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Investigating fish migration, mortality and physiology to improve conservation planning of anadromous salmonids: a case study on the endangered North Sea houting (*Coregonus oxyrinchus*)

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Abstract: Understanding migratory behavior, mortality and physiology is essential for conservation of many species, in particular anadromous fish. In this study, freshwater and marine migrations of the endangered salmonid North Sea houting (*Coregonus oxyrinchus*, Linnaeus, 1758) were investigated using telemetry. Furthermore, physiological samples were collected from North Sea houting and from resident and anadromous populations of the closely related European whitefish (*Coregonus lavaretus,* Linnaeus 1758) to compare hypo-osmotic tolerances. On average, North Sea houting spent 193 days at sea where the mortality was 36%. Most fish returned from sea in the autumn, and river entry correlated inversely with river temperature and positively with discharge. Fish spent an average of 49 days in the estuarine area. Artificial lakes negatively affected migration speeds. Migration speeds did not differ consistently between individuals (i.e. not a repeatable trait), but correlated positively with water temperature. Fish arrived at spawning areas in November. In the post-spawning state, Na^+/K^+-ATPase activities were elevated in North Sea houting and anadromous whitefish compared to resident whitefish, while osmolality was elevated only in North Sea houting. Our study provides important information for conservation planning related to the Habitat Directive of the European Union that lists the North Sea houting as critically endangered.

Introduction

Knowledge of habitat use and movements between habitats is essential for conservation of threatened species (Simpson and Mapleston 2002; Ebner and Thiem 2009), because diversity in habitat use and movements enable animals to respond to changing environmental conditions and maximize growth, reproductive success and survival (Kahler et al. 2001; Eggeman et al. 2016; Rolandsen et al. 2017). For example, many species increase fitness by performing seasonal migrations between disparate habitats. Anadromous fish species reproduce in freshwater habitats, while a major part of the somatic growth takes place in marine environments (Thorstad et al. 2016). This strategy can be advantageous, as migrants often benefit from faster growth rates and exhibit elevated reproductive output (Bohlin et al. 2001). However, migrants may also experience elevated levels of predation risk (Gowans et al. 2003; Wright et al. 2007), disease exposure (Halttunen et al. 2018), osmoregulatory requirements (Jensen et al. 2015b) and energetic costs (Forseth et al. 1999; Boel et al. 2014), as well as difficult access to the spawning areas (Aarestrup and Jepsen 1998; Svendsen et al. 2004; Thorstad et al. 2008).

The North Sea houting (*Coregonus oxyrinchus* Linnaeus, 1758) is an anadromous and iteroparous salmonid fish endemic to the Wadden Sea (Svendsen et al. 2018). The River Vidaa in Denmark supports the only indigenous population of North Sea houting left in the world. Previous reports have indicated that adult North Sea houting migrate into rivers to reproduce during the autumn and winter months. Larvae hatch in the early spring and presumably rely on lentic nursery areas within the river system for foraging (Jensen et al. 2015b). Juvenile North Sea houting stay in the river until they reach 3-5 cm in body length. At this point, they develop the ability to hypo-osmoregulate and presumably migrate into the Wadden Sea (Jensen et al. 2015b). After a period of 2-4 years at sea, the adults return to the natal river to spawn.

Historically, North Sea houting was widespread throughout the Wadden Sea. A dramatic decline of the species began in the early twentieth century, leading to extirpations of the species in both the Netherlands and Germany. These extirpations are attributed to a combination of pollution, overfishing, habitat loss as well as fragmentation caused by the establishment of migratory barriers in the rivers (Borcherding et al. 2010). Since the 1970s, numerous projects have been carried out to conserve the North Sea houting, but with

limited success (Stoltze and Pihl 1998; Pihl and Laursen 2002; Jepsen et al. 2012; Poulsen et al. 2012; Svendsen et al. 2018).

In River Vidaa, projects eliminated migratory barriers (e.g. low head weirs) and created two artificial lakes to provide lentic foraging areas for the early life stages of North Sea houting. While the lakes may provide foraging areas for the young North Sea houting, lakes could also hamper the migration performed by later life stages of the species. Several studies have revealed migratory delays and elevated mortality when smolts (migrating juvenile salmonid) travel through lakes and reservoirs (Jepsen et al. 1998; Olsson et al. 2001; Aarestrup and Koed 2003; Stich et al. 2015). In contrast to the smolt migration, effects of artificial lakes on the migration performed by adult salmonids are largely unknown. Although artificial lakes may not elevate the mortality of the adult fish, as much as juveniles, partly because of their larger body size, artificial lakes could also delay migrating fish, because navigational cues present in the river (e.g. water current; Braithwaite and Girvan 2003)) may be absent in the lake.

In many migrating animals, it is increasingly recognized that individual decisions may have important implications (Chapman et al. 2011; Svendsen et al. 2011; Hewson et al. 2016; Crozier et al. 2017; Rolandsen et al. 2017). For example, in migrating fish, return probability and mortality rate may vary with individual behavioural traits (Hulthén et al. 2017; Armstrong et al. 2018), making measures of individual behaviours an important topic in conservation biology (Killen et al. 2016; Hirsch et al. 2017; Merrick and Koprowski 2017). If individual behaviours are repeatable (or consistent) across time and space, the behaviours may be targeted by selection and could have fitness implications. A first step towards understanding the consequences of individual variation in behaviour is therefore to assess whether traits are repeatable in individual fish i.e. whether behavioural traits differ consistently between individuals. On this basis, studies are increasingly examining the repeatability of various migratory behaviours (Vardanis et al. 2016; Hasselquist et al. 2017; Villegas-Ríos et al. 2017). Although a previous study reported repeatable circadian rhythms in migrating North Sea houting (Jensen et al. 2018b), the repeatability of other migratory behaviours in the species is unknown.

The taxonomic status of North Sea houting remains controversial. Based on morphological characters, Freyhof and Schöter (2005) declared North Sea houting extinct. According to Freyhof and Schöter (2005),

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the true North Sea houting was confined to the Rhine area in Germany and thus, the eradication of this population meant extinction of the species. The authors suggested that the remaining population in River Vidaa belongs to *Coregonus maraena* (Bloch, 1779) and not North Sea houting. This assessment was based on different numbers of gill rakers, assumed to represent genetic differences unambiguously. However, several genetic analyses have revealed that such morphological traits are homoplastic and not necessarily useful for depicting genetic inheritance (Østbye et al. 2005; 2006; Etheridge et al. 2012; Jacobsen et al. 2012).

Physiological traits are often connected to migratory behaviours, especially when the migration involves exposure to disparate environments. Anadromous fishes migrating from freshwater into saltwater are challenged by differences in salinity. During the transition between the two environments, salmonids change from hyper- to hypo-osmoregulation, often with implications for levels of gill Na^+/K^+-ATPase and regulation of blood osmolality. Some physiological changes start prior to the environmental transition, as a preparation for the new environment (Boel et al. 2014). Therefore, future seaward migration of individual brown trout *Salmo trutta* (Linnaeus, 1758) can be predicted based on levels of gill Na^+/K^+-ATPase several weeks prior to the migration (Nielsen et al. 2004). Seasonal changes, and differences between residents and migrants, in terms blood osmolality and plasma $[Ca^{++}]$, $[K^+]$ and $[Na^+]$ are usually weaker than gill Na^+/K^+-ATPase (McCormick et al. 1989; McCormick and Björnsson 1994; Young et al. 1995; Reis-Henriques et al. 1996), suggesting that blood osmolality is a relatively weak predictor of migration. In the post-spawning state, North Sea houting are believed to migrate into full strength saltwater in the Wadden Sea ($\geq$ 30‰), whereas populations of European whitefish (*Coregonus lavaretus* Linnaeus, 1758), either remain in freshwater or migrate into brackish waters ($\leq$ 15‰). While these behavioural differences might rely on physiological adaptations, it is unknown if the physiology of North Sea houting differs from populations of European whitefish in the post-spawning state.

The objective of this study was to inform conservation practitioners by investigating factors that influence the migration of the North Sea houting. To date, conservation efforts for the North Sea houting, including removal of migration barriers and habitat restoration, have been insufficient (Jensen et al. 2015*b*; Svendsen et al. 2018). This suggests that a better understanding of the factors important for population

development, such as migration and mortality, is much needed before successful conservation measures can be implemented. Specifically, we aimed to 1) estimate the marine mortality, 2) map the upstream spawning migration and the influence of environmental factors, and 3) compare traits related to osmoregulation in North Sea houting and European whitefish in the post-spawning state. To this end, we tagged fish with acoustic transmitters and monitored river entry and upstream migration using receivers positioned between the Wadden Sea and putative spawning areas in the River Vidaa. In addition, physiological gill and blood samples were collected from North Sea houting and European whitefish in the post-spawning state. Specifically, we tested four hypotheses: 1) river entry and migration speed are influenced by temperature and discharge, 2) artificial lakes situated in the River Vidaa affect migration speeds, 3) upstream migration speed is a repeatable trait in North Sea houting, and 4) North Sea houting exhibit elevated gill Na^+/K^+ ATPase activity compared to European whitefish in the post spawning state. In contrast, blood osmolality levels were not expected to differ between North Sea houting and European whitefish.

MATERIALS AND METHODS

Study area

The River Vidaa is a lowland river located in southwestern Denmark (54° 57.761' N; 8° 39.686' E) (Fig. 1). The catchment area is 1330 km² and the mean annual discharge is 13,400 l s^{-1} (Ovesen et al. 2000). At the river outlet, the water flow is regulated by a sluice, protecting the surrounding area from flooding. The spawning population of North Sea houting is unknown, but estimated to be about 3,500 in River Vidaa (Svendsen et al. 2018). In 2009, two artificial lakes, Lake Nørresø and Lake Hestholm Kog, were established on the river (Fig. 1) to provide nursery habitats for juvenile North Sea houting (Jensen et al. 2015*b*; 2018*b*).

Deployment of receivers

A total of 16 acoustic receivers (model VR2W; VEMCO, Bedford, Canada) were deployed in a fixed array throughout River Vidaa (Fig. 1). Coverage included the river mouth, the estuarine area, river sections with and without lakes, and ended near the putative spawning areas situated 25 km upstream from the Wadden Sea. Throughout the study period (November 11th 2014 - February 21st 2016) receivers were checked for

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debris and data were downloaded at weekly intervals. Receiver data were used to reveal river entry from the Wadden Sea and the subsequent riverine migration towards the spawning areas (Fig. 1). Previous studies have indicated that receivers deployed in lowland rivers similar to River Vidaa provide 100% detection probability of tagged fish migrating past receiver sites (Aarestrup et al. 2014; 2015). Similarly, during fish upstream migration in the present study, detection on one receiver was always associated with detections on the receiver further downstream, indicating a fish detection probability of 100%.

Capture and tagging

In total, 78 adult North Sea houting (total body length: 42.7 ± 0.7 cm (mean $\pm$ SE)) were captured in River Vidaa between 18th November 2014 and 16th March 2015 (Jensen et al. 2018*b*). Fish were captured using electrofishing or gillnetting (Jensen et al. 2018b). Each fish was anesthetized using benzocaine (VWR Chemicals; Radnor, Pennsylvania, USA; 2.55 mg l^{-1}) (Aarestrup et al. 2015; Baktoft et al. 2016), and surgically tagged with an individually coded acoustic transmitter (model V9-2L; VEMCO, Bedford, Canada). The transmitters (29 mm long; 4.7 g in air) were programmed to emit a signal every 30 to 60 s, providing a battery life of 378 days. Tagging followed standard procedures (Svendsen et al. 2011; Kristensen et al. 2017; Piper et al. 2017). Total body length (to nearest 0.1 cm) was measured while each fish was anesthetized. Fish were released near the capture location following operative recovery (Jensen et al. 2018*b*). The body sizes of the tagged fish ensured a low ratio of transmitter mass: fish mass ($\leq 2\%$) and within the range where effects on the behaviour of the fish often are negligible (Brown et al. 2010). No controls were used to evaluate the effect of tagging on fish health, behaviour and survival. Previous studies have indicated, however, that long term effects of surgically implanted transmitters are often negligible (Jepsen and Aarestrup 1999; Koed and Thorstad 2001; Wilson et al. 2017). The effects of implanted transmitters in salmonid fish are generally believed to be limited (Moore et al. 1995; Connors et al. 2002). All handling and tagging procedures were in compliance with the guidelines described in permission 2012-DY-2934-00007 from the Animal Experimentation Inspectorate of the Danish Ministry of Justice as well as permission NST-41501-00093 from the Danish Nature Agency.

Water temperature and river discharge

River water temperature (to nearest 0.1 °C) was measured at 30 min. intervals throughout the study period using temperature loggers (HOBO 64K Pendant logger; Onset Computer, Bourne, USA) attached to receivers 16, 10 and 5 (Fig. 1). River discharge (to nearest 10 l) measured at hourly intervals throughout study period at the river mouth (Fig. 1) was provided by Tønder Municipality.

Sampling of gill Na$^+$/K$^+$-ATPase and blood osmolality

To compare traits related to hypo-osmoregulation between North Sea houting and anadromous and resident populations of European whitefish, fish were sampled for measurements of gill Na$^+$/K$^+$-ATPase activity and blood osmolality (Saoud et al. 2007). In the spring 2016, 51 North Sea houting and 30 anadromous and 18 resident whitefish were caught using gill nets similar to previous studies (Jensen et al. 2018*b*). North Sea houting were captured in the fresh water reservoir near the river mouth of River Vidaa (Fig. 1), while anadromous and resident whitefish were captured in Ringkøbing Fjord (55° 59.645' N; 8° 13.958' E) and Lake Ring (55° 57.895' N; 9° 35.807' E) in western Denmark, respectively (Skall et al. 2004; Jacobsen et al. 2012). Fish were held in 60 l containers with aerated local water and transferred to a container with a solution of benzocaine (VWR Chemicals; Radnor, Pennsylvania, USA; 2.55 mg l^{-1}) prior to sampling. Data on total length (to nearest 0.1 cm) and body mass (to nearest 1 g) were collected. A volume of 0.1 ml of blood was collected from the caudal vein using a heparinized syringe and needle following standard procedures (Boel et al. 2014). Three to five gill filament tips, each 2-3 mm long, were removed with a pair of fine suture scissors and stored frozen in SEI-buffer (250 mM sucrose, 10 mM EDTA, 50 mM imidazole, pH 7.3) until analysis of Na$^+$/K$^+$-ATPase (McCormick 1993; Aarestrup et al. 2000). All samples were immediately transferred to a liquid nitrogen container (Model BS2004, CryoDiffusion, Verdun, France) and stored at minus 80 °C until analysed (Boel et al. 2014). After operative recovery, fish were released (Jensen et al. 2018*b*). All fish survived the procedure. No controls were used to evaluate the effect of sampling. This sampling method is, however, reported to have no effects on gill Na$^+$/K$^+$-ATPase activity, growth rate or survival of fish (Rodgers et al. 1987; Mccormick 1993). This suggests that the procedures had negligible effects on the sampled fish. Note that no fish sampled for gill Na$^+$/K$^+$-ATPase activity or blood osmolality

were used for the telemetry study. Gill Na^+/K^+-ATPase activity was analyzed by the standard method of

Mccormick (1993) in gill homogenates, using a microtitre plate reader (Spectramax Molecular Devices,

Sunnydale, CA, USA). Protein content in tissue homogenates was measured at 280 nm using a NanoDrop

Spectrophotometer (ND-1000, NanoDrop Technologies, Inc. Wilmington, USA) and calculated by using a

bovine serum albumine standard curve. Blood samples were diluted (1:5) in deionized water and total

osmolality was determined using a freezing point depression osmometer (Osmomat 030, Gonotec, Berlin,

Germany) (Piironen et al. 2013).

Data analyses

The seaward migration of the tagged North Sea houting in the spring 2015 was described by a previous study

(Jensen et al. 2018*b*). The present study examined time and mortality at sea and the subsequent upstream

migration towards the spawning areas (Fig. 1).

Time spent at sea was estimated as the temporal difference between the last detection on the most

downstream receiver (receiver 16; Fig. 1) during the downstream post-spawning migration in the spring of

2015 and the first subsequent detection on receiver 16 later in 2015. Marine mortality was estimated as the

proportion of individuals leaving the river during seaward migration (spring 2015) and not returning to the

river before the spawning season (i.e. before January 2016). To examine the influence of body size on

marine mortality, a binomial logistic regression model was fitted using the data describing mortality (1) or no

mortality (0) for the individual fish as the dependent factor and the associated body size as the independent

factor (Koed et al. 2006). Following previous salmonid studies (Aarestrup et al. 2014; 2015), the approach

does not account for the possibility of fish skipping a spawning season and returning to the river after two

summers in the Wadden Sea. The extent of skipped spawning in mature salmonids is largely unknown,

however, a previous study on North Sea houting suggested that the percentage of the mature population that

skip spawning is less than 5% (Christensen and Hvidt 1990).

The first detection of returning individual fish at the river mouth (i.e. receiver 16; fig. 1) was also used

to examine environmental variables affecting river entry from the Wadden Sea. Fish that did not return to the

river were excluded from these analyses. On a daily basis, receiver data were separated into river entry and

no river entry for the individual North Sea houting (Svendsen et al. 2004). Using these data, binomial logistic regressions with river entry data as the dependent factor and river discharge or temperature as independent factors were conducted (Svendsen et al. 2004).

For the individual fish, time spent between receiver 16 and receiver 13 was used to estimate time spent in the estuarine area (Fig. 1). Initiation of upstream migration was defined as the first detection on receiver 13, whereas the first detection on receiver 1, 2, 5 or 6 was used to estimate arrival time in the spawning areas (Fig. 1). Receivers 1, 2, 5 or 6 were positioned in the vicinity of the putative spawning areas (Fig. 1).

The duration of the upstream migration was estimated as the time spent between receiver 13 and the most upstream receivers (receiver 1, 2, 5 or 6; depending on migration route). The instantaneous loss per kilometer was calculated as $\ln(F_{mig} \times F_{up}^{-1}) \, D^{-1}$, where F_{mig} is the number of upstream migrating fish, F_{up} is the number of fish that reached one of the most upstream receivers (receivers 1, 2, 5 or 6) and D is the distance (river km) between receiver 13 and the most upstream receivers. Importantly, this analysis was only possible because the detection probability of fish passing receivers in the River Vidaa approached 100%, consistent with previous studies (Aarestrup et al. 2014; 2015).

To test for correlations between 1) time at sea and timing of river entry (receiver 16), as well as 2) time at sea and timing of arrival at the putative spawning sites (receivers 1, 2, 5 or 6), least square linear regressions were employed. For this purpose, days spent at sea were regressed against river entry date and spawning site arrival date, respectively.

To estimate upstream migration speeds, the river was diverted into five sections: A, B, C, D and E (Jensen et al. 2018*b*) (Fig. 1). For the individual fish, the migration speed through each section was estimated using receiver locations (Fig. 1) and the fish detection data. Specifically, migration speeds were calculated using the distances (m) between sequential receivers and the time (h) spent covering the distance. Following previous studies (Jensen et al. 2018*b*), these data were used to examine whether the two artificial lakes (Lake Nørresø and Lake Hestholm Kog; Fig. 1) affected upstream migration speeds. Migration speeds associated with the five river sections (A, B, C, D and E) were compared using generalized mixed effect models (GLMM) following Zuur et al. (2009). A model was fitted with migration speed as a function of length, fish ID and river section. To account for within-individual dependency, individual fish ID was included as a

random factor (Moe et al. 2016), while river sections were included as a fixed factor. Fish body length was included in the model to correct for any correlation between individual body length and migration speed. (Baktoft et al. 2016). The significance of each section on migration speed was tested using the Likelihood ratio test based on maximum likelihood estimation (Aarestrup et al. 2015). The model was fitted by assuming Gamma distribution of data. Using residual plots as model diagnostics, no sign of violation of model assumptions was found.

To further assess the effects of artificial lakes, least square linear regression was used to correlate the time spent in the artificial lakes with arrival date in the spawning areas.

Least square linear regression was employed to examine effects of river temperature on migration speeds. The analyses were restricted to river sections that included a temperature logger. Specifically, the influence of temperature on migration speeds was examined between six receiver pairs: 14-13, 12-10, 10-9, 8-7, 7-6 and 7-5 (Fig. 1). The average water temperature logged while the individual fish passed between the receiver pairs was regressed against the associated migration speed.

Similarly, individual upstream migration speeds between 12 receivers, (receiver 13-1; Fig. 1) were used to examine whether migration speed is a repeatable trait in the North Sea houting. To this end, the intra-class correlation coefficient (ICC) was quantified using a linear mixed model and the restricted maximum likelihood procedure (Nakagawa and Schielzeth 2010). Specifically, measures of repeatability reveal the proportion of phenotypic variation that can be attributed to between-subject variation (Nakagawa and Schielzeth 2010). The model included migration speed as a function of fish body length to correct for any correlation between migration speed and body length among individuals (Baktoft et al. 2016).

Individual estimates of gill Na^+/K^+ ATPase activity and blood osmolality were compared between the North Sea houting and anadromous and resident populations of European whitefish. To adjust for variation in body mass (g), data were regressed against individual body mass to estimate slope values. Slope values were subsequently compared between populations using analysis of covariance (ANCOVA) to test for differences in Na^+/K^+-ATPase activity and osmolality between the North Sea houting and anadromous and resident populations of European whitefish (Finley et al. 2016). Subsequently, post-hoc analyses based on the Holm-Šídák test were employed to identify differences.

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The statistical software R (R Development Core team 2016) was used for statistical analyses. Specifically, the analyses were based on the R-packages lme4 (Bates et al. 2014) and dunn.test (Dinno 2017). Results were considered significant at $P < 0.05$. All values are reported as means ± s.e.m. unless otherwise noted.

RESULTS

A total of 56 out of 78 tagged houting (72%) entered the Wadden Sea after the spawning season in the winter of 2014-2015. Among the 56 fish, 36 individuals subsequently returned to the river, indicating a marine mortality approaching 36%. The marine mortality did not appear to vary with fish body length (logistic regression, $P = 0.28$). On average, North Sea houting spent 193 ± 34 days (range 72-291 days) in the Wadden Sea. The fish arrived at the river mouth between 2nd July and 5th November (median date: 14th October), a period spanning 126 days. Most North Sea houting entered the river in October. Time spent at sea (i.e. days) was positively correlated with the river entry date ($R^2 = 0.7$, $P < 0.001$), indicating that a long period at sea was associated with late river entry. A previous study indicated that some individual post-spawning North Sea houting enter the Wadden Sea during the winter, whereas other North Sea houting enter the Wadden Sea in the spring (four months later; Jensen et al. 2018b). The present correlational analysis indicates that a late return to the river from the Wadden Sea is not just compensating for a late sea entry (e.g. in the spring), but instead allows the fish to spend a longer period in the marine environment.

Analyses indicated that the probability of river entry correlated negatively with water temperature (logistic regression; $P = 0.009$). The highest probability of river entry occurred between 8 and 9 ° C (Fig. 2a). In contrast, the probability of river entry correlated positively with river discharge, indicating a higher probability of river entry at elevated river discharges (logistic regression; $P = 0.042$) (Fig. 2b; Fig. 3).

Among the 36 fish that entered the river from the Wadden Sea, three individuals (8%) remained in the estuarine area (receivers 16-13; Fig. 1), whereas 33 individuals (92%) migrated further upstream (i.e. left receiver 13 in the upstream direction).

Migrating individuals spent 49 ± 8.5 days (range 0.04 - 250 days) in the estuarine area (receivers 16-13; Fig. 1) before the upstream migration, including one individual that only briefly left the river in March 2015 and spent the remaining time in the estuarine area instead of the Wadden Sea.

Upstream migration from the estuarine area (i.e. upstream of receiver 13; Fig. 1) started between 17th July and 23rd November (median date 22nd October). The majority of the fish (85%) started the upstream migration in October.

During the upstream spawning migration, eight fish (24%) were lost due to unknown circumstances, while 25 (76%) of the 33 fish reached the most upstream receivers (i.e. receivers 1, 2, 5 or 6). This loss rate corresponds to a potential mortality of 1.1% mortality per km. Three fish were lost in section C, corresponding to Lake Rudbøl and the lentic Magisterkogen, two fish were lost in section E, corresponding to the artificial Lake Nørresø, one fish was lost in section D, corresponding to the artificial Lake Hestholm Kog, one fish was lost in section A, corresponding to River Grønaa and finally one fish was lost after passing receiver no. 4 located upstream River Vidaa (Fig. 1).

The duration of the upstream migration (i.e. time between receiver 13 and receivers 1, 2, 5 or 6 depending on migration route) was 41 ± 6 days (range 5-141 days). Fish arrived at the putative spawning areas between 31st October and 23rd January (median date 26th November), but primarily during late November and early December.

Arrival date in spawning areas was not correlated with the time spent at sea (least square linear regression, $R^2 < 0.0001$, $P > 0.96$), indicating that a long period spent at sea did not result in late arrival in the spawning areas. Thus, there was no evidence of a trade-off between a long time spent at sea and early arrival in the spawning areas, presumably because early river entry was associated with a longer period of time spent in the estuarine area or slow upstream migration.

Analyses indicated that migration speeds differed between river sections (GLMM, L-ratio = 47.4, df = 4, $P < 0.001$) (Fig. 4; Fig. 1). Fastest migration speeds were observed in sections A, B and C, whereas significantly slower migration speeds were recorded in the sections with artificial lakes, i.e. sections D and E (Fig. 4). The slowest migration speeds were measured in section E (GLMM, Value = 28.5, SE = 7.63 df = 107, t-value = 3.7, $P < 0.001$), corresponding to passage of the artificial Lake Nørresø followed by section D

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(GLMM, Value = 5.2, SE = 1.8, df = 107, t-value = 2.8, $P < 0.01$), corresponding to passage of the artificial Lake Hestholm Kog (Fig. 1; Fig. 4).

Fish spent 13 ± 2 days (range 0.3 - 36 days) and 9 ± 3 (range 0.1-42 days) traversing Lake Nørresø and Lake Hestholm Kog, respectively. Time spent in the artificial lakes did not correlate with arrival date in the spawning areas (least square linear regression: $R^2 < 0.057$, $P > 0.25$), suggesting that a longer period of time spent in the artificial lakes was not associated with a late arrival time in the spawning areas.

Migration speeds correlated positively with water temperature, although the amount of variation explained was low (least square linear regression, $R^2 = 0.052$, $P < 0.01$).

Results from the repeatability analysis revealed no signs of subject based variance, according to the calculation of repeatability and a subsequent ANOVA analysis (linear mixed model, ICC = 0.004; ANOVA, $P = 1$). This indicated that migrating individuals did not travel consistently at a certain limited speed range during the upstream migration, but rather exhibited intra-individual variation in migration speeds through the different river sections.

Fish body mass (g) did not correlate significantly with gill Na^+/K^+ ATPase activity (ANCOVA, $P = 0.11$) or osmolality (ANCOVA, $P = 0.44$). Fish body mass was therefore left out of the subsequent analyses. Mean gill Na^+/K^+ ATPase activity differed significantly between North Sea houting caught in River Vidaa and resident and anadromous European whitefish caught in Lake Ring and Ringkøbing Fjord, respectively (ANOVA, $P < 0.007$) (Fig 5a). Significantly lower Na^+/K^+ ATPase activity levels were found in the samples from the resident population of European whitefish compared to North Sea houting (Holm-Šídák, $P = 0.009$) and anadromous European whitefish (Holm-Šídák, $P < 0.006$). No significant difference was found between the anadromous European whitefish and North Sea houting ($P > 0.6$) (Fig 5a). Mean osmolality differed significantly between North Sea houting and both resident and anadromous European whitefish (ANOVA, $P < 0.001$). Specifically, the osmolality in the North Sea houting was significantly higher than both the anadromous (Holm-Šídák, $P < 0.001$) and the resident (Holm-Šídák, $P < 0.008$) European whitefish (Fig. 5b).

DISCUSSION

In this study, we describe the marine mortality of the North Sea houting in the Wadden Sea and the subsequent upstream migration towards the spawning areas in the River Vidaa; the last known location in the world where the North Sea houting is spawning successfully. The marine mortality was 36% and exceeded previous mortality estimates (Jepsen et al. 2012). River entry from the Wadden Sea varied with river temperature and discharge, whereas the upstream migration speed correlated positively with river temperature. Analyzing individuals, there was no evidence of repeatability in upstream migration speed. Upstream migration was associated with a loss of 24% of the North Sea houting, and migration speeds declined during passage of artificial lakes. In the post-spawning state, the physiology of North Sea houting differed from populations of European whitefish.

The North Sea houting is living in the Wadden Sea, an area recognized as a World Heritage Site, and the fish is protected by the Bern Convention and the EU Habitat Directive. Despite these measures, the River Vidaa population remains critically low with only 3,500 adult fish left (Svendsen et al. 2018). Numerous conservation and restoration projects have failed to recover populations in rivers where the North Sea houting thrived historically (Svendsen et al. 2018). Investigating mechanisms leading to mortality and loss prior to spawning and relationships with environmental factors is therefore important to improve further conservation planning.

We found that 36% of the North Sea houting did not return to the River Vidaa after entering the Wadden Sea. Although straying (Keefer and Caudill 2014; Thorstad et al. 2016) and non-consecutive repeat spawning behavior (Rideout et al. 2005; Jonsson and Jonsson 2009) cannot be ruled out, we assume that the marine loss corresponded largely to mortality. In a previous long term study, the total annual mortality of adult North Sea houting was estimated to be 20% (Jepsen et al. 2012). While the data provided by Jepsen et al. (2012) may be influenced by catch efficacy, our data could be influenced by irregular spawning behavior (e.g. straying). Studies on other salmonids (brown trout; *S. trutta*) have provided mortality estimates that vary substantially between years and locations (Jonsson and Jonsson 2009; Aldvén et al. 2015). Marine mortality may range between 15% (Thorstad et al. 2016) and 70% (Berg and Jonsson 1990; Aarestrup et al. 2015). Thus, the present marine mortality estimate (36%) from one year and one location should be interpreted with caution.

Marine mortality of salmonids is influenced by several factors (Sobocinski et al. 2018), including body size (Berg and Jonsson 1990; Jonsson and Jonsson 2009), timing of seaward migration (Jonsson and Jonsson 2009; 2014), feeding efficiency and growth (Kennedy et al. 2008; Henderson et al. 2018; Jensen et al. 2018*a*), environmental conditions (Gosselin et al. 2018) pathogens (Gargan et al. 2012; Gjelland et al. 2014; Skaala et al. 2014; Halttunen et al. 2018) as well as predation by birds (Dieperink et al. 2002; Wiese et al. 2008) and seals. Harbour seals (*Phoca vitulina,* Linnaeus 1758) are abundant in the Wadden Sea (Reijnders et al. 2010) and are growing in numbers in the area (Jensen et al. 2015*a*; Aarts et al. 2019). Seal density often correlate negatively with salmonid productivity (Nelson et al. 2018) and seals may threaten salmonid species (Wright et al. 2007; Thomas et al. 2017). The marine migration of the North Sea houting remains to be mapped, and future studies should determine the specific factors that drive the mortality after the fish enter the Wadden Sea. Identifying mechanisms leading to marine mortality could be used to reduce the overall annual mortality of North Sea houting.

The total annual mortality of adult North Sea houting may also be influenced by the mortality in freshwater, especially during spawning (autumn) and post-spawning (spring) migrations. In the present study, eight adults (24%) were lost during the upstream migration, suggesting a mortality of 1.1% per km in the autumn. A previous study on the post-spawning individuals in freshwater suggested a slightly higher mortality of 1.4% per km in the spring (Jensen et al. 2018*b*). At least 30% of the loss (i.e. six adults) in the post-spawning state (i.e. spring) was inflicted by foraging cormorants (*Phalacrocorax carbo*, Linnaeus, 1758) (Jensen et al. 2018*b*). In the present autumn study, we were unable to determine the factors that induced the loss of the adults during the upstream migration. However, a marine mortality of 36%, combined with spring and autumn mortalities approaching 26% and 24%, respectively, in freshwater indicate that the annual mortality may be significantly higher than previously thought; warranting further studies that determine the factors that cause the mortality in freshwater and marine environments. The present mortality estimates are only valid for adult fish. The mortality of the juvenile fish is likely much higher.

On average, adult North Sea houting spent 193 days (range 72 - 291 days) in the Wadden Sea before returning to River Vidaa. In anadromous salmonids, it is well known that some individuals may return to the natal river many months prior to spawning (Quinn et al. 2016). An average of 193 days at sea is a longer

period of time than observed in a range of studies on other adult anadromous salmonids. In brown trout for example, the period spent at sea rarely approaches 193 days and typically ranges between 54 – 88 days (Berg and Berg 1989), 89-145 days (Bendall et al. 2005) and 78-191 days (Aarestrup et al. 2015). The period spent at sea is likely governed by latitude (Jonsson et al. 2007; Aarestrup et al. 2015), temperature (Berg and Berg 1989), difficult access to the river (Berg and Jonsson 1990), riverine competition for spawning areas and trade-offs involving growth and mortality rates in the marine and freshwater environments (Quinn et al. 2016). We suggest that the environmental conditions in the River Vidaa and the Wadden Sea favor a trade-off between growth and mortality where fish are spending a prolonged period of time at sea to recover energy reserves (Olsen et al. 2006) and maximize somatic growth (Brönmark et al. 2008) while facing relatively limited mortality risk.

North Sea houting river entry varied with environmental factors. Specifically, river entry peaked at increasing river discharges and at temperatures < 10° C. Salmonid upstream migration at increasing river discharges is commonly observed (Svendsen et al. 2004; Mitchell and Cunjak 2007; Bendall et al. 2012), although more complex patterns have also been reported (Jonsson et al. 2007). River entry at temperatures < 10° C is relatively cold compared to a number of previous studies (12 - 16° C (Borcherding et al. 2014); 10 - 15° C Jonsson et al. (2007)), but similar to brown trout > 30 cm in the River Imsa in southern Norway (Jonsson and Jonsson 2002). Our study suggests that North Sea houting river entry could be sensitive to factors that change river discharge or temperature. This could be important because changed timing of river entry may expose salmonids to elevated mortality (Berg and Jonsson 1990).

The upstream migration speed decreased when the fish traversed two artificial lakes. Decreased migration speeds were also observed when the fish traversed the artificial lakes in the downstream direction (Jensen et al. 2018b). The underpinning mechanisms are unknown but could be related to navigation through the lakes. In a recent study on brown trout passing a lake, Schwinn et al. (2017) suggested that migration speed is controlled by complex interactions between several factors, including turbidity, wind-induced currents and lake morphology that may affect navigation. Reduced migration speed through a reservoir may lead to increased mortality due to predation for example by cormorants (Jepsen et al. 1998; Olsson et al.

2001). In the present study, North Sea houting were lost in both artificial lakes, but the impacts on the population size are unknown.

Reduced upstream migration speeds through the artificial lakes could eventually delay spawning activities further upstream. Previous studies have reported that forced delays of spawning often reduce egg survival because of excessive egg ageing after ovulation (Gaudemar and Beall 1998; Samarin et al. 2015). It is well known that migratory delays can have severe negative consequences (Svendsen et al. 2011; Crozier et al. 2017; Schwinn et al. 2018); however, we found no correlation between the times spent traversing the artificial lakes and subsequent arrival dates in the spawning areas, suggesting that the reduced migration speeds through the lakes did not translate into delayed spawning.

The importance of behavioral phenotypes is increasingly recognized in conservation planning (Killen et al. 2016; Hirsch et al. 2017; Merrick and Koprowski 2017; Meager et al. 2018). A previous study revealed that circadian activity patterns are repeatable in North Sea houting, indicating that individual fish exhibit behavioral phenotypes in relation to migration activity through the diel 24 h period (Jensen et al. 2018*b*). In the present study we tested if individual fish exhibit behavioral phenotypes in relation to upstream migration speed. Unlike previous field studies (Hanson et al. 2008; Taylor and Cooke 2014; Baktoft et al. 2016), we found no evidence that upstream migration speeds are repeatable in individual fish. Behavioral field studies conducted over several months may provide data that are influenced by environmental conditions (Svendsen et al. 2004; Salinger and Anderson 2006; Bendall et al. 2012) and therefore more variable and less repeatable. We suggest future repeatability studies account for variable environmental conditions and include individual responses to changes in river discharge and temperature.

Our data revealed a positive relationship between water temperature and upstream migration speed, suggesting that North Sea houting were often migrating at temperatures below the optimum temperature (Salinger and Anderson 2006). It seems paradoxical that river entry correlated negatively with temperature, whereas upstream migration speed correlated positively with river temperature. If the fish had entered the river earlier (e.g. during the summer), river temperatures would have been warmer and upstream migration could have progressed faster. We suggest that the negative relationship between water temperature and river entry reflects fish that are extending the period of time spent foraging in the marine environment and

therefore tend to enter the river in relatively cold water. Due to the resulting cold conditions in the river, fish

end up migrating at river temperatures below the optimum temperature and make relatively slow progress

towards the spawning areas. This potential trade-off between time spent foraging in the marine environment

and time spent reaching the spawning areas warrants further study.

On average, the upstream migrating North Sea houting spent 49 days in the estuarine area before

proceeding further upstream. Similar observations were made in the post-spawning state when fish utilized

the estuarine area prior to entering the Wadden Sea (Jensen et al. 2018*b*). It is therefore likely that the

estuarine area represents an important habitat for North Sea houting. Therefore, it may be important to

protect or restore estuarine areas in River Vidaa and in other rivers where the goal is to establish viable North

Sea houting populations.

The North Sea houting is closely related to the European whitefish, but the North Sea houting has a

better capacity to tolerate high salinity. The European whitefish is unable to tolerate full marine salinities (>

30‰) (Madsen et al. 1996), whereas the North Sea houting live in the Wadden Sea for several months,

where such conditions occur frequently (Jensen et al. 2015*b*). In an attempt to address recent requests for

applying physiological measures in conservation research (Mckenzie et al. 2016; Mahoney et al. 2018), we

analysed gill Na^+/K^+ ATPase activity and blood osmolality in North Sea houting and resident and

anadromous populations of European whitefish in the post-spawning state. Consistent with our hypothesis,

Na^+/K^+ ATPase activity was elevated in post-spawning freshwater North Sea houting before they returned to

the Wadden Sea, in comparison with the freshwater resident European whitefish situated in freshwater. This

suggests a degree of pre-adaptation to the hypo-osmoregulatory state before returning to the marine

environment in the North Sea houting. However, the anadromous whitefish caught in brackish water in the

Ringkøbing Fjord had gill Na^+/K^+ ATPase levels in the same range as post-spawning houting in freshwater

and elevated compared to resident whitefish in freshwater. This supports previous findings that whitefish

increase gill Na^+/K^+ ATPase activity upon exposure to elevated salinity (Madsen et al., 1996). Blood

osmolality was consistently higher in North Sea houting than both anadromous and resident whitefish

populations (caught in brackish and freshwater environments, respectively), suggesting that the North Sea

houting deviate physiologically from populations of European whitefish. Our study is the first to compare

physiological traits in North Sea houting and European whitefish. Common garden experiments are required to reveal if the North Sea houting exhibits adaptations to the local environment, similar to other salmonid populations (Jensen et al. 2008). Assessing the value of habitats for endangered species often requires physiological knowledge, in particular for anadromous species. Although the present physiological data cannot be used directly in management, the data do suggest that North Sea houting and European whitefish differ in physiologically at least in terms of osmoregulation. These findings indicate that data on European whitefish may not be directly applicable for North Sea houting.

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Figure legends

Figure 1. Map of the study area. The map includes the River Vidaa in South Denmark and the 16 stationary acoustic receivers positioned in the river, numbered 16-1. The river drains into the Wadden Sea at receiver 16. Sections A and B cover natural river sections, whereas sections D and E cover artificial lakes. Section C covers a natural lentic area. Modified from Jensen et al. 2018*b* (Jensen, L.F., Rognon, P., Aarestrup, K., Bøttcher, J.W., Pertoldi, C., Thomsen, S.N., Hertz, M., Winde, J., and Svendsen, J.C. 2018*b*. 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. Ecol. Freshw. Fish, **27**(3): 672–685. doi:10.1111/eff.12383. Reproduced by permission of John Wiley and Sons.)

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Figure 2. The probability of river entry (0 = no entry, 1 = entry) as a function of [a] temperature (°C) and [b]

river discharge (l s^{-1}) in North Sea houting (Coregonus oxyrinchus). Each relationship was fitted using

logistic regression. The probability of river entry varied significantly with temperature and discharge. Low water temperatures and high river discharges elevated the probability of river entry.

Figure 3. River discharge (l s^{-1}) (●) and water temperature (°C) (○) were measured throughout the study period.

Figure 4. North Sea houting (Coregonus oxyrinchus) migration speeds (km h^{-1}) through river sections (sections A and B), the lentic Magisterkog (C) and the artificial Lake Hestholm Kog (D) and Lake Nørresø (E). Upper and lower 95% CI are shown with bars. Significant differences between sections are indicated by different letters ($P < 0.05$). See map in Fig. 1 for details. The slowest migration speeds were observed when the fish travelled through artificial lakes.

Figure 5. Values of gill Na$^+$/K$^+$ ATPase-activity (μ moles/ mg protein/ hour) and blood osmolality (mOsmol/ kg) differ between North Sea houting and resident (R) and anadromous (A) European whitefish. [a] Na$^+$/K$^+$ ATPase activity is significantly higher in North Sea houting and anadromous whitefish compared to resident whitefish. [b] Osmolality is significantly higher in North Sea houting compared to both anadromous and resident whitefish.
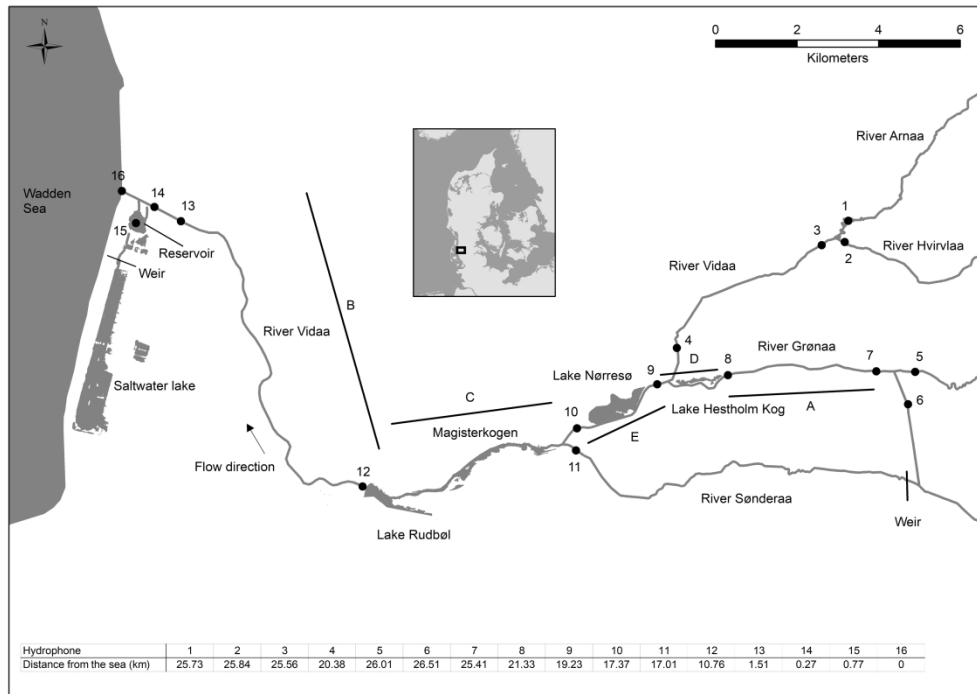
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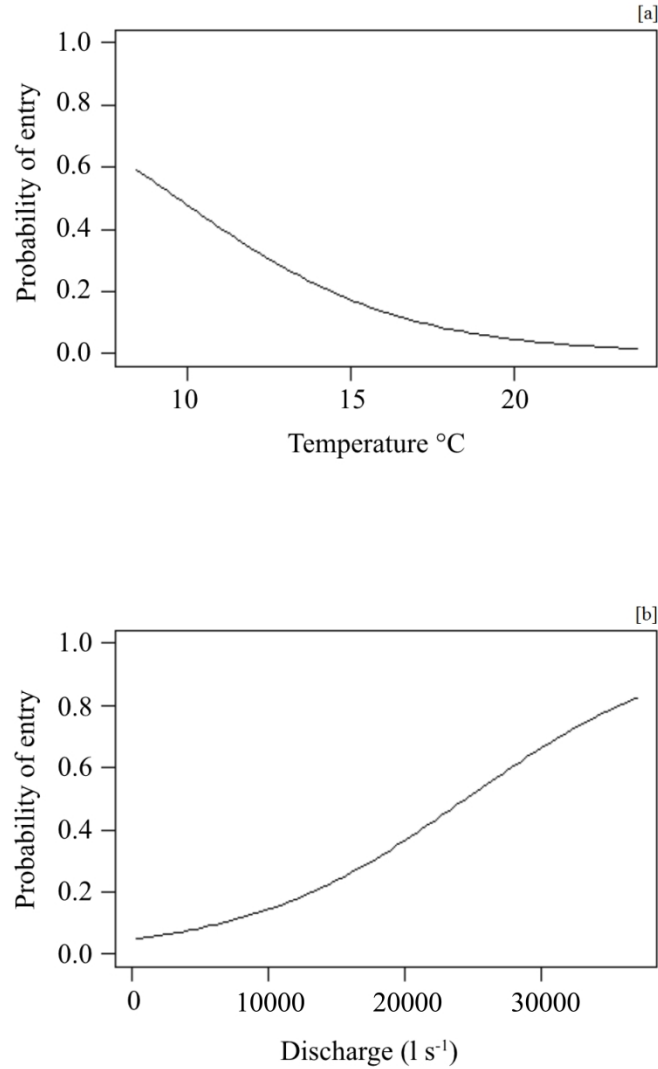
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Figure 2. The probability of river entry (0 = no entry, 1 = entry) as a function of [a] temperature (°C) and [b] river discharge (l s-1) in North Sea houting (Coregonus oxyrinchus). Each relationship was fitted using logistic regression. Temperature and discharge varied significantly with the probability of river entry. Low water temperatures and high river discharges elevated the probability of river entry.
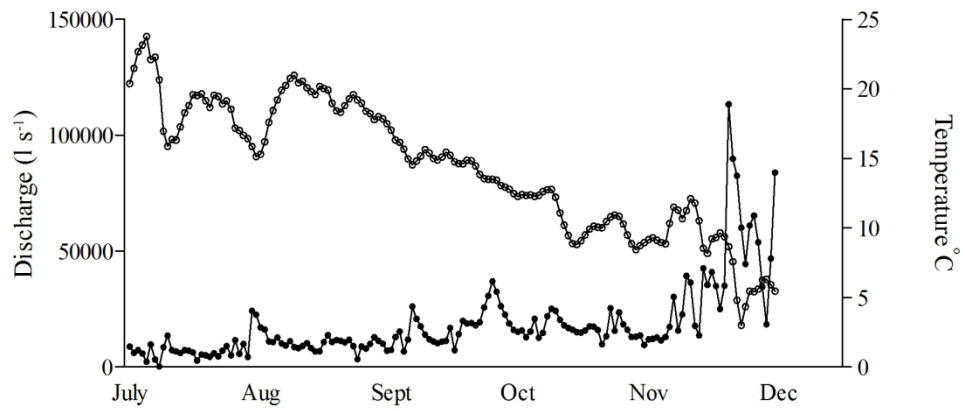
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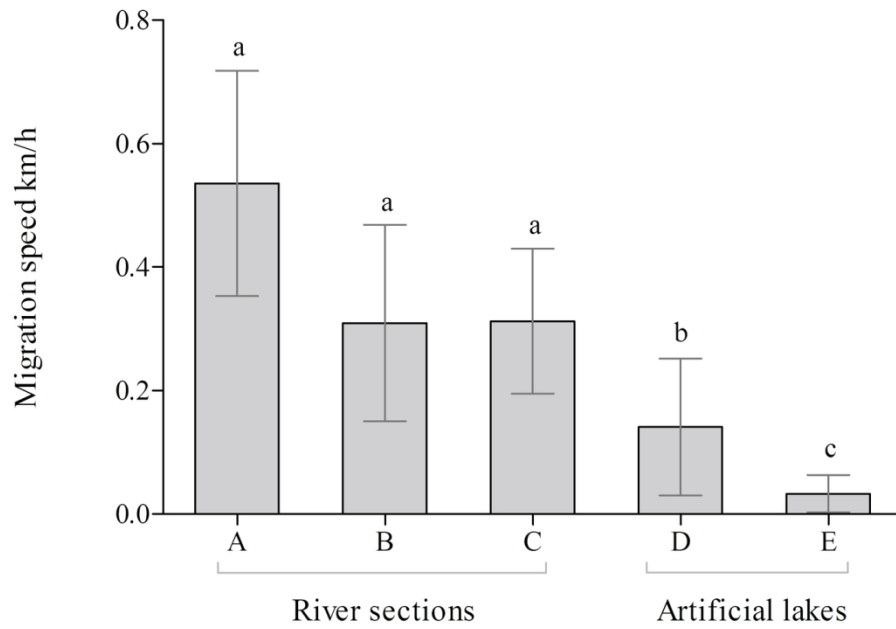
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Figure 4. North Sea houting (Coregonus oxyrinchus) migration speeds (km h-1) through river sections (sections A and B), the lentic Magisterkog (C) and the artificial Lake Hestholm Kog (D) and Lake Nørresø (E). Upper and lower 95% CI are shown with bars. Significant differences between sections are indicated by different letters ($P < 0.05$). See map in Fig. 1 for details. The slowest migration speeds were observed when the fish travelled through artificial lakes.
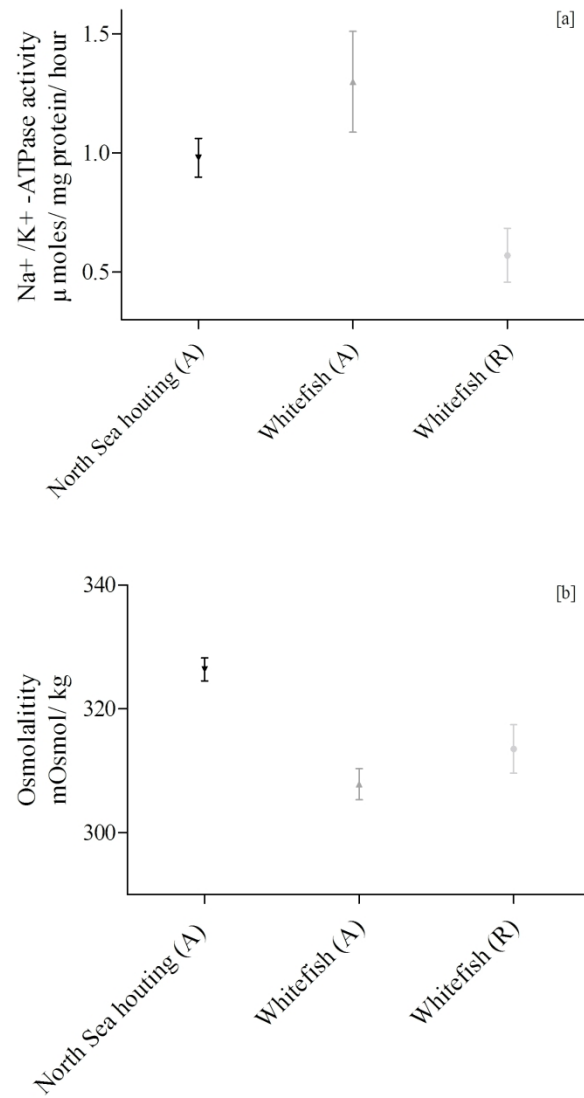
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Figure 5. Values of gill Na+/K+ ATPase-activity (μ moles/ mg protein/ hour) and blood osmolality (mOsmol/ kg) differ between North Sea houting and resident and anadromous European whitefish. [a] Na+/K+ ATPase activity is significantly higher in North Sea houting and anadromous whitefish compared to resident whitefish. [b] Osmolality is significantly higher in North Sea houting compared to anadromous and resident whitefish.

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