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Channel catfish BAC-end sequences for marker development and assessment of syntenic conservation with other fish species

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Summary

In the present study, 25 195 BAC ends for channel catfish (*Ictalurus punctatus*) were sequenced, generating 20 366 clean BAC-end sequences (BES), with an average read length of 557 bp after trimming. A total of 11 414 601 bp were generated, representing approximately 1.2% of the catfish genome. Based on this survey, the catfish genome was found to be highly AT-rich, with 60.7% A+T and 39.3% G+C. Approximately 12% of the catfish genome consisted of dispersed repetitive elements, with the Tc1/mariner transposons making up the largest percentage by base pair (4.57%). Microsatellites were detected in 17.5% of BES. Catfish BACs were anchored to the zebrafish and *Tetraodon* genome sequences by BLASTN, generating 16% and 8.2% significant hits ($E < e^{-5}$) respectively. A total of 1074 and 773 significant hits were unique to the zebrafish and *Tetraodon* genomes, respectively, of which 417 and 406, respectively, were identified as known genes in other species, providing a major genome resource for comparative genomic mapping.

Keywords BAC, catfish, comparative mapping, conserved synteny, end sequencing, fish, repeat.

Introduction

Teleost fish, accounting for over half of all vertebrate species, have in recent years been a testing ground for theories of genome duplication, divergence and speciation (for recent reviews, see Venkatesh 2003; Crollius & Weissenbach 2005). Genome-wide analyses of zebrafish (*Danio rerio*), pufferfish (*Takifugu rubripes*), *Tetraodon nigroviridis*, as well as medaka (*Oryzias latipes*; Taylor *et al.* 2003; Naruse *et al.* 2004; Woods *et al.* 2005), have lent support to the theory that two rounds of genome duplications occurred early in vertebrate history, followed by another whole-genome duplication event in ray-finned fishes after the split from mammals and before the teleost radiation (Holland *et al.* 1994; Amores *et al.* 1998, 2004). The predictive value of this theory appears to be restricted; however, by differing rates of gene retention and/or by duplication and divergence not only among teleost species but also among the gene families within a given teleost species (Dugas & Ngai 2001; Gloriam *et al.* 2005; Peatman *et al.* 2006). The traditional model species alone may provide an insufficient context to resolve complex questions of duplication and divergence.

Channel catfish, as the primary aquaculture species in the United States, has long been a research model for comparative immunology and toxicology but has until recently lacked genomic resources. Development and evaluation of large numbers of molecular markers (Kocabas *et al.* 2002; He *et al.* 2003; Serapion *et al.* 2004), construction of framework genetic linkage maps (Waldbieser *et al.* 2001; Liu *et al.* 2003), a successful EST project (Cao *et al.* 2001; Karsi *et al.* 2002; Kocabas *et al.* 2002) and the production of two BAC libraries using different restriction endonucleases (http://bacpac.chori.org/library.php?id=103, Quiniou *et al.* 2003) within the last 5 years have provided the foundation for large-scale genome research in catfish. However, genome infrastructure for physical mapping in catfish has not been developed, as already accomplished in Atlantic salmon (Ng *et al.* 2005). The objective of this study, therefore, was to produce a resource of catfish BAC-end sequences (BES) needed for physical mapping, comparative

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genome analysis, map integration and better utilization of the existing genomic information.

Materials and methods

BAC culture and end sequencing

The CHORI-212 Channel Catfish BAC library was used for BAC-end sequencing. BAC culture and sequencing reactions were conducted using standard protocols. The raw, untrimmed files were processed by PHRED software (Ewing & Green 1998; Ewing *et al.* 1998) within the Genome Project Management System (GPMS). The PHRED quality score cut-off value was set at 20 for the acquisition of Q20 values.

Sequence processing and bioinformatics

The BES were trimmed of vector sequences, filtered of bacterial sequences and stored in a local ORACLE database after base calling and quality assessment using GPMS, a local laboratory information management system for large-scale DNA sequencing projects (Liu *et al.* 2000). Quality assessment was performed using PHRED (Ewing & Green 1998; Ewing *et al.* 1998) with $Q \geq 20$ as a cut-off. Repeats were masked using REPEATMASKER (http://www.repeatmasker.org) before BLAST analysis.

BLASTX searches of the repeat-masked BES were conducted against the non-redundant protein database. A cut-off value of e^{-5} was used as the significance similarity threshold for the comparison. In order to anchor the catfish BES to the zebrafish and *Tetraodon* genomes, BLASTN searches of the repeat-masked catfish BES were conducted against the zebrafish and *Tetraodon* genome sequences.

Identification of microsatellites and determination of their polymorphism

Microsatellites and other simple sequence repeats were analysed using REPEATMASKER and VECTOR NTI SUITE 9.0 (Invitrogen, Carlsbad, CA, USA) as we previously described (Serapion *et al.* 2004). Polymerase chain reaction (PCR) primers were designed using the FASTPCR software package (http://www.biocenter.helsinki.fi/bi/Programs/fastpcr.htm). In order to assess the rate of polymorphism, 80 microsatellite loci (randomly picked) were tested within a resource family, F_1-2 (female) × Ch-6 (male), by PCR analysis.

Results

BAC-end sequencing statistics

A total of 25 195 BAC ends were sequenced from 12 672 BAC clones (1.84X clone coverage of the channel catfish genome) from both ends, resulting in 20 493 high-quality BES >200 bp in length (81.3% overall success rate). After filtering and trimming for *Escherichia coli* and vector sequences, a total of 20 366 BES were generated. The BES were of high quality as the Q20 length ranged from 200 to 810 bp, with an average Q20 read length of 557 bp, comparing favourably to BES produced from human (477 bp, Zhao *et al.* 2000), mouse (485 bp, Zhao *et al.* 2001) and cattle (515 bp, Larkin *et al.* 2003). All these BES have been deposited into the GenBank GSS database with consecutive accession numbers of DX083364–DX103729. A total of 11 414 601 bp of genomic sequences was generated from this study, representing approximately 1.2% of the catfish genome. The channel catfish genome appeared to be highly A+T-rich with 60.7% A+T and 39.3% G+C.

Repeat status of the catfish genome

The overall status of repetitive elements in the catfish genome was assessed by repeat-masking. Analysis using the 11 414 601 bp BES resulted in 10.86% of base pairs masked using the *Danio* repeat database and 7.31% of base pairs masked using the *Takifugu* repeat database. The use of both *Danio* and *Takifugu* repeat databases masked 11.91% (Table S1). These results suggested that while teleost fish share a high level of repetitive elements, a significant fraction of taxa-specific repeats exist. It appeared from the analysis that the zebrafish and catfish genomes shared a larger pool of repetitive elements than do the *Takifugu* and catfish genomes. It was also clear that the catfish and zebrafish genomes harboured a larger percentage of repetitive elements than the *Takifugu* genome, an expected result considering the compact size of the *Takifugu* genome.

The most abundant type of repeat encountered in the catfish genome was the DNA transposons (Fig. 1), the vast majority consisting of Tc1/mariner transposon-related sequences at 4.12% of all BES. Retroelements were the second largest fraction of repetitive elements, accounting for 3.13% of BES. Simple repeats, such as microsatellites, accounted for

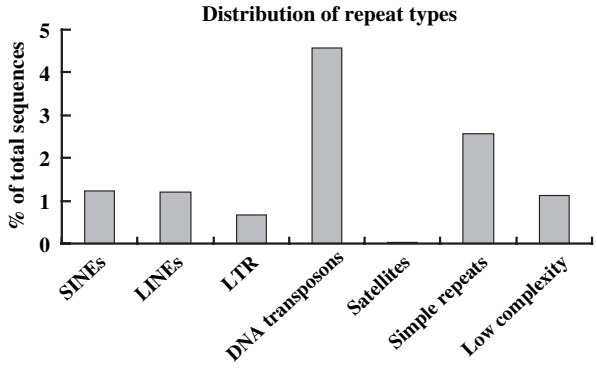

Figure 1 Distribution of major repeat types as revealed by REPEATMASKER analysis of the channel catfish BAC-end sequences (BES). The percentage indicates the percentage of total base pairs.

2.58%, with CA-, AT- and CT-type repeats accounting for 68% of all microsatellite types.

A total of 3748 BES were found to contain one or more stretches of microsatellite sequences. Of these, 2365 (63%) had sufficient flanking sequences on both sides, making them potentially useful as markers for genetic mapping. In order to assess the proportion of microsatellites useful for linkage mapping in our resource families, we conducted polymorphism analysis of 80 microsatellite loci. Approximately 55% of the tested microsatellites exhibited polymorphism in a F_1-2 (female) × Ch-6 (male) resource family. Based on the conservative 55% polymorphic rate by testing in only one resource family, approximately 1300 microsatellite markers can be developed from this BES resource without additional sequencing.

Mapping genes to BACs

BLASTX searches of the 20 366 BES resulted in 2351 BES with significant hits to 1877 unique genes. Of the 1877 gene hits, 1130 had an *E*-value smaller than e^{-10} in BLASTX searches with average alignment length of 73 amino acids and a range of 31–100% identity. An additional 747 gene hits were identified with an *E*-value between e^{-5} and e^{-10}, but these hits in many cases involved either short, high-quality alignments or long, highly divergent alignments.

In addition to unique BLASTX hits, we also found multiple BES (2–77) that hit a single gene. At the lower range, this result can be explained by redundant sequencing of the same gene harboured in different BAC clones in the 10X coverage library or by gene duplication. However, for some gene hits, a large number of BES were involved. For instance, six genes were hit by 10 or more BES, indicating the presence of large families or multiple copies of these genes in the catfish genome. BLASTX searches indicated their putative identities were *neurotactin* (10 hits), *CCHC-type and RNA-directed DNA polymerase* (15 hits), *gephyrin* (18 hits), *senescence-associated protein* (45 hits) and *rRNA intron-encoded homing endonuclease* (77 hits). Searches of the zebrafish and *Tetraodon* genomes revealed that all these genes existed in large copy numbers, suggesting conservation of large gene copy numbers or gene families in catfish as well.

Anchoring of channel catfish BES to zebrafish and *Tetraodon* genome sequences

BLASTN searches of the catfish BES against zebrafish and *Tetraodon* genome sequences resulted in 3251 (16%) and 1670 (8.2%) significant hits ($E < e^{-5}$) respectively. Repeated hits were then removed, resulting in 1074 unique significant hits to the zebrafish genome sequence. Similar BLAST searches against the *Tetraodon* genome resulted in 773 unique significant hits, suggesting that the number of genomic regions containing evolutionarily conserved sequences was greater between catfish and zebrafish than between catfish and *Tetraodon*, consistent with their phylogenetic relationships.

Of the 1074 unique significant hits to the zebrafish genome, 417 (38.8%) had significant BLASTX hits. Similarly, with *Tetraodon*, of the 773 unique significant hits, 406 had significant BLASTX hits. The similarity in number of significant BLASTX hits with the zebrafish and the *Tetraodon* genomes suggested that the majority of genes were conserved among catfish, zebrafish and *Tetraodon*. The greater number of unique BLASTN hits to the zebrafish genome was accounted for, in the most part, by non-gene genomic sequences, which reflects the level of conservation between the catfish and the zebrafish genomes.

To develop a set of gene markers for potential comparative genome analysis, the catfish BES were searched against the chromosomes of the zebrafish and *Tetraodon* genomes. The catfish BES had significant BLASTN hits to each of the 25 zebrafish chromosomes with a range of 16–66 hits per chromosome (Table 1). BLASTX searches against the NR database using catfish BES with unique BLASTN hits to the zebrafish genome resulted in 4–30 significant hits per chromosome. Similar but fewer unique hits were found with the *Tetraodon* genome (Table 1). Notably, only a single significant hit with BLASTN or BLASTX was found with *Tetraodon* chromosome 20, likely due to the small size of the chromosome and its low sequence coverage to date (http://www.genoscope.cns.fr/externe/tetranew/).

Discussion

Catfish and zebrafish, as Ostariophysian fishes, share much closer evolutionary relationships than does zebrafish with other fish model species, medaka, *Tetraodon* and *Takifugu*. One would predict, therefore, that the catfish and zebrafish genomes would show high levels of conservation. If catfish demonstrates high syntenic conservation with zebrafish, the future tasks of mapping and assembling the catfish genome would be simplified. Additionally, both catfish and zebrafish researchers could benefit from an exchange of information on gene duplication and divergence. In particular, a major catfish transcriptome project is ongoing with the Joint Genome Institute (JGI) for the sequencing of 600 000 ESTs. Once the physical framework is established, along with the anticipated identification of the vast majority of catfish genes through the JGI project, catfish genome information could be a substantial comparative resource for the studies of teleost genomes. The only points of genomic comparison between the two species prior to BAC-end sequencing have been small gene-based sequencing reports (e.g. Peatman *et al.* 2006; Wang *et al.* 2006a). The catfish BES provided a resource for anchoring catfish genomic sequences to the zebrafish and *Tetraodon* genomes. Over 3200 significant BLASTN hits were generated with the zebrafish genome sequence. Concentrating on unique hits alone, we gener-

Table 1 Distribution of unique BAC-end sequence (BES) significant BLASTN hits in the *Danio rerio* and *Tetraodon nigroviridis* genomes (the cut-off value was set at e^{-5}).

	Zebrafish		*Tetraodon*	
Chromosome	Unique BLASTN hits	BLASTX hits of catfish BES with unique BLASTN hits	Unique BLASTN hits	BLASTX hits of catfish BES with unique BLASTN hits
1	58	22	44	32
2	39	13	55	27
3	58	28	36	19
4	36	14	13	10
5	66	27	23	13
6	40	21	15	4
7	56	22	20	11
8	36	15	20	14
9	59	24	23	12
10	42	16	32	21
11	38	15	21	11
12	37	16	24	16
13	45	16	74	17
14	54	16	14	9
15	31	9	30	25
16	53	18	23	15
17	47	15	16	9
18	28	4	21	14
19	44	20	10	8
20	52	30	1	1
21	34	10	19	14
22	28	11		
23	54	20		
24	23	7		
25	16	8		
Undesignated			239	104
Total	1074	417	773	406

ated 1074 hits with the zebrafish genome. Only 417 of the hits appeared to be genes as revealed by BLASTX searches. The majority of these significant hits were to non-gene regions, indicating strong genome similarities between catfish and zebrafish.

The catfish genome contains a significantly lower proportion of repetitive elements when compared with the genomes of mammals. The fraction of repeat bases in the set of catfish BES was approximately 12% using REPEATMASKER with the zebrafish and *Takifugu* repeat databases. Even using the mammalian repeat database, overall masked repeats were still below 15%. Clearly, this fraction was underestimated, most likely because of the low ability of BAC-end sequencing to detect tandem repeats. We previously described the presence of a major class of tandem repeats named *Xba* elements (Liu *et al.* 1998) that accounted for about 5% of the catfish genome. These elements were not detected in the BES, because they lack the *Eco*RI restriction sites necessary for insertion into BAC clones. One might also argue that catfish may contain specific repeat types that would not have been detected by REPEATMASKER using existing repeat databases. However, extensive BLAST searches of the catfish BES against themselves did not result in the identification of highly repetitive elements except a few major multigene families (data not shown). Therefore, catfish genomes may harbour a significantly lower fraction of repetitive elements than mammals. Repetitive element percentages of 47% and 37% were found in cattle BES (Larkin *et al.* 2003) and mouse BES (Zhao *et al.* 2001) respectively. This result appears consistent with the overall smaller genome size of catfish in comparison with mammals.

Integration of physical and linkage maps can be approached from several directions. Markers from a linkage map can be hybridized to BAC libraries used in physical mapping, or markers discovered by sequencing BACs, if polymorphic, can be placed onto linkage maps. This study demonstrated that BAC-end sequencing was a highly efficient method for marker generation, gene localization and eventual map integration. We have in previous research utilized overgo hybridizations (Bao *et al.* 2005, 2006; Xu *et al.* 2005) to the catfish BAC library for gene localization (Baoprasertkul *et al.* 2005; Bao *et al.* 2005; Wang *et al.* 2006b). Despite efforts to increase efficiency by using a

two-dimensional design, only several dozen genes have been mapped to BAC clones to date. In contrast, at least 1130 genes were identified in the catfish BES. We also expect that mapping microsatellites uncovered in the BES to linkage maps will prove to be significantly more efficient than hybridizing microsatellite markers from the linkage maps to BACs. Attempts to use this latter approach in Atlantic salmon proved to be too labour intensive and were complicated by an abundance of repetitive elements in the genome (William Davidson, Simon Fraser University, personal communication). This set of BES should provide a solid foundation for future physical mapping, map integration and comparative genomics in catfish.

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Supplementary Material

The following supplementary material is available online at http://www.blackwell-synergy.com:

Table S1 Repeat composition of the channel catfish genome BAC-end sequences as assessed by REPEATMASKER using the combined repeat database of zebrafish and *Takifugu rubripes*.