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An AFLP-Based Genetic Linkage Map of Channel Catfish (*Ictalurus punctatus*) Constructed by Using an Interspecific Hybrid Resource Family

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ABSTRACT

Catfish is the major aquaculture species in the United States. The hybrid catfish produced by crossing channel catfish females with blue catfish males exhibit a number of desirable production traits, but their mass production has been difficult. To introduce desirable genes from blue catfish into channel catfish through introgression, a genetic linkage map is helpful. In this project, a genetic linkage map was constructed using amplified fragment length polymorphism (AFLP). A total of 607 AFLP markers were analyzed using 65 primer combinations and an interspecific backcross resource family. A total of 418 AFLP markers were assigned to 44 linkage groups. Among the remaining 189 markers, 101 were not used because of significant segregation distortion, 29 were unlinked, and 59 were eliminated because they span very large distances. The 418 AFLP markers covered 1593 cM Kosambi. The AFLP markers showed a high level of clustering that appears to be related to certain primer combinations. This linkage map will serve as the basis for mapping a greater number of markers to provide a map with high enough resolution for it to be useful for selective breeding programs using introgression.

CATFISHES are an ancient group of fish including 17 families and containing numerous species found everywhere except in the Arctic and Antarctic regions (Smitherman *et al.* 1978). The channel catfish is the most economically important catfish species in the United States with an annual production of 269,000 metric tons, which accounts for >60% of all U.S. aquaculture production (U.S. Department of Agriculture 2001). Blue catfish is also economically important because the hybrid catfish produced by channel catfish female × blue catfish male exhibit superior performance traits for aquaculture (Dunham *et al.* 1990).

Much of the genetic research effort has been on evaluation and selection of performance traits through crossbreeding and interspecific hybridization (Bondari 1983, 1984; Dunham and Smitherman 1983a,b; Hallerman *et al.* 1986; Dunham *et al.* 1987, 1993; Wolters and Johnson 1994, 1995; Padi 1995; Wolters *et al.* 1996; Dunham and Liu 2002). Heritabilities and genetic correlation for several important performance traits have been calculated (Patino 1986; Dunham and Argue 1998). To increase the efficiency of selection, particularly for complex traits such as disease resistance, feed conversion efficiency, and processing yields, trait-linked DNA markers are needed (Waldbieser *et al.* 1998). Molecular markers correlated with genetic loci controlling economic traits are needed to expedite development of superior brood stocks.

Research on catfish genomics is developing rapidly. Both channel catfish and blue catfish have 29 pairs of chromosomes (Wolters *et al.* 1981; LeGrande *et al.* 1984) with a genome size of $\sim 1 \times 10^9$ bp (Tiersch *et al.* 1990; Tiersch and Goudie 1993). Several highly repetitive to moderately repetitive elements have been characterized in channel catfish (Liu *et al.* 1998b, 1999d; Kim *et al.* 2000). Before this study was conducted, only a few genes had been mapped in catfish and several linkage groups were established using allozyme markers (Liu *et al.* 1992).

Linkage maps have become powerful research tools in genetic studies of many organisms (Rohrer *et al.* 1996; Kappes *et al.* 1997; Groenen *et al.* 2000), including several aquaculture species (Kocher *et al.* 1998; Robison *et al.* 2001; Waldbieser *et al.* 2001). A fine linkage map is necessary to efficiently carry out mapping for quantitative trait loci (QTL) to complement marker-assisted selection and to conduct comparative genome mapping (Lander and Botstein 1989). However, a fine linkage map requires large numbers of molecular markers. In channel catfish, several hundred microsatellite markers have been developed (Waldbieser and Bosworth 1997; Liu *et al.* 1999a,b; Tan *et al.* 1999) and 262 of them have been mapped (Waldbieser *et al.* 2001).

Amplified fragment length polymorphism (AFLP) is a PCR-based technique that is capable of producing multilocus and reliable fingerprints of genomes (Vos *et al.* 1995). It shows a greater level of polymorphism and informativeness than any other marker system in the organisms examined to date (Mackill *et al.* 1996).

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AFLP-based linkage maps have been constructed for various organisms (Becker *et al.* 1995; Alonso-Blanco *et al.* 1998; Hawthorne 2001; Tan *et al.* 2001) including those of tilapia, rainbow trout, and the Medaka (Kocher *et al.* 1998; Naruse *et al.* 2000; Robison *et al.* 2001). Our previous research demonstrated that AFLP rate was low within channel catfish (Liu *et al.* 1998a, 1999c), defeating the efficiency of AFLP. To exploit the holistic AFLP markers, in this research interspecific resource families were produced by backcrossing the F_1 hybrids of channel catfish females and blue catfish males. Using the interspecific hybrid backcross population, we report here an AFLP-based genetic linkage map of channel catfish.

MATERIALS AND METHODS

Resource families: F_1 interspecific hybrid catfish were made by mating channel catfish females with blue catfish males. F_1 (channel × blue) hybrid catfish, channel catfish, and blue catfish were screened prior to the 1997 spawning season to determine which matings of these parents were most informative. In the spawning season of 1997, backcross families were made by mating the F_1 fish with either channel catfish (channel catfish backcross) or blue catfish (blue catfish backcross). Reciprocal backcrosses were made by using the F_1 fish as maternal or paternal parent. Eight backcross families were produced, four from channel catfish and four from blue catfish backcrossed with the heterozygous F_1. These families were reared in 1000-liter tanks until collection of blood samples for genotyping. Individuals that were sampled for genotyping were heat branded for future identification.

Genomic DNA: Blood samples (0.5–1 ml) were collected in a 1-ml syringe and immediately expelled into a 50-ml tube containing 20 ml of DNA extraction buffer (100 mm NaCl, 10 mm Tris, pH 8, 25 mm EDTA, 0.5% SDS, and freshly added proteinase K, 0.1 mg/ml), and DNA was isolated using standard protocols as previously described (Liu *et al.* 1998a). Briefly, the blood samples were incubated at 55° overnight and DNA was extracted twice with phenol and once with chloroform. DNA was precipitated by adding a half volume of 7.5 m ammonium acetate and two volumes of ethanol. DNA was collected mostly by spooling onto a micropipette tip or, in some cases, by brief centrifugation; washed twice with 70% ethanol; air dried; resuspended in TE buffer (10 mm Tris-HCl, 1 mm EDTA, pH 7.5); and quantified with a spectrophotometer.

AFLP analysis: AFLP analysis system I (catalog no. 10544-013) was purchased from Life Technologies (Bethesda, MD). Primer combinations were abbreviated in a matrix manner (Liu *et al.* 1998a) and are listed in Table 1. *Eco*RI primers were designated with a letter, from A to I, and *Mse*I primers were designated by a number, from 1 to 8. Primer combinations were designated by a letter plus a number with *Eco*RI primer first (*e.g.*, E-AAG/M-CAC primer combination was identified as B2). *Eco*RI primers A, B, C, F, and I were labeled with IR700, and *Eco*RI primers D, E, G, and H were labeled with IR800 fluorescent dyes (LI-COR, Lincoln, NE). Genomic DNA was digested completely with *Eco*RI and *Mse*I as described by the supplier (Life Technologies). All reactions were carried out in 96-well microtiter plates (International Corp., Mount Prospect, IL). Briefly, the following were added to a 96-well plate: 1 μl restriction reaction buffer, 1 μl (∼50 ng) genomic DNA, 0.4 μl *Eco*RI/*Mse*I restriction endonucleases, and 2.6 μl water. The reaction was gently mixed by brief centrifugation for 5 sec in a Beckman (Fullerton, CA) GS-15 using an S2096 rotor. The reaction was incubated for 2 hr at 37° and then inactivated at 70° for 5 min. Adaptors for *Eco*RI and *Mse*I (4.8 μl) were added to the restriction fragments by ligation using T4 DNA ligase (0.2 μl) for 2 hr at 20°. After ligation, 90 μl of Tris-EDTA buffer (pH 8.0) was added to dilute the reactions 10 times. A fraction (1 μl each) was removed to a fresh 96-well plate and the remaining product was stored for future use. To the new 96-well plate, the following was added: 8 μl preamp primer mix, 1 μl 10× PCR buffer from the AFLP kit, and 0.2 μl *Taq* DNA polymerase. The samples were mixed by brief centrifugation. Preamplification was performed for 20 cycles with temperatures as follows: 94° for 30 sec, 56° for 60 sec, and 72° for 60 sec. After preamplification, 2 μl of the preamplification products was transferred to a fresh 96-well plate containing 98 μl of Tris-EDTA buffer (pH 8.0), diluting the samples 50 times. Selective amplification reactions contained the following: 1 μl preamplified DNA, 0.3 μl (1 pmol/μl) labeled *Eco*RI primer, 1 μl *Mse*I primer (with dNTPs), 0.03 μl *Taq* polymerase, 0.6 μl 10× PCR buffer for AFLP, and 2.07 μl double-distilled water. The selection amplification was performed with a touch down program for 13 cycles: 94° for 30 sec, 65° for 30 sec, 72° for 60 sec with a 0.7° decrease of annealing temperature each cycle, followed by 23 cycles of amplification at 94° for 30 sec, 56° for 30 sec, and 72° for 60 sec.

AFLP genotyping: All AFLP products were analyzed by using the LI-COR automatic sequencers using both IR700 and IR800, as appropriate with labeled primers. After PCR, 3 μl of formamide dye was added to each reaction. The samples were heated to 92° for 3 min and 0.6 μl was loaded onto the gel. Page Plus concentrate gel mix (40%, E562-500 ml) was diluted to 5.5% using 1× TBE (AMRESCO, Solon, OH). All 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. Genotyping was conducted using IMAGE software (LI-COR) and the genotypes were transferred to Microsoft Excel spread sheets and imported to Mapmaker software for linkage analysis.

Nomenclature of AFLP markers: The catfish AFLP markers were named with information of the species, primer combination, and the size of the AFLP bands. The first two letters of the marker indicate the species (*e.g.*, Ip for *Ictalurus punctatus*), followed by primer combination, and the size of the AFLP band separated with a hyphen. For instance, AFLP marker IpE2-155 indicates the AFLP marker of *I. punctatus* was produced from primer combination E2 (Table 1) with a size of 155 bp.

Linkage analysis: Parents and 71 offspring were genotyped. Chi-square tests were performed to determine if the segregation ratio of presence/absence in backcross progeny was significantly different from the expected ratio of 1:1. Markers deviating from the expected ratio at the $P = 0.05$ level of significance were eliminated. A data matrix was constructed with 1 representing presence and 0 representing absence of AFLP bands. This data matrix was imported into Mapmaker/Exp version 3.0b (Lander *et al.* 1987). Initial grouping of markers was performed using GROUP command at LOD score of 3.0 and maximum recombination fraction of 0.3. Then, the most informative subset in each linkage group was determined using the SUGGEST SUBSET command. The ORDER and COMPARE commands were employed to determine the most probable marker order within each linkage group. The maximum number of the most informative markers in each linkage group (LG) was kept at eight for the COMPARE procedure

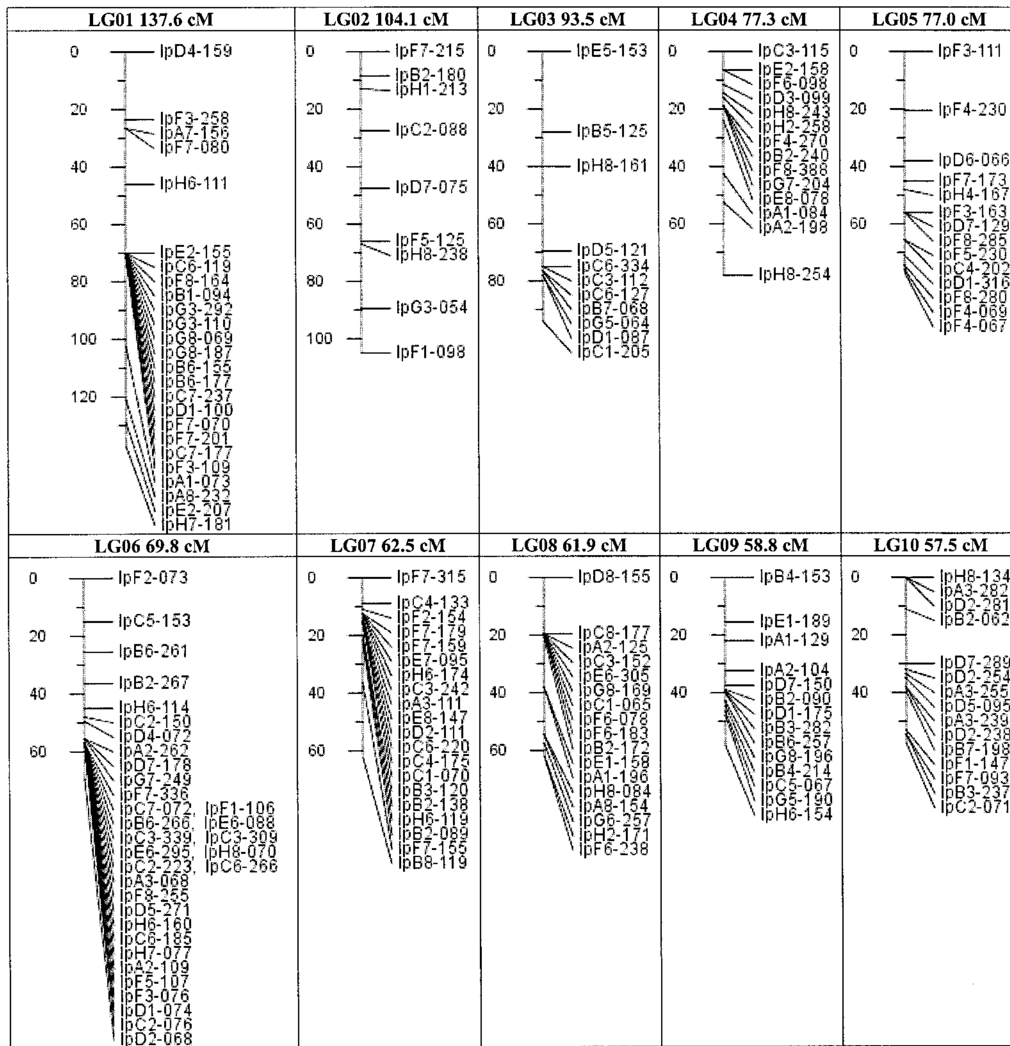

FIGURE 1.—AFLP genetic linkage map of the channel catfish genome. Size of each linkage group (LG) is marked at the top. Genetic distances between AFLP markers are shown at the left in centimorgans.

since this procedure takes a tremendous amount of computing time if more than eight markers are used. After defining the most probable marker order of the most informative subset of each group, TRY command was used to assign additional markers to the intervals. Final marker order was checked by RIPPLE command and maps were constructed by MAP command. The map figures were drawn by using MapCreator (http://www.wesbarris.com/mapcreator).

RESULTS AND DISCUSSION

The AFLP linkage map: A total of 607 polymorphic loci were produced with the 64 *Eco*RI/*Mse*I primer combinations using the resource family F_1–4 (female) × blue catfish-3 (male). Among the polymorphic AFLP markers, 101 markers (16.6%) were not used for the construction of the linkage map because they showed a significant distortion from the expected 1:1 ratio at $P = 0.05$ level. The remaining 506 markers were analyzed using the Mapmaker program. A total of 418 markers were assigned to 44 linkage groups (Figure 1). Among the remaining AFLP markers, 29 were unlinked, and 59 were eliminated because they span very large map distances. Given the dominant nature of AFLP markers, a conservative approach was taken to ensure that they did not span more than one linkage group.

The number of markers on the 44 linkage groups ranged from 2 to 25. There were 27 major linkage groups with 5–25 markers and 17 small linkage groups with 2–4 markers (Figure 1). The genomic coverage of this AFLP linkage map spans 1593 cM Kosambi. The largest linkage group spans 137.6 cM with 25 markers.

The haploid genome of catfish has 29 chromosomes and therefore the numbers of linkage groups are expected to be equal to the chromosome number. Our study produced 44 linkage groups. It is obvious that some linkage groups belong to the same chromosomes. A microsatellite-based map of catfish (WALDBIESER *et al.* 2001) also showed nonequivalence between chromosome number and linkage groups produced. More markers are needed to fill the gap to bring linkage groups belonging to the same chromosome together. Obviously, AFLPs are dominant markers that provide

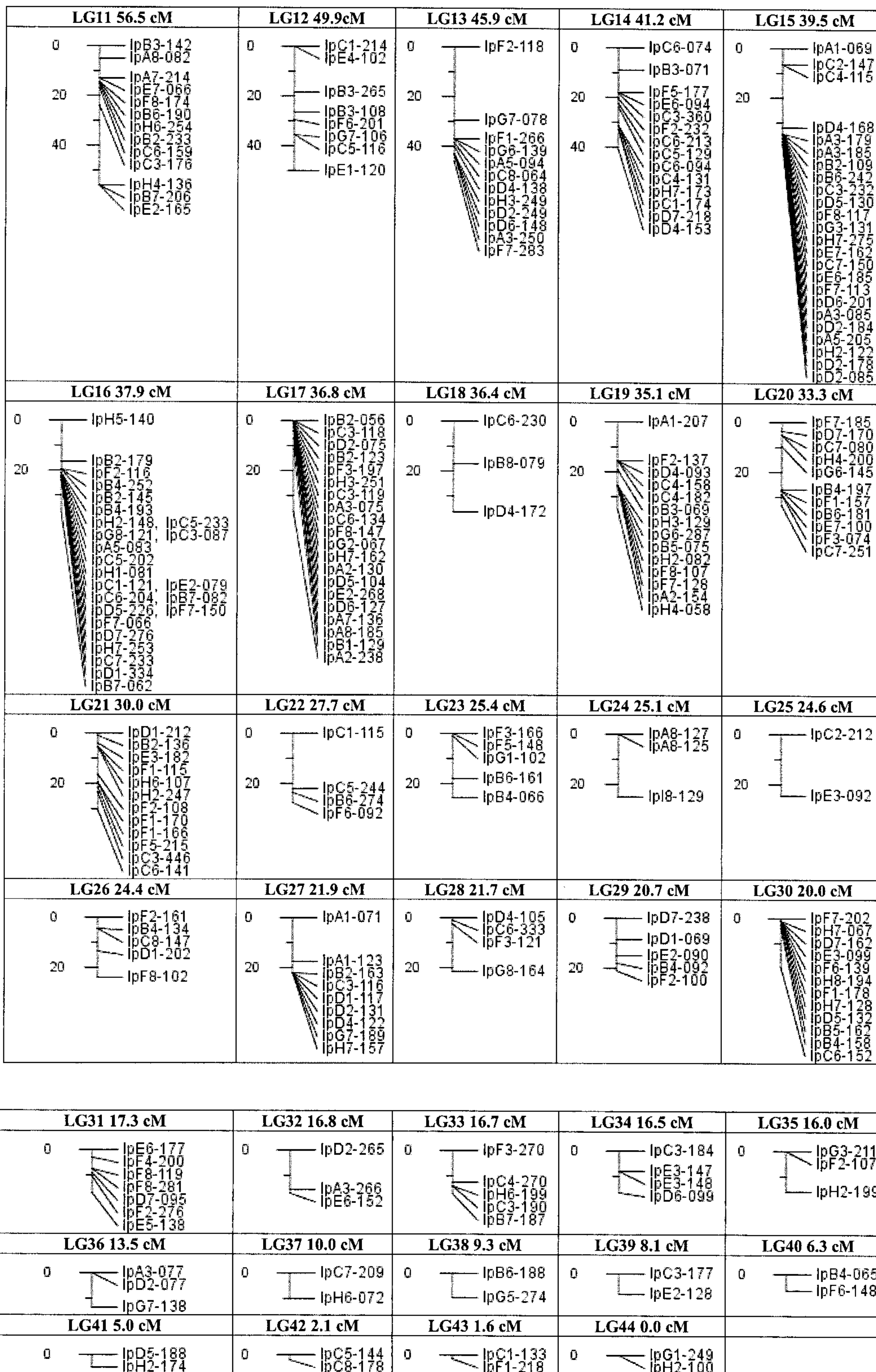

FIGURE 1.—*Continued.*

less genetic information as compared to microsatellite markers. Mapping of additional codominant markers to the AFLP-based map should eventually bring the number of linkage groups to the number of chromosomes.

Primer combinations, markers, and marker distribution: Table 1 shows the production of AFLP markers among the 64 primer combinations using the F_1–4 × blue catfish-3 backcross resource family. Various numbers of markers were produced depending on the

TABLE 1

Matrix identification of AFLP primer combinations in catfish and number of markers produced in the resource family F_1–4 × blue catfish-3

	M-CAA 1	M-CAC 2	M-CAG 3	M-CAT 4	M-CTA 5	M-CTC 6	M-CTG 7	M-CTT 8	Total
E-AAC: (A)	10	14	14	14	5	7	3	9	76
E-AAG: (B)	2	18	9	15	6	15	9	2	76
E-ACA: (C)	9	10	20	10	9	21	11	5	95
E-ACC: (D)	10	16	1	11	8	6	15	1	68
E-ACG: (E)	6	12	10	2	2	9	7	3	51
E-ACT: (F)	15	18	11	7	6	16	22	15	110
E-AGC: (G)	4	6	8	10	6	7	9	8	58
E-AGG: (H)	3	15	4	6	9	11	11	11	70
E-AA: (I)								3	3
Total	59	109	66	75	51	92	87	68	607

primer combinations. On average, 9.4 markers were produced from each of the 64 primer combinations. Several primer combinations such as C3, C6, and F7 produced over 20 useful AFLP markers. However, 6 primer combinations produced 2 or fewer AFLP markers (Table 1). The average number of markers produced from each primer combination was lower than we previously reported (Liu *et al.* 1999c). This difference was caused mainly by use of fluorescent labels in this study while primers were labeled with radioactive nucleotides in previous studies. It was difficult to produce reliable genotypes when bands were >350 bp using the 41-cm gel plates and fluorescent labels.

The AFLP markers showed an uneven distribution on the genetic linkage map. A highly clustered distribution was observed for 133 AFLP markers (Table 2). These markers tended to be distributed at the end of several major linkage groups (Figure 1). For instance, multiple markers were clustered at a small region of LG1, LG6, LG7, LG8, LG13, LG15, LG16, LG17, and LG19 (Figure 1). Their distribution at the end of these linkage groups did not indicate that they had the colocation close to the end of chromosomes. Instead, because the relationship of the linkage groups and the chromosomes has not been established, many linkage groups should represent the same chromosomes. Thus, many of the clustered AFLP markers could be at a position close to centromeres as well as at the end of chromosomes. As the chromosomes become defined in channel catfish, the locations of the clustered markers can be better defined. In *Arabidopsis thaliana*, highly clustered AFLP markers were found to be around the centromere regions (Alonso-Blanco *et al.* 1998). AFLP marker clustering has been observed on linkage maps of other species including those of potato (Van Eck *et al.* 1995), barley (Becker *et al.* 1995; Powell *et al.* 1997), and soybean (Keim *et al.* 1997). In fish, highly clustered AFLP markers were also reported in tilapia, rainbow trout, and the Medaka. It appeared that the level of AFLP clustering increased with the number of AFLP markers. For instance, a couple of highly clustered AFLPs were observed when 112 AFLP markers were mapped to the tilapia genome (Kocher *et al.* 1998); >5 highly clustered AFLPs were observed when 219 AFLP markers

TABLE 2

Distribution of clustered AFLP markers among primer combinations

Primer combination	1	2	3	4	5	6	7	8	Total
A	0	1	5	0	2	0	0	0	8
B	1	7	1	2	1	5	2	0	19
C	3	1	8	3	2	7	4	0	28
D	4	6	0	2	3	1	2	0	18
E	0	2	1	0	0	3	3	1	9
F	2	3	2	0	1	0	9	5	22
G	0	1	3	0	0	1	2	2	9
H	1	3	2	0	0	5	6	3	20
Total	11	24	22	7	9	22	28	10	133

TABLE 3

Distribution of markers deviating from the expected Mendelian segregation ratios

	M-CAA 1	M-CAC 2	M-CAG 3	M-CAT 4	M-CTA 5	M-CTC 6	M-CTG 7	M-CTT 8	Total
E-AAC: (A)	0	4	2	2	2	1	0	1	12
E-AAG: (B)	0	2	1	3	2	2	3	0	13
E-ACA: (C)	1	1	3	1	0	3	2	0	11
E-ACC: (D)	0	3	0	2	0	1	4	0	10
E-ACG: (E)	1	2	3	1	0	0	2	1	10
E-ACT: (F)	3	4	1	1	0	5	4	1	19
E-AGC: (G)	1	3	3	2	0	2	2	1	14
E-AGG: (H)	0	4	0	1	1	1	2	3	12
Total	6	23	13	13	5	15	19	7	101

were mapped to the rainbow trout genome (Robison *et al.* 2001); and, similar to our observation here in catfish, many highly clustered AFLPs were observed when 488 AFLPs were mapped to the Medaka genome (Naruse *et al.* 2000).

The reasons for the high level of marker clustering are not known at present. As discussed by Alonso-Blanco *et al.* (1998), it is possible that a small proportion of the clustered markers resulted from allelism between some AFLP bands since AFLP are allelic markers. However, a large proportion of the clustered markers could not be accounted for by allelism. Other potential causes include (i) a reduced recombination rate around centromere regions and/or telomere regions, (ii) a *bona fide* enrichment of AFLP markers in these regions due to uneven distribution of restriction sites, and (iii) presence of highly repetitive elements within these genomic regions with great variation in both the lengths and the sequences among the repetitive elements. In Arabidopsis, the pericentromeric regions contain mainly repeated sequences of unknown functions (Maluszynska and Heslop-Harrison 1991; Fransz *et al.* 1998). Nonetheless, such high levels of marker clustering hinder the effectiveness of AFLP markers and, therefore, it is warranted to study the nature of the genomic sequences surrounding the regions of clustering markers.

Segregation distortion: Segregation distortion was observed for 101 of 607 markers. When the distorted markers were correlated with the primer combinations, it appeared that large numbers of distortion markers occurred with certain primer combinations (Table 3). For instance, when primer *Mse*I-CAC was used, 23 markers segregated with deviation from Mendelian segregation ratios. Similarly, *Mse*I-CTG had a large number of markers segregating in a non-Mendelian fashion. Deviations from the expected Mendelian ratios have been observed in previous efforts to construct linkage maps using molecular markers. A distortion rate of 65% was reported for clubroot (Voorrips *et al.* 1997) and 54% was reported for silkworm (Tan *et al.* 2001) using AFLP markers. Here with catfish, the distortion rate was ∼16%. As previously reported, several reasons may account for the observed marker distortion, including competition among gametes for preferential fertilization (Lyttle 1991), sampling in finite mapping populations, or amplification of a single-sized fragment derived from several genomic regions (Faris *et al.* 1998). In channel catfish, Tc1-like transposable elements are highly abundant (Liu *et al.* 1999d), but there is no evidence that they are involved in the distorted AFLP markers. Involvement of this and other types of repetitive elements in marker segregation distortion is a possibility and should be further studied.

The interspecific hybrid resource families: Although only one interspecific hybrid resource family, F_1–4 (female) × blue catfish-3 (male), was used for the construction of the AFLP map of this project, eight interspecific hybrid resource families were made in consideration of the informativeness of markers in a given resource family. These backcross families should be useful resources for analysis of many markers that may not be informative in one family. Both backcross progeny were produced in consideration of the dominant markers for analysis of segregating markers from both channel catfish and blue catfish. Using the hybrid system for mapping would allow mapping of QTL from both species. The hybrid system also has utility for rapid application of marker-assisted selection in backcrossing programs to introgress the genomes of blue and channel catfish for production of new improved synthetic breeds. The interspecific hybrid system should facilitate rapid mapping of large numbers of molecular markers to the catfish linkage map and make it feasible to apply several types of molecular markers including isozyme markers, microsatellites, random amplified polymorphic DNA, AFLP, and single nucleotide polymorphism markers.

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