Received: 7 July 2023 | Revised: 11 September 2023 | Accepted: 12 September 2023

DOI: 10.1111/eff.12755

ORIGINAL ARTICLE

Ecology of FRESHWATER FISH WILEY

Smolting in post-sexually mature male Atlantic salmon (*Salmo salar* L.) parr in the wild

Angus J. Lothian[1,2] | Jessica Rodger[1,2] | Lorna Wilkie[2] | Marcus Walters[3] | Richard Miller[3] | Chris Conroy[2] | Shona Marshall[4] | Morven MacKenzie[4] | Colin E. Adams[1]

[1]Scottish Centre for Ecology and the Natural Environment, School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Rowardennan, UK

[2]Atlantic Salmon Trust, Perth, UK

[3]The Deveron, Bogie and Isla Rivers Charitable Trust, Avochie, UK

[4]West Sutherland Fisheries Trust, Gardeners Cottage, Scourie, UK

Correspondence
Angus J. Lothian, Scottish Centre for Ecology and the Natural Environment, Rowardennan, G63 0AW, UK.
Email: angus@atlanticsalmontrust.org and dr.ajlothian@gmail.com

Funding information
Grosvenor's Reay Forest Estate; Missing Salmon Alliance

Abstract

Conflicts can arise in developmental pathways that prevent an individual entering different developmental life stages that result in the expression of different phenotypes within a specific time period. In salmonids, theory suggests that sexual maturation may inhibit subsequent smolting within the same 12-month period and that this is partly the result of the time and the apparently conflicting physiological changes for these processes to occur, and partly because of the energy requirements for these physiologically taxing processes. This study tested whether sexually mature male Atlantic salmon (*Salmo salar* L.) parr, caught in the autumn, would subsequently smolt the following spring. Through individual identification using PIT telemetry, minimum estimates of 3.0% ($n = 6/203$) and 5.9% ($n = 1/17$) of Atlantic salmon parr that were sexually mature in two river catchments during the autumn were subsequently identified as smolts in the following spring. We therefore suggest that, in line with previous studies on domesticated Atlantic salmon and laboratory-based experiments, there is no developmental conflict but that life-history expression is mediated by environmental and genetic processes.

KEYWORDS
alternative life history, biotelemetry, cryptic mating, developmental conflict, migration, ontogenetic processes

1 | INTRODUCTION

Genetic variation between populations is known to influence the probability with which a trait may be expressed (Ferguson et al., 2019; Mobley et al., 2021; Rodger et al., 2021; Thorpe, 1994). However, conflicts within and between developmental pathways governed by resource acquisition and allocation may arise, thereby precluding the expression of multiple life history strategies and traits within set time frames. The concept that developmental constraints may limit the expression of one phenotype at the expense of another is most frequently described in the context of alternative life-history traits (Gould & Lewontin, 1979; Stearns, 1980). One example where this may occur is the apparent developmental conflict between the transformational processes of sexual maturation and smolting in salmonid fishes.

The Atlantic salmon (*Salmo salar* L.) is a diadromous fish which typically spends between 1 and 8 years in freshwater before migrating to nutrient-rich areas of the marine environment to grow for up to 7 years (Klemetsen et al., 2003). The sea-ward migration prior to marine residency is preceded by a complex series of physiological, morphological and behavioural changes that prepare the migrant for seawater entry. Together these changes are known as smolting (Hoar, 1988). Following its time at sea, the Atlantic salmon returns to freshwater to reproduce, having accrued size-related fitness advantages (i.e., larger females can carry more eggs and larger males can gain a fighting advantage over smaller males; Hutchings & Myers, 1994; Jonsson et al., 2016).

As an alternative life history strategy, Atlantic salmon frequently become sexually mature in freshwater as parr without having previously migrated to sea and thus at a relatively small size in comparison with their anadromous counterparts (Baum et al., 2004; Hutchings, 2011; Hutchings & Myers, 1994; Myers et al., 1986; Shaw, 1836). The vast majority of records of sexual maturation in Atlantic salmon parr are for males (Mobley et al., 2021; Myers, 1984; Myers et al., 1986); however, there are a few records of female parr becoming sexually mature before sea migration (Bagliniere & Maisse, 1985; Mills, 1971; Power, 1969; Prouzet, 1981). The fitness advantage of early sexual maturation is that there is a higher probability of surviving to sexual maturity, compared with the alternative strategy of becoming mature only after a long-distance migration to and from sea (Hutchings & Myers, 1994). Expression of this alternative life history strategy also promotes population stability as fish from any given year cohort exhibit alternate behaviours reducing the impact of catastrophic events on a population, as well as creating multi-year cohort breeding groups which limits the possibility of inbreeding (Mobley et al., 2021; Perrier et al., 2014).

Both smolting and sexual maturation are highly complex developmental processes. Maturation requires the development of gametes, but the process also includes a suite of physiological, morphological and behavioural changes for the process to result in successful breeding (Sutterlin & Maclean, 1984). Smolting, similarly, is a compliment of processes of morphology, physiology and behaviour change (Hoar, 1988; Langdon & Thorpe, 1985). A consequence of the complex nature of these changes is that they take time. Drawing together the results of experimental tank and field studies, Thorpe (1986) showed that the process of smolting in advance of sea migration begins in salmon parr in the summer approximately 9 months before migration. Similarly, the processes eventually leading to successful reproduction for parr begins in spring, approximately 8 months before the breeding season. Thus, it has been considered that smolting and maturation of parr are mutually exclusive processes within the same year because of these temporal conflicts (Mobley et al., 2021; Thorpe, 1986; Thorpe & Metcalfe, 1998; Thorpe & Morgan, 1980; Yevropeytseva, 1962).

Laboratory studies have, however, observed that smolting and maturation can occur within the same 12-month period. These studies include those whereby parr are retained in tanks until smolting (Berglund et al., 1991; Fjelldal et al., 2018; Saunders et al., 1982) or those where parr are held in tanks and then released into rivers immediately before smolting (Berglund et al., 1991, 1992; Hansen et al., 1989; Lundqvist et al., 1988). Arguably, in both cases, the developmental pathways may have already been initiated through parr being exposed to unnaturally stable or increased temperatures and food abundance and quality, both of which variables have been identified to influence smolting of parr and the maturation at any stage of the Atlantic salmon life cycle (Åsheim et al., 2023; Berglund et al., 1991, 1992; Jonsson et al., 2013). There is also some evidence of previously mature parr smolting in the wild, with spent males being found within smolt-capturing programs (Myers, 1984; Österdahl, 1969). However, in these studies as individual fish were not followed from maturation to smolting, the time frame over which this transition took place is unknown.

Recent research into these two developmental pathways in domesticated Atlantic salmon suggests that there is no developmental conflict between the two pathways (Fjelldal et al., 2018). Although both the maturation and the smolting processes are regulated by neuroendocrine pathways, namely the brain-pituitary-gonad system for maturation and the GH-IGF-I system and thyroid hormone for smolting (Björnsson et al., 2011), it has been suggested that as they ultimately culminate at different endpoints, the processes can develop in parallel without direct conflict (Fjelldal et al., 2018). However, these studies also identified that maturation in parr could significantly impair hypo-osmoregulation in smolts and in turn reduce a smolt's chance of surviving the transition to seawater (Berglund et al., 1992; Fjelldal et al., 2018). Therefore, some indirect conflict may exist which, under natural conditions with wild fish (rather than under laboratory conditions with either wild or domesticated strains), could prevent smolting and maturation within the same year.

This study aims to explore the potential for a developmental conflict in the maturation and smolting, in that order, of wild Atlantic salmon parr within a 12-month period in two geographically separated river catchments. Specifically, we hypothesise that, as a result of the perceived developmental conflict (Thorpe, 1986) and the impacts of maturing on hypo-osmoregulation (Berglund et al., 1992), male parr will be unable to smolt the spring after sexual maturity. Therefore, we test the null hypothesis that there is no developmental conflict and that mature male parr can smolt the following spring. A secondary aim of this study is to describe the relationship between length and weight of wild mature male and immature parr and smolting.

2 | METHODS

2.1 | Study site

The Deveron catchment is situated in Northeast Scotland and has an overall catchment area of 1266 km^2 and a length of 96 km. It rises 600 m above sea level and flows directly into the North Sea (Figure 1). The Laxford catchment is situated on Grosvenor's Reay Forest Estate in the remote North-west Highlands of Scotland and drains an approximate area of 118 km^2. Unlike the Deveron which is a river for its entire course, the Laxford flows through two lakes (Loch More and Loch Stack, approximately 65 m and 55 m above sea level, respectively), which are fed by a network of tributaries,

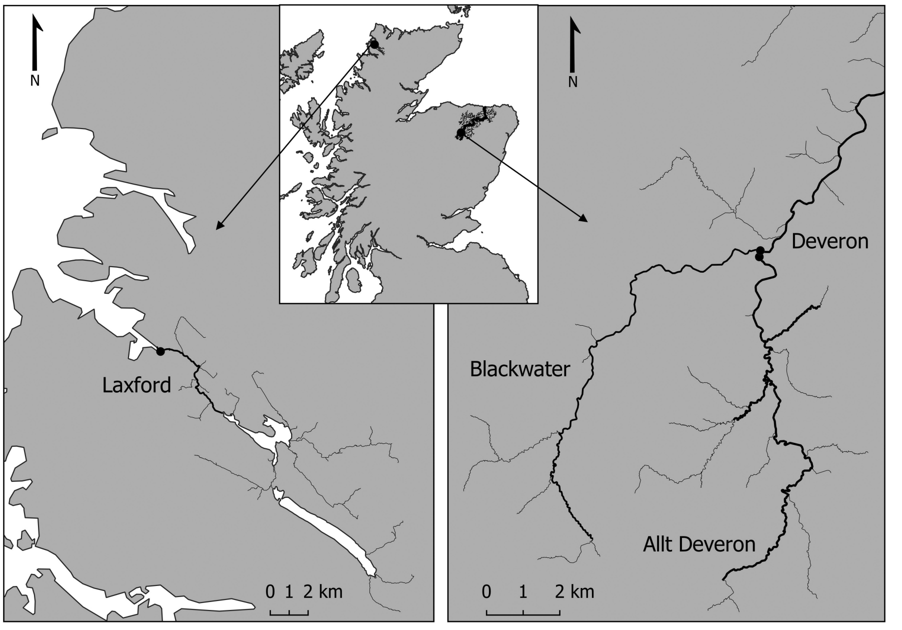

FIGURE 1 Map of the Laxford (left) and Deveron (right) study catchments with Rotary Screw Traps marked (dots).

before flowing for 7 km into the North Atlantic Ocean (Figure 1). In both catchments, Atlantic salmon tend to smolt and emigrate to sea at 2 years post-hatching, but records of up to four-year-old smolts have been recorded in the Deveron (A. Lothian, personal observation).

2.2 | Fish capture and tagging

Electrofishing was conducted over 6 days between 13th and 29th October 2021 in the Deveron and across 4 days between 29th October and 4th November 2021 in the Laxford by two independent teams experienced in electrofishing. Atlantic salmon parr were captured from the two major tributaries of the Deveron and six tributaries of the Laxford. All Atlantic salmon parr were held in containers (~75 L) filled with constantly aerated river water. Fish were individually anesthetised in a buffered solution of tricaine methanesulphonate (MS-222; 100 mg L^{-1}) and river water, before being measured for fork length (mm) and weight (g). The abdomens of each fish were then palpated to release gametes to determine whether any fish were of advanced sexual maturity. A small abdominal incision approximately 3–4 mm in length was made ventrally, anterior to pelvic girdle for those fish greater than 90 mm in length before a Passive Integrated Transponder (PIT) tag (12.5 × 2.15 mm; 0.11 g in air; Biomark) was implanted into the body cavity. No sutures were used to close the incision as it has been shown that PIT tag retention is high in juvenile Atlantic salmon without sutures (97% retention with 23 mm long PIT tags; Larsen et al., 2013). Fish were allowed to recover in aerated tanks (~75 L) of river water for 1–3 h before being returned to the river within 50 m of where they were captured. All methods and procedures were performed in accordance with the United Kingdom's Scientific Procedures Act 2003 and carried out under Home Office issued licence (Project Licence number PP0483054).

2.3 | Smolt recapture

To capture Atlantic salmon smolts during their downstream seaward migration, rotary screw traps were positioned mid-stream downstream of a natural narrowing in each of the two rivers in April and May 2022. In the Deveron, one rotary screw trap was positioned at each of the lower reaches of two tributaries, the Blackwater (57.36367702° N; 3.03180701° W) and the Allt Deveron (57.36213002° N; 3.0224341° W; Figure 1), just upstream of their confluence. These were operated from 27th March until 1st June 2022. On the River Laxford, a rotary screw trap was positioned near the tidal limit of the Laxford (58.37474528° N; 5.01656746° W; Figure 1) and operated between 13th April and 3rd May 2022. Traps were checked daily and all fish were removed. Atlantic salmon smolts were scanned with handheld PIT scanners (HPR Lite, Biomark) daily throughout the trapping period on the Deveron and across 4 days between 30th April and 3rd May 2022 on the Laxford. If a PIT tag was detected, the PIT tag ID was recorded. Mark-recapture trials conducted for the Deveron rotary screw traps in 2022 suggest capture efficiencies of 16% and 31% for Atlantic salmon smolts in the Allt Deveron and Blackwater, respectively (M. Walters, personal communication). The rotary screw trap on the Laxford was deployed for the first time in 2022 and so no efficiency estimates exist for this site.

2.4 | Statistical analyses

Welch's two sample *t*-tests were used to compare the differences in length and weight of immature and sexually mature parr captured in autumn 2021 in both river catchments due to the unequal sample sizes between the two maturity groups. Welch's two sample *t*-tests were also used to compare autumn length and weight between all fish that smolted and did not, as well as for mature fish that smolted and did not. Analyses carried out on recaptured fish were only performed for the Deveron due to the low number of recaptures in the Laxford. All analyses were performed in RStudio (2022.02.3) using R (4.1.2; R Core Team, 2021).

3 | RESULTS

In total, 1157 and 158 Atlantic salmon parr were captured and PIT tagged in the Deveron and Laxford catchments, respectively. The mean ± SD length (mm) and weight (g) of all Atlantic salmon parr for the Deveron were 109 ± 9 mm and 15 ± 4 g and for the Laxford were 101 ± 9 mm and 12 ± 4 g, respectively. For fish collected from the Deveron, 17.5% ($n = 203$) of all Atlantic salmon parr tagged in autumn 2021 were sexually mature males. Of the Atlantic salmon parr sampled from the Laxford in autumn 2021, 10.8% ($n = 17$) were sexually mature males. No sexually mature females were recorded from either site. At both study sites, sexually mature male parr were significantly greater in length (Deveron: Welch's two sample *t*-test, $t = 6.3$, $df = 247.6$, $p < .001$; Laxford: Welch's two sample *t*-test, $t = 3.9$, $df = 19.4$, $p < .001$) and weight (Deveron: Welch's two sample *t*-test, $t = 8.8$, $df = 231.6$, $p < .001$; Laxford: Welch's two sample *t*-test, $t = 4.7$, $df = 18.6$, $p < .001$) than those which were immature in autumn 2021 (Table 1; Figure 2).

Of the 1157 and 158 Atlantic salmon parr tagged and released into the Deveron and Laxford rivers, 63 (5.4%) and 6 (3.8%) fish were recaptured in the rotary screw traps, respectively, in spring 2022 as smolts. Of those recaptured smolts, 9.5% ($n = 6/63$) and 16.7% ($n = 1/6$) were fish that had been sexually mature in the autumn, indicating a minimum observed 3.0% ($n = 6/203$ tagged sexually mature parr) and 5.9% ($n = 1/17$ tagged sexually mature parr) of the Deveron and Laxford mature parr, respectively, smolted. In both catchments, the length and weight of the recaptured sexually mature fish (length and weight recorded at time of tagging) were greater than for those that were immature (Table 1). This difference was only significant for the weight of the fish at time of tagging in the Deveron (Welch's two sample *t*-test, $t = 3.2$, $df = 5.8$, $p = .02$) but not for length (Welch's two sample *t*-test, $t = 2.1$, $df = 5.9$, $p = .07$). Within the group of parr that were mature in the Deveron, there was no significant difference in the length (Welch's two sample *t*-test, $t = -1.6$, $df = 5.6$, $p = .16$) or weight (Welch's two sample *t*-test, $t = -1.6$, $df = 5.8$, $p = .17$) for those that were recaptured as smolts or not.

4 | DISCUSSION

Here we show clear evidence from the field of male parr that were sexually mature in late autumn also smolting and migrating to sea in the same year (6–7 months later). With 3.0% and 5.9% of those tagged sexually mature parr being observed as smolts in the Deveron and the Laxford, respectively, we also show that this may be more common than previously expected. This proportion fits with previously calculated estimates that 2–7% of mature 1-year-old parr undergo smolting and migrate to sea the following spring (Myers, 1984), although individual fish age was not investigated in the current study. The proportions of mature parr that were released and migrated downstream as smolts in this study must be assumed to be minimum estimates given the trapping technique. The traps in the Deveron only operated at an estimated maximum efficiency of 32% in 2022 (M. Walters, personal communication), and PIT scanning only occurred over 4 days in the Laxford, and so there is a high likelihood that more PIT tagged and released fish smolted. Therefore, if more smolts were captured in the trap, the proportion of PIT tagged mature parr that smolted may be higher than that estimated (given that the number of tagged fish remains the same). Irrespectively, this is the first evidence of the maturation and smolting developmental process occurring within the same 12-month period in wild Atlantic salmon populations (Fjelldal et al., 2018; Mobley et al., 2021).

Despite the fact that we show the process of smolting can occur rapidly following maturation in parr, this study was not able to determine whether the two developmental processes occur in tandem with each other or sequentially. However, given that Fjelldal et al. (2018) showed no intrinsic developmental conflict in domesticated Atlantic salmon, and experimental trials on wild and hatchery fish in laboratories have shown that maturation and smolting can occur within the same year under stable conditions (Berglund et al., 1991, 1992; Hansen et al., 1989; Lundqvist et al., 1988; Saunders et al., 1982), we also suggest that there exists no conflict between the two developmental pathways in the wild. Rather, environmental factors such as temperature and nutrient acquisition, along with genetic components (i.e., maturation genes such as *vgll3*; Åsheim et al., 2023; Niemelä et al., 2022) limit an individual's ability to undergo both energetically demanding process with the same 12-month period.

The majority of mature parr either delay smolting and migration or die shortly after spawning (Dalley et al., 1983; Myers, 1984;

TABLE 1 The number and mean ± SD length and weight of parr (measured during autumn sampling) of sampled fish that were deemed either mature or immature at time of autumn sampling.

	Mature			Immature		
Catchment	N	Length (mm)	Weight (g)	N	Length (mm)	Weight (g)
Autumn – Parr						
Deveron	203	114 ± 12	18 ± 6	954	108 ± 8	14 ± 4
Laxford	17	110 ± 10	16 ± 4	141	100 ± 9	11 ± 3
Spring – Smolt						
Deveron	6	120 ± 9	21 ± 4	57	111 ± 8	16 ± 3
Laxford	1	121	21	5	103 ± 6	11 ± 2

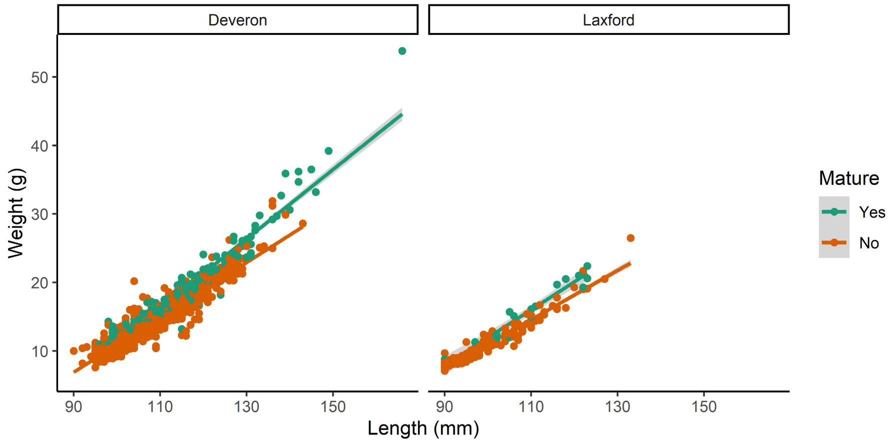

FIGURE 2 The length and weight relationship of sexually mature male parr and immature parr processed in the Deveron (left) and Laxford (right).

Saunders et al., 1982; Thorpe, 1994; Whalen & Parrish, 1999). In some populations, it has been estimated that 60% of parr that become mature do not smolt and migrate to sea (Myers, 1984). Those individuals that did mature and smolt in the current study are likely to be individuals that had participated in spawning, although this cannot be known for certain. Hansen et al. (1989) identified that those mature males which had been stripped of gametes at time of spawning in the autumn, thereby simulating a breeding attempt, were 20% more likely to initiate smolting and migration following spring. It could, therefore, be argued that there is a cost associated with re-absorption of gametes which might induce a delay in migration. Alternatively, a mature male parr that has not yet completed a breeding event could continue searching for potential breeding opportunities and thereby miss the potential smolting initiation window. This relationship between breeding success (or at least a completed attempt at breeding) and smolting may ultimately be identified by longitudinal studies on life history strategy with a focus on mature parr breeding success rates.

Several environmental variables are known to impact both the age of sexual maturity and smolting in salmonids (Åsheim et al., 2023; Berglund et al., 1991, 1992; Jonsson et al., 2013; Mobley et al., 2021). Several laboratory studies have now shown that temperature and food resource availability can increase the chances that maturity occurs in parr (Adams & Thorpe, 1989; Åsheim et al., 2023; Berglund et al., 1991; Debes et al., 2020; Thorpe, 1994). This is in part influenced by genetics, specifically the *vgll3* gene which can encode for late or early maturity (Åsheim et al., 2023; Niemelä et al., 2022). Although the *vgll3* gene was originally identified as a strong correlate with the number of years an individual spent at sea before returning to spawn (Barson et al., 2015), recent common garden experiments have shown that the gene may play a role in determining maturity pre-smolting (Åsheim et al., 2023). Those individuals with the early alleles may be more likely to mature pre-smolting than those with late alleles given the same resource availability. With temperature and resource acquisition known to influence smolting (Berglund et al., 1991), it might be that with climate change, and therefore greater river temperatures, a fixed level of resource acquisition could enable a greater occurrence rate of maturation and smolting in parr in the same 12-month period. Likewise, with salmon stocks declining around the world, it might be that less competition from reduced parr densities enables a greater resource acquisition to promote these processing occurring in tandem. The mechanisms for this to occur need further investigation. Using information acquired from the *vgll3* gene, fish sex and fish age could be a useful tool to disentangle the relationship between maturation and smolting in future studies.

It has been frequently shown that only the largest parr within a year class mature (Berglund et al., 1992; Dalley et al., 1983; Leyzerovich, 1973; Rowe & Thorpe, 1990; Saunders et al., 1982). Sexually mature male parr in this study were also significantly larger in terms of length and weight than those that were immature in the autumn sampling, fitting the trends seen in the literature. However, sexually mature male parr in this study showed a wide range of lengths, with the smallest being 90 mm in length. The literature also suggests that only the largest of the mature parr will smolt (Berglund et al., 1992). However, in this study, there was no statistically significant difference in the lengths of fish in autumn that were detected as smolts in spring compared with those that were not.

Although it is now well established, from laboratory and field studies, that Atlantic salmon that become sexually mature as parr in freshwater can, and do, eventually migrate to sea, more information is required to fully understand the long-term impacts of this behavioural phenotype and the associated developmental pathways in wild fish. Phenotypic and genetic diversity within populations expressed as alternative life histories are important within populations to dampen the impacts of catastrophic events, thusly increasing a species resilience to environmental change (King et al., 2007). This diversity is particularly important within the context of current climate change.

AUTHOR CONTRIBUTIONS

Angus J. Lothian: Conceptualisation; Methodology; Formal Analysis; Investigation; Writing – Original Draft; Writing – Review and Editing. **Jessica Rodger**: Conceptualisation; Investigation; Writing – Review and Editing. **Lorna Wilkie**: Investigation; Project Administration; Resources; Writing – Review and Editing. **Marcus Walters**: Investigation; Resources; Writing – Review and Editing. **Richard Miller**: Investigation;

Resources; Writing – Review and Editing. **Chris Conroy**: Investigation; Resources; Writing – Review and Editing. **Shona Marshall**: Investigation; Resources; Writing – Review and Editing. **Morven MacKenzie**: Investigation; Resources; Writing – Review and Editing. **Colin E. Adams**: Conceptualisation; Supervision; Writing – Review and Editing.

ACKNOWLEDGEMENTS

We would like to thank Jamie Carruth, Karen Muller, Steve Burns, Bev Winter, Kevin Greensil, David Allison, Robert King and Seamus Nairn for their help in capture and tagging of fish. Further thanks are extended to Grosvenor's Reay Forest Estate. Funding for PIT tags was provided by the Missing Salmon Alliance and Grosvenor's Reay Forest Estate as part of the Project Deveron and Project Laxford, respectively. We also extend our thanks to two anonymous reviewers for their helpful comments.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data will be made available upon reasonable request to the corresponding author, Angus J. Lothian.

ORCID

Angus J. Lothian https://orcid.org/0000-0002-4121-3817
Jessica Rodger https://orcid.org/0000-0003-1913-6533
Colin E. Adams https://orcid.org/0000-0003-2470-9754

REFERENCES

Adams, C. E., & Thorpe, J. E. (1989). Photoperiod and temperature influences on growth in juvenile Atlantic salmon (*Salmo salar* L.). *Aquaculture*, *79*, 403–409.

Åsheim, E. R., Debes, P. V., House, A., Liljeström, P., Niemelä, P. T., Siren, J. P., Erkinaro, J., & Primmer, C. R. (2023). Atlantic salmon (*Salmo salar*) age at maturity is strongly affected by temperature, population and age-at-maturity genotype. *Conservation Physiology*, *11*, coac086.

Bagliniere, J. L., & Maisse, G. (1985). Precocious maturation and smoltification in wild Atlantic salmon in the Armorican massif, France. *Aquaculture*, *45*, 249–263.

Barson, N. J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G. H., Fiske, P., Jacq, C., Jensen, A. J., Johnston, S., Karlsson, S., Kent, M., Moen, T., Niemelä, E., Nome, T., Næsje, T. F., Orell, P., Romakkaniemi, A., Sægrov, H., Urdal, K., … Primmer, C. R. (2015). Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature*, *528*, 405–408.

Baum, D., Laughton, R., Armstrong, J. D., & Metcalfe, N. B. (2004). Altitudinal variation in the relationship between growth and maturation rate in salmon parr. *Journal of Animal Ecology*, *73*, 253–260.

Berglund, I., Hansen, L. P., Lundqvist, H., Jonsson, B., Eriksson, T., Thorpe, J. E., & Eriksson, L.-O. (1991). Effects of elevated winter temperature on seawater adaptability, sexual rematuration, and downstream migratory behaviour in mature male Atlantic salmon parr (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 1041–1047.

Berglund, I., Schmitz, M., & Lundqvist, H. (1992). Seawater adaptability in Baltic salmon (*Salmo salar*): A bimodal smoltification pattern in previously mature males. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*, 1097–1106.

Björnsson, B. T., Stefansson, S. O., & McCormick, S. D. (2011). Environmental endocrinolgy of salmon smoltification. *General and Comparative Endocrinology*, *170*, 290–298.

Dalley, E. L., Andrews, C. W., & Green, J. M. (1983). Precocious male Atlantic salmon parr (*Salmo salar*) in insular Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*, 647–652.

Debes, P. V., Piavchenko, N., Erkinaro, J., & Primmer, C. R. (2020). Genetic growth potential, rather than phenotypic size, predicts migration phenotype in Atlantic salmon. *Proceedings of the Royal Society B*, *287*, 20200867.

Ferguson, A., Reed, T. E., Cross, T. F., McGinnity, P., & Prodöhl, P. A. (2019). Anadromy, potamodromy and residency in brown trout *Salmo trutta*: The role of genes and the environment. *Journal of Fish Biology*, *95*, 692–718.

Fjelldal, P. G., Schulz, R., Nilsen, T. O., Andersson, E., Norberg, B., & Hansen, T. J. (2018). Sexual maturation and smoltification in domesticated Atlantic salmon (*Salmo salar* L.) – Is there a developmental conflict? *Physiological Reports*, *6*, 1–18.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London B*, *205*, 581–598.

Hansen, L. P., Jonsson, B., Morgan, R. I. G., & Thorpe, J. E. (1989). Influence of parr maturity on emigration of smolting Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *46*, 410–415.

Hoar, W. (1988). The physiology of smolting salmonids. In W. Hoar & D. Randall (Eds.), *Fish physiology* (Vol. *XIB*, pp. 275–343). Academic Press.

Hutchings, J. A. (2011). Old wine in new bottles: Reaction norms in salmonid fishes. *Heredity*, *106*, 421–437.

Hutchings, J. A., & Myers, R. A. (1994). The evolution of alternative mating strategies in variable environments. *Evolutionary Ecology*, *8*, 256–268.

Jonsson, B., Jonsson, M., & Jonsson, N. (2016). Optimal size at seaward migration in an anadromous salmonid. *Marine Ecological Progress Series*, *559*, 193–200.

Jonsson, B., Jonsson, N., & Finstad, A. G. (2013). Effects of temperature and food quality on age and size at maturity in ecotherms: An experimental test with Atlantic salmon. *Jounral of Animal Ecology*, *82*, 201–210.

King, T. L., Verspoor, E., Spidle, A. P., Gross, R., Phillips, R. B., Koljonen, M.-L., Sanchez, J. A., & Morrison, C. L. (2007). Biodiversity and population structure. In E. Verspoor, L. Stradmeyer, & J. L. Nielsen (Eds.), *The Atlantic salmon: Genetics, conservation and management* (pp. 117–166). Blackwell.

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. *Ecology of Freshwater Fish*, *12*, 1–59.

Langdon, J., & Thorpe, J. (1985). The ontogeny of smoltification: Development patterns of gill Na/K- ATPase, SDH and chloride cells in juvenile Atlantic salmon *Salmo salar*. *Aquaculture*, *45*, 8–97.

Larsen, M. H., Thorn, A. N., Skov, C., & Aarestrup, K. (2013). Effects of passive integrated transponder tags on survival and growth of juvenile Atlantic salmon *Salmo salar*. *Animal Biotelemetry*, *1*, 1–7.

Leyzerovich, K. A. (1973). Dwarf males in hatchery propagation of the Atlantic salmon. *Journal of Icthyology*, *13*, 382–392.

Lundqvist, H., Clarke, W. C., & Johansson, H. (1988). The influence of precocious sexual maturation on survival to adulthood of river stocked Baltic salmon, *Salmo salar*, smolts. *Holarctic Ecology*, *11*, 60–69.

Mills, D. (1971). *Salmon and trout*. Oliver & Boyd.

Mobley, K. B., Aykanat, T., Czorlich, Y., House, A., Kurko, J., Miettinen, A., Moustakas-Verho, J., Salgado, A., Sinclair-Waters, M., Verta, J. P., & Primmer, C. R. (2021). Maturation in Atlantic salmon (*Salmo salar*, Salmonidae): A synthesis of ecological, genetic, and molecular processes. *Reviews in Fish Biology and Fisheries*, *31*, 523–571.

Myers, R. A. (1984). Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *41*, 1349–1353.

Myers, R. A., Hutchings, J. A., & Gibson, R. J. (1986). Variation in male parr maturation within and among populations of Atlantic salmon *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, *43*, 1242–1248.

Niemelä, P. T., Klemme, I., Karvonen, A., Hyvärinen, P., Debes, P. V., Erkinaro, J., Sinclair-Waters, M., Pritchard, V. L., Härkönen, L. S., & Primmer, C. R. (2022). Life history genotype explains variation in migration activity in Atlantic salmon (*Salmo salar*). *Proceedings of the Royal Society B*, *289*, 20220851.

Österdahl, L. (1969). The smoltrun of a small swedish river. In T. G. Northcote (Ed.), *Symposium on Salmon and Trout in streams – H.R. MacMillan lecture in fisheries* (pp. 2015–2215). University of British Columbia.

Perrier, C., Normandeau, É., Dionne, M., Richard, A., & Bernatchez, L. (2014). Alternative reproductive tactics increase effective population size and decrease inbreeding in wild Atlantic salmon. *Evolutionary Applications*, *7*, 1094–1106.

Power, G. (1969). *The salmon of Ungava Bay*. Arctic Institute of North America, Technical Paper No. 22, 1–73.

Prouzet, P. (1981). Observation d'une femelle de tacon de saumon atlantique (*Salmo salar* L.) parvenue a maturite sexuelle en riviere. *Bulletin Français de la Pêche et de la Pisciculture*, *282*, 16–19.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rodger, J. R., Honkanen, H. M., Bradley, C. R., Boylan, P., Prodöhl, P. A., & Adams, C. E. (2021). Genetic structuring across alternative life-history tactics and small spatial scales in brown trout (*Salmo trutta*). *Ecology of Freshwater Fish*, *30*, 174–183.

Rowe, D. K., & Thorpe, J. E. (1990). Differences in growth between maturing and non-maturing male Atlantic salmon, *Salmo salar* L., parr. *Journal of Fish Biology*, *36*, 643–658.

Saunders, R. L., Henderson, E. B., & Glebe, B. D. (1982). Precocious sexual maturation and smoltification in male Atlantic salmon (*Salmo salar*). *Aquaculture*, *28*, 211–229.

Shaw, J. (1836). An account of some experiments and observations on the parr and the ova of the salmon, proving the parr to be the young of the salmon. *The Edinburgh New Philosophical Journal*, *21*, 99–111.

Stearns, S. C. (1980). A new view of life-history evolution. *Oikos*, *35*, 266–281.

Sutterlin, A., & Maclean, D. (1984). Age at first maturity and the early expression of oocyte recruitment processes in two forms of Atlantic slamon *Salmo salar* and their hybrids. *Canadian Journal of Fisheries and Aquatic Sciences*, *41*, 1139–1149.

Thorpe, J. E. (1986). Age at first maturity in Atlantic salmon (*Salmo salar* L.) freshwater period influences and conflicts with smolting. In D. J. Meerburg (Ed.), *Salmonid age at maturity. Canadian Special Publications in Fisheries and Aquatic Science* (Vol. *89*, pp. 7–14). Natural Resource Council of Canada.

Thorpe, J. E. (1994). Reproductive strategies in Atlantic salmon, *Salmo salar* L. *Aquaculture Research*, *25*, 77–87.

Thorpe, J. E., & Metcalfe, N. B. (1998). Is smolting a positive or a negative developmental decision? *Aquaculture*, *168*, 95–103.

Thorpe, J. E., & Morgan, R. I. G. (1980). Growth-rate and smolting-rate of progeny of male Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology*, *17*, 451–460.

Whalen, K. G., & Parrish, D. L. (1999). Effect of maturation on parr growth and smolt recruitment of Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*, 79–86.

Yevropeytseva, N. V. (1962). *Comparative analysis of the process of desmoltification in the young of different ecological forms of the Atlantic salmon*. (Doctoral Thesis No 311). Leningrad State University, Russia.

How to cite this article: Lothian, A. J., Rodger, J., Wilkie, L., Walters, M., Miller, R., Conroy, C., Marshall, S., MacKenzie, M., & Adams, C. E. (2023). Smolting in post-sexually mature male Atlantic salmon (*Salmo salar* L.) parr in the wild. *Ecology of Freshwater Fish*, *00*, 1–7. https://doi.org/10.1111/eff.12755