





# Genetic structuring across alternative life-history tactics and small spatial scales in brown trout (*Salmo trutta*)

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## Abstract

Facultative migration occurs when, in response to prevailing conditions, individuals in a population may (or may not) undertake a migration. The brown trout (*Salmo trutta*) is a species that exhibits facultative migration, where some individuals within populations may move to mainstem rivers (fluvial-adfluvial migration), lakes (lacustrine-adfluvial migration), estuaries (partial anadromy) or sea (anadromy) to feed, while others remain resident. This study attempts to separate two alternative hypotheses for the population structuring that underpins the expression of facultative migration in this species: (a) that anadromous and nonanadromous fish comprise two gene pools; (b) that individual genetic variation or individual variation in gene-environment interactions is responsible for the expression of different life-history tactics within the same gene pool. The study design involved sampling and analyses of anadromous and nonanadromous brown trout from three independent tributary rivers known to produce (sea-run) trout within the same catchment. Results indicate that, in all cases, population genetic divergence was linked to geographical location and not to life-history tactics. Two genetically distinct coexisting population pairs were identified in two separate tributaries. Despite similar environmental conditions in both tributaries, the frequency of each life-history tactic (anadromy vs. nonanadromous) within these population pairs differed significantly. The results of this study support the hypothesis that facultative migration in brown trout is likely to be driven by a quantitative threshold trait, where the threshold value varies both among populations and among individuals within populations.

## KEYWORDS

anadromy, brown trout, co-habiting, facultative migration, life history, structuring

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## 1 | INTRODUCTION

Facultative migration occurs when an individual may or may not undertake a migration, and where the alternative options are influenced by context. If some individuals in a population do migrate and others do not, then “partial migration” is the term frequently used to describe this phenomenon, which is one of the most common migratory patterns observed in nature. Individuals expressing resident or migratory life-history tactics are most likely to segregate spatially either for foraging or breeding (Chapman, Brönmark, Nilsson, & Hansson, 2011). A wide range of species across multiple taxa exhibit migration patterns where, some but not all, individuals migrate. These include for instance, birds: for example lapwings (*Vanellus vanellus*) (Lundberg, 1988), mammals: for example savanna elephants (*Loxodonta africana*) (Purdon, Mole, Chase, & van Aarde, 2018) and fish: for example roach (*Rutilus rutilus*) (Brodersen et al., 2014). Even in the best studied systems, however, there is still an incomplete understanding of the mechanisms driving the migratory decision of individuals within populations (Chapman et al., 2011; Dodson, Aubin-Horth, Thériault, & Páez, 2013; Ferguson, Reed, Cross, McGinnity, & Prodöhl, 2019). The brown trout (*Salmo trutta* L.) provides an interesting example of a species characterised by resident and facultative migratory life-history tactics. For the former, brown trout can either be resident within rivers (river-resident) or lakes (lake-resident) for their entire life cycle. In both instances, localised dispersal movements are common (Jonsson, Jonsson, & Jonsson, 2018; Vøllestad et al., 2012). Most brown trout populations, however, are migratory with individuals moving between spawning (rivers) and feeding grounds on a regular basis, following a temporally predictable pattern. Migration can take place to a larger tributary or mainstem of a river (fluvial-adfluvial migration), to a lake (lacustrine-adfluvial migration), to an estuary (partial anadromy) or to the open sea (anadromy) (Charles, Roussel, & Cunjak, 2004; Ferguson et al., 2019; Hendry, Bohlin, Jonsson, & Berg, 2003; Klemetsen et al., 2003; Samuiloviené & Kontautas, 2012; Wysujack, Greenberg, Bergman, & Olsson, 2009). The process initiating which of these alternative tactics is to be adopted (to migrate or not migrate), is thought to be determined by a quantitative threshold trait controlled by multiple genes and modulated by environmental factors. The migration/ non-migration decision involves two components, a liability trait (or cue) consisting of a normally distributed trait explaining some features of the individual's condition controlled by both environmental signals and genes, and a genetically determined threshold for that condition (Ferguson et al., 2019). When the condition of an individual, which is sensitive to a continuously varying environmental cue (e.g. food availability and/ or temperature) exceeds the genetically predefined threshold value, residency occurs (i.e. no migration). On instances when the individual's condition is deficient and its physiological condition is lower than the threshold, it adopts a migratory strategy. In summary, the same genotype can result in different decisions regarding the life-history tactic as a consequence of environmental variability resulting in variation in the physiological condition cue (see Ferguson et al., 2019 for a comprehensive review). Thought to

be a consequence of homing behaviour to natal breeding sites, brown trout have been shown to form genetically discrete populations over relatively short geographic distances (Bernatchez, Guyomard, & Bonhomme, 1992; Carlsson, Olsen, Nilsson, Øverli, & Stabell, 1999; Crozier & Ferguson, 1986; Ensing et al., 2011; Ferguson, 1989, 2006; Finlay et al., 2020). In some places, this can lead to more than one brown trout population sharing the same local environment in the absence of obvious barriers to gene flow (Bernatchez et al., 1992; Carlsson et al., 1999; Finlay et al., 2020). Of particular interest, in the context of this study, are coexisting genetically distinct brown trout populations, which are known to produce anadromous (sea-run migratory) and nonanadromous (river resident) individuals. Populations differing in their relative composition of anadromous and nonanadromous brown trout sharing the same local environment may result from either of two main scenarios. In the first scenario, anadromous and nonanadromous brown trout may be comprised of two separate genetic groups. Under this hypothesis, the threshold value for migration differ between populations and drives the expression of migration differences. Thus, one population would have a lower average genetically predefined threshold trait value leading to a high incidence of one tactic while the other, with a higher average genetically predefined threshold trait value, would be characterised by a high incidence of the alternative tactics (Chapman et al., 2011; Dodson et al., 2013; Ferguson et al., 2019; Pulido, 2011).

An alternative scenario is that anadromous and nonanadromous brown trout belong to the same gene pool (i.e. Mendelian population). Under this scenario, the two life-history tactics are maintained by individual variation within a single population (Chapman et al., 2011; Dodson et al., 2013; Ferguson et al., 2019; Pulido, 2011) and, as summarised earlier, the decision to migrate or not is determined by the individual's physiological condition cue. Thus, any individual fish drawn from a single Mendelian population may differ in their genetically predefined threshold value for the expression of migration or in their exposure to environmental variables that result in the threshold being reached or a combination of both (Chapman et al., 2011).

Discriminating between these two hypotheses is challenging. Several studies have investigated whether anadromous and nonanadromous brown trout coexisting in the same area belong to the same population. With a few exceptions, most studies have shown no genetic differences between anadromous and nonanadromous brown trout (Charles, Guyomard, Hoyheim, Ombredane, & Baglinière, 2005; Charles, Roussel, Lebel, Baglinière, & Ombredane, 2006; Cross, Mills, & de Courcy Williams, 1992; Hindar, Jonsson, Ryman, & Ståhl, 1991; Petersson, Hansen, & Bohlin, 2001). In a few instances, however, genetic differences have been noted between anadromous and nonanadromous brown trout sharing the same local environment (Kreig & Guyomard, 1985; Skaala & Naevdal, 1989). One of the main problems of such studies is that it is difficult to differentiate between individuals adopting alternative life-history tactics. It is often the case that anadromous individuals can only be identified once they have become smolts. Thus, sampling juvenile brown trout before external indicators of this transformation are evident

can lead to misidentification of the life-history strategy adopted (Ferguson, 2006; Ferguson et al., 2019).

The aim of the work described here is to attempt to discriminate between the two alternative explanations for facultative migration to estuary or to sea (partial or complete anadromy) patterns in the wild. Specifically, this study examined associations between within-river genetic population structuring on the adoption of alternative life-history tactics by brown trout in the Foyle catchment, Ireland.

## 2 | MATERIALS AND METHODS

### 2.1 | Collection of samples

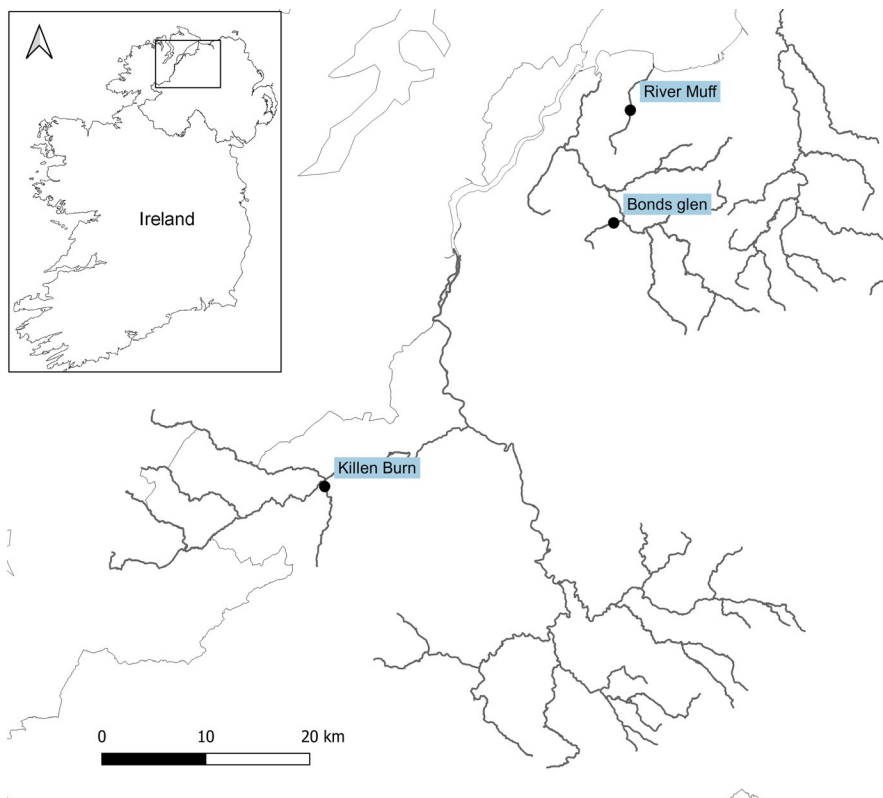
The River Foyle is a large dendritic river catchment of around 4,500 km<sup>2</sup> (Figure 1) (Dauphin, Prévost, Adams, & Boylan, 2010). Three tributary rivers (River Muff, Bonds Glen and Killen Burn) of the Foyle catchment, known for their sea trout runs, were selected for detailed examination of potential genetic structuring of coexisting anadromous and nonanadromous brown trout (Figure 1). Samples of anadromous and nonanadromous brown trout were collected at all three sites by electrofishing. The same one kilometre stretch of each tributary river was sampled in both 2013 and 2014 (Table 1). Anadromous brown trout were collected by electrofishing in April/May, and nonanadromous brown trout were collected in June–August from the same location (after the period of migration to sea for that year was complete). Only brown trout that met specific criteria for defining anadromous and nonanadromous were included in the study. Anadromous brown trout were defined by a silvering on

the epidermis and an elongated body (smolt stage). Nonanadromous brown trout were defined as those individuals lacking silvering on their epidermis, retaining their juvenile colouration and having a fork length (mm) greater than the longest anadromous brown trout caught at each individual site in each year. We acknowledge that the criteria employed to differentiate between anadromous and nonanadromous individuals are not without caveats. For instance, brown trout exhibiting potamodromy (fluvial–adfluvial and/or lacustrine–adfluvial migration) may also exhibit silvering (Ferguson et al., 2019). We argue, however, that since there are no lakes and/or large tributary rivers downstream of the sampling sites used in this study, it is unlikely that such fish formed part of our sampling. Furthermore, as outlined above, all three tributary rivers are known for the presence of sea trout. Thus, we are confident that all brown trout smolts identified in this study migrated to marine habitats.

Following the criteria described above, 217 individual brown trout were available for analysis (81 and 136 nonanadromous and anadromous individuals respectively). These were anaesthetised using clove oil and a nondestructive (fin-clip) tissue sample collected and stored in molecular grade ethanol. A measurement of fork length (mm) and weight (g) was also taken for each individual.

### 2.2 | Microsatellite analyses

Genomic DNA was extracted from ~20 mg of biopsy tissue samples using the Promega Wizard Genomic DNA Purification kit following the manufacturer's protocol ([www.promega.com](http://www.promega.com)). Extracted genomic DNA was quantified by comparison with a known DNA



**FIGURE 1** Sampling sites within the three studied tributary rivers, which from north to south are as follows: River Muff, Bonds Glen and Killen Burn

**TABLE 1** The number of nonanadromous and anadromous brown trout samples collected from each site

River	Year sampled	Life history	Sample size (N)
Bonds Glen	2013 and 2014	Nonanadromous	20
Bonds Glen	2013 and 2014	Anadromous	20
River Muff	2013 and 2014	Nonanadromous	37
River Muff	2013 and 2014	Anadromous	87
Killen Burn	2013 and 2014	Nonanadromous	24
Killen Burn	2013 and 2014	Anadromous	29

Note: Fork length range of anadromous brown trout varied between sampling sites and year. Adult nonanadromous brown trout used in this study were larger than the longest anadromous brown trout caught each year at each sampling site.

standard on 0.8% 0.5X TBE agarose gels and stained with ethidium bromide and, in all instances, diluted to working concentrations of ~5ng/μl. All samples were screened for 21 microsatellite markers (*Ssa85*, *Oneu9ASC*, *Ssa416UOS*, *Ssa406UOS*, *CA054565*, *CA048828*, *CA053293*, *One102a,b*, *One108*, *One103*, *ppStr2*, *SsaD48*, *Cocl-Lav-4*, *BG935488*, *CA060177*, *Ssa197*, *MHC-I*, *SasaTAPA2*, *SsaD71*, *ppStr3*, *Ssa410UOS*) in two separate multiplex PCR reactions. The rationale for the choice of markers and the specific PCR conditions (including source of PCR primers) for both panels are given in Keenen *et al.* (2013a). A sex identification marker, *salmoYF* (P. Prodöhl unpublished), was included in the second PCR reaction. Resulting PCR products were resolved on an ABI3730XL 96 capillary DNA analyser, and genotyping was carried out using Genemapper V4.1 (Thermo Fisher Scientific). *SsaD48* was removed from the analysis due to inconsistencies in banding patterns, making it unreliable for typing.

### 2.3 | Statistical analysis

Only samples that amplified for 14+ microsatellite marker loci (i.e. at least 70% of genotyped markers) were retained for further analyses. The program COLONY (Jones & Wang, 2010) was used to identify potential full-sibs among the samples. In those instances where full-sibs were identified, the recommendations of Hansen and Jensen (2005) were followed, and a maximum of three randomly selected individuals per family was retained for use in further analyses.

Potential patterns of population genetic structuring between anadromous and nonanadromous brown trout were investigated using the Bayesian statistical framework implemented in STRUCTURE (Pritchard, Stephens, & Donnelly, 2000). STRUCTURE was run hierarchically using 100,000 Markov Chain Monte Carlo steps after a burn-in period of 100,000. STRUCTURE was run 20 times (iterations) for each *K* value (presumed number of populations) that ranged from 1 to 10. The program STRUCTURE Harvester (Earl & von Holdt, 2012) was then used to determine the best *K* value explaining the data using the ad hoc method described by Evanno,

Regnaut, and Goudet (2005) and to produce the input files for CLUMPP (Jakobsson & Rosenberg, 2007), which was employed (using the "Greedy" option) to summarise results from multiple STRUCTURE runs for the best *K*. Resulting STRUCTURE bar plots were visualised using R studio (R Core Team, 2016).

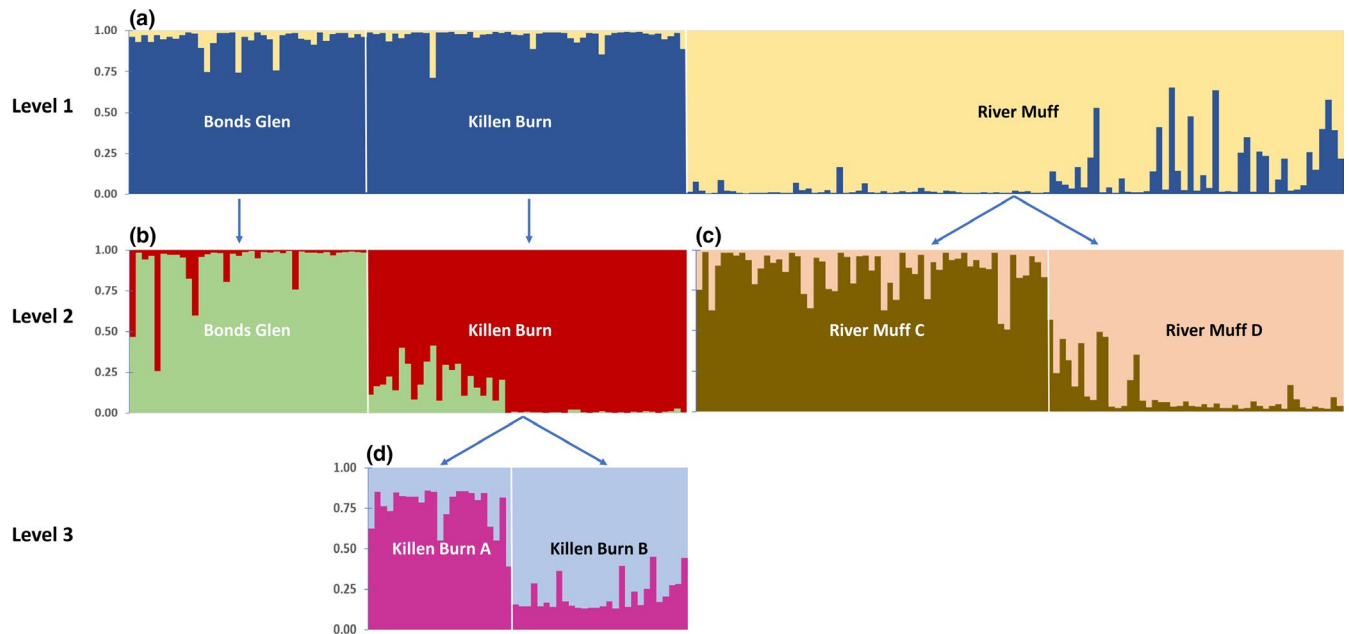
Summary statistics (e.g. allelic richness ( $A_r$ ), observed ( $H_o$ ) and expected ( $H_e$ ) heterozygosity) for the inferred populations were calculated using the R package "diveRsity" (Keenan, McGinnity, Cross, Crozier, & Prodöhl, 2013, R Core Team, 2016). Tests for departure from HWE and Linkage disequilibrium were carried out using "Genepop on the web" ([genepop.curtin.edu.au](http://genepop.curtin.edu.au)) (Raymond & Rousset, 1995; Rousset, 2008). In all instances, Bonferroni correction for multiple tests was employed to reduce the probability of Type 1 errors. Weir and Cockerham's (1984) equivalent ( $\theta$ ) of Wright's *F*-statistics and  $D_{JOST}$  metric of genetic differentiation (Jost, 2008) for both pairwise sample comparisons, and for the whole data set were estimated using "diveRsity." Statistical significance for these estimators was accessed by bootstrapping. Binomial tests were used to examine for potential deviations from the expected 1 male: 1 female sex ratio. These tests were performed between anadromous and nonanadromous brown trout within each genetically defined population.

## 3 | RESULTS

One hundred and ninety-four (74 nonanadromous and 120 anadromous) of the original 217 tissue samples yielded good quality genomic DNA that amplified for more than 70% of the microsatellite markers used.

### 3.1 | Population structure

The first level of analysis in STRUCTURE identified two major clusters, the River Muff and the combined Bonds Glen plus Killen Burn groups (Figure 2a). Thus, at this level, there was no indication of genetic differentiation driven by life-history tactic, only on geographic location. Subsequent hierarchical STRUCTURE analyses (Level 2) identified two groups within the River Muff (Figure 2c) and separated brown trout from Bonds Glen and the Killen Burn (Figure 2b). The third level of STRUCTURE analysis failed to identify additional sub-structuring within the River Muff clusters. Similarly, no further structuring was found in the Bonds Glen genetic cluster. At this level, however, two further genetic sub-clusters were identified within the Killen Burn (Figure 2d). No further structuring was observed for any of the previously identified groups. In summary, five Mendelian populations were identified from the three tributary rivers: one within the Bonds Glen and two coexisting within the River Muff and the Killen Burn respectively. In all instances, the identified populations were defined by geographical location with no evidence of structuring being linked to life-history tactic (Figure 2; Table 2).



**FIGURE 2** Barplots representing individual membership to inferred genetic clusters (represented by different colours) resulting from the hierarchical STRUCTURE analyses of samples derived from the three tributary rivers within the Foyle catchment. a–d represent the outcome results from the first, second and third levels of the hierarchical STRUCTURE analyses. Five genetically distinct populations (Bonds Glen, Killen Burn A, Killen Burn B, River Muff C and River Muff D) were identified within three tributary rivers

**TABLE 2** The number of nonanadromous and anadromous brown trout in each genetic cluster identified and the year(s) the fish were collected

Genetic cluster	Number of freshwater resident brown trout	Year(s) freshwater resident samples collected	Number of anadromous brown trout	Year(s) anadromous samples collected
River Muff C	28	2013/2014	30	2013/2014
River Muff D	6	2013/2014	41	2013/2014
Bonds Glen	18	2013/2014	20	2013/2014
Killen Burn A	20	2013/2014	9	2013/2014
Killen Burn B	2	2013	20	2013/2014

Summary population statistics for the five identified populations are displayed in Appendix (Table A1). There was no significant evidence for deviation from HWE and Linkage Disequilibrium within populations. Pairwise genetic differentiation between inferred populations, based on Weir and Cockerham's  $F_{ST}$ , ranged from 0.023 between Bonds Glen and Killen Burn A to 0.091 between Killen Burn B and River Muff D (Table 3). Equivalent  $D_{JOST}$  estimates ranged from 0.037 between River Muff B and River Muff C to 0.165 between River Muff B and Killen Burn A (Table 3). Overall levels of genetic differentiation were 0.052 (95% CI 0.044–0.060) and 0.113 (95% CI 0.093–0.134) for Weir & Cockerham's  $F_{ST}$  and  $D_{JOST}$  respectively.

While genetic structuring was primarily determined by geographical location, the proportion of anadromous and nonanadromous brown trout significantly differed between coexisting populations identified both in the River Muff and in the Killen Burn (Figure 2c,d; Table 4). Thus, population A in the Killen Burn had a significantly higher proportion of nonanadromous brown trout in comparison with population B and vice versa for anadromous brown trout

**TABLE 3** Pairwise genetic distances between genetically defined brown trout populations based on  $D_{JOST}$  (values below diagonal) and Weir and Cockerham  $F_{ST}$  (values above diagonal)

	Killen Burn A	Killen Burn B	River Muff C	River Muff D	Bonds Glen
Killen Burn A	–	0.031	0.046	0.077	0.023
Killen Burn B	0.060	–	0.056	0.091	0.042
River Muff A	0.072	0.089	–	0.038	0.033
River Muff B	0.165	0.152	0.037	–	0.070
Bonds Glen	0.057	0.103	0.044	0.141	–

Note: All pairwise distances showed a significant difference between population pairs based on the upper and lower 95% confidence intervals.

( $\chi^2 = 15.92_{(1)}$ ;  $p < .001$ ; Figure 2d; Table 4). Similarly, population C, in the River Muff, was characterised by a significantly higher proportion of nonanadromous brown trout in comparison to population D

**TABLE 4** The probability of anadromous and nonanadromous brown trout belonging to each of the two sympatric populations identified in the River Muff and Killen Burn, with significance tested for using a chi-squared test with Yates's correction

	Killen Burn A	Killen Burn B	River Muff C	River Muff D
Probability of anadromous brown trout belonging to cluster	0.31	0.69	0.42	0.58
Probability of nonanadromous brown trout belonging to cluster	0.91	0.09	0.82	0.176
$\chi^2$ (df), p-value	15.92(1); $p < .001$		13.37(1); $p < .001$	

**TABLE 5** The sex ratio of nonanadromous and anadromous brown trout for each population and the significance of the deviation from a 1:1 (female: males) ratio in a binomial test

River	Life history	N	Sex ratio (female: male)	p-value
River Muff C	Nonanadromous	28	3:25	<.001
River Muff C	Anadromous	30	21:9	.042
River Muff D	Nonanadromous	6	0:6	.031
River Muff D	Anadromous	41	25:16	.211
Bonds Glen	Nonanadromous	18	6:12	.238
Bonds Glen	Anadromous	20	16:4	.012
Killen Burn A	Nonanadromous	20	11:9	.824
Killen Burn A	Anadromous	9	5:4	1
Killen Burn B	Nonanadromous	2	1:1	1
Killen Burn B	Anadromous	20	13:7	.263

and vice versa for anadromous brown trout ( $\chi^2 = 13.37_{(1)}$ ;  $p < .001$ ; Figure 2c; Table 4). Therefore, the probability of anadromous brown trout belonging to population B in the Killen Burn and population D in the River Muff is greater than for population A in the Killen Burn and population C in the River Muff.

### 3.2 | Sex ratio

The overall sex ratio of both nonanadromous and anadromous brown trout deviated significantly from the expected 1:1 ratio. Among nonanadromous fish, across the three tributary rivers examined, there was one female for every 2.9 males (binomial test,  $p < .001$ ). Among anadromous brown trout, however, females dominated with two females for every one male (binomial test,  $p < .001$ ). Furthermore, the sex ratio for both nonanadromous and anadromous brown trout was found to be population specific (Table 5). Thus, the sex ratio of nonanadromous brown trout in River Muff C was highly skewed with one female for every 8.3 males (binomial test,  $p < .001$ ). A similar result was recorded in the River Muff D, where no females were present in the sample (binomial test,  $p < .001$ ). These were the only populations where the sex ratio of nonanadromous brown trout significantly deviated from the expected 1:1 sex ratio. For anadromous brown trout, both the River Muff C (2.3 females for every one male (binomial test,  $p < .001$ )) and Bonds Glen populations (four females for every

one male [binomial test,  $p = .012$ ]) had a significantly higher proportion of females than expected (Table 5).

## 4 | DISCUSSION

### 4.1 | Population structuring

Brown trout often form genetically differentiated populations separated by relatively short geographic distances (Carlsson et al., 1999; Finlay et al., 2020). Five populations were identified from three tributary rivers in this study: Bonds Glen, Killen Burn A, Killen Burn B, River Muff C and River Muff D. Thus, two coexisting populations were identified in each of the Killen Burn and River Muff. It is unlikely, that these coexisting populations are truly sympatric but are allopatric, utilising different areas for spawning. However, all five populations were comprised of a mixture of individuals adopting both anadromous and nonanadromous life-history tactics. This study found no evidence that population-level genetic differentiation was primarily driven by differences between brown trout exhibiting anadromous and nonanadromous life-history tactics. Genetic differentiation between and among populations was primarily driven by geography (albeit within the same catchment and in interconnected waters) and not life-history tactics. Thus, this investigation does not support scenario one, that the expressed migration tactic is simply the result of two genetically distinct groups each expressing one of two alternative life-history tactics. The result presented here are in line with the findings of other studies, such as on the River Jörlanda, Sweden where no genetic differentiation was detected between anadromous and nonanadromous brown trout based on the analyses of mitochondrial haplotypes and microsatellite markers (Petersson et al., 2001). Petersson and colleagues demonstrated that there was a greater genetic difference between populations above and below a migration barrier than there was between the coexisting nonanadromous and anadromous brown trout. Similarly, in the Voss River, Western Norway there were greater genetic differences between brown trout at different localities than between coexisting life-history tactics (Hindar et al., 1991). However, two pairs of genetically defined populations showed differences in the rate at which the alternative life histories examined here were expressed. This may in part explain results from some studies examining population genetic differences between anadromous and nonanadromous individuals in the same catchment (see e.g. Kreig & Guyomard, 1985; Skaala & Naevdal, 1989). Where the observed differences between



life-history tactics may, in reality, reflect structuring in populations, which in turn differ in the rate at which they express alternative life histories.

## 4.2 | Sex ratio

In this study, the sex ratio of brown trout adopting alternative migration life-history tactics deviated significantly from the expected 1:1 ratio. Such deviations have been shown elsewhere, for example in the Vangsvatnet Lake, Norway (Jonsson, 1985) and in the Kirk Burn, Scotland (Campbell, 1977). The costs and benefits of a migration, which is an energetic and metabolic demanding process, have been shown to be sex specific (Jonsson & Jonsson, 1993; Sahashi & Morita, 2013). For females, the costs of migration (in particular to the marine environment), which include a higher chance of mortality and a higher energy expenditure, are more likely to be outweighed by the fitness benefits accruing from the ability to reach a larger body size due to an increased food availability than for males. In females, a larger body size enables them to produce larger eggs and in greater numbers, gain better breeding territories, and have a higher success defending their nests (Dodson et al., 2013; Jonsson & Jonsson, 1993). On the other hand, for males, the benefits of a large body size accruing from anadromy are not as clear, as the energetic cost of gamete production is relatively low. Smaller males can thus use sneaker tactics for mating and become principle spawners in the absence of larger males (Ferguson et al., 2019; Jonsson & Jonsson, 1993).

This study suggests that deviations in sex ratio were not only specific to life-history tactic but was also site-specific, with anadromous brown trout in the River Muff and Bonds Glen and nonanadromous brown trout in the River Muff having a sex ratio that significantly deviated from the expected 1:1. The Killen Burn, having the longest migration distance to the sea, was the only sampling location with no deviation from an expected 1:1 sex ratio. Earlier studies have shown that the costs of adopting an anadromous life-history strategy increases with migration distance (e.g. Sahashi & Morita, 2013). Therefore, it is plausible that the higher chance of mortality and increased energy demand associated with the longer migration from the Killen Burn may mitigate any additional advantages for females to adopt an anadromous life-history strategy.

## 4.3 | Adoption of alternative life-history strategies

Although this study demonstrated that nonanadromous and anadromous brown trout were present in all populations, the frequency of each life-history strategy varied significantly between coexisting populations in the River Muff and Killen Burn. The environmental variables that trigger the physiological and behavioural processes leading to migration are, at least partly, understood for salmonids (Dodson et al., 2013; Ferguson et al., 2019). For example, it has been shown that food availability and temperature are among the main

environmental factors triggering facultative migration in brown trout (Nevoux et al., 2019; Peiman et al., 2017). However, it has also been shown that individual condition plays a similarly important role with smaller individuals and individuals in poor condition being more likely to adopt an anadromous life-history tactic (Peiman et al., 2017). Coexisting populations in the River Muff and Killen Burn showed different rates of expression of each of the two life-history tactics, despite being subject to the same broad environmental variables. There are two possible explanations for this. Firstly, nonanadromous and anadromous brown trout were sampled from the same stretch of river. Therefore, it is possible that a proportion of anadromous brown trout sampled during the smolt run originated from further upstream and the nonanadromous brown trout for this population were under-sampled. The second possibility is that this is the result of different inherited average thresholds between different populations (Dodson et al., 2013; Piché, Hutchings, & Blanchard, 2008). A common garden experiment or genomics approach would be needed to determine whether a difference in threshold trait is responsible for the difference in frequency of anadromy and nonanadromy in coexisting brown trout populations. However, despite evidence of between population variation in the expression of the alternative life-history traits of migration, the clear conclusion of this study is that the biggest driver in differences in the expression of these alternative life-history tactics is between individual variation in the probability of migration within a single population (scenario 2). There are three mechanisms through which this could occur. Thus, this could be the result of within family inherited differences in the quantitative threshold value of the traits that triggers migration (Dodson et al., 2013; Ferguson, 2006; Ferguson et al., 2019). This explanation is supported by the finding of differences in the expression of migratory life-history strategy of the coexisting populations (Killen Burn and River Muff) in this study. Alternatively, individual variation in the expression of the migratory life-history tactic may result from between individual differences in exposure to the environmental conditions that trigger migration (Metcalf, Huntingford, Graham, & Thorpe, 1989). We cannot discount this mechanism with the data from this study. The third, and most likely explanation, is that individual variation in expression of life-history tactic results from a combination of both genetic and environmental factors (Ferguson et al., 2019; Nevoux et al., 2019).

One consequence of migration as an adaptive trait being facultative is that, although directional selection may favour one migration tactic over another, it is less likely to result in the complete loss of the capacity to express that alternative migration tactic, as that phenotype is not likely to be expressed (as it is facultative) and, thus, will remain hidden from selection (Dodson et al., 2013). The expression of facultative migration as an adaptive trait would have significant fitness advantages for species that live in highly variable environments, such as brown trout. Thus, facultative migration will persist in a population when the relative costs and benefits of migration differs between individuals in the population. It is more likely to persist if the relative costs and benefits are also dependent upon the frequency of conspecifics adopting each

strategy. Under such conditions, different individuals may achieve high fitness through alternative routes and the relative proportion of the population expressing alternative migration tactics may fluctuate in response to the prevailing environmental conditions, such as food availability (Dodson et al., 2013; Ferguson et al., 2019; Roff, 1996).

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTIONS

The study was designed in detail and concept by Patrick Boylan, Paulo A. Prodöhl and Colin Adams. The field element of the study was executed by Jessica Rodger and Hannele Honkanen, the laboratory analysis by Jessica Rodger and Caroline R. Bradley. Data analysis was conducted by Jessica Rodger, Paulo A. Prodöhl and Caroline R. Bradley. All authors contributed to data interpretation and manuscript preparation and editing.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## APPENDIX

**TABLE A1** Summary statistics for populations which includes

River	N	A	%	Ar	H <sub>o</sub>	H <sub>e</sub>
Killen Burn A	29	197	81.1	8.06	0.7	0.73
Killen Burn B	22	150	68.2	6.62	0.67	0.69
River Muff C	47	168	71.5	6.57	0.63	0.64
River Muff D	58	138	59.7	5.61	0.58	0.61
Bonds Glen	38	202	83.8	8.05	0.69	0.71

N—The number of individual samples in each population, A—Number of alleles per population, %—Percentage of total observed alleles, Ar—Allelic richness, H<sub>o</sub>—observed heterozygosity and H<sub>e</sub>—expected heterozygosity.