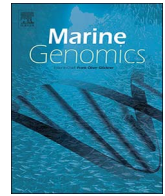




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Mapping of quantitative trait loci for temporal growth and age at maturity in coho salmon: Evidence for genotype-by-sex interactions

Miyako Kodama^{a,*}, Jeffrey J. Hard^b, Kerry A. Naish^a

^a School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98105, USA

^b National Marine Fisheries Service, Northwest Fisheries Science Center, Conservation Biology Division, Seattle, WA 98112, USA

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ABSTRACT

Phenotypic differences between males and females are ubiquitous throughout the animal kingdom. Therefore, investigating the extent to which sex-dependent genetic effects contribute to phenotypic variation is important in understanding the evolutionary response of each sex to natural and artificial selection. Sex-specific differences in growth patterns and age at sexual maturity have been observed in a number of anadromous salmonid fishes. In these species, faster growing individuals in a given cohort often mature earlier than conspecifics, and earlier maturing individuals are often males. The aim of this study was to determine whether sex-dependent genetic effects contribute to phenotypic variation in age at sexual maturity and growth in coho salmon reared through juvenile stages to first maturity. To achieve this aim, quantitative trait loci (QTL) underlying growth-related traits and age at first maturity were mapped across four families, and interactions between offspring sex and trait were examined by investigating the significance of genotype-by-sex (QTL × sex) interactions. Several temporally expressed growth-related QTL mapped to the same position, suggesting that these regions affected growth across many months. QTL × sex interactions were widespread, indicating that the effect of QTL on age at sexual maturity and growth over the course of development in coho salmon may be under sex-specific genetic control. We also found evidence for epistatic interactions between some growth traits. Our results provide insights into the genetic architecture underlying growth-related traits in coho salmon, and have implications for understanding the genetic and evolutionary basis of important fitness-related traits.

1. Introduction

Phenotypic differences in physiological, morphological, behavioral, or life-history traits are widespread between males and females in both animal and plant species (Andersson, 1994; Anholt and Mackay, 2004; Barrett and Hough, 2012; Foerster et al., 2007; Mackay, 2004; Williams and Carroll, 2009). Such differences are often attributed to sex-determining loci, as these are the only genomic regions that differ between the sexes (Mank, 2009; Rice, 1984). However, a growing body of studies suggests that genetic variation within the autosomal genome also affects a number of phenotypic traits differently between the sexes (Korstanje et al., 2004; Mackay, 2004; Ueno et al., 2004). Specifically, genotype-by-sex interactions or sex-specific quantitative trait loci (QTL) have been reported in a wide variety of species including humans, fruit flies, rats, mice and medaka (Ankra-Badu et al., 2010; Kawajiri et al., 2014; Korstanje et al., 2004; Krohn et al., 2014; Mackay, 2004; Mattson et al., 2007; Mogil et al., 1997; Ober et al., 2008; Ueno et al., 2004; Weiss et al., 2005, 2006).

Genotype-by-sex interactions occur when the same genotype in genes or genomic regions exerts differential effects on the expression of traits between the sexes (Singh and Uyenoyama, 2004). The effects of genotype-by-sex interactions may be sex-limited, sexually concordant or antagonistic, indicating that a genotype that is beneficial in one sex could be neutral, not as beneficial or even harmful in the opposite sex, respectively (Bonduriansky and Chenoweth, 2008; Chenoweth and McGuigan, 2010; Foerster et al., 2007; Foley et al., 2007; Poissant et al., 2012; Rice, 2000). Genotype-by-sex interactions may promote the accumulation of sex-specific genetic variance, reduce intersexual genetic correlations and resolve intralocus sexual conflicts (Barson et al., 2015; Chenoweth and McGuigan, 2010; Fox and Wolf, 2006; Singh and Uyenoyama, 2004). Because genotype-by-sex interactions may allow for the trait divergence between the sexes, evaluating the prevalence and degree of these interactions would provide insights into how sex-specific genetic control may contribute to the evolutionary dynamics of sexual dimorphism.

Growth and age at sexual maturity are important fitness-related

* Corresponding author at: School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA.

E-mail address: miyako.kodama@snm.ku.dk (M. Kodama).

¹ Current address: Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, 1350 Copenhagen, Denmark.

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traits in salmonids (Fleming, 1998; Gross, 1985; Kodama et al., 2012). Early growth is often phenotypically correlated with later growth, and variation in growth is linked to variation in age at maturity. Variation in size and age at sexual maturity tends to be larger in male salmonids due to the presence of several alternative mating tactics to achieve fertilization success. Smaller, younger-maturing males may adopt sneaking behavior to gain access to spawning females whereas large, late-maturing males may engage in courtship and fighting to gain access to females and outcompete smaller males (Fleming, 1998; Gross, 1985). In female salmon, size is linked to reproductive output and to the ability to select and defend nesting sites and therefore variation in size and age tends to be smaller than in males (Fleming, 1998). Correlations between growth and age at sexual maturity involve a shift in energy allocation from growth to reproduction (Hendry and Stearns, 2004; Roff, 1992). Maturation and growth are correlated in most salmonid species (Thorpe et al., 1983), where faster growing fish in a given cohort mature earlier than conspecifics (Hutchings and Jones, 1998; Shearer and Swanson, 2000). Thorpe et al. (1998) have proposed a model where growth performance during fall one year prior to and spring six months prior to spawning determine the age of sexual maturity (see also Larsen et al., 2006). Specifically, maturation is triggered if growth performance in an individual fish surpasses a genetically determined threshold level during the critical periods. The decision to mature occurs every year (Thorpe et al., 1998), resulting in variable age at maturity in many salmon species (Waples et al., 2009). The proportions of males and females from a given cohort maturing in any given year is expected to vary; therefore, knowledge on the presence and function of genotype-by-sex interactions would be crucial to study how such interactions may contribute to the sex-specific differences in growth and age at sexual maturity in salmon.

The genetic basis of growth and age at sexual maturity in salmonids has been widely investigated through QTL mapping (Gutierrez et al., 2014, 2012; Küttner et al., 2011; Martyniuk et al., 2003; Moghadam et al., 2007; Pedersen et al., 2013). Some of these studies observed that QTL for maturation timing mapped to similar regions as those for body lengths or weights at certain time points (Küttner et al., 2011; Martyniuk et al., 2003; Pedersen et al., 2013), indicating that pleiotropy or linked genes may be responsible for the correlation. Although little had been known about the genetic architecture underlying sex differences in growth and maturity, Barson et al. (2015) recently discovered that a gene controlling age at sexual maturity in Atlantic salmon exhibited sex-dependent dominance, resulting in earlier maturation in males but later maturation in females. Studies that incorporate sex-specificity into the QTL analyses using a suite of growth-related traits measured at regular intervals over the course of development will help identify novel QTL for growth and maturity that are influenced by sex in salmon. Such studies will demonstrate how genotype-by-sex interactions may lead to sex-specific differences in growth and age at sexual maturity, and provide insights into how the maturation decision might be genetically influenced by temporal growth performance.

The aim of this study was to characterize genotype-by-sex interactions via QTL mapping based on frequent measures of growth spanning the key maturation decision periods in a salmonid species with a simple life history, coho salmon (*Oncorhynchus kisutch*). This species is ideal to investigate the importance of genotype-by-sex interactions for growth and age at sexual maturity during juvenile and sub-adult stages because individuals can be readily sexed using the sex-determining gene (Yano et al., 2013). The species is also short lived and semelparous, with most individuals maturing at three years, but a fraction of males maturing as two year olds in natural environments (Sandercock, 1991). Given that age at sexual maturity is an observable binary trait in coho salmon, it is feasible to phenotype all individuals for this trait within two years. A domesticated aquaculture strain that has been selectively bred for large size and early maturation (two years) for over 15 generations (Myers et al., 2001) was available for this study, and was originally crossed

with individuals from a wild population that mature at the typical age of three years (McClelland et al., 2005; McClelland and Naish, 2010, 2008).

Measurements in an F4 outbred cross using this strain started during fall one year preceding the maturation conversion until the fall when maturation was initiated. Restriction site-associated DNA (RAD) sequencing (Baird et al., 2008) was performed on offspring, and sequences were aligned against a high-density linkage map for the species (Kodama et al., 2014) to locate QTL underlying the traits. Genotype-by-sex (QTL \times sex) interactions were incorporated into the QTL models. Significant interactions were interpreted as evidence for sex-dependent QTL effects on the phenotypic traits of interest. Our results were aimed at demonstrating how genotype-by-sex interactions may have resulted in sex-specific differences for growth and age at sexual maturity. Because frequent measures of growth spanning the key maturation decision periods were employed in this study, the results were also aimed at providing insights into how the maturation decision might be genetically influenced by temporal growth performance in male and female coho salmon, with the intention of improving our understanding of sex-specific life history evolution among salmonid species.

2. Materials and methods

2.1. Experimental crosses

In December 2010, F3 crosses were created from outbred experimental lines of coho salmon established in 2001 (McClelland and Naish, 2010). The F0 populations originated from naturally produced individuals derived from Bingham Creek (47°15'N, 123°40'W), a tributary to the Satsop River that drains to the Southwest Washington coast, and from the Domsea aquaculture line. These populations differ at growth-related traits such as length, weight and daily growth rate (McClelland et al., 2005). The Domsea commercial line originated in 1973 and 1974 from the Washington Department of Fish and Wildlife's (WDFW) Wallace River Hatchery (47°87'N, 121°71'W), and was selectively bred for early maturation (two years) and large size over 15 generations (Myers et al., 2001). The typical age at maturity at Bingham Creek is two years for precocious males and three years for adult males and all females (McClelland et al., 2005; McClelland and Naish, 2010, 2008). Four families of F4 offspring were selected for QTL analyses (Family_1, Family_2, Family_3, Family_4). All individuals were marked with PIT tags (Biomark Inc., Boise, ID, USA) in August 2011 at their parr stage (the juvenile stage prior to physiological transformation for saltwater adaptation) for individual identification. Each family was placed in a 76 cm diameter tank from August 2011 to August 2012 and then in a 180 cm diameter tank from September 2012 to January 2013. Throughout the course of the experiment, individuals were fed to satiation and reared in fresh water at a constant 10 °C.

This study was conducted in the aquaculture environment, where individuals were kept in captivity from birth to death. The advantage of this study was that the rearing conditions were kept identical, thus we avoided the potential effects of the environments on fish growth across different families; such setting allowed us to identify QTL linked with growth, without having to account for growth differences originating from differences in environmental conditions. However, such setting also means that our experimental setting did not allow us to investigate the influence of environment on growth, despite that a number of studies have suggested that such interactions also play a role in influencing age-at-sexual maturity.

2.2. Phenotypic measures

Growth-related and age at maturity traits were examined in two F4 families (Family_1 and Family_2). Lengths and weights were measured every six weeks from August 2011 when fish were approximately 8 months of age, to November 2012 when fish were approximately

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