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Quantitative trait loci map for growth and morphometric traits using a channel catfish × blue catfish interspecific hybrid system[1]

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ABSTRACT: Head length, head depth, head width, body depth, body width, caudal depth, and caudal width and total length and BW were measured for 71 backcross full sibs between the interspecific backcross F_1 (female channel catfish [*Ictalurus punctatus*] × male blue catfish [*Ictalurus furcatus*]) female × blue catfish male. Body measurements were corrected for both size and the relationship between relative body shape and size, which is critical but usually ignored in fish research. Amplified fragment length polymorphism analysis was used for construction of a QTL map with 44 linkage groups. Eleven of 44 linkage groups had at least 1 significant QTL ($P \leq 0.05$) and 11 of 44 at $P = 0.10$. Linkage group 19 was unique as it had multiple QTL for every trait measured, except for caudal width for which no QTL was identified on any linkage group. Approximately half of the markers measured were associated with positive effects (increase in size) on the traits and half had negative effects (decrease in size). Linkage groups 5, 9, 18, 20, 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 BW, total length, and the 7 morphometric traits indicated that multiple trait marker-assisted selection to simultaneously increase BW body depth, body width, and caudal depth while decreasing the head traits with the goal to increase body weight and carcass yield would be very difficult. Multiple genetic enhancement approaches would likely be needed to simultaneously improve BW and body conformation.

Key words: amplified fragment length polymorphism, BW and shape, catfish, linkage map, quantitative trait loci

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INTRODUCTION

Channel catfish (*Ictalurus punctatus*) and blue catfish (*Ictalurus furcatus*) have 29 pairs of chromosomes (LeGrande et al., 1984). The linkage map constructed using amplified fragment length polymorphism (**AFLP**) markers for channel catfish (Liu et al., 2003) identifies 44 linkage groups (**LG**).

In the case of fish, QTL have been identified for fitness (Cnaani et al., 2003), high temperature tolerance for cold water species (Cnaani et al., 2003; Somorjai et al., 2003), body mass and condition factor (Martyniuk et al., 2003), cold tolerance in warmwater species (Sun and Liang, 2004), time of hatch (Robison et al., 2001), and disease resistance (Ozaki et al., 2013). Three studies have examined QTL for morphology in marine fish, European sea bass, (*Dicentrarchus labrax*; Massault et al., 2010) and gilthead seabream (*Sparus aurata*; Boulton et al., 2011; Loukovitis et al., 2013), and 1 in freshwater fish, such as carp (Wang et al., 2013). Naturally, body measurements are highly correlated with BW, and the relative body shape also changes as a fish grows (Dunham and Smitherman, 1984; Dunham et al., 1986; Dunham, 2012). For any morphometric measurement, including QTL, to be meaningful in fish, the trait must be corrected both for size and the relationship between size and morphology, which has not been previously considered for QTL.

The primary objective of this study was to construct a QTL map for the 7 morphometric traits, head length, head depth, head width, body depth, body width, caudal depth, and caudal width, along with total length and BW and to identify the markers that have positive (increased

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Table 1. Mean, SD, maximum, minimum, range, variance, and CV for total BW, total length, head length, head depth, body depth, caudal depth, head width, body width, and caudal width of the interspecific backcross F_1 (female channel catfish [*Ictalurus punctatus*] × male blue catfish [*Ictalurus furcatus*]) female × blue catfish male in the small (aquaria 1) and large (aquaria 2) size groups

Trait	BW, 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
Small fish									
Mean	16.53	14.75	2.88	1.76	2.24	0.98	1.90	1.52	0.42
SD	10.11	3.00	0.51	0.41	0.52	0.20	0.36	0.40	0.10
Maximum	44.00	21.50	4.10	2.90	3.20	1.50	2.80	2.40	0.70
Minimum	4.00	9.90	1.80	1.10	0.90	0.60	1.20	0.90	0.30
Range	40.00	11.60	2.30	1.80	2.30	0.90	1.60	1.50	0.40
Variance	102.25	9.02	0.26	0.17	0.27	0.04	0.13	0.16	0.01
CV	61.18	20.37	17.72	23.32	23.19	20.82	19.08	26.09	23.29
Large fish									
Mean	74.50	23.47	4.60	2.85	3.59	1.56	3.13	2.36	0.78
SD	42.79	3.69	0.69	0.56	0.73	0.23	0.67	0.45	0.18
Maximum	185.00	30.00	5.80	3.90	5.00	2.00	4.50	3.10	1.20
Minimum	23.00	16.50	3.00	1.80	2.20	1.00	1.80	1.40	0.50
Range	162.00	13.50	2.80	2.10	2.80	1.00	2.70	1.70	0.70
Variance	1,831.32	13.63	0.47	0.31	0.53	0.05	0.45	0.20	0.03
CV	57.44	15.73	14.97	19.56	20.25	14.66	21.34	19.11	23.15

size) or negative effects (decreased size) on the trait identified by the map. To optimize body shape to increase carcass yield, it is desirable for relative head size to decrease and for the relative size of body width/depth and caudal traits to increase. The QTL reported here are the first for fish that have been corrected for both size and the relationship between size and morphology.

MATERIALS AND METHODS

All the procedures involving the handling fish during this study were approved by the Auburn University Institutional Animal Care and Use Committee. Tricaine methanesulfonate was used at 200 mg/L to euthanize a male for testes collection and at 100 mg/L to anesthetize experimental fish to collect blood.

The F_1 interspecific hybrids were produced by crossing a female channel catfish with a male blue catfish as described in Liu et al. (2003). A backcross family was then produced by mating an F_1 female with a blue catfish male, producing a blue catfish backcross. A total of 71 progeny were produced and evaluated (Liu et al., 2003). Blood was collected to sample the genomic DNA.

Brood stock were kept in earthen ponds at the E.W. Shell Fisheries Research Center (Auburn University, AL). Males and females were seined and selected by the visible reproductive readiness as indicated by head size for the male and abdominal distention for the female and transported to tanks for spawning.

The females were held in 227-L aquaria with 1 female per aquarium. The female was paired with 1 male. Spawning behavior was monitored and the females were removed to hand-strip and collect eggs when ovulation was observed.

The male catfish was sacrificed to obtain testes. The testes were removed, cleaned with saline solution, and trimmed with scissors to remove excess tissue and blood. The testes were manually macerated to release the sperm.

The eggs were fertilized within minutes of the eggs being stripped and weighed. 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 embryos were transferred to an egg basket in a paddle wheel hatching trough until hatch.

After the embryos hatched, the backcross family was divided into two 60-L aquaria. The fish were fed 1 time daily to satiation with 36% protein feed. Water flow and aeration were provided for the 2 aquaria. The fish were harvested from the aquaria to sample DNA and take phenotypic measurements. The mean BW was 74.5 and 16.5 g and the mean total length was 23.5 and 14.8 cm for the big fish from aquaria 2 and the small fish from aquaria 1 (Table 1).

Genomic DNA

Approximately 1 mL of blood was collected from each fish in a 1-mL syringe and immediately put into a 50-mL tube with 20 mL of DNA extraction buffer (100 m*M* NaCl, 10 m*M* Tris, pH 8, 25 m*M* EDTA, 0.5% SDS, and

proteinase K, 0.1 mg/mL) following the protocol described by Liu et al. (1998). The blood samples were incubated at 55°C overnight. The DNA was then extracted twice with phenol and once with chloroform. Deoxyribonucleic acid was precipitated by adding a half volume of 7.5 *M* ammonium acetate and 2 volumes of ethanol. The DNA was collected and then washed twice with 70% ethanol, dried, and then resuspended in Tris-EDTA (**TE**) buffer (10 m*M* Tris-HCl and 1 m*M* EDTA, pH 7.5). The DNA was then quantified with a spectrophotometer.

Amplified Fragment Length Polymorphism Analysis

Amplified fragment length polymorphism analysis system I (catalog number 10544-013) was purchased from Life Technologies (Bethesda, MD). Primer combinations were abbreviated in a matrix manner (Liu et al., 1998). *Eco*RI primers were designated with a letter from A to I. The *Mse*I primers were given a number from 1 to 8. The primer combinations were designated by a letter plus a number with *Eco*R1 primer first. Genomic DNA was digested completely with *Eco*R1 and *Mse*I following the manufacturer's instruction. The reactions were performed in 96-well microtiter plates (International Corp., Mount Prospect, IL). The reaction system was prepared as follows: 1 µL restriction reaction buffer, 1 µL (approximately 50 ng) genomic DNA, 0.4 µL *Eco*RI/*Mse*I restriction endonucleases, and 2.6 µL water. The reaction was centrifuged for 5 s at 500 × g at room temperature 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°C 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 h at 20°C. Following ligation, 90 µL of Tris-EDTA buffer (pH 8.0) was added to dilute the reactions to 10 times. One microliter of each dilution was transferred 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 for 5 s at 500 × g at room temperature and preamplification was performed for 20 cycles at the following temperatures: 94°C for 30 s , 56°C for 60 s , and 72°C for 60 s (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 to 50 fold. Selective amplification reactions were done with the following: 1 µL preamplified DNA, 0.3 µL (1 pmol/µL) labeled *Eco*RI primer, 1 µL *Mse*I primer (with deoxyribonucleotide triphosphates), 0.03 µL Taq polymerase, 0.6 µL 10x PCR buffer for AFLP, and 2.07 µL double distilled water. A touchdown program was used for the selective amplification for 13 cycles: 94°C for 30 s, 65°C for 30 s, and 72°C for 60 s with a 0.7°C decrease of annealing temperature each cycle followed by 23 cycles of amplification at 94°C for 30 s, 56°C for 30 s, and 72°C for 60 s (Liu et al., 2003).

Amplified Fragment Length Polymorphism Genotyping

The procedures for AFLP genotyping followed Liu et al. (2003). The AFLP products were analyzed using the LI-COR automatic sequencers, both the IR700 and the IR800 (LI-COR, Inc., Lincoln, NE), 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°C for 3 min, 0.6 µL was loaded onto the gel. Page Plus concentrate gel mix (40%, E562, 500 mL) was diluted to 5.5% using 1x Tris-borate-EDTA (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 (Microsoft Office 2007, Microsoft, Redmond, WA) and imported to Mapmaker software (Mapmaker/Exp 3.0; Lander et al.,1987) for linkage analysis.

Nomenclature of Amplified Fragment Length Polymorphism Markers

The AFLP markers were named for the species, primer combination, and the size of the AFLP bands. The first 2 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, and separated with a hyphen.

Linkage Analysis

Parents and 71 offspring were genotyped for AFLP. 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 where 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 logarithm of the odds (**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 LG was found. The ORDER and COMPARE commands were used to determine the most probable order within the LG. The maximum number of the most informative markers in each LG was kept at 8 for the COMPARE procedure because a number of about 8 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 by the RIPPLE command to check the marker order and then the MAP command to draw the map. The figures were drawn in MapCreator (www.wesbarris.com/mapcreator; Liu et al., 2003).

A total of 607 polymorphic AFLP loci were produced with the 64 *Eco*RI/*Mse*I primer combinations. A total of 101 markers (16.6%) were not used for the construction of the linkage map because they showed distortion—linkage disequilibrium—from the expected 1:1 ratio. Four hundred forty-five markers were assigned to 44 LG, with 29 markers unlinked, and 32 markers were excluded because of large map distances. The number of markers on the 44 LG ranged from 2 to 33.

Regression Analysis

The fish were measured in 2 groups from the 2 aquaria as mentioned above. The following measurements were taken: head length, head depth, head width, body depth, body width, caudal depth, caudal width, total length, and total BW (**TotalWeight**). The measurements were recorded on metric units in a single day per group. Fish in the 2 aquaria were significantly different in size. To correct the size difference, regression analysis was performed using PROC REG in SAS 9.1 (SAS Inst., Inc., Cary, NC). The fish were grouped into small- and big-size categories, with fish numbered 629 to 658 inclusive (18 fish, from aquaria 1) classified as big fish and the rest classified as small fish (53 fish, from aquaria 2). Mean of TotalWeight was computed for each category (**MeanTW$_c$**), in which the subscript *c* denotes category, that is, 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 2 environments.

Relative body shape changes as fish grow (Dunham and Smitherman, 1984; Dunham et al., 1986) and absolute morphometric measurements are partially dependent on BW. Therefore, all body measurements were corrected for BW. For each category, a regression of the form Body Part (**BodyP**) = *f*(TotalWeight) was run to obtain the coefficient BodyP*b*. The body parts for which regressions were run were 1) head length (**HeadL**), 2) head depth (**HeadD**), 3) body depth (**BodyD**), 4) caudal depth (**CaudalD**), 5) head width (**HeadW**), 6) body width (**BodyW**), and 7) caudal width (**CaudalW**) 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*, and 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 = BodyP – BodyP*b* × (TotalWeight – MeanTW$_c$), in which **BodyPC** denotes the corrected body part.

Explicitly, the 7 equations were

1) HeadLC (**HLC**) = HeadL – HeadL*b* × (TotalWeight – MeanTW$_c$),

2) HeadDC (**HDC**) = HeadD – HeadD*b* × (TotalWeight – MeanTW$_c$),

3) BodyDC (**BDC**) = BodyD – BodyD*b* × (TotalWeight – MeanTW$_c$),

4) CaudalDC (**CDC**) = CaudalD – CaudalD*b* × (TotalWeight – MeanTW$_c$),

5) HeadWC (**HWC**) = HeadW – HeadW*b* × (TotalWeight – MeanTW$_c$),

6) BodyWC (**BWC**) = BodyW – BodyW*b* × (TotalWeight – MeanTW$_c$), and

7) CaudalWC (**CWC**) = CaudalW – CaudalW*b* × (TotalWeight – MeanTW$_c$).

Measurement correction was done for all 71 fish, using original measurement for the fish's body part (HeadL, HeadD, etc.) regression coefficient (HeadL*b*, HeadD*b*, etc.) for the category to which the fish belonged, original measurement for the fish's TotalWeight, and 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$_c$, and 7) CWCMean$_c$.

A correction factor (Δ) was computed using the means of the 2 categories:

1) HLΔ = HLCMeansmall – HLCMeanbig,

2) HDΔ = HDCMeansmall – HDCMeanbig,

3) BDΔ = BDCMeansmall – BDCMeanbig,

4) CDΔ = CDCMeansmall – CDCMeanbig,

5) HWΔ = HWCMeansmall – HWCMeanbig,

6) BWΔ = BWCMeansmall – BWCMeanbig, and

7) CWΔ = CWCMeansmall – CWCMeanbig.

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 Δ. The equation used for adjustment is of the form BodyPA = BodyPC + BPΔ, in which BodyPC denotes corrected body part.

Explicitly, the equations were

1) HeadLA = HeadLC + HLΔ,

2) HeadDA = HeadDC + HDΔ,

3) BodyDA = BodyDC + BDΔ,

4) CaudalDA = CaudalDC + CDΔ,

5) HeadWA = HeadWC + HWΔ,

6) BodyWA = BodyWC + BWΔ, and

7) CaudalWA = CaudalWC + CWΔ.

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 comprised the corrected body parts HeadLC, HeadDC, …, and CaudalWC while the observations for the big category comprised the adjusted body parts HeadLA, HeadDA, …, and CaudalDA. Altogether, the observations form the standardized measurements for head length, head depth, body depth, caudal depth, head width, body width, and caudal width.

Quantitative Trait Loci Analysis

Quantitative trait loci analysis was performed using MapQTL 5 (Van Ooijen, 2004). 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). The significance threshold was set and evaluated at 0.05 and at 0.10.

The information was taken from MapQTL 5 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 MapQTL 5. The equation used to determine the additive variance was

mu_A – mu_H,

in which mu_A = the estimated mean of the distribution of the quantitative trait associated with "a" genotype and 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)/population variance,

in which 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 (Fig. 1) using the AFLP based map of Liu et al. (2003) containing more than 400 markers. This map represents the QTL found on all 44 LG analyzed. The means, SD, minimum, maximum, range, and CV for all traits for the corrected values are reported (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 (Table 2). All LG were then evaluated for an overall positive or negative effect (Table 3).

For body depth (Table 2), there were 4 markers that had a negative effect on the trait. The other 10 markers had a significant positive effect on the trait. The positive markers were all located in LG 19 and 29. The percent explained variation for every trait for every marker was calculated and reported in Table 2. In some cases, these numbers total more than 100% of the explained variation for a trait. This was a result of multiple AFLP markers being linked to the same QTL. Thus, the variation accounted for is being counted multiple times. This is also obvious because the explained variation and the additive variance for each of these markers are identical. For example, at LG 19 for the trait body depth there are 6 AFLP markers that are apparently linked to the same QTL as each identifies exactly 8.3% 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 4 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 2 QTL (Table 2), the least of any of the other traits measured, 1 on LG 39 and 1 on LG 19. Linkage 39 had a negative effect on the phenotypic traits, while linkage 19 had a positive effect on these traits (Table 3). There were no QTL discovered for caudal width.

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

Head length has 22 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 BW (Table 2) have 30 significant markers and 18 significant markers for the traits, respectively. For total length and BW, LG 5, 9, 39, and 40 had negative effects on both traits. Total length has 3 other LG with negative trait effects, LG 7, 18, and 20.

All of the phenotypic traits measured were found to be strongly correlated with each other (Table 4). Every trait was measured using PROC GLM in SAS 9.1 against every other trait to find significant ($P = 0.05$) phenotypic correlation.

For all 7 morphometric traits and 2 growth traits, there are 11 of the 44 LG that have at least 1 significant locus using a significance threshold of 0.05. At a significance threshold of 0.10, there are 11 LG that have at least 1 marker that is significant. Linkage groups 1, 2, 3, 6, 8, 10, 11, 12, 13, 15, 16, 17, 21, 22, 24, 25, 26, 27, 28, 30 through 38, 41, 42, and 44 contain no QTL for the measured traits. In LG 4, marker IpH8254 is significant ($P = 0.05$) for TotalWeight and total length (Fig. 1). Linkage group 5 has 4 markers identified as QTL. Marker IpF3111 is significant ($P = 0.05$) for body depth, head depth, head width, head length, total length, and total weight. Marker IpF4230 is significant at the $P = 0.05$ threshold for total weight and total length. On 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 7 has 2 significant markers less than 0.1 cM apart on the chromosome, IpE8147 ($P = 0.05$) and IpC6220 ($P = 0.10$) for total length. Linkage group 9 has 2 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 ($P = 0.10$) for total weight.

Linkage group 14 has 1 significant marker ($P = 0.10$) for head width and total weight. Linkage group 18 has 1 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 total weight 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 cM 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 3 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 last marker, IpH4058, located 35 cM 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 1 trait. Marker IpB4197 is significant ($P = 0.05$) for total length. Markers IpF1157, IpB6181, IpE7100,

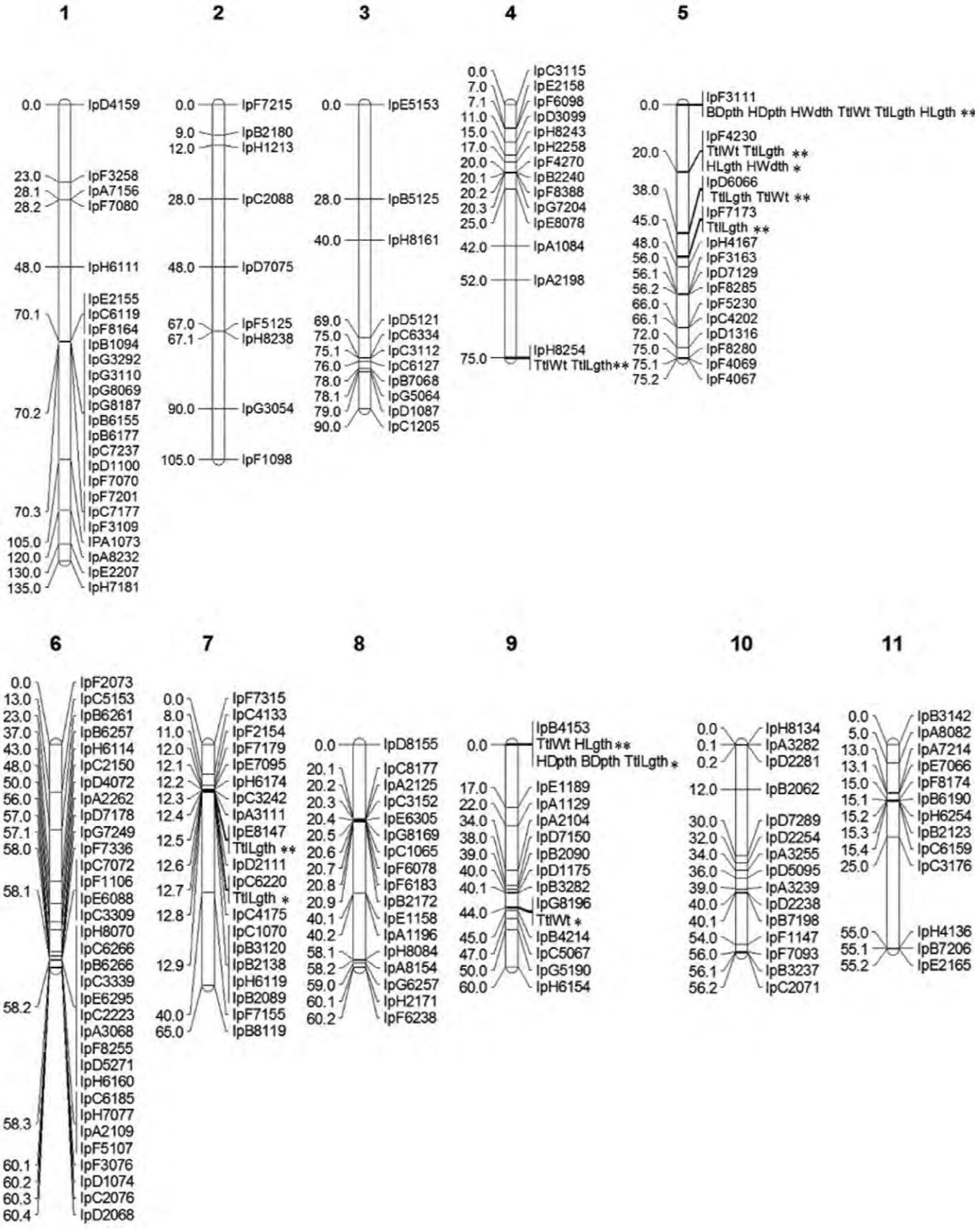

Figure 1. A QTL map of head length (HLgth), head depth (HDpth), head width (HWdth), body depth (BDpth), body width (BWdth), caudal depth (CDlDpth), caudal width (CWdth), total length (TtlLgth), and total BW (TtlWt) for the interspecific backcross F_1 (female channel catfish [*Ictalurus punctatus*] × male blue catfish [*Ictalurus furcatus*]) female × blue catfish male. No QTL were detected for caudal width. *QTL is significant at $P = 0.10$; **QTL is significant at $P = 0.05$.

Continued.

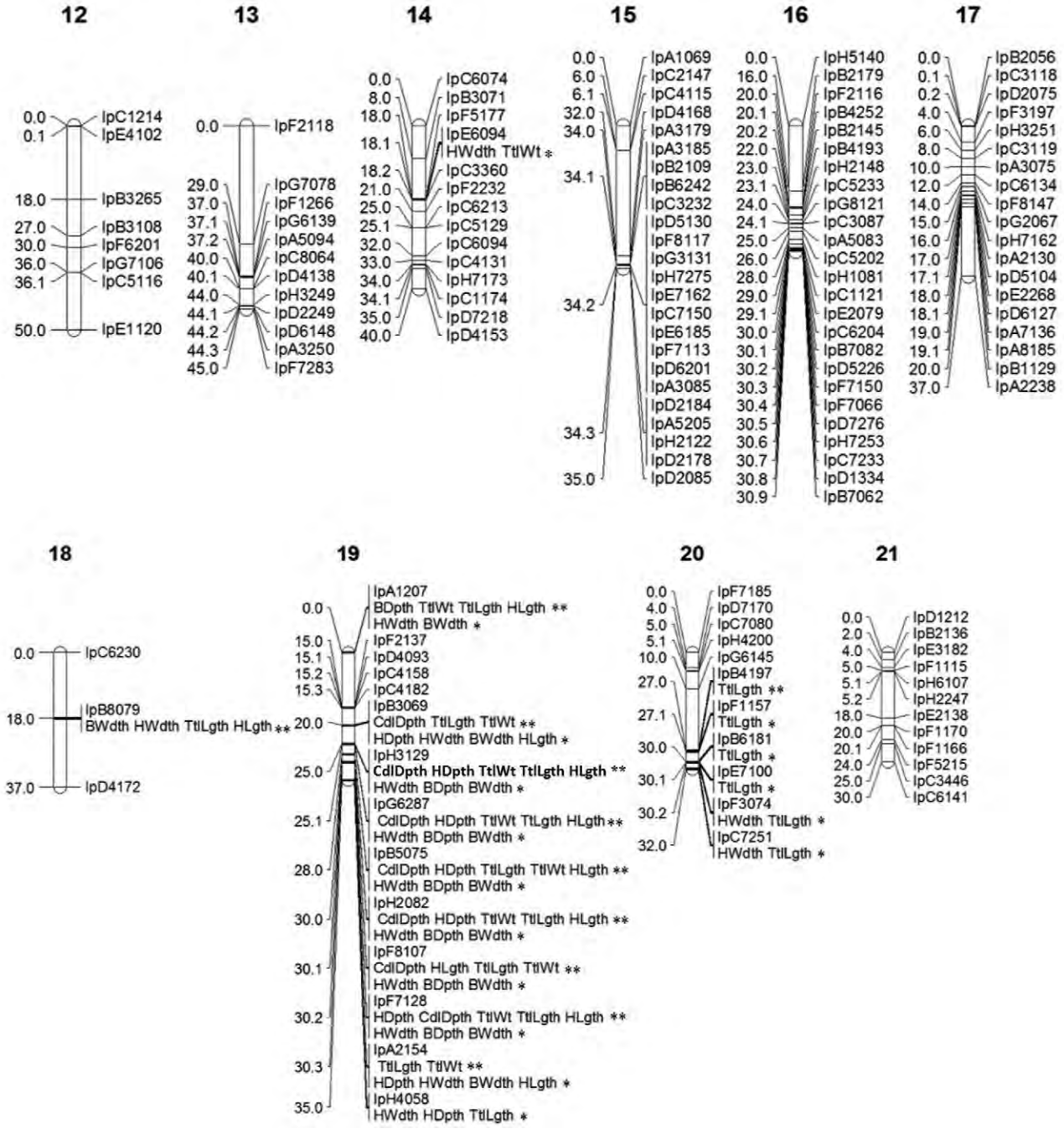

Figure 1. (cont.).

IpF3074, and IpC7251 are significant ($P = 0.10$) for total length with markers IpF3074 and IpC7251 also being significant ($P = 0.10$) for head width.

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 ($P = 0.10$) for head length. Markers IpG1102 and IpB6161 are significant ($P = 0.10$) for head width with IpG1102 also being significant for head depth. The final marker IpB4066, on the chromosome located 25.0 cM from the start of the chromosome, is significant ($P = 0.10$) for body width and total length.

Linkage group 29 has 5 markers that span 20 cM. Four of the 5 markers, IpD1069, IpE2090, IpB4092, and IpF2100, are significant ($P = 0.10$) for body width. 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 group 39 has QTL on both markers located 7 cM apart. IpC3177 is significant ($P = 0.05$) for head width, head depth, body depth, caudal depth, and total

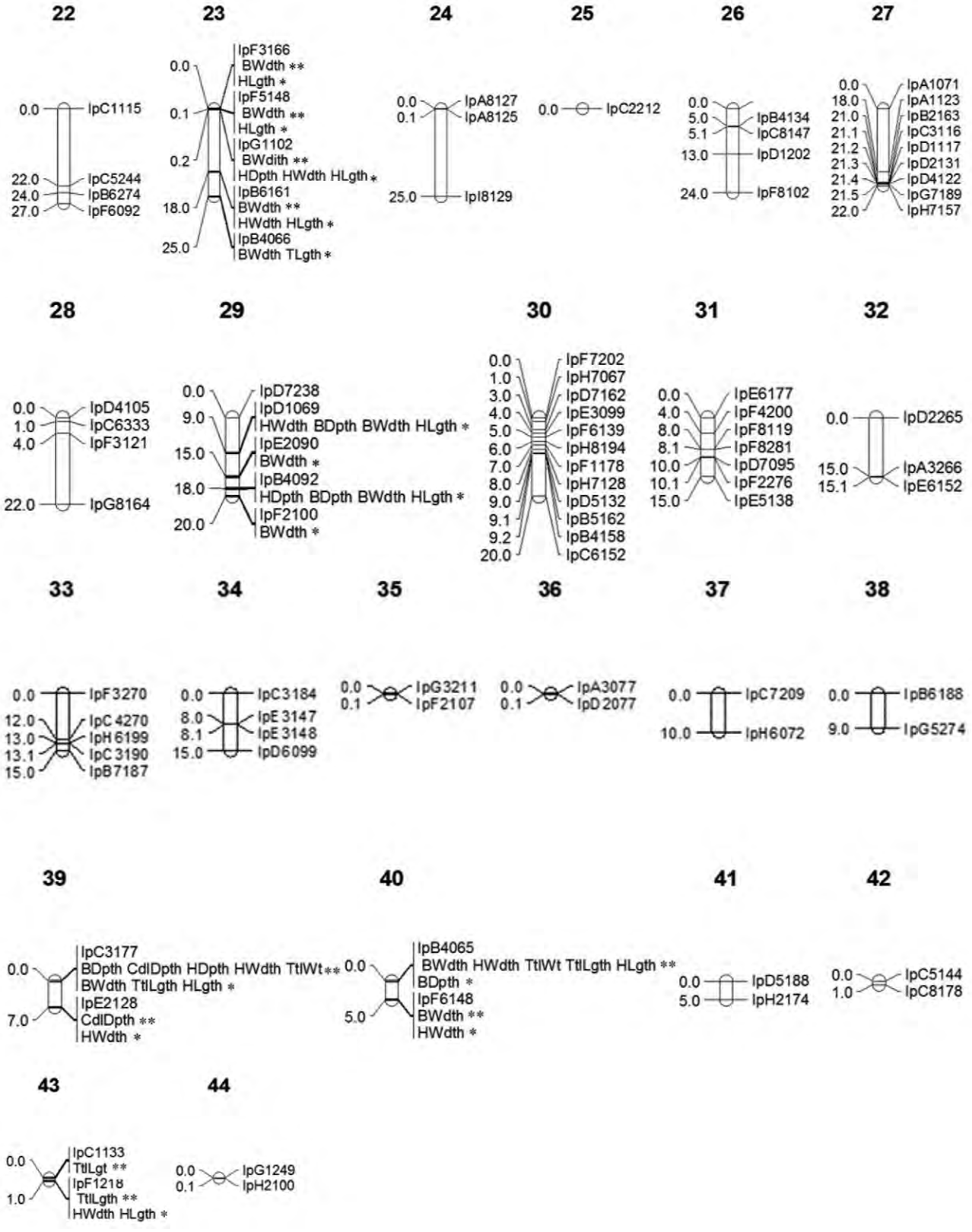

Figure 1. (cont.).

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 head width ($P = 0.10$). Linkage group 40 has 2 markers, both with QTL. 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 cM from

Table 2. Logarithm of the odds (LOD), genetic information coefficient (GIC), significance level, variance, percent variation explained, additive variance, and effect (positive is increased and negative is decreased size) on the trait by locus within linkage group for the interspecific backcross F_1 (female channel catfish [*Ictalurus punctatus*] × male blue catfish [*Ictalurus furcatus*]) female × blue catfish male. All traits were corrected for BW differences.

Trait[1]	Linkage group	Locus	LOD	GIC	Significance level	Variance	Percent explained	Additive variation	Effect on trait
BDPTH	19	IpA1207	1.43	0.488	0.05	0.61	8.9	0.49	Positive
BDPTH	19	IpA2154	1.22	0.452	0.1	0.62	7.6	0.45	Positive
BDPTH	40	IpB4065	1.09	–0.44	0.1	0.62	7	–0.44	Negative
BDPTH	29	IpB4092	0.96	0.402	0.1	0.63	6	0.4	Positive
BDPTH	9	IpB4153	1.36	–0.477	0.1	0.61	8.5	–0.48	Negative
BDPTH	19	IpB5075	1.33	0.471	0.1	0.62	8.3	0.47	Positive
BDPTH	39	IpC3177	1.28	–0.469	0.05	0.62	8	–0.47	Negative
BDPTH	29	IpD1069	1.1	0.447	0.1	0.62	7.2	0.45	Positive
BDPTH	5	IpF3111	2.32	–0.6622	0.05	0.58	14.3	–0.62	Negative
BDPTH	19	IpF7128	1.33	0.471	0.1	0.62	8.3	0.47	Positive
BDPTH	19	IpF8107	1.33	0.471	0.1	0.62	8.3	0.47	Positive
BDPTH	19	IpG6287	1.33	0.471	0.1	0.62	8.3	0.47	Positive
BDPTH	19	IpH2082	1.33	0.471	0.1	0.62	8.3	0.47	Positive
BDPTH	19	IpH3129	1.33	0.471	0.1	0.62	8.3	0.47	Positive
BWDTH	19	IpA1207	1.29	0.31	0.1	0.27	8.1	0.31	Positive
BWDTH	19	IpB3069	1.13	0.291	0.1	0.28	7.1	0.29	Positive
BWDTH	40	IpB4065	1.8	–0.368	0.05	0.26	11.1	–0.37	Negative
BWDTH	23	IpB4066	1.18	0.299	0.1	0.28	7.3	0.3	Positive
BWDTH	29	IpB4092	1.23	0.302	0.1	0.28	7.6	0.3	Positive
BWDTH	19	IpB5075	1.1	0.286	0.1	0.28	6.9	0.29	Positive
BWDTH	23	IpB6161	1.73	0.362	0.05	0.27	10.6	0.36	Positive
BWDTH	18	IpB8079	1.49	–0.353	0.05	0.27	10.4	–0.35	Negative
BWDTH	39	IpC3177	1.01	–0.279	0.1	0.28	6.4	–0.28	Negative
BWDTH	29	IpD1069	1.05	0.289	0.1	0.28	6.8	0.29	Positive
BWDTH	29	IpE2090	0.91	0.263	0.1	0.28	5.7	0.26	Positive
BWDTH	29	IpF2100	0.97	0.27	0.1	0.28	6.1	0.27	Positive
BWDTH	23	IpF3166	1.7	0.357	0.05	0.27	10.5	0.36	Positive
BWDTH	23	IpF5148	1.7	0.357	0.05	0.27	10.4	0.36	Positive
BWDTH	40	IpF6148	1.18	–0.305	0.05	0.28	7.4	–0.31	Negative
BWDTH	19	IpF7128	1.1	0.286	0.1	0.28	6.9	0.29	Positive
BWDTH	19	IpF8107	1.1	0.286	0.1	0.28	6.9	0.29	Positive
BWDTH	23	IpG1102	1.97	0.386	0.05	0.26	12	0.39	Positive
BWDTH	19	IpG6287	1.1	0.286	0.1	0.28	6.9	0.29	Positive
BWDTH	19	IpH2082	1.1	0.286	0.1	0.28	6.9	0.29	Positive
BWDTH	19	IpH3129	1.1	0.286	0.1	0.28	6.9	0.29	Positive
CDLDPTH	19	IpB3069	1.53	0.201	0.05	0.1	9.4	0.2	Positive
CDLDPTH	19	IpB5075	1.43	0.194	0.05	0.1	8.8	0.19	Positive
CDLDPTH	39	IpC3177	1.55	–0.205	0.05	0.96	9.7	–0.2	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	0.1	8.8	0.19	Positive
CDLDPTH	19	IpF8107	1.43	0.194	0.05	0.1	8.8	0.19	Positive
CDLDPTH	19	IpG6287	1.43	0.194	0.05	0.1	8.8	0.19	Positive
CDLDPTH	19	IpH2082	1.43	0.194	0.05	0.1	8.8	0.19	Positive
CDLDPTH	19	IpH3129	1.43	0.194	0.05	0.1	8.8	0.19	Positive
HDPTH	19	IpA2154	1.37	0.38	0.1	0.39	8.6	0.38	Positive
HDPTH	19	IpB3069	1.11	0.344	0.1	0.39	6.9	0.34	Positive
HDPTH	40	IpB4065	0.98	–0.333	0.1	0.39	6.4	–0.33	Negative
HDPTH	29	IpB4092	0.96	0.319	0.1	0.4	6	0.32	Positive
HDPTH	9	IpB4153	1.44	–0.388	0.1	0.38	8.9	–0.39	Negative
HDPTH	19	IpB5075	1.4	0.382	0.05	0.39	8.7	0.38	Positive
HDPTH	39	IpC3177	1.26	–0.369	0.05	0.39	7.9	–0.37	Negative

continued.

Table 2. (cont.)

Trait[1]	Linkage group	Locus	LOD	GIC	Significance level	Variance	Percent explained	Additive variation	Effect on trait
HDPTH	5	IpF3111	1.89	–0.445	0.05	0.38	11.7	–0.44	Negative
HDPTH	19	IpF7128	1.4	0.382	0.05	0.39	8.7	0.38	Positive
HDPTH	23	IpG1102	1.21	0.365	0.1	0.39	7.6	0.37	Positive
HDPTH	19	IpG6287	1.4	0.382	0.05	0.39	8.7	0.38	Positive
HDPTH	19	IpH2082	1.4	0.382	0.05	0.39	8.7	0.38	Positive
HDPTH	19	IpH3129	1.4	0.382	0.05	0.39	8.7	0.38	Positive
HDPTH	19	IpH4058	1.21	0.357	0.1	0.39	7.6	0.36	Positive
HLGTH	19	IpA1207	1.78	0.975	0.05	0.77	11	0.62	Positive
HLGTH	19	IpA2154	1.38	0.995	0.1	0.79	8.6	0.54	Positive
HLGTH	19	IpB3069	1.38	0.999	0.1	0.79	8.6	0.55	Positive
HLGTH	40	IpB4065	1.35	0.986	0.05	0.79	8.6	–0.55	Negative
HLGTH	29	IpB4092	1.06	1	0.1	0.81	6.6	0.48	Positive
HLGTH	9	IpB4153	1.7	1	0.05	0.77	10.4	–0.6	Negative
HLGTH	19	IpB5075	1.44	1	0.05	0.79	8.9	0.55	Positive
HLGTH	23	IpB6161	1.14	0.997	0.1	0.8	7.1	0.5	Positive
HLGTH	18	IpB8079	1.62	0.963	0.05	0.76	11.4	–0.63	Negative
HLGTH	39	IpC3177	1.04	0.986	0.1	0.81	6.6	–0.48	Negative
HLGTH	29	IpD1069	1.06	0.972	0.1	0.8	7	0.5	Positive
HLGTH	43	IpF1218	0.72	0.998	0.1	0.82	4.5	0.4	Positive
HLGTH	5	IpF3111	1.85	0.961	0.05	0.76	11.5	–0.63	Negative
HLGTH	23	IpF3166	1.07	1	0.1	0.8	6.7	0.49	Positive
HLGTH	5	IpF4230	1.55	0.994	0.1	0.78	9.6	–0.58	Negative
HLGTH	23	IpF5148	1.07	1	0.1	0.8	6.7	0.49	Positive
HLGTH	19	IpF7128	1.44	1	0.05	0.79	8.9	0.55	Positive
HLGTH	19	IpF8107	1.44	1	0.05	0.79	8.9	0.55	Positive
HLGTH	23	IpG1102	1.25	1	0.1	0.8	7.8	0.53	Positive
HLGTH	19	IpG6287	1.44	1	0.05	0.79	8.9	0.55	Positive
HLGTH	19	IpH2082	1.44	1	0.05	0.79	8.9	0.55	Positive
HLGTH	19	IpH3129	1.44	1	0.05	0.79	8.9	0.55	Positive
HWDTH	19	IpA1207	1.22	0.386	0.1	0.45	7.6	0.39	Positive
HWDTH	19	IpA2154	1.29	0.397	0.1	0.45	8	0.4	Positive
HWDTH	19	IpB3069	1.29	0.399	0.1	0.45	8	0.4	Positive
HWDTH	40	IpB4065	1.23	–0.402	0.05	0.45	8	–0.4	Negative
HWDTH	19	IpB5075	1.25	0.391	0.1	0.45	7.8	0.39	Positive
HWDTH	23	IpB6161	1	0.354	0.1	0.46	6.3	0.36	Positive
HWDTH	18	IpB8079	1.92	–0.524	0.05	0.42	14	–0.52	Negative
HWDTH	39	IpC3177	1.28	–0.401	0.05	0.45	8	–0.4	Negative
HWDTH	14	IpC6094	1.2	0.387	0.1	0.49	0.2	0.06	Positive
HWDTH	20	IpC7251	1.17	–0.38	0.1	0.45	7.3	–0.38	Negative
HWDTH	29	IpD1069	1.04	0.371	0.1	0.46	6.8	0.37	Positive
HWDTH	39	IpE2128	0.71	–0.299	0.1	0.47	4.5	–0.3	Negative
HWDTH	43	IpF1218	0.78	0.313	0.1	0.47	4.9	0.31	Positive
HWDTH	20	IpF3074	1.21	–0.386	0.1	0.45	7.6	–0.39	Negative
HWDTH	5	IpF3111	1.63	–0.448	0.05	0.44	10.2	–0.45	Negative
HWDTH	5	IpF4230	1.44	–0.419	0.1	0.45	9.2	–0.49	Negative
HWDTH	40	IpF6148	1.08	–0.382	0.1	0.46	7.1	–0.38	Negative
HWDTH	19	IpF7128	1.25	0.391	0.1	0.45	7.8	0.39	Positive
HWDTH	19	IpF8107	1.25	0.391	0.1	0.45	7.8	0.39	Positive
HWDTH	23	IpG1102	1.03	0.364	0.1	0.46	6.4	0.36	Positive
HWDTH	19	IpG6287	1.25	0.391	0.1	0.45	7.8	0.39	Positive
HWDTH	19	IpH2082	1.25	0.391	0.1	0.45	7.8	0.39	Positive
HWDTH	19	IpH3129	1.25	0.391	0.1	0.45	7.8	0.39	Positive
HWDTH	19	IpH4058	1.15	0.375	0.1	0.45	7.2	0.38	Positive
TTLLGTH	19	IpA1207	1.81	0.975	0.05	8,429.66	11.2	65.16	Positive
TTLLGTH	19	IpA2154	1.74	0.995	0.05	8,474.91	10.7	63.74	Positive

continued.

Table 2. (cont.)

Trait[1]	Linkage group	Locus	LOD	GIC	Significance level	Variance	Percent explained	Additive variation	Effect on trait
TTLLGTH	19	IpB3069	1.57	0.999	0.05	8,571.7	9.7	60.92	Positive
TTLLGTH	40	IpB4065	1.17	0.986	0.05	8,771.97	7.6	–54.35	Negative
TTLLGTH	23	IpB4066	1.2	1	0.1	8,779.02	7.5	53.99	Positive
TTLLGTH	9	IpB4153	1.32	1	0.1	8,714.26	8.2	–55.72	Negative
TTLLGTH	20	IpB4197	1.62	1	0.05	8,544.6	10	–62.56	Negative
TTLLGTH	19	IpB5075	1.58	1	0.05	8,566.73	9.7	60.79	Positive
TTLLGTH	20	IpB6181	1.12	1	0.1	8,825	7	–52.01	Negative
TTLLGTH	18	IpB8079	1.53	0.963	0.05	8,490.74	10.5	–63.23	Negative
TTLLGTH	43	IpC1133	1	0.998	0.05	8,895.89	6.3	49.35	Positive
TTLLGTH	39	IpC3177	0.97	0.986	0.1	8,903.93	6.2	–49.02	Negative
TTLLGTH	7	IpC6220	1.44	1	0.1	8,646.6	8.9	–58.57	Negative
TTLLGTH	20	IpC7251	1.41	0.998	0.1	8,658.23	8.8	–57.84	Negative
TTLLGTH	5	IpD6066	3.95	0.999	0.05	7,343.39	22.6	–92.9	Negative
TTLLGTH	20	IpE7100	1.27	1	0.1	8,741.35	7.9	–55	Negative
TTLLGTH	7	IpE8147	2.87	1	0.05	7,879.36	17	–80.47	Negative
TTLLGTH	20	IpF1157	1.18	0.996	0.1	8,787.52	7.4	–53.46	Negative
TTLLGTH	43	IpF1218	1.12	0.998	0.05	8,820.16	7.1	52.21	Positive
TTLLGTH	20	IpF3074	1.42	1	0.1	8,652.78	8.8	–58.03	Negative
TTLLGTH	5	IpF3111	2	0.961	0.05	8,289.65	12.7	–69.36	Negative
TTLLGTH	5	IpF4230	3.15	0.994	0.05	7,726.95	18.6	–84.06	Negative
TTLLGTH	19	IpF7128	1.58	1	0.05	8,566.74	9.7	60.79	Positive
TTLLGTH	5	IpF7173	1.6	0.999	0.05	8,552.35	9.9	–61.26	Negative
TTLLGTH	19	IpF8107	1.58	1	0.05	8,566.73	9.7	60.79	Positive
TTLLGTH	19	IpG6287	1.58	1	0.05	8,566.83	9.7	60.79	Positive
TTLLGTH	19	IpH2082	1.58	1	0.05	8,566.73	9.7	60.79	Positive
TTLLGTH	19	IpH3129	1.58	1	0.05	8,566.87	9.7	60.78	Positive
TTLLGTH	19	IpH4058	1.17	0.995	0.1	8,795.21	7.3	52.74	Positive
TTLLGTH	4	IpH8254	2.39	0.983	0.05	8,116.38	14.5	74.63	Positive
TTLWT	19	IpA1207	1.45	0.975	0.05	1,045.43	9	20.4	Positive
TTLWT	19	IpA2154	1.38	0.995	0.05	1,050.79	8.6	19.86	Positive
TTLWT	19	IpB3069	1.45	0.999	0.05	1,046.15	9	20.42	Positive
TTLWT	40	IpB4065	1.03	0.986	0.05	1,072.73	6.7	–17.76	Negative
TTLWT	9	IpB4153	1.92	1	0.05	1,014.74	11.7	–23.21	Negative
TTLWT	19	IpB5075	1.31	1	0.05	1,055.53	8.2	19.38	Positive
TTLWT	39	IpC3177	1.19	0.986	0.05	1,063.79	7.4	–18.74	Negative
TTLWT	14	IpC6094	1.16	0.994	0.1	1,141.54	0.7	5.61	Positive
TTLWT	5	IpD6066	1.66	0.999	0.05	1,131.82	10.2	–21.74	Negative
TTLWT	5	IpF3111	1.68	0.961	0.05	1,028.92	10.5	–21.98	Negative
TTLWT	5	IpF4230	1.84	0.994	0.05	1,019.44	11.3	–22.82	Negative
TTLWT	19	IpF7128	1.31	1	0.05	1,055.53	8.2	19.38	Positive
TTLWT	19	IpF8107	1.31	1	0.05	1,055.53	8.2	19.38	Positive
TTLWT	19	IpG6287	1.31	1	0.05	1,055.52	8.2	19.38	Positive
TTLWT	9	IpG8196	1.23	0.991	0.1	1,059.98	7.8	–18.92	Negative
TTLWT	19	IpH2082	1.31	1	0.05	1,055.53	8.2	19.38	Positive
TTLWT	19	IpH3129	1.31	1	0.05	1,055.52	8.2	19.38	Positive
TTLWT	4	IpH8254	1.72	0.983	0.05	1,027.09	10.6	22.26	Positive

[1]BDPTH = body depth; BWDTH = body width; CDLDPTH = caudal depth; HDPTH = head depth; HLGTH = head length; HWDTH = head width; TTLLGTH = total length; TTLWT = total BW.

the first marker, is significant ($P = 0.05$) for body width and is significant ($P = 0.10$) for head width.

Linkage group 43 has QTL on both markers, which are 1 cM 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

Using 7 morphometric and 2 growth traits, there are 11 of the 44 LG that have at least 1 significant locus using a significance threshold of 0.05. Using a significance threshold of 0.10, there are 11 LG that have at

least 1 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.

Thus, approximately 25% of the LG had QTL associated with morphology. Recently, Massault et al. (2010) and Boulton et al. (2011) also found QTL for morphology on approximately 25% of the LG for 2 marine fish species, European sea bass and gilthead seabream, suggesting some conservation regarding the organization of the genome in regards to the areas affecting body shape. In this discussion, we will make a series of comparisons between our research and that with the European sea bass and the gilthead seabream. However, these comparisons need to be partially tempered by the fact that the work with the European sea bass did not account for the fact that body measurements increase with size and the study on gilthead seabream did not account for the fact that the relative body shape of a fish changes as it grows. Thus, some of the findings with these 2 marine species could be artifacts of the measurement of BW or body length without correction.

Markers in LG 5, 7, 9, 18, 20, 39, and 40 had an overall negative effect on the QTL. The other 6 LG had a positive effect. The traits were all strongly correlated. If the traits were not correlated, the LG would likely be positive for some traits and negative for others within the LG rather than the LG having an overall positive or negative effect.

Linkage group 19 was unusual. It had multiple positive QTL for all traits. Linkage group 19 appears to have a significant effect QTL for body conformation as well as total length and BW. All of the traits measured were represented by at least 7 markers for every trait on LG 19. Massault et al. (2010) also found 1 LG in European sea bass that accounted for a major impact, accounting for 38% of the variation of morphology, but such a large effect was not found in gilthead seabream (Boulton et al., 2011). The LG 19 in catfish likely possesses genes or a series of genes that have positive effects on various growth traits. Again, this suite of QTL appear promising for multiple trait, marker-assisted selection (**MAS**), except they would likely increase head size, which would adversely affect carcass yield. The studies on the marine fish did not detect QTL associated with head size.

Table 3. Positive (increased size) or negative (decreased size) effect in all linkage groups with QTL for all traits for the interspecific backcross F_1 (female channel catfish [*Ictalurus punctatus*] × male blue catfish [*Ictalurus furcatus*]) female × blue catfish male

	Linkage group												
QTL/trait	4	5	7	9	14	18	19	20	23	29	39	40	43
BW	+	–		–	+		+				–	–	
Total length	+	–	–	–		–	+	–	+		–	–	+
Head depth		–		–			+		+	+	–	–	
Head width		–		–	+[1]	–	+	–	+	+	–	–	+
Head length		–		–		–	+		+	+	–	–	+
Body depth		–		–			+			+	–	–	
Body width						–	+		+	+	–	–	
Caudal depth							+				–		
Caudal width[2]													

[1]Explained a small amount of variation (25–50 fold less) compared to other QTL.

[2]No QTL were detected.

Quantitative trait loci for body depth are found on 6 different LG 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 LG 19 with markers being 10 cM apart.

Body width conformation is represented on 6 different LG, using the significance threshold of $P = 0.10$. Linkage group 23 has 5 markers with a total distance of 25 cM. Linkage groups 19, 23, and 29 have a strong positive effect on the trait. If selecting for body width, these 3 LG 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. The positive effects on body depth, body width, and caudal depth should have a positive effect on carcass yield if MAS is applied; however, again, gains could be negated

Table 4. Phenotypic correlations for total BW, total length, head length, head depth, body depth, caudal depth, head width, body width, and caudal width for the interspecific backcross F_1 (female channel catfish [*Ictalurus punctatus*] × male blue catfish [*Ictalurus furcatus*]) female × blue catfish male. Measurements are all corrected for BW

Phenotypic correlations[1]	BW	Total length	Head length	Head depth	Body depth	Caudal depth	Head width	Body width	Caudal width
BW	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

[1]All are significant ($P = 0.05$).

by the positive effects for head size, which would be negative in regards to carcass yield.

A QTL for body size sometimes represented both BW and total length (4 QTL). However, when a QTL represented just 1 of these it was usually total length, 6 QTL, rather than BW, 1 QTL. On only 1 occasion was a QTL representing total length and BW (LG 4) and once for total length (LG 7) not linked to any of the morphometric measurements. This may make it difficult to conduct MAS for BW without affecting the other traits. This could be a positive or a negative depending on the nature of these linkages. Linkage group 4 had a positive effect on size and thus was a good candidate for MAS; however, LG 7 had a negative effect on length. Linkage group 4 had a single QTL that affected both total length and BW. Additionally, this QTL was near the end of the LG.

All of the QTL for BW and total length explained similar amounts of the variation for those traits, so no major loci were identified. Similarly, Tanck et al. (2001) found 11 microsatellites that were correlated with mass and length in common carp (*Cyprinus carpio*). In contrast, Reid et al. (2005) found only 1 major and 1 minor locus (QTL) for growth rate and 1 major locus and 3 minor loci for condition factor in rainbow trout (*Oncorhynchus mykiss*). Reid et al. (2005) had the same findings in Arctic char (*Salvelinus alpinus*), opening the possibility that genetic relationships for the same traits and QTL may be similar in related species. However, (O'Malley et al., 2003) identified twice as many, 3 QTL for growth and 4 suggestive QTL for growth in rainbow trout, indicating either different experimental sensitivities, strain effects, or both. Also in contrast to our results, Cnaani et al. (2003) found 3 unlinked QTL for growth rate in tilapia, and in the European sea bass and gilthead sea bream 4 BW QTL were identified (Massault et al., 2010; Boulton et al., 2011). The greater number of QTL for size and morphology in catfish may indicate a different genomic arrangement and strategy for growth and morphometric traits; however, a more likely explanation is that the large numbers of markers used in the present study may have allowed a greater number of QTL to be identified. However, 1 definitive biological difference at this point of discovery was that no major locus for growth was identified in contrast to what was found in the salmonids. Another explanation for the larger number of QTL found in the present study is the use of the interspecific backcrossing, which may be a more powerful mapping technique for QTL compared to the intraspecific approaches used in the other studies discussed above.

Three LG had positive QTL for BW and 4 had negative effects on BW in catfish, narrowing the candidates for MAS. A similar result was observed for total length with 4 LG having positive effects and 7 having negative effects. Fortunately, no LG existed where total length and BW were antagonistic, which is consistent with the high phenotypic correlation of these 2 traits, and 2 LG, 4 and 19, had BW and total length QTL both positive.

If MAS for BW 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 such as is possessed by the paternal blue catfish, which would presumably result in higher carcass yield. However, the positive correlation between size and relative head size would result in a lower carcass yield. The phenotypic correlations indicate that it may be difficult to conduct multiple trait MAS for increased BW and decreased head size. Marker-assisted selection for increased BW, body depth, body width, and caudal width would be successful, which would theoretically 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 LG contained significant QTL. In each and every case, all QTL on a LG affected the trait in the same direction, all positive or all negative. This would prevent focusing multiple trait MAS on LG that have positive effects on BW and body and caudal morphometrics but negative effects on head size as such LG did not exist. The effects of the predicted theoretical positive correlated response among BW and head size traits, which should decrease carcass yield, appear to be more than offset by the positive correlated response among BW and body width and depth and caudal traits, which should increase carcass yield, as selection for BW in channel catfish resulted in small increases in carcass yield (Rezk, 1993).

Linkage group 4 would be a good LG for MAS since only BW and total length QTL were found; therefore, negative correlated responses for the other traits should not occur.

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

Linkage groups 5, 9, 39, and 40 all had negative effects on all 3 head size traits. However, they also had negative effects on BW and total length; therefore, undesired correlated responses to multiple trait MAS might occur. Quantitative trait loci negative for 1 to 2 head traits were found on LG 18 and 20. In this case, there were also negative QTL for total length. Perhaps since total length only and not BW QTL were found in

these LG, these may be the best LG and QTL for MAS of the head traits with the least potentially damaging effects on BW.

If the relationships on LG 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 LG 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 1 LG to another. Linkages were quite tight in many cases, but some were fairly distant.

The linkage relationships found among BW, total length, and the 7 morphometric traits indicated that multiple trait MAS to increase BW, body depth, body width, and caudal depth while decreasing the head depth, head length, and head width with the goal of improving BW and carcass yield simultaneously might be difficult. Certain QTL 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 LG were studied, but as channel catfish and blue catfish have 58 chromosomes, 29 LG should exist. The information generated should allow the initial evaluation of MAS for BW and morphology in catfish.

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