


Evidence of cormorant-induced mortality, **disparate migration strategies** and repeatable circadian rhythm in the endangered North Sea houting (*Coregonus oxyrinchus*): A telemetry study mapping the postspawning migration

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Abstract

Life history theory predicts a trade-off between migration and residency where migration is favoured when it infers elevated fitness. Although migration to more favourable environments may offer higher growth rates, migrants often experience increased mortality due to predation. Here, we investigated mortality and migration behaviour of the North Sea houting (*Coregonus oxyrinchus*), an anadromous salmonid endemic to the Wadden Sea. We used acoustic telemetry to map the migration of the only remaining indigenous population by applying stationary hydrophones combined with manual tracking. Data suggested a total mortality of 26%, with 30% of the total mortality attributed to predation by great cormorants (*Phalacrocorax carbo sinensis*), highlighting that North Sea houting conservation could be jeopardised by increased cormorant predation. Risk of cormorant predation was size-dependent, with smaller fish suffering higher risk of predation. The study found North Sea houting to exhibit disparate migration strategies and identified a lentic area in the estuary as an important habitat. Two newly established artificial lakes within the river system significantly reduced the migration speeds, possibly indicating constrained navigation through the lakes. The migration into the Wadden Sea correlated with temperature perhaps indicating osmoregulatory constraints of sea entry. Unlike many salmonid species, migration occurred both day and night. Moreover, fish exhibited repeatable individual differences in diel activity patterns, suggesting that individuals differ consistently in their migratory activity throughout the 24-hr period. Our study provides novel information on salmonid migration, which is crucial for the development of science-based conservation strategies.

KEYWORDS

artificial lakes, circadian rhythm, cormorant predation, repeatability, telemetry, whitefish

1 | INTRODUCTION

Migration is defined as synchronised movements between distinct habitats occurring at specific life stages (Lucas & Baras, 2002), and is a common phenomenon in many animals (Dingle & Drake, 2007) including mammals (Avgar, Street, & Fryxell, 2013), birds (Berthold, Gwinner, & Sonnenschein, 2013), amphibians (Sinsch, 2014) and fish (Secor, 2015). Migration is considered an adaptation to resources that fluctuate spatiotemporally, for example seasonally (Dingle & Drake, 2007). Although the fitness of migratory individuals often exceeds the fitness of residents, migratory individuals may experience increased mortality risk during the migration, because of elevated predation risk (Brönmark et al., 2014). In birds, predation risk during migration may shape the evolution of migration timing and routes (Lank, Butler, Ireland, & Ydenberg, 2003). Movement is often associated with elevated predation (Aarestrup, Jepsen, Koed, & Pedersen, 2005), and predation during migration may favour resident strategies over migratory strategies (Bohlin, Pettersson, & Degerman, 2001). To manage migratory populations, it is therefore important to know predation rates en route between different habitats. In fish, anadromy describes individuals that migrate between freshwater spawning habitats and marine foraging habitats. At high latitudes, early life stages of anadromous fishes may experience reduced predation risk in lotic freshwater habitats, while growth rates in marine habitats often exceed growth rates in freshwater habitats (McDowall, 2001). Therefore, assuming limited mortality during the migration, it may be adaptive to migrate between the disparate habitats.

In anadromous salmonids, increased mortality due to predation has been documented during migration in smolts (i.e., migrating juveniles) and adults (Gowans, Armstrong, Priede, & Mckelvey, 2003; Wright, Riemer, Brown, Ougzin, & Bucklin, 2007). Specifically, several studies have documented significant predation from piscivorous birds including heron (*Ardea cinerea*; Koed, Jepsen, Aarestrup, & Nielsen, 2002), great crested grebe (*Podiceps cristatus*; Jepsen, Aarestrup, Økland, & Rasmussen, 1998), common merganser (*Mergus merganser*; Wood, 1987) and cormorants (*Phalacrocorax carbo sinensis*; Koed, Baktoft, & Bak, 2006). Notably, avian predation may change both size distribution and abundance of several species within fish communities (Steinmetz, Kohler, & Soluk, 2003). These findings indicate that avian predation may impede sustainable management of migrating fish populations.

The North Sea houting (*Coregonus oxyrinchus*) is an anadromous salmonid species endemic to the Wadden Sea. Situated in the south-eastern corner of the North Sea, the Wadden Sea is the largest unbroken system of intertidal sand and mud flats in the world, and included on the World Heritage List. Historically, the North Sea houting was distributed across the entire Wadden Sea, however, habitat degradation, establishment of barriers within rivers, pollution and possibly overfishing caused severe declines and extirpation of populations throughout its native range (Jepsen, Deacon, & Koed, 2012). The only indigenous population remaining today at a global scale is found in River Vidaa in Denmark, although the species has been reintroduced in a few other rivers (Borcherding, Heynen, Jäger-Kleinicke, Winter, & Eckmann, 2010). On this basis, the North Sea houting is considered endangered

and is listed in the Bern Convention as well as on Appendixes II and IV in the EU Habitats Directive (Pihl et al., 2000).

Previous studies have indicated that adult North Sea houting migrate from the Wadden Sea into adjacent rivers to spawn in the autumn and winter (Borcherding, Breukelaar, Winter, & König, 2014; Jepsen et al., 2012). Eggs hatch in February and March, and larvae and juveniles presumably stay in lentic freshwater habitats until reaching 30–50 mm in body length, upon which they migrate into the Wadden Sea to forage (Jensen et al., 2015; Poulsen et al., 2010, 2012). Using stable isotopes from scale samples, Borcherding, Pickhardt, Winter, and Becker (2008) examined migration strategies in a reintroduced population of North Sea houting in the Dutch Lake IJsselmeer. The authors uncovered individuals that never left freshwater, a group that migrated to sea at an early age, and finally fish that migrated at a considerably older age, suggesting disparate migration strategies within the North Sea houting. Migration strategies of the indigenous population in River Vidaa have not been examined, but could reveal important riverine habitats, which would add valuable knowledge for future conservation plans. Restoration projects have created artificial lakes in River Vidaa to support the early life stages of North Sea houting (Jensen et al., 2015), but possible effects of the artificial lakes on the migration of adult North Sea houting remain uncertain.

As endothermic animals, the physiology of fish is strongly affected by temperature (Brett, 1964; Tirsgaard, Svendsen, & Steffensen, 2015), and fish migration often correlates with water temperature (Sims, Wearmouth, Genner, Southward, & Hawkins, 2004). In many salmonid species, such correlations have been widely documented (Jonsson, 1991; Svendsen, Koed, & Aarestrup, 2004; Thorstad, Whoriskey, Rikardsen, & Aarestrup, 2011). To date, it remains unknown if migration of North Sea houting correlates with temperature. In this context, migration between river and marine areas may be particularly interesting, because mechanisms to switch from hyper-osmoregulation to hypo-osmoregulation (Jensen et al., 2015) are influenced by temperature (Finstad, Staurnes, & Reite, 1988).

Recent studies have revealed repeatable interindividual variation in fish behaviour (Killen, Adriaenssens, Marras, Claireaux, & Cooke, 2016). In natural settings, fish may exhibit repeatable movement distances (Taylor & Cooke, 2014), routines (Baktoft et al., 2016), timing and destination of migration (Brodersen et al., 2012) and spawning locations (Forsythe, Crossman, Bello, Baker, & Scribner, 2012). Behavioural repeatability in North Sea houting has not been investigated. Although the importance of behavioural repeatability is increasingly recognised for conservation and management (Killen et al., 2016; Merrick & Koprowski, 2017), repeatability of circadian rhythm is largely unknown in migrating fish (Alós, Martorell-Barceló, & Campos-Candela, 2017). Circadian rhythm is a significant driver of behaviour in a diversity of animals (Aschoff, 1966; Bano-Otalora & Piggins, 2017; Moore, Watts, Herrig, & Jones, 2016; Wang, Harpole, Trivedi, & Cassone, 2012) including fish (Feng & Bass, 2016; Reeb, 2002). Most studies of circadian rhythms have used laboratory animals kept under stringently controlled conditions (Amin, Slabbekoorn, Schaaf, & Tudorache, 2016; Buck, 2016; Svendsen et al., 2014), however, observations in natural settings are important to understand the diversity and adaptive

significance of circadian rhythm and the mechanistic basis (Bulla et al., 2016; Merrick & Koprowski, 2017; Steiger et al., 2013; Stuber, Baumgartner, Dingemans, Kempnaers, & Mueller, 2016; Vanin et al., 2012; Závorka, Aldvén, Näslund, Höjesjö, & Johnsson, 2016).

Employing acoustic telemetry, we investigated migration of North Sea houting during the postspawning descent from freshwater spawning areas to the Wadden Sea. Using the only remaining indigenous population, we tested five hypotheses: (i) avian predation depends on fish body size, (ii) North Sea houting exhibit disparate migration strategies, (iii) fish travelling through artificial lakes exhibit reduced migration speeds, (iv) migration into the Wadden Sea correlates with water temperature and (v) individual fish that are migrating exhibit repeatable circadian rhythms.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted on the River Vidaa (Figure 1) located in south-west Denmark and draining into the Wadden Sea, a shallow

water area in the south-eastern corner of the North Sea. At the river outlet, the water flow is regulated by a sluice protecting the farmland and villages behind the dikes from flooding. The catchment area of the River Vidaa is lowland, and the area has been extensively drained and channelled and turned into farmland. The River Vidaa is formed by the confluence of the Rivers Arnaa and Hvirvlaa. Two other rivers, River Grønaa and River Sønderaa, join the river near the township of Tønder. These two rivers are thought to hold the main spawning areas for the North Sea houting, while access to the River Arnaa and River Hvirvlaa branch was only opened in 2009 by the removal of a 400-year-old barrier. The River Vidaa is 69 km long, the catchment area is 1,081 km² and the mean annual discharge is 13 m³s⁻¹ (Ovesen et al., 2000).

Four lakes and reservoirs form parts of the River Vidaa system (Figure 1). South of the sluice at the river outlet, a shallow artificial lake, acting as a daily water reservoir, connects to the River Vidaa. The reservoir is connected to a 250-ha artificial saltwater lake through a channel blocked by a weir impassable to fish. Given that the reservoir is located in the estuarine area, it could provide important habitat to the North Sea houting during the transition from the river into the Wadden Sea. Lake Rudbøl is situated 11 km upstream from the outlet,

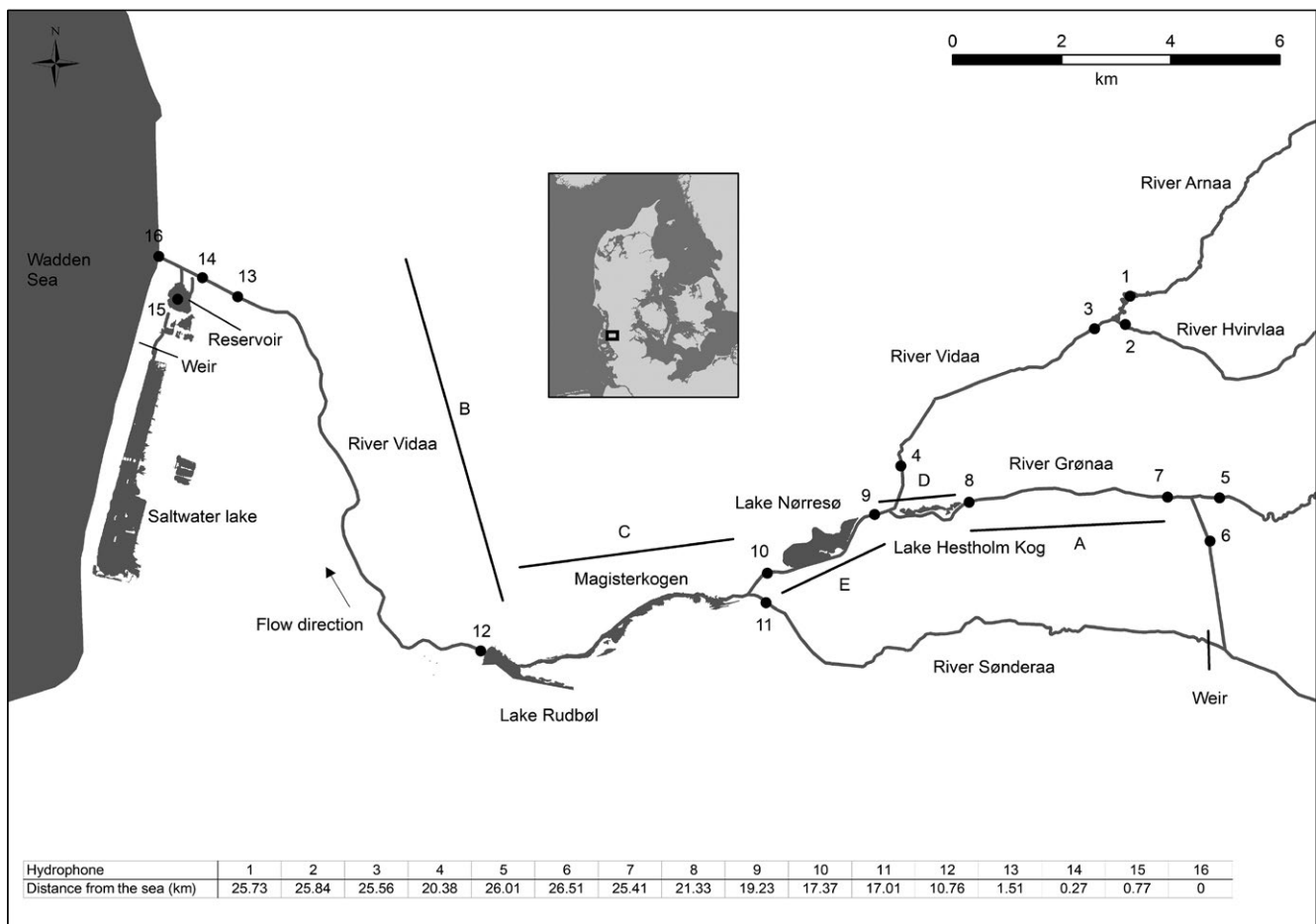


FIGURE 1 Location of the 16 stationary hydrophones in the River Vidaa system. The main spawning areas are believed to be situated upstream of hydrophones 5 and 6. Almost no water passes over the weir in River Sønderaa. Instead, water runs north and meets River Grønaa (and passes hydrophone 6). Water drains into the Wadden Sea at hydrophone 16. Sections A-E represent sections used in the analyses of differential migration speed displayed in Figure 5. Sections A and B represent river sections, while sections D and E represent artificial lakes. Section C represents a natural lentic area.

and Lake Nørresø (90 ha) is situated further upstream. This lake was re-established in 2009, after having been drained since 1930, to provide nursing habitat for juvenile North Sea houting. Within Lake Nørresø, a patch of old trees is used by resting cormorants (*Phalacrocorax carbo sinensis*). Finally, just upstream Lake Nørresø, a fourth lake called Hestholm Kog was established in parallel with Lake Nørresø. Hestholm Kog is connected to River Grønaa through two channels, but the area between the river and Hestholm Kog is flooded during periods of high water levels. In addition to the four lakes, a part of River Vidaa called Magisterkogen situated between Lake Nørresø and Lake Rudbøl is characterised by largely lentic water.

2.2 | Tracking equipment

Movements of adult North Sea houting were tracked using 16 stationary acoustic hydrophones (Vemco VR2W 69 kHz). In October 2014, the hydrophones were installed throughout the River Vidaa system. Figure 1 shows the location of each hydrophone along with river distances between hydrophones and the Wadden Sea. Hydrophones were installed both upstream and downstream of lakes and river bifurcations. Detection range of the hydrophones was evaluated using test transmitters attached to a float. Ranges varied from 50 m to more than 500 m depending on weather conditions, depth and obstacles. Detection ranges showed no overlap between hydrophones, except between hydrophones 13, 14 and 16 due to the channelisation of the most downstream part of the river system. For this reason, migration speed was not considered between those three hydrophones. Electrofishing surveys suggest that the spawning grounds are located just upstream of station 5 or 6.

In addition to the stationary hydrophones, manual tracking was conducted using a portable acoustic receiver (Vemco VR100) from boat. Manual tracking was carried out between November 2014 and June 2015 in River Grønaa (upstream of hydrophone number 5), Lake Nørresø and in the reservoir near the outlet of River Vidaa.

Water temperature in the river was logged using HOBO UTB-001 TidbiT V2 temperature loggers attached to hydrophones 5, 11 and 16. Temperature was logged every 30 min., throughout the study.

2.3 | Tagging and release

Forty-nine adult North Sea houting were caught by electrofishing in River Grønaa and River Sønderaa near the putative spawning areas during the spawning period in November 2014. In addition, 29 post-spawned adults were caught in gillnets near the outlet of the River Vidaa between January and March 2015. Gill nets were lifted and examined every 15 min to minimise any fishing-induced stress. Table 1 lists location, date, number of fish tagged and mean length of tagged fish. Fish with large wounds were excluded from the study. Sex was only determined for fish sampled during the spawning season as lack of sexual dimorphism (e.g., scale texture, presence of eggs and milt) outside the spawning period complicates consistent sex determination in live fish.

Fish were anaesthetised using benzocaine (7.5 ml per litre water; Sigma-Aldrich Chemie GmbH) and tagged with an acoustic transmitter

TABLE 1 Summary statistics of tagged North Sea houting

Date	Sample size	Locality	Mean length (cm)
18.11.2014	16	River Grønaa	47.4
20.11.2014	14	River Sønderaa	44.0
27.11.2014	19	River Grønaa	40.4
02.01.2015	2	Estuary	49.5
30.01.2015	9	Estuary	36.8
16.02.2015	15	Estuary	40.9
16.03.2015	3	Estuary	48.2

(Vemco coded tag, V9-2x, 69 kHz, 146 dB re 1µPa @1 m transmission delay of 30–60 s between signals.) surgically implanted into the body cavity. The surgery procedure applied the protocol used previously (Piper, Svendsen, Wright, & Kemp, 2017; Svendsen et al., 2011) in compliance with the guidelines described in permission 2012-DY-2934-00007 from the Animal Experimentation Inspectorate of the Danish Ministry of Justice and permission NST-41501-00093 from the Danish Nature Agency. Mean length of tagged fish was 42.7 ± 6.4 cm (mean \pm SD) allowing a low ratio of transmitter mass: fish mass (transmitter weight of 2.9 g) and within the range where effects on the behaviour of the fish are negligible (Brown et al., 2010). Generally, implantation of transmitters in salmonids is believed to have limited effects on behaviour, swimming performance, growth and mortality (Connors, Scruton, Brown, & McKinley, 2002; Mellas & Haynes, 1985; Moore, Russell, & Potter, 1990; Peake, McKinley, Scruton, & Moccia, 1997). Operative recovery lasted 5–15 min and was considered complete when fish restored a normal upright position, recovered activity levels and responded to tactile stimuli. After operative recovery, fish were released near the catch site. Data were collected between 18 November 2014 and 29 June 2015.

2.4 | Data analysis

Data were split into two parts: (i) the postspawning downstream migration from the spawning areas and (ii) the period of time in the estuarine area (salinity approx. 0.2 psu). The start of the postspawning migration was defined as the time of the last detection on hydrophones 5 or 6 located immediately downstream of the putative spawning areas. The end of the migration was marked by the first detection on hydrophone 13, which is located close to the sluice and the Wadden Sea (Figure 1). Similarly, the start of the estuarine residency was defined as the first detection on hydrophone 13 and ended when the fish left the river and entered the Wadden Sea. Fish that were detected by hydrophone 16 located at the sluice next to the Wadden Sea and subsequently not detected by the hydrophone, or any other hydrophones, were assumed to have left the river and entered the Wadden Sea.

Migration speed of each individual North Sea houting was calculated by dividing the river distance (to nearest 10 m) between hydrophones 5 or 6 near the spawning areas and hydrophone 13 near the estuary by the time (to nearest 1 s) spent covering the distance.

Similarly, migration speeds were calculated for each section between neighbouring hydrophones (Figure 1).

For a total of 32 North Sea houting tagged near the spawning grounds in River Grønaa and River Sønderaa, data on the complete migration from the spawning grounds to the sea were available. Applying the criteria (i) time in estuary/time in river >2 and (ii) time in estuary/time in river <0.5, the fish were grouped into distinct groups showing different migration patterns during the downstream migration to the sea.

Circadian repeatability, that is whether individual fish displayed consistent patterns in the diel timing of migration, was evaluated by calculating the repeatability, R (Hayes & Jenkins, 1997). Data used for the purpose were the first detection on individual hydrophones indicating active movement in either upstream or downstream direction. As individual behaviour is likely to differ between the postspawning migration and the estuarine period, each stage was analysed separately. Postspawning migration was defined as movement between hydrophones 1–13 (a total of 49 fish). Due to overlapping detection ranges, behaviour in the estuary was only represented by movements between hydrophones 15 and 16, 13 and 15 and 14 and 15 (a total of 45 fish).

2.5 | Statistical testing

All statistical analyses and graphics were carried out using the software package R (R Development Core Team, 2016). Due to the unbalanced nature of the data along with significant heteroscedasticity, nonparametric statistical tests were applied.

To investigate the influence of individual body size and sex on the mortality during migration, we used a binomial generalised fixed effect model with size and sex as independent variables and mortality as dependent variable. The analyses were carried out using the function `glm` in R. In the first analysis, only those individuals that were confirmed to be dead by locating their transmitters in cormorant resting areas during manual tracking were entered into the model as dead. Repeated electrofishing surveys from boat documenting the fish fauna in Lake Nørresø were used to ascertain the mortality. In a second analysis, those individuals that disappeared from the system without subsequently being located by manual tracking were also considered as dead and added as such to the data set to investigate whether “broad sense” mortality was size-dependent.

A Wilcoxon's rank-sum test was applied to test for differences between sexes in the onset of the downstream migration as well as sex differences in migration speeds. Spearman's rank-order correlations were applied to examine correlations between fish body size and migration speed and time spent in the estuary.

A Friedman test, taking into account repeated measures of individuals, was used to test whether migration speeds in the river sections differed significantly from migration speeds in the lake sections. For this analysis, migration speeds between hydrophones 7 and 8 (section A) and hydrophones 12 and 13 (section B) represent river sections immediately upstream of Lake Nørresø (section E between hydrophones 9 and 10) and downstream of the lentic Magisterkogen and Lake Rudbøl (section C between hydrophones 10 and 12) respectively

(Figure 1). Section D between hydrophones 8 and 9 covers a part of River Grønaa and Lake Hestholm Kog. Pairwise post hoc comparisons were performed using Wilcoxon signed-rank tests.

To investigate whether temperature had an effect on the entry into the Wadden Sea, the relationship between temperature and cumulative number of fish entering the Wadden Sea was analysed by fitting polynomial regression models.

A one-way ANOVA was applied to calculate the repeatability of timing of migration, following the method of Lessells and Boag (1987). R has been shown to be a robust estimator, even when the data set is unbalanced (Bell, Hankison, & Laskowski, 2009; Nakagawa & Schielzeth, 2010). Standard errors and confidence intervals were computed using the method of Nakagawa and Schielzeth (2010). The R package `circular` (Agostinelli & Lund, 2013) was used to account for the circular properties of the data. The repeatability reflects the intra-class correlation coefficient and is defined as the fraction of the total behavioural variation that is explained by variation between individuals (Bell et al., 2009). Thus, the repeatability estimate R can attain values from 0 to 1, with values close to 1 regarded as highly repeatable.

3 | RESULTS

From the time of release (varying between 18 November 2014 and 16 March 2015) to the end of data collection on 29 June 2015, 96% (75 individuals) of the tagged North Sea houting were detected at least once. Three individuals (4%) that were tagged near the spawning areas were not detected and are assumed to have died in the spawning areas.

At the termination of the data collection, 56 tagged North Sea houting had left the river and entered the Wadden Sea. Thirty-two of these were tagged in the winter 2014 in the vicinity of the spawning grounds, while 24 were tagged in the estuary in the spring 2015. At this point in time, two individuals were still located in the river and were active in the estuarine area. A total of 20 fish (26%) were lost during the study period. While 14 of these were not found (three individuals not detected during the study), six were located under a patch of trees in Lake Nørresø during manual tracking. Repeated electrofishing surveys in the lake (1 August 2015) showed no signs of North Sea houting, while simultaneous manual tracking confirmed the presence of the six transmitters. Electrofishing provided numerous roach (*Rutilus rutilus*), a few gudgeon (*Gobio gobio*) and a single northern pike (*Esox lucius*; <20 cm). Investigating the effect of sex and body size on survival, the generalised mixed model showed no significant effect of sex on mortality, when only entering transmitters located by manual tracking as dead ($p = .61$) and when entering all lost transmitters into the model as dead ($p = .12$). However, a significant positive correlation between body length and survival was found, when only considering those transmitters that were located under resting cormorants as dead ($p = .023$; Figure 2). When assuming mortality for all individuals that disappeared including those located under the resting cormorants, no significant correlation between body length and mortality was found ($p = .10$).

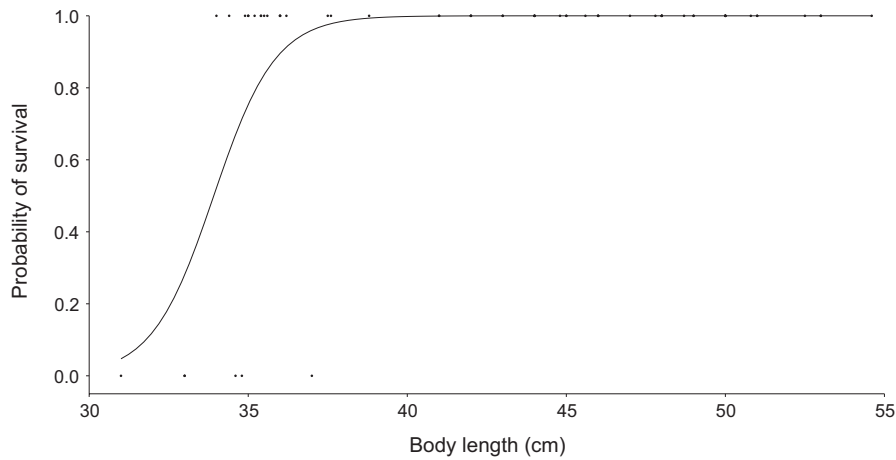


FIGURE 2 Probability of survival is body size-dependent in North Sea houting. The figure shows the probability of survival during the downstream migration in relation to body length ($p < .05$).

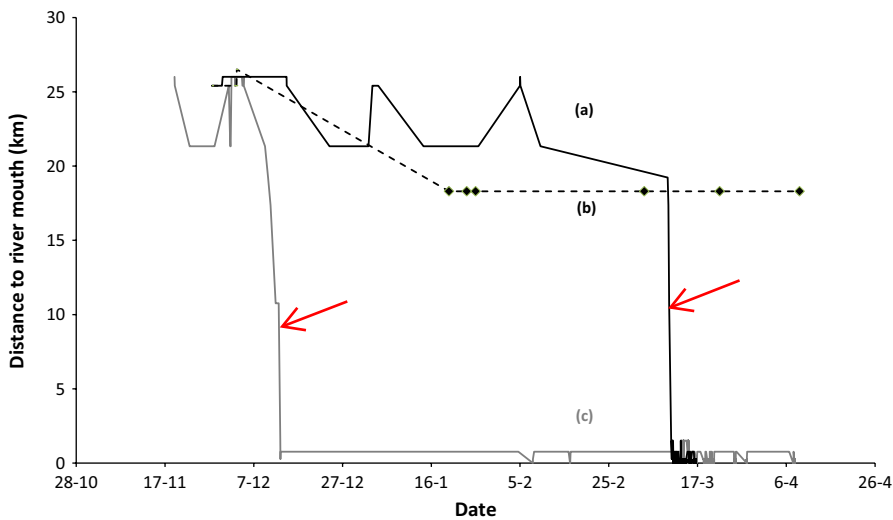


FIGURE 3 Individual North Sea houting exhibit different migratory strategies during downstream migration in the spring. The figure shows (a) a late migrating fish spending extra time in the vicinity of the spawning areas, (b) a dead fish detected in Lake Nørresø and (c) an early migrating fish spending less time in the vicinity of the spawning areas. Diamond-shaped data points originate from manual tracking

The onset of the downstream migration of North Sea houting, as defined by the last detection at station 5 or 6, varied between 28 November 2015 and 5 February 2015 with most fish starting the downstream migration in mid-December 2014. A significant difference in the onset of the downstream migration between sexes was revealed (Wilcoxon's rank-sum test, $p = .02$). Specifically, females (median: 7 December, IQR: 10.5) started the migration 6 days earlier than males (median: 13 December, IQR: 4.75), indicating that males were spending longer time in the spawning areas.

When grouping individuals into distinct migration patterns using the criteria (i) time in estuary/time in river >2 and (ii) time in estuary/time in river <0.5 , the group meeting criterion (i) represented 25% ($n = 8$) of the fish. These individuals initiated downstream migration soon after spawning with a median time spent in the river after spawning of only 6.5 days (interquartile range IQR = 13.25) before they arrived in the estuary, where they stayed for a period of 99.0 days (median; IQR = 47.75). The other group [meeting criterion (ii)], representing 66% ($n = 21$ of the 32 fish) of the tagged fish, spent considerably longer time in the upper reaches of the river (median of 88.5 days; IQR = 70.25), before they migrated quickly downstream to the estuary, where they spent only 2.0 days (median; IQR = 8.0). Three fish (9%) did not meet the criteria and spent relatively equal time in

the river and the estuary. Figure 3 shows the representative migration patterns for the two groups along with the pattern of a transmitter that was tracked manually in Lake Nørresø on six occasions.

Considering the complete migration from the putative spawning grounds (hydrophones 5 and 6) to the estuary (hydrophone 13), no difference in the duration of migration between males (median = 33.9 days, IQR = 71.7) and females (median = 24.5 days, IQR = 87.2) was observed (Wilcoxon's rank-sum test, $p = .50$). Similarly, when considering time spent in the estuary, that is from the first detection on hydrophone 13 to the last detection on hydrophone 16, no difference between males (median = 1.7, IQR = 35.7) and females (median = 1.3, IQR = 56.1) was observed (Wilcoxon's rank-sum test, $p = .31$). No correlation between body length and migration speed during the downstream migration from the spawning grounds to the estuary (Spearman's rank-order correlation, $p = .48$) as well as time spent in the estuary (Spearman's rank-order correlation, $p = .13$) was found.

Considering all fish detected in the estuary, that is both fish tagged near the spawning grounds and fish tagged in the estuary (excluding fish disappearing before entering the estuary), a total of 45 of 62 fish (73%) entered the reservoir near the estuary. The time spent in the reservoir varied between 1.25 hr and about 4 months (114 days), with

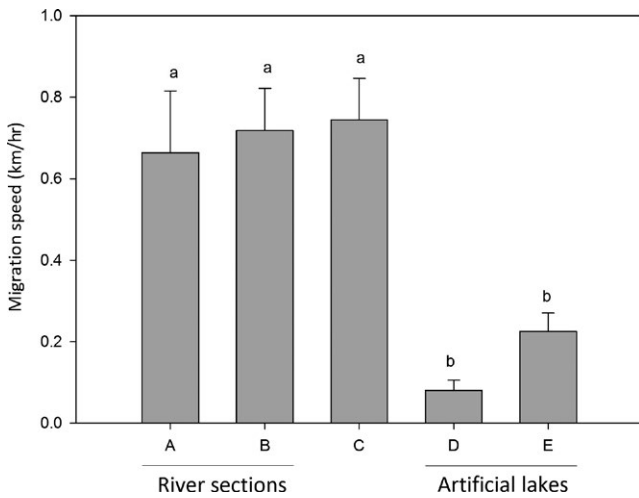


FIGURE 4 Migration speeds are reduced through artificial lakes. Mean migration speed in five sections representing two river stretches (sections A and B), the lentic Magisterkog and Lake Rudbøl (C) and the artificial Lake Hestholm Kog (D) and Lake Nørresø (E). In section D, fish can either enter Lake Hestholm Kog or remain in River Grønaa. Different letters indicate statistically significant differences ($p < .05$)

an average of 22.5 ± 30.6 days (mean \pm SD), excluding those fish that did not enter the reservoir.

The first fish entered the Wadden Sea on 19 December 2015, while the main migration into the Wadden Sea took place in March and April 2015, when 40 fish (72%) left the river. The average Julian day for entering the Wadden Sea did not differ between the two groups (Wilcoxon's rank-sum test, $p = .12$), as the group that initiated downstream migration soon after spawning arrived in the Wadden Sea on 23 March (median, IQR = 73), while the group spending time in the upper reaches of the river arrived in the Wadden Sea on 30 March (median, IQR = 30.75).

Comparing the average migration speed between the different sections of both river and lake revealed significant differences between sections (Friedman test, $p < .001$). Results from the post hoc

tests along with means and standard errors are presented in Figure 4. The highest migration speeds were found in the river sections between hydrophones 7 and 8 (section A) and hydrophones 12 and 13 (section B) and Magisterkogen (section C, spanning hydrophones 10 and 12), while migration speeds in the artificial lakes Hestholm Kog (section D between hydrophones 8 and 9) and Lake Nørresø (section E between hydrophones 9 and 10) were significantly reduced (Figures 1 and 5).

A significant relation between river temperature and cumulative number of fish in the Wadden Sea was found ($p < .001$), explaining 87% of the variation (Figure 5).

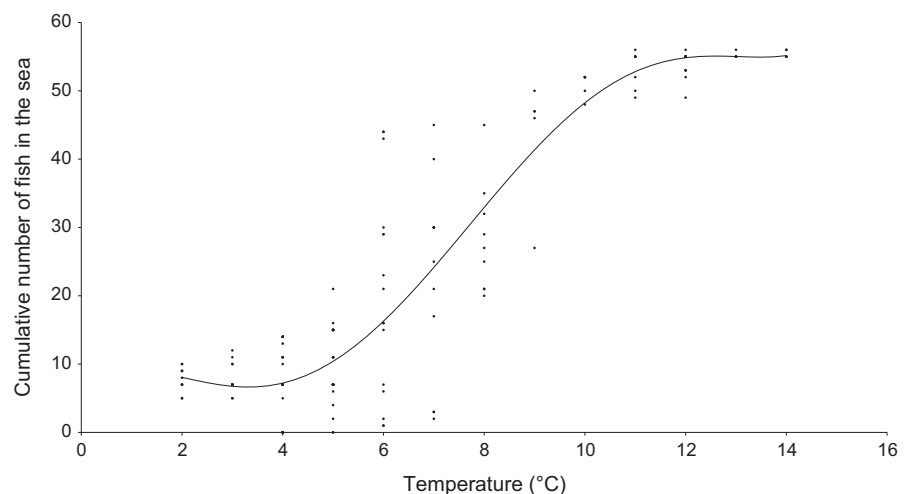
The diel activity pattern of North Sea houting during the migration from the putative spawning areas to hydrophone 13 is shown for each month in the rose diagram in Figure 6. Migrating North Sea houting were active all 24 hr of the diel period.

Results from the repeatability analysis are shown in Table 2. For individuals in both the estuary ($R = .16$) and the river ($R = .33$), repeatabilities were significantly higher than zero ($p < .01$ in both cases). Despite the large difference in repeatability between fish in the estuary and the river, the difference was not statistically significant, as revealed by the overlapping confidence intervals, following the procedure applied by Sprenger, Dingemans, Dochtermann, Theobald, and Walker (2012).

4 | DISCUSSION

In this study, a total of 20 fish disappeared during the study period. Although malfunctioning transmitters cannot be entirely ruled out, transmitter loss is most likely due to fish mortality (e.g., by avian removal from the system), returning an estimate of total mortality of 26%, corresponding to 1.4% mortality (or loss) per km following the procedure by Koed et al. (2006) and only considering those fish that were tagged near the spawning areas.* Of the total mortality, great cormorant predation accounted for at least 30%, represented by six transmitters (representing 8% of all fish tagged) located under a patch

FIGURE 5 North Sea houting enters the Wadden Sea when temperatures are increasing beyond 6°C in the spring. The figure shows a relationship between daily average river temperature and cumulative number of fish in the Wadden Sea by fitting polynomial regression models to the data. $p < .001$, $R^2 = 0.87$



*[Correction added on 20 November after first online publication: A sentence has been deleted in this section for clarity]

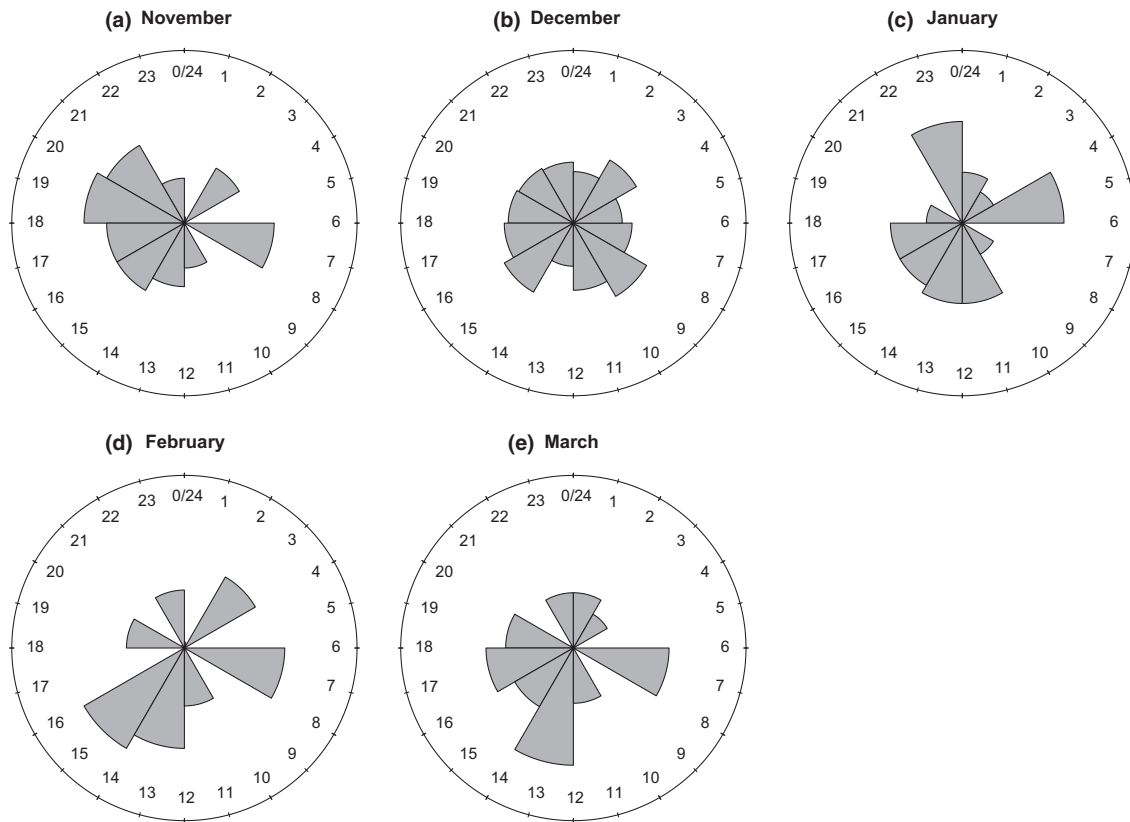


FIGURE 6 North Sea houting migrates throughout the 24-hr period. The figure shows the monthly timing of activity during the downstream migration from the spawning areas (hydrophones 5 or 6) to the estuary (hydrophone 13). The areas of each wedge correspond to the number of travels initiated in the corresponding time slot. (a) November, (b) December, (c) January, (d) February, (e) March. [Correction added on 20 November after first online publication: The sequence of the month in this figure was previously incorrect and has been corrected in this version].

of trees in Lake Nørresø used by resting cormorants. Electrofishing in the area, while confirming the presence of the transmitters, revealed only the presence of roach, gudgeon and a juvenile northern pike strengthening the conclusion that the transmitters were expelled by cormorants rather than representing live North Sea houting. The estimate of cormorant predation is highly conservative, given that only transmitters expelled by cormorants into the water under the path of trees were included. Manual tracking in the lakes and the river, including near the spawning areas, did not detect any additional transmitters, suggesting that the remaining lost transmitters were no longer submerged in water. Although some transmitters could have been washed ashore, this indicates that predation from birds or mammals such as otter (*Lutra lutra*) or American mink (*Neovison vison*) could be responsible (e.g., as seen in Aarestrup et al. (2005)). The lack of a significant size dependency of mortality when entering all lost fish as dead suggests that cormorants are not be responsible for the total loss, although mortality of larger fish from failed cormorant attacks cannot be ruled out. Mortality from angling is presumably limited as taking of the species is prohibited.

The great cormorant population in Europe, including Denmark, has increased substantially within recent decades, counting about 371,000 breeding pairs in 2012 (Bregnballe et al., 2014), corresponding to a total of about 2 million birds, applying a conversion factor of 2.8 (Steffens, 2011). Further, a change in foraging behaviour in great

cormorants has occurred in recent years. While previously mainly confined to coastal areas and estuaries, great cormorants are now colonising inland waters as well. Following the cold winter 2009/2010 in particular, cormorants increased foraging in Danish rivers at unprecedented levels (Jepsen, Skov, Pedersen, & Bregnballe, 2014).

The present findings of cormorant predation on the endangered North Sea houting suggest that cormorant may have a negative impact on the conservation status of the species. Several other studies have indicated that increased numbers of cormorants can cause damage to both freshwater and marine fish populations. For instance, Kennedy and Greek (1988) estimated that cormorant predation accounted for a loss of 51%–66% of wild salmon smolt in a river in Northern Ireland, and Steffens (2011) reported on losses of more than 80% in Austrian populations of grayling due to predation by cormorants. Likewise, cormorant predation may also cause poor recruitment in protected whitefish populations (*Coregonus lavaretus*) in the UK (Winfield, Crawshaw, & Durie, 2003). In a lentic ecosystem, Skov et al. (2014) found that cormorant predation caused altered age and size distributions in the fish fauna. Similarly, Sonnesen (2007) and Jepsen, Klenke, Sonnesen, and Bregnballe (2010) concluded that cormorants consumed a significant fraction of juvenile flounder (*Platichthys flesus*) in a Danish fjord and possibly caused a substantial decline in fishery landings. Despite several habitat restoration projects, the Danish populations of North Sea houting are in decline. Thus, in River Varde, the species is extirpated,

TABLE 2 The diel timing of North Sea houting activity is repeatable

Location	df1	df2	F-ratio	N_0	Repeatability	95% CI	p-Value
Estuary	47	273	2.239	6.69	0.16	0.049–0.263	<.001
River	44	994	12.29	23.09	0.33	0.223–0.434	<.001

The table shows the results from the repeatability analysis. *df1* and *df2* are respectively the numerator and denominator degree of freedom, N_0 is the corrected number of measures per fish following the procedure given by Lessells and Boag (1987) and 95% CI mark the lower and upper limits of the 95% confidence interval.

and in River Ribe, the population is declining with seemingly limited recruitment of new cohorts (Jepsen et al., 2012). In River Vidaa, the population also seems to be declining after years of stable population size. Whether the decline of North Sea houting populations is related to increased predation from great cormorants still awaits further research, but it is possible that increased predation on the adult cohorts could have a significant negative impact on small populations.

Koed et al. (2006) investigated mortalities of migrating Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolt in a river before and after an extensive restoration project, including the establishment of a lake within the river system. They found that in-river mortality doubled after the completion of the lake, mainly due to increased predation from cormorants using the newly established lake as resting area. In the River Vidaa system, an equivalent situation is found in the newly established Lake Nørresø, where numerous birds including cormorants rest. Our data did not, however, reveal any indication of predation of adult North Sea houting from great cormorants (or other birds) within the lake itself. Thus, among the six transmitters expelled in the lake by resting cormorants, three were last registered in the estuary, two in River Grønaa and one in River Sønderaa, both located upstream of Lake Nørresø. Thus, great cormorants seem to forage throughout the river system, but with highest intensity in the upper reaches of the river system more than 25 km from the outlet and in the estuarine area, while using Lake Nørresø as resting area.

Cormorant-induced mortality was found to be size-dependent, with fish smaller than 38 cm experiencing higher risk of predation. According to the model, predation risk of smaller fish (<32 cm) approached 100%, while predation risk of larger fish (>38 cm) approached 0%. The relationship between fish size and risk of cormorant-induced mortality found in this study corroborates previous studies, indicating that success rate for cormorants decreases with increasing prey size (Delmastro, Boano, Conte, & Fenoglio, 2015). The length distribution of fish sampled during this study, both tagged and nontagged, showed that 23% and 52% of the fish caught using electrofishing (November) and gill nets (January–March) respectively were under 38 cm in body length. Thus, a significant proportion of the North Sea houting population in River Vidaa would be vulnerable to cormorant predation.

Although smaller fish experience a higher risk of predation from cormorants, larger fish also risk increased mortality from cormorant attacks. During population surveys in December near the spawning sites in River Sønderaa and River Grønaa, 17% of the adult North Sea houting had lesions most likely inflicted during cormorant attacks. Similar observations were made during surveys near the sluice in spring 2015. Fish subjected to severe cormorant attacks are likely to suffer from elevated mortality due to the trauma or secondary bacterial or fungal

infections. It is well known that fish wounded from cormorant attacks are in significantly poorer nutritional condition than nonwounded fish (Adámek, Kortan, & Flajšhans, 2007; Kortan, Adamek, Flajshans, & Piackova, 2008). In a study on the endangered Cisalpine pike (*Esox cisalpinus*), Delmastro et al. (2015) found that 57% of the specimens (73% of the adults) carried wounds from cormorant attacks and conclude that cormorants could represent a serious threat to the conservation status of this endangered fish species.

In this study, we found North Sea houting to exhibit disparate migration strategies. Most notably, we were able to group the tagged individuals into two groups based on onset of migration and time spent in the river after spawning. These results suggest that the migration behaviour of North Sea houting in River Vidaa is more variable than previously thought. In a study based on stable isotopes from scale samples, Borcharding et al. (2008) examined migration strategies in a reintroduced population of North Sea houting in the Dutch Lake IJsselmeer. The authors uncovered disparate migration strategies by identifying individuals that never left freshwater, fish that migrated to sea at an early age and finally a group that migrated at a considerably older age. This apparent variability of the species should be taken into account in future conservation plans. Moreover, the fact that some individuals spend considerable time, that is months, in the river system before returning to the Wadden Sea imposes a need for conservation strategies to also consider the lotic habitat in relation to adult North Sea houting outside the spawning period.

Reservoirs and artificial lakes may delay fish migration (Stich, Kinnison, Kocik, Zydlewski, & Krkošek, 2015). In this study, we found significant differences in migration speeds between different sections of the river system. Thus, migration speeds through sections D and E representing River Grønaa/Lake Hestholm Kog and Lake Nørresø respectively were significantly reduced compared to the nearby river sections (sections A and B) as well as section C covering the lentic Magisterkogen and Lake Rudbøl. Both Lake Hestholm Kog and Lake Nørresø were established in 2009 to provide nursery habitat for juvenile North Sea houting. The low migration speed found in section D may indicate that migrating North Sea houting enter Lake Hestholm Kog, rather than travelling exclusively in the River Grønaa. Whether the descending North Sea houting reduce migration speed in the artificial lakes due to preference for the lentic habitat or due to difficulties navigating through the lakes is unknown. However, the high migration speeds, similar to river sections, observed in the lentic Magisterkogen and Lake Rudbøl may indicate that artificial lakes constrain navigation and downstream progress. Several studies on migrating brown trout and Atlantic salmon smolts have demonstrated significant reductions in migration speed through artificial lakes within river systems

(Aarestrup, Jepsen, Rasmussen, & Økland, 1999; Aarestrup & Koed, 2003; Olsson, Greenberg, & Eklöv, 2001) often associated with high mortalities (Koed et al., 2006). Further studies on the detailed movements within artificial lakes in relation to hydrological and bathymetric conditions are needed.

The reservoir near the river outlet appeared to be an important habitat for North Sea houting as 73% of the tagged fish entered the reservoir and spent on average 22.5 days in the area. Possibly, the residency in the estuarine area and the reservoir in particular were due to osmoregulatory difficulties coping with low temperatures and high salinity in the Wadden Sea (mean approx. 30 psu). This is supported by the significant relationship between temperature and number of fish having entered the Wadden Sea explaining 87% of the variation. Generally, euryhaline fish, such as anadromous salmonids, have difficulties maintaining homeostasis in sea water, when temperatures are low (Finstad et al., 1988; Handeland et al., 2014). Osmoregulatory capabilities in whitefish are believed inferior to many other euryhaline fish such as Atlantic salmon and anadromous brown trout. Thus, Madsen, Larsen, and Jensen (1996) found that even adult whitefish (*Coregonus lavaretus*) did not tolerate salinities of 32 psu. Adult North Sea houting are generally believed to exhibit greater hyper-osmotic tolerance than other whitefish, but no studies have investigated osmoregulatory capabilities in adult North Sea houting. Further studies are required to examine whether postspawning North Sea houting require access to a large estuarine area (e.g. the reservoir) that favours foraging in the spring while temperatures are increasing.

In the present study, adult North Sea houting were found to be actively migrating throughout day and night. This contrasts to, for example, anadromous Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*), where studies have found patterns of pronounced nocturnal postspawning downstream migration (Aldvén, Hedger, Økland, Rivinoja, & Höjesjö, 2015; Bendall, Moore, & Quayle, 2005; Scruton et al., 2007), but contrasting findings of mainly daily or diurnal postspawning migration in anadromous brown trout have also been reported (Aarestrup et al., 2015; Östergren & Rivinoja, 2008). In migrating Atlantic salmon smolts, the diel activity pattern is generally dependent on temperature, with higher nocturnal activity at lower temperatures (Svendsen, Eskesen, Aarestrup, Koed, & Jordan, 2007) and increased diurnal activity at higher temperatures (Ibbotson, Beaumont, Pinder, Welton, & Ladle, 2006; Thorpe, Metcalfe, & Fraser, 1994). Nocturnal migration is generally believed to reflect an adaptive behaviour to avoid predation from visual predators (Moore, Potter, Milner, & Bamber, 1995). Possibly, temperature dependency of neuromuscular escape responses ultimately drives the diel behavioural changes as a slow escape response favours nocturnal activity (Thorpe & Moore, 1996). Temperature in River Vidaa during the downstream migration averaged 5°C in the period December-March, when the majority of the tagged fish descended the river. Thus, the lack of a clear nocturnal migration pattern at these low temperatures does not seem consistent with temperature-dependent behaviour. The lack of any preference for nocturnal migration of postspawning North Sea houting could make them vulnerable to predation from visual predators, including the cormorant.

At the level of individual fish, significant repeatability in the diel patterns of migration was found, indicating consistent individual differences in migration behaviour. These findings imply diverse circadian behavioural phenotypes where individuals tend to be active during different time intervals over the 24-hr cycle. To our knowledge, this is the first study to investigate repeatability in anadromous fish diel migration behaviour. The consistency of individual behavioural patterns in fishes has been addressed for a number of behavioural characters (Bell et al., 2009) including mating preferences (Lehtonen & Lindström, 2008), aggression (Riddell & Swain, 1991), predator evasion (Fuiman & Cowan, 2003) and foraging (Martins, Schrama, & Verreth, 2005). Recently, Alós et al. (2017) found consistent between-individual differences in three circadian behaviours (awakening time, rest onset and rest duration) in pearly razorfish (*Xyriichthys novacula*), and Taylor and Cooke (2014) found significant repeatability of movement distances over seasons (spring and autumn) as well as over diel periods in bull trout (*Salvelinus confluentus*) using radio telemetry. A heritable component to animal personality traits has been established in a number of studies (van Oers, Jong, van Noordwijk, Kempenaers, & Drent, 2005; Petelle, Martin, & Blumstein, 2015) and could be under the influence of natural selection (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Smith & Blumstein, 2008; Wolf & Weissing, 2012). Assuming a heritable component to the observed repeatability of diel migration pattern, increased predation from visual predators, such as great cormorants, might change the behavioural pattern towards nocturnal migration over time. Although not statistically significant, repeatability in the estuary ($R = .16$) was lower than during the downstream migration ($R = .33$). This might indicate a change in behaviour upon reaching the lower parts of the river system. Generally, repeatability estimates from populations in nature are often higher than corresponding estimates under laboratory conditions (Bell et al., 2009). Uncontrolled environmental effects in the wild could inflate estimates of repeatability resulting in pseudo-repeatability (Killen et al., 2016). Such context dependency of trait repeatability is expected to be most pronounced during long-term studies. It is not known if the repeatability observed in the present study was influenced by context dependency.

In this study, we demonstrated that (i) the endangered North Sea houting is vulnerable to cormorant predation, (ii) the species exhibits disparate migration strategies, (iii) artificial lakes seem to delay the postspawning migrating fish, (iv) entry into the Wadden Sea is temperature-dependent and finally (v) individual fish exhibit repeatable circadian rhythms. Together, these results add to our knowledge base on the biology of North Sea houting supporting implementation of improved conservation plans. However, significant knowledge gaps are still challenging management of the species. For instance, although cormorant predation could negatively affect the North Sea houting population in River Vidaa, further studies are needed to provide insight into the general decline of the North Sea houting populations in Denmark. This includes additional studies of adult mortality during pre- and postspawning migration as well as during the marine phase in terms of, for example, mortality, habitat preferences and detailed migration patterns. Moreover, further research directed at recruitment and the early life stages of North Sea houting is needed and should be fed into management plans and targeted conservation measures.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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