Maturation in Atlantic salmon (*Salmo salar*, Salmonidae): a synthesis of ecological, genetic, and molecular processes

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Abstract

Over the past decades, Atlantic salmon (*Salmo salar,* Salmonidae) has emerged as a model system for sexual maturation research, owing to the high diversity of life history strategies, knowledge of trait genetic architecture, and their high economic value. The aim of this synthesis is to summarize the current state of knowledge concerning maturation in Atlantic salmon, outline knowledge gaps, and provide a roadmap for future work. Our summary of the current state of knowledge: 1) maturation in Atlantic salmon takes place over the entire life cycle, starting as early as embryo development, 2) variation in the timing of maturation promotes diversity in life history strategies, 3) ecological and genetic factors influence maturation, 4) maturation processes are sex-specific and may have fitness consequences for each sex, 5) genomic studies have identified large-effect loci that influence maturation, 6) the brain-pituitary-gonadal axis regulates molecular and physiological processes of maturation, 7) maturation is a key component of fisheries, aquaculture, conservation, and management, and 8) climate change, fishing pressure, and other anthropogenic stressors likely have major effects on salmon maturation. In the future, maturation research should focus on a broader diversity of life history stages, including early embryonic development, the marine phase and return migration. We recommend studies combining ecological and genetic approaches will help disentangle their relative contributions to maturation. Functional validation of large-effect loci should reveal how these genes influence maturation. Finally, continued research in maturation will improve our predictions concerning how salmon may adapt to fisheries, climate change, and other future challenges.

Introduction

Sexual maturation (hereto forward maturation, **Box 1**) is a key process necessary for reproduction in a variety of organisms. Maturation encompasses a variety of developmental, physiological, and behavioral processes ultimately leading to reproductive capacity. Maturation processes are energetically costly, and therefore maturation involves trade-offs with other fitness components such as growth and survival (Bernardo, 1993; Roff, 1993; Stearns, 1992). It is well known that a variety of environmental factors can influence maturation and some, such as dietary requirements for normal reproductive development, are ubiquitous. Recent research has shed light on how maturation is shaped by the underlying genetic architecture demonstrating that key molecular pathways are shared among a variety of vertebrate species (Barson et al., 2015; Laan et al., 2002; Liang et al., 2016). Currently, maturation research is flourishing and a wide variety of studies aimed at understanding the relative contributions of ecological and genetic factors on maturation processes are underway.

The timing of maturation (**Box 1**) contributes to the remarkable variation in the life history strategies of organisms (Healy et al., 2019) and is highly variable both within and among fishes (He & Stewart, 2001). Time from birth to maturity can be as short as three weeks in turquoise killifish, *Nothobranchius furzeri* (Vrtílek, Žák, Pšenička, & Reichard, 2018), while spiny dogfish, *Squalus acanthias*, can take over 35 years for half of the adults to mature (Saunders & McFarlane, 1993). Maturation may also be highly variable within and among populations due to various ecological and genetic influences (e.g., Reznick, Bryant, & Holmes, 2006) and the presence of alternative reproductive strategies (Gross, 1996; Taborsky, 2008). Salmonids, in particular, exhibit high variation in the timing of maturation within species and this variation is

Box 1. Definitions

Alevin: Recently hatched juveniles that still retain a yolk sac.
Condition factor: The relationship between body length and somatic mass used as a proxy for nutritional status and health.
Freshwater age: The amount of time an individual spends in fresh water prior to smoltification, measured in years. Also known as river age or smolt age.
Fry: Recently hatched, free-swimming juveniles that have absorbed their yolk sac and have begun to feed independently.
Genome-wide association study (GWAS): Study using a set of molecular markers (most often SNPs) covering the entire genome aiming to identify genetic variant(s) associated with a phenotypic trait.
Grilse: Adult that has returned to fresh water to spawn after spending one winter at sea.
Kelt: An adult individual that has recently spawned, often in poor condition.
Maturation: Developmental, physiological, morphological, and behavioral processes leading to reproductive capacity.
Mature male parr: Male parr with mature gonads capable of reproduction. Also known as precocious parr.
Parr: Juveniles that are independently feeding in fresh water. Commonly identified by vertical stripes and colored spots.
Post-smolt: A marine-phase adult that has spent less than one winter in the marine environment.
Puberty: Development of mature gonads and gametes and other secondary sexual characteristics.
Quantitative trait locus (QTL): A locus that correlates with phenotypic trait variation in a population.
Repeat-spawn: Marine-phase adults that spawn in two or more years. Also known as previous-spawner or iteroparous adults.
Return migration: Returning from the marine environment to fresh water to spawn after a variable number of years at sea. Also known as spawning migration.
Sea age: The amount of time an individual spends in the marine environment prior to returning to fresh water to spawn, commonly measured in sea winters (SW). Also known as sea age at maturity. Individuals that spend a portion of their life at sea before returning to spawn are called anadromous adults.
Single nucleotide polymorphism (SNP): A molecular marker representing variation in a single base-pair of DNA. Currently the most commonly used type of molecular marker.
Smolt: A parr that has undergone smoltification to migrate from fresh water to the marine environment.
Smoltification: The physiological, morphological, and behavioral processes enabling transition from fresh water to the marine environment.
Spermiation: Late stage of spermatogenesis when mature sperm are released from Sertoli cells.
Timing of maturation: Age at which an individual reaches reproductive capacity. Also known as age at first reproduction.

responsible for the remarkable life history diversity in this family of fishes (Stearns, 1992).

Atlantic salmon, (*Salmo salar* L. 1759, Salmonidae) is an emerging model system for maturation research in fishes and other vertebrates (**Box 2, Fig. 1**). Life history traits vary widely across populations and latitudes) and are particularly variable in landlocked populations (Hutchings et al., 2019). Atlantic salmon exhibit high diversity in life history strategies due, in part, to considerable variation in the timing of maturation and the number of reproductive episodes (iteroparity *vs.* semelparity) and the potential for males to participate in reproduction at the parr stage (Einum, Thorstad, & Næsje, 2002; Erkinaro et al., 2019; Hutchings et al., 2019; Jonsson & Jonsson, 1993; Jonsson & Jonsson, 2011; Thorpe, 2007). For example, up to 120 different There are also a number of well-monitored natural systems that provide detailed long-term data on maturation strategies and/or reproductive success over the distribution range of the species (Bacon et al., 2015; Chaput et al., 2018; Erkinaro et al., 2019; Jonsson, Jonsson, & Hansen, 1990; McGinnity et al., 2003)life histories have been reported among anadromous Atlantic salmon in a single river across a 40 year time series (Erkinaro et al., 2019). Maturation in Atlantic salmon is strongly influenced by ecological and genetic factors that affect the duration of particular life stages (Barson et al., 2015; Good & Davidson, 2016; Jonsson & Jonsson, 2011). Taken together, these features make Atlantic salmon an excellent system for addressing questions concerning the causes and consequences of variation in maturation (Barson et al., 2015; Dodson, Aubin-Horth, Thériault, & Páez, 2013; Jonsson & Jonsson, 2011; Stearns, 1992).

Atlantic salmon have a number of additional key features that make them an appealing species for maturation research. For instance, the economic importance of the species means that hatchery facilities for common-garden rearing and controlled treatments are abundant

(Fleming, Jonsson, Gross, & Lamberg, 1996; Skaala et al., 2019).

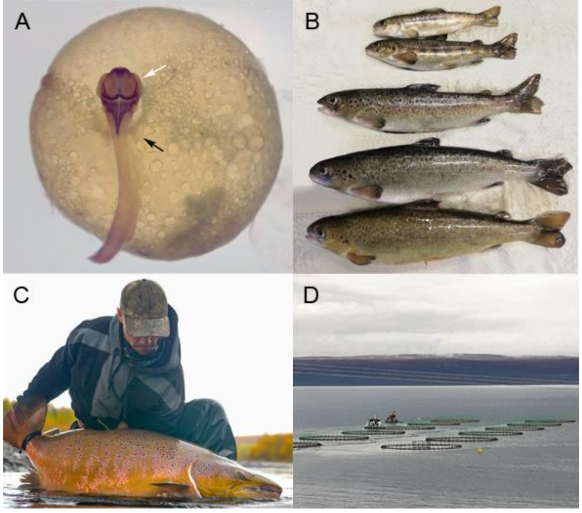

Fig. 1. Atlantic salmon in maturation research. A) Slow development times and large embryo size make Atlantic salmon a good model system for developmental biology. Pictured an Atlantic salmon embryo from the eyed-egg stage stained for the expression of the gene notch1b, which is seen in the developing central nervous system (white arrow indicates to eye, black arrow indicates pectoral fin). Image by J. Moustakas-Verho. B) Atlantic salmon show remarkable life history variation. Two year-old male mature parr (top two) represent an alternative reproductive strategy and are smaller than mature post-smolt males (bottom three) of the same age reared in common-garden conditions. Image by A. House. C) Maturation affects a variety of life history traits including body size and reproduction. Long-term monitoring of natural populations can aid conservation and management programs. Image by M. Ellmen. D) Atlantic salmon are an economically important species. Maturation research may help to increase sustainability of exploited fish stocks and yield in commercial aquaculture. Image by K. B. Mobley.

Further, genomic resources for this species are well-advanced, with a high quality genome assembly (Lien et al., 2016), commercially-available single nucleotide polymorphism (SNP) arrays (Barson et al., 2015), and ongoing initiatives to improve functional genome annotation (Macqueen et al., 2017). Finally, historical scale archives containing up to hundreds of thousands of samples are available for a number of populations. These scale archives provide access to historical composition of life history variation as well as genetic material (Johnston et al., 2013; Nielsen & Hansen, 2008; Perrier, Guyomard, Bagliniere, Nikolic, & Evanno, 2013) (**Fig. 2**).

Understanding maturation in Atlantic salmon has a number of practical benefits. Atlantic salmon aquaculture is a multi-billion dollar industry where early maturation in cultivation results in significant economic losses (Good & Davidson, 2016). Further, wild populations of Atlantic salmon have significant socio-economic importance: they are an important component of indigenous cultures and artisanal fisheries (COSEWIC, 2010; Lam & Borch, 2011). Atlantic salmon are also a primary target of recreational and commercial fisheries that can bring significant income to remote regions (Pokki, Artell, Mikkola, Orell, & Ovaskainen, 2018). For example, the annual value of recreational fishing trips to a single remote Atlantic salmon river system have been estimated to range from € 2.6 to 3.7 million (Pokki et al., 2018). Moreover, information concerning the timing of maturation is needed for developing accurate models for sustainable recreational and commercial fisheries (Kuparinen & Hutchings, 2017, 2019; Kuparinen & Merilä, 2007; Oomen et al., 2020) and for predicting evolutionary change as a result of exploitation and climate change (de Roos, Boukal, & Persson, 2006).

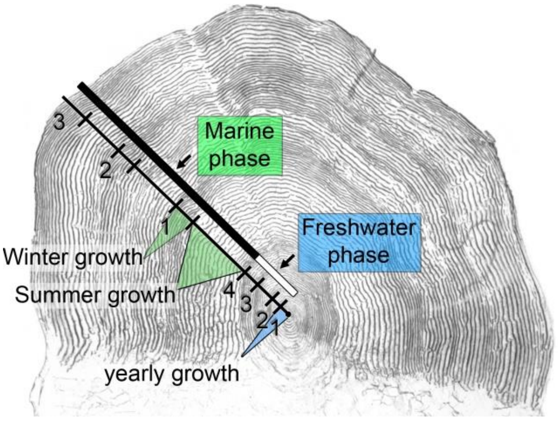

Fig. 2. Salmon scale samples contain important life history information. Time spent in the freshwater phase (freshwater age) and marine phase (sea age) can be accurately calculated based on scale growth rings (circuli). Repeat spawning (iteroparous) individuals can also be identified by scale samples. Location, weight, body size, and sex of the individual are often recorded at the time of collection. DNA of sufficient quality for genetic analyses can be extracted from scales (Johnston et al., 2013). This adult spent four years in the freshwater phase (blue), and three years in the marine phase (green), before it was collected on the spawning ground. Image of scale, Natural Resources Institute Finland (Luke).

In this synthesis, we review recent advances in the study of maturation in Atlantic salmon. We first provide a brief overview of maturation at different life history stages. We then summarize the current state of knowledge of the ecological

Box 2. Atlantic salmon as a model system in maturation research

Atlantic salmon is an emerging model system to study maturation processes in fishes, and vertebrates in general (**Fig. 2**). Compared to a plethora of other organisms, salmonids have slow development times, longer lifespans, reproduce later in life, and therefore occupy the slow-end of the fast-slow pace-of-life continuum (Damsgård et al., 2019; Healy, Ezard, Jones, Salguero-Gómez, & Buckley, 2019). Atlantic salmon therefore offer a natural contrast to the fast-end of the pace-of-life continuum fish species currently used to investigate the relationship between behavior, physiology, life history traits and maturation such as zebrafish, *Danio rerio* (Laan, Richmond, He, & Campbell, 2002; Uusi-Heikkilä et al., 2015), mosquitofish, *Gambusia holbrooki* (Polverino, Santostefano, Díaz-Gil, & Mehner, 2018), three-spine sticklebacks, *Gasterosteus aculeatus* (Norton & Gutiérrez, 2019), the turquoise killifish, *Nothobranchius furzeri* (Kim, Nam, & Valenzano, 2016), and the Trinidadian guppy, *Poecilia reticulata* (White, Kells, & Wilson, 2016). In this manner, Atlantic salmon can act to complement and broaden our understanding of maturation beyond fast pace-of-life model species.

Atlantic salmon can also contribute to investigations of molecular pathways related to vertebrate maturation evolution. Ample genomic resources, including a high-quality genome assembly (Lien et al., 2016), make inquiries concerning the genetic basis of maturation traits possible. Recent research has demonstrated that some components of the genetic basis of maturation are conserved among vertebrates including the *vgll3* locus (Barson et al., 2015; Laan et al., 2002; Liang et al., 2016). Given that the same molecular pathways have been proposed as key players in salmon maturation as in other vertebrates, including humans (Kjærner-Semb et al., 2018; Kurko et al., 2020), salmon are included in a list of models showing promise for informing human pubertal timing research (Chakradhar, 2018).

Atlantic salmon are also a model species for understanding the adaptive evolution of the timing of maturation and maturation related traits. The timing of maturation can be under strong selection and this selection can vary spatially and temporally between life history stages, the sexes, and populations (Czorlich, Aykanat, Erkinaro, Orell, & Primmer, 2018; Mobley et al., 2020; Mobley et al., 2019). This variation in the timing of maturation makes maturation traits important targets of natural and sexual selection that can be monitored efficiently in the wild and under experimental conditions. Understanding how selection affects maturation within and among salmon populations can therefore may aid our understanding of evolutionary processes such as the genetic architecture of adaptive traits, local adaptation, and sexual conflict (Mank, 2017; Mobley et al., 2019; Oomen, Kuparinen, & Hutchings, 2020).

There are several advantages for using Atlantic salmon as a model system to study developmental processes related to maturation. Compared to the main fish model in developmental biology, the zebrafish (Lele & Krone, 1996), salmon embryos are larger and develop slower (Gorodilov, 1996; Gorodilov, 2010). This slower development rate makes specific embryonic developmental endpoints easier to target.

factors, genetic architecture, and molecular and physiological processes that direct maturation in Atlantic salmon. We also provide a guide to practical considerations of maturation to use in conservation, management, and aquaculture efforts. Looking forward, we outline key fields for future research that should help fill critical gaps in our knowledge. We conclude by providing a brief summary and recommendations to solve outstanding questions concerning maturation in this species.

Maturation in life history stages

Maturation in Atlantic salmon takes place over several distinct phases of their life cycle. The traditional view is that maturation begins at puberty (**Box 1**). This transition involves the development of functional gonads, the production of viable gametes and the development of secondary sexual traits related to reproduction. However, it is now recognized that developmental processes initiated during embryonic development can also influence maturation via sex-specific gene expression and maternal effects (e.g., Jonsson & Jonsson, 2018; Thorpe, 1994; von Schalburg et al., 2011). Moreover, Atlantic salmon have the ability to reproduce at different times throughout the life cycle and may renew this ability annually as an adult (Thorpe, 2007). Based on these observations, we take an inclusive view of maturation and include maturation processes that begin after fertilization, through puberty until reproductive capacity, and these processes may be renewed cyclically until reproductive senescence or death. In **Box 3**, we briefly summarize the life cycle of anadromous Atlantic salmon to help understand how maturation occurs in key life history stages and transitions.

Box 3. Life cycle of Atlantic salmon

Atlantic salmon have a complex life cycle consisting of distinct juvenile, adult, and reproductive life history stages (**Fig. 3**). Atlantic salmon are generally anadromous, although populations of non-anadromous (i.e., 'landlocked') salmon that spend their entire life cycle in fresh water occur in northern Europe and eastern North America (reviewed in Hutchings et al., 2019). Sexually mature anadromous adults reproduce in fresh water during the fall and winter months. Fertilization of eggs takes place externally in gravel nests (redds) excavated by females in river beds (Fleming & Einum, 2011; Jonsson & Jonsson, 2011). Developing embryos spend a variable amount of time in the gravel bed before hatching the following spring as alevins (**Box 1**). Post-hatching, alevins continue to gain nutrition from the yolk sac for several weeks and remain in the relative safety of the redd. Once the yolk sac is fully absorbed several weeks to months after hatching, alevins 'swim-up' from the redd, becoming fry (**Box 1**), and commence feeding. Fry then develop into parr (**Box 1**), shifting from a diet of microscopic invertebrates to larger invertebrate prey (Jonsson & Jonsson, 2011). Parr remain in fresh water for a variable number of years before they are able to transition to the marine phase. The morphological, physiological, and behavioral transformation to migrate from the fresh water to the marine phase is known as smoltification (Jonsson & Jonsson, 2011; Jonsson & Jonsson, 2003; McCormick, Hansen, Quinn, & Saunders, 1998) (**Box 1**). However, some males may develop mature gonads and participate in reproduction at the parr stage, prior to smoltification (Fleming & Reynolds, 2004; Fleming, 1996). These mature male parr (**Box 1**) represent an alternative male reproductive strategy (Gross, 1996; Myers, 1984). Females initiate maturation during or after smoltification (Fjelldal et al., 2018) but typically do not obtain reproductive capacity until several months at sea. In the marine phase, salmon spend a number of years feeding and growing at an accelerated rate compared to the freshwater phase (Friedland & Haas, 1996; Nicieza & Braña, 1993; Salminen, 1997). The most common maturation strategy is to obtain sexual maturity during a return migration (**Box 1**) to fresh water after a varying number of years (1-5 SW) spent in the marine environment (Erkinaro et al., 2019; Jonsson & Jonsson, 2011). Atlantic salmon can repeat-spawn (**Box 1**) and a small portion of Atlantic salmon may return to spawn over multiple years (Fleming & Einum, 2011; Hutchings & Morris, 1985; Jonsson & Jonsson, 2011).

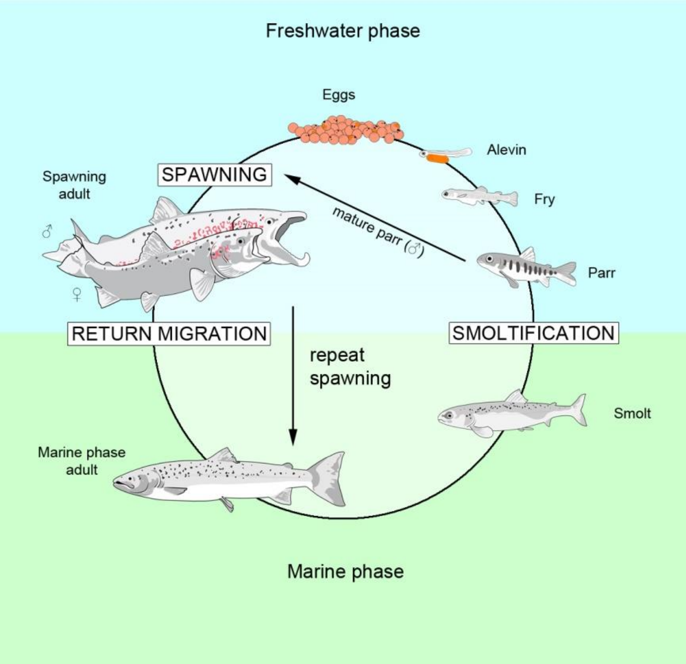

Fig. 3. Atlantic salmon life cycle.

Freshwater phase

The freshwater phase is characterized by embryonic development, hatching, and growth until smoltification. Several aspects of growth and development in the freshwater phase have strong effects on maturation. For example, larger eggs develop faster and hatch earlier than smaller eggs (Einum, 2003; Gilbey, McLay, Houlihan, & Verspoor, 2005). Earlier hatching times give rise to larger alevins and fry that can be more dominant and have a competitive fitness advantage (Einum, 2003; Gilbey et al., 2005; Metcalfe & Thorpe, 1992). For example, it has been shown that a difference of less than one week in commencement of first feeding can spell the difference between smolting in the natal year or spending two summers in fresh water (Metcalfe & Thorpe, 1992). Maternal effects may contribute to this phenomenon as larger and older females generally have larger eggs (Heinimaa & Heinimaa, 2004; Kazakov, 1981; Van Leeuwen et al., 2016) and higher offspring survivorship (Einum & Fleming, 2000). Paternal effects on egg size are also evident and may play a role in maturation (Houde, Fraser, O'Reilly, & Hutchings, 2010; Pakkasmaa, Peuhkuri, Laurila, Hirvonen, & Ranta, 2001). Paternal effects may also influence juvenile growth (Garant, Fontaine, Good, Dodson, & Bernatchez, 2002; Van Leeuwen et al., 2016).

Freshwater age (**Box 1**) is highly variable within and among populations and can range anywhere from one to eight years after hatching (Erkinaro et al., 2019; Friedland & Haas, 1996; Økland, Jonsson, Jensen, & Hansen, 1993). In general, freshwater age increases with latitude due to a shorter growing season (Metcalfe & Thorpe, 1990). Freshwater age is largely determined by growth in the freshwater phase and affects maturation by influencing growth in the marine phase (Jonsson & Jonsson, 2007; Metcalfe, 1998; Thorpe, 1986). For example, faster growth in the freshwater phase increases the chance of an earlier transition to the marine environment (Metcalfe, 1998; Thorpe, 1986) and a higher chance of male parr maturation (Aubin-Horth & Dodson, 2004; Thorpe, 1986). Smaller smolt size, in turn, can result in faster growth in the marine phase (Jonsson & Jonsson, 2007).

Mature male parr

During the freshwater phase, male parr may become sexually mature in prior to the annual spawning season (reviewed in Fleming, 1996; Hutchings & Myers, 1994). The percentage of mature male parr in different populations can vary widely, ranging from completely absent to all individuals sampled (Heinimaa & Erkinaro, 2004; Myers, 1984; Myers, Hutchings, & Gibson, 1986). The causes for variation in parr maturation is likely a combination of population-specific ecological and genetic factors influencing growth. Faster growth and larger size at hatching increases the potential for males to mature at the parr stage (Aubin-Horth & Dodson, 2004; Thorpe, 1986). However, once males start to mature as parr, growth is decreased by two fold compared to immature parr (Thorpe, 1986; Whalen & Parrish, 1999) presumably because they are allocating resources to reproduction rather than growth. Male parr maturation is costly in the wild and reduces the probability of the male surviving and smolting the following year by as much as 44% (Letcher, Gries, & Juanes, 2002; Myers, 1984; Whalen & Parrish, 1999). This low probability of survival is also likely a result of investment into reproduction. However, a number of experimental studies have not found an association with male parr maturation and the probability of smolting (Debes, Plavchenko, Erkinaro, & Primmer, 2020; Duston & Saunders, 1997) suggesting that these two processes may be decoupled.

Mature male parr participate in reproduction (Bacles et al., 2018; Richard, Dionne, Wang, & Bernatchez, 2013; Saura, Caballero, Caballero, & Morán, 2008; Taggart, McLaren, Hay, Webb, & Youngson, 2001; Tentelier et al., 2016; Weir, Breau, Hutchings, & Cunjak, 2010). The reproductive contributions of male mature parr can vary greatly among different populations. On the high end of the spectrum, mature male parr sired up to 87% of offspring in the Nivelle River, France (Grimardias et al., 2010). However, the individual contributions of mature male parr tend to be smaller than anadromous adult males, on average. For example, compared to mature male parr, anadromous males successfully mated four times and sired 12 times more offspring in the same population from the Nivelle River (Tentelier et al., 2016). Similarly, anadromous males were estimated to have sired 8-10 fold more offspring than mature male parr in an experiment with wild caught Canadian fish (Jones & Hutchings, 2002). Body size may play a role in mature male parr reproduction. For instance a strong positive correlation between parr body size and reproductive success was reported in at least one breeding experiment (Thomaz, Beall, & Burke, 1997). However, other studies have found either no relationship (Jones & Hutchings, 2002) or a negative relationship (Tentelier et al., 2016) between parr body size and reproductive success. Currently, the genetic factors influencing male parr maturation are not well understood and detailed information from multi-generational pedigrees and longitudinal studies may shed light on this topic in the future.

Smoltification

Smoltification is an important stage in salmon life history demarcating the transition from freshwater to marine phases in anadromous salmon. The age at smoltification is a function of growth and body size obtained in the freshwater phase and ecological and genetic factors. During smoltification, juveniles undergo morphological, physiological, and behavioral changes to enable the transition to the marine environment. Smolts take on a silvery coloration and become more streamlined (Jonsson & Jonsson, 2011). Physiological transformation includes changes in lipid storage and ion-regulation enabling physiological adaptation to higher salinity (Sheridan, 1989). Hormones such as prolactin, growth hormone (Gh), insulin-like growth factor (Igf), and cortisol, increase during smoltification (Sheridan, 1989). Smolts lose their positive rheotactic behavior (facing upstream) in order to migrate to sea (Specker, Eales, Tagawa, & Tyler, 2000; Veselov, Kazakov, Sysoyeva, & Bahmet, 1998). In some instances, the process of smolting is reversed (i.e., desmoltification) and these fish remain in the freshwater phase until conditions are met for resmoltification (Fraser, Fjelldal, Schulz, Norberg, & Hansen, 2019; Hansen, Jonsson, Morgan, & Thorpe, 1989; Thorpe, 1994).

The age at smoltification is likely determined by physiological trade-offs in the freshwater environment associated with growth-resource availability. Previous studies have shown that time spent in the freshwater phase is similar between the sexes and larger, faster growing parr tend to smolt earlier than smaller, slower growing parr (Jonsson & Jonsson, 2011; Thorpe, 1986, 1994; Thorpe, Mangel, Metcalfe, & Huntingford, 1998). However, smolt size is positively correlated with freshwater age; fast growing parr smolt at an earlier age and therefore smaller size in Norwegian salmon (Einum et al., 2002; Økland et al., 1993). Thorpe et al. (1998) proposed that a suite of developmental thresholds and growth parameters such as weight and lipid levels determine smolt timing. Juveniles that have sufficient overwinter lipid stores will smolt the following spring, while those that do not postpone smoltification (Metcalfe, 1998; Thorpe et al., 1998).

Among anadromous salmon, females generally mature in the marine phase after the smolting process. Males, on the other hand, can mature before or after smolting. However, mature male parr do not appear to smolt in the same year (Thorpe & Morgan, 1980). This observation suggests that males do not have enough energy to support maturation and smolting within the same year. and a trade-off between male parr maturation and smolting exists. However, males that smolt can mature at sea within the same year (Thorpe & Morgan, 1980).

The age at smoltification has direct effects on sea age (**Box 1**) and reproductive fitness. Earlier smolting individuals tend to spend more time at sea before returning to rivers to spawn (Erkinaro et al., 2019; Jonsson & Jonsson, 2011; Salminen, 1997) and have higher reproductive fitness due to generally achieving larger size (Mobley et al., 2020). There may also be a sex-specific relationship between growth and time spent in fresh water. For example, females that spend more time in fresh water show reduced pre- and post-smolt (**Box 1**) growth (Einum et al., 2002), signifying a trade-off between growth at sea and the time spent in fresh water. A recent study demonstrated that females that spend more time in fresh water spend less time at sea than earlier smolting individuals, and suffer a reduction in reproductive success (Mobley et al., 2020). However, smolting early potentially exposes these individuals to higher predation at sea, highlighting a potential trade-off between smolting and survival (McCormick et al., 1998).

Marine phase

The marine phase is associated with rapid growth and fat accumulation that subsequently fuels gonadal development and maturation (O'Connell, Dempson, & Chaput, 2006). Maturation in the marine phase is suggested to be a threshold response that is triggered by body size and/or condition during the spring and fall (Jonsson, Jonsson, & Finstad, 2013). Larger body size at the onset of seaward migration and faster post-smolt growth is generally associated with younger sea age (e.g., Chaput et al., 2018; Hutchings & Jones, 1998; Jonsson & Jonsson, 2007; Salminen, 1997). However, in Baltic Atlantic salmon, smaller smolt size is associated with faster growth followed by earlier maturation, suggesting that the relationship between post-smolt size and maturation may be population-specific (Jonsson & Jonsson, 2007).

The marine phase is marked by high mortality, which, in turn, may affect the timing of maturation (Olmos et al., 2019). Tagging studies estimate mortalities as high as 70 to 93% (Armstrong, McKelvey, Smith, Rycroft, & Fryer, 2018; Gregory, Armstrong, & Britton, 2018; Hutchings & Jones, 1998; Michielsens et al., 2006; Peyronnet, Friedland, & Ó Maoileidigh, 2008; Strøm et al., 2019; Webb, Verspoor, Aubin-Horth, Romakkaniemi, & Amiro, 2007). Marine survival of Atlantic salmon is size- and age-dependent with orders of magnitude higher mortality rates at the post-smolt stage, compared to older and larger adults (Chaput, Caron, & Marshall, 2003; Chaput et al., 2018; Michielsens et al., 2006). High mortality in the marine phase may confer a selective advantage to earlier maturation, such that higher probability of survival before reproduction may offset the advantage of being older and larger at maturity (Hard et al., 2008; Mobley et al., 2020; Thorpe, 2007).

Return migration and spawning

During the return migration, Atlantic salmon return to fresh water to spawn, often to their natal rivers. This ability is known as homing (Hendry, Castric, Kinnison, & Quinn, 2003; Quinn, 1993). Atlantic salmon commonly spend one to three years (but can be up to 5 years) in the marine environment before returning to fresh water to spawn for the first time (Jonsson & Jonsson, 2011; Webb et al., 2007). Every additional year in the marine environment results in doubling of individual mass; individuals returning after one year are typically 1-3 kg and 50-65 cm, compared to 10-20 kg and >100 cm after spending three or more years in the marine environment (Hutchings & Jones, 1998; Mobley et al., 2020). The main determinants of return migration timing are likely a mixture of the ecological factors, genetics, and the physiological state of the fish.

Females typically spend more years at sea than males (Barson et al., 2015; Mobley et al., 2020; Niemelä, Erkinaro, et al., 2006). This additional time is required as females need approximately six times more energy than males for gonad development and egg production (Fleming, 1996; Jonsson, Jonsson, & Hansen, 1997). In general, large, multi-seawinter adults arrive earlier on the spawning grounds (Armstrong et al., 2018; Harvey, Tang, Wennevik, Skaala, & Glover, 2017; Jokikokko, Kallio-Nyberg, & Jutila, 2004; Jonsson et al., 1990; Jutila, Jokikokko, & Julkunen, 2003; Niemelä, Erkinaro, et al., 2006; Quinn, McGinnity, & Cross, 2006; Shearer, 1990).

Fecundity, the number of offspring (reproductive success) and the number of mating partners (mating success) increases with larger body size and later timing of maturation (Fleming, 1998; Fleming, 1996; Heinimaa & Heinimaa, 2004; Mobley et al., 2020; Mobley et al., 2019). The timing of maturation in Atlantic salmon represents a classic evolutionary trade-off: individuals that spend more time at sea before returning to fresh water to spawn have higher reproductive success due to their larger size but also have a higher risk of mortality prior to first reproduction (Fleming & Einum, 2011; Mobley et al., 2020). Increased reproductive success among older, and therefore larger, individuals is potentially due to their increased competitive ability on the spawning grounds. Differences in competitive ability are likely mediated by size- and age-related differences in aggression and courtship behaviors, gamete competition, as well as mate choice (Auld, Noakes, & Banks, 2019; Fleming, 1998; Gage et al., 2004; Mjølnerod, Fleming, Refseth, & Hindar, 1998). For example, body size affects dominance hierarchies, with larger females defending high quality spawning areas [e.g., fast flowing water (Crisp & Carling, 1989)] and thus obtaining higher mating and reproductive success (Fleming, 1996; Fleming & Einum, 2011). Larger males also compete more successfully for access to nesting females (Fleming, 1998; Fleming, 1996; Fleming & Gross, 1994). There is also the potential for sex-specific selection and/or sexually antagonistic selection (e.g., sexual conflict) over reproduction to affect maturation in Atlantic salmon (Barson et al., 2015; Mobley et al., 2020) (**Box 4**).

Repeat spawning and reproductive senescence

In some populations of Atlantic salmon, a proportion of adults may return to spawn in several different years, although the number of these repeat-spawners is generally low (< 10%) (Fleming & Reynolds, 2004; Fleming, 1996). Individuals that repeat spawn usually overwinter in fresh water following their first spawning event prior to returning to sea and are known as kelts (**Box 1**). Currently, reproductive senescence (Lemaître & Gaillard, 2017) is unknown in Atlantic salmon and they are assumed to reproduce throughout their lifetime. For example, one of the oldest recorded Atlantic salmon is a 14-year-old female from the Teno River with four spawning migrations and a total of six years at sea prior to capture (Erkinaro et al., 2019). Fourteen-year-old individual has also been reported among landlocked salmon (Hutchings et al., 2019).

Alternative reproductive strategies

Males with distinct sexual maturation phenotypes coexist in many salmon populations (Fleming, 1996; Hutchings & Myers, 1994). This phenotypic diversity can give rise to different male reproductive strategies based on size and maturation at different life-history phases (Aubin-Horth & Dodson, 2004; Hutchings & Myers, 1994). For example, anadromous males guard and court females, while mature male parr attempt to sneak copulations without investing in courtship and mate defense (Fleming, 1998; Gage, Stockley, & Parker, 1995; Hutchings & Myers, 1994). Compared to anadromous males, mature male parr have significantly smaller gonads in terms of absolute size, a greater proportion of motile spermatozoa, and greater sperm adenosine triphosphate (ATP) content (Vladić, 2001; Vladić, Afzelius, & Bronnikov, 2002). Thus, mature parr invest relatively more in sperm quality and sperm numbers in relation to body size than anadromous males in order to compete for fertilizations. Evidence supports the adoption of a particular reproductive strategy being a threshold trait and may be genetically determined in different populations (Hutchings, 2011; Hutchings & Myers, 1994; Piché, Hutchings, & Blanchard, 2008).

In populations that have polymorphism in sea age, there is a strong positive correlation between sea age, and therefore body size, and reproductive fitness (Mobley et al., 2020). However, smaller anadromous males may be able to obtain some reproductive success by sneaking copulations or mimicking female behaviors allowing them to remain near spawning pairs (Fleming & Einum, 2011; Foote, Brown, & Wood, 1997).

Females do not appear to display alternative reproductive strategies. Females may mature at a small size in some landlocked populations (Gibson, Williams, McGowan, & Davidson, 1996; Hutchings et al., 2019), although evidence for females to mature at the parr stage is scant (Bagliniere & Maisse, 1985; Power, 1958).

Ecological factors affecting maturation

A variety of abiotic and biotic ecological factors influence maturation in Atlantic salmon, and these factors generally reflect the habitats and conditions that Atlantic salmon encounter during different times during their life. Here, we present ecological patterns and processes that have been shown to affect maturation during different life history phases.

Freshwater phase

Numerous environmental factors can influence the embryonic stage, affecting development and survival, which in turn can influence maturation processes in later life history stages (**Table 1**). For example, developing embryos are sensitive to temperature, oxygen levels, and sedimentation (Hamor & Garside, 1976; Julien & Bergeron, 2006; Peterson, Spinney, & Sreedharan, 1977). Normal embryonic development takes place at a narrow band of temperatures with high mortality at the low and high extremes (Hamor & Garside, 1976). Under experimental conditions, higher incubation temperatures during embryonic development increase growth and performance in juveniles (Burgerhout et al., 2017; Finstad & Jonsson, 2012), that in turn may affect reproductive allocation in adults (Finstad & Jonsson, 2012; reviewed in Jonsson & Jonsson, 2014; Jonsson & Jonsson, 2016; Jonsson, Jonsson, & Finstad, 2014). However, faster development comes at a cost to growth, as embryos incubated in warmer water are generally smaller than those that are raised in lower temperatures (Peterson et al., 1977). Incubation temperature does not appear to influence growth to first feeding (Peterson & Martin-Robichaud, 1989). Jonsson and Jonsson (2018) demonstrated that embryos experimentally reared in warmer water temperatures delayed their return spawning migration by two weeks indicating that incubation temperature may influence maturation in later stages.

Temperature continues to be important for growth, physiology, and behavior during the alevin and parr stages (Adams & Thorpe, 1989; reviewed in Elliott & Elliott, 2010; Koskela, Pirhonen, & Jobling, 1997). Metabolic processes are sensitive to environmental changes, and increasing water temperatures can elicit an increase in food consumption and vice versa (Elliott, 1991; Koskela et al., 1997; Oligny-Hébert, Senay, Enders, & Boisclair, 2015). Higher temperature may also increase male parr maturation (Fjelldal, Hansen, & Huang, 2011), although this temperature effect is not found in all studies (Baum, Laughton, Armstrong, & Metcalfe, 2005).

Water flow can also influence juvenile growth (reviewed in Finstad, Armstrong, & Nislow, 2011). An increase in water flow generally results in increased food abundance but a decrease in the capture efficiency of prey (Metcalfe, Valdimarsson, & Fraser, 1997). Moreover, competition for food resources is intense and salmon fry disperse to alleviate intraspecific competition (Brännäs, 1995; Gibson, 1993). Juvenile salmon become territorial and individuals compete with each other for optimal habitat (Keenleyside & Yamamoto, 1962). Here, the supposition is that individuals that are more competitive occupy better habitat and grow faster than those that do not. Earlier feeding fry are more dominant, and therefore individuals that hatch earlier than others may outcompete and mature earlier than their conspecifics (Metcalfe & Thorpe, 1992). However, emerging earlier from the redd may come at a cost of higher predation risk (Brännäs, 1995).

Smoltification

The length of photoperiod that signals changes in season is an important cue for smoltification (McCormick, Shrimpton, Moriyama, & Björnsson, 2002; McCormick, Shrimpton, Moriyama, & Björnsson, 2007; Metcalfe & Thorpe, 1990; Saunders & Henderson, 1970). Photoperiod affects hormonal levels such as insulin-like growth factor (Igf), and growth hormone that are associated with smoltification (McCormick et al., 2002). Experiments that increase temperature and photoperiod demonstrate that these factors interact to increase growth and maturation during and after smoltification (Fjelldal et al., 2011; Imsland, Handeland, & Stefansson, 2014; McCormick et al., 2002; McCormick et al., 2007). Food restriction (Thorpe & Metcalfe, 1998) and reduced water flow (Hosfeld et al., 2008) can also increase the time to smoltification.

A recent common garden study that partitioned genetic and environmental effects found that environmental factors such as water temperature were important for smoltification. However, for a given temperature, there was a greater importance of genetic factors predicting smoltification probability than other environmental effects (Debes et al., 2020).

Marine phase

Numerous ecological factors may influence salmon maturation during the marine phase (**Table 1**). However, due to the vast geographical distances that salmon cover at this stage (O'Connell et al., 2006), it is currently difficult to pinpoint the specific ecological factors influencing maturation at sea (Thorpe et al., 1998). Despite this, a variety of methods such as mark-recapture and common garden experiments, and scale analyses (**Fig. 2**) have provided insights on the environmental factors that likely drive maturation in the marine phase. For example, temperature, diet, photoperiod, and salinity all likely contribute to variation in maturation during the marine phase (reviewed in Good & Davidson, 2016; Jonsson & Jonsson, 2011).

Temperature is perhaps the best studied environmental factor influencing Atlantic salmon maturation in the marine phase (reviewed in Good & Davidson, 2016; Jonsson & Jonsson, 2011) (Table 1). In general, higher water temperatures are associated with earlier maturation in the marine phase (reviewed in Jonsson & Jonsson, 2011). In the wild, warmer conditions during the post-smolt stage are associated with increased mortality in North American Atlantic salmon (Friedland, Chaput, & MacLean, 2005; Friedland, Reddin, & Castonguay, 2003). In contrast, higher sea surface temperature (SST) in North European coasts is associated with higher growth and survivorship of 1SW grilse (Friedland, Hansen, Dunkley, & MacLean, 2000) (**Box 1**). The temperature effect on maturation may also interact with nutrition (Friedland et al., 2005). For example, higher temperatures increase the likelihood of early maturation in conjunction with the presence of abundant and high quality food items (e.g., high lipid content) (Handeland, Imsland, & Stefansson, 2008; Jonsson et al., 2013). On the other hand, increased temperatures may enhance basal metabolic activity of individuals and negatively affect growth and/or survival via density-dependent effects (Friedland et al., 2003).

Salmon use seasonal changes in photoperiod as a proximate maturation cue during the marine phase (reviewed in Bromage, Porter, & Randall, 2001; Hansen, Stefansson, & Taranger, 1992; Schulz, Andersson, & Taranger, 2006; reviewed in Taranger et al., 2010; Taranger et al., 1999). Experimentally manipulating photoperiods, such as shortening day length in the fall), can increase the proportion of fish that delay maturation to the next spawning season (reviewed in Taranger et al., 2010). Maturation is also affected by the interaction between photoperiod and water temperature (Imsland et al., 2014). Elevated temperature combined with continuous light can trigger male Atlantic salmon to mature during and immediately after smoltification (Fjelldal et al., 2011; Imsland et al., 2014). Atlantic salmon spawning rivers cover a wide range of latitudes, and therefore the use of photoperiod as a maturation cue may be population-specific. For instance, photoperiod-associated responses may be mismatched with other environmental cues of maturation, such as temperature, resulting in maladaptive or mismatching phenotypic expression. However, this possibility has not yet been investigated, but may be an important future consideration in the face of climate change.

In general, the initiation of maturation in salmonids is associated with a higher condition factor and therefore is likely dependent upon nutritional status during the marine phase (reviewed in Jonsson & Jonsson, 2011). A study on Atlantic salmon in sea cages showed that low food resources during winter affected growth and condition, resulting in lower proportions of earlier maturing salmon (Duston & Saunders, 1999). During the post-smolt stage, salmon that feed on marine fish larvae and crustaceans show an increase in growth (Hvidsten et al., 2009; Rikardsen et al., 2004; Salminen, Erkamo, & Salmi, 2001). This rapid accelerated growth then influences maturation during the first year at sea (Friedland & Haas, 1996; Friedland, Moore, & Hogan, 2009; Jonsson, Finstad, & Jonsson, 2012; Jonsson & Jonsson, 2003; Nicieza & Braña, 1993).

The effect of diet on maturation is less well known in the open sea, due both to the difficulty in tracking individuals as well as analyzing dietary composition. However, post-smolts are known to be generalist feeders and adopt a more piscivorous diet later in life (Jacobsen & Hansen, 2001). Salmon post-smolt appear to utilize high-lipid, high-energy forage fish such as capelin, herring and lantern fishes that may influence early maturation (Rikardsen & Dempson, 2010). Currently, it is unclear how genetic factors interact with diet to influence maturation during the marine phase. A recent study by Aykanat et al. (2020) quantified the stomach contents of wild adult Atlantic salmon and demonstrated that the *six6* genomic region is linked to gut fullness as well as prey composition, while *vgll3* was marginally linked to prey composition. These results suggest that Atlantic salmon is not only a diet specialist governed by genetic variation in *six6*, but that the genetic basis of diet variation is linked to maturation. Thus, the maturation status of Atlantic salmon populations is likely to have an evolutionary response to alteration in food web structures and changes in resource composition (Bentley, Serpetti, & Heymans, 2017; Daufresne, Lengfellner, & Sommer, 2009; Pershing et al., 2015).

Return migration and spawning

Thorstad, Økland, Aarestrup, and Heggberget (2008) comprehensively reviewed a variety of ecological factors affecting the return migration of anadromous Atlantic salmon. Briefly, older and larger salmon may encounter difficulties migrating to breeding grounds in rivers or tributaries with low water flow due to their inaccessibility (Jonsson, Hansen, & Jonsson, 1991). As a likely consequence, older and larger salmon are commonly observed spawning in the mainstem of rivers and large tributaries (Erkinaro et al., 2019; Vähä, Erkinaro, Niemelä, & Primmer, 2007). Furthermore, freshwater temperature is a potential factor regulating the return migration of Atlantic salmon (Moore et al., 2012). However, the mechanisms that trigger fish to return migrate to spawn are likely both genetically and environmentally determined (Barson et al., 2015). Future research investigating how genetics may interact with ecological conditions to influence the decision on when and where to spawn would be beneficial.

Genetics of maturation

Maturation processes during different life history stages have been shown to have a heritable basis. As early as 1978, Nævdal, Holm, Ingebrigtsen, and Møller noted that prevalence of grilsing differed among populations when reared in a common environment suggesting a genetic basis of mature male parr and early maturation. During the decades that followed, evidence for heritability of maturation processes has accumulated (reviewed in Garcia de Leaniz et al., 2007). For example, the timing of smoltification (Páez et al., 2011), sea age at maturity (Gjerde, 1984; Reed et al., 2018; Sinclair-Waters et al., 2020), and male parr maturation (Debes et al., 2019) all have high heritabilities. These results have generated interest in elucidating genomic regions and molecular functions linked to maturation traits. Recently, considerable progress in identifying genes that influence maturation in the marine phase have sprung from genome-wide association studies (GWAS, **Box 1**) (Ayllon et al., 2015; Barson et al., 2015). However, less is known concerning what genes are responsible for variation in maturation-related processes in other life history stages such as the freshwater phase and smoltification. Likewise, the exact location of genomic polymorphisms within these regions that are causally linked to trait variation, and the underlying molecular functions have yet to be uncovered.

Freshwater phase

Given the heritability of life history traits such as male parr maturation and smoltification timing, there is concerted interest in identifying genetic variation that underlies these traits. Studies examining tens to hundreds of single nucleotide polymorphism (SNP, **Box 1**) markers aim to identify quantitative trait loci (QTLs, **Box 1**) associated with the probability of male parr maturation. For instance, Lepais, Manicki, Glise, Buoro, and Bardonnet (2017) identified a handful of QTLs associated with male parr maturation (**Table 2**). One large effect QTL was found on chromosome 25 that explained 20.6% of the variation in male parr maturation threshold values (Lepais et al., 2017). This QTL region spans the *vgll3* gene, which has been previously identified as a large-effect locus for Atlantic salmon sea age (Ayllon et al., 2015; Barson et al., 2015) and its association with male parr maturation has recently been further supported in controlled experiments in several salmon populations (Debes et al., 2019; Verta et al., 2020). This result strongly suggests that the *vgll3* locus plays a key role in sexual maturity in the freshwater phase. Another study by Pedersen et al. (2013) identified multiple QTLs associated with male parr maturation providing further evidence that the trait has a polygenic architecture (Pedersen et al., 2013) (**Table 2**). However, the mapping of these male parr maturation QTLs is coarse due to low SNP density used in this study, as well as low recombination rate in male Atlantic salmon (Lien et al. 2011). Pedersen et al. (2013) also identified several genomic regions associated with smoltification timing (**Table 2**). This included regions containing genes known to undergo expression changes [*sparc* (Seear et al., 2010)] or potentially influence hormonal changes during smoltification [*ghrh* (McCormick, Ryen, Munday, & Walker, 2010) (**Table 2**)]. Yet, for both male parr maturation and smoltification, an examination of the link between genotype and phenotype using denser marker coverage (e.g., >10,000 SNP markers) is still lacking. A high density genome scan approach that covers a greater number of haplotype blocks is likely to provide a more detailed understanding of the genetic architecture, including structural variation and single variants, underlying traits influencing maturation in the freshwater phase of the Atlantic salmon life cycle.

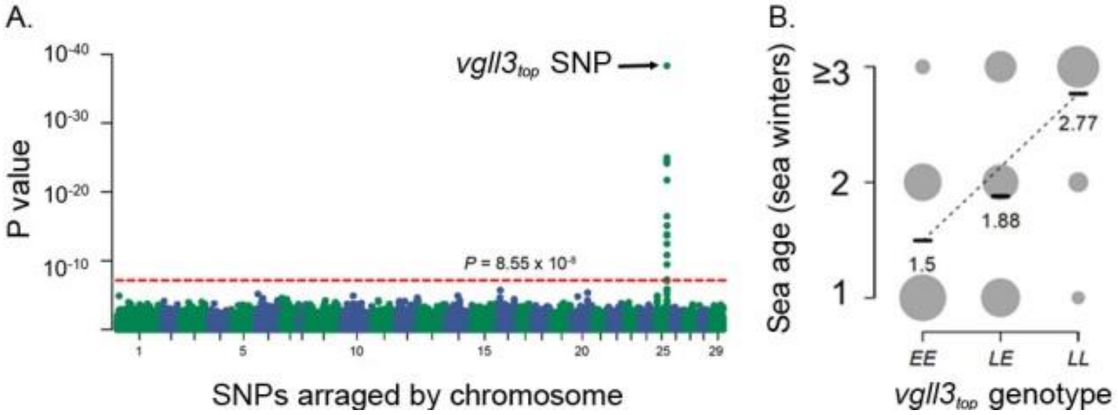

Fig. 4. A. Genome-wide association plot (Manhattan plot) of 220k SNPs showing the association between sea age and SNP loci on chromosome 25. Points above the dashed line indicate significant SNPs associated with sea age. The SNP locus with the strongest association, located near the *vgll3* gene, is labelled *vgll3*$_{top}$. B. Sea age (in seawinters) in relation to *vgll3*$_{TOP}$ genotype. Alleles linked with early and late maturation are labelled *E* and *L*, respectively. Circle areas are proportional to sample size (total n = 1404). Black bars indicate mean sea age for each genotype class. Data from Barson et al. (2015).

Marine phase

Early studies aiming to identify the genetic basis of sea age generally lacked statistical power and/or genomic coverage sufficient for giving a clear picture of the genomic regions underlying the trait (**Table 2**). The age of genomics eliminated these limitations, giving rise to several studies that identified a large-effect locus on chromosome 25 that explains up to 39% of the variation in sea age (Ayllon et al., 2015; Barson et al., 2015) (**Fig. 4**). The primary candidate gene in the genome region, *vgll3* (*vestigial-like family member 3*), encodes a transcription cofactor involved in adipogenesis regulation (Halperin, Pan, Lusis, & Tontonoz, 2013) and therefore potentially plays a pivotal role in lipid storage and metabolism in Atlantic salmon. The gene is associated with, amongst other things, pubertal timing, growth, and body condition in humans (Cousminer et al., 2013; Elks et al., 2010; Tu et al., 2015). The alternative alleles at the highest associated SNP in the *vgll3* locus conferred either early (*E*) or late (*L*) sea age (Barson et al., 2015). The *vgll3* locus exhibits incomplete sex-specific dominance that may partially resolve potential sexual conflict in this locus (**Box 4, Fig. 5**). Furthermore, Christensen, Gutierrez, Lubieniecki, and Davidson (2017) found that after accounting for *vgll3* genotypes, *tead3* (*TEA domain transcription factor 3*) was associated with early maturation. *Tead3* codes for a transcription factor that the *vgll3*-encoded cofactor binds to in order to regulate the Hippo signaling pathway (Figeac et al., 2019; Kjærner-Semb et al., 2018; Kurko et al., 2020; Simon, Thézé, Fédou, Thiébaud, & Faucheux, 2017) . This indicates that the *tead3* gene may affect early maturation via an interaction with *vgll3*.

The effect of *vgll3* on sea age appears to be conserved across all European Atlantic salmon lineages (Atlantic, Barents/White Sea and Baltic Sea lineages), and influences sea age in both males and females (Barson et al., 2015) (**Table 2**). Furthermore, a higher proportion of late maturation alleles of *vgll3* are found in late-maturing females than in early-maturing individuals from populations of North American Atlantic salmon suggesting *vgll3* may also be associated with sea age in this lineage (Kusche et al., 2017). Although several GWAS have found a significant association between the *vgll3* region and maturation (Ayllon et al., 2015; Ayllon et al., 2019; Barson et al., 2015), others examining single north American aquaculture strains have not (Boulding, Ang, Elliott, Powell, & Schaeffer, 2019; Mohamed et al., 2019). This discrepancy may be due to different genetic architecture or variable gene-environment interactions among populations/strains. Alternatively, this may be merely due to low genetic variation at the *vgll3* locus in the study samples and/or some studies being underpowered to detect such an association. Future research should investigate the exact function of *vgll3* in Atlantic salmon and other genes in the same highly associated region.

A second gene in the genome region significantly associated with sea age on chromosome 25 is the *akap11* gene encoding the A-kinase anchor protein (Barson et al., 2015). Akap11 protein belongs to a family of A-kinases that are expressed throughout spermatogenesis and is important for sperm motility (Reinton et al., 2000). *Akap11* and *vgll3* have recently been shown to have correlated expression in various juvenile life history stages (Kurko et al., 2020). It is therefore possible that

Box 4: Sexual conflict and the *vgll3* locus

Atlantic salmon is an interesting model system to investigate questions related to sexual conflict (Barson et al., 2015; Mank, 2017). Intra-locus sexual conflict potentially exists at the *vgll3* locus (Barson et al., 2015). Differing phenotypic optima for males and females over the sea age and body size at maturation may result in a genetic "tug-of-war" between the early (*E*) and late (*L*) alleles at the locus (Barson et al., 2015) (**Fig. 4**). Repeat-spawning is also linked to the *vgll3* locus (Aykanat et al., 2020) and early maturing individuals may recover additional reproductive success if they survive to reproduce again. A survey of 57 populations has shown that *vgll3* alleles are maintained at intermediate frequencies in many populations (Barson et al., 2015), which may be indicative of balancing selection, predicted under intra-locus sexual conflict (Connallon & Clark, 2014).

An interesting twist to this scenario is the observation of sex-dependent dominance of the *vgll3* locus, allowing the maintenance of the two allelic forms of *vgll3* in populations of Atlantic salmon (Barson et al., 2015; Kuparinen & Hutchings, 2019). Due to the apparent dominance of the *E* allele in males, *EL*, heterozygote males behave like homozygote *EE* males by returning to spawn after 1SW, whereas heterozygote females return to spawn at an intermediate age between both homozygotes (**Fig. 4**). Potential consequences of sex-specific dominance and additive effects on selection at sea inducing variation in sex-specific allele frequency patterns are supported by simulations and empirical data (Czorlich et al., 2018). Future research should investigate the potential causes and consequences of sexual conflict in this species.

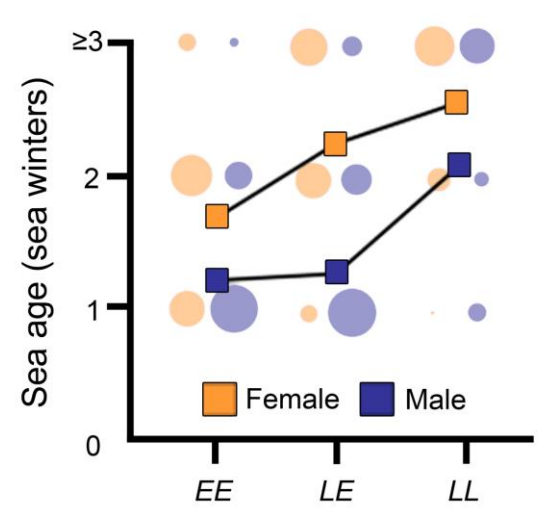

Fig. 5. Sex-specific differences in sea age maturation and incomplete dominance of *vgll3* genotypes. Sea age of females (n = 693) and males (n = 711) in relation to *vgll3* genotype (*E* = early, *L* = Late). Points indicate predicted average sea age using a logit transformation model (see Barson et al., 2015 for details). Circles are proportional to the number of spawning adults used in the study. Figure based on data from Barson et al. (2015).

akap11, along with *vgll3,* may serve important roles in processes leading to sexual maturation.

A number of loci in other genome regions have been linked with sea age at maturity (**Table 2**). For example, early isozyme work on Iberian Atlantic salmon populations found slight, yet significant, allele frequency differences in grilse versus multi-sea winter individuals at one protein locus, MEP-2. Additionally, two QTLs located on chromosomes 10 and 21 associated with early maturation in males and one QTL associated with late maturation (chromosome 18) have been identified in aquaculture strains (Gutierrez, Yá, Fukui, Swift, & Davidson, 2015). However, these findings are not ubiquitous across studies linking genetics and maturation timing. Higher-powered association studies involving a broad range of populations and aquaculture strains may help to elucidate why such discrepancies are observed. One recent example examining over 11,000 adults from a single aquaculture strain, identified over 100 candidate genes associated with maturation (Sinclair-Waters et al., 2020). This demonstrates the importance of increasing sample sizes in order to detect genes of smaller effects. However, to better understand the links of these smaller-effect genes with maturation, we require a high level of individual sampling across a broader range of populations and aquaculture strains. Additionally, new evidence suggests that some genes (e.g., *magi2* & *picalm*) may have sex-specific effects on maturation (Mohamed et al., 2019). Studies with large sample sizes and good representation of sexes will be vital to determine the extent that sex-specific genetic architectures for maturation traits exist in Atlantic salmon (**Box 4**).

Sinclair-Waters et al. (2020) identified another candidate genome region on chromosome 9, including the gene *six6* (*SIX homeobox 6*), that is strongly associated with maturation. *Six6* encodes a transcription factor of the brain-pituitary-gonadal axis, and is also associated with height and age-at-maturity in humans (Perry et al., 2014) and puberty in cattle (Cánovas et al., 2014). The same region was also strongly associated with maturation in Johnston et al. (2014) and Barson et al. (2015), but following correction for population stratification, the association signal of significance was lost. This may suggest that the region is associated with a correlated trait (e.g., body size or return migration timing) that is also associated with an environmental factor [e.g., river catchment area, (Pritchard et al., 2018)]. Furthermore, a locus (*lrrc9*) associated with spawning site selection in sockeye salmon, *Oncorhynchus nerka*, is located in the same significant genomic region as *six6* suggesting that this genomic region plays a role in maturation and sexual reproduction in other salmonids (Pritchard et al., 2018; Veale & Russello, 2017). The *six6* locus is also associated with variation in return migration timing among Scottish Atlantic salmon populations (Cauwelier, Gilbey, Sampayo, Stradmeyer, & Middlemas, 2018).

Molecular & physiological processes of maturation

Besides the basic molecular and physiological processes required to maintain normal development, growth, and homeostasis, several regulatory processes are key for maturation in Atlantic salmon. These processes include hormonal control of maturation, gene expression pathways related to maturation processes, and gonadal development. The brain-pituitary-gonadal (BPG) axis is a central player in maturation in vertebrates, including salmon (Taranger et al., 2010). Genetic and ecological factors may also interact with these regulatory processes. Here, we provide an overview of our current understanding of the molecular and physiological processes governing maturation in Atlantic salmon.

The brain-pituitary-gonadal axis

The BPG axis regulates maturation via neurological and hormonal feedback and is analogous to the hypothalamic-pituitary-gonadal axis in other vertebrates (Ellis, 2013). The activation of the BPG axis is induced by different internal and external stimuli, including growth, adiposity, sex hormones, photoperiod, temperature, salinity and social cues (Choi, Kim, Shin, & Choi, 2014; Gielen, Goos, Peute, van den Bosch, & van Oordt, 1982; Melo et al., 2014; Taranger et al., 2010). Many of these stimuli are functionally related to growth and/or energy acquisition and storage, which in turn affect the rate of lipid acquisition and storage, and achieving sufficient lipid reserve levels sufficient for reaching key growth and condition thresholds for maturation at different life history stages (Jonsson & Jonsson, 2003; Rowe, Thorpe, & Shanks, 1991; Taranger et al., 2010). The onset of maturation can be modulated by the rate of lipid storage in the body and the specific levels and types of lipids stored, whereby low lipid levels act as a factor limiting early maturity in salmonids (Jenkins et al., 2019; Rowe et al., 1991; Sheridan & Harmon, 1994; Silverstein, Shimma, & Ogata, 1997).

Considerable research has been conducted on understanding how the different components of the BPG axis regulate maturation in salmon and related species. Thus far, less effort has been placed in understanding the specific links between environmental and molecular/physiological factors that affect maturation. We therefore first consider the brain, pituitary and gonad components of the BPG axis separately and summarize gene expression studies related to the maturation process in Atlantic salmon (**Table 3**). Finally, we consider molecular and physiological factors affecting variation in maturation timing.

Brain

The brain is the first organ in the BPG axis that integrates cues of factors affecting maturation. The main brain hormone that induces this axis is gonadotropin-releasing hormone (GnRH) which is secreted from the GnRH neurons that form during early embryonic development (Parhar, Iwata, Pfaff, & Schwanzel-Fukuda, 1995). A well-known molecular mediator of GnRH release in mammals, the neuropeptide kisspeptin, has been examined recently in fish (Ohga, Selvaraj, & Matsuyama, 2018), but its role in fish remains controversial. In Atlantic salmon, co-expression of the kisspeptin receptor gene, *skissr*, and sGnRH3 in the brain indicates that kisspeptin may affect GnRH secretion directly, primarily during at the onset of maturation and later stages of gonad development (Chi, Li, Liu, & Liu, 2017). Different internal and external cues are known to induce the BPG axis and GnRH release, one of the most important being photoperiod changes which are sensed both in the hypothalamus and saccus vasculosus, a special sensor of seasonal changes in day length in the fish brain (Nakane et al., 2013). Long photoperiod has been shown to increase expression of both *skissr* and *gnrh3* in the hypothalamus and saccus vasculosus in salmon, suggesting that photosensing has a direct effect on the BPG axis via the kisspeptin system (Chi et al., 2017).

The link between energy stores, especially that of lipids, and reproduction is conserved in vertebrates (see above), and leptin hormone is one of the molecules conveying such metabolic signals to the brain. Although leptin influences Atlantic salmon fat accumulation, its role seems to be something other than adiposity signaling via the BPG axis, as sexual maturation does not directly induce expression changes in the leptin receptor gene, *lepr*, in the brain (Trombley, Mustafa, & Schmitz, 2014). However, long photoperiod has been shown to reduce leptin receptor A1 gene, *AsLRa1*, expression levels in both the hypothalamus and saccus vasculosus, thereby increasing appetite and food intake which, in turn, results in higher growth rate, another important cue for maturation, in Atlantic salmon (Chi, Li, Liu, & Liu, 2019).

In mature male parr, there is an upregulation in genes involved in energy production and homeostasis, metabolism, growth, and feeding, such as pro-opiomelanocortin and melanin-concentrating hormone 2(Aubin-Horth, Landry, Letcher, & Hofmann, 2005; Aubin-Horth, Letcher, & Hofmann, 2009; Guiry et al., 2010; Kawauchi, 2006; Takahashi, Kobayashi, Amano, & Yamanome, 2009), and genes regulating lipid metabolism, for example, apolipoproteins and glycerol-3-phosphate dehydrogenase (Aubin-Horth et al., 2009) (**Table 3**).

In addition to the upregulation of genes associated with energy status and metabolism during maturation, differential gene expression patterns have been reported in the brain of maturing male parr. Some of these associated genes are involved in spatially and temporally correct navigation, maintenance of osmotic balance, body color modification and coping with mechanical and social stress (**Table 3**). This suggests that molecular signals originating from the brain prepare salmon physiologically and behaviorally for maturation. Accordingly, expression changes have been observed in genes encoding prolactin involved in migration and osmoregulation (Whittington & Wilson, 2013), Na/K ATPase alpha regulating in osmotic balance of neuronal cells (Vornanen & Paajanen, 2006), and pro-opiomelanocortin and melanin-concentrating hormone 2 controlling pigmentation (Kawauchi, 2006; Takahashi et al., 2009). Additional genes associated with maturation include ependymin which is essential in long-term memory (Piront & Schmidt, 1988), as well as vasotocin and isotocin involved in circadian and seasonal cycles, responses to stress, cardiovascular function, osmoregulation and regulation of social behavior (Balment, Lu, Weybourne, & Warne, 2006; Chou, Hung, Wu, Hwang, & Hwang, 2011; Godwin & Thompson, 2012; Kasper et al., 2017)(**Table 3**). Although the details are not well understood, signals from the brain trigger the production and/or release of hormones in the next component of the BPG-axis, the pituitary.

Pituitary

The pituitary is a key organ translating signals from the brain into endocrine signaling hormones that influence maturation and e.g. regulate gonad and germ cell development. The main pituitary hormones in the BPG axis are two gonadotropins, follicle-stimulating hormone (Fsh) and luteinizing hormone (Lh), which are secreted from specific gonadotropic cells in the pituitary (Nozaki et al., 1990) by GnRH stimulation from the brain (Amano, Urano, & Aida, 1997). This hormonal signaling has mainly been studied in other salmonid species, but recent gene expression studies have confirmed these findings also in Atlantic salmon (**Table 3**). Upregulation of the gene paralogs encoding the GnRH receptor [*gnrhr4* (Melo et al., 2014; Schulz et al., 2019) and *gnrhr2bbα* (Ciani et al., 2020)] is seen in the pituitary of maturing males. Increased expression of *fshb* and *lhb* (coding for Fsh and Lh beta-subunits, respectively) is detected in the pituitaries of both maturing males (Ciani et al., 2020; Maugars & Schmitz, 2008a; Melo et al., 2014; Schulz et al., 2019; Trombley et al., 2014) and females (Andersson et al., 2013). These molecular genetic studies found that during gametogenesis, *fshb* expression is highest during early and mid-stage of spermatogenesis and oogenesis. In contrast, expression of *lhb* peaks at spermiation (**Table 1**) and the onset of ovulation.

Environmental cues affect hormonal signaling in the pituitary. Exposure of salmon males to salt water increases *gnrhr4* and *fshb* expression, and induces stronger stimulation of the onset of spermatogenesis compared to fresh water (Melo et al., 2014). Decreasing photoperiod induces more efficient *lhb* expression and, therefore, faster completion of spermatogenesis than longer exposure to light (Melo et al., 2014).

Released gonadotropins circulate in the blood and bind to their corresponding receptors in the developing gonads (testes and ovaries) where they contribute to regulating expression of the gonad-secreted sex hormones (Miwa, Yan, & Swanson, 1994; Yan, Swanson, & Dickhoff, 1992). Fsh is mainly required to induce and maintain gonadal growth, as evidenced by increased levels of Fsh in the plasma at the onset of vitellogenesis (yolk formation) and spermatogenesis, while Lh peaks in the plasma during spawning, suggesting that it is required for final gonad maturation (Breton, Govoroun, & Mikolajczyk, 1998; Gomez et al., 1999; Prat, Sumpter, & Tyler, 1996; Suzuki, Kanamori, Nagahama, & Kawauchi, 1988).

Beyond gonadotropins, additional pituitary hormones affecting gonad development and other processes involved in maturation include the somatotropin hormone family members. It has been shown that genes encoding somatotropin (i.e., growth hormone, Gh) and somatolactin are upregulated in the pituitary of mature females (Benedet, Andersson, Mittelholzer, Taranger, & Bjornsson, 2010; Benedet, Bjornsson, Taranger, & Andersson, 2008) (**Table 3**). Both of these hormones are known to influence steroid biosynthesis, gonad development generally, and spawning (Benedet et al., 2008; Le Gac et al., 1993). More specifically, somatolactin is suggested to be involved in the regulation of body coloration, plasma calcium and phosphate metabolism during vitellogenesis, maturation-induced fasting, and lipid metabolism in oocyte maturation (Benedet et al., 2008). Taken together, it is clear that pituitary-derived hormonal regulation is a complex process aiming to ultimately produce mature gametes via gradual development of the gonads.

Gonads

The final phase of maturation in the BPG axis is the development of mature gonads. Gonadal differentiation starts during embryonic development, and ovaries and testes are already distinguishable a few weeks after hatching (von Schalburg et al., 2011). The main inducers of the gonad development are sex hormones stimulated by the pituitary-secreted gonadotropins, Fsh and Lh, (see previous section) which bind to their corresponding receptors in the ovary and testis. In the Atlantic salmon ovary, the Fsh receptor gene, *fshr*, is expressed at a stable basal level during maturation and upregulated only post ovulation (Andersson et al., 2013) which differs from male parr in which *fshr* expression is upregulated in maturing testis and peaks during late spermatogenesis (Maugars & Schmitz, 2008a) (**Table 3**). These studies also show that the Lh receptor gene, *lhcgr*, is upregulated in both maturing ovaries and testes and peaks at ovulation and spermiation, respectively. In contrast to parr, in grilse testes, both *fshr* and *lhcgr* downregulate towards the late stages of spermatogenesis (Schulz et al., 2019) (**Table 3**).

In male salmonids, 11-ketotestosterone (11KT) is the primary androgen (male sex hormone) (Antonopoulou & Borg, 2016). 11KT secretion in testes is induced by Fsh during early spermatogenesis (Maugars & Schmitz, 2008a) when it stimulates spermatogonial differentiation with the help of testosterone (T) (Melo et al., 2015). Later in spermiogenesis, the release of 11KT is mediated by Lh instead of Fsh (Maugars & Schmitz, 2008a). In addition to spermatogenesis, 11KT is also known to influence secondary male, and also female, sexual characteristics in salmonids (Idler, Bitners, & Schmidt, 1961; Kudo et al., 2018). During spermiation, the plasma levels of 11KT and T decline (Baynes & Scott, 1985; Planas & Swanson, 1995; Sakai, Ueda, Suzuki, & Nagahama, 1989) while levels of the main maturation-inducing hormone, Lh-induced 17α,20β-dihydroxy-4-pregnen-3-one (17,20P) increase to finalize sperm maturation (Baynes & Scott, 1985; Fitzpatrick, Van der Kraak, & Schreck, 1986; Le Gac & Loir, 1988; Planas & Swanson, 1995; Sakai et al., 1989; Ueda, Young, Crim, Kambegawa, & Nagahama, 1983). 17,20P is also suggested to induce sperm motility in the sperm duct (Miura, Yamauchi, Takahashi, & Nagahama, 1992) and be associated with the control of the ionic composition of seminal plasma (Baynes & Scott, 1985).

Fish gonads are comprised of both mitotic (males: Sertoli and Leydig cells; females: granulosa cells) as well as meiotic (spermatozoa, ova) cell types that are connected to the endocrine networks regulating maturation. The function of Sertoli cells in males is to support the differentiation of germ cells into functional sperm and phagocytize residual cell bodies (França, Nóbrega, Morais, De Castro Assis, & Schulz, 2015). In seasonal breeders such as Atlantic salmon, Sertoli cells also phagocytize unejaculated seminal fluid and spermatozoa. The number and function of Sertoli cells in fish including salmon are dynamic and change as a function of maturation status (França et al., 2015).

The early stages of male maturation involve mitotic proliferation of Sertoli cells, which is required for increases in undifferentiated spermatogonia (Schulz et al., 2005). Sertoli cell proliferation during maturation is connected to endocrine factors such as estrogens, androgens, progestins, and thyroid hormone (Morais et al., 2013; Schulz et al., 2005). Sertoli cells express key genes that control whether or not male germ cells differentiate, undergo meiosis, and mature into functional sperm (**Table 3**). Along with Fsh (see previous section), androgen-regulated Sertoli cell factors Anti-Müllerian hormone, Amh, insulin-like growth factor 3, Igf3 (sometimes also called igf1), and insulin-like 3, Insl3, constitute a core regulatory network that activates the early stages of spermatogenesis before meiosis (spermatogonial phase) (Crespo et al., 2019; Maugars & Schmitz, 2008b; Morais et al., 2017; Nóbrega et al., 2015; Sambroni, Rolland, Lareyre, & Le Gac, 2013; Schulz et al., 2019; Skaar et al., 2011; Skaftnesmo et al., 2017). Additionally, expression of two genes encoding transforming growth factor beta (TGF-beta) factors have been shown to be associated with maturation in Sertoli cells: *gsdf, gonadal soma-derived growth factor*, is downregulated and *inha*, *protein inhibin alpha chain*, upregulated in mature testis (Kleppe et al., 2020)(**Table 3**).

In female salmonids, Fsh enhances the production of estradiol (E2) (Montserrat, Gonzalez, Mendez, Piferrer, & Planas, 2004; Oppen-Berntsen et al., 1994; Suzuki, Nagahama, & Kawauchi, 1988), that induces zonagenesis and vitellogenesis (i.e., eggshelladiata protein and vitellogenin production, respectively) of maturing oocytes (Celius & Walther, 1998; Oppen-Berntsen, Gram-Jensen, & Walther, 1992). When approaching ovulation, the levels of E2 decrease and, instead, Lh stimulates the production of 17,20P (Suzuki, Nagahama, et al., 1988) to induce the final oocyte maturation and ovulation (Fitzpatrick et al., 1986; Nagahama & Adachi, 1985; Nagahama et al., 1983; Scott, Sheldrick, & Flint, 1982; Suzuki, Nagahama, et al., 1988; Young, Crim, Kagawa, Kambegawa, & Nagahama, 1983).

Early gonadal development in female salmon starts with transformation of primordial germ cells into primary oocytes, after which the oocytes stay quiescent and meiosis is stalled until puberty is reached. Pubertal stages include vitellogenesis (growth) and the completion of meiosis, ending in ovulation (Lubzens, Young, Bobe, & Cerdà, 2010). Gene expression changes at different stages of oocyte growth indicate that in addition to Fsh, Amh and Gsdf seem to play a role in regulating the onset of female puberty in coho salmon (Luckenbach, Iliev, Goetz, & Swanson, 2008). In Atlantic salmon, however, *gsdf* expression has been shown to stay unchanged, but, instead, *inha* is upregulated in granulosa cells of early vitellogenic ovary during puberty (Kleppe et al., 2020) (**Table 3**).

Molecular factors resulting in variation in maturation

One of the most important molecular processes that controls sexual maturation is cell fate commitment regulation, the potential for cells to proliferate and differentiate into particular kinds of cells (Plusa & Hadjantonakis, 2018). From the maturation perspective, this is a key process as it is linked with decisions related to allocating resources between e.g. growth vs gonadal development (Jonsson & Jonsson, 2003). Two key molecular pathways, Hippo and Wnt signaling, are known to be involved in this process. These two pathways interact with each other (Varelas et al., 2010) to regulate body axis patterning and organ size during development by controlling cell proliferation, differentiation and migration, and they are conserved in both vertebrates and invertebrates (Halder & Johnson, 2011; Meng, Moroishi, & Guan, 2016; Petersen & Reddien, 2009; Teo & Kahn, 2010). Studies show that both pathways regulate gonad development in salmonids such as Atlantic salmon (Kjærner-Semb et al., 2018; Skaftnesmo et al., 2017) and rainbow trout (Sambroni et al., 2013).

In Atlantic salmon post-smolts, downregulation of the Hippo signaling genes *vgll3* and *tead3*, both associated with sea age, and *neurofibromin 2*, *nf2*, is seen in maturing testis compared to that of immature salmon, whereas the same genes are upregulated in regressing testis (Kjærner-Semb et al., 2018) (**Table 3**). These findings, combined with the localization of *vgll3* expression in testicular Sertoli cells, suggest that Vgll3 and other members of the Hippo signaling pathway may function as inhibitors of Sertoli cell proliferation in immature testis (Kjærner-Semb et al., 2018). In female salmon, however, the opposite pattern of *vgll3* expression has been reported (Kjærner-Semb et al., 2018). Further, a sex-specific expression pattern is seen in the *vgll3* paralogs. For example, the sea age-associated paralog on chm25 is expressed in testis and a second paralog on chromosome 21 is expressed in the ovary (Kurko et al., 2020). In addition to taking part in Sertoli cell proliferation inhibition, Vgll3 is also a central actor in the decision of mesenchymal stem cell commitment by inducing chondrocyte and osteocyte differentiation and inhibiting adipocyte maturation as seen in a murine cell line (Halperin et al., 2013). This commitment decision is likely critical to the sexual maturation process of salmon to enable allocation of fat-derived energy for gonad development at the right time. Cell fate commitment regulation by Vgll3 has been suggested to be conducted via actin cytoskeleton assembly control with assistance from Akap11 (Kurko et al., 2020), encoded by another gene associated with sea age in Atlantic salmon.

An additional gene associated with maturation, *six6*, encodes a transcription factor that has been shown to regulate maturation of the GnRH neurons and expression of GnRH in the mice hypothalamus (Larder, Clark, Miller, & Mellon, 2011), as well as transcription of the gonadotropin genes in the gonadotrope cell line in mice (Xie et al., 2015). Its expression has been detected also in the Atlantic salmon brain and testis (Kurko et al., 2020) and shown to be upregulated in mature parr testis (Guiry et al., 2010), suggesting its importance in the BPG axis in salmon as well. Genetic variation in *six6* associated with age-at-maturity may influence differential timing of the BPG axis activation via the role of Six6 in regulating neuronal and hormonal development. Moreover, expression of two genes, *slc38a6* and *rtn1*, encoding proteins involved in neuroendocrine secretion in the BPG axis and located in the same genomic region as *six6*, is shown to correlate with *six6* expression in several salmon juvenile life history stages (Kurko et al., 2020). This further emphasizes the importance of this genomic region and the BPG axis in the regulation of maturation.

Physiological status and maturation

After embryonic development, Atlantic salmon fry need to initiate feeding as early as possible to allow for adequate lipid storage which affects the timing of maturation (Rowe et al., 1991). In Atlantic salmon males, there is a positive correlation between storage lipids and allocation of resources to gonadal development during summer months (Rowe et al., 1991). Fasting during the spring delays maturation because stored lipid reserves are required for maturation the following autumn (Herbinger & Friars, 1992; Rowe et al., 1991). If feeding is not sufficient, maturation will be inhibited until the following year (Thorpe, 2007).

The gene leptin has roles in feeding, adiposity, metabolism, and reproduction (Park & Ahima, 2015). Leptin is thought to affect food intake in a wide range of vertebrate taxa and monitor energy reserves to regulate pubertal development in eutherian mammals (Sprent, Jones, & Nicol, 2012). In salmon, leptin is expressed at low levels in the liver. Leptin receptor genes are expressed at low levels in testis of non-maturing male parr during periods of fat accumulation and growth (Trombley et al., 2014). In mature males that have already allocated energy from fat stores to developing gonads, leptin is upregulated (Trombley et al., 2014).

Atlantic salmon expend a substantial part of their somatic energy reserves during upstream migration and spawning. For example, the total body lipid content dropped from 11% before upstream migration to less than 2% after spawning (Jonsson et al., 1997). A significant component of this large depletion of lipids goes to gametogenesis and reproductive behavior since feeding is arrested during the return migration (Rowe et al., 1991; Thorpe, 1994). During this time, females expend 20-25% of their weight into gonads for egg production, whereas males are invest 3-9% of body weight into gonads (Rowe et al., 1991; Thorpe, 1994).

Practical applications

Due to the high economic value and significant cultural importance of the species (Houston & Macqueen, 2019), a brief overview of how knowledge of Atlantic salmon maturation can be applied in practice is warranted. Here, we focus on how understanding variation in maturation trajectories may inform conservation and management efforts, commercial and recreational fisheries, and aquaculture.

Conservation of genetic diversity

Life history features of Atlantic salmon such as being long lived, having a wide diversity in life history strategies (to which variation in maturation is a major contributor) and thereby, overlapping generations (Chaput, Dempson, Caron, Jones, & Gibson, 2006; Erkinaro et al., 2019; Hutchings & Jones, 1998) can improve the abundance, genetic diversity, and the ability of populations to adapt to new environmental conditions. The presence of individuals with alternative reproductive strategies in a population also has the potential to reduce inbreeding by increasing the occurrence of matings between individuals from different cohorts. For instance, the contribution of mature male parr to spawning has been shown to increase the genetic diversity of populations and effective population size (N_e), as anadromous females are more likely to be older and from a different cohort than their mature male parr mates (Juanes, Perez, & Garcia-Vazquez, 2007; Perrier, Normandeau, Dionne, Richard, & Bernatchez, 2014). Jones & Hutchings (2002) estimated the reproductive contributions of mature male parr to moderately increase N_e in a mating experiment with anadromous adults. In wild populations**,** Perrier et al. (2014) showed a 1.8 fold increase in the effective number of breeders and Saura et al. (2008) a two to three-fold increase in N_e due to mature parr spawning. Perrier et al. (2014) also reported an 11% increase in the number of alleles in progeny due to contribution of mature male parr. They found that relatedness between mature parr and anadromous females was significantly lower than between anadromous adults, suggesting that alternative reproductive strategies may reduce long-term inbreeding depression at the population level.

Variation in maturation may improve population genetic diversity. For instance, Vähä et al. (2007) reported that the proportion of late maturing (multi-sea winter) females was the best predictor of genetic diversity among four landscape variables and explained ~80% of the observed variation in allelic richness at microsatellite loci in several populations of the Teno River in Northern Europe. Life history diversity and overlapping generations may also stabilize variance in genetic diversity (Gaggiotti & Vetter, 1999; Vähä et al., 2007) and the abundance of individuals over time via the portfolio effect (see also Anderson, Cooper, & Dulvy, 2013; Schindler et al., 2010). Simply stated, the portfolio effect is the diversification of risks reducing the overall impact of negative effects, e.g. environmental disturbances occurring at particular locations and/or during a limited period of time (Schindler, Armstrong, & Reed, 2015; Tilman, Lehman, & Bristow, 1998). Schindler et al. (2010) also exemplified the commercial significance of life history diversity in sockeye salmon *O. nerka* by calculating that losing population and life history diversity would result in ten times more frequent fishery closures.

Fisheries management

Understanding maturation processes is central to fisheries as management programs are often based on estimation of the minimum size required for sexual reproduction (Coggins, Catalano, Allen, Pine, & Walters, 2007; Erkinaro et al., 2019; Uusi-Heikkilä et al., 2015). This consideration is particularly important as late-maturing salmon are becoming rarer in many wild Atlantic salmon populations (Chaput, 2012; Erkinaro et al., 2019).

Fishery management based on body size limits likely select individuals with different maturation strategies within the same population. In salmon, the situation is complicated because individuals are harvested at different life history stages and maturation states. For example, salmon are fished when immature in marine feeding grounds, or when mature or maturing in coastal waters or in the river. Mixed-stock fisheries may alter the timing of maturation in different populations if maturation strategies differ among populations. The influence of male parr maturation may also be relevant to fisheries management. For instance, it is estimated that approximately 60% of the adult male salmon production is lost due to male parr maturation in a natural population in southwest Newfoundland (Myers, 1984). As a result, fisheries may have different ecological and evolutionary consequences for each population of the mixed stock, unless both the population of origin and the life history composition of each population of the mixed stock are taken into account. Molecular and scale age approaches now enable detailed life history information to be estimated with relatively straightforward approaches (e.g., Johnston et al., 2013; Johnston et al., 2014; Vähä, Erkinaro, Falkegård, Orell, & Niemelä, 2017). However, the economic loss due to male parr maturation in wild populations remains an open question.

Fishing pressure targeting individuals differently according to their size may play a role in the observed reduction in the frequency of late-maturing Atlantic salmon (Czorlich et al., 2018), but evidence for this is inconclusive. The effect of genetic changes associated with fishing, i.e., fishing-induced evolution (Conover, Arnott, Walsh, & Munch, 2005; Reznick & Ghalambor, 2005), on salmon sea age may be more difficult to predict and interpret than has been assumed based on phenotypic and ecological data (Kuparinen & Hutchings, 2017, 2019). The results of Kuparinen and Hutchings (2017, 2019) and Oomen et al. (2020) demonstrate how the outcomes of size-selective fishing can depend on the genetic architecture behind the trait being selected for, and highlight the unpredictability of the evolutionary outcomes of different fishing strategies.

The timing of the salmon return migration preceding the reproductive season is used to determine the time window of when fishing is permitted in a riverine fishery in northern Finland and Norway (Erkinaro et al., 2019) and also the mixed-stock fishery in the northern Baltic Sea (Suuronen & Jounela, 2010). This is because females and large, multi-sea winter, and repeat-spawning salmon tend to return to rivers early in the season (Erkinaro, Dempson, Julkunen, & Niemelä, 1997; Jokikokko et al., 2004; Jonsson et al., 1990; Jutila et al., 2003; Niemelä, Erkinaro, et al., 2006; Niemelä, Orell, et al., 2006; Quinn et al., 2006; Shearer, 1990). Therefore, fishing of individuals returning early in the season may lead to relative over-harvesting of females and later maturing salmon (Erkinaro et al., 2019; Niemelä, Erkinaro, et al., 2006). As return migration timing appears to be a highly heritable trait (Stewart, Smith, & Youngson, 2002), such exploitation may contribute to long-term declines in the abundance of large adult salmon that usually enter rivers early in the season (Quinn et al., 2006). For example, it has been suggested that in some rivers prohibiting fishing in the early season may favor the spawning of multi-sea winter salmon and lead to their proportional increase in the stock (Kallio-Nyberg, Saloniemi, Jutila, & Jokikokko, 2011) and this is being implemented in some systems (Anonymous, 2018; Jokikokko & Jutila, 2005). Because of these aspects, temporal regulation of fisheries is a valuable tool for protecting maturation-related diversity of salmon stocks.

Restocking

Supplementing natural populations of Atlantic salmon through hatchery restocking programs in a manner that retains biodiversity is challenging (Fraser, 2008). Retaining diversity in maturation timing is no exception. Supplementing natural populations of Atlantic salmon through hatchery restocking programs requires thoughtful consideration of maturation. For exploited fish populations to recover from undesired consequences of fishing pressure or other causes of population decline, it is essential that fishing selection has not eroded population genetic variability in traits such as age at maturity and size (Hard et al., 2008). Knowledge of the *vgll3* locus (Ayllon et al., 2015; Barson et al., 2015) may be used to promote diversity in wild salmon populations and hatchery broodstocks for restocking purposes. Here, targeted assays can rapidly and cost-effectively genotype the genomic region containing the *vgll3* locus in large numbers of fish (Bernatchez et al., 2017; Czorlich et al., 2018). These assays may predict the age when stocked adults return to fresh water to spawn, and be used to control the frequency of the late maturation allele in parr and/or smolts that are released into the wild. This approach could help guide breeding programs to produce late maturing individuals of salmon and possibly other exploited fish species if they exhibit similar shifts in the timing of maturation. However, this strategy has the potential to backfire, if the environmental conditions selecting against large, late maturing individuals are not well understood (Kostow, 2004). In addition, populations in captive breeding programs may rapidly lose genetic diversity and fitness (reviewed in Fraser, 2008). Thus, caution is warranted in applying “gene-targeted” conservation and management planning (Kardos & Shafer, 2018; Pearse, 2016) by selective breeding and reintroductions of late maturing fish into wild populations.

Recreational angling

Maturation affects size and abundance of Atlantic salmon and the presence of prized large salmon is essential to recreational fisheries to attract anglers (Anderson & Lee, 2013; Beardmore, Hunt, Haider, Dorow, & Arlinghaus, 2015). Across the species distribution, recreational fishing of Atlantic salmon is of great economic importance (Myrvold, Mawle, Andersen, & Aas, 2019). A number of country- and river-specific economic assessments support the high economic value of recreational fisheries (e.g., Butler, Radford, Riddington, & Laughton, 2009; Gardner, 2011; Pohja-Mykrä et al., 2018; Pokki et al., 2018). In total, anglers of wild salmon across the North Atlantic were estimated to spend 300-500 million euros in 2017 in expenditures related to angling (Myrvold et al., 2019).

The decrease in the frequency of late maturing, large Atlantic salmon in many populations (Chaput, 2012) likely impacts recreational fisheries. First, larger adults produce more offspring (Fleming, 1998; Mobley et al., 2020; Mobley et al., 2019) and are therefore important for the long-term viability and sustainability of natural salmon populations. Second, the opportunity to catch large salmon is an important draw for recreational fishers, such as tourist anglers who typically prefer larger sizes of fish (Anderson & Lee, 2013; Beardmore et al., 2015). Because selective harvesting can influence trends in body size and migration timing in Atlantic salmon (Quinn et al., 2006), it is important to carefully consider the sex and age at maturity of salmon harvested by recreational anglers when developing management regulations. The substantial economic benefits provided by regional recreational fisheries may also affect the optimal design of commercial fishing strategies, fishing allocation policies, and international fisheries management of Atlantic salmon stocks on a larger scale (Oinonen et al., 2017). Taken together, efforts to maintain and increase the attractiveness of Atlantic salmon to recreational anglers should take into account variation in age at maturity when selecting optimal fishing strategies and conservation measures that aim to maximize the economic benefits of different fisheries.

Aquaculture

Similar to wild populations, aquaculture Atlantic salmon face a trade-off between growth and maturation. However, early sexual maturation in aquaculture is problematic because it decreases size and flesh quality (reviewed in: Good & Davidson, 2016; Taranger et al., 2010) and represents a large economic loss for the industry (Johnston et al., 2006; McClure, Hammell, Moore, Dohoo, & Burnley, 2007). When farmed salmon become sexually mature, their growth rate decreases (Gjerde, 1984). This decrease in growth occurs because energy stores are primarily used for sexual development (Hendry, Berg, & Quinn, 1999). During this time, feed consumption is reduced or completely stopped prior to, or during, maturation (Kadri, Mitchell, Metcalfe, Huntingford, & Thorpe, 1996). For these reasons, fish farms harvest at the onset of sexual maturation (Aksnes, Gjerde, & Roald, 1986; Taranger & Hansen, 1993).

In aquaculture, the timing of maturation is controlled by manipulating environmental maturation parameters such as photoperiod and temperature (Bromage et al., 2001; King & Pankhurst, 2007; Mohamed et al., 2019; Pankhurst & Porter, 2003). However, these manipulations only partially reduce the problem of early maturation (Taranger et al., 2010). McClure et al. (2007) estimated in Canadian sea farms that economic losses are in the range of $11 - $24 million CAD per year for the early maturation in salmon. In Chile, 50% of the total costs of production can be required for feed (Bjørndal, 2002). The feed conversion ratio (FCR) decreases during maturation, resulting in large economic losses. Stead, Houlihan, McLay, and Johnstone (1999) reported that a low FCR resulted in economic losses in a study of feed consumption and growth performance in maturation in salmon. Despite the huge economic losses resulting from of early maturation, a study using growth-selected salmon lines demonstrated a 7-10% reduction in the proportion of mature male parr (Debes & Hutchings, 2014). This result suggests that economic loss due to male parr maturation may decrease in commercial salmon lines.

Future outlook

Our current understanding of maturation in Atlantic salmon has gained a new perspective due to recent breakthroughs in comprehending the ecological conditions, genetic-based traits, and molecular and physiological processes underlying maturation. Looking toward the future, we provide an overview of research areas that we think will be important next steps for maturation research.

Understanding how previous life-history stages affect maturation: the value of technological advances in longitudinal studies

In section 2, we noted that maturation is a continuous process and that developmental processes initiated during embryonic development may influence maturation. However, we have only fragmented knowledge of how genetics and ecological factors related to specific developmental stages affect maturation during later stages, how these processes interact and/or accumulate during maturation, and how these processes ultimately affect fitness. Progress to date is thanks, in large part, to the ability to track monitor maturation of the same individuals at different points in their life-history. For example, longitudinal studies using traditional approaches including common garden studies (Debes et al., 2020; O'Toole et al., 2015; Skaala et al., 2019), tagging (Chaput et al., 2018; Thorpe, Ross, Struthers, & Watts, 1981), inferring life history strategies via scale readings (e.g., Erkinaro et al., 2019; Mobley et al., 2020), or a combination of several of these (Norrgård, Bergman, Schmitz, & Greenberg, 2014) have illuminated patterns of maturation in a variety of ecologically relevant settings.

Currently, trade-offs related to the specific methodological approaches limit possibilities to generalize, and often result in a focus on interactions between a limited number of life history stages. For example, common garden studies allow environmental manipulation, but the environment is generally not reflective of what would be experienced in the wild. Tagging experiments are prone to low sample sizes in later life-history phases due to poor survival and these, but also studies utilizing scale-inferred life-history information, generally have limited scope regarding the specific environmental conditions individuals have experienced, particularly in the poorly understood marine phase.

We view recent and future technological advances in longitudinal studies as playing a pivotal role in linking maturation between different life history stages at the level of the individual. For example, although cost and size remains prohibitive for use in large numbers and at all life-history stages, satellite tags hold great potential to provide individual-level information about location and environmental conditions in the future (e.g., Strøm, Thorstad, Hedger, & Rikardsen, 2018). Advances in stable isotope composition analysis can provide more detailed insights into long distance migrations without the need for tagging (Matsubayashi et al., 2020), while decreasing costs for genetic tagging offer opportunities for improving sample sizes via “close-kin mark-recapture” (Bravington, Grewe, & Davies, 2016). Finally, eDNA techniques may be used to determine kinship, sex ratios, population size, and density, although its application for longitudinal studies at the individual level is unclear based on current practices (Adams et al., 2019; Spear, Embke, Krysan, & Vander Zanden, 2020). In the future, studies that incorporate such technological advances should help to reveal how genetic and environmental factors influence maturation over the course of an individual’s lifetime.

Ecological factors affecting maturation: unraveling maturation during the marine phase

The majority of studies that experimentally test how ecological factors affect maturation have focused on the freshwater phase (**Table 1**). This is mostly due to practical reasons associated with capturing, rearing, and tracking individuals. Juveniles can be electrofished from streams in high abundance compared to seafaring post-smolts and adults, embryos and parr are much smaller than their post-smolt counterparts and thus do not require as extensive facilities for rearing and monitoring, and mature male parr can be reared within one year. Such studies have provided a wealth of information on the ecological factors affecting maturation during the early life stages. However, knowledge gaps remain concerning later life history stages. For example, gaining a better understanding of the ecological factors that affect the less understood female maturation process is particularly important since reproduction is ultimately dependent upon female fecundity (Fleming, 1998; Fleming, 1996; Heinimaa & Heinimaa, 2004). A second limitation of the focus on pre-marine migration maturation is that other critical maturation time points, such as the ecological factors that affect maturation during the marine phase, are not well understood.

In the marine phase, the factors that influence maturation timing and the return migration are partially genetically determined, yet growth and diet still play a role in determining maturation. A better understanding of how maturation is triggered at sea is partially obscured by the difficulty of tracking individuals on their return migration from feeding grounds. One way to overcome this stumbling point is to combine long-term climate and prey species data and monitoring of salmon at sea with genetic and diet studies, at different times of the year. For example, focusing on the return migrating salmon during the summer and fall may help to understand the physiological changes linked with maturation.

Further, studies accurately estimating reproductive fitness in entirely natural systems are few. How maturation at different time points influences fitness is little known both in experimental conditions and in natural populations (Fleming, 1998; Mobley et al., 2020). This can be solved by long-term pedigree studies, breeding experiments and modeling approaches aimed at understanding the ecological factors and underlying genetics of reproductive fitness (e.g., McGinnity et al., 2003; Mobley et al., 2020; O'Sullivan et al., 2019). For example, noting the strong effect of incubation temperature on the growth and timing of the return migration, how incubation temperature affects the reproduction and survivorship of the F1 generation is still unknown. This could be important for adaptation in the face of climate change.

There are also new opportunities for understanding ecological factors linked with maturation thanks to the recent advances in understanding the genetic basis of maturation strategies. Large-effect maturation loci, such as *vgll3*, can be used as ‘markers’ of the likely future life history strategy of individuals already during the earliest developmental stages. Thus merging genetic information with ecological data may help to disentangle differences in maturation strategies during different life history stages.

Genetics of maturation: Functional validation of genes associated with maturation

Functional validation of genes in candidate regions associated with maturation is a logical next step to confirm their role in Atlantic salmon maturation. Validation should include *in vitro* (cell line), *in vivo* (tissue, whole organism) and *in silico* (computational modelling) studies during different developmental life history stages to further our understanding of the roles of these genes. Some achievements have already been accomplished, for example, in functional studies of *vgll3*, *akap11* and *six6* (Kjærner-Semb et al., 2018; Kurko et al., 2020; Verta et al., 2020), but more research is required to fully understand the molecular roles of these genes, as well as genes they interact with, in the maturation process.

Further research on gene expression at both transcriptional (mRNA) and translational (protein) level, as well as on epigenetic modifications, will be necessary to determine, potentially complex, molecular pathways that candidate genes with different genotypes take part in, ultimately leading to phenotypic variation directly in maturation or maturation-related processes. Molecular functions of target genes can be studied in a detailed manner at the cellular level by examining, for example, mRNA expression by single-cell qPCR and RNAseq or cellular location of mRNA and protein using *in situ* hybridization and antigen labelling techniques, respectively. Further, there are several techniques to study protein-protein interactions which can reveal novel information on potential binding partners of candidate genes. In the case of *vgll3* and *six6* encoding transcription factors, chromatin immunoprecipitation assay (ChIP-Seq) would provide interesting knowledge about the transcriptional targets of these proteins. Additionally, reporter assays enabling studying promoter activity could shed light on whether noncoding regions with SNPs associating with age-at-maturity [e.g., the noncoding region between *vgll3* and *akap11*, (Barson et al., 2015)] are actually regulatory regions and how genetic variation in these regions affects regulation of the target gene expression.

An exciting new way to study the functional importance of candidate genes is to use genome editing techniques. CRISPR-Cas9 technology is being increasingly used to knock-out or edit genes, whereas RNA interference (RNAi) can be used to knock down expression, at the organismal or cellular level to examine the effect on the phenotype and downstream molecular pathways. The CRISPR-Cas9 technique has already been successfully implemented in Atlantic salmon (Datsomor et al., 2019). Gene editing by the CRISPR-Cas9 system would allow for converting a certain genotype to another. For example, modifying a *vgll3 EE* genotype into an *LL* genotype and *vice-versa* in a fertilized egg would demonstrate if an artificial *vgll3* genotype has the same influence on phenotypic variation as a natural *vgll3* genotype. Provided appropriate experimental and ethical safeguards were in place, experiments such as the one outlined above would allow a deeper understanding of the regulatory pathways controlling maturation.

Maturation candidate genes identified via QTL and genetic studies differ across studies. Determining the reasons these differences are observed is key for understanding the genetic architecture of Atlantic salmon maturation. Lack of power in some studies may have given rise to such differences, however, it remains unknown whether in some cases this is a result of differences in the effect of these genes among populations or lineages. Future work on identifying candidate genes should aim to survey a wide range of populations representing all lineages of Atlantic salmon. Additionally, examining population-specific gene-by-environment effects may help to elucidate why differences in gene effects may occur due to differences in life history traits and ecological factors experienced in different populations. Furthermore, sex-dependent dominance at the *vgll3* was observed in European wild populations (Barson et al., 2015). However, no dominance pattern was observed in males from a Norwegian aquaculture strain (Sinclair-Waters et al., 2020). This raises the question whether sex-dependent dominance at the *vgll3* locus exists in all populations and if there are specific conditions in the wild that give rise to this dominance effect (e.g. limited food availability). Lastly, gene effects may differ among sexes and future work should investigate sex-specific maturation genes.

Molecular and physiological mechanisms of maturation: incorporating a greater diversity of life history stages and molecular approaches

Beyond the functional validation of genes associated with maturation is the need for a systemic approach that integrates molecular and physiological communication across the organism. The function of each part of the BPG axis is well known with regards to maturation and its timing in salmonids. Still obscure is the causality between activation of the BPG axis and initiation of the maturation process, and whether inter-individual variation in the elements of the BPG axis can explain variation in maturation.

Currently, it is unclear how genetic variation in life history genomic regions interacts with the BPG axis, though it is likely that *six6* is involved in neuronal development and hormonal regulation of this axis, as in mice (Larder et al., 2011; Xie et al., 2015). Genetic variation in *six6* (Barson et al., 2015; Sinclair-Waters et al., 2020) and other genomic regions may explain differences in the timing of BPG axis activation, and, therefore, in maturation. The molecular role of *six6* and the link between its genetic variation and functional outcome in the BPG axis should be examined in salmon. Future questions need to address the evolution of the BPG axis in populations with known genetic backgrounds and maturation status. Studies addressing these questions should include more profound and global approaches to discover novel genes that regulate maturation.

How environmental influences, such as changes in photoperiod, temperature, salinity, interspecific competition, and diet, affect gene expression, hormonal regulation, and lipid metabolism has been extensively studied with respect to maturation. Future research would benefit not only from the addition of genetic background information and population structure, but also from more extensive application of “big data” approaches such as metabolomics and lipidomics (broad-scale analyses of hundreds or thousands of metabolites and lipid species, respectively) to provide a broader profile of the molecules involved in the maturation process as well as their associations and interactions.

Climate change and other anthropogenic issues affecting maturation: can salmon adapt?

Given the close relationship of salmon maturation with several environmental factors including temperature, it is no surprise that range-wide rapid decline in salmon stocks has been linked to global climate change (Lehnert et al., 2019; Mills, Pershing, Sheehan, & Mountain, 2013). In particular, declines of large, later maturing individuals of up to 88% have been observed in regions across the Atlantic salmon range (Chaput, 2012). How well Atlantic salmon can adapt to a changing climate may be limited, in part, by the species’ evolutionary response to selection (Radchuk et al., 2019). Therefore, a major goal of future research should be to investigate how predicted increases in temperature will affect the timing of maturation, reproductive fitness of different life history strategies, and the long-term persistence of natural salmon populations (Cline, Ohlberger, & Schindler, 2019; Hedger et al., 2013; Sundt-

Hansen et al., 2018). Understanding how future climate change scenarios will impact Atlantic salmon will require better knowledge of how temperature at different stages of life history (e.g., freshwater vs marine phases) influences maturation trajectories, as well as how temperature interacts with genetic factors (Debes et al., 2020).

Climate change can also be expected to have a number of indirect effects of significance for salmon maturation. For example, altered climatic conditions in the marine environment, either directly due to temperature increase, or altered current patterns, are affecting key prey species of salmon (Todd et al., 2008), and thus may affect prey abundance and distribution. This can have knock-on effects affecting growth and adiposity, and thereby, maturation. Such changes can be predicted to affect alternative life history strategies in a different manner. For example, the negative effects of reduced marine prey abundance may be greater for individuals spending multiple years at sea before reproduction (Czorlich et al., 2018). In the riverine environment, in the event of reduced rainfall, decreased water flow can decrease oxygen saturation levels, which in turn can affect metabolism, feeding rates, and growth rates (Hosfeld et al., 2008), all of which have the potential to affect maturation trajectories. Decreased water flow can also decrease the ability of large, late-maturing, individuals to reach spawning areas that were previously accessible in higher flow conditions.

Besides climate change, a variety of pernicious anthropogenic threats may influence salmon maturation in unpredictable ways. Pollution from industrial waste and pharmaceuticals, particularly those that potentially alter behavior (Klaminder et al., 2019) or interfere with normal hormonal regulation such as endocrine disrupting compounds, may alter development and maturation (Björnsson, Stefansson, & McCormick, 2011; Duffy, Iwanowicz, & McCormick, 2014; McCormick, O'Dea, Moeckel, Lerner, & Björnsson, 2005). More generally, any anthropogenic factor that can affect growth or survival has the potential to alter maturation trajectories of individuals. Therefore, invasive species (Mo et al., 2018), habitat degradation (Einum, Nislow, Reynolds, & Sutherland, 2008), barriers to migration (Marschall, Mather, Parrish, Allison, & McMenemy, 2011), over-exploitation by fisheries (Czorlich et al., 2018; Saura et al., 2010), aquaculture escapees, and inappropriate stocking (Einum & Fleming, 2001) can all potentially affect maturation of wild Atlantic salmon.

Fishing and aquaculture: potential benefits of utilizing recent discoveries

The long-term success of fisheries is highly dependent on the potential of fish stocks to adapt to changing environments. However, how salmon respond to selection has rarely been considered in fishing policies (Hard et al., 2008). This may change in the future as we gain a better understanding of the ecological and genetic factors influencing maturation in Atlantic salmon (Barson et al., 2015; Czorlich et al., 2018; Sinclair-Waters et al., 2020).

Knowledge of the genetic control of the timing of maturation is critical for understanding and predicting the evolutionary impact of fishing (Kuparinen & Hutchings, 2017; Kuparinen & Merilä, 2007). Quantifying the effects of fishing on known candidate genes (e.g. monitoring population allele frequency changes over time) will help to elucidate how maturation variability may change under different kinds of harvesting pressure. The timing and locality of fishing, and gear used, may select for individuals with differing maturation strategies, and are therefore factors to consider when quantifying the effects of fishing. Furthermore, models predicting the effects of fishing on maturation have considered a polygenic genetic architecture (i.e. many small-effect genes) and a single large-effect locus without sexual selection (Kuparinen & Hutchings, 2017). Next steps should aim to incorporate knowledge of estimated effect sizes for known candidate genes in such models. Additionally, it may be valuable to consider how linkage disequilibrium patterns within the genome may modify the effects that fishing has on maturation (see Oomen et al., 2020). Integrating new information of genes involved in maturation will help enhance and inform management strategies aimed at maintaining variability in the timing of maturation in salmon populations.

New information on genes involved in maturation, and how they function in salmon, has potential value for selection aimed at optimizing the timing of maturation in aquaculture strains. For example, new genetic knowledge could help reduce the frequency of mature male parr in aquaculture strains, and thus decrease the amount of resources and individuals with undesirable maturation trajectories. Accounting for this could help make aquaculture more sustainable. In addition, understanding how maturation is genetically correlated with other traits can help define limits of artificial selection on the timing of maturation.

Conclusions and recommendations

The ever-increasing research on Atlantic salmon maturation consolidates the species as a tractable vertebrate model system for studying various aspects of maturation (Chakradhar, 2018). Our goal for this synthesis is to provide a current overview of research on maturation in Atlantic salmon with the express purpose to identify major themes where information is lacking and thus highlight potential areas for future research. Here, we proffer our major conclusions and recommendations for the field as it moves forward.

1. ***Maturation occurs throughout the life cycle, starting from embryonic development and throughout each distinct life history stage****.* However, our knowledge of maturation during some life history stages is incomplete. For example, ecological investigations mostly focus on freshwater life-history stages, whereas less is known about maturation in the marine phase. In contrast, few genomic studies investigating maturation-related traits have been conducted on early embryonic and juvenile phenotypic traits of importance during the freshwater phase. Moreover, gene expression studies overwhelmingly focus on maturation in male parr while much less is known concerning gene expression patterns prior to the return migration and in maturing females. Finally, we still lack basic knowledge concerning how ecological and genetic factors influence embryonic development. Future research should address these gaps in our knowledge in order to pinpoint critical developmental time points and life history phases that are key to sexual reproduction in this species.

2. ***Variation in the timing of maturation promotes diversity in life history strategies.*** We are now coming to an understanding that the timing of maturation during different life history phases drives the exceptionally high life history diversity of within this species. However, many questions remain. For example, what is the genetic architecture of male parr maturation and iteroparity? How does development in one life history phase affect maturation in later stages? What is the relative fitness of different life history strategies in different environments? A combination of common garden experiments, wild pedigrees, longitudinal studies, and modeling approaches may help to answer these questions in the future.

3. ***Ecological and genetic factors influence maturation****.* A range of ecological factors, most notably temperature and photoperiod, affect maturation at different life history stages while several genetic factors including large-effect loci influence maturation during the marine phase. However, research on these factors is not yet sufficiently integrated. For example, although there is considerable knowledge of i) how ecological factors influence maturation and ii) the molecular processes of maturation generally, our understanding of how i) affects ii) and *vice versa* is much more limited. Studies that combine ecological and molecular approaches, e.g., common garden experiments, may help to disentangle the relative contributions of each of these factors to the maturation process.

4. ***Maturation processes are sex-specific and may have fitness consequences for each sex***. Males and females mature at different ages and have different physiological and metabolic requirements for reproduction*.* These differences in the timing of maturation between the sexes may start as early as embryonic development and may drive intra-locus sexual conflict at large-effect loci related to maturation. Moreover, the maintenance of alternative mating strategies and the relative contribution of male mature parr to reproductive fitness is not well understood in nature. In the future, studies that investigate differences between the sexes in traits and gene expression patterns and how these differences translate into reproductive fitness during different life stages and alternative reproductive strategies will help to illuminate sex-specific maturation processes.

5. ***Molecular and physiological maturation pathways are affected by large-effect loci***. Maturation during the marine phase is affected by large-effect loci suggesting a relatively simple genetic architecture, yet the details of how this is achieved are not well understood. Future research should take advantage of this simplified genetic architecture to identify the causal genes within the identified large-effect genomic regions associated with maturation and identify the functions of these genes using functional validation techniques.

6. ***The brain-pituitary-gonadal axis is a central player that regulates molecular and physiological processes of maturation in Atlantic salmon****.* While we are beginning to unravel the intricacies of the BPG axis, it is unclear how variation in large-effect loci controlling maturation processes and ecological factors interacts with the BPG axis. In addition, how downstream physiological and metabolic processes such as lipid metabolism and storage are regulated by the BPG axis in salmon is not well understood. Future research should focus on feedback between external ecological factors, the genetic architecture and the internal physiological processes to better understand how maturation occurs at the molecular level.

7. ***Knowledge of maturation is a key component of conservation and management programs in many populations and stocks***. Variation in maturation has positive consequences for population genetic diversity and thus its preservation can preserve the adaptive potential of populations. Moreover, genetic markers linked to large-effect maturation loci offer new avenues to further develop management and conservation tools for preserving variation in life history strategies.

8. *Climate change, fishing pressure, and other anthropogenic stressors likely have major effects on salmon maturation*. Due to their direct and indirect effects on growth and survival, various anthropogenic factors have been shown to have significant effects on maturation trajectories. Such knowledge can improve predictions concerning how populations may respond to different harvest regimes or fishing restrictions. However, considering the combined effects of harvesting and other anthropogenic factors on life-history diversity, as well as incorporating knowledge of maturation trait genetic architecture into forecasts has rarely been achieved. This would be an ambitious, yet worthy, goal for future population management aimed at preserving variation in life history strategies.

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Table 1. Examples of ecological factors affecting maturation in Atlantic salmon. Studies are listed chronologically according to life history stage and factor with a summary of the major findings.

Phase/Stage	Factor(s)	Summary of findings	References
Freshwater Phase			
Embryo	Temperature Oxygen Water exchange	Increased incubation temperature increased development rate and decreased survival. Developmental rate and survival increase with increasing dissolved oxygen and with increasing rate of water exchange.	(Hamor & Garside, 1976)
Embryo	Temperature	Increased incubation temperature decreased size of eyed eggs and alevins.	(Peterson et al., 1977)
Embryo	Temperature	Incubation temperature prior to swimup had no effect on fry growth during initial feeding. Increased temperature at first feeding increased growth of fry.	(Peterson & Martin-Robichaud, 1989)
Embryo	Temperature	Parr growth was higher in warmer incubation temperature treatments. Temperature experienced after embryo incubation did not affect growth performance of juveniles.	(Finstad & Jonsson, 2012)
Embryo	Temperature	Increased incubation temperature influenced egg size and gonad mass of males and females relative to body size. Incubation temperature did not influence age at maturity or fecundity in either sex.	(Jonsson et al., 2014)
Embryo	Temperature	Increased incubation temperature in the two months prior to hatching increased mass of eggs in next-generation (F1) females.	(Jonsson & Jonsson, 2016)
Embryo	Temperature	A 4˚C increase in incubation temperature doubled the growth as measured by weight gain in later stages (start feeding -> adult at harvest). Variation in epigenetic methylation patterns may help to explain differences in skeletal muscle growth and thermal plasticity.	(Burgerhout et al., 2017)
Embryo	Temperature	Embryos incubated in warmer temperatures returned to spawn earlier than those incubated in colder temperatures as adults.	(Jonsson & Jonsson, 2018)
Embryo	Sedimentation	Increases in fine sediment decreases survival of embryos.	(Julien & Bergeron, 2006)
Fry	Interspecific competition	Early immerging fry are more at risk to predation than later immerging fry.	(Brännäs, 1995)
Fry	Interspecific competition	Earlier-feeding fry are dominant over later immerging fry. Dominant individuals have a higher growth rate.	(Metcalfe & Thorpe, 1992)
Parr	Temperature	Increased temperature increased feed intake and growth rate among hatchery-raised 1+ parr. Lipid deposition increased with temperature.	(Koskela et al., 1997)

Parr	Temperature	Increased temperature increases metabolic rate of parr.	(Oligny-Hébert et al., 2015)
Parr	Temperature and photoperiod	Increase in 5°C above ambient temperature increased male maturation and increased oocyte size in females. Advanced photoperiod did not affect maturation.	(Adams & Thorpe, 1989)
Parr	Water flow, Nighttime light intensity	Optimal foraging efficiency is influenced by an interaction between water velocity and nighttime light intensity. On darker nights, parr prefer slower moving currents and vice versa.	(Metcalfe et al., 1997)
Parr	Interspecific competition	Dominant individuals are associated with optimal growth and survival.	(Keenleyside & Yamamoto, 1962)
Mature male parr	Temperature	Male parr maturation increases with increased temperature during the first winter in fresh water.	(Duston & Saunders, 1997)
Smolt	Photoperiod	Increased photoperiod during the spring increases growth and smoltification.	(Saunders & Henderson, 1970)
Smolt	Temperature and photoperiod	Age at smoltification was positively correlated with latitude. 82% of variation in age at smoltification was explained by growth as a function of temperature and photoperiod.	(Metcalfe & Thorpe, 1990)
Smolt	Temperature and food availability	A 2^{o}C temperature difference increased 1+ parr smoltification probability from 0.42 to 0.76, but a 6 week food restriction the previous autumn did not affect smoltification probability	(Debes et al., 2020)
Parr, Smolt	Temperature and photoperiod	Increased temperature increases growth and osmoregulatory activity. Photoperiod cues hormonal signaling to advance smoltification.	(McCormick et al., 2002)
Parr, Smolt	Temperature and photoperiod	Increased photoperiod increases hormones associated with smoltification in smolts but not parr.	(McCormick et al., 2007)
Parr and smolt	Photoperiod and temperature	Higher temperature and continuous light triggers maturation during and after smoltification in male salmon	(Fjelldal et al., 2011)
Pre and post-smolt	Temperature and photoperiod	Growth and maturation highest in continuous light. Higher proportion of male maturation was greater under higher temperature. Temperature and photoperiod interact to determine maturation.	(Imsland et al., 2014)
Smolt	Food availability	Food-restricted individuals are smaller and had lower survivorship during seawater challenge.	(Thorpe & Metcalfe, 1998)
Smolt	Oxygen	Smolts experimentally exposed to high oxygen environments had higher growth and were in better condition in both freshwater and saltwater environments.	(Hosfeld et al., 2008)
Marine phase			

Post-smolt (<1SW)	Temperature	Post-smolt survival is negatively affected by earlier than normal increases in temperature in nursery areas.	(Friedland et al., 2003)
Post-smolt (<1SW)	Temperature	Contrasting evidence that post-smolt growth during the first year at sea is negatively or positively correlated with sea surface temperature.	(Friedland et al., 2005)
Post-smolt (<1SW)	Temperature	Temperature significantly influences post-smolt growth rate, feed intake and feed conversion efficiency and stomach evacuation rate.	(Handeland et al., 2008)
Post-smolt (<1SW)	Temperature Food quality	Increased temperature and increased food quality (higher lipids to protein ratio) increased growth rate and early male maturation.	(Jonsson et al., 2013)
Grilse (1SW)	Temperature	Enhanced growth and higher survivorship of 1SW fish correlated with higher sea surface temperature.	(Friedland et al., 2000)
Grilse (1SW)	Food availability	Dietary restriction decreased condition factor and maturation of both male and female grilse.	(Duston & Saunders, 1999)
Multi-seawinter	Temperature	Increased sea temperature is associated with larger numbers of >1SW fish and fewer grilse (1SW).	(Martin & Mitchell, 1985)
Post-smolt (<1SW)	Photoperiod	Artificially longer photoperiods increased growth rate and maturation percent and advanced ovulation time of females.	(Hansen et al., 1992)
Adult	Photoperiod	Exposing salmon to constant light in winter reduces male maturation then those exposed to a natural photoperiod.	(Schulz et al., 2006)
Adult	Temperature Prey availability	Increased seawater temperature at smoltification positively increased proportion of returning adults and may be related to diet.	(Hvidsten et al., 2009)

Table 2. Examples of associations between genomic regions and maturation traits in Atlantic salmon. Maturation traits are listed chronologically according to life history stage with a summary of genetic associations found and relevant references. Positions of genes or loci have the nomenclature “chromosome ID:position” in accordance to the most recent Atlantic salmon genome assembly (ICSASG_v2) (Lien et al., 2016).

Life-history Stage/Trait	Method	Summary of associations between maturation traits and genomic regions	References
Freshwater phase			
Male parr maturation	QTL analysis (100-300 SNPs)	3 QTLs reach genome-wide significance* for male parr maturation: ssa07, ssa12, ssa20. 4 QTLs reach chromosome-wide** significance for male parr maturation: ssa05, ssa09, ssa10, ssa16. (N=493)	(Pedersen et al., 2013)
Male parr maturation	QTL analysis (40 SNPs)	1 QTLs reaches genome-wide significance for male parr maturation: ssa25. 3 QTLs reach chromosome-wide significance: ssa14, ssa19, ssa25. (N=142)	(Lepais et al., 2017)
Male parr maturation	Common garden experiment of parr with known *vgll3* genotypes	Male parr with the *vgll3*EE* genotypes reared in common garden conditions had a 10x higher maturation frequency than males with the *vgll3*LL* genotype, while *vgll3* heterozygotes were intermediate (N=384)	(Verta et al., 2020)
Early smoltification	QTL analysis (100-300 SNPs)	1 QTL reaches genome-wide significance: ssa23. 3 QTLs reach chromosome-wide significance: ssa05, ssa08, ssa13. (N=755)	(Pedersen et al., 2013)
Marine phase			
Early maturation (=1SW)	QTL analysis (6.5K SNP array)	1 QTL reaches chromosome-wide significance for male early maturation: ssa21. 1 QTL reaches suggestive significance for male early maturation: ssa10. (N=81)	(Gutierrez et al., 2014)
Early maturation (=1SW)	GWAS (6.5K SNP array)	5 SNPS reach genome-wide significance for early maturation: ssa10, ssa02, ssa12, ssa13, ssa25. (N=626)	Gutierrez et al. (2015)
Early maturation (=1SW)	Targeted genotyping of 1 SNP in *tead3*	Association with *tead3* (ssa12:79,047,648-79,123,946) and early maturation in males (*P*-value=0.046). (N=79)	(Christensen et al., 2017)
Early maturation (=1SW)	GWAS (50K SNP array)	Polygenic and sex-specific genetic architecture. 13 SNPs reach chromosome-wide significance for freshwater maturation. (N=1,846) 48 SNPs reach chromosome-wide significance for sea age at maturity. (N=2,721). No overlap between male and female associations. Two notable candidate loci include *magi2* (ssa10:60,175,081), *picalm* (ssa11:81,521,399)	(Mohamed et al., 2019)
Early maturation (=1SW)	GWAS (50K SNP array)	SNPs in *vgll3* region that are associated with sea age at maturity in European lineages were not associated with early maturation in	(Boulding et al., 2019)

		the North American lineage. However, the early alleles occurred at low frequencies in the study samples. 3 SNPs on ssa21 reach genome-wide significance for early maturation (N=773)	
Late maturation (≥2SW)	QTL analysis (100-300 SNPs)	2 QTLs reach chromosome-wide significance: ssa21 and ssa23. Ssa21 and ssa23 are homologous to chromosomes with maturation QTLs in rainbow trout. (N=81)	(Pedersen et al., 2013)
Late maturation (≥2SW)	GWAS (6.5K SNP array)	4 SNPS reach genome-wide significance for late maturation: ssa01, ssa28 6 SNPS reach chromosome-wide significance for late maturation: ssa01, ssa07, ssa16, ssa21. (N=466)	(Gutierrez et al., 2015)
Late maturation (≥2SW)	QTL analysis (6.5K SNP array)	1 QTL reaches chromosome-wide significance for late maturation: ssa18. (N=195)	(Gutierrez et al., 2014)
Sea age	Isozyme analysis (6 loci)	Non-random distribution of alleles at 1 isozyme locus, MEP-2, in 1SW vs multi-SW individuals. (N=291-648)	(Consuegra, De Leániz, Serdio, & Verspoor, 2005)
Sea age	GWAS 220K SNP array	Strong association with *vgll3* (ssa25:28654947-28659019) and sea age at maturation. Evidence of sex-dependent dominance at *vgll3* locus. (N=1,404)	(Barson et al., 2015)
Sea age	GWAS pooled sequencing. Targeted sequencing of 2 SNPs in *vgll3*	Strong association with *vgll3* (ssa25:28654947-28659019) and sea age at maturity. 74 significant SNPs (0.1% FDR) outside *vgll3* region: ssa01-ssa07, ssa09-24, ssa27-29. (N=20 per pool, 6 pools)	(Ayllon et al., 2015)
Sea age	Targeted genotyping of 2 SNPs in *vgll3* region	Correlation between *vgll3* and probability of maturing after multi-SW versus after 1 SW in three populations in Québec, Canada. Strength of correlation varies across study populations. (N=1,505)	(Kusche et al., 2017)
Sea age	Analysis of 2 SNPs genotyped using combination of qPCR and Sequenom MassArray	Association between *vgll3* and sea age at maturity in males (N=308), but not females (N=304), from the *Mowi* strain of domesticated Atlantic salmon.	(Ayllon et al., 2019)
Iteroparity	Targeted genotyping of 194 SNPs	Individuals homozygous for early allele at *vgll3* locus are 2.4 times more likely to spawn a second time than individuals homozygous for late allele. (N=1,135)	(Aykanat et al., 2019)

*Genome-wide significance level is determined according to a Bonferroni threshold that accounts for the total number of tested SNPs in the entire genome (0.05/# of tested SNPs)
**Chromosome-wide significance level is determined according to a Bonferroni threshold that accounts for only the number of tested SNPs on the focal chromosome (0.05/# of tested SNPs on focal chromosome)

Table 3. Examples of gene expression studies related to maturation in Atlantic salmon. Gene expression studies are listed according to life history stage comparisons. The method, target tissue, summary of gene expression patterns genes that show differential expression during maturation and relevant references are also listed.

Comparison	**Method, *target tissue***	**Summary of gene expression patterns during maturation**	**References**
Immature vs. mature male parr	Microarray, qPCR *Brain*	*Prl* (prolactin) and *pomc* (pro-opiomelanocortin), and other genes in biological processes such as circadian rhythm, neural plasticity, reproduction, growth, metabolism, and energy production and feeding are upregulated in mature compared to immature parr.	(Aubin-Horth et al., 2005)
Immature vs. mature male parr	Microarray, qPCR *Brain*	*Hba1* and *hba4* (alpha globin 1 and 4), *hbb* (beta globin), *apoe* (apoliporotein E), *ciapin1* (anamorsin), *ctsd* (cathepsin D), isotocin 2, vasotocin 1 and *cof2* (cofilin 2) genes are downregulated and *ctnnbip1* (beta-catenin interacting protein 1), *mch2* (melanin-concentrating hormone 2) and *tgfb2* (transforming growth factor beta 2) are upregulated among other genes in mature compared to immature parr.	(Guiry et al., 2010)
Immature vs. mature male parr, early male and female migrants (smoltification in present year) vs. late male and female migrants (smoltification next year or later)	Microarray *Brain*	Globin alpha and beta and retinol binding protein genes are upregulated both in mature parr and early migrants compared to immature parr and late migrants, respectively. Apolipoprotein, cGMP-phosphodiesterase, class III alcohol dehydrogenase, ependymin, glycerol-3-phosphate dehydrogenase, godonadotropin alpha 1, gonadotropin alpha 2, gonadotropin beta (Fsh), Na/K ATPase alpha, prolactin, pro-opiomelanocortin, rod-like opsin, selenoprotein, somatolactin, somatotropine, thr3 and transposase genes are upregulated in mature parr but downregulated in early migrants compared to immature parr and late migrants, respectively.	(Aubin-Horth et al., 2009)
Immature vs. maturing male parr	qPCR *Pituitary*	*Fshb* (follicle-stimulating hormone β-subunit) and *lhb* (luteinizing hormone β-subunit) are upregulated in maturing compared to immature parr. Expression of *fshb* increases during early spermatogenesis and remains high until late spermatogenesis but slightly decreases at spermiation. *Lhb* expression slightly increases during early- and mid-spermatogenesis and then highly raises at late spermatogenesis and peaks at spermiation.	(Maugars & Schmitz, 2008a)

Immature vs. maturing male parr	qPCR *Pituitary*	*Fshb* and *lhb* are upregulated in maturing compared to immature parr. Expression of *fshb* declines at late spermatogenesis. *Lhb* expression gradually increases during spermatogenesis and peaks at spermiation.	(Trombley et al., 2014)
Immature vs. maturing male parr	qPCR *Pituitary*	*Fshb*, *lhb* and *gnrhr2bbα* are upregulated in maturing compared to immature parr. Expression of *gnrhr2bbα* increases from early to late spermatogenesis.	(Ciani et al., 2020)
Immature vs. maturing male parr	ddPCR *Testes plus 9 other tissues*	Temporal analysis of *vgll3* expression in ten tissues across the first year of salmon development revealed a 66% reduction in testicular *vgll3* expression in maturing male parr. *vgll3*LL* genotype was associated with a tendency to delay puberty and also with expression of a rare transcript isoform of *vgll3* pre-puberty.	(Verta et al. 2020)
Immature vs. maturing male grilse	qPCR *Pituitary*	*Fshb*, *lhb* and *gnrhr4* (gonadotropin-releasing hormone II receptor) are upregulated in maturing compared to immature grilse. Expression of *fshb* increases during early- and mid-spermatogenesis but declines at spermiation. *Lhb* expression slightly increases during early- and mid-spermatogenesis and then peaks at spermiation. Expression level changes during spermatogenesis were modest for *gnrhr4*.	(Schulz et al., 2019)
Immature vs. maturing male post-smolts	qPCR *Pituitary*	*Fshb*, *lhb* and *gnrhr4* are upregulated in maturing compared to immature post-smolts. Expression of *fshb* increases during early and mid-spermatogenesis while decreases until spermiation. *Lhb* and *gnrhr4* mRNA levels increase gradually and peak at spermiation.	(Melo et al., 2014)
Immature vs. maturing female post-smolts	qPCR *Pituitary*	*Fshb* and *lhb* are upregulated in maturing compared to immature post-smolts. Expression of *fshb* gradually increases from oil droplet stage to mid-vitellogenesis with secondary yolk vesicles and maintains at a high level during late vitellogenesis with larger oocytes in tertiary yolk stage. *Fshb* mRNA level increases again and remains high during ovulation and post ovulation. *Lhb* expression increases gradually from oil droplet stage to late vitellogenesis and peaks at the onset of ovulation.	(Andersson et al., 2013)
Immature vs. maturing female post-smolts	qPCR *Pituitary*	*Sl alpha* and *sl beta* (somatolactin) are upregulated in maturing compared to immature post-smolts. Expression of *sl alpha* and *sl beta* increases during late vitellogenesis and again during ovulation, and decreases post ovulation.	(Benedet et al., 2008)

Immature vs. maturing female post-smolts	qPCR *Pituitary*	*Gh* (growth hormone) is upregulated in maturing compared to immature post-smolts. Expression of *gh* is increased during early and mid-vitellogenesis and decreased during ovulation but raised again post ovulation.	(Benedet et al., 2010)
Immature vs. maturing female post-smolts	qPCR *Ovary*	*Fshr* (follicle stimulating hormone receptor) is expressed at relatively stable level during vitellogenesis and maturation but upregulated post ovulation. *Lhcgr* (luteinizing hormone receptor) is upregulated in maturing compared to immature post-smolts. Expression of *lhcgr* gradually increases from oil droplet stage to late vitellogenesis and ovulation but decreases post ovulation.	(Andersson et al., 2013)
Immature vs. early maturing female post-smolts	qPCR *Ovary*	*Vgll3* (vestigial-like family member 3) is upregulated during early vitellogenesis (early maturing) compared to oil drop (maturing) stage in post-smolts.	(Kjærner-Semb et al., 2018)
Immature vs. maturing females	RNA-seq, qPCR *Ovary*	*Inha* (protein inhibin alpha chain) is upregulated in maturing (early vitellogenic) compared to immature females.	(Kleppe et al., 2020)
Immature vs. maturing male parr	qPCR *Testis*	*Fshr* and *lhr* are upregulated in maturing compared to immature parr. Expression of *fshr* and *lhr* increases during early and mid-spermatogenesis. *Fshr* mRNA levels peak at spermiogenesis, but *lhr* mRNA levels continue to rise at spermiation.	(Maugars & Schmitz, 2008a)
Immature vs. mature male parr	Microarray, qPCR *Testis*	*Amh* (anti-Müllerian hormone), alpha and beta globin, *col1a2* and *col1a3* (collagen 1A2 and 1A3), transferrin and zinc finger protein genes are downregulated and *apoe* and *apoc1* (apolipoproteins E and C-1), *lpl* (lipoprotein lipase), anti-leukoproteinase precursor and *six6* (SIX homeobox 6) are upregulated among other genes in mature compared to immature parr. *Amh* is downregulated in mature compared to immature adult.	(Guiry et al., 2010)
Immature vs. maturing male parr	qPCR *Testis*	*Ff1b* (FTZ-F1 homolog), *3b-HSD* (3b-hydroxysteroid dehydrogenase/D5–D4–isomerase), *11b-HSD* (11b-hydroxysteroid dehydrogenase), *StAR* (steroidogenic acute regulatory protein), *P450scc* (cytochrome P450 cholesterol side-chain cleavage enzyme), *P450c17* (cytochrome P450 17a-hydroxylase/17,20-lyase) and *P45011b* (cytochrome P450 11b-hydroxylase) are upregulated in maturing compared to immature parr. Expression of *3b-HSD*, *11b-HSD* and *P450scc* gradually increases throughout spermatogenesis.	(Maugars & Schmitz, 2008b)

		P450scc mRNA levels strongly peak at spermiation. *StAR* and *P450c17* expression increases during early spermatogenesis, decreases during mid-spermatogenesis, increases again during spermiogenesis and peaks at spermiation. *P45011b* mRNA levels increase during spermiogenesis. *Amh* is downregulated during early to mid-spermatogenesis and further spermiogenesis in maturing compared to immature parr, but reaches its initial level at spermiation.	
Immature vs. maturing male parr	qPCR *Testis*	*Lepr* (leptin receptor) is upregulated in maturing compared to immature parr. Expression of *lepr* increases throughout mid- to late spermatogenesis.	(Trombley et al., 2014)
Immature vs. maturing male grilse	qPCR *Testis*	*Fshr*, *lhr, ara1*, *ara2* (androgen receptor type a 1 & 2) and *amh* are downregulated gradually during spermatogenesis in maturing compared to immature grilse. The lowest expression for these genes is seen at spermiogenesis and spermiation. *Igf3* (insulin-like growth factor 3) is upregulated in maturing compared to immature grilse and high levels were maintaned during progress of spermatogenesis.	(Schulz et al., 2019)
Immature vs. maturing male post-smolts	RNA-seq, qPCR *Testis*	*Igf3* is upregulated and *amh* downregulated in maturing testis. Pathways that are enriched in immature compared to maturing testis include fatty acid metabolism, biosynthesis of unsaturated fatty acids, cell cycle, mitophagy, vegf signaling and progesterone-mediated oocyte maturation. Enriched pathways in maturing compared to immature testis include Wnt signaling, insulin signaling, apelin signaling, foxo signaling and autophagy.	(Skaftnesmo et al., 2017)
Immature vs. maturing male post-smolts	Microarray, qPCR *Testis*	*Insl3* (insulin-like 3) is upregulated and *amh* downregulated in maturing compared to immature post-smolts. Genes inmetabolic, purine and pyrimidine metabolism, glycerolipid metabolism, regulation of actin cytoskeleton, cell cycle and Wnt signaling pathways are upregulated in maturing compared to immature post-smolts.	(Crespo et al., 2019)
Immature vs. maturing male post-smolts	RNA-seq, qPCR *Testis*	The Hippo signaling genes such as *vgll3*, *tead3* (TEA domain transcription factor 3) and *nf2* (neurofibromin 2), and *amh* are downregulated, and *pcna* (proliferating cell nuclear antigen) is upregulated in maturing compared to immature post-smolts.	(Kjærner-Semb et al., 2018)
Immature vs. mature adult males	RNA-seq, qPCR *Testis*	*Inha* is upregulated, while *gsdf* (gonadal soma-derived growth factor) is downregulated in mature compared to immature	(Kleppe et al., 2020)

		adults.	
Immature vs. maturing male parr	qPCR *Liver*	*Lepa1* and *lepa2* (leptin) are upregulated in maturing compared to immature parr. Expression of *lepa1* and *lepa2* increases throughout mid- to late spermatogenesis and peaks at spermiation.	(Trombley et al., 2014)