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Sequence of formation and inheritance of meristic variation in the post-cranial axial skeleton of Atlantic salmon (*Salmo salar*)

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Abstract

Atlantic salmon is an important aquaculture species that has fascinated naturalists for centuries, resulting in its biology being widely characterized. Certain details about the early development and the inheritance of meristic variation in the post-cranial axial skeleton are, however, largely unexplored. The present study gives a detailed description of the sequence of formation of the post-cranial axial skeleton based on whole-mount staining and used radiology to investigate the inheritance of meristic variation in isogenic hybrid all-male families of Atlantic salmon (∼4 kg). Eight different families were created by crossing two homozygous double haploid XX females (dam A, B) with four different double haploid homozygous YY super males (sires a to d). In the caudal fin complex, the first bone to form is hypural 1 and its associated lepidotrichia followed by a bidirectional formation of new bones. In the dorsal and anal fins, development starts in the cranial part, and new bones form bidirectionally towards the head and tail fin. The neural and haemal arches start to form at segment 43, and further development is bidirectional. The first parapophysis form in the caudal part of the abdomen followed by a unidirectional completion cranially. The first ribs form at segment 3 and new ribs develop unidirectional caudally. Chordacentra formation starts at segment 24 followed by formation of chordacentrum number 58 (caudal-most vertebra). New chordacentrae form bidirectionally from segment 24 in parallel with the formation of chordacentrum number 57. The first epineuralia form at segment 1 followed by a unidirectional completion caudally until segment 30. The first supraneuralia to develop is number 10 closely followed by number 1, then new supraneurals form bidirectionally from number 10. Analysis of the inheritance on the post-cranial axial skeletal bones showed a strong maternal effect on total vertebrae centra and tail fin lepidotrichia counts. For these skeletal counts, dam A produced offspring with modes of 58 and 45 respectively, while dam B produced offspring with modes of 59 and 42. The higher number of total vertebrae centra produced by dam B was associated with additional abdominal and/or transitional vertebrae. The completion of formation in different post-cranial axial skeletal parts are either bi- or unidirectional, and the initiation of formation is site specific for each skeletal part with some inter-part similarities. Further, the present results may suggest that there has been a maternally driven selection for more abdominal vertebrae associated with a higher number of total vertebrae, and more tail fin lepidotrichia associated with a lower number of total vertebrae. These changing meristic counts may impact on important fitness-related traits, such as fecundity and swimming ability, making the present findings relevant for both ecological and aquaculture sciences.

KEYWORDS

Atlantic salmon, inheritance, lepidotrich, meristic, pterygiophore, vertebra

1 | INTRODUCTION

Atlantic salmon (*Salmo salar* L. 1758) is an anadromous teleost with a complex life history. The skeleton of the Atlantic salmon has fascinated scientists for decades (Sanford, 2000). The skull of maturing male fish was most appealing for pioneers (Tchernavin, 1938), while deformity development in salmon aquaculture has driven the research focus towards the vertebral column (Witten et al., 2005). There are several studies that have investigated the early development (Grotmol et al., 2003, 2006; Grotmol, Kryvi, & Totland, 2005; Grotmol, Nordvik, et al., 2005), anatomy (Nordvik et al., 2005), and growth and mineralization (Fjelldal et al., 2005, 2006; Kryvi et al., 2017, 2021) of the vertebral column in Atlantic salmon. The cartilage of the neural and haemal arch are the first structures to differentiate (Grotmol et al., 2003). Segmentation of the notochord initiates the formation of the vertebral centra (Fleming et al., 2004; Grotmol et al., 2003, 2006; Grotmol, Kryvi, & Totland, 2005; Grotmol, Nordvik, et al., 2005; Pogoda et al., 2023). Somite-derived cells contribute to the growth of the centra and other vertebral column skeletal structures (Witten & Hall, 2022). The fully developed vertebral column is equipped with ribs, epineurals, and haemal and neural arches and spines, depending on the region (Nordvik et al., 2005). The morphology of the vertebral column changes during smoltification and migration to seawater towards relatively larger vertebrae in the tail region (Fjelldal et al., 2006). The vertebral column together with the supraneurals and median (unpaired) fins (dorsal, anal, and tail fins) make up the post-cranial axial skeleton in fish.

Kryvi et al. (2017) gave a detailed description of the developmental sequence of the post-cranial axial skeleton in Atlantic salmon. Between 370 and 640 day-degrees (d°) the skeletal parts started to develop in the following order: (i) dorsal and anal fin lepidotrichia along with caudal fin hypurals (370 d°); (ii) neural and haemal arches (400 d°); (iii) lateral ribs and intramuscular bones (560 d°); (iv) vertebral chordacentra (640 d°). However, further details on the sequence of formation within each skeletal part have not been described. One exception is the vertebral column, where the first complete chordacentra forms in the region beneath the dorsal fin, from where successive chordacentra developed bidirectionally towards the head and tail (Grotmol, Nordvik, et al., 2005).

The genetic makeup and the environment during early development are factors that affect post-cranial axial skeletal meristic counts in teleost fish (Ando et al., 2010, 2011, 2017; Berg et al., 2018; Fowler, 1970; Harrington Jr & Crossman Jr, 1976; Leary et al., 1985; Lindsey, 1988; Lindsey & Harrington Jr, 1972; Orska, 1963; Swain & Lindsey, 1986; Taniguchi et al., 1996; Tibblin et al., 2016). Mid-parent values have been used to study the inheritance of meristic variation (Kiso et al., 2012; Leary et al., 1985). There are, however, studies that have described maternal effects in chum salmon (*Oncorhynchus keta* Walbaum 1792) (Ando et al., 2017) and paternal effects in Atlantic cod (*Gadus morhua* L. 1758) (Løken & Pedersen, 1996) on the total vertebral counts. However, these studies did not investigate vertebrae counts in different regions of the vertebral column. Indeed, other studies have shown that variation in vertebrae counts may be restricted to certain regions of the vertebral column, e.g., in masu salmon (*Oncorhynchus masou* Brevoort 1856) (Ando et al., 2008), three spine-sticklebacks (*Gasterosteus aculeatus* L. 1758) (Hermida et al., 2002; Lindsey, 1962), and Chinook salmon (*Oncorhynchus tshawytscha* Walbaum 1792) (De Clercq et al., 2018).

Recently, Sankar et al. (2024) developed a radiographic method for vertebral column regionalization for salmonids based on specific radiographic hallmarks. The method allows the assessment of individual-based vertebrae counts within the post-cranial, abdominal, transitional, caudal, and ural regions of the vertebral column. Applying this method in meristic studies has the potential of providing useful information regarding evolutionary and ecological adaptions (Ando et al., 2008; Ford, 1937; Kiso et al., 2012; Swain, 1992a, 1992b). There is, however, no knowledge covering these aspects in Atlantic salmon. Indeed, homozygous clonal fish lines can be used to refine studies on how genetics impact on the meristic characters (Bergot et al., 1981; Grageda et al., 2005; Nakajima et al., 1996; Nichols et al., 2004; Taniguchi et al., 1996; Young et al., 1995). For instance, using isogenic hybrids, offspring of homozygous parents, is one possible, yet unexplored, solution to further target possible parental contributions more specifically (Fjelldal et al., 2020; Young et al., 1995). We recently established homozygous double-haploid female (Hansen et al., 2020) and male (Fjelldal et al., 2020) lines of Atlantic salmon, enabling the production of isogenic hybrids.

An improved understanding about how the different parts of the post-cranial axial skeleton develop and the parental contribution to their meristic variation will be useful for both ecological and aquaculture sciences studying Atlantic salmon. It can help to understand local adaptions, possible impacts of a changing environment, and the development of early life defects and implications of selective breeding in aquaculture. To pursue this, the present study describes the sequence of formation of post-cranial axial skeletal bones and explores the parental contributions to post-cranial axial skeletal meristic counts in Atlantic salmon including vertebral column regions. An outbred strain was used to study the sequence of formation, and adults from eight different isogenic hybrid all-male families were used to study the inheritance of meristic variation.

2 | MATERIALS AND METHODS

The study consisted of two separate parts. The first part described the sequence of formation of the post-cranial axial skeleton using whole-mount staining during embryogenesis. This study used an outbred strain of Atlantic salmon. The second part was on the inheritance of meristic variation in the post-cranial axial skeleton using radiology on adults from different heterozygous isogenic hybrid families. These families were created by crossing different homozygous double-haploid male and female Atlantic salmon.

2.1 | Ethics statement

The care and use of experimental animals complied with the Norwegian Animal Welfare Act, guidelines, and policies as approved by the Norwegian Food Safety Authority, permit number 17127.

2.2 | Part 1: Sequence of formation

2.2.1 | Fish and rearing conditions

Atlantic salmon (*Salmo salar*) embryos and alevins were supplied from local hatcheries in western Norway (Tveitevåg, Askøy). The various stages were kept in flow-through systems. Developmental stages are classified by day-degrees (d°), the sum of mean ambient temperature (°C) for each day of development. For the embryonic stages, water temperature was maintained at 8.0°C. Embryos hatched at approximately 500 d°, at which time water temperature was raised to 8.5°C and maintained at this temperature until the alevins had consumed their yolk sacs, at approximately 850 d°. Fish were examined at approximately 50-d° intervals starting at 110 d°, when notochords are present, until 850 d°. Before all preparative procedures, embryos and alevins were anaesthetized with 5% benzocaine dissolved in water.

2.2.2 | Whole-mount staining

For studying the sequence of development in different post-cranial axial skeletal parts in the growing embryos, eggs and larvae were treated as described by Nordvik et al. (2005). The cartilage and bones were stained with Alcian blue and Alizarine red, respectively. Five specimens were sampled approximately every 100 d°, whereupon they were stained, dehydrated, and stored in glycerol.

2.3 | Part 2: Inheritance of meristic variation

2.3.1 | Fish and rearing conditions

Sex determination in Atlantic salmon is genetic, having the male heterogametic (sdY) system (XX female and XY male) (Yano et al., 2013). Eggs from two different homozygous double-haploid isogenic XX females (A and B) (Hansen et al., 2020) were fertilized with four different doubled haploid homozygous YY supermales (a, b, c, d) (Fjelldal et al., 2020) to produce eight all-male families (Aa, Ab, Ac, Ad, Ba, Bb, Bc, Bd). The families were created in November 2019, incubated at a stable temperature of 8°C, produced as under-yearling smolts as described by Fjelldal et al. (2006), transferred to seawater in December 2020, and reared in seawater until February 2022, when they were euthanized at a body weight of ~4 kg by an overdose of anesthetics (0.5 g L^{-1}, Finquel vet; MSD Animal Health Norge AS). In total, 80 fish were sampled with 10 fish per family ($n = 80$, mean length 64.58 ± 0.56 cm [standard error] and mean weight 3.851 ± 0.115 kg).

2.3.2 | Dissection, radiology, and meristic counts

The lateral musculature was carefully removed from each specimen. The remaining post-cranial axial skeletal bones (vertebral column, supraneurals, and fin lepidotrichia and pterygiophores) were subjected to further analysis. First the complete – lepidotrichia and pterygiophores – dorsal, anal, pectoral, and pelvic fins were dissected free from the vertebral column and radiographed (Amos et al., 1960). Next, the vertebral column was radiographed in a lateral view. Radiographs were taken using a direct radiology system (resolution 4.0 Ip/mm; Canon CXDI410C Wireless, Canon Inc.) and portable X-ray unit (Portable X-ray unit Hiray Plus, Model Porta 100 HF, Job Corporation) with 40 kV and 4 mA input at 88 cm distance. The digital Tagged Image File Format images were used to analyze for structure and region-specific counts (vertebrae, supraneurals, fin lepidotrichia and pterygiophores). Vertebral column regions were defined using

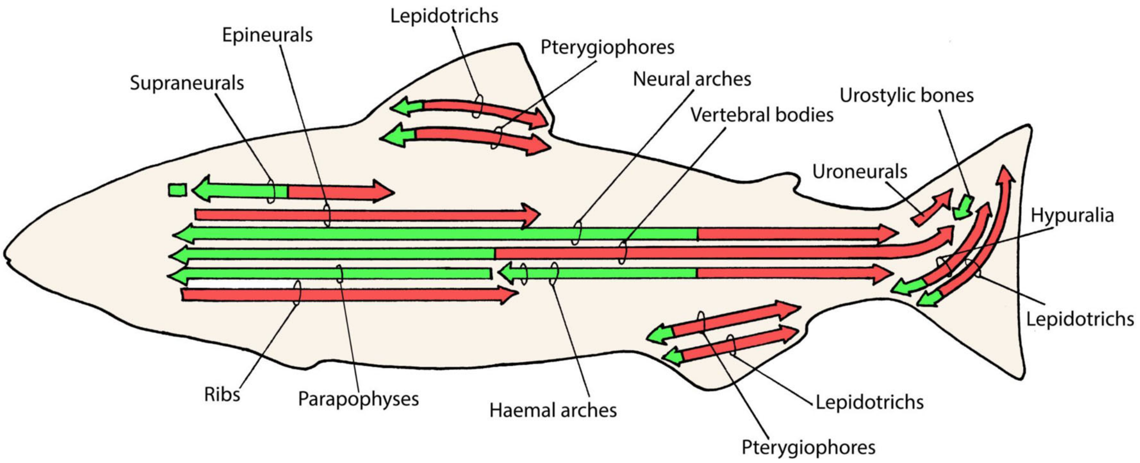


FIGURE 1 Schematic depiction of sequence of formation for the post-cranial axial skeleton.

radiographic hallmarks according to the method developed by Sankar et al. (2024), allowing region-specific vertebrae counts within the post-cranial, abdominal, transitional, caudal, and ural regions of the vertebral column.

2.4 | Statistical analysis

The data were transferred to the R Statistical software (version 4.0.4; R Core Team, 2021) for all analyses. The packages “nlme” (Pinheiro et al., 2022), “MuMIn” (Barton, 2024), “emmeans” (Lenth, 2021), and “ggplot2” (Wickham, 2016) were used for analysis and graphical presentation. Throughout, model diagnostics were assessed via q-q plots and standardized versus predicted residual plots. When assessing which fixed effects/interactions to include in the final models, we considered the model with the lowest Akaike information criterion corrected for small sample sizes (AICc) to best describe the data when weighted against complexity (Hurvich & Tsai, 1991).

Exploratory statistics were used to explore the relationships between all meristic counts which showed variation at the population level. A correlation matrix was created using the “rcorr” function from the “Hmisc” (Harrell, 2022) package and the Spearman rank test with no corrections for multiple comparisons.

To assess maternal and paternal effects, five proportional odds logistic regression models were fitted to the total vertebrae count data and fin lepidotrichia and pterygophors data which showed variation between family. The most complex included the fixed effects for dam (two levels) and sire (four levels) and their interaction.

3 | RESULTS

3.1 | Sequence of formation in the post-cranial axial skeleton

Figure 1 shows the sequence of formation and direction of completion within the different parts of the post-cranial axial skeleton.

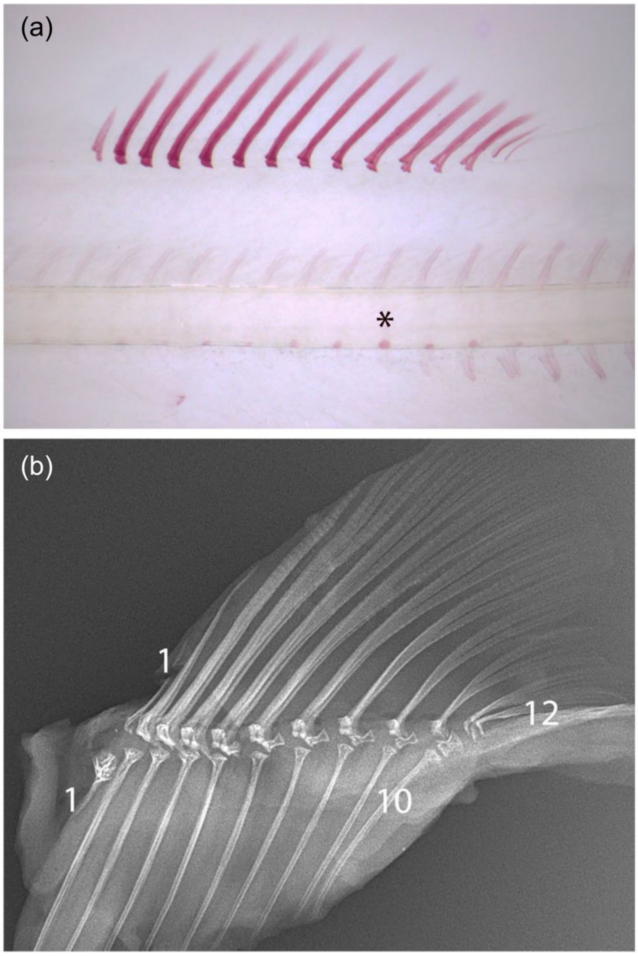


FIGURE 2 (a) Whole-mount alizarine red staining showing formation of the first chordacentra (the first chordacentrum is indicated with a black asterisk). (b) Radiographic image of the anal fin in adult salmon. Pterygiophore and lepidotrich numbers are indicated.

Figure 2a shows whole-mount staining of the first forming chordacentra as an example of the staining method used. In the caudal fin complex, the first structure to form is hypural 1 and its associated lepidotrichia, followed by a bidirectional development. Dorsal and anal fin pterygiophores and lepidotrichia start to form near their cranial ends and then complete their development in a bidirectional manner. The neural and haemal arches start to form at segment 43 in the caudal region and develop from there in a bidirectional manner. The first fused neural and haemal spine forms at segment number 53 and fused spines continue to form cranially to segment 27 and caudally to segment 56. The first parapophysis forms in the caudal part of the abdomen and these structures continue to form cranially. The first ribs occur in the cranial part of the abdomen and new ribs continue to form caudally. The two most cranial segments do not develop ribs. The anlage of the vertebral bodies (chordacentra) starts to form at segment 24 followed by chordacentrum number 58 (caudal most vertebra). Then new chordacentra start to form bidirectionally from segment 24 in parallel with the formation of chordacentrum number 57 (the second most caudal vertebra). Intermuscular epineuralia start to protrude from the neural arch at segment 1 and thereafter appear caudally until segment 30. The supraneurals form in the epaxial median septum, and the first supraneuralium to form is number 10 closely followed by number 1, then new supraneurals form bidirectionally from number 10.

3.2 | Inheritance of meristic variation in the post-cranial axial skeleton

Figure 2b shows a radiograph of the anal fin as an example for the radigraphic method used. The most appropriate models for total, abdominal, and transitional vertebrae counts included both dam and sire (Table 1). There was a significant effect of dam, but not sire, for total vertebral counts (Figure 3), while both dam and sire had a significant effect on the vertebral counts of the abdominal (Figure 4) and transitional (Figure 5) regions. The statistical significance was stronger for dam than for sire for both the abdominal and transitional vertebral counts (Table 1). For total vertebral counts, dam A had a mode of 58, while it was 59 for dam B **(**Figure 2**)**. With respect to caudal and ural region-specific vertebral counts, the most appropriate models included sire and dam only, respectively (Table 1). Sire had a significant effect (Table 1) on caudal vertebral counts (Figure 6) and dam had a significant effect (Table 1) on ural vertebral counts (Figure 7). For the fin ray counts the most appropriate model for anal fin pterygiophore and lepidotrich counts included dam only, while for the tail fin lepidotrichia it included both dam and sire (Table 1). Dam had a significant effect (Table 1) on anal fin pterygiophore (Figure 8) and lepidotrich counts (Figure 9), and both dam and sire had a significant effect (Table 1) on tail fin lepidotrich counts (Figure 10). For tail fin lepidotrichia, dam A had a mode of 45 whilst dam B had a mode of 42 (Figure 10). There was also evidence of a sire effect on the tail fin lepidotrich count, although the mode was 42 for all sires (Figure 10). Histograms showing data from all the eight family groups for each region/skeletal part are shown in Figures S1–S4.

3.3 | Various associations

A correlation analysis at the population level found numerous highly significant relationships. Most notably, for the vertebral counts, there was a significant negative association between abdominal and transitional vertebral counts (Figure 11). These trends were also mostly true within families, but sires a and b gave the strongest correlations for dam A while sires c and d gave the strongest correlations for dam B (Figures S5–S12). Total vertebral counts were positively associated with abdominal vertebral counts at the population level (Figure 11).

TABLE 1 Results from proportional-odds logistic regression for each trait.

Trait	Model rank[a]	Model terms	χ^2	*df*	*p*
Total vertebrae	1	Dam	53.0	2	<0.001***
		Sire	8.9	4	0.064
Abdominal	1	Dam	14.1	1	<0.001***
		Sire	11.3	3	0.010*
Transitional	1	Dam	17.8	1	<0.001***
		Sire	13.4	3	0.004**
Caudal	1	Sire	16.0	3	0.001**
Ural	1	Dam	18.7	1	<0.001***
Anal fin lepidotrichia	1	Dam	11.1	1	<0.001***
Anal fin pterigophors	1	Dam	17.2	1	<0.001***
Dorsal fin lepidotrichia	2	Dam	1.2	1	0.272
Dorsal fin pterigophors	2	Dam	0.7	1	0.404
Supraneurals	2	Sire	5.62	3	0.132
Tail fin lepidotrichia	1	Dam	45.7	1	<0.001***
		Sire	10.5	3	0.015**

[a] See Tables S1 and S2 for full ranking. If the top ranked model was the null model, then the second-ranked model was used.

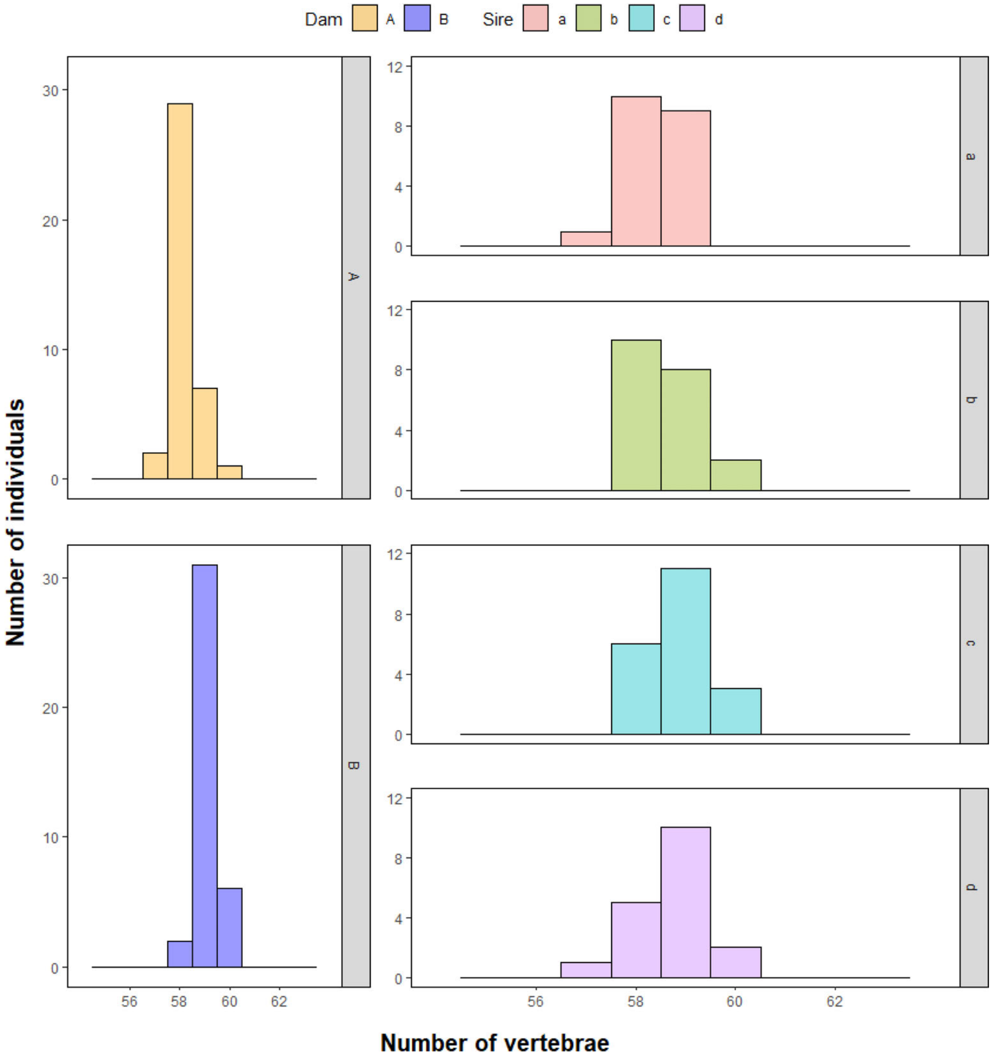


FIGURE 3 Histograms of total vertebrae count split by dams and sires. Both dam and sire were in the final model, but there was no interaction.

However, this trend was only obvious in some families, while in others the association was even reversed (Figures S5–S12).

Total vertebral counts showed a significant negative association with tail fin lepidotrich counts at the population level (Figure 11), but not at the family level (Figures S5–S12). There were significant negative associations between transitional vertebrae counts and anal fin pterygiophore and lepidotrich counts at the population level (Figure 11), and within families this association seem to depend on the sire more than the dam (Figures S5–S12). For example, for sire a the association was strong for both dams A and B, while for sire d it was not.

4 | DISCUSSION

The present study shows that the sequence of skeletogenesis varies between different post-cranial axial skeletal parts, and that there is a strong maternal effect on the number of total vertebrae and the tail fin lepidotrich counts.

4.1 | Sequence of formation in the post-cranial axial skeleton

Kryvi et al. (2017) described the developmental sequence of the different parts of the post-cranial axial skeleton in Atlantic salmon. Continuing this research, the present study revealed the sequence of formation within each skeletal part. For the vertebral column, the present study showed that the first chordacentrum to form was number 24, followed by number 58. Which chordacentrum forms first varies between teleosts. The first chordacentrum to form are number 1–2 (cranial) in sargo, *Anisotremus davidsonii* Steindachner 1876 (Watson & Walker Jr, 1992), number 2 (cranial) in sea bream, *Sparus aurata* L. 1758 (Faustino & Power, 1999), number 2–3 (cranial) in common dentex, *Dentex dentex* L. 1758 (Koumoundouros et al., 1999), number 3 (cranial) in Atlantic cod, *Gadus morhua* L. 1758 (Fjelldal et al., 2013; Sæle et al., 2017), number 2–4 (cranial) in long tooth grouper, *Epinephelus bruneus* Bloch 1793 (Iwasaki et al., 2018), number 1–4 (cranial) in turbot, *Scophthalmus maximus* L. 1758 (Tong et al., 2012), number 3 and 4 (cranial) in zebra fish, *Danio rerio* F. Hamilton 1822

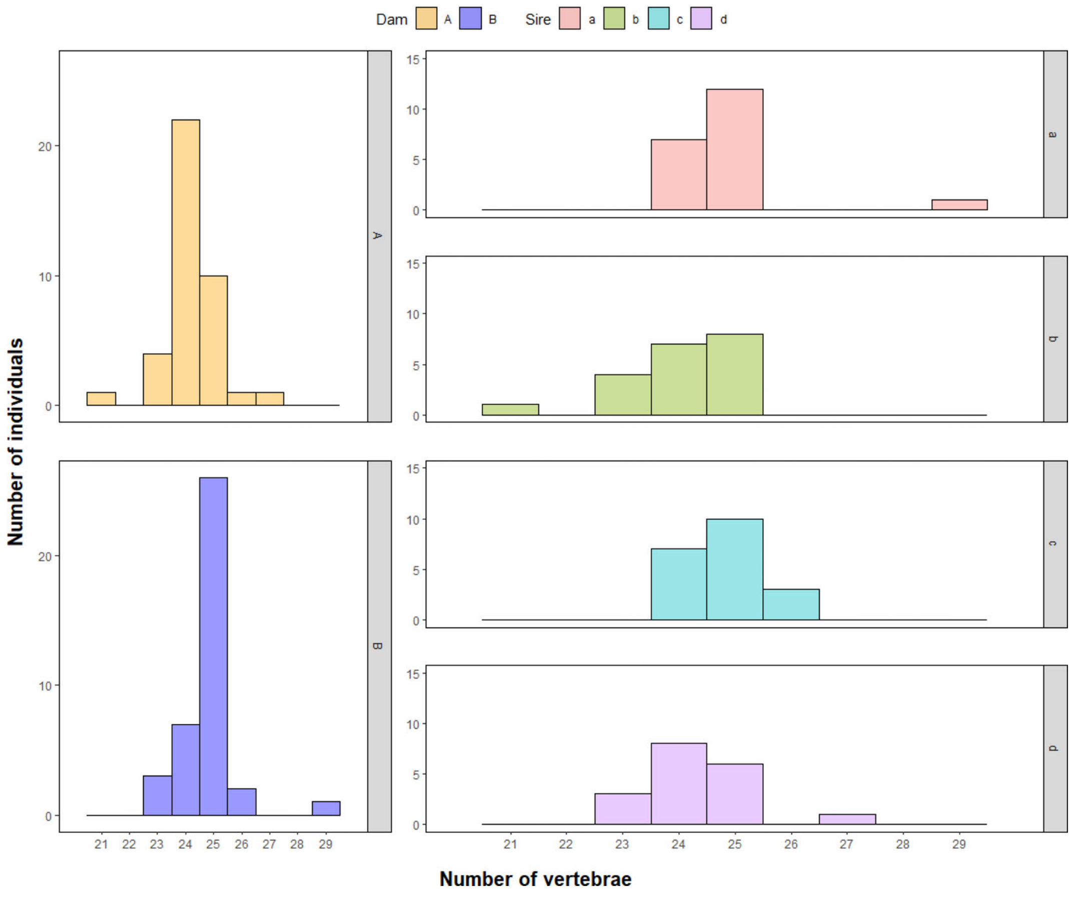


FIGURE 4 Histograms of abdominal vertebrae count split by dams and sires. Both dam and sire were significant, but there was no interaction.

(Bensimon-Brito et al., 2012; Bird & Mabee, 2003), at the border between the abdominal and caudal region in Atlantic halibut (*Hippoglossus hippoglossus* L 1758) (Lewis & Lall, 2006), and the preural centra in Atlantic thread herring, *Opisthonema oglinum* Lesueur 1818 (Richards et al., 1974). Similar to the present observation in Atlantic salmon, two initiation sites for chordacentra formation, the first one cranial and the second one ural, have also been observed in other species such as sargo, *Anisotremus davidsonii* Steindachner 1876 (Watson & Walker Jr, 1992), snook, *Centropomus undecimalis* Bloch 1792 (Potthoff & Tellock, 1993), sea bream (Faustino & Power, 1998), and common dentex (Koumoundouros et al., 1999). On the other hand, Richards et al. (1974) found that chordacentra formation started in the ural region and later in vertebra number 12 in thread herring.

The reason behind the development of the species-specific chordacentra initiation site is at present unknown but may be related to functional anatomy or phylogeny, or an interplay between these two. The inherited anterior to posterior sequence of development controlled by Hox genes (Ozernyuk & Schepetov, 2022), together with the selective forces caused by the physical environment where the fish are raised, may have created these species-specific developmental patterns (Cote et al., 2002). An interesting example is the initiation of chordacentra formation in turbot and halibut. The species have substantially different origin sites for chordacentra formation (Lewis & Lall, 2006; Tong et al., 2012) but belong to two closely related families of the order Pleuronectiformes, flatfishes (Chanet et al., 2020). Their diverging formation patterns may indeed be linked to the large differences in the physical and biological environment during early life development between the two species (Haug, 1990; Tong et al., 2012).

Development of the first chordacentrum is at somite number 24, which is the most common initiation site for the development of vertebral deformities during the freshwater life stage in farmed Atlantic salmon (Fjelldal et al., 2012). Several teleosts, including Atlantic salmon, start to form chordacentra in the ural region before the posteriorly advancing ossification of the vertebral column reaches the caudal complex, while it is vice versa in thread herring. This may suggest that selective forces caused by functional demands have framed the evolution of these developmental patterns. As such, functionally demanding vertebral regions may be most prone for deformity development under certain unnatural farming conditions. Formation of the first neural and haemal arch is at somite number 43, which is the most common initiation site for vertebral deformity development during the seawater life stage in farmed Atlantic salmon (Fjelldal et al., 2012). Based on the ontogenetic distance between the events, a rationale connecting them is, however, difficult to construct.

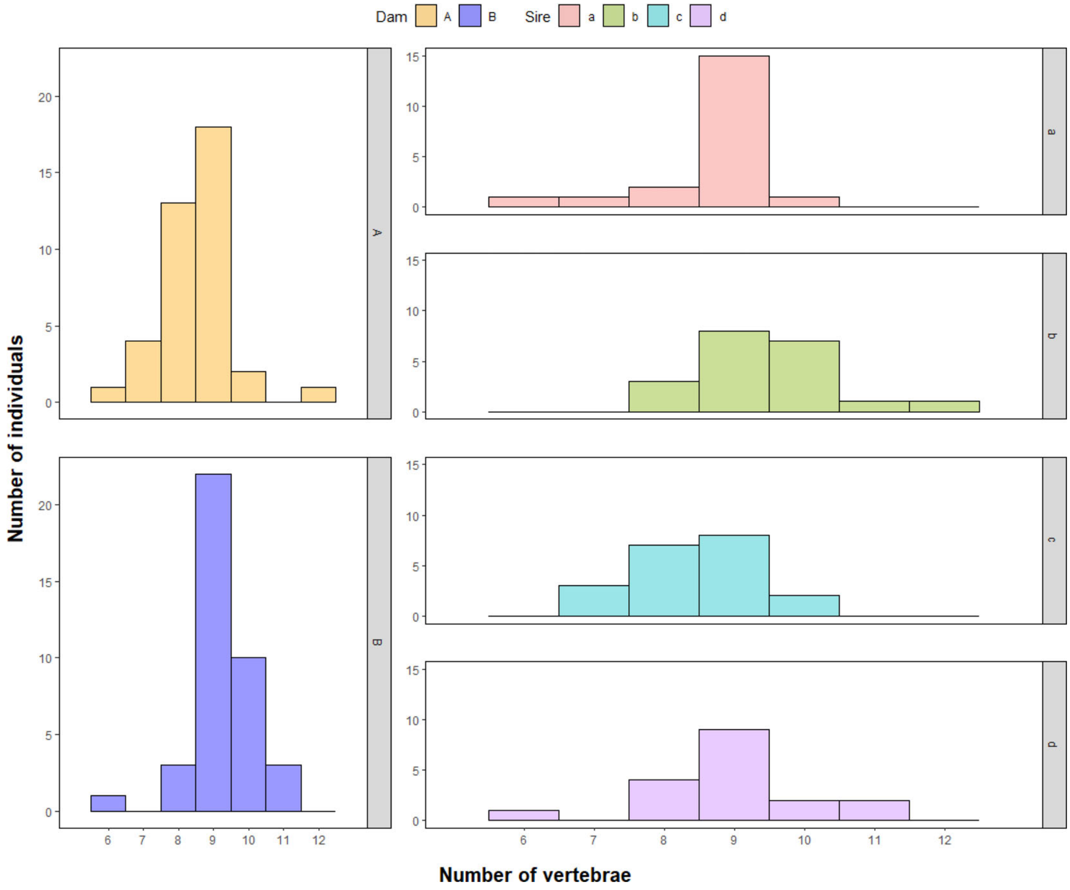


FIGURE 5 Histograms of transitional vertebrae count split by dams and sires. Both dam and sire were significant, but there was no interaction.

In the caudal fin complex, hypural 1 and parhypural are formed first in zebra fish (Bird & Mabee, 2003; Mabee et al., 2002) and sharp snout seabream, *Diplodus puntazzo* Walbaum 1792 (Sfakianakis et al., 2005), which was similar to the present study. Hypural 1 and hypural 2 appear first in the caudal fin complex of the white sea bream, *Diplodus sargus* L. 1758 (Koumoundouros et al., 2001), common pandora, *Pagellus erythrinus* L. 1758 (Sfakianakis et al., 2004), Senegal sole, *Solea senegalensis* Kaup 1858 (Gavaia et al., 2002), yellow catfish, *Pelteobagrus fulvidraco* J. Richardson 1846 (Huang et al., 2016), and Asian seabass, *Lates calcarifer* Bloch 1790 (Fraser et al., 2004). In black-head sea bream, *Acanthopagrus schlegelii* Bleeker 1854, both neural and hypural processes are the first bones to form in the vertebral column (Hu et al., 2019). The dorsal and anal fins starting to form at their cranial ends may have a functional application, allowing for further formation in a more “sheltered” environment caudally. The development of ribs starts in segment number 5, and the first supraneural to form is number 5 in zebra fish (Bird & Mabee, 2003; Mabee et al., 2002), while these bones start to form at numbers 3 and 10 in Atlantic salmon. The only skeletal parts that follow a strict anterior to posterior direction of development in Atlantic salmon are the ribs and epineurals. This may suggest that the inherited developmental pattern has overruled the selective forces imposed by the environment, or that these inputs have concerted during the formation of these bones.

4.2 | Inheritance of meristic variation in the post-cranial axial skeleton

There was a stronger maternal compared to paternal effect on number of total vertebrae in male offspring of Atlantic salmon. This agrees with Ando et al. (2017), who described a strong maternal effect on the number of total vertebrae in the pacific chum salmon (*Oncorhynchus keta* Walbaum 1792). Further, the present study showed a marked maternal effect on abdominal, transitional, ural, and total vertebrae counts, and a stronger paternal effect on caudal vertebrae counts. Ando et al. (2008) reported that the number of abdominal (including post-cranial, abdominal, and transitional vertebrae) and caudal vertebrae (including caudal and ural vertebrae) is governed by genetics in masu salmon (*Oncorhynchus masou masou* Brevoort 1856), without elaborating parental region-specific contributions. In medaka (*Oryzias latipes* Temminck & Schlegel 1846), variation in the number of vertebrae in wild populations is associated with variation in the abdominal region (Yamahira et al., 2009), which was shown to be

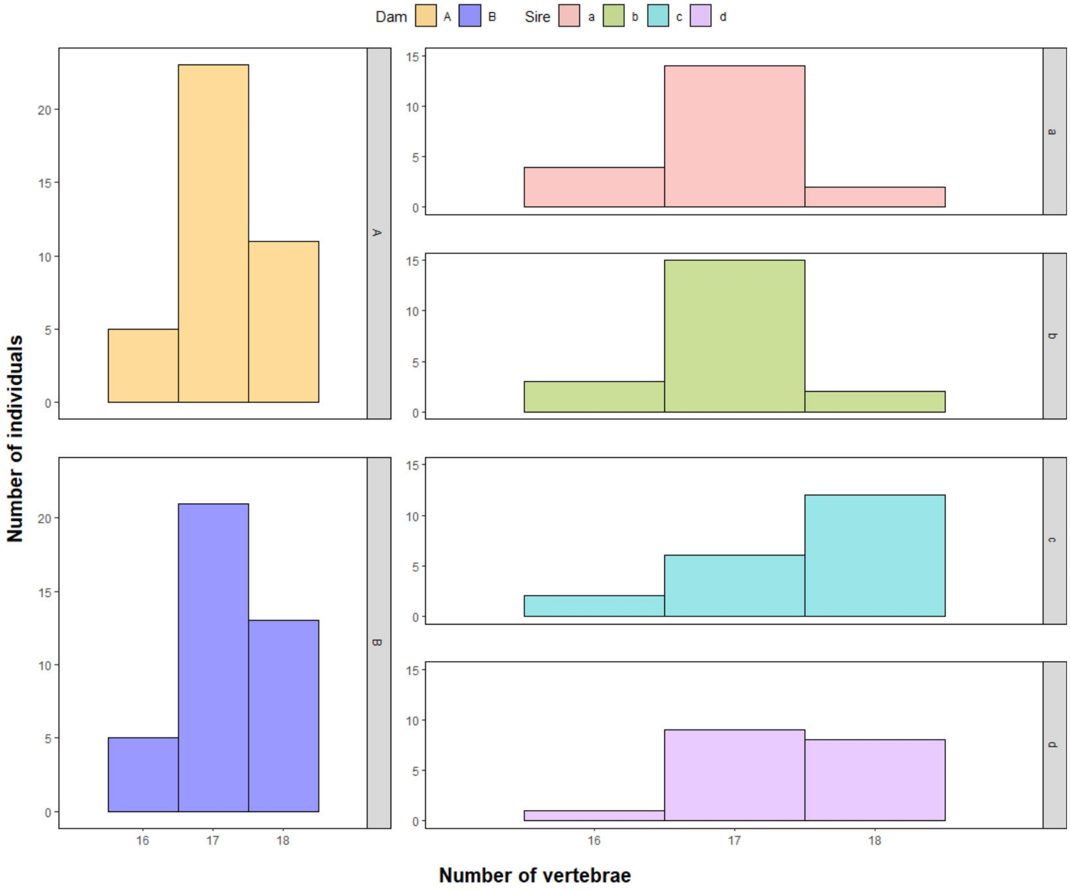


FIGURE 6 Histograms of caudal vertebrae count split by dams and sires. Only the sire was significant.

highly heritable in a laboratory study comparing populations from different latitudes (Kiso et al., 2012). These authors suggest that abdominal and caudal vertebrae are controlled by separate developmental modules in medaka. However, their study used mid-parent values and did not elaborate maternal versus paternal contribution. Indeed, Hermida et al. (2002) suggested that in three-spined stickleback (*Gasterosteus aculeatus* L. 1758) there is a maternal effect on caudal and abdominal vertebrae in the natural environment, and that it is to some extent impossible to rule out sex-limited inheritance for the latter. Lindsey (1962) postulated that variability in the number of abdominal vertebrae is strongly sex-limited and is transmitted between females in the three-spined stickleback. The present study compared different families that all contained genetically identical heterozygous all-male individuals that were created by crossing double-haploid homozygous fish. In both wild and farmed populations there is genetic diversity with a variable degree of heterozygosity. It is not clear if our findings are directly transferable to such fish, if crosses of heterozygous fish would produce similar significant results, or if offspring sex matters. Further examinations should elaborate this. Another factor that may complicate transferability of the present results to natural conditions is the environmental influence; a significant interaction between family and incubation temperature on total vertebrae number have been reported in chum salmon (*Oncorhynchus keta* Walbaum 1792) (Ando et al., 2011) and northern pike (*Esox Lucius* Linnaeus 1758) (Tibblin et al., 2016). Nonetheless, in support of the present findings, more recent studies have shown a significant genetic component for total vertebrae number in Atlantic herring (*Clupea harengus* Linnaeus 1758) (Berg et al., 2018) and indicated that stock enhancement programs affect the total vertebrae number in wild masu salmon (*Oncorhynchus masou* Linnaeus 1758) populations (Ando et al., 2019). Genomic research on 13 Nicaraguan Midas cichlid species (*Amphilophus* spp.) pointed out the potential for genomic co-segregation of the lateral line and vertebrae numbers on two chromosomes based on QTL analysis (Ehemann et al., 2024). In some species, variation in total vertebrae number may impact on body form, as observed in the neotropical fish *Rhoadsia altipinna* (Fowler 1911), where fineness ratio (ratio between standard length and body depth) accounted for 10.3% of the variation in vertebrae number (Aguirre et al., 2019).

We have described a positive association between the number of abdominal and total vertebrae, and a negative association between the number of abdominal and transitional vertebrae in the present study. There was a stronger maternal than paternal effect on these traits, and dam A produced higher counts for all of them compared to dam B. Hence, there is a maternal contribution to the number of vertebrae connected to the abdominal cavity, which may make this part of the body proportionally larger. This may represent a maternally driven selection towards a larger abdominal cavity in certain phenotypes, which may possibly enhance egg-bearing capacity. Interestingly,

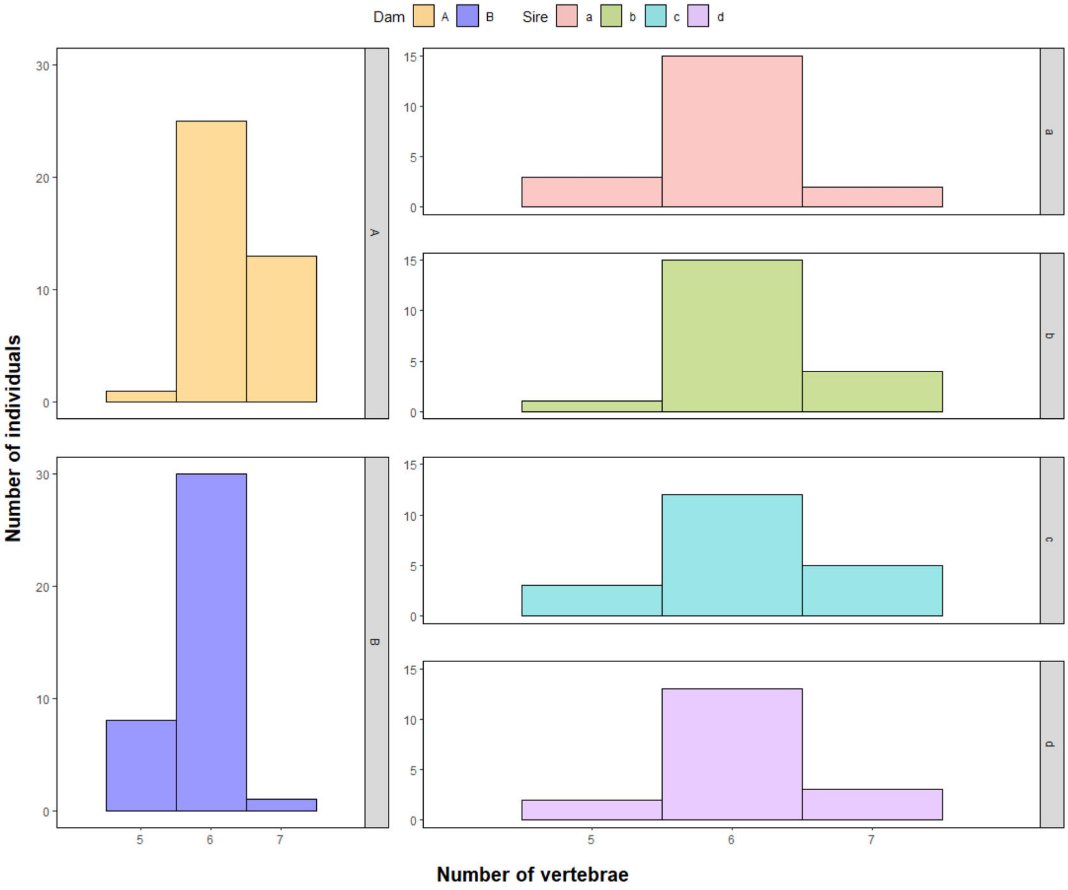
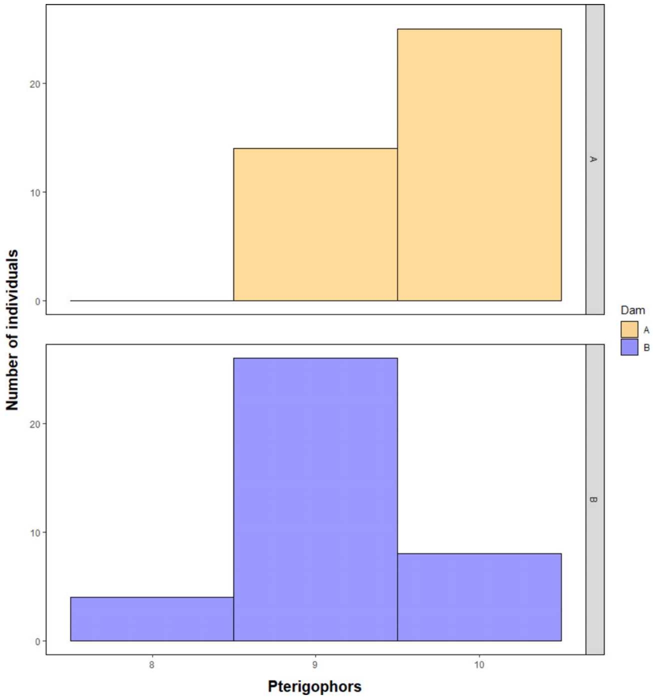


FIGURE 7 Histograms of ural vertebrae count split by dams and sires. Only the dam was significant.



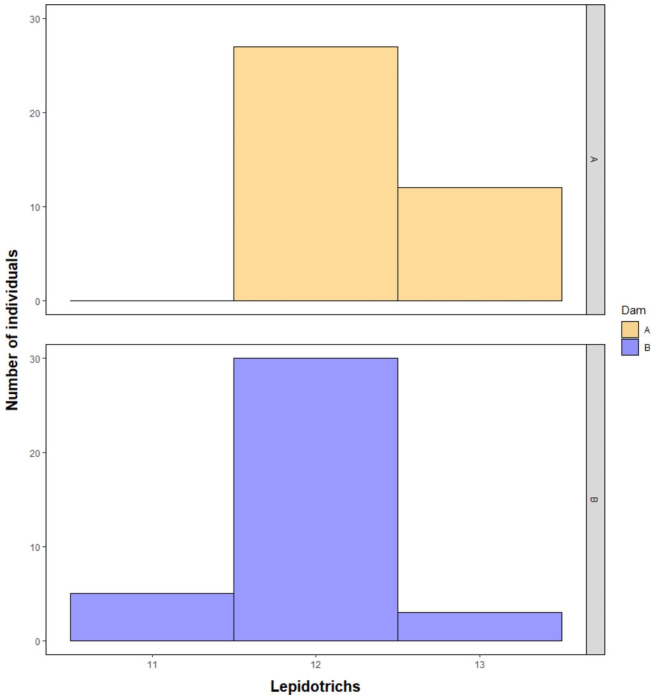


FIGURE 8 Histograms of anal fin lepidotrichia split by dam. Only the dam was significant.

FIGURE 9 Histograms of anal fin ray (lepidotrich) counts split by dam. Only the dam was significant.

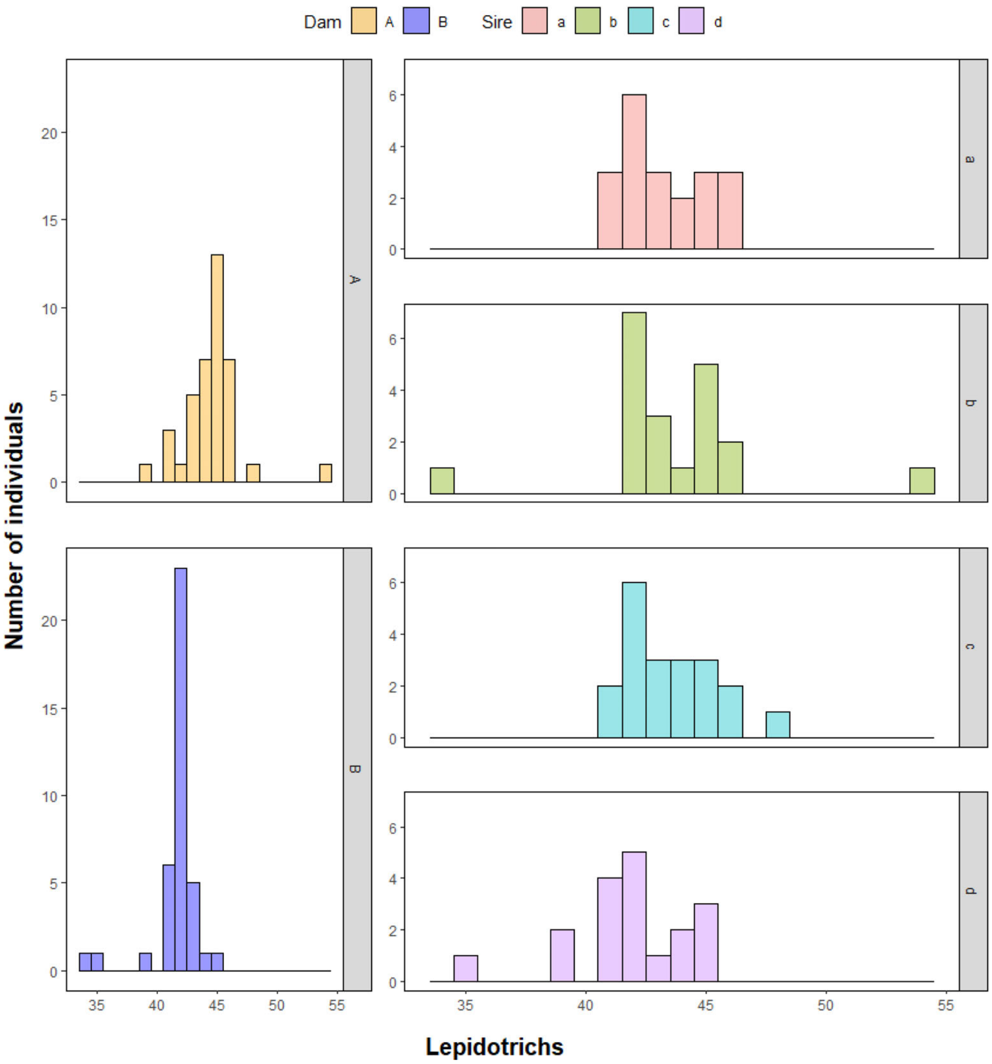
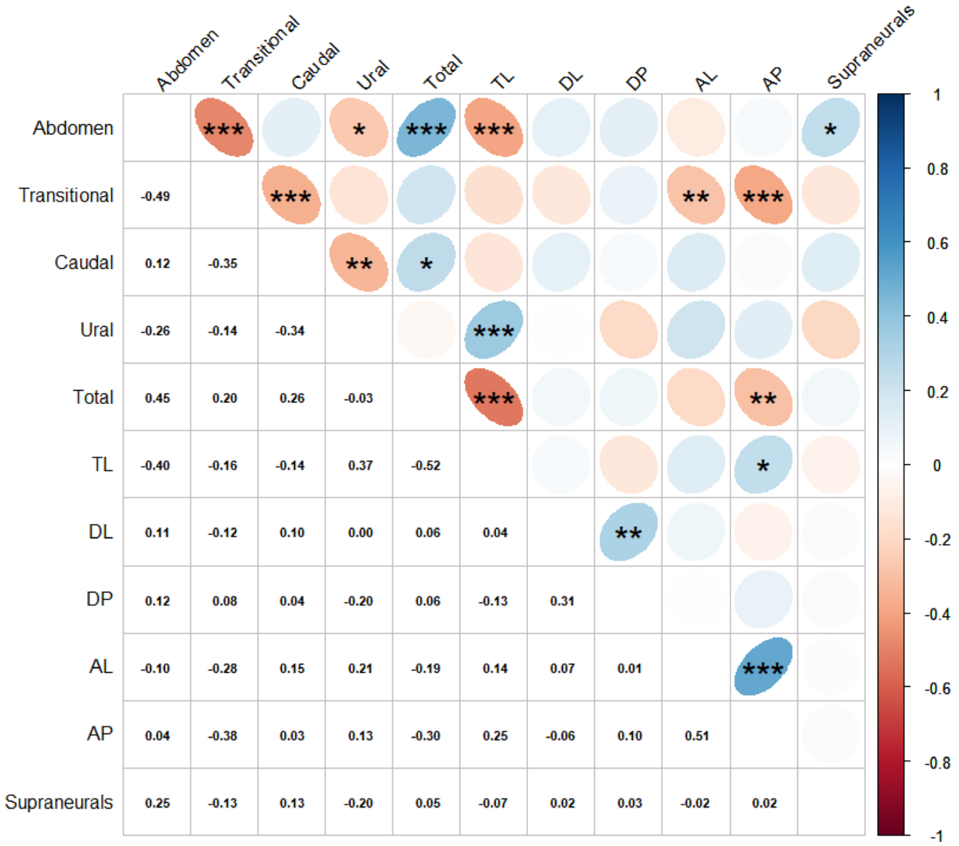


FIGURE 10 Histograms of tail fin ray (lepidotrich) counts split by dam and sire. Both dam and sire were significant, but there was no interaction.

the number of vertebrae, especially abdominal vertebrae, may be related to fecundity, as indicated in common roach (*Rutilus rutilus* L. 1758) (Komova, 2023), and naturally spawning early migrating chum salmon possess more vertebrae compared to later migrators within the same river system (Ando & Sato, 2018). The number of vertebrae and region-specific counts may also affect other traits that can affect fitness. In the three-spined sticklebacks, the ratio between the number of abdominal and caudal vertebrae has been shown to affect predation survival (Swain, 1992a, 1992b). In Arctic char (Salvelinus alpinus), vertebral number affected escape performance, but the regional identity of vertebrae was, however, not addressed in that study (Campbell et al., 2021) .

Compared to maternal, there was a weaker paternal contribution to the number of abdominal and transitional vertebrae. There were strong negative offspring correlations between the number of abdominal and transitional vertebrae when dam A was crossed with sires a and b, and when dam B was crossed with sires c and d. Dam A and sires a and b produced modes of 58 vertebrae, while dam B and sires c and d produced modes of 59 vertebrae. This may indicate that at the individual level, extra-abdominal vertebrae result in less transitional vertebrae or vice versa for certain mating combinations. A rational explanation for this mating specific pattern is at present difficult to construct.

There was a maternal effect on anal fin pterygiophores and lepidotrichia, and caudal fin lepidotrichia. Indeed the most dramatic difference produced in the present study was the modes of 45 in dam A and modes of 42 for dam B for caudal fin lepidotrichia. Interestingly, Beacham (1990) found a maternal effect on caudal fin width in chum salmon, without counting ray numbers. How fin size affects the swimming capacity within species is poorly understood. Nicoletto (1991) found no difference in critical swimming speed between male guppies (*Poecilia reticulata* W. Perters 1859) that differed in their caudal fin shape, but not caudal fin area. Webb (1973) found no effect of tail fin amputation on swimming kinematics or standard and active metabolic rate in sockeye salmon (*Oncorhynchus nerka* Walbaum 1792). Plaut (2000) found lower critical swimming speed and activity level in zebrafish with either no tail fin or a long tail fin compared to wild type. In the present study, caudal fin size was not assessed. There is no available literature linking intra-species caudal fin lepidotrich number to heritability, parental contribution, or functional applications. This



	Abdomen	Transitional	Caudal	Ural	Total	TL	DL	DP	AL	AP	Supraneurals
Abdomen		***		*	***	***					*
Transitional	-0.49		***						**	***	
Caudal	0.12	-0.35		**	*						
Ural	-0.26	-0.14	-0.34			***					
Total	0.45	0.20	0.26	-0.03		***				**	
TL	-0.40	-0.16	-0.14	0.37	-0.52					*	
DL	0.11	-0.12	0.10	0.00	0.06	0.04		**			
DP	0.12	0.08	0.04	-0.20	0.06	-0.13	0.31				
AL	-0.10	-0.28	0.15	0.21	-0.19	0.14	0.07	0.01		***	
AP	0.04	-0.38	0.03	0.13	-0.30	0.25	-0.06	0.10	0.51		
Supraneurals	0.25	-0.13	0.13	-0.20	0.05	-0.07	0.02	0.03	-0.02	0.02	

FIGURE 11 Correlation matrix of the general population (all families). The lower triangle contains the *r* values (from a Spearman's rank correlation) while the upper triangle is a visual representation of the strength of the relationships indicated by the size (stronger relationships are more elliptical) and color (blue for positive, red for negative) of the ellipses. The asterisks in the upper panel indicate tests which were significant; *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. AL, anal fin lepidotrichia; AP, anal fin pterygiophores; DL, dorsal fin lepidotrichia; DP, dorsal fin pterygiophores; TL, tail fin lepidotrichia.

should be further investigated. The present strong negative association between total vertebrae and tail fin lepidotrich counts further supports that there is a strong maternal effect on these traits. Indeed, dam A produced offspring with modes of 58 vertebrae and 45 tail fin lepidotrichia, while dam B produced offspring with modes of 59 vertebrae and 42 tail fin lepidotrichia. An increase in tail fin lepidotrich count in response to a lowering in vertebrae count or vice versa may be an evolutionary adaptation to maximize swimming ability. This could be especially important in anadromous Atlantic salmon, which relies on long-distance ocean migrations and maximum swimming performance during its freshwater life stage in rivers where it is challenged by waterfalls and high water current speeds.

5 | CONCLUSIONS

The initial site of formation is specific for each part of the post-cranial axial skeleton, with some inter-part similarities. The variation may reflect an interplay between the inherited anterior to posterior sequence of development and the selective forces caused by the physical environment. The results of the present investigation suggest a strong maternal effect on tail fin lepidotrichia and the number of total vertebrae in Atlantic salmon, and that an increased number of total vertebrae facilitates an increased number of abdominal vertebrae, and associates with lower tail fin lepidotrichia counts. These meristic changes may affect important fitness-related traits such as fecundity and swimming ability, highlighting that post-cranial axial skeletal meristic counts should be included in both ecological and aquaculture-based sciences on Atlantic salmon. Further research should explore possible interactions between incubation temperature and genetics on meristic variation in both isogenic and outbred strains of Atlantic salmon, and explore possible impacts of interbreeding between escaped farmed and wild Atlantic salmon.

AUTHOR CONTRIBUTIONS

M.S.: Methodology, validation, investigation, writing – original draft. T.W.K.F.: Validation, writing – review and editing, visualization, data curation, formal analysis. K.N.: Methodology, validation, investigation, writing – review and editing, visualization. A.J.P.P.: Project administration, funding acquisition, writing – review and editing. S.R.: Methodology, resources, writing – review and editing. T.J.H.: Methodology, resources, writing – review and editing P.E.W.: Conceptualization, methodology, validation, writing – review and editing. H.K.: Conceptualization, methodology, validation, investigation, writing – review and editing, visualization. P.G.F.: Conceptualization, methodology, validation, investigation, writing – original draft, visualization.

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SUPPORTING INFORMATION

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

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