Behaviour of veteran sea trout *Salmo trutta* in a dangerous fjord system

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ABSTRACT: The behaviour and survival of sea trout *Salmo trutta* L. in marine environments remains scarcely described despite the widespread ecological and cultural importance of the species. We tracked 160 wild, post-spawned sea trout in 2 Danish river systems using acoustic tags to examine their behaviour in a fjord system characterized by a scarcity of refuges and a high abundance of mammalian and avian predators. The fjord has an eastern opening 120 km from the river outlets and a western opening 110 km from the river outlets. All surviving fish left the fjord through the eastern outlet, except for 2 surviving individuals that stayed in the fjord. We observed the lowest marine survival (15%) and the fastest progression rates documented for the species in marine environments. After a variable period of residency close to the river mouths, the fish moved through the fjord within a short window of time at gradually increasing speeds (mean: 1.1 km d^{-1} in the fjord compartment they entered, mean: 43.4 km d^{-1} in the final fjord compartment before reaching the sea). We found no statistically significant differences between exit timing, migration behaviour (speed and time) and survival of fish from the 2 river systems. The results suggest that migrating quickly through the dangerous fjord system and exiting at a specific time is important to succeed in the area. Our results distinguish themselves from those obtained in similar studies of sea trout elsewhere and provide new insights on factors influencing survival and migration behaviour of salmonids.

KEY WORDS: Behaviour · Fjord · Trout · Kelt · Migration · Salmonidae · Survival · Adaptation

1. INTRODUCTION

Migratory behaviours are individuals′ responses to interactions between environmental (e.g. food availability, predation or changes in temperatures) and internal (e.g. stress levels, food assimilation) factors (Lucas & Baras 2001). As such, migration is thought to be an adaptive response to a changeable environment, which ultimately increases reproductive success of individuals (Hendry et al. 2004, Cucherousset et al. 2005). Sea trout *Salmo trutta* (also commonly known as sea-run brown trout) exhibit anadromy, where individuals move from freshwater to saltwater to feed, and return to freshwater to spawn (Gross et al. 1988). By exploiting better feeding habitats, sea trout reach larger sizes and, thus, higher reproductive potential than conspecifics that remain in fresh-

water, especially in females (Jonsson & Jonsson 1993, Hendry et al. 2004).

Sea trout populations are capable of adapting to local conditions over time (Svärdson & Fagerström 1982, Fraser et al. 2011), and sea trout kelts (individuals that have spawned and are returning to sea) show great variability in their migration timing, speed and marine survival. Studies have reported marine survival from 18 to 86% (Bendall et al. 2005, Bordeleau et al. 2018) and speed of migration in marine environments up to 32 km d^{-1} in an English estuary where most sea trout used the ebbing tide to make a fast progression (Bendall et al. 2005). In Norway, studies have documented that sea trout generally reside in many of the fjords (Jensen et al. 2014, Flaten et al. 2016). For example, in a central Norwegian fjord, 58% of post-spawned sea trout individuals were

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never more than 13 km away from their natal river during their marine phase (Eldøy et al. 2015). The overall preference for short marine migrations seems common for the species, where detection or recapture of individuals farther than 100 km from the natal river is rare (Thorstad et al. 2016). Some sea trout populations, such as Danish sea trout, appear to favour longer migrations towards the sea, and individuals from these sea-bound populations could migrate farther than 100 km away from the natal river mouth while at sea, though no equipment has been in place to document such migrations (Aarestrup et al. 2015, Kristensen et al. 2018a). Long-distance migrations to the sea, however, are energetically costly due to the resources needed for osmoregulation and swimming and ecologically costly due to the increased risk of predation, injury and encounters with gill- and pound nets (Gross et al. 1988, Jonsson & Jonsson 1993, Ward & Hvidsten 2010). Nonetheless, individuals that successfully repeat spawning can constitute a large proportion of the spawning population (L'Abée-Lund 1989, Aarestrup & Jepsen 1998) and contribute a disproportionately high production of juveniles due to the higher fecundity of large individuals that produce larger eggs, which increases the subsequent chances of survival of the fry (Pemberton 1976).

In the last few decades, the abundance of sea trout has decreased considerably in many regions, and scientists have speculated that this is due to low marine survival (Milner et al. 2006). This decline is exacerbated by the fact that most sea trout are females, so marine mortality has an accentuated effect on population recruitment (Jensen et al. 2012). Furthermore, given the iteroparous nature of this species, recruitment depends considerably on the abundance of repeat spawners (Pemberton 1976), making the survival of this life stage particularly crucial. Understanding the factors that make kelts successful in their outgoing and incoming migration is thus necessary to focus management efforts. For this reason, the marine phase of the brown trout lifecycle is of particular interest, although it has received considerably less attention than the freshwater phase (Drenner et al. 2012). The ecological drivers that may cause individual fish to migrate further despite the costs that come with doing so remain poorly understood. We currently lack basic knowledge regarding migration speed and survival to identify potential risks and threats to be addressed in management schemes. Furthermore, few attempts have been made to characterize environmental and behavioural aspects that make individuals successful in reaching the sea (but see Aarestrup et al. 2015, Eldøy et al. 2015, Bordeleau et al. 2018).

The Limfjord is the largest fjord in Denmark and offers an interesting site for investigating adaptive behavioural responses during the marine phase in sea trout kelts. It is a soft-sediment system with a scarcity of submerged macrophytes or other potential refuges (Jørgensen 1977, Olesen 1996), making fish more vulnerable to predation (Peterson 1979) from harbour seals *Phoca vitulina* and great cormorants *Phalacrocorax carbo sinensis* (Andersen et al. 2007). Genetic analysis of the sea trout population in the Karup River, the main river running into the fjord, revealed that millions of stocked, non-native trout failed to survive and reproduce sufficiently to have a significant impact on the genetic composition of the wild population (Ruzzante et al. 2004). This strong selection against non-native individuals appeared to have taken place in the marine environment. A study of the behaviour and survival of sea trout smolts (first-time marine migrants) from the fjord suggested that all surviving individuals (20%) left the fjord in the eastern direction (Kristensen et al. 2018b). It is unknown if kelts from the same rivers behave similarly or have different preferences in terms of prey items and predator evasion, or if they exhibit a higher preference for fjord residency as seen in Norwegian fjord systems of similar size (Eldøy et al. 2015).

We acoustically tagged 160 mature sea trout kelts to investigate the migratory behaviour and subsequent survival of these fish in different parts of the Limfjord. Individuals were tagged in the Karup and Simested Rivers, 2 important sea trout rivers in the region which flow into the central/southern parts of the Limfjord. Our hypothesis was that, in order to survive their relatively long seaward migration distance, these fish would display unique behaviours in terms of migration speed, timing and directionality compared to sea trout from other fjord systems.

2. MATERIALS AND METHODS

2.1. Study site

Post-spawned sea trout were captured and tagged in the Karup and Simested Rivers (Fig. 1), 2 Danish lowland rivers on the Jutland Peninsula with catchment areas of 763 and 241 km^2, respectively, and mean discharge rates of 9300 and 2000 l s^{-1}, respectively. The rivers run into the central/southern part of the 160 km long Limfjord, a shallow, microtidal fjord, with a mean depth of 4.5 m, a tidal amplitude of 0.1–0.2 m and a scarcity of submerged macrophytes due to eutrophication (Dolmer & Frandsen 2002,
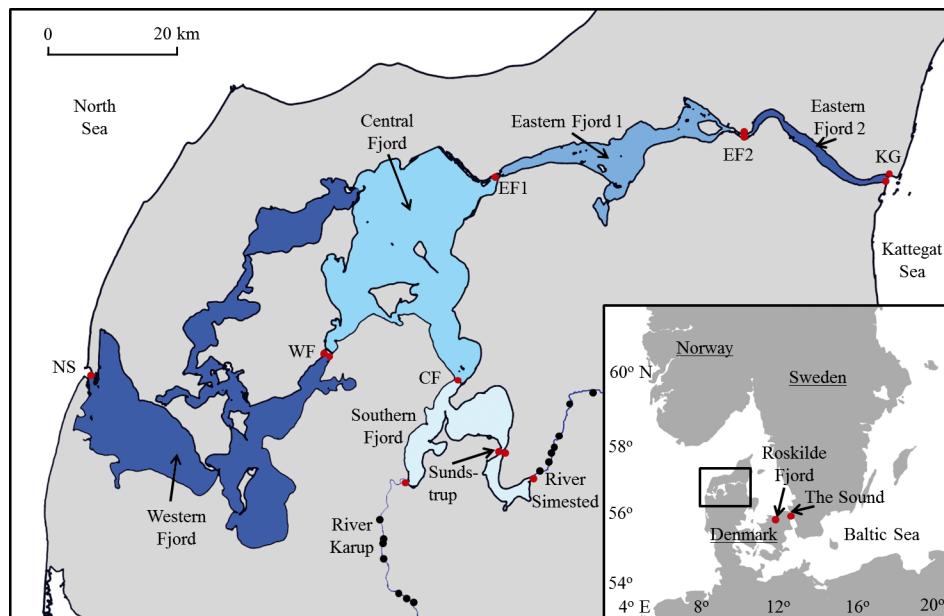
Fig. 1. Study area in northern Denmark, showing the location of individual receivers (red circles), tagging locations (black circles) and the fjord compartments (different shades of blue). The Limfjord runs between site NS in the west and KG in the east. Inset: locations (red dots) of receivers in another telemetry study conducted in Roskilde Fjord in 2017 and 2018 (unpubl. data) and in The Sound between Sweden and Denmark in 2017

Wiles et al. 2006). The Limfjord has a western opening to the saline (30–34 PSU) North Sea and an eastern opening to the more brackish (19–27 PSU) Kattegat. Water currents and mixing regimes in the fjord are complex and influenced by meteorological forcing (Wiles et al. 2006). Parts of the fjord frequently switch between stratified and mixed conditions, with anoxic conditions occurring near the bottom (Hofmeister et al. 2009).

Total fisheries landings from the Limfjord were relatively stable (3000–5000 t) during the 20th century until the 1970s, when most fish stocks collapsed. Trawl surveys found decreasing yields from 15 kg 30 min^{-1} in 1984 (after the collapse in commercial landings) to a stable level of approximately 1 kg 30 min^{-1} in the 1990s (Hoffmann 2000). At present, sea trout and Atlantic herring *Clupea harengus* are the most abundant fish species in the fjord.

The fjord hosts a population of harbour seals and grey seals *Halichoerus grypus*, while great cormorants are also abundant in the region (Andersen et al. 2007). Grey seals mainly inhabit the western part of the fjord, while the population of harbour seals in the central fjord was estimated to be roughly 800 individuals in the early 1990s and 1000 individuals at present (Dept. of Bioscience, University of Aarhus, Denmark, unpubl. data). Seal predation is a reason for conflict in the region, as seals have started foraging well upstream (>30 km) in the rivers for sea trout.

This is particularly pronounced in Karup River, where a permit to regulate seals entering the river has been issued.

2.2. Fish capture and tagging

In both 2017 and 2018, 40 post-spawned sea trout were captured at different sites in each river (N = 160, length range 46–80 cm, Table 1) via electrofishing and immediately placed in a 500 l container of fresh, oxygenated stream water. Within 3 min of capture, fish were sampled for blood (0.3 ml) at the caudal vasculature using a 3.8 cm 25-gauge heparinized needle for a separate study (unpubl. data). The fish were held in freshly oxygenated water until further processing. Some fish had minor damages and fungus infections following spawning activities but were still tagged to avoid possible bias of only selecting fish in better condition.

Fish were anesthetized (300 ppm benzocaine) until their opercular rate became slow and irregular (2–4 min), and their total body length and wet body mass were measured. Each fish was given an acoustic tag (ID-LP13, ThelmaBiotel, 28 mm length by 13 mm diameter, 9.2 g in air, 5.5 g in water) through a 2 cm incision on the left side of the fish, anterior to the pelvic fins. The gills of the fish were irrigated with fresh water once or twice during surgery. The inci-

Table 1. Year, tagging date, distance from tagging site to river mouth, number of fish tagged (n), mean length and mass (parentheses: range), mean velocity from the river to fjord, survival to the fjord and mortality per km on the way to the fjord of acoustically tagged post-spawned sea trout *Salmo trutta* in the Simested and Karup Rivers. Range is provided in brackets where applicable

Year	Date	Distance (km)	n	Length (cm)	Mass (kg)	Mean velocity (m s^{-1})	Survival (%)	Mortality per km (%)
Simested								
2017	01 Feb	1.0	7	64.3 (56–79)	2.2 (1.3–4.3)			
2017	01 Feb	6.2	6	60.8 (55–64)	1.9 (1.5–2.3)			
2017	02 Feb	9.1	4	60.3 (55–67)	1.7 (1.4–2.3)			
2017	02 Feb	19.8	8	64.9 (55–75)	2.4 (1.3–3.6)			
2017	06 Feb	10.9	8	55.9 (51–61)	1.6 (1.1–2.7)			
2017	15 Feb	21.9	7	64.7 (52–78)	2.2 (1.2–3.6)			
2018	05 Feb	6.3	6	57.3 (47–59)	1.5 (0.9–1.9)	17.5 (0.2–58.6)	83	2.7
2018	05 Feb	14.3	6	55.6 (51–67)	1.4 (1.1–2.5)	4.9 (0.2–25.3)	100	0.0
2018	20 Feb	31.8	3	64.3 (54–73)	2.0 (1.2–2.8)	29.4 (0.7–58.0)	67	1.0
2018	21 Feb	19.6	6	56.8 (49–73)	1.5 (0.9–2.9)	3.4 (0.6–13.4)	83	0.9
2018	21 Feb	28.5	5	58.0 (51–65)	1.6 (1.0–2.3)	1.5 (1.4–1.6)	80	0.7
2018	21 Feb	30.0	6	66.0 (56–80)	2.5 (1.4–4.1)	0.8 (0.7–0.9)	100	0.0
2018	22 Feb	28.1	8	63.6 (53–75)	2.1 (1.2–3.3)	1.2 (0.7–2.7)	100	0.0
Summary			80	61.0 (49–80)	1.9 (0.9–4.3)	5.9 (0.2- 58.7)	90	0.7
Karup								
2017	30 Jan	15.3	9	59.7 (54–67)	1.9 (1.4–2.8)	13.7 (0.9–56.0)	89	0.7
2017	30 Jan	17.8	12	66.6 (56–78)	2.5 (1.4–4.7)	6.8 (0.5–51.3)	92	0.5
2017	31 Jan	29.9	7	68.9 (61–78)	2.8 (1.8–4.0)	15.9 (0.5–68.3)	71	1.0
2017	31 Jan	31.9	12	67.0 (59–76)	2.4 (1.5–4.1)	11.1 (0.5–91.2)	83	0.5
2018	07 Feb	11.8	1	74.3	3.5		0	8.5
2018	07 Feb	14.2	5	60.2 (51–73)	1.8 (1.2–3.2)	11.8 (0.2–56.7)	100	0
2018	08 Feb	29.5	1	58	1.37	0.5	100	0
2018	08 Feb	31.6	6	66.5 (55–73)	2.5 (1.3–3.6)	27.4 (0.6–54.8)	67	1.0
2018	08 Feb	33.8	6	56.8 (51–72)	1.6 (1.0–3.1)	14.4 (1.0–56.7)	83	0.5
2018	09 Feb	24.7	7	57.6 (55–65)	1.6 (1.1–2.5)	27.1 (0.4–66.9)	100	0
2018	09 Feb	26.5	8	56.3 (49–73)	1.5 (1.0–2.7)	14.0 (0.5–54.3)	75	0.9
2018	09 Feb	27.3	6	62.0 (54–78)	2.2 (1.4–4.6)	2.4 (0.4–10.0)	83	0.6
Summary			80	62.8 (51–78)	2.1 (1.0–4.7)	16.0 (0.4–91.2)	85	0.7

sions were closed with 2 sutures (4-0 vicryl absorbable sutures), and scales and a fin clip were also obtained from each individual. The scales provided information on the age, number of spawnings and marine experience (years at sea) of individuals (Rifflart et al. 2006). Fish were then left to recover in a 200 l container of fresh stream water. All tagged fish recovered from the procedure and were subsequently released at the site of capture. The operation lasted between 1 and 2 min, and the recovery time was 2–5 min. All procedures were carried out in accordance with the Danish Experimental Animal Committee (2017-15-0201-01164). The acoustic tags transmitted their unique IDs at a random interval between 30 and 90 s (mean: 60 s) at 150 dB re 1 µPa at 1 m and had an expected battery life of 24 mo.

2.3. Hydrophone deployment

Vemco VR2W-69 kHz or ThelmaBiotel TBR700 receivers were placed at the river mouths and at 7 transects on narrow parts of the fjord (Fig. 1) to track the tagged sea trout as they moved from the rivers into the fjord and out to sea. Receivers in both river mouths were located roughly 200 m before the actual fjord entry. The location of the transects was mainly based on logistical considerations (narrow passages are more easily covered with receivers). Detailed bathymetry charts were used to assure that there were no 'deaf zones' between the receivers, which was unlikely since the depth profile of the fjord is U- or V-shaped in most locations. When possible, receivers were placed on permanent structures such as beacons, bridge pillars or harbour fronts. The remaining hydrophones were placed on buoys in 2017 and deployed underwater in 2018, since the 2017 setup was subject to loss of hydrophones. Hydrophones that were deployed underwater were painted with anti-fouling paint and mounted either on a Sub Sea Sonic AR-50 automatic release system (n = 3) or tied to an anchor and a float (n = 6). The hydrophones that were deployed using the automatic release system were positioned 2 m above the bottom, while the

hydrophones deployed with anchor and floats were positioned 2–3 m below the surface. The maximum distance between hydrophones at any receiver gate was 390 m. The receiver efficiency is reported in Table S1 in the Supplement at www.int-res.com/articles/suppl/m616p141_supp.pdf.

The receiver at the mouth of the Simested River was lost and replaced on 26 May 2017, resulting in the loss of the outmigration data from that river in that year. Several hydrophones were lost in 2017, and site EF2 (see Fig. 1) was therefore used to determine whether a fish had left the fjord that year. No fish were lost between sites EF2 and KG in 2018. In 2018, 2 of the 3 hydrophones were lost at site CF, likely due to trawl fishing. Despite this loss in hydrophones, we were able to track sea trout with high receiver coverage as the fish moved from the river, through the fjord and out to sea.

2.4. Environmental data

Water temperatures were measured in Karup River at the receiver site, 200 m from the river mouth. Satellite-measured fjord and sea temperatures were downloaded from the Copernicus Marine Environment Monitoring Service (marine.copernicus.eu). Temperatures were downloaded for the entire fjord as daily means from the top 2.0 m of the water column during the night (21:00 and 07:00 h).

2.5. Data analysis

The fjord was considered as the compartment between the river mouths and site NS site in the west and site EF2 in the east. For 2018, residence times, migration speeds and survival were calculated for each fjord compartment between the receiver gates: Southern Fjord, Central Fjord, Eastern Fjord 1 and Eastern Fjord 2 (Fig. 1). For the Southern and Central Fjord compartments, values were estimated based on the individuals that had been detected at site CF, as receiver coverage was not 100% at this transect. A registration on a receiver was interpreted as an individual having moved past the receiver. The first detection at a given transect was considered the time of detection at the site. Absolute mortality was calculated by dividing the number of fish that disappeared in a compartment by the total number of tagged fish. Relative mortality was calculated by dividing the number of fish that left a compartment by the number of fish that entered it.

A linear mixed effects model was used to test whether river of origin, fish length and fjord compartment affected progression speeds through the fjord for the 24 fish (12 from each river) that were detected in all 4 compartments and hence successfully migrated to sea. Fish identification number was entered as a random effect. A gamma distributed model from the 'glmmTMB' package (Brooks et al. 2017) was used in order to allow for heteroscedasticity in the data, as was necessary due to heterogeneity of variance between the compartments. Diagnostic plots were inspected visually and analysed with a smoother from the 'mgcv' package (Wood 2017) for each variable to test for patterns in the residuals. Significance of the smoother was p = 0.950–0.973 (adjusted R^2 = 0.03) for the compartments, p = 0.737 (adjusted R^2 = 0.01) for fish length and p = 0.418 (adjusted R^2 = 0.07) for river of origin, suggesting no patterns in the residuals. Residuals are reported in Fig. S1 in the Supplement. The following model was fitted, where the j observed progression speed of fish i is modelled as the common intercept α, the covariates, a random intercept a_i (accounting for different intercepts between individuals and assumed to be normally distributed around 0) and residuals $ε_{ij}$:

$$\text{speed}_{ij} = \ + \text{comp}_{ij} + \text{length}_{ij} + \text{river}_{ij} + a_i + ε_{ij} \qquad (1)$$

A binomial regression model was used to test whether year, river of origin, fish length, condition ($K = 100\frac{\text{mass (g)}}{\text{length (cm)}^3}$), temperature at the fjord entry, previous number of spawning migrations and fungus or wounds on the fish when tagged had an effect on the likeliness of survival through the fjord. The following model was fitted:

$$\text{Logit(survival)} = α + \text{covariates} \qquad (2)$$

where α denotes a common intercept and the remaining term represents the covariates of interest. Year and river of origin were entered as factors and the other terms as continuous variables. Model diagnostics showed no sign of under- or over-dispersion (dispersion statistic = 1.29).

The vif-function and the visual plotting options provided in the R-package 'car' (Fox & Weisberg 2011) were used to test for collinearity between the variables. Variance inflation factor values of 1.08 (condition), 1.33 (length), 1.43 (year), 1.22 (temperature), 1.08 (number of spawning events) and 1.13 (wounds or fungus) suggested no issues with collinearity (Fox & Weisberg 2011). McFadden's pseudo-R^2 value (0.10) of the model was calculated with the 'PR2' function in the package 'pscl' (Jackman 2017).

Table 2. Fate of the 160 acoustically tagged post-spawned sea trout *Salmo trutta* from the Simested and Karup Rivers. Shown are the number of individuals, with corresponding percentages in brackets

	Tagged	Lost in river	Lost in fjord out	Lost at sea	Lost in fjord returning	Resided in fjord	Survived river, sea, river	Total survival
Simested								
2017	40	Unknown	Unknown	7 (17%)	7 (17%)	0	3 (8%)	3 (8%)
2018	40	4 (10%)	19 (48%)	7 (17%)	4 (10%)	1 (1%)	5 (13%)	6 (15%)
Karup								
2017	40	6 (15%)	20 (50%)	7 (18%)	1 (1%)	1 (1%)	5 (15%)	6 (15%)
2018	40	6 (15%)	20 (50%)	8 (20%)	0	0	6 (15%)	6 (15%)

All analyses and modelling of the data were performed in R Studio version 1.0.136 running on basic R version 3.5.1. (R Development Core Team 2013).

3. RESULTS

3.1. River phase

In both 2017 and 2018, 34 of 40 tagged kelts outmigrated from the Karup River, suggesting a minimum survival of 85% through the river phase (Table 2). Outmigration from the river occurred between 2 February and 31 March 2017 and between 31 January and 22 April 2018. In 2018, 36 of 40 tagged kelts (90%) migrated out of the Simested River between 6 February and 9 April. This information is not available for 2017 due to the lost receiver at the river mouth.

Of 160 tagged individuals, 29 (18%) had fungus or wounds. Eight of these fish disappeared in the rivers, corresponding to 50% of the 16 fish that potentially died in the river.

Pronounced activity occurred at the mouths of the rivers (Fig. 2). Forty-one percent (28 of 68 individuals) of the Karup fish and 44% (16 of 36 individuals in 2017) of the Simested fish did not make a direct movement into the fjord. These individuals either waited at the river mouth or left and returned multiple times for an average of 17.3 d (Karup, median: 15.0 d, range: 2.1–43.5 d) and 20.3 d (Simested, median: 14.5 d, range: 2.2–52 d) before the final detection (assumed to represent the final movement into the fjord).

3.2. Marine phase

The fish entered the fjord when surface water temperatures were between −1 and 5°C but showed little activity during winter and early spring. Only 3 detections occurred at receiver sites within the actual fjord until 26 March, when the fish started migrating towards the exit.

There was no significant difference in progression rates between fish from different rivers in 2018 (p = 0.70, n = 70) or among fish of different lengths (p = 0.26). Progression rates were lowest in the southern fjord compartment and increased towards the fjord exit (p < 0.001, Table 3).

Progression rates increased from the river through the various fjord components (i.e. fish progressed faster as they approached the Kattegat; Fig. 3). The fastest progression rates in the study were observed
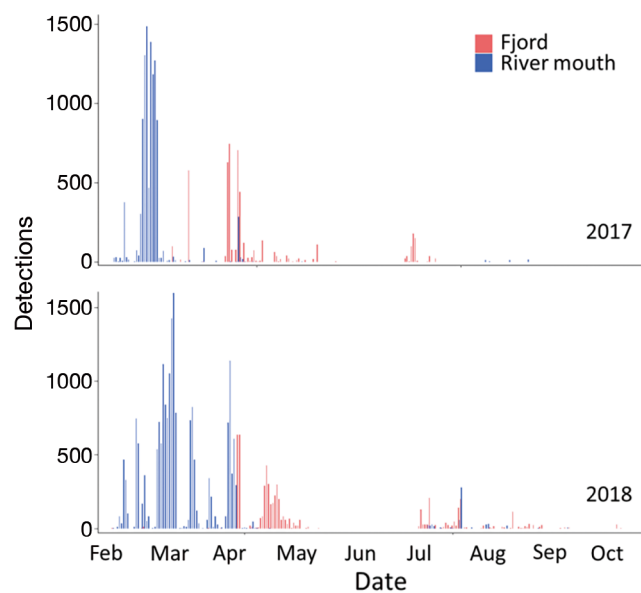

Fig. 2. Total number of detections of acoustically tagged post-spawned sea trout *Salmo trutta* each day at river mouth and fjord receivers in 2017 and 2018. Note that in 2017, the Karup River was the only river with a receiver at the river mouth during the outmigration. The movement into the fjord and further out to sea occurred later in 2018. After the fish leave the fjord, there is a period of 'silence' before they start returning again during summer

Table 3. Output for explanatory variables included in the linear mixed effects model analysing progression rates of acoustically tagged post-spawned sea trout *Salmo trutta*. AIC: Akaike's information criterion

	AIC	Log-likelihood	p
Full model	615.0	−299.5	
Compartment	788.2	−389.1	<0.0001
Fish length	614.3	−300.1	0.257
River	613.2	−299.6	0.701

in the 29 km long Eastern Fjord 2 compartment (mean: 43.3 km d^{-1}, range: 10.5–86.0 km d^{-1}). Progression rates, survival and behaviour from the present study are compared with reports from other studies of horizontal migration of sea trout kelts in Table 4. The onset of migration toward the sea was simultaneous among fish from both rivers, and coincided with sudden increases in fjord temperatures (Fig. 4). Outmigration from the fjord occurred when temperatures were between 3.9° and 13.2°C, but 95% of all fish left at temperatures between 5.8° and 11.0°C.

Some individuals migrated together, particularly in the early part of the outmigration through the fjord. Fourteen of the 49 Simested fish detected at Sundstrup were detected within 30 min of another tagged fish, and 9 individuals had overlapping detections with another tagged fish. Some of these fish both
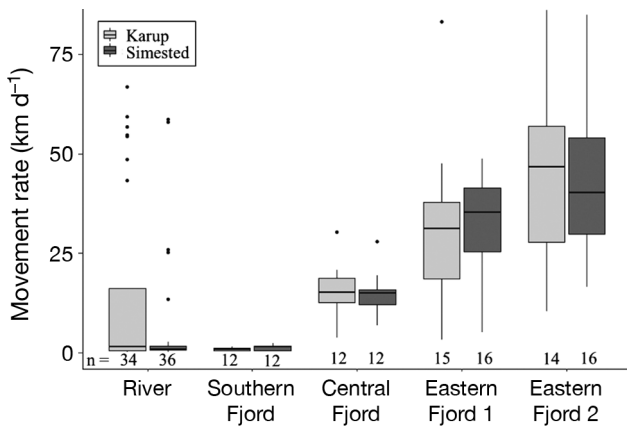

Fig. 3. Progression through different compartments in the Limfjord (see Fig. 1) in 2018 for acoustically tagged post-spawned sea trout *Salmo trutta* that both entered and left a given compartment (River = from release site to river mouth). The numbers of contributing individuals in each compartment are noted along the *x*-axis. Fewer individuals contributed in the Southern and Central Fjord due to the lack of detections at site CF. Black horizontal line = median values, box hinges = interquartile range (IQR), whiskers = 1.5× IQR, black dots = data points outside the IQR

Table 4. Metrics extracted from existing published records of post-spawned sea trout *Salmo trutta* horizontal migration behaviour in marine environments. The studies are listed based on the recorded minimum survival (for the entire marine period), displayed in decreasing order from the top and down. Note the negative correlation of this with reported progression rates that increase from the top and down. The study by Bendall et al. (2005) took place in an estuary with tidal amplitudes of roughly 3 m, enabling most fish to escape the estuary within a single ebbing tide. These studies are not directly comparable to one another given differences in categorization, speed measurement approaches and study sites, but offer some perspective on the results from the present study

| Minimum survival (%)	Mean progression (km d^{-1})	Behaviour	Location	Study area	n	Study
86	Not unidirectional	48% stayed in inner fjord (<21 km)	Central Norway	47 km fjord	32	Bordeleau et al. (2018)
82	Not unidirectional	50% stayed within 19 km	Northern Norway	29 km fjord	20	Jensen et al. (2014)
56	Not unidirectional	58% stayed within 13 km	Central Norway	20 km fjord	115	Eldøy et al. (2015)
29	2.4	All survivors left	Denmark	29 km fjord	49	Aarestrup et al. (2015)
Not reported	5.1 (inner), 14.7 (outer), 11.2 (coastal)	All survivors left	Sweden	2.5 km estuary + 1.5 km coastal	40	Aldvén et al. (2015)
18	~32	All survivors left	England	8 km estuary/tidal zone	45	Bendall et al. (2005)
15	1.1 (Southern), (Central), 32.6 (Eastern 1), 43.3 (Eastern 2)	97% of survivors left	Denmark	160 km sound	160	Present study
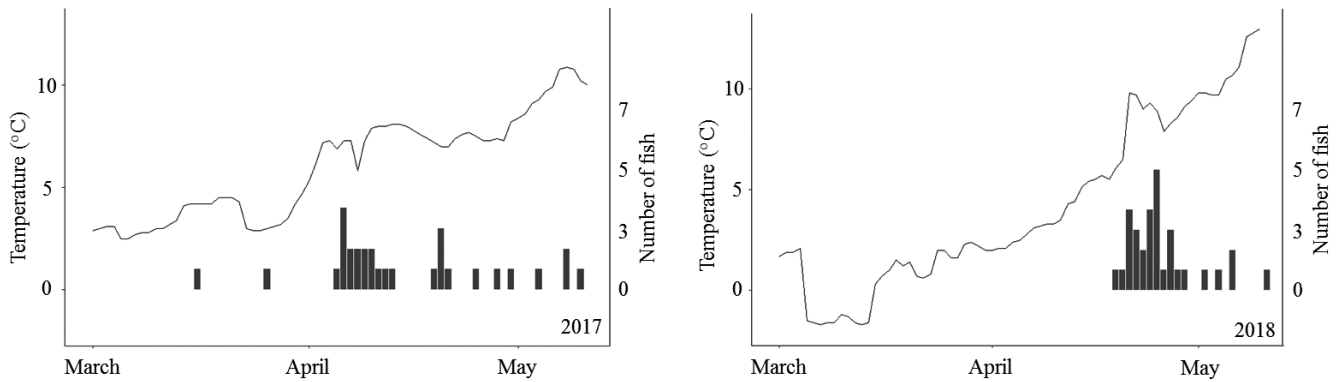
Fig. 4. Fjord surface water temperature (line) and the number (bars) of acoustically tagged post-spawned sea trout *Salmo trutta* leaving the fjord each day in spring 2017 and 2018. A total of 30 tagged fish left the fjord each year

entered and left the Sundstrup site only a few minutes apart, but were not detected together at subsequent receiver sites.

Outmigration through the fjord took take place mainly when daylight was present (Fig. 5). Ninety-one percent of all first registrations at receiver sites within the fjord occurred during daytime or civil twilight.

Fish spent an average of 88.6 d at sea in 2017 (median: 88.9 d, range: 54.4–123.1 d) and 98.4 d at sea in 2018 (median: 102.7 d, range: 64.6–163.4 d), before returning to the fjord. Receivers deployed in The Sound (206 km from the last fjord receiver gate) in 2017 detected 6 of the 30 fish (20%) that left the Limfjord that year. Three fish were detected in The Sound during summer and subsequently moved across the Kattegat with linear progression rates of 33.1–58.6 km d^{-1}. In addition, 2 fish from the Karup River were detected in Roskilde Fjord, 165 km from the Limfjord in 2018.

The fish returned gradually to the fjord during summer and autumn and spent an average of 5.3 d
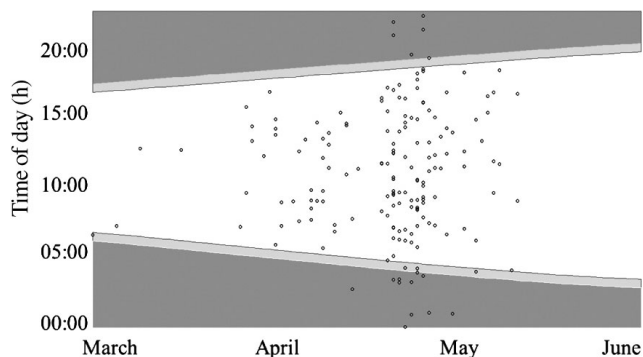

Fig. 5. Time of first registrations for acoustically tagged post-spawned sea trout *Salmo trutta* at the receiver sites in the fjord during late February–May. White areas represent day-time, light grey areas represent civil twilight time, and dark grey areas represent night-time

(median: 4.6 d, range: 2.2–14.9 d) migrating through the fjord and back into the river. The progression rates of individuals outmigrating and return migrating through the fjord were not correlated (see Fig. S2).

3.3. Survival

Eighty-seven percent of the tagged kelts outmigrated from the rivers. In both 2017 and 2018, 34 of the 40 tagged fish (85%) outmigrated from the Karup River, corresponding to a mortality of 0.7% km^{-1} in the freshwater phase (Tables 1 & 4). In the Simested River, 36 of the 40 tagged fish outmigrated from the river in 2018, corresponding to a similar mortality of 0.7% km^{-1} in the freshwater phase.

In both years, survival was lower in the fjord than in freshwater. A total of 30 fish (16 from Simested and 14 from Karup) successfully outmigrated from the fjord, and 1 individual spent its entire marine period within the fjord in each study year, corresponding to a total fjord survival of 44% of the 70 fish that entered the fjord each year. Mortality was particularly high in the early phase of the fjord migration for both groups of fish (Table S2). Length was positively correlated to the probability of survival through the fjord (Table 5, Fig. 6). Survival at sea was also higher than in the fjord. Fifty-two percent (46% for Karup fish and 56% for Simested fish) returned from the sea to the fjord in total.

4. DISCUSSION

Salmonids display great variation in their migratory tendency over spatial and temporal scales, making them interesting organisms to explore how

Table 5. Binomial regression modelling of the probability of acoustically tagged post-spawned sea trout *Salmo trutta* surviving through the fjord as a function of condition (*K*), body length, year, temperature, experience and damage when tagged (fungus or wounds). Parameter estimates are on the scale of the linear predictor

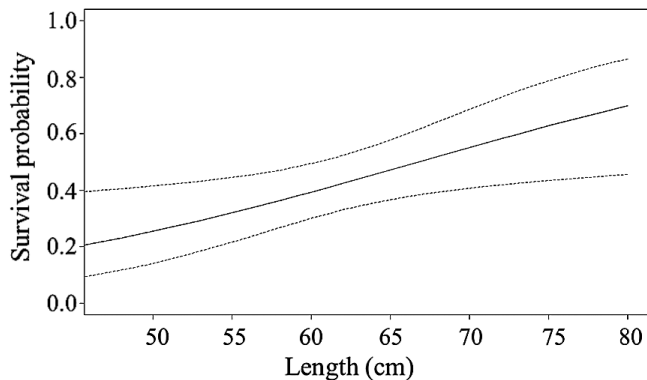|	Estimate	SE	*z*	p(<|z|)
Intercept	−2.131	3.411	−0.625	0.532
K	−5.245	3.291	−1.594	0.111
Length	0.085	0.032	2.664	0.008
Year	0.623	0.539	1.155	0.248
Temperature	0.113	0.165	0.686	0.493
Experience	−0.015	0.584	−0.026	0.979
Damage	0.853	0.572	1.491	0.135

Fig. 6. Model-derived probability of survival as a proportion between 0 and 1 (±95% CI, dashed lines) of acoustically tagged post-spawned sea trout *Salmo trutta* through the fjord versus fish length

and why migration has evolved (Hendry et al. 2004). Brown trout display a great deal of plasticity in behaviour and life-history strategies in rivers, which may extend into the marine environments for sea-run individuals, making this species an ideal candidate to explore factors shaping migration strategy (Aarestrup et al. 2018). We therefore acoustically tagged 160 post-spawned sea trout from 2 rivers in a unique fjord system where large numbers of non-native sea trout had been stocked but had failed to survive and reproduce at levels significantly influencing the genetic composition of the wild population (Ruzzante et al. 2004). We hypothesized that wild fish from these rivers exhibited specific, potentially adaptive behaviours increasing their survival in the fjord. Our work attempts to increase knowledge on how salmonids may cope and adapt to different types of fjords and estuarine systems.

4.1. Receiver gate efficiency

No detected fish had escaped detection at previous receiver sites except at Hvalpsund, where 2 of 3 receivers were lost during the time of outmigration. Range testing revealed high detection efficiency at WF, except at the outermost and shallow positions, where fish could have avoided detection. However, no fish were detected further west at NS. Conditions at this receiver gate can be particularly difficult, potentially creating windows for poor detection where individual fish could avoid detection (Thorstad et al. 2000). While single fish may have avoided detection at both WF and NS going west, we find it unlikely that our setup has failed to detect a significant movement through the western part of the fjord during the migration in and out of the fjord, especially given the high efficiency at WF.

4.2. River phase

The progression rates down the rivers were similar to those observed for sea trout kelts in England (Bendall et al. 2005) and in the Gudenaa River in Denmark (Aarestrup et al. 2002). Some tagged fish appeared to leave and return to the rivers several times during winter and early spring, a strategy that to our knowledge has not been previously reported for trout. Kelts are energy depleted, and the physiological stress associated with residing in the cold waters of the fjord (Sakamoto et al. 1993, Watz & Piccolo 2011) could make them more vulnerable to predation, especially in the predator-rich environment of the southern Limfjord where seals are abundant. We therefore hypothesize that this behaviour of repeatedly leaving and returning may be a trade-off between better feeding opportunities (Ebert 2004) and greater risks of predation in the fjord compared to the river.

4.3. Marine phase

The vast majority of kelts outmigrated from the fjord, and did so in the eastern direction, thus behaving similarly to the sea trout smolts observed by Kristensen et al. (2018b). We found no significant differences in terms of migration speed and timing between fish from the Simested and Karup Rivers in the Limfjord. The behaviour of trout in the fjord was unlike that reported for this species in other systems. After a period of residency close to the river mouth,

the fish migrated 120 km to the eastern fjord exit in relatively few days with the highest progression speeds observed in marine environments for the species. This strategy is unlike the directed movement through the relatively short (~8 km) estuary at the mouth of the Fowey River in south-west England (Bendall et al. 2005) or the gradually decreasing movement speed observed through a 29 km long Danish fjord system (Aarestrup et al. 2015) and in a Swedish estuary and coastal area (Aldvén et al. 2015). The strategy of trout in the Limfjord is also in stark contrast to the preference to stay within fjords or close to the river mouth during the entire marine period observed in Norwegian fjords (Jensen et al. 2014, Eldøy et al. 2015). Previous mark–recapture studies throughout Europe have indicated a preference for sea trout to stay relatively close to their natal river during the marine phase, with relatively few trout being caught more than 100 km from home (Thorstad et al. 2016). With nearly all individuals (except 2) migrating a minimum of 120 km to leave the Limfjord, the behaviour of the Karup and Simested fish differs from what has typically been described for sea trout migratory behaviour. Several of the fish were detected at even further distances away including The Sound (206 km from the easternmost receivers in the Limfjord, n = 6) and Roskilde Fjord (165 km from the easternmost receivers in the Limfjord, n = 2), although these sites only cover a few of the potential areas of migration of Limfjord sea trout.

Long-distance migrations to sea such as those performed by the Karup and Simested trout are associated with high energetic demands, as well as increased risks of predation and injury (Gross et al. 1988, Ward & Hvidsten 2010). However, these risks may be outweighed by the higher risk of predation in the Limfjord. Conditions in the fjord, including a high concentration of predators, may have historically favoured fast progression rates as a kind of 'fleeing' tactic where individuals leave the system quickly to avoid predation. Today, there are large populations of seals and cormorants in the Limfjord, and these predators have few fish species to target due to the collapse of most of the other fish stocks in the fjord in the 1970s (Hoffmann 2000). While predation pressure has likely played an important role in shaping the migratory behaviour of sea trout through the fjord, other factors such as potentially better foraging opportunities outside the fjord, avoidance of warm temperatures in the shallow fjord in summer and avoidance of anoxic conditions within the fjord may have also played a role (Hofmeister et al. 2009).

For instance, sea surface (0–2 m) temperatures as warm as 23°C were measured in the central fjord in 2018 (http://marine.copernicus.eu), which is well above the 12–17°C range where optimal growth rates have been reported for sea trout (Ojanguren et al. 2001, Larsson 2005).

The exclusive preference for leaving the fjord through the eastern exit is identical to that of smolts from the same rivers (Kristensen et al. 2018b), despite the western exit being approximately 10 km closer. This may be an inherited preference due to the historical (pre-1865) lack of a western exit, which has been maintained due to higher salinities to the west, the location of predator colonies in the western fjord and current directions.

The timing of migration was relatively consistent between rivers, although it appeared to vary slightly between years, extending later into spring in 2018. In both years, outmigration activity through the fjord increased during or directly after a sudden increase in the temperature of fjord waters, perhaps to reach the sea in times of particularly optimal feeding opportunities there (Satterthwaite et al. 2014). Although speculative, this suggestion is also brought forward by Aarestrup et al. (2015). In that study, sea trout kelts gathered in the outer compartment of a fjord located 40 km south of the Limfjord before entering the Kattegat Sea at roughly the same time as the kelts from the present study. Alternatively, it is possible that migration timing is a trade-off between optimal migration temperature (the higher, the better for the fish) and the risk of predation when staying in the fjord for longer time. This may explain why some individuals went back and forth between the river and the fjord, and others appeared to migrate simultaneously, perhaps as a way to decrease the likelihood of being detected by a predator (Magurran 1990). A similar behaviour was observed at Sundstrup, where the fish have to move through a 26 m wide passage before entering the next compartment. Seals are often present in relatively great numbers at this site, and the behaviour may have been a consequence of fish postponing their passage due to predator activity at the site. This suggests that manmade structures or narrow passages may cause delays or make the fish more vulnerable to predation as seen elsewhere in the marine environment (Yurk & Trites 2000) and in freshwater (Aarestrup & Koed 2003).

The observed preference for migration during daytime or crepuscular hours is in line with other telemetry studies of sea trout kelts moving in the marine environment (Aarestrup et al. 2015, Aldvén et al. 2015). However, it differs from the preference for

movement during evening or night-time observed for the Limfjord postsmolts, where 80.2% of all first registrations at receiver gates occurred between 16:00 and 04:00 h (Kristensen et al. 2018b). The different movement strategies could reflect a form of adaptation by kelts to avoid predation from seals that hunt efficiently during the night (Hobson 1966, Renouf 1989). By being more active during the day, kelts are more exposed to avian predators that prefer hunting during daylight (White et al. 2008) but may be more easily escaped compared to seals. These results also suggest that kelts may rely more on the angle of the sun to navigate compared to postsmolts (Hasler et al. 1958).

The detection of a total of 6 tagged fish in The Sound and 2 in Roskilde Fjord, 206 and 165 km from the easternmost receiver gate, respectively, confirms previous observations from mark–recapture studies, where trout from the Limfjord were caught throughout the Kattegat and western Baltic region (Pedersen et al. 2006). The 6 fish detected at The Sound in 2017 were only detected on 1 occasion, suggesting that the trout may follow different routes on their way to and from the Baltic Sea, or that receiver efficiency was poor at the site. The movement rate of 33.1–58.6 km d⁻¹ between The Sound and the Limfjord for the fish that were detected during summer suggests that these individuals took a direct path back toward the fjord. The horizontal progression rates of the returning kelts are similar to, though somewhat faster than, those documented by Tanaka et al. (2005) for chum salmon *Oncorhynchus keta* migrating through open sea to return to their native river (36.4 ± 15.2 km d⁻¹).

4.4. Survival

Survival in the freshwater phase was relatively high (85–90%), and comparable to what other studies have reported in Danish rivers (Aarestrup et al. 2002, 2015). Survival in the marine phase (from the river to the sea, and back to the river) was similar between years and rivers (15%), but was considerably lower than that reported for other veteran migrants (29%) in the area (Aarestrup et al. 2015). A recent Norwegian study reported marine survival of sea trout kelts as high as 86% (Bordeleau et al. 2018). Survival at sea (52%) in the present study was similar to the 45% reported by Aarestrup et al. (2015) that was performed in a system just south of the Limfjord, with an exit into the Kattegat. The particularly low overall survival through the entire marine phase in

the current study, in combination with a relatively large proportion of fish being lost in the fjord during their outmigration, highlight the importance of mortality as a potential selective force acting in the Limfjord. Mortality was particularly pronounced in the southern fjord compartment, which aligns well with previous studies documenting the dangers associated with entering the marine environment (Thorstad et al. 2012). The much longer residence times of trout in this southern compared to the central and eastern compartments likely contributes to this high mortality.

Although the exact extent of mortality from different predators is unknown, harbour seals are known to prey on adult salmonids (Wright et al. 2007), and have started to enter the Karup River to forage there, as has been reported in other rivers (Middlemas et al. 2005). The large presence of seals in the Limfjord may have resulted in some level of increased mortality in the present study, as seals can hear the 69 kHz acoustic transmitters (Kastelein et al. 2009). The effect of this is not well covered in the scientific literature. A study has found a survival ratio of 0.79–1.05 of acoustically-tagged versus passive integrated transponder (small, non-transponding tags) tagged salmonid smolts in systems with mammalian predators (Columbia River, USA; M. Rubb unpubl. data), although some of this difference could also been attributed to increased tag-burden from the larger and heavier acoustic tags.

The present study documents a special behaviour in sea trout entering a dangerous fjord system. Tagged individuals originated from 2 different rivers entering different compartments of the fjord and behaved almost identically, yet differently from sea trout populations elsewhere. The tagged individuals entered the fjord gradually but exited it towards the sea within a short window of time and moved with the highest progression rates documented for the species in marine environments on their way out. The fjord system has a western and an eastern opening to the sea, but migration through the fjord occurred exclusively along the longer, eastern route. The special behaviour exhibited by the tagged individuals could reflect important local adaptations to survive the marine phase in the region, potentially explaining why wild fish outcompeted non-native fish stocked in the region during the 20th century. The results highlight the adaptability of sea trout and increase our knowledge on factors influencing behaviour and survival of salmonids in marine environments. Future studies should continue using acoustic telemetry to investigate behavioural pat-

terns in other systems, which may reveal the under-pinnings of local adaptations in salmonid populations. Three-dimensional acoustic arrays may be of particular interest, where specific aspects of survival and behaviour including real distance covered, delays at man-made barriers and exact locations and magnitudes of predation can be documented.

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