

ARTICLE

Evaluating the importance of accurate sex ratios on egg deposition targets and conservation limit compliance for Atlantic salmon (*Salmo salar* L.) in the River Tamar, south-west England

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Abstract

Effective management of Atlantic salmon requires a suite of metrics that are fed into stock assessment models to assess stock compliance within individual rivers in relation to estimated conservation limits. Key among metrics required to assess compliance are the number of adult female spawners within each adult sea age class and their corresponding egg deposition rates. Owing to the current need to conserve salmon stocks, adult sex ratios used to calculate egg deposition estimates often depend on data derived from historic lethal sampling. Using non-invasive sampling and an accurate genetic sex test, we determined the proportion of female fish in two adult life history stages (one sea winter and two sea winter) of Atlantic salmon from the River Tamar, an Environment Agency (England) Monitored River. Our results suggested that phenotypic-based sexing of Tamar salmon was unreliable, especially for early run fish and that the proportion of female salmon has been under-estimated, thereby leading to consistent under-estimation of egg deposition rates.

KEYWORDS

Atlantic salmon, conservation limit, egg deposition, fisheries management, sdY gene, stock assessment

1 | INTRODUCTION

The Atlantic salmon (*Salmo salar* L.) is an iconic fish species with significant cultural, ecological and economical importance. Due to their predominantly anadromous life history, Atlantic salmon (hereafter, salmon) are subjected to multiple stressors in both freshwater and marine habitats (Gillson et al., 2022; Thorstad et al., 2021) which have led to populations across the entire species' range dramatically declining in abundance over the last 40 years (ICES, 2019). To enable informed fisheries management, stock assessment models are used to predict numbers of recruits

to a population (often referred to as a stock) over a given period, ordinarily based on returning stock estimates from the preceding year (Ó Maoiléidigh et al., 2004). Such models require detailed knowledge of numbers of adult female returnees and egg deposition rates. However, egg numbers are not calculated directly, but rather, are estimated from counts and length of returning adults, with estimates of sex ratio for each sea age class within the annual salmon run (White et al., 2016). However, sex ratios vary among life history stages, between years and among stocks (Chadwick, 1985; O'Connell et al., 2006), while the sex ratios used in models are often based on historic values (White et al., 2016)

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that may be out-of-date or are averages derived from multiple catchments (Scottish Government, 2019). Precise knowledge of the sex ratio for multiple life history stages is essential for incorporation into stock assessment models (Crozier et al., 2018; Rivot et al., 2019), and up-to-date information is needed to inform fisheries management decisions (ICES, 2019).

Management of salmon fisheries in England and across most of the North Atlantic depends on river-specific conservation limits (the spawning stock level that produces maximum sustainable yield—NASCO, 2009). The English Environment Agency conducts an annual conservation limit compliance assessment for each of the 42 principal salmon rivers in England based on annual Returning Stock Estimates, calculated either from direct counts of upstream migrants using automated fish counters or from declared salmon rod catch data. Within the returning stock estimate, proportions of one sea winter (1SW) and two sea winter (2SW) salmon in the annual run are estimated, which is combined with an estimate of the sex ratio and weight-related fecundity of female fish within each sea age class to estimate annual egg deposition.

A reliable estimate of the number of female fish present within each sea age class of adult salmon within the annual run is critical to ensure that estimates are updated and re-assessed, especially where sex ratios may be influenced by environmental, anthropogenic or biological factors (Martins et al., 2012; Spidle et al., 1998; Thompson et al., 2016). Currently, for conservation limit compliance in England, the proportion of female fish used nationally for each salmon sea age class was set in the Salmon Action Plan Guidelines (Environment Agency, 2003). For 1SW fish, the proportion of females for a given river is derived from a formula relating catchment area to female proportion data for 10 British, Irish and French rivers, while for 2SW salmon, the value is fixed at 0.687, the mean proportion of 2SW females from six British and French catchments (Environment Agency, 2003).

Ideally, where possible, the most recent, catchment-specific metrics should be used in conservation limit compliance assessments. However, salmon stock data cannot be collected on every catchment because costs can be prohibitive, when most rivers lack trapping infrastructure. For this reason, monitored rivers (formally Index Rivers) are used to provide biological metrics to inform management of salmon stocks on other river catchments, especially those with similar salmon run characteristics or within the same broad geographical area. The River Tamar (south-west England) is one of the three river catchments intensively monitored by the Environment Agency in England. The river is subjected to monitoring to both inform and improve wider management of migratory salmonids, including extensive juvenile electrofishing surveys, trapping and tagging of smolts during spring migration, and trapping of returning adults (Environment Agency, 2020). Thus, the River Tamar provides an ideal catchment to assess sex ratios across multiple salmon life history stages over multiple years.

Determination of sex of adult salmon is generally difficult from external physical characteristics, especially if fish recently entered fresh water from their marine feeding migration (Gray, 1986;

ICES, 2010). Such fish rarely display the overt signs of sexual maturity that are very evident in salmon in fresh water as they approach spawning condition. Sexing individuals based on single sexually dimorphic phenotypic characters is sometimes successful (Maise et al., 1988; Prévost et al., 1991), but, ultimately, sex determination is most reliable from internal examination; however, this generally requires lethal sampling (ICES, 2010). Continued declines in Atlantic salmon stocks (ICES, 2019) renders such an approach undesirable.

Increasingly, genetic markers to determine the sex of fish are being incorporated into fisheries management and assessment studies in a wide range of fishes, including salmonids (Bouchard et al., 2022; McKinney et al., 2022; Webster et al., 2021). However, to our knowledge, no studies have compared phenotypically determined and genetically determined sexes in a management context.

Here, we sought to determine if sex ratios for two salmon life histories (1SW and 2SW adults) within the River Tamar derived from non-lethal sampling were the same as a highly accurate genetic sex test (King & Stevens, 2020). Using samples collected over multiple years, we quantified short-term temporal variability in proportions of female:male fish and evaluated how values for adult females corresponded to historic default values currently used to assess conservation limit compliance for the River Tamar (0.453 and 0.687, respectively, for 1SW and 2SW adult sea age classes). Additionally, we evaluated how our more recent, contemporary sex ratios affected salmon egg deposition estimates for the Tamar compared to historic estimates.

2 | METHODS

2.1 | River Tamar salmonid monitoring programme

Adult salmon were caught during their upstream spawning migration in a purpose-designed fish trap associated with a fish pass located on a weir at the tidal limit at Gunnislake, Cornwall (Figure 1 – grid reference 50.519, -4.206). The annual adult salmon run is typically between March and the end of November, peaking between May and late August, and principally comprises two stock components. Early running spring salmon (pre-1st June) tend to be Multi-Sea-Winter (MSW) fish, most of which have spent two winters at sea. One-sea-winter fish (also known as grilse) typically begin to enter fresh water at the end of June. From June until the end of November, the salmon run includes both 1SW and 2SW salmon. At the Gunnislake trap, biological measurements include weight to the nearest 10 g, fork length to the nearest mm, girth, physical condition assessments (sea lice burden and damage, extent of wounds, that is, net marks, scale loss, split fins and lamprey marks), presence of notable health issues (ulcerative lesions, presence of fungal infections, etc.) and phenotypic sex determination (male, female or undetermined). Sex is determined from phenotypic characters, including head shape (more elongated in males), body shape (females often have a fatter and deeper body shape in

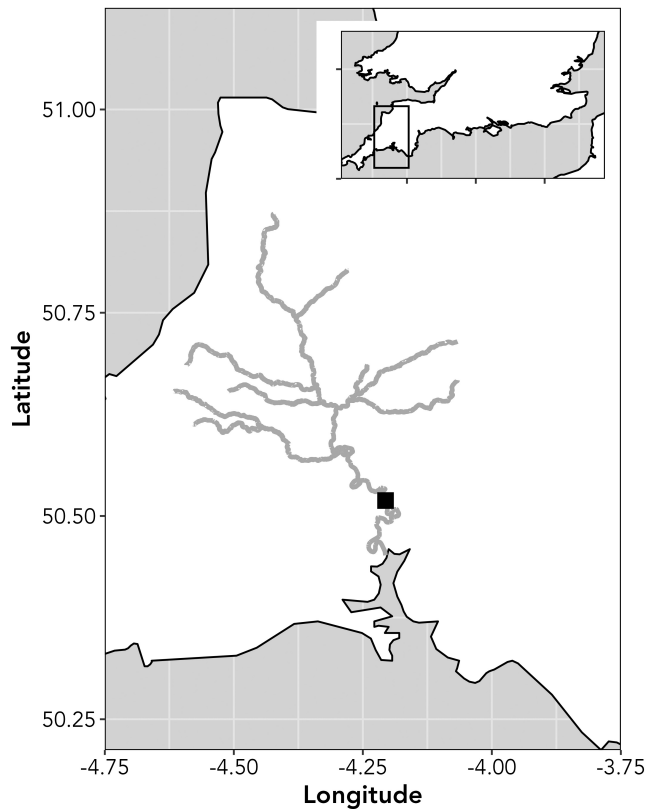


FIGURE 1 Map of the River Tamar catchment showing the location of the adult trap at Gunnislake weir (black square). Inset shows southern UK with map area shown within the black rectangle.

TABLE 1 Summary of samples obtained for molecular sex testing of River Tamar Atlantic salmon adults.

Year	1SW	2SW	Other ^a
2007	419	68	3
2008	152	126	3
2009	192	111	10
2015	182	90	3
2016	226	80	2
2017	101	97	2
2018	160	93	5
2019	166	99	1
2020	307	139	1
Total	1905	903	30

Abbreviations: 1SW, one sea winter; 2SW, two sea winter.

^aFish with sea ages other than 1SW or 2SW that is, 3SW, 1+SM+ or fish with only replacement scales available.

the belly region), colour (red to coppery in males) and presence of pronounced teeth and a kype in males. The presence of a coded-wire tag (CWT) or lack of an adipose fin (indicating that the fish was trapped and clipped as a smolt during downstream migration) is also noted for marine mortality estimates.

2.2 | Sample collection

Scales were obtained from every fifth adult fish caught in the Gunnislake weir trap during 2007–2009 and 2015–2020. Age was estimated from scales to determine fresh water and sea age of each adult fish. The total data set consisted of 2838 fish (Table 1).

2.3 | Molecular methods

Genomic DNA was extracted from fin clips and scales following the method of Truett et al. (2000). Molecular sex was assigned using a duplex polymerase chain reaction (PCR) using primers that amplify a portion of the male-specific *sdY* (sexually dimorphic on the Y-chromosome) gene and primers for the fatty acid-binding protein *6b* (*fabp6b*) gene (amplification-positive controls) as described in King and Stevens (2020). Two sets of *sdY* primers were used. For the 2007–2009 adult scale samples, we used primers *Salmo-sdY-F* and *Salmo-sdY-R* (Quéméré et al., 2014) that amplify a product of 179 to 193 bp in male fish only. For the 2015–2020 adult samples, we used two primers *Ss sdy Ex1F* and *SS sdy AS* (King & Stevens, 2020; Yano et al., 2013) that amplify a product of ~700 bp in male fish only. These *sdY* primer combinations correctly assign sex in samples from known male and female salmon (King & Stevens, 2020; R.A. King, unpublished data). The *fabp6b* primers amplify a product of ~450 bp in both male and female fish. Amplifications were in a 10 µl volume comprising 5 µl of HotStar Taq Master Mix Kit (Qiagen), 0.1 µM of *fabp6b* primer, 0.2 µM of *sdY* primer, 0.1 µl of bovine serum albumin (20 mg/ml—New England Biolabs) and 1 µl of extracted DNA. PCR cycling conditions were 95°C for 5 min, followed by 35 cycles of 94°C for 30 s, 60°C (*Ss sdy Ex1F* & *SS sdy AS*) or 56°C (*Salmo-sdY-F* & *Salmo-sdY-R*) for 30 s, 72°C for 40 s and a final extension at 72°C for 10 min. PCR products were visualised on ethidium bromide stained 1.5% agarose gels. A negative control (water only template) and two positive controls (DNA from one known male and one known female salmon) were included in each batch of amplifications. To test correspondence of results from both *sdY* primer sets, sex was assigned to a subset of samples (200 from 2019) using both the *Ss sdy Ex1F* and *SS sdy AS*, and *Salmo-sdY-F* and *Salmo-sdY-R* primer combinations.

2.4 | Data analysis

The proportion of female fish (P_f), with 95% binomial confidence intervals, was estimated for 1SW and 2SW salmon from 2007–2009 and 2015–2020 using the *Mkinfer* R package (Kohl, 2020). A Chi-squared test with p values computed using Monte Carlo simulation (10^6 simulations), was used to test for deviations from a 1:1 sex ratio (R version 4.0.4; R Core Team, 2019).

Binomial generalised linear modelling (GLM) was used to test correspondence between phenotypic sex (determined “in hand” at

TABLE 2 Values of parameters used to assess the effect of changing proportion of females (P_f) on the River Tamar Atlantic salmon egg deposition for 2015–2020.

Parameters	2015		2016		2017		2018		2019		2020	
	1SW	2SW	1SW	2SW	1SW	2SW	1SW	2SW	1SW	2SW	1SW	2SW
Historic default P_f	0.453	0.687	0.453	0.687	0.453	0.687	0.453	0.687	0.453	0.687	0.453	0.687
Annual genetically determined P_f	0.511	0.789	0.407	0.925	0.436	0.742	0.569	0.785	0.337	0.798	0.420	0.730
2015–2020 average genetically determined P_f	0.447	0.795	0.447	0.795	0.447	0.795	0.447	0.795	0.447	0.795	0.447	0.795
Number of spawners ^a	2215	1834	2889	1047	2061	1855	1302	1309	1326	1162	3189	1277
Average length (mm)	584.7	736.8	567.5	749.6	572.4	734.6	584.7	755.1	569.3	748.9	598.4	752.8
Average eggs per female	3455	7164	3144	7564	3231	7093	3455	7740	3176	7540	3717	7667

Abbreviations: 1SW, one sea winter; 2SW, two sea winter.

^aTotal number of spawners, adjusted accounting for freshwater mortality and rod catch.

the Gunnislake weir trap) and genetic sex, across the run for the subset of individuals having estimates of sex for both methods (glm() function, R version 4.0.4, R Core Team, 2019). Analyses were performed on the combined data for each sex within each of the two sea age classes. Data were coded as 1 (match between phenotypic and genetic sex) or 0 (mismatch between phenotypic and genetic sex). Trapping date of each individual was taken as the number of days after 1st January. A Z-test was used to test for statistical differences in the proportion of female fish for individuals assigned a sex both phenotypically and genetically (see <http://www.socscistatistics.com/tests/ztest/Default2.aspx>).

2.5 | Estimation of annual egg deposition rates

The proportion of female fish in each sea age class, an important metric in salmon stock assessment models, was evaluated using our updated sex ratios on egg deposition estimates for the Tamar, during 2015–2020. River-specific egg deposition estimates are based on the estimated number of annual adult salmon returning. For the Tamar, the returning stock estimate is based on counts of fish from an automated resistivity counter associated with the adult trap at Gunnislake weir, with corrections for salmon that may migrate upstream via alternative routes (i.e. over the weir). The returning stock estimate is divided into constituent run components to estimate the annual total number of fish returning to the Tamar within each adult sea age class. The estimate is further adjusted to account for rod fishery exploitation and mortality within fresh water (assumed to be 20% for rod-caught and released fish and 9% for uncaught fish—Environment Agency, 2015). Additionally, weight–length data and scale samples are obtained from a representative sample of adult fish trapped throughout the annual run period. Female salmon fecundity was estimated using a River Tamar-specific relationship based upon historic hatchery records that use the average length of salmon within each sea age class sampled each year:

$$\text{Log}_{10}\text{fecundity} = -5.188178 + 3.153893 \times \text{Log}_{10}\text{length (mm)}$$

Where reliable catchment-specific data were not available, default sex ratio estimates for each adult sea age class were derived from other river catchments in England, France, Ireland and Scotland, from historic lethal sampling in fish trapping programmes and net fishery sampling. For the Tamar, historic default P_f values were 0.453 for 1SW and 0.687 for 2SW adult sea age classes.

To determine the influence of changing sex ratios on estimated annual egg deposition rates, we compared the use of default historic and genetically estimated proportions of females in each sea age class in the 2015 to 2020 annual runs, while keeping all other stock-specific parameters constant (Table 2). Sex ratio data were as follows:

1. Default historic P_f (0.453 for 1SW and 0.687 for 2SW classes);
2. A genetically determined annual P_f for each sea age class (Table 2);



3. Average genetically determined P_f values (0.447 for 1SW and 0.795 for 2SW classes) for 2015–2020.

3 | RESULTS

Of 2838 adult salmon analysed, 67.12% were 1SW and 31.82% were 2SW fish (Table 1). Only 30 were of other sea ages, mostly repeat spawners or 3SW fish (Table 1). Therefore, subsequent analyses were restricted to 1SW and 2SW adult salmon. Genetic sex determination was identical between primer sets for 200 fish analysed using both Ss sdy Ex1F and SS sdy AS, and Salmo-sdY-F and Salmo-sdY-R combinations.

3.1 | Sex ratios

Proportions of genetically determined females differed between 1SW and 2SW sea-age adult salmon. 1SW salmon had similar numbers of males and females across 9 years (Figure 2; mean $P_f = 0.457$), but varied among individual years from a strong male bias (min $P_f = 0.337$) to a slight excess of females (max $P_f = 0.560$). In 2016 ($P_f = 0.407$, $\chi^2 = 7.805$, $p = 0.006$), 2019 ($P_f = 0.337$, $\chi^2 = 17.566$, $p = 2.8 \times 10^{-5}$) and 2020 ($P_f = 0.420$, $\chi^2 = 7.821$, $p = 0.006$), the sex ratio differed significantly from 1:1. For 2SW fish, the sex ratio was significantly biased towards females in all 9 years (Figure 2; mean $P_f = 0.800$, min $P_f = 0.734$, max $P_f = 0.925$).

3.2 | Correspondence between phenotypic and genetic sex

Across 9 years, for 1812 individuals assigned to a phenotypic sex at the Gunnislake weir fish trap ($P_f = 0.59$ for 1SW and 0.66 for 2SW fish), the genetically determined P_f was lower for 1SW ($P_f = 0.49$)

and higher for 2SW ($P_f = 0.78$) fish (Table S1). Over all samples and years, assignment rates using external characteristics were correct for 72.4% of 1SW and 83.0% of 2SW males, and 92.5% of 1SW and 79.7% of 2SW females (Table S1). Phenotypic sexing over-estimated P_f for 1SW fish in 4 of 6 years, whereas phenotypic and genetic P_f estimates did not differ significantly among years for 2SW fish (Figure S1). The probability that genetically determined males and females were correctly assigned a sex phenotypically varied between sexes. For females, phenotypic and genetic sex corresponded well and were independent of sampling date (Figure 3, Table 3). In contrast, many early running males of both sea age classes, especially 1SW fish, were mis-assigned based on phenotypic characters (Figure 3, Table 3). Phenotypic sex assignment of males was reliable (>0.9 probability) after day 288 (14th October) for 1SW and day 224 (11th August) for 2SW (Figure 3) fish.

3.3 | Egg deposition estimates

Use of genetically determined sex ratios increased egg deposition estimates (Figure 4). Annual P_f estimates increased estimated deposition by 9.65% (range = 0.25%–16.83%) compared to historic default estimates. For 2020, default and annual egg deposition estimates were similar (0.25%, ~30,000 eggs). The average sex ratio during 2015–2020 increased average estimated egg deposition by 10.41% (range = 8.15%–11.86%) above the historic default ratio (Figure 4). Across all years and P_f estimates, 2SW females contributed 70% of eggs to average estimated egg deposition (range = 55.61%–83.13%; Figure 4; Figure S2).

4 | DISCUSSION

Sex ratios of adult salmon from the River Tamar differed between the 1SW age class (slight male bias) and the 2SW class (strong female

FIGURE 2 Proportion of female (P_f) Atlantic salmon (with 95% confidence intervals) in samples of one sea winter (1SW) and two sea winter (2SW) adult fish captured at Gunnislake weir on the River Tamar during 2007–2009 and 2015–2020. Black dashed line = current P_f used in setting salmon conservation limits on the River Tamar (0.453 for 1SW and 0.687 for 2SW); grey dashed line = average P_f across 9 years. Significance of deviation from equal sex ratio, as determined by a chi-squared test, is shown above each bar (ns—non-significant, ** $p < 0.01$, *** $p < 0.001$).



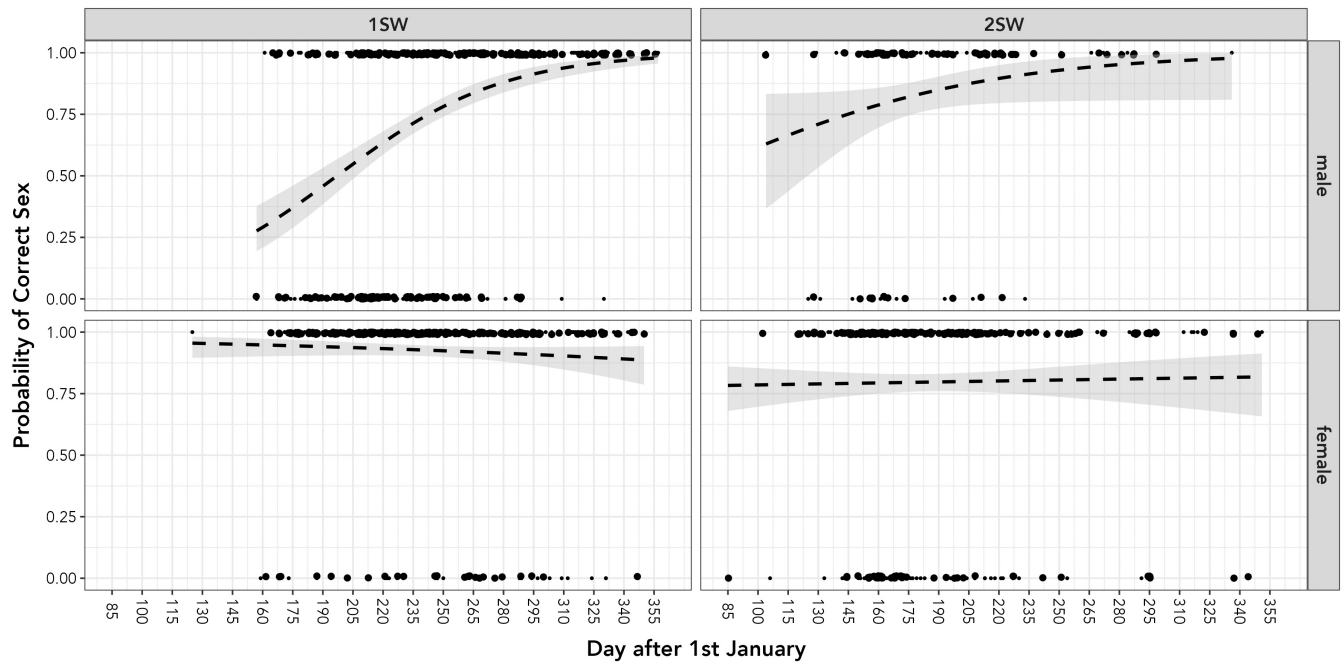


FIGURE 3 Generalised linear models summarising the association between correspondence of phenotypic- and genetical-derived sex of Atlantic salmon one sea winter (1SW) and two sea winter (2SW) genetic males and females and day of sampling for 9 years of data (2005–2007 and 2015–2020). Dashed line is the predicted probability that phenotypic sex = genetic sex and the grey area is the 95% confidence interval.

Sex/sea age	Coefficient estimate	Standard error	z value	p
Male 1 sea winter	0.0241	0.0029	8.191	2.59×10^{-16}
Female 1 sea winter	-0.0044	0.0035	-1.274	0.203
Male 2 sea winter	0.0139	0.0072	1.947	0.052
Female 2 sea winter	0.0008	0.0025	0.325	0.745

TABLE 3 Results of binomial generalised linear modelling to investigate the correspondence between phenotypic and genetic sex of River Tamar Atlantic salmon.

bias) (Thériault et al., 2007). Male reproductive success is limited by availability of mates (Thériault et al., 2007), with small anadromous and fresh water resident males (precocious parr) being able to reproduce by adopting “sneaker” tactics (Fleming, 1996; Tentelier et al., 2016). Conversely, in salmonid fishes, female fecundity strongly depends on body size (Goodwin et al., 2016; Mobley et al., 2019; Ohlberger et al., 2020; Thériault et al., 2007), with female Atlantic salmon displaying a strong positive relationship between body length and number of ova (Moffett et al., 2006). Larger female Atlantic salmon also produce higher quality eggs (in terms of energy content), which may increase alevin and fry survival (Heinimaa & Heinimaa, 2004). Similar to previous studies of salmonids (e.g. Ohlberger et al., 2020), we found that older, larger 2SW females contributed significantly more eggs to estimated egg deposition than 1SW females in the River Tamar. On the River Tamar, these large early running 2SW salmon are protected by obligatory catch-and-release bylaws to maximise potential egg deposition.

For both sea age classes, sex ratios differed significantly among years in the River Tamar, which may be common for Atlantic salmon

populations (Czorlich et al., 2021; O’Connell et al., 2006, Table S2) because of inter-annual variation in survival of males and females at sea (Olsen et al., 2006; Tamate & Maekawa, 2004), possibly driven by direct and indirect effects of prey availability and fishing mortality (Czorlich et al., 2021). Alternatively, annual variability could be caused by variation in sex-specific maturation schedules driven by growth in fresh water and the first summer at sea (Tréhin et al., 2021). Age at maturity in Atlantic salmon has also been shown to be under strong genetic control, with sex-dependent dominance at the *vgll3* gene maintaining variation in age at maturity (Barson et al., 2015). Mechanisms underlying temporal variation in sex ratio are likely multifactorial and worthy of further research to determine the relative contribution of different factors.

Consistent with other studies (i.e. Gray, 1986), sex assignment of adult salmon at the Gunnislake trap using external phenotypic characters was unreliable at certain times across the annual run, especially for males early in the run. As such, this finding will have implications for rivers where sex ratios based on the external examination are used to calculate egg deposition. Misclassification

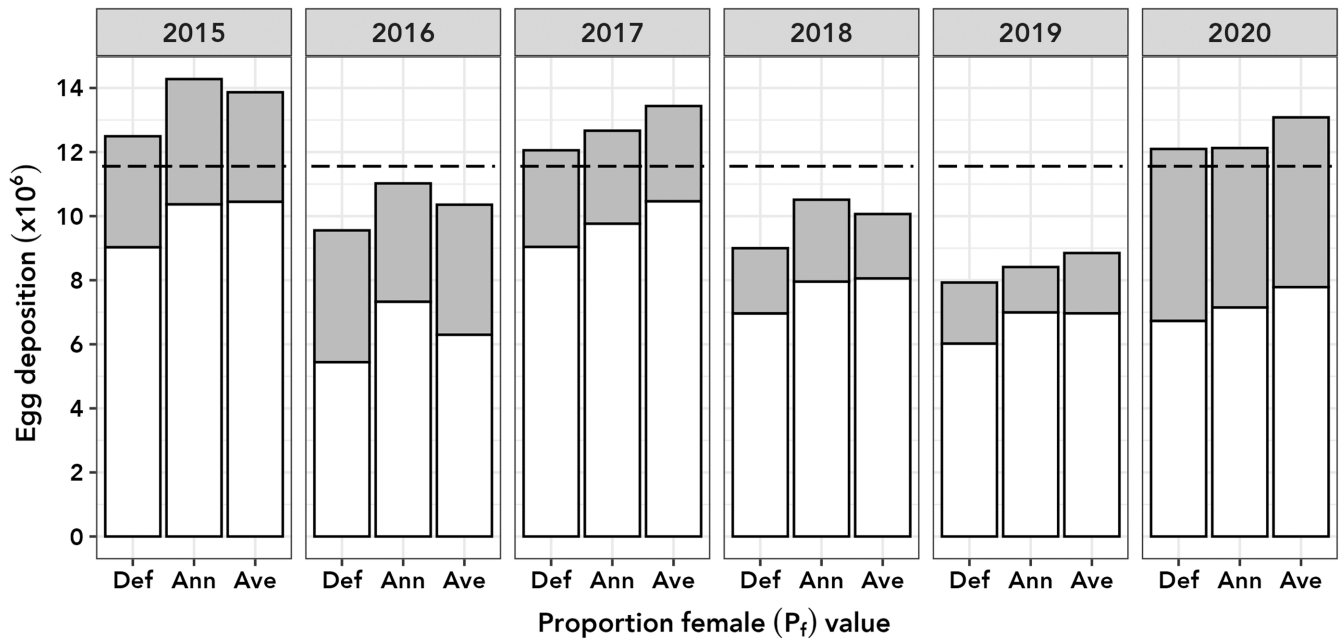


FIGURE 4 Effect on egg deposition estimates of different values of the proportion of females (P_f) for River Tamar Atlantic salmon during 2015–2020. Estimates are based on historic default (Def), annual (Ann—determined by genetic sex testing) and the 2015–2020 average (Ave) genetically determined P_f values (Table 2). The black dashed line is the conservation limit egg deposition target (11.56×10^6 eggs). Grey and white portions of each bar represent the contribution from one sea winter and two sea winter females to the total estimated egg deposition.

of males would inflate the proportion of female fish, thereby over-estimating egg deposition, which could result in rivers being falsely classified in excess of the conservation limit and negative consequences for management of salmon stocks.

For 1SW salmon, the average genetically determined proportion of females across 9 years ($P_f = 0.457$) was similar to the default historical value ($P_f = 0.453$) used to calculate egg deposition for the River Tamar, which provides some confidence for previous River Tamar salmon stock assessment results, particularly because 1SW salmon have been the numerically predominant sea age class within the River Tamar adult salmon run for many years. In contrast, for 2SW salmon, the historic default value ($P_f = 0.687$) was lower than the genetically determined proportion of females across 9 years ($P_f = 0.800$). Female 2SW fish contribute a higher proportion of total egg deposition, so this difference can significantly influence conservation limit compliance for the River Tamar. Depending on the genetically determined P_f used (annual or 6-year average), total egg deposition was generally under-estimated when using the default historic P_f value. Updated 1SW and 2SW P_f values from 2015 to 2017, when used in 2018 and 2019, improved accuracy of salmon conservation limit compliance calculations for the River Tamar (Environment Agency, 2020). Genetically determined estimates of the proportion of females during 2015–2020 will be used in future stock assessments.

Use of current information can dramatically affect egg deposition estimates (e.g. O'Connell et al., 2008). For example, in Atlantic salmon populations of eastern Canada, egg deposition differed by 30%–75% using annual length-weight fecundity estimates,

compared to default values. Similarly, natural variability in weight, run size, proportions of sea age classes and length–fecundity relationships have been shown to affect conservation limits of Irish salmon populations, although fixed sex ratios were used because no new information was available for Irish stocks and no systematic studies allowing variation in this parameter to be used in calculations of conservation limits (White et al., 2016). Results and methodology of this study provide a blueprint for estimating egg deposition and conservation limit compliance for any salmon populations where samples are available for genetic analysis.

Genetic techniques have generally been underutilised in fisheries management (Martinson et al., 2019), but their use is increasing, especially in mixed-stock analyses of commercial, subsistence and recreational fisheries (Bradbury et al., 2018, 2021; King et al., 2016). Accurate and non-invasive sex determination of adult Atlantic salmon will be useful to managers if resulting estimates of sex ratios are incorporated into conservation limit compliance assessments. To be useful, genetically determined sex assignments must be timely and cost-effective. Based on our experience, several hundred scales can be easily analysed in a week using basic molecular biological methods: DNA extraction, PCR, electrophoresis and gel staining and visualisation, without the need to use more expensive genomic methods.

Overall, our investigation highlights the need to collect accurate, up-to-date data to inform and update salmon stock assessments. Our finding that the proportion of female 2SW salmon entering the Tamar has been consistently under-estimated is an important result because these larger, more fecund individuals contribute the most to annual egg deposition in the River Tamar. The genetic techniques



described herein also provide a unique opportunity to investigate and update the observed relationship between 1SW salmon sex ratios and catchment area. From a fisheries management perspective, the average P_f for 1SW and 2SW age classes during 2015–2020 will be used by the Environment Agency (England) to assess future conservation limit compliance for the River Tamar.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest for this article.

DATA AVAILABILITY STATEMENT

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

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