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A call for a paradigm shift: assumed-to-be premature migrants actually yield good returns

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Running title: Return rate of autumn migrants
Abstract

Animals with complex life cycles often display plasticity in the timing of transitions across life stages. The brown trout, *Salmo trutta*, highlights such phenotypic plasticity with its alternative migratory tactics. Downstream migration of smolts exemplifies one of the many ways in which brown trout display plasticity. The timing of this migration is assumed to be in the spring, though recent evidence suggests an autumn migration is also present. While the proximate and ultimate causes for this autumn migration remain unclear, it was hypothesized that leaving in the autumn may have short-term benefits (e.g., lower competition) but that these individuals are maladapted to life at sea, and yield poor adult returns. To test this hypothesis, 1370 wild juvenile brown trout from a Danish stream were tagged with PIT tags. Individuals were then divided into autumn and spring migrants depending on the timing of their outmigration to saltwater, and their return to freshwater was followed. Inconsistent with the hypothesis that autumn migrants yield poor returns, our findings suggest that autumn migrants yield similar return rates to spring migrants, with no observed differences in length, mass and condition upon tagging, nor in average time spent at sea. Our findings suggest that autumn migrants may not be maladapted to marine environments in a way that affects their survival, and call for a paradigm shift in the current description of the brown trout lifecycle.

Keywords: anadromous fish, lifecycle, migration, paradigm shift, phenotypic plasticity, salmonids
Introduction

In species with complex lifecycles, variations in the timing of transitions from one life stage to the next may convey fitness advantages at an individual (Roff, 2002), population (Charlesworth, 1994) and community level (Shreiber and Rudolf, 2008). Migratory species often display such variations in their spatial and temporal migratory behavior (Nathan et al., 2008; Chapman et al., 2011). In the Salmonidae for example, observations of this variation is plentiful (Dodson et al., 2013). The brown trout, Salmo trutta L., is perhaps the most variable of the salmonids as it displays alternative migratory tactics from resident to anadromous forms (Jonsson & Jonsson, 2011), and year-round migratory movements.

Downstream migration of smolts exemplifies one of the many ways in which brown trout display plasticity. While the classical description of the brown trout lifecycle suggests that juveniles migrate from freshwater to marine environments in the spring, evidence for a class of anadromous autumn migrants is growing in the field. In Atlantic salmon (Salmo salar), these early movements are well recognized and are considered pre-smolt migrations (e.g., Jonsson & Jonsson, 2014; Taal et al., 2014). In brown trout, these movements are less well recognized (though see Jonsson & Jonsson, 2009; Marine Institute, 2013; Taal et al., 2014), and were first hypothesized to be merely potamodromous or performed by unsmoltified individuals (Poole et al., 1996) which were maladapted to face marine environments, and thus had poor return rates. However, accumulating findings appear to support a pre-smolt migration (Winter et al., 2016; Aarestrup et al., 2018). In fact, autumn migrants seem to be similar to their spring counterparts in terms of length, mass, condition and sex ratio both upon tagging (see Winter et al., 2016) and upon migration (see Aarestrup et al., 2018). Whether these autumn migrants come back to contribute to the population (i.e., spawning) has received little attention however. Few studies showed that autumn migrants do in fact constitute a part of the reproducing population, though the extent of this contribution
appeared to be small compared to spring migrants (Poole et al., 1996; Jonsson & Jonsson, 2009). In the current study, we aimed to test the existing hypothesis that autumn migrants are less likely to return to their native river than their spring counterparts using Passive Integrated Transponder (PIT) telemetry. We further investigated the influence of length, mass and condition upon tagging on migration timing (autumn vs. spring) and likelihood of return, as well as the influence of migration season on time spent at sea.

Materials and Methods

Study site
The Gudsø stream is located in the southern region of Kolding, Jutland, Denmark (Figure 1). The stream is approximately 6 km long, and is home to a wild population of partially migrant brown trout (Salmo trutta), where both migratory and resident phenotypes coexist within the same population. Two PIT stations (allowing determination of directionality), are located approximately 500 and 600 m from the outlet to Kolding fjord. Fish from this population typically have freshwater residencies between 0.5 to 2 years, unless they assume complete freshwater residency, and typically spend no more than 1 to 2 years at sea. Straying to other rivers is unlikely given that there are no nearby rivers to Gudsø, but not impossible as other rivers exit into Kolding fjord. Our set up does not allow us to detect strayers however, because no other PIT stations are present in the area.

Fish capture and tagging
Between 2012 and 2015, a total of 1370 juvenile brown trout (ranging 12 to 18 cm) were captured via electrofishing and PIT-tagged during four tagging events (6 – 12 March 2012, 4 – 7 November 2012, 11 – 18 March 2013, 21 October – 3 November 2015). Fish were captured throughout the stream, starting at least 1.0 km upstream of the PIT stations. All fish
were anesthetized with 0.03 g l⁻¹ benzocaine in fresh stream water, measured and weighed. Fish were then tagged with a 23 mm PIT tag (Texas Instruments, RI-TRP-RRHP, 134 Hz, 0.6 g mass in air, Plano, Texas, USA) and left to recover in freshly oxygenated stream water. Following the procedure (less than 1 minute per fish), fish were released at their site of capture. All procedures were carried out in conformation to the Danish Experimental Animal Inspectorate (2017-15-0201-01164).

PIT data

Data from the PIT stations were downloaded in November 2017. Time of downstream migration (i.e. river exit) was determined as the last detection on the downstream-most PIT station. Time of upstream migration (i.e. river reentry) was determined as the first detection at the downstream-most PIT station. Only fish detected at the upstream and downstream stations in that order were considered to have migrated out to sea; only fish detected at the downstream and upstream stations in that order were considered to have returned. Fish detected only once (whether at the upstream or the downstream station) were excluded from the analysis (n = 28) to ensure downstream directionality (detection efficiency = 93.7 %). Time spent at sea was calculated as the number of days between time of downstream and time of upstream migration. Fish detected to come back to freshwater within less than one month (30 days) were excluded from the analysis.

Data analysis

Tagged fish from all study years were pooled together for the analysis, with tagging year as a random effect. Fish detected at the antennas between August and January were categorized as “autumn migrants”, while those detected between February and July were categorized as “spring migrants”. Fish were categorized in this way to encompass the autumn and spring
migrations at both lower and higher latitudes (i.e., to make our data comparable in other geographical regions where the timing of autumn and spring migrations may vary), but also to include individual fish that may migrate outside normal peak periods. However, given that we cannot identify the cohort to which each tagged fish belongs (because fish between 12.0 and 18.0 cm likely belong to at least two cohorts), we cannot categorize the fish into “early” or “late” autumn migrants (i.e., whether fish from a cohort migrate as half or 1.5 year olds in the autumn).

All data showed homogeneous variance and presented no outliers. We used two-way ANOVAs to examine differences in length, mass and condition at the time of tagging between spring and autumn migrants that had returned to the river or not. We also used a goodness-of-fit test to determine whether autumn migrants were less likely to return to the river than their spring counterpart, and to determine whether larger fish were more likely to return. We further tested whether migration season affected time spent at sea using a goodness-of-fit test. All statistical analyses were performed in JMP version 13.0.0 (SAS Institute).

**Results**

A total of 413 individuals migrated out of the river; 305 spring migrants and 108 autumn migrants. No fish tagged in the spring migrated the following autumn. Within spring migrants, 62 (20.3 %, mean length: 14.4±1.4 cm, mean mass: 27.7±8.1 g) individuals returned and 243 (79.8 %, mean length: 14.3±1.3 cm, mean mass: 27.0±7.2 g) did not. Within autumn migrants, 17 (15.7 %, mean length: 14.2±1.6 cm, mean mass: 27.8±9.6 g) individuals returned, and 91 (84.3 %, mean length: 14.3±1.4 cm, mean mass: 28.2±8.1 g) did not. We found no differences in length, mass and condition at the time of tagging between spring and autumn migrants that returned or not (\(P > 0.05\), *Figure 2*). Furthermore, autumn migrants
were equally likely to return to their natal river compared to spring migrants (goodness-of-fit, \( \chi^2 = 1.12, P = 0.29 \), **Figure 3, 4**). Larger fish were not more likely to return (goodness-of-fit, \( \chi^2 = 0.09, P = 0.76 \)). Autumn migrants spent on average 209.4±170.7 days at sea, while spring migrants spent on average 247.7±159.3 days at sea, but this difference was not significant (goodness-of-fit, \( \chi^2 = 0.76, P = 0.38 \), **Figure 5**).

**Discussion**

The classical description of the salmonid lifecycle (or “salmonid paradigm”) includes smolts migrating downstream and out to sea during the spring (Klemetsen et al., 2003). Variation in this spring migration depending on latitude has long been acknowledged; for example, smolts in Denmark migrate mostly between March and May, while those in northern Norway migrate mostly between May and July. A growing number of observations however, suggest that many individuals migrate outside the classical spring smolt migration period. In consensus with findings from Winter et al. (2016) and Aarestrup et al. (2018), we found that individuals migrating in the autumn did not differ in length, mass or condition to the spring migrants at the time of tagging. Fish tagged in the autumn which migrated the following spring may have undergone some growth during the winter, and may therefore have been somewhat larger than their autumn counterparts at the time of migration. Growth rate was not measured in this study, but a recapture or a trap study could be used to answer this question for future research.

We further found that autumn and spring migrating classes did not differ in return rates; autumn migrants were not less likely to return than spring migrants, as was initially described in the literature (Poole et al., 1996). This may support the hypothesis that autumn migrants are in fact pre-smolts and fit enough to enter marine environments, assuming that autumn migrants migrate earlier than spring migrants from the same cohort (i.e., early
autumn migrants, 0.5 year migrants). If however autumn migrants migrated in the following autumn (i.e., late autumn migrants, 1.5 year migrants), this class may be comprised of individuals not fit enough to migrate in their first year. A limitation to our study is the fact that aging was not performed on fish, and thus fish cannot be associated to a specific cohort. Regardless of whether autumn migrants are “early” or “late” migrants however, the finding that they are equally likely to return as their spring counterparts suggest that they are perhaps equally adapted to face marine environments as their spring counterparts. Previously observed return rates of autumn migrants were lower than those of spring migrants (Poole et al., 1996). These low returns were perhaps in part due to juvenile autumn migrants having had to migrate past weirs and dams on their way to sea. On the contrary, their spring counterparts may have had free passage since in spring, spillways are often opened during peak migration periods. Delayed mortality of individuals passing barriers (e.g., predation, injuries) may have reduced the overall return rate of these autumn migrants. An investigation of autumn migration/returns in highly fragmented rivers would provide some valuable information in that regard.

The proximate and ultimate causes for migrating in the autumn remain unclear at this point however. Various mechanisms have been proposed including density-dependent displacements of subordinates by dominant individuals (Bjornn, 1971; Mason, 1976) and the search for more suitable habitat, perhaps where food availability is greater or competition is lower (Riley et al., 2008). Alternatively, individuals of varying sizes may have the ability to exploit other resources, perhaps at sea, hence why they migrate sooner (Rincón and Lobón-Cerviá, 2002). Future research should focus on the mechanisms that regulate the timing of downstream juvenile migrations.

True autumn migrants (i.e., fish leaving the river to go to sea) may however only be observed in areas where rivers exit into weakly saline and/or brackish environments, such as
the Baltic Sea, where high osmoregulatory competency is not required for survival (Taal et al., 2014). This is the case for Kolding fjord, where fish exited in this particular study.

Varying levels of salinity may thus affect the survival and return rates of autumn migrants, and provides an interesting avenue for future research. For example, how do return rates of autumn migrants compare across populations entering low-, medium- and high-salinity areas? We further wish to note that propensity to migrate outside the peak smolt season as well as survival at sea and return rates may differ between brown trout and Atlantic salmon given the plastic nature of brown trout life-histories. Return rates of autumn-migrating Atlantic salmon may be low compared to brown trout because their marine life stage typically involves long-distance migrations to areas of high-salinity, and thus physiological readiness for sea life may be more necessary in salmon than trout. Another interesting avenue for future research would be to investigate egg quality, offspring survival and other fitness traits in relation to autumn-migrating mothers, given the tight link between early maternal experience and offspring performance (Burton et al., 2013). While autumn migrants are as likely to return to freshwater as spring migrants, our study did not allow us to examine individual fecundity; how much do these individuals contribute to the population in reproductive potential? We found that autumn and spring migrants did not differ significantly in the amount of time individuals spent at sea (though autumn migrants spent on average 40 days less at sea), perhaps suggesting that fish attained similar sizes, and reached similar reproductive potential. We observed great variation among individuals of both migratory phenotypes in time spent at sea. At this point, it is impossible to say whether spending 40 days less at sea is ecologically relevant; larger sample sizes of returning adults from both phenotypes would be necessary to do so. Future research should also consider recapturing individuals once back into freshwater to provide some insight on the fecundity of autumn migrants.
Over the years, highly cited studies have dismissed or avoided investigating individuals migrating outside the peak season, despite the fact that these individuals represented a significant proportion of the relative spring numbers (Elliott, 1986, 1994). In anadromous species, the freshwater output of a river is typically measured as the production of spring migrants (Ibbotson et al., 2013). However, this assumption creates two major issues in systems where autumn migrants are present: (1) it underestimates the productivity of the river, and (2) it overestimates the return rate of spawning adults. We therefore urge the salmonid research community to acknowledge and consider autumn migrants as true contributors to populations, and encourage a shift in the so-called salmonid paradigm.

Investigations in the physiological readiness of these autumn migrants to face saltwater – as was done in *S. salar* (Riley et al., 2008) – would make a valuable contribution to our understanding of this phenomenon, and would enable researchers to make predictions about how this autumn phenotype may respond under varying climate.

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Figure Captions

Figure 1. Gudsø stream, southeastern Jutland, Denmark.

Figure 2. Length (cm), mass (g) and condition (Fulton’s K) of brown trout (Salmo trutta) spring and autumn migrants which (left) returned (spring $n = 62$, autumn $n = 17$) to Gudsø stream, and (right) did not return (spring $n = 243$, autumn $n = 91$).

Figure 3. Percentage of brown trout (Salmo trutta) spring and autumn migrant classes that returned and did not return to Gudsø stream.

Figure 4. A) Number of migrating brown trout (Salmo trutta) per month. B) Relative return rate of brown trout per month. All study years are pooled ($n = 79$). Black bars represent autumn migrants; white bars represent spring migrants. NB: we caution that only two and one fish migrated in June and August, respectively, and that in each case, the fish returned (hence 100% return rate in panel B).

Figure 5. Time spent at sea (days) of brown trout (Salmo trutta) as a function of month migrated out. Black markers represent autumn migrants ($n = 17$); white markers represent spring migrants ($n = 62$).
Figure 1.
Figure 2.
Figure 3.

- **Spring**
- **Autumn**

% of migratory class

Not returned

Returned

0 10 20 30 40 50 60 70 80 90
Figure 4.
Figure 5.