Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part D

journal homepage: www.elsevier.com/locate/cbpd

Review

Development of genomic resources in support of sequencing, assembly, and annotation of the catfish genome☆

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ARTICLE INFO

Article history:
Received 15 February 2010
Received in revised form 15 March 2010
Accepted 16 March 2010
Available online 25 March 2010

Keywords:
Catfish
Fish
Genome
EST
Marker
Physical map
Linkage map

ABSTRACT

Major progress has been made in catfish genomics including construction of high-density genetic linkage maps, BAC-based physical maps, and integration of genetic linkage and physical maps. Large numbers of ESTs have been generated from both channel catfish and blue catfish. Microarray platforms have been developed for the analysis of genome expression. Genome repeat structures are studied, laying grounds for whole genome sequencing. USDA recently approved funding of the whole genome sequencing project of catfish using the next generation sequencing technologies. Generation of the whole genome sequence is a historical landmark of catfish research as it opens the real first step of the long march toward genetic enhancement. The research community needs to be focused on aquaculture performance and production traits, take advantage of the unprecedented genome information and technology, and make real progress toward genetic improvements of aquaculture brood stocks.

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Contents

1. Introduction . . . 11
2. The catfish industry in the United States . . . 12
3. Important catfish traits and the need for genome-based tools for selection . . . 12
4. Development of DNA markers . . . 13
5. Development of catfish genome resources in support of the whole genome sequence assembly . . . 13
 5.1. Linkage mapping of the catfish genome . . . 13
 5.2. Physical mapping of the catfish genome . . . 13
 5.3. BAC-end sequences . . . 13
 5.4. Integration of genetic linkage and physical maps . . . 13
 5.5. Genome repeat structures . . . 13
6. Development of catfish genome resources in support of the whole genome sequence annotation . . . 14
 6.1. EST resources . . . 14
 6.2. Full-length cDNAs . . . 14
 6.3. Microarrays and functional studies . . . 14
 6.4. Characterization of catfish genes . . . 14
7. Whole genome sequencing . . . 14
8. Concluding remarks . . . 15
Acknowledgements . . . 15
References . . . 15

1. Introduction

The availability of a draft whole genome sequence significantly enhances genome research and applications of genome-based technologies for improving agricultural production and quality. As such, whole

☆ This paper stems from a presentation at the Genomics in Aquaculture Symposium held at Bodø on 5th–7th July 2009. This was the first international meeting devoted exclusively to this field and it was funded by the Research Council of Norway (grant 192126/S40).

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1744-117X/$ – see front matter © 2010 Elsevier Inc. All rights reserved.
doi:10.1016/j.cbd.2010.03.001

genome sequences are available or nearly available for major livestock species including cattle, swine, chicken, and horse. With the recent advances in sequencing technologies, it is likely that draft genome sequences will be made available for all agriculturally important species in the near future including those of aquaculture species.

In spite of its importance, whole genome sequencing with aquaculture species has lagged behind other species. However, more than a decade of preparation coupled with advances in sequencing technology has led to rapid recent progress. Of the six aquatic species groups included in the US Animal Genome NRSP-8 program, whole genome sequencing projects are underway for at least four: tilapia, Atlantic salmon, catfish, and oyster. The tilapia-genome project was funded by NIH, and it is being sequenced at the Broad Institute (http://www.broad.mit.edu/science/projects/mammals-models/vertebrates-invertebrates/tilapia/ tilapia-genome-sequencing-project). Organized by the Oyster Genome Consortium, the oyster genome is being sequenced at the Beijing Genome Institute (http://www.intl-pag.org/17/abstracts/W45_PAGXVII_329.html). Sequencing of the Atlantic salmon genome is more complex as the salmon genome is derived from a whole genome duplication approximately 20–120 million years ago (Ohno, 1970; Allendorf and Thorgaard, 1984). However, highly productive research projects, particularly those funded by Genome Canada, have prepared a solid foundation for sequencing the salmon genome. Recent communications with Dr. Willie Davidson (Simon Fraser University) and Ben Koop (University of Victoria) confirmed the initiation of salmon genome sequencing as a cooperative project between Canada, Norway, and Chile. Several countries including China, Thailand, Japan, and the US are discussing strategies for sequencing the shrimp genome.

The Blueprint for USDA Efforts in Agricultural Animal Genomics calls for the production of a draft genome sequence for catfish, and the drastic reduction in sequencing costs recently has made it now possible to sequence the whole genome of catfish. Very recently, USDA approved funding for the generation of channel catfish whole genome sequence using the next generation sequencing. However, the usefulness of the whole genome sequence relies on the efficient sequence assembly and adequate sequence annotation, which in turn depends on the availability of a number of genome resources. In this communication, I will focus on several major lines of research leading to the development of genome resources in catfish in recent years in support of the whole genome sequencing, assembly, and annotation.

2. The catfish industry in the United States

Catfish is the primary aquaculture species in the U.S., accounting for over 60% of all US aquaculture production (USDA, 2000, 2006). Catfish production includes channel catfish (*Ictalurus punctatus*), blue catfish (*I. furcatus*), and their F1 hybrid. However, the major species in aquaculture production is channel catfish. The channel catfish female x blue catfish male F1 hybrid catfish exhibit a high level of heterosis and is a preferred genotype for aquaculture production, but due to reproduction isolation, artificial fertilization is required for the production of the interspecific hybrid. Major progress has been made in recent years for the efficiency of the hybrid production, but the quantities produced are still not sufficient for the entire catfish industry. The catfish industry is valued at approximately two billion dollars with value added, and 509 million pounds were processed in 2008. Catfish is one of the top agricultural commodities and in the southeastern United States, particularly so in the state of Mississippi and Alabama.

In recent years, the catfish industry in the United States has encountered unprecedented challenges due to devastating diseases, high feed and energy costs, and fierce international competition. As a result, both the production and acreage has declined somewhat from the industry high record set in 2003. For instance, total catfish production had a reduction of 28% in 2008 compared to the best production year in 2003. The acreage has reduced from 115,000 acres to 67,000 acres during the last 7 years accounting for 40% in reduction. Many catfish producers are not profitable due to the very high feed costs and energy and transportation costs. Therefore, genetically enhanced brood stocks are needed, along with the best practices involving all the steps from ponds to plates.

3. Important catfish traits and the need for genome-based tools for selection

Several performance and production traits are very important for the catfish industry including, but not limited to, growth rate, feed conversion efficiency, disease resistance, processing yield, seinability, stress tolerance, and tolerance to low dissolved oxygen. Growth rate is a primary trait for production because producers need to complete the production cycle in approximately 18 months to allow aquaculture ponds to be used with two years for a single crop. As feed accounts for over 50% of all variable costs, enhanced feed conversion efficiency will help to reduce feed costs and increase profit margins. Disease problems constitute the largest single cause of economic losses in aquaculture. Diseases cause major losses, up to one third of the industry every year. Enteric septicemia of catfish (ESC) caused by *Edwardsiella ictaluri* and columnaris disease caused by *Flavobacterium columnare* are the major causes of losses. In addition, channel catfish virus disease, the protozoan parasite *Ichthyophthirius multifiliis*, and motile aeromonad septicemia caused by *Aeromonas hydrophila* can also cause major economic losses. Processing yield is important because most catfish are processed into fillet for marketing. Seinability is a very important trait because any fish that is left in the pond after seining can significantly reduce the feed conversion efficiency. Stress tolerance and low dissolved oxygen tolerance are important because these traits affect survival rates and affect energy consumption due to the use of aerators. Stress tolerance is also important immediately before processing of catfish during transportation because stress of catfish can lead to the so-called red flesh disease, a consequence of high levels of stress during harvesting and transportation immediately before processing. While most of these traits can be affected by the environment and environment x genotype interactions, genetic factors play a crucial role in determination of many of these traits.

Genetic selection holds great potential to improve production efficiency in farm-raised catfish. Although current breeding stocks have retained a considerable amount of genetic variation as measured by allelic heterozygosity, outbred catfish stocks are readily accessible in freshwater systems. Molecular markers linked to favorable genetic variation can be used for broodstock selection for traits that have low heritability, or are difficult, expensive, or lethal to measure (e.g. resistance to pathogen infection, carcass yield). Marker-assisted selection depends on the identification of marker alleles that are in linkage disequilibrium with alleles that positively influence production phenotypes. Such markers can serve as proxies for desired haplotypes, but become useless if linkage disequilibrium is disrupted or if the marker allele is not present in the population of interest. These caveats are less likely as marker density increases throughout the genome, ultimately to the level of complete genome sequence. Because catfish stocks are relatively outbred compared with traditional livestock species, haplotype blocks will likely be smaller. Therefore high marker densities are required throughout the genome in order to effectively select for beneficial haplotypes.

Although channel catfish is the major species used in aquaculture, blue catfish possess several superior traits including high resistance against ESC disease, greater processing yield due to its uniform body shape, and high seinability due to its higher position in the water column than channel catfish. The interspecific hybrid catfish are fertile, and as a matter of fact, higher generations of hybrid catfish have been produced. Therefore, interspecific introgression is a viable breeding strategy to introgress genes involved in the superior traits harbored by blue catfish. Toward this direction, genetic linkage mapping has been conducted in the interspecific resource families (Liu et al., 2003; Kucuktas et al., 2009).

4. Development of DNA markers

In the past decade, one of major efforts of catfish genome research was to develop polymorphic markers (reviewed by Liu and Cordes, 2004). Much of this effort in the early days of catfish genome research was devoted in marker types that were readily available without the availability of genome information or resources. This included the application of RAPD and AFLP markers (Liu et al. 1998a,b, 1999a,b; reviewed by Liu, 2003). These efforts certainly contributed to the genome program development at that time, but in terms of polymorphic DNA markers in the long term, these dominant markers are not very useful. Since 1997, great effort has been devoted to microsatellite development in catfish. Several approaches were adopted including construction of microsatellite-enriched genomic libraries (Waldbieser and Bosworth, 1997; Liu et al., 1999c,d; Tan et al., 1999;), targeted sequencing (Serapion et al., 2004a), and identification of microsatellites through data mining using genome resources such as expressed sequence tags (ESTs) or BAC-end sequences (Liu et al., 1999e; Serapion et al., 2004b; Xu et al., 2006; Li et al., 2007; Somridhivej et al., 2008; Liu et al., 2009; Wang et al., 2010). It is now clear that the largest numbers of useful microsatellites have been obtained through genome sequence surveys such as BAC-end sequencing, and through EST data mining.

Most recently, the effort of marker development was shifted to the identification of single nucleotide polymorphism (SNPs, He et al., 2003). This shift was driven by the demand of even larger numbers of polymorphic markers at the level of tens of thousands or hundreds of thousands, and by the demand of automated genotyping for a large number of markers and a large number of genomes. In the absence of a whole genome sequence, we have used EST resources to mine SNPs (Wang et al., 2010) and identified over 300,000 putative SNPs. However, a key issue of EST-derived SNPs is the possibility of sequencing errors that are subsequently interpreted as potential SNPs by data mining. In order to circumvent this problem, we have established quality standards for EST-derived SNPs. It appears that two factors are the most important: the contig size and the minor sequence allele frequency. Contigs with at least four sequences with the minor allele sequence being represented at least twice provided a high rate of SNP validation (Wang et al., 2008). Most recently, we have started sequencing of reduced representation libraries to generate additional SNPs. However, we believe that generation of whole genome sequence using the next generation sequencing technology with a high level of genome coverage is the most efficient way of producing the highly needed SNPs. This work is now in progress.

5. Development of catfish genome resources in support of the whole genome sequence assembly

A number of genome resources are required in support of efficient whole genome sequence assembly. In catfish, these resources included genetic linkage maps constructed in channel catfish and channel x blue catfish backcross populations, two BAC contig-based physical maps that are to be integrated to reduce the number of contigs, a large database of BAC-end sequences, integrated genetic and physical maps, and a large database of EST sequences. In addition, we have characterized the structure of interspersed repeats in the catfish genome.

5.1. Linkage mapping of the catfish genome

On the basis of the framework linkage maps constructed several years ago (Waldbieser et al., 2001; Liu et al., 2003), we have recently made significant progress in linkage mapping. Such progress includes placing 331 gene-associated markers to 29 linkage groups (Kucuktas et al., 2009). With the availability of a large number of microsatellite sequences within BAC-end sequence, over 2000 microsatellites have been placed on the genetic linkage map, allowing establishment of scaffolds of the catfish genome (Ninwichian et al., in preparation). This genetic linkage map will serve to validate the whole genome assembly and anchor the assembly to chromosomes.

5.2. Physical mapping of the catfish genome

Two channel catfish BAC libraries have been constructed and characterized (Quiniou et al., 2003; Wang et al., 2007). BAC contig-based physical maps of the channel catfish genome have been generated using high information content fingerprinting (Quiniou et al., 2007; Xu et al., 2007). Fingerprinting of 46,548 BAC clones (6.8× genome coverage) from the CCBL1 BAC library developed from an inbred meiotic gynogen permitted the assembly of 1782 contigs (Quiniou et al., 2007). Fingerprinting of 34,580 BAC clones (5.6X genome coverage) from CHORI 212 BAC library developed from an outbred male permitted assembly of 3307 contigs (Xu et al., 2007). The CCBL1 BAC library was based on *Hin*dIII partial digestion of genomic DNA while the CHORI 212 BAC library was based on *Eco*RI partial digestion, so we expect many genomic regions not covered within one library could have been covered in the other. We plan to integrate these physical maps to close some gaps.

5.3. BAC-end sequences

Over 61 Mb of BACX end sequences have been generated using Sanger sequencing (6% of catfish genome) with 103,000 BAC-end sequences from the two catfish BAC libraries (Xu et al., 2006; Liu et al., 2009; Quiniou, unpublished data). The total BAC-end sequences represent, on average, one sequence tag per 9.7 kb of the catfish genome. The majority of BAC-end sequences (88,000 sequences from 44,000 BAC clones) were mate-paired and thus highly useful for assisting the whole genome assembly.

5.4. Integration of genetic linkage and physical maps

We have identified a large number of microsatellites from BAC-end sequences (Somridhivej et al., 2008; Liu et al., 2009). To date, we have placed over 2000 BAC-end-associated microsatellites on the linkage map. Thus almost two-thirds of the CHORI212 BAC contigs have been placed on the linkage map to establish BAC scaffolds. These scaffolds contain large numbers of BAC-end sequences, and they will be extremely useful in guiding the assembly of the reference whole genome sequence. The existing linkage and physical maps, along with the BAC-end sequences, will serve as a framework for the whole genome sequence assembly, and the sequence assembly will permit additional BAC-end anchored microsatellites and SNP markers to be mapped *in silico*.

5.5. Genome repeat structures

While we do not have a complete understanding of the genome repeat structure in catfish, we have characterized several major classes of repeats in the catfish genome. The most abundant repeat class is an approximately 325 bp A/T-rich *Xba* element with approximately 150,000 copies in the catfish genome arranged in head-to-tail tandem arrays primarily in centromeric regions (Liu et al., 1998c; Quiniou et al., 2005). The catfish genome also contains approximately 9000 copies of 57-bp *Mermaid* and approximately 1200 copies of 64-bp *Merman* elements, which are short interspersed repetitive elements found in many bony fish (Kim et al., 2000). We reported a highly abundant (32,000 copies) non-autonomous *Tc1*-element named *Tipnon* (Liu et al., 1999f) dispersed in the catfish genome. Through genome sequence surveys using BAC-end sequences, we estimated that Tc-1/mariner DNA transposons are the major dispersed repetitive elements, representing approximately 4–5% of catfish genome sequence (Xu et al., 2006; Nandi

et al., 2007; Liu et al., 2009). EST analysis indicated that the Tc-1 elements are associated with 0.6% of the catfish transcripts (Nandi et al., 2007). Such information is crucial not only for entire genome sequencing and assembly but also for comparative genome analysis and the establishment of conserved syntenies. Because the *Tc1*-like elements are highly repetitive and may contain segments of other genes, special caution is needed for establishment of orthologies involving such sequences.

6. Development of catfish genome resources in support of the whole genome sequence annotation

A major challenge in a whole genome project is the proper annotation of the genome sequences. Specifically, gene models and gene structures need to be supported by experimental data; exon–intron borders need to be defined; alternative splicing and differential polyadenylated transcripts need to be identified; and expression and function of the genes need to be studied. Genome resources such as full-length cDNA sequences and ESTs are particularly useful in support of genome annotation. Toward that goal, we have constructed 32 uni-directional plasmid cDNA libraries (10 libraries were normalized) from various tissues of channel catfish and blue catfish (Li et al., 2007; Wang et al., 2010), and generated a large set of ESTs. Work toward generating a set of full-length cDNAs are in progress.

6.1. EST resources

To date, GenBank dbEST contains 493,852 catfish ESTs based on Sanger sequencing, with 354,377 entries for channel catfish and 139,475 entries for blue catfish (Ju et al., 2000; Cao et al., 2001; Karsi et al., 2002a; Kocabas et al., 2002a,b; Nonneman and Waldbieser, 2005; Li et al., 2007; Wang et al., 2010). Clustering of EST sequences with CAP4 software resulted in 45,306 contigs and 66,272 singletons. All ESTs have been annotated with putative gene identification based on sequence homology (Wang et al., 2010). Over 35% of the unique sequences had significant similarities to known genes, allowing the identification of 14,776 unique genes in catfish. Ongoing research includes a comprehensive transcriptome project that utilizes high throughput Illumina sequencing, with both pooled cDNAs from many tissues and samples from tissues important to the immune system. Such transcriptome information will also greatly facilitate annotation of the reference sequence assembly.

6.2. Full-length cDNAs

The catfish EST sequences provide a platform for the identification and characterization of full-length cDNA clones. A total of 10,037 channel catfish and 7382 blue catfish putative full-length cDNA were identified from the catfish EST assemblies (Wang et al., 2010). A well characterized full-length cDNA set from catfish will be crucial in ongoing studies of teleost gene duplication and gene family structure, as well as aiding in annotation of the catfish whole genome sequence. Current efforts are focused, therefore, on characterization and re-sequencing of these full-length cDNAs.

6.3. Microarrays and functional studies

Initial work of microarrays involves only a small number of 660 genes (Ju et al., 2002; Kocabas et al., 2004). Recently, microarray platforms with 19K- and 28K-genes have been developed and used for the analysis of genes involved in immune and disease responses of both channel catfish and blue catfish (Li and Waldbieser, 2006a; Peatman et al., 2007, 2008; Liu et al., 2008). Continued research is ongoing to identify expression candidate genes involved in various biological processes. Such expression information should help with the whole genome annotation.

6.4. Characterization of catfish genes

A large number of catfish genes have been characterized including important genes involved in growth such as growth regulators and stress regulators (Karsi et al., 1998, 2004; Kim et al., 2000; Leonard et al., 2001; Liu et al., 2001a,b; Kocabas et al., 2002a,b; Clay et al., 2005; Kaiya et al., 2005; Peterson et al., 2005; Goto-Kazeto et al., 2009; Small et al., 2009), important genes involved in reproduction (Liu et al., 1997a,b, 2001a,b; Xia et al., 1999; Chen et al., 2002; Kazeto and Trant, 2005; Kazeto et al., 2005; Mosadeghi et al., 2007; Small et al., 2009; Goto-Kazeto et al., 2009). A large number of genes involved in catfish immunity have been cloned and characterized, and analyzed in relation to immune and defense responses including immunoglobulins (Ghaffari and Lobb, 1999), MHC complexes (Antao et al., 1999, 2001; Godwin et al., 2000), immune cell surface markers and receptors (Wilson et al., 1998; Edholm et al., 2007; Evenhuis et al., 2007; Jaso-Friedmann et al., 2004; Stafford et al., 2006a,b; Yeh and Klesius, 2007, 2009), complement factors (Abernathy et al., 2009; Li and Waldbieser, 2006b), antimicrobial peptides (Bao et al., 2005, 2006a; Wang et al., 2006a,b; Xu et al., 2005), Toll-like receptors and their accessory protein genes (Bilodeau and Waldbieser, 2005; Baoprasertkul et al., 2006, 2007a,b), NOD-like receptors (Sha et al., 2009), a large number of chemokines (He et al., 2004; Baoprasertkul et al., 2004, 2005; Chen et al., 2005; Bao et al., 2006b; Wang et al., 2006c; Peatman et al., 2006, Peatman and Liu, 2007), and many other genes involved in the innate and adaptive immunity of catfish such as Mx genes (Plant and Thune, 2004, 2008), odorant receptors (Ngai et al., 1993) iron regulatory and response proteins (Liu et al., 2010a, b; Takano et al., 2008), interferons and death-inducing signaling complexes (Long et al., 2004, 2006; Milev-Milovanovic et al., 2006;), tumor necrosis factors (Zou et al., 2003), tumor suppressors (Luft et al., 1998), proteinases (Yeh and Klesius, 2008a,b,c; Jiang et al., 2010), and warm temperature acclimation proteins (Sha et al., 2008). All 79 ribosomal protein genes have been characterized (Karsi et al., 2002b; Patterson et al., 2003). These genes and their expression information should be a valuable resource for the annotation of the catfish genome sequence.

7. Whole genome sequencing

In spite of our great progress in the development of molecular tools, a key challenge in utilizing genome-wide selection remains the lack of whole genome sequence. Without a draft genome sequence, our genetic and physical maps cannot provide the resolution for genome-based selection, and construction of higher resolution maps is highly costly and labor-intensive. Through years of efforts, we have placed approximately 3000 markers on the genetic map, but large gaps still exist on the map due to marker clustering. We are currently identifying tens of thousands of SNP loci in catfish populations using 2nd generation DNA sequencing technology, but placement of SNP markers on the genetic map depends on polymorphism within reference families and sufficient levels of recombination to resolve marker order without excessive marker clustering. High throughput genotyping of 50,000 catfish SNP markers in hundreds of offspring will be expensive, so the choice of which SNP loci to map is extremely important. A more logical approach would be to map the SNP sequences to the whole genome sequence, and then identify the SNPs that provide the best genome coverage. In addition, sufficient flanking sequences are needed for the SNP analysis; many of the SNPs identified through the deep sequencing technology, for instance, are located close to the end of the fragments with simple sequences not suitable for SNP analysis. SNPs identified from ESTs are gene-associated, but their analysis can be complicated by the presence of introns. A whole genome sequence would alleviate all these problems. Fortunately, recent advances in sequencing technologies have led to both huge increases in throughput and drastic reduction in costs that have made the previously impossible sequencing tasks immediately feasible.

Very recently, USDA approved funding for the generation of a draft whole genome sequence for catfish using the next generation sequencing technology. In this project, a doubled haploid channel catfish (Waldbieser et al., 2009) will be used as template, simplifying the complications caused by genome duplication. The launch of the catfish whole genome sequencing project is historic. The genome sequence will not only permit efficient identification of sequence polymorphism, but also allow their *in silico* mapping. The genome sequence assembly will facilitate 1) genome-wide comparative analysis, enabling scientific insight into evolutionary biology and genome function; 2) establishment of gene orthologies with other vertebrate species, which will greatly facilitate functional genomic studies and candidate gene identification for performance traits; and 3) haplotype mapping to provide the basis for genome-based selection. The catfish is positioned basally in the teleost phylogeny, so its genome assembly will be useful in genome alignments with other fish (e.g. rainbow trout, Atlantic salmon, zebrafish, pufferfish, medaka, and stickleback) to inform teleost evolution and function. Comparison of the blue and channel catfish genomes will help researchers investigate mechanisms and consequences of speciation. It will also facilitate introgression of blue catfish genomic regions into the channel catfish genome for production of self-reproducing hybrid catfish.

The genome sequence assembly will expedite the identification and location of SNP and microsatellite markers evenly spaced throughout the genome. It will also enable the identification of insertions/deletions, segmental duplications, multi-copy loci, and changes in local DNA topography (Freeman et al., 2006; Parker et al., 2009) to permit researchers to investigate the contribution of these types of genomic variation toward phenotypic variation.

Annotation of the assemblies through transcript mapping and putative annotation based on comparative sequence information will permit researchers to identify virtually all coding regions in the catfish genome and enable comprehensive functional genomics research. The whole genome sequences will permit production of more complete microarray platforms. The assemblies will also enable quantification of gene expression by mapping large numbers of cDNA sequences produced by 2nd generation sequence technology. This approach is inefficient with the current state of knowledge of the catfish transcriptome because 1) many catfish ESTs are 3′ end sequence that currently lack sequence homology with annotated genes and 2) we may not efficiently identify duplicated genes based on transcript sequence.

8. Concluding remarks

More than two decades of animal genomics research have demonstrated that whole genome sequence is the most significant essential genome tool and resource, lack of which severely limits genetic improvements using genome-based technologies. However, genome resources in support of whole genome sequence assembly and annotation are essential in order to make the whole genome sequence highly useful. To this end, we have generated many of the needed genome resources for the assembly and annotation of the whole genome sequence in catfish. However, generation of the whole genome sequence only opens the real first step of the long march toward genetic enhancement, but by no means draws a period of it. The research community needs to be focused on aquaculture performance and production traits, take advantage of the unprecedented genome information and technology, and make real progress toward genetic improvements of aquaculture brood stocks.

Acknowledgements

Our research is supported by the USDA CSREES National Research Initiative NRICGP (award# 2009-35205-05101), and the USDA NIFA Agricultural and food Research Initiative (AFRI) award# 2010-65205-20356). The author is grateful to his hard-working staff, postdoctoral fellows and graduate students, and thanks his postdoctoral fellow Dr. Hong Liu for technical assistance of this review. The author is grateful to the works that were the basis of this review done by the catfish genome community and the Catfish Genome Consortium listed here in alphabetic order: Jason Abernathy, Jerald Ainsworth, Ihan Altinok, Cova R. Arias, Joel A. Bader, Anita L. Bilodeau, Baolong Bao, Puttharat Baoprasertkul, Eva Bengten, Curtis Bird, Jan Bogerd, Brian G. Bosworth, Richard C. Bruch, Karen Burnett, John T. Caprio, Jesse Chappell, Nagaraj Chatakondi, Fei Chen, Gregory Chinchar, Walton W. Dickhoff, Richard T. DiGiulio, Cunming Duan, Mary V. Duke, Rex A. Dunham, Steve Gabel, Troy A. Giambernardi, WL Gray, Eric D. Green, Larry A. Hanson, Michael Hardman, Chongbo He, Jun-ichi Hikima, Alison Hutson, Liliana Jaso-Friedmann, Yanliang Jiang, Zhenlin Ju, Ludmilla Kaltenboeck, Attila Karsi, Kevin Kelley, David Kingsley, Conrad Kleinholz, Philip H. Klesius, Arif Kocabas, Huseyin Kucuktas, Won Kyo Lee, Yoona Lee, Mara Lennard, Ping Li, Erika Lindquist, Wayne Litaker, Gary W. Litman, Hong Liu, Lei Liu, Shikai Liu, Craig J. Lobb, Jianguo Lu, Susan Lucas, George Luker, Brad G. Magor, Thomas J. McConnell, Norman Miller, William Muir, Christopher Murdock, Samiran Nandi, Edward Noga, Kenneth Nusbaum, Donald D. Ourth, Victor Panangala, Reynaldo Patino, Eric Peatman, Brian C. Peterson, Ronald Phelps, Karen P. Plant, John H. Postlethwait, Jonas Quilang, Sylvie Quiniou, Herbert E. Quintero, Paul Richardson, Daniel Rodriguez, Daniel Rokhsar, Holly L. Saunders, Brian Scheffler, Tom Schwedler, Zhenxia Sha, Richard A. Shelby, William Simco, Craig A. Shoemaker, Brian C. Small, Benjaporn Somridhivej, Letong Tang, Tomokazu Takano, Jeff Terhune, Jyothi Thimmapuram, Ronald L. Thune, Terrence R. Tiersch, John Trant, Deepika Vullaganti, Geoff Waldbieser, Mei Wang, Qun Wang, Shaolin Wang, Wenqi Wang, Yaping Wang, Gregory W. Warr, Thomas Welker, Monte Westerfield, Kristie L. Willett, Kenneth Williams, Melanie Wilson, Richard Winn, Lilian Wong, Changgong Wu, Dehai Xu, Peng Xu, Roger Yant, Hung -Y. Yeh, Yonathan Zohar, and Jun Zou.

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