Running Head: Brown trout phenology.

Investigating the phenology of juvenile potamodromous brown trout (*Salmo trutta* L.) in two large lake catchments.

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Abstract

There is growing interest in the phenology of juvenile *Salmo trutta* and evidence of significant downstream migration during the autumn in some anadromous populations. The present study used acoustic telemetry to examine the phenology of potamodromous trout parr across a region encompassing two large lake catchments. 167 trout parr were tagged in late summer across 4 lake tributaries between 2018-2020. In total, 75 tagged parr migrated into the lakes with 67 (89%) migrating between September-December and 8 (11%) migrating between March-June. Autumn migration was highly prevalent across all the tributaries, with 16-66% of each tagged sample exhibiting autumn migration, and 0-15% of each tagged sample exhibiting spring migration. Autumn migrants were significantly longer and heavier than spring migrants but condition factor was similar. Autumn migrants were associated with higher river discharge levels and lower water temperatures than spring migrants. The management challenges posed by extensive autumn migration behavior in migratory trout stocks are examined and discussed.

INTRODUCTION

Brown trout (*Salmo trutta* L.) display remarkable diversity in genetics, morphology, behaviour, phenology and life-history strategies across their geographical range (Pakkasmaa & Piironen, 2001; Jonsson & Jonsson, 2011; Drinan *et al.,* 2012; Birnie-Gauvin *et al*., 2019; Ferguson *et al.*, 2019). This inherent genetic diversity and consequential adaptability have enabled the species to occupy a wide-range of riverine, lacustrine, estuarine and coastal habitats throughout their natural distribution and to successfully establish populations in many areas outside of the species' native geographical range, following anthropogenic introductions (Budy & Gaeta, 2018; Hasegawa, 2020). Many *S. trutta* populations incorporate a migratory phase during their life-cycle with significant variation often evident in the extent and timing of movement patterns between and even within populations (Birnie-Gauvin *et al*., 2019). Ferguson *et al*., (2019) documented seven potential migratory behaviours in *S. trutta*, ranging from more limited within river migrations up to adfluvial anadromy. Recent work has also challenged the traditional assumption that juvenile anadromous *S. trutta* only migrate during the spring period and has suggested that many stocks may also exhibit significant migration at other times of the year (Birnie-Gauvin *et al*., 2019). For example several recent studies have demonstrated that significant numbers of juvenile sea trout migrate to the sea during the autumn (Taal *et al*., 2014; Winter *et al*., 2016; Aarestrup *et al*., 2018; Birnie-Gauvin & Aarestrup, 2018). A bi-seasonal migration pattern, often peaking in the spring and again in the autumn, has been observed in some potamodromous salmonid populations (Bjornn, 1971; Leathe *et al*., 2014). Boel *et al*., (2014) suggested that the migration strategy of juvenile *S. trutta* was directly influenced by physiological status, and demonstrated that potamodromous migrants moved shorter distances and had lower lipid reserves than longer ranging anadromous migrants.

The phenology of *S. trutta* stocks is relatively under-reported and more research is needed to more fully understand the range of migratory behaviours expressed and the ecological significance of migration outside of the spring period (Birnie-Gauvin *et al*., 2019). Potamodromous brown trout populations often support important recreational, and sometimes commercial, fisheries (Kennedy *et al*., 2021) and juveniles migrating to lakes may have to move substantial distances to reach their lacustrine feeding areas. Owing to their migratory habit, potamodromous parr are vulnerable to a wide range of pressures including water abstraction, riverine obstacles and predation, and therefore knowledge of the key downstream migration periods is fundamental for effective management.

The freshwater environment in Northern Ireland is dominated by two large lake catchments, Loughs Neagh and Erne, both of which contain stocks of economically important potamodromous *S. trutta* (Crozier, 1985; Kennedy *et al*., 2021). An extensive study was undertaken between 2018-2021 to investigate the migration of potamodromous trout parr into these large lakes using acoustic telemetry. The study sought to tag a representative sample of >0+ trout parr, captured close to known lake trout spawning sites, and determine the subsequent extent and timing of lake migration. The biological characteristics of autumn migrants and spring migrants were also investigated and compared.

MATERIALS & METHODS

Study Sites

Lough Neagh is the largest lake, by area, in Britian and Ireland with a surface area of 392 km^2 and drains a large catchment encompassing around 4,550 km^2 (Fig 1). Lough Neagh has few islands or sheltered inlets and is largely an open expanse of water. The lake is fed by 6 main tributaries, has a single outflow to the North Atlantic on the north coast of Ireland and is home to a variety of fish species including potamodromous *S. trutta* known locally as dollaghan. The Sixmilewater and Ballinderry rivers are two important spawning tributaries for potamodromous trout in Lough Neagh. Lower Lough Erne is the second largest lake in Northern Ireland with a surface area of 110 km^2 and drains into the North Atlantic ocean on the west coast of Ireland. Lough Erne, by contrast to Neagh, has an abundance of islands and sheltered inlets and bays. This lake also supports stocks of potamodromous *S. trutta*. The Ballinamallard and Garvary rivers are two of the main spawning tributaries for potamodromous trout in the Erne catchment (Kennedy *et al*., 2021).

Sampling and Tagging

One electric fishing site was sampled at each of four study rivers during late summer-early autumn during 2018-2020 (Table I). Survey sites were located adjacent to heavily used potamodromous trout spawning beds, based on historical lake trout redd count records (Kennedy *et al*., 2021), local knowledge from fishery officers and by direct observations during the previous spawning season. On each sampling occasion an electric fishing team of 4-6 operatives and a smaller tagging team of two people were present. The electric fishing protocol entailed isolating a standard site between two 5 mm diameter mesh, stop nets before undertaking at least three fishing passes of the enclosed habitat. The electric fishing work employed e-fish 500W backpacks, with one set used for every 3.5m of channel width at the site. A random sub-sample of 20-40 parr-marked trout >140 mm fork length (L_F) was removed from the catch after the first pass and retained in a large 200 L aerated tank by the tagging team. The presence of parr-markings was used as a phenotypic indicator of juvenile state and it was assumed that all tagged fish were immature. It is possible that a small proportion of the tagged samples, particularly males, could have matured in the autumn following tagging (Forty *et al*., 2016; Lothian *et al*., 2020). After each pass the electric fishing team identified and counted all fish before L_F (mm) and weight (g) were measured, with the additional biological data from the tagging sub-sample collated and added later. Scale samples were removed from a sub-sample of trout for aging. Trout were divided into 3 age groups (0+, 1+ and >1+) on the basis of length frequency distributions, confirmed by scale reading. Density estimates were produced for each age class, assuming constant effort in each sequential pass (Zippin, 1958). The length-frequency profile, age structure, population density and biomass of the trout population were determined for each site in accordance with Kennedy *et al*., (2012).

Trout were tagged using individually coded ultrasonic acoustic tags (7 mm diameter, 23 mm length, 2.7 g, INNOVASEA Ltd.). The acoustic tags had a frequency of 69 kHz, nominal delay settings of 120 s and a minimum life expectancy of >10 months. Prior to tagging, trout were anaesthetised in a bath of 100 mg l^{-1} tricane (MS-222). L_F was measured to the nearest mm, body mass to the nearest g and a small scale sample of 4-6 scales removed for aging. The acoustic transmitter was activated, sterilised in 100% ethanol and inserted into the body cavity through a mid-ventral incision, anterior to the pelvic girdle. The incision was closed with one single absorbable suture (vicryl 4-0) before tagged fish were allowed to recover for 1 hour in a netted $1.5m^2$ enclosure in the river. Once fully recovered, all tagged trout were released back into the river at the initial capture site. The tagged batches across all sites were released during the day between 13:00 – 14:00 h. Ethical issues were carefully considered and all tagging work was conducted under a UK Animals Scientific Procedures Act licence (Project Licence Number - 2869).

The movement of tagged trout was monitored by a network of hydroacoustic receivers (VR2W, VR2AR INNOVASEA Ltd.) positioned at strategic locations along each study river corridor and through-out each lake (Fig. 1). Receiver arrays were deployed by boat into the lakes. On each river a VR2W receiver was placed at the tagging site, one c. 500m upstream of the tagging site, 1-3 units were then placed progressively downstream from the tagging site and finally a detection ‘gate’ was arranged at the river mouth. The lake confluence ‘gate’ had 2

VR2W units placed sequentially in the river c. 50-100m immediately upstream of the lake confluence and a further VR2AR unit was placed onto the lake bed c. 50-100m directly out from the river mouth. The detection gate was designed to ensure optimal detection coverage for tagged trout parr leaving the river and entering the lake. Deployment locations in rivers were typically deeper, slower flowing areas, which optimised the acoustic transmission range from the tags. Two further receivers were placed in the outflows from each lake to monitor for any fish leaving the lakes towards the sea. In the Lough Neagh catchment, 7 receivers were placed in the Sixmilewater, 5 in the Ballinderry, 15 in the lake and 1 in the outflow. In the Erne catchment, 5 receivers were placed in the Garvary, 5 in the Ballinamallard, 17 in the lake and 1 in the outflow (Fig. 1).

The fate of each tagged trout was classified into one of 4 categories. Since no tagged fish entered the lake in January or February, those detected entering the lakes between September – December were classed as *autumn migrants* whilst fish detected entering the loughs between March – June the following year were classed as *spring migrants*. Tagged fish which were not detected after release or stopped being detected on the river arrays prior to the time of battery expiry (11 months after tagging) were classed as *missing*. Those individuals that continued to be actively detected on the in-river arrays by the time of battery expiry were classed as *river residents*. River residency rates represented *minimum* estimates because some fish that were not detected (missing) on the passive in-river arrays may have simply moved within the river and taken up station outside the detection range of adjacent receivers. Given the inherent uncertainty in the classification of river residents subsequent statistical comparisons focused on autumn and spring migrants.

The date on which fish were detected passing through the lower gate into the lake was taken as the migration date. Any downstream migrants which were no longer detectable prior to the gate were excluded from further temporal analysis. The migration pattern for each river was collated and the overall temporal pattern across all samples and years plotted as a cumulative frequency distribution.

Detection patterns from tagged trout after lake entrance provided a useful proxy for survival. Previous telemetry work on potamodromous trout in Lough Erne indicated that surviving individuals tended to move actively within the lake, continuously registering on numerous receivers across the array (Kennedy *et al*., 2021) whilst predated individuals either disappeared following avian predation or became static following consumption by larger predatory fish (Kennedy *et al*., 2018). Tagged fish that were detected actively moving around the lake arrays by the time of tag battery expiry were assumed to be alive. It is possible that some fish may have remained alive but were not actively moving or detected on the lake arrays, and some fish may have expelled their tags (Kennedy *et al*., 2020), therefore these data were taken only as a proxy for *minimum* survival rates in the lake.

Data analysis

The biological characteristics of autumn and spring lake migrants, L_F (mm), body mass (g) and Condition Factor (CF – Fulton's Index) at the time of tagging, were analysed using a generalised linear mixed model (GLMM; REML procedure, VSNi Software). The main effects of migratory fate (autumn or spring) and river (Ballinderry, Ballinamallard, Garvary and Sixmilewater), and their interaction were fitted as fixed effects with year as the random effect.

RESULTS

A total of 102 trout parr were tagged in the Lough Neagh catchment, comprising 69 on the Sixmilewater and 33 on the Ballinderry (Table II). In the Erne catchment, a total of 65 trout parr were tagged between the Garvary (46) and Ballinamallard rivers (19). The length-frequency distribution of tagged parr were not significantly different to the background population, sampled by electric fishing, on the Sixmile (*Kolmogorov-Smirnov Test*; D = 0.27; P >0.05) and Ballinderry rivers (*Kolmogorov-Smirnov Test*; D = 0.31; P > 0.05). Insufficient additional electric fishing samples were available from the Garvary and Ballinamallard rivers for comparison and the samples were assumed to be reflective of the background population. The largest parr were encountered on the Sixmilewater in 2019 (Mean L_F 198 mm) and smallest on the Garvary river in 2020 (Mean L_F 159 mm) (Table II). In total, 118 tagged trout were 1+ and 49 were >1+ age class. The biomass of >0+ trout was highest on the Sixmilewater in 2018 (1748 g $100m^{-1}$) and lowest on the Garvary river in 2020 (601 g $100m^{-1}$). The condition factor of trout was relatively high across all catchments and consistently exceeded 1.2 (Table II).

In total 75 tagged fish migrated successfully into the lakes with 21 (32%) detected in Lough Erne and 54 (53%) in Lough Neagh. One tagged parr in the Sixmilewater was detected moving downstream in October 2019 but ceased to be detected before the river-lake gate. None of the successful lake migrants were subsequently detected in the outflow from either lake. The detection efficiency of all the river-lake gates were assessed to be 100% (supplementary material) because all tagged individuals detected on the lake arrays had initially registered on their respective river gate.

The Sixmilewater parr showed high levels of autumn migration with 66% and 55% of all the tagged parr moving into the lake in the autumns of 2018 and 2019, respectively (Fig. 2). The other river samples showed a variation in autumn migration levels ranging from 16% on the Ballinamallard river to 45% for the Garvary river sample in 2020 (Fig 2). Spring migrants were detected on all catchments except the Sixmilewater and in all cases occurred in lower numbers than the respective autumn migrants, ranging from 4% on the Garvary river 2019 to 15% on the Ballinderry sample (Fig 2). The minimum levels of river residency across the study rivers ranged from 0% (Garvary 2019 & 2020) up to 21% on the Ballinamallard river. Most river residents were detected moving upstream from the tagging site and were detected periodically between the tagging site and upstream receiver site.

Across all samples and years, 67 tagged fish were detected entering the lakes during the autumn/winter period between 1st September - 22nd December, with the mean migration date on the 25th October. No migrants entered the lake during January or February. In total 8 tagged parr entered the lakes during the spring/early summer period between 27th March – 4th June, with a mean migration date on the 7th May. The pooled cumulative frequency distribution indicated that 89% of the migrants moved during the autumn period with 66% migrating during October and November (Fig. 3).

Detection patterns from tagged trout after entering the lakes provided a useful proxy of minimum lake survival rates. Lough Neagh had 49 autumn migrants of which 36 (73.5%) were still actively moving around the lake array by the time of battery exhaustion in the following summer, and 5 spring migrants of which 2 (40%) remained active until battery exhaustion. Lough Erne had lower overall survival levels with 18 autumn migrants of which 4 (22.2%) were still active by the following summer, and 3 spring migrants of which 0 (0%) remained active at battery termination.

The GLMM analysis indicated that significant differences were evident in L_F for the main effects of migration timing (autumn or spring) and river ($F_{Timing\ (1,\ 67.05)} = 6{\cdot}63$, $P < 0{\cdot}05$; $F_{River\ (3,\ 66.13)} = 14{\cdot}44$, $P < 0{\cdot}05$) but not for the interaction of the main effects ($F_{Timing:River\ (1,\ 67.05)} = 0.22$, $P > 0{\cdot}05$). Significant differences were also evident for weight across the main effects ($F_{Timing\ (1,\ 67.11)} = 5{\cdot}60$, $P < 0{\cdot}05$; $F_{River\ (3,\ 62.22)} = 10{\cdot}43$, $P < 0{\cdot}05$). There were no significant effects of migration timing or river, or their interaction, for condition factor. Spring migrating trout were significantly smaller (167 mm mean L_F) than autumn migrating trout (178 mm mean L_F) at the time of tagging, whilst mean condition factor was similar at 1·22 and 1·23 for spring and autumn migrants respectively (Fig 4a). Spring migrants tended to emigrate at higher mean ambient water temperatures (12·5 ^{o}C) than autumn migrants (9·9 ^{o}C) whilst spring migrants moved at much lower discharge levels (Q 83) than autumn migrants (Q 18) (Fig 4b).

DISCUSSION

Juvenile trout migration patterns are generally under-reported, poorly understood and subject to broad assumptions with respect to phenology (Birnie-Gauvin *et al*., 2019). The current study provides a striking example of an autumn migratory habit where 89% of the tagged trout which emigrated, did so in the autumn or the early winter. These data suggest extensive migration of potamodromous trout outside of the generally assumed spring smolt window. The extent of autumn migration in these tagged potamodromous parr was dramatic and much exceeded levels of c. 20% recorded from anadromous stocks (Aarestrup *et al*., 2018). Higher levels of autumn migration have however been observed for trout stocks with a potential potamodromous option, with levels up to 57% recorded on the Irish Burrishoole catchment (Marine Institute, 2014) and 46% noted on the Deerness River in England (Winter *et al*., 2018). It is acknowledged that the current study focused on >0+ age class parr due to the size limitations (>140 mm L_F) imposed by implantation of 7mm acoustic tags. It is possible that some fast growing 0+ trout could have potentially bolstered the spring run in the following year as young 1+ spring migrants such that the autumn migration figure (89%) may be an over-estimate at a population level. Nevertheless, larger migrants often contribute more heavily to subsequent adult returns in many anadromous salmonids (Gregory *et al*., 2019) and the phenology of older migrant parr is likely to be critical to the productivity of potamodromous stocks.

The traditional view of juvenile trout migration, whether to coastal, estuarine or lacustrine feeding grounds, has been based around a dominant spring movement cycle. This narrative however, is being increasingly challenged, as this study and other telemetry research provide more examples of significant autumn migrations in juvenile trout across various stocks (Taal *et al*., 2014; Winter *et al*., 2016; Aarestrup *et al*., 2018; Birnie-Gauvin & Aarestrup, 2018). The current work focused on potamodromous trout parr, which do not need to smoltify but nonetheless must often undertake extensive downstream migrations to access their lake feeding grounds. Potamodromous trout experience similar biological tradeoffs to anadromous stocks with pressure to emigrate from the natal stream to access better feeding opportunities balanced against potentially increased predation risk from large lake predators such as pike (*Esox lucius* L.). Long term tag activity, as a proxy for survival, was higher for autumn migrants on both lakes and may be indicative of better overall survival for juveniles entering the lake during colder months. Kennedy *et al.,* (2018) showed high predation losses on *S. salar* smolts entering Lough Erne in the spring, due principally to the close proximity of post-spawned *E. lucius* to marginal shorelines and river mouths at that time of year. Autumn migrants may experience lower predation pressure than spring migrants and more telemetry research into this issue using calibrated predation tags (Hanssen *et al*., 2021), to compare seasonal predation rates, would be valuable. Lough Neagh showed higher overall lake survival rates than Lough Erne. This differential could be related to greater predation pressure in Lough Erne which is much more suitable for *E. lucius* than Lough Neagh, where pike are considerably less common.

Winter *et al.,* (2016) found no significant differences in the length or mass of spring or autumn juvenile migrants from populations dominated by sea trout, at the time of tagging, on the Deerness or Villestrup rivers. Some other studies, by contrast, found that autumn migrants were significantly larger than spring migrants of the same year class (Huntingford *et al*., 1992; Holmes *et al*., 2014). Jonsson & Jonsson (2009) suggested that autumn migrants may be predominately fast growing fish which need to translocate to more productive habitats for feeding and continued growth. The present study found that autumn migrants were larger and heavier whilst condition factor was similar at the time of tagging. These results support the view that larger, faster growing fish tend to migrate earlier. In addition, the river with the highest growth rate (Sixmilewater), as evidenced by the largest 1+ parr at the time of tagging (Table II), only exhibited autumn migration behaviour, perhaps reflecting the pressure on fast growing young fish to relocate in search better feeding opportunities. Birnie-Gauvin *et al*., (2021) suggested that autumn migrating *S. trutta* parr had lower condition than spring migrants, suggestive that energy depletion was an important driver of early (autumn) emigration. Jonsson & Jonsson (2009) postulated that autumn migration may provide juvenile sea trout with a head start on the best feeding opportunities available in the early spring. The completion of lake-ward migration in the autumn may also allow overwintering trout to rapidly exploit increased prey abundance in the early spring or even during the colder winter months. Lough Erne and Neagh both support high biomasses of *Mysis salemaai*, which tend to switch from open water pelagic behaviour to marginal semi-benthic behaviour in winter (Griffiths *et al*., 2015). These crustaceans may provide good feeding opportunities for young autumn migrant trout and encourage winter lacustrine residence. The thermal regime of larger lakes also facilitates a degree of heat retention, cooling more slowly than their respective influent rivers and this may provide an opportunity for extended autumn/winter feeding and growth in the lake relative to the tributaries. An investigation of the comparative activity levels and energetics between lake dwelling and river resident *S. trutta* could be a useful focus for future research.

In the present study many young trout had to migrate up to 20 km in order to reach the lake and autumn migrants used much higher mean flows (11·8 m^3s^{-1}; Q value = 19) than those migrating in spring (1·5 m^3s^{-1}; Q value = 83). Youngson *et al.*, (1983) suggested that autumn migration in Atlantic salmon smolts was stimulated primarily by increasing water discharge on the Girnock Burn in Scotland. Similarly, Winter *et al.*, (2016) found that increasing water level had the greatest influence on autumn migration of sea trout parr in study catchments in Denmark and England. Migration in association with increased river discharge is potentially beneficial for downstream moving fish due to decreased energetic expenditure and protection from predators due to rapid movement and reduced visibility in turbid water (Hvidsten & Hansen, 1988). Long term analysis of hydrometric data from a range of rivers across Great Britain and Northern Ireland has shown a trend towards increased autumn flows whilst spring flows tended towards stability or declines during 1969-2008 (Hannaford & Harvey, 2010). It is possible that long term selective pressures consequent to local hydrological patterns may have favoured autumn migration and that such pressure may be magnified in the future if longer term climate change predictions for wetter autumn-winters and drier spring-summers are realised (Hannaford & Buys, 2012). It is likely that an evolutionary balance has developed between growth rate, population density, predation and climate such that selection will favour the migratory strategy best able to maximise future reproductive success. The timing of outward migration is therefore a critical decision point in the life history of migratory trout and thus a robust understanding of phenology is consequentially important for effective management.

Assumptions on migration timing can easily feed through into management practices and result in the implementation of fishery protection measures targeted across traditional or perceived migratory periods. In Northern Ireland for example, fisheries legislation requires that protections for juvenile migratory salmonids are implemented between 1st March - 30th May. The legislative protections for young actively migrating salmonids are varied and include control of water abstractions, passage around hydro-electric stations, management of flow in regulated rivers and authorisation of predator controls. The current work has indicated the importance of autumn migration in potamodromous trout across a geographical region and challenges fishery managers to reconsider stock phenology and the protections offered outside of the traditional spring smolt period.

The smoltification process in anadromous salmonids involves an intricate physiological transition cued by specific environmental conditions (Morera *et al*., 2021), with peak migration often associated with, but not exclusive to, the spring period (Birnie-Gauvin & Aarestrup, 2018). Del Villar-Guerra *et al*., (2019) further demonstrated that various developmental stages of anadromous *S. trutta* were capable of successful migration to sea during the spring period. Freshwater migrating trout do not need to transition into saltwater, have no need to smoltify and therefore may be unrestricted in the timing of their behavioural responses to favourable environmental conditions, such as high river discharge in the autumn. It is possible that autumn migration of potamodromous juveniles represents a relatively plastic behaviour, and that the extent of autumn migration may vary with annual discharge. Longer time-series data comparing phenology patterns, environmental conditions and climate could provide valuable insights into variability in, and factors affecting, migration timing in trout populations.

Acknowledgements

Thanks to A. Kane, M. Horton, E. McFadden and J. McGauran for practical assistance. Thanks to N. Reid for support on the Sixmile.

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