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Probabilistic reaction norm reveals family-related variation in the association between size, condition, and sexual maturation onset in Atlantic salmon (*Salmo salar*)

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Abstract

This study investigated the relationship between the size, condition, year class, family, and sexual maturity of Atlantic salmon (*Salmo salar*) using data collected in an aquaculture selective breeding programme. Males that were sexually mature at 2 years of age (maiden spawn) have, on average, greater fork length and condition factor (K) at 1 year of age than their immature counterparts. For every 10-mm increase in fork length or 0.1 increase in K at 1 year of age, the odds of sexual maturity at 2 years of age increased by 1.48 or 1.22 times, respectively. Females that were sexually mature at 3 years of age (maiden spawn) have, on average, greater fork length and K at 2 years of age than their immature counterparts. For every 10-mm increase in fork length or 0.1 increase in K at 2 years of age, the odds of sexual maturity at 3 years of age increased by 1.06 or 1.44 times, respectively. The family explained 34.93% of the variation in sexual maturity among 2-year-old males that was not attributable to the average effects of fork length and K at 1 year of age and year class. The proportion of variation in sexual maturity among 3-year-old females explained by the family could not be investigated. These findings suggest that the onset of sexual maturation in Atlantic salmon is conditional on performance (with respect to energy availability) surpassing a threshold, the magnitude of which can vary between families and is determined by a genetic component. This could support the application of genetic selection to promote or inhibit the onset of sexual maturation in farmed stocks.

KEYWORDS

aquaculture, growth, puberty, reproduction, selective breeding

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1 | INTRODUCTION

Salmonines (species of *Salmo*, *Salvelinus*, and *Oncorhynchus* genera) are characteristically annual spawners (generally in autumn or winter), although they exhibit a great diversity in age at maiden spawn and the interval between repeated spawns. For example, 120 different life-history strategies (including combinations of sea age at spawning migration and duration between repeated spawning migrations) were demonstrated in a single wild Atlantic salmon (*Salmo salar*) population over a 40-year period (Erkinaro et al., 2019). In any reproductive season, spawning is conditional on the onset of sexual maturation, which can become histologically evident 8 months before spawning (Andersson et al., 2013; Campbell et al., 2003). It is thought that an individual's performance (with respect to energy availability) must surpass a threshold at a specific seasonal time (critical period) for sexual maturation to ensue; otherwise, sexual maturation will be postponed until at least the following year (Jenkins et al., 2023; Thorpe, 1994). Such a gating mechanism indeed seems intuitive, considering the substantial energetic costs associated with reproduction in this taxon (Bowerman et al., 2017; Jonsson et al., 1997; Penney & Moffitt, 2014).

The physiological basis by which performance is assessed during the critical period remains unclear, although the proximate signal(s) appears to be associated with body length (Simpson, 1992), mass (Shearer et al., 2006), condition (Bohlin et al., 1994; Kadri et al., 1996), adiposity (Rowe et al., 1991), and plasma triglyceride content (Jenkins et al., 2019). For instance, 2-year-old mature male Chinook salmon and Arctic charr (*Salvelinus alpinus*) were significantly heavier at ~1 year of age than their immature counterparts (Adams & Huntingford, 1997; Clarke & Blackburn, 1994). Similarly, 3-year-old mature male and female Atlantic salmon had significantly greater condition at ~2 years of age than their immature counterparts (Duston & Saunders, 1999). Furthermore, interventions that led to reduced growth, condition, and/or lipid accumulation within 12 months before spawning reduced the incidence of sexual maturation in Atlantic salmon (Martinez et al., 2022; Norrgård et al., 2014; Rowe & Thorpe, 1990), Chinook salmon (*Oncorhynchus tshawytscha*) (Hopkins & Unwin, 1997; Larsen et al., 2013, 2006; Shearer et al., 2006), coho salmon (*Oncorhynchus kisutch*) (Appleby et al., 2003), and lake trout (*Salvelinus namaycush*) (Henderson & Wong, 1998).

The magnitude of the performance threshold for sexual maturation onset is suggested to vary between individuals of the same species (Thorpe et al., 1998). Several studies have investigated this by comparing the estimates of the probabilistic maturation reaction norm (PMRN) (i.e., the relationship between body size and the probability of sexual maturity; see Heino et al., 2002) between genetically distinct populations when reared in a common setting (Harvey et al., 2018; Larsen et al., 2019; Piché et al., 2008). One study found that the fork length associated with a 50% probability of sexual maturity at 2 years of age for males differed by 11.1 mm (~9%) between two Chinook salmon stocks (Spangenberg et al., 2015). In another study, the mass associated with a 50% probability of sexual maturity at 2 years of age for males ranged from 24.1 to 42.2 g among 10 different Chinook salmon stocks (Larsen et al., 2022). These studies support the occurrence of individual variation in performance thresholds for sexual maturation onset, at least at the interpopulation level (i.e., between

individuals from different stocks). Yet few studies have investigated variation at the intrapopulation level (i.e., between individuals from the same stock). In this regard, one study on Atlantic salmon found family-related differences in the PMRN between male half-sibs sired by a parr or an anadromous male (with a common dam) (Lepais et al., 2017). The prospect of family-related variation is significant not only as a contribution to basic understanding but also in that it could support the application of genetic selection to promote or inhibit sexual maturation onset in farmed stocks.

The present study utilized mass, fork length, and sexual maturation data collected in the Salmon Enterprises of Tasmania Pty. Ltd. (SALTAS) Atlantic salmon selective breeding programme. Because all individuals measured in the SALTAS selective breeding programme are pedigreed, the data provide the opportunity to account for genetic factors influencing variation in sexual maturity at age. The aims of this study were twofold: first, to determine if size and condition are positively associated with sexual maturation onset in the SALTAS population; and, second, to determine whether the SALTAS population exhibits between-family variation in the performance threshold for sexual maturation onset.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

This research used only historic commercial data collected from animals as part of normal commercial operations. This research did not involve any animal experimentation or harm and required no permits. SALTAS is fully accredited with the Best Aquaculture Practices, Aquaculture Stewardship Council, and Global Good Agriculture Practices standards.

2.2 | Overview of the SALTAS Atlantic salmon selective breeding programme

The SALTAS Atlantic salmon selective breeding programme has been described in detail previously (Elliott & Kube, 2009; Verbyla et al., 2021). Briefly, ~200 pedigreed families are produced annually (using a partial factorial mating design where each male and female are crossed twice) and communally reared from the eyed-egg stage (~250 eggs per family; ~50,000 eggs total) at a SALTAS hatchery, Wayatinah, Tasmania. At 1 year of age, each year class is reduced to ~11,000 randomly selected individuals (mixed-sex and immature-mature parr are intentionally excluded), which are measured (fork length and mass), tagged with a passive integrated transponder tag, and genotyped for pedigree determination and genomic selection. Cohorts of ~2500 randomly selected individuals are transferred each to a sea pen in southeastern Tasmania. A cohort of ~3000 randomly selected individuals are transferred to a freshwater hatchery in South Springfield, Tasmania. The remaining ~3000 individuals are retained in fresh water in Wayatinah. At 2 years of age, all individuals from each cohort are measured (fork length and mass) and assessed for

sexual maturity. Thereafter, the South Springfield and Wayatinah cohorts are each reduced to ~1000 individuals (selected on genetic merit) and assessed again for sexual maturity at 3 years of age.

2.3 | Detailed fish husbandry and data collection

This study refers only to husbandry and data collected from the Wayatinah (freshwater) cohort in the 2016–2018 year classes.

Each year class was fertilized in May of that year. Embryos and alevins were housed within a recirculating aquaculture system (RAS) at the SALTAS Wayatinah hatchery and reared at ~8°C in complete darkness (0:24 light/dark [LD]). Following complete yolk-sac absorption in August/September, fry were reared in a 4000-L tank under constant dusk lighting (24:0 LD) first at 12°C and later at 15°C. In February of the year following fertilization, parr were transferred to a 62,000-L tank within an outdoor flow-through system and reared under ambient photoperiod and temperature conditions (42.39°S, 146.49°E). In June/July of the year following fertilization, juveniles were transferred to a 215,000-L tank in a RAS and thereafter reared under simulated natural photoperiod and artificial temperature conditions.

The dates of fertilization, 1-year- and 2-year-old measures, and sexual maturity assessments (at 2 and 3 years of age) for each year class are presented in Table S1. At the 1-year-old measure, fork length was measured to the nearest millimeter and mass to the nearest gram (5 g for the 2018 year class). At the 2-year-old measure, fork length was measured to the nearest millimeter and mass to the nearest 5 g. Sexually mature fish were identified by the presence of external secondary sexual characteristics including darkened skin colouration, presence of kype (males), protruding ovipositor, and extended abdomen (females) (Davidson et al., 2021). Fulton's condition factor (K) was calculated at each measure using the formula $K = 10^n(W/L^3)$, where $n = 5$, W = mass (g), and L = fork length (mm).

2.4 | Summary of the datasets and data cleaning

Data were separated into four datasets: two for males (M2 and M3) and two for females (F2 and F3). The M2 and F2 datasets contained

1-year-old fork length, mass, and K measurement data and 2-year-old sexual maturation data. The M3 and F3 datasets contained 2-year-old fork length, mass, and K measurement data and 3-year-old sexual maturation data. Only fish that were sexually immature at the time of the 2-year-old assessment were included in the M3 and F3 datasets. This was to eliminate any confounding effect of 2-year-old sexual maturation outcome on fork length, mass, and K at the time of the 2-year-old measure (Leclercq et al., 2010).

Box plots were used to visualize outliers in K of immature and mature fish from each year class in each dataset. All outliers with $K < 0.9$ or $K > 2.1$ were removed, as these ranges were considered to indicate erroneous measure data. There were between zero and seven individuals removed from each dataset. The number of individuals and families remaining and the incidence of sexual maturation for each year class in the cleaned data are summarized in Table 1. As there was <5% incidence of sexual maturation in females at 2 years of age in each of the studied year classes, the F2 dataset was not used in this study.

2.5 | Statistical analyses

All statistical analyses were performed using R 4.2.1 (www.r-project.org). Statistical significance was considered at a level of $p < 0.05$.

2.5.1 | Comparison of size and condition between sexually mature and immature fish

For each sex, a two-tailed independent t -test (homogeneity of variance assumed) or two-tailed Welch's t -test (homogeneity of variance not assumed) was used to compare within each year class the mean fork length, mass, and K (at the 1-year or 2-year-old measure) between fish that were immature and mature (at the 2-year or 3-year-old sexual maturity assessment, respectively). The assumption of homogeneity of variance was checked by examining the residual plotted against the fitted values and using the Levene's test on the residuals. The assumption of normal distribution was checked using a quantile–quantile plot and Shapiro Wilk test on the residuals. Where necessary, transformations were used to correct for non-normal distributions (Table S2).

TABLE 1 Summary of the datasets used in the present study.

| Dataset | Year class | Number of individuals | Number of families | Incidence of sexual maturation (%) |
|---------|------------|-----------------------|--------------------|------------------------------------|
| M2 | 2016 | 1032 | 107 | 54.46 |
| | 2017 | 1076 | 182 | 38.38 |
| | 2018 | 1400 | 157 | 28.64 |
| M3 | 2016 | 152 | 53 | 65.79 |
| | 2017 | 183 | 91 | 62.30 |
| | 2018 | 264 | 105 | 70.45 |
| F3 | 2016 | 640 | 97 | 58.75 |
| | 2017 | 395 | 137 | 41.01 |
| | 2018 | 497 | 129 | 34.61 |

2.5.2 | Influence of size and condition on the odds of sexual maturity

Data were analysed using a multiple logistic regression (LR) model with sexual maturity (yes = 1; no = 0) as the dependent variable. Size and K (and the interaction) effects on the odds of sexual maturity (odds = $p/[1 - p]$, where p is the probability of sexual maturity) were tested by fitting size, K , and year class as fixed effects. Size and K data were zero-centered. The model was run twice for each dataset: once when size was represented by fork length and once when size was represented by mass. As fork length and mass were highly correlated (Figure S1), they were not included in the same model. The AIC was used to select the best-fit model (Symonds & Moussalli, 2011). Only findings from the best-fit model were subject to visualization and interpretation. When the effects of both size and K were significant, the magnitude of their respective effects was ranked by comparing standardized β coefficients (Schielzeth, 2010). The assumption of absence of multicollinearity was checked using variance inflation factors. The assumption of linearity in the logit for continuous independent variables was checked visually. The assumption of lack of strongly influential outliers was checked using Cook's distance statistic. No transformations or removal of outliers from the data were required to meet the model assumptions.

2.5.3 | Assessment of between-family variation in the PMRN

Only families with ≥ 10 measured individuals were considered in the analysis to increase precision of family-based estimates. In the M2 dataset, there were 52, 34, and 66 families with ≥ 10 measured individuals in the 2016, 2017, and 2018 year classes, respectively. These families were represented by a total of 781, 467, and 862 individuals, respectively. The M3 and F3 datasets were not subjected to the following analysis as there were few families with ≥ 10 measured individuals.

Using the lme4 R package 1.3.1 (Bates et al., 2015), data were analysed using a generalized linear mixed-effect (LME) logistic regression model with sexual maturity (yes = 1; no = 0) as the dependent variable. Fork length, K , and year class were fitted as fixed effects, and family was fitted as a random (intercept) effect. Fork length and K data were zero-centered. Variance attributable to family was expressed as a proportion of the total variance using the formula $\sigma_i^2/(\sigma_i^2 + \sigma_e^2)$, where σ_i^2 = random family effect variance and σ_e^2 = residual variance, assumed to be $\pi^2/3$ (Nakagawa & Schielzeth, 2010). Assumptions of the model were checked as described in Section 2.5.2. No transformations were required, although one outlier was removed from the data to meet the model assumptions. Variation in the PMRN between families within each year class was examined visually.

3 | RESULTS

3.1 | Comparison of size and condition between sexually mature and immature fish

3.1.1 | Males

Sexual maturity at 2 years of age

Mean fork length, mass, and K at 1 year of age were significantly greater in sexually mature compared to immature 2-year-old males for each year class (Figure 1a-c; Table S2). The difference in mean fork length at 1 year of age between sexually mature and immature 2-year-old males was 13.74, 16.69, and 17.14 mm for the 2016, 2017, and 2018 year classes, respectively. The difference in mean mass at 1 year of age between sexually mature and immature 2-year-old males was 36.07, 38.23, and 35.59 g for the 2016, 2017, and 2018 year classes, respectively. The difference in mean K at 1 year of age between sexually mature and immature 2-year-old males was 0.04, 0.03, and 0.03 for the 2016, 2017, and 2018 year classes, respectively.

Sexual maturity at 3 years of age

Mean fork length and mass at 2 years of age were not significantly different between sexually mature and immature 3-year-old males for the 2016 and 2017 year classes but were significantly greater in sexually mature 3-year-old males for the 2018 year class (Figure 2a,b; Table S2). The difference in mean fork length at 2 years of age between sexually mature and immature 3-year-old males was 15.08 mm for the 2018 year class. The difference in mean mass at 2 years of age between sexually mature and immature 3-year-old males was 229.45 g for the 2018 year class. Mean K at 2 years of age was not significantly different between sexually mature and immature 3-year-old males for any year class (Figure 2c; Table S2).

3.1.2 | Females

Sexual maturity at 3 years of age

Mean fork length at 2 years of age was significantly greater in sexually mature compared to immature 3-year-old females for the 2016 and 2018 year classes but not for the 2017 year class (Figure 3a; Table S2). The difference in mean fork length at 2 years of age between sexually mature and immature 3-year-old females was 8.20 and 10.45 mm for the 2016 and 2018 year classes, respectively. Mean mass and K at 2 years of age were significantly greater in sexually mature compared to immature 3-year-old females for each year class (Figure 3b,c; Table S2). The difference in mean mass at 2 years of age between sexually mature and immature 3-year-old females was 170.82, 124.03, and 257.24 g for the 2016, 2017, and 2018 year classes, respectively. The difference in mean K at 2 years of age between sexually mature and immature 3-year-old females was 0.06, 0.08, and 0.07 for the 2016, 2017, and 2018 year classes, respectively.

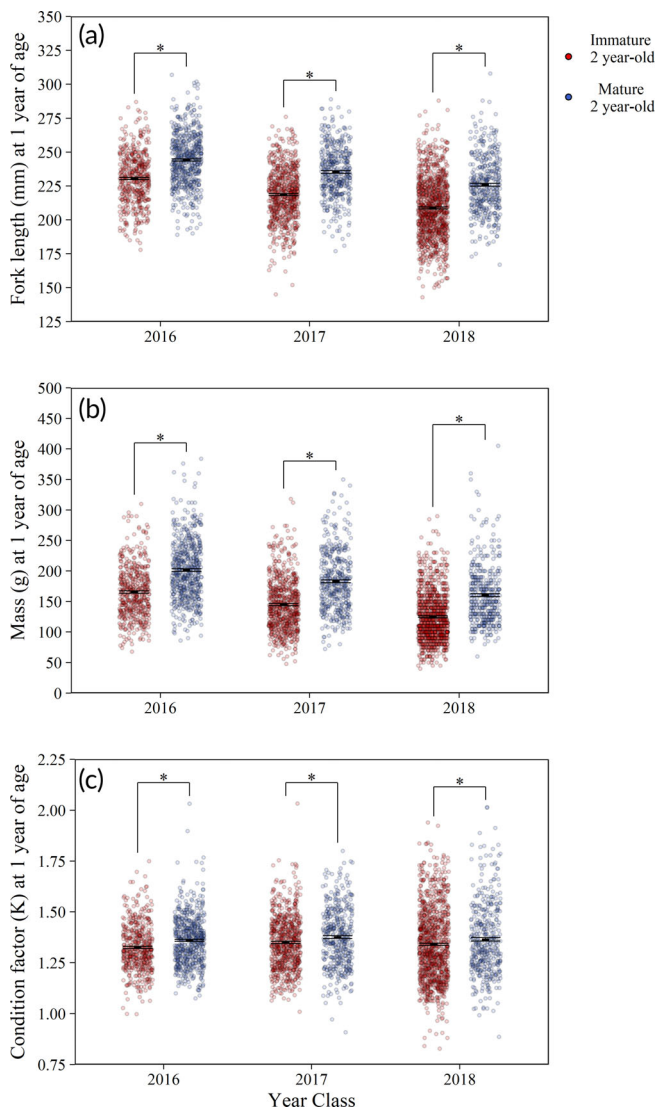


FIGURE 1 (a) Fork length, (b) mass, (c) and condition factor at 1 year of age in immature and mature 2-year-old male Atlantic salmon (*Salmo salar*) from the SALTAS population. Mean (\pm s.e.) is indicated by a black bar. *, Significant differences between the means of immature and mature fish within a year class ($p < 0.05$).

3.2 | Influence of size and condition on the odds of sexual maturity

3.2.1 | Males

Sexual maturity at 2 years of age

The best-fit model was produced when size was represented by fork length (Table S3). Significant main effects of fork length (LR: $z = 19.64$, $p < 0.0001$) and K (LR: $z = 7.31$, $p < 0.0001$) were observed on the odds of sexual maturity at 2 years of age. For every 10-mm increase in fork length at 1 year of age, the odds of sexual maturity at 2 years of age increased by 1.48 times (95% C.I. = 1.42–1.54). The relationship between fork length at 1 year of age and the probability of sexual maturity at 2 years of age is illustrated graphically (Figure 4a). For every 0.1 K increase in condition at 1 year of age, the

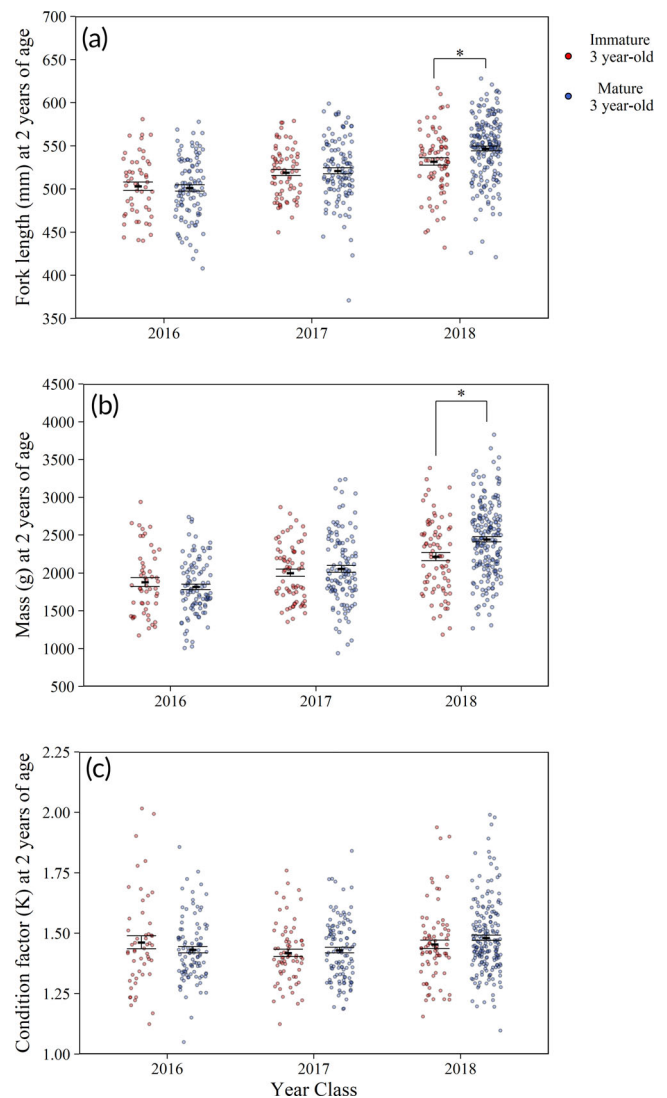


FIGURE 2 (a) Fork length, (b) mass, and (c) condition factor at 2 years of age in immature and mature 3-year-old male Atlantic salmon (*Salmo salar*) from the SALTAS population. Mean (\pm s.e.) is indicated by a black bar. *, Significant differences between the means of immature and mature fish within a year class ($p < 0.05$).

odds of sexual maturity at 2 years of age increased by 1.22 times (C.I. = 1.15–1.28). The relationship between K at 1 year of age and the probability of sexual maturity at 2 years of age is illustrated graphically (Figure 4b). Comparison of the standardized β coefficients indicated that fork length at 1 year of age had a greater effect than K on the odds of sexual maturity at 2 years of age. No significant interaction effect between fork length and K at 1 year of age was observed on the odds of sexual maturity at 2 years of age (LR: $z = 0.58$, $p > 0.05$).

Sexual maturity at 3 years of age

The best-fit model was produced when size was represented by mass (Table S3). A significant main effect of mass (LR: $z = 2.58$, $p < 0.01$) was observed on the odds of sexual maturity at 3 years of age. For every 100 g increase in mass at 2 years of age, the odds of sexual maturity at 3 years of age increased by 1.06 times (C.I. = 1.01–1.10).

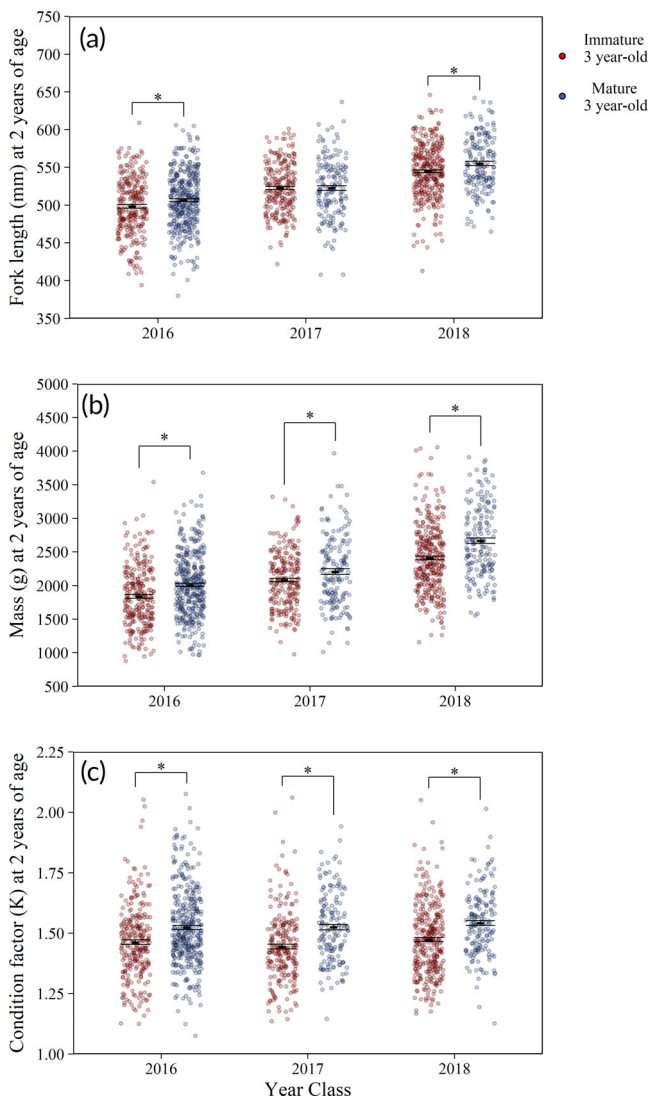


FIGURE 3 (a) Fork length, (b) mass, and (c) condition factor at 2 years of age in immature and mature 3-year-old female Atlantic salmon (*Salmo salar*) from the SALTAS population. Mean (\pm s.e.) is indicated by a black bar. *, Significant differences between the means of immature and mature fish within a year class ($p < 0.05$).

The relationship between mass at 2 years of age and the probability of sexual maturity at 3 years of age is illustrated graphically (Figure 5). No significant main effect of K or interaction effect between mass and K at 2 years of age was observed on the odds of sexual maturity at 3 years of age (LR: $z = -0.38$, $p > 0.05$ and $z = -1.34$, $p > 0.05$, respectively).

3.2.2 | Females

Sexual maturity at 3 years of age

The best-fit model was produced when size was represented by fork length (Table S3). Significant main effects of fork length (LR: $z = 4.03$, $p < 0.0001$) and K (LR: $z = 9.08$, $p < 0.0001$) were observed on the odds of sexual maturity at 3 years of age. For every 10-mm increase

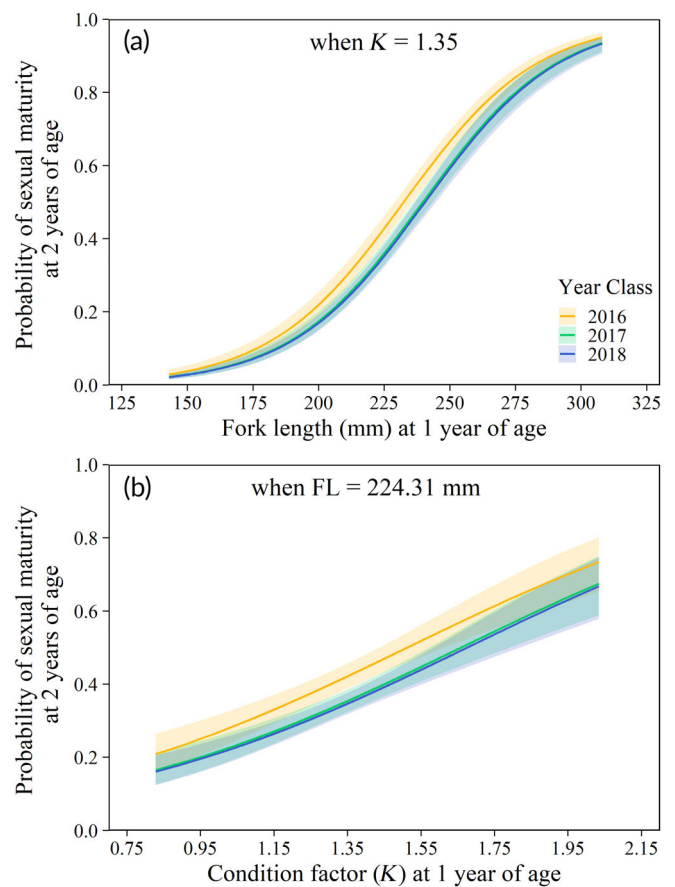


FIGURE 4 Fitted logistic regression of the probability of sexual maturity at 2 years of age based on (a) fork length and (b) condition factor at 1 year of age in male Atlantic salmon (*Salmo salar*) from the SALTAS population. The 95% C.I. is represented by the shaded area. FL, fork length; K , condition factor.

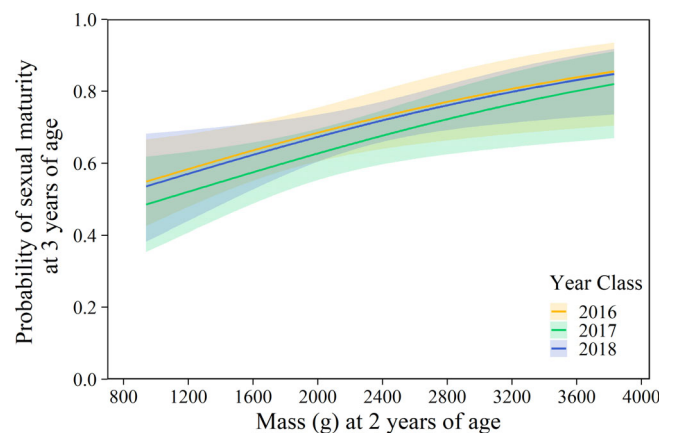


FIGURE 5 Fitted logistic regression of the probability of sexual maturity at 3 years of age based on mass at 2 years of age in male Atlantic salmon (*Salmo salar*) from the SALTAS population. The 95% C. I. interval is represented by the shaded area.

in fork length at 2 years of age, the odds of sexual maturity at 3 years of age increased by 1.06 times (C.I. = 1.03–1.09). For every 0.1 K increase in condition at 2 years of age, the odds of sexual maturity at

3 years of age increased by 1.44 times (C.I. = 1.33–1.56). Comparison of the standardized β coefficients indicated that K at 2 years of age had a greater effect than fork length on the odds of sexual maturity at 3 years of age. There was a significant interaction effect between fork length and K at 2 years of age on the odds of sexual maturity at 3 years of age (LR: $z = 2.737$, $p < 0.01$). The relationship between fork length at 2 years of age and the probability of sexual maturity at 3 years of age at different levels of K (mean $-$ s.d., mean, mean $+$ s.d.) is illustrated graphically (Figure 6a–c). The relationship between K at 2 years of age and the probability of sexual maturity at 3 years of age

at different levels of fork length (mean $-$ s.d., mean, mean $+$ s.d.) is illustrated graphically (Figure 6d–f).

3.3 | Assessment of between-family variation in the PMRN

There was a significant main effect of fork length and K on the odds of sexual maturity at 2 years of age in males (LME: $z = 14.00$, $p < 0.0001$ and $z = 5.73$, $p < 0.0001$, respectively). The proportion of

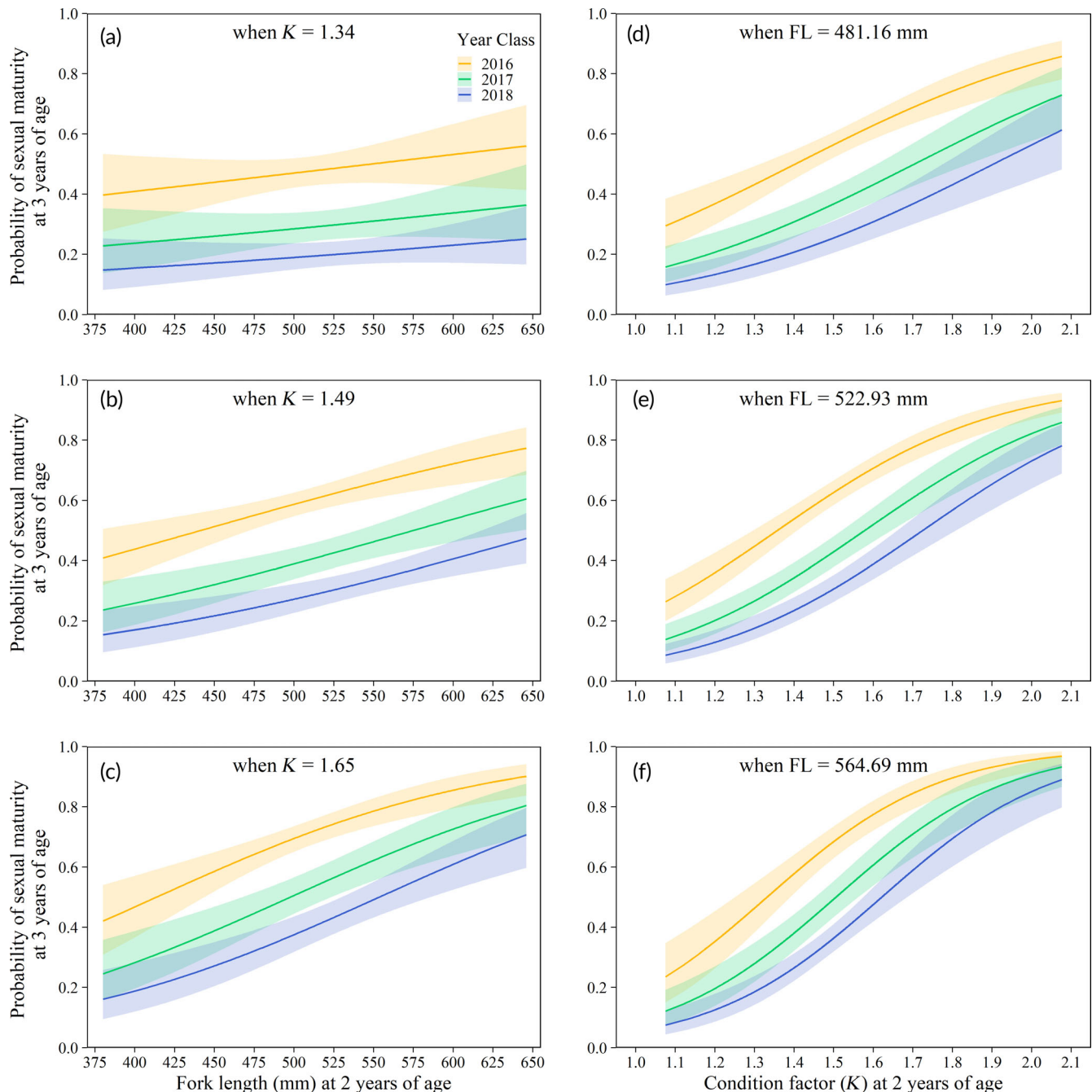


FIGURE 6 Fitted logistic regression of the probability of sexual maturity at 3 years of age based on (a–c) fork length and (d–f) condition factor at 2 years of age in female Atlantic salmon (*Salmo salar*) from the SALTAS population. The 95% C.I. interval is represented by the shaded area. FL, fork length; K , condition factor.

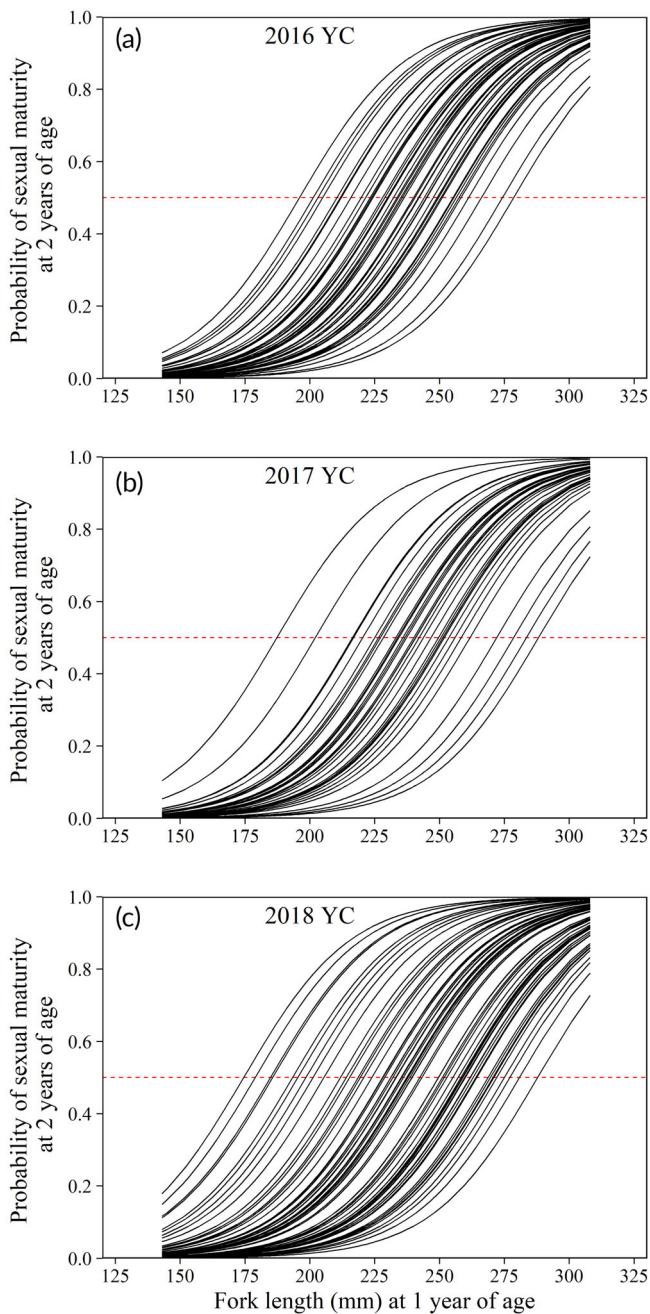


FIGURE 7 Estimated probabilistic maturation reaction norm (PMRN) for families from the (a) 2016, (b) 2017, and (c) 2018 year classes of the SALTAS Atlantic salmon (*Salmo salar*) population. A logistic regression of the probability of sexual maturity at 2 years of age was fitted, based on fork length and condition factor (K) at 1 year of age in males. ---, Estimated PMRN for a single family; —, probability of sexual maturity at 2 years of age equal to 0.5.

variance in the model explained by family was 34.93%. The relationship between fork length at 1 year of age and the probability of sexual maturity at 2 years of age for each family (with ≥ 10 measured males) from the 2016 to 2018 year classes is illustrated graphically (Figure 7).

4 | DISCUSSION

This study investigated the association between size, condition, year class, family, and sexual maturity in the SALTAS Atlantic salmon population. Within any single year class, males and females that were sexually mature at 2 and 3 years of age (maiden spawn), respectively, tended to have greater fork length, mass, and K than did their immature counterparts at 1 and 2 years of age, respectively. Consistent with this, previous studies on Atlantic salmon in the wild (Prévost et al., 1992), laboratory (Duston & Saunders, 1999), and aquaculture setting (Kadri et al., 1996) showed that fork length, mass, and K was greater in sexually mature compared with immature groups approximately 1 year before spawning. Collectively, these findings highlight a strong association between size, condition, and sexual maturation onset in Atlantic salmon.

The probability of sexual maturity at 2 years of age was positively associated with size and condition at 1 year of age in males. The probability of sexual maturity at 3 years of age was positively associated with size at 2 years of age in males and size and condition at 2 years of age in females. These findings suggest that variation in sexual maturity among individuals from the SALTAS Atlantic salmon population is related in part to size and condition 1 year before spawning, irrespective of age or sex. This is in line with the hypothesis that the onset of sexual maturation in Atlantic salmon is conditional on performance (with respect to energy availability) surpassing a threshold (Thorpe, 1994). Other studies on male Atlantic salmon have also demonstrated a positive association between size, condition, and probability of sexual maturity (Åsheim et al., 2023; Oldham et al., 2023). Notably, Åsheim et al. (2023) found that, for a given level of mass and condition, the probability of sexual maturity was higher in individuals reared in a warm temperature regime compared to a cool temperature regime. A similar observation of variation in the association between fork length, condition, and sexual maturity under different temperature regimes was also made in an earlier study on male Atlantic salmon (Duston & Saunders, 1997). In addition, a study on white spotted charr (*Salvelinus leucomaenis*) showed that, for a given level of fork length, the probability of sexual maturity was higher in individuals maintained in a narrow section of river compared to a wide section of river (Morita et al., 2009). Thus, it is apparent that the association between size, condition, and probability of sexual maturity can vary among different environments. Indeed, in the present study there was significant variation among year classes (Table S4), which may reflect differences in rearing environment as well as genetics and age at measure.

That the association between size, condition, and probability of sexual maturity can vary among different environments is significant from both basic and applied perspectives. At an applied level, it suggests that the targeted modulation of size and condition in farmed stocks could lead to varied rates of sexual maturation among cohorts. This presents as an important management consideration for farmers because reliable control of sexual maturation is needed to reduce costs of broodstock production (Berlinsky et al., 2020), accelerate

genetic improvement in selective breeding programmes (Houston et al., 2020), and prevent adverse effects on efficiency, quality, and welfare in commercial production (Taranger et al., 2010). At a basic level, one interpretation is that, in addition to size and condition, other biological processes subject to environmental influence are involved in regulating sexual maturation onset (Åsheim et al., 2023). Alternatively, the performance threshold for sexual maturation onset could be plastic and adaptive to the favorability of the environment for reproductive success (e.g., refuge availability) (Morita et al., 2009). We posit that size and condition per se do not regulate sexual maturation onset and are simply correlated (disproportionately under different environments) with proximate signals of energy availability (Fraser et al., 2023). This is in general agreement with the view in mammals that body composition and reproduction are not causally related but rather independent (generally correlated) responses to energy availability (Wade & Jones, 2004). A focus of future studies should be to identify the proximate signals of energy availability involved in the regulation of sexual maturation onset. Such knowledge might support diet formulation or the development of management strategies for consistent control over the incidence of sexual maturation in farmed stocks (Berlinsky et al., 2020).

In the present study family explained a considerable proportion (~35%) of the variation in sexual maturity at 2 years of age among males that was not attributable to the average effects of size, condition, and year class at 1 year of age. In some cases, there were large differences in the estimated PMRN between families from the same year class (i.e., reared in a common setting), with estimates of the probability of sexual maturity for a given fork length ranging from 6.93% to 80.41%, 4.46% to 86.23%, and 4.53% to 92.10% for families from the 2016, 2017, and 2018 year classes, respectively. This suggests that the magnitude of the performance threshold (with respect to energy availability) for sexual maturation onset varies between families in the SALTAS population. The level of family-related variation observed here may not necessarily be representative of other Atlantic salmon stocks. Because the families were reared in separate incubation units from fertilization up to the eyed-egg stage, it is possible that an incubator effect contributed in part to the family-related variation observed. However, the separate rearing of families to the eyed-egg stage is known to have a negligible effect on most traits in the SALTAS population. Variation in the PMRN was also found between families of Atlantic salmon from the Oir River, France (Lepais et al., 2017), and Chinook salmon from the Yakima River, U.S. (Galbreath et al., 2022). Family-related variation in the PMRN was clearly linked with sire phenotype (parr, anadromous) in the previous study on Atlantic salmon (Lepais et al., 2017) but not on Chinook salmon (Galbreath et al., 2022). In the latter study, family-related variation was attributed to individual sire and dam effects that were unrelated to broodstock age, spawning date, dam size, or egg size (Galbreath et al., 2022). Evidence for intrapopulation variation in the PMRN was also demonstrated in Atlantic salmon from the Neva and Oulu stocks in Finland with differing *vestigial-like family member 3* (*vglI3*) genotypes (Åsheim et al., 2023). *VglI3* is known to explain a large proportion (~33%–39%) of variation in age at first sexual maturity in Atlantic salmon of European origin (Ayllon et al., 2015; Barson

et al., 2015) and to influence seasonal changes in body condition (House et al., 2023). Significantly though, *vglI3* is not associated with age at first sexual maturity in Atlantic salmon from the SALTAS population (Mohamed et al., 2019). When taken together, these findings provide a strong case for a genetic component affecting the magnitude of the performance threshold for sexual maturation onset.

Genetic selection for sexual maturity at age has been used to support control of sexual maturation in farmed Atlantic salmon (Verbyla et al., 2021). With reference to the “critical period” hypothesis (Thorpe, 1994), sexual maturity at any age is simply a consequence of an individual's performance in a prior season, relative to a performance threshold. Thus, from a biological perspective, sexual maturity at age could be considered a ratio of two-component traits. Performance (notionally represented by size or condition) and the performance threshold for sexual maturation onset (notionally represented by the value for size or condition that gives a 50% probability of sexual maturity) are the component traits that determine (and are likely the subject of genetic influences on) sexual maturity at age. Application of genetic selection pressure directly on a ratio trait can exert disproportionate selection pressure on its component traits, making genetic progress difficult to predict (Gunsett, 1984). Therefore, directing genetic selection pressure on component traits can be a more effective strategy for improving ratio traits than directing genetic selection on the ratio itself (Zetouni et al., 2017). With this in mind (and that selection for growth is already typical of Atlantic salmon selective breeding programmes), one idea for consideration is whether directing genetic selection pressure on the performance threshold for sexual maturation onset (again, notionally represented by the value for size or condition that gives a 50% probability of sexual maturity) or sexual maturity at age is the best approach to support control of sexual maturation in farmed stocks. To explore its potential as an alternative target for genetic selection, further study is needed to evaluate the genetic parameters of the performance threshold for sexual maturation onset.

In summary, this study on Atlantic salmon from the SALTAS population showed that the probability of sexual maturity at 2 or 3 years of age was positively associated with size and condition in the previous year. These findings support the hypothesis that the onset of sexual maturation is conditional on a performance threshold (with reference to energy availability) being surpassed (Thorpe, 1994). Studies are needed to identify the proximate signals of energy availability involved in regulating sexual maturation onset. Family accounted for a considerable proportion of the variation in sexual maturity that is not attributable to size, condition, and year class. This suggests the magnitude of the performance threshold can vary between families and is determined by a genetic component. Evaluation of the genetic parameters for the performance threshold may support the application of genetic selection to control the incidence of sexual maturation in farmed stocks.

AUTHOR CONTRIBUTIONS

Morgan S. Brown: study conceptualization, data analysis methodology, formal data analysis, manuscript preparation. Roberto Carvalheiro: study conceptualization, data analysis methodology, manuscript

revision and editing. Richard S. Taylor: funding acquisition, manuscript revision and editing. Wagdy Mekky: data analysis methodology, manuscript revision and editing. Timothy D.W. Luke: data analysis methodology, manuscript revision and editing. Lewis Rands: study conceptualization, data collection, manuscript revision and editing. Damien Nieuwesteeg: data collection, manuscript revision and editing. Brad S. Evans: funding acquisition, manuscript revision and editing. Nicholas M. Wade: funding acquisition, manuscript revision and editing. Curtis E. Lind: funding acquisition, manuscript revision and editing. Pollyanna E. Hilder: funding acquisition, manuscript revision and editing.

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