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Time spent in distinct life history stages has sex-specific effects on reproductive fitness in wild Atlantic salmon

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Abstract

In species with complex life cycles, life history theory predicts that fitness is affected by conditions encountered in previous life history stages. Here, we use a 4-year pedigree to investigate if time spent in two distinct life history stages has sex-specific reproductive fitness consequences in anadromous Atlantic salmon (*Salmo salar*). We determined the amount of years spent in fresh water as juveniles (freshwater age, FW, measured in years), and years spent in the marine environment as adults (sea age, SW, measured in sea winters) on 264 sexually mature adults collected on a river spawning ground. We then estimated reproductive fitness as the number of offspring (reproductive success) and the number of mates (mating success) using genetic parentage analysis (>5,000 offspring). Sea age is significantly and positively correlated with reproductive and mating success of both sexes whereby older and larger individuals gained the highest reproductive fitness benefits (females: 62.2% increase in offspring/SW and 34.8% increase in mate number/SW; males: 201.9% offspring/SW and 60.3% mates/SW). Younger freshwater age was significantly related to older sea age and thus increased reproductive fitness, but only among females (females: −33.9% offspring/FW and −32.4% mates/FW). This result implies that females can obtain higher reproductive fitness by transitioning to the marine environment earlier. In contrast, male mating and reproductive success was unaffected by freshwater age and more males returned at a younger age than females despite the reproductive fitness advantage of later sea age maturation. Our results show that the timing of transitions between juvenile and adult phases has a sex-specific consequence on female reproductive fitness, demonstrating a life history trade-off between maturation and reproduction in wild Atlantic salmon.

KEYWORDS
life history, mating success, reproductive success, sexual conflict, sexual selection, trade-off

1 | INTRODUCTION

Many organisms have complex life cycles and undergo discrete life history stages in two or more distinct habitats (Moran, 1994). Transitions between these life history stages are typically accompanied by major shifts in physiology, behaviour and ecology, making them inherently risky and energetically expensive. Life history theory predicts that fitness in one life history stage may depend upon the allocation of resources in previous life history stages (Bernardo, 1993; Metcalfe & Monaghan, 2001; Roff, 1993; Stearns, 1992). To maximize fitness, trade-offs between the duration of time spent at specific life history stages, such as the timing to switch to a new feeding habitat or when to achieve sexual maturity, are hypothesized (Roff, 1993; Stearns, 1992). A negative relationship between growth and the time spent in each stage may in turn affect adult fitness. For example, earlier development in one life history stage may increase the probability of surviving to reproduction (Day & Rowe, 2002). However, increased survivorship may come at a cost of reduced size at reproduction. Smaller individuals may produce fewer offspring through mechanisms such as lower fecundity, increased predation and increased mating competition (Day & Rowe, 2002; Roff, 2000; Stearns, 1992). In sexually reproducing species, optimal strategies for growth, survival and reproduction can also differ between the sexes driving sexual conflict over these traits (Arnqvist & Rowe, 2005; Winemiller, 1992). Therefore, investigating how trade-offs in the duration of time spent in specific life history stages shape reproductive fitness between the sexes may help to understand the evolutionary causes and consequences of sexual conflict.

Atlantic salmon (*Salmo salar*) have a complex life cycle consisting of distinct juvenile, adult and reproductive life history stages (Jonsson & Jonsson, 2011). Atlantic salmon are anadromous; sexually mature adults reproduce in fresh water, eggs hatch and juveniles stay in freshwater anywhere between 1 and 8 years before migrating to sea (Erkinaro et al., 2019; Friedland & Haas, 1996; Jonsson & Jonsson, 2011; Økland, Jonsson, Jensen, & Hansen, 1993). Freshwater age is the amount of time spent in the juvenile freshwater environment before migration to sea. The process of transitioning to seawater is known as smoltification and is associated with morphological, physiological and behavioural changes (Jonsson & Jonsson, 1993, 2011; McCormick, Hansen, Quinn, & Saunders, 1998). At sea, salmon spend a number of years feeding and growing at an accelerated rate before returning to freshwater to spawn (Fleming, 1996, 1998; Jonsson & Jonsson, 2011). The time spent at sea before returning to spawn is known as sea age and is commonly measured in sea winters (SW). Atlantic salmon exhibit wide variation in both freshwater and sea age, and this variation affects growth and the timing of reproduction (Einum, Thorstad, & Næsje, 2002; Erkinaro et al., 2019; Jonsson & Jonsson, 1993, 2011). As a result, Atlantic salmon is an excellent model system for addressing questions related to life history evolution (Barson et al., 2015; Jonsson & Jonsson, 2011; Stearns, 1992).

A trade-off between freshwater age and sea age on the reproductive fitness of Atlantic salmon has been proposed by theoretical

models and empirical studies (Einum et al., 2002; Jonsson & Jonsson, 1993; Thorpe, Mangel, Metcalfe, & Huntingford, 1998; Thorpe & Metcalfe, 1998). Previous studies have shown that time spent in freshwater habitats is similar between the sexes and that larger, faster growing individuals tend to spend less time in the freshwater habitat than smaller, slower growing individuals (Jonsson & Jonsson, 2011; Thorpe, 1986; Thorpe et al., 1998). These individuals that spend less time in freshwater generally spend more time at sea and thus attain sexual maturity later before returning to rivers to spawn (Erkinaro et al., 2019; Jonsson & Jonsson, 2011; Randall, Thorpe, Gibson, & Reddin, 1986). Spending more time at sea has direct reproductive fitness consequences as larger body size is related to higher fecundity (i.e., mature eggs) in females (Heinimaa & Heinimaa, 2004) and higher reproductive success in both males and females (Fleming, 1998; Mobley et al., 2019a). However, spending more time at sea may come with a high cost to survivorship as fewer older individuals return to mate, presumably due to high predation at sea (McCormick et al., 1998; Thorpe, 1994). To our knowledge, the hypothesis that a trade-off exists between time spent in the freshwater environment and time spent at sea to maximize reproductive fitness has not yet been tested.

To date, few studies have investigated how time spent at discrete life history stages affects reproduction in Atlantic salmon. Previous studies have mainly focused on sea age rather than the potential for freshwater age to influence reproductive fitness (Mobley et al., 2019a). This is probably due, in part, to the relatively long reproductive cycle of Atlantic salmon and the low survivorship to sexual maturity in natural populations. Previous experimental studies in seminatural settings have shown that body size is an important determinant of reproduction and is related to fecundity (numbers of eggs) in females and to mate monopolization in males (Fleming, Jonsson, Gross, & Lamberg, 1996; Fleming, Lamberg, & Jonsson, 1997). These studies have been instrumental to our understanding of the positive relationship between body size and reproductive success in Atlantic salmon but were conducted in controlled settings using populations with limited life history variation (e.g., wild salmon males all 1 SW, females 1–2 SW; Fleming et al., 1997) and did directly measure reproductive success via genetic parentage reconstruction. Garant, Dodson, and Bernatchez (2001, 2003) also found evidence for a relationship between body size, reproductive success and mating success in Atlantic salmon in 1 SW and 2 SW males and 2 SW females, but did not characterize freshwater age, rendering comparisons between relevant life history stages incomplete. Building on more recent developments in genetic techniques, sex-specific life history trade-offs can measure the reproductive success of spawning adults by reconstructing pedigrees over multiple years (Christie, McNickle, French, & Blouin, 2018; Mobley et al., 2019a).

In the present study, we use data from Mobley et al. (2019a) to dig deeper into how sex-specific effects of the timing of two major life history stages, freshwater age and sea age, can affect reproductive fitness. The optimal time spent in the freshwater and marine environment may differ between male and female Atlantic salmon in order to maximize reproductive fitness. The data set

used consists of parentage analysis on 264 adults with life history information and >5,000 juveniles collected for over four cohort years from a population of wild Atlantic salmon from northern Finland. We first tested for a sex-specific relationship between freshwater age and sea age to see if time in freshwater affects the time spent in seawater differently between the sexes. Second, we investigated the relationship between adult body size (e.g., weight, length and condition) and freshwater age and sea age to determine whether time spent at these life history stages affected the overall size and condition at reproduction. Third, we tested whether males and females differed in the relationship between reproductive success and mating success, also known as the Bateman gradient (β, Arnold & Wade, 1984; Jones, 2009). A higher significant estimate of β generally corresponds to the strength of sexual selection and can indicate whether sexual selection is acting more strongly on males or females (Anthes, Häderer, Michiels, & Janicke, 2017; Henshaw, Kahn, & Fritzsche, 2016; Jones, 2009). Finally, we looked for sex-specific differences in the relationship between the effect of freshwater age and sea age on reproductive and mating success. The nature of these relationships was first tested using a complete data set with all adults including those that did not have offspring in our sample (all adults). We also tested these relationships using reduced data sets that only included breeding adults (breeding adults) and only first-time spawning adults excluding repeat-spawning individuals (first-time spawners).

2 | METHODS

Anadromous adults were sampled in September–October 2011–2014 at the lower Utsjoki spawning grounds at the mouth of the Utsjoki tributary of the Teno River in northern Finland (69°54′28.37″N, 27°2′47.52″E; for further details on sampling location see Mobley et al., 2019a). Fishing permission for research purposes was granted by the Lapland Centre for Economic Development, Transport, and the Environment (permit numbers 1579/5713-2007, 2370/5713-2012 and 1471/5713-2017). Adults were primarily captured by gill nets at night to minimize handling stress. A few males (n ~ 5) were captured by rod and reel angling. All adults were assessed for signs of maturity during sampling (presence of secondary sexual characteristics, presence of sperm from striping males and visual inspection of females) and all adults appeared to be in, or very near, spawning condition. Adults were weighed and total length was recorded. Condition was calculated as the residual from a linear model of weight predicted by length for each sex and spawning cohort (Mobley et al., 2019a; Patterson, 1992). Scales were collected for age analysis and a small piece of anal fin was collected for genetic analysis before release near the site of capture. Juveniles were sampled by electrofishing shallow areas in the region of the spawning grounds 10–11 months later, which is 2–3 months after they are expected to have emerged from the nests in the stream bed gravel (Mobley et al., 2019a). Genetic samples were collected from all juveniles by collecting a

small piece of adipose and/or anal fin tissue, after which they were immediately returned to the river (Mobley et al., 2019a). Four parent–offspring cohorts were sampled in this manner between 2011 and 2015.

2.1 | Age determination

Freshwater age, defined as the number of years spent in freshwater before migrating to sea, and sea age, defined as the number of years an individual overwintered at sea before returning to spawn, was determined for adults captured on the spawning ground using scale growth readings as outlined by Aykanat et al. (2015). Freshwater age could not be determined on 25 individuals (three females, 22 males) using scale data. Sea age could not be determined for 16 adults >1 SW (one female, 15 males) using scale data and was therefore extrapolated based on calculated distributions of weight of known sea age individuals (see Mobley et al., 2019a; Table S4). However, freshwater age was not extrapolated based on weight due to the poor relationship between weight and freshwater age (see Section 3). Therefore, these individuals were excluded from statistical analyses. Repeat spawners that were spawning for a second time were also determined using scale data. Thirteen individuals (six females, seven males) were identified as repeat spawners by scale ageing analysis. The mean sea age of repeat spawning females was 3.2 ± 0.4 SE (range 2–4 SW) and all repeat spawning males had spent 1 year at sea before the first spawning migration and another year at sea before returning to spawning for the second time (i.e., all male repeat spawners were 2 SW).

2.2 | Parentage analysis

Molecular parentage analysis was conducted according to Mobley et al. (2019a). Briefly, all adults and juveniles were genotyped using 13 microsatellite loci previously used for parentage analyses in this species (Aykanat et al., 2014). Pedigrees were constructed for each parent–offspring cohort separately using the package MASTERBAYES version 2.55 (Hadfield, Richardson, & Burke, 2006) in the R programming environment (R Core Team, 2018). Genotyping error rate was calculated as per Mobley et al. (2019a). The distribution of unsampled population sizes (mothers and fathers separately) were given a prior mean of twice the sampled population size, following Aykanat et al. (2014), with a variance calculated as 1.5 − 0.25 × sampled population size, which encompassed probable parameter space. The pedigree was run for 30,000 iterations after a burn-in of 5,000. We then extracted the mode of the posterior distribution of pedigrees, and removed assignments with a likelihood of <90%. Offspring assigned to a known parent were either confidently (>90% likelihood) assigned to two sampled adults, or one parent confidently assigned to a sampled adult and the other confidently assigned to an unsampled adult. In this manner, an offspring that contributed to our reproductive fitness measures was either assigned to both a sampled

sire and a sampled dam, or to either a sampled sire or a dam and an unsampled adult (Mobley et al., 2019a).

2.3 | Reproductive fitness estimates

Reproductive success was quantified as the number of offspring assigned to an adult, following parentage assignment of all offspring. Mating success was estimated as the number of unique mates per individual identified within our sample by parentage analysis (Mobley et al., 2019a).

2.4 | Statistical analyses

We tested for a sex difference in the relationship between freshwater age and sea age and their interaction using a linear regression model. Sex differences in the relationship between weight, body length and condition, and their interaction with sex were tested in linear models for freshwater age and sea age separately. We also tested for a sex difference in the relationship between reproductive success and mating success using a linear regression model. Effect sizes for sex are presented as a comparison of males to females for linear regressions. Power or the probability of a hypothesis test to detect an effect if there is one is calculated for linear models using the package PWR for R using α = 0.05. Power for all effect sizes in linear models was >0.99.

We tested for a sex difference in the relationship between reproductive success and mating success using zero-inflated mixture models in a generalized linear model (GLM) approach fitting separate models for freshwater age and sea age. All these models of reproductive and mating success included an offset of the number of offspring sampled in the relevant year, log-transformed for consistency with the models' link functions to account for between-year variation in sampling effort. We applied zero-inflated models using the function zeroinfl() from the package PSCL (Jackman, 2017; Zeileis, Kleiber, & Jackman, 2008) because estimates of mating success and reproductive success contained a high proportion of individuals without any offspring, and hence mates, assigned. Zero-inflated mixture models consisted of a binomial model for the frequency of zeros and, conditional on this, a count model using a Poisson distribution. Effects of freshwater and sea age were tested only in the count model, but both count and binomial models included an offset to account for differences in sampling effort between years. For reproductive success, an effect of sex was also included in the binomial model because a much greater proportion of males did not have any sampled offspring compared to females. For mating success, sex was not a significant predictor in the binomial model and hence was not included in the final models. All response variables for models were first tested with a full initial model consisting of an interaction between sex and the relevant explanatory variable and their main effects for all adults (all adult data set). Nonsignificant (p > .05) explanatory variables were removed step-wise from the model to obtain

a minimal model in which all predictors had a significant effect. In all models, the four sampling years were pooled to maximize sample sizes as patterns in reproductive success have been shown to be consistent across years (Mobley et al., 2019a).

Models of weight, length, condition, reproductive success and mating success were also tested on two additional reduced data sets. The "breeding adults" data set consisted only of those individuals that were assigned offspring in our sample (nonzero number of offspring and mates). Because repeat spawning may influence reproductive fitness, the breeding adults data set was further reduced to include only "first time spawners," thereby excluding the 13 repeat spawners. For reproductive success and mating success, reduced data sets were not zero-inflated and hence were modelled using a negative binomial GLM in the R package MASS for reproductive success, and using a quasipoisson GLM in the R package STATS for the number of mates. Variance distributions were chosen based on dispersion behaviour of model residuals. All statistical models were performed in R (R Core Team, 2018) and all means are reported ±*SEM*.

3 | RESULTS

A total of 230 adult males, 34 adult females and 5,223 juvenile offspring (<1 year old) were collected over the four cohort years. At the time of spawning, females were larger, heavier and had older sea age than males, on average (Table 1). However, both sexes had similar condition estimates at spawning (Table 1). Means and sample sizes for body weight, length, condition, freshwater age, sea age, reproductive success and mating success for all adults, breeding adults (adults with offspring assigned from our sample) and first-time spawners (excluding repeat-spawners) pooled across cohort years are reported in Table 1 and are summarized by freshwater age and sea age in Table S1.

Females spent less time, on average, in the juvenile freshwater environment than males before migrating to sea (Table 1, Figure 1). Mean sea age, by contrast, was higher in females than in males (Table 1, Figure 1). We found a sex-specific effect between freshwater age and sea age: older freshwater age females returned to spawn at younger sea ages, whereas freshwater age had no effect on sea age in males (freshwater age: −0.45 ± 0.16, $t_{1,238}$ = −2.756, p < .0001; sex: −2.67 ± 0.65, $t_{1,238}$ = −4.105374, p < .0001; sex × freshwater age: 0.42 ± 0.18, $t_{1,238}$ = 2.343, p = .0200; Figure 1). However, only the sex difference in sea age was significant when restricting analyses to breeding adults and first-time spawner data sets (Table S2).

Mirroring the negative sex-specific relationship between freshwater age and sea age, females that spent more time in freshwater were not as heavy at sexual maturity than those females that spent less time in freshwater (sex: −10.63 ± 3.04, $t_{1,238}$ = −3.497, p = .0006; freshwater age: −1.721 ± 0.77, $t_{1,238}$ = −2.242, p = .0259; sex × freshwater age: 1.70 ± 0.83, $t_{1,238}$ = 2.037, p = .0427; Figure 2a). However, only the sex difference in weight was significant while restricting analyses to the breeding adults and first-time spawner data sets

TABLE 1 Summary of body size, age and reproductive fitness estimates for all adults pooled across cohort years, only breeding adults, and first-time spawners (breeding adults without respawners)

	n	Weight (kg)	Length (cm)	Condition	Freshwater age[a]	Sea age	Number of offspring	Number of mates
All adults								
Females	34	7.61 ± 0.63	89.2 ± 2.3	0.00 ± 0.19	3.58 ± 0.12	2.41 ± 0.13	26.5 ± 6.4	2.47 ± 0.36
Males	230	3.65 ± 0.21	70.0 ± 0.9	0.00 ± 0.05	3.65 ± 0.04	1.35 ± 0.05	6.1 ± 1.0	0.71 ± 0.06
Breeding adults								
Females	28	8.23 ± 0.66	91.6 ± 2.1	0.01 ± 0.18	3.54 ± 0.13	2.54 ± 0.14	32.2 ± 7.4	3.00 ± 0.37
Males	115	4.54 ± 0.39	74.1 ± 1.6	−0.04 ± 0.09	3.63 ± 0.06	1.53 ± 0.08	12.3 ± 1.8	1.43 ± 0.07
First-time spawners								
Females	22	7.43 ± 0.59	89.2 ± 1.9	−0.17 ± 0.14	3.57 ± 0.15	2.41 ± 0.13	27.0 ± 6.3	3.05 ± 0.43
Males	111	4.49 ± 0.40	73.8 ± 1.7	−0.03 ± 0.09	3.64 ± 0.06	1.51 ± 0.08	12.2 ± 1.9	1.44 ± 0.07

Note: The number of adults (*n*) and mean weight (kg), length (cm), condition, freshwater age (years), sea age (sea winters), reproductive success (number of offspring) and mating success (number of mates) for each sex ± *SE* are given.

[a]Freshwater age *n* (males, females): all adults = 31, 211; breeding adults = 26, 102; first-time spawners = 21, 89).
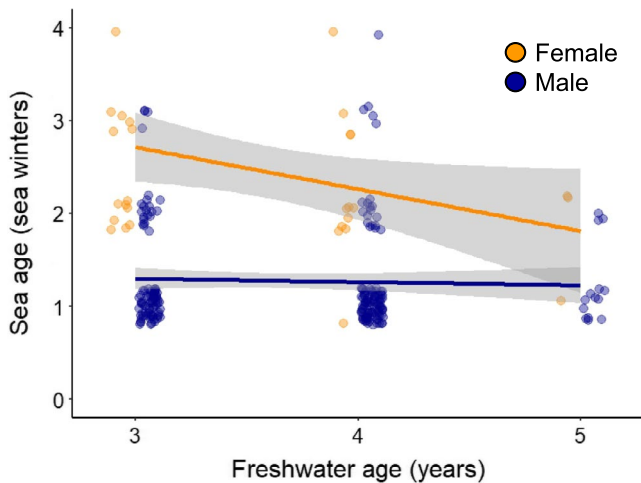

FIGURE 1 Sex difference in the relationship between freshwater age and sea age in the "all adults data set." Coloured lines represent linear regression for each sex and grey areas represent 95% confidence intervals (CI). Circles show individual data points. For clarity, individual points are jittered on the *x*- and *y*-axis [Colour figure can be viewed at wileyonlinelibrary.com]

(Table S3). Adults that spent more time at sea were heavier and no sex difference was discerned (sex: −0.09 ± 1.35, $t_{1,261}$ = −0.066, *p* = .9470; sea age: 17.98 ± 0.64, $t_{1,261}$ = 27.988, *p* < .0001; Figure 2b). When restricting the analyses to the breeding adults and first-time spawners, significant effects of both sex and sea age were apparent (Table S3).

Freshwater age did not affect body length in either females or males (sex: −21.46 ± 2.30, $t_{1,239}$ = −9.320, *p* < .0001; freshwater age: −2.28 ± 1.27, $t_{1,239}$ = 1.800, *p* = .0731). Sea age, as expected, was positively and significantly related to length, and this relationship was similar between the sexes (sex: −0.09 ± 1.89, $t_{1,245}$ = −0.066, *p* = .947; sea age: 17.98 ± 0.64, $t_{1,245}$ = 27.988, *p* < .0001; sex × sea age, 2.77 ± 1.49, $t_{1,244}$ = 1.855, *p* = .0649).

Relationships between length and freshwater age and sea age were similar when analysing only breeding adults or first-time spawners with the exceptions that sex differences in body length and a significant interaction between sex and sea age was observable (Table S4).

Freshwater age did not affect overall condition in either females or males (sex: −0.13 ± 0.15, $t_{1,239}$ = −0.862, *p* = .3890; freshwater age: 0.06 ± 0.82, $t_{1,239}$ = 0.669, *p* = .5040). Similarly, sea age did not affect condition at spawning (sex: 0.12 ± 0.18, $t_{1,261}$ = 0.666, *p* = .5060; sea age: 0.11 ± 0.08, $t_{1,261}$ = 1.476, *p* = .1410). However, condition was significantly higher in higher sea age individuals in the restricted breeding adult and first-time spawner data sets (Table S5).

Bayesian parentage analysis had high confidence to assign offspring to at least one parent including unsampled adults (2011:99.8%; 2012%: 99.9%; 2013:99.3%; 2014:99.9%) with a combined exclusion probability > .999 across all 13 microsatellite loci. Parentage analysis assigned 1,987 of the offspring (38%) to at least one sampled adult with confidence (Mobley et al., 2019a; Table S4). Based on parentage analysis, 83.9 ± 5.1% of sampled females and 51.5 ± 2.1% of sampled males over the four cohort years had at least one offspring in our sample. Based on the total size of the breeding population calculated by the MASTERBAYES program, we estimate that, on average, 21.4% of sires and 18.8% of dams in the breeding population were sampled (Mobley et al., 2019a; Table S1).

Based on estimates of the number of offspring and mates assigned to adults from parentage analysis, females, on average, had higher reproductive and mating success than males. Females had a mean of 26.5 ± 6.5 offspring (range 0–177) and 2.47 ± 0.36 mates (range 0–8, Table 1). Females gained an average of 5.10 ± 1.56 offspring/ kg ($t_{1,32}$ = 10.68, *p* < .0026) and 0.22 ± 0.09 mates/kg ($t_{1,32}$ = 5.73 3, *p* = .0227, Figure 3). Males had a mean of 6.1 ± 1.0 offspring (range 0–145) and 0.71 ± 0.05 mates (range 0–5, Table 1). Males gained an average of 2.87 ± 0.25 offspring/kg ($t_{1,228}$ = 134.33, *p* < .0001) and 0.10 ± 0.02 mates/kg ($t_{1,228}$ = 32.80, *p* < .0001; Figure 3).
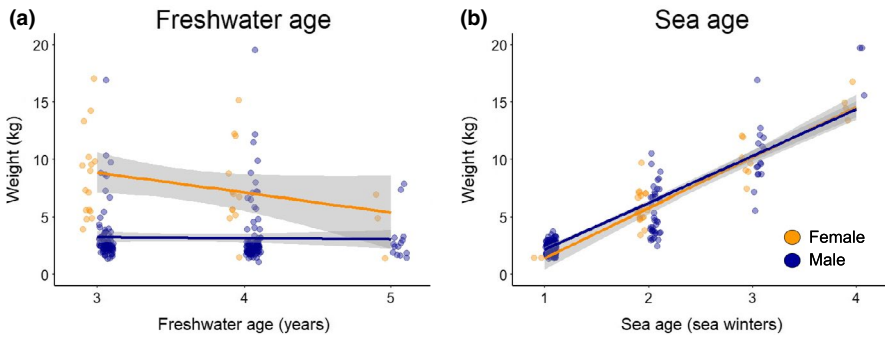
FIGURE 2 The influence of (a) freshwater and (b) sea age on weight at reproductive maturity for males and females in the "all adults data set." Coloured lines represent linear regression for each sex and grey areas represent 95% confidence intervals (CI). Circles show individual data points. For clarity, individual points are jittered on the x- and y-axis [Colour figure can be viewed at wileyonlinelibrary.com]
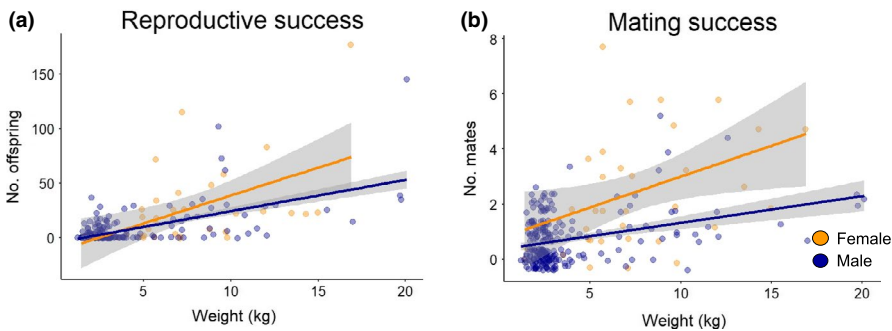

FIGURE 3 The relationship of (a) reproductive success (number of offspring) and and (b) mating success (number of mates) and weight (wet mass) of male and female Atlantic salmon in the "all adults data set." Coloured lines represent linear regression for each sex and grey areas represent 95% confidence intervals (CI). Circles show individual data points. For clarity, individual points are jittered on the x- and y-axis [Colour figure can be viewed at wileyonlinelibrary.com]
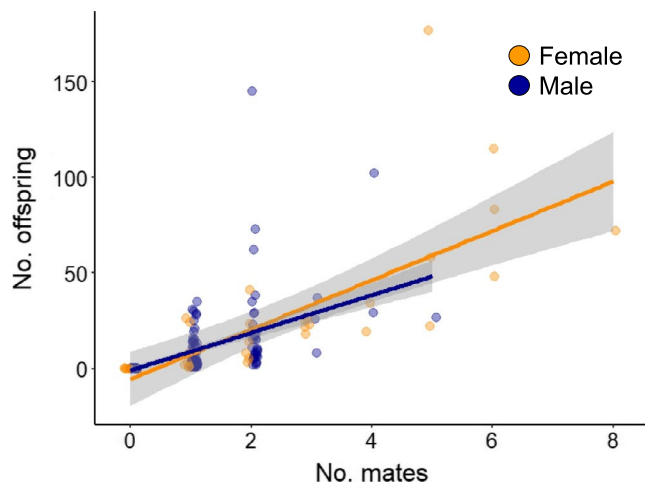

FIGURE 4 The Bateman gradient, β, or the relationship of reproductive success (number of offspring) with mating success (number mates) for males and females in the "all adults data set." Coloured lines represent linear regression for each sex and grey areas represent 95% confidence intervals (CI). Circles show individual data points. For clarity, individual points are jittered on the x- and y-axis [Colour figure can be viewed at wileyonlinelibrary.com]

The Bateman gradient, β, was similar between males and females (mates: 11.25 ± 0.83, $t_{1,261} = 13.557$, $p < .0001$; sex: -0.62 ± 3.11, $t_{1,261} = -0.199$, $p = .842$; sex × mates, -3.065 ± 1.658, $t_{1,260} = -1.849$, $p = .0656$; Figure 4). These results were also similar when analysing only breeding adults or first-time spawners (Table S6).

There was a negative relationship between freshwater age and reproductive and mating success in females (-9.01 ± 10.60

offspring FW^{-1}, $t_{1,29} = -0.85$, $p = .4024$, decrease of 33.9% of offspring FW^{-1}; -0.80 ± 0.57 mates FW^{-1}, $t_{1,29} = -1.40$, $p = .1720$, decrease of 32.4% mates FW^{-1}). In contrast, no relationship between reproductive and mating success and freshwater age in males was found (0.52 ± 1.48 offspring FW^{-1}, $t_{1,209} = 0.35$, $p = .7286$, 0.05 ± 0.09 mates FW^{-1}, $t_{1,209} = 0.57$, $p = .5676$). Both reproductive success and mating success showed positive relationships with sea age in females, although only reproductive success was significant at $\alpha = 0.05$ (16.53 ± 7.99 offspring SW^{-1}, $t_{1,32} = 2.07$, $p = .0466$, increase of 60.3% offspring SW^{-1}; 0.86 ± 0.45 mates SW^{-1}, $t_{1,32} = 1.90$, $p = .0671$, increase of 34.8% mates SW^{-1}). Both reproductive and mating success were positively correlated to sea age in males (12.45 ± 1.19 offspring SW^{-1}, $t_{1,228} = -5.91$, $p < .0001$, increase of 201.9% offspring SW^{-1}; 0.44 ± 0.08 mates SW^{-1}, $t_{1,228} = 5.54$, $p < .0001$, increase of 60.3% mates SW^{-1}).

Results of generalized linear mixed model (GLMMs) demonstrated that more time spent in the juvenile freshwater habitat was associated with reduced reproductive success, but only in females (Table 2, Figure 5a). However, adults that spent more time at sea had greater reproductive success, with a steeper relationship in females, and females had greater reproductive success overall (Table 2, Figure 5b). However, when restricting the data set to breeding adults and first-time spawners, no effect of freshwater age on reproductive success was significant whereas the effect of sea age and sex remained significant (Table S7).

Patterns in mating success mirrored those in reproductive success. Females that spent longer in the juvenile freshwater habitat showed reduced mating success, while male mating success was not affected by freshwater age (Table 2; Figure 5c). A general increase in the number of mates with sea age in both males and females was

TABLE 2 Results of GLMMs showing the effect of sex differences on freshwater (FW) age and sea age and on reproductive success and mating success

	Effect size	SE	z	Pr(>|z|)
Reproductive success				
Freshwater age				
Intercept	−2.22	0.20	−10.85	<0.0001
FW age	−0.40	0.06	−6.86	<0.0001
Sex	−3.61	0.28	−13.09	<0.0001
FW age × Sex	0.64	0.08	8.33	<0.0001
Zero inflation (Intercept)	−8.82	0.49	−17.96	<0.0001
Zero inflation (Sex)	1.64	0.51	3.21	0.0010
Sea age				
Intercept	−5.12	0.12	−44.12	<0.0001
Sea age	0.57	0.04	14.07	<0.0001
Sex	−1.09	0.13	−8.18	<0.0001
Sea age × Sex	0.23	0.05	4.78	<0.0001
Zero inflation (Intercept)	−8.74	0.45	−19.21	<0.0001
Zero inflation (Sex)	1.46	0.47	3.09	0.0020
Mating success				
Freshwater age				
Intercept	−4.39	0.71	−6.18	<0.0001
FW age	−0.49	0.20	−2.37	0.0180
Sex	−3.78	0.90	−4.22	<0.0001
FW age × Sex	0.66	0.25	2.61	0.0090
Zero inflation (Sex)	−9.15	0.48	−19.21	<0.0001
Sea age				
Intercept	−7.21	0.24	−29.96	<0.0001
Sea age	0.42	0.08	5.41	<0.0001
Sex	−0.93	0.16	−5.75	<0.0001
Zero inflation (Sex)	−9.41	0.53	−17.14	<0.0001

Note: Effect sizes for age are shown per year, and for sex, for males compared to females, with the response transformed according to the relevant link function. Freshwater age, sea age, and sex are count data whereas zero inflation terms are binomial.

observed (Table 2, Figure 5d). All of these effects remained significant within the restricted data sets among breeding adults and first-time spawners (Table S4).

4 | DISCUSSION

In this study, we investigated sex-specific trade-offs in reproductive fitness and the time spent during two life history stages of anadromous Atlantic salmon. A sex-specific trade-off between time spent in

the freshwater stage and reproductive fitness was apparent among females. Females that remained longer in freshwater spent less time at sea before returning to spawn, and were smaller, suffering a slight but significant reduction in both reproductive and mating success. In contrast, males spent less time at sea than females but showed no indication that freshwater age influenced reproductive fitness. The time spent at sea had a substantial positive influence on weight, body length and reproductive fitness of both sexes and condition among breeding adults. Moreover, any negative effect of longer time spent in freshwater on reproductive fitness in females was masked by the strong positive relationship between sea age, body weight/length and reproductive fitness.

In our study, females were larger and spent more years at sea than males, as is the case for most populations of Atlantic salmon (Barson et al., 2015). Females also had more mates and produced more offspring than males. We found a significant positive Bateman gradient in both male and female Atlantic salmon, indicating that having more mating partners results in more offspring in both sexes similar to reports in North American Atlantic salmon (Garant, Dodson, & Bernatchez, 2001). The relationship between reproductive success and mating success does not differ between the sexes, demonstrating that the strength of sexual selection is similar between males and females (Anthes et al., 2017; Arnold & Duvall, 1994; Janicke, Häderer, Lajeunesse, & Anthes, 2016; Jones, 2009). This result is surprising, as it is generally thought that sexual selection is stronger among males in Atlantic salmon (Fleming, 1996, 1998; Fleming & Einum, 2011). We expected sexual selection to be greater in males as there was a significant male bias in the sex ratio of adults caught on the spawning grounds (Mobley et al., 2019a). Based on mating system theory, a male-biased sex ratio should drive higher levels of mate competition among males for available females (Emlen & Oring, 1977; Mobley, 2014; Shuster & Wade, 2003). Potentially, high levels of sneaking by younger anadromous males and mature male parr (pre-smolting individuals that have not yet transitioned to the marine environment) can decrease sexual selection among males (Jones, Walker, Kvarnemo, Lindstrom, & Avise, 2001). However, we should be careful with this interpretation as no information on reproductive success of these parr in our study population is currently available, yet the occurrence of mature male parr in the region is estimated to be around 10% (Heinimaa & Erkinaro, 2004). Further research is warranted to uncover the extent to which sexual selection operates on males and females in this and indeed other species of salmonids (Auld, Noakes, & Banks, 2019).

The strong positive relationship between sea age and weight, body length, and reproductive fitness estimates in both sexes is probably related to genetic and environmental factors controlling sea age at maturation. Sea age is partially under genetic control of the *vgll3* locus in this population (Ayllon et al., 2015; Barson et al., 2015; Czorlich, Aykanat, Erkinaro, Orell, & Primmer, 2018) explaining nearly 40% of the variation in sea age. This same genomic region may also influence the potential for repeat spawning (iteroparity) in this species (Aykanat et al., 2019). Environmental factors may also
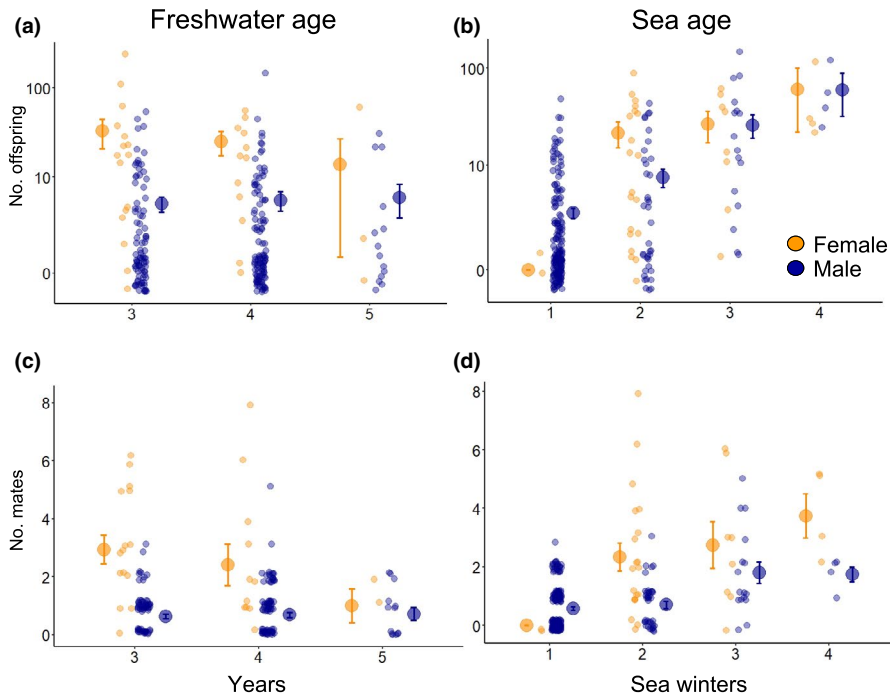
(a) Freshwater age

(b) Sea age

(c)

(d)

Years

Sea winters

FIGURE 5 The relationship of reproductive success (number of offspring) with (a) freshwater age and (b) sea age, and mating success (number of mates) with (c) freshwater age and (d) sea age in male and female Atlantic salmon in the "all adults data set." Large circles with error bars represent the mean ± *SE*, while small circles show individual data points. For clarity, individual points are jittered on the *x*- and *y*-axis and the *y*-axis for reproductive success is $\log_{10}$-transformed [Colour figure can be viewed at wileyonlinelibrary.com]

affect sea age, including salinity, photoperiod and temperature (Fjelldal, Hansen, & Huang, 2011; Melo et al., 2014).

Compared to our understanding of the genetic and environmental underpinnings of sea age, the conditions responsible for the timing of smoltification in Atlantic salmon are less well understood. The decision to leave the freshwater juvenile environment probably depends upon the balance between growth and survival at sea (McCormick et al., 1998; Thorpe, 1994). Earlier smolting individuals spend more time at sea where they are potentially exposed to higher predation (McCormick et al., 1998). Previous studies do not appear to show clear patterns concerning a fitness trade-off between freshwater age and sea age. For example, a negative relationship between smolt size, pre-smolt growth and post-smolt growth was reported earlier in female Atlantic salmon from Norway (Einum et al., 2002), yet no relationship between mean growth and sea age at maturity was found in Spanish Atlantic salmon (Nicieza & Braña, 1993). Other species of salmonids, steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*), show a weak positive association between pre- and post-smolt growth, indicating no trade-off between freshwater age and sea age in these species, at least under artificial hatchery conditions (Johnsson, Blackburn, Clarke, & Withler, 1997). Environmental conditions may also affect smolt timing as smoltification is also associated with higher water temperatures (Duston & Saunders, 1997). Currently, it is unknown whether genes associated with *vgll3* affect freshwater age, and future studies should investigate the genetic and environmental factors underpinning sex differences in smolt timing in an effort to understand their relative contributions to reproductive fitness.

Our study demonstrates a sex-specific trade-off in maturation timing such that females that spend more time in freshwater spend less time in the marine environment before returning to spawn and

suffer a decrease in reproductive fitness. Male maturation, by contrast, does not appear to be affected by freshwater age. Previous studies have shown that females that spend more time in freshwater often spend less time in the marine environment before returning to spawn in populations in northern Finland (Erkinaro et al., 2019; Erkinaro, Dempson, Julkunen, & Niemelä, 1997). Our results therefore indicate that time spent in freshwater is more critical to female reproduction than to males. However, a previous study investigating 20 natural populations of Canadian Atlantic salmon found no relationship between either freshwater age and sea age or freshwater age and sex (Bielak & Power, 1986), suggesting that the importance of freshwater age on female reproduction may be population-specific.

In our study, we were able to confidently assign 37.5% of offspring to at least one sampled adult (Mobley et al., 2019a; Table S4). Because it is often difficult to recover all breeding individuals and offspring in large, open, natural populations, missing parentage data can potentially bias estimates of mating and reproductive success (Mobley, 2014; Mobley & Jones, 2013). For example, adults that produced offspring but were not recovered in our sample would have their overall contributions to reproduction underestimated. However, the results of our zero-inflated models for male and female mating and reproductive success that accounted for individuals that did not have offspring in our sample were generally supported by analyses that excluded individuals that did not produce offspring in our sample (breeding adults) and excluding multiyear spawners (first-time spawners; Table S7). These results demonstrate that our analyses are generally robust to the exclusion of these individuals.

The lower Utsjoki spawning ground showed a significant 7:1 male bias that was consistent over the four cohort years (Mobley et al., 2019a). Sex ratios are commonly male-biased in Atlantic

salmon populations (Fleming, 1996, 1998; Fleming & Reynolds, 2004). Within the Teno river and its tributaries, sex ratios can vary widely (Erkinaro et al., 2019; Mobley et al., 2019a; Niemelä et al., 2006). The sex ratio of freshwater juveniles at the lower Utsjoki site is approximately equal (Czorlich et al., 2018), suggesting that the male-biased sex ratio is the result of higher female mortality at sea. However, it is conceivable that there could be some bias towards capturing males as they are more active than females and move more during the spawning season (J. Erkinaro, unpublished data), which may make them more vulnerable to gill net capture (i.e., the primary means of adult capture in the study). However, MASTERBAYES estimated that a similar proportion of males and females were sampled from the total breeding population and thus a bias in capture rate seems unlikely.

Our reproductive fitness estimates, reproductive success and mating success, are based on samples of <1-year-old juveniles collected on the spawning grounds. Therefore, our reproductive fitness estimates include aspects of sexual selection, including mate choice and mate competition, as well as natural selection on offspring survivorship and early life-history characteristics. After emergence from the gravel, offspring may stay near the redd or may drift to less densely populated areas downstream presumably to avoid intraspecific competition (Bujold, Cunjak, Dietrich, & Courtemanche, 2004). Spatial analysis of juveniles collected at 20 different locations within the lower Utsjoki study site indicates that offspring assigned to sampled males and females were collected on multiple locations and varied according to density (K. B. Mobley et al., unpublished data). This information, combined with the estimated one-third of offspring assigned to at least one sampled parent, suggests that a fairly high proportion of offspring stay within the spawning ground and should not bias reproductive fitness estimates.

Reproductive fitness estimates may also be influenced by parental effects and thus have the potential to bias our estimates of mating and reproductive success toward parental combinations that produce fitter offspring. For example, larger Norwegian Atlantic salmon females produce fewer, yet larger, offspring that generally show higher survivorship (Einum & Fleming, 2000). Therefore, it is possible that our estimates of offspring fitness are potentially biased toward older females. However, we do not feel that this is a major limitation to our study, as juveniles collected after the critical hatching and first feeding stages marked by high mortality (Mackenzie & Moring, 1988; Pauwels & Haines, 1994) provide a better estimate of offspring that may survive and reproduce and thus may in fact give more accurate estimates of reproductive fitness.

The results reported here serve to identify the source, and quantify the extent, of the reproductive advantage achieved by larger and later maturing (i.e., older sea age) males and females on the spawning grounds. Despite the advantage of later maturation in both sexes, many populations have experienced a decline in this life history strategy in recent decades (Chaput, 2012). A higher proportion of early maturation life history strategies suggests that there has been a change in the balance of natural selection in the sea and sexual selection on the spawning grounds, such that across the entire life history, the fitness of the smaller, earlier maturing anadromous adults has been increasing despite their lower reproductive fitness. There are other factors that may also help to compensate for this apparent reduced reproductive fitness of individuals that return after only one year at sea. For example, it is possible that these individuals will gain further reproductive fitness by repeat spawning. Although the majority of individuals spawn after only one SW, Atlantic salmon are iterparous, and both males and females can return to spawn over multiple years (Hutchings & Morris, 1985; Jonsson & Jonsson, 2011; Niemelä et al., 2006). A recent study has shown in a pacific salmon, *O. mykiss*, that repeat-spawning individuals may obtain 2.5 times the lifetime reproductive success of single spawners (Christie et al., 2018). Indeed, the proportion of repeat spawners has also been increasing in the Teno River populations (Erkinaro et al., 2019). Furthermore, it has recently been shown that the potential for repeat spawning in Atlantic salmon is associated with the *vgll3* locus and is tied to the decision to return earlier from sea to spawn for the first time (Aykanat et al., 2019). However, only a small number of repeat spawners were captured on the spawning grounds and our results were robust to the exclusion of these individuals (Table S7). Thus, we lack sufficient data to address this topic at present and hope that it can be analysed in the future with the addition of more cohort years.

5 | CONCLUSION

A fundamental goal of evolutionary biology is to understand how life-history trade-offs affect individual fitness. This study contributes to this goal by investigating reproductive fitness of the timing of transitions at two critical life history stages and demonstrating that there is a sex-specific life history trade-off between maturation and reproduction in a wild population of anadromous salmon. Indirect costs may also play a role in life history stages, as early smolting individuals may be at greater risk of mortality via predation at sea yet may also have a higher chance of multiple reproductive seasons. Future research should investigate sex-specific growth rates and the timing of smoltification, as well as mortality at sea, to uncover the potential hidden costs associated with maturation at specific life history stages.

Environment (permit numbers 1579/5713-2007, 2370/5713-2012 and 1471/5713-2017).

CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

K.B.M. and C.R.P. conceived the study. M.E., P.O. and J.E. coordinated and/or participated in sample collection. C.R.P coordinated the molecular data generation. K.B.M. and H.G.-W. analysed the data. K.B.M. drafted the manuscript, with input from all other authors.

DATA AVAILABILITY STATEMENT

Adult phenotypic and reproductive fitness data and parent-age analysis assignments of offspring are available on DRYAD 10.5061/dryad.4b8gtht8j (Mobley et al., 2020). Microsatellite genotype data for adults and offspring are available on DRYAD 10.5061/dryad.3ss2t53 (Mobley et al., 2019b), genotypes.csv.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.