




Sex- and length-dependent variation in migratory propensity in brown trout

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Funding information

Eawag Swiss Federal Institute of Aquatic Science and Technology; Swiss National Science Foundation grant (31003A_153296)

Abstract

In partially migratory species, individuals either migrate at some point(s) in life or reside within their natal habitat throughout life. For salmonid fish, migration creates opportunities for feeding and growth, but it is also associated with increased mortality risk. Such trade-offs likely differ between the sexes, since reproductive output is more closely tied to body size in females than males. However, testing hypotheses on sex-specific migratory behaviour in would-be first-time migratory salmonids is difficult, since sexes are generally morphologically indistinguishable prior to maturation. Previous studies have evaluated the influence of sex on migration based on dissection of migratory juveniles or the sex ratio of returning adults. However, both approaches are potentially biased by differential survival during migration. Here, we utilise advances in minimally invasive genetic sex-determination methods for salmonids to investigate sex-specific, spring out-migration propensity in potamodromous brown trout (*Salmo trutta*) in a pre-Alpine, central European lake. We show that there are marked differences in migratory behaviour between males and females, with small (~10 cm) females being approximately twice as likely to migrate out of their natal river in spring compared to similarly sized males, which generally migrate for the first time at larger sizes (in similar proportions to larger females). This study highlights how novel genetic sex-determination techniques can provide insight into the sex- and size-specific life-history trade-offs that shape migration propensity. Moving forward, these techniques should become useful tools for ecologists and fisheries managers.

KEYWORDS

migration, passive telemetry, potamodromy, predation-growth trade-off, *Salmo trutta*, sdY gene

Edward Lavender and Yannick Hunziker should be considered joint first author.

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1 | INTRODUCTION

Migrations occur throughout the animal kingdom and allow individuals to exploit spatio-temporal variation in resource availability (Fudickar et al., 2021; Hays et al., 2016). While migrating can be advantageous, for example, in terms of better feeding and growth opportunities and ultimately higher reproductive output, it can also incur significant costs, such as increased energy use or mortality (Chapman et al., 2011; Sabal et al., 2021). In evolutionary ecology, these conflicts are formalised in terms of evolutionary trade-offs (Chapman et al., 2011; Sabal et al., 2021; Stearns, 1989). In the presence of trade-offs, variation in individual traits within a population and their interaction with extrinsic factors can lead to partial or facultative migration, with some individuals migrating, while others stay resident (Berg et al., 2019; Brodersen et al., 2014; Chapman et al., 2011; Menz et al., 2019). While the drivers of partial migration are not fully understood, studies show that migration propensity is shaped by both genetic factors and phenotypic plasticity, and dependent upon many intrinsic (e.g. sex and size) and extrinsic (e.g. predation risk and temperature) conditions (Hulthén et al., 2015; Pearse et al., 2019; Pulido, 2011; Wysujack et al., 2009). For example, in many systems, the predation risk–growth (P/G) trade-off model appears to explain at least some variation in migration propensity, with smaller, more vulnerable individuals often (but not exclusively) less likely to risk migration than larger individuals, who preferentially undertake migration to realise enhanced growth opportunities (Brönmark et al., 2008; Dermond et al., 2019; Skov et al., 2014). However, understanding how the balance between the risks and opportunities of migration is shaped by intrinsic and extrinsic factors remains a key area of research in evolutionary ecology (Sabal et al., 2021).

Sex is a fundamental intrinsic trait that influences many aspects of life history (Stearns, 1992; Trivers, 1972). Sex-specific differences are often linked to a disparity between the size of eggs and sperm (i.e. anisogamy), such that females typically invest more energetic reserves in gamete production than males (Hayward & Gillooly, 2011; Trivers, 1972). This means that female fecundity is often limited by gamete production, while male fecundity is constrained by access to females (Trivers, 1972). In fishes, these constraints have been suggested to impose a strong selection pressure on female body size, which is closely associated with egg production (Barneche et al., 2018; Parker, 1992). This effect may be amplified in species that rely on external fertilisation, where fecundity is often increased to counterbalance the low survival prospects of offspring (Pianka, 1970). In males, female choice and competition can favour larger body sizes too (Kim et al., 2021; Rueger et al., 2016; Scherer et al., 2018), but smaller (subordinate) males can also sire offspring through other mechanisms, such as sneak spawning, which may weaken the size–fecundity relationship in some settings (Kim et al., 2021; Ota et al., 2014). In partially migrating taxa, and in the context of a P/G trade-off, these observations lead to the general prediction that (all else being equal) the optimal balance between minimising predation risk and maximising growth should be reached

at smaller sizes in females, such that females (and especially small females) should be more likely to migrate (and migrate earlier) than similarly sized males.

In salmonids, partial migration is widespread (Arostegui & Quinn, 2019a; Ferguson et al., 2019; Klemetsen et al., 2003). All offspring hatch and undergo juvenile development in the natal habitat, but some individuals mature and reproduce within the same area, while others migrate to oceans (anadromy) or lakes/larger rivers (potamodromy) to exploit enhanced feeding and growth opportunities (Arostegui & Quinn, 2019a; Ferguson et al., 2019). Migratory individuals then return to their natal habitat to spawn at considerably larger sizes than resident conspecifics (Ferguson et al., 2019; Fleming & Reynolds, 2004). Migratory females typically have a higher fecundity and tend to produce larger eggs (Bagenal, 1969), which correlates positively with offspring survival (Einum & Fleming, 1999). Larger, migratory males also have higher success in competitions for females, but smaller, resident males can achieve mating success via sneak or mimetic reproductive strategies (Esteve, 2005; Garcia-Vazquez et al., 2001; Sloat et al., 2014). Collectively, these observations suggest a difference between male and female salmonids in the optimal balance of the P/G trade-off as it pertains to migration. However, most studies to date have been conducted on anadromous populations, and the movements of potamodromous populations remain less well studied (Arostegui & Quinn, 2019a; Ferguson et al., 2019). Furthermore, since salmonids are generally indistinguishable before maturation, previous studies of sex-specific differences in migratory propensity have focused on the sex ratio of individuals during or following migration, based on dissection of out-migrating juveniles or observations of returning adults, making it difficult to separate differences in migration propensity from differential mortality (Aarestrup et al., 2018; Jonsson, 1985). As a result, differences in the migration propensity of would-be first-time male and female salmonid migrants remain poorly understood.

Novel genetic sex-determination methods provide a unique means to assess (early) life-history differences between sexes in monomorphic taxa. In salmonids, a male-specific sexual dimorphism on the Y-chromosome (the sdY gene) was previously identified in rainbow trout (*Oncorhynchus mykiss*) and later found in 15 other species from all three salmonid subfamilies (Yano et al., 2012, 2013). These discoveries led to the development of molecular methods to distinguish genetically male and female juvenile salmonids, such as the duplex real-time PCR protocol (Anglès d'Auriac et al., 2014).

In this study, we coupled recent advances in salmonid genetic sex-determination with passive telemetry to investigate sex- and size-specific differences in the migratory propensity of brown trout (*Salmo trutta*) in afferent streams near Lake Lucerne in Switzerland. In this system, we have observed partial potamodromous (lacustrine–adfluvial) migration, with a portion of individuals remaining resident in natal streams while others migrate into the lake in spring for a period of growth, before returning to streams from September–January to overwinter (Dermond et al., 2019). Previous work in this system has suggested that variation in migration propensity can be partly explained by a version of the P/G trade-off model, with

smaller individuals tending to migrate later in the season as their growth potential outweighs elevated predation risks in the lake (Dermond et al., 2019). However, the differential benefits of larger sizes between would-be first-time female and male migrants remain unstudied. In this study, we hypothesised a sex- and size-dependent P/G trade-off shapes initial migration propensity. We tested two specific predictions of this hypothesis, denoted P1–P2:

(P1) Females are more likely to migrate, especially at smaller body sizes, into the lake than males.

(P2) First-time female migrants should migrate earlier in spring than equivalently sized males.

2 | MATERIALS AND METHODS

2.1 | Study area

We studied the migratory propensity of brown trout in seven groundwater-fed streams that drain into Lake Lucerne, a large (114 km²), pre-alpine lake in central Switzerland (Figure 1, Table A1, Appendix S1.1). Five of the studied streams drain directly into the lake; two are located further afield and mouth into a larger stream (the Urner Reuss) that drains into the lake (Figure 1, Table A1). All selected groundwater-fed streams host resident and migratory trout and are consistently characterised by stable flow and temperatures,

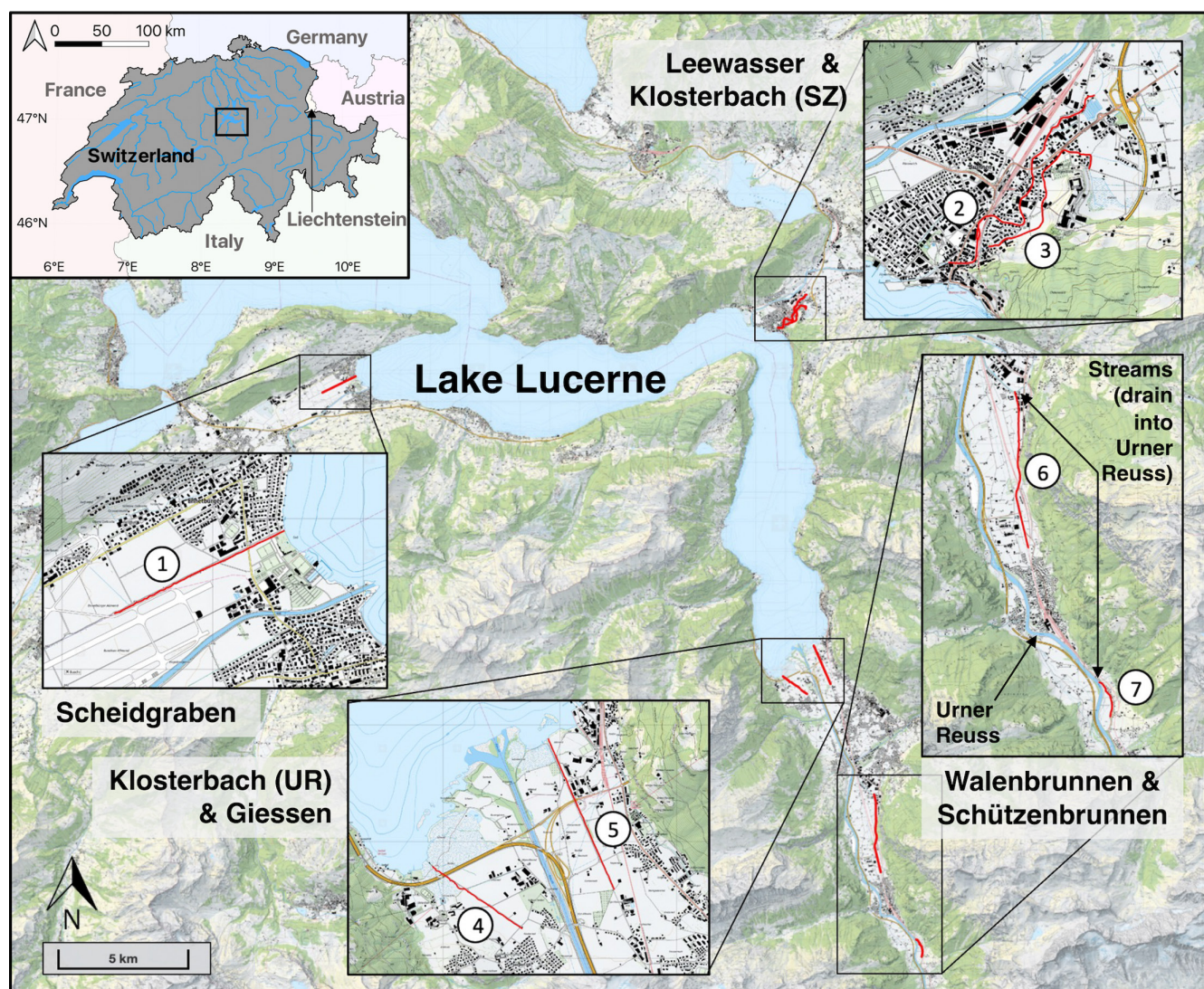


FIGURE 1 The study area. The inset shows the location of Lake Lucerne (enclosed) in Switzerland. The main panel shows the locations of sampled streams: (1) Scheidgraben, (2) Leewasser (Schwyz), (3) Klosterbach (Schwyz), (4) Klosterbach (Uri), (5) Giessen (Uri), (6) Walenbrunnen (Uri) and (7) Schützenbrunnen (Uri). Streams 1–5 drain directly into the lake. Streams (6–7) are located further afield and are tributaries of a larger stream (the Urner Reuss) that drains into the lake. Electrofishing and tagging were conducted in multiple sections along streams. All PIT antennas were located at, or close to, the mouth of each stream (i.e. adjacent to the lake for streams 1–5 and the Urner Reuss in the case of streams 6–7). The latter is a highway for migrating fish but is artificially channelised and subject to hydropeaking in this area and thus not suitable habitat for resident fish. For further details, see Tables A1–A3. Data sourced from the Database of Global Administrative Areas and the Swiss Federal Office of Topography.

making them well suited to studies of migration propensity due to intrinsic factors (namely, sex and size). Most spawning migratory trout in this system are 40–50 cm in length but occasionally can exceed 90 cm (Dermond et al., 2019). In the streams, predation risk is thought to be relatively low (compared to the lake), with the main risk coming from grey heron (*Ardea cinerea*). In the lake, brown trout are principally exposed to predation from perch (*Perca fluviatilis*) and pike (*Esox lucius*), with the latter reaching over 1 m in size (Dermond et al., 2019). All fieldwork in this region was reviewed by Eawag and the Veterinary Office of the Four Cantons and authorised under research permits LU01/14.

2.2 | Sampling

Streams were divided into sections for the study, from section one, situated as close as possible (≈ 50 m) to the stream mouth, to additional sections further upstream (Tables A1 and A2). Fish were captured in February and March 2015 by electrofishing, following the methods described in Dermond et al. (2019) (Tables A1–A3). Electrofishing locations were situated 0–1787 (median = 605) m from the first section (or 74–11,962 [median = 1148] m from the lake) (Figure 1, Table A2). Each stream was fished on 2–3 occasions, resulting in similar numbers ($n = 76$ –98) of captured individuals across streams (Table A1). Total body length and standard body length (± 0.1 cm) were measured from the most anterior point of the head to the tip of the tail and the most posterior point of the hypural plate respectively. Fish exceeding a total length of 10.5 cm (≈ 8.9 cm standard length and ≥ 1 year old) were anaesthetised, using a MS222 solution (1 g Tricaine-S/15 L stream water), and tagged with a Passive Integrated Transponder (PIT) tag (model: 23 mm HDX+ PIT Tag; weight: 0.6 g; manufacturer: Oregon RFID, Portland, USA). The tag was inserted into the abdominal cavity via a small abdominal incision that was sealed with Koi Med Wound Snow antifungal powder. The 10.5 cm threshold approximately corresponds to the 10 cm fork length recommended for Atlantic salmon (*S. salar*) by Larsen et al. (2013) and was selected to minimise possible effects of tagging on growth rate or mortality effects. A small sample of adipose fin tissue was taken and stored in 100% analytical standard ethanol at -20°C for subsequent genetic analysis. Prior to release in the capture section, tagged fish were held in an oxygenated recovery tank. For this study, we focused on $n = 629$ potential first-time migrants (which are generally juvenile) identified from phenotypic examination (pre-migratory individuals are generally red-brown in colour, lacking the silvery seen in migratory individuals and have smaller, less fusiform bodies) (Arostegui & Quinn, 2019b; Holecek et al., 2012; Piironen et al., 2013; Schulz, 1999).

2.3 | Passive telemetry

At the start of the first (most downstream) section in each stream, we placed two stationary PIT antennas (Oregon RFID, Portland,

USA), separated by a distance of approximately 10 m, to identify migration events (Figure 1, Table A1). The antennas act as high-frequency readers that detect tags within range, up to 14 times per second. We identified individuals as 'downstream migrants' if both of the following criteria were met: (1) a detection was recorded between the date of tagging and 30 June, 2015 (i.e. during the normal period of downstream migration) (Dermond et al., 2019) and (2a) the final detection in the migratory period was recorded at the antenna nearest to the stream mouth or (2b), for fish only detected at the upstream antenna, the duration between the first and last detection was less than 10 s. The alternative criterion (2b) comes from the observation that individuals moving rapidly downstream may not be detected by both antennas, due to high velocity or sideways drift (PIT tags need to move at an approximately perpendicular angle to an antenna to be detected). The 10 s threshold assumes that individuals that were only detected at the upstream antenna for a short period were 'downstream migrants' (given the lack of subsequent detections) while excluding individuals exploring or foraging in this area. For the two streams draining indirectly into the lake (via the Urner Reuss), we are confident that antenna detections indicate migration as the downstream environment of the Urner Reuss, which is artificially channelised and subject to hydropeaking, is not a suitable habitat for residency (Figure 1).

2.4 | Sex-determination (duplex PCR)

In 2018, we used a sex-determination method based on the duplex real-time PCR method to identify the sex of individuals captured and tagged in the telemetry study from tissue samples (Anglès d'Auriac et al., 2014; Quéméré et al., 2014). This method targets the sdY gene (present on the Y chromosome in males) and an 18S positive control (present in both sexes). Individuals that result in amplification of both PCR products are identified as genetically male, while individuals that only result in amplification of the 18S PCR product are identified as genetically female (Figure A1).

DNA was extracted from tissue samples using a standard Chelex extraction protocol. Each tissue sample was extracted in 165 μL of Chelex extraction buffer (150 μL of 5% Chelex solution + 10 μL of TE buffer + 5 μL of Proteinase K). After the addition of the tissue to the Chelex buffer, the tubes were vortexed, briefly centrifuged and then incubated in a Labcycler Thermoblock 96 PCR machine (SensoQuest GmbH, Göttingen, Germany) at 55°C for 2 h, followed by 10 min at 99°C , with a final holding temperature of 4°C . For the PCR, we used the same primer sequences as in Anglès d'Auriac et al. (2014) but applied them to a conventional duplex PCR protocol (Table A4). The reason for applying the sdY assay to a conventional PCR setup is that it utilises more readily available equipment, facilitating uptake of the method by fish biologists. Several different reaction set-ups and thermal profiles were tested; however, the following protocol was found to yield the clearest PCR products. Each reaction contained 25 μL of Master Mix (Qiagen GmbH, Hilden, Germany), 400 nM and 100 nM of both forward and reverse

sdY and 18S primers, respectively, 12.5 µL of H₂O and 10 µL of DNA (200 ng), adding up to a total volume of 50 µL. The PCR thermal profile was as follows: 95°C for 15 min, followed by 35 cycles of 94°C for 30 s, 63°C for 90 s and 72°C for 90 s, with a final extension step of 10 min at 72°C. PCR reactions were performed in 96-well plates and on a Labcycler Thermoblock 96 PCR machine. PCR products were separated using a 1.5% agarose gel (Promega Corporation, Madison, USA) in 1X TBE buffer (BioConcept Ltd., Allschwil, Switzerland). A total quantity of 5 µL of each PCR product was run with 4 µL of loading dye (Gel Loading Dye 6x, BioLabs, Ipswich, USA) alongside a BenchTop 100 bp Ladder (Promega Inc., Madison, USA). Gels were then stained in a 2% ethidium bromide solution for 10 min, before being visualised with a Fusion Fx7 UV illuminator (Witec AG, Sursee, Switzerland). An image of each UV illuminated gel was captured using FusionCapt Advance software (Vilber Lourmat, Marne-la-Vallée, France).

We validated the above protocol for genetic sex-determination with a sample of 20 adult fish (10 females, 10 males) of known sex, captured in November 2018. The genetic sex of each individual was determined from anonymised PCR results. Genetic sexes were compared against phenotypic sexes, determined from assessment of secondary sexual characteristics (e.g. the hooked lower jaw in males) and gametes. All 20 fish were successfully assigned the correct sex. We therefore proceeded to determine individual sex using this method for all studied individuals.

2.5 | Statistical analyses

Statistical analyses were implemented in R, version 4.2.3 (R Core Team, 2023). To test for sex- and size-dependent differences in the probability of spring out-migration (P1), we modelled downstream migration (0, 1) as a Bernoulli random variable in relation to an interaction between sex and standard length, with additional terms included to account for variation in the time (*day*) of tagging (T), between stream sections (within streams) and among streams. We considered generalised linear and additive mixed model (GLMM and GAMM) formulations (i.e. linear and non-linear forms of the interaction between sex and standard length) but a GAMM formulation was preferable (see Appendix S1.2). The best model took the form:

$$\begin{aligned} \text{migration}_{i,j,k} &\sim \text{Bernoulli}(p_{i,j,k}) \\ \text{logit}(p_{i,j,k}) &= \text{sex}_i + f(\log(\text{length}_i), \text{sex}_i) + g(\text{day}_i^T) + \zeta_{j[i]}^{\text{stream}} + \zeta_{k[j[i]]}^{\text{section}} \\ \text{logit}(p_{i,j,k}) &= \log\left(\frac{p_{i,j,k}}{1-p_{i,j,k}}\right) \\ \zeta_{j[i]}^{\text{stream}} &\sim N(0, \sigma_{\text{stream}}^2) \\ \zeta_{k[j[i]]}^{\text{section}} &\sim N(0, \sigma_{\text{section}}^2) \end{aligned} \quad (1)$$

where *i*, *j* and *k* index observations (individuals), streams and sections within streams, *f* is a thin plate regression spline of the effect of standard length by sex, *g* is a cyclic cubic regression spline (with knots at 0 and 365) and ζ denotes random effects for stream and sections within streams with variance σ_{stream}^2 and $\sigma_{\text{section}}^2$. This model fits sex-specific

smooth functions, each with their own degree of 'wiggleness', for the effect of standard length on migration probability (Pedersen et al., 2019). Using this model, we quantitatively compared the predicted probability of migration between 'small' (10 cm) and 'large(r)' (15 cm) females and males (with tagging day held at the median value and excluding the random effects). We also visually evaluated model predictions for the probability of migration in relation to (i) the observed proportion of migrants (out of all individuals) and (ii) the observed proportion of migratory males versus migratory females (out of all migratory individuals), calculated for each 1.5 cm standard length class.

We tested for differences in the timing of out-migration in males and females of different lengths (P2) in a similar way. For this analysis, we evaluated four candidate models of the timing (*day*) of migration (*M*), including two models with sex-specific smoothers of the effect of standard length, one model with sex- and stream-specific effects of standard length and one model that incorporated a main effect of sex and separate stream-specific effects of standard length on migration timing (see Appendix S1.3). The best-supported model included the main effect of sex and stream-specific effects of standard length, and is described by the equation:

$$\begin{aligned} \text{day}_{i,j,k}^M &\sim N(\mu_{i,j,k}, \sigma^2) \\ \mu_{i,j,k} &= \text{sex}_i + f(\log(\text{length}_i), \text{stream}_{j[i]}) + g(\text{day}_i^T) + \zeta_{j[i]}^{\text{stream}} + \zeta_{k[j[i]]}^{\text{section}} \end{aligned} \quad (2)$$

where all terms are as previously defined. We visually compared observations to predictions from this model and quantitatively estimated the expected standard lengths of individuals in selected streams migrating at different times (following the methodology of the previous analysis).

All GAMs were fitted via *mgcv* using restricted maximum likelihood (Wood, 2017). Smooth functions for continuous variables were represented with the default basis dimension (*k* = 10), except for *day*^T for which we deliberately restricted the basis dimension (*k* = 5) to enforce interpretability. We confirmed the default basis dimension was sufficient using the *k*-index diagnostic test implemented by *mgcv*. Model predictions were generated using standard *mgcv* functions. Residuals were evaluated using *mgcv* and DHARMA (Hartig, 2022; Wood, 2017).

3 | RESULTS

Of the 629 fish sampled, 47% (*n* = 298) were female and 53% (*n* = 331) were male (Table A5). Individuals varied in standard length from 8.9 to 24.3 cm, but approximately 95% of individuals were 9.5–18.4 cm and we obtained few samples of either sex from larger individuals (Figure A2). While fish age was not measured, the smallest individuals in this size range are likely to be 1-year-old; individuals ~10–15 cm are expected to be 2 years old; and larger individuals are expected to be at least 3 years old (Figure A2). The sex ratio of sampled individuals varied among streams, ranging from 1:0.63 (male dominance) to 1:1.58 (female dominance). Of all sampled individuals, 247 downstream migrants were identified. Of these, 54% (*n* = 133) were female and 46% (*n* = 144) were male (Table A5).

The propensity of spring out-migration (P1) differed significantly by sex, standard length and stream (Figures 2 and A3, Tables A6 and A7). There was evidence for an interaction between sex and standard length. At small (10 cm) sizes, the expected probability of migration was approximately twice as high (a difference of 15%) on average in females ($\hat{p} = 0.29$) as in males ($\hat{p} = 0.14$), although there was considerable variation (with 95% confidence intervals ranging between 0.15–0.48 and 0.07–0.27 respectively). In both sexes, the expected probability of migration broadly increased and became more similar at larger sizes, with the expected probabilities for an individual of 15 cm ranging between $\hat{p} = 0.41$ (0.25–0.59) and $\hat{p} = 0.35$ (0.21–0.52) for females and males respectively (Figure 2). Accordingly, at small (~10 cm) sizes, approximately 60% of migrant individuals were female, but by 13–15 cm migratory sex ratios approached equality (Figure 3). At larger sizes (from >15 to 24.3 cm), there appeared to be no further, consistent change in the probability of migration (Figure 2), or the relative proportion of male and female migrants (Figure 3), but there is uncertainty in this result given available data. Across all streams, the model of migration propensity fitted the observed proportion of out-migrants in different size classes reasonably well, but both sexes showed some indication of a peak in migration probability for individuals 12.5–14.0 cm in size (with migration probability in males peaking at the larger size) that the model did not fully capture. Overall, deviance explained was 13% (Table A7). Predictions for individual streams followed a similar pattern, but there was substantial variation within streams undescribed by the model (Figure A3).

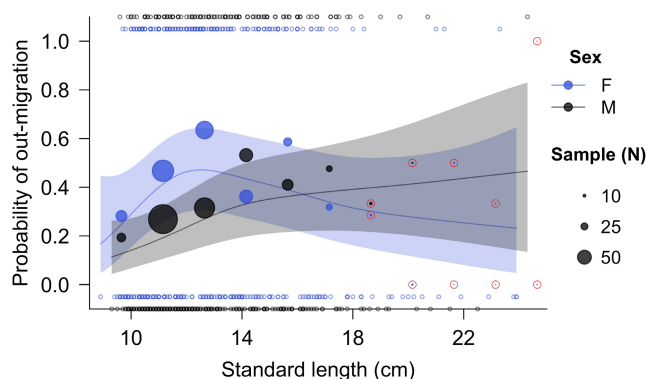


FIGURE 2 The relationship between spring out-migration probability and standard body length in males and females. Filled points mark the observed proportion of migrants in each 1.5 cm length class (and include individuals tagged at different times in different streams/stream sections). Points are shown at the midpoint length for each class. Point size is proportional to the number of individuals in each class. The smallest points are highlighted in red. Lines and envelopes are predictions and 95% confidence intervals from a Bernoulli generalised additive model for migration probability in relation to sex, length, day of tagging, stream and stream section. Predictions are shown for the median tagging day (February 27, 2015) but excluding the random stream and stream/section effects. Open points mark the lengths of resident (top) and migrant (bottom) individuals.

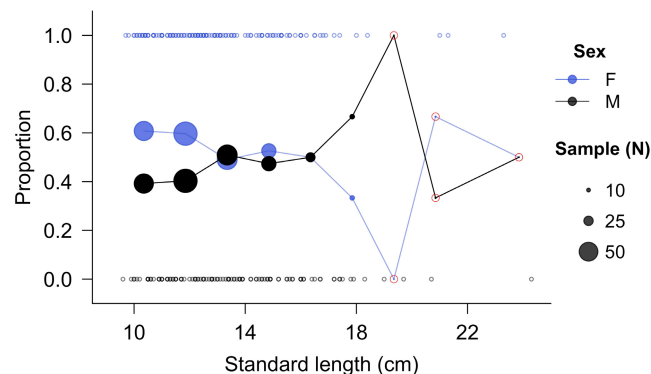


FIGURE 3 The proportion of male versus female migrants at different standard body lengths. Filled points mark the observed proportion of male or female individuals, out of the total number of migrants, in each 1.5 cm length class. Points are shown at the midpoint length for each class. Point size is proportional to the total number of migrants (males and females) in each class. The smallest points are highlighted in red. Open points mark the lengths of migrant males and females.

Among migrant individuals, the timing of migration was significantly associated with standard length, tagging date, stream and section but not sex (Figure 4, Tables A8 and A9). In most (5/7) streams, the first spring migrants were consistently larger than later migrants, irrespective of sex (Figure 4). For example, in Giessen, the expected migration date for 'large' (15 cm) females (20th [11th–29th] April) was approximately 1 month earlier than for smaller (10 cm) individuals (15th [5th–25th] May). These results were similar for males and in the other streams, with the exception of Klosterbach (SZ) and Scheidgraben (Figure 4). In Klosterbach (SZ), there was evidence that larger individuals migrate earlier on average, but the largest (21.3 cm) female migrant remained within the stream for 1 month longer than the next largest (12.1 cm) individual (until mid-June). In Scheidgraben, the largest (≥ 21 cm) individuals were relatively early migrants, but the remaining samples comprised individuals within a small size range (~10–14 cm) making inference difficult. This model explained 53% of the deviance (Table A9). In both the analyses, standard residual diagnostic checks suggest model assumptions were met satisfactorily.

4 | DISCUSSION

This study demonstrates marked differences in the migratory behaviour of male and female brown trout. By coupling a genetic sex-determination protocol with passive telemetry, we show for the first time that the sex-specific propensity of lacustrine-adfluvial out-migration in would-be first-time migratory salmonids is length dependent. At small (~10 cm) sizes, females were approximately twice as likely to undertake spring migration as similarly sized males, while at larger sizes, migration probability increased and became more similar between the sexes, in line with theoretical expectations. The result is a relatively similar sex ratio on average between female

versus male migrants (54: 46%). Among migratory individuals, the timing of migration was notably mediated by length, with larger individuals migrating earlier than smaller individuals, irrespective of sex. Taken together, these results indicate that the 'decision' to migrate depends on both sex and length but, given a decision to migrate, length is the more important mediator of migratory timing.

In line with our first prediction (P1), we found that initial, spring migration propensity from natal tributaries into Lake Lucerne was higher for young female brown trout compared to males. At small sizes, females accounted for approximately 60% of migratory individuals. These results are consistent with the observation that gamete production in females is more expensive than in males and the hypothesis that females have more to gain from migration (Fleming, 1996; Nevoux et al., 2019). A likely part of the explanation for this pattern is the correlation between female body size and fecundity (Klemetsen et al., 2003), such that gaining a larger body size can contribute more to fecundity in females than in males (Fleming & Reynolds, 2004; Nevoux et al., 2019; Sloat et al., 2014). At the same time, it seems likely that smaller (more vulnerable) males may be selected to delay migration (until autumn or the following year), or become residents, and instead mature early as precocious parr, because in so doing, they can minimise predation risks and exploit female mimicry or sneak mating to achieve fertilisation (Esteve, 2005; Garcia-Vazquez et al., 2001; Sloat et al., 2014). In other systems, precocious parr have been documented in brown trout from 1 year

of age (Dębowski & Dobosz, 2017; Pavlov et al., 2020), suggesting this is a potentially relevant consideration across the range of males tagged in this study.

Previous studies have demonstrated sex-specific differences in migratory propensity and/or sex ratios, but the structuring influence of size on the effect of sex has received less attention (Aarestrup et al., 2018; Jonsson, 1985; Nevoux et al., 2019). In a study in Western Norway, Jonsson (1985) showed that female brown trout were more likely than males to smoltify and undertake the spring migration into coastal waters, accounting for ~60% of such individuals. In line with our results, younger female migrants (sea age ≤ 3 years) were also generally smaller than male migrants of a similar age, with this difference disappearing with age. In a related study of seaward autumn migration in Denmark, Aarestrup et al. (2018) estimated that 68% of out-migrating juvenile brown trout (averaged across all sizes) were female (based on dissection and genitalia identification of a sample of 84 individuals undergoing migration), but there was no difference in the average size of male and female migrants. These figures, and others published for anadromous trout (Nevoux et al., 2019), exceed our estimate for the average prevalence of female migration (54%), suggesting that the cost-benefit ratio of migration in males versus females varies across systems in relation to local circumstances, as illustrated in other settings (Pavlov et al., 2008; Pavlov & Savvaitova, 2008). One possible explanation for this discrepancy is relatively higher growth opportunities for migratory females in the

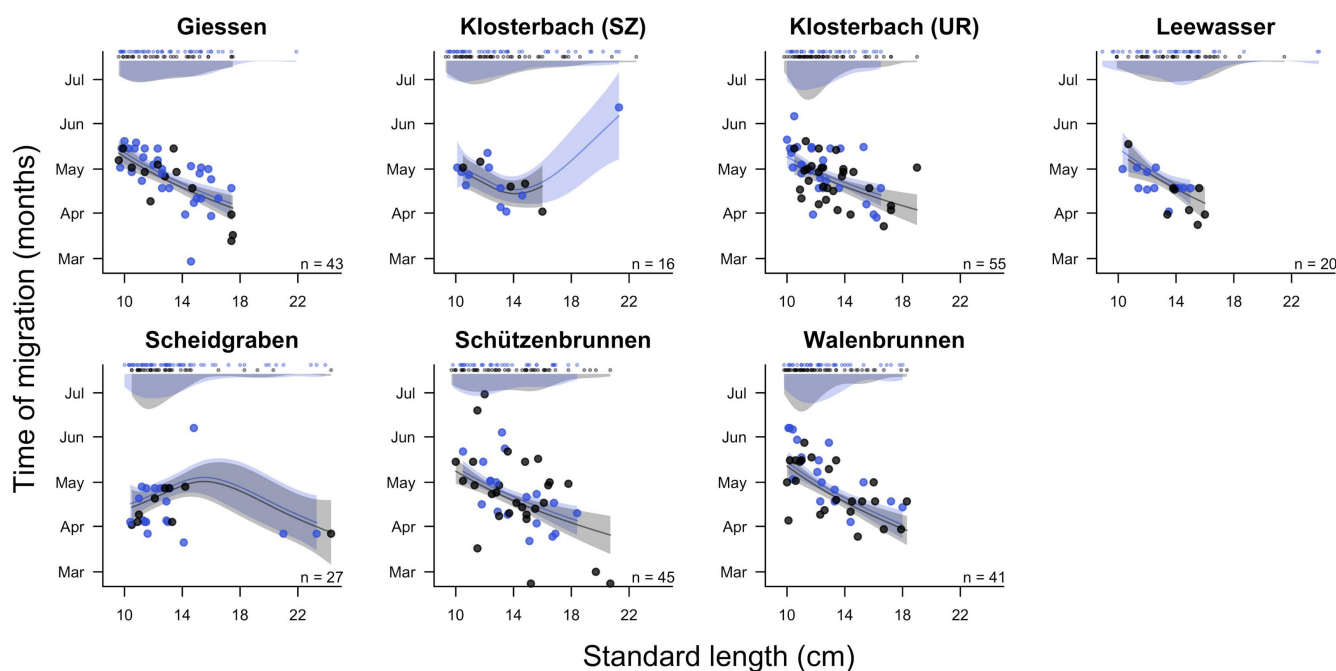


FIGURE 4 Spring migration timing in relation to standard body length in males and females, by stream. Panels separate streams. In each panel, black and blue colours distinguish males and females respectively. Filled points mark observations. Note that observed data were collected from individuals tagged at different times and in different stream sections. Lines and envelopes are predictions and 95% confidence intervals from a Gaussian generalised additive model of migration day in relation to sex, length, day of tagging, stream and stream section. Predictions are shown for the median tagging day (February 27, 2015) across the range of lengths observed for males and females in each stream, excluding the stream/section random effect. The number of observations in each stream is denoted *n*. The distribution of body lengths across all (migratory and non-migratory) individuals in each stream is shown for context at the top of each panel by the points and accompanying Gaussian kernel density estimates.

Norwegian and Danish study systems, which might reflect a difference between potamodromy and anadromy more widely (Nevoux et al., 2019). At the same time, elevated challenges (such as predation pressure) in marine environments may restrict migration by smaller females, resulting in a similar size distribution among the individuals that do migrate in some settings. However, it is difficult to draw firm conclusions about the drivers of variation among studies given substantial differences in study methodology, timing and context, and in the absence of information on sex ratios before migration and the size structure of migrating individuals. A key goal for future work should be to unpick the factors structuring variation in migration propensity within and among systems.

In both sexes, migration propensity appeared to increase with standard body length from the smallest sizes (≥ 8.9 cm). In females, the rate of increase in the probability of out-migration occurred more quickly with respect to increasing length than in males. This result fits with the hypothesis that the P/G trade-off shifts more quickly in females than males, either because females are relatively less vulnerable to predation (at a given length) and/or because they have elevated energetic requirements and/or more to gain from growth opportunities (Nevoux et al., 2019). At larger sizes (~ 12 – 14 cm), migration became more common in both females and males, as expected from the observation that larger individuals are frequently less vulnerable to migration-associated predation than smaller individuals and/or need to satisfy higher energy requirements (Dermond et al., 2019; Dill, 1983; Ibbotson et al., 2006). Beyond 15 cm, we obtained little data from either sex and model predictions were highly uncertain. However, it seems likely that the marginal gains of migration will decline with continued growth beyond a certain size, leading to the prediction that the largest individuals should not migrate in the absence of significant 'push' factors (such as food limitation). While further work is required to confirm this hypothesis, it is notable that at larger sizes, migration propensity was more commonly overpredicted by our flexible regression model. However, with more data, this modelling framework is well suited to examination of these kinds of non-linear relationships and studies in this area would be worthwhile.

Among migrant individuals, we found that larger individuals were more likely to migrate earlier, in line with previous work (Bohlin et al., 2001; Dermond et al., 2019; Nevoux et al., 2019). There were differences among streams in this effect, as encapsulated by the stream-specific smoothers of the effect of standard length, but these appeared to be driven by variation in data availability and/or individual variation rather than representing distinct functional responses. Alongside the length effect, we expected juvenile females to migrate earlier than similarly sized males (to gain an early growth advantage), but we did not find a substantial sex effect on migration timing. Given the emphasis on sex in the literature (Ferguson et al., 2019; Nevoux et al., 2019), this is a notable result, but its explanation remains unclear. One possibility is that early migration happens during a low-growth period of the year, at a time when the balance between predation risk and growth may be sufficient to favour migration for larger fish (the early migrants), but insufficient

to favour migration in smaller fish, even if they are female. Another option is that earlier migrants are influenced by necessity (trading off safety for food) rather than opportunity (Brodersen et al., 2008; Dodson et al., 2013; Nevoux et al., 2019). While these hypotheses remain to be tested, it is worth noting that differences in the timing of return migration in male and female salmonids are widely documented, with males often returning before females (protandry) (Esteve, 2005; Finlay et al., 2020; Morbey, 2000). This pattern has been linked to male–male competition for territories, during which time females continue to exploit feeding opportunities in migratory habitats for as long as possible.

While our predictions were broadly supported, considerable variation in migration propensity and (to a lesser extent) timing among individuals remained unexplained by our models. This variation is probably structured by processes operating at multiple scales. At the individual level, factors such as energetic constraints (Brodersen et al., 2008), personality (Chapman et al., 2011) and genetics (Giger et al., 2006), can shape migratory costs, benefits and propensity (Nevoux et al., 2019). For example, previous work on Pacific salmon (*Oncorhynchus* spp.) has shown that body condition can influence predation risk (Tucker et al., 2016) and, according to the genetic/environmental trait-threshold model, individuals may take this into account when it comes to the 'decision' to migrate and/or migratory timing (Ferguson et al., 2019; Phillis et al., 2016). This points towards the need for research into the vulnerability of fish to predation, not only in relation to standard body length but other morphometrics and individual traits as well. Within and among streams, other variables such as management, density, food availability, habitat, predation risk and distance (horizontal and altitudinal) to the migratory habitat are likely to shape migratory propensity (Chapman et al., 2011; Ferguson et al., 2019; Nevoux et al., 2019; Tanaka et al., 2021). In our model, these factors are broadly captured by the random-effects terms but, where data are available, it would be worthwhile to study their specific influences on migration propensity. In the Lake Lucerne system, we anticipate that variation in most of these factors may influence migratory propensity, but the influence of distance from the migratory habitat is likely to be limited, since horizontal and altitudinal distances are small (< 10 km and < 50 m respectively), relative to the mobility of trout, and migratory routes (including the Urner Reuss) are free from barriers. However, in other systems, these factors can be important drivers of migration propensity (Bohlin et al., 2001; Nevoux et al., 2019).

Three methodological caveats in this work may further contribute to the residual variation in migration propensity. The first caveat concerns sex assignment. In fishes, mismatches in phenotypic and genetic sex assignments have been documented (Hattori et al., 2019) and, since the identification of the sdY (maleness) gene in salmonids, infrequent mismatches have been noted in brown trout and Atlantic salmon, with phenotypic females occasionally exhibiting a positive signal for sdY (Ayllon et al., 2020; Brown et al., 2020; Quéméré et al., 2014). Recent studies have suggested that 0%–4% of individuals may be misidentified in this way (based on samples of 65–2025 individuals) (Ayllon et al., 2020; Brown et al., 2020; Quéméré

et al., 2014; Yano et al., 2013). One explanation for mismatches is the presence of a non-functional, autosomal copy of the sdY gene in a small proportion of females, but other hypotheses have also been put forward (Ayllon et al., 2020; Brown et al., 2020). While all 20 test individuals were correctly assigned in this study, the prevalence of mismatches in larger samples suggests that a small number of females could have been misidentified as males, which may (partly) cloud the observed differences in migratory propensity between the sexes. However, further studies of phenotypic versus genetic sex discordance in brown trout would help to clarify the scale of this phenomenon.

A second caveat in our study concerns the potential influences of tag loss and in-stream mortality prior to migration on apparent migration propensity. In our system and others, tag loss in both male and female juveniles is relatively rare (occurring in <8% of individuals) (Hanson et al., 2020; Saboret et al., 2021), and likely negligible, but variation in in-stream mortality remains poorly studied. This process could contribute towards apparently low migration propensity in smaller individuals, which are likely to have lower survivorship (Costa-Pereira et al., 2018; Dermond et al., 2019; Nilsson & Brönmark, 2000). Differential mortality between the sexes, with relatively higher in-stream male mortality, could also contribute towards apparent differences in migratory propensity between the sexes at small sizes, but this hypothesis remains to be tested.

The third caveat in this study concerns the potential, occasional misidentification of resident and migratory fish from antenna data. Detection efficiency (i.e. the probability of detecting a migrating fish) in antenna systems is typically high (~96%–100%) (Connolly et al., 2008) but a proportion of downstream migrants are expected to be missed, especially in structurally complex habitats with features that enable migrating fish to evade detection (Weber et al., 2016). Our model of migratory propensity accounted for stream-wide differences in apparent migratory propensity, but individual characteristics, such as ontogeny, can also influence detection probability and we did not account for this (Kelly et al., 2017). However, while detection efficiency is an issue that deserves further study across much of the field of movement ecology, in general, we expect the influence of detection efficiency in PIT antenna systems to be negligible in studies with large sample sizes. A related issue in PIT systems is that partially nomadic individuals, which move sporadically between natal and downstream habitats, may be mis-identified as migrants from detections at antennas (Brodersen et al., 2019). While our experience suggests these movements are rare in the Lake Lucerne system, longer term study of arrhythmic dynamics and their influence on migration analyses would be worthwhile.

Beyond the factors structuring unexplained variation in migratory propensity, a broader limitation in this work (and many similar studies) is the restricted spatiotemporal scale of sampling (Ferguson et al., 2019). We show that spring migratory propensity within a given year is sex- and length-dependent, but it remains for future work, spanning the entire lifetime of individuals, to investigate the extent to which the potential first-time migrants that do not migrate in a given season are temporarily delaying migration (until later in the

year or the following year) versus becoming lifetime residents, and the factors that shape these 'decisions' throughout life (Ferguson et al., 2019; Forseth et al., 1999; Jonsson, 1985). Further research is also needed to understand what drives variation in migratory patterns among systems. With the establishment of semi-permanent passive telemetry systems in a variety of locations, these important questions should become tractable in the coming years.

In conclusion, this study uniquely demonstrates the value of integrating genetic sex-determination protocols with passive telemetry to quantify migration patterns in brown trout. Despite uncertainties, we identified marked differences in migratory propensity between males and females of differing sizes that align with predictions from theory. We anticipate that the discovery of the sdY gene and the development of associated molecular methods for analysis, together with tissue samples collected at the time of sampling, have the potential to become important resources for ecologists and fisheries managers in other systems (Anglès d'Auriac et al., 2014; Quéméré et al., 2014; Yano et al., 2012, 2013). Building on this work and the wider literature on salmonid genomics and partial migration (Arostegui et al., 2019; Ferguson et al., 2019; Kelson et al., 2019), we strongly recommend that tagging programmes store genetic samples for future genomic analyses that may not currently be available.

AUTHOR CONTRIBUTIONS

Jakob Brodersen and Darryl McLennan conceptualised and designed the study. Philip Dermond, Yannick Hunziker and Jakob Brodersen collected the field data. Yannick Hunziker and Darryl McLennan sexed individuals in the laboratory. Edward Lavender and Yannick Hunziker analysed the data. Edward Lavender and Yannick Hunziker wrote the article; and all authors contributed critically to drafts and approved publication.

ACKNOWLEDGEMENTS

We gratefully thank Salome Mwaiko for her assistance in the laboratory and Brigitte Germann, Lauren McIntyre, Julia Wouters and other field team members for collecting the empirical fish data. We also thank Andreas Scheidegger and Helen Moor for insightful discussions. Tom Reed and two anonymous reviewers provided helpful comments that greatly improved the article. Open access funding provided by ETH-Bereich Forschungsanstalten.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

FUNDING INFORMATION

This study was supported by an Anakom grant from Eawag Swiss Federal Institute of Aquatic Science and Technology and a Swiss National Science Foundation grant (31003A_153296) to JB. EL was supported by a postdoctoral researcher position at Eawag, funded by the Department of Systems Analysis, Integrated Assessment and Modelling. DS was supported by a PhD position at Eawag, funded by the Swiss Federal Office for the Environment (FOEN). DM was also funded by FOEN (Framework Hydrological Engineering and Ecology).

DATA AVAILABILITY STATEMENT

The empirical fish data and code are available on GitHub (<https://github.com/edwardlavender/eawag-hunziker>) and archived on Zenodo (DOI: 10.5281/zenodo.8146370).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Lavender, E., Hunziker, Y., McLennan, D., Dermond, P., Stalder, D., Selz, O., & Brodersen, J. (2024). Sex- and length-dependent variation in migratory propensity in brown trout. *Ecology of Freshwater Fish*, 33, e12745. <https://doi.org/10.1111/eff.12745>