

## **A method to geolocate eastern Baltic cod by using Data Storage Tags (DSTs)**

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### **Abstract**

DSTs can be used to investigate horizontal and vertical migrations in relation to the spawning and feeding grounds, and to estimate rates of migration and dispersion for different localities and seasons, for example with respect to hydrographic features. Our aim here is to present a new geolocation methodology which will be used to reconstruct migration pathways of individual eastern Baltic cod. The method is based on combined data of pressure, temperature and salinity obtained by DSTs attached to cod with a length greater than 45 cm. Hydrographic fields obtained from hydrodynamic modeling are used as a geolocation database in order to identify individual tracks of Baltic cod by comparison with the environmental data collected by each DST. A state-space Kalman filter was used to estimate geolocation errors, movement parameters, and most probable tracks from the derived locations. We present migration routes of 9 selected tagged cod released in the Bornholm Basin of the Baltic Sea in early spring 2003.

### **Introduction**

Investigations on fish migration patterns, based on fishery data, tagging experiments, and surveys revealed that foraging and spawning are the main reasons for fish to move over long distances. Throughout a migration, each fish experiences a change in environmental conditions as a consequence of changing depth and geographical area. There has been a marked resurgence of interest in biotelemetry as newer equipment has become available and novel research possibilities have been created. The development of

faster and cheaper microprocessors, coupled with the development of sophisticated software, means that complex algorithms can easily be incorporated into new tracking systems. Recent developments in technology now offer a variety of methods to identify behaviour and migration routes of individual fish in their natural environment (Robichaud and Rose, 2001; Thorrold et al., 2001). Environmental information obtained by Data Storage Tags (DSTs), also known as archival tags, from recaptured fish can provide a considerable amount of information which can be used to directly estimate the geographical position of individual fish throughout the time they were at liberty (e.g. Block et al., 2001; Hunter, 2001). Geolocation is a technique that can relate the movements of individuals directly to environmental parameters like temperature, salinity, light, and additional information such as bottom depth and tidal patterns (e.g. Hill, 1994; Hunter et al., 2003). The precision of estimates of geographic position can be improved by combining more than one variable in the analysis (Block et al., 2001). Investigations on fish migration patterns, based on fishery data, tagging experiments, and surveys revealed that foraging and spawning are the main reasons for fish to move over long distances. DSTs can be used to investigate on an individual basis horizontal migrations in relation to spawning, nursery and feeding grounds. These investigations will serve to estimate population rates of migration and dispersion for different localities and seasons in relation to hydrographic features.

The Baltic Sea is a semi-enclosed brackish water system. Temperature, salinity and oxygen content are vertically stratified on the scale of meters and show horizontal gradients on the scale of tens of kilometers. A permanent halocline separates low saline (< 8) surface water from high saline deep water (11-18). Below the halocline, salinity increases progressively with depth, while oxygen content usually decreases. The upper trophic ecosystem levels in the Central Baltic Sea are dominated by cod (*Gadus morhua*) as the top predator and sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) as its most important prey. The success of cod reproduction in the eastern Baltic is restricted to the deep basins (Gotland Basin, Gdansk Deep, and Bornholm Basin; Fig. 1), as a minimum salinity of 11 is required for fertilization of eggs and attaining neutral buoyancy (Westin and Nissling, 1991). The eastern Baltic cod stock is at a historically low level due to heavy fishing and recruitment failure caused by e.g. the lack of renewal of deep water (Köster et al., 2001) and mismatch of larval cod with its predominant prey species (Hinrichsen et al., 2002). Baltic cod use separate locations and habitats for spawning, larval development, juvenile and adult feeding (Fig. 1). Such complex life history requires a successful temporal and spatial linkage between these locations to integrate the whole life-cycle.

The primary aim of this paper is to present a new geolocation methodology which will be used to reconstruct migration pathways of individual eastern Baltic cod. The methodology is based on combined data of pressure, temperature and salinity obtained by DSTs attached to adult cod. Hydrographic fields obtained from hydrodynamic modelling are used as a geolocation data base to identify individual pathways of Baltic cod by comparison with environmental data collected by each DST.

In the first part of this manuscript we will demonstrate the utilization of our geolocation method by tracking an artificial cod. Secondly, we will present migration routes of selected real tagged cod released in the Bornholm Basin area of the Baltic Sea (Fig. 1) in early spring 2003.

## **Material and Methods**

### *Tagging*

Baltic cod > 45 cm were caught on a long-line in the Bornholm Basin at ca. 30-40 depth. After capture, the cod were transferred into a 0.75 m<sup>3</sup> tank and observed. Those cod that were

swimming on the bottom of the tank after ca. 1 to 6 hours were used for tagging. Total length ( $L_T$ ) was measured, a haemoglobin sample was taken and the cod were injected with Sr in order to put a mark on the otolith. A bit of piano-wire was attached at each end of the DST. The two wire ends were passed through the back of the fish from one side to the other below the 1<sup>st</sup> dorsal fin by use of an injection needle. This way, the DST was placed on one side of the back of the fish, and a PE-disc was fixed to the other side passing the wire ends through two holes of the disc (of a similar spacing as between the wire ends on the DST) and, then, twisting them. Finally, redundant wire material was pinched off, and the twisted part squeezed towards the disc. The cod were then carefully put into the water again. The whole tagging procedure took ca. 2 minutes per fish.

The tags were of the type *Star-Oddi CTD*, and each was programmed to record depth, ambient temperature, and salinity once every hour for 2 years. We also programmed the tags to archive the hydrographic data in between with a sampling interval of 5 minutes in order to check if the cod showed a different vertical activity on this time scale.

### *Geolocation*

For the reconstruction of migration routes of individual cod we have created a comprehensive geolocation database containing the spatial and temporal development of the relevant hydrographic conditions in the Baltic Sea. The most important hydrographic features with respect to geolocation of tagged fish are generated by a hydrodynamic model for the Baltic Sea. The hydrodynamic model is based on the free surface Bryan-Cox-Semtner model (Killworth et al., 1991) which is a special version of the Cox numerical ocean general circulation model (Bryan, 1969; Semtner, 1974; Cox, 1984). A detailed description of the equations and modifications made, necessary to adapt the model to the Baltic Sea can be found in Lehmann (1995) and (Lehmann and Hinrichsen, 2000a). A detailed analysis of the Baltic Sea circulation has been performed by Lehmann and Hinrichsen (2000b) and by Lehmann et al. (2002). Physical properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (for further description see Lehmann, 1995; Hinrichsen et al., 1997; Lehmann and Hinrichsen, 2000a). The model domain comprises the entire Baltic Sea including the Gulf of Bothnia, Gulf of Finland, Gulf of Riga as well as the Belt Sea, Kattegat and Skagerrak. The horizontal resolution is 5 km, with 60 vertical levels specified. The thickness of the different levels is chosen to best account for the different sill depths in the Baltic. The Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI: Norrköping, Sweden) and river runoff taken from a mean runoff database (Bergström and Carlsson, 1994). The meteorological database covers the whole Baltic Sea drainage basin with a grid of 1° x 1° squares. Meteorological parameter, such as geostrophic wind, 2-m air temperature, 2-m relative humidity, surface pressure, cloudiness and precipitation are stored with a temporal increment of 3 hours. Prognostic variables of the hydrodynamic model are the baroclinic current field, the three-dimensional temperature, salinity and oxygen distributions, the two-dimensional surface elevations and the barotropic transport. These prognostic variables have been extracted from the model every 6 hours, and form the geolocation database for the subsequent analysis.

However, longer circulation model runs will provide increasing uncertainties in the simulated physical property fields, and hence in the geolocation of tagged individual fish. These uncertainties may arise from errors in the specified forcing, boundary and initial conditions, and subgrid scale processes not resolved by the model dynamics. To overcome at least some of these problems the utilization of assimilation techniques are extremely important for long-term simulations. As initial conditions, the three-dimensional distributions of temperature, salinity and oxygen concentrations were taken from a hydrographic survey prior to the tagging period (15-March-2003) of Baltic cod covering different subareas of the Baltic Sea.

During the survey the hydrographic property distributions in the Kattegat, the western Baltic, the Arkona Basin, the Bornholm Basin, and the Stolpe Trench (Fig. 1) were recorded. A prerequisite for data assimilation as it was utilized here are hydrographic field measurements on an approximately regular grid. The observation must be horizontally distributed to ensure a smooth merging of observations with model data at the edges of the hydrographic field. It was also assumed that the field observation taken during one hydrographic survey were quasi-synoptic. Horizontal maps were constructed interpolating the physical property data onto the model grid by objective analysis (Bretherton et al., 1976). An isotropic covariance function

$$f(r) = \sigma^2 \exp(-r^2/R^2) \quad (1)$$

was used with  $R = 25$  km and  $\sigma^2$  the variance and  $r$  the distance between data points. It was assumed that the error variance due to measurement errors and small scale noise amounts in 15% of the total variance of the fields. For those areas where the expected r.m.s error was < 50%, observations substituted model data on the model grid, for those areas where the r.m.s. error was > 50% the following function was used to merge observations with model data.

$$T_m(x,y) = T_{\text{mod}}(x,y) - \alpha [T_{\text{mod}}(x,y) - T_{\text{obs}}(x,y)] \quad (2)$$

with

$$\alpha = \begin{cases} 1, & \text{rms} < 50\% \\ \exp[-((\text{rms}-50)/12.5)^2], & \text{rms} > 50\% \end{cases} \quad (3)$$

$T_m$  represents the merged temperature and salinity fields,  $T_{\text{mod}}$  the model data prior to the assimilation, and  $T_{\text{obs}}$  are the field observations. Data outside the surveyed area were taken from a previous model run representing similar seasonal hydrographic conditions as for the observational period. Although not recorded by DSTs, oxygen concentrations could be used as a supplementary database to geolocate Baltic cod, we have calculated this parameter by a function dependent on temperature and salinity. At the sea surface, as a boundary condition, oxygen saturation was set 100%. In order to take into account consumption of oxygen by biological processes, a constant depletion rate (Wieland, 1995) has been implemented. Further re-initializations of the physical property fields have been performed for April, May, July, August and November 2003.

A geolocation method has been developed to corroborate temperature and salinity records recovered from DSTs deployed in the Baltic Sea with hydrographic data obtained from hydrodynamic model fields calculated for the tagging period in 2003. The key to our method is that each combination of salinity and temperature at a given depth is unique for a very small area in the Baltic Sea. Therefore, the DST-derived knowledge about the fishes' depth and the temperature and salinity in the surrounding water can be used to estimate the fish's position. The model derived average salinity gradient in the Bornholm Basin has a maximum of ca. 0.33 per 5 km at around 60 m depth in the Bornholm Basin. At 50 m and at 70 m depth the salinity gradient is ca. 0.2 per 5 km (Figure 2 A). In contrast to the salinity gradient, the average temperature gradient is maximal at ca. 70 m depth, with an average temperature change of ca. 0.75 °C per 5 km (Fig. 2 B).

Hence, the geographic position of each fish from release to recapture was determined by comparing the DSTs temperatures and salinities with the environmental variables as obtained from the highly temporally and spatially resolved hydrodynamic model output fields. The method requires representation of all available parameter (ptag, ttag, stag) to estimate the daily and subdaily geographical positions of individual fish by minimizing the residuals

between DST data and model output ( $p_{\text{mod}}, t_{\text{mod}}, S_{\text{mod}}$ ) which is commonly known as the ‘least square approach’.

$$w_1 * (p_{\text{tag}} - p_{\text{mod}})^2 + w_2 * (t_{\text{tag}} - t_{\text{mod}})^2 + w_3 * (S_{\text{tag}} - S_{\text{mod}})^2 = \min \quad (4)$$

$p_{\text{tag}}, T_{\text{tag}}$  and  $S_{\text{tag}}$  represent the DST measured pressure, temperature and salinity data,  $p_{\text{mod}}, T_{\text{mod}}$  and  $S_{\text{mod}}$  the model data as the geolocation database. Weights are allocated to the various parameters according to environmental variability and instrument precision; for each parameter  $i$ , the corresponding weight  $w(i)$  is determined as the ratio between the instrument precision and the largest variance of the parameter found in the field. Weighting factors are necessary in order to make parameters of incommensurable units comparable, which means that information obtained from each parameter is of identical quality. The accuracy of the geographic positions along the migratory route of a tagged cod will be improved wherever possible through the use of other datasets where appropriate (e.g. bottom topography, oxygen concentrations).

### *Statistical modeling*

The daily geolocation estimates are post-processed by a state-space model similar to the one proposed in Sibert et al (2003). This model uses the Kalman filter to obtain estimates of the daily locations when the entire track is taken into account. A slightly improved version of this method is used. Instead of using the standard Kalman filter in combination with an ad hoc linearization of the model, we used the extended Kalman filter (Harvey 1990). The extended Kalman filter uses a local Taylor expansion around the previous state. The method for reconstruction of the track is also updated. Instead of using the 'prediction track', where each estimated geolocation is derived from previous points only, we used the entire track to estimate each geolocation. This approach reduces the uncertainties and gives a smoother reconstructed track.

## **Results**

In order to demonstrate how geolocation of DST tagged Baltic cod could be performed, we have chosen an artificial Baltic cod which started its migration in spring time in the near of Gedser (Fig. 3). Recapture was assumed to take place 35 days later in the Gdansk Deep (Fig. 3) which is approximately 500 km farther east of the original start location. The prescribed migration route of the cod passed through the Arkona Basin, the Strait of Bornholm into the Bornholm Basin where the fish performed an anti-cyclonic loop within the center area (Fig. 3). In vicinity of 55°N30', 15°E30' it was assumed that the cod remained for a time period of  $x$  days. After leaving the deep central area of the Bornholm Basin the artificial cod directly swam to the Gdansk Deep (Fig. 3), where recapture was prescribed to take place at the 5<sup>th</sup> May. Along the migration path, the cod recorded its ambient physical environment. These environmental data were taken for April conditions from 4-years averages of the 6 hourly resolved model fields (Lehmann and Hinrichsen, 2000b). As a next step the geolocation method recalculated the migration route of the cod by utilization of (4). For this purpose, only the environmental data recorded by the artificial fish were considered. In order to create realistic measurement errors and small scale noise of the environmental data, we have used randomly distributed individual parameter perturbations in the range of the instrument precision of the DST.

From most of the data the originally prescribed positions of the artificial cod could be recovered. However, for some data points, the geographical positions were identified to be located far away from the original track position. These locations were outside the range of a

cod's swimming ability, which has been recorded to be on average not higher than one body length per second. Thus, in order to calculate the fish's migration route based on realistic behaviour, a first modified version of our method includes two additional constraints: i) their subsequent geographical positions must be reached by a cod in an appropriate time period with respect to swimming ability, and ii) the recapture position has to be reached for a cod by its average swimming speed in the remaining time frame of the individual fish tagging period. Taking into account these biological constraints, the 'known' and the simulated migration routes are close together (Fig. 3) with the differences between the prescribed and recovered positions of the cod is on average  $2.9 \text{ km} \pm 4.7 \text{ km}$ .

The estimated tracks from 9 recaptured cod displayed in Fig. 4 show migrations of individual cod during 54 to 126 days. Two cod moved from the tagging location at the east-coast of Bornholm to the west coast (Fig. 4 A and E), but returned and were re-captured close to the tagging location. Three other cod visited Slupsk Furrow (Fig. 4 F,H, and I) after tagging. 6 out of the 9 cod we tracked were re-captured close to the release point.

We selected the track displayed in Fig. 4 E in order to explain the potential in the usage of the Kalman-Filter. Based on 81 geolocations for this cod on 81 subsequent days (Fig. 5), the estimated standard deviation of the geolocations based on the hydrodynamic model was  $0.07 \pm 0.02$  [degree] in the x-direction (longitude) and  $0.03 \pm 0.01$  [degree] in the y-direction (latitude). The longitudinal ( $u$ ) and latitudinal ( $v$ ) components which in combination give the vector describing the mean rate of displacement for the cod were estimated to  $u = 0.039 \pm 0.518$ , and  $v = 0.067 \pm 0.518$  [ $\text{nm d}^{-1}$ ], and the rate  $D$  at which the uncertainty of the position estimate increases over [zweiter halbsatz] time was estimated to  $10.751 \pm 2.167$  [ $\text{nm}^2 \text{d}^{-1}$ ].

## Discussion

The suitability of the geolocation methodology of tagged eastern Baltic cod for predicting their migration routes is clearly indicated in this coupled field and modelling exercise. Geolocating fish by this method has no inherent limits to accuracy, as for example in geolocation by light intensity (Metcalf 2001). The accuracy of the geolocation is determined by the measurement accuracy of the tag and the accuracy of the hydrodynamic model. After calibration with known salinities, the tag measurements of salinity have an accuracy of about  $\pm 0.5$ . The same is the case for the temperature measurements, where accuracy is ca.  $\pm 0.1$  °C. An additional problem with the temperature measurements is the sensor delay. The temperature sensor is located inside the tag that has a ceramic housing. Although heat is transported quickly by the housing material, the sensor response is lagged within the order of minutes, for example when temperature changes from 7° C to 4° C. If the cod perform rapid vertical migrations, the archived temperature might hence not match completely the archived salinity. However, our DST records of depth indicate strongly, that such rapid vertical migration occur seldom. Furthermore, a possible outlier in the geolocations, based on a wrong combination of temperature and salinity would very probably be spotted by the Kalman filtering.

The hydrodynamic model has been updated regularly by assimilating data from hydrographic surveys. The observed hydrographic data from surveys allowed for a test of the performance of the hydrodynamic model. The model error increases the longer the model runs without assimilating survey data. The maximum deviations of the model from the observed environmental conditions during the hydrographic survey after ca. 1 month modelled hydrographic development were about 1 in salinity (in the halocline) and 1° C in temperature (in the thermocline). These deviations, considered separately, correspond to a horizontal mismatch of 5.5 to 8.3 nm.

The Kalman filter produces estimates of geolocation errors for individual fish and movement parameters applicable in order to describe changes in the distribution on population-scale (Sibert *et al.* 2003). The standard deviation of the geolocations is in the same order of magnitude as the deviations solely based on tag measurement error and model error. Translated to distance for the central Baltic Sea, a longitudinal standard deviation of 0.07 degrees corresponds to 2.1 nm, and a latitudinal standard deviation of 0.03 degrees corresponds to 1.8 nm. Taking 2 standard deviations, each geolocation lies hence within a circle of approximately 4 nm radius.

Future management measures based on effort allocation within specific areas needs a more complete understanding on the horizontal movements of cod. For instance, to regulate fishing activity, the design and effectiveness of 'Marine Protected Areas' could be based on tagging data of migrating fish. However, the precision of assessments from tag recoveries will depend on the number of releases, but based on actual recapture rates, simulation studies can be performed to estimate the number of releases needed to obtain a certain precision (Xiao, 1996).

Subsequent studies on horizontal movements of tagged fish will provide valuable information on timing of migration, migration rates and migration distances of Baltic cod, and thus on their spawning and feeding habitats as well as on stock boundaries and stock mixing.

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### **References**

Bergström, S., Carlsson, B., 1994. River runoff to the Baltic Sea: 1950-1990 *Ambio* 23 (nos. 4-5), 280-287

Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L.H., Seitz, A., Walli, A., Fudge, D. 2001. Migratory movements, depths preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293:1310-1314.

Bretherton, F.P., R.E. Davis, and C.B. Fandry, 1976: A technique for objective analysis and design of oceanographic experiments applied to MODE-73. *Deep-Sea Res.*, 23, 559-582

Bryan, K., 1969: A numerical method for the study of the circulation of the world ocean. *J. Phys. Oceanogr.*, 15, 1312-1324

Cox, M.D., 1984: A primitive equation 3-dimensional model of the ocean. GFDL Ocean Group Tech. Rep. No. 1, GFDL/Princeton University

Harvey, A.C., 1990: Forecasting, structural time series models and the Kalman Filter. Cambridge University Press.

Hill, R. 1994. Theory of geo-location by light levels. In: Le Boeuf, B.J., Laws, R.M. (eds) *Elephant seals population ecology, behaviour and physiology*. University of California Press, Los Angeles, pp 227-236

- Hinrichsen, H.-H., Lehmann, A., St.John, M.A. and Bruegge, B. (1997) Modelling the cod larvae drift in the Bornholm Basin in summer 1994. *Cont. Shelf Res.*, Vol. 17, No. 14, 1765-1784
- Hinrichsen, H.-H., Moellmann, C., Voss, R., Koester, F.W., Kornilovs, G. 2002. Bio-physical modelling of larval Baltic cod (*Gadus morhua* L.) growth and survival. *Can. J. Fish. Aquat. Sci.* 59: 1858-1873
- Hunter, E., Aldridge, J.N., Metcalfe, J.D., Arnold, G.P. 2003. Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables. *Marine Biology*. 142: 601-609.
- Hunter, E. 2001. Migration, distribution and spatial dynamics of plaice in the North Sea- Final Report. Report FAIR PL96-2079 to the EU
- Killworth, P.D., D. Stainforth, D.J. Webbs, and S.M. Paterson, 1991: The development of a free-surface Bryan-Cox-Semtner ocean model. *J. Phys. Oceanogr.* 21, 1333-1348.
- Koester, F.W., Hinrichsen, H.-H., St.John, M.A., Schnack, D., MacKenzie, B.R., Tomkiewicz, J., Plikshs, M., 2001. Developing Baltic cod recruitment models II: Incorporation of environmental variability and species interaction. *Can. J. Fish. Aquat. Sci.* 58: 1535-1557
- Lehmann, A., 1995. A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. *Tellus* 47A, 1013-1031
- Lehmann, A., Hinrichsen, H.-H., 2000a. On the thermohaline variability of the Baltic Sea. *J. Mar. Syst.* 25: 333-357
- Lehmann, A., Hinrichsen, H.-H., 2000b. On the wind driven and thermohaline circulation of the Baltic Sea. *Phys. Chem. Earth (B)* 25, 183-189
- Lehmann, A., Krauss, W., Hinrichsen, H.-H., 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus* 54A, 299-316
- Metcalfe, J.D., 2001: Summary report of a workshop on daylight measurements for geolocation in animal telemetry. In: *Electronic Tagging and Tracking in Marine Fisheries Reviews: Methods and Technologies in Fish Biology and Fisheries*. J. Sibert and J. Nielsen (eds.) Dordrecht: Kluwer Academic Press, pp. 343-368.
- Robichaud, D. and Rose G.A., 2001: Multiyear homing of Atlantic cod to a spawning ground. *Can. J. Fish. Aquat. Sci.* 58(12):2325-2329.
- Semtner, A.J., 1974: A general circulation model for the World Ocean. UCLA Dept. of Meteorology Tech. Rep. No. 8, 99p.
- Sibert, J.R., Musyl, M.K., Brill, R.W. (2003) Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging data. *Fish. Ocean.* 12(3): 141-151.



Thorrold, S.R., Latcozy, C., Swart, P.K., Jones, C.M., 2001: Natal homing in a marine fish metpopulation. *Science* 291(5502):297-299.

Westin, L., Nissling, A., 1991. Effects of salinity on spermatozoa motility, percentage of fertilized eggs and egg development of Baltic cod *Gadus morhua*, and implications for cod stock fluctuations in the Baltic. *Marine Biology* 108: 5-9

Wieland, K., 1995: Einfluss der Hydrographie auf die Vertikalverteilung und Sterblichkeit der Eier des Ostseedorsches (*Gadus morhua callarias*) im Bornholm Becken, suedliche zentrale Ostsee, Ber. Inst. f. Meeresk. Kiel, 266, 114pp

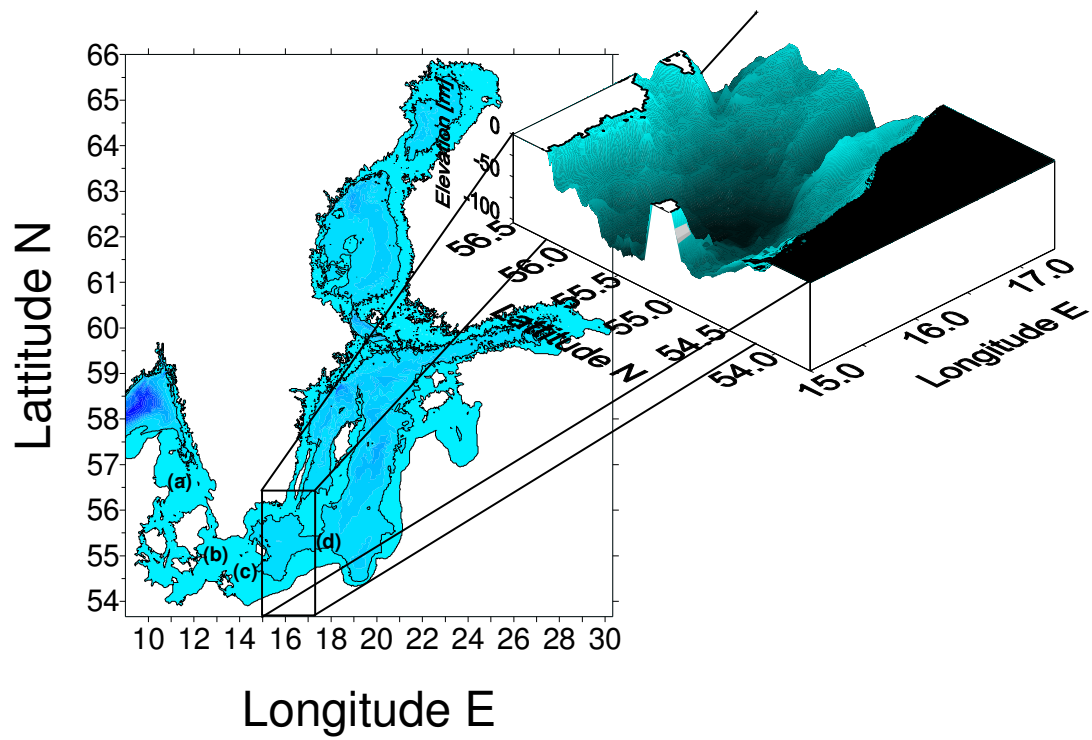


Figure 1:  
 The Baltic Sea (map) and the Bornholm basin as surface plot. (a) Kattegat, (b) the western Baltic, (c) the Arkona Basin, and (d) the Stolpe Trench.

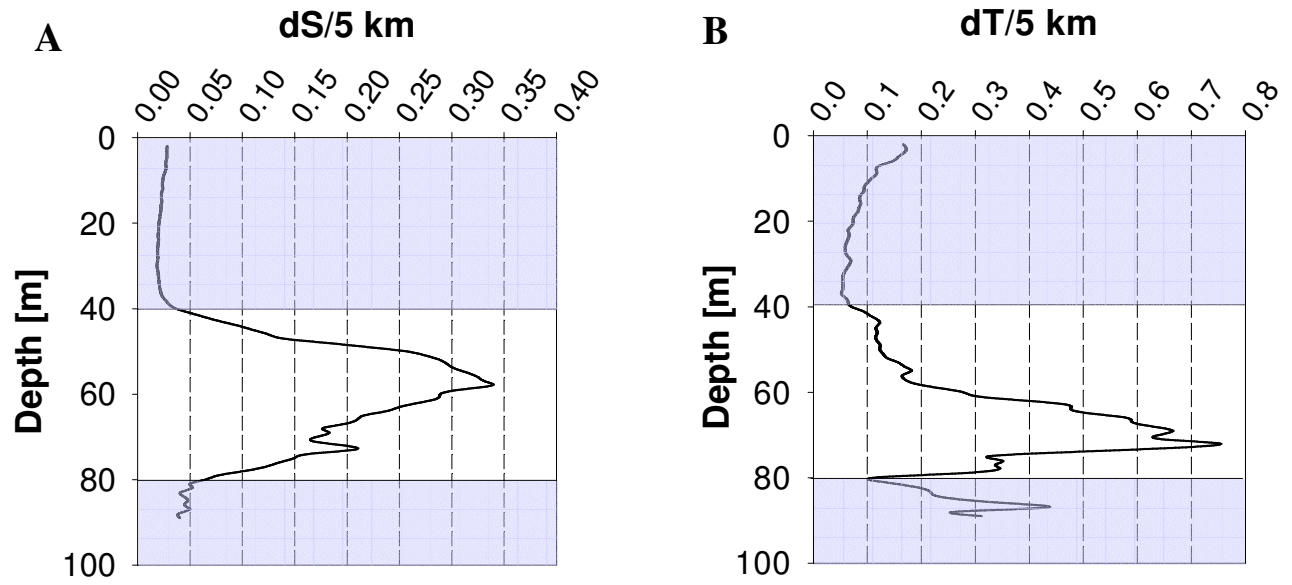


Figure 2:  
 Average gradients of salinity (A) and temperature (B) at depth for the Bornholm Basin. The depth range between 40 m and 80 m mark the main distribution area for cod in the Basin.

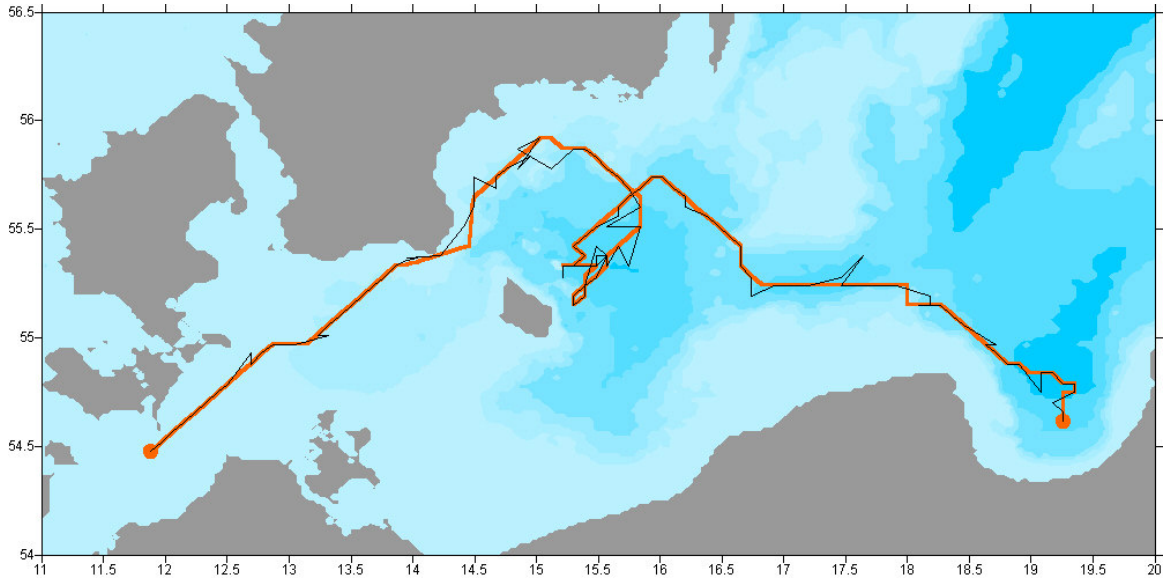


Figure 3:  
Simulated track (thick line) and estimated track (thin line) .

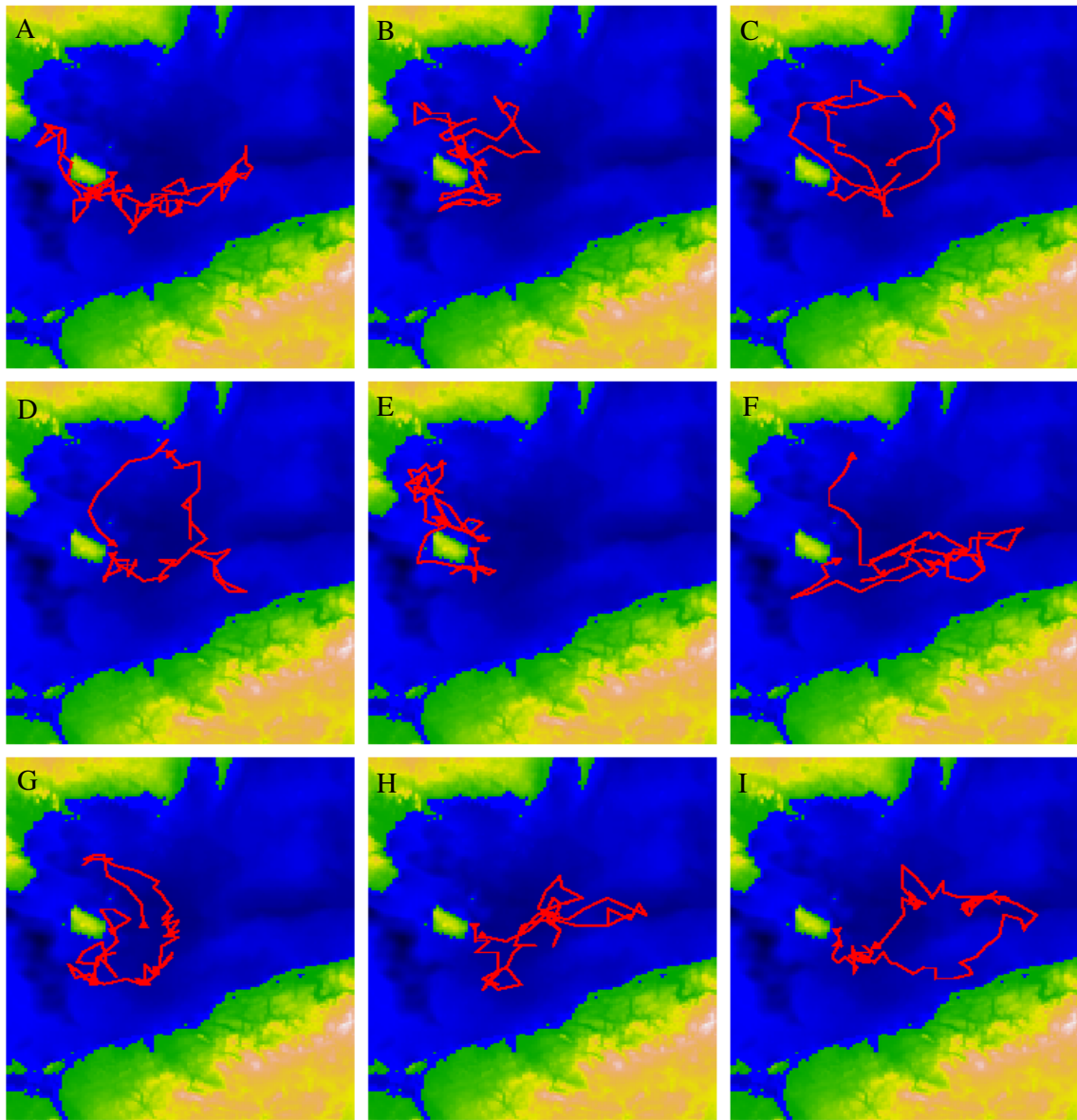


Figure 4:  
(A) – (I) estimated tracks from recaptured cod.

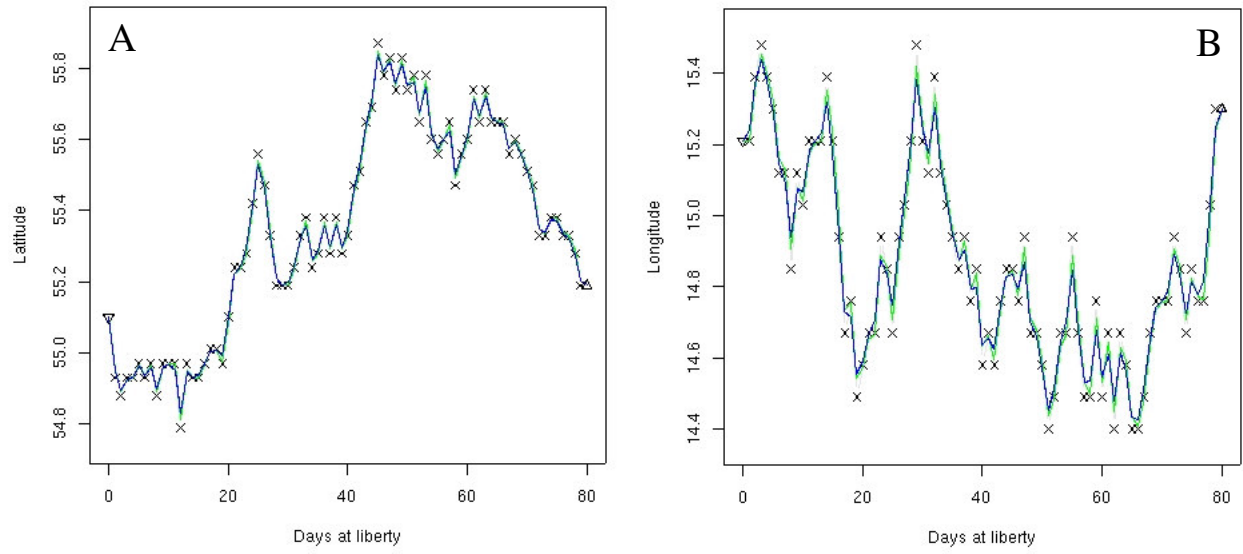


Figure 5:  
Estimated latitude (A) and longitude (B) (solid line) and daily geolocations (crosses) for the track in Fig. 4 (e).