Aquaculture 358–359 (2012) 61–70

Contents lists available at SciVerse ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aqua-online

Genetic mapping of quantitative trait loci (QTL) for body-weight in Atlantic salmon (*Salmo salar*) using a 6.5 K SNP array

Alejandro P. Gutierrez [a], Krzysztof P. Lubieniecki [a], Evelyn A. Davidson [a], Sigbjørn Lien [b], Matthew P. Kent [b], Steve Fukui [c], Ruth E. Withler [d], Bruce Swift [e], William S. Davidson [a,*]

[a] *Department of Molecular Biology and Biochemistry, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6*
[b] *CIGENE, Norwegian University of Life Sciences, P.O. Box 5003, Ås, 1432, Norway*
[c] *Mainstream Canada, 203-919 Island Highway, Campbell River, British Columbia, Canada V9W 2C2*
[d] *Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, British Columbia, Canada V9T 6N7*
[e] *TRI-GEN Fish Improvement Ltd., 2244 Wilson Road, Agassiz, British Columbia, Canada V0M 1A0*

ARTICLE INFO

Article history:
Received 20 March 2012
Received in revised form 11 June 2012
Accepted 18 June 2012
Available online 26 June 2012

Keywords:
Atlantic salmon
Quantitative trait loci
Body-weight
Breeding program

ABSTRACT

We examined five families from the Mainstream Canada Atlantic salmon broodstock program to identify quantitative trait loci (QTL) associated with body-weight at four time points during a commercial production cycle. The parents and 49–65 progeny from each family were genotyped using a 6.5 K single nucleotide polymorphism (SNP) array. Uninformative markers were removed from each family dataset, and approximately 2500 informative markers per family were positioned on male and female linkage maps, which had been constructed using the same SNP array. QTL analysis was carried out using GridQTL software utilizing the Sib-Pair model to take advantage of the full-sib nature of the families. We also did half-sib analyses to identify segregating alleles from dams or sires with a QTL. Significance thresholds to assess QTL effects were obtained from a 10,000 permutation test. We identified genome-wide significant QTL ($P<0.05$) linked to chromosomes Ssa02, Ssa07, Ssa13, Ssa09, Ssa17 and Ssa26, and also several chromosomes which contain significant ($P<0.01$) and suggestive QTL ($P<0.05$) associated with body-weight. Some of these QTL have previously been identified as being associated with body-weight in Atlantic salmon. Our findings provide useful evidence of QTL associated with body-weight traits. These QTL should be valuable candidates for use in the Mainstream Canada marker-assisted selection breeding program. Moreover, it is an important step towards the identification of genes and the understanding of the genetic components underlying growth and body-weight in Atlantic salmon.

1. Introduction

Growth is a high-interest trait in economically important livestock, including aquaculture species such as Atlantic salmon (*Salmo salar*). In salmonids, as in other species, genetic and environmental factors control the complex physiological processes of growth, including qualitative and quantitative aspects of nutritional availability, behavioral interactions conditioned by intra- and inter-specific demographics and seasonal changes (Sumpter, 1992). The effect of these factors on important growth traits and their heritable variation between and within populations of Atlantic salmon has been reviewed by Garcia de Leaniz et al. (2007). In spite of the high number of environmental factors that may directly or indirectly influence growth rates, moderate levels of heritability have been reported in most cases (Garcia de Leaniz et al., 2007; Gjerde et al., 1994; Jónasson and Gjedrem, 1997; Quinton et al., 2005).

Over the past decades, advances in genomic research have significantly improved the tools available for the genetic improvement of livestock. In particular, the development of genetic markers and linkage maps has permitted great advances in the quantitative analyses of commercially important traits. Quantitative trait loci (QTL) analyses not only have allowed the identification of genetic markers associated with the genetic variation underlying several traits, but also the identification of candidate genes (Mackay et al., 2009). The ability to map the chromosomal regions that influence economically important traits has led to the implementation of selective breeding based on improved genetic selection practices by identifying animals with favorable genotypes. In Atlantic salmon aquaculture, marker-assisted selection (MAS) could be a valuable addition to current selective breeding programs by improving the accuracy of selection, and therefore the genetic gain (Sonesson, 2007a), especially for those traits (e.g., disease resistance, flesh quality) that are difficult to measure on the actual broodstock (Sonesson, 2007b). The ability to carry out whole-genome selection based on several genetic markers at once is a goal for aquaculture breeding programs.

* Corresponding author. Tel.: +1 778 782 5637; fax: +1 778 782 5530.
E-mail address: wdavidso@sfu.ca (W.S. Davidson).

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doi:10.1016/j.aquaculture.2012.06.017

QTL are regions of the genome that have an effect on phenotypic traits, and they usually contain genes associated with the particular quantitative trait of interest (Lynch and Walsh, 1998). The use of molecular markers and inference of the effects of allele segregation throughout the genome are employed to determine the number, positions and the magnitude of the QTL affecting a trait by statistical associations between marker genotypes and particular trait phenotypes. Several QTL associated with growth traits have been described for salmonid species, including Atlantic salmon (Baranski et al., 2010; Boulding et al., 2008; Houston et al., 2009; Reid et al., 2005), rainbow trout (Haidle et al., 2008; Martyniuk et al., 2003; O'Malley et al., 2003; Wringe et al., 2010), coho salmon (McClelland and Naish, 2010; O'Malley et al., 2010) and Arctic charr (Küttner et al., 2011; Moghadam et al., 2007b). Moreover, linkage maps for these species have been described (Woram et al., 2004; Danzmann et al., 2008; McClelland and Naish, 2008; Moen et al., 2008;). The studies that identified some major QTL also produced evidence for the existence of homologous and homeologous chromosomes between and within some salmonid species, the latter a result of the whole-genome duplication event in their common ancestor (Allendorf and Thorgaard, 1984). However, most of these QTL studies were based on the use of a limited number of microsatellite markers, and many regions of the genome were sparsely represented. Thus, it was not possible to obtain precise and complete information about the number and locations of the QTL.

Recent advances in genome research have provided new techniques for constructing high-density genetic maps. The development of new sequencing technologies has made it possible to obtain thousands of single nucleotide polymorphism (SNP) markers for genotyping, and new genotyping technologies enable the simultaneous analysis of a large number of these markers, which allows the construction of high-density genetic maps (Goddard and Hayes, 2009). These techniques are now being widely used in species of agricultural importance, and have led to the development of dense SNP arrays (Gabreski et al., 2009; Kijas et al., 2009; Matukumalli et al., 2009; Muir et al., 2008; Ramos et al., 2009; Yan et al., 2010). However, for aquaculture species, the availability of SNPs is still somewhat limited, with a large number of SNPs being reported only for catfish species (Wang et al., 2010), Atlantic cod (Hubert et al., 2010), rainbow trout (Hohenlohe et al., 2011; Miller et al., 2012; Sanchez et al., 2009) and Atlantic salmon (Hayes et al., 2007). A custom Illumina iSelect SNP-array containing approximately 6.5 K SNP markers from Atlantic salmon has been developed (Kent et al., 2009) and used to construct a relatively dense SNP linkage map for this species (Lien et al., 2011).

The aims of this study were to identify and map QTL related to body-weight at four stages in a commercial production cycle of Atlantic salmon. The genetic mapping of QTL was performed in five families of a European strain of Atlantic salmon, which are part of a commercial broodstock development program, utilizing the 6.5 K SNP array and the linkage map described by Lien et al. (2011). Our results will lead to a better understanding of the genetics underlying the control of growth in Atlantic salmon and by extension provide a basis for comparative studies among salmonid species.

2. Materials and methods

2.1. Mapping families and phenotype data

The families were part of a commercial broodstock program initiated by Mainstream Canada in 1995 and based on the Mowi strain of Atlantic salmon, which is derived from a breeding program established using Norwegian populations (Gjedrem et al., 1991). In November/December 2005, 130 single-pair mating families were made. The parents were selected based on estimated breeding values (EBV), which took into account both growth rate and low maturation/grilsing rate. Pedigree records indicated that none of the parents were related to one another. Each sire and dam was used only once in the production of the families. This procedure gave a series of full-sib families. At the fry stage (February 2006), 120 offspring from each family were pooled (15,600 fish in total) and grown communally at the Oceans Farms Hatchery, Vancouver Island. At ~25 g (September/October 2006), 5,000 of the fish were PIT (passive integrated transponder) tagged, and phenotypic measurements including weight (W1) were taken. In November 2006, the PIT-tagged fish had their adipose fins removed for DNA analyses. When the fish were 90–120 g (February/March 2007), they were transferred to the Cypress Harbour, Vancouver Island saltwater broodstock facility and placed in a single smolt cage. In August 2007 when the fish were ~500 g (W2), they were transferred into a single grow-out net pen. As the fish were grown communally throughout the production cycle, this eliminated potential differences within or between families due to environmental conditions associated with a tank-effect. Phenotypic measurements were taken in February 2008 (1st sea winter, W3) and again in January 2009 (2nd sea winter, W4).

2.2. DNA extraction and parental assignments

DNA was extracted from the adipose fins of the PIT-tagged progeny and from the parents used to produce the 130 families (Withler et al., 2005). The DNA then was genotyped using eight microsatellite markers, and parental assignment was carried out as described by Withler et al. (2007).

2.3. SNP array and linkage mapping

Five families were selected for SNP array analysis based on the number of progeny and the range of phenotypes of interest. The SNP genotyping was carried out at CIGENE, Norwegian University of Life Sciences, Ås using an Atlantic salmon 6.5 K Illumina iSelect SNP-array (Kent et al., 2009). Analyses were based on an Atlantic salmon linkage map, which contains ~5,650 SNPs and was constructed using genotyping data from 143 families comprising 3,297 fish (Lien et al., 2011). This map contains 29 linkage groups, each of which was assigned to its specific chromosome according to the nomenclature established by Phillips et al. (2009). SNP array data were edited to remove all non-informative markers from the datasets, and subsequently independent male and female linkage maps were generated for each family based on the order and genetic distances between the markers in the maps constructed by Lien et al. (2011). In addition, we identified those informative markers shared by all five families and constructed male and female maps from these markers for comparative purposes.

2.4. QTL analyses

QTL analyses were performed using a regression-interval mapping method available through the GridQTL portlet (available at http://www.gridqtl.org.uk/), which allows the analysis of extensive datasets (Seaton et al., 2006). The datasets were analyzed using two different strategies. The first strategy involved an independent analysis for each family dataset using all informative markers. Although many of the markers were not shared among the families, every chromosome was covered. The second strategy we utilized was to identify those markers that were informative and shared among all five families, and then to test for the presence of QTL using those markers. By combining the data from the five families into one analysis and also by analyzing within each family separately, we were able to identify which family was informative for the presence of a specific QTL.

The analyses were carried out using two different approaches. The first approach involved using a sib-pair model, which utilized a variance method to analyze linkage, based on alleles that are identical-by-descent (IBD). Individuals with similar phenotypes are expected to show alleles sharing IBD (Haseman and Elston, 1972). IBD probabilities of full-sib families (known parents) are calculated using an exact