Chapter

Sexual Maturation in Farmed Atlantic Salmon (*Salmo salar*): A Review

Patricia Rivera, José Gallardo, Cristian Araneda and Anti Vasemägi

Abstract

The sexual maturation of Atlantic salmon *Salmo salar* is a multifactorial process in which fish acquire somatic characteristics to reproduce. In salmon farming has been described a high variability in the trait age at maturation derived from wild reproductive strategies. Early maturation is a phenotype that generates serious economic repercussions on both, sea cage and on land-based aquaculture systems. In view of the challenges of this problem for the global salmon farming industry, it is essential to thoroughly understand the influencing factors of early and late maturation to find efficient alternatives for managing the phenomenon. This review briefly describes sexual maturation in *S. salar*, its variability in cultures, and the factors influencing the maturation age trait at the physiological, genetic and environmental levels. The control of early maturity through changes to the natural photoperiod and through the use of genetic markers are discussed.

Keywords: sexual maturation, *Salmo salar*, multifactorial, reproduction, cultures, variability, photoperiod, physiological, genetic markers, GWAS

1. Introduction

Sexual maturation in *S. salar* is a complex and multifactorial process whose purpose is to acquire the somatic and behavioral conditions necessary to perform reproductive functions. In both wild and domesticated populations, there is variability in the age at maturation – a characteristic known as a life history trait – which can occur at an early or late stage in both males and females. These reproductive strategies were adopted by wild congeners to increase their reproductive success, perpetuate the species, and promote population sustainability.

Some salmon farms worldwide, including large industries in countries such as Canada [1], land-based aquaculture systems [2], and others, have experienced significant economic losses associated with salmon presenting advanced maturation, either in the freshwater cycle or, with greater repercussions, in fattening stages prior to harvest. These losses occur because when maturation is reached, fish divert energy from body reserves to reproduction, resulting in salmon with a smaller body size and lower organoleptic quality of the fillet. During meat evaluation in processing plants, any degraded physical characteristic will result in a decrease in the commercial value of the fish.

The time and degree of maturation in *S. salar* are influenced by several factors, which can be intrinsic, such as genetic makeup, body composition and metabolic status, or environmental, and these factors can affect anatomical and physiological processes. Among environmental factors, photoperiod is considered a major determinant of the maturation of most cultured teleosts [3], and temperature influences the variation in age and size at maturity in salmonids [4].

Several strategies have been used by the industry to control early maturation in salmon cultures. Among these, photoperiod manipulation has been an alternative that has provided better results in terms of reducing the advanced-maturation phenomenon. Currently, thanks to knowledge regarding the genetic component of sexual maturation, new approaches are being investigated, such as molecular marker-assisted selection. Knowing that the goal of salmon farmers is to maintain salmon in an immature stage to preserve the quality of the product and ensure sustainable production, this review presents a summary of the following topics: life cycle and sexual maturation in *S. salar*; maturation variability in cultures; and physiological, genetic and environmental factors influencing maturation.

2. Life cycle of Atlantic salmon

Atlantic salmon is an anadromous species whose life cycle (**Figure 1**) in the wild can include a reproduction and rearing phase in freshwater and a growth and sexual maturation initiation phase in the ocean [5, 6]. In this general pattern, there are some alternative strategies, developed mainly by males, that can be very successful in the natural environment, such as, 1) sexual maturation in freshwater as precocious male parr; 2) sexual maturation of fish known as jacks, which mature prematurely in freshwater prior to sea transfer or which reach a body size of approximately 0.5 kg in the sea before maturation [7]; and 3) maturation of fish known as grilse, which reach maturity, with a body size of typically 2 to 5 kg, after 1.5 years in the sea [8] cited in [9]. In all the cases described above, reproduction and spawning occur in the autumn so that the eggs incubate in the gravel substrate during the winter and hatch after two or three months depending on the water

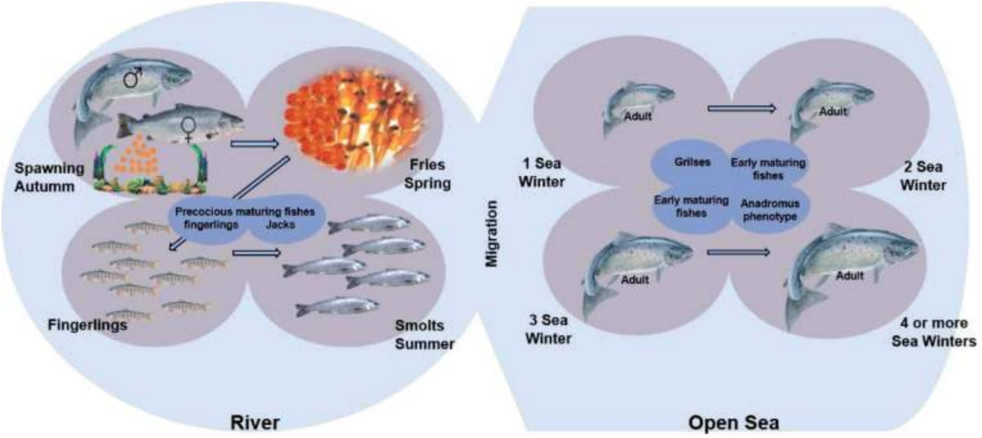

Figure 1.

Life cycle of Atlantic salmon. Both males and females of Atlantic Salmon, in the spawning season in autumn, fertilize and incubate eggs which, in spring hatch and will become fries. After a few months, the fries become to be fingerlings, and one to five years after hatching S. salar *juveniles typically descend as smolts to the ocean to feed and, return to the rivers of origin to a new cycle as adults. Early maturation could be presented in freshwater (precocious male parr); in freshwater prior to sea transfer (jacks), in the first sea winter after transfer to sea (grilse), and in a second or third winter (early maturation). While those adult salmon that mature after 4 or more years in the sea are known as anadromous or late maturing fish.*

temperature [10], so in some environments this process could be delay by the low temperatures of the water. One to five years after hatching, *S. salar* juveniles typically descend as smolts to the ocean to feed and, return with a high degree of fidelity to the rivers of origin to spawn and start a new cycle [11].

3. Maturation in domesticated populations of *S. salar* and its implications in production

The presence of different reproductive and maturation strategies among individuals within a wild population of Atlantic salmon has shown to reflect its genetic diversity [12]. That is, to maintain the natural sustainability of the species, sexual maturation in salmon occurs early or late in different proportions of individuals in both the freshwater and ocean environments [13]. This variability is common and is part of the life history of Atlantic salmon to perpetuate the species and maintain genetic diversity.

Variation in the maturation phenotypes beneficial to population survival in wild populations of Atlantic salmon can be undesirable in domesticated populations. For example, early maturation, especially in fattening stages prior to harvest, affects the profitability of commercial production because it is associated with the expression of secondary sexual characteristics [14]. Losses have also been observed due to the use of body reserves for gamete formation [9] and to decreased growth and degradation of fish meat [15]. These circumstances together hinder not only the profitability of fish farms but also the management, care, and survival of animals [14].

The strong negative impacts caused by the presence of high proportion of early maturing animals are especially noticable in large-scale commercial operations. [2] describe a serious production disaster in a land-based aquaculture system in which 80% of male salmon matured earlier than the harvest time, with recorded weights of 4 to 5 kg, forcing the fish farmers to close their facilities. In economic terms, [1] estimated significant losses of up 4,4% which represented between 11 to $24 million in 2002 in the salmon industry of New Brunswick, Canada, due to this phenomenon. As noted in both cases, early maturation often has irreparable economic consequences.

The incidence of the early maturation of individuals in domesticated populations is influenced by production goals because the industry seeks to obtain animals with a greater body weight in less time. [1] describe the main risk factors that cause early maturity in salmon; these factors include the intensity of feeding diets with a high fat content, the exaggerated manipulation of photoperiod regimes to delay spawning, and differences in water temperature, among others. As noted, the management of cultures in controlled environments contributes to the risk of early maturation, which is why fish farms find it necessary to resort to other control alternatives.

4. Physiology and factors that influence maturation in Atlantic salmon

Maturation is a process intrinsically governed by genetic makeup, body composition and metabolic status and by environmental factors [16]. Animals exhibit biological rhythms that are usually in step with environmental factors, which are also known as proximate and ultimate causes or factors [17]. Proximate factors affect anatomical and physiological processes, and ultimate factors underlie adaptation and diversification [18]. Therefore, integration of the totality of these signals in the brain is the main trigger for maturation and reproduction.

Of the environmental factors that can be categorized as proximate, photoperiod is the most important and is considered the main determinant of the maturation of most cultured teleosts [3], it has effects such as delayed onset of sexual maturity in salmonids [16] and increased maturational steroids and gonadal development [19]. In contrast, the temperature influences the variation in the age and size at maturity in salmonids [4] and can alter the time of ovulation [20]. Finally, inter and intra-specific competition maximize reproductive success within the limitations imposed by the opposite sex, the environment and phylogeny [21]. Together, all these factors modulate the maturational and reproductive patterns of salmon. The integration of all these signals when processes in the brain of the fish, especially seasonal changes in the photoperiod, triggers the beginning of maturation and modulates the seasonal patterns of endocrinological activity regulating the cyclic process, whose purpose is to achieve optimal reproduction. Notably, reproductive events occur at times during which salmon determine the survival of their progeny by ensuring the hatching of their larvae in seasons with abundant food resources [22].

In salmonids, the pineal gland and the brain play important roles in the activity of the reproductive axis because they develop light-perceptive, integrative and executive functions [23]. Light perception in these fish occurs through their photoreceptor organs, which transmit an electrical message at night that results from the release of melatonin [24]. The directive derived from this is the secretion of gonadotropin-releasing hormone (GnRH) by hypothalamic neurons and, subsequently, the secretion of gonadotrophins, follicle-stimulating hormone (FSH) and luteinizing hormone (LH), which regulate gametogenesis and gonadal steroidogenesis [3].

The intrinsic factors acting on the physiology of maturation include genetic component. Gene expression of the *vgll3* and variation together with other genomic regions associated with the hypothalamic pathway are analyzed in [25–27]. Based on the results from these studies, it could be suggested the aspects conducive to the maturation process, beginning with the expression of the *ywhab* gene, which contributes to the cytoplasmic retention of the *yap/taz* gene complex, which in turn acts as a cofactor for the expression of the *tead3* gene, ultimately interacting with the *vgll3* gene for the translation of the Vgll3 protein. The vgll3 gene has two alleles; the early maturity allele is expressed in Sertoli cells in males and in granulosa cells in females and acts in cell proliferation processes [27]. However, further research is still needed to understand the biological functions attributed to the genomic regions associated with maturation.

In summary, in a physiological context, sexual maturation can be understood as the process in which an animal begins the development of reproductive competencies through the integration of intrinsic and extrinsic factors. The maturational process is accompanied by a cascade of hormone secretion that modulates gonadal function in specific stages prior to reproduction, where the action of FSH occurs in early stages of gametogenesis, promoting the synthesis of sex steroids for spermatogonial proliferation in males and the progression of vitellogenesis in females and, subsequently, LH acts in the formation of maturational steroids [3].

5. Control of maturation in farmed Atlantic salmon

During fattening at sea, salmon must be maintained in an immature stage to preserve the quality of the product and ensure a good selling price. Therefore, various strategies have been implemented that help mitigate sexual maturation. For example, a common practice, but only effective in the short term, is eliminating or discarding early maturing males prior to entering the sea. Other alternatives are, for example, those described by [16], who cite, the induction of polyploidy mainly triploidy, modification of genes and the manipulation of environmental factors, especially photoperiod and temperature as [19]. Finally, recent findings regarding genomic regions that govern sexual maturation in Atlantic salmon [28] have shed light on the genetic determinants of this trait. Next, the use of photoperiod and genetic markers for the control of early sexual maturation is discussed in more detail.

5.1 Control of early maturation by photoperiod in marine cages and land-based aquaculture systems

Atlantic salmon marine cage aquaculture centers work with photoperiod protocols that seek to reduce the fish's perception of seasonal changes in photoperiod, mainly the decrease in daylight hours from summer to winter, thus inhibiting maturation. Examples of reductions in early maturation in cultures with different photoperiod regimes include the study by [29], who work with one-year-old Atlantic salmon smolts in the northern hemisphere treated with three different photoperiod regimes between January to July, with what, the proportion of sexually maturing fish was significantly lower among both sexes, from 91 to 9% in females and from 74 to 16% in males, in the groups treated from January with natural light + continuous additional light which was not switched off during daytime and was supplied by a 1300-W quartz halogen light. Additionally, in a study by [15], similar results were obtained, with 50% maturation in salmon reared under natural light and only 0.8% in males treated with artificial light for 9 months. More recently, the effectiveness of different alternative sources of artificial light has also been investigated. For example, [30] investigated the incidence of early sexual maturation in a culture of *S. salar* subjected to continuous artificial light, including five different LED light intensities, a single light intensity from a metal halide source and a control treatment with natural light; the results indicated that sexual maturation in males (6.1% under natural light) was arrested uniformly at all intensities. With this, the usefulness of this alternative light source on the control of maturation was confirmed, and widely used in fattening at sea.

The advancement of land-based aquaculture technologies has allowed salmon to complete the life cycle fully in these systems, but early maturation has been reported as a significant problem [19]. To address this issue, several studies have evaluated the efficacy of photoperiod manipulation to control early sexual maturation in these systems. For example, [31] showed that compared with Atlantic salmon exposed to continuous light for 24 hours during the first year, Atlantic salmon exposed to a reduced photoperiod of 18 hours of light from the first feeding to 1 year after hatching in a freshwater recirculation aquaculture system (RAS) showed a significantly higher proportion of mature males despite regimes of photoperiod, so fishes sampled at 19-months, were 50.0% grilse in the 18 h group and 33.3% grilse in the 24 h group. Additionally, [19] showed that the combination of spectral composition, photoperiod and light intensity can be used effectively to suppress or delay the gonadal development of Atlantic salmon reared in RAS. In summary, considerable number of studies demonstrate that photoperiod can be used effectively for the control of early maturation in both marine cages and land-based aquaculture systems.

5.2 Control of early maturation by genetic markers

Age of maturation in Atlantic salmon is a heritable trait so it should be possible to prevent early maturation using selective breeding [32–34]. Early records of high heritability on age at maturation (0.48 ± 0.20) and therefore great opportunity to control early maturation in Atlantic salmon were described from the mid-1980s [32]. High heritability values are usually expressed as large differences in the proportion of grilse between families of the same population. However, the systematic elimination of grilse in domesticated populations did not generate the expected results for reasons that will be explained later. This led, during the growth of the Atlantic salmon aquaculture in the 1990s, to the elimination of populations characterized as having high levels of grilse. More recent studies confirm that the age at sexual maturation [14] or some associated traits such as maturation in fresh water [6] or the proportion of grilse [35] have from medium to large heritable component and that there are significant differences between populations.

With the identification of the first genetic markers associated with the age of maturation trait in Atlantic salmon [14, 22], not only has a genetic explanation emerged for the variation previously described in early sexual maturation but foundations have also been laid to initiate more effective control of early maturation through the selection of fish that possess late-maturing genotypes (**Table 1**). The seminal studies of [14, 22], first allowed recognizing that there is a major/effect locus that controls the age of maturation, which has sex-dependent dominance and favors early maturation in males and late maturation in females [22]. This phenomenon may partially explain the great diversity of reproductive strategies observed in *S. salar*, particularly in male precocious parr, jacks and grilses. In addition, this phenomenon may also explain why the phenotypic elimination of early males does not have an impact on the control of early maturation in the long term, as heterozygous females can maintain the early maturation allele and pass it to their offspring. Those authors also identified that the locus with the largest effect on chromosome 25 is associated with the *vgll3* gene (vestigial-like family member 3 gene). This gene explained between 33 and 39% of the variation in age at maturation, an unexpectedly large proportion for a highly complex trait [14, 22].

In addition to abovementioned works, several genome-wide association studies (GWAS) and whole-genome sequencing studies (WGS) have identified additional genetic variants associated with sexual maturation in different wild and domesticated salmon populations. For example, [35], identified another quantitative trait locus (QTL) associated with the age of maturation in North American wild salmon populations; this marker is located on chromosome 6 and explained 6% of the variation in the early maturation phenotype. They also described that the frequency of the early genotype of the *vgll3* gene is lower in this population, contrary to that observed in European populations in which the early genotype is quite common. In turn, [28] reported contrasting results demonstrating that the *vgll3* gene was not associated with maturation in females in a domesticated population, known as Mowi, suggesting that other unidentified genomic regions control the age of maturation. More recently, based on the most extensive GWAS analysis in Atlantic salmon to date, [34] found significant associations with age of maturation in 28 of 29 chromosomes, including two very strong signals that spanned the regions of genes *six6* and *vgll3* on chromosomes 9 and 25, and this study for early maturation demonstrates that using very large sample sizes it is possible to reliably identify loci with small effect.

Regarding the molecular action of these variants on the physiology of maturation, there are several hypotheses related mainly to the *vgll3* gene. *Vgll3* is a regulator of adiposity in vertebrates [38]. Because the fat reserve level is considered a key element in the control of the initiation of maturation [39], its association with the age of maturation in Atlantic salmon seems clear and direct. The *vgll3* gene has two missense mutations strongly associated with age at maturation at amino acids 54 and 323 [14]. The haplotype associated with late maturation (e.g., 3 sea winters) codes for the amino acids threonine (Thr) and lysine (Lys), while those associated with early maturation (1 sea winter) code for methionine (Met) and aspartic acid (Asp). To date, it is unknown how the other markers, such as SNPs found in the *ndufs4*, *rora*,

Population/ Strain	Origin	Gene	Chr	Applied statistics	Method used	Reference
Wild	Norway	vgll3, akap11	Ssa25	Logit model	GWAS	[22]
		six6	Ssa09			
	Norway	vgll3, chmp2B, akap11	Ssa25	Cochran–Mantel–Haenszel test (CMH)	GWAS	[14]
	France	vgll3, akap11	Ssa25	Latent environmental threshold model (LETM)	Genotyping by sequencing and linkage map	[26]
Mowi	Canada	E2F4, MDH, PQLC2, PGRC1, SYAP1, FRA10AC1, PAPL, 14–3–3 beta/alpha	Ssa10, Ssa02, Ssa13, Ssa16, Ssa28, Ssa01, Ssa01	Mixed model and scoring tests	GWAS	[36]
Mowi	Norway	vgll3, mst1, nf2, tead3, ywhab, taz	—	—	qPCR	[14]
AquaGen					Analysis of global gene expression with RNAseq	[27]
Saint John-SJR	Canada	ropn1	Ssa21	Mixed model and principal components analysis	GWAS	[35]
SALTAS	Tasma-nia	lefty2, adpgk, scrib, ppp1r9a, pou6f2, cfap299, slitrk6, smarcd3, maggi2, picalm, ctnna2, rapgef2, cldn4, caln1, tsku, ser1, nlrp12	Ssa9, Ssa29, Ssa14, Ssa24, Ssa17, Ssa10, Ssa11, Ssa09, Ssa04, Ssa05, Ssa01	Mixed linear method	GWAS	[6]
Neva River	Finland	arhgap6e, akap11a, yap1 rd3l	—	—	NanoString transcription profiling	[37]
AquaGen	Norway	ndufs4, rora, cntn4	Ssa15, Ssa16, Ssa22	Mixed linear model	GWAS	[34]

Table 1.
Genes associated with age at maturation in wild and domesticated populations of Salmo salar.

cntn4 genes [34], influence the process of sexual maturation. Therefore, it is essential to continue functional genetic research to fill this knowledge gap in the future.

6. Conclusions

Early maturation is a serious problem for fish farms due to the economic losses, especially in periods close to harvest. Faced with this problem, various control strategies have been used, with photoperiod manipulation on sea cage being widely used in Atlantic salmon. In addition, triggered by fast development of the field of genomics, and based on growing knowledge on genetic components of sexual maturation, the genetic control of maturation is actively being implemented in selective breeding programs. The integration of both strategies should allow progress towards an effective control of early maturation in salmon aquaculture, both in marine aquaculture and in land-based aquaculture.

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Conflict of interest

The authors declare that they have no conflicts of interest.

Author details

Patricia Rivera[1], José Gallardo[1]*, Cristian Araneda[2] and Anti Vasemägi[3]

1 Laboratory of Genetics and Genomics Applied of Aquaculture, Pontificia Universidad Católica de Valparaíso (Pontifical Catholic University of Valparaíso), Chile

2 Faculty of Agronomic Sciences, Department of Animal Production, Laboratory of Genetics and Biotechnology in Aquaculture, University of Chile, Santiago, Chile

3 Department of Aquatic Resources, Swedish University of Agricultural Sciences, Drottningholm, Sweden

*Address all correspondence to: jose.gallardo@pucv.cl

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