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Migration routes and habitat use of a highly adaptable salmonid (sea trout, *Salmo trutta*) in a complex marine area

Martin Lykke Kristensen^{1*} , Martin Wæver Pedersen², Uffe Høgsbro Thygesen³, Diego del Villar-Guerra⁴, Henrik Baktoft¹ and Kim Aarestrup¹

Abstract

Background: Understanding fish movements and migrations are paramount for management and conservation efforts. By applying Hidden Markov Models (HMMs) on records from electronic tags, migration routes of tagged fish can be reconstructed and new insights to the movement ecology of a species can be gained. We demonstrate the usability of HMMs on a widespread, iteroparous salmonid (sea trout, *Salmo trutta*) in a complex marine area with highly variable temperatures and salinities within small geographic distances. Understanding how the highly adaptable sea trout cope with these complex conditions could shed new light on factors driving the movement ecology of salmonids. Migration tracks of fish migrating at sea are reconstructed by applying an HMM on temperature and depth records from eight wild post-spawned sea trout from four Danish rivers.

Results: The fish migrated at sea for 47–142 days. Estimated positions of all fish were close to the coast (< 100 km) throughout the marine period, but migrations along coastlines up to 580 km away from the natal river occurred. Seven of eight individuals resided in or actively migrated into stratified or shallow marine areas that heat up fast during spring, while all eight individuals resided in deeper and more heterogeneous areas that heat up slow during summer. All fish entered the Skagerrak (located between Denmark and Norway) at some stage during summer. Migrations were directed into less saline areas during the first 15 days at sea for all individuals. Mean linear progression of the fish was 16 km day⁻¹ (range 0–58 km day⁻¹).

Conclusions: The results corroborate the expectation that sea trout are more coastally orientated than other salmonids, but also suggest that longer migrations occur in the seas surrounding Denmark compared to elsewhere. This could be a consequence of the fish seeking out habitats with optimal conditions (e.g. salinity, temperature, predation and foraging options) for growth in different parts of the year. The coinciding movement from shallow or stratified marine areas that heat up fast during spring to deeper, more well-mixed areas that heat up slow during summer suggested that some habitat selection had occurred. These results shed new light on factors influencing marine migrations in salmonids and demonstrate how HMMs can expand our knowledge on behaviour and movement ecology of marine fishes.

Keywords: Salmonid, Hidden Markov Model, Migration, Kelt, Sea trout, Data storage tags, Archival tags, Geolocation, Habitat use, Movement ecology

*Correspondence: makri@aqu.dtu.dk

¹ Technical University of Denmark, National Institute for Aquatic Resources, 8600 Silkeborg, Denmark

Full list of author information is available at the end of the article



Background

The ability to select environments favouring different requirements through different parts of a lifecycle is a key element to success for many marine species [1]. Detailed knowledge of movement ecology is, therefore, paramount for understanding and managing fish and fisheries [2]. Technological constraints have, however, made it difficult to acquire such knowledge for many species [3].

Salmonids are prized target species among recreational anglers and have high economical and societal importance in their distribution areas [4–6]. To successfully manage and conserve them, basic knowledge regarding their habitat preferences and ability of individuals to seek out areas with more favourable predator/prey abundances or specific ranges of metabolic influencers such as food, temperature and salinity is needed [3, 7].

Although generally orientated towards the surface during their marine period, substantial differences in movement ecology and temperature use exist between iteroparous salmonids such as Arctic charr *Salvelinus alpinus*, Atlantic salmon *Salmo salar* and steelhead *Oncorhynchus mykiss*, potentially affecting their tolerance to environmental alterations and climate change [8]. Arctic charr generally have short (1–2 months) marine periods in cold (<11 °C) water close to their natal river [9], while Atlantic salmon from North America [10] and Europe [11–13] tend to perform long migrations into the relatively cold Labrador Sea or North Atlantic Ocean. Steelhead also migrates into the open ocean, but disperse across the Pacific into a wider temperature range [8].

Less is known about the behaviour at sea of sea-run brown trout (hereafter termed as sea trout): an iteroparous salmonid, dispersed across all continents except Antarctica and known for exhibiting large variability and adaptability to local conditions in terms of life strategy and movement ecology [14]. Although scarcely described in the sea, marine migration strategies in fjords and estuaries are known to be complex for sea trout [7]. Individuals may opt for a sedentary migration strategy and stay within fjord and estuary systems during the entire marine period in some regions [9, 15, 16] while estuaries and fjords are used as short-term migration corridors to the sea by sea trout in other areas [17–19]. Factors such as predator/prey abundances, temperature and salinities may influence the overall strategy employed by sea trout populations in different regions [20].

Temperature and salinity affect the metabolism of fish [21–23], although the metabolic cost associated with osmoregulation in salmonids is still subject to debate [24, 25]. The seas surrounding Denmark respond to meteorological forcing at different speeds with some areas warming up much faster than others during spring and summer.

Additionally, a salinity gradient stretches between the North Sea (30–35 PSU) on the western side of Denmark and the Baltic Sea (8–14 PSU) on the eastern side [26]. Conditions in the seas surrounding Denmark, therefore, provide sea trout with the option to migrate towards marine areas with lower salinities and different temperatures at different times of the year. Understanding how a highly adaptable salmonid like sea trout copes with the special conditions of the seas surrounding Denmark may, therefore, shed new light on factors shaping marine migrations in salmonids.

We used a Hidden Markov Model (HMM) to investigate migration behaviour by reconstructing the migration tracks of eight sea trout kelts (individuals that had spawned at least once). This is a follow-up study to investigate the geographical distribution of the fish, as a previous study documented that the tagged sea trout were residing in waters warmer than the mean in the seas surrounding Denmark during spring and colder than the mean during summer [27]. By recreating the migration tracks of the fish, we were able to investigate how individuals migrated in the complex seas surrounding Denmark and whether they used specific areas at different times of the year. The HMM computed the tracks based on temperature and depth measurements from the fish recorded by data storage tags. We expected the kelts to be mainly shelf-sea orientated and that migrations would generally be towards areas with temperatures favourable for growth and possibly towards lower salinities.

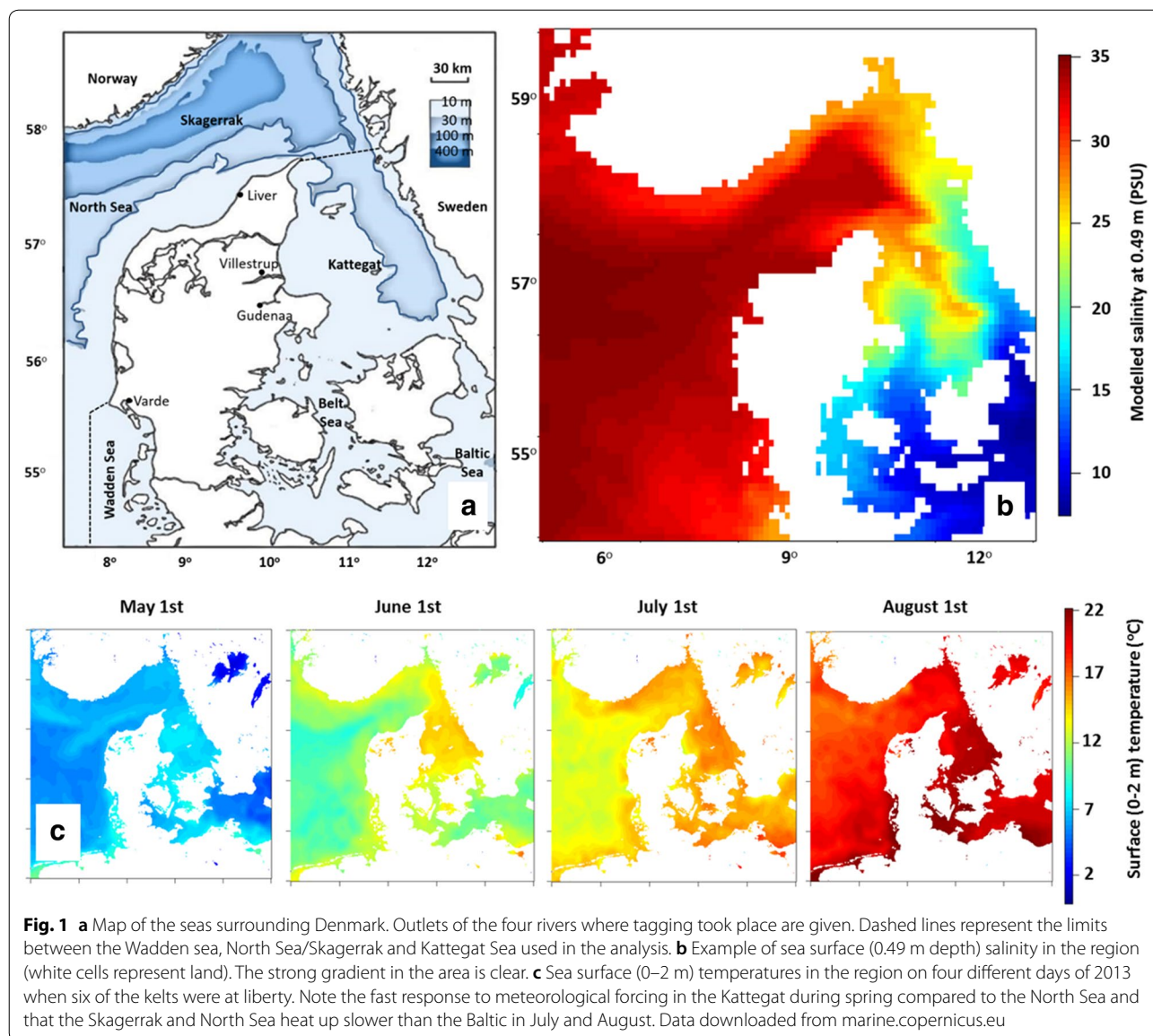
Materials and methods

Study site

The seas surrounding Denmark are generally shallow (<50 m deep) and characterized by a strong halocline between the North Sea and the Baltic Sea [26]. The limited depths and lack of mixing to depths deeper than 5–15 m enables sea surface temperatures to change quickly in the Kattegat and Belt Sea area, while surface temperatures in the North Sea and Baltic Sea respond slower to meteorological forcing [26, 28]. The southwesternmost part of the North Sea (hereafter referred to as the Wadden Sea) is shallow but well mixed by tidal and wind force. Sea surface salinities in the Skagerrak, Kattegat and Belt seas depend on wind speed and direction in the region, but generally decrease towards the Baltic Sea (Fig. 1).

Tagging with DSTs

A total of 125 sea trout kelts were tagged with G5 long-life DSTs (CEFAS Technology, <http://www.cefastechnology.co.uk>) fitted with a string of 11-mm diameter floats (the same diameter as the tag) to facilitate retrieval after shedding or death. The total tag length with floats was



approximately 140 mm, weight in air was 9.8 g and the net buoyancy was 0.009 N, corresponding to a negative weight in water of 0.9 g. The floats were covered in silicon rubber (Dow Corning, 734) that is biologically inactive and harmless to the fish [29]. The tags recorded temperature and depth of the fish every 5 min. For a full description of the tags used, see [27].

Sea trout kelts were electro-fished or captured in traps during downstream migration in the rivers Liver, Gudena, Villestrup and Varde (Fig. 1) during winter or spring. The fish were anesthetized with benzocaine and the DST was implanted in the body cavity by an experienced fish surgeon in accordance with the permission

2012-DY-2934-00007 from the Danish Experimental Animal Committee. The surgical procedure lasted 1–2 min and is described in full in [27].

Eight tags were recovered from fish that had performed a full marine cycle (Table 1). Six of these were recovered by recreational anglers who had caught the fish after it had returned to the river. The seventh tag was found on a river bank (without the fish) while the eighth tag was recovered from a fish that was electro-fished. An additional 25 tags were recovered from fish that had died or lost the tag at sea, but these datasets are not included as their mean survival time at sea was 14.3 days [30].

Table 1 Tagging information from eight sea trouts and summary data from their marine period

Fish no.	Tag ID	River of origin	Weight at release (g)	Length at release (cm)	Gender	Date of tagging	Date of sea entry	Time at sea (days)
1	A08546	Liver	7150	91.5	Female	16-Mar-2012	27-Apr-2012	47
2	A08543	Gudena	2400	58	Female	27-Mar-2013	30-Apr-2013	89
3	A08549	Gudena	2480	58	Female	27-Mar-2013	09-May-2013	87
4	A08577	Liver	1736	55	Male	12-Dec-2012	06-May-2013	142
5	A08578	Gudena	1850	56.5	Male	27-Mar-2013	24-Apr-2013	105
6	A08609	Varde	1650	54	Female	08-Apr-2013	10-Apr-2013	94
7	A08634	Varde	1650	57	Female	08-Apr-2013	14-Apr-2013	87
8	A08640	Villestrup	1860	60.5	Female	13-Apr-2015	28-Apr-2015	118
Mean	–	–	2597 (SE: 660)	61.4 (SE: 4.4)	–	–	–	96.1 (SE: 9.7)

Fish from the Gudena, Varde and Villestrup rivers migrated through fjords or estuaries before entering the sea

Data analysis

The day of sea entry and exit was defined as the first and last day of entry to depths deeper than 10.0 m. For justification of the method, see [27]. Fjord and estuary residence was discarded from the present dataset.

A Hidden Markov Model (HMM) was used to compute discrete probabilities of kelts residing in a given area on a given day [31]. The model assumes that the fish performs a random walk between discrete grid cells, and computes the posterior probabilities of residence given observations of temperatures and depths. Specifically, displacements between consecutive days in the longitudinal and latitudinal direction were assumed to be independent Gaussian random variables with zero mean and a variance which is estimated from data using the Maximum Likelihood principle. Temperature and maximum visited depths experienced by the kelts vs. satellite-measured temperatures and bathymetry charts of the region were used to compute the likelihood of residence in cells of a 1 × 1 km grid covering the area from –10° to 18° E and 50° to 66° N. The relatively large area was included to ensure that modelled migration tracks were not restricted by the geographical extent of the dataset.

Conceptually, depth measurements constrain the residence, in that the model assumes that the fish could not reside in areas with shallower depths than the maximum visited depth on a given day. At the same time, temperatures experienced by the fish should be close to that of the satellite-measured sea surface temperatures. The heterogeneity of sea surface temperatures in the area (Fig. 1c) made it a suitable region for this type of analysis.

Maximum visited daily depth was extracted for each day from each individual fish during its residence at sea. Temperature at the surface (0–2 m) in the area of residence of the fish was obtained for each day as a mean of measurements between 21:00 and 07:00 h. Only measurements where the fish had resided at depths of

0–2 m for a minimum of 20 consecutive minutes were included in the mean. The 20-min delay was necessary to allow the temperature of the implanted DST to reach ambient levels after visits to deeper waters by the fish [32].

Depth charts were downloaded from <http://www.gebco.net> and sea surface (0–2 m) temperatures for the region were downloaded from marine.copernicus.eu (product name: SST_BAL_SST_L4_NRT_OBSERVATIONS_010_007_b). The temperatures represented a mean of a series of infrared satellite measurements from depths of 0–2 m between 21:00 and 07:00 h each day for a 1 × 1 km grid. The uncertainty of the temperature data was reported for each cell for each day and was approximately 0.5 °C in general.

To assign gradually decreasing chances of residence in a cell the farther the measurements from the fish deviated from the satellite measurements and bathymetry data, the `dnorm()` and `pnorm()` functions of the stats package in R were used. This also avoided assignment of strictly binary outcomes for the cells.

The `dnorm` function was used for temperature with the error of the satellite-measured temperatures entered as the standard deviation. Assigned likelihood of residence in a cell was, thus, closer to 1 the closer the mean satellite-measured temperatures was to the temperature measured in the fish and the smaller the error was for the satellite data of the given cell. Potential uncertainty in the temperatures measured by the tag were not accounted for in the likelihood function.

The `pnorm` function was used for depth where standard deviation was defined as the standard deviation of depths in the cells surrounding a given cell in the bathymetry chart. This assigned likelihoods of residence close to 1 in cells deeper than the maximum daily visited depth of the fish and values close to zero for

cells shallower than the maximum visited depth with a gradual transition between 1 and 0 from depths 1–3 m deeper to 1–3 m shallower than the maximum visited depth.

Depth was included as all fish visited depths deeper than 40 m at some stage, thus enabling the exclusion of residence in large areas on some days. Including both depth and temperature, however, also introduced some uncertainty to the modelled position due to the discrete nature of the dataset (i.e. the fish could have visited deep water in the morning and moved into shallower and warmer waters during night when temperatures were measured). This could introduce an overestimation of the modelled distance to land, particularly in the early part of the marine migration phase when the fish sought out warm waters, likely found closer to the coast [27].

The overall likelihood for residence in each cell was calculated by multiplying the respective temperature and depth data frames together. The likelihood of residence in

cells on land was set to 0. When done for each day in all cells in the entire grid, probability distributions like those on Fig. 2 were obtained.

A discrete state Hidden Markov Model (HMM) was used to combine likelihoods from consecutive days and reconstruct the migration track of each individual [31]. The HMM can filter out areas where probability of residence may have been high from a raw temperature/depth-based assessment of data from the specific day (Fig. 2) but where the fish could not possibly have resided due to its natural restrictions in daily movement [33]. The method has previously been used on Atlantic cod *Gadus morhua* [34], southern bluefin tuna *Thunnus maccoyii* [35] and Atlantic salmon [10, 13]. HMMs estimate the posterior distribution at each discrete time step by a two-step forward running Bayesian filter, followed by a backward smoothing step refining marginal distributions conditional on all data [31]. In essence, the HMM, therefore, computes the migration track of the fish by a

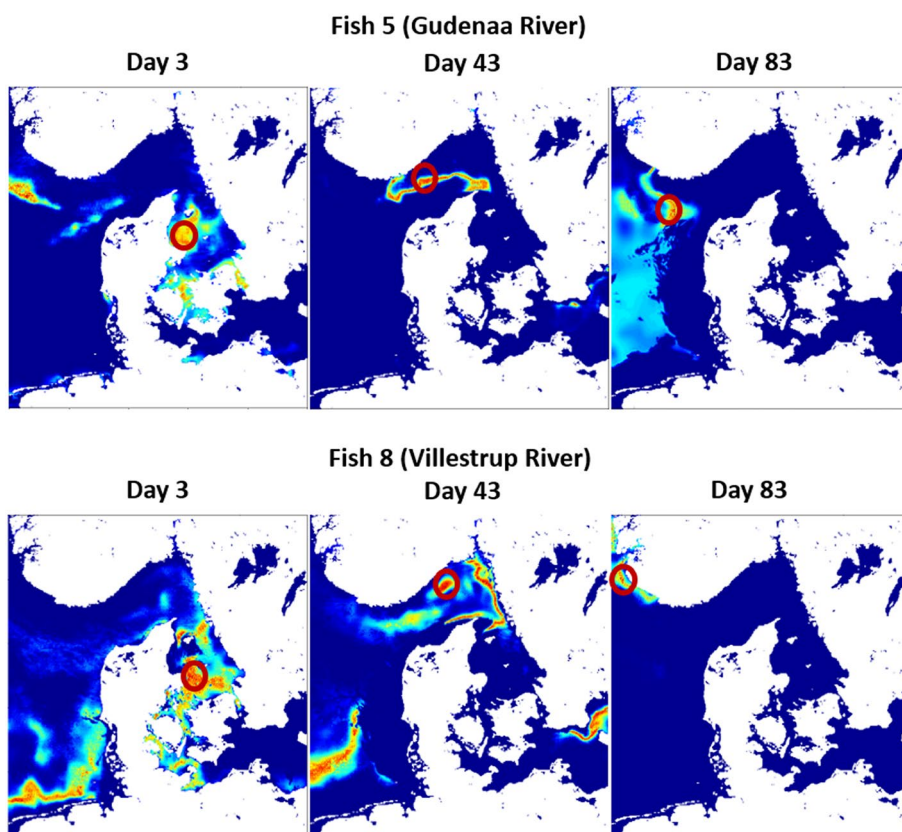


Fig. 2 Likelihoods of residence on days 3, 43 and 83 after sea entry for Fishes 5 and 8 that both migrated towards the Norwegian coast. Positions according to the reconstructed track on the same days are marked with red circles. Red areas represent high likelihood of residence while dark blue areas represent ≈ 0 likelihood of residence. Likelihoods are calculated by multiplying temperature values from the *dnorm* function (values range from 0 to infinity, but rarely exceed 2.0 in practice due to the uncertainty in the SST measurements) and depth likelihoods (ranging between 0 and 1)

stepwise assessment of raw, daily probability distributions and a subsequent smoothing of the track. We refer to [31] for a full explanation of the mathematical background of the models. Filtering and smoothing was carried out in Matlab R2019a.

The migration tracks from the HMM were inspected for correlation with raw temperature/depth probabilities (i.e. compare reconstructed positions with likelihood distributions in Fig. 2). To further evaluate the performance of the model, endpoints at the natal river were removed to see how this affected the track, and fish temperatures were shifted up and down by 0.5 °C before calculating the raw probabilities to see how this affected the subsequent track.

Some of the fish avoided the surface for consecutive days or weeks during their time spent at sea [27]. This mostly occurred in the last week of the marine period of the kelts. At this stage, the impact on the modelled tracks was minor, as the position on the last day at sea was known (fjord/estuary entry point or natal river mouth). Fish 4 was an exception to this, as it stayed at sea until September and generally avoided the sea surface for several consecutive weeks during July and August when sea surface temperatures were high. The track was, therefore, only reconstructed for the first 71 days at sea for Fish 4 as the surface avoidance became pronounced after this.

Estimated salinities

Daily positions from the migration track were used to estimate the salinity experienced by the fish. This was done by extracting the mean salinity for each estimated position of the fish from modelled salinity data downloaded from marine.copernicus.eu [36]. The downloaded salinity data had a resolution of 1°/12° (approximately 5.2 × 9.2 km on 55° N) and reported the mean daily salinity on a depth of 0.49 m (see example on Fig. 1b). Data were downloaded for this relatively shallow depth, as the kelts were generally surface orientated between dives in the first weeks at sea [27].

Salinity at the estimated positions on the first 15 days at sea were analysed using a generalized linear mixed effect model from the glmmTMB package in R [37] using fish ID as random effect. As seawater salinity is continuous and strictly positive, a gamma distribution was used/assumed. Only the first 8 days of sea residency was entered for Fish 5 due to a bimodal likelihood distribution (the fish could be on either side of an island) making the estimated position of this fish uncertain after this period (see later paragraph). The following model was fitted, where salinity estimated from the position of fish i on day j is modelled as the common intercept α , the covariate (days since sea entry), a random intercept a_i (assumed to be normally distributed around zero):

$$\text{Salinity}_{ij} \sim \text{Gamma}(\mu_{ij}, \tau)$$

$$\log(\mu_{ij}) = \alpha + \text{day}_{ij} + a_i$$

$$a_i \sim N(0, \sigma^2).$$

Diagnostic plots were inspected visually and analysed with a smoother from the mgcv package [38] to test for patterns in Pearson residuals. Significance of the smoother applied to the residuals was $P=0.410$ (adjusted $R^2=0.02$), suggesting patterns were not significant. Visual inspection of residuals (Additional file 1: Fig. S1), however, indicated potential non-linear temporal patterns not captured by the model, suggesting that the effect of days at sea on experienced salinity might not be linear and a more complex model such as a GAMM might be more appropriate. However, we refrain from applying more complex models as we believe a larger dataset would be required for doing so when considering the inherent uncertainties in estimated positions and thus experienced salinities.

Results

Individuals included in the study

Of 125 tagged individuals, 53 tags (42%) were recovered, in most cases due to the floating characteristic of the tag. Eight kelts survived the full marine period (i.e. returned to their natal river) and are included in the present study. Seven of these kelts were between 54.0 and 60.5 cm when tagged while one individual was 91.5 cm.

Performance of the HMM

Evaluation of the estimated positions and the raw likelihoods revealed that the HMM created credible tracks. Modelled tracks with or without endpoints added were almost similar with the exception that the return migration from, e.g. the Skagerrak to the natal river was not correctly reconstructed (Additional file 1: Figs. S2–S8). The model was challenged here as several fish avoided the warm surface waters on their way back and, therefore, provided poor data for the model to reconstruct their return migration without knowing its endpoint. Shifting temperatures up and down by 0.5 °C had little effect on the overall migration tracks, but did lead to minor (<50 km) adjustments of parts of the tracks. For Fish 2 (Additional file 1: Fig. S9), shifting the temperatures upwards by 0.5 °C resulted in a bimodal likelihood distribution around the island of Zealand for a period of 10 days similar to that of Fish 5, but the track was similar to the non-adjusted track otherwise.

The mean uncertainty (± 1 standard deviation) of the estimated daily positions was 0.21° for latitude (range 0.09°–0.58°) and 0.31° (range 0.11°–0.59°) for longitude, corresponding to 23.1 km (9.9–63.8 km) and 19.2 km

(range 6.8–36.6 km), respectively. The position of Fish 5 was particularly uncertain for days 8–13 after reaching the sea due to a bimodal likelihood distribution suggesting that the fish could have resided on either side of an island.

Migrated distance

The daily progression was estimated from first differences of the estimated position. This is the minimum variance estimate of daily displacements, but tends to underestimate distance travelled since it cannot capture movements on finer scale than a single day, and due to the smoothing in the HMM filter. The estimated values range between 0 and 58 km day⁻¹ with several fish exhibiting periods of days or weeks with very little horizontal movement (Fig. 3). The mean progression was 16 km day⁻¹ for the entire modelled period in all kelts. The kelts migrated a mean of 1540 km during their entire marine period (range 550–1960 km, Fish 4 is excluded). Maximum linear distance away from the natal river was 580 km in fish 6 while fish 1 peaked at a distance of 130 km from the natal river (Table 2). Progression during the first and last day of sea residence is associated with some uncertainty due to lack of knowledge on the exact timing of sea entry and exit for the kelts.

Migration routes

The migration tracks for all eight kelts are presented in Fig. 4. No kelts migrated into the open ocean, although fishes 5 and 8 were getting close to the Atlantic Ocean before turning back. No fish apparently exceeded distances more than 100 km from land during the migration. The kelts migrated towards or stayed within the Kattegat region in the beginning of the marine period except Fish 1 that stayed in the Skagerrak and Fish 7 that moved towards the Wadden Sea before moving northwards. Note that the track from Fish 4 is terminated after 71 days due to the changed behaviour described in a previous paragraph. All fish visited the Skagerrak during summer and no fish resided in the warm Kattegat Sea during summer, except when returning back towards the natal river. The residence areas of the fish are summarized on Fig. 5.

Estimated salinities

Movement during the first 15 days at sea revealed that the kelts moved towards less saline areas in all or part of the period. This was corroborated by the mixed effects model (Table 3, Fig. 6) that found a significantly negative correlation between salinity of the estimated position and days spent at sea ($P < 0.0001$). This relationship was generally discontinued later in the season, where several fish re-entered areas with higher salinities.

Discussion

Fish included in the study

Although the number of fish in this study was small, it is similar to other electronic tag studies on Atlantic salmon ($n = 4$ in [13] and $n = 16$ in [10]). The tagged sea trout were comparable in size (54–91 cm) with kelts from other Danish studies (30–87 cm in [17] and 54–79 cm in [18] but larger than sea trout kelts studied elsewhere (e.g. 29–59 cm in [19] and 28–58 cm in [39]). Seven of the tagged kelts were, however, comparable in size (54–60 cm) with the large individuals included in studies of sea trout elsewhere while Fish 1 was substantially larger (91 cm). Larger sea trout individuals are expected to take on longer migrations into pelagic areas [40, 41]. However, the large Fish 1 appeared to have spent its entire marine period in the Skagerrak, relatively close (< 130 km) to its natal river unlike the other individuals that migrated farther away. All individuals included in the present study, therefore, appeared to have reached a size where other factors than length defines the migratory strategy.

Migration behaviour

Migration patterns revealed an initial movement into shallow or highly stratified marine areas (Kattegat or the Wadden Sea) during the first weeks at sea followed by a migration into deeper and more well-mixed areas (The North Sea and Skagerrak) during the end of May and beginning of June. The Kattegat and Wadden Sea heat up more quickly than the North Sea and Skagerrak, and the reconstructed tracks, therefore, provide a geographic layer of explanation to the direct measurements reported in [27] where the kelts resided in waters warmer than the mean for the region when mean temperatures were below 15 °C and colder than the mean when mean temperatures were above 15 °C. Although the migrations are on a different scale, this horizontal migration has similarity with that observed for sea trout within a Norwegian fjord system [9]. In addition, the kelts in the present study migrated into areas with lower salinities during their first 15 days at sea ($P < 0.0001$). The migration of the fish may, thus, optimize their aerobic scope and support growth [21–23].

The apparent preference for longer migrations in Danish sea trout compared to the mainly fjord-bound Norwegian trout [9, 15] could be a consequence of Danish sea trout migrating farther to utilize the unique possibilities of the seas surrounding Denmark in terms of highly variable salinities and temperatures or potentially a different availability of food items suiting the fish at different times of the season. Norwegian trout entering a fjord system with higher temperatures and lower salinities close to the river outlet may have no metabolic advantage of leaving the fjord, and the high

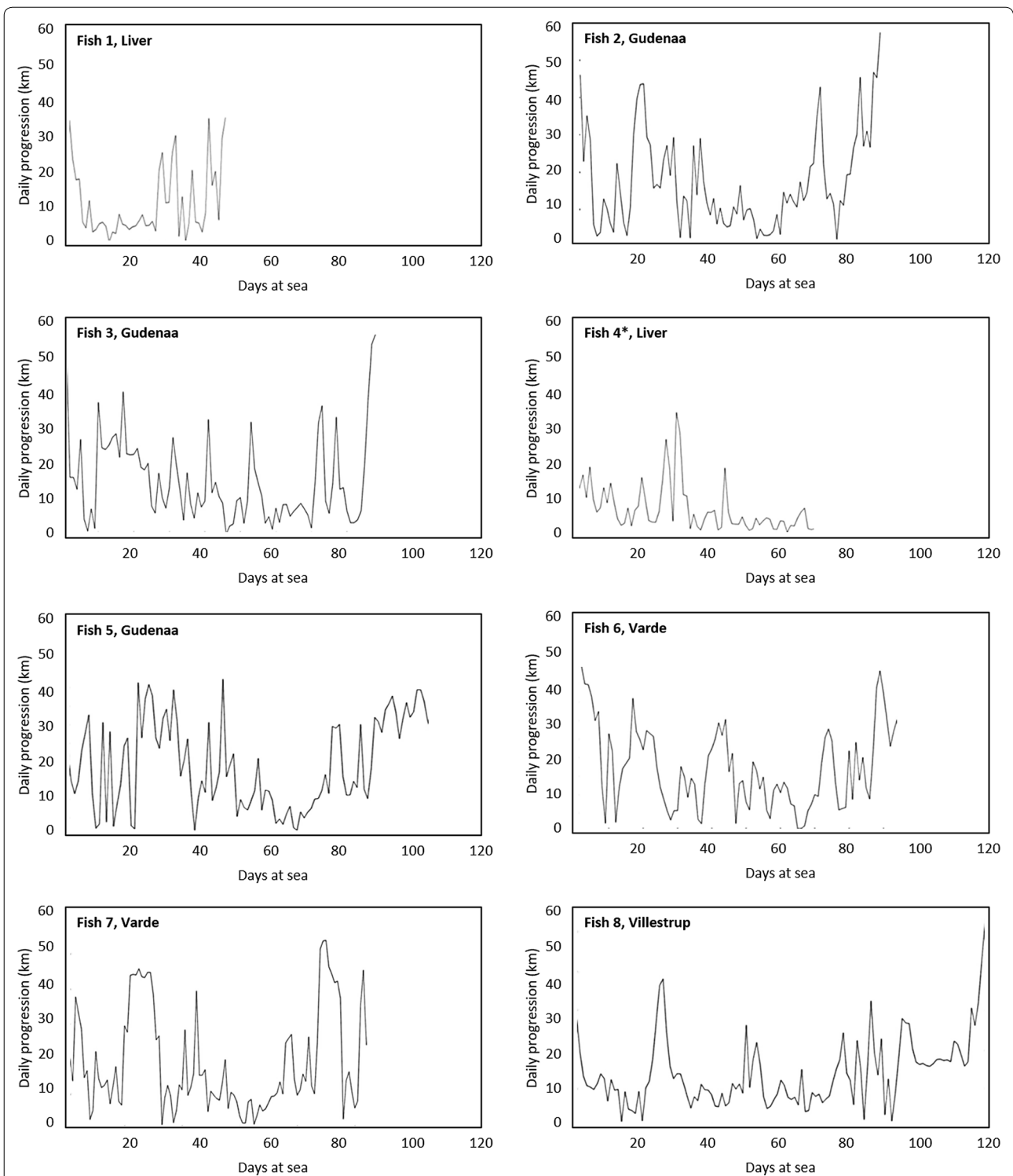


Fig. 3 Daily horizontal progression in all eight fish. Fish 4 spent 142 days at sea, but only modelled for 71 days as it avoided the surface for several weeks during summer, thus disabling a credible track to be modelled after 71 days. All eight kelts have periods of several consecutive days of weeks with relatively small movement rates (< 10 km)

Table 2 Model summary data for the eight sea trout

Fish no.	Days modelled	Max dist. natal river	Distance migrated	Daily progress (km)
1	47	130	550	12
2	89	290	1590	18
3	87	250	1380	16
4	71*	–	480	7
5	105	410	1960	19
6	94	580	1680	18
7	87	410	1960	23
8	118	490	1640	14

Max distance to the natal river represents the shortest possible route from the natal river outlet to the estimated position farthest from the river outlet. Km migrated is the total covered distance in the modelled period while the daily progress is the mean daily horizontal progression in the modelled period

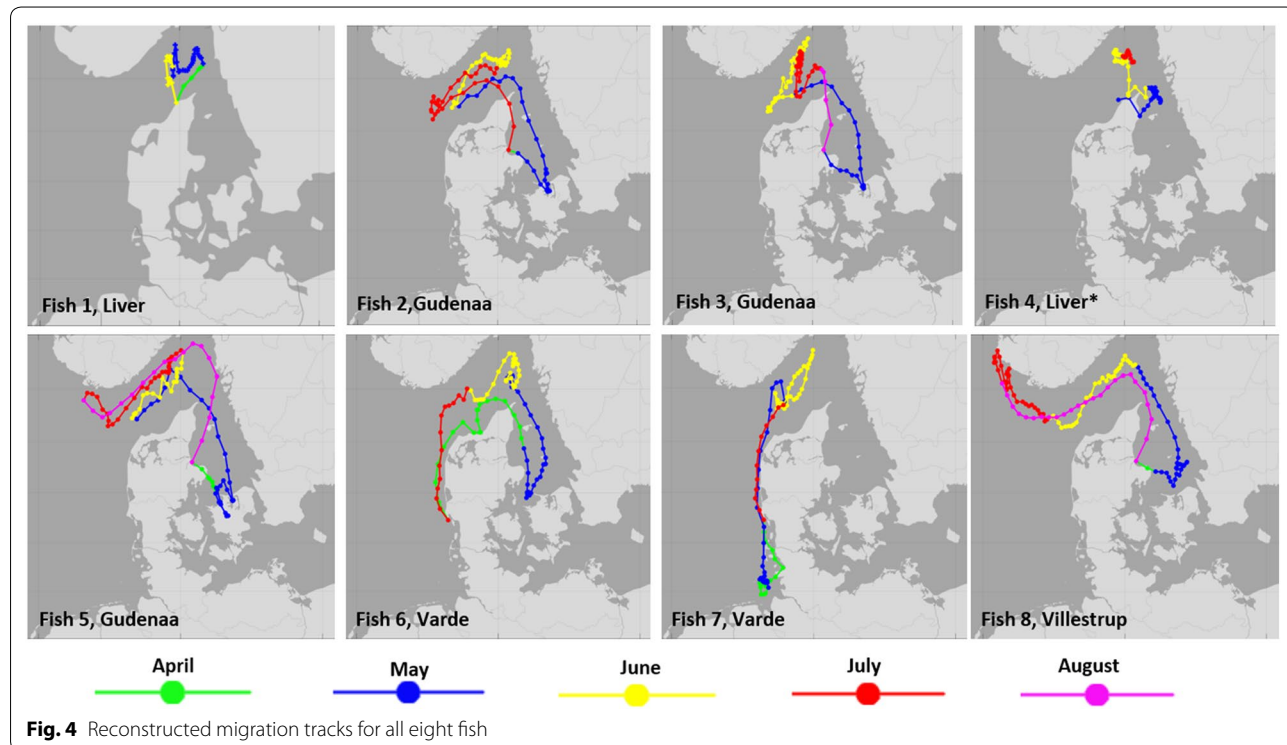
*Note that the migration route of Fish 4 was only reconstructed for 71 days as the fish avoided the surface for too long to reconstruct a credible migration track after this day

return rates of Norwegian sea trout (e.g. 86% in [42] suggests that staying in the fjord is safe). This is contradicted by Danish fjords, where 26% [17] and 57% [18] of tagged sea trout kelts were lost in two fjord systems although the kelts generally migrated through the systems within a month. We are not able to determine if the tracks reflect a movement to optimize metabolic scope or if other factors, e.g. predator/prey abundances

could also drive the migrations. The fact that the fish left the warmer and less saline (but supposedly also more dangerous) fjords in the first place provides an indication that migratory behaviour of sea trout can be shaped by complex interactions between predator/prey abundances and temperature and salinity preferences.

The salinity front in the Skagerrak results in complex mixing of surface waters [26], and trawl surveys have revealed that the area is home to a variety of demersal and pelagic prey items for sea trout [43]. All kelts performed dives deeper than 40 m in the Skagerrak [27], suggesting that they were foraging there. With a combination of available prey items, temperatures normally closer to the range optimal for growth in sea trout during summer and supposedly lower predation pressure than in the fjords and more coastal habitats, residency in the North Sea/Skagerrak or open seas in general may offer the best overall conditions for the trout during summer in this region. Investigation of detailed movement ecology of other species in the region could shed light on predator/prey interactions and identify potential reasons for sea trout to reside in the shallow or stratified areas during spring and the deeper and more well-mixed areas during summer.

The reconstructed migration tracks reinforce the picture of sea trout not migrating far into open oceans as opposed to other salmonids where HMMs have been used to reconstruct migration routes [10, 13]. The sea



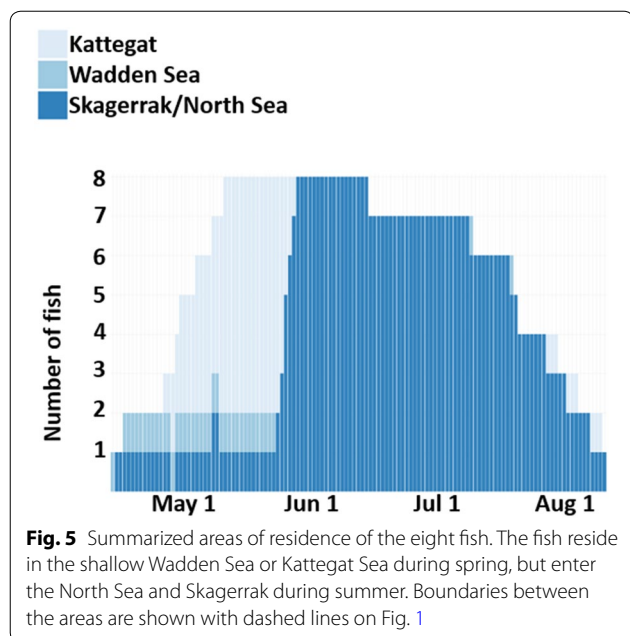


Fig. 5 Summarized areas of residence of the eight fish. The fish reside in the shallow Wadden Sea or Kattegat Sea during spring, but enter the North Sea and Skagerrak during summer. Boundaries between the areas are shown with dashed lines on Fig. 1

Table 3 Summary of the gamma distributed mixed model

	Value	SE	z value	P
Intercept	3.276	0.096	34.11	<0.0001
Days at sea	-0.016	0.002	-6.62	<0.0001

The model analysed salinity for the estimated positions of the first 15 days at sea for the sea trout kelts. Model parameter estimate, associated SE, z values and P values are given

trout from the present study were, however, migrating long distances compared to the general expectation of individuals of the species to reside within 100 km from the natal river mouth [7], and especially compared to the more northern conspecifics [9, 15]. The migration tracks suggested that all eight fish had resided more than 100 km from their natal river at some point, while Fish 6 peaked at a distance of 580 km from the natal river. Although this opposes the expected preference for shorter migrations of sea trout in general, it was not unexpected for Danish sea trout considering the results from mark-recapture studies (K. Aarestrup, DTU Aqua, Denmark, unpubl. results) and genetic origin assignment of captured trout (D. Bekkevold, DTU Aqua, Denmark, unpubl. results). Linear progression rates up to 59 km day⁻¹ have been recorded in acoustically tagged sea trout crossing the Kattegat, suggesting that sea trout are capable of navigating and progressing efficiently through the region [18].

Actual migrated distance of the kelts may be substantially longer than the linearly progressed distance [16], making the migration energetically costly [44]. The sea

trout in the present study appeared to be foraging (diving) on their way [27] similar to observations in Atlantic salmon [45]. Although migrating farther, it is possible that the kelts from the present study were not swimming more than sea trout elsewhere, but that their movements were more unidirectional. For example, [16] found that sea trout post-smolts entering a Norwegian fjord were actively swimming with mean speeds of 0.68 bl s⁻¹ but that their swimming direction was chaotic as opposed to Atlantic salmon smolts entering the same fjord and swimming more directly through it and into the ocean. If moving with similar speeds of 0.68 bl s⁻¹, the kelts of the present study could have moved a mean of 36 km day⁻¹, which is well above the reported mean of 16 km day⁻¹ of the HMM. The longer migrations observed by some salmonids could, therefore, reflect a more linear movement pattern rather than more energy being allocated for movement. Studies with accelerometers on adult Pacific salmon found that the fish had progressed farther than they actually swam (according to the accelerometer data) during a long distance migration in the sea, thus suggesting that the fish had used passive transportation from ocean currents and moved fairly unidirectionally [46]. Danish sea trout generally experience some of the highest marine growth rates observed for the species [47, 48] while apparently also having a preference for longer migrations compared to their conspecifics elsewhere. Future studies linking horizontal progression with total marine growth in salmonids could, therefore, shed new light on the cost associated with the highly variable migration strategies observed between, e.g. Arctic charr [9, 41], Atlantic salmon [10, 13], Steelhead [8] and sea trout [7].

Performance of the HMM

Removing the endpoints of migration and shifting temperatures of the fish up and down by 0.5 °C only had minor effects on the migration tracks. This suggests that the method was robust and that the vast temperature differences occurring over small distances in the region make it suited for this type of analysis—particularly during spring and early summer when temperature differences are greatest.

The mean linear distance between estimated daily positions according to the HMM was 16 km (SE: 1.34 km) with daily linear progression ranging between 0 and 58 km. Actual movement may differ due to the uncertainty associated with each daily position. There are no published records of linear progression speeds of sea trout at sea, but eight acoustically tagged Danish sea trout have been documented to move 280 km across the Kattegat Sea with linear progression rates of 9–59 km day⁻¹ [18]. Mean progression rates for 24 sea trout kelts

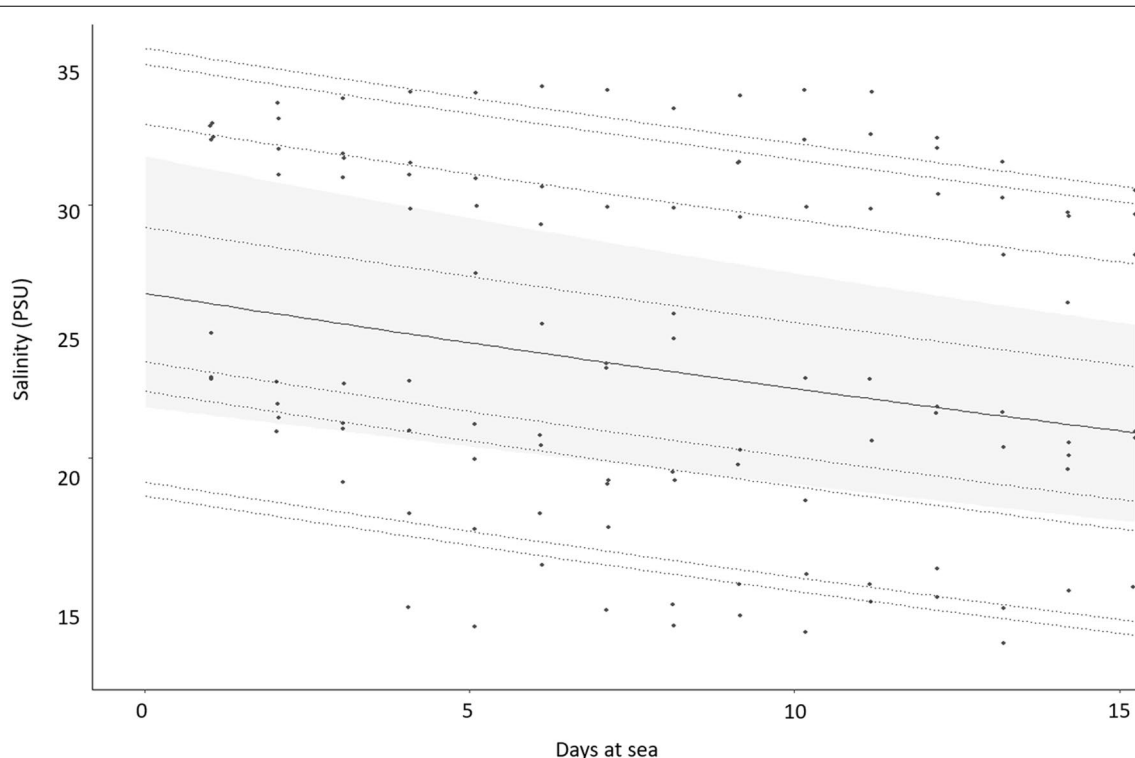


Fig. 6 Relationship between salinity of the estimated position and days spent at sea for the eight kelts during the first 15 days at sea, modelled with a mixed effects model. Shaded areas represent 95% confidence intervals of the model, while points represent actual observations. Dotted lines represent trend lines for each of the eight kelts. Residuals for the model are presented in Additional file 1: Fig. S1. Salinity on the estimated position after 15 days at sea was lower than at sea entry for all eight kelts

migrating through an open (> 15 km wide) part of a Danish fjord system was 15.0 km day^{-1} (SE: 1.26) [18]. The underlying movement scheme of the HMM, therefore, appeared realistic for sea trout.

Inspection of the tracks in comparison with the raw likelihoods suggested that the HMM provided a credible way of reconstructing migration tracks of sea trout. The problems with bimodal likelihoods distributed on each side of an island on days 8–12 in fish 5, however, also reveal that this type of model is challenged in reconstructing fine-scale movements in areas with islands or narrow passages [33]. Similar problems have not occurred in other studies with HMMs that have been carried out in more open marine areas [10, 13]. The Belt seas connecting the Kattegat to the Baltic Sea are narrow, which decreases the chance of a reconstructed migration track going through the Belt Sea with the approach used in the present study. As a consequence, sea trout kelts may utilize the Baltic region to a higher extent in reality than reflected by the reconstructed tracks of the present study. A different mathematical approach could be used to investigate the probability of fish migrating on either side of an island or, e.g. into the Baltic as described by

[33]. Future studies with salinity measurements included in the data storage tags would also provide an efficient method to improve the performance of the HMM, as salinity measurements would remove any questions as to whether a fish was in the North Sea, Kattegat, Belt Seas or Baltic Sea, due to the general high salinity gradient.

Another challenge of using HMMs on a near-coastal species like sea trout is that the fish could seek out areas within few metres from land where temperatures could deviate from measurements in the $1 \times 1 \text{ km}$ satellite grid. This could lead to discrepancies in the raw likelihood grid and subsequently cause the HMM to miscalculate the migration track. The temperature reports from [27] suggest that this would mainly be a challenge in the early marine phase but not later on when the fish appeared to have entered open sea. Again, a repetitive study with salinity measurements could establish whether this was a problem or if the fish were actually migrating as reported by the HMM.

Conclusion

In total, we reconstructed credible migration tracks for sea trout kelts migrating at sea using an HMM. The tracks were credible for the entire time spent at sea in six of the kelts while one track suffered from a bimodal likelihood distribution in the initial part of the migration and one had to be discontinued after 74 days at sea due to lack of data after this point in time. The kelts were migrating farther away from their natal river outlet (130–580 km) than generally expected for the species but stayed in near-coastal areas (<100 km from land). This was particularly true in the early marine phase, where the kelts entered areas with lower salinities and higher temperatures, possibly to increase their aerobic scope. The unique hydrographic conditions of the sea surrounding Denmark may cause the fish to migrate farther to utilize habitats that provides optimal conditions in different parts of the year. Understanding the cost of such migration versus the gain of performing them is crucial to understand the movement ecology of salmonids and assess their robustness to environmental changes. It remains unknown if Danish sea trout move more than their conspecifics or if they move in less random directions, thus covering larger areas during their marine period. Additional studies on sea trout in Denmark and elsewhere, coupling the observed migration behaviour with physio-chemical conditions, weight gained during the marine period and predator/prey distributions could expand our knowledge on preferred habitats of sea trout in marine environments and provide valuable inputs to managers and stakeholders. Marine survival and behaviour of salmonids may vary considerably, and we, therefore, call for further studies of factors affecting the behaviour, success and survival of salmonids at sea.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s40317-019-0185-3>.

Additional file 1. Additional figures.

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Authors' contributions

KA conceived and designed the study, DdV assisted with the field work, HB contributed with tools for the data analysis, MWP and UHT wrote the code for the HMM, MLK analysed the data and wrote the paper. All the co-authors provided comments and changes for the paper during the writing process. All the authors read and approved the final manuscript.

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Availability of data and materials

The data and computational codes used in the current study are available from the corresponding author upon reasonable request.

Ethics approval and consent to participate

The study was carried out in accordance with the permission 2012-DY-2934-00007 from the Danish Experimental Animal Committee.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

¹ Technical University of Denmark, National Institute for Aquatic Resources, 8600 Silkeborg, Denmark. ² ENFOR A/S, 2970 Hørsholm, Denmark. ³ Department of Applied Mathematics and Computer Science, Technical University of Denmark, 2800 Lyngby, Denmark. ⁴ Loughs Agency, 22 Victoria Rd, Londonderry BT47 2AB, UK.

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References

1. Harden Jones FR. Fish migration. London: St. Martin's Press, Inc.; 1968.
2. Allen AM, Singh NJ. Linking movement ecology with wildlife management and conservation. *Front Ecol Evol.* 2016;3:155.
3. Drenner SM, Clark TD, Whitney CK, Martins EG, Cooke SJ, Hinch SG. A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. *PLoS ONE.* 2012;7(3):e31311.
4. Blicharska M, Rönnbäck P. Recreational fishing for sea trout—resource for whom and to what value? *Fish Res.* 2018;204:380–9.
5. Loomis J. Use of survey data to estimate economic value and regional economic effects of fishery improvements. *N Am Fish J Manage.* 2011;26:301–7.
6. Cook BA, McGaw RL. Sport and commercial fishing allocations for the atlantic salmon fisheries of the Miramichi River. *Can J Agr Econ.* 1996;44:165–71.
7. Thorstad EB, Todd CD, Uglem I, Bjørn PA, Gargan PG, Vollset KW, Halttunen E, Kålås S, Berg M, Finstad B. Marine life of the sea trout. *Mar Biol.* 2016;163:47.
8. Hayes SA, Kocik JF. Comparative estuarine and marine migration ecology of Atlantic salmon and steelhead: blue highways and open plains. *Rev Fish Biol Fisher.* 2014;24:757–80.
9. Jensen JLA, Rikardsen AH, Thorstad EB, Suhr AH, Davidsen JG, Primicerio R. Water temperatures influence the marine area use of *Salvelinus alpinus* and *Salmo trutta*. *J Fish Biol.* 2014;84:1640–53.
10. Strøm JF, Thorstad EB, Chafe G, Sørbye SH, Righton D, Rikardsen AH, Carr J. Ocean migration of pop-up satellite archival tagged Atlantic salmon from the Miramichi River in Canada. *ICES J Mar Sci.* 2017;74:1356–70.
11. Finstad B, Økland F, Thorstad EB, Bjørn PA, McKinley RS. Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *J Fish Biol.* 2005;66:86–96.
12. Hedger D, Rikardsen AH, Strøm JF, Righton DA, Thorstad EB, Næsje TF. Diving behaviour of Atlantic salmon at sea: effects of light regimes and temperature stratification. *Mar Ecol Prog Ser.* 2017;574:127–40.
13. Strøm JF, Thorstad EB, Hedger JD, Rikardsen AH. Revealing the full ocean migration of individual Atlantic salmon. *Anim Biotelem.* 2018;6:2.
14. Lobón-Cerviá J, Sanz N. Brown trout: biology, ecology and management. New York: Wiley; 2018.

15. Eldøy SH, Davidsen JG, Thorstad EB, Whoriskey F, Aarestrup K, Næsje TF, Rønning L, Sjørnsen AD, Rikardsen AH, Arnekleiv JV. Marine migration and habitat use of anadromous brown trout (*Salmo trutta*). *Can J Fish Aquat Sci.* 2015;72:1366–78.
16. Thorstad EB, Økland F, Finstad B, Sivertsgård R, Bjørn PA, McKinley RS. Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. *Environ Biol Fish.* 2004;71:305–11.
17. Aarestrup K, Baktoft H, Thorstad E, Svendsen J, Höjesjö J, Koed A. Survival and progression rates of anadromous brown trout kelts *Salmo trutta* during downstream migration in freshwater and at sea. *Mar Ecol Prog Ser.* 2015;535:185–95.
18. Kristensen ML, Birnie-Gauvin K, Aarestrup K. Behaviour of veteran sea trout *Salmo trutta* L. in a dangerous fjord system. *Mar Ecol Prog Ser.* 2019;616:141–53.
19. Bendall B, Moore A, Quayle V. The post-spawning movements of migratory brown trout *Salmo trutta* L. *J Fish Biol.* 2005;67:809–22.
20. Kristensen ML. The marine life of sea trout (*Salmo trutta* L.). Ph.D. thesis. Silkeborg: Technical University of Denmark; 2019.
21. Baeuf G, Payan P. How should salinity influence fish growth? *Comp Biochem Phys C.* 2001;130:411–23.
22. Ojanguren AF, Reyes-Gavilan FG, Braña F. Thermal sensitivity of growth, food intake and activity of juvenile brown trout. *J Therm Biol.* 2001;26:165–70.
23. Larsson S. Thermal preference of Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta*—implications for their niche segregation. *Environ Biol Fish.* 2005;73:89–96.
24. Morgan JD, Iwama GK. Effects of salinity on growth, metabolism, and ion regulation in juvenile rainbow and Steelhead Trout (*Oncorhynchus mykiss* and Chinook Salmon *Oncorhynchus tshawytscha*). *Can J Fish Aquat Sci.* 1991;46:2083–94.
25. Morgan JD, Iwama GK. Energy cost of NaCl transport in isolated gills of cutthroat trout. *Am J Physiol Reg.* 1999;(277):R631–9.
26. Rasmussen B. Stratification and wind mixing in the Southern Kattegat. *Ophelia.* 1995;42:319–34.
27. Kristensen ML, Righton D, del Villar-Guerra D, Baktoft H, Aarestrup K. Temperature and depth preferences of adult sea trout *Salmo trutta* L. during the marine migration phase. *Mar Ecol Prog Ser.* 2018;599:209–24.
28. Pedersen FB. Fronts in the Kattegat: the hydrodynamic regulating factor for biology. *Estuaries.* 1992;16:104–12.
29. Thorstad EB, Økland F, Westerberg H, Aarestrup K, Metcalfe JD. Evaluation of surgical implantation of electronic tags in European eel and effects of different suture materials. *Mar Freshw Res.* 2013;64:324–31.
30. Kristensen ML, Righton D, del Villar-Guerra D, Baktoft H, Aarestrup K. Behaviour of adult sea trout *Salmo trutta* that survive or die at sea. *Estuar Coast Shelf S.* 2019;227:106310.
31. Pedersen MW. Hidden Markov modelling of movement data from fish. Ph.D. thesis. Kongens Lyngby: Technical University of Denmark; 2010.
32. Reddin DG, Downton P, Fleming IA, Hansen LP, Mahon A. Behavioural ecology at sea of Atlantic salmon (*Salmo salar* L.) kelts from a Newfoundland (Canada) river. *Fish Oceanogr.* 2011;20:174–91.
33. Thygesen UH, Pedersen MW, Madsen H. Geolocating fish using hidden markov models and data storage tags. In: Nielsen JL, Arrizabalaga H, Frago N, Hobday A, Lutcavage M, Sibert J, editors. Tagging and tracking of marine animals with electronic devices. Reviews: methods and technologies in fish biology and fisheries. Berlin: Springer; 2009. p. 277–93.
34. Pedersen MW, Righton D, Thygesen UH, Andersen KH, Madsen H. Geolocation of North Sea cod (*Gadus morhua*) using hidden Markov models and behavioural switching. *Can J Fish Aquat Sci.* 2008;2008(65):2367–77.
35. Pedersen MW, Patterson TA, Thygesen UH, Madsen A. Estimating animal behavior and residency from movement data. *Oikos.* 2011;120:1281–90.
36. Poulsen JW, Berg P. More details on HBM—general modelling theory and survey of recent studies. DMI Technical Report No. 12–16. 2012.
37. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 2017;9:378–400.
38. Wood SN. Generalized additive models: an introduction with R. 2nd ed. Boca Raton: Chapman and Hall/CRC; 2017.
39. Eldøy SH, Davidsen JG, Thorstad EB, Whoriskey FG, Aarestrup K, Næsje TF, Rønning L, Sjørnsen AD, Rikardsen AH, Arnekleiv JV. Marine depth use of sea trout *Salmo trutta* in fjord areas of central Norway. *J Fish Biol.* 2017;91:1268–83.
40. Knutsen JA, Knutsen H, Gjøsæter J, Jonsson B. Food of anadromous brown trout at sea. *J Fish Biol.* 2001;59:533–43.
41. Klemetsen A, Amundsen P-A, Dempson JB, Jonsson N, O'Connell MF, Mortensen E. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol Freshw Fish.* 2003;12:1–59.
42. Bordeleau X, Davidsen JG, Eldøy SH, Sjørnsen AD, Whoriskey FG, Crossin GT. Nutritional correlates of spatiotemporal variations in the marine habitat use of brown trout (*Salmo trutta*) veteran migrants. *Can J Fish Aquat Sci.* 2018;999:1–11.
43. Casini M, Cardinale M, Hjelm J, Vitale F. Trends in cpue and related changes in spatial distribution of demersal fish species in the Kattegat and Skagerrak, eastern North Sea, between 1981 and 2003. *ICES J Mar Sci.* 2005;62:671–82.
44. Hendry AP, Bohlin T, Jonsson B, Berg OK. To sea or not to sea? Anadromy versus non-anadromy in salmonids. In: Hendry AP, Stearns SC, editors. Evolution illuminated: salmon and their relatives. Oxford: Oxford University Press; 2004. p. 92–125.
45. Friedland KD, Walker RV, Davis KD, Myers KW, Boehlert GW, Urawa S, Ueno Y. Open-ocean orientation and return migration routes of chum salmon based on temperature data from data storage tags. *Mar Ecol Prog Ser.* 2001;216:235–52.
46. Tanaka H, Naito Y, Davis ND, Urawa S, Ueda H, Fukuwaka M. First record of the at-sea swimming speed of a Pacific salmon during its oceanic migration. *Mar Ecol Prog Ser.* 2005;291:307–12.
47. Jonsson B, L'Abée-Lund JH. Latitudinal clines in life-history variables of anadromous brown trout in Europe. *J Fish Biol.* 1993;43:1–16.
48. Frier J-O. Bevaring af øredbestande i Danmark. Reports from the Nordic Seminar. 1993. p. 644.

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