

# HAF- OG VATNARANNSÓKNIR

MARINE AND FRESHWATER RESEARCH IN ICELAND

Göngur þorsks út frá sjávarföllum

*Cod migration based on tidal signatures*

*Ingibjörg G. Jónsdóttir, Höskuldur Björnsson, Siv Nam Khang Hoff, Sissel Jentoft, Christophe Pampoulie, Bruce McAdam*



**HAFRANNSÓKNASTOFNUN**

Rannsókná- og ráðgjafarstofnun hafs og vatna

**MARINE & FRESHWATER RESEARCH INSTITUTE**

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## Ágrip

Rafeindamerki (DST) skrá samfelld gögn um hita og dýpi og veita mikilvægar upplýsingar um atferli fiska. Við Ísland hafa gögn úr rafeindamerkjum leitt í ljós tvær ólíkar fargerðir þorsks (*Gadus morhua*): grunnfarsþorsk sem dvelur að mestu leyti á grunnsævi (< 200 m) árið um kring, og djúpfarsþorsk sem heldur sig á meira dýpi í hitaskilum yfir fæðutímenn. Ef fiskur liggur nógu lengi við sjávarbotn má sjá sjávarföll í dýptarferlinum. Þau er hægt að nota til að bera saman við sjávarfallalíkan á útbreiðslusvæði fisksins og finna þannig líklegustu staðsetningu hans en það var einmitt meginmarkmið þessa verkefnis. Stærsti hluti verkefnisins fólst í því að uppfæra sjávarfallalíkanið sem notað er þannig að það myndi ná yfir stærra hafsvæði og að færa kóðann úr Matlab yfir í R. Einnig var kannað hvort hægt væri að sjá mun í erfðafræði grunn- og djúpfarsfiska með það að markmiði að geta greint þá í sundur án þess að skoða gögn úr rafeindamerkjum. Verkefnið var styrkt af Verkefnasjóði sjávarútvegsins. Í þessari skýrslu er tekin saman framvinna verkefnisins og helstu niðurstöður þess kynntar.

**Lykilorð:** göngur, sjávarföll, þorskur, grunnfar, djúpfar

## Abstract

*Data storage tags (DSTs) continuously record temperature and pressure-derived depth data, offering insights into the behaviour of fish. In Icelandic waters, DST data have previously revealed two distinct ecotypes of Atlantic cod (*Gadus morhua*): coastal cod, which mainly remain at shallow depths (< 200) year-round, and frontal cod, which migrate to deeper offshore waters during the feeding season. If cod remain on the seabed, tidal signals can be detected within the DST depth profile. These signals can be compared with predictions from a tidal model developed for the Icelandic shelf to geolocate the fish, which is the main objective of this project. A major component involves upgrading a tidal geolocation model to expand its geographical range and reimplementing the code in R. Furthermore, we investigated whether genetic analysis can distinguish between coastal and frontal cod, making it possible to identify the ecotypes without relying on DST data. The project was supported by Verkefnasjóður sjávarútvegsins. This report synthesizes the project's progress, outlines the development of the analytical framework, and presents the main outcomes.*

**Keywords:** *cod, migration, tidal signature, coastal cod, frontal cod*

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# 1 Introduction

The life cycle of many fish species is characterized by seasonal migrations, where individuals or groups move regularly between different areas. This migration pattern causes population density to vary according to both area and season. Tagging has been used to study cod migrations in Icelandic waters for over a century (Jónsdóttir et al. 2021). T-bar tags are the most common, but they provide information about the tagging location and the recapture location but there is no information about what happens between these two points. Data storage tags (DSTs) have also been used extensively in Iceland. They collect data continuously until the tag memory is full or until the fish is recaptured and the measurement is stopped. These tags measure temperature and pressure, which are converted to depth. In addition to knowing where the fish was tagged and recaptured, DSTs provide information about its behaviour, specifically, at what depth and at what temperature it stays at any given time during liberty.

Data from DSTs have revealed different migration patterns in cod off Iceland; cod that mainly remains shallow (< 200 m) all year round (coastal cod) and cod that move to greater depths during the feeding season (frontal cod) (Figure 1). Still other cod do not follow these migration patterns but instead move both shallowly and deeply in search of food.

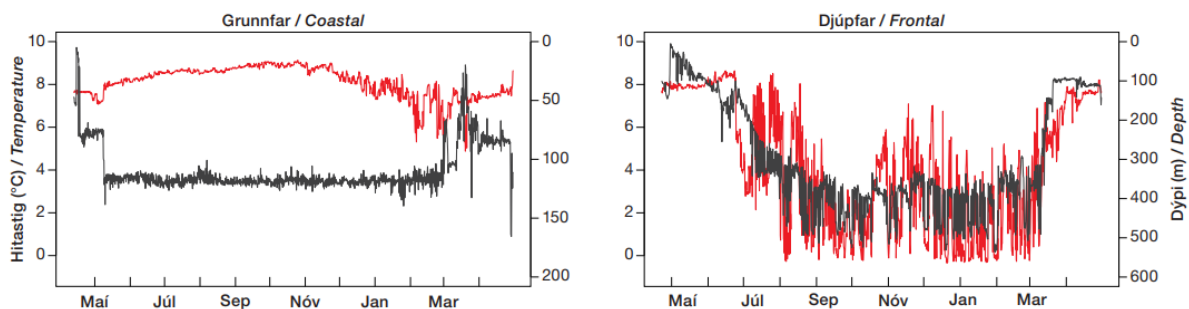


Figure 1. Typical coastal and frontal behaviour types. Red profiles indicate temperature and black profiles depth.

If cod remain on the seabed, tidal signals can be detected within the depth profile recorded by the DSTs (Figure 2). These profiles can be compared with predictions from a tidal model developed for the Icelandic shelf (Thorsteinsson et al. 2012). This approach makes it possible to geolocate the fish, though the position is limited to an accuracy of approximately 10x10 km. The tidal model used was developed by Gunnar G. Tómasson and Ólöf R. Káradóttir in 2005 (Tómasson and Káradóttir 2005). At that time, there were few cod migrations out of Icelandic ecoregion, and the model is limited to 29 degrees west longitude. Therefore, it is not fully effective when examining data from cod that were tagged and/or recaptured on Dohrnbanki. There is a need to update the model so that it can be better utilized for these DSTs, thereby increasing our knowledge of cod migrations within the Icelandic ecoregion as well as towards Dohrnbanki. The model also needs to be calibrated. For this purpose, tidal measurements need to be obtained at sea, which is done by deploying four buoys with electronic sensors that measure depth for one month.

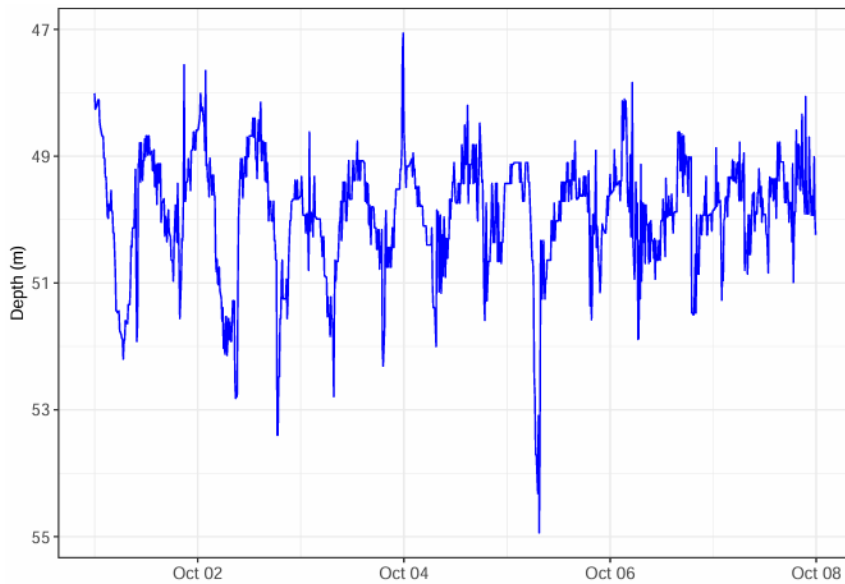


Figure 2. Depth profile from October 1-7 showing tidal signatures within a DST depth profile. DST tag number 1B4618.

It is necessary to go through the data profiles from recaptured DSTs and evaluate their locations over the entire period the tag recorded. A considerable amount of time is spent reviewing the DSTs and assessing probable locations. Temperature and depth profiles are used as a reference to evaluate whether locations are likely, given the temperature and depth in the area that the model estimates as most probable. With genetic analysis of the fish, it is possible to confirm both the behaviour and the likely origin of the fish.

The overall aim of this project is to study migration patterns of Icelandic cod by investigating tidal signals in DST depth profiles, thereby estimating specific locations of cod migration. A main part of this project involves developing the analytical tool required to perform this analysis. This will be done through several steps:

- Produce a tool for estimating locations
  - update the existing tidal model
  - calibrate the tidal model
  - write R code for scientists to use to estimate locations based on tidal signals in the DST profiles
  - add temperature and depth into the tidal model to improve its accuracy and reliability of the location data
- Study migration patterns
  - go through profiles of recaptured DSTs and track migration of cod based on tidal signals
- distinguish between coastal and frontal cod with genetics
  - analyse cod genome from coastal and frontal cod

The Ministry of Food, Agriculture and Fisheries awarded a grant for this project through *Verkefnasjóður sjávarútvegsins* in November 2024. The estimated duration for this work was approximately 16 months, and the project was officially completed on March 31, 2026. In this report we go over the progress within the project steps and outline the key milestones achieved during the reporting period.

## 2 Tidal model update

### 2.1 Current tidal geolocation model

The tidal geolocation model currently used at the Marine and Freshwater Research Institute (MFRI) is based on Matlab code by Pedersen (2010) to perform the geolocation and uses tidal parameters from the Icelandic tidal prediction model of Tómasson and Káradóttir (2005).

#### 2.1.1 Current tidal prediction model

The Tómasson and Káradóttir (2005) model covers a geographic range from 62° to 68° N at a resolution of 0.1°, and 9° to 29° W at a resolution of 0.25°. Tides are composed of a set of wave forms (components) with different periods causing diurnal (daily) and lunar monthly tides as well as variation from year-to-year. For each spatial location in the geographic extent the phase and amplitude of a set of seven tidal components (M2, S2, K2, N2, K1, O1, and Q1) are recorded allowing prediction of tidal heights at that location and at any time point over a multi-decadal time period. Figure 3 shows the phase and amplitude of the M2 tidal component that drives the diurnal tidal cycle. These parameters allow the model to calculate tidal height at any location at any point in time.

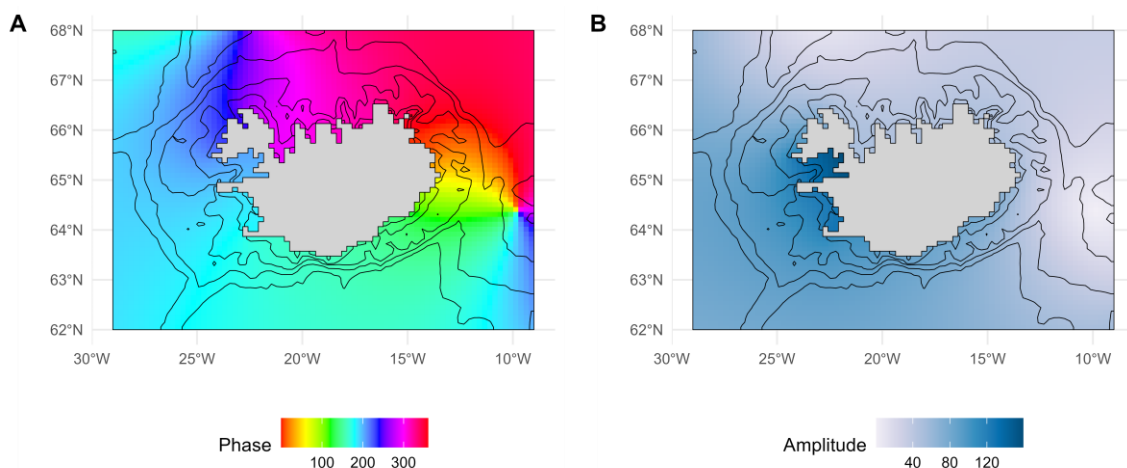


Figure 3. Parameters of the Tómasson and Káradóttir (2005) tidal prediction model used in the original geolocation system. A: phases in degrees of M2 tidal component. B: amplitude in cm of M2 tidal component. Depth contours at 50, 100, 200, 500 and 1000 m (taken from the original geolocation system).

The tidal geolocation model is written as Matlab code, which has subsequently been edited to run in the open source Octave programming language (Eaton et al. 2019).

Applying the model to DST data requires several steps. First, data must be prepared by identifying the relevant date range of the DST data (i.e. excluding any period that the tag was active but not attached to a fish) and recording the release and recapture locations. Secondly, the Matlab model scans through the DST data to identify days on which tidal signatures can be identified ('tidal days'), optionally these can be manually checked to remove false positives.

Having identified the tidal days, the third step is to calculate the likelihood of the fish being at any location for each of these days. To do this, the model calculates tidal heights at every location for the same time period as the DST data. The difference between the modelled tidal height and the observed height from the DST data is then used to calculate the likelihood for that location. Figure 4 shows example DST data and the likelihood. The result of this is a map of likelihoods for each tidal day.

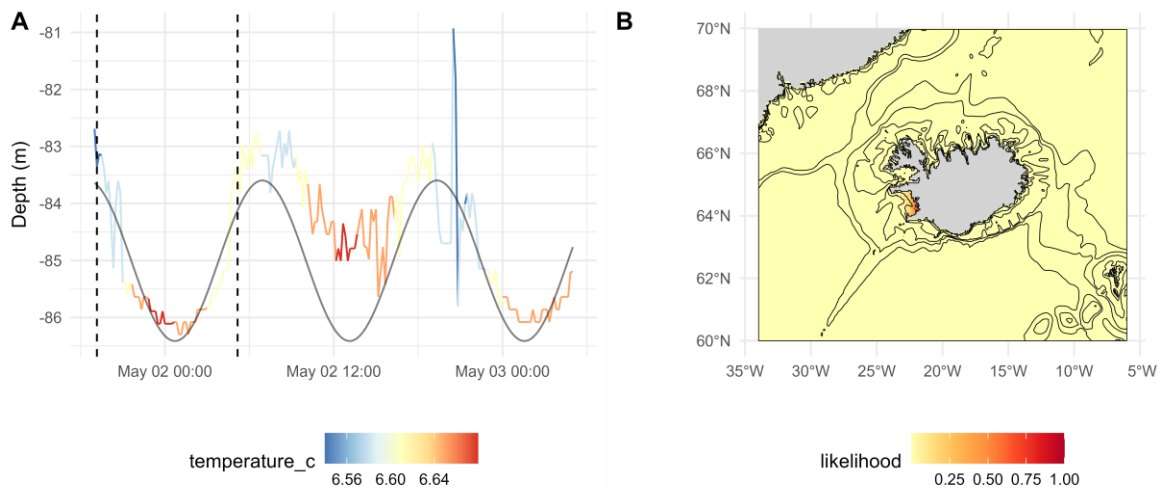


Figure 4. Example of geolocating using a tidal signature (A) Observed DST data and the best fit tidal signature, dotted lines indicate the time period that best fits the tidal signature. (B) Likelihood of this DST data being obtained at each location on the map. Likelihood is on an arbitrary scale and does not account for bathymetry (depth the fish was observed, compared to sea depth) as this is accounted for at a different stage of the model.

At this stage, the tidal days have been analysed independently, but there are also time periods in which no tide could be identified, and therefore geolocation was not possible. The fourth and final stage of geolocation is to use a diffusion model to calculate the likelihood of each location on each day (tidal days and non-tidal days), given the likelihoods on the preceding and following days. This stage of the model effectively tracks the probable locations of the fish from day to day from its release to recapture location. Optionally a track of maximum likelihood locations can be generated (the maximum probability track, MPT), but in practice this is not used because it understates the uncertainty in the model, particularly in periods when few tidal signatures were identified.

## 2.2 Update of the tidal model

The current tidal prediction model has limited extent and resolution. Because of concerns that fish may have greater migration distances than are covered by this extent, it is desirable to use an alternative model with greater geographic extent.

### 2.2.1 The TPX010 tidal model

The TPX010-atlas-v2 tidal model (Egbert and Erofeeva 2002) is a global tidal model at 1/30 degree resolution incorporating eight major tidal components and another 7 minor components. Data are

available under a free non-commercial license and thus present an opportunity to improve the resolution of the tidal geolocation model as well as to extend its geographic scope.

### 2.2.2 Extracting relevant data from TPXO10

TPXO10 tidal component data are available as NetCDF files with a global extent. Each file contains a single tidal component in the form of complex harmonic amplitudes for every 1/30 degree grid square. An additional bathymetry file gives depth for each grid square. For consistency with the current implementation, we obtained the data for tidal components M2, S2, K2, N2, K1, O1, Q1.

A script in R was produced to load the tidal components; crop the geographic extent to 60-70 degrees north latitude and 6-34 degrees west longitude; convert the complex harmonic amplitudes to phase in degrees and amplitude in mm; save the resulting data in the text file format required by the Matlab code. The script also saves the bathymetry data in the same format. Figure 5 shows the phase and amplitude of the M2 component in the TPXO10 model. Compare with Figure 3 showing the current implementation. The script could be used in future to extract different geographic extent. The script could also be modified to alter the spatial resolution of the model, if the full 1/30 degree resolution is not needed.

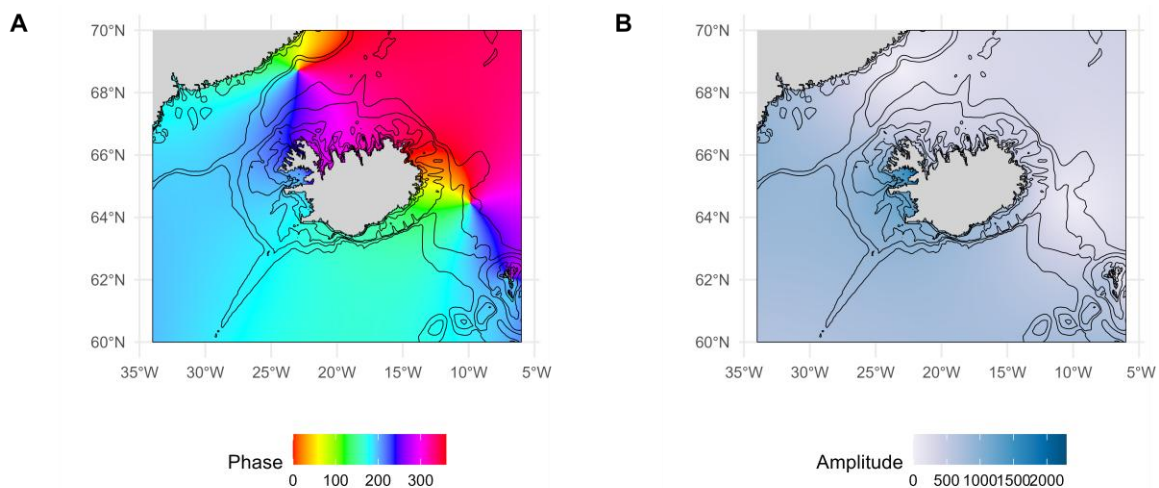


Figure 5. Parameters of the TPXO10 (Egbert and Erofeeva 2002) tidal prediction model used in the new geolocation system. A: phase in degrees of M2 tidal component. B: amplitude in mm of M2 tidal component. Depth contours at 50, 100, 200, 500, 1000 m (taken from the original geolocation system).

### 2.2.3 Updating the existing model to use TPXO10

The existing Matlab/Octave implementation of tidal geolocation was edited to make use of the TPXO10 data, allowing the same geolocation procedure to be carried out over a larger geographic area and at higher resolution.

## 2.3 Calibration of the tidal model

In the beginning, the plan was to deploy specific buoy to collect data on tidal signals from Icelandic waters. During the project, the decision was made to change this approach and instead use existing data from DSTs that were attached to gillnets during the annual gillnet survey. Even though this does not give a whole month of continuous data, this approach gave the opportunity to use data from multiple locations and years.

## 2.4 R code to run the tidal model

### 2.4.1 Issues with current Matlab/Octave implementation

While the current implementation running in Octave has performed very well, there are potential issues with its ongoing use. The code was originally written for the commercially licensed Matlab language, but as most researchers at MFRI do not have access to this, the code was modified to be compatible with the open source Octave language, however in doing this some functionality that was not available in Octave has been removed (principally producing some of the maps). The software has become difficult to maintain because few MFRI staff are familiar with the Matlab/Octave language; making it desirable to reimplement in a way that more researchers will be familiar with.

The software does not save outputs or accept its input data in any standard geographic information system (GIS) data file formats, making it hard to use the outputs in other software (for example to draw maps in a GIS, or to perform statistical analysis of outputs using statistics in R). This also leads to additional data processing stages if new data is integrated with the model (see above for the steps that were required to include TPXO10 tidal model data). For input DST data, the software is not integrated with the SQL database that is used to store DST data and instead reads the text files exported from the DST reading software, but this process can be problematic because of inconsistent formatting (units of measurement and date format) between files.

The software does not make use of standard libraries for its geographic data processing or statistical calculations. This makes the code complex, can make it hard to ensure correctness, and means it cannot take advantage of more efficient code that may be found in standard libraries (for example for parallelising geographic calculations).

These limitations of working in Octave suggest that re-implementation in another language may be worthwhile in order to have a system that can be more easily maintained and extended in future.

### 2.4.2 Potential for re-implementation in R

Existing work on tidal geolocation has made use of R for plotting outputs as maps and graphs, and for statistical analysis of the geolocation output. This has been done by importing saved Matlab binary data files into R using the *R.matlab* library (Bengtsson 2022). Loading this data is not trivial because the multidimensional arrays representing the maps of likelihood must be carefully interpreted because the files lack information such as the geographic extent, resolution, and in some data objects it is not clear how to interpret the dates.

As part of the work carried out in this project, R was used to import the TPXO10 netCDF data files, extract an appropriate geographic extent, and export as text files suitable for the current geolocation model. The R *stars* library (Pebesma and Bivand 2023) was used extensively in this process to load data from NetCDF files, process the data (such as subsetting the geographic extent and performing calculations at every geographic location), and to plot the output. Data manipulation using this library was relatively straightforward and allowed calculations to be carried out across the geographic extent in a single line of code, without having to specify looping structures. Plotting good quality maps (for example adding depth contours from other sources) was also straightforward.

This work with R, particularly manipulating geographic data with the *stars* library suggested it would be feasible to reimplement tidal geolocation using R, and that this would produce more robust, flexible and easier to maintain code.

### 2.4.3 Examples on tidal geolocation in R

Calculating likelihoods based on the tidal model do not show specific coordinate points, but rather a bounded areas where the fish most likely remained (Figure 6). The model has been tested on a few individuals. Likely locations can only be estimated during months when tidal signals are present within the depth profiles. The number of detectable tidal signals is highly variable between individuals. Coastal cod exhibit more demersal behaviour than frontal cod, and in general, a greater number of tidal signals are found within their profiles. For example, cod 1B3947 most likely remained in outer Breiðafjörður in July (Figure 6). Furthermore, data from an individual displaying tidal signals across multiple months show that coastal cod 1B3950 remained around the Reykjanes peninsula between September and December (Figure 7).

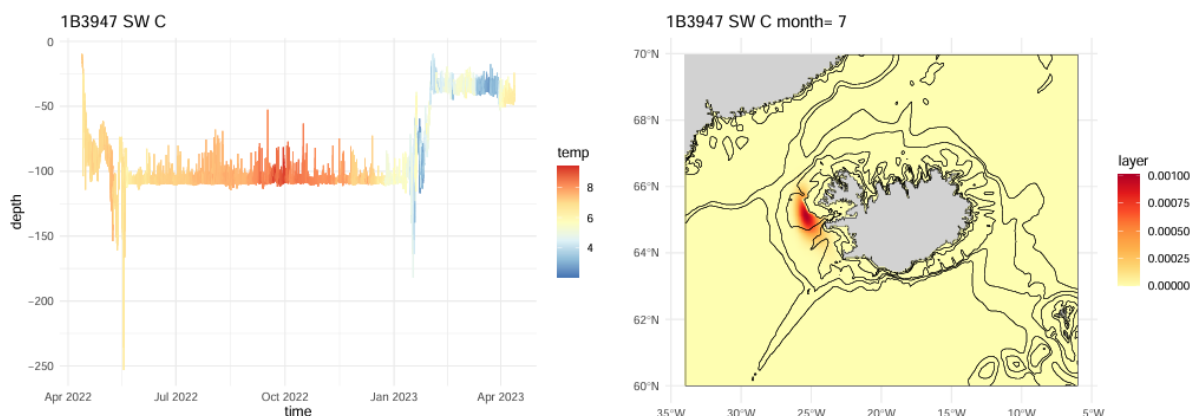


Figure 6. On the left: An example of a DST profile showing depth over a year for a coastal cod tagged Southwest of Iceland. Colour represent temperature. On the right: Most likely locations in July based on tidal signature in the DST depth profile of cod 1B3947. The red colour scale shows relative likelihood (the numeric values are not directly meaningful), when the likelihood is concentrated in a small area, the red colour appears less distinct, but represents a high likelihood over a smaller area.

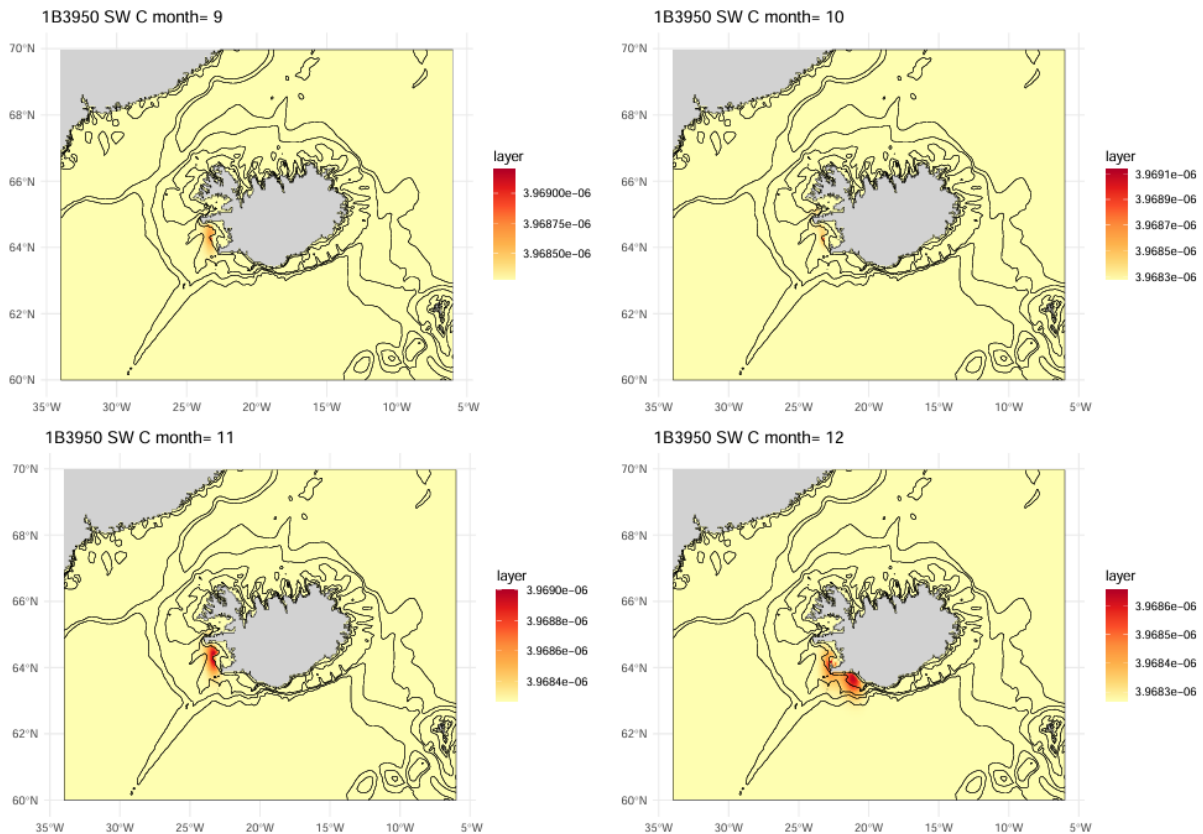


Figure 7. Most likely locations in September to December based on tidal signature in the DST depth profile of cod 1B3950. The red colour scale shows relative likelihood (the numeric values are not directly meaningful), when the likelihood is concentrated in a small area (e.g. month 10 in this figure), the red colour appears less distinct, but represents a high likelihood over a smaller area.

#### 2.4.4 Work carried out on temperature-based geolocation in R

The DSTs record temperature as well as depth, and this has proven valuable when analysing data to establish behavioural patterns and temperature niches (Grabowski et al. 2011), however currently temperature is not used during tidal geolocation. Temperature is of potential value in geolocation as it may distinguish regions with similar tides that experience different climates. For example, similar phases are found between the Westfjords and Greenlandic coast as north of Faroe, but very different mean temperatures.

Using ocean temperature to establish the likelihood of a fish being in a particular location is challenging for two key reasons: firstly, temperatures are highly variable over time, and secondly, we do not have temperature data and must rely on oceanographic models that reconstruct likely temperatures. Using data from the Copernicus Global Ocean Physics Analysis and Forecast (E.U. Copernicus Marine Service Information) we constructed two data sets: monthly mean temperatures for each location and depth slice, and standard deviation in temperature for the same points. We then calculated likelihoods by treating DST temperature as a random variable drawn from a normal distribution described by these means and standard deviations (an example of the temperatures and resultant likelihoods are shown in Figure 8). This has the potential to improve tidal geolocation, and to provide approximate locations when no tidal signature is detected. The methods will need to be validated because we cannot be

certain how well the modelled oceanographic temperatures correspond to the observed temperatures from DSTs.

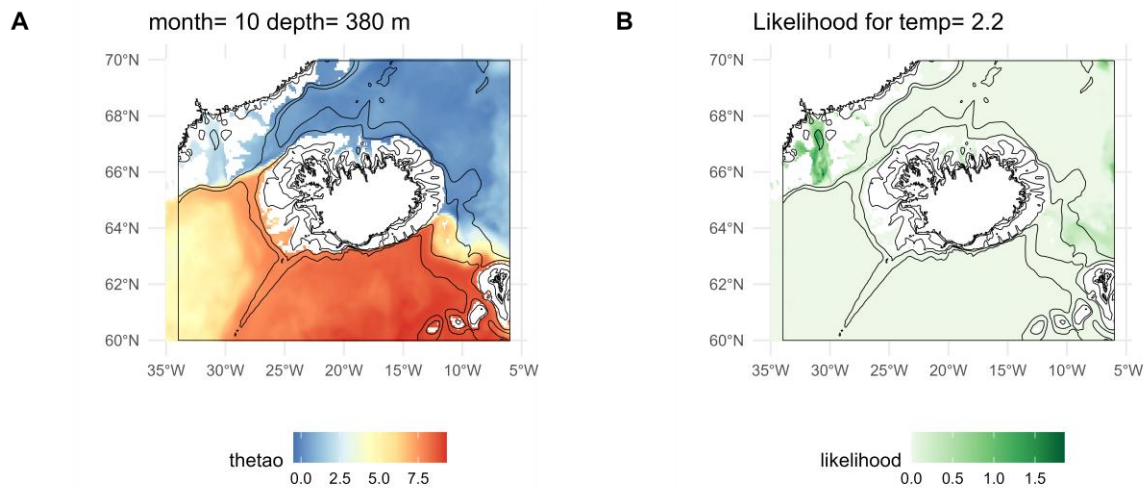


Figure 8. DST data located a fish at 380 m depth and a temperature of 2.2°C during October. A: mean temperatures for this time period and depth. B: likelihood of observed DST temperature of 2.2° at each location (likelihood is measured on an arbitrary relative scale).

### 3 Genomic characterization of the Icelandic coastal and frontal ecotypes

So far, the potential genetic differentiation of the coastal and frontal Icelandic cod ecotypes has mainly been investigated using single genes approaches, e.g. the Pantophysin (*Pan 1*) and Rhodopsin (*RH1*) genes (Pampoulie et al. 2008, 2015). While differentiation could be detected among ecotypes classified as coastal and frontal cod ecotypes using tagging methods (DSTs), some individual's genetic characteristics remained ambiguous. To characterize further the genetic background/divergence between the two ecotypes of Atlantic cod in Iceland, we genome sequenced specimens ( $n=40$ ) that have previously been tagged with DSTs and identified to be either of the frontal or coastal ecotypes using DST profiles. Of these samples, each ecotype (15 coastal and 15 frontal) were older specimens tagged and sampled in 2003, while 5 individuals of each ecotype were more recent specimens, tagged and sampled in 2022 and 2023. In order to maximize the possibility of capturing fine-scale population structuring, variant calling, i.e., identification of single-nucleotide polymorphisms (SNPs), was performed by including an extended set of cod samples from both Iceland ( $n=144$ ) and other locations across the North Atlantic Ocean ( $n=467$ ).

General population genomic analyses were carried out on putative neutral loci to assess signals of spatial genomic structure, i.e. gene flow, including Principal Component and Admixture (Alexander et al. 2009), and the results suggest very low levels of genome-wide differentiation among the Icelandic samples, including between the DST-assigned frontal and coastal cod. In an effort to characterize genomic differences between the two ecotypes, we utilized the DST samples and performed several analyses, including different outlier (loci under selection) detection methods using PCAadapt (Privé et

al. 2020), BayPass (Gautier 2015), and HacDivSel (Carvajal-Rodríguez 2017). Moreover, we estimated the genomic differentiation between the DST-assigned coastal and frontal cod measured as Weir and Cockerham's  $F_{st}$  using VCFtools (Danecek et al. 2011). The results from these analyses suggest overall low levels of genomic differentiation between the frontal and coastal ecotypes, outside four large chromosomal inversions, while substantial differentiation was detected within the inversions, in line with previous reports on Icelandic cod (Berg et al. 2017). Therefore, genomic differences were found at loci putatively under selection (four inversions) while neutral loci showed high level of gene flow between both ecotypes.

Based on these results, focusing on the reference dataset of the known frontal and coastal cod (the DST-assigned individuals in the current analyses), we developed an assignment test, i.e., a probability score based on genotype status of the four inversions discriminating the ecotypes. When testing this assignment method on the larger dataset of individuals collected at several Icelandic spawning grounds without prior information on their migration behaviour, we were able to assign all spawning cod from spawning locations as being either frontal or coastal cod. This resulted in only 3% of the specimens being potentially ambiguous to assign with 0.555 or 0.549 probability of being coastal, and 0.445 or 0.451 probability of being frontal, respectively.

These preliminary results using this assignment approach suggest that this method could be a promising and feasible tool to use in the future to delineate ecotype composition of each spawning ground of the Icelandic cod stock and could provide valuable insight for stock assessment and management of the Icelandic cod.

## 4 Final remarks

Through the development of this project, we have established a robust analytical framework for the long-term study of cod migration. By updating and calibrating the tidal model and implementing the workflow into R, this tool can be applied to the extensive MFRI database spanning the past 30 years. Furthermore, by integrating depth and temperature data with the tidal signatures, it is now possible to investigate seasonal migrations and behavioural differences driven by region, age, sex and temporal shifts. A significant advantage of this framework is that it can be utilized for any fish species tagged with DSTs within the Icelandic ecoregion. This approach expands our analytical capabilities across multiple taxa, such as Atlantic wolffish, plaice, saithe and haddock, allowing for a more holistic understanding of ecoregion-wide migration patterns and habitat use.

Understanding behavioural patterns are important because the two distinct behavioural types, coastal and frontal cod, utilize different feeding grounds. Consequently, fishing activities may exert varying levels of pressure on these two behaviours depending on the fleet's location. This impact has already been documented in Icelandic waters, specifically through the decline of *Pan1<sup>BB</sup>* individuals (frontal) between 1948 to 2002 (Jakobsdóttir et al. 2011). Since the current proportion of these behavioural types on spawning grounds are unknown, the genetic analysis completed during this project demonstrates that it is now possible to quantify these ratios for the first time.

By successfully delivering both an R-based geolocation framework for spatial tracking and a genetic approach to resolve ecotype proportions, this project significantly expands our capabilities for monitoring Icelandic fish stocks.

## Acknowledgements

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## References

- Alexander DH, Novembre J, Lange K (2009) Fast model-based estimation of ancestry in unrelated individuals. *Genome Res* 19:1655–1664. doi: 10.1101/gr.094052.109
- Bengtsson H (2022) R.matlab: Read and write MAT files and call MATLAB from within R. In: <https://CRAN.R-project.org/package=R.matlab>.
- Berg PR, Star B, Pampoulie C, Bradbury IR, Bentzen P, Hutchings JA, Jentoft S, Jakobsen KS (2017) Trans-oceanic genomic divergence of Atlantic cod ecotypes is associated with large inversions. *Heredity* (Edinb) 119:418–428. doi: 10.1038/hdy.2017.54
- Carvajal-Rodríguez A (2017) HacDivSel: Two new methods (haplotype-based and outlier-based) for the detection of divergent selection in pairs of populations. *PLoS One* 12:e0175944. doi: 10.1371/journal.pone.0175944
- Danecek P, Auton A, Abecasis G, Albers CA, Banks E, DePristo MA, Handsaker RE, Lunter G, Marth GT, Sherry ST, McVean G, Durbin R (2011) The variant call format and VCFtools. *Bioinformatics* 27:2156–2158. doi: 10.1093/bioinformatics/btr330
- Eaton JW, Bateman D, Hauberg S, Wehbring R (2019) GNU Octave version 5.2.0 manual: a high-level interactive language for numerical computations. In: <https://www.gnu.org/software/octave/doc/v5.2.0/>.
- Egbert GD, Erofeeva SY (2002) Efficient inverse modeling of barotropic ocean tides. *Journal of Atmospheric and Oceanic Technology* 19:183–204. doi: [https://doi.org/10.1175/1520-0426\(2002\)019%3C0183:EIMOBO%3E2.0.CO;2](https://doi.org/10.1175/1520-0426(2002)019%3C0183:EIMOBO%3E2.0.CO;2)
- E.U. Copernicus Marine Service Information <https://doi.org/10.48670/moi-00016>.
- Gautier M (2015) Genome-wide scan for adaptive divergence and association with population-specific covariates. *Genetics* 201:1555–1579. doi: 10.1534/genetics.115.181453
- Grabowski TB, Thorsteinsson V, McAdam BJ, Marteinsdottir G (2011) Evidence of segregated spawning in a single marine fish stock: Sympatric divergence of ecotypes in Icelandic cod? *PLoS One*. doi: e17528 10.1371/journal.pone.0017528
- Jakobsdóttir KB, Pardoe H, Magnússon Á, Björnsson H, Pampoulie C, Ruzzante DE, Marteinsdóttir G (2011) Historical changes in genotypic frequencies at the Pantophysin locus in Atlantic cod (*Gadus morhua*) in Icelandic waters: evidence of fisheries-induced selection? *Evol Appl* 4:562–573. doi: 10.1111/j.1752-4571.2010.00176.x

- Jónsdóttir IG, Sólmundsson J, Hjörleifsson E, Thorlacius M, Karlsson H (2021) Göngur og atferli þorsks: Þorskmerkingar við Ísland í rúma öld. Náttúrufræðingurinn 91:5–15.
- Pampoulie C, Jakobsdóttir KB, Marteinsdóttir G, Thorsteinsson V (2008) Are vertical behaviour patterns related to the Pantophysin locus in the Atlantic cod (*Gadus morhua* L.)? Behav Genet 38:76–81. doi: 10.1007/s10519-007-9175-y
- Pampoulie C, Skirnisdóttir S, Star S, Jentoft S, Jónsdóttir IG, Hjörleifsson E, Thorsteinsson V, Pálsson ÓK, Berg PR, Andersen Ö, Magnúsdóttir S, Helyar SJ, Daníelsdóttir AK (2015) Rhodopsin gene polymorphism associated with divergent light environments in Atlantic cod. Behav Genet 236–244. doi: 10.1007/s10519-014-9701-7
- Pebesma E, Bivand R (2023) Spatial Data Science. Chapman and Hall/CRC, New York
- Pedersen MW (2010) Hidden Markov modelling of movement data from fish.
- Privé F, Luu K, Vilhjálmsson BJ, Blum MGB (2020) Performing highly efficient genome scans for local adaptation with R Package pcadapt Version 4. Mol Biol Evol 37:2153–2154. doi: 10.1093/molbev/msaa053
- Thorsteinsson V, Pálsson ÓK, Tómasson GG, Jónsdóttir IG, Pampoulie C (2012) Consistency in the behaviour types of the Atlantic cod: repeatability, timing of migration and geo-location. Mar Ecol Prog Ser 462:251–260. doi: 10.3354/meps09852
- Tómasson GG, Káradóttir ÓR (2005) A two dimensional numerical model of astronomical tide and storm surge in the North Atlantic Ocean. In: Viggosson G (ed) Second International Coastal Symposium in Iceland. Höfn, Hornafjörður, 5-8 June, pp 266–267



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