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A first genetic linkage map of bluegill sunfish (*Lepomis macrochirus*) using AFLP markers

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Abstract Genetic linkage maps were constructed for bluegill sunfish, *Lepomis macrochirus*, using AFLP in a F_1 inter-population hybrid family based on a double-pseudo testcross strategy. Sixty-four primer combinations produced 4,010 loci, of which 222 maternal loci and 216 paternal loci segregated at a 1:1 Mendelian ratio, respectively. The female and male framework maps consisted of 176 and 177 markers ordered into 31 and 33 genetic linkage groups, spanning 1628.2 and 1525.3 cM, with an average marker spacing of 10.71 and 10.59 cM, respectively. Genome coverage was estimated to be 69.5 and 69.3% for the female and male framework maps, respectively. On the maternal genetic linkage map, the maximum length and marker number of the linkage groups were 122.9 cM and 14, respectively. For the paternal map, the maximum length and marker number of the linkage groups were 345.3 cM and 19, respectively, which were much greater than those on the maternal genetic linkage map. The other genetic linkage map parameters of the paternal genetic linkage map were similar to those in the maternal genetic linkage map. For both the female and male maps, the number of linkage groups was greater than the haploid chromosome number of bluegill ($2n = 48$), indicating some linkage groups may distribute on the same chromosome. This genetic linkage mapping is the first step toward to the QTL mapping of traits important to cultured breeding in bluegill.

Keywords AFLP · Genetic linkage map · Bluegill sunfish · *Lepomis macrochirus* · Double-pseudo testcross strategy

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Introduction

The bluegill sunfish, *Lepomis macrochirus*, is a freshwater fish species native to North America and distributed widely in rivers, ponds and lakes. This species has already been introduced into other countries, such as Japan and Korea (Kouichi et al. 2006). Bluegill sunfish have increasingly become an economically important fish because of both the perspective of their developing use in aquaculture and their recreational value in North America. In some states like Ohio and Michigan, bluegill has been listed as one of the top three culture species of fish because of their desirable characteristics for production and the demand for them in the marketplace (Lewis and Heidinger 1978; McLarney 1987; Ehlinger 1989). However, reports of slow and variable growth from commercial producers of bluegill have heightened the need for enhancing growth and reducing grow-out time. The prolific nature and precocious maturation of the bluegill have long been recognized as the cause of over-crowding and stunting in culture situations. One recent study showed that bluegill males grow twice as fast as females (Hayward and Wang 2006). Consequently, much interest has been generated concerning the development of monosex male populations and fast-growing strains through selective breeding. As part of the effort to enhance aquaculture production of bluegill, the Ohio State University has undertaken an O'GIFT (Ohio Genetic Improvement of Farmed-fish Traits) program to improve aquaculture production traits for bluegill sunfish and other species through selective breeding.

Genetic linkage maps have become important tools in many areas related to genetic research and have been constructed for several aquaculture species (Kocher et al. 1998; Young et al. 1998; Lundin et al. 1999; Sakamoto et al. 2000; Agresti et al. 2000; Waldbieser et al. 2001; Liu et al. 2003; Sun and Liang 2004; Zimmerman et al. 2005). Furthermore, genetic maps and related research could be applied to MAS (marker-assisted selection) and genetic improvement programs in the future.

AFLP (amplified fragment length polymorphism) can produce a large number of polymorphic markers without any prior information of DNA sequences for the organism (Vos et al. 1995). Initial genetic linkage maps have been successfully constructed for several fish species mainly relying on AFLP markers (Coimbra et al. 2003; Poompuang and Na-Nakorn 2004; Agresti et al. 2000; Felip et al. 2005).

Genetic linkage mapping could provide the basis for detection of important commercial traits, such as growth and other quantitative trait loci (QTL), and determination of the sex determination mechanism for a bluegill breeding program. Based on a fine genetic linkage map, we expect to apply QTL mapping to detect the distribution of interested QTL that are associated with growth. Although several SSR (simple sequence repeat) loci in bluegill are available (Neff et al. 1999; Neff 2001), it is not feasible to construct an elementary saturated genetic linkage map using these limited SSR loci. To date, no preliminary genetic linkage map of DNA markers has been constructed in bluegill sunfish.

In this study, a single-pair parent family of bluegill was employed in the genetic linkage mapping of AFLP markers using a pseudo-testcross strategy (Grattapaglia and Sederoff 1994). Based on the differences existing between paternal and maternal genetic linkage maps, we discussed the possible sex chromosome type and sex determination mechanism of bluegill sunfish.

Materials and methods

Mapping population

An inter-population hybrid family was used in this study as the mapping population. The female parent was selected from a group of fish that was derived from a wild population in northern Ohio in 2004. The male parent was selected from a population caught from a lake in southern Ohio in 2003. This pair of parents were fin-clipped and placed into an isolated 1 m^3 round tank with artificial nests for spawning in October 2006 to produce the mapping population. One hundred F_1 juvenile progeny (2–3 cm in length) from this family were randomly sampled after depriving feeding for 6 h and stored at −20°C for DNA extraction. DNA samples from 90 juveniles and 2 parents were involved in the linkage analysis.

Genomic DNA preparation

DNA used in genetic linkage mapping was extracted from whole juveniles and the fin clips of their parents. For each specimen, tissue was digested in 100 mM Tris–HCl (pH 8.0), 50 mM EDTA (pH 8.0), with a final concentration of 0.05% SDS and 300 μg/ml proteinase K. After protein digestion, ammonium acetate was added to achieve a final concentration of 1.75 M. The solution was well shaken and put on ice for 5 min, then centrifuged for 6 min at 12,000 r/min at 10°C. Clear supernatant fluid was carefully transferred to another centrifuge tube, and the same volumes of isopropyl alcohol and 5 μl POLYACRYL CARRIER (Molecular Research Center, Inc) were added and mixed well. The DNA solution was centrifuged at 12,000 r/min at 4°C for 30 min to precipitate DNA. Isolated DNA was rinsed twice using 70% alcohol, dried and resuspended with ddH_2O.

AFLP procedure, band score and nomenclature

The AFLP procedure closely followed the methods of Vos et al. (1995) with a slight modification. Genomic DNA (200–250 ng) was first digested with *Eco*R I and *Mse* I in a double enzyme digestion buffer system (Promega) before ligating restriction site-specific adapters. Adapter-specific primers (Table 1) with a single selective base were used in pre-amplification, the product of which was diluted 20-fold with 0.1 TE (Tris–HCl, pH 8.0, EDTA, pH 8.0). Selective PCR was conducted using primers with two additional selective bases each (Table 1). Amplified fragments were separated using 5% denatured (7.0 M urea) acrylamide gel with DNA ladder (Promega G2101) and visualized using silver staining.

The AFLP markers for bluegill were labeled with species name, selective primer combinations and the size of the bands. The first two letters were the abbreviation of the scientific name of bluegill (for example, "lm" represents *Lepomis macrochirus*), followed by the primer combination (Table 2), and the size of the bands preceded with a hyphen. For instance, lm35-156 means the AFLP marker of bluegill was produced from selective combination 35 (E3-ACA and M5-CTA, Table 2) with a 156 bp size.

Generally, the AFLP are accepted as the dominant markers, and therefore, the polymorphism among bluegill resulted from the presence/absence of the restriction enzyme-specific recognized locus or the polymorphism in the flanking sequence. In a few cases, however, if the polymorphism existed between two restriction enzyme-recognized loci, and this part of the DNA fragment could be amplified, then the co-dominant segregating pattern

Table 1 The adapters, common primers and selective primers applied in this study

Primer	Primer sequence (from 5′ to 3′ direction)
EcoR I adapter1	CTC GTA GAC TGC GTA CC
EcoR I adapter2	AAT TGG TAC GCA GTC
Mse I adapter1	GAC GAT GAG TCC TGA G
Mse I adapter2	TAC TCA GGA CTC AT
Mse I common primer	GAT GAG TCC TGA GTA AC
EcoR I common primer	GAC TGC GTA CCA ATT CA
E1	GAC TGC GTA CCA ATT CAAC
E2	GAC TGC GTA CCA ATT CAAG
E3	GAC TGC GTA CCA ATT CACA
E4	GAC TGC GTA CCA ATT CACT
E5	GAC TGC GTA CCA ATT CAGA
E6	GAC TGC GTA CCA ATT CAGC
E7	GAC TGC GTA CCA ATT CATC
E8	GAC TGC GTA CCA ATT CATG
M1	GAT GAG TCC TGA GTA ACAT
M2	GAT GAG TCC TGA GTA ACAA
M3	GAT GAG TCC TGA GTA ACCA
M4	GAT GAG TCC TGA GTA ACCT
M5	GAT GAG TCC TGA GTA ACTA
M6	GAT GAG TCC TGA GTA ACTT
M7	GAT GAG TCC TGA GTA ACGA
M8	GAT GAG TCC TGA GTA ACGC

Table 2 AFLP primer combinations used in the linkage group analysis, and number of segregating loci produced by each primer combination

	E1-AAC	E2-AAG	E3-ACA	E4-ACT	E5-AGA	E6-AGC	E7-ATC	E8-ATG	Total
M1-CAT	2	7	4	8	2	15	9	11	58
M2-CAA	6	7	9	14	4	13	9	7	69
M3-CCA	4	9	11	7	9	8	4	7	59
M4-CCT	7	10	4	9	8	8	6	5	57
M5-CTA	6	4	6	9	10	9	9	5	58
M6-CTT	8	8	7	13	15	5	10	10	76
M7-CGA	2	3	2	3	4	5	5	3	27
M8-CGC	4	1	5	7	6	3	4	4	34
									438

could be observed from the AFLP-PCR products. In this case, maternal and paternal contributions were "absent" and "present" in two band positions, respectively, and the progenies shared only one of these two bands from the parents. Thus, the two bands detected in one of parents were recorded as alleles of one locus instead of two independent dominant loci. This type of co-dominant marker was suffixed with a letter "C" behind the band size.

Linkage analysis

The 64 primer combinations used in linkage analysis are listed in Table 2. Mapping data were obtained by visual scoring. Only the clear bands that were present in either the maternal or the paternal groups and segregated in the progeny were scored. A Chi-square test was performed to identify distorted deviation from a 1:1 Mendelian ratio at $P < 0.01$ level. After discarding the distorted deviation loci, maternal and paternal data sets were used to construct their linkage groups, respectively. Linkage groups were analyzed using MAPMAKER/EXP3.0 (Whitehead Institute, ftp://ftp-genome.wi.mit.edu/distribution/software/mapmaker3), and linkage group drawings were performed with Mapdraw software (Liu and Meng 2003). An LOD score of 4.0 and a maximum distance of 50 cM were set as the linkage group threshold for grouping markers at the initial analysis, and the groups with less than eight markers were analyzed using multipoint mapping function with the following successive commands: COMPARE, ORDER and MAP. The groups with more than eight markers were first subjected to the SUGGEST SUBSET command to select the most informative markers, and then the COMPARE, TRY and MAP commands were used successively. Incorporation of unlinked markers that did not map into previous groups was attempted using the TRY command under less stringent conditions (LOD = 3.0 and a maximum distance of 50.0). All the marker orders were verified by the RIPPLE command.

Estimation of genome size

The genome size and map coverage were estimated based on the mapped markers. Two approaches were used to assess the estimated genome size (*Ge*) of bluegill. *Ge*1, the estimated genome length, was calculated by adding 2*s* to the length of each linkage group to account for chromosome ends, where *s* is the average spacing between markers (Fishman et al. 2001). *Ge*2, an estimated genome length, was calculated by multiplying the length of each linkage group by $(m + 1)/(m - 1)$, where m is the number of framework markers in each group (Chakravarti et al. 1991). The average of the two estimates was used as the estimated genome length (*Ge*) for the bluegill. Observed genome lengths (*Goa*) were calculated as the total length considering all markers. The observed genome coverage was determined by *Goa*/*Ge*.

Results

Segregating analysis

Those bands that were present in one parent and absent in the other parent, and segregating in the progeny, were scored for linkage analysis. Goodness-of-fit of observed-to-expected allelic ratios was analyzed using Chi-square test, and markers that did not significantly depart from Mendelian ratios at $\alpha = 0.01$ level were used in the linkage analysis. Markers that segregated according to a 1:1 segregation pattern were involved in the genetic linkage mapping of maternity and paternity maps. Sixty-four AFLP primer combinations produced 4,010 AFLP loci. In total, 438 loci (10.92%) showed 1:1 segregation ratio. The numbers of segregating loci for each primer pair ranged from 1 to 15 (Table 2). Of them, nine co-dominant loci (four were from maternity and five were from paternity), 222 maternal loci and 216 paternal loci segregated at 1:1 ratio (Table 2). After sequential Bonferroni

correction, only 6 (2.7%) and 4 loci (1.9%) deviated significantly from 1:1 ratio in maternal and paternal data sets, respectively (Table 3).

Genetic linkage maps

The genetic linkage maps were constructed for female and male, respectively. The female genetic linkage map consisted of 192 markers including 4 co-dominant markers. A total of 176 markers were assigned to 31 linkage groups (more than three markers), which covered 1628.2 cM in length with an average interval of 10.71 cM. The length of the linkage groups ranged from 10.5 to 122.9 cM, and the number of markers per group varied from 3 to 14 (Table 3). The remaining 16 markers were grouped as 8 doublets.

For the paternal map, 177 linked markers including 3 co-dominant markers were distributed onto 33 linkage groups, which covered 1525.3 cM in length with an average interval of 10.59 cM (Table 3; Fig. 2). The maximum length and maximum marker number of male linkage groups were 345.3 cM and 19, respectively.

The AFLP markers were not evenly distributed in the genetic linkage maps. By visual observation, two clusters phenomena were found on two linkage groups (LG8 and LG11, Fig. 1) of the female map; however, the number of marker clusters on the male map was slightly more than those of the female map. Three clusters were observed on three linkage groups (LG11, LG28 and LG29, Fig. 2). Additionally, no visual correlation between the size of the linkage group and the number of AFLP markers on the linkage groups was observed.

The genome lengths estimated by the two methods were similar, being 2393.6 and 2292.3 cM in female, while 2193.2 and 2208.9 cM in male. The expected genome sizes for the female and male were 2343.0 and 2201.1 cM, respectively. Based on the expected

Table 3 Summary of segregating markers and linkage groups of bluegill sunfish (*Lepomis macrochirus*)

	Maternal	Paternal
Total number of markers scored	222	216
Distorted segregation loci	6	4
Marker number in linkage analysis	216	212
Number of markers mapped (including doublets)	192	191
Unlinked marker number	24	21
Linkage groups	31	33
Number of doublets	8	7
Average markers number per linkage group	5.9	5.4
Minimum length of linkage group (cM)	10.5	2.3
Maximum length of linkage group (cM)	122.9	345.3
Minimum markers number per group	3	3
Maximum markers number per group	14	19
Average marker interval (cM)	10.71	10.59
Observed genome length (*Goa*) (cM)	1628.2	1525.3
Estimated genome length 1 (*Ge1*) (cM)	2393.6	2193.2
Estimated genome length 2 (*Ge2*) (cM)	2292.3	2208.2
Estimated genome length (*Ge*) (cM)	2343.0	2201.1
Genome coverage (%)	69.5	69.3

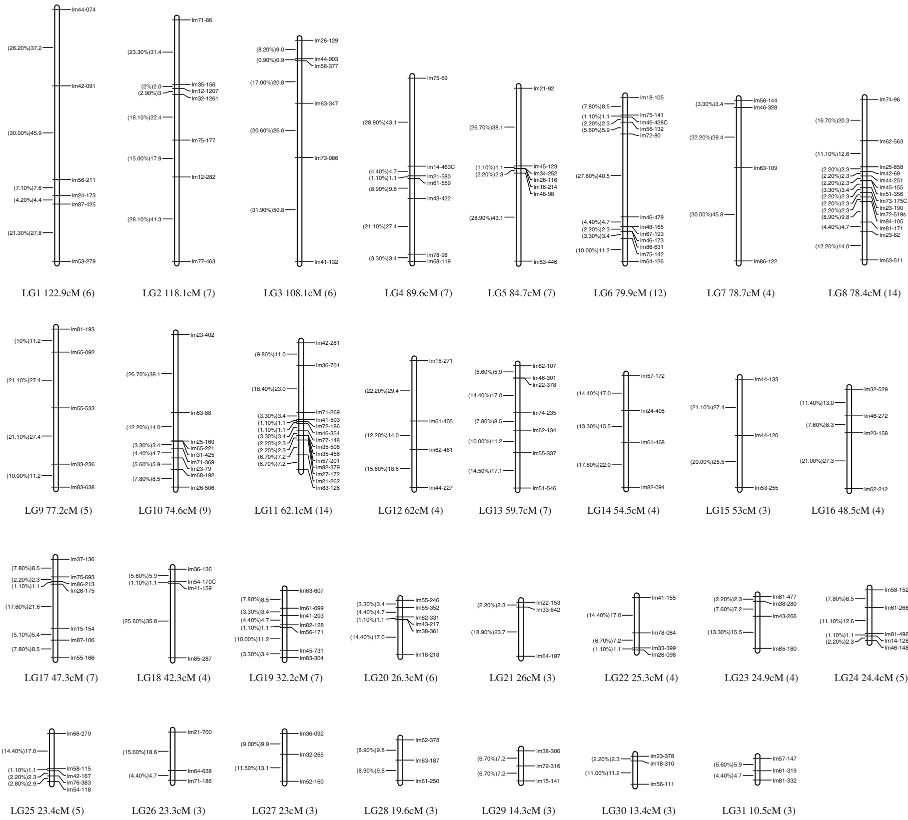

Fig. 1 Female linkage groups of AFLP markers of bluegill sunfish (*Lepomis macrochirus*). Suffixes with *C* behind the band size indicate co-dominant markers. The marker names are shown to the *right* of linkage groups, and the percentage of refraction ratio (%, *in parenthesis*) and marker spaces (cM) are shown to the *left* of the linkage groups. Linkage groups were arranged according to its length (cM) and named as LG with a suffix taxis number at the *bottom* of linkage groups, the *number in the parentheses* was the linked markers number in this LG

genome lengths, the genome coverage of the female and male framework genetic linkage maps were 69.5 and 69.3%, respectively.

Discussion

This study resulted in the first maternal and paternal genetic linkage maps of AFLP markers in bluegill sunfish based on a pseudo-testcross strategy. This strategy originated from eucalyptus (*Eucalyptus grandis*) genetic mapping of RAPD markers (Grattapaglia and Sederoff 1994) and has been used in genetic mapping of many aquatic animals (Li et al. 2003; Perez et al. 2004; Yue et al. 2004; Wang et al. 2006). In the present study, a double-pseudo testcross strategy was used in the genetic linkage mapping of paternity and maternity of bluegill. The efficiency of this strategy depends on the genetic heterogeneity between two parents. It was more suitable to construct genetic linkage mapping between allied-inter-species or different populations with obvious genetic variety, because the more

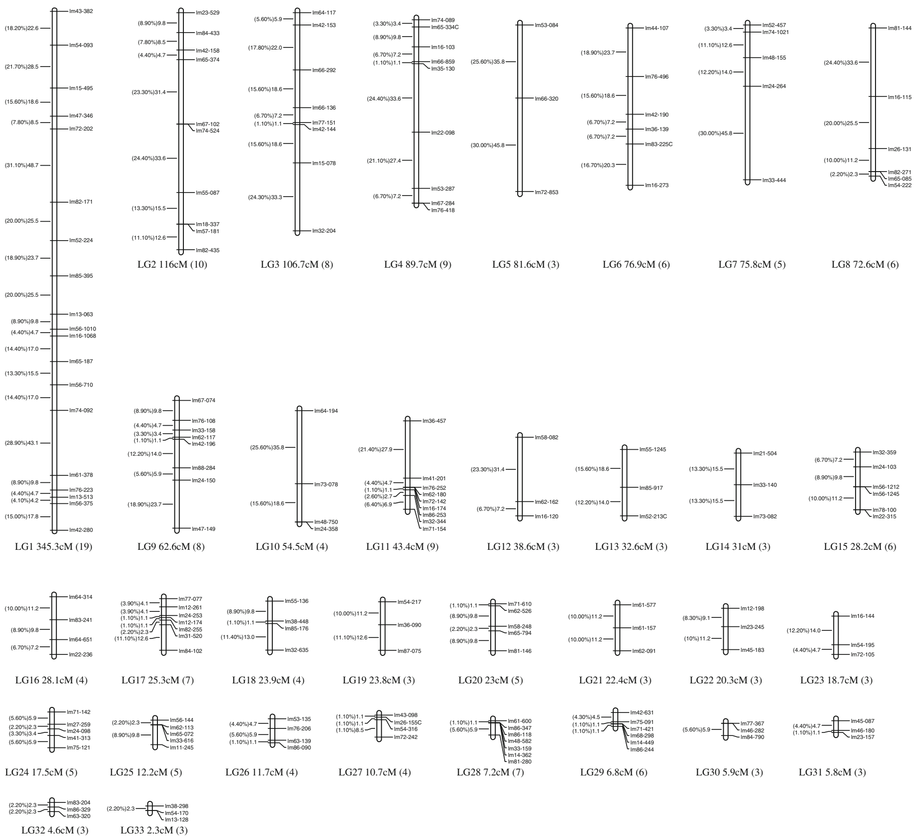

Fig. 2 Male linkage groups of AFLP markers of bluegill sunfish (*Lepomis macrochirus*). The suffixes with *C* behind band the size indicate co-dominant markers. The marker names are shown to the *right* of the linkage groups. The percentages of refraction ratio (%, *in parenthesis*) and marker spaces (cM) are shown to the *left* of the linkage groups. Linkage groups were arranged according to its length (cM) and named as LG with a suffix taxis number at the *bottom* of linkage groups, the *number in the parentheses* was the linked markers number in this LG

heterozygous the parents were, the more chance the segregating loci in progeny would be detected. The parent fish in this mapping family were from distinct geographical populations, which might partly increase the segregating loci number involved in the genetic linkage mapping. Dominant anonymous markers, such as AFLP and RAPD, cannot discriminate dominant homozygosity and heterozygosity just according to the "band" in the electrophoresis pattern. However, this type of shortage could be avoided in the linkage mapping approach that is based on a pseudo-testcross strategy, since only a 1:1 ratio segregant loci could be recorded in the linkage mapping, and the "band" in the electrophoresis pattern of progeny would only correspond to heterozygosity and not to dominant homozygosity.

Because of its ability to identify a large number of polymorphic bands without any prior knowledge of DNA sequences in the organism, the AFLP technique is generally accepted as a very powerful and efficient tool in the preliminary genetic linkage mapping in aquatic animals (Liu et al. 2003; Li et al. 2003, 2005; Perez et al. 2004). Compared with the other

markers, such as SSRs and RAPDs, the assay efficiency index of AFLP is about tenfold higher (Pejic et al. 1998), so it has the potential to create high-resolution maps around target loci, which could facilitate gene detection and isolation (Li et al. 2003). Although the AFLP markers are not easy to transfer among different populations and families, which would without doubt limit the further development and application of the maps, AFLP fragments correspond to unique positions in the genome. Therefore, these loci could be expected to be used as landmarks in future genetic and physical mapping with appropriate isolation and sequencing.

Of all the 438 segregating loci scored, only 10 (2.28%) loci showed distorted segregation at the $P < 0.01$ level. Generally, including the progeny population size, the segregation distortion could be caused by many factors, such as genetic drive, ultra-selfish DNA elements, sex chromosome drive and lethal effects caused by recessive homozygote in the juvenile period. For example, in the Pacific oyster (*Crassostrea gigas*), selection acted early in the life cycle against homozygotes for recessive deleterious mutations, which increased distortion of segregation ratio in the following genetic linkage mapping process (Lyttle 1991; Hubert and Hedgecock 2004). Distorted segregation may affect the organism's fitness directly or indirectly. To eliminate the potential effects caused by segregating distortion in older progeny, we selected juveniles for the linkage analysis of bluegill. Hubert and Hedgecock (2004) applied a similar strategy to reduce the segregating distorters in Pacific oyster (*Crossostrea gigas*) linkage analysis using SSR markers.

The numbers of linkage groups were 31 and 33 for the female and male maps (not including the doublets), respectively, which are higher than the haploid chromosome number of bluegill ($n = 24$, Roberts 1964). For a complete genetic linkage map, the number of male or female linkage groups is supposed to be equal to the haploid chromosome number. It is obvious that some linkage groups belong to the same chromosome in this study. Two genetic linkage maps of channel catfish (*Ictalurus punctatus*) using AFLP and SSR markers also showed this difference existing between chromosome number and linkage group number (Liu et al. 2003; Waldbieser et al. 2001). To fill the gap existing among some linkage groups, more markers, either dominant such as AFLP or co-dominant such as SSR, need to be added, which could ultimately make the number of linkage groups correspond to the chromosome number. Because of the cluster phenomena of AFLP markers in linkage analysis and from the aspect of improving genetic linkage mapping efficiency, it would be wiser to add some co-dominant markers to fill the gaps existing among some linkage groups.

It is well known that AFLP markers in linkage analysis tend to cluster together, and the level of clustering increases with the marker number (Liu et al. 2003). Two female linkage groups and three male linkage groups presented slight clusters in the maternal and paternal genetic linkage maps of bluegill, respectively, while the other markers in the other linkage groups showed an even distribution. The tendency of AFLP markers to cluster in one region of a linkage group may be attributed to the following: some regions on the genomic DNA owned abundant restriction enzyme digestion loci and displayed a high exchange fraction during meiosis. Interestingly, highly clustered AFLP markers were found around the centromere region (Alonso-Blanco et al. 1998), suggesting some relationship between cluster region on linkage groups and the chromosome region. The relationship of the linkage groups and the chromosomes of bluegill sunfish has not been reported prior to this study; thus, our results may indicate that many of the clustered AFLP markers could be at a position close to centromeres as well as at the end of chromosomes. In the genetic linkage maps of other species, including rainbow trout (Young et al. 1998), and tilapia (Agresti et al. 2000), the AFLP markers in linkage groups also showed clustering. Nevertheless,

clustered AFLP markers can inhibit the effective use of genetic linkage mapping. Adding some other type of markers, such as SSR, could make the marker distribution more even.

In the present study, a preliminary genetic linkage map was constructed in *L. macrochirus*, a species that was relatively lacking in genetic information, using the AFLP technique. However, it is still necessary to construct a moderately or highly saturated genetic linkage map for the successive QTL mapping and marker-assisted selections. Concerning the universal use of genetic linkage maps, co-dominant markers, including SSR, SCARs (sequence-characterized amplified regions), and SNP (single nucleotide polymorphisms) should be placed on this map to improve its applicability as a tool in a genetic, selective breeding program. In addition, there is a need of confirming the correspondence relationship between linkage groups and chromosomes for the QTL mapping and physical map construction in the future.

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References

Agresti JJ, Seki S, Cnaani A et al (2000) Breeding new strains of tilapia: development of an artificial center of origin and linkage map based on AFLP and microsatellite loci. Aquaculture 185:43–56

Alonso-Blanco C, Peeters AJM, Koornneef M et al (1998) Development of an AFLP based linkage map of L*er*, Col and Cvi *Arabidopsis thaliana* ecotypes and construction parative karyology of three species of North American catfishes of a *Ler/Cvi* recombinant inbred line population. Plant J 14:259–271

Chakravarti A, Lasher LK, Reefer JE (1991) A maximum likelihood method for estimating genome length using genetic linkage data. Genetics 128:175–182

Coimbra RM, Kobayashi K, Koretsugu S et al (2003) A genetic linkage map of the Japanese flounder, *Paralichthys olivaceus*. Aquaculture 220:203–218

Ehlinger T (1989) Learning and individual variation in bluegill foraging: habitat-specific techniques. Animal Behavior 38:643–658

Felip A, Young WP, Wheeler PA et al (2005) An AFLP-based approach for the identification of sex-linked markers in rainbow trout (*Oncrohynchus mykiss*). Aquaculture 247:35–43

Fishman L, Kelly AJ, Morgan E et al (2001) A genetic map in the *Mimulus guttatus* species complex reveals transmission ratio distortion due to heterospecific interactions. Genetics 159:1701–1716

Grattapaglia D, Sederoff R (1994) Genetic linkage maps of *Eucalyptus grandis* and *Eucalyptus urophylla* using a pseudo-testcross mapping strategy and RAPD markers. Genetics 137:1121–1137

Hayward RS, Wang HP (2006) Rearing male bluegills indoors may be advantageous for producing food-size sunfish. J World Aquac Soc 37:496–508

Hubert S, Hedgecock D (2004) Linkage maps of microsatellite DNA markers for the Pacific oyster. Genetics 168:351–362

Kocher TD, Lee WJ, Sobolewska H et al (1998) A genetic linkage map of a cichlid fish, the tilapia (*Orechromsi niloticus*). Genetics 148:1225–1232

Kouichi K, Ryuji Y, Osamu K et al (2006) Origin and dispersal of bluegill sunfish, *Lepomis macrochirus*, in Japan and Korea. Mol Ecol 15:613–621

Lewis WM, Heidinger RC (1978) Use of hybrids in the management of small impoundments. In: Novinger GD, Dillard JC (eds) New approaches for the management of small impoundments North Central Division. American Fisheries Society, Special Publication 5, Bethesda, pp 104–108

Li YT, Byrne K, Miggiano E et al (2003) Genetic mapping of the kuruma prawn *Penaeus japonicus* using AFLP markers. Aquaculture 219:143–156

Li L, Xiang JH, Liu X et al (2005) Construction of AFLP-based genetic linkage map for Zhikong scallop, *Chlamys farreri* Jones et Preston and mapping of sex-linked markers. Aquaculture 245:63–73

Liu RH, Meng JL (2003) Mapdraw: a Microsoft excel macro for drawing genetic linkage maps based on given genetic linkage data. Heraditas 25:317–321
Liu ZJ, Karsi A, Li P et al (2003) An AFLP-based genetic linkage map of channel catfish (*Ictalurus punctatus*) constructed by using an interspecific hybrid resource family. Genetics 165:687–694
Lundin M, Mikkelsen B, Moran P et al (1999) Cosmid clones from Atlantic salmon: physical genome mapping. Aquaculture 173:59–64
Lyttle TW (1991) Segregation distorters. Annu Rev Genet 25:511–557
McLarney W (1987) Characteristics of important cultured animals summarized. In: The freshwater aquaculture book. Hartley and Marks, Point Roberts, Washington, pp 485–508
Neff BD (2001) Genetic paternity analysis and breeding success in bluegill sunfish (*Lepomis macrochirus*). J Hered 92:111–119
Neff BD, Fu P, Gross MR (1999) Microsatellite evolution in sunfish (Centrarchidae). Can J Fish Aquat Sci 56:1198–1205
Pejic I, Ajmone-Marsan P, Morgante M et al (1998) Comparative analysis of genetic similarity among maize inbred lines detected by RFLP, RAPD, SSR, and AFLPs. Theor Appl Genet 97:1248–1255
Perez F, Erazo C, Zhinaula M et al (2004) A sex-specific linkage map of white shrimp *Penaeus* (*Litopenaeus*) *vannamei* based on AFLP markers. Aquaculture 242:105–118
Poompuang S, Na-Nakorn U (2004) A preliminary genetic map of walking catfish (*Clarias macrocephalus*). Aquaculture 232:195–203
Roberts FJ (1964) A chromosome study of twenty species of Centrarchidae. J Morph 115:401–408
Sakamoto T, Danzmann RG, Gharbi K et al (2000) A microsatellite linkage map of rainbow trout (*Oncorhynchus mykiss*) characterized by large sex-specific differences in recombination rates. Genetics 155:1331–1345
Sun XW, Liang LQ (2004) A genetic linkage map of common carp (*Cyprinus carpio* L.) and mapping of a locus associated with cold tolerance. Aquaculture 238:165–172
Vos P, Hogers R, Bleeker M et al (1995) AFLP: a new technique for DNA fingerprinting. Nucleic Acid Res 23:4407–4414
Waldbieser GC, Bosworth BG, Nonneman DJ et al (2001) A microsatellite-based genetic linkage map for channel catfish, *Ictalurus punctatus*. Genetics 158:727–734
Wang WJ, Kong J, Dong SR et al (2006) Genetic mapping of the Chinese shrimp *Fenneropenaeus chinensis* using AFLP markers. Acta Zoologica Sinica 52:575–584
Young WP, Wheeler PA, Coryell VH et al (1998) A detail linkage map of rainbow trout produced using doubled haploids. Genetics 148:839–850
Yue ZQ, Wang WJ, Kong J et al (2004) Construction of genetic linkage maps of *Fenneropenaeus chinensis* based on "double pseudo-testcross" strategy and AFLP markers. High Technol Lett 5:88–93
Zimmerman AM, Wheeler PA, Ristow SS et al (2005) Composite interval mapping reveals three QTL associated with pyloric caeca number in rainbow trout, *Oncorhynchus mykiss*. Aquaculture 247:85–95