SCIENCE CHINA
Life Sciences

• RESEARCH PAPER •

April 2013 Vol.56 No.4: 351–359
doi: 10.1007/s11427-012-4427-3

# A consensus linkage map of common carp (*Cyprinus carpio* L.) to compare the distribution and variation of QTLs associated with growth traits

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Received July 30, 2012; accepted December 3, 2012; published online March 12, 2013

The ability to detect and identify quantitative trait loci (QTLs) in a single population is often limited. Analyzing multiple populations in QTL analysis improves the power of detecting QTLs and provides a better understanding of their functional allelic variation and distribution. In this study, a consensus map of the common carp was constructed, based on four populations, to compare the distribution and variation of QTLs. The consensus map spans 2371.6 cM across the 42 linkage groups and comprises 257 microsatellites and 421 SNPs, with a mean marker interval of 3.7 cM/marker. Sixty-seven QTLs affecting four growth traits from the four populations were mapped to the consensus map. Only one QTL was common to three populations, and nine QTLs were detected in two populations. However, no QTL was common to all four populations. The results of the QTL comparison suggest that the QTLs are responsible for the phenotypic variability observed for these traits in a broad array of common carp germplasms. The study also reveals the different genetic performances between major and minor genes in different populations.

**common carp, consensus map, comparative QTL analysis, growth-related traits**

**Citation:** Zheng X H, Kuang Y Y, Lv W H, et al. A consensus linkage map of common carp (*Cyprinus carpio* L.) to compare the distribution and variation of QTLs associated with growth traits. Sci China Life Sci, 2013, 56: 351−359, doi: 10.1007/s11427-012-4427-3

Over the last 20 years, genetic and genome technologies have promoted significant advances in the molecular study and genetic improvement of aquaculture animals [1,2]. Common carp is the most widely cultivated freshwater fish in the world and is an important model species for many research areas. Significant progress has been made in the genetics and genome research of common carp. The current genomic resources available for common carp include a large number of polymorphic genetic markers [3–5]; genetic maps based on haploid and outbred mapping panels [6–8]; large expressed sequence tag (EST) databases and reference transcriptome (unpublished); a bacterial artificial chromosome (BAC) library [9]; a large dataset of BAC-end sequences(BES) [10]; and a BAC-based physical map [11].

Many quantitative trait loci (QTLs) have been identified for various economic traits, such as cold-tolerance [6], growth-related traits [12,13], muscle quality [14], feed conversion efficiency [15], and amino acid content [16] in common carp. However, all of these QTL studies were carried out in populations of progeny derived from single crosses. Combination QTL analysis of multiple populations provides improved power to detect QTLs, more precise estimates of their effects and positions, and a better understanding of their functional allelic variation and distribution

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across more diverse germplasms [17]. Therefore, an integrated genetic map is needed to enable fine mapping and to improve the accuracy of QTLs for use in marker-assisted selection (MAS) programs to improve common carp germplasm and aquaculture production. In this study, three sets of connected full-sib families and one $F_2$ population were used to construct an integrated genetic map and to compare the distribution and variation of QTLs.

To go beyond a simple comparison of results between populations, the authors propose to analyze the different populations jointly. Many multiple population QTL studies have been carried out in plants [18–20] and animals [21–23], and there are some reports on aquatic species [24,25]; however, to date, no studies have been carried out on common carp. Here, we present an integrated common carp map, including the position of QTLs controlling growth-related traits to provide a genomic framework for quantitative trait loci identification and for comparative mapping, map-based cloning, assessment of genetic diversity, and applied breeding in MAS schemes.

## 1 Materials and methods

### 1.1 Populations and phenotypic data

The four populations used in this study are described in Table 1. The number of progeny in each population varied from 68 to 159 lines. Population C was used for the construction of the first generation comparative map [7]. Briefly, a total broodstock containing 75 brooders, comprising 29 females and 46 males cultivated by the SongPu Aquaculture Experimental Station, was genotyped with 30 polymorphic microsatellites. According to genetic differences, 40 full-sibling families were produced. After hatching, groups of fry were selected for rearing in ponds for 6 months. In this study, we selected another two populations, A and B, from 40 full siblings: A and B were derived from the same dam, A and C were derived from the same sire. D is an $F_2$ population whose linkage map has been described previously [8]. We scored the following growth traits: body weight (W, g), standard length (SL, cm), body depth (H, cm) and body thickness (BT, cm) from the four populations, according to the Part 3: measurement of characters of inspection of germplasm for cultured fishes reference standard (GB/T 18654.3-2008). The mean, standard deviation, and range for the four traits within each population are described in Table S1.

Blood samples from parents and fin clips from their progeny were collected. DNA was isolated using a standard proteinase K/phenol-chloroform extraction protocol. The quality of DNA was checked on 1% agarose gel and quantified with spectrophotometry (Nanodrop 8000, Thermo Scientific, Germany). The DNA concentration of the sample from each fish was adjusted to 2.5 ng $\mu L^{-1}$ and arrayed into 96-well PCR plates for later use.

### 1.2 Genotypic data and map construction

In this study, genotype data for 200 microsatellites and 250 SNPs in populations A and B were selected from the linkage map based on population C. Microsatellites were genotyped using an automated DNA sequencer (LI-COR 4300) and SNPs were genotyped using an illumine GoldenGate platform, as described previously [7].

Linkage maps were constructed for each mapping panel by JoinMap 4.0 [26] using the Cross Pollinator (CP) model. Marker segregation distortion was estimated by a Chi-square test. Given that the goal was to generate a consensus map for further comparison of detected QTLs, marker distortion was considered significant at $P<0.005$; the C and D linkage maps were also reconstructed using the same mapping method. For all crosses, a minimum logarithm of odds (LOD) score of 3.0 and a maximum distance of 30 cM determined the assignment of markers to linkage groups (LGs). We removed all markers mapping at the end of any LG (>20 cM away from any other marker) and all markers that caused large increases in the distance between flanking loci. Map distances were calculated using the Kosambi mapping function [27].

For the construction of a consensus linkage map, LGs that did not share common markers were discarded. Groups with at least two markers in common were integrated into one dataset with the "combine groups for map integration" module of JoinMap 4.0 using the following parameters: Kosambi's mapping function LOD >2, REC (recombination fraction) <0.4, goodness of fit jump threshold for removal of loci=5, performing ripple after adding one locus and the third integration round=Yes.

### 1.3 QTL analysis

Shapiro-Wilkins and Kolmogorov-Smirnov tests for normality found no deviation from a standard normal distribution for W, SL, H or BT in any family (Table S1).

QTL analysis was performed using MapQTL® 6.0 [28] with genotype data and phenotype data of each population. Interval mapping and multiple QTL model (MQM) mapping were used to detect any significant effect on growth traits. The LOD score significance thresholds were calculated by permutation tests, with a genome-wide significance level of $\alpha<0.05$, $n=1000$ for significant linkages and a linkage-group-wide significance level of $\alpha<0.05$, $n=1000$ for suggestive linkages. A 2-LOD support interval was taken as a confidence interval for a putative QTL.

### 1.4 Comparative QTL analysis

For comparative purposes, unique QTLs in the four populations were placed into 15 cM regions of a consensus genetic map on the basis of the position of homologous flanking markers. If a flanking marker defining a QTL was not in-

cluded in the framework map during the merging process, the next most closely linked marker was chosen for representation in the integrated map. Where only a single marker was associated with a QTL, the marker position was used as both the start and stop position of the QTL.

### 1.5 Potential candidate gene locations

For those markers positioned near or overlapping with QTL peaks, a BLAST search was performed of the flanking sequences of microsatellites and whole sequences of SNPs to identify potential candidate genes. BLAST searches were performed against the genomes of zebrafish ($E$-value<$e^{-10}$) in the current ENSEMBL release version at http://www.ensemble.org and against all known sequences in GenBank.

## 2 Results

### 2.1 Linkage maps and consensus map construction

A genetic map was constructed for each population. The main features (number of markers, map length, and marker interval) of these maps are shown in Table 1. Two hundred microsatellites and 250 SNPs were selected for genotyping in populations A and B. For population A, 380 loci were used toconstruct the map, which comprised 306 loci spanning 1040.2 cM, with an average loci distance of 4.0 cM over 46 linkage groups. For population B, 364 loci were available for map construction. Ultimately, the B map comprised 285 loci spanning 1106.7 cM, with an average loci distance of 4.6 cM over 45 linkage groups. The C and D maps contain 402 and 433 loci spanning 1743.5 cM and 1933.9 cM, respectively.

Common markers among homologous LGs allowed for a comparison of marker order among the four mapping populations. Four hundred and thirteen markers were common to at least two populations, of which 105 (25.4%) were common to the four mapping panels. The consensus map spans 2371.6 cM across the 42 common carp LGs and comprises 678 markers (257 microsatellites and 421 SNPs), with a mean marker interval of 3.7 cM/marker.

### 2.2 QTL detection

Sixty-seven QTLs associated with four growth-related traits were detected in the four populations (Table S2, Figure 1). The 14 QTLs detected in population A were located on eight consensus map LGs, among which one QTL was significant at the genome-wide level in group H13. The contributions to phenotypic variation explained (PVE) for a single QTL varied between 12.1% and 25.1%. In population B, 21 QTLs were detected with contributions to PVE ranging from 11.7% to 35.1%. Among these, two QTLs, located in H16 and H34, surpassed the genome-wide threshold for significance. In population C, 17 QTLs were detected on nine consensus map LGs, with contributions to PVE varying from 11.8% to 26.3%. However, no QTLs reached the genome-wide level of significance. In population D, 15 QTLs (among which five SL QTLs have been described by Zhang et al. [29]) were identified on 10 consensus map LGs, which explained 13% to 47% of the PVE. Only one significant genome-wide QTL was detected in group H10.

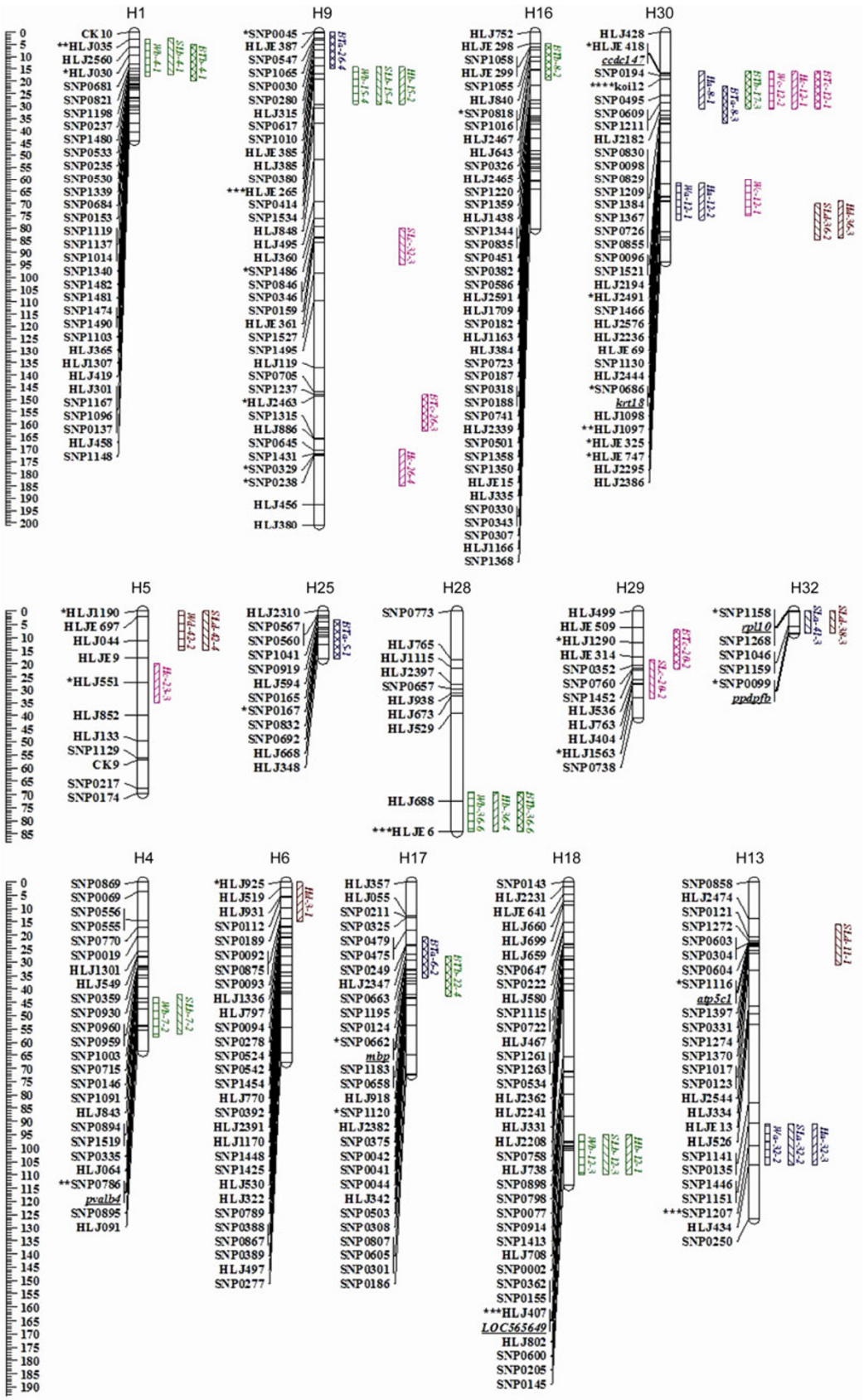
### 2.3 QTL comparison across four populations

One QTL (*BTa-8-3/BTb-17-3/BTc-12-1*) was identified in three populations and nine QTLs were detected in two populations (Table 2). However, no QTL was common to all four populations. W QTLs, *Wa-43-3*/*Wc-40-3* and *Wa-12-1*/*Wc-12-1*, were all detected in populations A and C. Only one SL QTL, *SLa-41-3/SLd-38-3*, was identified in populations A and D. Three H QTLs, *Hc-19-2/Hd-8-2*, *Ha-8-1*/*Hc-12-1* and *Ha-12-2/Hd-36-3*, were detected in populations C and D, A and C, A and D, respectively. Of the BT QTLs, three and one were commonly identified in two populations and three populations, respectively. *BTa-8- 3/BTb-17-3/BTc-12-1* were detected in A, B and C. *BTa-43- 5/BTd-6-1*, *BTa-6-2/BTb-22-4* and *BTc-45-4/BTd-56-4* were identified in A and D, A and B, and C and D, respectively.

As shown in Figure 1, the different traits have common QTLs in individual populations. For example, in H1, W (*Wb-4-1*), SL (*SLb-4-1*) and BT (*BTb-4-1*) were identified in population B; in H13, W (*Wa-32-2*), SL (*SLa-32-2*) and H (*Ha-32-3*) were detected in population A. Moreover, the different traits also have common QTLs among or between populations. For instance, H (*Ha-8-1*) and BT (*BTa-8-3*) in A, BT (*BTb-17-3*) in B, and W (*Wc-12-1*), H (*Hc-12-1*) and BT (*BTc-12-1*) in C were identified as having common or overlapping QTL intervals in the H30 consensus group.

**Table 1** Marker type, interval, and map lengths observed in individual population and consensus maps

| Population | No. of progeny | No. of each type of marker | | Map Length (cM) | Marker interval (cM) |
|---|---|---|---|---|---|
| | | SSR | SNP | | |
| A | 143 | 113 | 193 | 1040.2 | 4.0 |
| B | 141 | 110 | 175 | 1106.7 | 4.6 |
| C | 159 | 177 | 225 | 1743.5 | 4.9 |
| D | 68 | 150 | 283 | 1933.9 | 5.1 |
| Consensus maps | – | 257 | 421 | 2371.6 | 3.7 |


H1
H9
H16
H30
H5
H25
H28
H29
H32
H4
H6
H17
H18
H13

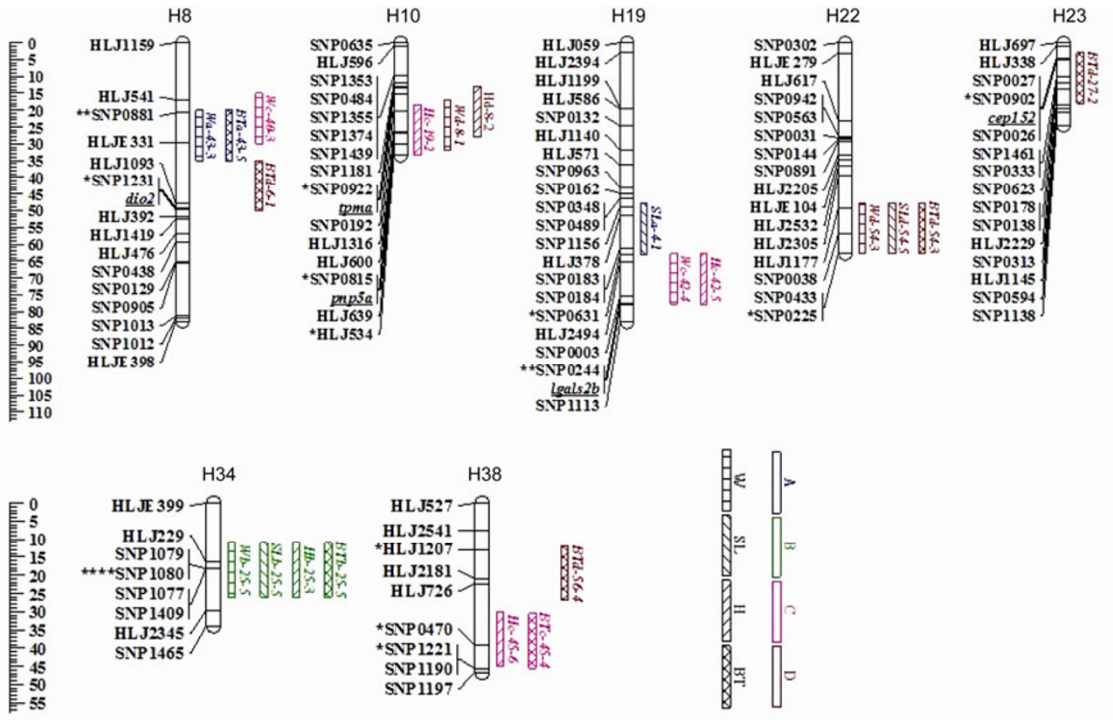



**Figure 1** QTL positions in integrated maps. Different colors represent the different populations and different shadings indicate the different traits, * represents the frequency of QTL loci for different traits.

**Table 2** Comparison of QTLs of the same trait across four populations

| Traits | LG | A | | | B | | | C | | | D | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | QTL | LOD | PVE (%) | QTL | LOD | PVE (%) | QTL | LOD | PVE (%) | QTL | LOD | PVE (%) |
| W | H8 | *Wa-43-3* | 2.6 | 14.3 | | | | *Wc-40-3* | 2.6 | 21.8 | | | |
| | H30 | *Wa-12-1* | 2.7 | 21.8 | | | | *Wc-12-1* | 2.3 | 22.0 | | | |
| SL | H32 | *SLa-41-3* | 2.0 | 12.1 | | | | | | | *SLd-38-3* | 2.6 | 31 |
| H | H10 | | | | | | | *Hc-19-2* | 2.1 | 16.2 | *Hd-8-2* | 3.0 | 34.6 |
| | H30 | *Ha-8-1* | 2.5 | 13.7 | | | | *Hc-12-1* | 3.0 | 18.5 | | | |
| | H30 | *Ha-12-2* | 2.6 | 15.5 | | | | | | | *Hd-36-3* | 2.1 | 14.8 |
| BT | H8 | *BTa-43-5* | 2.9 | 16.6 | | | | | | | *BTd-6-1* | 3.0 | 42.7 |
| | H17 | *BTa-6-2* | 3.7 | 24.2 | *BTb-22-4* | 1.3 | 13.4 | | | | | | |
| | H30 | *BTa-8-3* | 3.6 | 22.1 | *BTb-17-3* | 2.9 | 35.1 | *BTc-12-1* | 2.6 | 26.3 | | | |
| | H38 | | | | | | | *BTc-45-4* | 2.4 | 21.2 | *BTd-56-4* | 2.1 | 13 |

Similar situations also existed in the H8, and H10 groups.

### 2.4 Potential candidate genes in QTL intervals

The sequences of 37 marker loci that occurred next to QTL peaks were BLAST-searched against the entire zebrafish genome. The results indicated that 70.3% (26/37) of the sequences had significant hits to the zebrafish genome. Further analysis showed that 14 sequences had very high similarity to annotation genes of zebrafish (Table S3). Most of them are potential candidates for growth-related genes, e.g., SNP1116 showed a very high similarity to the *atp5c1* (ATP synthase) gene of zebrafish and Atlantic salmon, SNP0922 corresponded to the *tpma* (alpha-tropomyosin) gene of zebrafish. Strikingly, 6 of the 10 common QTLs have existing genes.

## 3 Discussion

### 3.1 Advantages of integrated maps

This study used 732 markers (289 SSRs and 443 SNPs) from four different populations to make an integrated map comprising 678 markers (257 SSRs and 421 SNPs). Construction of a genetic map is the basis for QTL location, cloning, and overall genome study, all of which require a high-density genetic map that relies on sufficient polymorphic molecular markers. Previously constructed common

carp maps used a single mapping panel in which polymorphic markers were quite limited. Using multiple, highly differentiated populations, it is possible to construct the high-density maps required. This study found 414, 402, 552 and 553 polymorphic markers in populations A, B, C, and D, respectively. Combining the four linkage maps generated 732 polymorphic markers. This represents 179 markers more than population D and 245 more than D after final integration. Each LG adds about five markers and shortens the inter-marker intervals by 1.4 cM. Covering the entire common carp genome clearly gives better results. A single population map means that either one LG is separated into two smaller groups or marker gaps will exist because of a lack of marker loci. Map integration of multiple populations is necessary and advantageous because it allows us to correct these defects. For example, in this study, LG8 and LG10 of population A correspond to the integrated map H30; LG1 and LG2 of population B correspond to the integrated map H1; and LG9 and LG10 of population C correspond to the integrated map H12.

### 3.2 Marker order and accuracy of integrated map

There are at least 413 common makers between two populations in this study. One hundred and five are common markers in four populations, and 165 are common to three populations, which provide the preconditions for consistent comparison of the marker order between four individual maps and one integrated map.

The integrated map and the zebrafish genome have a linear relationship, which, to some extent, reflects the accuracy of the integrated map [7]. In addition, the marker orders in the integrated map and the four individual maps are highly consistent. However, the location of a few markers changed. For example, HLJ519 is in LG4 of the population D map and consensus group H6, SNP0211 and SNP0324 are in LG13 of the population C map and consensus group H17 (Figure 2). This phenomenon has also been recorded in other plants and animals [30–32]. It is likely that this occurs because of size differences of communities used for making the separate maps and not by the actual combination [33].

### 3.3 The superiority of the comparison of QTLs from multiple populations

QTL location and genetic effect will differ according to their parental genetic background. By analyzing QTLs from multiple population, the credibility of minor QTLs will improve. Many minor QTLs cannot be detected if the LOD value is set too high. To increase the amount of valuable information obtained, the LOD can be lowered; however, this may lead to false-positives. The comparison and analysis of QTL results from different populations can partly resolve this conflict. If a minor QTL is detected in different populations then the LOD value is credible, even though it is lower. For example, the QTL LOD value in population B is 1.3, but in population A it is 3.7. Therefore, the QTL detected in B is credible. The fine mapping of genes and the creation of clones also prove that the QTLs with lower LOD values may be credible. The nonsignificant QTLs in some tests could reach significance in future tests or in other populations [34,35].

Figure 3 illustrates that HLJ1097 and SNP0686 in population B are not linked. Although there is polymorphism in population D, there is no genetic difference and the contribution to the trait is not significant. It is possible that polymorphic alleles at QTLs in one population may be monomorphic in another. In addition, it is possible that the effects on expression of body weight loci are genome dependent [36]. Such QTL markers, which have different polymorphisms and genetic contributions, are problematic to QTL linkage analysis and molecular marker assisted breeding. Testing different populations allows us to investigate more QTL locations. Full identification of the location on a chromosome of genes controlling a trait and major genes is the basis of the genetic study of QTLs. The common QTLs that exist between different populations or families are not only more valuable in molecular-marker-assisted breeding, but probably represent relatively stable gene sites during long periods of species evolution [37,38]. By studying those gene sites, it is possible to predict the location of important QTLs in a species and permit the analysis of the evolutionary process. Therefore, it is necessary to identify the QTLs of different families or populations to more accurately locate gene sites controlling traits of interest.

### 3.4 The characteristics of common QTLs

By BLAST-searching QTL loci sequences, 14 markers with related genes and relevant function annotation were identified. The functions of these genes are mainly energy storage, protein binding and synthesis, regulation of protein activity, cellular components and transport, cell differentiation, ion binding and transport, signal transduction, and unclear functional genes. The authors believe that QTLs related to growth are not necessarily the axis of growth regulation genes, and may also be associated with cell differentiation, ion transport, signal transduction, and may even include genes of unknown function. Therefore, most of these genes can be used as candidate growth genes. Furthermore, 6 of the 10 common QTL intervals represent existing genes. Four of the common QTLs were found in populations with different genetic backgrounds (three in A and D, one in C and D). These can be considered as major QTLs that control traits. Usually the genes in QTL intervals controlling the traits are major genes. Therefore, the major genes that control traits in QTL intervals are probably the basis of shared QTLs in different populations.

During the comparative analysis of QTLs in the four populations, very few QTLs of the same trait were identi-

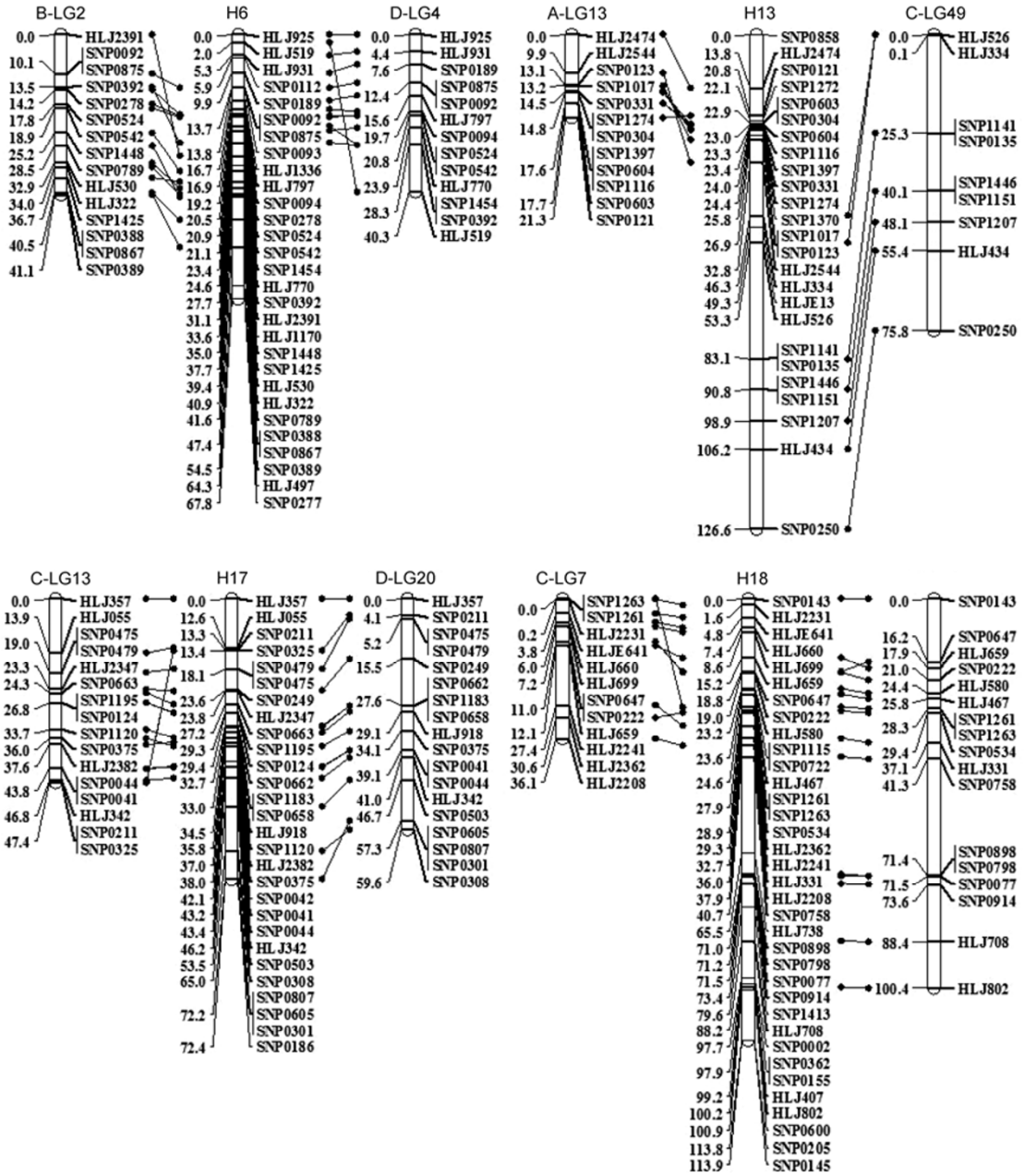



**Figure 2** Compared marker order of the composite map to the individual linkage maps. A, B, C, and D represent the four individual maps, H represents the consensus map, with straight line connecting the same markers.

fied as being common across populations. Only 21 out of 67 QTLs provided 10 common QTL pairs. They are two between A and B, three between A and C, two between B and C, two between C and D, and none between B and D. This reflects the fact that the degree of QTL commonality is, to some extent, related to genetic diversity in the parents. For example, A, B, and C are from populations with the same parents and are half siblings. Similar genetic backgrounds and relatedness resulted in seven common QTLs in the first three populations, but only two in population D. Location results of individual populations may be inconsistent because of differences in the parental backgrounds of the populations [34]. This would explain why the QTL controlling one trait is different in each population.

Common QTL traits also showed phenotypic variability. In terms of body weight (W) (Figure 3), the phenotypic variability of QTL markers in each population varied. For example, HLJE747, HLJ1097, SNP0686, HLJ541, and SNP0881 accounted for more than 20% of PVE in population A and C, but 5% in B and D. HLJE418 explained more than 20% of the phenotypic variation in A, B, and C; however, it accounted for less than 5% in D. HLJ035 and SNP1080 accounted for a high percentage, 19% and 29%, respectively, of PVE in population B, but was absent or

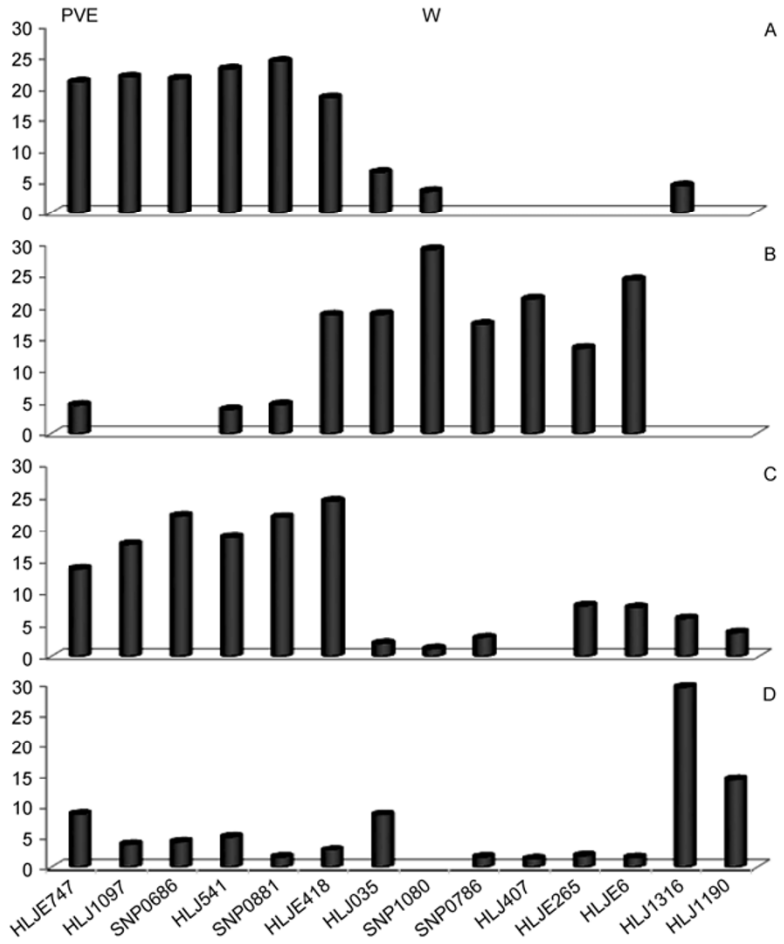



**Figure 3** Hereditary effects on the variation of QTL markers affecting body weight (W) in four populations. Abscissa represents loci, the ordinate represents phenotypic variance explained (PVE), the space in the diagram represents markers with no polymorphisms or significant QTLs detected.

detected with very low polymorphism in the other three populations. This study has revealed that major and minor genes differ in their genetic performance. Therefore, we conclude that the major gene is undergoing change and remains unfixed in these populations. Further work is needed to identify shared QTLs in populations or families. In view of the high cost of QTL mapping experiments, it would be advantageous if QTL regions were consistent among crosses. Only the most suitable flanking marker and the sign of the QTL allele would have to be determined for each population [39]. Efficient QTL detection would permit the location of more QTLs. QTLs are not often repeated within populations. However, to confirm the reliability of QTL results, information on populations should be shared, which will require significant coordination.

In conclusion, to the best of our knowledge, this is the first integrated map of common carp. The alignment of framework markers and the position of growth-related QTLs in the integrated map will facilitate comparative QTL analyses among populations of different origins. This will provide deeper insights into the genetic control of the diverse phenotypic variability observed in the common carp germplasm.

*This work was supported by the National Basic Research Program of China (2010CB126305), the Special Fund for Agro-scientific Research in the Public Interest (200903045) and National High Technology Research and Development Program of China (2011AA100402).*

1 Liu Z J. Aquaculture genome technologies. Oxford: Blackwell Publishing, Ames, IA, 2007
2 Gui J F, Zhu Z Y. Molecular basis and genetic improvement of economically important traits in aquaculture animals. Chin Sci Bull, 2012, 57: 1751–1760
3 Crooijmans R, Poel J J, Groenen M A M, et al. Microsatellite markers in common carp (*Cyprinus carpio* L.). Anim Genet, 1997, 28: 129–134
4 David L, Rajasekaran P, Fang J, et al. Polymorphism in ornamental and common carp strains (*Cyprinus carpio* L.) as revealed by aflp analysis and a new set of microsatellite markers. Mol Genet Genomics, 2001, 266: 353–362
5 Hou N, Li D Y, Li Y, et al. Development of 10 tri- and tetranucleotide microsatellite loci for population studies in the common carp (*Cyprinus carpio* L.). Mol Ecol Resour, 2008, 8: 1357–1359
6 Sun X W, Liang L Q. A genetic linkage map of common carp (*Cyprinus carpio* L.) and mapping of a locus associated with cold tolerance. Aquaculture, 2004, 238: 165–172
7 Zheng X H, Kuang Y Y, Zhang X F, et al. A genetic linkage map and comparative genome analysis of common carp (*Cyprinus carpio* L.) using microsatellites and snps. Mol Genet Genomics, 2011, 286:

261–277
8 Wang X P, Sun X W, Li W S, et al. The construction of genetic linkage map of common carp (*Cyprinus carpio* L.) (in Chinese). J Shanghai Ocean Univ, 2011, 20: 641–648
9 Li Y, Xu P, Zhao Z X, et al. Construction and characterization of the bac library for common carp *Cyprinus carpio* L. and establishment of microsynteny with zebrafish danio rerio. Mar Biotechnol, 2011, 13: 706–712
10 Xu P, Li J, Li Y, et al. Genomic insight into the common carp (*Cyprinus carpio*) genome by sequencing analysis of BAC-end sequences. BMC genomics, 2011, 12: 188
11 Xu P, Wang J, Wang J T, et al. Generation of the first BAC-based physical map of the common carp genome. BMC genomics, 2011, 12: 537
12 Zheng X H, Kuang Y Y, Lu C Y, et al. Quantitative trait locus analysis of standard length, body depth and body thickness in mirror carp (*Cyprinus carpio* L.) (in Chinese). Yi Chuan, 2011, 33: 1366–1373
13 Zhang Y, Liang L Q, Chang Y M, et al. Mapping and genetic effect analysis of quantitative trait loci related to body size in common carp (*Cyprinus carpio* L.) (in Chinese). Yi Chuan, 2007, 29: 1243–1248
14 Zhang Y, Xu P, Lu C Y, et al. Genetic linkage mapping and analysis of muscle fiber-related QTLs in common carp (*Cyprinus carpio* L.). Mar Biotechnol, 2011, 13: 376–392
15 Wang X P, Zhang X F, Li W S, et al. Mapping and genetic effect analysis on quantitative trait loci related to feed conversion ratio of common carp (in Chinese). Acta Hydrobiol Sin, 2012, 36: 177–196
16 Mao R X, Liu F J, Zhang X F, et al. Studies on quantitative trait loci related to activity of lactate dehydrogenase in common carp (*Cyprinus carpio*) (in Chinese). Yi Chuan, 2009, 31: 407–411
17 Coles N D, McMullen M D, Balint-Kurti P J, et al. Genetic control of photoperiod sensitivity in maize revealed by joint multiple population analysis. Genetics, 2010, 184: 799–812
18 Liu T, Zhang Y, Xue W, et al. Comparison of quantitative trait loci for 1000-grain weight and spikelets per panicle across three connected rice populations. Euphytica, 2010, 175: 383–394
19 Marcel T C, Varshney R, Barbieri M, et al. A high-density consensus map of barley to compare the distribution of QTLs for partial resistance to puccinia hordei and of defence gene homologues. Theor Appl Genet, 2007, 114: 487–500
20 Martin M, Miedaner T, Schwegler D D, et al. Comparative quantitative trait loci mapping for gibberella ear rot resistance and reduced deoxynivalenol contamination across connected maize populations. Crop Sci, 2012, 52: 32–43
21 Liu G, Kim J J, Jonas E, et al. Combined line-cross and half-sib QTL analysis in duroc-pietrain population. Mamm Genome, 2008, 19: 429–438
22 Nagamine Y, Haley C S, Sewalem A, et al. Quantitative trait loci variation for growth and obesity between and within lines of pigs (*Sus scrofa*). Genetics, 2003, 164: 629–635
23 Walling G, Visscher P, Wilson A, et al. Mapping of quantitative trait loci for growth and carcass traits in commercial sheep populations. J Anim Sci, 2004, 82: 2234
24 Wang C M, Lo L C, Feng F, et al. Identification and verification of QTL associated with growth traits in two genetic backgrounds of barramundi (*Lates calcarifer*). Anim Genet, 2008, 39: 34–39
25 Hayes B J, Gjuvsland A, Omholt S. Power of QTL mapping experiments in commercial atlantic salmon populations, exploiting linkage and linkage disequilibrium and effect of limited recombination in males. Heredity, 2006, 97: 19–26
26 Van Ooijen J. JoinMap® 4, software for the calculation of genetic linkage maps in experimental populations. The Netherlands: Kyazma BV, Wageningen, 2006
27 Kosambi D. The estimation of map distances from recombination values. Ann Eugen, 1944, 12: 172–175
28 Van Ooijen J. MapQTL® 6, software for the mapping of quantitative trait loci in experimental populations of diploid species. The Netherlands: Kyazma BV, Wageningen, 2009
29 Zhang T Q, Zhang X F, Tan Z J, et al. Mapping and genetic effect analysis of quantitative trait loci related to body length in mirror carp (*Cyprinus carpio* L.) (in Chinese). Yi Chuan, 2011, 33: 1245–1250
30 Millan T, Winter P, Jüngling R, et al. A consensus genetic map of chickpea (*Cicer arietinum* L.) based on 10 mapping populations. Euphytica, 2010, 175: 175–189
31 Gustafson J P, Ma X F, Korzun V, et al. A consensus map of rye integrating mapping data from five mapping populations. Theor Appl Genet, 2009, 118: 793–800
32 Li H, Kilian A, Zhou M, et al. Construction of a high-density composite map and comparative mapping of segregation distortion regions in barley. Mol Genetics Genomics, 2010, 284: 319–331
33 Lombard V, Delourme R. A consensus linkage map for rapeseed (*Brassica napus* L.): construction and integration of three individual maps from dh populations. Theor Appl Genet, 2001, 103: 491–507
34 Wang L, Liu W, Xu Y, et al. Genetic basis of 17 traits and viscosity parameters characterizing the eating and cooking quality of rice grain. Theor Appl Genet, 2007, 115: 463–476
35 Barton N H, Keightley P D. Understanding quantitative genetic variation. Nat Rev Genet, 2002, 3: 11–21
36 Beavis W, Grant D, Albertsen M, et al. Quantitative trait loci for plant height in four maize populations and their associations with qualitative genetic loci. Theor Appl Genet, 1991, 83: 141–145
37 Hill W G. Understanding and using quantitative genetic variation. PhilosoT R Soc B, 2010, 365: 73–85
38 Farrall M. Quantitative genetic variation: A post-modern view. Hum Mol Genet, 2004, 13: R1–R7
39 Mihaljevic R U, Melchinger H F, Albrecht E. Congruency of quantitative trait loci detected for agronomic traits in testcrosses of five populations of european maize. Crop Sci, 2004, 44: 114



## Supporting Information

**Table S1** Descriptive statistics for four traits (body weight, standard length, body depth and body thickness)

**Table S2** QTL results for all populations

**Table S3** Blast results of peak QTL loci

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