Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system

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Synopsis

We recorded the observed and actual swimming speeds of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system, and initiated studies on the orientation mechanisms of the post-smolts. We tracked Atlantic salmon and sea trout with acoustic transmitters for up to 14 h after release. The actual swimming speed and direction of a fish relative to the ground is the vector sum of the observed movements of the fish and the movements of the water. We determined actual swimming speeds and directions of the post-smolts, which reflect their real swimming capacities and orientation, by corrections for the speed and direction of the water current. The post-smolts were actively swimming. The observed direction of movement was dependent on the actual movement of the fish and not the water current. Water currents were not systematically used as an orientation cue either in Atlantic salmon or sea trout, as the actual movements were random compared to the direction of the water current. The actual movement of sea trout were in all compass directions, with no systematic pattern. The Atlantic salmon also moved in all compass directions, but with the lowest frequency of actual movement towards the fjord.

Introduction

Anadromous salmonids move from fresh water to the ocean to gain weight, but Atlantic salmon, *Salmo salar* L., and sea trout, *Salmo trutta* L., differ in their strategies during the sea phase. Atlantic salmon migrate to the open ocean (e.g. Hansen et al. 2003), whereas the sea trout remain in the inner fjord systems (e.g. Jonsson 1985, Knutsen et al. 2001). The understanding of the early marine phase of the Atlantic salmon and the environmental factors that may influence their behaviour and distribution in the sea is limited (Moore et al. 2000), and even less is known about the sea trout. This lack of information is particu-

larly critical because the heaviest mortality of salmon in the sea apparently takes place during the first months after the smolts leave fresh water (see Hansen et al. 2003).

During the last decades, intensive fish farming in fjord and coastal areas has led to higher concentrations of salmon lice, *Lepeophtheirus salmonis* Krøyer (Heuch & Mo 2001), and salmon lice infestations have been reported to cause significant sub-lethal and lethal effects on wild Atlantic salmon and sea trout (Tully et al. 1999, Bjørn et al. 2001, Heuch & Mo 2001, Tully & Nolan 2002). The developing fish farming industry has been charged with reducing the negative effects of sea lice on wild salmonid populations. One strategy is

to locate fish farms in areas where the risk of salmon lice infestations is reduced. This requires information on migratory routes of the post-smolts and the amount of time they spend in different fjord areas. However, knowledge about migratory routes, geographical distribution and swimming speeds of post-smolt salmonids in fjord and near shore areas is sparse (Voegeli et al. 1998, Lacroix & Voegeli 2000, Moore et al. 2000). The aim of the present study was, therefore, to record observed and actual swimming speeds of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system, and to initiate studies on the orientation mechanisms of the post-smolts.

Material and methods

Study area

The study was carried out in the inner part of the Romsdalsfjord system (Figure 1). The difference between low and high tide is approximately 1.6 m. Important Atlantic salmon and sea trout rivers, such as the River Eira, empty into the system (Figure 1). The River Eira has a mean annual water discharge of 15.5 m^3 s^{-1}.

We measured water temperature and salinity 2002 at four stations in the middle of Eresfjord, from the release site to 10 km from the river mouth (Figure 1). The water temperature at the surface was 8.6–10.3°C on 14 May and 10.5–14.5°C on 2 June. At 1 m depth, the water temperature was 9.2–9.9°C on 14 May and 12.0–12.5°C on 2 June. The salinity increased along the fjord towards the sea, and was 29.3–30.1 ppt at the surface on 14 May and 24.2–26.4 ppt on 2 June. At 1 m depth, the salinity was 29.3–30.1 ppt on 14 May and 24.2–26.4 ppt on 2 June.

Handling, tagging and release of fish

We tagged hatchery-reared Atlantic salmon (n = 5) and wild sea trout (n = 4) smolts with acoustic transmitters (VEMCO Ltd., Canada, V8SC-6L, 9 × 20 mm, mass in air of 3.3 g) at the Statkraft hatchery in Eresfjord. The Atlantic salmon (mean total length 26.3 cm, range 22.6–30.0; mean mass 181 g, range 105–278) were 2-year old smolts from the hatchery. A seawater tolerance test (Blackburn & Clarke 1987) performed on the hatchery-reared salmon on 3 May revealed plasma chloride levels at 130 mM, indicating that they had smolted (Sigholt & Finstad 1990). The salmon were also ready to actively migrate, as indicated by salmon from the same group that were tagged with coded transmitters and recorded by automatic listening stations 48 km from the release site on average 65 h later (i.e. minimum migration speed of 0.69 body lengths per second, own unpublished data). We caught the sea trout (mean total length 20.3 cm, range 18.1–24.5, mean mass 62 g, range 43–100) in a trap during downstream migration in the River Eira and transported them in a tank with
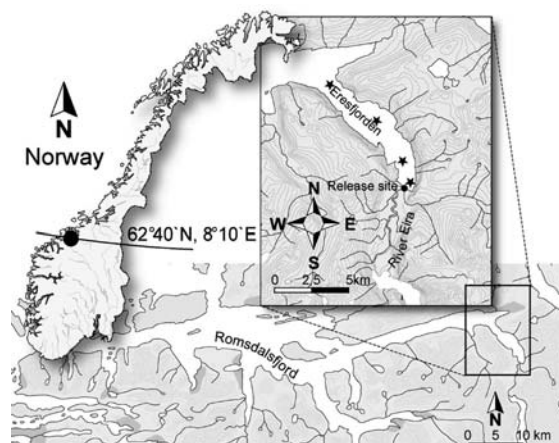

Figure 1. The Romsdalsfjord system in Middle Norway. Site for release of acoustically tagged smolts (•) and stations for temperature and salinity recordings (★) are indicated.

oxygenated water to the hatchery. We allowed the fish to recover from the stress of being captured, and we tagged the individuals that seemed most robust after 0–6 days.

We anaesthetised the fish by a 3-min immersion in an aqueous solution of 2-phenoxy-ethanol (EC No 204-589-7, SIGMA Chemical Co., USA, 0.5 ml L^{-1}). We made a 1.2–1.3 cm incision on the ventral surface posterior to the pelvic girdle. We inserted the transmitter through the incision and pushed it forward into the body cavity. We closed the incision using two independent silk sutures (4/0 Ethicon). Mean handling time was 2.8 min.

We transported tagged smolts in plastic bags with water to a cage in the fjord at the mouth of the River Eira (mean time from anaesthetisation to release in the cage was 17 min), where they could recover from anaesthesia and tagging without being prone to predation for 1–3 days before release. The cage (90 cm diameter × 75 cm) was constructed of knotless nylon net (mesh size 13 × 13 mm). We released the fish together with 25–30 non-tagged hatchery-reared Atlantic salmon smolts.

Fish tracking and simultaneous current measurements

We tracked the fish manually from a boat using a VEMCO VR60 receiver in the period 10 May to 1 June 2003. We fixed the fish position every 10th minute after release using a GPS. We followed individual fish for up to 14 h (salmon average 9.3 h, range 6.6–13.9; trout average 8.6 h, range 6.1–13.9).

To correct fish swimming speeds and directions for the water current, a separate boat and crew used a current drift drogue to simultaneously record the speed and direction of the water current. Every 30th minute, the current drift drogue was put into the water at the site where the fish was recorded. After 10 min, we recorded the position of the current drift drogue using GPS. The current drift drogue was made of canvas, and had three wings (57 cm wide and 1 m deep) mounted at 120° angles to each other. The current drift drogue was attached 30 cm below a floater at the surface and, hence, reflected the current at 0.3–1.3 m depth. Atlantic salmon post-smolts usually swim close to the surface, in the upper brackish layer (Fried et al.

1978, LaBar et al. 1978, Holm et al. 2003), which was also assumed to be true for sea trout in an estuary (Moore et al. 1998).

We calculated actual swimming speeds and directions of the fish by vector analysis based on observed movements of the fish and the direction and speed of the water current. We preformed statistical analyses with SPSS 11.5 and the GPS mapping software OziExplorer 3.90.3a.

Results

Swimming speeds

Mean observed migration speed was 1.27 bl s^{-1} (SD = 0.43, individual means from 0.94 to 2.00) for Atlantic salmon and 0.56 bl s^{-1} (SD = 0.23, individual means from 0.33 to 0.88) for sea trout. When corrected for the speed and direction of the water current, the actual swimming speed was on average 1.32 bl s^{-1} (SD = 0.28, individual means from 1.10 to 1.79) for Atlantic salmon and 0.68 bls^{-1} (SD = 0.29, individual means from 0.48 to 1.11) for sea trout. The actual migration speed (bls^{-1}) was not dependent on time from release (linear regression, r^2 = 0.004, p = 0.48).

The fish did not follow a straight route seaward along the fjord (see below). The most seaward position of the Atlantic salmon during the tracking period was on average 4702 m (range 2195–10 022 m) from the release site, and of the sea trout 1687 m (range 113–3702 m). This corresponds to a mean net rate of seaward movement of 506 m h^{-1} for Atlantic salmon and 196 m h^{-1} for sea trout.

Orientation

The current direction varied considerably during tracking, however, the highest number of recordings showed the current flowing out of the fjord (Figure 2). Mean current speed was 0.16 m s^{-1} (range 0–0.74, SD = 0.13).

The highest frequency of observed movements of the Atlantic salmon was out of the fjord (northern and western to northern directions, Figure 2). The actual movement, when corrected for the speed and direction of the water current, revealed the lowest frequencies in towards the
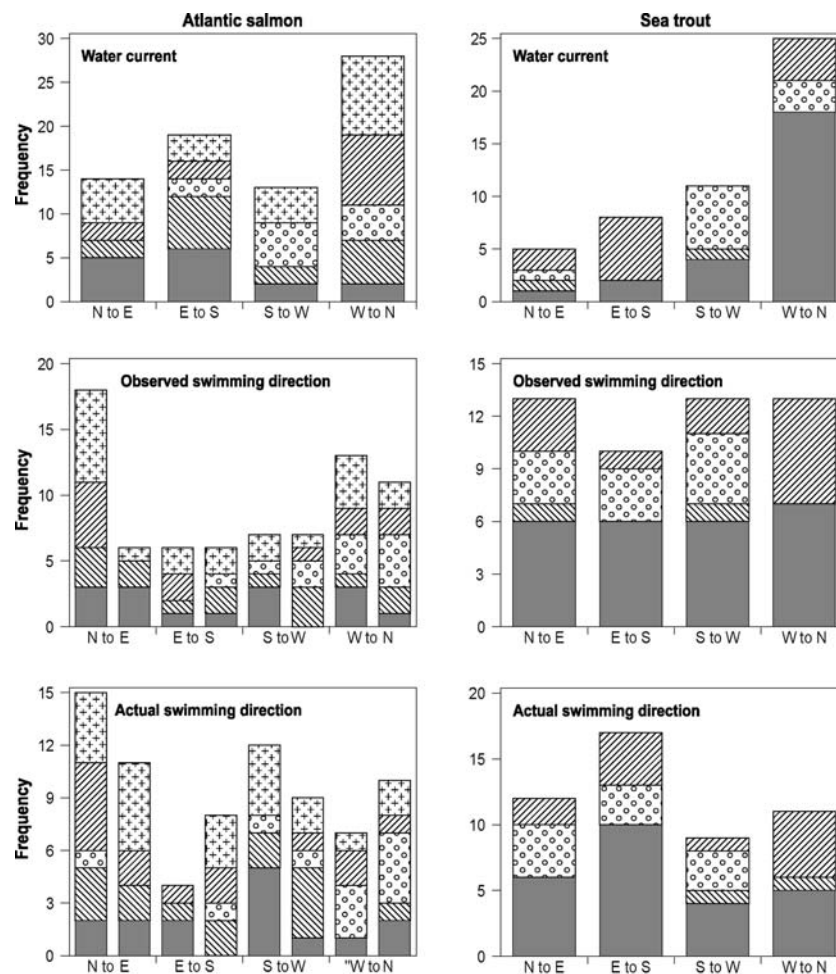
Figure 2. Directions of the water current and observed and actual (i.e. after correcting for the speed and direction of the water current) movements of Atlantic salmon (n = 5) and brown trout (n = 4) post-smolts tagged with acoustic transmitters and manually tracked in a Norwegian fjord. The figures show the frequency of 10-min recordings in the directions north to east (N to E, 0°–90°), east to south (E to S, 90°–180°, i.e. inwards the fjord), south to west (S to W, 180°–270°) and west to north (W to N, 270°–360°, i.e. outwards the fjord). In the inner part of the fjord, migration in northern directions, as performed by some salmon, will also be more or less directed seaward. For the salmon, each group of directions was therefore divided into two bars to present the data in more detail (N to E is presented as one bar for 0°–45° and one bar for 46°–90°). Stacked bars indicate contribution from each individual.

fjord (eastern to southern directions, Figure 2). For Atlantic salmon, the direction of neither observed nor actual movement was dependent on the direction of the water current (linear regressions, observed: $r^2 = 0.021$, $p = 0.22$, actual: $r^2 = 0.009$, $p = 0.42$). However, the direction of the observed movement was dependent on the actual movement (linear regression, $r^2 = 0.78$, $p < 0.001$).

The sea trout had less directed movement patterns than the Atlantic salmon, and no patterns in the direction of observed or actual movement were seen (Figure 2). As for the salmon, neither the direction observed nor the actual movement was dependent on the direction of the water current (linear regressions, observed: $r^2 = 0.029$, $p = 0.24$, actual: $r^2 = 0.005$, $p = 0.64$), but the direction of the observed movement was dependent on the actual movement (linear regression, $r^2 = 0.50$, $p < 0.001$).

Mean distance to shore was 374 m for the Atlantic salmon (based on individual means,

which ranged from 146 to 468 m) and 125 m for the sea trout (individual means from 26 to 468 m).

Discussion

The present study showed that both the Atlantic salmon and sea trout post-smolts were not passively drifting with the current, but actively swimming (actual swimming speeds of 1.3 bl s^{-1} for Atlantic salmon and 0.7 bl s^{-1} for sea trout). There was no relationship between the direction of observed movement and the direction of the water current, indicating that the post-smolts were moving in random directions in relation to the water current. The strong relationship between the direction of the actual and observed movement of the post-smolts indicates that the observed directions of movement were highly dependent on the actual movement of the fish and not of the water current.

In contrast to the results in the present study, several other studies suggest that water currents are the major transport factor in seaward migration of Atlantic salmon smolts, although most studies also emphasize observations of active directed swimming (Fried et al. 1978, LaBar et al. 1978, Lacroix & McCurdy 1996, Moore et al. 2000). The actual movements of the fish may have been masked by strong water currents in some of these studies. The active swimming component by the fish may be easier to detect when recording migrations in a fjord system with relatively light currents, as in the present study. The differences between the present study and previous studies may also be a result of the detailed and simultaneous water current recordings made in the present study, as compared to studies with a few current recordings at fixed stations, or corrections based solely upon the direction of the tidal flow. However, another explanation for differences between studies could be that post-smolts are not swimming actively in strong currents.

In Norway, most of the Atlantic salmon post-smolts leave the rivers from May to July (Hvidsten et al. 1998) and migrate to the open ocean (Moore et al. 2000). In contrast, sea trout seem to remain in the inner fjord systems (e.g. Jonsson 1985, Knutsen et al. 2001), which may be the reason why we recorded what seemed to be a slower and less

directed migration closer to shore for the sea trout than for the Atlantic salmon. Even less is known about the marine phase of sea trout than of Atlantic salmon, and we know no other publications of telemetry studies of the marine migration of sea trout, except estuarine studies by Moore & Potter (1994) and Moore et al. (1998). The sea trout post-smolts were passively moving with the ebb tide in the upper sections of the estuaries, but were actively swimming in the lower sections (Moore & Potter 1994, Moore et al. 1998), as they did in the fjord areas in the present study.

Orientation mechanisms used by migrating salmonid smolts and post-smolts apparently differ among species and habitats (Groot 1965, LaBar et al. 1978, Thorpe et al. 1981, Quinn & Brannon 1982, Moser et al. 1991). Landmarks, celestial cues, currents, electric and magnetic fields and olfaction are among suggested orientation and navigation cues for fishes (e.g. Stasko et al. 1973, Lucas & Baras 2001). Water currents seemed not to be systematically used as an orientation cue by either Atlantic salmon or sea trout in the present study. However, the sea trout were predominantly recorded relatively close to the shore, hence, the shoreline may be used to orient. Magnetic material has been found in the lateral line of Atlantic salmon, and in the nose of several fish species, which may enable them to use the earth's magnetic field for navigation (Potter & Moore 1991, Lucas & Baras 2001). However, the lack of highly directional movements in this study did not indicate precise navigation, although the lowest frequency of movements of Atlantic salmon post-smolts was in towards the fjord, resulting in a net seaward movement.

The high swimming speeds recorded in the present study indicates that Atlantic salmon post-smolts have the potential to pass fjord areas with fish farms and high concentrations of salmon lice during a relatively short period. However, the lack of directional movements will increase their stay in inner fjord areas and increase the vulnerability of being infested with sea lice. Based on the results in the present study, it seems difficult to predict migration routes of post-smolts based on currents, but similar studies in outer fjord systems could reveal other patterns. Sea trout post-smolts are clearly more vulnerable to sea-lice infestations in inner fjord areas than Atlantic salmon, with their

slower migration speeds and longer stay in these areas.

Wild Atlantic salmon smolts in most Norwegian watersheds are too small to be tagged with the acoustic transmitters that are currently available. Migratory routes of wild and hatchery-reared Atlantic salmon were similar in the studies of Lacroix & McCurdy (1996) and Voegeli et al. (1998). However, we suggest that the approach in the present study should be further explored with wild fish, and extended to a longer time period during their outward migration.

Acknowledgements

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