GENOMIC ENABLEMENT OF AQUACULTURED SPECIES

A White Paper Submitted by
the Aquaculture Genome Coordinating Committee
on behalf of the 300 authors

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Summary

This document has been generated by an open community of academic, government, and industry researchers, as well as commercial aquaculture producers committed to advancing genomic sciences in cultured aquatic species. It presents the significance of research conducted in these species, emphasizes the role that genomic research with these species has played in bringing us to our current state of knowledge, and argues that there is a critical need for increased genomic research on key aquaculture species. This White Paper is divided into three sections. 1) An introduction, presenting the importance of cultured aquatic species not only for agriculture, but also in a broader biological context that includes developmental biology and evolution, and environmental/ecological studies. 2) A summary of the current status of genomic research on aquacultured species, identifying the gaps in our knowledge. 3) A strategy for funding. In this section a variety of mechanisms to accelerate the development of genomic science for aquacultured species is considered, including current grant programs, novel partnerships and shared resources.

1) Introduction: the Significance of Aquacultured Species

The aquacultured species within the NRSP-8 initiative at USDA are catfish, salmonids, tilapia, striped bass, shrimp and oyster (Table 1).

Table 1: U.S. Consumption, Production, and Economic Value of Aquacultured Species in 2003*

Species	U.S. Consumption (lbs x 1000)	U.S. Production** (lbs x 1000)	Economic Value*** ($ x 1000)	Percent Production from Aquaculture
Shrimp	1,690,375	104,000	5,100,000	30.3%
Catfish	666,934	661,504	1,984,000	~100.0%
Trout/ Salmon	525,785	53,169	1,004,727	69.0%
Tilapia	400,516	20,000	768,991	57.7%
Oyster	73,723	19,000	55,000	95.9%
Striped Bass	13,000	12,000	40,000	87.7%
TOTAL	3,370,333	869,673	8,952,718	73.43%

*Values taken or extrapolated from *Johnson, 2004; **USDA Aquaculture Outlook 2004 <http://usda.mannlib.cornell.edu/reports/erssor/livestock/ldp-aqs/>. ***Numbers include value-added portions for catfish produced in the U.S. Average consumption of seafood per capita in the US is approximately 16 lbs per year.*

This diverse collection of commercially-important species is also linked by 2 features: 1) their shared aquatic habitat and 2) the fact that they have only recently (in comparison with terrestrial farm animals) been domesticated. For striped bass, shrimp and oyster their domestication is still very much a work in progress. In all other respects the aquacultured species are a remarkably diverse collection, spanning 3 phyla (*chordata, arthropoda, mollusca*) and inhabiting every permutation of fresh and salt, cold and warm water. This heritage of diversity and recent domestication is in one sense a disadvantage, as research efforts are invested in multiple species with an uneven and usually limited body of literature and knowledge. However, the diversity of aquacultured species, and their recent domestication, has distinct value when regarded in a broader context. First, the wide taxonomic spread of the cultured aquatic species means that basic information derived in these animals will contribute to deeper understanding of biological diversity in many areas including genetics, physiology, growth and development, and evolution. Second, the recent domestication of aquacultured species means that in essentially every case the wild populations from which the domesticated stocks were derived are still present in the natural environment. This is true for all of the 6 key aquacultured species, and thus knowledge of a cultured species yields insight into the wild members of the same (and closely-related species). Thus, tools developed to study the genetics and physiology of aquacultured species can readily be applied to many other important fields of study. For example, gene microarrays developed to study the molecular physiology of aquacultured species such as salmonids, shrimp and oysters are being applied to studies of the responses of wild populations to environmental stressors and contaminants. The field of Ecogenomics (ecological genomics, Chapman, 2001) will be greatly advanced by the application of tools developed for the study of aquacultured species to wild populations of their relatives. Third, the recent establishment of cultured lines implies that substantial genetic variation in quantitative traits likely exists in most if not all established strains, which can be further selected by traditional breeding strategies. Even in salmonids where the culture history is the longest and most intense for an aquacultured species, recent publications have shown that within-strain variation in quantitative traits is still substantial (Martyniuk *et al.* 2003). Thus, the potential to improve a host of important quantitative traits including disease resistance, growth, and food conversion efficiency by selective breeding strategies remains strong for the aquaculture species. This should impact

favorably on the economic growth of the related industries and on food production. Fourth, the often intimate relationship between the marine ecosystem and human health has been recognized by the "Oceans and Human Health" initiatives at the NSF, NIEHS, and NOAA and is a prominent feature of the recently released report to the President by the US Commission on Ocean Policy (http://www.oceancommission.gov/documents/welcome.html). The "Oceans and Human Health" initiatives support significant research efforts on marine species, including wild populations of cultured marine species such as oysters, salmonids and shrimp. Genomic enablement of these species will inform and accelerate research on the ecology and environmental biology of these species, as well as providing critical information for the development of these species as food resources, and their relationship to the health of the human population, from consumption of seafood to recreation and residence in the coastal zone.

This significance of each of the aquacultured species, not only in agricultural terms, but also in the broader context of basic and applied biological science, is summarized below.

Catfish: Catfish is the most important aquacultured species in the US. Of the five most consumed seafoods in the U.S., catfish is the only one that is primarily produced by aquaculture. In 2003, over 660 million pounds of pond-reared catfish were produced in the US (USDA Aquaculture Outlook). The aquacultured species of catfish (channel and blue) are native to American freshwater rivers and lakes, and the larger specimens are much sought by recreational fishermen, contributing significantly to the local economy of some regions. The catfish is a well established model system for basic research in neurobiology, (Lee and Bai, 2002; Davis and Linn, 2003; Sundin et al., 2003), chemosensory and mechanosensory physiology, (Hansen et al., 2003; New, 1999), behavior (including unique antipredator responses, Brown et al., 2003) and in studies of toxicology and ecology (Leaner and Mason, 2002; Tilton et al., 2002; Gray et al., 2003). However, the catfish is unique amongst the fish for the depth of knowledge of its immune system, and it has become the premier species for the study of fish immune function. This is for a number of reasons. First, culture conditions for the *in vitro* study of catfish immune cell function have been established (Miller and Clem, 1984). Second, there are many established *in vitro* growing clonal cell lines, including B, T, macrophage, and alloantigen specific cytotoxic T cell and NK cell lines (Miller et al. 1994; Stuge et al. 2000; Zhou et al. 2001; Shen et al. 2004). These cell lines are readily available and have been widely distributed. Third, many immune-function genes have been cloned and sequenced (see Zou et al., 2003; He et al., 2004; Bao et al., 2005; Long et al., 2004 for recent examples), and monoclonal antibodies are available to significant numbers of cell-surface markers and immune-function proteins. Genomic studies should also allow exploitation of both channel catfish and blue catfish using the already popular interspecific hybrids or synthetic breeds for combined benefits, thus providing sustainability to the catfish industry.

Salmonids: The rainbow trout (*Oncorhynchus mykiss*) was the leading salmonid species in U.S. aquaculture, with production of around 51 million pounds in 2003 (as compared to around 40 million pounds of farmed salmon production). Collectively, the salmonid species are the most culturally significant fish in the US. There is a large recreational and tourist industry built around salmon and trout fishing, and salmonid species have attracted widespread interest as symbols of a pristine natural environment. More is known about the physiology and biology of salmonids than of any other fish. The rainbow trout, and all other species in the family Salmonidae, are descended from a single tetraploidization event that occurred approximately 25-100 million

years ago (Allendorf and Thorgaard 1984). Thus, the salmonid genome provides a natural laboratory for following the process of evolution by gene duplication (Ohno, 1970), a process which is continuing in these fishes (Force et al., 1999). The trout is also an important experimental model for biomedical research. The strongest applications of the rainbow trout model lie in carcinogenesis and toxicology research, and as a comparative immunology model (Thorgaard et al., 2002). Excellent and complementary knowledge is also available in the related fields of physiology, nutrition (Hardy, 2002) and disease pathogenesis (Ozaki et al., 2001). Fundamental processes such as vision (Julian et al., 1998), olfaction (Laberge and Hara, 2001), exercise physiology (Kieffer, 2000), excretion (Wood, 2001), osmoregulation (Perry et al., 2000) and stress response (Iwama et al., 1998) have been intensively studied.

Tilapia: Tilapia was, in 2003, eighth on the seafood consumption list for the US, with around 5% of the total of 400 million pounds coming from domestic production (Johnson, 2004). Tilapia are members of the *Cichlidae*, a Family of *Perciform* fish that includes over 3000 species. This diversity of cichlid fish, extraordinary amongst the vertebrates, has in some cases arisen by recent rapid radiations. For example, the species flocks of Lakes Tanganyika and Malawi each contain >700 species that have arisen within the last 1 million years (Meyer 1993; Klett and Meyer, 2002). Thus, the cichlid species are important models for the study of major issues in evolution, including the genetics of speciation, the genetics of behavior, and the evolution of development (e.g. Albertson et al., 2003a, b; Hofmann and Fernald, 2001). The cichlid fish are also important models for physiological studies of growth and reproduction, ion transport, stress and immune responses, and for the study of aquatic toxicology (e.g. Palacio et al.,, 2002; Sarder et al., 2001; Rowell et al., 2002).

Striped Bass: Striped bass (*Morone saxitilis*), white bass (*M. chrysops*) and their hybrids (which are preferred for commercial aquaculture) were, in 2003, the 5th most significant cultured fish in the US, at 13 million pounds (Johnson, 2004). The members of the family *Moronidae* (order *Perciformes)* are the subject of substantial research in areas that include infectious disease and immunity (Gauthier et al., 2003; Lauth et al., 2005) responses to environmental contaminants (Regala and Rice, 2004), reproductive physiology (Hiramatsu et al., 2002, 2004), neuroendocrinology (Klenke and Zohar 2003), and behavior (Salek et al., 2002). The regulatory biology of osmoregulation and growth also has received considerable attention in *Morone* species (Fruchtman et al. 2000, Rodgers et al. 2001).

Oysters. There are two species of oyster of significance in the US: the Eastern Oyster, *Crassostrea virginica,* and the Pacific Oyster, *C. gigas*. The economic importance of these species can readily be understood: the Pacific Oyster alone has global distribution and for the past several years the highest annual production of any freshwater or marine organism, at 4 million metric tons worldwide, worth $3.4 billion. Approximately 35,000 metric tons (meat weight) of Eastern Oyster was supplied to the US market in 2003 (Johnson, 2004). However, the significance of oyster research extends beyond aquaculture: oysters have fundamental evolutionary interest not only as representatives of the *Lophotrochozoa*, an understudied major branch of eukaryotic life, but also as examples of highly fecund animals, which in many ways resemble plants rather than the more familiar and better-studied terrestrial animals (Williams, 1975). Oysters play an important role in the ecology of estuarine and coastal marine habitats, where an increasing proportion of humans live and where environments are rapidly degrading. The relationship between oysters, their physical environment, human pathogens, oyster

pathogens, the ecology of the coastal environment, and the accumulation of anthropogenic contaminants in oyster tissues is very complex, and the dissection of this relationship is being undertaken by many investigators using not only traditional cellular and biochemical studies, but also functional genomic approaches, which offer the possibility of great acceleration in the pace of discovery.

Shrimp: US consumption of shrimp approached 800,000 metric tons (heads-off weight) in 2003 (Johnson, 2004), with US production (including landings) accounting for around 13% of this total. World-wide, aquaculture accounts for 30% of shrimp production, and declines in native stocks, environmental damage from shrimp aquaculture facilities, and the global emergence of shrimp pathogens such as White Spot Syndrome Virus and Taura Syndrome Virus that threaten the environment as well as the aquaculture industry (Lo et al., 1996; Nunan et al., 2001; Chapman et al., 2004) have prompted urgently-needed research into the relationship between shrimp, the marine environment, and emerging crustacean pathogens. The need for basic research has given added emphasis to the development of genomic tools that can be applied generally to studies of shrimp health and disease. The recent realization that shrimp possess inducible innate antiviral responses (Robalino et al., 2004) should lead to the elucidation of enhanced molecular understanding of shrimp/pathogen/environment interactions.

The above brief summary emphasizes that the aquacultured species have an importance that extends beyond the agricultural context: they are important subjects for our understanding of evolutionary genetics and developmental biology, as models for the physiology of aquatic organisms, and for unraveling the complex interrelationships between marine organisms, environmental stress, pathogens and human health. Progress in all of these areas of research will be accelerated by the ongoing genomic enablement of these species.

2) Gaps in our Knowledge

In order to avoid presenting, in the body of this document, a large amount of detailed technical information, a summary of the current status of genomic research in each of the aquacultured species is presented in Appendix I. This summary supports a strong conclusion that what we know of aquaculture genomics is far exceeded by the gaps in our knowledge (see Table 2 below). However, rather than proceeding, species by species, and constructing a detailed list of resources that are needed for each of them, we suggest that it makes more sense to ask the question: ***"What is the minimal set of resources required for efficient genomic research regardless of species?"*** Once a satisfactory answer to this question has been formulated, then the list of resources available to any species can be compared to this standard, and the missing resources easily identified. The above question has been phrased with the qualifier "minimal" inserted deliberately, since we recognize that whole genome sequencing, the ultimate "genomic enablement" is not going to be attainable for every species of interest in the near future.

We thus propose a set of standards which should be met before research on any species can be considered genomically enabled.

There should be: 1) a linkage map with resolution of <1cM, 2) Large insert, deep coverage BAC libraries, 3) An EST database of sufficient breadth (tissue and developmental stage) and depth that much of the organism's transcriptome has been captured, 4) A microarray that includes the maximum set of unigenes identifiable in the

EST database, 5) "Sample sequencing" of the genome sufficient to provide initial resources for gene identification, assessment of synteny conservation, repeat content, and polymorphism and 6) Stable infrastructure, both physical and bioinformatic, to ensure the continued maintenance and public availability of genomic resources. For example there should be two repositories for the maintenance of clones and other physical resources to insure against catastrophic loss, and central bioinformatics support that maintains, updates and ensures continuous availability of annotated sequence databases, maps, microarray specifications and results, etc . Each of these is considered in more detail below.

1) Maps: Linkage maps are the foundation of genetic knowledge for any species. Because maps, even after whole-genome sequencing, are always works in progress it is difficult to specify an ideal density of markers that should be on any linkage map. However, a higher resolution than 1cM is desirable, and the map should be anchored (e.g. by fluorescent *in situ* hybridization techniques, FISH) to the chromosomes.
2) BAC libraries: these are a resource that should be arrayed, archived, propagated and made publicly available (as libraries, clones and filters). Large insert, deep-coverage (>10 haploid genomes) BAC libraries must be available for several reasons. BAC libraries hold the key to additional advances in genomic enablement, for example by large-scale high resolution fingerprinting (physical mapping) and by BAC-end sequencing. Genetic maps can be linked to the chromosomes by *in situ* hybridization (FISH) using BACs, and local regions of the genome can be mapped by focusing on the relevant BAC contig. However, BAC libraries also serve the humble but highly important role of permitting the cloning of specific, individual genes of interest. Any researcher should be able to screen the BAC library filters for clones that contain a specific gene, and then take delivery of the BAC clone for detailed study.
3) An EST database. Comprehensive coverage of the transcriptome is key to an EST database serving the community as a resource for the discovery of novel genes and for *in silico* "data mining" for development of a SNP database. Thus, EST libraries of low redundancy and representing different tissues and developmental or physiological stages should be exploited to generate a substantial database. The best-studied model organisms have EST databases that extend well into the hundreds of thousands, or millions in some cases. A reasonable minimal goal for an EST collection for a species would be between 100,000 and 200,000, with an expectation that up to 35 – 40,000 unigenes should be identifiable.
4) A microarray (or arrays) carrying all the identified unigenes of a species. Although specific research projects that utilize functional genomic approaches can typically focus, very beneficially, on a subset of informative genes, it is important to have a "starting array" in which the transcriptome is as broadly represented as possible. Once the informative genes have been identified, these can then be selected for a second generation custom array tailored to the project's needs. This 2 step approach is especially important in organisms (such as oyster and shrimp) where annotation is problematic; 50% or more of the unigenes lack homologues in the GenBank databases and therefore have no known functions. Unless such unigenes are included on a microarray, their transcriptomic response and clues to their potential function will be missed.
5) The value of limited genomic sequence information is hard to overestimate. This is illustrated in the case of the dog (Kirkness et al., 2003), where "sample genomic

sequencing" equivalent to only 1.5x coverage permitted the annotation of over 18,000 genes or gene fragments, the assessment of conserved synteny and repeat content of the genome, and determination of mutation rates and phylogenetic relationships, as well as identifying polymorphisms of value as genetic markers. Sample sequencing can be approached by random shotgun sequencing of clones, or, where BAC libraries are available, by BAC-end sequencing, an approach that can tie the primary sequence data to the physical and genetic maps of the organism.

6) The financial investment in each of the above items is significant, and the commitment of ongoing support necessary to ensure the long term protection and continuity of these resources is essential. A coordinated plan for the maintenance and distribution of biological resources generated for the aquacultured species is clearly in order. Adequate ongoing bioinformatic support is also essential for all aspects of genomic enablement. In particular, it is important that there be a commitment to continuous, long-term maintenance of websites and databases where EST collections, maps, and other genomic data are archived. It is more efficient for a single entity to support a single community of researchers than for multiple small bioinformatics operations to exist for communities with narrowly-defined interests and needs.

Table 2: Current Status and Required Genomic Resources in the Aquacultured Species.

Genome resources	**Species that require additional resources**
1. Development of a moderate-density genetic linkage map (with 1-2 cM resolution)	Catfish, oyster, shrimp, striped bass, tilapia
2. Development of large-insert genomic libraries such as BAC libraries	Shrimps, striped bass
3. Development of BAC-based physical maps	Catfish, trout, oysters, shrimps, and striped bass
4. Merging linkage maps with physical maps to produce integrated maps	All six species
5. Large collection of ESTs with a minimal number of 100,000 ESTs	Catfish, oysters, shrimps, striped bass, and tilapia
6. Development of cDNA or oligo microarrays	Catfish, oysters, shrimps, striped bass, and tilapia
7. Databases and bioinformatics resources	All six species
8. Partial or complete genome sequencing	All six species

We believe that if we compare the "minimal genomic enablement" defined above, with the brief survey of the state of genomic enablement of the aquacultured species (Appendix I and Table 2) two major conclusions can be drawn. First, when we compare the aquacultured animals with the major domesticated species (e.g. cow, pig, chicken, dog) and with major models of biomedical research (e.g. mouse, rat, *Drosophila, C. elegans*) there is a huge "knowledge gap" in terms of genomic enablement. This gap exists even when we examine the most extensively studied aquacultured species, the salmonids and the catfish. Second, genomic enablement of the aquacultured species, as it gathers momentum, results in rapid increases in our knowledge of the

fundamental biology of the organism. The best examples of this are again the most-studied teleost fish species (the salmonids and the catfish) but the same process of accelerated progress is underway in all of the species. Clearly genomic enablement is good value. Increases in knowledge that result from genomic enablement come across a broad spectrum of the fundamental biology of the organisms, extending well beyond the issues of selective breeding, and elevating the level at which essentially all aspects of fundamental biological research in a species is possible.

The last section of this White Paper considers ways in which momentum towards the genomic enablement of aquacultured species can be maintained and enhanced.

3) A Strategy for Funding

A shared vision for genomic enablement of aquacultured species has been laid out above: but what are the practical means by which this can be achieved? We believe that there are three answers to this question. First, by maintaining existing programs that promote genomic enablement. Second, by forming open, inclusive, comprehensive consortia of researchers united in their advocacy of genomic enablement. Such consortia should have, as a priority, partnering with established researchers at major genome centers to ensure that the expertise and efficiency they offer can enhance the investment of resources in aquacultured species. Third, by ensuring that the community of researchers on aquaculture species have appropriate input to Federal Agencies whose mission includes research on aquacultured species. Thus, when the status of genomic research is evaluated by such agencies, and when their programs, policies and initiatives in genomic science are discussed, the voice of the aquaculture community should be heard.

Maintaining Existing Programs that Facilitate Genomic Enablement

Programs that were established to facilitate the generation of genomic tools and reagents have been, and continue to be, of the greatest importance to the aquacultured species. We argue very strongly for the retention and continued substantial support of programs that the aquacultured species are only now poised to take full advantage of. The programs of particular value to the aquaculture research community include, but are not limited to:

1) The Genomic Tools and Reagents program of USDA
2) The BAC Resource Network of the NHGRI
3) The Community Sequencing Program of the Joint Genome Institute.

Partnerships to Advance Aquaculture Genomics

There can be no argument with the proposition that a community of researchers wishing to advance the genomic enablement of their species has to be open, inclusive, and comprehensive if they wish to succeed. The aquaculture community is well on the way to forming genome consortia for their species. Genome Consortia have been formed for Oysters, the Cichlid fish, Catfish, and Shrimps. We believe that each species group should form an open, inclusive Genome Consortium that unites all the academic researchers and producers and speaks with a single, positive voice to advocate genomic enablement of their species. The NRSP-8 Aquaculture species group will then serve as a forum through which the individual species Genome Consortia can integrate their communication and advocacy. In addition, these Genome Consortia for the aquacultured species should reach out beyond the community of researchers working on their

species. It is important that the aquaculture genomics community form liaisons with and engage the collaboration and support of investigators at major national and international genome centers. The field of genomics has expanded dynamically and the pace of technological and bioinformatics advance has been dramatic. The huge investment in whole-genome sequencing drove the development of large scale, high-throughput genomics centers with tremendous technical expertise and efficiency. The past history of these centers has been one of consolidation, and this trend will likely continue. Genomic initiatives in the aquaculture species should engage these centers. The truly advanced expertise resides in these centers, and the funding agencies can be assured that the proven expertise and efficiency of these centers will be applied to the development of aquacultured species. Such approaches have shown success already: researchers at Auburn University have joint funded projects on catfish with the Keck Center for Functional and Comparative Genomics. Partnerships with commercial concerns are also appropriate and valuable; a collaboration between researchers on Pacific oyster and Lynx Therapeutics has resulted in the donation of 4.6 million ESTs.

The fact that commercially-important aquacultured species are often major experimental models for investigative biology, as well as important components of natural ecosystems, opens the possibility for multi-agency partnerships at the national and international level to promote genomic enablement of these species. The authors of this White Paper urge that the potential for such partnerships between federal agencies be vigorously explored.

A commitment to full public availability of genomic resources. The authors of this White Paper support the position (see e.g. http://www.genome.gov/10506376) that there must be full public availability of all genomics resources that are developed. Forming research partnerships with large Genome Centers and commercial partners will facilitate the wide distribution and public availability of both tangible and bioinformatics resources for the genomic enablement of the aquacultured species.

Aquaculture: A Seat at the Table

The aquacultured species are, as we have demonstrated above, important for reasons that go far beyond food production. These reasons extend in one direction to fundamental issues of basic science such as developmental biology and evolution, and in another direction to ecology and environmental issues, including emerging infectious diseases and conservation biology. Thus, it is appropriate for the aquacultured species (through the community of engaged researchers) to be considered when policy, programs and initiatives in genomic research are under discussion. Thus, the aquaculture community should be represented at the table when federal agencies that support genomic research relevant to these species review the status of the field of genomics, formulate new initiatives, and plan changes to programs and policies that deal with genomic sciences. Such Agencies include not only the USDA, but the NSF, the NIH, the Department of Commerce, and the Department of Energy. Given that the significance of the aquacultured species cuts across many areas of research, from food production to developmental biology, evolutionary genetics, environmental science and human health, it would seem particularly appropriate that this community be represented when Inter-Agency Working Groups seek input and advice from the research community.

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Appendix I: Current Status of Genomic Research on Aquacultured Species

This Appendix is a highly condensed review of current genomic enablement for the aquacultured species, and the narrative provides information that supports the summary provided in Table 2 of this White Paper.

In considering genomic enablement of any species, there are several stages or mileposts that can be defined and that are summarized below.

1. The development of a moderate density linkage map (1-2 cM resolution) using highly polymorphic DNA markers.
2. The development of physical maps, using techniques that include the fingerprinting of BAC libraries, FISH (Fluorescence in-situ hybridization) on chromosomes, and exploitation of radiation hybrid panels.
3. The fusion of linkage and cytogenetic maps with the physical map is an important stage in the genomic enablement of a species, which then permits the identification of synteny with model organisms.
4. Capture of large proportions of the transcriptome as tissue- and developmental stage-specific collections of ESTs.
5. Databases of single nucleotide polymorphisms (SNP). These are readily extracted from large EST collections and facilitate the development of high-density maps and marker-assisted selective breeding.
6. Printing and utilization of microarrays to study patterns of gene expression.
7. Genomic sequencing. This ranges in extent from initially limited (so-called “sample” or “light”) genome sequencing, to whole genome draft sequencing, to (quite rarely) a fully-finished whole genome sequence.

8. Bioinformatic Resources. Genomic enablement, no matter the path it takes, is critically dependent on the parallel development of the bioinformatics resources needed to house, analyze, and make publicly available the information that is generated.

Based on these stages, a summary can drawn up (Table 2) that provides both the current status of genomic research in the aquacultured species, and the additional genomic resources that are needed.

Catfish:

Linkage Maps: Two linkage maps have been published, based on microsatellite loci (Waldbieser et al., 2001) and AFLP loci (Liu et al., 2003). The addition of markers to these maps is ongoing at Auburn University, with the identification of a large number of type I microsatellite markers in the catfish EST database (Serapion et al., 2004).

BAC Libraries: Two catfish BAC libraries have been produced, arrayed and are publicly available as libriaries, clones and filters. The CHORI-212 library was produced from a diploid male, represents 10-fold genome coverage, and is available from Dr. Waldbieser, Dr. Liu, and BACPAC resources. The CCBL1 library (Quiniou et al., 2003), maintained by Dr. Waldbieser at the Catfish Genetics Research Unit (CGRU), was produced from a 3rd generation gynogenetic female and has a nominal 7-fold genome coverage. At the current stage of catfish genomics, construction of a BAC-based physical map is critically demanded for the identification of regional markers for fine linkage and QTL mapping, and for comparative genome analysis. Teams at Auburn University and CGRU are working to secure funding to construct the physical map using the two libraries.

EST Collections and Microarrays: Over 45,000 EST sequences for *Ictalurus punctatus* and 10,500 EST sequences for *I. furcatus* (Ju et al., 2000; Cao et al., 2001; Karsi et al., 2002; Kocabas et al., 2002; He et al., 2003; Liu, unpublished) have been deposited in dbEST, and over 44,000 of these have been incorporated into the TIGR catfish gene index (www.tigr.org). Two catfish microarrays are now commercially available. A cDNA microarray representing 2821 channel catfish genes has been generated in collaborations involving Mississippi State University, the CGRU and the University of Mississippi Medical Center. 2020 of the sequences are from the channel catfish fry EST project and 530 are "putative immune function" cDNAs from the Jx13 channel catfish mixed leukocyte culture EST project. In addition CGRU has developed (and conducted preliminary experiments with) an oligonucleotide microarray consisting of 18,989 unique catfish expressed sequences. Each sequence is represented by ten matching 24-mer oligonucleotides designed throughout the entire sequence, and ten more oligonucleotides containing two mismatched nucleotides at positions 13 and 19. In spite of these development in microarrays, the Affymetrix- or NimbleGen-styled microarrays are still too costly for catfish researchers to conduct large scale microarray-based studies. cDNA-based microarrays are greatly demanded for wide applications in catfish research.

Salmonids:

***Linkage Maps*:** Genetic linkage maps have been developed for the rainbow trout (Sakamoto et al; 2000; Nichols et al., 2003), and over 1000 polymorphic microsatellite markers are being genotyped for the creation of a high-density microsatellite genetic map at NCCCWA.

BACs: Four BAC libraries (see below) have been constructed from the rainbow trout and are being used for genomic sequencing and mapping of type I markers (ESTs), and to produce a sequence-ready BAC contig map (Phillips et al. 2003; Gahr et al. 2004). BACs from 2 of the

libraries have been used as probes in fluorescence in situ hybridization to anchor the genetic linkage map to specific chromosomes (Phillips et al., 2003). A publication using BAC probes and type I and II markers to anchor every chromosome to the linkage groups on the genetic map of Nichols et al., (2003) is in preparation.

***EST Collections and Microarrays*:** A major effort is now focused on increasing the number of sequences in the rainbow trout EST database (Rexroad et al., 2004). The total number of rainbow trout ESTs currently available exceeds 250,000, with the existing EST database being augmented with an additional 80,000 ESTs from the collaborative genome project of NCCCWA and West Virginia University, and over 100,000 from the French INRA project The salmonid research community is quickly moving into functional genomics, and two high-throughput microarrays became publicly available in 2004. A rainbow trout 8000 feature cDNA-based microarray has been constructed by Dr. Paul Coussens at Michigan State University based on the first version of the TIGR rainbow trout gene index. A second salmonid cDNA based microarray has been generated by the GRASP (http://web.uvic.ca/cbr/grasp/) project and represents 16,000 expressed sequences. Over 15% of the GRASP sequences are derived from rainbow trout, and experimental evidence with previous versions of this array (3700 gene array) has shown that cross-species hybridization works well between salmonids (Rise et al., 2004a; 2004b).

BAC Libraries: Four BAC libraries of the rainbow trout genome have been constructed to date. The 2 most recently constructed BAC libraries are from the OSU female homozygous line and the Swanson male homozygous line and were commercially constructed by Amplicon Express Inc. The OSU BAC library has 96,768 clones arrayed in 384 well plates with an average insert size of 110 kb (4.5X coverage). The Swanson BAC library has 184,704 clones arrayed in 384 well plates with an average insert size of 130 kb (10X). DNA fingerprinting was used for local physical mapping of 20 genes in the Swanson library, which demonstrated its utility for identifying duplicated loci and confirmed its 10X coverage (most probes yielded two sets of contigs with an average of ~10 BAC clones each, Palti et al. 2004).

Tilapia:

Linkage Maps: A map constructed from the F_2 hybrid offspring of a cross between *O. niloticus* and *O. aureus* has been published by Lee et al. (2004) and contains ~550 microsatellites and ~20 genes on 24 linkage groups, with an average marker spacing of ~3cM. A genetic map for haplochromine cichlids has been published by Albertson et al. (2003a). This map contains ~130 microsatellites in 24 linkage groups spanning 845 cM. The data so far available (~180 markers) indicate nearly complete co-linearity of the two maps. Progress on constructing a physical map will be considered in the next section.

***BAC Libraries*:** Four *Oreochromis niloticus* (Nile tilapia) BAC libraries, collectively providing deep coverage, have been constructed (Katagiri et al. 2001). A library from the Lake Victoria haplochromine *Paralabidochromis chilotes* has been constructed by Watanabe et al. (2003). These 78,000 clones average 128kb and provide 10x coverage of the genome. A collaboration between Axel Meyer (U. Konstanz) and Chris Amemiya (Benaroya Res. Inst. At Virginia Mason) has produced a BAC library for *Astatotilapia burtoni*, of average insert size 150kb and 12x coverage. Progress towards physical mapping of the tilapia genome has been achieved: A restriction fingerprint database representing a nominal 5x genome coverage) has been assembled from the 2 largest Nile tilapia BAC libraries (http://hcgs.unh.edu/fpc/image.php). The number of contigs resolved is ~3500.

***EST Collections and Microarrays**:* In excess of 33,000 ESTs from diverse tissue sources of 6 species of cichlid fish (*Oreochromis niloticus*, *Metriaclima zebra*, *Astatotilapia burtoni*, *Lipochromis "matumbi hunter"*, *Ptyochromis 'redtail sheller'*, *Paralabidochromis chilotes*) have been generated in an effort that is ongoing. Initial studies suggest that cichlid sequences have sufficient sequence identity that excellent cross-species hybridization should be expected.

Striped Bass:
Although individual laboratories have used molecular genetic approaches to study the striped bass growth (Rodgers et al. 2001), reproduction (Hiramatsu et al. 2004, Holland et al. 2002), and immune function (Walker et al., 1994; Shike et al., 2002, Lauth et al., 2004, Regala and Rice, 2004), the systematic development of genetic and genomic resources for *Morone spp* has only just begun. At a landmark meeting entitled, "Workshop on Genetic Improvement and Selective Breeding for the Hybrid Striped Bass Industry", held at the USDA/ARS Harry K. Dupree Stuttgart National Aquaculture Research Center (SNARC) in October 2003, a National Program of Genetic Improvement and Selective Breeding for the Striped Bass Industry was established as a cooperative venture between scientists in academia, government, and industry. One goal of the Program is to establish fundamental genetic resources needed to undertake the breeding effort. No linkage maps, BAC libraries, or EST collections currently exist for the *Morone* species although a collaboration is ongoing between researchers at North Carolina State University, the USDA National Center for Cool and Coldwater Aquaculture (Kearneysville, WV), and Kent SeaTech Corporation to develop 100 highly polymorphic microsatellite DNA markers for striped bass. This effort is funded by the University of North Carolina System Genomics Initiative to develop informative markers for linkage mapping as well as to track pedigrees in an established *Morone spp* breeding program. At present, 200 microsatellite primer sets have been designed and optimized, and are currently being screened for polymorphism. A subset of these markers are currently being applied to assign parentage of fingerlings grown in "common garden" performance trials conducted with multiple genotyped families produced from domesticated striped bass (4^{th} generation) and white bass (7^{th} generation) broodstocks maintained at the NCSU-Pamlico Aquaculture Field Laboratory (Aurora, NC).

Oyster:
***Linkage Maps*:** Low resolution linkage maps have been generated for both *C. gigas* (Hubert & Hedgecock 2004) and *C. virginica* (Yu and Guo, 2003).
***BAC libraries*:** The Oyster Genome Consortium, a non-exclusive group of 54 researchers on oysters, wrote a successful White Paper to NHGRI for construction of *C. virginica* and *C. gigas* BAC libraries. High quality large insert deep coverage (>10x) libraries were constructed in 2004 and are available from Clemson University Genomics Institute (https://www.genome.clemson.edu).
***EST collections and microarrays*:** An international group of researchers has come together to print a multi-species first generation microarray containing sequences from *C. gigas, C. virginica* and *Perkinsus marinus*, the causative agent of Dermo disease. cDNA clones representing >5000 unigenes from *C gigas* and *C. virginica* developed by groups in Charleston SC (www.marinegenomics.org), Auburn AL, Montpellier, France(www.ifremer.fr/GigasBase/) and Bergen (Norway), as well as 384 unigene clones from the oyster parasite *Perkinsus marinus* (Baltimore, MD), have been assembled in Charleston. Amplicons are being generated, and the printing of microarrays will be accomplished in 2004. These microarrays will, after validation, be made available to the Oyster Genome Consortium and other interested researchers. In addition,

a remarkable library of 4.6 million Pacific oyster ESTs is available from a *pro bono*, genome-wide survey of gene expression in inbred and hybrid Pacific oysters carried out by Lynx Therapeutics, using Megaclone and massively parallel signature sequencing or MPSS technologies (Brenner et al. 2000a, 2000b). Each sequence consists of a 17bp read from the 3' end of a unique cDNA clone; the collection of 4.6 million sequences comprises 53,771 unique signatures.

Shrimp:

***Linkage Maps*:** A low-resolution map generated by Dr Kate Wilson for *Penaeus monodon* is now available at <http://www.aims.gov.au/pages/research/shrimpmap/pages/sm-00.html>. An AFLP map for *Marsupenaeus japonicus*, has been published (Li et al., 2003). Maps for *Litopenaeus vannamei,* and *Fenneropenaeus chinensis* are still under development.

***BAC Libraries*:** No BAC libraries for shrimp species are currently available.

***EST Collections and Microarrays*:** The collection of >10,000 shrimp ESTs from *L. vannamei* and *L. setiferus* (www.marinegenomics.org) is currently the only publicly available resource containing significant numbers of shrimp ESTs. The ~3000 unigenes represented in the collection from the Marine Genomics Group in Charleston (www.marinegenomics.org) have been amplified and the first generation *L. vannamei* microarray will be printed in 2004.

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