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Research Paper

Migration patterns of the Faroe Plateau cod (*Gadus morhua*, L.) revealed by data storage tags

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ABSTRACT

Spawning cod were tagged in March 2002, 2003 and 2004 on the Faroe Plateau with Data Storage tags, recording temperature and depth. Migration routes were reconstructed for 23 recaptured individuals using a state-space model and analysed focusing on horizontal and vertical migration behaviour in relation to spawning, feeding and areas closed to trawling. The state-space model is constrained by homogeneous temperatures and depths however the Faroe Plateau is ideal in this regard. Although our inference is based on limited data we here demonstrate a proof of concept.

Regarding horizontal movement, a log-normal distribution of daily displacement was found with a significantly higher daily displacement during spawning than during feeding season. This indicates a clear distinction between spawning and feeding behaviour. However, while food availability did not affect the migration routes cod did avoid the trawled areas. Regarding vertical behaviour, cod stayed within 10 m from the bottom more than 90% of the time. Yet, individuals caught with longline had a stronger affinity to the bottom than cod taken by other gears such as trawl, suggesting that the use of trawl as survey gear should be continued in this area.

The information, available from the simulated migration routes is a great improvement compared to the information achieved from conventional tagging when studying individual fish behaviour. The results can be used to support fisheries data, i.e. survey, logbook, stock assessment or acoustic data that lack resolution to evaluate individual fish.

1. Introduction

To ensure fitness, animals need to be efficient feeders, avoid predators and to reproduce. Natural habitats do not always provide locations where all these needs are simultaneously fulfilled and occasional migration is therefore advantageous despite energetic costs (Nikolsky, 1963; Sutherland, 1996). Harden Jones (1968) describes fish migration by a migration triangle where spawning, nursery and feeding areas represent the three corners. However the latest period of advances in technology has showed that migration behaviour is more diverse (Secor, 2015). Many fish populations migrate distances of more than 1000 km (Bergstad et al., 1987; Harden Jones, 1968; Opdal, 2010; Opdal and Jørgensen, 2015), however this paper focuses on Faroe Plateau Atlantic Cod (*Gadus morhua*), where distances between known spawning, feeding and nursery areas are of the order of 50 km (Joensen et al., 2005).

The Faroe Plateau, here defined as the area around the Faroe Islands shallower than ~500 m, is approximately 40 thousand square kilometres and has a spatial extent of approximately 220 × 200 km (Hansen, 2006). Strong tidal currents with a clockwise residual flow dominate the plateau. The Faroe Shelf Front, located on 80–130 m depth, separates the always well mixed and relatively cold central shelf water from the outer, seasonally stratified water masses (Larsen et al., 2008, 2002). Inside the front the temperature varies from 6 to 11 °C between March and August. Outside the front, the sea surface temperature is higher by 0.5–1 °C (Larsen et al., 2008).

Many fish species spawn just inside the tidal front where appropriate food for the larvae is abundant and the risk that eggs and larvae are flushed away is low (Gaard and Steingrund, 2001). The 500 m isobaths is usually considered an approximate outer boundary for the

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Faroe Plateau cod (Joensen et al., 2005; Steingrund et al., 2009; Strubberg, 1933, 1916; Tåning, 1940) and the cod are distributed over the entire plateau, albeit scarcely distributed in areas deeper than 200 m (Tåning, 1940). The main spawning areas are located at two specific areas north and south west of the islands, between 80 and 150 m depth (Tåning, 1943) (Supplementary material, Fig. S1).

Cod in this region spawn between February and May with peak spawning in the second half of March (Jákupstovu and Reinert, 1994). Cod, spawning in the northern spawning area, move eastward or westward after spawning, and eventually distribute all over the plateau during the feeding season. Generally, cod spawning in the south western spawning area, move south after spawning and distribute on the southern part of the plateau during the feeding season, although deviations from this pattern have been observed (Joensen et al., 2005; Steingrund et al., 2009; Tåning, 1940). Faroe Plateau cod show a strong site fidelity to both spawning and feeding area (Steingrund et al., 2009; Tåning, 1940) and are therefore classified as 'accurate homers' (Robichaud and Rose, 2004). Even though cod is known to navigate by spatial memory of landmarks and bathymetry (Robichaud and Rose, 2002), this has so far not been demonstrated for Faroe Plateau cod. During the feeding season cod are distributed over the entire Plateau, however they are very stationary (Joensen et al., 2005; Strubberg, 1933, 1916). In areas shallower than 200 m, cod feed primarily on sandeels and benthic crustaceans, with sandeels being the preferred prey. In deeper waters cod feed primarily on norway pout and blue whiting (du Buis, 1982; Rae, 1967).

The fishery for groundfish species on the Faroe Plateau can roughly be divided into two groups: trawlers primarily targeting saithe at depths from 100 to 150 m down to 500 m and longliners primarily targeting cod and haddock in shallower waters (ICES, 2016). The separation of the gear, trawl and longline, is enforced by a number of area closures, with exceptions, that are too complex to explain in detail here (Gaard et al., 2014). In addition there are specific area closures for longliners as well as trawlers during spawning time to protect the spawning of cod. Jiggers are, however, not constrained by any of these area closures. The area closures have been unchanged since the effort management system was introduced in 1996 (ICES, 2016). Despite area closures, there are no area that is closed to all types of fishing during the whole calendar year on the Faroe Plateau. This is especially true for cod that are caught by all gears, i.e. jigging, longline and trawl. In practice, longliners have traditionally taken 30–70% of the cod catches since 1985, and 50-60% during the tagging period 2002–2006(ICES, 2016).

Faroe Plateau cod enter the fishery at age 2 years and are fully recruited to the fishery at age 4 (ICES, 2016). The catch ranged between 18 and 40 thousand tons during nearly a century (1906–1990) but decreased to less than 10 thousand tons in 1991–1994 and in the period after 2006 (Supplementary material, Fig. S2).

Previous analyses of Faroe Plateau cod migration pattern rely on mark-recapture data, obtained using conventional tags, which only provide information on release and recapture location. Data Storage Tags (DSTs) continually record temperature and depth while attached to individual fish. As the spatial distribution of conventional and DST tagged cod has showed to be similar, these data can upon recapture be used to infer movements during the time at liberty (Righton et al., 2007).

This paper presents the first estimation of migration routes of Faroe Plateau cod using DSTs. Migration routes were reconstructed using a state-space model, in which observations of depth and temperature and vertical behaviour were used as input. We aim to describe the Faroe Plateau cod migration and to show the possibilities of this method by relating it to homing to spawning areas, potential navigational mechanisms, habitat use in relation to feeding and trawled areas, horizontal movement pattern (daily displacement), vertical migration into the water column and vulnerability to fishing gears (including survey gears).

2. Material and methods

2.1. Data storage tags and tagging

Cod were caught by RV "Magnus Heinason" on March 26th 2002 and March 20th and 21st 2004 and by a hired commercial trawler on March 28th and 29th 2003 (Supplementary material, Table S1). The cod were caught at the spawning areas north and south west of the islands at 102–113 m depths (Supplementary material, Table S1). The mesh size was 135 mm in the cod-end and all cod in good conditions were transferred to tanks with running seawater. The DSTs (DST-milli, Star-Oddi, Iceland) were implanted into the body cavity of 180 cod. The tags, which record temperature and depth with 0.2 °C and 2 m precision respectively, were set to log every ten minutes for the first two days and thereafter every third hour for the next 12 days. This routine was repeated every 14 days. Date, time, position, depth and fish length (rounded down to the nearest cm) were recorded for each tagged fish before release.

The tagging was announced in local newspapers and on the website of the Faroe Marine Research Institute. A reward of 100 DKK was paid for each tag returned and if tag and carcass were returned, 300 DKK and 20 DKK per kilo of the carcass were paid. An annual lottery of 10,000 DKK was arranged, where tags with a carcass had a threefold probability to win. Recapture date (registered either as a specific date or as a date interval), recapture position (a GPS position accompanied by an error estimate as a diameter in nautical miles) and recapture gear were recorded. For returned carcasses, length (rounded down to nearest cm), weight, gutted weight, liver weight, gonad weight, sex, maturity state and otolith age were also recorded.

Of the 36 cod recaptured (Supplementary material, Table S1), ten tags were disregarded due to poor data quality, data exceeding the model grid in time and space, or inability of the model to find optimal parameters (lack of convergence and therefore inability to produce a track). Moreover, three tags were excluded as the estimated migration routes proved to be sensitive to the choice of the parameter S, which defines the pelagic and demersal behavioural states (see model description). Thus, it was possible to estimate migration routes for 23 cod (Supplementary material, Fig. S3 and Table S2). Tag number 1445, 1483 and 1498 in 2002 all stopped logging before recapture. The average length of these was 67 cm at release and only three of the 23 cod were at liberty until the following year.

2.2. Model

We used a state-space model (SSM), including behaviour switching, to simultaneously estimate movement and behaviour of each individual fish (Pedersen et al., 2011). Overall, this model connects the release and recapture positions by fitting the time series of temperature and depth data, by using the restrictions set by the bathymetry (Simonsen et al., 2002) and a simulated temperature field (Rasmussen et al., 2014). For our study region we use bathymetric information resolved on a 300 × 300 m grid in the latitude longitude range: (59.11N–63.71N) (12.55W–14.5W). The code was run in Matlab based on a modification of the code from (Pedersen et al., 2008a).

The behavioural model has two states: in state one ($i = 1$) the fish is located close to the bottom and in state two ($i = 2$) the fish is located away from the bottom (pelagic). Thus, behaviour is interpreted in terms of vertical placement relative to the bottom.

The switching between the two behavioural states is governed by a Markov chain with transition probabilities p_{12} and p_{21}, i.e. the probabilities of switching from state 1 to state 2 and vice versa. The process equation describing the horizontal movement of the fish was a random walk given by

$$x_t = x_{t-1} + e_t,\ e_t \sim N(0, s^2),$$

where x_t is the horizontal location of the fish at time t and e_t is the distance travelled in one time step. The notation $e_t \sim N(0, s^2)$ indicates a normal distribution with zero mean and s^2 variance. The variance parameter s^2 is related to the movement rate of the fish.

The SSM has two observation equations, one for each of the two data types. The depth observation (d_t) is the deepest depth, recorded in each three hour interval, and the d_t temperature observation (y_t) is the temperature recorded at the time of

2.2.1. Depth observation equation

The likelihood for the depth observation depends on the behavioural state, *i*. For the state where the fish is close to the bottom ($i = 1$) the observation equation is:

$$d_t = abs(D_t),$$

where $abs()$ means absolute value and $D_t \sim N[B(x_t), S^2]$. Thus, d_t follows a half-normal distribution (Johnson et al., 1994). The parameter S determines how close to the bottom the fish is expected to be located, with smaller values indicating higher bottom closeness. The function B returns the bathymetric value at location x_t.

For the "pelagic" state ($i = 2$) d_t follows a probit shape with inflection point located at $B(x_t) - 2S$ and standard deviation equal to $S/2$ (Supplementary material, Fig. S4). The parameter S determines the vertical distribution of the fish when exhibiting "bottom"-behaviour or "pelagic"-behaviour. The "bottom"-state refers to the range between the bottom level to 2S m above the bottom (Supplementary material, Fig. S4) and the "pelagic"-state refers to the remaining part of the water column. The value of S could in principle be estimated together with the other model parameters by using maximum likelihood, however by fixing the value of S it is possible to estimate the time spent in a particular part of the water column and thus the potential exposure to different fishing gear. For example, this can be achieved by setting $2S$ to a fixed value representing the height of a trawl net.

The data products available influence how finely one can expect to resolve the vertical behaviour of the fish. Coarsely resolved bathymetric information in a region containing high variability in depth would restrict S to values above some threshold. To assess whether this threshold is larger than the values of S of interest, the model was run for a range of S-values and the values resulting in biologically impossible movement estimates (i.e. erratic movement as a result of numerical divergence) were excluded. The value of S was then selected among the values that were not excluded.

2.2.2. Temperature observation equation

The observation equation for the temperature is somewhat simpler than for the depth:

$$y_t \sim N[T(t, x_t, d_t) + b_t, S_T^2],$$

Again N represents a normal distribution. The function T is the predicted temperature at a given d_t time t, location x_t, and depth

In this study we used temperature predictions from a high resolution HYCOM model of the Faroe Shelf (Rasmussen et al., 2014). Predicted temperature data were extracted from the model with a vertical resolution of 10 m. The extracted data for 2002 had a 5 × 5 km horizontal resolution, whereas data from 2003 and onward had a 1 × 1 km horizontal resolution. Rasmussen et al. (2014) compared modelled temperatures at a fixed location with corresponding observed temperatures, and this indicated that the predicted temperature was higher than the observed temperature in particular during the winter months. Therefore, b_t represents a time varying bias in the difference between the model and the recorded temperature and this bias was estimated to oscillate between 0.44 °C in the summer season and 0.92 °C in the winter season.

The parameter S_T indicates the strength of random noise inherent in the difference between the hydrographic model and the recorded temperature. We assumed that $S_T = S_M + S_O$, where S_M=0.10 °C is the residual standard error derived from comparing modelled temperatures with corresponding temperature observations at a fixed location (61.9073N, 6.8805W). As it was unrealistic to assume that S_M is representative for the whole study region, we added an additional contribution, S_O, to account for the likely inflated error in regions away from the reference location. The value of S_O was unknown and therefore had to be estimated.

2.2.3. Estimating unknown parameters

The unknown parameters of the SSM were the movement rate s, the transition probabilities p_{11} and p_{21}, and S_O. The parameters s, p_{12} and p_{21} were estimated with maximum likelihood as in Pedersen et al. (2011). It was not feasible to include S_O directly in the set of optimised parameters because this would entail prohibitively large computational requirements. Instead, we ran the model (i.e. estimated s, p_{12} and p_{21}) for a number of fixed values of $S_O(S_O = \{0.1, 0.2, 0.3, 0.4, 0.5\}°C)$. We did this for the tags: 4408, 4729, 4743, 4749 and 4750. For all tags $S_O = 0.1$ °C resulted in the highest likelihood value. We therefore used $S_O = 0.1$ °C for all remaining analyses. This estimation approach can be regarded as a simple profile likelihood estimation.

The value of S was set to 5 m to investigate the time spent within $2S = 10$ m off the bottom. This range was chosen to be able to determine whether the Faroe Plateau cod was strictly demersal or also has a pelagic state.

From the estimated switching probabilities p_{12} and p_{21} the stationary distribution (δ_1, δ_2) of the behavioural process were calculated (Zucchini and MacDonald, 2009). The values of δ_1 and δ_2 can be interpreted as the expected proportion of time spent in the two different vertical zones as defined by S. However, as it is doubtful whether electronic tagging data can be interpreted as the output of a stationary (i.e. non-transitory) process the calculated stationary distribution should not be taken literally, but only be used as a helpful summary of the results.

The estimated horizontal movements are summarised by calculating the mean track of the smoothed probability distribution of the location. The estimated vertical behaviour was summarised by the probability of being in the "bottom" state.

2.3. Movement

The year has been divided into three seasons: Spawning season (February–May), feeding season 1 (June–September) and feeding season 2 (October–January). All the following statistical tests are described in Sokal and Rohlf (1995) and performed in R (R Core Team, 2013).

2.3.1. Spawning

The relation to the spawning area (Supplementary material, Fig. S1) was done by visual evaluation of the estimated migration routes in relation to navigation and homing in the peak spawning period (March 15th -30th).

2.3.2. Feeding

The area between 70 and 150 m depth on the Faroe Plateau was grouped into areas categorized as either 'sandeel' or 'crustacea' based on stomach content analysis from the bottom trawl survey in August 1997–2006 (Supplementary materials, Figs. S5 and S6). Sandeel and crustacean areas are based on pooled stomach data due to limited stomach data from each single year. The location of the areas does however not change from year to year. Of the total area, 58 and 42% was classified as sandeel and crustacean respectively (Fig. 1). Residence time based on the estimated migration routes in sandeel and crustacean areas was calculated for the individual fish in the spawning season and feeding season 1 (Supplementary material, Table S3). Since only few cod were at liberty during feeding season 2, this period was disregarded from all analysis. A binomial test was invoked to compare the time cod spent in sandeel areas against the time they spent in crustacean areas in

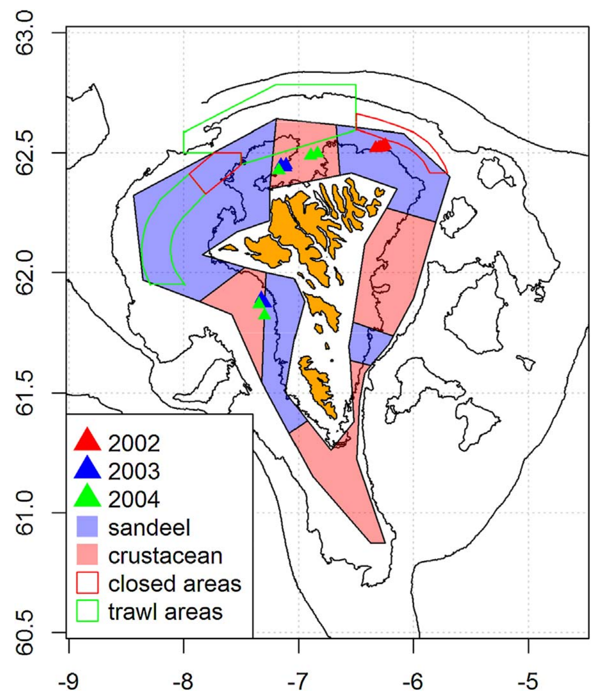

Fig. 1. Faroe Plateau with tagging locations, two areas open to trawl and two areas closed to trawl and areas with sandeels or crustaceans. Triangles show tagging positions for the year 2002 (red), 2003 (blue) and 2004 (green). Sandeel and crustacean areas are shown in respectively blue and red filled polygons. Closed and trawl areas are shown in respectively red and green open polygons. Bathymetric contours indicate 100, 200 and 500 m depth.

the spawning season and in feeding season 1.

2.3.3. Avoidance of trawled areas

Two closed and two adjacent areas, open to trawl with similar depths as the closed areas, were chosen to investigate whether cod avoided trawled areas. The trawled areas comprised 19% of the total area of trawled and closed areas (Fig. 1). Residence time based on the estimated migration routes in the closed and trawled areas were estimated for the spawning season and for the feeding season 1 and a binomial test was used to compare the results. Cod spending less than five following days in the closed and trawled areas were excluded from the analysis.

2.3.4. Daily displacement

Daily displacements, defined as the difference in mean position from the estimated migration routes from one day to the next, were calculated.

A *t*-test was applied to compare the mean daily displacements during the spawning season and the feeding season 1.

The mean daily displacement during feeding season 1 was tested statistically by an ANCOVA having year (2002, 2003 or 2004) as a categorical variable and the mean daily displacement of the same individuals during spawning season as a covariate.

When comparing the mean daily displacements of the three years 2002, 2003 and 2004 separately, a one-way ANOVA was used.

2.3.5. Vertical migration

The state-space model also includes proximity to the bottom, described by the parameters $\delta1$(demersal) and $\delta2$(pelagic) (Supplementary material, Table S2). Linear regression was used to compare the time spent pelagic ($\delta2$) and the mean daily displacement for the spawning season and for the feeding season 1. An F-test was used to compare the proportion of time spent pelagic ($\delta2$) and the type of gear the fish was caught by (longlines vs. trawl or jigging reels).

3. Results

3.1. General movement pattern

Cod were predominantly found at depths shallower than 200 m however the mean depth varied over the years (109 m in 2002, 90 m in 2003 and 124 m in 2004). There was a large individual variation in the distances travelled, e.g. cod with tag no. 1438 and 4750 were both at liberty around six months (Fig. 2) but travelled 1400 and 436 km respectively. The time in which the cod were at liberty varied from 39 days to 460 days. Five out of the 23 tagged cod (1472, 4407, 4427, 4433, 4762) travelled nearly all the way around the islands. A distinction between the spawning and feeding migration was not possible by visual evaluation of the estimated migration routes (Fig. 2).

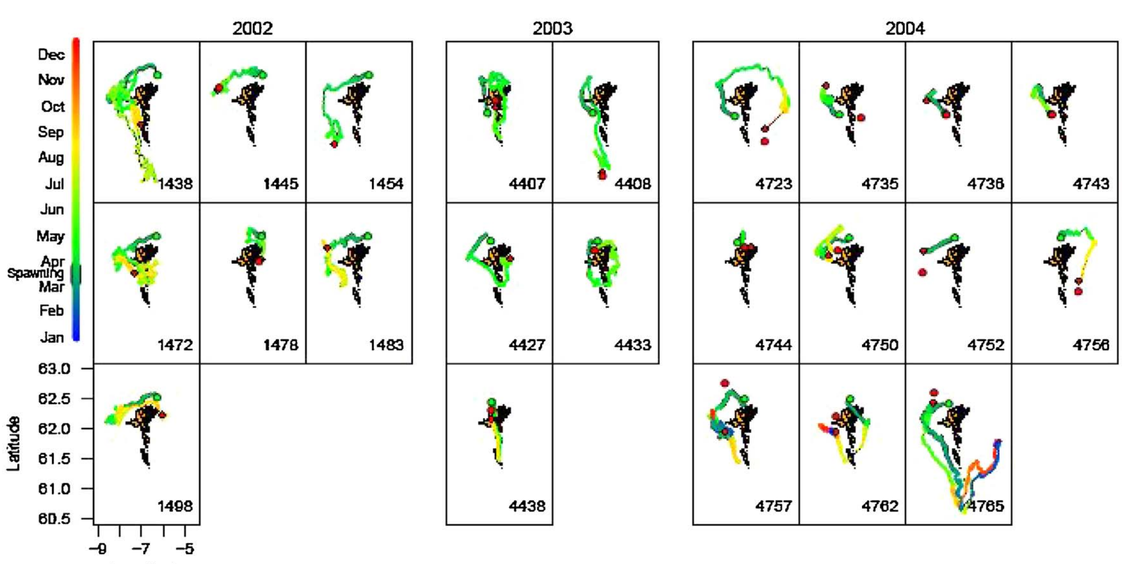

Fig. 2. Estimated migration routes of the 23 DST tagged cod from 2002, 2003 and 2004. Green square indicates estimated release position and green dots reported release position. Red square indicates estimated catch position and red dots reported catch position. Colours on track indicate the month of the year. Bold green colour indicates peak spawning period (March 15th -30th).

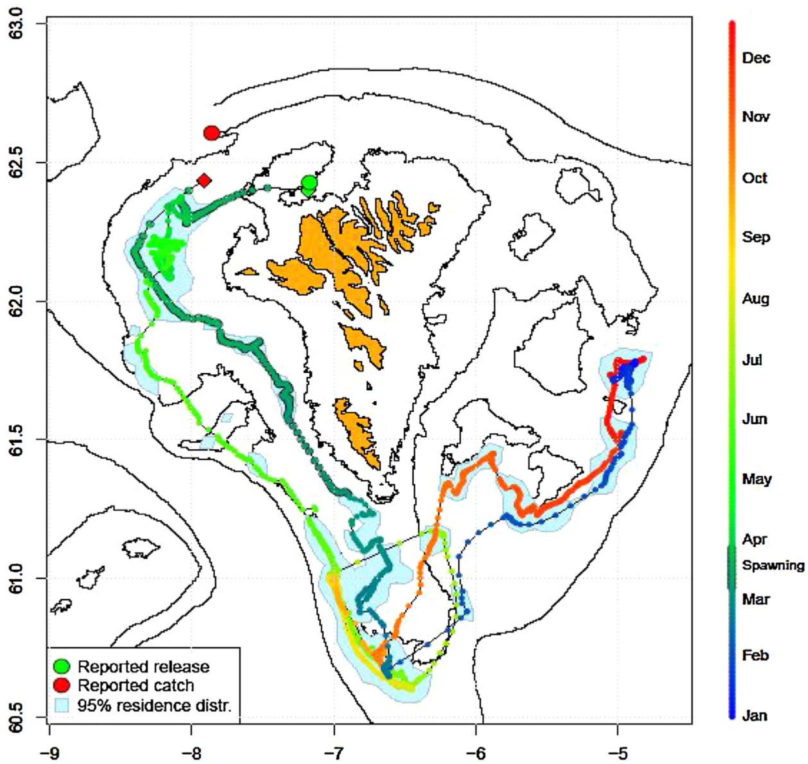

Fig. 3. Estimated migration route for cod tagged with DST no. 4765. The green square indicates estimated release position and green dot reported release position. The red square indicates estimated catch position and red dot reported catch position. Colours on track indicate the month of the year. Bold green colour indicates peak spawning period (March 15th–30th). Light blue colour indicates the 95% residence distribution. Depth contours are at 100, 200 and 500 m.

3.2. *Movement*

3.2.1. *Spawning*

Of the 17 cod released at the northern spawning area (2002–2004) 13 cod went westward, two eastward, one southward and one stayed close to the release position (Fig. 2). Two cod changed direction and one was caught within the first month at liberty. All six cod tagged at the south western spawning area (2003, 2004) went in a northern direction after release (Fig. 2). After one month at liberty two changed direction and one was caught.

Two cod were at liberty for two consecutive spawning seasons. Cod with tag no. 4757 was released at the northern spawning area and was recaptured at the south western spawning area the following spawning season. Cod with tag no. 4765 (Fig. 3) was also released at the northern spawning area and recaptured the following spawning season north west of the islands, after migrating through the south western spawning area during the spawning season. The 95% residence distribution, the area where the fish was expected to reside within 95% of the time at liberty, confirm this pattern (Fig. 3).

3.2.2. *Feeding*

During the spawning season (February–May), 14 out of 23 cod were found to spend more time in the sandeel areas than the size (58%) of these areas would suggest. During feeding season 1 (June–September), 7 out of 13 cod were found more than 58% of the time in the sandeel areas. None of these proportions were significantly different from a probability of 0.5 (binomial test, $p = 0.20$ and 0.5).

3.2.3. *Avoidance of trawled areas*

During the spawning season (February–May), 14 of 23 cod spent more than 5 consecutive days in the two closed and two trawled areas. Three of these 14 cod spent more time in the trawled areas than the size (19%) of these areas would suggest, which is significantly different from a probability of 0.5 (binomial test, $p = 0.03$). During feeding season 1 (June–September), 5 of 23 cod spent more than 5 consecutive days in the closed and trawled areas. One of the 5 cod spent more time in the trawled areas. Although this is not significantly different from a probability of 0.5 (binomial test, $p = 0.19$), due to the low number, it is much in line with what was found for the spawning season.

3.2.4. *Daily displacement*

Most of the time, daily displacements were less than 10 km/day, although displacements of up to 49 km/day were observed (Fig. 4). There was a significant difference between the mean daily displacements in the spawning season and feeding season 1 (*t*-test, $p = 0.02$) with higher mean daily displacement during spawning season than during feeding season 1, also when one outlier was removed ($p = 0.04$). However, the mean daily displacements during feeding season 1 was highly correlated with the mean daily displacements during the spawning season (ANCOVA, $p < 0.001$) and this relationship was not dependent on the year ($p = 0.6$). Cod tagged in 2002 and 2003 had a higher mean daily displacement than cod tagged in 2004 (one-way ANOVA, $p = 0.006$), also when one outlier was removed ($p = 0.01$).

Daily displacement (all individuals and seasons pooled) was grouped on a log scale, and the frequency calculated, reveal a dome shaped distribution, which broadly resembles a normal distribution (Fig. 5). The normal distribution was not fitted to the lowest velocity bin since the mean position per day is probably not accurate enough to allow this.

3.2.5. *Vertical migration*

22 of 23 cod stayed near the bottom (closer than 10 m) more than 90% of the time (Supplementary material, Table S2). There was a positive correlation between the time spent pelagic ($\delta 2$) and the mean daily displacement during the spawning season (linear regression, $p = 0.02$), also when one outlier was removed ($p = 0.02$). Vertical movements for cod with tag 4762 show that days with pelagic movements were scattered during the feeding season 2, Fig. 6, however the second feeding season is not included in the analysis and there was no correlation between $\delta 2$ and the mean daily displacement during the feeding season 1 (linear regression, $p = 0.44$), also when one outlier was removed ($p = 0.08$). Cod caught on longlines showed less variation in the probability to stay pelagic than cod caught by other gears (trawl

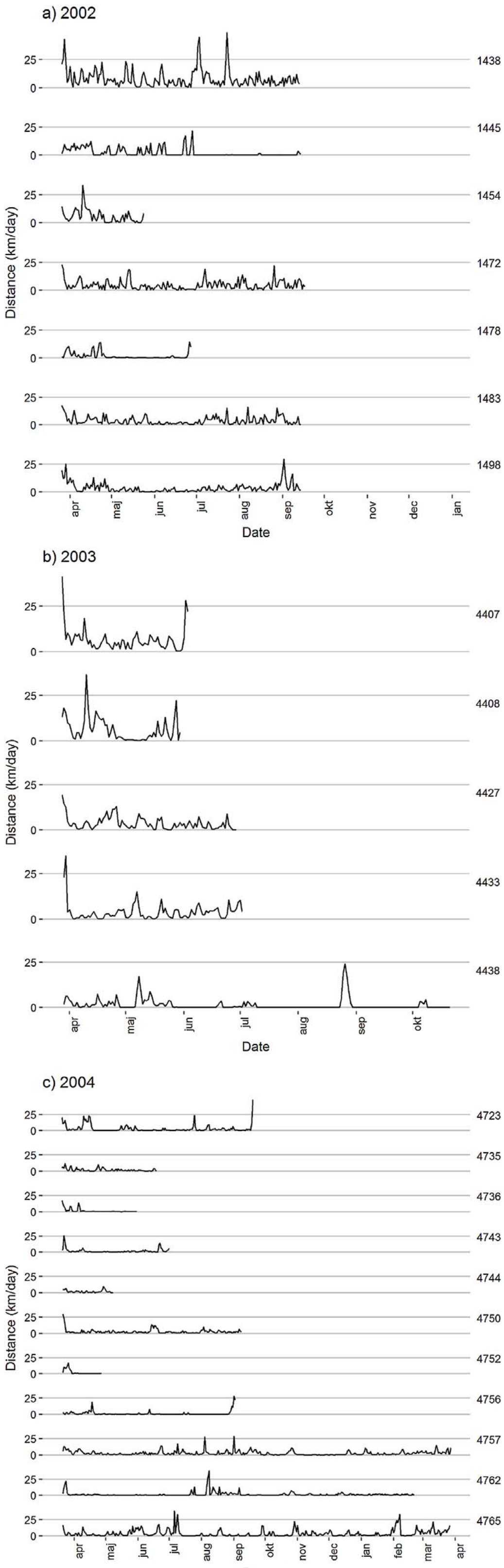

Fig. 4. Mean daily displacements (km/day) for 23 DST cod from a) 2002, b) 2003 and c) 2004. Tag number is shown on the right.

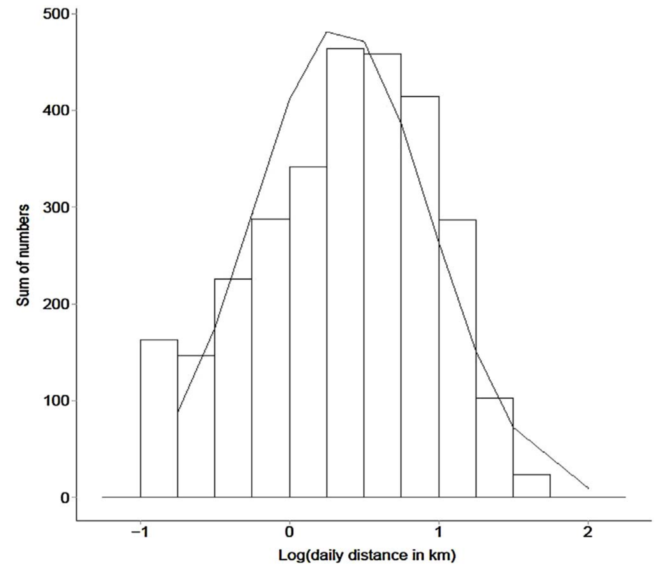

Fig. 5. Histogram of the frequency distribution of daily displacement distances on a log scale.

or jigging reels) (F-test, p = 0.007).

4. Discussion

4.1. General movement pattern

Modelling high-resolution data from DST coupled with environmental information, reveals likely migration routes and enable ecological inferences such as preferred habitats, feeding and spatial management interactions. In addition, fewer tag recoveries are needed to collect detailed information to describe animal behaviour than low-resolution conventional tagging data. The location of this study is ideal for DST studies due to the well-defined cod stock inhabiting an area with great ranges of temperatures and depths which help to improve the accuracy of the model. Further the tagged cod are accessible to fishing gears during their entire distributional area on the Faroe Plateau and the entire year if they stay close (< 10 m) to the bottom.

The estimated migration routes presented here are based on data collected in the DST tagging program, 2002–2006, that covers the last period before the Faroe Plateau stock declined. The tagged cod migrated predominantly at depths less than 200 m, in accordance with Tåning (1940), and stayed closer than 10 m from the bottom. However cod generally moved more and showed less site fidelity to spawning and feeding area than anticipated from conventional tagging (Steingrund and Mouritsen, 2009). This is in line with Secor (2015) where more diverse migration patterns are suggested than the migration triangle presents.

4.2. Movement

4.2.1. Spawning

The behaviour of the 23 tagged cod was mainly in accordance with the spawning migration routes described by Steingrund and Mouritsen (2009). All 23 cod were tagged in the spawning season and dispersed all over the Faroe Plateau after spawning.

However, all six cod tagged in the south western spawning area moved northward after the tagging, even though two changed direction towards west/south after one month at liberty. This is not in line with Joensen et al. (2005), who found that cod spawning in the south western spawning area mainly move southwards after spawning. This result suggests that alternative migration patterns for cod spawning in the south western spawning area are maybe more common than previously

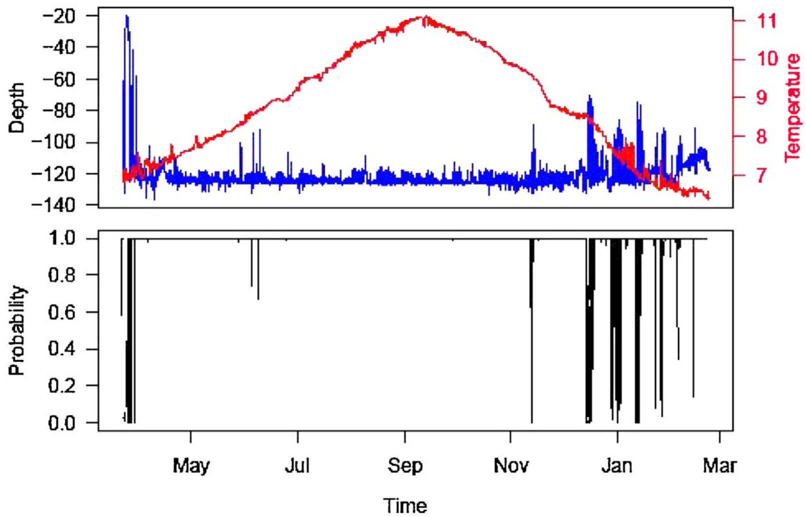

Fig. 6. Temperature and depth profiles for cod with tag no. 4762 (upper panel) and the associated probability to stay within 10 m from the bottom (lower panel).

thought.

Earlier studies of conventionally tagged cod have found that the Faroe Plateau cod has a strong site fidelity to spawning area (Steingrund and Mouritsen, 2009; Tåning, 1940) and this is also in accordance with studies of cod tagged with ultrasonic transmitters in Placentia Bay, Newfoundland (Robichaud and Rose, 2001). Nevertheless, although males usually are considered more stationary during spawning than females (Dean et al., 2014; Robichaud and Rose, 2003), the two male cod (4757 and 4765), which were at liberty for the two consecutive spawning seasons, apparently did not show site fidelity to the spawning area where they were tagged, and both cod visited both spawning areas. Cod with tag no. 4765 moved from one spawning area to the other within one week during the spawning season and did not migrate by the same route to and from the spawning area (Fig. 3; Supplementary material, Fig. S7) indicating that this fish did not migrate based on spatial memory of landmarks and bathymetry (Robichaud and Rose, 2002). However a migration based on previous experience as migration aggregation as suggested by Rose (1993) is still a possibility.

The fact that two individual cod covered more than one spawning area during the same spawning season is not necessarily a contradiction to homing to spawning areas in general, since the spawning areas on the Faroe plateau are only ~50 km apart, and thus very close compared to other regions. Further here we evaluate homing in relation to peak spawning period and not the whole spawning period. In general, the migration of individual fish are expected to be variable and do not necessarily represent the whole population (Leggett, 1977).

4.2.2. Feeding

Interestingly, cod did not prefer sandeel areas over crustacean areas. This result must be interpreted cautiously, since the definition of areas are based on stomach analysis (Supplementary material, Figs. S5 and S6) and thus are very coarse. However here we demonstrate that it is possible to infer ecological behaviour from modelled movement data.

4.2.3. Avoidance of trawled areas

Fish are known to show avoidance reactions when they are in close proximity to demersal trawls (Engås, 1994). Survey results show that the catch rates of cod in trawled areas at the Faroe Plateau was considerably lower (by factor 6) compared with areas closed to trawling (Gaard et al., 2014), either because cod avoided trawled areas altogether or became less vulnerable to the gear.

The migration pattern by individual fish could in principle be affected by fishing activity either by an attraction to longline areas (feeding on baits) or an avoidance of trawled areas. This is partly addressed by comparing the residence time of individual fish in areas that are close to the dispersal routes from the spawning areas. Our study shows that cod avoided the trawled areas. These results are in agreement with the results from Dean et al. (2012). However the motivation for moving out of the trawled areas could also be due to less favourable conditions. Although our inference is based on limited data, the process could benefit future studies.

4.2.4. Daily displacement

A seasonal pattern in daily displacements, which also has been shown for the southern North Sea cod (Righton et al., 2007, 2001) and in conventional tagging experiments (Joensen et al., 2005), was observed. Importantly, the DST-data seem to provide a basis to regard the long-term (over months or years) displacement of cod as a sum of daily displacements which to our knowledge, has not been demonstrated earlier for cod by empirical data. As presented in Fig. 5 the frequency distribution of the daily displacement, pooled for all individuals over their entire period at liberty, resembles closely a log-normal distribution. The long-term displacement, based on conventional tagging, also conforms to a log-normal distribution for a number of cod populations along the Norwegian coast and at the Faroe Islands (Pedersen et al., 2008b).

Cod tagged in 2002 and 2003 had a higher daily displacement than cod tagged in 2004 while the amount of sandeel was high in 2002 but lower in 2003 and 2004 (ICES, 2014). This result indicates that high abundances of sandeel on the Faroe Plateau cause the cod to visit the pelagic zone for hunting more frequently. These results are moreover supported by conventional tagging results from the Faroe Plateau in the period 1997–2015, where a positive correlation between the daily displacement and the amount of sandeel is found (Faroe Marine Research Institute, unpublished data). In the Barents Sea, Strand and Huse (2007) extended such a relationship even further by predicting a shift to strict pelagic lifestyle if only pelagic prey was available.

4.2.5. Vertical migration

Knowledge on the vertical migration of cod is essential for evaluating the reliability of survey estimates used in stock assessments. Even though pelagic cod behaviour has been reported (Godø, 1994; Godø and Michalsen, 2000; Rose, 1993), this study confirms that the Faroe Plateau cod is demersal since it stayed within 10 m off the bottom over 90% of the time. In practical terms cod are available to the survey gear all the time and potential mismatches between back-calculated population numbers from the catch-at-age and the relative population numbers from the tuning series must be caused by other sources of error than a time-varying vertical migration.

The inclination to stay close to the bottom makes Faroe Plateau cod more vulnerable to commercial fishing gears than some other cod stocks in the North Atlantic (e.g. in the Barents Sea, Godø and Michalsen (2000)).

There was a positive correlation between the time spent pelagic and the average daily displacement (Supplementary material, Table S2). As mentioned above, the tendency for cod to have a higher average displacement when sandeels are abundant may be caused by the foraging behaviour of cod on sandeels. It could be speculated that cod preying on sandeels chase sandeels in the water column part of the time and during this time of active foraging cod could be displaced for a longer distance.

There was also a relationship between the tendency to stay pelagic and the probability to be caught on longlines, i.e., there was much less variation in δ_2 for cod caught on longlines compared with other gears (trawl or jigging reels) (Supplementary material, Table S2). This indicates that longline-caught cod have a close affinity with the bottom. Finally, if the variability in δ_2 reflects behavioural variation of individual cod in the cod population, then trawl as a survey tool is better suited than longline since trawl catches a broader range of individuals.

4.3. Assumptions potentially influencing the results

Estimating movement using hydrographical data products has the inherent assumption that the data product is representative of reality. The simulated temperatures, used in this study, are generally higher than corresponding observations (Rasmussen et al., 2014). We have accounted for this by adding a residual standard error, S_M which accounts for the general bias, and an additional noise parameter, S_O, which was estimated using a simple profile likelihood approach. Investigation of independent temperature data from several moorings within the study region is recommended for future projects, but was outside the scope of the current study.

The data resolution of the bottom topography in the 2002 simulation was coarser than the resolution used in the 2003 and 2004 simulations, which could be the reason for the lower δ_1 value in 2002. However, this does not affect the conclusion that the Faroe Plateau cod stays within 10 m off the bottom more than 90% of the time.

5. Conclusion

We have shown that simulation of detailed migration routes enables evaluation of fish behaviour, such as navigational mechanisms, site fidelity, habitat use both horizontally and vertically, in relation to food and areas closed to trawling, foraging behaviour and vulnerability to fishing gears. We found a log-normal distribution of daily displacement with significantly higher daily displacement during spawning than during feeding season indicating a clear distinction between spawning and feeding behaviour. We found that food availability did not affect the migration routes however the daily displacement was greater in years where sandeels were abundant. Further cod avoided the trawled areas. Cod stayed within 10 m from the bottom more than 90% of the time however, individuals caught with longline had a stronger affinity to the bottom than cod taken by other gears such as trawl, suggesting that trawl should be used as survey gear in this area. However, the results presented here are constrained by low amount of data, however the analysis demonstrates methods that could be useful to others.

The information, available from the simulated migration routes is of great value when studying individual fish behaviour. It is a great improvement compared to the information achieved from conventional tagging and can be used to support fisheries data, i.e. survey data, logbook data, stock assessment data or acoustic data, which all operate on groups of fish but lack resolution to evaluate individual fish.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.06.014.

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