

Mapping QTLs for Swimming Ability Related Traits in *Cyprinus carpio* L.

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Abstract Body height (BH), head length (HL), snout length (SL), and tail length (TL) are important traits related with swimming ability of fish. Therefore, improving these traits will increase the production which is the basic goal of aquaculture breeding. To understand the genetic basis of swimming ability related traits in *Cyprinus carpio* L., a high-density linkage map spanning 3,301 cM in 50 linkage groups was utilized for quantitative trait locus (QTL) mapping. Mapping family comprised 190 offspring and 627 molecular markers were genotyped with average distance of 5.6 cM. A total of 15 QTLs including four (*qBH13*, *qBH30*, *qBH33*, *qBH48*) for BH, four (*qHL10*, *qHL18*, *qHL29*, *qHL48*) for HL, three (*qSL24*, *qSL27*, *qSL45*) for SL, and four (*qTL15*, *qTL17*, *qTL18*, *qTL44*) for TL were detected on 13 linkage groups LG10, LG13, LG15, LG17, LG18, LG24, LG27, LG29, LG30, LG33, LG44, LG45, and LG48. Each LG consisted on single QTL except LG18 and LG48. LG18 was found with two QTLs associated with HL and TL. While LG48

was comprised, the QTLs related with BH and HL. The phenotype variance was recorded from 12.6 to 40.6 %. Five QTLs, *qHL48*, *qSL45*, *qTL15*, *qTL18*, and *qTL44*, explained phenotype variance of >20 % with a significant levels of 0.047, 0.049, 0.037, 0.025, and 0.023, respectively. The neighbored loci of these QTLs were considered as main region of chromosomes controlling the traits. These identified genetic regions will be the main source of discovering gene(s) associated with swimming ability related traits in *C. carpio* L.

Keywords Body height · *Cyprinus carpio* L · Head length · QTL · Snout length · Tail length

Introduction

Organisms face two important challenges in order to survive, which are to obtain energy and avoid predators. Fishes commonly swim up to a prey item and utilize a combination of ram (swimming) and suction feeding for prey capture (Emily and Higham 2011). Whereas, ram feeding relies on predator speed to overtake the prey (Liem 1980; Norton and Brainerd 1993). There is a relationship between body shape and swimming performance that affects the feeding and avoiding predators (Reid and Catherine 2010). Hence, swimming ability directly or indirectly affects the growth and production of the fish. When we look closer at nature's design of a low friction, fish morphology has a great importance to swim easily in the water. Body shape is related to swimming ability and can affect swimming performance of fish (Walker 2007). The talk about the tail being the only part of fishes related with swimming ability is not true because it is just a helping organ in swimming that plays an important role in changing the direction. Fishes swim by moving their bodies and the tail area (Küllü et al. 2010). Hence, some major body parts of fish such as body height (BH), head length

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(HL), snout length (SL), and tail length (TL) collectively play a vital role in swimming. These traits have a great importance due to influence on the swimming ability. The virtual mass of water depends on the local body height, and the local velocity perpendicular to the surface of the body changes with the amplitude of the lateral movement from head to tail (Videler 1993). Likewise, reactive force propels the fish forward. High BH functions like keel helps fish to move fast. At the same time, HL and SL help fish to reduce the friction in the water and move ahead easily, while tail length may be considered as a powerful tool that forces fish to speed up. By reducing friction, fish not only saves energy but also speeds up to catch the prey or avoid to be preyed. Hence, BH, HL, SL, and TL simultaneously play an important role during swimming and are considered as important traits associated with swimming ability. Collective efforts of these traits optimize the swimming speed of fish. Consequently, improving the trait related with swimming ability will increase the survival rate, in case of predation, and increase the feeding ability as well as saving energy consumed during tough locomotion. Hence, that reserved energy will be conserved in the growth. Overall, the advantage of improving such complex trait is to increase fish production.

Quantitative trait locus (QTL) study attributes in better understanding the effect and number of genes controlling such important traits. Hence, this will contribute to improve the efficiency of selective breeding programs in aquaculture species (Liu and Cordes 2004). Some QTLs associated with fin position have been reported in aquaculture species such as Asian sea bass (Wang et al. 2011), Atlantic salmon (Boulding et al. 2008), European sea bass (Chatziplis et al. 2007; Massault et al. 2010), silver carp and bighead carp (Wang et al. 2013), and three-spined stickleback (Albert et al. 2008). However, limited research was conducted on the length of tail.

Cyprinus carpio L. is one of the important aquaculture species cultures for decades. A decade practice of selective artificial breeding shows significant difference in body shape of carp population (Shen and Yan 1985). Morphological description of strains has a great importance that focuses on characteristics and facilitates identification of an ideal breed or strain (Rege and Okeyo 2011). In particular, investigating the QTL affecting the body shape related swimming ability traits of *C. carpio* provides an opportunity to improve the trait for marker-assisted selection program. QTL analysis of various traits has been studied in this commercially important fish, mostly focused on economical traits such as activity of lactate dehydrogenase (LDH) (Mao et al. 2009), body shape related trait (Zhang et al. 2013), body weight, length and condition factor (Laghari et al. 2013a), cold tolerance (Sun and Liang 2004), eye cross and diameter trait (Jin et al. 2012), feed conversion ratio (Li et al. 2009), growth rate trait (Laghari et al. 2013b), growth traits (Zheng et al. 2011; Wang et al. 2012; Laghari et al. 2013c), head size (Liu et al. 2009), and muscle fiber related trait (Zhang et al. 2011).

Wang et al. (2012) and Zhang et al. (2013) identified the QTLs related with tail length in *C. carpio* by using 43 F₂ specimens and 92 F₁ progenies, respectively. A total of 469 and 307 molecular markers were utilized for genetic linkage map construction, separately. The accuracy of QTL location depends upon the number of markers and size of samples (Wang et al. 2006). Recently, a high-density genetic map with 627 molecular makers covering 5.6-cM average distance was constructed (Zhang et al. 2012). Taking an advantage of such high-density genetic linkage map, a family comprised of 190 progenies was utilized for QTL mapping. Such genetic map with high-density molecular markers and large number of samples may increase the accuracy of QTL mapping, which is a great advantage of this study. Particular traits related with the swimming ability, BH, HL, SL, and TL, were used in QTL analysis. We expect that the result of this study may play a key role in genetic breeding program in future and may be applied for decreasing mortality and increasing production in future.

Material and Method

Sampling and Genetic Map Construction

Swimming ability related traits as BH, HL, SL, and TL of F₁ *C. carpio* family, comprised of 190 progenies, were utilized. The experimental fishes were kept in a series of water circulating aquarium system, temperature and oxygen levels were maintained throughout the experiment. Fish were fed with local commercial fish feed at the same ratio three times a day. Four traits (BH, HL, SL, TL) of 300 days post-hatch (dph) individuals were measured by measuring tape (see Fig. 1). The phenotype data of all four traits were normalized to the standard body length of the fish for further QTL analysis to increase the accuracy. The blood samples were collected for DNA isolation. DNA was isolated with a QIAamp DNA Blood Midi Kit (QIAGEN, Shanghai, China) for genotyping. A genetic map, relying on 627 markers (617 SSRs and 10 SNPs) and spawning 3,301 cM with an average distance of 5.6 cM, with 50 linkage groups (LGs), was constructed (Zhang et al. 2012) and utilized for QTL mapping. Briefly, microsatellite markers were developed by BAC-end sequence and whole-genome shotgun sequences generated from the Roche 454

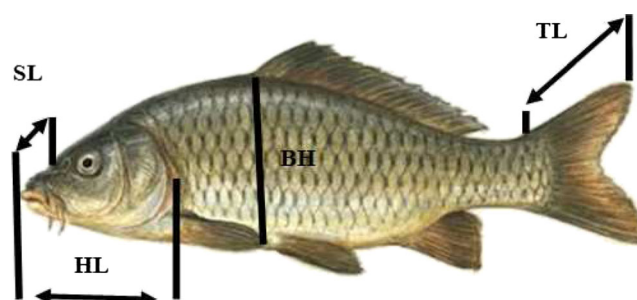


Fig. 1 Morphometric measurement of *C. carpio* L. BH body height, HL head length, SL snout length, and TL tail length

platform. Primer 3.0 software was utilized for primers design and a tailed primer protocol (Schuelke 2000) was used for PCR reaction. Microsatellite was genotyped on Genetic Analyzer 3130XL (Applied Biosystem, Foster City, CA, USA). Genotype was confirmed with LIZ-500 size standards (Applied Biosystems), using GeneMapper 4.0 software (Applied Biosystems) (Zhang et al. 2012). The JoinMap 4.0 (Van Ooijen 2006) software package, with default significance levels from 4.0 to 10.0 logarithm of odds (LOD), was used for genetic linkage map construction. A threshold of 5.0 was set to detect suspect linkage possibly resulting from allele coding errors. Marker position was confirmed by using up to three rounds of the mean chi-square test (Stam 1993).

QTL Mapping

QTLs were analyzed by using MapQTL 4.0 program (Van Ooijen et al. 2002), and Multiple QTL Mapping (MQM) method was employed to detect any significant associations between swimming ability related traits and marker loci. Significant LOD thresholds were calculated by permutation test of $\alpha < 0.05$ and $n = 10,000$ for significant linkage. Empirically, a QTL is claimed when LOD is larger than a critical value predetermined by permutation, if LOD score in several flanking marker intervals are larger than the critical value. Hence, two-LOD support interval determined by the range of the highest LOD minus two LODs provides an empirical confidence interval. One-way ANOVA (SAS Institute) was carried out for significant QTL markers with four alleles to determine the differences among the genotypes of markers that were nearest to each QTL. For markers with two alleles, two-tailed *t* test was used with Welch's correction for unequal variances. The genotypes of the marker locus lying closest to the peak in each of the QTL-containing genomic regions were defined as m1f1, m1f2, m2f1, and m2f2, where m1 and m2, and f1 and f2 denote the genotypes of the mother and father, respectively.

Result

Trait Measurements and Genetic Mapping

A total of four swimming ability related traits, BH, HL, SL, and TL, of 190 F1 individuals were measured. The average values of BH, HL, SL, and TL traits calculated were 6.833 ± 0.851 , 4.372 ± 0.432 , 1.682 ± 0.252 , and 2.802 ± 0.301 cm, respectively.

QTL Analysis

Fifteen QTLs associated with swimming ability related traits were detected, four for each BH, HL, and TL, while three for

SL, on 13 linkage groups LG10, LG13, LG15, LG17, LG18, LG24, LG27, LG29, LG30, LG33, LG44, LG45, and LG48 (Fig. 2). Among these, LG18 was found with the QTLs associated with HL and TL (*qHL18*, *qTL18*), while LG48 was related with the QTLs of two traits, BH and HL (*qBH48*, *qHL48*). And, all other 11 linkage groups had single QTL each. Minimum and maximum LOD scores remained at 3.18 and 5.11, respectively. The highest phenotype variance of 40.6 and the lowest of 12.6 % were recorded (Table 1).

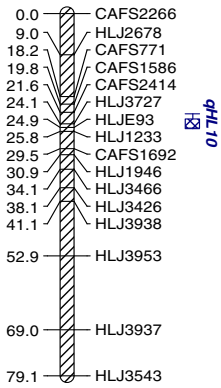
Four QTLs, *qBH13*, *qBH30*, *qBH33*, and *qBH48*, associated with BH were identified on LG13, LG30, LG33, and LG48 at the nearest markers CAFS1429, HLJ1275, HLJ2179, and HLJ1145, separately (Fig. 3). The LOD scores and phenotypic variance values recorded were 4.05, 3.4, 3.58, and 3.88, and 15.3, 15.7, 18.2, and 12.6 %, respectively, responding to each QTL. ANOVA and *t* test, of nearest marker of QTL, suggested a significant increase ($p < 0.05$) in the BH.

Four QTLs, *qHL10*, *qHL18*, *qHL29*, and *qHL48*, related with HL were located on LG10, LG18, LG29, and LG48 at the nearest markers HLJE93, HLJ752, CAFS1846, and HLJ1145, respectively (Fig. 3b). The LOD scores recorded were 3.18, 3.76, 3.82, and 3.8, respectively, for each QTL. While, phenotypic variance values recorded were 14.4, 15.8, 16.0, and 25.3 %, separately, for each nearest marker. ANOVA test of nearest marker for HL QTLs resulted in a significant increase ($p < 0.05$) in HL. Only *qHL48* with the nearest marker HLJ1145 shows higher phenotype variance of > 20 % than other QTLs related with HL.

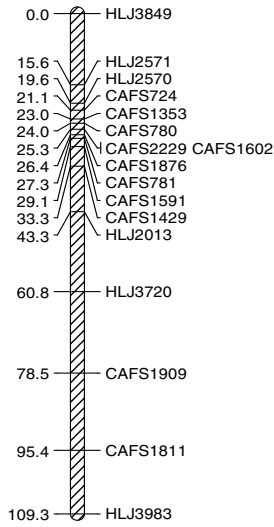
There were three QTLs, *qSL24*, *qSL27*, and *qSL45*, associated with SL found on LG24, LG27, and LG45 at the nearest markers HLJ1944, HLJ3751, and HLJ3885, separately (Fig. 3c). The LOD scores were 3.28, 3.56, and 3.6, corresponding to each detected QTL of SL. Observed phenotypic variance values were 13.5, 14.4, and 28.3 % for each nearest locus separately. ANOVA and *t* test of neighbored loci for SL QTLs resulted in a significant increase ($p < 0.05$) in SL. Only *qSL45* shows higher phenotype variance of > 20 % than the other two QTLs.

Four QTLs, *qTL15*, *qTL17*, *qTL18*, and *qTL44*, related with TL were located on LG15, LG17, LG18, and LG44 at the nearest markers HLJ2682, CAFS230, CAFS893, and CAFS834, respectively. The LOD scores recorded were 3.98, 3.29, 5.11, and 4.64, and phenotypic variance values were 20.3, 17.1, 40.6, and 29.0 %, respectively, for each nearby marker of detected QTL (Fig. 3d). ANOVA and *t* test of neighbored loci for TL QTLs resulted in a significant increase ($p < 0.05$) in TL. Out of four detected QTLs, associated with TL, *qTL15* and *qTL18* show higher phenotype variance of > 20 %.

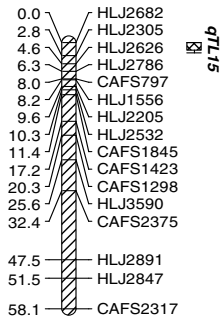
LG10



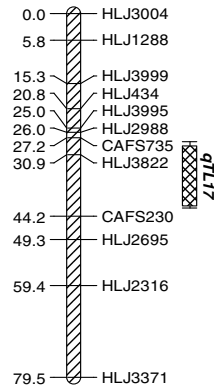
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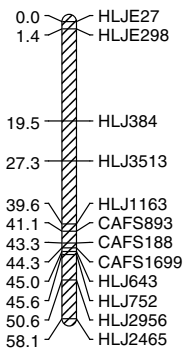
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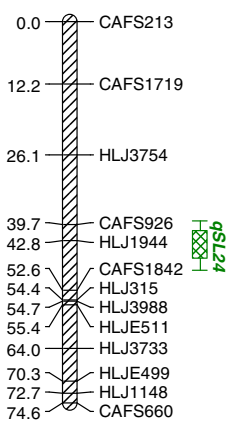
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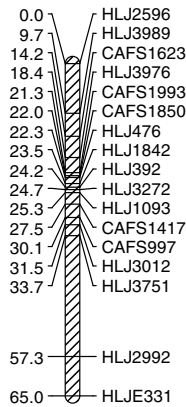
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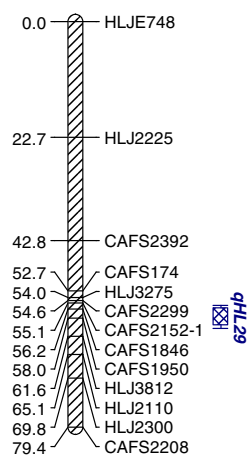
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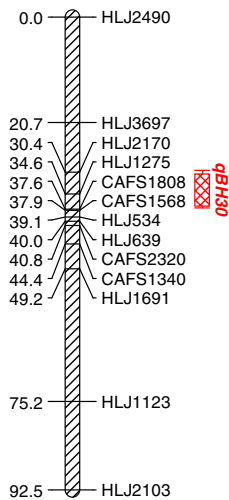
LG27



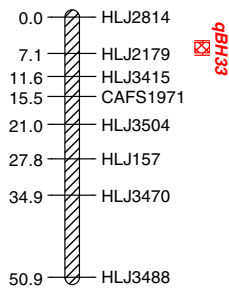
LG29



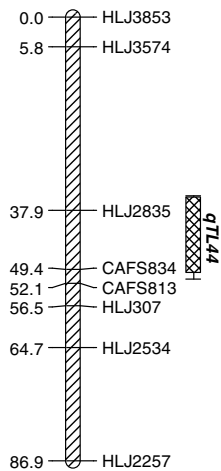
LG30



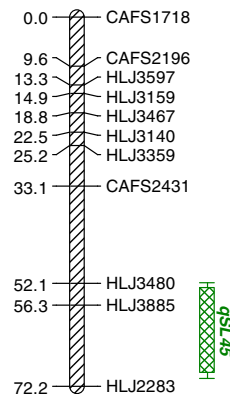
LG33



LG44



LG45



LG48

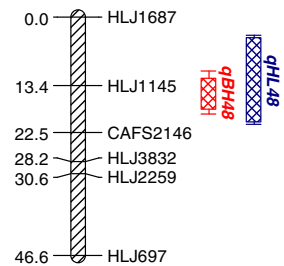


Fig. 2 Thirteen LGs consisted on QTLs associated with swimming ability related traits in *C. carpio* L. Red mark indicates body height QTLs, blue head length, green snout length, and black tail length associated QTLs (Color figure online)

Statistical Analysis

ANOVA and *t* test of neighbored loci for all QTLs resulted in a significant increase ($p < 0.05$) in related traits. Further, one-way ANOVA for four allele combinations (m1f1, m1f2, m2f1, m2f2) and *t* test for two allele combinations (m1f1, m2f1) from markers nearest to each QTL were performed to investigate the association between the phenotype trait and genotype (Table 1). The two nearest markers HLJ2179 and HLJ1145 related to BH show significantly highest height ($p < 0.05$) in m1f1 offspring. While, CAFS1429 and HLJ1275 show significantly highest height ($p < 0.05$) in m2f1 and m2f2 offspring, respectively (Table 1).

Among neighbored markers related to HL trait, HLJE93 and CAFS1846 with offspring genotype of m1f1 were found

with significantly longest length ($p < 0.05$) of head. HLJ752 and HLJ1145 show a significant increase ($p < 0.05$) in m1f2 and m2f2 offspring, respectively.

QTLs associated with SL, progeny with m1f1, at nearest markers HLJ1944 and HLJ3751 show significant increase ($p < 0.05$) in m1f1 offspring length, and the other nearest marker HLJ3885 shows a significant increase ($p < 0.05$) in m2f2 individuals.

Among four nearest markers of QTLs related with TL, two markers, CAFS230 and CAFS893, showed higher phenotype value at m1f1 and the other two markers HLJ2682 and CAFS834 showed significant increase in the offspring with genotype of m1f2 and m2f2 (Table 1).

Further, to analyze the effects of alleles, within parents and their interactions, a single marker nearest to each QTL was used. Eight QTLs (*qBH30*, *qBH33*, *qBH48*, *qHL10*, *qSL27*, *qTL15*, *qTL17*, *qTL18*) showed significant effects within mother alleles, six (*qBH13*, *qHL18*, *qHL29*, *qHL48*, *qSL45*, *qTL44*) within father alleles, and only one *qSL24* exhibits effect within both mother and father parent alleles (Table 1).

Table 1 Detected QTLs associated with swimming ability related traits in *C. carpio* L.

Trait	QTL	LG	Nearest marker	LOD	LOD threshold	PVE%	Phenotype mean				Significance <i>p</i>
							m1f1	m1f2	m2f1	m2f2	
Body height (cm)											
BH											
	qBH13	13	CAFS1429	4.05	3.71	15.3	6.493±0.716	6.425±0.653	7.050±0.623	6.446±0.573	0.045
	qBH30	30	HLJ1275	3.4	3.19	15.7	6.463±0.683	6.477±0.618	6.490±0.648	6.978±0.589	0.042
	qBH33	33	HLJ2179	3.58	3.4	18.2	6.912±0.659		6.464±0.633	0.041	
	qBH48	48	HLJ1145	3.88	3.5	12.6	6.981±0.649		6.423±0.635	0.043	
Head length (cm)											
HL											
	qHL10	10	HLJE93	3.18	2.8	14.4	4.383±0.427		4.060±0.438	0.042	
	qHL18	18	HLJ752	3.76	2.92	15.8	4.049±0.465	4.423±0.462	4.102±0.442	4.138±0.377	0.035
	qHL29	29	CAFS1846	3.82	3	16	4.560±0.445	4.269±0.449	4.366±0.389	4.311±0.390	0.005
	qHL48	48	HLJ1145	3.8	3.12	25.3	4.148±0.436		4.393±0.429	0.047	
Snout length (cm)											
SL											
	qSL24	24	HLJ1944	3.28	2.8	13.5	1.745±0.341	1.335±0.178	1.348±0.252	1.501±0.226	0.05
	qSL27	27	HLJ3751	3.56	2.91	14.4	1.697±0.219		1.269±0.212	0.045	
	qSL45	45	HLJ3885	3.6	2.98	28.3	1.421±0.270		1.680±0.231	0.049	
Tail length (cm)											
TL											
	qTL15	15	HLJ2682	3.98	3	20.3	2.807±0.286	2.868±0.285	2.741±0.302	2.727±0.321	0.037
	qTL17	17	CAFS230	3.29	2.77	17.1	2.805±0.286		2.692±0.305	0.046	
	qTL18	18	CAFS893	5.11	4.5	40.6	2.9±0.290	2.819±0.305	2.742±0.266	2.736±0.325	0.025
	qTL44	44	CAFS834	4.64	3.85	29	2.669±0.296		2.822±0.303	0.023	

Phenotypic means (±standard error) are listed for each genotype at the marker with the peak LOD score for each trait. Analyzed phenotypic means for each allele and significant mean phenotypic differences between alleles are noted in the “Significance” column

QTL quantitative trait locus, LG linkage group, PVE phenotype variance (%), *f1* and *f2* father alleles, *m1* and *m2* mother parent alleles

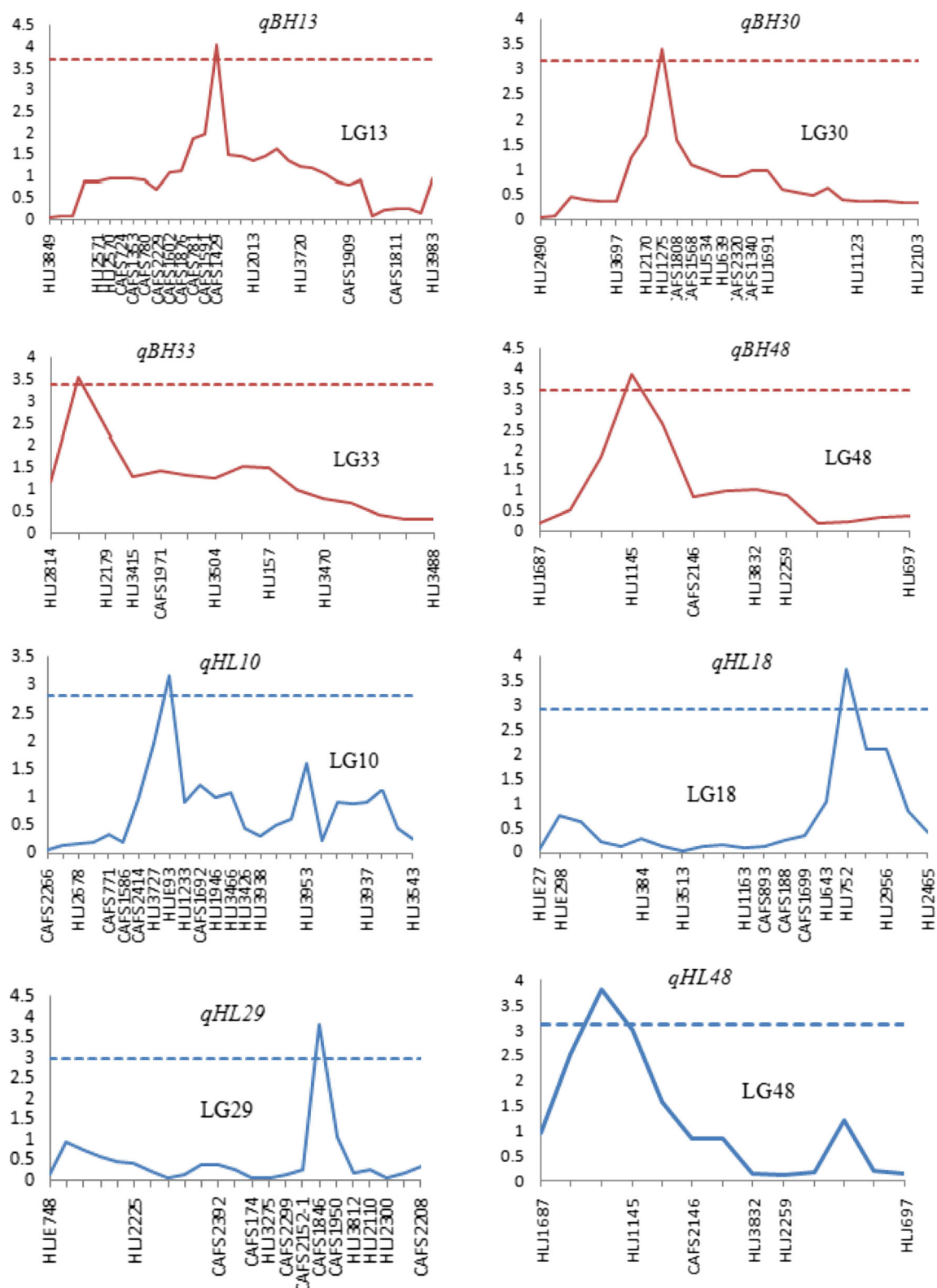


Fig. 3 The LOD curve of quantitative trait locus (QTL) detected for BH trait in 190 progenies of *C. carpio* L. The y axis shows LOD values of QTL and the x axis locates position of markers

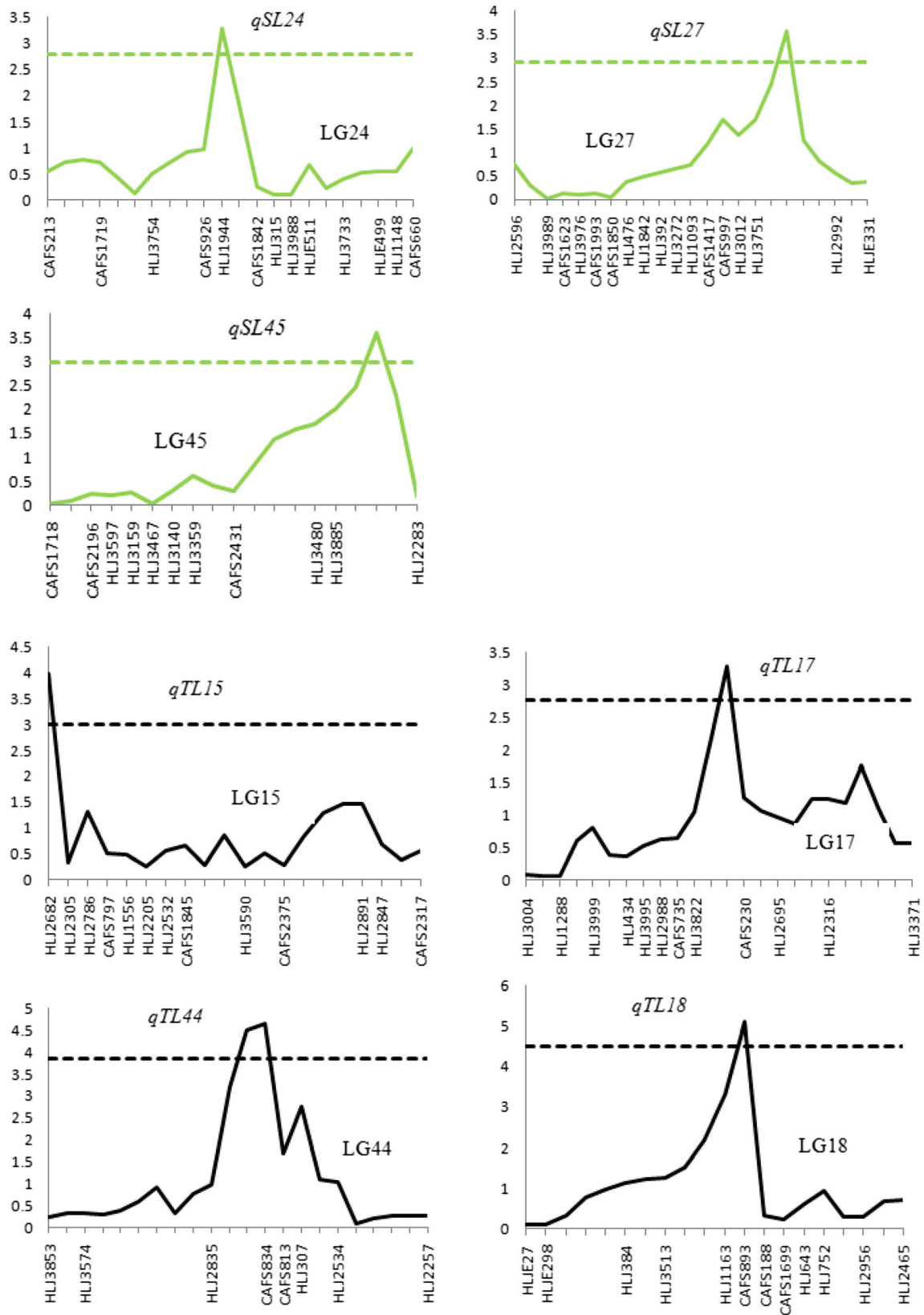


Fig. 3 (continued)

Discussion

Accuracy of QTLs depends on the sample size of progeny and density of molecular markers used for QTL analysis. In previous studies employing QTL mapping, a small number of individuals and lowest density genetic map had been analyzed for QTL detection in *C. carpio* L. Hence, a family with 190 progenies and a genetic linkage map with 627 molecular markers were utilized for QTL mapping in this study. The objective of this study was to locate the QTLs associated with swimming ability related traits. The genetic linkage map is a prerequisite tool for genetics and genomic research. In the present study, F1 progeny of common carp was generated to construct the genetic map. A genetic linkage map relying on 627 molecular markers was constructed (Zhang et al. 2012) and used for preliminary QTL mapping to locate the markers related with swimming ability related traits. As low marker density and a small number of samples influence the QTL accuracy, therefore, high marker density and increased number of samples were utilized in this study than earlier QTL studies on *C. carpio* (Zhang et al. 2007, 2008, 2010, 2013; Zheng et al. 2011; Wang et al. 2012; Laghari et al. 2013a, b).

In this study, we located a total of 15 QTLs related with BH, HL, SL, and TL on 13 linkage groups of genetic map. Out of these, four (*qBH13*, *qBH30*, *qBH33*, and *qBH48*) for BH, four (*qHL10*, *qHL18*, *qHL29*, and *qHL48*) for HL, three (*qSL24*, *qSL27*, and *qSL45*) for SL, and four (*qTL15*, *qTL17*, *qTL18*, and *qTL44*) for TL were detected. Wang et al. (2012) found eight QTLs related with TL on six LGs, and Zhang et al. (2013) located two QTLs related with TL on two LGs. While, there was not any overlap resulted when compared with Zhang et al. (2013).

LG18 was found with the QTLs associated with HL and TL at different locations, while LG48 was found with QTLs related with BH and HL traits at the same region, HLJ1145. All other LGs were found with QTLs of single trait. At some chromosomal regions, QTLs controlling more than one swimming ability traits were detected, suggesting either the linkage of two or more QTLs or the presences of a single QTL on each LG with pleiotropic effects. Overall, dissimilar locations were found for controlling all of four traits. Therefore, it could be concluded that all of these four traits are controlled by a different region of the chromosome and controlling gene would be different. More interesting is that *qBH48* and *qHL48* resulted overlap in the present study, and interval is also <20 cM. Therefore, this region needed more consideration for further gene prediction. Isolation of additional microsatellites and SNPs are still underway, to allow for the construction of a high-resolution linkage map for fine mapping of QTL and gene of interest.

It is expected that focusing on these markers, related with the traits of interest, will be fruitful for investigating genes. This is because the identification of QTLs influencing several

traits could increase the efficiency of MAS and will enhance genetic progress (Upadyayula et al. 2006).

ANOVA test resulted that all neighbored markers of QTL are significantly ($p < 0.05$) related with the traits. *qHL48*, *qSL45*, *qTL15*, *qTL18*, and *qTL44* explained phenotype variance of >20 % with significant levels of 0.047, 0.049, 0.037, 0.025, and 0.023, respectively. Involving locus in above QTLs could be considered as major genomic region controlling the respective traits. The genotypes at these marker loci may be useful for growth improvement through marker-assisted selection in this family. Identified markers on genetic map in this study can be a main source of discovering genes associated with swimming ability related traits in *C. carpio*.

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