

Perspectives: Gene expression in fisheries management

Jennifer L. NIELSEN^{1*}, Scott A. PAVEY^{2,3*}

¹ US Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA

² Department of Biological Sciences, Simon Fraser University, Burnaby, B. C., V5A 1S6, Canada

³ National Park Service, Katmai National Park, King Salmon, AK 99613, USA

Abstract Functional genes and gene expression have been connected to physiological traits linked to effective production and broodstock selection in aquaculture, selective implications of commercial fish harvest, and adaptive changes reflected in non-commercial fish populations subject to human disturbance and climate change. Gene mapping using single nucleotide polymorphisms (SNPs) to identify functional genes, gene expression (analogue microarrays and real-time PCR), and digital sequencing technologies looking at RNA transcripts present new concepts and opportunities in support of effective and sustainable fisheries. Genomic tools have been rapidly growing in aquaculture research addressing aspects of fish health, toxicology, and early development. Genomic technologies linking effects in functional genes involved in growth, maturation and life history development have been tied to selection resulting from harvest practices. Incorporating new and ever-increasing knowledge of fish genomes is opening a different perspective on local adaptation that will prove invaluable in wild fish conservation and management. Conservation of fish stocks is rapidly incorporating research on critical adaptive responses directed at the effects of human disturbance and climate change through gene expression studies. Genomic studies of fish populations can be generally grouped into three broad categories: 1) evolutionary genomics and biodiversity; 2) adaptive physiological responses to a changing environment; and 3) adaptive behavioral genomics and life history diversity. We review current genomic research in fisheries focusing on those that use microarrays to explore differences in gene expression among phenotypes and within or across populations, information that is critically important to the conservation of fish and their relationship to humans [*Current Zoology* 56 (1): 157–174, 2010].

Key words Fish genome, Fisheries management, Conservation, Gene expression

1 Introduction

Revolutionary advances in genomics, molecular technology and biotechnology have set a new path for understanding ecological variation and adaptation in animals. Perhaps because of a strong link to commercial fisheries harvest and the “stock” concept in Pacific salmonids (Utter et al., 1987), fisheries genetics has been slow to accept the challenge of modern molecular approaches. For more than 60 years, bi-allelic diversity visualized through allozyme electrophoresis was considered standard for genetic stock identification in fisheries (Avise, 1974; Utter, 2004). The value of early allozyme studies to harvest allocation and fisheries management in the late 20th century is undeniable, but it also delayed acceptance and application of new molecular technologies. Some of the earliest studies and applications of DNA technologies were in fish conservation, but without allozyme support these early studies remained in question. The 1990s saw rapid developments in the use of polymorphic DNA markers (mtDNA

haplotypes, microsatellites, SNPs) in the study of evolution and natural history (see reviews Avise, 2004; Schwartz et al., 2006; Verspoor et al., 2007). Analysis and monitoring of highly polymorphic allelic frequencies in fish populations across multiple spatial and temporal scales required a significant change in the way genetics was applied to fisheries management and policy (Allendorf et al., 1997). The prevailing idea that phenotypically similar fish populations, hatchery or wild, were manageable as one stock began to change (Conover et al., 2006). Allozymes were eventually replaced by neutral DNA-based molecular markers in fisheries science and management.

With the dawn of highly polymorphic neutral genetic markers, population-scale applications became important even in unexploited fish species. Dynamic changes in our knowledge of the distribution and abundance of fish populations again altered the questions asked by management. The first decade of the 21st century has generated a significant dialogue on fish culture and artificial propagation and their impacts on wild populations

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* Corresponding author. E-mail: jlnielsen@usgs.gov, scott_pavey@nps.gov

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(Ferguson et al., 2007; McClure et al., 2008). Additional concerns have emerged about fisheries-induced selection in commercially harvested species (Marshall and Browman, 2007; Biro and Post, 2008). Human perturbation of habitats and a rapidly changing climate have created the need for new molecular approaches addressing physiological limitations in natural populations (Wikelski and Cooke, 2006; Waples and Hendry, 2008). Managers are looking for interdisciplinary research exploring how animals adapt to rapidly changing

environments and what physiological thresholds limit such adaptations at the molecular level (Crozier et al., 2008; Cooke et al., 2008). To help address these issues, fisheries geneticists are starting to investigate approaches and analytical techniques first developed from the Human Genome Project over the last two decades. Fisheries science is rapidly entering the era of functional genes using new molecular tools of genomics and gene expression covering an extensive array of studies and applications (Table 1).

Table 1 A partial list of literature (2001–2009) on genomic and gene expression applications in non-model species important to fisheries conservation and management

Topic	Group/species	Tools	Applications	Literature
General review papers			Background and evolving technologies	
	General	Microarrays	Experimental design	Kerr & Churchill 2001
	Rainbow trout	Genomics	Applied research	Thorgaard et al. 2002
	Bony fish	Genomics	Reviews applications	Clark 2003
	General	Genomics	Functional genomics	Hofman 2003
	Non-model species	Microarrays	Comparative physiology	Gracey & Cossins 2003
	Catfish	Genomics	Review	Liu 2003
	Salmonids	Microarrays	Methodology	Rise et al. 2004
	General	Microarrays	Methodology	Renn et al. 2004
	Cichlids	Candidate genes	Behavioral ecology	Fitzpatrick et al. 2005
	Marine fishes	Genomics	Ecology & physiology	Hofmann et al. 2005
	Fish	Microarrays	Lists various applications	Douglas 2006
	Non-model species	Microarrays	Environmental genomics	Buckley 2007
	Biological systems	Microarrays	Ecological genomics	Kammenga et al. 2007
	Biological systems	Microarrays	Ecological genomics	Landry & Aubin-Horth 2007
	Biological systems	Microarrays	Ecological genomics	Kassahn 2008
	Fish	Microarrays	Methods and applications	Miller & Macclean, 2008
	Atlantic salmon	Genomics	Tool development	Von Schalburg et al. 2008
	Fisheries	Microarrays	Genotype & phenotype	Naish & Hard 2008
	Fisheries	Genomics	Methods and applications	Hauser & Seeb 2008
	Marine fishes	Genomics	Review of applications	Nielsen et al. 2009
Evolutionary and adaptive genomics			Biodiversity, adaptation and speciation	
	Fishes	microarrays	Exogenous estrogen	Denslow et al. 2001
	Non-model species	Microarrays	Natural expression diversity	Oleksiak et al. 2002
	Catfish	EST	Cold acclimation	Ju et al. 2002
	African cichlids	Microarrays	Comparative genomics	Renn et al. 2004
	Stickleback	EST	Developmental traits	Kingsley et al. 2004
	Salmonids	Linkage maps	Recombination rates	Danzmann et al. 2005
	General	Microarrays	Multispecies divergence	Gilad et al. 2005
	Teleost fish	Sequence	Evolution of genes	Volff 2005
	Atlantic salmon	Microarrays	Expression change in farmed fish	Roberge et al. 2006
	Rainbow trout	Microarrays	Toxicant exposure	Hook et al. 2006
	Chum salmon	Microarrays	Genetic stock ID	Moriya et al. 2007
	Salmonids	EST	Gene duplication	Koop et al. 2008
	Goby	Microarrays	Phenotypic plasticity	Gracey 2008
	Atlantic salmon	Microarrays	Farmed and wild fish	Roberge et al. 2008
	African cichlids	EST	Adaptive radiation	Salzburger et al. 2008
	General	Genomes	Phylogeny	Boore & Fuerstenberg 2008
	Aquaculture	Microarrays	Culture profiles	Zhang et al. 2009
	Tuna	Microarrays	Endothermy	Castilho et al. 2009

EST = expression sequence tags. Additional applications and references are found in the text.

Applications of these new technologies are not without drawbacks (Zhang, 2002; Kammenga et al., 2007). Finding and identifying candidate genes linked to different physiological pathways can require considerable time, effort and costs, especially in non-model species for which we lack full genome data. The \$1,000 genome remains a necessary but evasive goal (Mardis, 2006). With ever-cheaper access to complete genomes for non-model animals, however, there exists the challenge of extensive data and the question of what elements of functional genomics to use in developing criteria for research or management. Current technology has the capacity to identify candidate loci that exhibit subtle differences in gene expression clearly associated with adaptive variation linked to various physiological development pathways, responses to a changing environment, and the expression of different life history tactics. Analysis of microarray data for gene expression is confounded by several factors and assumptions. Genes that share similar expression profiles across a set of conditions may not share similar functions. Genes can interact with each other in many ways, and not all interactions will have similar transcriptional profiles. These challenges are not insurmountable, and limitations reflect the early stage of development of this rapidly evolving technology. It is difficult to predict what other applications will evolve as our knowledge of functional genomes in fishes matures.

This scale of data was not available with earlier techniques, and direct hypotheses are just starting to organize in fisheries (Hauser and Seeb, 2008; Nielsen et al., 2009). Much of the research in gene expression in fishes has been directed at “model” animals, including the zebrafish *Danio rerio*, medaka *Oryzias latipes*, pufferfishes (*Tetraodon nigroviridis* and *Takifugu rubripes*), and threespined stickleback *Gasterosteus aculeatus* (Douglas, 2006). Genomic applications in aquaculture have focused on commercially important species such as salmonids, catfish, cod, and flatfish, with thousands of expressed sequence tags (EST) available for some species (see reviews in Dunham, 2004 and Wenne et al., 2007). More recently, studies have begun to apply genomic and gene expression tools to questions in non-commercial fish populations (Volf, 2005; Miller and Maclean, 2008), especially in the investigations of adaptive function at the molecular level (Hofmann et al., 2005).

Changes in environmental conditions can lead to rapid shifts in allele frequencies. Neutral genetic markers can reflect these shifts, especially in species with

short generation times (Carroll et al., 2007). There are many examples in which evolutionary response to selection appears limited (Blows and Hoffmann, 2005), but adaptive response to changing conditions is often the product of physiological tolerance reflected in phenotypic change, not genetic constraint (Hoffmann and Willi, 2008). The workings of genes linked to adaptive biological function are not static, and their behavior and efficiency can be influenced by many factors driven by evolutionary history, developmental status, and age, as well as by the environment (Oleksiak et al., 2002; Jaenish and Bird, 2003). RNA can be analyzed as variation in genes expressed within the organism, in specific tissues, among populations in different habitats, or even at specific stages of development or ontogeny for a single animal. In a way, this reflects a return to early research on functional genes using allozymes, but with increased molecular rigor. Gene expression is only part of the story, but it is an important part that has been missing in fisheries management.

A good example is found in the progression of genetic studies in the teleost fish *Fundulus heteroclitus* on the eastern coast of the U.S. Early allozyme research on coastal populations of *F. heteroclitus* demonstrated local adaptation in temperature tolerance and physiological performance along a natural temperature gradient of 10°C linked to allelic variance at the lactate dehydrogenase-B (*Ldh-B*) locus (DiMichele and Powers, 1982; Powers et al., 1991; Powers and Schulte, 1998). Differences in *Ldh-B* expression among phenotypes was maintained even after long-term acclimation to common temperatures in the laboratory, suggesting genetic changes among geographic populations beyond adaptive acclimation effects (Schulte et al., 1997). Schulte et al. (1997) found significant differences in reporter gene activity driven by flanking regions, both in cell culture and *in vivo*. Schulte et al. (2000) further demonstrated sequence changes 400–500 bp upstream of the transcription start site that resulted in a two fold difference in reported gene transcription, which could account for the twofold differences in *Ldh-B* transcription between northern and southern populations (Glémet et al., 1999). Significant variation in gene expression in cardiac cDNAs was found among individuals within *F. heteroclitus* populations by Oleksiak et al. (2002 and 2005). In these studies, inference originally drawn from allozymes led to documentation that minor changes in cis-acting DNA regulatory sequences can have important impacts on gene expression and the ability of wild fish populations to respond to stressful environments

(Picard and Schulte, 2004).

Despite the fact that very little is currently known about the molecular mechanisms underlying adaptively significant patterns in gene expression in non-model fishes, there has been a steady increase in the literature documenting use of molecular technologies to study physiology, adaptive response to the environment, life history, and rapid microevolution in fishes (Schulte, 2001; Douglas, 2006). The marriage of gene expression and high-throughput functional genomics marks the latest sea change, in which molecular approaches augment previous approaches in fisheries genetics (Hauser and Carvalho, 2008). Recent studies of Atlantic salmon *Salmo salar* life histories have shown how different evolutionary inference can be gained using gene expression analyses. Male Atlantic salmon are developmentally plastic, with life history types ranging from precocious parr (males that develop more quickly in early life, mature sexually at a young age, and “sneak” breeding opportunities with large anadromous females) to large anadromous males that return to breed after 3 – 7 years at sea and compete for reproductive females in riverine spawning habitats (Jordan et al., 2007). Aubin-Horth et al. (2005a) investigated the nature and extent of brain transcription profiles in these two extremes of life history in Atlantic salmon males. Consistent patterns of gene expression were found for individuals with the same reproductive life history, demonstrating the viability of the technique in life history analyses for salmon. Most interestingly, the results of their gene expression analyses suggested that delayed maturation and sea migration in anadromous males result from active inhibition of molecular developmental pathways exhibited in sneaker males. This contradicts the traditional concept of maturation and development in salmonids males, in which anadromy and large size are thought to be the default life history. This association between the two life history strategies sheds new light on the long-standing discussion about the evolution of anadromy in salmonids and if the genus was originally derived from marine or freshwater species (McDowall, 2002; Thorpe, 2007).

A variety of transcriptome profiling technologies are currently available (Renn et al., 2004; Yauk et al., 2004). Recent advances in new technologies which allow sequencing of entire transcriptomes, thus providing enriched profiles of gene expression, such as Applied Biosystem’s Illumina Genome Analyzer and Roche’s 454 Life Sciences’ SAGE systems, are pushing gene expression further into the digital age (Sultan et al., 2008). But high-throughput sequencing comes with sig-

nificant cost and still has numerous high-level complications and data interpretation problems (Blow, 2009). Currently, microarrays tend to offer researchers standardized techniques and will continue to offer array-based tools for preparatory experiments, especially for organisms for which we lack complete genomes or adequate linkage maps. Goetz and Mackenzie (2008) provide a review of the various advantages and disadvantages of different approaches.

Microarray analysis of gene expression profiles has become the most widely used functional genomics tool in fisheries. The examination of gene expression using microarrays has proven tremendously valuable for identification of candidate genes involved in a variety of physiological processes in fish (Table 1). There are several standard techniques for analysis of gene expression using microarrays. The regulation of gene expression begins with the level of transcription of DNA in living cells into mRNA. The scale at which a gene is up-regulated (high transcription rate) or down-regulated (low transcription rate) can provide information about gene function. Gene expression profiles provide insights into complex physiological processes that are the result of coordinated interactions of sets of genes. These profiles have also revealed temporal and tissue-specific changes and patterns of activity critical to intact living animals.

In most approaches, RNA is extracted from one or more tissues of the organism to develop an expressed sequence tag (EST) library (Schena et al., 1995; Fig. 1). ESTs are single-pass, partial sequences of cDNA clones used extensively for gene discovery and mapping (Schuler, 1997). Normally, cDNA clones are selected to represent as many unique transcripts as possible (Kerr and Churchill, 2001). The ESTs are then sequenced and assembled to represent full-length coding regions of genes as well as untranslated regions (UTRs). These elements are then placed (or “printed”) in individual wells (spots) on an oligonucleotide array created for analysis. Both the slide surface and the spotting buffer are critical for reproducible, high-fidelity microarray analysis. Array printing can be done using microarray spotting robots; however, pre-printed arrays are commercially available for many fish species. Many important gene sequences or genes are highly conserved, allowing useful cross-species amplification of gene profiles from arrays developed for closely related taxa (Cossins and Crawford, 2005).

Gene expression array experiments require hybridizing a “target” (labeled cDNA from a sample) in solution to a probe (fixed, known and unlabeled sequence) found

in isolated spots or wells on the array. A single microarray can provide information on the expression of tens of thousands of genes using different probes (Stoeckert et al., 2002). Targets for microarray analysis are prepared from RNA templates by incorporation of fluorescently labeled deoxyribonucleotides during first-strand cDNA synthesis. Fluorescently labeled quantities of target ma-

terial are added to the array spots containing the probe. The goal of hybridization is to obtain high specificity by maximizing measurable fluorescence from the array while minimizing background. Gene expression levels at each array spot are compared according to their fluorescence intensities to detect variation in up- or down-regulated genes (Fig. 2). The complete process

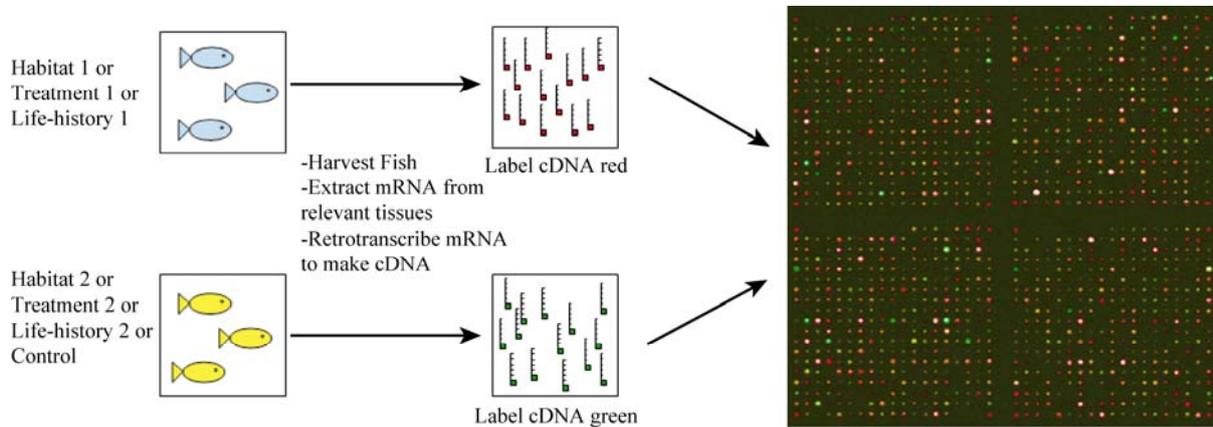


Fig. 1 Schematic illustrating the development of a gene expression microarray for two populations of fish with different habitats and life histories

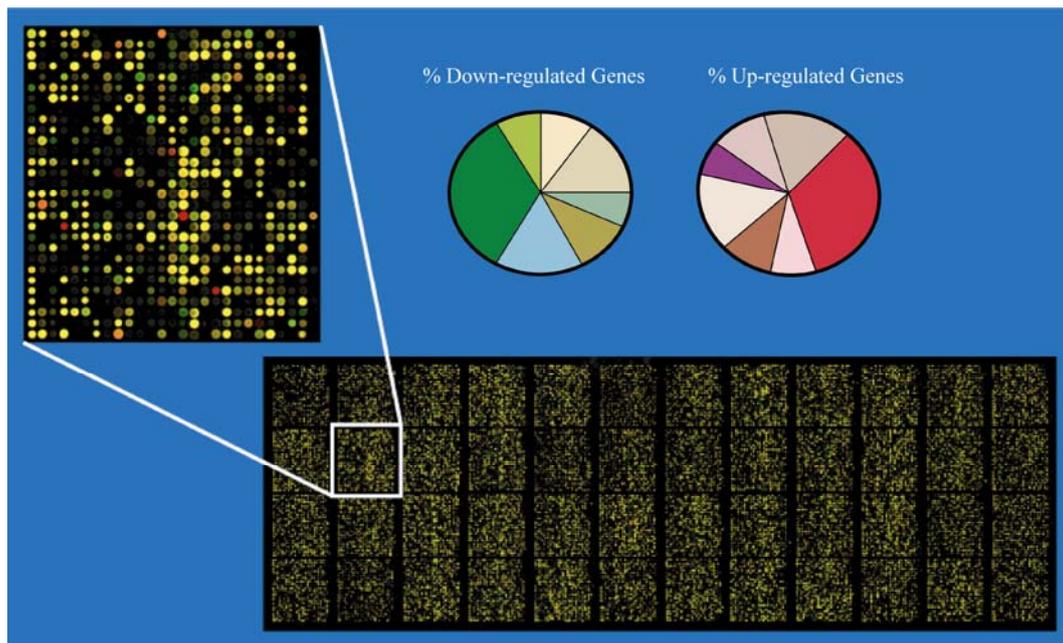


Fig. 2 Hypothetical microarray showing variation in gene expression across a range of colors based on up-regulated (red) and down-regulated (green) genes in a diversity of characters or states

The scale of fluorescence indicates the amount of expression recorded in individual wells or spots on the array. Genes in this hypothetical might include those involved in general cell maintenance, physiological function, or biochemical pathways depending on the case study. These may include various percentages of genes with specific function such as (rotating clockwise from largest percentage) down-regulated genes: 38% cell division (HMG-Y and proliferating nuclear antigen); 6% globins synthesis (globin bA1); 12% cell structure/motility (creatine kinase M2 and M3, actin alpha, keratin type II, myosin light chain 1b); 16% cell/organism defense (BiP and heat shock cognate 70); 4% signaling/communications (RanBP1); 10% glycolysis/TCA (phosphoglycerate kinase, malate dehydrogenase, and aldolase); 14% protein expression (ribosomal protein L5B and L10). Up-regulated genes might include (rotating clockwise from largest percentage): 34% cell structure/motility (thromyosin alpha, thronin C skeletal and cytokeratin S); 5% protein expression (ribosomal protein S10); 12% metabolism (ATPase 8, ATPase calcium, NADH and cytochrome c oxidase subunit VIII); 18% signaling/communication (ras-related nuclear protein ran and ras-related GTP-binding protein rap 2b); 3% cell division (histone H3); 11% cell/organism defense (DNA repair protein RAD52 and heat shock protein 30); 17% glycolysis/TCA (enolase, lactate dehydrogenase, and adenine homocysteine hydrolase).

has been reviewed in Goetz and MacKenzie (2008). Experimental design of microarrays can vary greatly. Most arrays require samples from different experimental conditions, i.e., different tissues or treatments, or tissues from different species (Thomas and Klaper, 2004). There are many different methods for comparing samples on the arrays, including direct, indirect, and loop designs. There are differences in the number of chips used as well, as the amount of biological and technical replication and the analytical protocol are likely to continue to evolve (Ball et al., 2003; Naidoo et al., 2005). There are several different techniques for normalization, quality control, quantifying spot intensity, and correcting for multiple tests (Kerr et al., 2000; Tseng et al., 2001). Public-domain microarray databases have developed, and open access analysis programs are now available for gene expression (Lash et al., 2000; Edgar et al., 2002; McLachlan et al., 2004).

In this paper, we look at the new genomics revolution, with special focus on gene expression for functional and adaptive genes, in relation to applications in fisheries management. We discuss current fisheries research using gene expression microarrays and project ways that these approaches may continue to contribute to fisheries management in aquaculture, harvest allocations, and conservation management.

2 Gene Expression in Aquaculture Management

2.1 Culture-developed molecular tools

The effort to compensate for the recent loss of commercially valuable fishes has led to a strong focus on artificial propagation and aquaculture (Stickney, 2007). Although artificial supplementation of fish has not always been environmentally responsible (Utter and Epifanio, 2002; Bartley, 2007; McClure et al., 2008), commercial aquaculture applications have been the primary motivation for the development of many fish microarray technologies. Aquaculture arrays have been used to test experimental models for developmental physiology, environmental toxicology, and endocrinology research (reviewed in Miller and Maclean, 2008). Aquaculture genomic studies frequently focus on improved growth and development rates (Douglas et al., 2008), food efficiencies (Taggart et al., 2008), increased resistance to disease and pathogens (Gonzales et al., 2004; Baerwald et al., 2008; Liu et al., 2008), and molecular phenotypic selection for improved broodstock characteristics (Malamed et al., 2001). Important molecular processes linked to gene ontologies are well described for many

aquaculture species that serve as platforms for expression research in other fishes (Liu and Cordes, 2004; Zhang et al., 2009).

Microarray analyses of differential gene expression have been used to help solve production problems in commercially valuable fish species, such as Atlantic halibut *Hippoglossus hippoglossus*, during the early stages of aquaculture development (Douglas et al., 2008). Genomic research and studies of gene expression in aquaculture species will continue to play a significant role in the development of future propagation efforts, especially in transgenic fish studies and in fish species with little remaining genetic diversity (Hew et al., 1999; Hill et al., 2000). Culture-developed molecular tools transfer important information and technologies to conservation and management of hatchery and wild fish populations.

2.2 Impacts of cultured fish

The exchange of molecular tools and information between culture and conservation is a two-way street. Gene regulation and expression are thought to play important roles in adaptive evolution in fishes (Cresko et al., 2004; Derome et al., 2006). Genetic mechanisms underlying adaptive differences in important physiological traits, however, have been poorly described for most aquaculture species even though directional selection is common in the culture of fishes (Garcia de Leaniz et al., 2007). The impact of artificial selection on local adaptation has been an important criticism of aquaculture in salmonids, especially considering the potential impacts of artificially propagated fish on wild populations (Hindar and Fleming, 2007; Araki et al., 2008). This is especially true when close polygenetic relatedness between wild populations and propagated fish makes it difficult to easily discriminate among different groups (Bert, 2007). Additional research is needed to test the hypothesis that rapid phenotype divergence can occur during artificial propagation of fishes taken from the wild. How does directional selection in broodstock (intended or not) affect variation in gene expression and subsequent phenotypes? It is equally important to test the hypothesis that potential divergence generated through selection in aquaculture will ultimately pass on maladaptive traits to wild fish through interbreeding.

Understanding the dynamics of phenotype development and limitations to adaptation that can be passed on to subsequent generations in aquaculture species is critical for efficient production and sustainability of broodstock, as well as for understanding the impacts

aquaculture releases may have on wild populations. Phenotypic plasticity represents the range of character states that an individual genotype can exhibit in different habitats. This is especially important for most adaptive traits. Phenotypes can vary continuously (reactive norms developed in response to environmental variation) or discretely (polyphenism based on threshold developmental pathways) (Nijhout, 2003). Biological factors common in aquaculture, such as crowding, diet, hormone levels, and environmental gradients, have been shown to underlie phenotype development for many organisms (Mangel et al., 2007; Gagliano et al., 2007; Carlson and Seamons, 2008). There are fewer papers documenting direct genetic effects contributing to distinct phenotypes in fish (see, however, Shapiro et al., 2004). A large collection of recent literature has provided empirical evidence supporting the inference of changes in gene regulation and expression as the foundation of phenotypic plasticity in many adaptive traits, especially micro-evolutionary changes in morphology (Carroll et al., 2006; Roberge et al., 2007; Wray, 2007; Whiteley et al., 2008; St-Cry et al., 2008). Gene expression profiles and physiological genomics applied to questions in aquaculture and fisheries dependent on artificial propagation will clearly benefit from these new technologies and significantly change the way culture management uses genetic information in the future.

3 Gene Expression in Harvest Management

3.1 Selection resulting from harvest

In the last 60 years, many aquatic species have suffered globally due to degradation and fragmentation of habitats, poor resource management practices (terrestrial and marine), regional exploitation, and overfishing leading to dramatic changes in local populations (Hutchings and Reynolds, 2004; Hendry et al., 2008; Waples et al., 2008). The harvest of fish by humans can have many different direct or indirect effects on populations (Allendorf and Hard, 2009; Cooke et al., 2009). The concept that fish may have an evolutionary response to commercial exploitation is complex and controversial (Morita and Fukuwaka, 2007; Naish and Hard, 2008; Sharpe and Hendry, 2009). Data in support of an evolutionary response to harvest have been reported in recent studies demonstrating changes in important fitness and life history traits linked to intensely harvested fish populations (Olsen et al., 2005; Walsh et al., 2006; Law, 2007; Conover and Baumann, 2009). Most studies have focused on potential harvest effects on growth and

maturation reaction norms. Hypothetically, when harvests select for larger fish, the exploited population will tend to shift to reproduction at a smaller size (Gagliano et al., 2007; Wright, 2007). Under these circumstances, disentangling phenotypic plasticity from genetic change with potential evolutionary effects can be difficult (Dieckmann and Heino, 2007; Kraak, 2007; Wang and Höök, 2009). Controlled selection experiments have confirmed gene-based changes in life history under intense harvest (Conover and Munch, 2002; Conover et al., 2006). However, local adaptation can be a dynamic process that can vary greatly in space and time (Hendry and Day, 2005; O'Malley et al., 2007; Nielsen et al., 2009). Selection differentials can be population-dependent (Hindar et al., 2007; Hilborn and Minte-Vera, 2008).

Most estimates of selection due to harvest have not been standardized to probable deviations in phenotypic response (Naish and Hard, 2008). Many fish species exhibit a broad diversity of life history strategies that remain flexible across generations, including rapid shifts in growth, fecundity, age structure dynamics, and senescence. Iteroparity and the possibility of freshwater residency in Atlantic salmon and anadromous steelhead trout *Oncorhynchus mykiss* are startling examples of phenotypic plasticity in salmonids that carry across many generations. How flexibility in life history traits interacts with the evolutionary trajectory of these species is just beginning to be studied (Aubin-Horth et al., 2005a, b; Garcia de Leantz et al., 2007; Thorpe, 2007). It seems likely that further research in gene expression will reveal additional fitness and selection factors contributing to our understanding of different species' evolutionary and demographic responses to harvest.

3.2 Species identification in harvest and marketing

Fish biodiversity is important economically and culturally (Volf, 2005). Sustainable harvests require management focused on diversity and conservation of unique populations, increasing the need for genetic assessments at the population level. There are many ways humans compile and catalogue biodiversity, and genetics clearly has played a significant role (Hutchings and Baum, 2005; Ogden, 2008). Genetics has long been useful for species identification to prevent fraud during harvest and when marketing seafood products (Wilson et al., 1967; Withler et al., 2004; Rasmussen and Morrissey, 2008). More recently, an international research collaboration, FISH-BOL (Fish Barcode of Life campaign), intends to catalogue 648 base pairs of the mitochondrial cytochrome *c* oxidase sub-unit I (COI) gene

for all freshwater and marine fish species to serve as a standard for species identification in harvest and marketing (Ward et al., 2009). More than 5000 fish species have been catalogued to date, with an average of five specimens per species. The FISH-BOL program claims that their mitochondrial DNA index can separate 93% – 98% of the described freshwater and marine fish species (Ward et al., 2009). While this represents an easy and cheap methodology for species identification, using a single gene to describe taxonomy in fishes has many problems, including issues of hybridization, recent radiations, regional divergence, nuclear integrated mtDNA sequences, and, more specific to this paper, differences in gene function and expression.

Misidentification of fish or fish products can result in inaccurate estimates of harvest allocations and stock size and adversely affect sustainable fisheries management and marketing. Proponents of FISH-BOL have stated that evolutionary issues are of little concern in the majority of specimens included in their inventory. It is difficult to address issues of heterogeneity (geographic or adaptive) with a sample size of as few as five fish per species, typical of the FISH-BOL diversity baseline. A logical extension to this approach would include consideration of local adaptation in many underreported species. To our knowledge, no research on variation of bar code candidate genes using gene expression has been published. This is especially important in many ray-finned fishes, for which a well-documented genome duplication and significant variation in duplicate gene retention have been reported (Allendorf, 1978; Liu, 1980; Taylor et al., 2003; Volff and Schartl, 2003). Indeed, closely related fish species have been shown to freely exchange mtDNA haplotypes (presumably with similar biotic function) to produce viable hybrids (Bartley et al., 1990; Wilson and Bernatchez, 1998). Since most published examples are from salmonids, mitochondrial hybrids may happen more often than we expect in underreported species.

Just as it is accepted that the mtDNA locus may not represent the true evolutionary phylogeny of important fish species (White et al., 2008), it is also true that phylogenetic inference built on genomic sequences may not reflect important differences found in the expression of adaptive genes. Fish with the same DNA sequence can have potentially divergent expression profiles (Oleksiak et al., 2005). The example of *LDH-B* variation in *F. heteroclitus* (see introduction) shows how DNA sequence of a gene may not be sufficient to explain critical adaptation within a species. The traditional view is that gene

expression is primarily driven by genomic differences in one or more genes and/or associated genetic mechanisms. More recently, the range of functions attributed to non-coding microRNA has expanded to include catalysis of critical cellular processes including mRNA splicing, translational inhibition, mRNA degradation, and protein synthesis (Ason et al., 2006; Stefani and Slack, 2008). Many of these microRNAs are phylogenetically conserved (Ambros, 2004). MicroRNA has been linked to developmental processes and changes in expression profiles in model fish (Schier and Giraldez, 2006). Barcoding fish with mtDNA will reveal none of these important and potentially adaptive molecular processes.

After a long history of overexploitation, the impacts of harvest can affect populations in many ways, including size-dependent growth, maturation, timing of migration, and collapse of target and non-target species (Worm et al., 2009). The range and limits of adaptive response to demographic and ecosystem change based on gene expression seem important to identifying sustainable populations of harvestable fish. Recent analyses of gene expression indicate that natural selection has the power to shape expression phenotypes even when genetic mutations at specific genes are in the nearly neutral range (Bedford and Hartl, 2009). An understanding of the distribution and function of the diversity of molecular phenotypes linked to adaptive expression profiles in harvestable animals is important if we are to fully implement the primary goals of biodiversity management and conservation of species and populations embedded in the FISH-BOL program.

4 Gene Expression in Conservation of Wild Fish

4.1 Evolutionary genomics and biodiversity

In the last half century, molecular sequence data has revolutionized our understanding of evolutionary relationships in fishes (Bernatchez, 1995; Crespi and Fulton, 2004). Molecular data have contributed to the integration and reevaluation of classical systematics and our definition of biodiversity in fishes (Volff, 2005). Through the study of genomics and how genes work through expression and regulation of physical function, we are developing a better understanding of molecular mechanisms affecting morphology, ecology, and behavior in fishes. Interspecific comparisons of gene expression continue to increase our knowledge about the mechanisms of transcription and to identify genes subjected to natural selection. Fisheries scientists are start-

ing to map molecular pathways for functional characteristics such as skeleton structure and bone development in evolutionary speciation (see Shapiro et al., 2004). Determining the presence of particular biochemical pathways in gene transcription and regulation linked to morphological and adaptive characteristics may again change our view on systematics and species biodiversity (Volf and Schartl, 2003; Boore and Fuerstenberg, 2008).

Genetic differentiation critical to the conservation of biodiversity can occur at multiple scales, not just at the biological species level. Phenotypic differentiation between allopatric populations is also a critical component of diversity in many fish species (Ward et al., 1994; Skúlason et al., 1996; Wilson et al., 2004; Bernier et al., 2008). The conservation community generally accepts that the genetics of natural populations reflect deep evolutionary histories tied to long-term patterns in selection and migration. A review of the conservation status for Pacific salmonids in the U.S. provided the first use of genetics to define a species under the U.S. Endangered Species Act (ESA) (Waples et al., 1990; Waples, 1995). This conservation policy is based on defining evolutionarily significant units (ESUs), which represent an important component of the evolutionary legacy of the species (Waples, 1991). Under this policy, an animal's evolutionary legacy is thought to hold the adaptive potential for the future of the species and is therefore deemed worth conserving. However, considerable uncertainty remains as to how the "evolutionary legacy of the past" can reflect the future adaptive needs of fish, especially in light of the influence of artificial propagation, overharvest, and significant environmental change (Reed and Frankham, 2001; McClure et al., 2008). Confusion about which population segments require conservation protection often occurs when genetic diversity also reflects population structure at least partially derived from recent manipulations (such as selection during hatchery propagation) or rapid adaptations to environmental change.

Phenotypic and life history traits such as size-at-age, fecundity, migration timing, age, and time of spawning are assumed to reflect adaptations with evolutionary importance, but we know little about how these traits evolve. Tools available through genomics and gene expression allow critical research in adaptation in fitness and life history traits that may not be reflected in the way we currently monitor evolutionary legacy for conservation with neutral genetic markers (Crozier et al., 2008; Derome et al., 2008; Waples and Hendry, 2008;

Whitley et al., 2008). As first suggested by Waples (1991), the process of evolution and differentiation within and between species is manifest in so many different ways that no simple yardstick is universally applicable. It has long been recognized that phenotypic trait evolution can result from random genetic drift and natural selection (Lande, 1976; Felsenstein, 1988). It is also generally assumed that stabilizing selection works to promote optimum phenotypes as well as genotypes. Variation in gene expression represents a molecular phenotype that can be linked to important developmental and adaptive traits in fishes (Shapiro et al., 2004). Molecular phenotypes are hypothesized to play a major role in adaptation across taxa (King and Wilson, 1975; Carroll et al., 2001). A large collection of recent literature has provided empirical evidence supporting the inference that changes in gene regulation and expression are the foundation of many ecologically important adaptive traits (Carroll et al., 2006, 2007; Wray, 2007; see Table 1). However, the extent to which stabilizing selection limits divergence in gene expression remains controversial (Drummond et al., 2005; Hoekstra and Coyne, 2007).

4.2 Adaptive physiology

Global climate change has the potential to greatly impact biodiversity by changing the dynamics and evolutionary potential of many species (Parmesan, 2006; Botkin et al., 2007; Eckert et al., 2008). The distribution and range of many aquatic organisms have already shifted around the globe in response to climate change, resulting in changes in population structure and community dynamics (Perry et al., 2005; Reist et al., 2006; Ficke et al., 2007). Dynamic population structure can result in novel inter- and intra-specific associations, which can increase environmental stressors and shift biotic demand (Root et al., 2003; Williams et al., 2007; Preston et al., 2008). Gene expression profiles linked to natural and anthropogenic stressors, including climate-induced changes in sea temperature, have been demonstrated in both coral reef fishes and the corals on which they depend (Wiens et al., 2000; Edge et al., 2005; Kassahn et al., 2007). Interpreting physiological responses to environmental change on individual and community scales is especially important when marine reserves are part of the conservation efforts in fisheries (Araújo et al., 2004). Significant evolutionary process has been shown to occur in fish over what are considered ecological time scales, i.e., tens of generations or less (Yoshida et al., 2003; Stockwell et al., 2003; Carroll et al., 2007). Evidence for natural variation in gene ex-

pression with ecological consequences has been shown in many recent studies: adaptation to hypoxia in burrow-dwelling goby fish *Gillichthys mirabilis* (Gracey et al., 2001); the development of sympatric ecotypes of lake whitefish *Coregonus clupeaformis* (Derome et al., 2006; Whiteley et al., 2008); ecological convergence between two limnetic coregonine fishes (Derome and Bernatchez, 2006); adaptation to different oceanic conditions in European flounder *Platichthys flesus* (Larsen et al., 2007); and physiological changes in Atlantic salmon (Giger et al., 2008) and brown trout *Salmo trutta* (Larsen et al., 2008) entering sea water. Studies suggest that our understanding of gene expression cannot ignore the potential ecological effects of rapid adaptation to altered fitness requirements in novel habitats (Nielsen et al., 2009).

Genetic implications of redistribution of organisms due to a rapidly changing climate are multifaceted and hard to predict. We do know that animals that cannot adapt through phenological response to a changing climate will most likely suffer diminished recruitment and declines in population size, ultimately leading to erosion of genetic variability across natural landscapes (Thorsten et al., 2007; Bradshaw and Holzapfel, 2008; Bell and Collins, 2008). The power of microarray technology to identify candidate loci that exhibit subtle differences in gene expression associated with adaptive variation linked to a response to climate change seems important to our understanding and conservation of biodiversity. Researchers working on fishes have provided innovative insights that can be used to address some of these questions (Oleksiak et al., 2002; Aubin-Horth et al., 2005a,b; Amstutz et al., 2006; Giger et al., 2008).

But this approach is not lacking challenges (Kammenga et al., 2007). Genetic profiles associated with spatial structure in fitness and complex life history traits can flux rapidly, with highly variable results (Bradshaw and Holzapfel, 2001, 2006; Moczek and Nijhout, 2003; McClelland and Naish, 2007). Theoretical hypotheses about the components of phenotypic variability, their measurement, and biological factors contributing to their expression are just starting to be tested (Willmore et al., 2007). Microarrays offer a means of generating data from specific tissues and life history stage under variable environments that may help link evolutionary potential to the stresses of climate change. Knowledge about the role and limits of adaptation linked to important physiological traits can provide significant information for conservation efforts in altered climates and environments (Bradshaw and Holzapfel, 2001; Reusch and

Wood, 2007; Preston et al., 2008).

4.3 Behavioral genomics

Fish express a complex set of behaviors that can be explored using gene expression and microarrays. An important topic of discussion in relationship to climate change, dispersal, and colonization behavior in migratory fishes is the question of local adaptation. Dispersal and gene flow among populations is assumed to dilute population genetic structure and be antagonistic to local adaptation. This view of dispersal assumes that fish stray randomly. However, strays are known to sample different environments and select those best fitted to their phenotype, leading to directed gene flow, local adaptation, and increased genetic structure (Edelaar et al., 2008). Whether phenotype-dependent dispersal (straying) is random or directed will have significant implications in the response to climate change experienced by highly migratory fishes (Armsworth and Roughgarden, 2005). Understanding the limits and costs of plasticity in specific behavioral traits may resolve some of the questions matching habitat choice with range expansion and colonization.

Recent studies have shown that behavior correlated to variation in gene expression in the central nervous system can improve our understanding of the processes involved in gene flow and connectivity among groups or populations within a species. For example, the work of Aubin-Horth et al. (2005a,b) on gene expression in the brains of young male Atlantic salmon have provided important insights into the molecular mechanisms underlying developmental plasticity and age at reproduction in this species. Implications of these studies on male reproductive plasticity and gene expression called into question the evolutionary history of anadromy in salmonids, a topic of great interest in the conservation of iteroparous species. Another genomic study of Chinook salmon by Bernier et al. (2008) showed that genes expressed in the brain exhibited strong differentiation across seasonal migratory groups in fish from the same population. The gene ependymin exhibited stronger transcription in the fall migrating fish than in the spring migration. This gene has been shown to affect long-term memory formation in fish. These data suggest that transcriptional changes in this gene may play an important role in behavioral variation in homing and spawning in salmon.

Changes in gene expression and their contribution to behavioral variation and phenotypic plasticity represent relatively new approaches in behavioral ecology. Other applications of behavioral genomics using gene expression with implications in fisheries management include

recent studies looking at differences between farmed and wild Atlantic salmon (Roberge et al., 2006 and 2008); how environment influences the development of behavioral plasticity and social structure in fish (Sneddon et al., 2005); genomic effects of handling stress (Krasnov et al., 2005); and the ongoing argument about the ability of fish to experience pain (Reilly et al., 2008). As the study of gene expression and candidate genes in different behavioral phenotypes expands, we will be able to ask questions about the underlying genetic processes of adaptive behavior. Are the genes that influence behavior in one species or organism likely to influence similar behavioral responses in others? How has selection shaped the limits of behavioral phenotypic response in fish to changing ecology and environments? This approach will be a useful tool linking genetic experimentation with our knowledge of gene function and local adaptation.

5 Discussion

Many of our questions about ecosystem condition and species survival center on the ability of an organism to adapt to its environment (Forcada et al., 2008; Tomanek, 2008). We are quickly learning that how genes work is as important as what genes are conserved. Gene expression profiles reflect a critical part of the interaction among an organism's evolutionary history, local environment, behavioral plasticity, and ability to adapt (Fig. 3). It is still difficult to determine if measurable

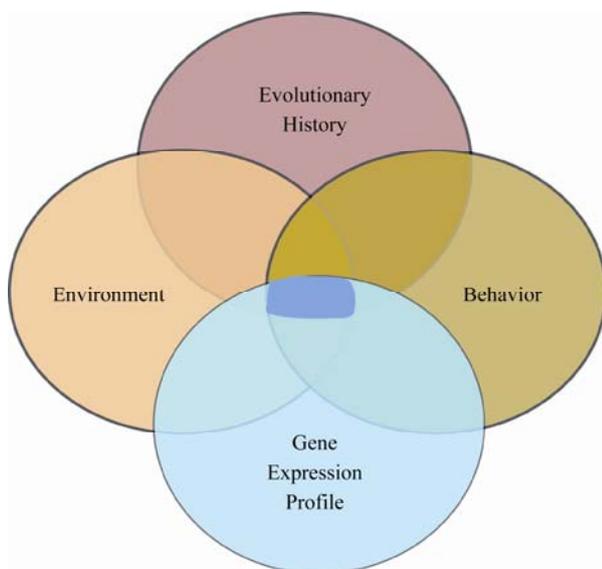


Fig. 3 Hypothetical relationship among evolutionary history, environment, behavior, and gene expression for adaptive trait contributing to an animal's composite phenotype under conditions of climate change

fitness traits are associated with changes in one or a few major genome regions. We also know little about how these regions help to integrate the complex physiological, morphological, and behavioral conditions associated with variation in adaptive traits. However, once critical gene complexes responsible for fitness traits are identified in model animals (Haffter et al., 1996) or are isolated from different species, surveying functional variation will be informative in the management and conservation of both propagated and wild fish populations (Kinnison and Hendry, 2001; Thrower et al., 2004; Nichols et al., 2008).

For several decades, fisheries regulations have been implemented in an effort to conserve biodiversity of known stocks that support sustainable harvests of wild fish populations around the globe (Ryman et al., 1995). Declines in the distribution and abundance of fish worldwide have changed the focus of fisheries management from harvest to restoration (Worm et al., 2009). Addressing conservation and restoration of global fish stocks, especially with a rapidly changing climate, will involve important questions concerning adaptation and fitness. These approaches require the application of genomic tools that may change our perspective of fisheries management and conservation. In light of the focus on restoration, we ponder the question of whether DNA technologies demonstrating the evolutionary history of a species are correctly focused on the true evolutionary potential of the resource. How do we define threatened or endangered status for populations as they migrate into different latitudes, colonize new habitats, develop new species complexes, and face different diseases and stressors?

Our concepts of threatened status, local extinctions, and dispersal/invasion biology are going to change as we recognize the implicit reality and biological implications of climate change (Carlson and Seamons, 2008). Even though natural populations of fish can tolerate a broad array of environmental conditions, global climate change will alter the selection regime for most biota (Reusch and Wood, 2007). Projected changes in climate forcing variables such as temperature and precipitation can have a wide range of impacts on future distributions and abundances of northern fishes (Parmesan, 2006). How will different species or populations respond to potential range expansions as the oceans warm? As the effects of climate change continue to shift environmental factors, especially in the large northward-flowing river of Siberia and northern Canada, many cold-water species are likely to extend their geographic range into the Arctic (Reist et al., 2006). Ocean

warming has resulted in frequent and unpredictable shifts in marine distributions of salmon in the North Pacific Ocean (Myers et al., 2007), with reproductive adults straying into Arctic waters (Babaluk et al., 2000; Stephenson, 2006). Commercially valuable fish species have also been moving into Arctic North Atlantic waters as a result of considerable oceanic warming (Rose, 2005). What evolutionary mechanisms sustain rapid colorizations in novel habitats?

Exploitation of commercially important Arctic fishes is already part of U.S. policy. The North Pacific Fishery Management Council recently released a management plan for commercial fisheries in the Arctic Ocean (NPFMC, 2009¹). This plan stipulates that no commercial fisheries can be harvested in the U.S. Arctic Management Area in the Beaufort and Chukchi seas at this time. Any authorized commercial fisheries in this area will require “judicious and responsible fisheries management practices, based on sound scientific research and analysis.” Are sustainable harvests of Arctic fish populations possible based on classical management and the “stock” concept? What type of genetic information can best inform fisheries managers through “sound science” in the Arctic?

As we learn more about genes and gene function in fishes, the question of what we can and will manage for human consumption will change (Muir, 2005). Current conservation efforts based on different measures of evolutionary history may well give way to arguments on genetic variation in fitness traits, measures of adaptive potential, and the evolutionary limits to adaptation. Interesting topics based on human evolution linked to unique pathways of gene function and adaptation (see Tang et al., 2007) will eventually transfer into natural resource questions. The future management of fisheries will need to consider fine-scale differentiation of factors contributing to an organism’s micro-evolutionary potential as well as the species’ long-term evolutionary history. We suggest that the study of gene expression using microarrays can play a significant role in our ability to address conservation and management issues in fisheries and will continue to grow in importance in the future.

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