



# Composite interval mapping reveals three QTL associated with pyloric caeca number in rainbow trout, *Oncorhynchus mykiss*

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## Abstract

The pyloric caeca of fishes are a major site for nutrient digestion and absorption. Some studies have reported an association between increased caeca number, improved feed efficiency and faster overall growth in rainbow trout. However, little is known concerning the genetic basis underlying pyloric caeca development in any fish species. We have identified two clonal rainbow trout lines that differ in pyloric caeca number. Doubled haploid progeny produced from an F<sub>1</sub> hybrid of these lines were used to evaluate the possibility of joint segregation of pyloric caeca phenotype with 330 amplified fragment length polymorphic (AFLP) markers and 39 microsatellites genotyped in 54 individuals. A genetic map has been constructed based on these genotypes and composite interval mapping revealed three major quantitative trait loci (QTL) associated with pyloric caeca number. These QTL respectively explain 19.2%, 18.6% and 13.5% of the variation in pyloric caeca number observed within the doubled haploid progeny. Because these QTL span 3 separate linkage groups, our results demonstrate the phenotype of pyloric caeca number is a polygenic trait in rainbow trout.

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## 1. Introduction

The growth rates of animals are fundamentally dependent upon the anatomical system where digestive and absorptive processes occur. Within vertebrates, elaborate modifications of the gastrointestinal tract include the presence of protuberances called caeca at various positions along the intestine. In

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some fishes, modifications of the digestive tract also include the presence of sac-shaped structures called pyloric caeca. These caeca extend from the upper regions of the small intestine at positions directly distal to the pyloric sphincter (or pylorus) of the stomach (Rust, 2002). In contrast to the caeca of higher vertebrates, fish pyloric caeca lack resident microflora and therefore do not serve as primary sites for bacterial fermentation of feedstuffs (Budington and Diamond, 1987). Histologically, fish pyloric caeca resemble the fish small intestine as each caeca lumen is lined by an epithelium dense in secretory cells (Beorlegui et al., 1992). These cells secrete a variety of digestive enzymes including trypsin and elastase (Rae and Walther, 1989; Dimes et al., 1994; Kristjansson, 1991; Olli et al., 1994; Pavlisko et al., 1997, 1999; Harpaz and Uni, 1999; Toyota et al., 2002). The inner lumens of fish pyloric caeca are also extensively folded resulting in the presence of large numbers of microvilli (Rust, 2002). Collectively, these properties facilitate the enzymatic breakdown of proteins (Byun et al., 2002; Toyota et al., 2002), hydrolysis of lipids (Bauermeister et al., 1979; Sire et al., 1981), absorption of amino acids, fats, water, sodium and other nutrients (Marcotte and De La Noue, 1984; Boge et al., 1988).

The recruitment of pyloric caeca in salmonids begins early in larval development and continues throughout the fry and alevin stages (Northcote, 1960). Within rainbow trout, pyloric caeca numbers appear to become fixed as fish reach sizes of approximately 4 cm and these numbers remain constant into adult stages (Bergot et al., 1981a). Total numbers of pyloric caeca within adult rainbow trout have been found to range from 31 to 147 depending upon the strain (Northcote, 1960; Blanc et al., 1979; Bergot et al., 1981b). Some studies have found families of rainbow trout with higher pyloric caeca numbers exhibit better food conversion ratios when compared to families possessing fewer pyloric caeca (Bergot et al., 1981a). Selection for higher pyloric caeca numbers at the Less-Athas hatchery (France) was also shown to increase overall growth rates in hatchery progeny (Bergot et al., 1981a). The precise relationship between pyloric caeca number and nutrient utilization remains unclear, however, as other studies have reported a lack of correlation between increased pyloric caeca number and fat and

protein digestibility (Choubert et al., 1991) and overall growth rate in rainbow trout (Ulla and Gjedren, 1985).

The capacity to locate and subsequently identify genes controlling traits such as food conversion efficiency and overall growth rate are of particular significance for domestic animal production. Such complex phenotypes are generally expected to be determined simultaneously by environmental effects, a few loci with large effects (quantitative trait loci, QTL), and with many other loci accounting for the remainder of the difference (Falconer and Mackay, 1996). Molecular approaches have greatly facilitated the identification of QTL in animal models for which two key resources are available, namely, strains that are genetically divergent for the phenotype of interest and animal models for which genetic linkage maps based on crosses of divergent strains have been developed (Lander and Botstein, 1989).

The availability of highly polymorphic DNA markers has made it possible to construct genetic linkage maps for economically important fish species such as rainbow trout. Currently, several rainbow trout genetic maps (Young et al., 1998; Sakamoto et al., 2000; Robison et al., 2001; Nichols et al., 2003a,b; Zimmerman et al., 2004) based on both experimental and outbred populations have been developed. These maps have facilitated QTL analysis of several complex phenotypes in rainbow trout including: spawning date (Sakamoto et al., 1999); albinism (Nakamura et al., 2001); resistance to infectious pancreatic necrosis virus (Ozaki et al., 2001); upper thermal tolerance (Perry et al., 2001); embryonic development rate (Robison et al., 2001); meristic traits (Nichols et al., 2003a) and natural killer cell-like activity (Zimmerman et al., 2004).

In the present study, we identify two rainbow trout clonal lines that differ in phenotypic numbers of pyloric caeca. Using a genetic linkage map based on progeny obtained from a cross of these two clonal lines (Zimmerman et al., 2004), we were able to identify 3 QTL associated with pyloric caeca number in rainbow trout. Our study validates a genetic approach towards understanding a complex phenotype in fish and provides insights into the genetic control of pyloric caeca development in rainbow trout.

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