Freshwater Biology

WILEY

Freshwater Biology

ORIGINAL ARTICLE OPEN ACCESS

Anadromous Brown Trout (*Salmo trutta*) Contribute Disproportionally to Recruitment: Insights From Genomics and Multi-Tissue Stable Isotope Chemistry

J. I. Jones[1] | R. A. King[2] | A. M. Sturrock[3] | H. Wei[1,4] | J. R. Stevens[2] | R. B. Lauridsen[5,6]

[1]School of Biological and Behavioural Sciences, Queen Mary University of London, London, UK | [2]Department of Biosciences, Faculty of Health and Life Sciences, University of Exeter, Exeter, UK | [3]School of Life Sciences, University of Essex, Colchester, UK | [4]Key Laboratory of Alien Species and Ecological Security (CAFS), Pearl River Fisheries Research Institute, Chinese Academy of Fisheries Science, Guangzhou, Guangdong, China | [5]Six Rivers Iceland, Vopnafjörður, Iceland | [6]Game and Wildlife Conservation Trust, Salmon & Trout Research Centre, Dorset, UK

Correspondence: J. I. Jones (j.i.jones@qmul.ac.uk)

Received: 27 March 2025 | **Revised:** 27 June 2025 | **Accepted:** 31 July 2025

Funding: This work was supported by Interreg France (Channel) England, Salmonid Management Around the Channel and Natural Environment Research Council, MR/V023578/1.

Keywords: eye lens | fisheries | life history diversity | migration | otolith | Salmonid

ABSTRACT

1. Brown trout (*Salmo trutta* L.) exhibit a variety of life-history strategies. The two physiological and phenotypic extremes are represented by freshwater residents that remain in freshwater for their entire life and anadromous sea trout that migrate to sea to grow. The cue to initiate anadromy appears to be a combination of environmental factors, genetics, and non-genetic parental effects. We currently lack a systematic understanding of the interplay between these two life-history strategies, in particular their relative importance in the recruitment of populations displaying facultative migration.
2. We assessed the importance of anadromous females in the recruitment of *S. trutta* at sampling locations 16–44 river km upstream of the tidal limit in a productive chalk stream using a combination of tissue stable isotope ratios and SNP genotyping of newly emerged fry, with a primary goal of understanding the migratory strategy of their mother and hence the relative contribution of the two strategies to recruitment. A secondary goal was to test a new method of assessing maternal strategy using the $\delta^{13}C$ of the core of the eye lens.
3. By combining information from muscle tissue and eye lens core stable isotope ratios, and SNP genotyping, we were able to allocate 97.5% of fry to either anadromous or freshwater-resident mothers. In most cases, the $\delta^{13}C$ of the core of the eye lens appeared to provide greater discrimination among maternal strategies than muscle tissue. Given the inert nature of this archival structure, lens core chemistry represents a promising approach to assess maternal strategy in any aged fish.
4. Anadromous females contributed disproportionately to recruitment throughout the catchment, where the proportion of fry with anadromous mothers followed a non-linear decline with increasing distance from the tidal limit. Close to the tidal limit (16 river km upstream) 100% of fry had anadromous mothers, declining to 43% at the site furthest from the tidal limit (44 river km upstream). As well as a disproportionate contribution of anadromous fish to young-of-the-year, the number of full-sibling family groups involving anadromous mothers was higher than for freshwater resident mothers at all sites.
5. Anadromous *S. trutta* mothers contribute disproportionately to recruitment even in the headwaters of a productive chalk stream. Whilst we do not know how the contribution of anadromous mothers influences the balance of the two life history strategies, recruitment appears highly dependent on unobstructed migration pathways to and from the marine environment.

1 | Introduction

Human activities are causing rapid and significant declines in many species across the globe. The impact is particularly pronounced for migratory species, where one in five of the species listed by the Convention on the Conservation of Migratory Species of Wild Animals are threatened with extinction, and many are undergoing population declines (Davis et al. 2024). Migratory species are exposed to a diverse range of anthropogenic pressures, including habitat loss, overexploitation, pollution and climate change. Due to their use of multiple locations through their life history, the management and conservation of migratory species is particularly challenging and often involves international cooperation. Yet many species are capable of facultative migration (sometimes called partial migration) where individuals within a population vary in their migratory tendencies. Facultatively migratory populations comprise a mixture of migrant and resident individuals, with migration typically occurring to take advantage of alternative foraging opportunities or to avoid adverse conditions (Chapman et al. 2011a). The decisions involved in such migrations are shaped by a complex interplay between extrinsic and intrinsic factors, where both the factors driving individuals to undertake them and the subsequent implications for the population are often opaque (Chapman et al. 2011b; Brönmark et al. 2013).

Brown trout (*Salmo trutta* L.) exhibit a highly variable life-history strategy (Klemetsen et al. 2003; Birnie-Gauvin et al. 2019; Ferguson et al. 2019). Populations often display facultative migration across a continuum of migration strategies. Some individuals may remain in freshwater for their entire life (freshwater resident), either remaining in the natal habitat or undertaking migration to more productive feeding grounds within the natal catchment, whereas other individuals may adopt an anadromous life history strategy (sea trout) where they migrate to the marine environment (Ferguson et al. 2019). The anadromous strategy is energetically costly, involving substantial journey distances, changes in osmoregulation and ionic regulation, and other phenotypic changes to cope with the move between fresh and salt water. Yet, marine habitats can also provide improved growth opportunities and thus increased fitness (Gross 1987). The 'decision' to migrate (or not) is thought to be controlled by ecophysiological thresholds, underpinned by an individual's genotype, physiological state, and its interactions with its immediate environment (Ferguson et al. 2019).

Anadromy provides access to better feeding opportunities, in terms of prey quantity and quality, frequently resulting in sea trout attaining a larger size than river residents, which translates into a greater contribution to recruitment, particularly for females (Acolas et al. 2008; Fleming and Reynolds 2004; Goodwin et al. 2016; Jonsson and Jonsson 2006). However, migration involves increased physiological and metabolic costs and an enhanced risk of predation and disease compared with those experienced by river residents (Brönmark et al. 2013). The balance between these spatially variable costs and benefits appears to determine the chosen strategy in terms of both the population and individual, best explained by the 'environmentally cued threshold model' (Tomkins and Hazel 2007). This model assumes that the frequencies of the alternative strategies are controlled by the relationship between an environmentally sensitive trait and a genetically variable threshold. Whilst there is variation in the propensity to migrate among populations, an experimentally reduced rate of supply of food encourages anadromy, even in ostensibly freshwater-resident populations (Archer et al. 2019, 2020). Hence, it appears that the cue to initiate anadromy is physiological condition (Klemetsen et al. 2003), which is influenced by a combination of environmental factors, genetics and non-genetic parental effects (e.g., egg quality, timing of spawning), where an individual's condition is set against a genetically predetermined threshold.

Given the interplay between genetic variation and environmental heterogeneity in determining life history strategy, the relative importance of freshwater-resident and anadromous forms for *S. trutta* population persistence is far from clear. Anadromous and freshwater-resident trout freely interbreed and produce fertile offspring (Charles et al. 2006; Goodwin et al. 2016). In an English chalk stream, a combination of stable isotope and genetic analysis attributed (at least) 76% of juveniles to anadromous mothers, compared with 2.5% to freshwater-resident mothers (Goodwin et al. 2016). On the other hand, studies of trout populations from less productive environments using genetics and long-term monitoring (Duval et al. 2021) or otolith chemistry (Losee et al. 2023) have suggested that a substantial proportion of anadromous individuals had freshwater-resident parents.

Studies using stable isotopes have shown differences in the contribution of anadromous and freshwater-resident mothers to recruitment among sites (McCarthy and Waldron 2000; Charles et al. 2004; Goodwin et al. 2016; Rohtla et al. 2017). However, the factors influencing the relative contributions of the two strategies have not been explored. It is typically assumed that the costs of migration restrict anadromous trout to the lowest reaches of catchments (Bohlin et al. 2001; Klemetsen et al. 2003). In anadromous populations, recruitment declines linearly with distance from the sea, an effect that does not influence recruitment in freshwater resident populations (Bohlin et al. 2001). How the two life-history strategies interact in populations displaying facultative migration is unknown. Yet, such an understanding is important. In most systems, sea trout stocks are under increasing pressure (Fiske et al. 2024) from migratory obstructions such as dams and diversions, pollution, fish farms and associated sea lice infestations, and over-exploitation. The cumulative outcome of such pressures disproportionately impacts anadromous forms. An understanding of how the relative importance of anadromous individuals for recruitment varies with distance from the sea would enable more informed management of such impacts. Here we used a combined analytical approach to address the question, 'How important are anadromous mothers for recruitment in a *S. trutta* population displaying facultative migration, and how do contribution rates vary with distance from sea?'

A secondary goal was to test a new method of assessing maternal strategy using carbon isotope ratios in the core of the offspring's eye lens. Fish eye lenses are metabolically inert, proteinaceous

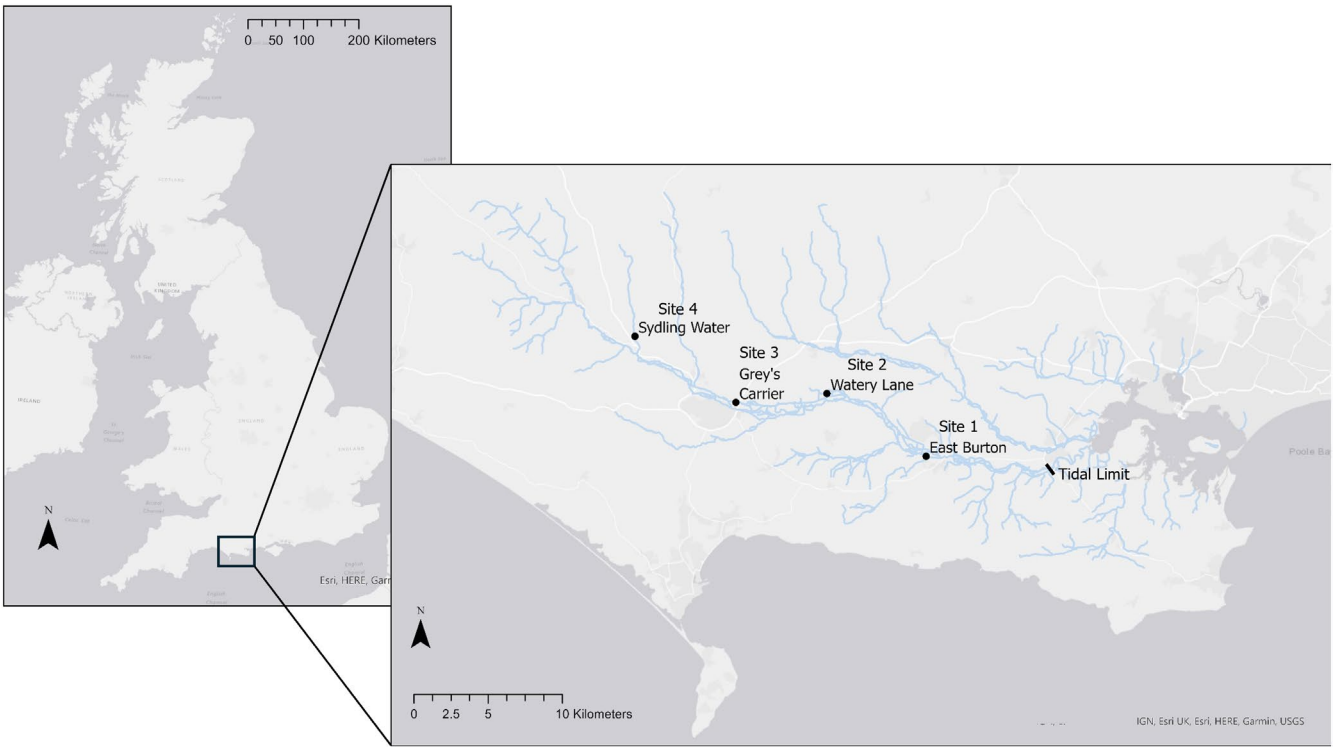

FIGURE 1 | Location of the four sampling sites within the River Frome catchment, Dorset, UK.

structures that grow incrementally in layers (laminae) from birth to death (Quaeck-Davies et al. 2018). The lens core is formed while the individual is in the egg being nourished by the yolk (produced by the mother while feeding in the sea, if anadromous, or river, if resident), and should closely reflect the isotopic composition of the mother. A similar mechanism has been used to assess maternal strategy based on strontium concentrations (Zimmerman et al. 2009) and isotope ratios (Courter et al. 2013) in the otolith core, as these markers can also covary with salinity. The benefit of using archival structures over soft tissues such as muscle is that the core can be isolated and subsequent layers influenced by exogenous feeding excluded from the analysis. This new method could open new avenues to look at the contribution rates of the two strategies to young of the year, and to assess differential survivorship of the offspring into adulthood.

We determined the importance of anadromous females in the recruitment of a *S. trutta* population at various distances from the sea in a productive chalk stream. We primarily used carbon and nitrogen isotope ratios in the muscle of newly emerged fry to identify the migratory strategy of their mother. We also used a novel technique, the stable isotopes of eye lens tissues, together with kinship analysis using single nucleotide polymorphisms (SNPs), to improve our ability to assign maternal strategy to fry where isotopic assignments were less clear. Due to the increased costs involved in a long migration from the headwaters to the sea, we hypothesised that the anadromous forms would only play an important role in recruitment close to the tidal limit (Bohlin et al. 2001). Further towards the headwaters, we assumed that the costs of migration and availability of food in this productive river would favour the river resident strategy.

TABLE 1 | Physical characteristics of the sampling locations within the Frome catchment.

Site	Distance from tidal limit (km)	Mean width (m)
1. East Burton	16	5.3 ± 0.8
2. Watery Lane	26	7.1 ± 1.0
3. Grey's Carrier	34	5.2 ± 0.8
4. Sydling Water	44	4.8 ± 0.9

2 | Methods

2.1 | Collection of Trout

The River Frome is a productive lowland chalk stream in Dorset, UK, flowing through highly braided but largely non-impounded channels characterised by pool, riffle, and glide habitats (Figure 1). The Frome rises at Evershot (50°50′24″N, 02°36′12″W) ~264 m a.s.l. and drains a catchment area of 463 km^2. The main stem is 59 km long to the tidal limit at Wareham (50°40′38″N, 02°07′03″W), prior to entering Poole Harbour estuary and then the English Channel. For the period 1965–2022, the mean annual discharge at the East Stoke gauging station was 6.7 m^3s^{-1} and as a groundwater dominated chalk stream, it has a very stable flow regime with a baseflow index of 0.86 (National River Flow Archive 2024).

Thirty trout fry were collected from each of four sampling sites within the catchment at varying distances from the tidal limit (Table 1), over the period 14–24 March 2019 by point sampling with an electro-fisher. The four sampling sites were chosen such

that they had similar physical characteristics: shallow, generally less than 50 cm deep, and a substrate dominated by gravel (Table 1). The furthest upstream (site 4) was a tributary headwater; the other three sites were carriers of the main river in the highly braided River Frome catchment. The timing of the fry collection period was based on the emergence date predicted from the degree day model of Elliott (1994) based on spawning date and temperature. Random points along the margins of approximately 200 m of river were sampled at each site using a Smith-Root LR-24 backpack electro-fisher. Pulsed DC was used where the output waveform was a square wave fished at 100 Hz, 250 V and 20% duty cycle.

Fry were mainly caught in the margins, shallows, and slow-flowing areas, typical habitats for newly emerged fry (Greenberg et al. 1996). Once captured, the fry were kept alive in a holding container until the whole stretch was fished; then euthanised humanely using a schedule I method. Upon return to the laboratory, each fry was weighed (wet weight), fork length measured to the nearest 1 mm, the presence of yolk recorded and frozen. The relationship between fry length and weight was determined using least squares regression, and differences among sites tested using ANOVA, both in R (R Core Team 2023).

2.2 | Stable Isotope Analysis—Muscle Tissue

Muscle flank was dissected from the posterior portion of each fry, washed in deionised water, dried at 85°C for 48 h, and ground to a fine powder using a mortar and pestle. Approximately 0.8 mg of ground tissue was loaded into individual 4 × 6 mm tin capsules (Elemental Microanalysis, Oakhampton). The samples were combusted, and isotope ratios were determined at Queen Mary University of London using a mass spectrometer system in the continuous-flow (CF-IRMS) mode, with a Carlo Erba elemental analyzer (CHN 1110) coupled to a Delta Plus mass spectrometer (Thermo Scientific). All isotope values are presented in parts per thousand (‰) using the delta notation (δ), which represents the deviation of stable isotope ratios (^{13}C:^{12}C and ^{15}N:^{14}N) from universal standards: Pee Dee Belemnite limestone standard for carbon and atmospheric nitrogen for nitrogen. Replicate samples of an internal standard (Casein) yielded results that were precise and accurate, $\delta^{13}C = -26.90 \pm 0.09‰$ (mean ± SD, $N = 20$), $\delta^{15}N = 5.94 \pm 0.21‰$ (mean ± SD, $N = 20$).

To identify individual fry as having freshwater-resident or anadromous brown trout mothers, we applied the same method as in Goodwin et al. (2016). This method was based on a single isotope ($\delta^{13}C$), two-source mixing model (IsoError Version 1.04; Phillips and Gregg 2001) returning an exact mathematical solution of the relative proportions of anadromous or river resident signal that would produce the isotopic ratio of the fry. The returned value was used to determine the probability of the fry having an anadromous or river resident mother. Isotopic ratios for muscle flank tissue of mature freshwater-resident or anadromous brown trout mothers were obtained from studies on the Tadnoll Brook, a tributary of the Frome (Lauridsen et al. 2012; Goodwin et al. 2016). These isotopic ratios were based on multiple individuals collected from the study catchment over several years and are considered to give the best estimate of the average and variance in maternal ratios in this trout population. Any effect of increasing atmospheric carbon (Suess effect) over the intervening years approximates measurement error and is likely to have less influence than spatial variation in marine feeding grounds among anadromous mothers (Artero et al. 2025). As a consequence of discriminative fractionation during the development of lipid-rich egg tissues (DeNiro and Epstein 1978), trout embryos are depleted in ^{13}C and ^{15}N relative to their respective maternal parents (Curry 2005). To account for this, an independently derived fractionation value (Grey 2001) was applied to adult ratios before analysis (mother—unreleased egg: $\Delta^{15}N$ −0.8, $\Delta^{13}C$ −1.5). Standard deviation was calculated for both adult life history strategies and used along with the mean to determine what proportion of the fry lay within the 95% interval (mean $\pm 1.96\sigma$) of expected ratios based on those of the adults. As it is evident that the isotopic ratios of newly emerged fry change as they start feeding on exogenous sources (Goodwin et al. 2016), a second wider interval was used that encompassed 99.7% of the expected ratios based on those of the adults (mean $\pm 3\sigma$).

2.3 | Stable Isotope Analysis—Eye Lens Tissue

To ground-truth the new technique of using the eye lens core isotopic composition to infer maternal strategy, both eye lenses were extracted from a subset of fry ($n = 21$) using fine-tipped forceps. Under a dissecting binocular microscope, a small droplet of deionised water was added to hydrate each lens, and the outermost laminae were peeled away until only the lens core remained. The 'core' was defined here as the point at which laminae became difficult to separate from the innermost material (at a diameter of *c.* 200 μm). Cores from both eyes were added to a single tin cup and encapsulated. All samples were < 0.1 mg.

Due to their small size, the lens core samples were analysed for $\delta^{13}C$ at the SEAPORT laboratory at the National Oceanography Centre using a vario PYRO cube elemental analyser (CN mode) coupled with visION isotope ratio mass spectrometer. Sulfanilamide was used as an elemental standard, and fish muscle standard ERM-BB422 (sample no. 0487 certified reference material fish muscle, European Commission, JRC, Geel, Belgium) yielded $\delta^{13}C$ results that were precise and within 0.03‰ of the SEAPORT laboratory's long-term average ($\delta^{13}C = -19.26 \pm 0.10‰$, mean ± SD, $N = 20$). The relationship between the isotopic composition of eye lens core and flank muscle from the same individual was determined by least squares regression using R (R Core Team 2023).

2.4 | Molecular Methods

Genomic DNA was extracted from muscle tissue dissected from the anterior portion of each individual fry following the HotSHOT method of Truett et al. (2000). All individuals were screened for variation at 95 biallelic SNP loci (Osmond et al. 2023). SNP genotyping was undertaken on the Standard Biotools EP1 Genotyping System using 96.96 Dynamic Genotyping Arrays and scored using the Standard Biotools SNP Genotyping analysis software. Genotyping plots of each locus were manually inspected for the quality of individual genotyping and clustering. Each run included two positive (individuals of known genotype) and two negative controls.

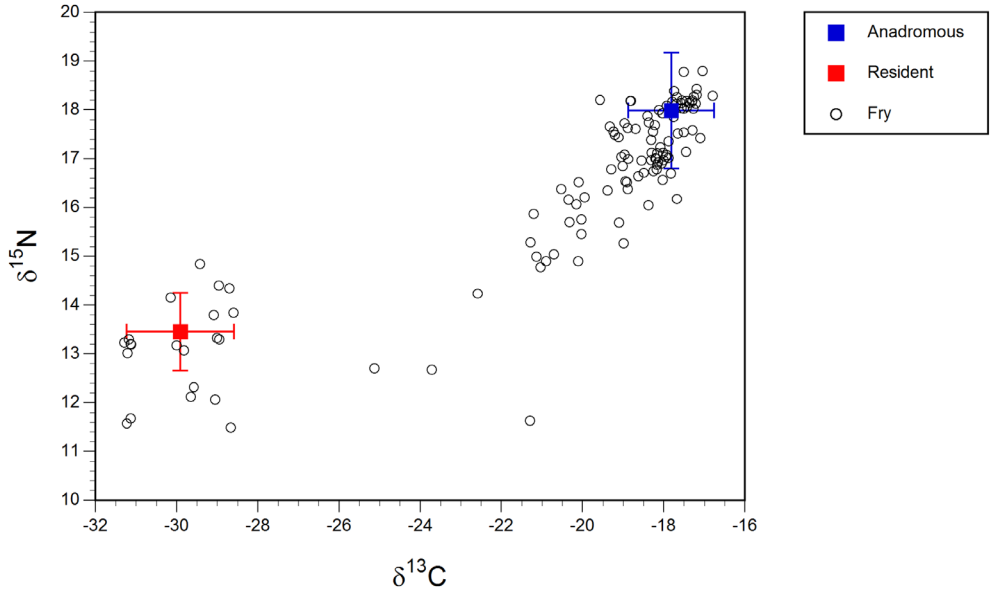

FIGURE 2 | $\delta^{13}C$ and $\delta^{15}N$ of recently emerged trout fry collected from four locations in the River Frome, together with the mean (±SD) of adult anadromous and freshwater-resident brown trout accounting for fractionation mother-egg.

2.5 | Sibship Analysis

To identify full siblings within each sampling site, we used a maximum-likelihood method, implemented in COLONY v 2.0 (Jones and Wang 2010). Settings were high precision medium length run, assuming both male and female polygamy without inbreeding. To check for consistency, analyses were run twice using different random number seeds.

For each of the four sample sites, we tested the power of the SNP panel to recover true full-sib relationships and to establish whether unrelated individuals could be falsely classified as full sibs. We simulated unrelated genotypes, the number equal to the sample size for each site, using HYBRIDLAB (Nielsen et al. 2021). The simulated datasets were analysed in COLONY using the same settings as given above.

2.6 | Allocation of Fry to Maternal Life History Strategy

A tiered allocation of fry to their mother's life history strategy was used. Based on the isotopic ratio of their muscle tissues, fry that the isotopic mixing model placed within 95% of the expected ratios based on the adults, i.e., the isotopic ratios of the fry were statistically indistinguishable from those of their mothers, were allocated to either anadromous or freshwater-resident mothers with high confidence. The fry that had isotopic ratios that fell outside the 95% range but within 99.7% of the expected ratios based on the adults were allocated to either anadromous or freshwater-resident mothers with lower confidence. These individuals had a muscle $\delta^{13}C$ value that was towards the edge of the range of expected isotopic ratios of fry that had not started feeding exogenously but were included as it was evident that many fry had been feeding exogenously based on their capture weight, creating the observed deviations from the predicted yolk values. The fry whose muscle tissue fell outside of these isotopic limits, but whose eye lens core fell within limits (i.e., suggesting that they had been feeding exogenously), were reallocated to the maternal life history strategy based on the eye lens core and the confidence limits described above. Finally, any fry that were part of a family group defined by SNP genotyping that included full siblings allocated to a maternal life history strategy based on isotope ratios were allocated to the maternal strategy with the highest confidence attained by any of the siblings in the group, i.e., where we were confident of one member of the family group, all siblings were allocated with the same confidence. No family groups contained siblings with isotope ratios that would suggest different maternal life history strategies.

For fry allocated to anadromous mothers, to support acceptance of the lower level of confidence, a linear model was used to determine if the relationship between $\delta^{13}C$ and $\delta^{15}N$ differed among the two levels of confidence using R (R Core Team 2023). All fry allocated to freshwater-resident mothers were assigned high confidence.

3 | Results

3.1 | Stable Isotope Analysis—Muscle Tissue

None of the fry caught had visible yolk reserves, indicating that they had emerged prior to capture and were likely to have started feeding on exogenous sources. The fry varied in size, where there was a strong relationship between the length and mass of the fry ($R^2 = 0.657$, $t = 14.708$, $p < 0.001$) but there was no difference in the size of fry sampled among sites ($F = 0.931$, $p = 0.354$). There was clear differentiation in the isotopic composition of the adult fish according to their life history strategy, where adult anadromous trout had both a higher $\delta^{15}N$ and a less negative $\delta^{13}C$ than adult freshwater-resident trout (Figure 2). When considered collectively from all four sites, the fry did not form two distinct clusters around the adults based on their isotopic ratios (Figure 2). Rather, one group formed a cluster with similar $\delta^{13}C$ and either a similar or lower $\delta^{15}N$ than adult freshwater-resident

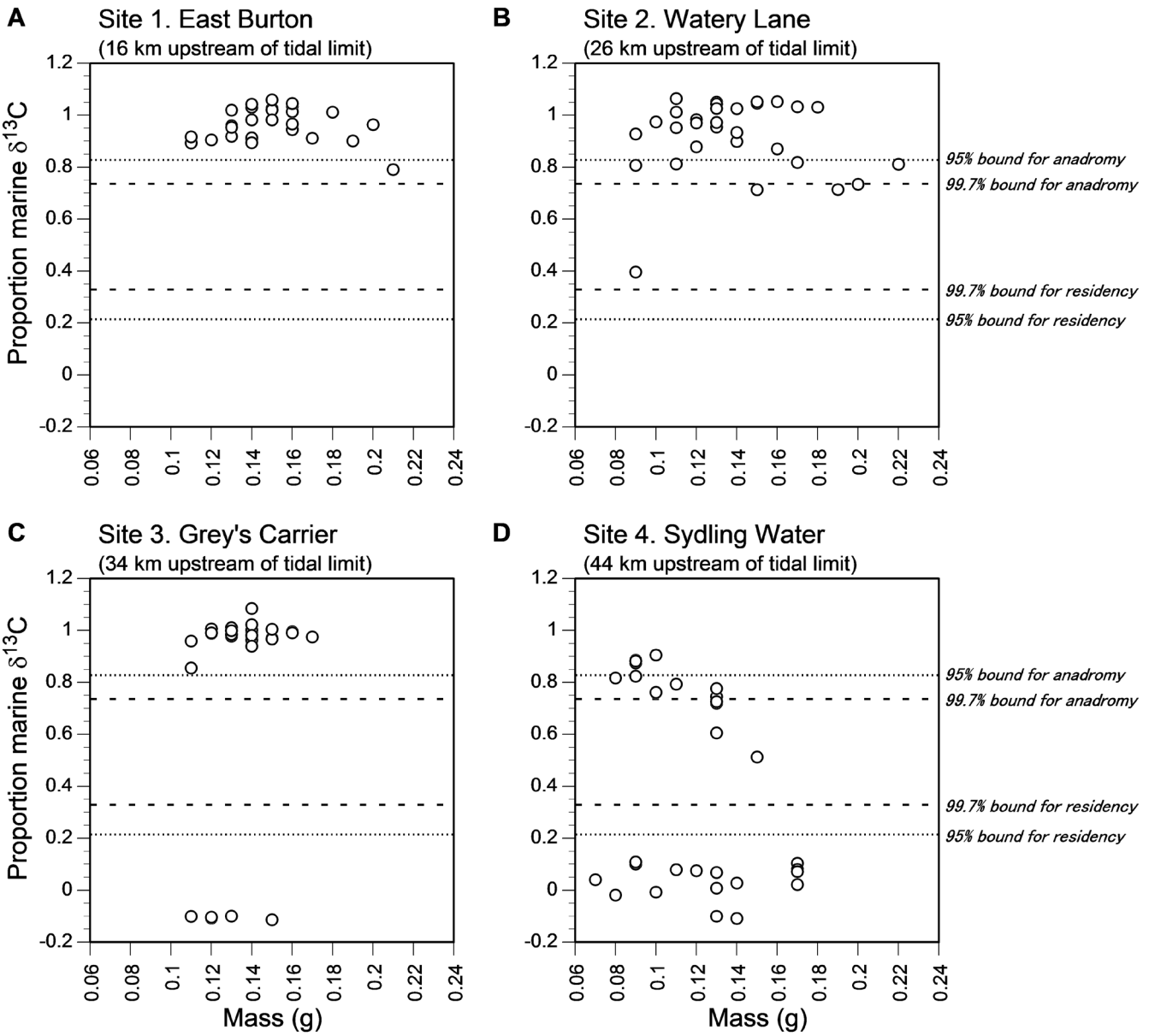

FIGURE 3 | Relationship between the proportion of marine derived carbon in individual offspring (from mixing model based on muscle tissue) and mass of trout fry collected from four locations in the River Frome (0% marine carbon corresponds to mean freshwater-resident adult trout, 100% marine carbon corresponds to mean anadromous adult trout). The ranges corresponding to 95% (small dashed line) and 99.7% (large dashed line) of adult observations were used to define intervals that corresponded to the respective life-history strategies.

trout, whilst the other group was scattered along a gradient of $\delta^{13}C$ and $\delta^{15}N$ which included fry with ratios similar to those of adult anadromous trout (accounting for fractionation mother-egg) at the upper end.

There were pronounced differences among the four sites in terms of where the mixing model placed the fry (Figure 3). At the most downstream site (Site 1, 16 km upstream of tidal limit), the mixing model placed most of the fry within the bounds that delimited anadromous maternal life history strategy with high confidence (i.e., 95% of expected ratios based on anadromous adults) except for the largest individual, which was allocated to maternal life history strategy with less confidence (i.e., outside the 95% but within the 99.7% bounds: Figure 3A). At site 2 (26 km upstream of tidal limit), four fry were placed outside the 95% but within the 99.7% bounds of expected ratios based on anadromous adults, and three fry outside the bounds for either maternal life history strategy, one of which was small and placed close to the 99.7% bound for having a freshwater-resident mother (Figure 3B). The remainder were all within the 95% bound for having an anadromous mother. At site 3 (34 km upstream of tidal limit), five fry were within the 95% bound for having a freshwater-resident mother and all the others within the 95% bound for having an anadromous mother. At the most upstream site (site 4: 44 km upstream of tidal limit), 16 fry of various sizes were placed within the 95% bound for having a freshwater-resident mother. Of the remaining, four fry were placed within the 95% bound for having an anadromous mother, whereas the others were distributed across a gradient of decreasing proportion of marine $\delta^{13}C$ with increasing mass where the

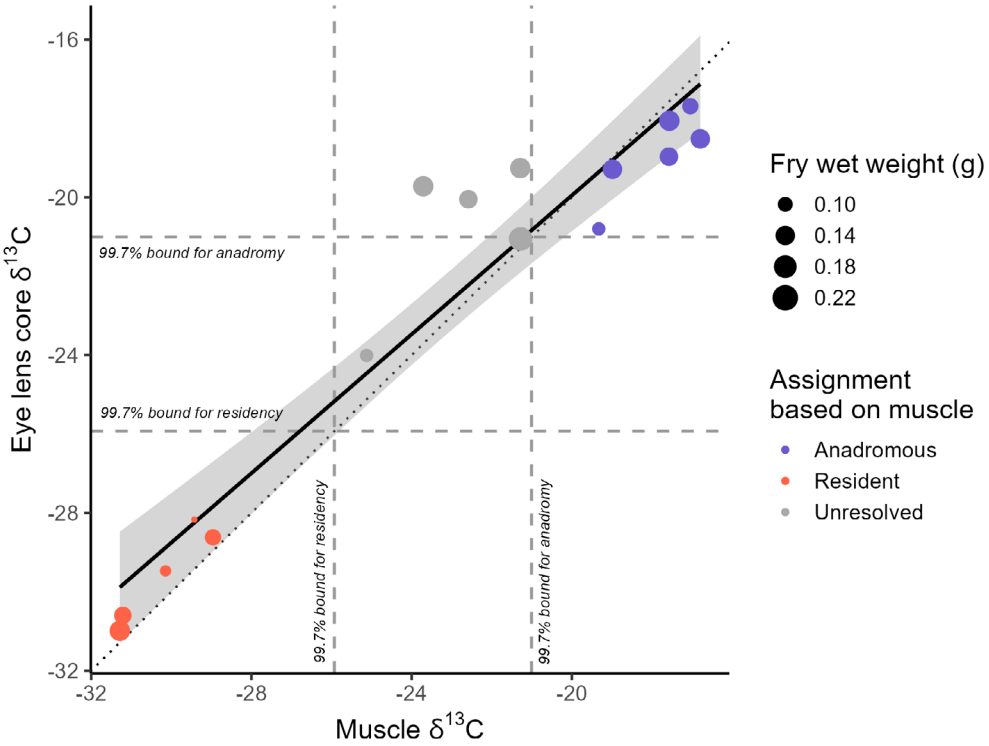

FIGURE 4 | Relationship between $\delta^{13}C$ of eye lens core and $\delta^{13}C$ of muscle of recently emerged fry, showing the linear regression line (thick black line) ± 95% confidence interval (grey area). The 1:1 line is indicated by a black dotted line. Data points are sized by fish weight and coloured by their assignment based on muscle $\delta^{13}C$ relative to the 99.7% bounds for residency and anadromy (dashed lines).

smaller fry were within the bounds for having an anadromous mother (Figure 3D).

3.2 | Stable Isotope Analysis—Eye Lens Tissue

Of the 21 lens core samples submitted for $\delta^{13}C$ analysis, five samples were below the limit of detection of the EA-IRMS. However, for the remainder, there was a strong positive relationship between eye lens and muscle $\delta^{13}C$ (Figure 4: $R^2 = 0.92$, $p < 0.001$). Two of the five individuals that were outside the bounds for either maternal life history based on muscle $\delta^{13}C$ also exhibited an intermediate lens core $\delta^{13}C$; albeit that one was very close to the 99.7% bound of expected ratios based on anadromous adults. However, three of these five 'intermediate' fry exhibited a lens core $\delta^{13}C$ that was within the range for having an anadromous mother (Figure 4).

3.3 | Molecular Methods—Sibship Analysis

Of the 95 SNP markers, two were monomorphic in all samples. Seven samples, all from site 4, failed the genotyping process due to the extraction of poor-quality DNA. The final dataset for the COLONY analysis was therefore 114 individuals scored at 93 SNP markers. Simulated data showed that we could reliably identify full sibship relationships with no spurious full-sib relationships among the simulated unrelated genotypes.

COLONY identified six family groups containing multiple fry at sites 1 and 2, five at site 3, and four at site 4 (Figure 5). All other fry had no full-sib relationships with the other individuals at the site. There were no relationships (full- or half-sib) between individuals at different sites. At site 3, all fry that were allocated to freshwater-resident mothers based on their muscle stable isotope composition were from the same family group (Figure 5C). At site 4, the fry that were allocated to freshwater-resident mothers based on the stable isotope composition of their muscle tissue comprised two family groups containing multiple fry and several fry with no identified full siblings (Figure 5D). At both sites 2 and 4, some of the fry whose muscle tissue was outside the bounds of expected ratios for anadromous mothers were members of family groups that also contained fry, typically smaller, that were within the bounds (Figure 5B,D). As well as sharing a sibling that was identified as having an anadromous mother based on the isotopic composition of their muscle tissue, the data from the eye lens core of two of these fry indicated that they had anadromous mothers, supporting the use of the eye lens core to identify maternal life-history strategy.

3.4 | Maternal Life History Strategy

By combining information from muscle tissue and eye lens core stable isotope ratios, and SNP genotyping, we were able to allocate all but three fry to either anadromous or freshwater-resident mothers (Figure 6). All fry with freshwater-resident mothers were allocated with high confidence. Of the 97 fry that were allocated to anadromous mothers, 12 were allocated with lower confidence. However, the level of confidence in the attribution of fry to anadromous mothers had no significant influence on the relationship between $\delta^{13}C$ and $\delta^{15}N$, i.e., the high and low confidence groups of fry were on the same trajectory of declining $\delta^{13}C$ and $\delta^{15}N$: the difference in isotopic ratios of

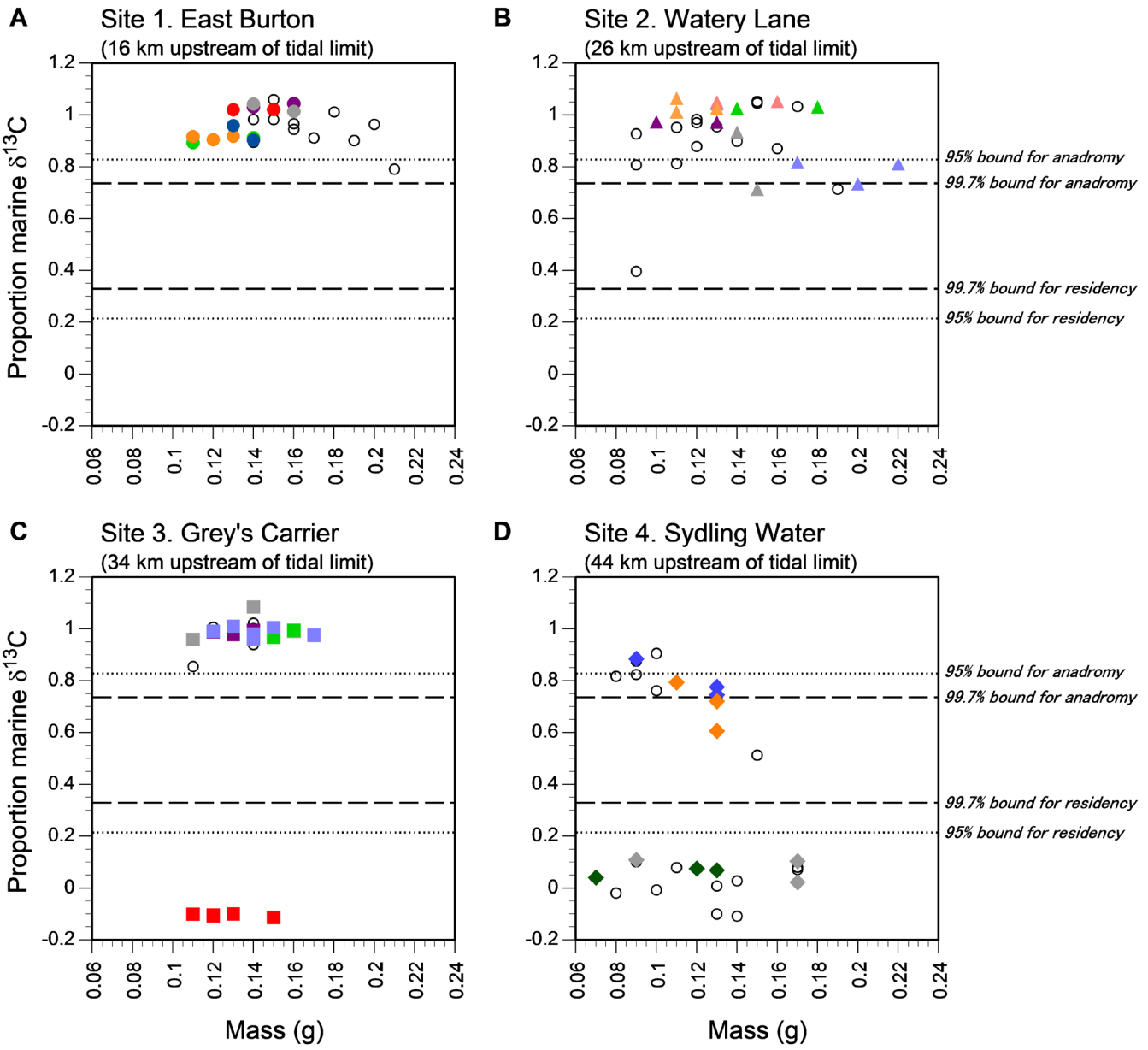

FIGURE 5 | Relationship between the proportion of marine derived carbon in individual offspring (from mixing model based on muscle tissue) and mass of trout fry collected from four locations in the River Frome (0% marine carbon corresponds to mean freshwater-resident adult trout, 100% marine carbon corresponds to mean anadromous adult trout). The ranges corresponding to 95% (small dashed line) and 99% (large dashed line) of adult observations were used to define intervals that corresponded to the respective life-history strategies. Open symbols indicate fry without siblings, filled symbols indicate siblings within family groups where each different colour/symbol combination indicates a different family group. No relationships (full- or half-sib) were found between fry at different sites.

larger fry from those expected in egg matter was a consequence of exogenous feeding on freshwater prey,'dampenin' the marine signal transferred by anadromous mothers to their offspring's tissues via the yolk (Figure 6). The three fry where the mother's life-history strategy was unresolved also sat on this isotopic trajectory; however, one of them was smaller than fry of similar isotopic position, suggesting minimal exogenous feeding post-emergence (Figure 6). The eye lens core of this small unresolved fry also exhibited an intermediate $\delta^{13}C$ (Figure 4).

Across the four sites, it was apparent that the proportion of fry with anadromous mothers followed a non-linear decline with increasing distance from the tidal limit (Figure 7A). All fry had anadromous mothers at site 1, 16 river km upstream of the tidal limit, and just under half (0.43) at site 4, 44 river km upstream of the tidal limit. Correspondingly, the proportion of fry with river-resident mothers followed a non-linear increase with increasing distance from the tidal limit, with no fry attributed to river-resident mothers at either of the two sites closer to the tidal limit and just over half (0.53) at site 4, 44 km upstream of the tidal limit (Figure 7A). The proportion of family groups attributable to mothers of the two life-history strategies followed a similar pattern of non-linear change with distance upstream. All family groups were attributable to anadromous mothers nearest to the tidal limit and approximately equal proportions attributable to the two life-history strategies at the site furthest from the tidal

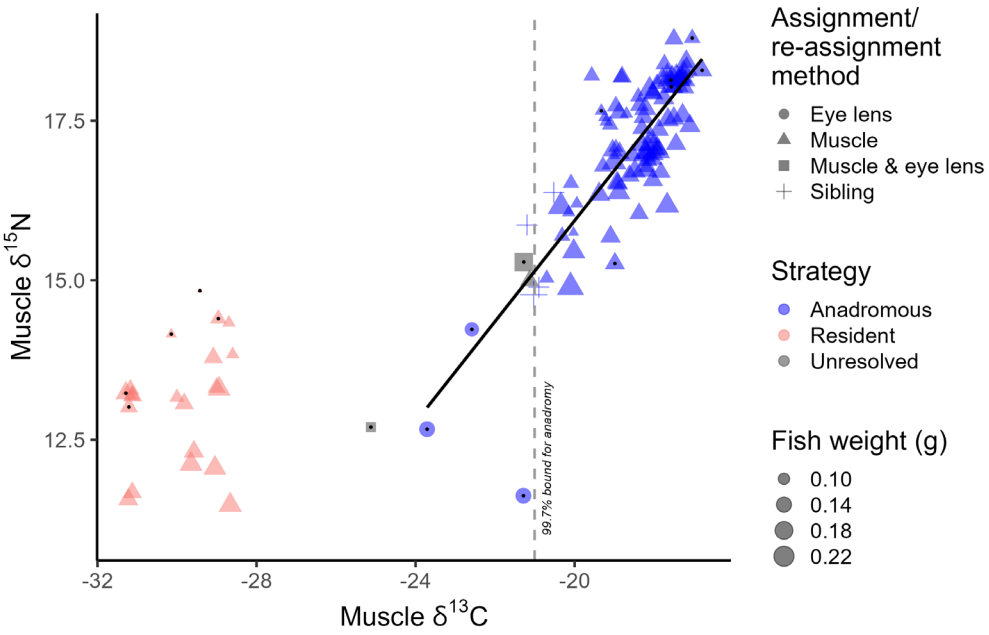

FIGURE 6 | Muscle $\delta^{13}C$ and $\delta^{15}N$ of recently emerged trout fry assigned to anadromous or freshwater-resident mothers collected from four locations in the River Frome. Samples with paired eye lens $\delta^{13}C$ data are indicated by a small black spot inside the symbol, with three individuals (blue circles) reassigned as anadromous based on the lens data (muscle $\delta^{13}C$ values below the −21.01‰ bound for anadromy, lens $\delta^{13}C$ values above it). See text for assignment rules. No fry were allocated to freshwater-resident mothers with lower confidence. Line fitted to fry with anadromous mothers ($R^2 = 0.6549$, $p < 0.0001$; influence of confidence class, $p = 0.4773$).

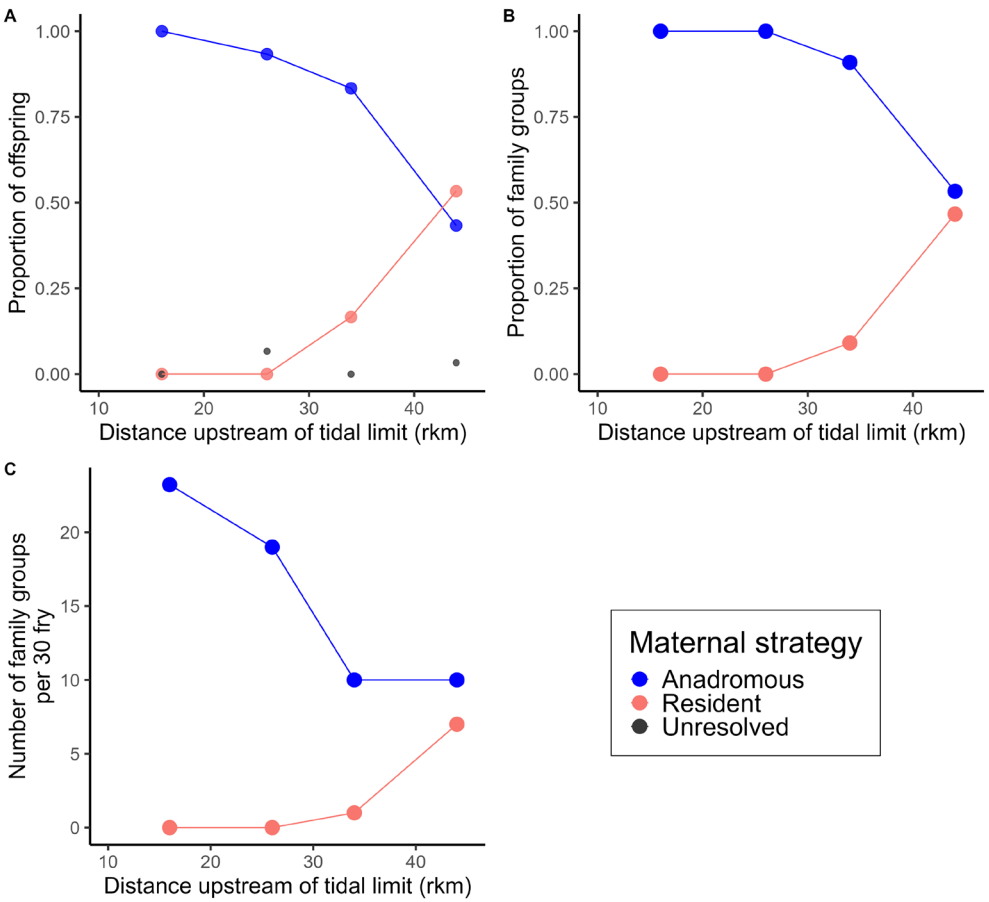

FIGURE 7 | Relationship between distance from the tidal limit and (A) the proportion of fry sampled that were attributed to anadromous or resident mothers, or unresolved, (B) the proportion of attributable family groups with anadromous or resident mothers, and (C) the number of family groups that were attributed to anadromous or resident mothers.

limit (Figure 7B). However, the number of family groups with an anadromous mother declined with distance from the tidal limit (Figure 7C). At the most upstream site, site 4, 10 family groups had anadromous mothers.

4 | Discussion

Our data indicate that anadromous mothers contribute disproportionally to the recruitment of *S. trutta*, and that this influence extends a considerable distance upstream, into the headwaters of the productive chalk stream that was the focus of this study. Whilst in the reach closest to the tidal limit (16 river km upstream) all fry had anadromous mothers; approximately half of the fry had anadromous mothers at the site furthest from the tidal limit (44 river km upstream). This finding is contrary to the expectation that the influence of anadromous mothers would be restricted to reaches close to the tidal limit, highlighting the importance of anadromous fish for recruitment throughout the catchment, even in productive systems.

To determine the maternal life-history of fry we primarily used the stable isotopic composition of their muscle tissue. As reported previously (Goodwin et al. 2016) there was clear differentiation in the isotopic composition of muscle from adult fish exhibiting resident vs. anadromous life history strategies. However, in contrast with previous reports (Doucett et al. 1999; McCarthy and Waldron 2000; Charles et al. 2004), this was not always true of the fry. As the tissues of offspring initially comprise matter derived from the mother via the egg, the isotopic composition of newly hatched fry reflects the habitat where the mother fed during vitellogenesis. Once offspring begin feeding exogenously, organic matter is taken up from the surrounding habitat, gradually replacing the maternal isotopic ratio with one characteristic of the environment they are feeding in (Doucett et al. 1999; Goodwin et al. 2016). For offspring of anadromous mothers, this corresponds with a gradual shift to a more deplete $\delta^{13}C$ as their tissues start to reflect the freshwater rather than the marine habitat. On the other hand, there is no change in $\delta^{13}C$ of fry with freshwater-resident mothers. Both groups of fry shift to a lower $\delta^{15}N$ as they feed lower in the food web than their mothers (Woodward et al. 2010). The effect of exogenous feeding on $\delta^{15}N$ is most pronounced in fry of anadromous mothers, which tend to have a more piscivorous diet at sea (Roche et al. 2017), resulting in a higher starting $\delta^{15}N$ value in their offspring. This shift in isotopic composition of fry with anadromous mothers was clear in our data. Despite these changes, our approach using isotopic ratios of muscle and eye lens cores, combined with SNP genotyping, was able to attribute 97.5% of the fry to either freshwater-resident or anadromous mothers.

The eye lens cores exhibited similar $\delta^{13}C$ values to the muscle samples from the same individuals, providing confidence in this technique. Moreover, in most cases the lens core appeared to provide greater discrimination among maternal strategies than muscle tissue: 60% of the fry with an undefined maternal strategy based on muscle could be confidently attributed to an anadromous mother based on eye lens core $\delta^{13}C$. This suggests that the muscle samples in these individuals had been affected by feeding on freshwater prey after emergence, incorporating matter with a lower $\delta^{13}C$ into their body tissues. Interestingly, one fry exhibited intermediate $\delta^{13}C$ values in both muscle and lens tissue, suggesting an intermediate migratory form where the mother spent extended periods in estuaries (known as a 'slob' trout; Ferguson et al. 2019) or moved frequently between fresh and marine waters during vitellogenesis. The main disadvantage of using lens cores compared with muscle tissue is that they are very small, making them more difficult to handle and to obtain reliable isotope measurements. Nevertheless, lens cores could be a powerful tool for reconstructing maternal strategy in older fish. While otolith core chemistry can provide analogous information using strontium concentrations and isotope ratios (Zimmerman et al. 2009; Courter et al. 2013), lens cores are easier to extract, and $\delta^{13}C$ analyses tend to be cheaper and more readily available. This opens new doors to compare the contribution rates of different strategies across more meaningful time periods. Our data along with those of Goodwin et al. (2016) suggest that despite resident fish being abundant throughout the system, anadromous mothers contribute disproportionately to trout recruitment. It is not known if these offspring survive to adulthood and maintain this higher contribution in subsequent cohorts. Whereas it is known that smolt size, sex and migration timing can impact the maiden marine migration (Gillson et al. 2025) and marine migration routes (Artero et al. 2025) of anadromous individuals, more work is required to determine which factors in the juvenile freshwater stages influence life-history outcomes and the implications for growth, migratory behaviour, and survival.

In this productive chalk stream catchment, we found that both the proportion of offspring and the proportion of family groups with anadromous mothers declined monotonically with distance upstream of the tidal limit. All fry had anadromous mothers at the lowest site, declining to approximately half at the highest site, 44 km from the tidal limit. The disproportionate contribution of anadromous fish to young-of-the-year did not simply reflect the difference in fecundity of anadromous compared with freshwater resident females (due to the difference in size/egg production): the number of family groups, indicative of the number of females involved in reproduction, was higher for anadromous mothers than for freshwater resident mothers at all sites. A decline in the numbers of anadromous fish with distance upstream was expected due to individuals halting their migration, due to homing, encountering suitable spawning sites, or obstructions to passage. This was reflected in the decline in number of family groups with anadromous mothers. Whilst we did not expect anadromous females to access the headwaters in high numbers, the number of family groups suggests slightly more pairings involving anadromous mothers than freshwater-resident mothers at the most upstream site. However, as we only considered full siblings in family groups (in order to accurately determine the life-history strategy of the mother), we cannot directly translate the number of family groups into numbers of anadromous mothers accessing the headwaters. Goodwin et al. (2016) found that anadromous females, which tend to be larger, mated with multiple males, both freshwater resident and anadromous, increasing the number of family groups per female. As males contribute little mass to the developing offspring, paternity can only be determined with knowledge of the father's genetics, which we lacked. Nevertheless, the maternal contribution of the two

strategies to recruitment at the most upstream site (44 km from the tidal limit) appeared to be approximately equal.

Whilst the implications of the disproportionate importance of anadromous females for trout recruitment are clearly apparent, resident fish can produce anadromous offspring and vice versa (Archer et al. 2019; Losee et al. 2023). As we do not fully understand the consequences of maternal life history strategy for the migration choices of the offspring, the consequences of the input of anadromous females to recruitment for the density of resident trout are less clear. Furthermore, the techniques we used here do not provide information on the importance of anadromous males. Goodwin et al. (2016) found that anadromous males contribute disproportionately (siring 63% of offspring) though not to the same extent as females. As the selective pressure differs between males and females (Klemetsen et al. 2003; Goodwin et al. 2016; Ferguson et al. 2019), it is likely that anadromous males do not penetrate as far upstream as females. Other strategies, e.g., sneaker mating, may offer distinct advantages to resident males and precocious parr, though to what extent this strategy is used by brown trout is unclear (Garcia-Vazquez et al. 2001; Vladić 2006). We do not know how the paternal contribution of the two life-history strategies to recruitment varies with distance from the sea, but note that recruitment is more likely to be limited by the production of eggs than by sperm.

Our findings have practical implications for the management of *S. trutta*, an economically important species. Whilst the typically larger anadromous fish are highly prized by anglers and to some extent support commercial fisheries, river resident fish also support valuable recreational fisheries. Sea trout are under considerable pressure, and widespread declines have been reported (Fiske et al. 2024). Pollution, over-exploitation, obstructions to passage, and coastal fish farms have all been implicated in reductions in the number of returning anadromous adult trout (Costello 2009; Fiske et al. 2024), with those factors that hamper migration having a pronounced and specific impact on anadromous individuals. Whilst the effect of barriers to the movement of obligate migratory species is well known and profound (Davis et al. 2024), the implications for facultative migratory species are unknown. Selective mortality on populations can cause shifts in the prevalence of alternative life history strategies (DeFilippo and Ohlberger 2021), and there are consequences for population size where mortality is size selective (Swain et al. 2007). Here we have shown that in a population displaying facultative migration, anadromous mothers contribute disproportionately to recruitment even in the headwaters of a productive chalk stream. Whilst we do not know the implications of this contribution for the balance of the two life history strategies, across all sites at least half of the fry were from anadromous mothers, such that recruitment to the stock of trout in the river appears highly dependent on unobstructed migration pathways to and from the marine environment.

Author Contributions

Conceptualisation: J.I.J., R.B.L. Developing methods, data analysis, preparation of figures and tables: J.I.J., R.A.K., R.B.L., J.S., A.M.S. Conducting the research, data interpretation, writing: J.I.J., R.A.K., R.B.L., J.S., A.M.S., H.W.

Acknowledgements

This research was part-funded by the European Union Interreg France (Channel) England programme project 'Salmonid Management Around the Channel' (SAMARCH). Funding was also provided to A.M.S. by a UKRI Future Leaders Fellowship (MR/V023578/1).

Ethics Statement

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The work was undertaken with the approval of the Environment Agency.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

References

Acolas, M. L., J. M. Roussel, and J. L. Bagliniere. 2008. "Linking Migratory Patterns and Diet to Reproductive Traits in Female Brown Trout (*Salmo trutta* L.) by Means of Stable Isotope Analysis on Ova." *Ecology of Freshwater Fish* 17: 382–393. https://doi.org/10.1111/j.1600-0633.2007.00290.x.

Archer, L. C., S. A. Hutton, L. Harman, et al. 2019. "The Interplay Between Extrinsic and Intrinsic Factors in Determining Migration Decisions in Brown Trout (*Salmo trutta*): An Experimental Study." *Frontiers in Ecology and Evolution* 7: 222. https://doi.org/10.3389/fevo.2019.00222.

Archer, L. C., S. A. Hutton, L. Harman, et al. 2020. "Metabolic Traits in Brown Trout (*Salmo trutta*) Vary in Response to Food Restriction and Intrinsic Factors." *Conservation Physiology* 8: 96. https://doi.org/10.1093/conphys/coaa096.

Artero, C., J. F. Strøm, G. Bennett, et al. 2025. "Diversity of Sea Trout Marine Migration Routes in the English Channel." *Animal Biotelemetry* 13: 18. https://doi.org/10.1186/s40317-025-00413-5.

Birnie-Gauvin, K., E. B. Thorstad, and K. Aarestrup. 2019. "Overlooked Aspects of the *Salmo salar* and *Salmo trutta* Lifecycles." *Reviews in Fish Biology and Fisheries* 29: 749–766. https://doi.org/10.1007/s11160-019-09575-x.

Bohlin, T., J. Pettersson, and E. Degerman. 2001. "Population Density of Migratory and Resident Brown Trout (*Salmo trutta*) in Relation to Altitude: Evidence for a Migration Cost." *Journal of Animal Ecology* 70: 112–121. https://doi.org/10.1111/j.1365-2656.2001.00466.x.

Brönmark, C., K. Hulthén, P. A. Nilsson, et al. 2013. "There and Back Again: Migration in Freshwater Fishes." *Canadian Journal of Zoology* 92: 467–479. https://doi.org/10.1139/cjz-2012-0277.

Chapman, B. B., C. Brönmark, J.-Å. Nilsson, and L.-A. Hansson. 2011a. "Partial Migration: An Introduction." *Oikos* 120: 1761–1763. https://doi.org/10.1111/j.1600-0706.2011.20070.x.

Chapman, B. B., C. Brönmark, J.-Å. Nilsson, and L.-A. Hansson. 2011b. "The Ecology and Evolution of Partial Migration." *Oikos* 120: 1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x.

Charles, K., J. M. Roussel, and B. Cunjack. 2004. "Estimating the Contribution of Sympatric Anadromous and Freshwater Resident Brown Trout to Juvenile Production." *Marine and Freshwater Research* 55: 185–191.

Charles, K., J. M. Roussel, J. M. Lebel, J. L. Baglinière, and D. Ombredane. 2006. "Genetic Differentiation Between Anadromous and Freshwater Resident Brown Trout (*Salmo trutta* L.): Insights Obtained

From Stable Isotope Analysis." *Ecology of Freshwater Fish* 15: 255–263. https://doi.org/10.1111/j.1600-0633.2006.00149.x.

Costello, M. J. 2009. "How Sea Lice From Salmon Farms May Cause Wild Salmonid Declines in Europe and North America and Be a Threat to Fishes Elsewhere." *Proceedings of the Royal Society B: Biological Sciences* 276: 3385–3394. https://doi.org/10.1098/rspb.2009.0771.

Courter, I. I., D. B. Child, J. A. Hobbs, T. M. Garrison, J. J. G. Glessner, and S. Duery. 2013. "Resident Rainbow Trout Produce Anadromous Offspring in a Large Interior Watershed." *Canadian Journal of Fisheries and Aquatic Sciences* 70: 701–710. https://doi.org/10.1139/cjfas-2012-0457.

Curry, R. A. 2005. "Assessing the Reproductive Contributions of Sympatric Anadromous and Freshwater-Resident Brook Trout." *Journal of Fish Biology* 66: 741–757. https://doi.org/10.1111/j.0022-1112.2005.00636.x.

Davis, F., A. Szopa-Comley, S. Rouse, et al. 2024. "State of the World's Migratory Species." UNEP-WCMC, Cambridge, UK. State of the Worlds Migratory Species report_E.pdf (cms.int).

DeFilippo, L. B., and J. Ohlberger. 2021. "Stochastic Recruitment Alters the Frequencies of Alternative Life Histories in Age-Structured Populations." *Fish and Fisheries* 22: 1307–1320. https://doi.org/10.1111/faf.12588.

DeNiro, M. J., and S. Epstein. 1978. "Influence of Diet on the Distribution of Carbon Isotopes in Animals." *Geochimica et Cosmochimica Acta* 42: 495–506. https://doi.org/10.1016/0016-7037(78)90199-0.

Doucett, R. R., W. Hooper, and G. Power. 1999. "Identification of Anadromous and Nonanadromous Adult Brook Trout and Their Progeny in the Tabusintac River, New Brunswick, by Means of Multiple-Stable-Isotope Analysis." *Transactions of the American Fisheries Society* 128: 278–288. https://doi.org/10.1577/1548-8659(1999)128<0278:IOAANA>2.0.CO;2.

Duval, E., O. Skaala, M. Quintela, et al. 2021. "Long-Term Monitoring of a Brown Trout (*Salmo trutta*) Population Reveals Kin-Associated Migration Patterns and Contributions by Resident Trout to the Anadromous Run." *BMC Ecology and Evolution* 21: 143. https://doi.org/10.1186/s12862-021-01876-9.

Elliott, J. M. 1994. *Quantitative Ecology and the Brown Trout*. Oxford University Press.

Ferguson, A., T. E. Reed, T. F. Cross, P. McGinnity, and P. A. Prodöhl. 2019. "Anadromy, Potamodromy and Residency in Brown Trout *Salmo trutta*: The Role of Genes and the Environment." *Journal of Fish Biology* 95: 692–718. https://doi.org/10.1111/jfb.14005.

Fiske, P., T. Forseth, E. B. Thorstad, et al. 2024. "Novel Large-Scale Mapping Highlights Poor State of Sea Trout Populations." *Aquatic Conservation: Marine and Freshwater Ecosystems* 34: e4067. https://doi.org/10.1002/aqc.4067.

Fleming, I. A., and J. D. Reynolds. 2004. "Salmonid Breeding Systems." In *Evolution Illuminated: Salmon and Their Relatives*, edited by A. P. Hendry and S. C. Stearns, 264–294. Oxford University Press. https://doi.org/10.1093/oso/9780195143850.001.0001. Online ISBN: 9780197700907; Print ISBN: 9780195143850.

Garcia-Vazquez, E., P. Moran, J. L. Martinez, J. Perez, B. de Gaudemar, and E. Beall. 2001. "Alternative Mating Strategies in Atlantic Salmon and Brown Trout." *Journal of Heredity* 92: 146–149. https://doi.org/10.1093/jhered/92.2.146.

Gillson, J. P., R. E. Blackwell, S. D. Gregory, et al. 2025. "Do the Biological Characteristics of Trout (*Salmo trutta*) Smolts Influence Their Spring Migration Timing and Maiden Marine Sojourn Duration?" *Journal of Fish Biology*. https://doi.org/10.1111/jfb.16040.

Goodwin, J. C. A., R. A. King, J. I. Jones, A. Ibbotson, and J. R. Stevens. 2016. "A Small Number of Anadromous Females Drive Reproduction in a Brown Trout (*Salmo trutta*) Population in an English Chalk Stream." *Freshwater Biology* 61: 1075–1089. https://doi.org/10.1111/fwb.12768.

Greenberg, L., P. Svendsen, and A. Harby. 1996. "Availability of Microhabitats and Their Use by Brown Trout (*Salmo trutta*) and Grayling (*Thymallus thymallus*) in the River Vojman, Sweden." *Regulated Rivers: Research & Management* 12: 287–303. https://doi.org/10.1002/(SICI)1099-1646(199603)12:2/3<287.

Grey, J. 2001. "Ontogeny and Dietary Specialization in Brown Trout (*Salmo trutta* L.) From Loch Ness, Scotland, Examined Using Stable Isotopes of Carbon and Nitrogen." *Ecology of Freshwater Fish* 10: 168–176. https://doi.org/10.1034/j.1600-0633.2001.100306.x.

Gross, M. R. 1987. "Evolution of Diadromy in Fishes." *American Fisheries Society Symposium* 1: 14–25.

Jones, O. R., and J. Wang. 2010. "COLONY, a Program for Parentage and Sibship Inference From Multilocus Genotype Data." *Molecular Ecology Resources* 10: 551–555. https://doi.org/10.1111/j.1755-0998.2009.02787.x.

Jonsson, B., and N. Jonsson. 2006. "Life History of Anadromous Brown Trout." In *Proceedings of the First International Sea Trout Symposium, July, Cardiff, Wales, UK 2004. Sea trout: Biology, Conservation & Management*, edited by G. S. Harris and N. J. Milner, 196–223. Blackwell Publishing, Oxford, England.

Klemetsen, A., P.-A. Amundsen, J. B. Dempson, et al. 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. https://doi.org/10.1034/j.1600-0633.2003.00010.x.

Lauridsen, R. B., F. K. Edwards, M. J. Bowes, et al. 2012. "Consumer–Resource Elemental Imbalances in a Nutrient-Rich Stream." *Freshwater Science* 31: 408–422. https://doi.org/10.1899/11-052.

Losee, J., A. Claiborne, D. Palm, et al. 2023. "Migratory Behavior and Maternal Origin of Anadromous Brown Trout in the Baltic Sea." *Marine Ecology Progress Series* 722: 145–155. https://doi.org/10.3354/meps14433.

McCarthy, I. D., and S. Waldron. 2000. "Identifying Migratory *Salmo trutta* Using Carbon and Nitrogen Stable Isotope Ratios." *Rapid Communications in Mass Spectrometry* 14: 1325–1331. https://doi.org/10.1002/1097-0231(20000815)14:15<1325::AID-RCM980>3.0.CO;2-A.

National River Flow Archive. 2024. "44001—Frome at East Stoke Total." https://nrfa.ceh.ac.uk/data/station/info/44001.

Nielsen, E. E., L. A. Bach, and P. Kotlick. 2021. "HYBRIDLAB (Version 1.0): A Program for Generating Simulated Hybrids From Population Samples." *Molecular Ecology* 6: 971–973. https://doi.org/10.1111/j.1471-8286.2006.01433.x.

Osmond, D. R., R. A. King, B. Stockley, S. Launey, and J. R. Stevens. 2023. "A Low-Density Single Nucleotide Polymorphism Panel for Brown Trout (*Salmo trutta* L.) Suitable for Exploring Genetic Diversity at a Range of Spatial Scales." *Journal of Fish Biology* 102: 258–270. https://doi.org/10.1111/jfb.15258.

Phillips, D. L., and J. W. Gregg. 2001. "Uncertainty in Source Partitioning Using Stable Isotopes." *Oecologia* 127: 171–179. https://doi.org/10.1007/s004420000578.

Quaeck-Davies, K., V. A. Bendall, K. M. MacKenzie, S. Hetherington, J. Newton, and C. N. Trueman. 2018. "Teleost and Elasmobranch Eye Lenses as a Target for Life-History Stable Isotope Analyses." *PeerJ* 6: e4883. https://doi.org/10.7717/peerj.4883.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Roche, W., N. Milner, C. Davies, et al. 2017. "Feeding Ecology of Sea Trout in the Irish Sea. Chapter 20." In *Sea Trout: Science and Management:*

Proceedings of the 2nd International Sea Trout Symposium, edited by G. Harris. Matador.

Rohtla, M., L. Matetski, R. Svirgsden, et al. 2017. "Do Sea Trout *Salmo trutta* Parr Surveys Monitor the Densities of Anadromous or Resident Maternal Origin Parr, or Both?" *Fisheries Management and Ecology* 24: 156–162. https://doi.org/10.1111/fme.12214.

Swain, D. P., A. F. Sinclair, and J. M. Hanson. 2007. "Evolutionary Response to Size-Selective Mortality in an Exploited Fish Population." *Proceedings of the Royal Society B: Biological Sciences* 274: 1015–1022. https://doi.org/10.1098/rspb.2006.0275.

Tomkins, J. L., and W. Hazel. 2007. "The Status of the Conditional Evolutionarily Stable Strategy." *Trends in Ecology & Evolution* 22: 522–528.

Truett, G. E., P. Heeger, R. L. Mynatt, A. A. Truett, J. A. Walker, and M. L. Warman. 2000. "Preparation of PCR-Quality Mouse Genomic DNA With Hot Sodium Hydroxide and Tris (HotSHOT)." *BioTechniques* 29: 52–54. https://doi.org/10.2144/00291bm09.

Vladić, T. 2006. "Sperm Quality and Egg Size in the Brown Trout: Implications for Sperm Competition and Cryptic Male Choice." *Verhandlungen—Internationale Vereinigung fur Theoretische und Angewandte Limnologie* 29: 1331–1340. https://doi.org/10.1080/03680770.2005.11902898.

Woodward, G., J. Blanchard, R. B. Lauridsen, et al. 2010. "Individual-Based Food Webs: Species Identity, Body Size and Sampling Effects." *Advances in Ecological Research* 43: 211–266. https://doi.org/10.1016/B978-0-12-385005-8.00006-X.

Zimmerman, C. E., G. W. Edwards, and K. Perry. 2009. "Maternal Origin and Migratory History of Steelhead and Rainbow Trout Captured in Rivers of the Central Valley, California." *Transactions of the American Fisheries Society* 138: 280–291. https://doi.org/10.1577/T08-044.1.