ANIMAL GENETICS Immunogenetics, Molecular Genetics and Functional Genomics

doi: 10.1111/age.12372

High-density interspecific genetic linkage mapping provides insights into genomic incompatibility between channel catfish and blue catfish

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Summary

Catfish is the leading aquaculture species in the United States. The interspecific hybrid catfish produced by mating female channel catfish with male blue catfish outperform both of their parent species in a number of traits. However, mass production of the hybrids has been difficult because of reproductive isolation. Investigations of genome structure and organization of the hybrids provide insights into the genetic basis for maintenance of species divergence in the face of gene flow, thereby helping develop strategies for introgression and efficient production of the hybrids for aquaculture. In this study, we constructed a high-density genetic linkage map using the hybrid catfish system with the catfish 250K SNP array. A total of 26 238 SNPs were mapped to 29 linkage groups, with 12 776 unique marker positions. The linkage map spans approximately 3240 cM with an average intermarker distance of 0.25 cM. A fraction of markers (986 of 12 776) exhibited significant deviation from the expected Mendelian ratio of segregation, and they were clustered in major genomic blocks across 15 LGs, most notably LG9 and LG15. The distorted markers exhibited significant bias for maternal alleles among the backcross progenies, suggesting strong selection against the blue catfish alleles. The clustering of distorted markers within genomic blocks should lend insights into speciation as marked by incompatibilities between the two species. Such findings should also have profound implications for understanding the genomic evolution of closely related species as well as the introgression of hybrid production programs in aquaculture.

Keywords hybrid catfish, hybrid incompatibility, Interspecific crossing, segregation distortion, single nucleotide polymorphism

Introduction

Channel catfish (*Ictalurus punctatus*) is the most important aquaculture species in the United States. Its closely related blue catfish (*I. furcatus*) is also extremely important for aquaculture. In particular, the interspecific hybrids produced by artificially mating female channel catfish with male blue catfish are superior to either of their parental species in a number of production traits such as growth rate, disease resistance, processing yield and seinability (Dunham & Argue 1998; Masser & Dunham 1998; Argue & Dunham 1999; Argue *et al.* 2003). It is widely believed that interspecific hybrids have the potential to revolutionize the US aquaculture industry, but mass production of fingerlings has been difficult due to reproductive isolation of the two parental species, presumably due to genomic incompatibility.

Genetic linkage mapping is an efficient way to investigate genome structure, function and evolution. Genetic maps provide frameworks for detecting quantitative trait loci (QTL), allowing for identification of genomic regions underlying important production traits (Du *et al.* 2010; Fife *et al.* 2011; Hernandez *et al.* 2014) and ecological and evolutionary characteristics (Bradshaw *et al.* 1995; Rieseberg *et al.* 2003; Araripe *et al.* 2010; Ostberg *et al.* 2013). Genetic mapping enables the understanding of hybridization and introgression between species (Rieseberg & Linder 1999; Fishman *et al.* 2001; Fitzpatrick *et al.* 2009; Ostberg *et al.* 2013). On the basis of genetic mapping, chromosome rearrangements have been revealed as barriers to gene flow by suppressing recombination between rearranged chromosomes (Rieseberg *et al.* 1995; Panithanarak *et al.* 2004;

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Accepted for publication 30 August 2015

Stevison *et al.* 2011). Genetic mapping has been used to identify genomic incompatibilities based on the detection of segregation distortion (Fishman *et al.* 2001; Moyle & Graham 2006; Kulmuni *et al.* 2010; Moyle & Nakazato 2010; Brennan *et al.* 2014).

Segregation distortion, a phenomenon that the observed genotypic frequencies of a locus deviate from the expected Mendelian inheritance, can be a reflection of selection against particular hybrid genotype combinations at those loci (Fishman *et al.* 2001; Moyle & Graham 2006; Brennan *et al.* 2014). Segregation distortion loci are frequently observed in genetic mapping when interspecific mapping populations are used (Fishman *et al.* 2001; Yamanaka *et al.* 2001; Lu *et al.* 2002; Woram *et al.* 2004; Recknagel *et al.* 2013; Xie *et al.* 2014). Genetic mapping with segregation-distorted markers is useful to identify intrinsic incompatibility between species and to reveal the nature of such incompatibility at both the genetic and genomic levels. Genetically incompatible loci identified based on segregation distortion between species have been reported in many organisms, including lake whitefish (Rogers & Bernatchez 2007; Rogers *et al.* 2007; Gagnaire *et al.* 2013), cichlids (Recknagel *et al.* 2013), trout (Ostberg *et al.* 2013), Drosophila (Phadnis & Orr 2009), moth (Streiff *et al.* 2014), Nasonia (Niehuis *et al.* 2008; Beukeboom *et al.* 2010) and several plant species (Foolad *et al.* 1995; Whitkus 1998; Fishman *et al.* 2001; Myburg *et al.* 2004; Skrede *et al.* 2008; Shirasawa *et al.* 2010; Brennan *et al.* 2014).

With channel catfish and blue catfish, their F_1 interspecific hybrids are fertile because of the identical karyotypes of channel catfish and blue catfish such that higher generations of hybrids can be made (Dunham & Argue 2000). However, the fertilization and hatching rates of interspecific hybrids for generating higher generations of hybrids are very low. Therefore, we exploited a backcross strategy to backcross the male F_1 hybrid catfish with channel catfish for effective production of the interspecific backcross progenies, such that segregation of chromosomes within the F_1 hybrids could be investigated. Such backcross progenies have been used as major resources for linkage and QTL analysis (Liu *et al.* 2003; Kucuktas *et al.* 2009; Ninwichian *et al.* 2012; Hutson *et al.* 2014). However, in previous studies, the marker densities were relatively low. Recent advances in sequencing technologies allow rapid discovery of SNPs (Davey *et al.* 2011; Liu *et al.* 2011; Sun *et al.* 2014). With the availability of a large number of SNPs from catfish, high-density SNP arrays have been developed for high-throughput and efficient genotyping (Liu *et al.* 2014).

In the present study, we conducted genetic linkage analysis with the catfish 250K SNP array using three backcross resource families (Liu *et al.* 2014) with the objectives of (i) construction of a high-density genetic map in hybrid catfish, (ii) identification of segregation distortion loci and their chromosomal locations to provide insights into genomic incompatibilities of the two species and (iii) identification of major chromosomal rearrangements between the two species.

Methods

Resource families

The resource families for linkage mapping used in this study were generated as previously described (Liu *et al.* 2003). F_1 interspecific hybrid catfish were produced by mating female channel catfish with male blue catfish. Backcross families were generated by mating the F_1 hybrid catfish males with either channel catfish or blue catfish females. Specifically, three backcross families (hyb220, hyb225 and hyb230), generated by mating one F_1 hybrid male (hybrid #7) with three respective channel catfish females (Marion #220, Marion #225 and Marion #230), were selected for this project. All experiments involving the handling and treatment of fish were approved by the Institutional Animal Care and Use Committee (IACUC) at Auburn University.

Genomic DNA isolation

A total of 288 backcross progenies with 96 individuals from each of the three backcross families were sampled for SNP genotyping. 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 of NaCl, 10 mM Tris, pH 8, 25 mM EDTA, 0.5% SDS and freshly added proteinase K 0.1 mg/ml). DNA was isolated using the Puregene DNA Isolation Kit (Gentra Systems) as previously described (Liu *et al.* 2003; Kucuktas *et al.* 2009; Ninwichian *et al.* 2012). PicoGreen dye (Quant-iT PicoGreen; Invitrogen) was used to quantify double-stranded DNA according to the manufacturer's protocol. The integrity of DNA samples was checked by 1% agarose gel electrophoresis stained with ethidium bromide.

SNP genotyping and filtering

The SNP genotyping and analysis were conducted as previously described (Liu *et al.* 2014). Briefly, genomic DNA samples from each family were arranged in a 96-well microtiter plate and outsourced for genotyping by GeneSeek with the catfish 250K SNP array (Liu *et al.* 2014). The raw data CEL files were analyzed for quality control and SNP genotype calling using Affymetrix GENOTYPING CONSOLE (GTC, version 4.0) software. Samples passing the quality check (Dish QC value >0.85) and sample call rate threshold (>97%) were retained. The genotyping outputs were post-processed and filtered for polymorphic markers with high genotyping quality using the R/SNPolisher (Affymetrix). The genotypes in CHP files were imported into SNP & VARIATION SUITE (SVS version 7; Golden Helix Inc.) for further filtering to exclude SNPs with missing genotypes >10% and

minor allele frequency <5%. Finally, a total of 286 samples from three resource families (two individuals from the hyb220 family being excluded for further analysis due to the low call rate) and a total of 17 401 SNPs from the hyb220 family, 18 619 SNPs from the hyb225 family and 11 509 SNPs from the hyb230 family were retained for linkage mapping.

Linkage mapping analysis

SNPs that were heterozygous in the male hybrid parent were used to construct the hybrid genetic map. Based on segregation, SNP markers were categorized into two types with AB × AB type (1:2:1) having segregated in both parents and AA/BB × AB type having segregated only in the male hybrid parent. Segregation distortion was detected by performing chi-square tests for goodness-of-fit. Markers that were distorted highly significantly with $P < 0.001$ were not used in the linkage mapping because they could create inaccurate distances and false linkages (Cervera *et al.* 2001; Recknagel *et al.* 2013).

Linkage maps were initially developed independently for the three mapping families as previously described (Li *et al.* 2015). In brief, we conducted linkage analysis and constructed genetic maps using R/ONEMAP (Margarido *et al.* 2007) and JOINMAP4 (Van Ooijen 2006). Markers were first allocated into linkage groups (LGs) using R/ONEMAP (Margarido *et al.* 2007). This package uses hidden Markov model algorithms for outbred species and implements Wu's methodology (Wu *et al.* 2002) in parallel to calculate the most probable linkage phases. LGs were formed using a minimum logarithm of the odds (LOD) score of 6 and a maximum recombination fraction of 0.35. To reduce the computational requirement for linkage mapping of large numbers of markers, we picked up only one marker with the most informative meiosis as the representative marker from each 'stacked cluster of markers' where no recombination events occur during meiosis (Li *et al.* 2015).

The orders of markers in each LG were then determined with the regression mapping algorithm using JOINMAP4 (Van Ooijen 2006). The use of a regression mapping algorithm and accounting for potential genotypic errors can reduce the tendency to erroneously derive oversized LGs, which is commonly observed in the construction of high-density genetic maps (Cartwright *et al.* 2007). Map distances were calculated in centiMorgans (cM) using the Kosambi mapping function. Markers falling into 'zero recombination clusters' that were excluded during linkage map construction were anchored to the maps based on the positions of their corresponding representative markers. The consensus genetic map was established by integrating individual maps from three resource families through shared markers using MERGEMAP (Wu *et al.* 2011). Genetic linkage maps were graphically represented using the program MAPCHART 2.2 (Voorrips 2002).

Segregation distortion analysis

Segregation distortion analysis was performed as described in a previous study (Brennan *et al.* 2014). In brief, genotype frequencies of each mapped marker were tested for Mendelian inheritance using chi-square tests in the three resource families. To correct for multiple hypothesis testing, we applied a false discovery rate (FDR) correction (Benjamini & Hochberg 1995) to compute FDR-adjusted *P*-values using the 'p.adjust' function with parameter 'BH' in the R statistical package (http://www.r-project.org/). The distribution of loci showing segregation distortion was presented by plotting distorted markers onto their genetic map positions. The number of distinct segregation distortion loci across the genetic map was assessed as the number of clusters of distorted markers. The distorted SNPs with 1:1 segregation (AA/BB × AB) were used to identify patterns of preferential genotypes existing among the distorted markers within families and across LGs. Biases of genotypes from distorted markers were investigated on the LGs with at least 20 markers to achieve reliable statistical significance. The differences were determined with chi-square tests against the null hypothesis of equal quantity.

Analysis of recombination differences

To determine whether introgression affects recombination in the hybrids, we compared the consensus hybrid genetic map with the consensus male channel catfish genetic map that was constructed in a separate study (Li *et al.* 2015). The genetic distances of markers used for comparison were normalized with total genetic lengths of respective LGs to account for variations derived from the use of different numbers of markers and individuals. Comparative analysis of genetic maps was graphically represented using the program MAPCHART 2.2 (Voorrips 2002) with common markers.

The comparison of recombination rates was conducted following a previous study (Ostberg *et al.* 2013). Only common markers ($n = 609$) that had consistent marker orders between channel catfish male map and the hybrid map were retained for analysis. Markers used to compare recombination rates generally covered a substantial proportion of each LG and were not restricted to areas of low recombination or areas of high recombination. The differences in recombination rate across the LGs were tested against the null hypothesis that no differences in recombination rates exist. Intermarker distances of two adjacent common markers were compared to assess the recombination differences ($n = 580$) using G-tests. Intermarker distances of 0 cM from either genetic map were excluded for analysis ($n = 14$). The G-tests were first conducted for each genetic distance of two adjacent markers to test the difference with the R package's 'RVAideMemoire' (Hervé 2013). Significant differences of LG-wide recombination

rates were then determined by summing G-test values and degrees of freedom from each comparison across the LG. To account for multiple testing, FDR-adjusted *P*-values were computed from the nominal *P*-values using the R function 'p.adjust' with the parameter of 'BH' (Benjamini & Hochberg 1995).

Results

Linkage mapping

Linkage maps were first constructed for each of the three resource families with 17 401, 18 619 and 11 509 SNPs respectively (Table 1). The proportion of AA/BB × AB and AB × AB type SNPs was approximately 2:1 within each family, with an average of 11 687 SNPs segregating only in the hybrid parent and 6233 SNPs segregating in both parents. For all three mapping families, 29 LGs were obtained, which was consistent with the catfish haploid genome chromosome number. A total of 12 776 markers with distinct genetic positions (hereafter referred to as unique markers) were placed on the consensus linkage map, which included 5037 SNPs from the hyb220 family, 4854 SNPs from the hyb225 family and 4758 SNPs from the hyb230 family (Table 1). After anchoring the previously excluded markers that fell into 'zero recombination clusters' based on the genetic positions of representative markers, a total of 26 238 SNP markers were placed onto the current hybrid catfish linkage map (Tables 1 & 2).

The consensus genetic map spans a total of approximately 3240 cM, with an average intermarker distance of 0.25 cM (Table 2). The genetic sizes varied from 81.99 cM (LG7) to 144.07 cM (LG4). The average number of mapped markers with distinct genetic positions per LG was 440, ranging from 331 markers on LG9 to 569 markers on LG3. The consensus hybrid catfish linkage map is presented in Fig. 1. It is apparent that the SNP markers were distributed relatively evenly across all 29 LGs, with some highly dense clusters formed by many stacked markers with minimal numbers of recombination in each LG (Fig. 1). Detailed information of the consensus hybrid genetic map is provided in Table S1.

Table 1 Summary of linkage mapping using three interspecific hybrid catfish resource families and SNP markers genotyped from the catfish 250K SNP array.

	Family hyb220	Family hyb225	Family hyb230	Total
Number of SNPs used	17 401	18 619	11 509	39 885
Mapped SNPs	10 943	12 361	10 674	26 238
Unique marker positions	5037	4854	4758	12 776

Table 2 Summary of consensus genetic map for hybrid catfish.

Linkage group	No. of mapped markers	No. of mapped unique markers	Genetic size (cM)	Average marker interval
1	1084	490	122.81	0.25
2	934	447	114.8	0.26
3	1117	569	129.45	0.23
4	1143	563	144.07	0.26
5	968	442	92.10	0.21
6	1101	450	137.88	0.31
7	751	338	81.99	0.24
8	1082	494	114.89	0.23
9	426	331	121.57	0.37
10	947	463	96.62	0.21
11	1067	489	133.06	0.27
12	1108	536	119.03	0.22
13	845	463	142.38	0.31
14	818	386	92.51	0.24
15	704	393	100.97	0.26
16	970	484	123.54	0.26
17	767	412	105.82	0.26
18	969	442	93.44	0.21
19	916	514	142.97	0.28
20	1025	509	100.4	0.20
21	809	349	94.61	0.27
22	975	430	105.68	0.25
23	917	437	101.55	0.23
24	711	398	95.27	0.24
25	1011	450	139.97	0.31
26	794	339	87.28	0.26
27	713	340	88.14	0.26
28	933	416	109.51	0.26
29	733	402	108.26	0.27
Total	26 238	12 776	3240.57	0.25

Segregation distortion analysis

Segregation distortion was observed for the mapped markers in the hybrid genetic map, with 986 markers (7.7% of 12 776) significantly deviating from the Mendelian ratio of segregation with FDR-adjusted *P*-values between 0.05 and 0.001 (Table S2). Markers showing genotypic segregation distortion were not randomly distributed across the linkage maps, with the vast majority of distorted markers clustering on several LGs (Fig. 2). The distorted markers were clustered to form major blocks located in 15 LGs including LG1, LG2, LG5, LG8, LG9, LG10, LG11, LG13, LG14, LG15, LG16, LG17, LG18, LG22 and LG25 (Figs. 1 & 2). The vast majority (71.2%) of segregation-distorted markers were located on five LGs: LG15, LG9, LG8, LG16 and LG18.

Further analysis of distorted marker genotypes indicated that a significantly high frequency of maternally inherited alleles were observed, displaying an excess of homozygotes of channel catfish alleles (Table 3). With regard to specific LGs, LG8, LG9, LG15 and LG16 had distorted markers exhibiting a higher ratio of maternally inherited alleles, whereas distorted markers on LG11 tended to display an excess of heterozygotes, but no highly significant statistical difference was found.

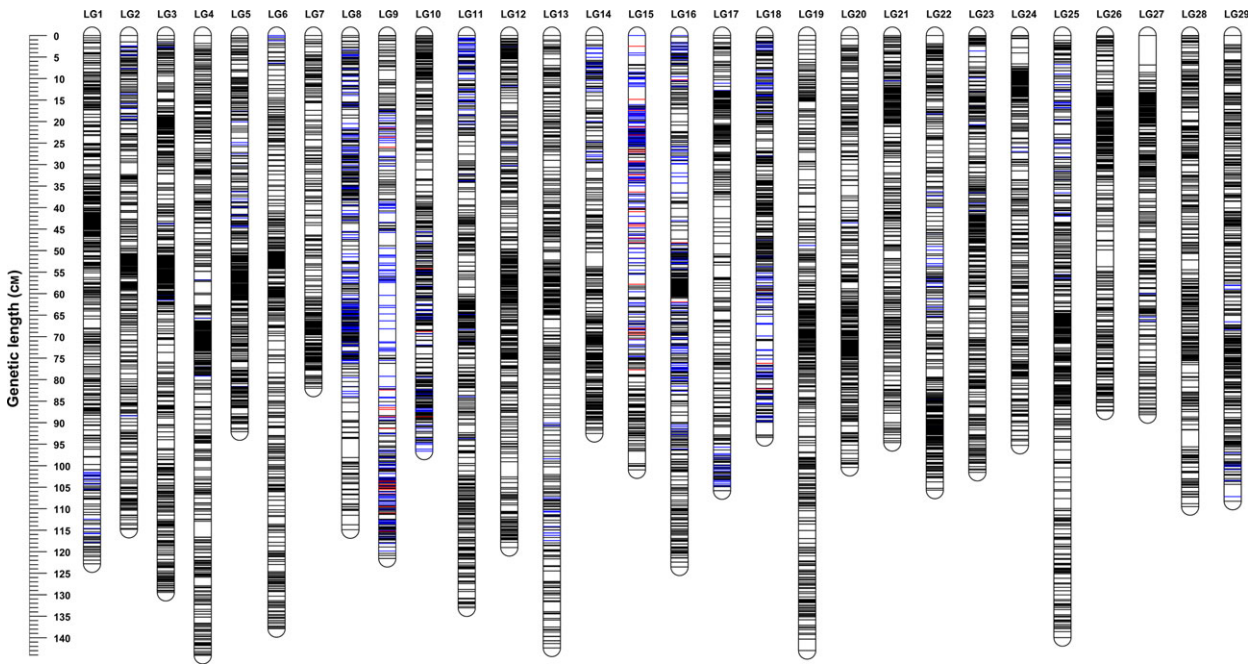

Figure 1 Graphical presentation of hybrid catfish genetic linkage map. The vertical bars represent 29 linkage groups (LGs), and the horizontal lines in those bars represent markers. The segregation-distorted markers (false discovery rate-adjusted $P < 0.05$) are highlighted in blue, and the segregation-distorted markers present in more than one family are highlighted in red.

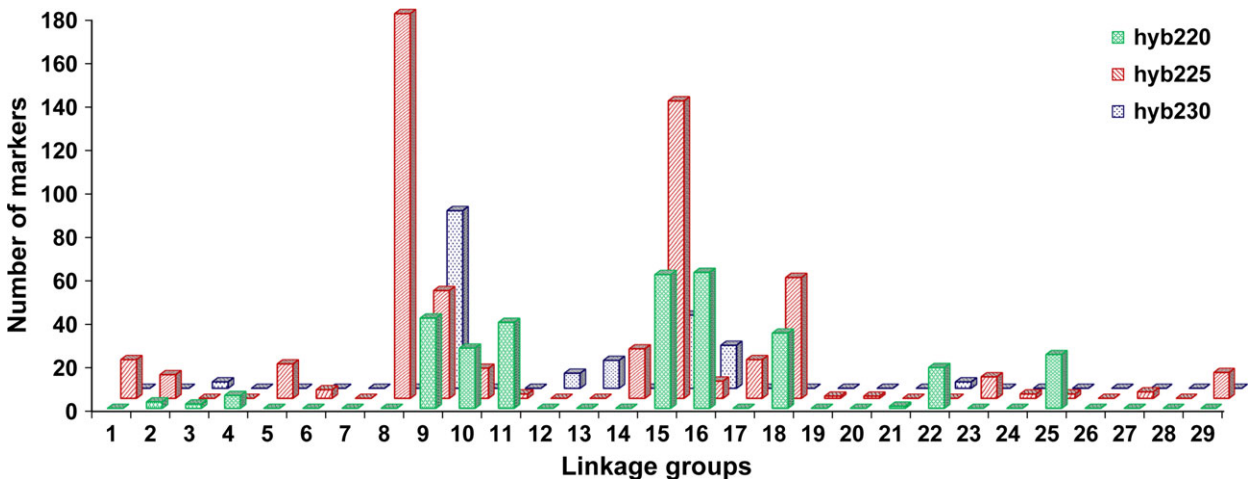

Figure 2 Distribution of distorted markers across linkage groups (LGs) detected in three resource families. The 29 LGs are indicated on the bottom of the figure from 1 to 29. The *Y*-axis represents the number of segregation-distorted markers with the statistical significance of false discovery rate adjusted $P < 0.05$.

Table 3 Identification of biased genotypes of SNPs with segregation distortion among three resource families. Only SNPs with 1:1 segregation (AA/BB × AB) were used for the analysis.

Resource family	Homozygous (AA or BB): channel catfish	Heterozygous (AB): hybrid catfish	*P*-value (χ^2 test)
hyb220	128	82	1.50E-03
hyb225	324	124	3.42E-21
hyb230	62	7	3.56E-11
Total	478	209	1.03E-24

The distorted markers varied among the three resource families used. It is notable that, in a number of cases, the number of distorted markers was high among all three resource families, including LG9, LG15 and LG16. However, in many instances, a large number of distorted markers were detected from only one or two of the three resource families (Fig. 2). For instance, a large number of distorted markers were detected only from family hyb225 in LG8, LG1, LG5, LG14 and LG17. Similarly, large numbers of distorted markers were found from family hyb220 in LG11,

LG22 and LG25 and from family hyb230 in LG12 and LG13 (Fig. 2).

Recombination differences

A comparison of the consensus hybrid genetic map with the channel catfish genetic map indicated that several major chromosome rearrangements likely occurred in the channel catfish vs. the blue catfish genomes. Most notably, these included chromosomal regions in LG5, LG12 and LG27 (Fig. 3). This observation is of sufficient interest to warrant future investigations of genome comparative analyses once the channel catfish and blue catfish genome sequences are available. Major differences in recombination rates were also observed between hybrid catfish and channel catfish. When the recombination rates were compared between LGs on the channel catfish linkage map and on the hybrid linkage map, 14 LGs exhibited major differences in recombination rates (FDR-adjusted $P < 0.05$), with 10 LGs having greater recombination rates on the channel catfish linkage map and four LGs having greater recombination rates on the hybrid map (Fig. 4). In the 10-LG group, for LG1, LG15, LG20 and LG24 recombination rates were significantly higher (FDR-adjusted $P < 0.01$) within channel catfish resource families, and in the four-LG group, for LG5 and LG17 the opposite was observed with greater recombination rates being observed from the hybrid map (Fig. 4).

Discussion

In this study, we report the construction of high-density genetic maps of interspecific hybrid catfish. With a total of 26 238 SNPs mapped to 29 LGs with 12 776 unique marker positions, this linkage map represents a linkage map with the highest density and coverage of markers among all available linkage maps for vertebrates. It harbors a similar density and similar set of markers as mapped to the channel catfish genome (Li *et al.* 2015), allowing comparative genome analysis using both genetic and genomic approaches. This high-density genetic linkage map is an important addition to the genomic resources for catfish genetics studies and is especially useful for investigations on genomic incompatibility for hybridization, genome evolution of closely related species and genetic enhancement programs in aquaculture.

The interspecific hybrids produced by crossing channel catfish with blue catfish exhibit strong heterosis and possess traits superior to their parental species, which enable the hybrid catfish system to be a great model for speciation studies of closely related species. Channel catfish and blue

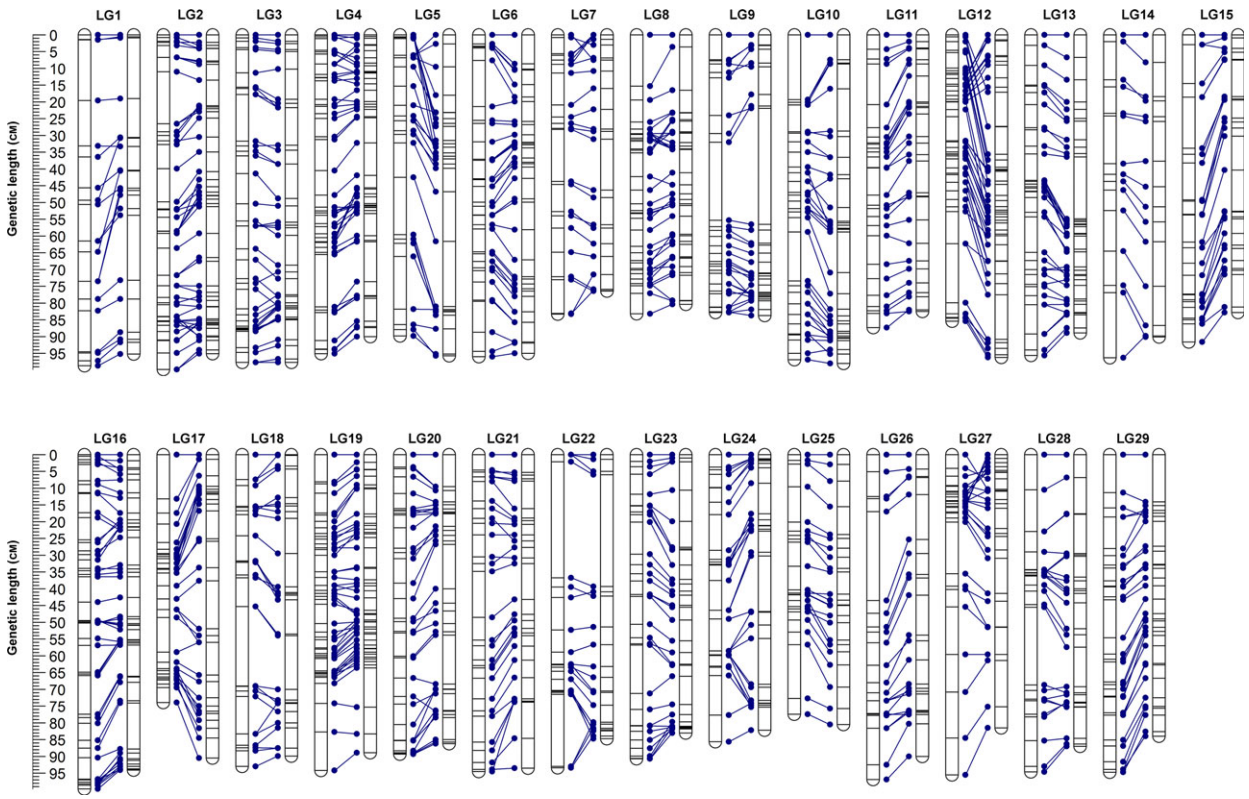

Figure 3 Graphical presentation of map comparisons between linkage maps from channel catfish and hybrid catfish. For each linkage groupwide comparison, the left panel denotes channel catfish linkage group (LG) and the right panel denotes the hybrid catfish LG. The common markers are indicated with lines.

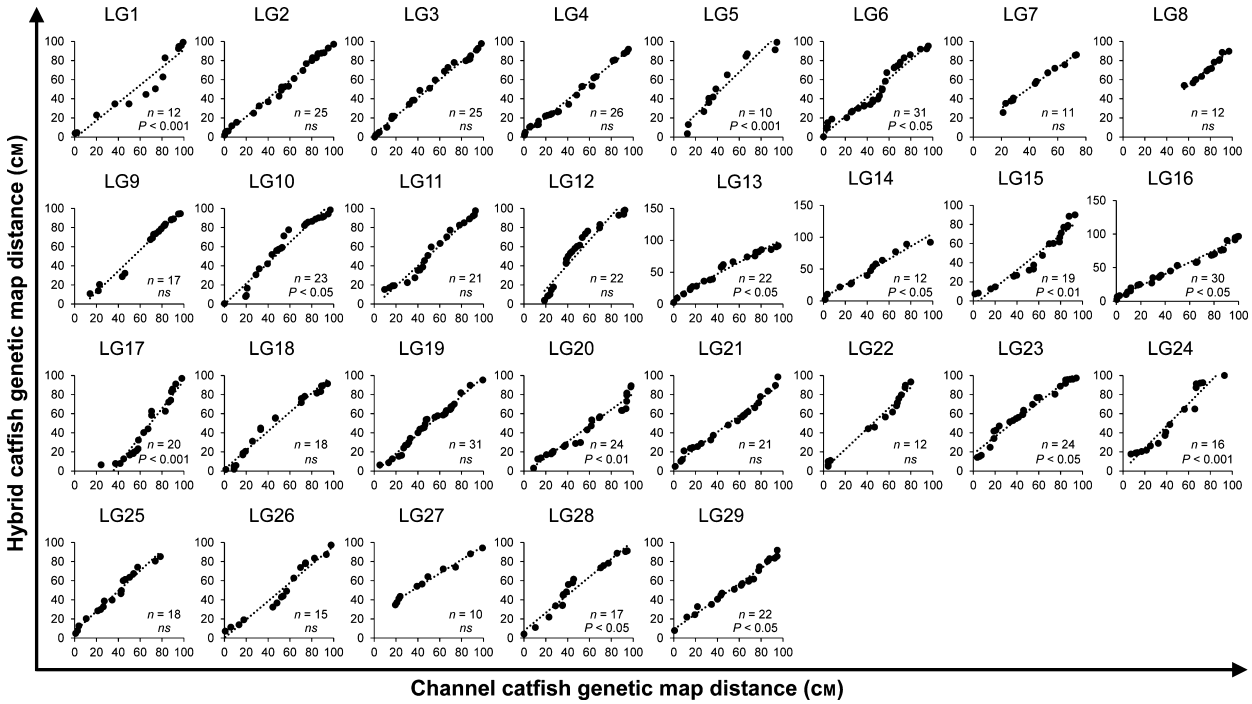

Figure 4 Comparison of map distance between the hybrid genetic map and the channel catfish genetic map. Map distances in centiMorgans (cM) across the same markers were compared between hybrid genetic map (*Y*-axis) and channel catfish genetic map (*X*-axis). Significant differences in recombination rates across linkage groups are indicated with *P*-values ($P < 0.05$) after multiple testing correction. ns, not significant; *n*, the number of map distances that were used for statistical tests.

catfish are recently divergent and exhibit a high level of similarity at the genome level (Wang *et al.* 2010). It is of interest to unravel how these two species have developed and maintain reproductive isolation. Besides pre-mating isolation, chromosomal rearrangements and/or genetic incompatibilities might act as isolating barriers to gene flow in post-zygotic reproduction (Coyne & Orr 2004). Analysis of markers with segregation distortion and recombination rate variation across the genome could provide insights into genomic regions underlying high levels of species divergence.

In our linkage mapping analysis, we found 986 markers that deviated from the expected Mendelian segregation ratio. Segregation distortion can result from genotyping errors and missing genotypes. However, the clustering of large numbers of distorted markers in local genomic regions, as observed in this work, should be attributed to biological causes and probably infers genomic incompatibilities between divergent parental species. We believe that the observed marker distortion in the hybrid catfish system indeed reflected genomic regions of incompatibility. This belief is supported by the fact that, in most instances, the distorted markers were biased for a significantly high frequency of maternally inherited alleles. With the hybrid catfish mapping families, the mapping population of backcross progenies was generated by mating the channel catfish female with the F_1 hybrid catfish male. Theoretically, the alleles within the F_1 hybrid were segregating with a 1:1 possibility of being the channel catfish allele or the blue catfish allele in the gametes. The observed bias with significantly more homozygous alleles (Table 4) suggests selective survival of the homozygous individuals with channel/channel combinations, whereas the heterozygous channel/blue combinations had a low odd of survival, suggesting their incompatibility.

The number of distorted markers varied among the three resource families, although a common set of LGs with high numbers of distorted markers was identified. Therefore, it seems reasonable to believe that there were chromosomal regions of generally high incompatibilities between the two species, but in addition, there appeared to be regions that were incompatible only within specific families.

Table 4 Preferential genotypes of segregation-distorted markers across linkage groups (LGs). SNPs with 1:1 segregation (AA/BB × AB) and LGs with at least 20 segregation-distorted markers were used for analysis. The shaded rows indicated highly significant differences (*P*-value < 0.01).

Linkage group	Homozygous (AA or BB): channel catfish	Heterozygous (AB): hybrid catfish	*P*-value (χ^2 test)
8	111	42	2.43E-08
9	60	18	1.98E-06
11	10	21	0.05
15	138	30	7.92E-17
16	60	9	8.27E-10
18	41	37	0.65

Comparative analysis of the hybrid catfish genetic map with the channel catfish genetic map revealed that recombination rates were generally similar between the hybrid catfish and channel catfish. Although the total genetic size of the male genetic linkage map from using channel catfish resource families was estimated to be 2593 cM (Li *et al.* 2015), which is smaller than the male genetic size from using the hybrid mapping families, this could be caused by the larger number of markers used in this study rather than increased recombination rates in the hybrids. When the recombination rates were compared in a pairwise fashion between LGs, a larger number of LGs on the hybrid map exhibited suppressed recombination than on the channel catfish map using intraspecific resource families. Ten LGs had lower recombination rates on the hybrid map than on the channel catfish map, whereas only four LGs had higher recombination rates on the hybrid map than on channel catfish map (Fig. 4).

Suppressed recombination in hybrid catfish was previously observed in linkage mapping with ~2500 microsatellite markers (Ninwichian *et al.* 2012). In this study, with a much larger number of markers, we focused on the examination of recombination rate variation in the hybrid catfish by comparative analysis of genetic maps. Conclusions of recombination differences made based on such comparisons need to be made with caution because recombination varies among related species (Smukowski & Noor 2011) as well as among individuals within species (Gharbi *et al.* 2006; Ostberg *et al.* 2013). In addition, recombination differences can be affected by the accuracy of marker orderings and differences in the number of mapped markers and individuals, which influence estimation of map distance (Ostberg *et al.* 2013). However, in the present study, we sought to examine the recombination differences across the genome on a broad scale and performed the genetic map comparative analysis using normalized genetic distances. On a broad scale, recombination rates tend to be conserved between closely related species (Smukowski & Noor 2011); that is, similar recombination rates are expected between channel catfish and blue catfish. Therefore, the trends revealed by the comparative analyses should provide an overview of recombination differences in the hybrids. These findings are of interest to warrant further investigations on comparative genome analysis to identify potential chromosome rearrangements and determine the recombination landscape across the genome once the channel catfish and blue catfish reference genome sequences are available.

Acknowledgements

We thank Miyako Kodama (University of Washington) for the discussion on linkage mapping using R/ONEMAP. This project was supported by Agriculture and Food Research Initiative (AFRI) Competitive Grants (Nos. 2015-67015-22907 and 2015-67015-22975) from the USDA National Institute of Food and Agriculture (NIFA) and by USDA Aquaculture Research Program Competitive Grant (No. 2014-70007-22395).

Conflict of interests

The authors declare that they have no conflict of interests with regard to this work.

Authors' contributions

SL and YL carried out the linkage mapping and genetic analysis. ZQ, XG and LB assisted with genetic analysis. LK, HK and RD contributed to the sample collection and DNA preparation. SL and ZL wrote the manuscript. ZL supervised the whole project.

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Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Markers and positions for the consensus hybrid genetic map.

Table S2 A list of the 986 segregation-distorted markers with false discovery rate-adjusted P-value < 0.05.