

Research Advances of Fish Genomics in China [Version 2]

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Abstract

Recent advances in DNA sequencing with higher efficiency and lower cost, along with the advanced developments in bioinformatics, enable us to effectively sequence and assemble the whole genome of any organism, including fish. Since the first fish (zebrafish) genome report in 2001, whole genomes of up to 40 fish species had been published thus far. Chinese scientists have contributed over 10 of them within the past 3 years (2014-2016), and large-scale genomics projects to sequence ~100 fish genomes and ~1,000 fish transcriptomes were initiated in China. In this review, we provide a brief summary of the recent advances of fish genomics in China, and anticipate how these genomic researches speed up their applications in basic science and important economic fields (such as molecular breeding and drug discovery).

Keywords

Fish; Whole Genome Sequencing; Transcriptome Sequencing; China

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Introduction

Fishes, with nearly 33,300 species recorded in Fish Base (<http://www.fishbase.org>), represent over 50% of all known vertebrate creatures [1] and show a great diversity in phylogeny, morphology, and ecology. As a consequence, tremendous attentions have been obtained by them for an extensive range of basic and applied scientific proposes. The recent advances in DNA sequencing enable higher efficiency and lower cost for generating whole genome sequences of any organisms. Therefore, whole genome sequencing (WGS) has been widely applied to various fish species, ranging from the model species zebrafish (*Danio rerio*) [2] and medaka (*Oryzias latipes*) [3] to commercially or ecologically important species such as the common carp (*Cyprinus carpio*) [4] and Japanese eel (*Anguilla japonica*) [5]. By far, genomes of nearly 40 fish species have been published by researchers all over the world (Table 1).

Among the above-mentioned fish genomes, more than 10 were finished by Chinese groups, suggesting a great contribution from the Chinese scientists to the global fish genomic study. Interestingly, the Chinese genome papers had been published within a recent narrow period (2014-2016), and BGI (the biggest genomics research center in the world) has been involved in most of the works.

Table 1: List of fishes with published genome data (updated by September 2016).

| No. | Scientific name | Common name | Citation |
|-----|--------------------------------------|-------------------------------|--|
| 1 | <i>Anguilla japonica</i> | Japanese eel | Henkel et al. 2012 [5] |
| 2 | <i>Astatotilapia burtoni</i> | Burton's mouthbrooder | Brawand et al. 2014 [6] |
| 3 | <i>Astyanax mexicanus</i> | Mexican tetra | McGaugh et al. 2014 [7] |
| 4 | <i>Boleophthalmus pectinirostris</i> | Great blue-spotted mudskipper | You et al. 2014 [8] |
| 5 | <i>Clupea harengus</i> | Atlantic herring | Barrio et al. 2016 [9] |
| 6 | <i>Ctenopharyngodon idellus</i> | Grass carp | Wang et al. 2015 [10] |
| 7 | <i>Cynoglossus semilaevis</i> | Tongue sole | Chen et al. 2014 [11] |
| 8 | <i>Cyprinus carpio</i> | Common carp | Xu et al. 2014 [4] |
| 9 | <i>Danio rerio</i> | Zebrafish | Howe et al. 2013 [2] |
| 10 | <i>Dicentrarchus labrax</i> | European seabass | Tine et al. 2014 [12] |
| 11 | <i>Electrophorus electricus</i> | Electric eel | Gallant et al. 2014 [13] |
| 12 | <i>Esox lucius</i> | Northern pike | Rondeau et al. 2014 [14] |
| 13 | <i>Gadus morhua</i> | Atlantic cod | Star et al. 2011 [15] |
| 14 | <i>Gasterosteus aculeatus</i> | Three-spined stickleback | Jones et al. 2012 [16] |
| 15 | <i>Ictalurus punctatus</i> | Channel catfish | Liu et al. 2016 [17], Chen et al. 2016 [18] |
| 16 | <i>Larimichthys crocea</i> | Large yellow croaker | Wu et al. 2014 [19], Ao et al. 2015 [20] |
| 17 | <i>Lates calcarifer</i> | Barramundi perch | Domingos et al. 2015 [21] |
| 18 | <i>Latimeria chalumnae</i> | African coelacanth | Amemiya et al. 2013 [22] |
| 19 | <i>Maylandia zebra</i> | Zebra mbuna | Brawand et al. 2014 [6] |
| 20 | <i>Neolamprologus brichardi</i> | Lyretail cichlid | Brawand et al. 2014 [6] |
| 21 | <i>Nothobranchius furzeri</i> | Turquoise killifish | Harel et al. 2015 [23] |
| 22 | <i>Notothenia coriiceps</i> | Black rockcod | Shin et al. 2014 [24] |
| 23 | <i>Oncorhynchus mykiss</i> | Rainbow trout | Berthelot et al. 2014 [25] |
| 24 | <i>Oreochromis niloticus</i> | Nile tilapia | Guyonet et al. 2012 [26] |
| 25 | <i>Oryzias latipes</i> | Japanese medaka | Kasahara et al. 2007 [3] |
| 26 | <i>Periophthalmodon schlosseri</i> | Giant mudskipper | You et al. 2014 [8] |
| 27 | <i>Periophthalmus magnuspinnatus</i> | Giant-fin mudskipper | You et al. 2014 [8] |
| 28 | <i>Poecilia reticulata</i> | Guppy | Fraser et al. 2015 [27] |
| 29 | <i>Pseudopleuronectes yokohamae</i> | Marbled flounder | Arthofer et al. 2015 [28] |
| 30 | <i>Pundamilia nyererei</i> | Flame back cichlid | Brawand et al. 2014 [6] |
| 31 | <i>Salmo salar</i> | Atlantic salmon | Davidson et al. 2010 [29] |
| 32 | <i>Scartelaos histophorus</i> | Walking goby | You et al. 2014 [8] |
| 33 | <i>Scleropages formosus</i> | Asian bonytongue | Austin et al. 2015 [30], Bian et al. 2016 [31] |
| 34 | <i>Sinocyclocheilus anshuensis</i> | Golden-line barbell (Anshui) | Yang et al. 2016 [32] |
| 35 | <i>Sinocyclocheilus grahami</i> | Golden-line barbell (Dianchi) | Yang et al. 2016 [32] |
| 36 | <i>Sinocyclocheilus rhinoceros</i> | Golden-line barbell (Xijiao) | Yang et al. 2016 [32] |
| 37 | <i>Takifugu rubripes</i> | Torafugu | Kai et al. 2011 [33] |
| 38 | <i>Tetraodon nigroviridis</i> | Spotted green pufferfish | Jaillon et al. 2004 [34] |
| 39 | <i>Thunnus orientalis</i> | Pacific bluefin tuna | Nakamura et al. 2013 [35] |
| 40 | <i>Xiphophorus maculatus</i> | Southern platyfish | Schartl et al. 2013 [36] |

Background and History of Whole Genome Sequencing

In the original era of fish genomes, the Sanger sequencing with the whole genome shotgun strategy was the most prevailing approach for sequencing the fish genomes, like medaka [3] and Tetraodon [34] genomes. As the first generation of sequencing platform, the ABI3730 adopting the technology of Sanger sequencing can yield long and highly accurate sequencing reads. Nevertheless, its limited throughput and the high costs of sequencing provided large barriers for massive scientists who had great interests for genome researches of fish species. Due to the rapid advancements of sequencing technology, the next generation sequencing (NGS) platforms, such as Illumina Hiseq, ABI SOLiD and Roche454, which gradually dominated the sequencing area because they can generate extremely high-throughput reads with low sequencing fee.

Compared with other NGS platforms, the Hiseq platform have been considered as the most outstanding representative with remarkable ability to yield longer reads than SOLiD and also with lower error rates than Roche454. Almost all the published fish genomes from Chinese scientists were sequenced by the Hiseq platform. Hiseq Xten, as the most advanced Hiseq platform by far, can yield 800 ~ 900 Gb data within 3 days and 1,000 dollars of expenditure. Generally speaking, the most popular Hiseq platforms in China have been facilitating the efficiency of genome sequencing and improving the Chinese fish genomic studies.

Fish Genomes Sequenced and Published by Chinese Scientists

Chinese scientists initiated their first fish genome paper in 2014 and the target species was the half-smooth tongue sole (*Cynoglossus semilaevis*) [11], which is also the world's first sequenced pleuronectiformes fish. The high-quality genome assembly uncovered that sex chromosomes of this fish were derived from the same ancestral vertebrate protochromosome as the avian W and Z chromosomes, and *dmrt1* was proposed to be an important sex-determining gene in the tongue sole as in chicken on basis of comparative genomic analysis.

In the same year, WGS data of representative mudskippers, one from each of the four genera (*Boleophthalmus*, *Scartelaos*, *Periophthalmodon* and *Periophthalmus*), were generated by our group. The assembled genome sizes of the four species were 0.966, 0.715, 0.720 and 0.683 Gb, respectively [8]. Comparative analysis among the four mudskippers revealed that several genetic changes are associated with their terrestrial adaptation, including loss and mutations in vision genes, expansion of innate immune genes, and positive selection of genes involved in ammonia excretion pathways.

Also in 2014, the genome of Chinese large yellow croaker (*Larimichthys crocea*) was firstly sequenced and assembled into

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a 728-Mb genome holding 19,362 protein coding genes [19]. Further genomic, transcriptomic and proteomic analyses uncovered a well-developed innate immune system in this fish. In the next year, another Chinese group (including us) sequenced and assembled a high-quality genome of this fish using a bacterial artificial chromosome (BAC) and whole-genome shotgun hierarchical strategy, and finally obtained a 679-Mb genome holding 25,401 protein coding genes [20]. Our improved data showed that in addition to the previously mentioned innate immune system [19], the fish also owns a well-established adaptive immune system with the majority of the Th1, Th2 and CD8⁺ T cell-related genes identified in the genome [20].

Chinese groups also sequenced the genomes of two carps, which are on the list of “four major Chinese carps”, in 2014 and 2015. Xu et al. [4] provided a draft genome for domesticated common carp (*Cyprinus carpio*), whose genome size was estimated to be 1.69 Gb and contained 52,610 protein-coding genes. Genomic resequencing of 33 individuals from 10 representative strains worldwide suggested a single origin for *C. Carpio* in 2 subspecies (*C. Carpio Haematopterus* and *C. Carpio-carpio*). Genomic as well as transcriptomic analyses were performed to identify genetic loci, functional genes and signaling pathways related to scaling patterns and skin color. Wang et al. [10] generated a 0.9-Gb genome assembly of a gynogenetic female adult and a 1.07-Gb draft genome of a wild male adult of grass carp (*Ctenopharyngodon idellus*), and proposed that the grass carp was divided from zebrafish at 49-54 million years ago. The paper also provided genetic basis for the grass carp’s transfer from a carnivorous to an herbivorous diet.

At the beginning of 2016, WGS of three *Sinocyclocheilus* species (*S. Grahami*, *S. Rhinocerosus* and *S. Anshuiensis*) were reported by our group aiming to unveil the mystery of cave life [32]. Genomes of the three fishes were a bit larger than expected with sizes of 1.75, 1.73 and 1.68 Gb, respectively. Comparative analysis among these species uncovered some important genetic changes (such as gene loss, pseudogenes, mutations, deletions and down-regulation) for the cave adaptation, and provided a fundamental resource for a better understanding of cave fish biology.

In 2016, a high-quality chromosome-level reference genome of the golden arowana [31; Li et al., accepted for publication in Scientific Data], and draft genomes of red and green arowana [31] were assembled. The genome sizes were estimated to be 779, 753 and 759 Mb respectively. The Phylogenomic analysis proposed a novel idea to support a sister group relationship between Osteoglossomorpha (*bony tongues*) and Elopomorpha (eels and relatives), with the two clades together forming a sister group of Clupeocephala which includes all the remaining teleosts. The genomic sequences combined with karyotype analysis identified putative sex chromosomes and suggested a ZW/ZZ sex determination in the Asian arowana.

Independent of the American group [17], we published the WGS data of channel catfish (*Ictalurus punctatus*) in the August of 2016 [18]. Our group sequenced the genome from an individual inbred in China for more than three generations, although it was originally imported from the North America. The obtained high-quality genome sequences, comparable to those reported for the “Coco” channel catfish [17], were assembled to be 845 Mb covering 66,332 contigs and 31,979 scaffolds, with a contig N50 of 48.5 kb and a scaffold N50 of 7.2 Mb [18].

On-going Fish Genomes and Large-Scale Projects in China

In addition to these published genomic data and papers produced by Chinese groups, more genome manuscripts have been submitted or even accepted for publication although they are not yet available now. For example, WGS data of tiger tail seahorse (*Hippocampus comes*), accepted for publication in Nature with partial contribution from us, showed that it’s the fastest-evolving fish sequenced so far and the specific gene (*tbox4*) related to the ‘pelvic fin-loss’ phenotype has been functionally proved after knocking out the gene in zebrafish (Lin Q. et al., unpublished data). In-depth WGS of the Chinese ricefield eel (*Monopterus albus*), along with our subsequent analysis on evolutionary origin and trajectories of the Z chromosome, clarified a molecular mechanism of developmental activation of male sex through spatiotemporal expression of four types of genes on the Z chromosomes (Luo M. et al., unpublished data). Genome and transcriptome sequencing of the Japanese flounder (*Paralichthys olivaceus*) pointed to several signaling pathways that are involved in the establishing of asymmetric pigmentation (Shao C. et al., unpublished results). WGS of the Chinese clear head icefish (*Protosalanx hyalocranius*) has also been completed by our group, and the genome provides a valuable genetic resource to reveal molecular mechanisms for the cavefish-like characters in this migratory fish (Liu K. et al., unpublished data).

China has been continuing to fulfill fish genomic researches by establishing large-scale genome and transcriptome projects. For example, the China Aquatic 10-100-1,000 Genomics Program is a joint scientific project, initiated by Chinese Academy of Fishery Sciences (CAFS) and Shenzhen BGI Fisheries Sci & Tech Co. Ltd. (BGI Fisheries) in 2016, with the principal aim to conduct molecular breeding of ~10 aquaculture species and complete whole genome sequencing of ~100 and transcriptome sequencing of ~1,000 aquatic species (recently an instructive white paper was submitted to Science China; Liu Y. et al., unpublished data). Our group at the BGI Fisheries, as the core initiator of the 10-100-1,000 program, is also leading the Fish-T1K (Transcriptomes for 1,000 Fishes) project (<http://www.fisht1k.org>), in which we have sequenced transcriptomes of more than 140 fish species by far [37] covering about 110 families and 51 orders.

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Prospects

These genomic data are going to lay a solid foundation for many basic and applied researches on fishes. For example, while using the reference genome of Chinese orange-spotted grouper (*Epinephelus coioides*; Zhang Y. et al., unpublished data) and restriction-site associated DNA (RAD) sequencing, we constructed high-density genetic linkage maps [38,39], along with identification of 27 significant growth-related quantitative trait loci (QTLs) and 17 putative genes [39]. These results could promote the development of marker-assisted selection (MAS) program for molecular breeding of groupers in China. Genomic, transcriptomic and proteomic studies on Chinese yellow catfish helped us to identify 15 putative toxin proteins [40], which may serve as novel active ingredients for drug development. Based on the available genomic data from a variety of fish species, we conducted comparative analysis on some important enzymes, for instance, the aralkylamine *N*-acetyl transferase [41] related to melatonin synthesis and biological rhythms, to interpret the molecular evolution of specific genes. In addition, our genomic and transcriptomic data were also valuable for unveiling the molecular mechanisms of some biological traits, including the growth superiority in a novel grouper hybrid [42] and formation of the arm-like pectoral fins in amphibious mudskippers [43].

We are definitely sure that more and more fish genomes and transcriptomes will be sequenced at a faster and faster pace within the coming years. Omics data and the deeper understanding of fishes enabled by them will eventually contribute to the related practical applications for human lives, such as providing new breeds of economically important species, novel components for medical drugs, special insights into the origin and evolution of vertebrates, and possible solutions to the protection of the endangered species and sustention of the ecosystem.

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