A QTL MAP FOR GROWTH AND MORPHOMETRIC TRAITS USING A CHANNEL CATFISH X BLUE CATFISH INTERSPECIFIC HYBRID SYSTEM

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Alison M. Hutson

Certificate of Approval:

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| _____ | _____ |
| Jeffery Terhune<br>Associate Professor<br>Fisheries and Allied Aquacultures | Rex A. Dunham, Chair<br>Professor<br>Fisheries and Allied Aquacultures |
| _____ | _____ |
| Daryl L. Kuhlers<br>Professor<br>Animal Sciences | Zhanjiang Liu<br>Professor<br>Fisheries and Allied Aquacultures |

_____
George T. Flowers
Dean
Graduate School

# A QTL MAP FOR GROWTH AND MORPHOMETRIC TRAITS USING A CHANNEL CATFISH X BLUE CATFISH INTERSPECIFIC HYBRID SYSTEM

Alison M. Hutson

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Alison M. Hutson



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Alison M. Hutson

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Date of Graduation

# VITA

Alison M. Hutson graduated from Purdue University with a Bachelors of Science degree in Fisheries and Aquatic Science. She came to Auburn University to pursue a Masters of Science degree in Fisheries and Allied Aquacultures. She graduated in August 2006 and continued at Auburn to pursue a doctoral degree. Alison was married in 2004 to her husband, Ryan Hutson, and has two children, Charlie and George.

DISSERTATION ABSTRACT

# A QTL MAP FOR GROWTH AND MORPHOMETRIC TRAITS USING A CHANNEL CATFISH X BLUE CATFISH INTERSPECIFIC HYBRID SYSTEM

Alison M. Hutson

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Many genetic programs have been designed to enhance performance for different desired traits in ictalurid catfish. Using quantitative trait loci (QTL) analysis, specific culture traits can be identified so that the performance of individuals can be improved using marker assisted selection (MAS). Using a combination of QTL analysis and MAS, overall genetic gain per generation might be increased compared to traditional selection because of the potential for increased intensity and accuracy of selection. The channel catfish, *Ictalurus punctatus*, and blue catfish, *I. furcatus,* each have superior traits that could be incorporated into a synthetic breed. For instance, a backcross population offers the potential of a fish with the growth rate of a channel catfish and the body conformation of a blue catfish, possibly increasing dressing percentage per fish.

Head length, head depth, head width, body depth, body width, caudal depth, and caudal width, total length, and body weight were measured for 71 backcross full sib individuals. These individuals were genotyped using AFLP analysis and used for construction of a QTL map. The nine traits were strongly correlated ($P \leq 0.05$).

As expected the morphometric traits have minimal variation while body weight and total length had large components of variation.

For all seven morphometric traits and two growth traits, 9 of 44 linkage groups had at least one significant QTL ($P \leq 0.05$) and 12 of 44 at $P = 0.10$. Linkage group 19 was unique as it had multiple QTLs for every trait measured, except for caudal width for which no QTL was indentified on any linkage group. Caudal depth is represented on the map by the fewest linkage groups, being significant ($P = 0.05$) in two groups.

Approximately, half of the markers measured were associated with positive effects on the traits and half had negative effects. Linkage groups 5, 7, 9, 39, and 40 were significant for multiple traits and always had a trait negative effect. Total length is represented on the map by the most linkage groups and the most markers.

The linkage relationships found among body weight, total length and the 7 morphometric traits indicated that multiple trait MAS to increase body weight, body depth, body width and caudal depth while decreasing the other traits measured body weight and carcass yield simultaneously might be difficult. Certain QTLs seemed more promising for accomplishing the goal, and focusing on MAS on these markers might yield positive results.

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# INTRODUCTION

Catfish farming was initiated in the 1930s in Kansas and in the 1940s in Mississippi and in Arkansas, and the production of channel catfish in hatcheries and commercial farms has continued to grow until 2005 when production decreased. The price of catfish received by producers from processors bottomed at 56.8 cents per pound in 2002 with the month of January being the lowest price at 52.9 cents. The total sales for catfish in the United States were $444,835,000 in 2007 (NASS 2008) down slightly from the total sales of $450,178,000 in 2005 (NASS 2007). The July 2008 price paid to producers was 81.8 cents per pound (NASS 2008). The average price paid per pound in 2005 was $0.70 (NASS 2007) down from $0.84 in 2003 (NASS 2005). Even with the increase in price, there has been a huge increase in production costs primarily due to rising prices of feed and fuel. According to the Agricultural Statistics Board, many surface acres are being taken out of production. The total acres taken out of production in 2008 in Alabama, Mississippi, Arkansas, and Louisiana were 11,435 acres, up from 3,860 in 2007 (NASS 2008). To remain competitive in a global aquaculture economy, producers need to produce fish that are resistant to diseases, have a low feed conversion ratio, have a fast growth rate and are easily seined to reduce production costs.

To increase performance for different desired traits, researchers are using different methods to genetically enhance the channel catfish, *Ictalurus punctatus*, and

blue catfish, *I. furcatus*. Growth traits have been improved (Dunham and Smitherman 1983; Dunham et al. 1987; Dunham and Smitherman 1987; Dunham and Brummett 1999; Dunham et al. 1999; Rezk et al. 2003) via mass selection. Intraspecific crossbreeding has also improved performance in channel catfish (Dunham and Smitherman 1983; Padi 2003).

Traditional selection breeding programs only improve one or a few traits at a time. The interspecific hybrid, channel catfish female X blue catfish male, exhibits heterosis for many traits in a single generation. The hybrid is a combination of the two most promising culture catfish species in the United States (Dunham et al. 1993). Some culture traits that have been improved by producing a hybrid catfish include faster growth rates to market size (Giudice 1966; Dunham and Smitherman 1981; Smitherman et al. 1983; Dunham et al. 1987; Dunham et al. 1990; Dunham and Brummett 1999) and uniformity in growth rates for a cohort (Giudice 1966; Dunham et al. 1982; Smitherman et al. 1983; Argue et al. 2003). Disease resistance has been improved in the hybrid using a combination of hybridization and selection (Dunham et al. 1990). The hybrids also exhibit an increased tolerance to low dissolved oxygen (Dunham et al. 1983) and uniformity in body shape (Dunham et al. 1982).

The hybrid catfish has many traits that are beneficial for culturing catfish on a commercial level. One major drawback is that hybrids must be artificially produced. Interspecific backcrossing may be an alternative to introgress beneficial culture traits from the blue catfish and the channel catfish to develop a synthetic breed, which might also overcome the natural reproductive isolating mechanisms between the two species.

With new technologies becoming available, genotyping of organisms is becoming faster and less expensive. This allows many organisms to be genotyped. Marker assisted selection (MAS) is a more recent technology that is being developed based on the genotyped individuals that allows selection based on the presence or absence of specific alleles. These alleles are identified using a variety of molecular techniques. MAS can be used when traditional selection methods are not effective (Weller 2001).

Marker assisted selection could be beneficial when a trait has low heritability, when traits cannot be scored on all individuals, when negative genetic correlations exist among traits, when significant non-additive genetic variance (dominance, epistasis) exists, and when cryptic genetic variation exists (Weller 2001). MAS could also be beneficial for interspecific backcrossing to develop synthetic breeds. A quantitative trait locus analysis provides basic information needed for MAS.

A quantitative trait locus segregates for alleles that have measurable expression of a quantitative trait. A QTL affects quantitative traits that are mapped on chromosomes. The QTL map combines the information from a linkage map with the phenotypic information of the individuals. QTL mapping is the calculation of QTL position on a linkage map in experimental populations of diploid species (van Ooijen 2004). The higher the resolution of the linkage map the higher the power will be for the QTL map. Linkage maps are a powerful tool for analysis in many organisms including the channel and blue catfish (Rohrer et al. 1996, Kappes et al. 1997, Groenen et al. 2000, Liu et al. 2003).

Channel catfish and blue catfish each have 29 pairs of chromosomes (Wolters et al. 1981, LeGrande et al. 1984). The genome is approximately 1 X $10^9$ bp (Tiersch et al.

1990, Tiersch and Goudie 1993). The linkage map constructed using Amplified Fragment Length Polymorphism (AFLP) markers for channel catfish (Liu et al. 2003) identifies 44 linkage groups. Because the number of markers was small, the map could not be refined to the actual 29 linkage groups and have a significant LOD, log of odds (Barnard 1949) score.

Ideally, a codominant marker system such as microsatellites produces the most detailed linkage maps, increasing the accuracy of the map and therefore the accuracy of the QTL map. A map using microsatellites has been constructed for channel catfish (Waldbieser et al. 2001). A less expensive alternative to microsatellites are AFLP markers. AFLP markers are used because of their reproducibility (Jones et al. 1997, Bagley et al. 2001). The major drawback with the AFLPs is that they are inherited in a dominant fashion, thus homozygote dominant and heterozygote genotypes are indistinguishable on the gel.

Among plants and animals, many QTLs have been identified for traits of economic importance. In maize (*Zea mays*, L.), a QTL for feed drying rate has been found (Sala et al. 2005). This is an economically important trait in areas with a mid to short growing season. In a durum wheat cross, QTLs were identified for pre-harvesting sprout, which reduces commercial grade (Knox et al. 2005).

In the case of fish, only a few QTLs have been identified for performance traits. In a tilapia hybrid (*Oreochromis mossambicus* X *Oreochromis aureus*) several QTLs were found affecting fitness traits using 20 microsatellites and then a second experiment confirmed the findings using six microsatellites in one linkage group (Cnaana et al. 2003). In Rainow trout, *Oncorhyncus mykiss*, QTLs for high temperature tolerance were

found using backcrosses (Jackson et al. 1998) and $F_2$ or crossbreeds (Perry et al. 2001, Cnaani et al. 2003). The correlation between growth related traits and male age at maturation was also studied in Rainbow trout (Martyniuk et al. 2003). QTLs were found for body mass and condition factor (Martyniuk et al. 2003). Sun and Liang (2004) identified a locus associated with cold tolerance that will be used as a starting point for QTL identification in the common carp (*Cyprinus carpio* L.).

QTLs have been found for other traits in fish. In Arctic Charr, (*Salvelinus alpinus*) two QTLs were found for upper temperature tolerance (Somorjai et al. 2003). Two QTLs influencing time of hatch were found in Rainbow trout (*Oncorhynchus mykiss*) (Robison et al. 2001). In Atlantic salmon, a multistage analysis for QTLs was performed for disease resistance traits, and two QTLs affecting disease resistance were found (Moen et al. 2004).

QTL mapping can be accomplished using a variety of methods. The Kruskal-Wallis method of analysis is a non-parametric method using the rank sum test to find the probability distributions of the quantitative traits (van Ooijen 2004). Interval mapping is another method of analysis developed by Lander and Botstein (1989) which creates a QTL likelihood map. Every position on the genome is evaluated for the presence of a segregating QTL (van Ooijen 2004). Multiple-QTL-model (MQM) mapping utilizes multiple QTL models (Jansen 1993, Jansen 1994, Jansen and Stam 1994). This method of mapping currently is used by making the markers cofactors with additive and dominant gene interactions (van Ooijen 2004). This method can also incorporate gene-environment interactions and gene-gene interactions although the analysis becomes very difficult even when using a computer program. The permutation test can also be used to

determine the threshold of the LOD score, or deviance (van Ooijen 2004). This can be done during interval mapping and provides a significance level for evaluation.

QTL data is utilized in a marker assisted selection program. Based on the LOD score, a trait can be evaluated and used in part of a marker assisted selection program. QTL data can also be incorporated into a BLUP model to predict breeding values.

Using QTL mapping, the phenotypes of the organisms could be studied, as in phenomics. Phenomics is the systematic correlation of phenotype with genotype (Hegele and Oshima 2007). Phenomics is defined by Hegele and Oshima as the "integrated multidisciplinary research to understand the complex consequences of genomic variation through systematic evaluation and cataloguing of standardized phenotypes"( Hegele 2004, Pollex and Hegele 2006, Hegele and Oshima 2007). Phenotypes are "observable structures and functions arising from the effects of molecules, cells, tissues and organs"(Hegele and Oshima 2007). Phenomics requires phenotypic information, genotypic information, environmental relationships, and any other information that would affect the phenotype of the organism. Mutations can be induced to result in the loss of function of a gene that allows a different observable phenotype.

In a study conducted by the Washington University School of Medicine in St. Louis, Missouri, several complex disease traits were phenotyped. Using a survey on phenotypic traits for the mouse PHENOME projects instituted by the Jackson laboratory (www.jax.org/phenome), 40 strains form 59 inbred lines of mice with a wide range of genetic variation were phenotyped. Some of these traits were cardiovascular disease, cancer, and diabetes. Behavioral traits such as immunological, metabolic, and reproductive traits were measured. To identify the genetic basis of these traits, QTLs

were identified using genome- wide association (GWA) scans. A GWA scan is the association of a mouse phenotype with SNP markers on the genome using linear regression mixed models. For obesity, a gene was found (Gpr39) to have knockout phenotypes for both obesity and plasma levels. Another QTL was found affecting total cholesterol and non –HDL cholesterol levels. Using GWA scans provided high resolution abilities to detect QTL that have a direct effect on a variety of phenotypes (Lui et. al., 2007).

Quantitative trait loci are also being incorporated into traditional selection programs to increase selection power for economically important traits. Incorporating QTL into a selection index to calculate breeding values allows for all of the genetic information to be used in selection. This allow for traits that are difficult to measure quantitatively, such as disease resistance, flesh quality or color, and survival, to be incorporated with the traits that can be measured such as growth rate or feed conversion ratio (Davis and Hetzel 2000). The amount of improvement depends on the genetic variation in the population (Davis and Hetzel 2000). From this information, a selection index could also be calculated so that the animals could be assigned breeding values based on economic importance.

There are many reasons a selection program can stop progressing, and reach a selection plateau. Using traditional selection methods alone may not be able to overcome selection plateaus, and QTL analysis coupled with maker assisted selection, MAS, may enable faster rates of genetic gain and improve the ability to break out of the selection plateaus. All selection programs will eventually reach a selection plateau, some traits will plateau sooner than others. The problem is overcoming these plateaus and finding

ways to select for traits that are currently difficult using traditional selection methods. Traits that can reach plateaus such as growth rate are economically important for any program and using QTLs coupled with MAS may overcome these plateaus effectively in the shortest amount of time.

Catfish performance needs to be improved to address the industry problems. Growth rate is obviously an important trait and, body conformation may affect dressing percentage (Dunham et al. 1984). One potential solution is the interspecific backcrossing to introgress the growth rate of a channel catfish and the body conformation of a blue catfish, leading to a faster growing fish with a higher dressing percentage. If this were successful, other traits may be introgressed as well A potentially efficient way to integrate the two catfish may be to generate a QTL map followed by MAS.

The primary objective of this study was to construct a QTL map for the seven morphometric traits, head length, head depth, head width, body depth, body width, caudal depth, and caudal width, along with total length and body weight. The secondary objectives of this project were to use the QTL map to evaluate the percent of the variation described by the QTL, to identify correlated traits and how they relate to the map, and, finally, to identify the markers that have positive or negative effects on the trait identified by the map.

# MATERIALS AND METHODS

The $F_1$ interspecific hybrids were produced by crossing a female channel catfish with a blue male catfish as described in Liu et al. (2003). Backcross families were then produced by mating the $F_1$ female with a blue catfish male and female, producing a blue catfish backcross. Blood was collected to sample the genomic DNA.

Brood stock was kept in earthen ponds throughout the year at the E.W. Shell Fisheries Research Center. The male and female were seined and transported to tanks to be prepared for spawning. Males and females were selected by the visible reproductive readiness as indicated by head size for the male and abdominal distention for the female.

The female for spawning were held in 227 liter aquaria with one female per aquarium. The female was paired with one male. When the pair began spawning behavior they were monitored so that the female could be removed to strip spawn and collect the eggs.

The male catfish was brought into the laboratory and sacrificed to obtain sperm. The males were weighed, sacrificed and then their testes were removed. The testes were cleaned with saline solution and trimmed with scissors to remove excess tissue and blood.

## *Injections*

To induce ovulation, the females received two injections of liquid carp pituitary extract. The female was given a priming dose of 2 mg per kg of female body weight

and a resolving dose of 8 mg per kilogram of female body weight 12 hours later. The injections were given intraperitoneally. The females had to be weighed before the first injection to deliver the appropriate dose. The fish were held in aquaria with males after injections until they began to release eggs.

*Artificial spawning for backcross population*

When the female was giving eggs freely, they were placed in a solution with 200 ppm tricaine methanesulfonate (MS 222) and 200 ppm sodium bicarbonate until her movement slowed. The fish was then dipped into a tank of freshwater while the vent was covered by a finger to keep the eggs from leaking out while rinsing off the anesthesia. The fish was placed on a dry towel and the head was covered with a towel to catch any water leaking from the gill cavity. The fish was then taken to the stripping table and hand stripped. The eggs were stripped into 23 cm diameter round coated pans greased with a thin layer of vegetable shortening to prevent sticking. The female was stripped of eggs until the eggs no longer flowed.

*Fertilization*

The eggs were fertilized within minutes of the eggs being stripped and weighed. The eggs were rinsed with saline solution to remove all the blood and excess tissue from the female. If no blood was present, the eggs were not rinsed. The sperm was added to

the egg mass in a circular motion to expose all the eggs to the sperm solution. Dechlorinated water was then added to the egg mass and sperm solution in the pan to activate the eggs and begin the fertilization process. The eggs and sperm were gently swirled. The fertilized egg masses were then allowed to sit for 2-10 min until they formed a mass and were then transferred to a water hardening trough. The eggs remained in the water hardening trough for at least 15 minutes. In the water hardening trough, there was constant water flow and aeration. The eggs were transferred to an egg basket in a paddle wheel hatching trough. The troughs had an air supply and a paddle wheel which was turned on when the youngest egg mass in the trough was at least 3 hours old.

*Incubation*

The eggs were held in tanks with paddlewheels until hatch. The eggs treatment began 12 hours after they were fertilized. The eggs were treated three times daily, every 8 hours, with 100 ppm formalin.

After the eggs hatched, the backcross family was divided into two 60 liter aquaria. The fish were fed one time daily to satiation with 36% protein feed. Water flow and aeration were provided for the two aquaria. All fish were from the same female and the same age. The fish were harvested from the aquaria to sample DNA and take phenotypic measurments. The mean body weight was 31.23 g and the mean total length was 70.52.

*Genomic DNA*

The procedures for genomic DNA sequencing came from Liu et al., 1998. Approximately one half to 1 ml of blood was collected from each fish in a 1ml

syringe and immediately put into a 50 ml tube with 20 ml of DNA extraction buffer (100 mM NaCl, 10 mM Tris, pH 8, 25 mM EDTA, 0.5% SDS, and proteinase K, 0.1 mg/ml) Lui et al. The blood samples were incubated at 55˚ overnight. The DNA was then extracted twice with phenol and once with chloroform. DNA was precipitated by adding a half volume of 7.5M ammonium acetate and two volumes of ethanol. The DNA was collected and then washed twice with 70% ethanol, dried, and then resuspended in TE buffer (10mM Tris-HCl, 1mM EDTA, pH 7.5). The DNA was then quantified with a spectrophotometer.

*AFLP analysis*

AFLP analysis system I (catalog no. 10544-013) was purchased from Life Technologies (Bethesda, MD). Primer combinations were abbreviated in a matrix manner (Liu et al. 1998). EcoRI primers were designated with a letter for A to I. The MseI primers were given a number from 1 to 8. The primer combinations were designated by a letter plus a number with EcoR1 primer first. Genomic DNA was digested completely with EcoR1 and MseI as described by Life Technologies. The reactions were carried out in 96-well microtiter plates (International Corp., Mount Prospect, IL). To the 96-well plate, the following were added: 1µl restriction reaction buffer, 1 µl (~50 ng) genomic DNA, 0.4 µl *Eco*RI/*Mse*I restriction endonucleases, and 2.6 µl water. The reaction centrifuged for 5 sec in a Beckman (Fullerton, CA) GS-15 using an S2096 rotor. It was then incubated for 2 h at 37˚C and then inactivated at 70˚ for 5 min. Adaptors for *Eco*RI and *Mse*I (4.8 µl) were added to the restriction fragments

by ligation using T4 DNA ligase (0.2 µl) for 2 hr at 20˚. Following ligation, 90 µl of Tris-EDTA buffer (pH 8.0) was added to dilute the reactions 10 times. 1 µl each was removed to a fresh 96-well plate and stored for future use. The following was added to the new plate: 8 µl preamp primer mix, 1 µl 10X PCR buffer from the AFLP kit, and 0.2 µl Taq DNA polymerase. The samples were briefly centrifuged ad preamplification was performed for 20 cycles at the following temperatures: 94˚ for 30 sec, 56˚ for 60 sec, and 72˚ for 60 sec (Liu et al. 2003). After preamplification was completed, 2 µl of the product was transferred to a new 96-well plate containing 98 µl of Tris-EDTA buffer (pH 8.0), diluting the samples 50 times. Selective amplification reactions were done with the following: 1 µl preamplified DNA, 0.3 µl (1 pmol/ µl) labeled EcoRI primer, 1 µl MseI primer (with dNTPs), 0.03 µl Taq polymerase, 0.6 µl 10 X PCR buffer for AFLP, and 2.07 µl double distilled water. A touch down program was used for the selective amplification for 13 cycles: 94˚for 30 sec, 65˚ for 30 sec, 72˚ for 60 sec with a 0.7˚ decrease of annealing temperature each cycle, followed by 23 cycles of amplification at 94˚ for 30 sec, 56˚ for 30 sec and 72˚ for 60 sec (Liu et al. 2003).

*AFLP Genotyping*

The procedures for AFLP genotyping came from Liu et al. (2003). The AFLP products were analyzed using the LI-COR automatic sequencers, both the IR700 and the IR800, as appropriate with labeled primers. After the PCR was completed, 3 µl of formamide dye was added to each reaction. After being heated to 92˚ for 3 minutes, 0.6 µl was loaded onto the gel. Page Plus concentrate gel mix (40%, E562-500ml) was diluted to 5.5% using 1 X TBE (AMRESCO, Solon, OH). Gels were run on a 41-cm gel

with 0.2 mm spacer. Molecular weight standard (LI-COR, Lincoln, NE) was run on the first and last lane of the gels. Using IMAGE software (LI-COR), genotyping was conducted and the genotypes were then transferred to Microsoft Excel® spreadsheets and imported to Mapmaker ® software for linkage analysis.

*Nomenclature of AFLP Markers*

The AFLP markers were named for the species, primer combination, and the size of the AFLP bands. The first two letters indicate the species (e.g., Ip for *Ictalurus punctatus*), followed by the primer combinations, and the size of the AFLP marker, in base pairs, separated with a hyphen.

*Linkage Analysis*

Parents and 71 offspring were genotyped for AFLPs. The expected ratio of segregation was 1:1. A chi-square test was performed to test if the presence/absence ratio in the backcross population differed from the expected ratio. Markers that differed from the expected ratio (P= 0.05) were eliminated. A data matrix was constructed were 1 represented the presence and 0 the absence of AFLP bands. This was imported into Mapmaker/Exp version 3.0b (Lander et al. 1987). Using a LOD score of 3.0 and a maximum recombination frequency of 0.3, the initial groupings of the markers was done using the GROUP command in Mapmaker (Liu et al. 2003). Using the SUGGEST SUBSET command, the most informative sunset in each linkage group was found. The ORDER and COMPARE commands were used to determine the most probable order within the linkage groups. The maximum number of the most informative makers in

each linkage group (LG) was kept at eight for the COMPARE procedure because a number of about eight takes a tremendous amount of computing power. The most probable marker order was determined and the TRY command was used to assign additional markers to the intervals. This was followed but the RIPPLE command to check the marker order and them the MAP command to draw the map. The figures were drawn in MapCreator (http://www.wesbarris.com/mapcreator) (Liu et al. 2003).

*Regression Analysis*

The fish were measured in two groups. The following measurements were taken: head length, head depth, head width, body depth, body width, caudal depth, caudal width, total length, and total weight. The measurements were recorded on metric units in a single day per group. Fish in the two aquaria were significantly different in size. To correct for the size difference, regression analysis was performed using PROC REG in SAS 9.1. The fish were grouped into small- and big-size categories, with fish numbered 629 to 658 inclusive (18 fish) classified as big fish, and the rest classified as small fish (53 fish). Mean of total body weight was computed for each category ($MeanTW_c$), where the subscript c denotes category, *i.e.*, big or small, to be used for body part measurement correction. The data was then adjusted according to the regression coefficient to account for the size difference due to the two environments.

Relative body shape changes as fish grow (Dunham et al. 1984, Dunham et al. 1986) and absolute morphometric measurements are partially dependent on body weight. Therefore, all body measurements were corrected for body weight. For each category, a regression of the form $BodyPart = f(TotalWeight)$ was run to obtain the coefficient

BodyP*b*. The body parts for which regressions were run were:1 – HeadLength, 2 – HeadDepth, 3 – BodyDepth, 4 – CaudalDepth, 5 – HeadWidth, 6 – BodyWidth, 7 – CaudalWidth, and the corresponding regression coefficients obtained were: 1 – HeadL*b*, 2 – HeadD*b*, 3 – BodyD*b*, 4 – CaudalD*b,* 5 – HeadW*b*, 6 – BodyW*b,* 7 – CaudalW*b*. Based on the 2 categories and 7 body parts, 14 regressions were run, and 14 regression coefficients were obtained, that is, 7 regressions and 7 regression coefficients for each category.

The next step was to compute corrected body part measurements within each category. The equation used for correction is of the form $BodyPC = BodyPart -$ BodyP$b*(TotalWeight - MeanTW_c)$, where *BodyPC* denotes Corrected Body Part.

Explicitly, the 7 equations were:

1 – $HeadLC = HeadLength$ – HeadL$b*(TotalWeight – MeanTW_c)$

2 – $HeadDC = HeadDepth$ – HeadD$b*(TotalWeight – MeanTW_c)$

3 – $BodyDC = BodyDepth$ – BodyD$b*(TotalWeight – MeanTW_c)$

4 – $CaudalDC = CaudalDepth$ – CaudalD$b*(TotalWeight – MeanTW_c)$

5 – $HeadWC = HeadWidth$ – HeadW$b*(TotalWeight – MeanTW_c)$

6 – $BodyWC = BodyWidth$ – BodyW$b*(TotalWeight – MeanTW_c)$

7 – $CaudalWC = CaudalWidth$ – CaudalW$b*(TotalWeight – MeanTW_c)$

Measurement correction was done for all 71 fish, using original measurement for the fish's BodyPart (HeadLength, HeadDepth, etc.), regression coefficient (HeadL*b*, HeadD*b*, etc.) for the category to which the fish belonged, original measurement for the fish's TotalWeight, and mean total body weight ($MeanTW_c$) for the category to which the fish belonged.

Mean of corrected body parts were computed for each category. The computed means were: 1 – $HLCMean_c$, 2 – $HDCMean_c$, 3 – $BDCMean_c$, 4 – $CDCMean_c$, 5 – $HWCMean_c$, 6 – $BWCMean_c$, 7 – $CWCMean_c$.

A correction factor ($\Delta$) was computed using the means of the two categories:

1 – $HL\Delta = HLCMean_{small} - HLCMean_{big}$

2 – $HD\Delta = HDCMean_{small} - HDCMean_{big}$

3 – $BD\Delta = BDCMean_{small} - BDCMean_{big}$

4 – $CD\Delta = CDCMean_{small} - CDCMean_{big}$

5 – $HW\Delta = HWCMean_{small} - HWCMean_{big}$

6 – $BW\Delta = BWCMean_{small} - BWCMean_{big}$

7 – $CW\Delta = CWCMean_{small} - CWCMean_{big}$

The final step was to standardize the measurement of all fish to the corrected small size measurement by adjusting the measurement of the big fish using $\Delta$. The equation used for adjustment is of the form $BodyPA = BodyPC + BP\Delta$, where *BodyPC* denotes corrected body part. Explicitly, the equations were:

1 – $HeadLA = HeadLC + HL\Delta$

2 – $HeadDA = HeadDC + HD\Delta$

3 – $BodyDA = BodyDC + BD\Delta$

4 – $CaudalDA = CaudalDC + CD\Delta$

5 – $HeadWA = HeadWC + HW\Delta$

6 – $BodyWA = BodyWC + BW\Delta$

7 – $CaudalWA = CaudalWC + CW\Delta$

The above computations were done only for fish under the “big” category.

Finally, all corrected observations were pooled together to create the data set used for QTL analysis. The observations for the small category were comprised of the corrected body parts HeadLC, HeadDC, …, CaudalWC while the observations for the big category were comprised of the adjusted body parts HeadLA, HeadDA, …, CaudalDC. Altogether the observations form the standardized measurements for HeadLength, HeadDepth, BodyDepth, CaudalDepth, HeadWidth, BodyWidth, and CaudalWidth.

*Quantitative Trait Loci Analysis*

Quantitative trait loci analysis was performed using MapQTL 5. The linkage map used for analysis was constructed as described above in linkage analysis. The information was put into a plain text file to import into MapQTL 5. Phenotypic measurements and AFLP information was also imported into MapQTL 5 as a plain text file. An interval analysis was performed as described by van Ooijen (1992). The likelihood of finding a segregating QTL is determined for each position on the genome while also calculating the genetic effects of the QTL and the residual variance are calculated (van Ooijen 1992). To determine the significance threshold for the LOD scores determined in the interval analysis, a permutation test was performed using 10,000 permutations as recommended by van Ooijen (1992). Two separate maps were made, one where the significance threshold was set at 0.05 and at 0.10.

The information was taken from MapQTL5 and supplied into MapChart (Voorrips 2002) to construct the map images.

The correlation of the traits was calculated using PROC GLM in SAS 9.1, all possible comparisons were made at the significance level P= 0.05.

To determine if the trait had a positive or negative effect, the additive variance was calculated using Map QTL5. The equation used to determine the additive variance was: mu_A – mu_H where:

mu_A = the estimated mean of the distribution of the quantitative trait associated with "a" genotype.

mu_H = the estimated mean of the distribution of the quantitative trait associated with "h" genotype.

The percent variation described by the QTL was then calculated. For each locus, a value was calculated using MapQTL5 (van Ooijen 2004) that describes the percent of variation described by that locus using the following equation:

$$100^* (H0\_var - var) / \text{population variance}$$

where H0_var = residual variance under current null hypothesis (van Ooijen 2004). However, when this is done using interval mapping, if the markers are linked, the values are not simply a series of values totaling 100%.

# RESULTS

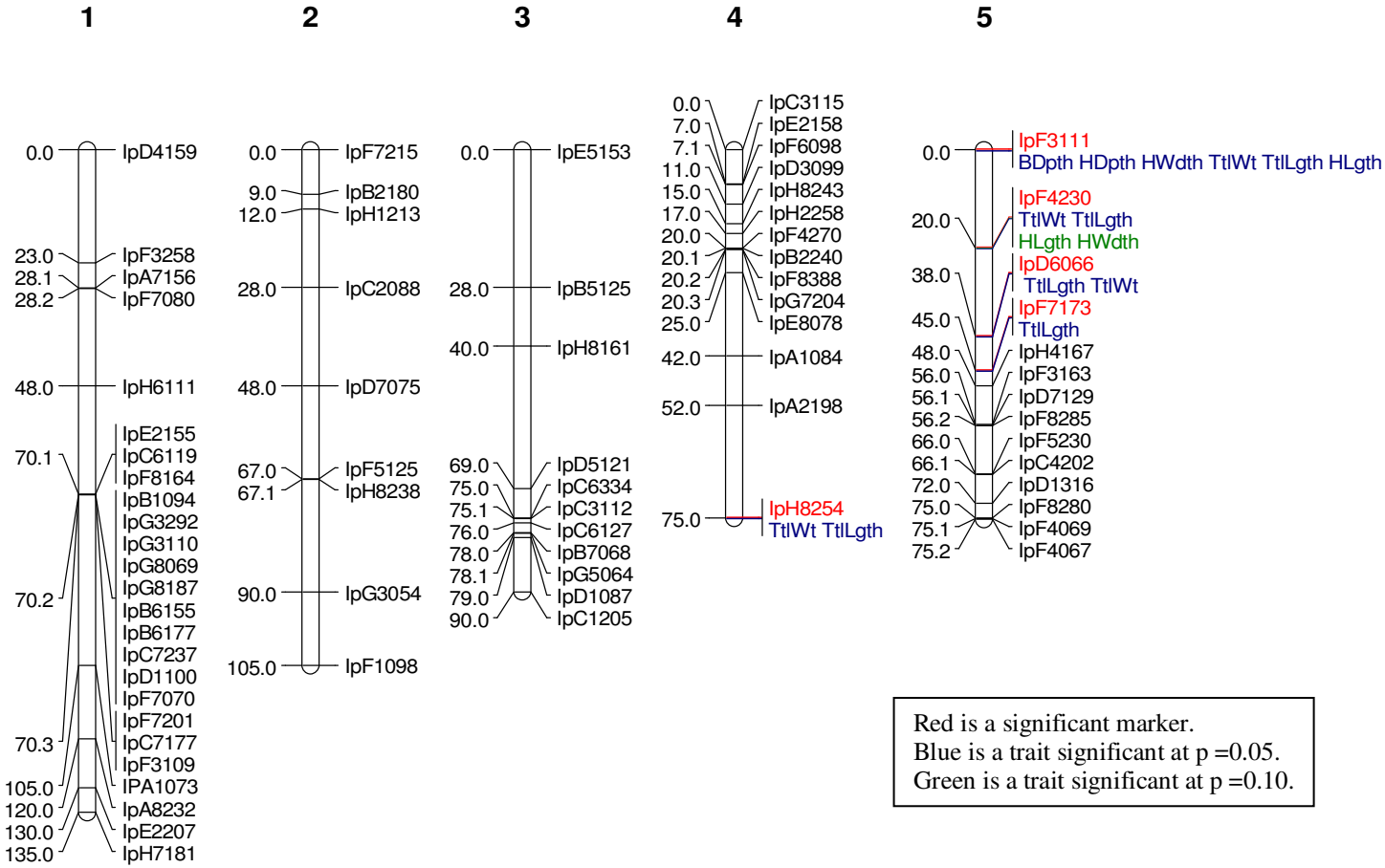
A QTL map was constructed (Figure 1). This map represents the QTLs found on all 44 linkage groups analyzed.

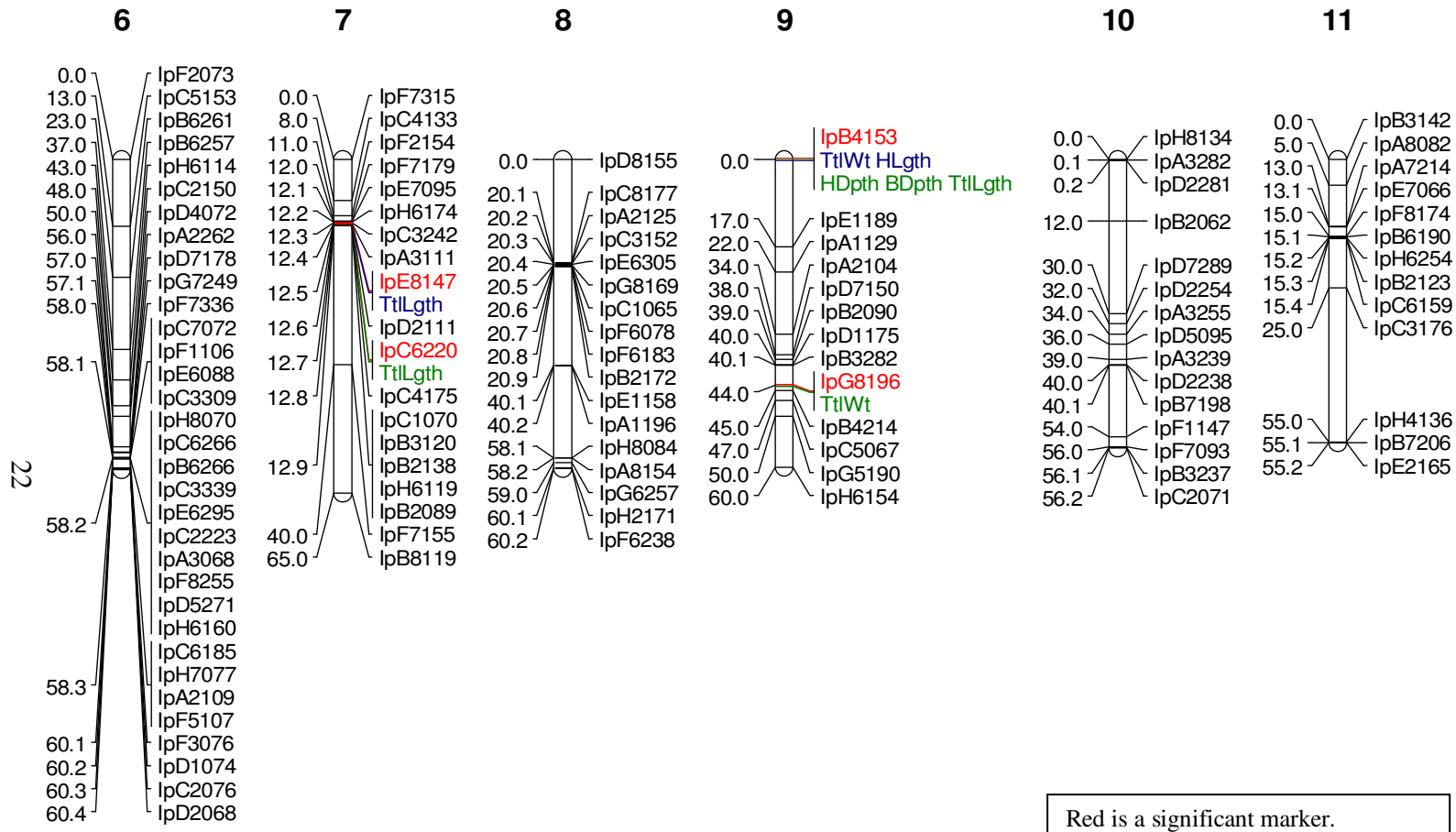
The means, standard deviations, minimum, maximum, range, and coefficient of variance for all traits for the corrected values are reported in Table 1. Each marker that was found to have a significant effect on the QTL was then evaluated to see if the marker had a positive or negative effect on the trait and are reported in Table 2. All linkage groups were then evaluated for an overall positive or negative effect Table 3. For body depth, Table 2, there were four markers that had a negative effect on the trait. The ten other markers had a significant positive effect on the trait. The markers were all located in linkage group 19 and 29. The percent explained variation for every marker was calculated and reported in Table 2. In some cases, these number total more than 100% of the explained variation. Because these markers are closely linked on the chromosome, the variation cannot simply be added to account for the total.

Body width had four markers that had a negative effect on the QTL (Table 2). All other significant markers had a positive effect on the QTL.

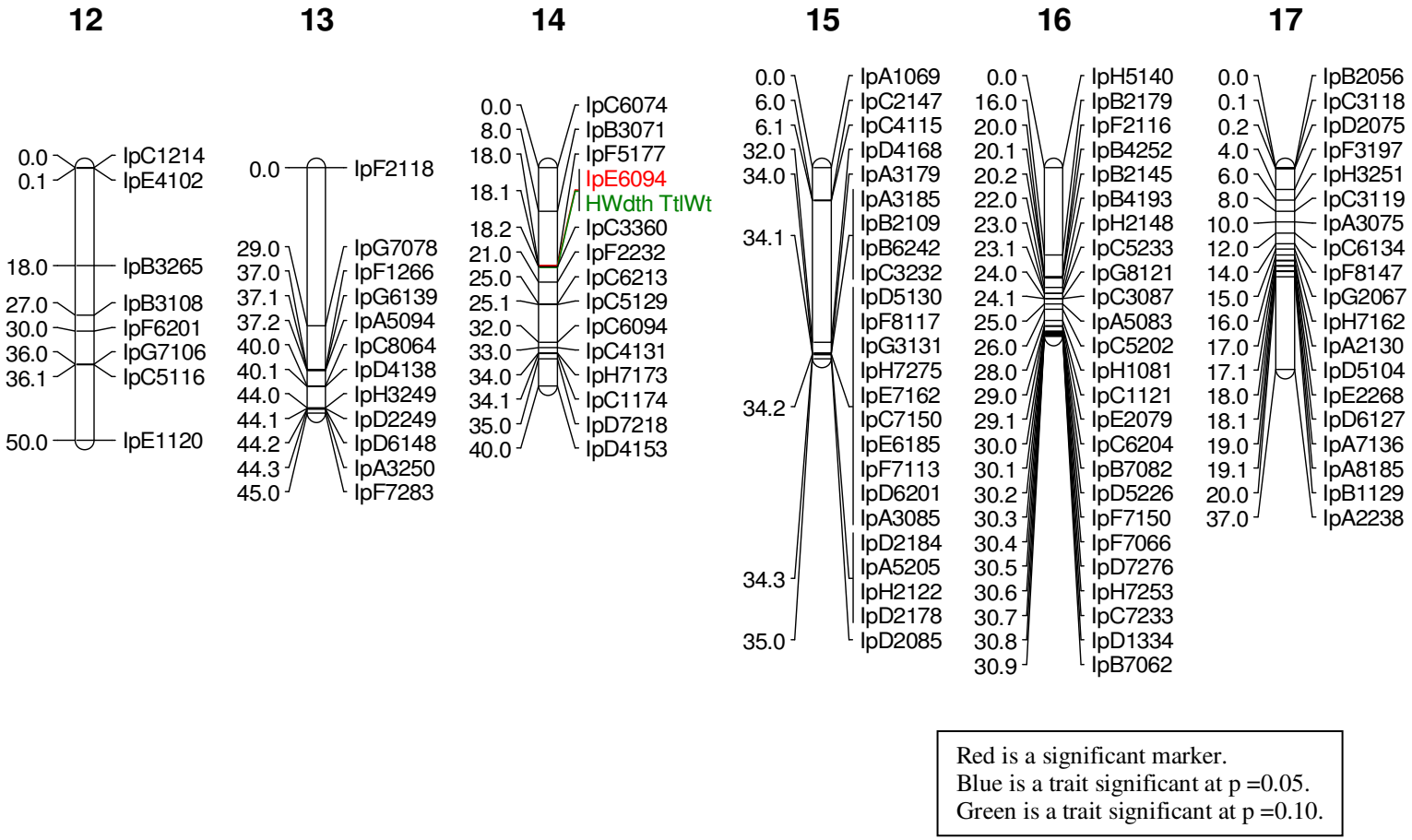
Caudal depth had two markers that had negative effects on the QTL (Table 2). Linkage group 39 had a negative effect on body depth, body width and caudal depth. Caudal depth was only seen on 2 linkage groups, the least of any of the other traits measured. Like the other traits, linkage group 19 is represented by the most significant markers.

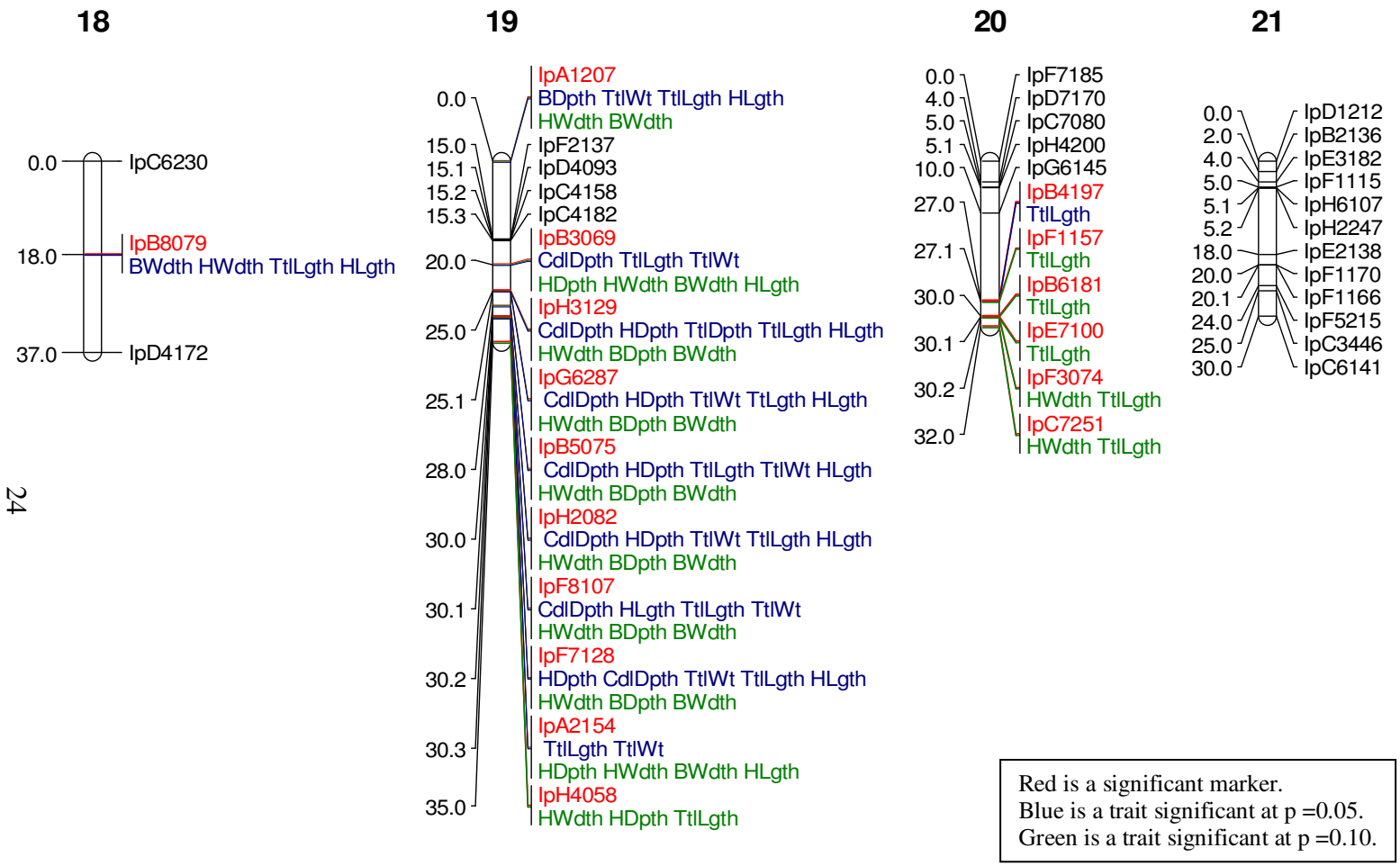
Figure 1. A QTL map of head length (HLgth), head depth (HDpth), head width (HWdth), body depth (BDpth), body width (BWdth), caudal depth (CDpth), caudal width (CWdth), total length (TtlLgth), and total weight (TtlWt) for the blue backcross spawned in aquaria.






Red is a significant marker.
Blue is a trait significant at p =0.05.
Green is a trait significant at p =0.10.


12
13
14
15
16
17
0.0 IpC1214
0.1 IpE4102
18.0 IpB3265
27.0 IpB3108
30.0 IpF6201
36.0 IpG7106
36.1 IpC5116
50.0 IpE1120
0.0 IpF2118
29.0 IpG7078
37.0 IpF1266
37.1 IpG6139
37.2 IpA5094
40.0 IpC8064
40.1 IpD4138
44.0 IpH3249
44.1 IpD2249
44.2 IpD6148
44.3 IpA3250
45.0 IpF7283
0.0 IpC6074
8.0 IpB3071
18.0 IpF5177
IpE6094
HWdth TtlWt
18.1
18.2 IpC3360
21.0 IpF2232
25.0 IpC6213
25.1 IpC5129
32.0 IpC6094
33.0 IpC4131
34.0 IpH7173
34.1 IpC1174
35.0 IpD7218
40.0 IpD4153
0.0 IpA1069
6.0 IpC2147
6.1 IpC4115
32.0 IpD4168
34.0 IpA3179
IpA3185
IpB2109
34.1 IpB6242
IpC3232
IpD5130
IpF8117
IpG3131
IpH7275
34.2 IpE7162
IpC7150
IpE6185
IpF7113
IpD6201
IpA3085
IpD2184
34.3 IpA5205
IpH2122
IpD2178
35.0 IpD2085
0.0 IpH5140
16.0 IpB2179
20.0 IpF2116
20.1 IpB4252
20.2 IpB2145
22.0 IpB4193
23.0 IpH2148
23.1 IpC5233
24.0 IpG8121
24.1 IpC3087
25.0 IpA5083
26.0 IpC5202
28.0 IpH1081
29.0 IpC1121
29.1 IpE2079
30.0 IpC6204
30.1 IpB7082
30.2 IpD5226
30.3 IpF7150
30.4 IpF7066
30.5 IpD7276
30.6 IpH7253
30.7 IpC7233
30.8 IpD1334
30.9 IpB7062
0.0 IpB2056
0.1 IpC3118
0.2 IpD2075
4.0 IpF3197
6.0 IpH3251
8.0 IpC3119
10.0 IpA3075
12.0 IpC6134
14.0 IpF8147
15.0 IpG2067
16.0 IpH7162
17.0 IpA2130
17.1 IpD5104
18.0 IpE2268
18.1 IpD6127
19.0 IpA7136
19.1 IpA8185
20.0 IpB1129
37.0 IpA2238
Red is a significant marker.
Blue is a trait significant at p =0.05.
Green is a trait significant at p =0.10.




Red is a significant marker.
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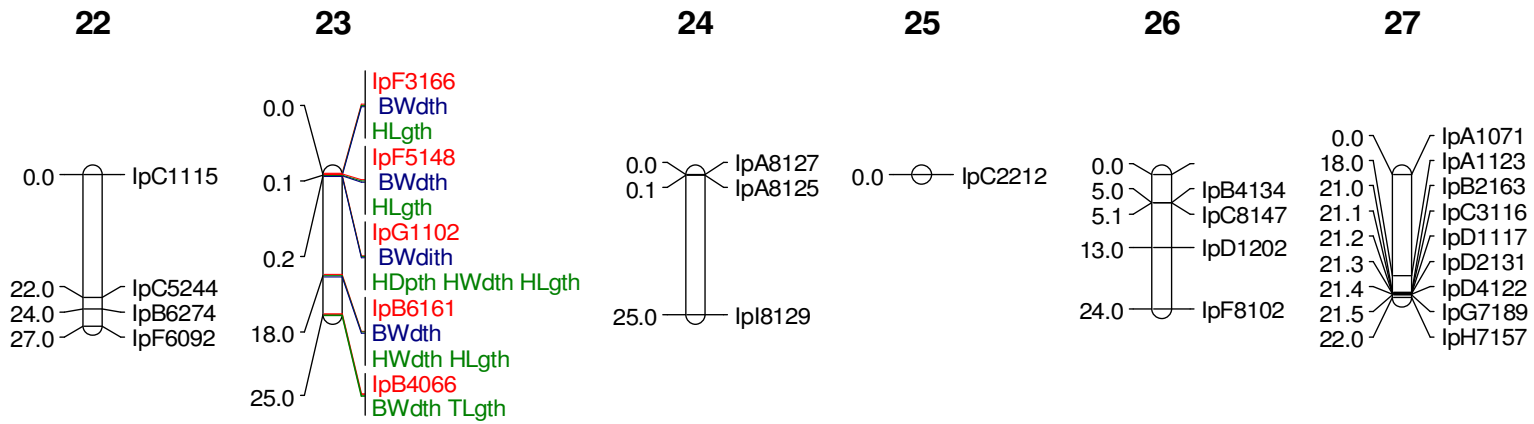
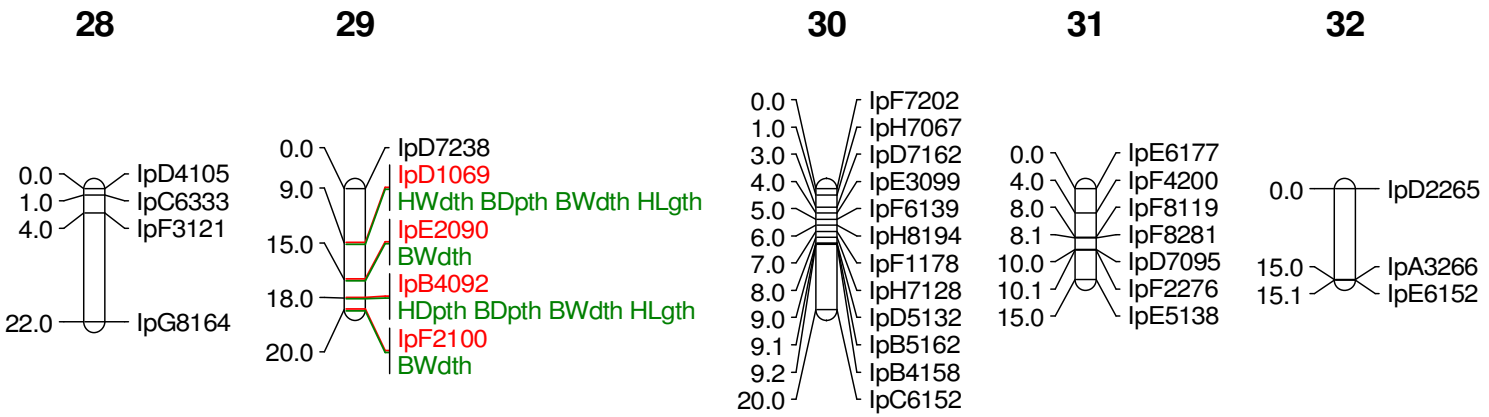
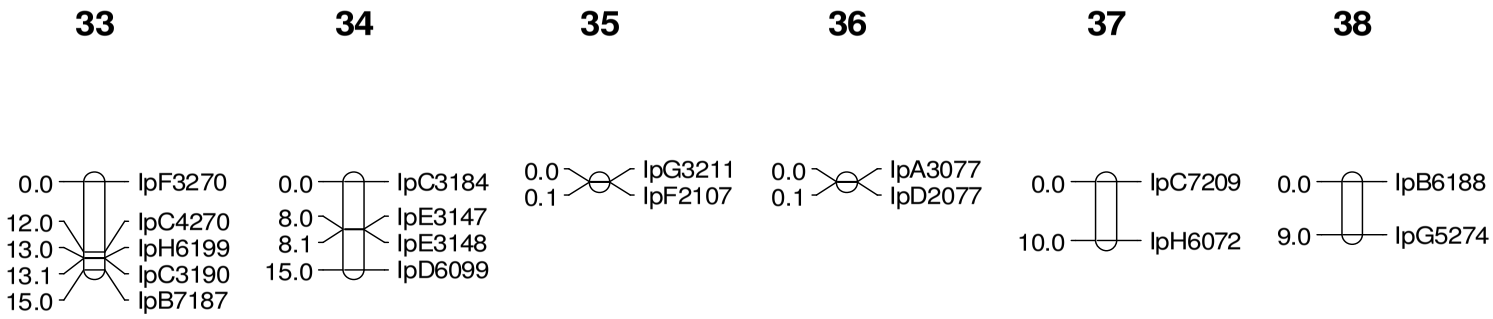
Green is a trait significant at p =0.10.



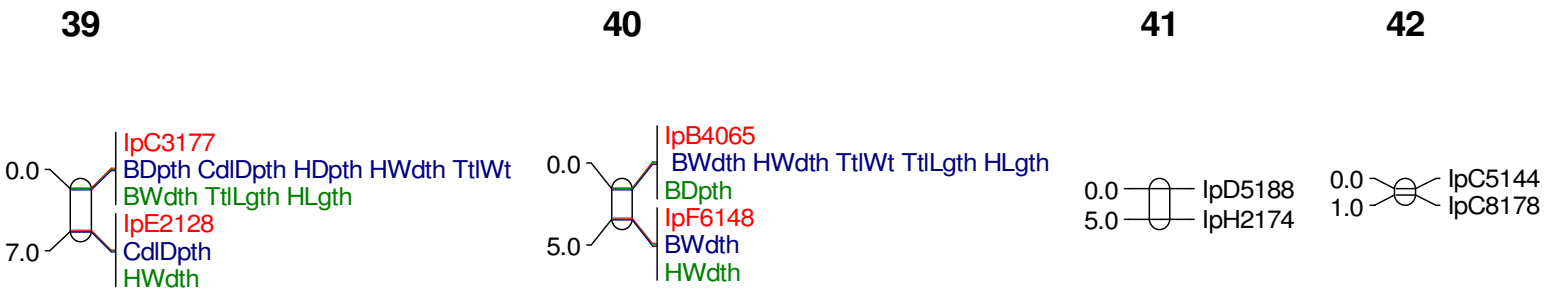

Red is a significant marker.
Blue is a trait significant at p =0.05.
Green is a trait significant at p =0.10.




Red is a significant marker.
Blue is a trait significant at p =0.05.
Green is a trait significant at p =0.10.

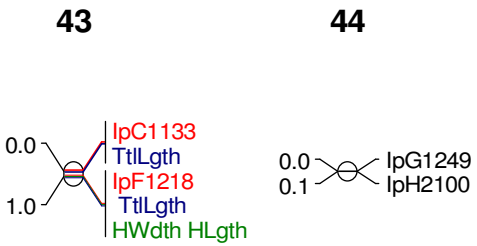



Red is a significant marker.
Blue is a trait significant at p =0.05.
Green is a trait significant at p =0.10.






Red is a significant marker.
Blue is a trait significant at p =0.05.
Green is a trait significant at p =0.10.




Red is a significant marker.
Blue is a trait significant at p =0.05.
Green is a trait significant at p =0.10.

Table 1. Mean, standard deviation, maximum, minimum, range, variance, and coefficient of variance for body weight, total length, head length, head depth, body depth, caudal depth, head width, body width, and caudal width of the blue backcross spawned in aquaria.

| Trait | Body Weight (g) | Total Length (cm) | Head Length (cm) | Head Depth (cm) | Body Depth (cm) | Caudal Depth (cm) | Head Width (cm) | Body Width (cm) | Caudal Width (cm) |
|---|---|---|---|---|---|---|---|---|---|
| Mean | 31.23 | 70.52 | 3.32 | 2.04 | 2.58 | 1.12 | 2.22 | 1.73 | 0.51 |
| Standard deviation | 34.14 | 98.11 | 0.94 | 0.65 | 0.83 | 0.33 | 0.70 | 0.55 | 0.20 |
| Maximum | 185.00 | 300.00 | 5.80 | 3.90 | 5.00 | 2.00 | 4.50 | 3.10 | 1.20 |
| Minimum | 4.00 | 9.90 | 1.80 | 1.10 | 0.90 | 0.60 | 1.20 | 0.90 | 0.30 |
| Range | 181.00 | 290.10 | 4.00 | 2.80 | 4.10 | 1.40 | 3.30 | 2.20 | 0.90 |
| Variance | 1165.81 | 9625.95 | 0.87 | 0.43 | 0.68 | 0.11 | 0.50 | 0.30 | 0.04 |
| Coefficient of Variance | 109.32 | 139.12 | 12.05 | 31.86 | 32.17 | 29.46 | 31.53 | 31.79 | 39.22 |

Table 2. LOD score, GIC (genetic information coefficient), significance level, variance, percent variation explained, additive variance, effect on the trait for body depth by locus within linkage group for the blue backcross spawned in

| Trait | Linkage Group | Locus | LOD | GIC | Significance Level | Variance | Percent Explained | Additive Variation | Effect on Trait |
|---|---|---|---|---|---|---|---|---|---|
| BDDPTH | 19 | IpA1207 | 1.43 | 0.488 | 0.05 | 0.61 | 8.9 | 0.49 | Positive |
| BDDPTH | 19 | IpA2154 | 1.22 | 0.452 | 0.10 | 0.62 | 7.6 | 0.45 | Positive |
| BDDPTH | 40 | IpB4065 | 1.09 | -0.44 | 0.10 | 0.62 | 7.0 | -0.44 | Negative |
| BDDPTH | 29 | IpB4092 | 0.96 | 0.402 | 0.10 | 0.63 | 6.0 | 0.40 | Positive |
| BDDPTH | 9 | IpB4153 | 1.36 | -0.477 | 0.10 | 0.61 | 8.5 | -0.48 | Negative |
| BDDPTH | 19 | IpB5075 | 1.33 | 0.471 | 0.10 | 0.62 | 8.3 | 0.47 | Positive |
| BDDPTH | 39 | IpC3177 | 1.28 | -0.469 | 0.05 | 0.62 | 8.0 | -0.47 | Negative |
| BDDPTH | 29 | IpD1069 | 1.10 | 0.447 | 0.10 | 0.62 | 7.2 | 0.45 | Positive |
| BDDPTH | 5 | IpF3111 | 2.32 | -0.6622 | 0.05 | 0.58 | 14.3 | -0.62 | Negative |
| BDDPTH | 19 | IpF7128 | 1.33 | 0.471 | 0.10 | 0.62 | 8.3 | 0.47 | Positive |
| BDDPTH | 19 | IpF8107 | 1.33 | 0.471 | 0.10 | 0.62 | 8.3 | 0.47 | Positive |
| BDDPTH | 19 | IpG6287 | 1.33 | 0.471 | 0.10 | 0.62 | 8.3 | 0.47 | Positive |
| BDDPTH | 19 | IpH2082 | 1.33 | 0.471 | 0.10 | 0.62 | 8.3 | 0.47 | Positive |
| BDDPTH | 19 | IpH3129 | 1.33 | 0.471 | 0.10 | 0.62 | 8.3 | 0.47 | Positive |
| BDWDTH | 19 | IpA1207 | 1.29 | 0.31 | 0.10 | 0.27 | 8.1 | 0.31 | Positive |
| BDWDTH | 19 | IpB3069 | 1.13 | 0.291 | 0.10 | 0.28 | 7.1 | 0.29 | Positive |
| BDWDTH | 40 | IpB4065 | 1.80 | -0.368 | 0.05 | 0.26 | 11.1 | -0.37 | Negative |
| BDWDTH | 23 | IpB4066 | 1.18 | 0.299 | 0.10 | 0.28 | 7.3 | 0.30 | Positive |
| BDWDTH | 29 | IpB4092 | 1.23 | 0.302 | 0.10 | 0.28 | 7.6 | 0.30 | Positive |
| BDWDTH | 19 | IpB5075 | 1.10 | 0.286 | 0.10 | 0.28 | 6.9 | 0.29 | Positive |
| BDWDTH | 23 | IpB6161 | 1.73 | 0.362 | 0.05 | 0.27 | 10.6 | 0.36 | Positive |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| BDWDTH | 18 | IpB8079 | 1.49 | -0.353 | 0.05 | 0.27 | 10.4 | -0.35 | Negative |
| BDWDTH | 39 | IpC3177 | 1.01 | -0.279 | 0.10 | 0.28 | 6.4 | -0.28 | Negative |
| BDWDTH | 29 | IpD1069 | 1.05 | 0.289 | 0.10 | 0.28 | 6.8 | 0.29 | Positive |
| BDWDTH | 29 | IpE2090 | 0.91 | 0.263 | 0.10 | 0.28 | 5.7 | 0.26 | Positive |
| BDWDTH | 29 | IpF2100 | 0.97 | 0.27 | 0.10 | 0.28 | 6.1 | 0.27 | Positive |
| BDWDTH | 23 | IpF3166 | 1.70 | 0.357 | 0.05 | 0.27 | 10.5 | 0.36 | Positive |
| BDWDTH | 23 | IpF5148 | 1.70 | 0.357 | 0.05 | 0.27 | 10.4 | 0.36 | Positive |
| BDWDTH | 40 | IpF6148 | 1.18 | -0.305 | 0.05 | 0.28 | 7.4 | -0.31 | Negative |
| BDWDTH | 19 | IpF7128 | 1.10 | 0.286 | 0.10 | 0.28 | 6.9 | 0.29 | Positive |
| BDWDTH | 19 | IpF8107 | 1.10 | 0.286 | 0.10 | 0.28 | 6.9 | 0.29 | Positive |
| BDWDTH | 23 | IpG1102 | 1.97 | 0.386 | 0.05 | 0.26 | 12.0 | 0.39 | Positive |
| BDWDTH | 19 | IpG6287 | 1.10 | 0.286 | 0.10 | 0.28 | 6.9 | 0.29 | Positive |
| BDWDTH | 19 | IpH2082 | 1.10 | 0.286 | 0.10 | 0.28 | 6.9 | 0.29 | Positive |
| BDWDTH | 19 | IpH3129 | 1.10 | 0.286 | 0.10 | 0.28 | 6.9 | 0.29 | Positive |
| CDLDPTH | 19 | IpB3069 | 1.53 | 0.201 | 0.05 | 0.10 | 9.4 | 0.20 | Positive |
| CDLDPTH | 19 | IpB5075 | 1.43 | 0.194 | 0.05 | 0.10 | 8.8 | 0.19 | Positive |
| CDLDPTH | 39 | IpC3177 | 1.55 | -0.205 | 0.05 | 0.96 | 9.7 | -0.20 | Negative |
| CDLDPTH | 39 | IpE2128 | 1.06 | -0.169 | 0.05 | 0.99 | 6.7 | -0.17 | Negative |
| CDLDPTH | 19 | IpF7128 | 1.43 | 0.194 | 0.05 | 0.10 | 8.8 | 0.19 | Positive |
| CDLDPTH | 19 | IpF8107 | 1.43 | 0.194 | 0.05 | 0.10 | 8.8 | 0.19 | Positive |
| CDLDPTH | 19 | IpG6287 | 1.43 | 0.194 | 0.05 | 0.10 | 8.8 | 0.19 | Positive |
| CDLDPTH | 19 | IpH2082 | 1.43 | 0.194 | 0.05 | 0.10 | 8.8 | 0.19 | Positive |
| CDLDPTH | 19 | IpH3129 | 1.43 | 0.194 | 0.05 | 0.10 | 8.8 | 0.19 | Positive |
| HDDPTH | 19 | IpA2154 | 1.37 | 0.38 | 0.10 | 0.39 | 8.6 | 0.38 | Positive |
| HDDPTH | 19 | IpB3069 | 1.11 | 0.344 | 0.10 | 0.39 | 6.9 | 0.34 | Positive |
| HDDPTH | 40 | IpB4065 | 0.98 | -0.333 | 0.10 | 0.39 | 6.4 | -0.33 | Negative |
| HDDPTH | 29 | IpB4092 | 0.96 | 0.319 | 0.10 | 0.40 | 6.0 | 0.32 | Positive |
| HDDPTH | 9 | IpB4153 | 1.44 | -0.388 | 0.10 | 0.38 | 8.9 | -0.39 | Negative |
| HDDPTH | 19 | IpB5075 | 1.40 | 0.382 | 0.05 | 0.39 | 8.7 | 0.38 | Positive |

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|---|---|---|---|---|---|---|---|---|---|
| HDDPTH | 39 | IpC3177 | 1.26 | -0.369 | 0.05 | 0.39 | 7.9 | -0.37 | Negative |
| HDDPTH | 5 | IpF3111 | 1.89 | -0.445 | 0.05 | 0.38 | 11.7 | -0.44 | Negative |
| HDDPTH | 19 | IpF7128 | 1.40 | 0.382 | 0.05 | 0.39 | 8.7 | 0.38 | Positive |
| HDDPTH | 23 | IpG1102 | 1.21 | 0.365 | 0.10 | 0.39 | 7.6 | 0.37 | Positive |
| HDDPTH | 19 | IpG6287 | 1.40 | 0.382 | 0.05 | 0.39 | 8.7 | 0.38 | Positive |
| HDDPTH | 19 | IpH2082 | 1.40 | 0.382 | 0.05 | 0.39 | 8.7 | 0.38 | Positive |
| HDDPTH | 19 | IpH3129 | 1.40 | 0.382 | 0.05 | 0.39 | 8.7 | 0.38 | Positive |
| HDDPTH | 19 | IpH4058 | 1.21 | 0.357 | 0.10 | 0.39 | 7.6 | 0.36 | Positive |
| HDLGTH | 19 | IpA1207 | 1.78 | 0.975 | 0.05 | 0.77 | 11.0 | 0.62 | Positive |
| HDLGTH | 19 | IpA2154 | 1.38 | 0.995 | 0.10 | 0.79 | 8.6 | 0.54 | Positive |
| HDLGTH | 19 | IpB3069 | 1.38 | 0.999 | 0.10 | 0.79 | 8.6 | 0.55 | Positive |
| HDLGTH | 40 | IpB4065 | 1.35 | 0.986 | 0.05 | 0.79 | 8.6 | -0.55 | Negative |
| HDLGTH | 29 | IpB4092 | 1.06 | 1 | 0.10 | 0.81 | 6.6 | 0.48 | Positive |
| HDLGTH | 9 | IpB4153 | 1.70 | 1 | 0.05 | 0.77 | 10.4 | -0.60 | Negative |
| HDLGTH | 19 | IpB5075 | 1.44 | 1 | 0.05 | 0.79 | 8.9 | 0.55 | Positive |
| HDLGTH | 23 | IpB6161 | 1.14 | 0.997 | 0.10 | 0.80 | 7.1 | 0.50 | Positive |
| HDLGTH | 18 | IpB8079 | 1.62 | 0.963 | 0.05 | 0.76 | 11.4 | -0.63 | Negative |
| HDLGTH | 39 | IpC3177 | 1.04 | 0.986 | 0.10 | 0.81 | 6.6 | -0.48 | Negative |
| HDLGTH | 29 | IpD1069 | 1.06 | 0.972 | 0.10 | 0.80 | 7.0 | 0.50 | Positive |
| HDLGTH | 43 | IpF1218 | 0.72 | 0.998 | 0.10 | 0.82 | 4.5 | 0.40 | Positive |
| HDLGTH | 5 | IpF3111 | 1.85 | 0.961 | 0.05 | 0.76 | 11.5 | -0.63 | Negative |
| HDLGTH | 23 | IpF3166 | 1.07 | 1 | 0.10 | 0.80 | 6.7 | 0.49 | Positive |
| HDLGTH | 5 | IpF4230 | 1.55 | 0.994 | 0.10 | 0.78 | 9.6 | -0.58 | Negative |
| HDLGTH | 23 | IpF5148 | 1.07 | 1 | 0.10 | 0.80 | 6.7 | 0.49 | Positive |
| HDLGTH | 19 | IpF7128 | 1.44 | 1 | 0.05 | 0.79 | 8.9 | 0.55 | Positive |
| HDLGTH | 19 | IpF8107 | 1.44 | 1 | 0.05 | 0.79 | 8.9 | 0.55 | Positive |
| HDLGTH | 23 | IpG1102 | 1.25 | 1 | 0.10 | 0.80 | 7.8 | 0.53 | Positive |
| HDLGTH | 19 | IpG6287 | 1.44 | 1 | 0.05 | 0.79 | 8.9 | 0.55 | Positive |
| HDLGTH | 19 | IpH2082 | 1.44 | 1 | 0.05 | 0.79 | 8.9 | 0.55 | Positive |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| HDLGTH | 19 | IpH3129 | 1.44 | 1 | 0.05 | 0.79 | 8.9 | 0.55 | Positive |
| HDWDTH | 19 | IpA1207 | 1.22 | 0.386 | 0.10 | 0.45 | 7.6 | 0.39 | Positive |
| HDWDTH | 19 | IpA2154 | 1.29 | 0.397 | 0.10 | 0.45 | 8.0 | 0.40 | Positive |
| HDWDTH | 19 | IpB3069 | 1.29 | 0.399 | 0.10 | 0.45 | 8.0 | 0.40 | Positive |
| HDWDTH | 40 | IpB4065 | 1.23 | -0.402 | 0.05 | 0.45 | 8.0 | -0.40 | Negative |
| HDWDTH | 19 | IpB5075 | 1.25 | 0.391 | 0.10 | 0.45 | 7.8 | 0.39 | Positive |
| HDWDTH | 23 | IpB6161 | 1.00 | 0.354 | 0.10 | 0.46 | 6.3 | 0.36 | Positive |
| HDWDTH | 18 | IpB8079 | 1.92 | -0.524 | 0.05 | 0.42 | 14.0 | -0.52 | Negative |
| HDWDTH | 39 | IpC3177 | 1.28 | -0.401 | 0.05 | 0.45 | 8.0 | -0.40 | Negative |
| HDWDTH | 14 | IpC6094 | 1.20 | 0.387 | 0.10 | 0.49 | 0.2 | 0.06 | Positive |
| HDWDTH | 20 | IpC7251 | 1.17 | -0.38 | 0.10 | 0.45 | 7.3 | -0.38 | Negative |
| HDWDTH | 29 | IpD1069 | 1.04 | 0.371 | 0.10 | 0.46 | 6.8 | 0.37 | Positive |
| HDWDTH | 39 | IpE2128 | 0.71 | -0.299 | 0.10 | 0.47 | 4.5 | -0.30 | Negative |
| HDWDTH | 43 | IpF1218 | 0.78 | 0.313 | 0.10 | 0.47 | 4.9 | 0.31 | Positive |
| HDWDTH | 20 | IpF3074 | 1.21 | -0.386 | 0.10 | 0.45 | 7.6 | -0.39 | Negative |
| HDWDTH | 5 | IpF3111 | 1.63 | -0.448 | 0.05 | 0.44 | 10.2 | -0.45 | Negative |
| HDWDTH | 5 | IpF4230 | 1.44 | -0.419 | 0.10 | 0.45 | 9.2 | -0.49 | Negative |
| HDWDTH | 40 | IpF6148 | 1.08 | -0.382 | 0.10 | 0.46 | 7.1 | -0.38 | Negative |
| HDWDTH | 19 | IpF7128 | 1.25 | 0.391 | 0.10 | 0.45 | 7.8 | 0.39 | Positive |
| HDWDTH | 19 | IpF8107 | 1.25 | 0.391 | 0.10 | 0.45 | 7.8 | 0.39 | Positive |
| HDWDTH | 23 | IpG1102 | 1.03 | 0.364 | 0.10 | 0.46 | 6.4 | 0.36 | Positive |
| HDWDTH | 19 | IpG6287 | 1.25 | 0.391 | 0.10 | 0.45 | 7.8 | 0.39 | Positive |
| HDWDTH | 19 | IpH2082 | 1.25 | 0.391 | 0.10 | 0.45 | 7.8 | 0.39 | Positive |
| HDWDTH | 19 | IpH3129 | 1.25 | 0.391 | 0.10 | 0.45 | 7.8 | 0.39 | Positive |
| HDWDTH | 19 | IpH4058 | 1.15 | 0.375 | 0.10 | 0.45 | 7.2 | 0.38 | Positive |
| TTLLGTH | 19 | IpA1207 | 1.81 | 0.975 | 0.05 | 8429.66 | 11.2 | 65.16 | Positive |
| TTLLGTH | 19 | IpA2154 | 1.74 | 0.995 | 0.05 | 8474.91 | 10.7 | 63.74 | Positive |
| TTLLGTH | 19 | IpB3069 | 1.57 | 0.999 | 0.05 | 8571.70 | 9.7 | 60.92 | Positive |
| TTLLGTH | 40 | IpB4065 | 1.17 | 0.986 | 0.05 | 8771.97 | 7.6 | -54.35 | Negative |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| TTLLGTH | 23 | IpB4066 | 1.20 | 1 | 0.10 | 8779.02 | 7.5 | 53.99 | Positive |
| TTLLGTH | 9 | IpB4153 | 1.32 | 1 | 0.10 | 8714.26 | 8.2 | -55.72 | Negative |
| TTLLGTH | 20 | IpB4197 | 1.62 | 1 | 0.05 | 8544.60 | 10.0 | -62.56 | Negative |
| TTLLGTH | 19 | IpB5075 | 1.58 | 1 | 0.05 | 8566.73 | 9.7 | 60.79 | Positive |
| TTLLGTH | 20 | IpB6181 | 1.12 | 1 | 0.10 | 8825.00 | 7.0 | -52.01 | Negative |
| TTLLGTH | 18 | IpB8079 | 1.53 | 0.963 | 0.05 | 8490.74 | 10.5 | -63.23 | Negative |
| TTLLGTH | 43 | IpC1133 | 1.00 | 0.998 | 0.05 | 8895.89 | 6.3 | 49.35 | Positive |
| TTLLGTH | 39 | IpC3177 | 0.97 | 0.986 | 0.10 | 8903.93 | 6.2 | -49.02 | Negative |
| TTLLGTH | 7 | IpC6220 | 1.44 | 1 | 0.10 | 8646.60 | 8.9 | -58.57 | Negative |
| TTLLGTH | 20 | IpC7251 | 1.41 | 0.998 | 0.10 | 8658.23 | 8.8 | -57.84 | Negative |
| TTLLGTH | 5 | IpD6066 | 3.95 | 0.999 | 0.05 | 7343.39 | 22.6 | -92.90 | Negative |
| TTLLGTH | 20 | IpE7100 | 1.27 | 1 | 0.10 | 8741.35 | 7.9 | -55.00 | Negative |
| TTLLGTH | 7 | IpE8147 | 2.87 | 1 | 0.05 | 7879.36 | 17.0 | -80.47 | Negative |
| TTLLGTH | 20 | IpF1157 | 1.18 | 0.996 | 0.10 | 8787.52 | 7.4 | -53.46 | Negative |
| TTLLGTH | 43 | IpF1218 | 1.12 | 0.998 | 0.05 | 8820.16 | 7.1 | 52.21 | Positive |
| TTLLGTH | 20 | IpF3074 | 1.42 | 1 | 0.10 | 8652.78 | 8.8 | -58.03 | Negative |
| TTLLGTH | 5 | IpF3111 | 2.00 | 0.961 | 0.05 | 8289.65 | 12.7 | -69.36 | Negative |
| TTLLGTH | 5 | IpF4230 | 3.15 | 0.994 | 0.05 | 7726.95 | 18.6 | -84.06 | Negative |
| TTLLGTH | 19 | IpF7128 | 1.58 | 1 | 0.05 | 8566.74 | 9.7 | 60.79 | Positive |
| TTLLGTH | 5 | IpF7173 | 1.60 | 0.999 | 0.05 | 8552.35 | 9.9 | -61.26 | Negative |
| TTLLGTH | 19 | IpF8107 | 1.58 | 1 | 0.05 | 8566.73 | 9.7 | 60.79 | Positive |
| TTLLGTH | 19 | IpG6287 | 1.58 | 1 | 0.05 | 8566.83 | 9.7 | 60.79 | Positive |
| TTLLGTH | 19 | IpH2082 | 1.58 | 1 | 0.05 | 8566.73 | 9.7 | 60.79 | Positive |
| TTLLGTH | 19 | IpH3129 | 1.58 | 1 | 0.05 | 8566.87 | 9.7 | 60.78 | Positive |
| TTLLGTH | 19 | IpH4058 | 1.17 | 0.995 | 0.10 | 8795.21 | 7.3 | 52.74 | Positive |
| TTLLGTH | 4 | IpH8254 | 2.39 | 0.983 | 0.05 | 8116.38 | 14.5 | 74.63 | Positive |
| TTLWGHT | 19 | IpA1207 | 1.45 | 0.975 | 0.05 | 1045.43 | 9.0 | 20.40 | Positive |
| TTLWGHT | 19 | IpA2154 | 1.38 | 0.995 | 0.05 | 1050.79 | 8.6 | 19.86 | Positive |
| TTLWGHT | 19 | IpB3069 | 1.45 | 0.999 | 0.05 | 1046.15 | 9.0 | 20.42 | Positive |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| TTLWGHT | 40 | IpB4065 | 1.03 | 0.986 | 0.05 | 1072.73 | 6.7 | -17.76 | Negative |
| TTLWGHT | 9 | IpB4153 | 1.92 | 1 | 0.05 | 1014.74 | 11.7 | -23.21 | Negative |
| TTLWGHT | 19 | IpB5075 | 1.31 | 1 | 0.05 | 1055.53 | 8.2 | 19.38 | Positive |
| TTLWGHT | 39 | IpC3177 | 1.19 | 0.986 | 0.05 | 1063.79 | 7.4 | -18.74 | Negative |
| TTLWGHT | 14 | IpC6094 | 1.16 | 0.994 | 0.10 | 1141.54 | 0.7 | 5.61 | Positive |
| TTLWGHT | 5 | IpD6066 | 1.66 | 0.999 | 0.05 | 1131.82 | 10.2 | -21.74 | Negative |
| TTLWGHT | 5 | IpF3111 | 1.68 | 0.961 | 0.05 | 1028.92 | 10.5 | -21.98 | Negative |
| TTLWGHT | 5 | IpF4230 | 1.84 | 0.994 | 0.05 | 1019.44 | 11.3 | -22.82 | Negative |
| TTLWGHT | 19 | IpF7128 | 1.31 | 1 | 0.05 | 1055.53 | 8.2 | 19.38 | Positive |
| TTLWGHT | 19 | IpF8107 | 1.31 | 1 | 0.05 | 1055.53 | 8.2 | 19.38 | Positive |
| TTLWGHT | 19 | IpG6287 | 1.31 | 1 | 0.05 | 1055.52 | 8.2 | 19.38 | Positive |
| TTLWGHT | 9 | IpG8196 | 1.23 | 0.991 | 0.10 | 1059.98 | 7.8 | -18.92 | Negative |
| TTLWGHT | 19 | IpH2082 | 1.31 | 1 | 0.05 | 1055.53 | 8.2 | 19.38 | Positive |
| TTLWGHT | 19 | IpH3129 | 1.31 | 1 | 0.05 | 1055.52 | 8.2 | 19.38 | Positive |
| TTLWGHT | 4 | IpH8254 | 1.72 | 0.983 | 0.05 | 1027.09 | 10.6 | 22.26 | Positive |

Table 3. Positive or negative effect in all linkage groups with QTLs for all traits for the blue backcross spawned in aquaria.

| | Linkage Group | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| QTL/Trait | 4 | 5 | 7 | 9 | 14 | 18 | 19 | 20 | 23 | 29 | 39 | 40 | 43 |
| Body Weight | + | − | | − | + | | + | | | | − | − | |
| Total Length | + | − | − | − | | − | + | − | + | | − | − | + |
| Head Depth | | − | | − | | | + | | | | − | − | |
| Head Width | | − | | − | +* | − | + | − | + | + | − | − | + |
| Head Length | | − | | − | | − | + | | + | + | − | − | + |
| Body Depth | | − | | − | | | + | | | + | − | − | |
| Body Width | | | | | | | + | | + | + | − | − | |
| Caudal Depth | | | | | | | + | | | | − | | |
| Caudal Width | | | | | | | | | | | | | |

* Explained a small amount of variation compared to other QTLs

Head depth has a similar trend as the other traits (Table 2). Like body depth, the markers in linkage groups 5, 9, 39 and 40, all had a negative trait effect. Linkage group 19 is represented by 8 markers.

Head length has 21 markers significant for a QTL (Table 2). Linkage groups 5, 9, 18, 39 and 40 have negative effects on the QTL. All other markers have a positive effect.

Head width has 23 markers significant for a QTL (Table 2). Linkage groups 5, 18, 20, 39 and 40 have negative trait effects. All other markers have a positive effect.

Total length (Table 2) and body weight (Table 2) have 29 significant markers and 17 significant markers for the traits. For total length and body weight, linkage groups 5, 9, 39 and 40 had negative effects on both traits. Total length has two other linkage groups with negative trait effects, linkage groups 7 and 20.

All of the phenotypic traits measured were found to be strongly correlated with each other (Table 3). Every trait was measured using PROC GLM in SAS 9.1 against every other trait to find significant (P= 0.05) phenotypic correlation.

Table 4. Phenotypic correlations for total body weight, total length, head length, head depth, body depth, caudal depth, head width, body width, and caudal width.

| Phenotypic Correlations | Body Weight | Total Length | Head Length | Head Depth | Body Depth | Caudal Depth | Head Width | Body Width | Caudal Width |
|---|---|---|---|---|---|---|---|---|---|
| Body Weight | NA | 0.84 | 0.90 | 0.89 | 0.90 | 0.87 | 0.90 | 0.83 | 0.92 |
| Total Length | | NA | 0.86 | 0.80 | 0.79 | 0.83 | 0.84 | 0.74 | 0.85 |
| Head Length | | | NA | 0.95 | 0.96 | 0.96 | 0.96 | 0.93 | 0.95 |
| Head Depth | | | | NA | 0.94 | 0.95 | 0.93 | 0.90 | 0.91 |
| Body Depth | | | | | NA | 0.95 | 0.94 | 0.93 | 0.92 |
| Caudal Depth | | | | | | NA | 0.93 | 0.92 | 0.94 |
| Head Width | | | | | | | NA | 0.91 | 0.91 |
| Body Width | | | | | | | | NA | 0.91 |
| Caudal Width | | | | | | | | | NA |

For all seven morphometric traits and two growth traits, there are 9 of the 44 linkage groups that have at least one significant locus using a significance threshold of 0.05. At a significance threshold of 0.10, there are 12 linkage groups that have at least one marker that is significant. In LG4, marker IpH8254 is significant (P= 0.05) for total weight and total length (Figure 1). Linkage group 5 has four markers identified as QTLs. Marker IpF3111 is significant (P= 0.05) for body depth, head depth, head width, head length, total length, and total width. Marker IpF4230 is significant at the P= 0.05 threshold for total weight and total length. One the same marker, a QTL using P= 0.10 is found for head length and head width. Marker IpD6066 is significant (P= 0.05) for total length and total weight. The final significant (P= 0.05) marker is IpF7173 for total length.

Linkage group 6 contains no QTLs for the measured traits. Linkage group 7 has two significant markers less than 0.1 centimorgans apart on the chromosome. IpE8147 is significant (P= 0.05) for total length. Marker IpC6220 is significant (P= 0.10) for total length as well. Linkage group 9 has two significant markers. Marker IpB4153 is significant (P= 0.05) for head length and total weight and significant (P= 0.10) for head depth, body depth, and total length. Forty four centimorgans away from IpB4153, marker IpG8196 is significant (P= 0.05) for total weight.

Linkage groups 10 to 13 have no QTLs for the seven measured traits. Linkage group 14 has one significant marker (P= 0.05) for head width and total width. Linkage groups 15, 16, and 17 have no QTLs. Linkage group 18 has one marker, IpB8079, significant (P= 0.05) for head length, head width, body width, and total length.

Linkage group 19 has 14 markers. Of the 14 markers, 9 have significances using P= 0.05 as threshold and a total of 10 using P= 0.10 as the threshold. Marker IpA1207 is

significant (P= 0.05) for head length, body depth, total length, and total weight, and is significant (P= 0.10) for head width and body width. Twenty centimorgans away, marker IpB3069 is significant (P= 0.05) for caudal depth, total length, and total weight, and is significant (P= 0.10) for body width, head depth, head width, and head length. IpH3129 is significant (P= 0.05) for caudal depth, head depth, head length, total length, and is significant (P= 0.10) for head width, body depth, and body width. Markers IpG6287, IpB5075, IpH2082, and IpF7128 are significant (P= 0.05) for caudal depth, head depth, head length, total length, and total weight, and are significant (P= 0.10) for head width, body depth and body width. Marker IpF8107, located between IpH2082 and IpF7128, 0.2 centimorgans apart, is significant (P= 0.05) for caudal depth, head length, total length, and total weight, and is significant (P= 0.10) for the same three traits as the previous markers. IpA2154 is significant for total length and total weight using 0.05 as the significance threshold and body width, head depth, head length, and head width at the 0.10 significance level. The final marker, located 35 centimorgans from the first marker on the chromosome, is significant (P= 0.10) for head depth, head width, and total length. Linkage group 20 has 6 markers significant for at least one trait. Marker IpB6145 is significant (0.05) for total length. Markers IpF1157, IpB6181, IpE7100, IpF3074, and IpC7251 are significant (P= 0.10) for total length with markers IpF3074 and IpC7251 also being significant (0.10) for head width.

Linkage groups 21 and 22 have no QTLs. Linkage group 23 has 5 markers, all significant for a QTL. Markers IpF3166, IpF5148, IpG1102, and IpB6161 are significant (P= 0.05) for body width and all these same markers are significant (0.10) for head length. Markers IpG1102 and IpB6161 are significant (0.10) for head length with

IpG1102 also being significant for head depth. The final marker on the chromosome located 25.0 centimorgans from the start of the chromosome, is significant (P= 0.10) for body width and total length.

Linkage groups 24- 28 have no QTLs for the traits measured. Linkage group 29 has 5 markers that span 20 centimorgans. Four of the five markers are significant (P= 0.10) for body width, IpD1069, IpE2090, IpB4092, and IpF2100. Markers IpD1069 and IpB4092 are significant (P= 0.10) for head length and body depth. IpD1069 is significant (P= 0.10) for head width and IpB4092 is significant (P= 0.10) for head depth. Linkage groups 30- 38 have no QTLs.

Linkage group 39 has QTLs on both markers located 7 centimorgans apart. IpC3177 is significant (P= 0.05) for head width, head depth, body depth, caudal depth, and total weight and is significant (P= 0.10) for head length, body width, and total length. Marker IpE2128 is significant (P= 0.05) for caudal depth and is significant (P= 0.10) for head width. Linkage group 40 has two markers, both with QTLs. IpB4065 is significant (P= 0.05) for head width, head length, body width, total length, and total weight and is significant (P= 0.10) for body depth. Marker IpF6148, located 5 centimorgans from the first marker, is significant (P= 0.05) for body width and is significant (P= 0.10) for head width. Linkage groups 41 and 42 have no QTLs.

Linkage group 43 has QTLs on both markers which are 1 centimorgan apart. IpC1133 is significant (P= 0.05) for total length. IpF1218 is significant (P= 0.05) for total length and is significant (P= 0.10) for head width and head length.
Linkage group 17 has no QTLs. Linkage group 18 has one marker, IpB8079, significant (P= 0.05) for head length, head width, body width, and total length.

Linkage group 19 has 14 markers. Of the 14 markers, 9 have significances using P= 0.05 as threshold and a total of 10 using P= 0.10 as the threshold. Marker IpA1207 is significant (P= 0.05) for head length, body depth, total length, and total weight, and is significant (P= 0.10) for head width and body width. Twenty centimorgans away, marker IpB3069 is significant (P= 0.05) for caudal depth, total length, and total weight, and is significant (P= 0.10) for body width, head depth, head width, and head length. IpH3129 is significant (P= 0.05) for caudal depth, head depth, head length, total length, and is significant (P= 0.10) for head width, body depth, and body width. Markers IpG6287, IpB5075, IpH2082, and IpF7128 are significant (P= 0.05) for caudal depth, head depth, head length, total length, and total weight, and are significant (P= 0.10) for head width, body depth and body width. Marker IpF8107, located between IpH2082 and IpF7128, 0.2 centimorgans apart, is significant (P= 0.05) for caudal depth, head length, total length, and total weight, and is significant (P= 0.10) for the same three traits as the previous markers. IpA2154 is significant for total length and total weight using 0.05 as the significance threshold and body width, head depth, head length, and head width at the 0.10 significance level. The final marker, located 35 centimorgans from the first marker on the chromosome, is significant (P= 0.10) for head depth, head width, and total length. Linkage group 20 has 6 markers significant for at least one trait. Marker IpB6145 is significant (0.05) for total length. Markers IpF1157, IpB6181, IpE7100, IpF3074, and IpC7251 are significant (P= 0.10) for total length with markers IpF3074 and IpC7251 also being significant (0.10) for head width.

Linkage groups 21 and 22 have no QTLs. Linkage group 23 has 5 markers, all significant for a QTL. Markers IpF3166, IpF5148, IpG1102, and IpB6161 are significant

(P= 0.05) for body width and all these same markers are significant (0.10) for head length. Markers IpG1102 and IpB6161 are significant (0.10) for head length with IpG1102 also being significant for head depth. The final marker on the chromosome located 25.0 centimorgans from the start of the chromosome, is significant (P= 0.10) for body width and total length.

Linkage groups 24- 28 have no QTLs for the traits measured. Linkage group 29 has 5 markers that span 20 centimorgans. Four of the five markers are significant (P= 0.10) for body width, IpD1069, IpE2090, IpB4092, and IpF2100. Markers IpD1069 and IpB4092 are significant (P= 0.10) for head length and body depth. IpD1069 is significant (P= 0.10) for head width and IpB4092 is significant (P= 0.10) for head depth. Linkage groups 30- 38 have no QTLs.

Linkage group 39 has QTLs on both markers located 7 centimorgans apart. IpC3177 is significant (P= 0.05) for head width, head depth, body depth, caudal depth, and total weight and is significant (P= 0.10) for head length, body width, and total length. Marker IpE2128 is significant (P= 0.05) for caudal depth and is significant (P= 0.10) for head width. Linkage group 40 has two markers, both with QTLs. IpB4065 is significant (P= 0.05) for head width, head length, body width, total length, and total weight and is significant (P= 0.10) for body depth. Marker IpF6148, located 5 centimorgans from the first marker, is significant (P= 0.05) for body width and is significant (P= 0.10) for head width. Linkage groups 41 and 42 have no QTLs.

Linkage group 43 has QTLs on both markers which are 1 centimorgan apart. IpC1133 is significant (P= 0.05) for total length. IpF1218 is significant (P= 0.05) for total length and is significant (P= 0.10) for head width and head length.

# DISCUSSION

As expected, all of the morphometric measurements had very little variation, however, total length and body weight, were highly variable. The fish were all relatively proportioned even though some were larger than others. Since all of the fish were from the same family, this may have also contributed to the small amount of variation in their body conformation.

Using 7 morphometric and 2 growth traits, there are 9 of the 44 linkage groups that have at least one significant locus using a significance threshold of 0.05. Using a significance threshold of 0.10, there are 12 linkage groups that have at least one marker that is significant for a trait. The markers that were closely positioned on the chromosome had, in general, the same positive or negative effect on the trait.

Markers in linkage groups 5, 7, 9, 20, 39, and 40 were significant. All of these linkage groups had an overall negative effect on the QTL. All other linkage groups had a positive effect. The traits were all strongly correlated. If the traits were not correlated, the linkage groups would likely be positive for some traits and negative for others.

Linkage group 19 was unusual. It had multiple positive QTLs for all traits. Linkage group 19 appears to have a significant effect QTLs for body conformation as well as total length and body weight. All of the traits measured were represented by at least 7 markers for every trait on chromosome 19. The linkage group likely possesses genes or a series of genes that have positive effects on various growth traits. Again, this

suite of QTLs appear promising for multiple trait MAS, except they would likely increase head size.

QTLs for body depth are found on 6 different linkage groups with a majority of the markers being in LG 19. When using the practical significance threshold of 0.10, body depth is tightly linked on linkage group 19 with markers being 10 centimorgans apart.

Body width conformation is represented on 6 different linkage groups, using the significance threshold of P= 0.10. Linkage group 23 has five markers with a total distance of 25 centimorgans. Linkage groups 19 and 23 have a strong positive effect on the trait. If selecting for body width, these two linkage groups would be extremely important. Body depth, caudal depth, head width, head depth, head length, head width, total length, and body width all have similar trends.

Usually a QTL for body size represented both body weight and total length (13 QTLs). However, when a QTL represented just one of these it was usually total length, 7 QTLs, rather than body weight, 2 QTLs. On only one occasion was a QTL representing total length and body weight (linkage group 4) and once for total length (linkage group 7) not linked to any of the morphometric measurements. This may make it difficult to conduct marker assisted selection for body weight without affecting the other traits. This could be a positive or a negative depending upon the nature of these linkages. Linkage group 4 had a positive effect on size, thus a good candidate for MAS, however, linkage group 7 had a negative effect on length. Linkage group 4 had a single QTL that affected

both total length and body weight. Additionally, this QTL was near the end of the linkage group.

All of the QTLs for body weight and total length explained similar amounts of the variation for those traits, so no major loci were identified. Three linkage groups had positive QTLs for body weight and 4 had negative effects on body weight, narrowing the candidates for MAS. A similar result was observed for total length with 4 linkage groups having positive effects and 6 having negative effects. Fortunately, no linkage groups existed where total length and body weight were antagonistic, which is consistent with the high phenotypic correlation of these 2 traits, and 2 linkage groups, 4 and 19, had body weight and total length QTLs both positive.

If MAS for body weight or total length were to be conducted, what effect would there be on the morphometric traits or vice versa? All of the phenotypic correlations were very high. Assuming that they are an accurate reflection of genetic correlations, the general response should be a series of positive correlated responses. However, as body size increases the desired correlated response is a decrease in head size like the parental blue catfish, which would presumably result in higher carcass yield. The phenotypic correlations indicate that it may be difficult to conduct multiple trait MAS for increased body weight and decreased head size, but multiple trait MAS for increased body weight, body depth, body width and caudal width would be successful, which should result in increased carcass yield. However, there would likely be a correlated gain in head size, which might negate the gains made in carcass yield. This is reinforced by the nature of the linkages. Thirteen linkage groups contained significant QTLs. In each and every case, all QTLs on a linkage group affected the trait in the same direction, all positive or all

negative. This would prevent focusing multiple trait MAS on linkage groups that have positive effects on body weight, body and caudal morphometrics, but negative effects on head size as such linkage groups did not exist.

There are not many studies currently identifying QTLs for morphometric traits or growth in fish. One study on rainbow trout identified three QTLs for growth and four suggestive QTLs for growth (O'Malley et al. 2003). No other measurements were taken during this study and there was no comparison between traits because the main objective was identifying spawning date. For the blue backcross, nine linkage groups with QTLs were determined (P= 0.05).

In chickens, body weight determination was studied in an $F_2$ intercross (Le Rouzic 2008). Greater than 15 loci were found to contribute to body weight determination. For the blue backcross, 16 loci were found to contribute to body weight. The blue backcross has the same complex determination of growth as the chicken.

Linkage group 4 would be a good linkage group for MAS since only body weight and total length QTLs were found, thus negative correlated responses for the other traits should not occur.

Linkage group 14 is also a good candidate as a positive QTL exists for body weight. There is also a positive QTL for head width on this linkage group, but it explains only a vary minor portion of the variation for head width. Thus, any negative correlated response for this trait would probably be inconsequential.

Linkage groups 5,3, 9 and 40 all had negative effects on all 3 head size traits. However, they also had negative effects on body weight and total length, therefore, undesired correlated responses to multiple trait MAS might occur. QTLs negative for 1-

to- 2 head traits were found on linkage groups 18 and 20. In this case, there were also negative QTLs for total length. Perhaps since total length only and not body weight QTLs were found in these linkage groups, these may be the best linkage groups and QTLs for MAS of the head traits with the least potentially damaging effects on body weight.

If the relationships on linkage groups 5, 9, 18, 19, 23, 29, 39 and 40 are examined, they show a very tight relationship among body depth and width and the head traits in both the positive and negative directions. This may indicate that it would be relatively easy to make this suite of traits larger or smaller simultaneously, but may be very difficult to select for them in different directions.

The QTL map also provides some indication on how difficult it may be to break up some of the linkage groups and change the nature of genetic and phenotypic correlations during long-term selection. If some of these linkages were weak, multiple trait MAS would be more successful in the long term. The relationships varied from one linkage group to another. Linkages were quite tight in many cases, but some were fairly distant.

The linkage relationships found among body weight, total length and the 7 morphometric traits indicated that multiple trait MAS to increase body weight, body depth, body width and caudal depth while decreasing the head depth, head length and head width with the goal of improving body weight and carcass yield simultaneously might be difficult. Certain QTLs seemed more promising for accomplishing the goal, and focusing on MAS on these markers might yield positive results.

Future research should include creating a more detailed and more precise QTL map. Forty-four linkage groups were studied, but as channel catfish and blue catfish have

58 chromosomes, 29 linkage groups should exist. There is a possibility that some of the linkage groups in this study actually belong together, which could influence the interpretation of the results and their use. The information generated should allow the initial evaluation of MAS for body weight and morphology in catfish.

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