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ORIGINAL ARTICLE

Quantitative trait locus analysis of hatch timing, weight, length and growth rate in coho salmon, *Oncorhynchus kisutch*

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In quantitative genetics, multivariate statistical approaches are increasingly used to describe genetic correlations in natural populations, yet the exact genetic relationship between phenotype and genotype is often unknown. Quantitative trait locus (QTL) analyses can be used to describe the molecular basis of this relationship. In salmonids, growth and development are important fitness traits that are phenotypically correlated with each other and with other life-history traits, and an understanding of the molecular basis of these relationships is valuable for future evolutionary studies. Here, a QTL analysis using an outbred cross was initiated to determine the molecular basis of phenotypic correlations between such growth traits in coho salmon (*Oncorhynchus kisutch*), an important fish species distributed throughout the North Pacific Ocean. Fifty-three QTL for growth rate, length and weight at eight time periods were located on seven linkage groups (OKI03, OKI06, OKI18, OKI19, OKI23, OKI24 and an unnamed linkage group) or associated with five unlinked markers (*Omm1159*, *Omm1367/i*, *Omy325UoG*, *OmyRGT55TUF* and *OtsG422UCD*). One QTL for hatch timing was associated with the marker, *Omm1241*. All QTL were of minor effect, explaining no more than 20% of the observed variation in phenotypic value. Several instances of colocalization of QTL weight, length and growth rate were observed, suggesting a genetic basis for phenotypic correlations observed between these traits. This study lays the foundation for future QTL mapping efforts, for detailed examinations of the genetic basis of phenotypic correlations between growth traits, and for exploring the adaptive significance of growth traits in natural populations.
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Introduction

Growth is an important fitness trait and is one factor affecting survival and fecundity across a wide range of taxa (Arendt, 1997). Growth rates may be correlated with other life-history traits including development rate and size at age (Cheverud *et al.*, 1983; Mangel and Stamps, 2001). Whether such traits are positively or negatively correlated may be strongly influenced by environmental conditions (Lankford *et al.*, 2001; Sundstrom *et al.*, 2005; Gregersen *et al.*, 2008). For example, both timing of development and large body size are often crucial for exploiting ephemeral resources or avoiding predation (Sundstrom *et al.*, 2005; Biro *et al.*, 2006). However, depending on resource availability, some species may adopt a strategy of allocating energy toward rapid development rather than toward achieving large body size. Other species may maximize efficiency of resource use rather than total resource utilization, resulting in a negative correlation between growth and development (Arendt, 1997).

Genetic correlations between traits have implications for the adaptation and evolution of a species. Evolutionary response is determined by phenotypic variation, by the strength and direction of selection, by the underlying genetic variation within a population and by the genetic covariance between traits (Falconer and Mackay, 1996). Genetic correlations limit the number of trait combinations that are advantageous and thus constrain the evolution of correlated phenotypes (McGuigan, 2006). Statistical quantitative techniques have often been used to examine the genetic variance and covariance of fitness traits (Lynch and Walsh, 1998). This type of analysis has been very illuminating but often fails to fully describe the genetic basis of complex traits and interactions between such traits. As a first step toward a more mechanistic understanding of these interactions, quantitative trait locus (QTL) analyses can be conducted to directly identify regions of the genome that might affect a suite of correlated traits.

QTL are regions of the genome that affect polygenic, continuously varying phenotypic traits. QTL are typically located in the genome by detecting the association of phenotypes with marker genotypes (Lynch and Walsh, 1998). In a recent review, Gardner and Latta (2007) found that correlated trait pairs tended to share a higher proportion of QTL than did uncorrelated traits. Therefore, mapping QTL underlying multiple traits within the same study can indicate if pleiotropic effects, where one

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locus affects more than one trait, explain genetic correlation between these traits (Lynch and Walsh, 1998). In addition, QTL analysis offers insight into the number of loci affecting a trait as well the relative distribution of the effects of such loci (Lynch and Walsh, 1998).

In salmonids, growth and development are important traits with fitness effects throughout their life history. Salmon are anadromous, rearing in freshwater for varying lengths of time (depending on species) before migrating to salt water where resources are more abundant and growth rates are high (Quinn, 2005). Large size and rapid growth are thought to be important during the freshwater phase, because salmon must compete with conspecifics for resources and escape from predation (Sundstrom et al., 2005). Salmon eggs are deposited in gravel of lakes and streambeds. Eggs hatch into alevin that rear in the gravel until they are able to begin exogenous feeding, at which time they emerge into the water column (Quinn, 2005). Rapidly developing embryos may have more access to resources, because they emerge from the gravel first and have more opportunity for feeding early in the season, resulting in larger size as fry (Beacham et al., 1988; Einum and Fleming, 2000). Greater size at the fry stage is positively correlated with freshwater overwintering survival (Quinn and Peterson, 1996). However, when predation is density dependent, early development and corresponding high growth rates as fry may increase an individual's exposure to predation risk and result in lower fitness (Sundstrom et al., 2005). In chinook salmon, juvenile growth rates are also positively correlated with the age and timing of smoltification, the physiological process of adapting to salt water (Beckman and Larsen, 1998), and with increased marine survival during the first winter at sea in coho salmon (Beamish et al., 2004). In contrast to these findings, a study in Atlantic salmon showed a negative correlation between pre-smolt size and post-smolt size, suggesting that the adaptive benefit of size varies across ages and species (Einum et al., 2002). Salmon spend a variable number of years in salt water and then return to freshwater to spawn (Quinn, 2005). Growth rates at critical periods in the 2 years before spawning may determine the age of maturation, and in particular, whether males will exhibit precious maturation or 'jacking' (Shearer and Swanson, 2000). In females, large size is correlated with fecundity, and large females tend to have both larger and more abundant eggs (Fleming and Gross, 1990; Campbell et al., 2006). Finally, egg size is positively correlated with the size of fry (Heath et al., 1999), which is important for survival as described above.

Recent QTL-based studies in salmonids have detected genetic correlations between growth traits and life-history traits, and have identified major and minor QTL for growth and development traits. In rainbow trout, QTL for length after emergence and time to hatching mapped to the same region of the genome, indicating possible pleiotropic effects on size and development rate (Robison et al., 2001; Nichols et al., 2008). Length has been phenotypically correlated with upper thermal tolerance, a physiological trait; two minor QTL for length and thermal tolerance mapped to the same region (Perry et al., 2005). These studies typically examine only a few traits at one or two time periods. This study will extend the work on salmonids by examining growth traits in coho salmon, *Oncorhynchus kisutch*, over a longer time period than previous studies, offering a more complete analysis of QTL from hatching up until the age coho typically undergo the physiological process of smoltification.

In this study, we use an outbred pedigree in coho salmon to map QTL underlying phenotypic traits related to growth and early development; namely, hatch timing, weight, length and growth rate. Outbred designs have the ability to expose more of the variation present in the originating populations because multiple QTL alleles can segregate in experimental families, thus potentially uncovering more evolutionarily important variation than inbred designs (Erickson et al., 2004). Response to selection on correlated traits in experiments using inbred lines has often differed from the predicted response given the correlations observed between the traits studied (Roff, 2007a). Use of populations that exhibit more of the genetic variation and genetic interactions present in natural populations may be useful in understanding the response to selection in the wild and the maintenance of long-term genetic variation (Roff, 2007a; Naish and Hard, 2008). Identification of genomic regions associated with growth traits in coho salmon is an important first step in locating genes of interest and in determining how genes may interact to affect evolution of fitness traits in this species.

Methods

Experimental crosses and trait measurements

An outbred pedigree was established using individuals from two populations of coho from Washington State, USA. Females were obtained from the Bingham Creek hatchery, which is located on a tributary to the Satsop River in southwest Washington. This hatchery takes wild broodstock into the hatchery each year. Juveniles are released into the wild annually and thus experience natural selection for a substantial portion of their lives. Males were provided from the Domsea broodstock farm located near Olympia, Washington. The Domsea broodstock has been selectively bred for large size and early maturation for over 15 generations (Myers et al., 2001a). These populations have previously been shown to differ at traits relating to growth rate, and size at alevin and juvenile life-history stages (McClelland et al., 2005).

Twenty F1 hybrid crosses were established in December 2005 by mating each male with two females. Fertilized eggs were incubated in Heath trays at a constant 10 °C. On day 30 after fertilization, 1000 eggs from two paternal half-sib families were transferred to 100-well incubation boxes to minimize the influence of hatching enzyme on unhatched eggs (Robison et al., 1999). Half-sib families were selected by egg size; one female had relatively small eggs (average egg diameter was 7.14 ± 0.08 mm) and the other female had relatively large eggs (average egg diameter was 8.30 ± 0.09 mm). The program IncubWin (Jensen and Jensen, 1999) was used to estimate the start of hatching using water temperatures. Eggs were inspected every 6–8 h from the estimated start of hatching (38 days or 380.8 degree-days) until all eggs had hatched; no eggs hatched before the estimated start time. All embryos that hatched within

Table 1 Approximate life-history stage, sampling date, sampling as days after fertilization and the trait measured for QTL analysis

Life-history stage	Date	Days since fertilization	Measurements taken
Fertilization	06 January 2006	0	
Start hatch	17 January 2006	42	time to hatching
End hatch	22 January 2006	47	
Start exogenous feeding	27 February 2006	83	
Juveniles (pre-smolt)	07 July 2006	213	weight, length
Juveniles (pre-smolt)	23 August 2006	260	weight, length
Juveniles (pre-smolt)	06 October 2006	304	weight, length
Juveniles (pre-smolt)	16 November 2006	346	weight, length
Juveniles (pre-smolt)	05 January 2007	395	weight, length
Juveniles (pre-smolt)	14 February 2007	435	weight, length
Juveniles (smolts)	30 March 2007	479	weight, length
Juveniles (smolts)	16 May 2007	526	weight, length

Growth rates were calculated from the weight measurements taken at each sampling period.

a given 6–8 h interval were assigned to the same hatching group, removed from the incubator boxes and reared together in a different incubator. Once yolk absorption was complete (day 83 after fertilization), hatching groups were placed in $1 \times 1 \times 0.5$ m nets arrayed within a single 4 m diameter broodstock tank. If hatching groups were large, fish were divided between several nets so that no net had more than 60 individuals. Throughout the course of the experiment, fry were reared at a constant 10 °C and fed to satiation. When fry reached approximately 3 g on average, 308 fish, selected proportionally from the different hatching groups, were marked with PIT tags (Biomark Inc., Boise, ID, USA) for individual identification and fin clips were collected for DNA extraction. At this time all fish were placed into the same 4 m diameter tank. Although smoltification traits were not quantified, smolts were first noted on day 345 after fertilization (November 2006). Length and weight measurements were taken every 6 weeks through June 2007 when fish were approximately 18 months of age (Table 1). Measurements were taken relatively frequently to ensure that growth during key intervals (for example, during the spring before smoltification and fall following) were assessed. Growth rates were calculated as the average daily change in body weight between measurement dates. The half-sib family that was the progeny of the dam with the larger diameter eggs was selected for further analysis.

Statistical methods
The hatch-timing data were treated categorically rather than as a continuous variable because phenotypes were recorded as the time interval in which an individual hatched. These data were not normally distributed. Phenotypic correlations between all traits were tested using Spearman's nonparametric rank test. Spearman's rank test is more appropriate for categorical data and data with non-normal distributions but is also a robust method of analyzing normally distributed, continuous data. Use of the nonparametric test facilitated analyses and comparisons between all traits. P-values were corrected using the sequential Bonferroni method with $\alpha = 0.05$ and $k = 276$ (Rice, 1989). Because hatching groups were reared at slightly different densities, analysis of variance was used to determine whether there was an effect of hatching group on size at the different sampling periods according to the model:

$$Y_{ijk} = \mu + \alpha_j + \beta_k + \alpha_j\beta_k + \varepsilon_{ijk}$$

where Y_{ijk} is the phenotype of the ith individual (in this case, length or weight for a given period), μ the population mean, α_j the affect of the jth hatching time, β_k the random affect of the kth net, $\alpha_j\beta_k$ the interaction between hatch time and net, and ε_{ijk} the random error. This analysis of variance takes into account any potential rearing group effects when determining the effect of hatching group on length or weight at age. The trait rank of fish over the course of the experiment was tested using Friedman's rank test for k paired samples. All statistical tests were implemented using SPSS v 14.0 (SPSS Inc., Chicago, IL, USA).

Genotyping
Phenotypic information for hatch timing and growth traits was available for 308 individuals. Sixty-six individuals were chosen for genotyping based on their hatch timing. Thirty-three individuals hatched during the earliest 10% of the trait distribution and 33 were in the latest 10%. Use of individuals representing extreme trait values, termed selective genotyping, can increase the power to detect QTL (Darvasi and Soller, 1992; Lynch and Walsh, 1998). When multiple traits are analyzed it is difficult to find individuals that represent the extremes for each trait unless traits are highly correlated (Darvasi and Soller, 1992). The individuals selected for hatch timing represented the range of values seen in the other traits measured. Fin clips were taken for DNA samples. Total genomic DNA was extracted using a DNeasy kit (Qiagen, Valencia, CA, USA). Microsatellite markers were chosen from a previously generated linkage map (McClelland and Naish, 2008); markers were selected to represent all known linkage groups with at least three markers per group. A total of 142 markers were screened in the parents of the mapping family. Both parents were homozygous for 56 of these markers, an additional 13 markers amplified duplicated loci for which it was not possible to determine parental haplotypes, and 3 loci had null alleles. The 66 individuals selected for QTL mapping were genotyped at the 70 loci which emerged from the marker screening process (Supplementary Materials). Microsatellites were amplified in 10 μl reactions containing 30 ng genomic DNA, $1 \times$ buffer (10 mM Tris-HCl, 50 mM KCl, 0.1% Triton X-100), 1.0–2.5 mM MgCl$_2$, 200 μM

each dNTP, 2 pmol each of forward and reverse primer and 0.5 units *Taq* (GeneChoice, Frederick, MD, USA). Thermal cycling conditions consisted of a 5 min denaturing step at 95 °C followed by 12 cycles of 95 °C for 45 s, 60 °C stepping down in 0.5 °C increments to a final temperature of 54 °C, 72 °C for 1 min. The touchdown sequence was followed by 20 cycles of 95 °C for 45 s, 54 °C for 45 s and 72 °C for 1 min with a final extension step of 72 °C for 45 min.

Linkage analysis

Salmonids can have large differences in recombination rates between the sexes so it is necessary to generate sex-specific linkage maps (Sakamoto *et al.*, 2000). Linkage groups were determined using the program LINKMFEX v2.1 (Danzmann and Gharbi, 2001). Using this program, we performed pairwise comparisons between loci separately for the dam and sire, and the 66 mapping progeny at all 70 microsatellite loci. A log of odds score of 3.0 was set as the threshold for clustering markers into linkage groups. Marker order was established using MAPORD and distances between markers was calculated using MAPDIS (both available as part of the LINKMFEX package). MAPORD attempts map construction using both a linear method, which minimizes the recombination distance between neighboring markers, and a matrix approach, which considers distances between each pair of markers in turn (Danzmann and Gharbi, 2001). MAPDIS uses phase-corrected genotypic data to establish mapping distances for each linkage group; mapping distances are representative of recombination frequencies between loci (Danzmann and Gharbi, 2001). Graphical representations of linkage groups were created using MapChart (Biometris, Wageningen, Netherlands; Voorrips, 2002). Linkage group names were assigned after the convention described in a previously defined coho linkage map (McClelland and Naish, 2008).

QTL analysis

The statistical power to detect QTL by interval mapping without selective genotyping and a sample size of 66 was calculated using the method developed by Hu and Xu (2008) for a backcrossed design. The method assumes a 'worst case scenario' where the QTL is located in the middle of a marker interval rather than immediately adjacent to a marker. A test statistic, λ, is defined such that, if the QTL overlaps an informative marker, the statistic will follow an F-distribution with degrees of freedom 1 and n, where n is the sample size and will follow a noncentral F-distribution when the QTL does not overlap an informative marker. The noncentrality parameter is defined as follows:

$$\delta = n\sigma_x^2 \frac{a^2}{\sigma^2}$$

where n is the sample size, σ_x^2 is the variance of the genotype distribution, α^2 is the additive genetic effect and σ_x^2 is the estimated residual error. The $1-\alpha$ percentile of the F-distribution is calculated as: $\lambda_{1-\alpha} = F^{-1}(\lambda_{1-\alpha} | 1, n, 0)$ where α is the Type I error. Type II error is then defined as $\beta = F(\lambda_{1-\alpha} | 1, n, \delta)$ and statistical power as $\gamma = 1-\beta$ (Hu and Xu, 2008). The power analysis was performed for QTL in both large (25 cM) and small intervals (5 cM) to determine the power to detect QTL, with $\alpha = 0.05$, of

three effect sizes: major effect (percent explained variation, PEV, of 0.25), nonmajor effect (PEV of 0.15) and small effect (PEV of 0.05).

QTL analyses were performed separately for male and female parents because markers and QTL in individuals used to create outbred crosses can be in different linkage phases (Lynch and Walsh, 1998). Before QTL analysis, phase-corrected data were generated for each mapping parent separately using the program GENOVECT (part of the LINKMFEX package).

QTL analysis was performed with MultiQTL v2.5 (MultiQTL Ltd., Haifa, Israel) using a simple interval model (Lander and Botstein, 1989). Interval mapping locates QTL between markers but does not account for the effect QTL in nearby intervals may have on marker–trait associations. The single-trait and two-trait models were both used, however, as the results did not differ, only the single-trait analyses are discussed here. To account for the differences in linkage maps, we analyzed dam and sire components separately using a backcross model to examine association between phenotypes and the two alleles from a given parent. Thus, for the analysis using the female parent, the effect of alleles segregating in the female (Bingham) line is averaged over the male alleles. The hatch-timing data were analyzed using a selective genotyping model because genotyped fish fell into the upper and lower 10% of the hatch-timing distribution. Other data were analyzed with the default, or reduced, model, which assumes no variance or covariance effects and no epistasis. Data other than hatch timing were not analyzed with the selective genotyping options because individuals genotyped represented the range of phenotypes for length, weight and growth rate. Linked markers were analyzed by interval analysis using the reduced model assuming equal variances. Significance levels were estimated using the permutation test of Churchill and Doerge (1994) with 10 000 permutations of the trait data with an experiment-wise false detection rate of 0.01. *P*-values less than 0.05 from the interval analysis permutation test were considered indicative of a significant QTL effect. Unlinked markers were analyzed using the marker option of MultiQTL and significance was determined by permutation testing as above. *P*-values for single-marker analyses are less conservative than for interval mapping (O'Malley *et al.*, 2003) so *P*-values of 0.01 were considered indicative of significant QTL effect. QTL that explained more than 25% of the variance (PEV) in the trait value were considered to be major QTL (Bradshaw *et al.*, 1998). The substitution effect ($|d|$), the phenotypic difference between progeny with alternate alleles, was also estimated. The substitution effect reflects the additive component of variance; it was not possible to estimate dominance or epistatic effects due to the depth of the pedigree and the constraints of the backcross model in MultiQTL.

Results

Statistical analysis of phenotypic correlation between traits

Hatching occurred over a 96 h time period. The distribution of hatch timings was skewed with 28% of fish hatched during the first hatching period (1008 to 1014 h

after fertilization), 52% of fish hatched over the course of the subsequent 12 h and 73% of fish had hatched by the end of the first 30 h. Of the 276 pairwise comparisons for correlations between traits, 251 comparisons were found to be correlated (Spearman's rank test, $P<0.0001$, Bonferroni-adjusted $\alpha=0.002$); 253 comparisons were correlated before Bonferroni correction. Hatch timing was positively correlated with length and weight on day 213 after fertilization (Spearman's rank test, $P>0.0001$, Bonferroni-adjusted $\alpha=0.002$) but was not correlated with length, weight or growth rate on any other days ($P>0.01$, Bonferroni-adjusted α ranged from 0.003 to 0.050). Weights and lengths at each sampling date were correlated with both weights and lengths on all other sample dates (for each test $P<0.0001$, Bonferroni-adjusted $\alpha=0.002$). Growth rates on each sample date were also correlated with all other weights and lengths (for each test $P<0.0001$, Bonferroni-adjusted $\alpha=0.002$), with the exception of growth rates from day 260 to 304 and from day 302 to 346 after fertilization that were not correlated with weight or length on day 213 (Spearman's rank test, Bonferroni-adjusted $\alpha>0.05$). Nets in which fish were reared from hatching until day 213 held unequal numbers of individuals, ranging from 17 to 60 fish per net with a median of 51.5 fish per net. However, there was no effect of fish density on weight, length or growth rate ($P>0.05$). Fish that hatched at 1026 and 1057 h (10 260 and 10 570 degree-hours, respectively) after fertilization consistently had greater weights, lengths and faster growth rates over all sampling time periods than did fish from other hatching groups (nested analysis of variance, $P<0.05$). Individual ranks for the traits did not change significantly over the time of the experiment (weight: $\chi_r^2=1001.9$, $P<0.001$; length: $\chi_r^2=1791.9$, $P<0.001$; growth rate: $\chi_r^2=1022.4$, $P<0.001$).

Genetic map

Sixty microsatellites were informative for generating the female map whereas 50 were informative for the male map. Six markers amplified duplicated loci, although in three cases only one copy could be assigned to a linkage group; the other copy was unlinked. Duplicated loci are designated by /i or /ii after the locus name. In the female map, 41 markers assigned to 16 linkage groups and in the male map, 31 markers assigned to 9 groups. Nineteen loci remained unlinked in both maps. Of these 19 loci, 15 were mapped in the opposite sex or have been mapped previously (McClelland and Naish, 2008) so it was possible to assign them to linkage groups, although recombination distances between markers in the current map were not calculated. The female map coverage was 210.16 cm, whereas the male map coverage was 114.37 cm. The intervals between markers ranged from 0 to 21.5 cm in length. Total coverage is approximately 50% of previously published maps for each sex (McClelland and Naish, 2008). Although marker order was consistent between the previously published map and that generated for the QTL mapping family, recombination differences often varied. The difference in recombination rates between the sexes is consistent with previous observations in coho (McClelland and Naish, 2008). The male map represents 9 linkage groups out of the 22 mapped in an earlier study; the female map in this study comprises 12 of the 30 linkage groups previously

mapped (McClelland and Naish, 2008). However, eight of the unlinked markers in the female, and nine in the male, are found on some of the linkage groups defined by the earlier study.

QTL analysis

The power analysis indicated that there was good power for detection of QTL with a PEV of 0.25 particularly in intervals of 10 cm or less: $\gamma=0.75$ of 22 cm intervals, $\gamma \geqslant 0.81$ of 10 cm intervals and less. Power to detect QTL of small effect (PEV = 0.05) was quite low with $\gamma=0.21$ for 22 cm intervals rising to $\gamma=0.24$ for 5 cm intervals. QTL with PEV of 0.15 were intermediate with $\gamma=0.52$ for 22 cm intervals and $\gamma=0.60$ for 5 cm intervals. In all cases, power increased with an increase in marker density.

QTL for growth rate, weight, length or time to hatching mapped to seven regions of the coho genome (Figure 1, Table 2); an additional seven QTL were associated with individual markers only (Table 2). Twenty-two QTL, which mapped to three linkage groups and to two unlinked markers, were detected using segregation information from the dam. Thirty-five QTL, which mapped to four linkage groups and to four unlinked markers, were detected using the sire data (Table 2). Three of the regions (*Omm1295* to *Omm1265*; *Omy1011UW* to *Omm1310/Omm1154*; and *Omy325UoG* to *Omm1309/Omm1367/ii*) were associated with QTL for growth traits over the majority of sampling periods. Where markers or intervals were associated with fewer QTL, those QTL tend to be for traits on the same or proximate dates (Figure 1). For example, OKI24 contains QTL for length on day 479 after fertilization and for growth rate from day 479 to 526.

Only one QTL for hatch timing was observed, associated with *Omm1241* in the dam analysis (Table 2), and this marker was not associated with any other QTL. It is interesting to note that although most traits were phenotypically correlated, phenotypic correlation did not always correspond to shared QTL. It appears that 64.5% of pairwise phenotypic correlations correspond to colocalized QTL. None of the QTL for any of the traits was considered to be of major effect, although 30 explained between 10% and 20% of the variation for their respective traits ($0.10 \leqslant PEV \geqslant 0.20$; Table 2).

Discussion

Here we report genomic locations of QTL in coho salmon for hatch timing and for weight, length and growth rate over sampling periods spanning 2 years. Three genomic regions contained multiple QTL spanning many sample dates, whereas other regions were associated only with QTL for traits at later ages (day 479 after fertilization and later). It is therefore possible that some of the same loci, or linked loci, affect growth traits across all life-stages whereas other loci are expressed only during certain time periods. QTL for length at multiple ages mapped to the same location on OKI03, OKI19 and OKI23, suggesting that there may be pleiotropic effects on length across ages. Similar results were seen for weight at age and growth rate across ages. QTL for weight, length and/or growth rate at the same age also mapped to the same intervals on several linkage groups (OKI03, OKI19, OKI23, OKI24 and the unnamed linkage group), suggesting loci may have pleiotropic effects across traits
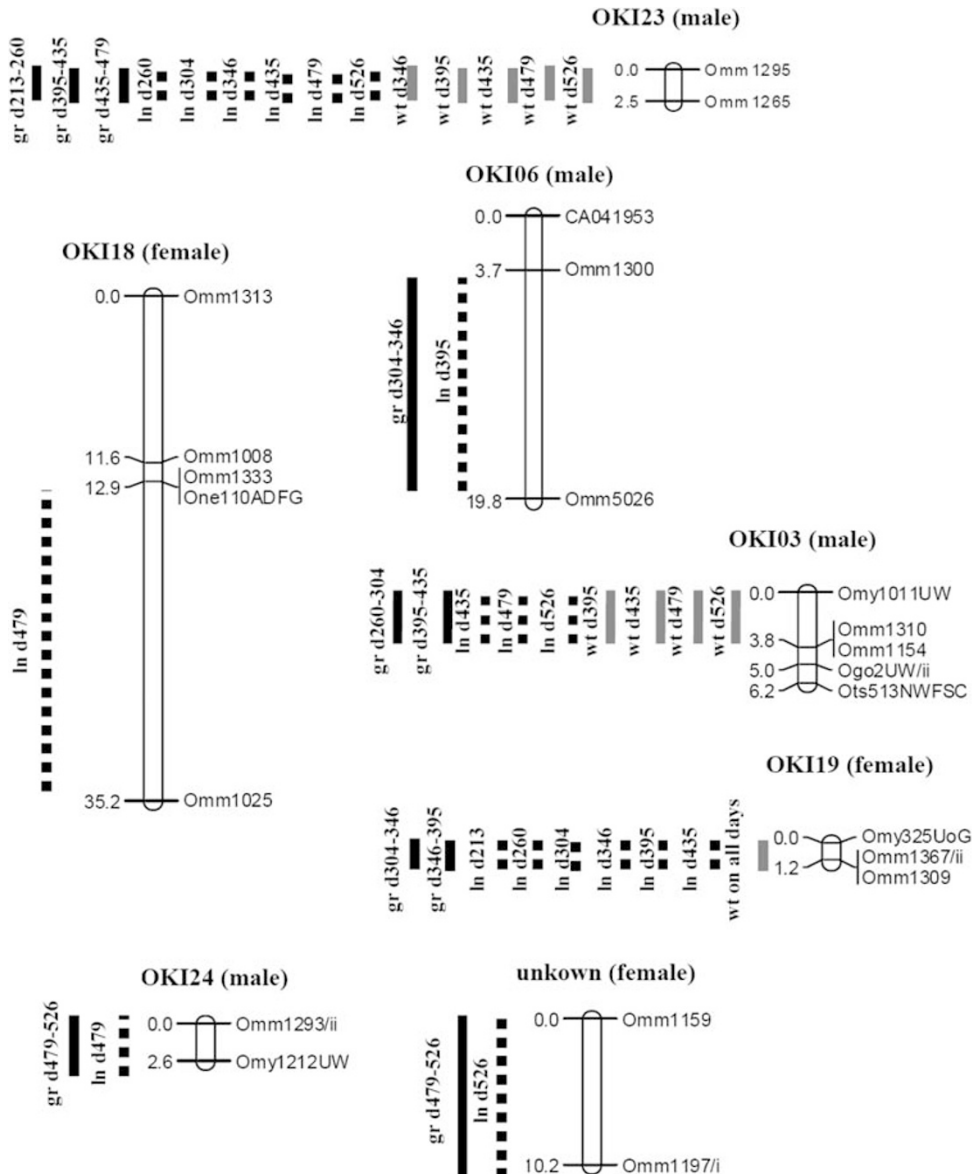
Figure 1 Linkage groups with quantitative trait locus (QTL). QTL for growth rate (gr), length (ln) and weight (wt) on various sampling days after fertilization that mapped to a marker interval on a linkage group. Linkage group names are as for previously published coho linkage groups (McClelland and Naish, 2008).

expressed at a specific age. All growth-related traits in this study were phenotypically correlated with each other and previous work on coho has shown high genetic correlations between weight and length at age (r ranges from 0.74 to 0.98; Myers *et al.*, 2001b; Neira *et al.*, 2004) and between weights at different ages (r ranges from 0.42 to 0.98; Hershberger *et al.*, 1990; Myers *et al.*, 2001b). QTL analyses are a first step in describing the genetic architecture underlying many of these genetic correlations.

All the QTL detected in this study were considered to be of minor effect because they each explain less than 25% of the variance of respective traits. The QTL for hatch timing had a particularly low PEV, explaining only 4.5% of the variation. Sample sizes below 300, as used here, typically have low power to identify QTL of small effect particularly at marker densities less than 15 cM

(Erickson *et al.*, 2004). Non-model organisms or outbred populations often have lower density linkage maps that increase the probability of failing to detect small effect QTL, if they exist (Lynch and Walsh, 1998). Selective genotyping can be used to increase the power to detect QTL while decreasing the number of individuals genotyped (Darvasi and Soller, 1992) as was performed for the hatch timing trait. However, this method can only be applied to one trait, except in the unlikely event that the trait distribution between individuals is maintained across all life-history stages (Darvasi, 1997). In this study, it is possible that QTL of small effect for growth related traits went undetected in this analysis. However, it is considerably less likely that QTL of major affect went undetected (probability of Type II error of 0.80). Some authors suggest that QTL of large effect are rare, whereas QTL of small effect are more commonly detected for

568

Table 2 Linkage groups and markers to which QTL mapped for hatch timing, growth rates, length and weight at different days (d) after fertilization

Trait	Linkage group	Marker	Source	LOD	Effect, m	Substitution effect, $|d|$	Residual variance	P	PEV
hatch timing	(OKI14)	Omm1241	dam	1.16	1025 h	9.27	21.44	0.009	0.045
growth_rate_d213-260	OKI23	Omm1295 Omm1265	sire	1.05	0.57 g	0.37	0.66	0.021	0.073
	unknown	Omm1367i	sire	1.52	0.62 g	0.45	0.65	0.002	0.106
growth_rate_d260-304	OKI03	Omy1011UW Omm1310/Omm1154	sire	1.56	0.89 g	0.86	0.87	0.011	0.196
	unknown	Omm1159	sire	1.45	0.96 g	0.84	0.87	0.009	0.187
growth_rate_d304-346	OKI19	Omy325UoG Omm1367/ii/Omm1309	dam	1.23	1.52 g	1.61	1.73	0.012	0.161
	OKI06	Omm1300 Omm5026	sire	1.10	1.61 g	1.48	1.74	0.042	0.152
growth_rate_d346-395	OKI19	Omy325 UoG Omm1367/ii/Omm1309	dam	1.23	1.45 g	1.51	1.70	0.019	0.089
growth_rate_d395-435	(OKI17)	OtsG422UCD	sire	2.25	1.65 g	0.93	1.03	0.002	0.167
	OKI03	Omy1011UW Omm1310/Omm1154	sire	1.11	1.77 g	0.64	1.08	0.046	0.080
	OKI23	Omm1295 Omm1265	sire	1.57	1.74 g	0.76	1.06	0.012	0.112
growth_rate_d435-479	OKI23	Omm1295 Omm1265	sire	1.00	2.36 g	0.97	1.61	0.048	0.083
	unknown	Omm1159	sire	1.60	2.41 g	1.21	1.58	0.008	0.128
growth_rate_d479-526	OKI24	Omm1293/ii Omy1212UW	sire	1.27	2.60 g	1.19	1.78	0.025	0.101
	unknown	Omm1159 Omm1197/i	dam	1.16	2.75 g	1.21	1.78	0.037	0.104
ln_d213	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.39	98.58 mm	12.35	19.21	0.018	0.094
ln_d260	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.69	134.53 mm	21.28	29.69	0.008	0.114
	OKI23	Omm1295 Omm1265	sire	1.06	132.20 mm	17.11	30.36	0.042	0.074
ln_d304	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.01	167.05 mm	25.50	46.88	0.043	0.069
	OKI23	Omm1295 Omm1265	sire	1.36	163.26 mm	29.53	46.32	0.020	0.092
ln_d346	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.25	190.03 mm	34.23	55.96	0.024	0.086
	OKI23	Omm1295 Omm1265	sire	1.24	185.82 mm	34.25	55.98	0.027	0.085
ln_d395	OKI06	Omm1300 Omm5026	sire	1.33	208.89 mm	40.10	62.32	0.041	0.096
	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.78	211.02 mm	46.10	61.23	0.005	0.124
ln_d435	(OKI17)	OtsG422UCD	sire	1.57	238.02 mm	45.14	61.08	0.009	0.120
	OKI03	Omy1011UW Omm1310/Omm1154	sire	1.53	245.22 mm	42.86	61.18	0.017	0.109
	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.36	245.31 mm	40.56	61.57	0.018	0.098
	OKI23	Omm1295 Omm1265	sire	1.00	241.71 mm	35.27	62.42	0.048	0.074
ln_d479	OKI03	Omy1011UW Omm1310/Omm1154	sire	1.04	277.05 mm	38.32	63.93	0.047	0.082

Table 2 Continued

Trait	Linkage group	Marker	Source	LOD	Effect, m	Substitution effect, |d|	Residual variance	P	PEV
	OKI18	One110ADFG/Omm1333 Omm1025	dam	1.36	280.06 mm	51.85	61.59	0.044	0.150
	OKI23	Omm1295 Omm1265	sire	0.96	275.75 mm	35.27	64.15	0.050	0.077
	OKI24	Omm1293/ii Omy1212UW	sire	0.32	276.22 mm	43.17	63.17	0.021	0.105
ln_d526	OKI03	Omy1011UW Omm1310/Omm1154	sire	1.41	311.54 mm	49.61	70.09	0.021	0.111
	OKI23	Omm1295 Omm1265	sire	1.20	310.8 mm	46.07	70.71	0.031	0.096
	unknown	Omm1159 Omm1197/i	dam	1.40	316.06 mm	49.87	70.11	0.022	0.112
wt_d213	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	0.98	13.0 g	3.88	7.24	0.048	0.067
wt_d260	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.68	38.0 g	17.47	24.43	0.007	0.113
wt_d304	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.26	83.0 g	53.82	61.49	0.025	0.161
wt_d346	(OKI27)	OmyRGT55TUF	dam	1.53	104.6 g	66.97	95.52	0.010	0.109
	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.34	114.6 g	63.53	99.95	0.017	0.092
	OKI23	Omm1295 Omm1265	sire	1.22	107.0 g	60.92	100.38	0.028	0.084
wt_d395	OKI03	Omy1011UW Omm1310/Omm1154	sire	1.12	151.3 g	80.46	136.37	0.039	0.080
	(OKI19)	Omy325UoG	sire	1.70	140.2 g	98.25	133.47	0.005	0.119
	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	2.01	156.0 g	106.23	131.93	0.004	0.139
	OKI23	Omm1295 Omm1265	sire	1.02	148.8 g	77.32	136.87	0.046	0.074
wt_d435	OKI03	Omy1011UW Omm1310/Omm1154	sire	1.31	224.9 g	111.68	172.94	0.025	0.094
	(OKI17)	OtsG422UCD	sire	1.57	208.2 g	126.43	171.29	0.008	0.120
	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.64	228.8 g	124.32	170.80	0.008	0.117
	(OKI27)	OmyRGT55TUF	dam	1.60	216.50	123.71	165.90	0.008	0.122
	OKI23	Omm1295 Omm1265	sire	1.33	221.2 g	112.76	172.82	0.022	0.096
wt_d479	OKI03	Omy1011UW Omm1310/Omm1154	sire	1.36	318.0 g	157.64	228.78	0.024	0.106
	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	1.12	326.0 g	143.71	231.10	0.033	0.088
	OKI23	Omm1295 Omm1265	sire	1.61	311.7 g	171.45	226.45	0.011	0.125
wt_d526	OKI03	Omy1011UW Omm1310/Omm1154	sire	1.55	432.1 g	216.71	290.58	0.014	0.122
	(OKI17)	OtsG422UCD	sire	1.79	405.3 g	240.17	287.75	0.004	0.148
	OKI19	Omy325UoG Omm1309/Omm1367/ii	dam	0.98	446.0 g	174.78	297.61	0.046	0.079
	OKI23	Omm1295 Omm1265	sire	1.24	429.2 g	195.57	294.38	0.027	0.099

Linkage groups given in parentheses indicate markers that were unlinked in the QTL cross but have been mapped previously in coho (McClelland and Naish, 2008). The parent in which the QTL was detected (source), max LOD score (LOD), effect (m) of the allele present on the trait, allelic substitution effect (\|d\|) at the QTL position, the residual (non-additive) variance, P-values for QTL (P), and the proportion of variance explained by the QTL marker (PEV) are shown. Markers grouped by a vertical line indicate that the maximum LOD score for that QTL was detected in the interval between those markers.

most traits (Lynch and Walsh, 1998; Mackay, 2004). Study results differ with respect to the number of major and minor QTL detected, and may relate both to the constraints of linkage map density as noted above and to breeding design (Roff, 2007b). In an inbred cross, for example, alleles of major effect can arise due to epistatic effects; these effects may be reduced in an outbred population in which a greater range of genetic backgrounds might be expected to occur (Roff, 2007b). Estimates of QTL effects in outbred populations are expected to be less precise than from inbred lines because QTL are expressed as genetic variances rather than means (Lynch and Walsh, 1998) and therefore some bias is likely with an outcross design. The range of effect sizes associated with QTL in this study are typical of other studies in outbred lines derived from natural populations of fishes (Peichel et al., 2001; Martyniuk et al., 2003; Rogers and Bernatchez, 2007). However, it would take further development of the coho linkage map to truly address the debate over the prevalence of small versus large effect QTL.

Although power to detect QTL is lower in outbred crosses than with inbred lines (Lynch and Walsh, 1998), there are many advantages to using an outbred design. Outbred designs are more likely to reveal the variation present in natural populations (Lynch and Walsh, 1998) and may thus be more relevant than inbred lines for determining the genetic basis of correlations in natural populations (Roff, 2007b). It has also been suggested that the colocalization of QTL for trait pairs is greater in natural populations (Gardner and Latta, 2007). In this study, QTL were mapped in the F1 generation; they therefore represent recombination events in the parents rather than in the F1 progeny. Because this study uses a single full-sib family for QTL mapping, the effect sizes of a QTL will incorporate the dominance interaction between parental alleles in the offspring (Lynch and Walsh, 1998). It is not immediately clear whether these dominance interactions will increase or decrease the apparent effect of the QTL on the marker in question (Lynch and Walsh, 1998). Additional studies mapping QTL in more families would be useful for elucidating the QTL effect across the population.

The Domsea broodstock are a domesticated line, and after several generations of selective breeding, inbreeding was estimated to be between 15% and 23% (Myers et al., 2001a). Although there was little change in average heterozygosity at allozyme loci in the Domsea line compared to their natural progenitors (Myers et al., 2001a), it is possible that the population has reduced variation at the growth traits under selection. If this outcome is true, there will be lower heterozygosity at marker loci (Lynch and Walsh, 1998). Fewer markers were mapped in the male (31 loci) compared to the female (41 loci), which may be indicative of a decrease in informative markers in the Domsea line generally. Further, there are two factors that may have affected the number of marker-trait associations detected in the male map. Variation in chromosomal locations flanking QTL might have been reduced due to strong artificial selection on growth traits in the Domsea fish (the paternal line), resulting in clustering of QTL and markers that are physically distant from each other. It is also important to point out that male salmonids generally exhibit reduced recombination compared to females (Sakamoto et al., 2000), thus distances between markers and QTL will be reduced in this sex. Reduced recombination in males might have also led to colocalization of QTL that would otherwise be physically distant from each other. It is therefore not possible in this study to resolve which factor, line or sex, has a greater influence on the number of markers linked to QTL, or to the observed colocalization of growth QTL. Increasing marker density for finer scale mapping, and focusing efforts on the female map would address this question in future work.

QTL for growth, length at age and weight at age were detected in both the sire and dam comparisons, indicating that these traits are segregating in both the Satsop and the Domsea populations. The genetic background in which a QTL is detected can affect the percentage of phenotypic variation (PEV) that a QTL explains (Chaib et al., 2006) and whether or not pleiotropy appears to affect a trait (Phillips and McGuigan, 2006). If one trait is segregating in the offspring but the other is not, pleiotropy may fail to be detected. In addition, alleles may vary in their pleiotropic effect (Phillips and McGuigan, 2006) so the identity of alleles present in the parents may impact the ascertainment of pleiotropy at different loci.

Hatch timing in coho salmon is phenotypically correlated with growth at day 213 after fertilization but not at later sample periods. The QTL analysis offers no evidence to suggest that there would be a molecular basis to any phenotypic correlation with this trait. This result was unexpected in light of previous ecological studies that suggest that hatch timing, as a measure of early development, is correlated with growth as alevin and fry (Beacham et al., 1988; Einum and Fleming, 2000; Sundstrom et al., 2005). In an inbred line of rainbow trout, one major QTL for hatch timing was associated with length at the start of exogenous feeding, suggesting a possible genetic correlation between development rate and later growth (Robison et al., 2001). However, undetected hatch-timing QTL of minor effect may be associated with QTL for other growth traits.

The one QTL for hatch timing, associated with marker Omm1241, was detected in the female line. This finding may be indicative of the variation for this trait in the parental lines. In the sire line, the Domsea broodstock, fish have been selected for large size and fast growth to maturity (Myers et al., 2001a) and, simultaneously, for high fecundity (Neely, 2006). There is a trade-off between egg number and egg size and, therefore, eggs from highly fecund females tend to be small (Fleming and Gross, 1990). In a study comparing the Domsea fish to their population of origin, it was observed that the Domsea fish produce smaller eggs than their progenitors (Neely, 2006). In salmonids, small eggs tend to develop more rapidly than do larger eggs (Valdimarsson et al., 2002) and thus selection for fecundity in the Domsea fish may also indirectly select for rapid early development. The dearth of QTL for hatch timing, particularly in the sire line, may indicate that there is little variation for this trait in the Domsea fish, perhaps due to generations of artificial selection, although the trait may still be segregating in the Satsop line. It is also possible that the individuals used in this cross did not capture the true extend of variation for hatch timing in these populations.

Comparisons with hatch timing QTL in other coho lines would be interesting in resolving this question.

QTL mapped in coho have previously been mapped to homologous linkage groups in other salmon species (Martyniuk et al., 2003; O'Malley et al., 2003; Reid et al., 2005). One QTL for body weight day 293 after fertilization was mapped to RT21 in rainbow trout (Martyniuk et al., 2003); this rainbow trout linkage group is homologous to coho linkage group OKI19 that contains QTL for body weight at all ages measured in this study. In the study of Martyniuk et al. (2003), it was postulated that pleiotropy affected body weight across several months of growth. QTL for body weight at age 1 year were mapped in Atlantic salmon to linkage group AS-18 (Reid et al., 2005) that is homologous to coho linkage group OKI24. Markers on OKI24 do not show any association with QTL for body weight in coho but are associated with other growth QTL (length and growth rate in the second year). In rainbow trout, studies have variously identified QTL of major and minor effect for hatch timing. Nichols et al. (2007) identified six minor QTL for hatch timing, one of which was located on rainbow trout linkage group RT14 (termed OC-14 in Nichols et al., 2007). In this study the QTL for hatch timing was associated with marker Omm1241 that has been mapped to OKI14, the coho linkage group homologous to RT14 (McClelland and Naish, 2008). Robison et al. (2001) identified two major QTL for hatch timing in rainbow trout; each QTL explained around 25% of the variation seen in the trait. Because different markers were mapped in the various studies, it is not possible to determine if QTL detected in other salmon species map to exactly the same chromosome regions as those in coho. However, presence of QTL for similar phenotypic traits along the same chromosome or chromosome arm may indicate some level of conservation of function across species. Because Atlantic and Pacific species have relatively recently diverged this finding is not particularly surprising. Other recent studies also found conservation of QTL across salmonids including Atlantic and Pacific salmon and Arctic charr (Somorjai et al., 2003; Reid et al., 2005; Moghadam et al., 2007).

Understanding the genetic correlations between traits is important when considering the constraints placed on the evolutionary response of complex traits. It has become increasingly common to use multivariate approaches to the breeder's equation to describe evolution in natural populations (McGuigan, 2006; Garant et al., 2008). In this type of approach, trait interactions are described by the **G** matrix, a matrix of the genetic variances and covariances between traits (McGuigan, 2006). Although very useful for describing evolution, this multivariate statistical approach assumes that all genetic change is due to additive variance and covariance, and that all underlying QTL are of small effect (Phillips and McGuigan, 2006; Roff, 2007a). QTL analysis, such as the one described here, can offer a more mechanistic understanding of complex traits and genetic correlations between traits, and explain whether the quantitative loci contribute equally to a phenotype. By identifying genomic regions that contribute to the variance of a trait, it becomes possible to further understand the ways in which covariance structures, as described by a **G** matrix, interact and change over time (Phillips and McGuigan, 2006), which is particularly relevant for

future efforts at integrating molecular and multivariate approaches to understanding evolutionary processes (Naish and Hard, 2008).

In this study we located QTL for length, weight, growth rate and hatch timing. This is the first study in salmon to map QTL over as great a range of sampling dates. Presence of multiple QTL mapping to the same location in the genome suggests that there is a genetic basis for the phenotypic correlation observed between many of the studied traits, although it is not possible in this study to distinguish between tightly linked loci and pleiotropy. QTL studies do not have the resolution to determine individual genes, so it is not possible to distinguish pleiotropy from strong linkage disequilibrium between sites (Gardner and Latta, 2007). Therefore, we postulate possible patterns of pleiotropy in this study. Future studies using denser genome maps and sequencing techniques could be used to further distinguish between linkage disequilibrium and pleiotropic effects. This study lays the foundation for future QTL mapping efforts, for location of candidate loci, for more detailed examinations of the genetic basis for phenotypic correlations between growth traits and for exploring the adaptive significance of growth traits in natural populations.

Conflict of interest

The authors declare no conflict of interest.

Acknowledgements

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Supplementary Information accompanies the paper on Heredity website (http://www.nature.com/hdy)