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Abstract

Located in the Pacific Northwest, the Columbia River basin provides important spawning and rearing habitat for Pacific salmon and steelhead (*Oncorhynchus* spp.). These species were historically abundant throughout the basin but have experienced extensive declines linked to a complex suite of factors. These declines, in tandem with their cultural and economic significance, have led Pacific salmon and steelhead to become one of the most intensely managed groups of species in North America. Management actions have increasingly recognized the importance of genetic resources and have expanded the use of genetic tools to provide powerful data for the conservation and management of Pacific salmon. We provide a summary of historic management actions in the basin with a focus on those relevant to genetic applications. We describe the initial recognition of genetic differences and distinction of population units, how genetics applies to the hatchery controversy, as well as the progression of genetic investigations and applications used in management. Further, we outline some emerging and potential future genetic tools.

Keywords: Columbia River basin, Pacific salmon, salmonid management, genetics

Introduction

The Columbia River basin (Figure 1) drains much of Idaho, Oregon, and Washington, portions of Montana, Nevada, Utah, and Wyoming in the United States as well as the southeastern portion of British Columbia, Canada. Prominent features of the landscape include the Columbia and Snake rivers which are fed by a complex network of tributaries stretching through the 668,000 km^2 basin. These drainage networks provide spawning and rearing habitat essential for five species of anadromous Pacific salmon and steelhead: Chinook salmon (*Oncorhynchus tshawytscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), steelhead trout (i.e., the anadromous form of rainbow trout) (*O. mykiss*), and sockeye salmon (*O. nerka*). These fishes were historically abundant throughout the basin, but have experienced widespread declines linked to direct exploitation (i.e., overfishing) as well as loss of habitat and connectivity, introgression with hatchery-origin fish, hydroelectric development, and water diversion projects, among other factors (Myers et al. 1998). It is estimated that prior to European arrival and development, the basin contained more than 200 healthy stocks of anadromous salmon (Chapman 1986, Nehlsen et al. 1991, Williams et al. 2006). These stocks were the basis for the regional economy and ecology for thousands of years. However, the number of healthy stocks was reduced to as few as nine by the late 1990s (Huntington et al. 1996). In response, extensive efforts have been employed to replace losses, making Pacific salmon one of the most intensely managed species groups in North America (Stouder et al. 1997, Dann et al. 2013).

Genetic resources have been increasingly recognized over time as important considerations for the conservation and management of Pacific salmon and steelhead in the Columbia River basin. There has been a transition from an early view that groups within a single salmonid species were interchangeable, to the present recogni-

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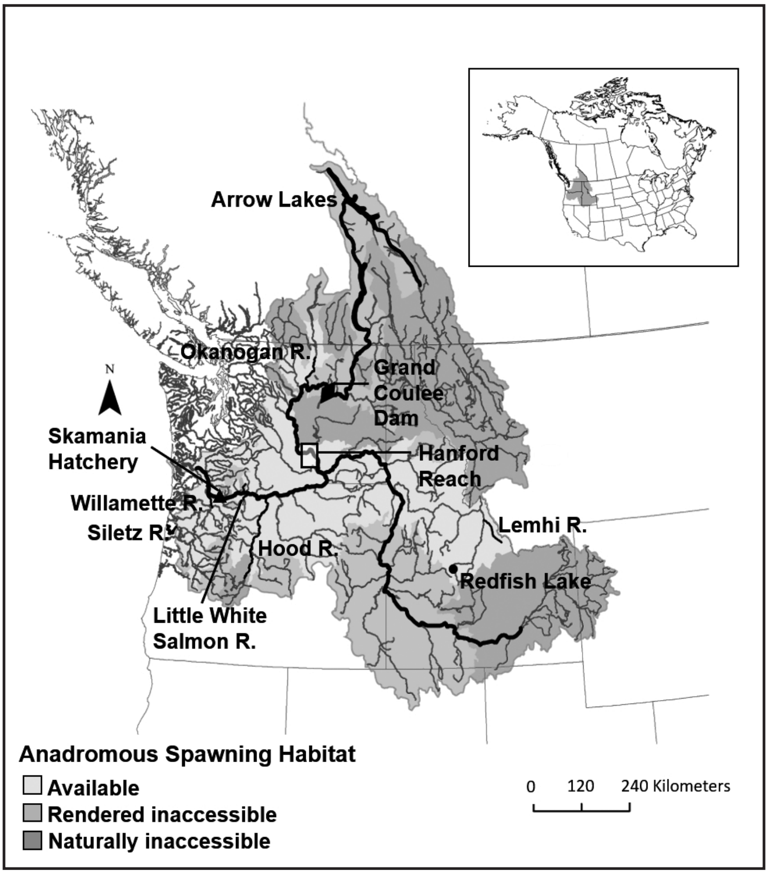

Figure 1. Map of the Columbia River Basin showing locations discussed in the manuscript. Basin (grey) is shaded to indicate areas historically (naturally) unavailable to anadromous salmon/steelhead as well as those rendered inaccessible by human influence. Habitat areas based on those developed by the Columbia River Inter-Tribal Fish Commission (CRITFC 2014).

tion that groups (i.e., populations or stocks) are important units of conservation. There has also been increasing recognition that genetic changes may take place after fish have been reared in a hatchery environment for even short periods of time and that these changes are relevant to their management. Here, we provide a background on a portion of relevant management actions, with a focus on those involving genetic applications. This review is not an exhaustive account of the dynamic history of fisheries management in the Columbia River basin. Instead, we hope to provide a concise and relevant summary that introduces non-specialists to the field and serves as a guide to some of the pertinent literature.

Early Recognition of Genetic Differences: Stocks and Evolutionary Significant Unit

The widespread historic practice of using eggs from distant sources in salmon enhancement programs within the Columbia Basin illustrated the prevailing view that units within salmon species were interchangeable. These transplants were typically monitored based on clipping of fins, the first of a wide range of marking and tagging techniques (Parker et al. 1990) that have culminated in the sophisticated use of genetic tags today. The key monograph by Ricker (1972) and report by Fulton and Pearson (1981) documented a number of such transplants. This practice continued into the 1980s, when the Idaho Department of Fish and Game imported sockeye salmon eggs from northern British Columbia (Babine Lake) in connection with a restoration effort for that species in central Idaho (Waples et al. 1991). That transplant, like many others, was unsuccessful.

One positive outcome of such wide transplants was the recognition that geographically local strains yielded the highest returns (Ricker 1972, Reisenbichler 1988). For example, there were no returns to the Lemhi River, Idaho of transplanted Little White Salmon River fall Chinook salmon from 1,100 km downstream, although returning fish were documented in the downriver fishery (Ricker 1972).

The realization that populations represented distinct units and needed to be considered as such for management and conservation purposes, (The Stock Concept; MacLean and Evans 1981, Carvalho and Hauser 1994, Booke 1999) became recognized as a fundamental concept in fishery management. Stock-based management and the ability to better define what constitutes a stock enabled fisheries to be targeted and to minimize the potential for overharvest. The application of the stock concept to salmonid populations and fisheries grew during the 1970s and 1980s (e.g., Simon and Larkin 1972, Berst and Simon 1981).

Studies in the Willamette River basin in Oregon involving transplants of summer-run steelhead gave a concrete example and mechanistic understanding of the importance of the stock concept. Efforts to introduce summer steelhead into the system had failed when a coastal strain from the Siletz River, Oregon had been utilized but succeeded when a Columbia Basin strain (Skamania) was used. This was attributed to the susceptibility of the Siletz (non-Columbia Basin) fish to the parasite *Ceratonovia shasta* which is endemic in the Columbia Basin (Buchanan et al. 1983). Similar resistance patterns were evident for other salmonid species (Zinn et al. 1977). Many other examples of local adaptation have been documented for a wide variety of traits in salmonid species, providing a practical rationale for conservation of local stocks. Local adaptation is also the rationale for many current hatchery and supplementation policies (to be discussed) (Taylor 1991, Fraser et al. 2011).

During this period, laboratory studies on genetic markers in Pacific salmon also reinforced the concept of genetic distinctions among stocks. Initial work with blood typing was supplanted by the widespread and successful use of protein electrophoresis for species and stock identification (Utter et al. 1973, Utter 1991). Protein electrophoresis provided a highly effective tool for addressing issues such as interspecific and intraspecific hybridization, within-species stock structure and management of mixed stock fisheries (Milner et al. 1985). Many issues related to Columbia Basin salmon stocks were investigated with this tool (e.g., Utter et al. 1995). Together, these studies demonstrating phenotypic and genetic marker differences among stocks set the stage for increasingly activist approaches to stock conservation.

Recognition of marked differences among salmon and steelhead populations and their continued demographic declines led to elevated concern for the conservation of many populations, including those in the Columbia River basin (Nehlsen et al. 1991). The decision to pursue listing of a salmon or steelhead population under the US Endangered Species Act (ESA) was initiated by a petition for listing of sockeye salmon in Redfish Lake, Idaho (Waples et al. 1991). The National Marine Fisheries Service of the National Oceanic and Atmospheric Administration (NOAA) ruled that listing of this population as an endangered species was warranted. Over subsequent years, a number of salmonid groups/populations within the Columbia Basin were approved for ESA listing (Waples et al. 2001). An important concept associated with these decisions was that of the Evolutionary Significant Unit (ESU), briefly defined as a group/population that is considered distinct for purposes of conservation (Waples 1991, 1995). This concept provided an operational process for identifying notable within-species groupings which merited protection. Detailed phenotypic and genetic studies followed to identify such conservation units within species (e.g., Waples et al. 2001, Brannon et al. 2004).

Hatchery vs. Wild Differences Emerge

Genetic tools have also been widely applied to hatchery operations. The use of hatcheries for mitigation and enhancement of fisheries in the Columbia Basin has a long history (Netboy 1980, Taylor 1999, Augerot and Foley 2005). Initially, hatcheries were widely equated to farms and hatchery success was evaluated by the same measures as traditional agriculture—production (Lichatowich 2001). However, even as hatcheries produced huge numbers of salmon, stocks continued to decline and the massive production efforts led to hatchery fish constituting the lion's share of many stocks in the basin (over 90 percent of coho salmon, more than 70 percent each of spring Chinook salmon, summer Chinook salmon, and steelhead, and half of the fall Chinook salmon) (NOAA 2017). Hatchery- and natural-origin fish, like fish from different geographic areas, were largely considered equivalent and interchangeable into the 1970s and 1980s. A pioneering study involving hatchery-origin and natural-origin summer-run steelhead in the Deschutes River, Oregon (Reisenbichler and McIntyre 1977) raised questions about their interchangeability. In this study of juvenile survival, hatchery fish were identified ("tagged") with a genetic marker detectable using protein electrophoresis. The progeny of hatchery-origin fish displayed greater survival in a hatchery environment, but demonstrated poorer survival in the wild than the progeny of natural-origin fish. Subsequent studies on hatchery- and natural-origin performance raised questions about their relative performance characteristics and often suggested that natural-origin fish show superior survival in nature (e.g., Chilcote et al. 1986, McLean et al. 2003) and that rivers with high proportions of hatchery steelhead show lower reproductive success than those with a predominance of wild fish (Chilcote et al. 2011, 2013). Most hatchery vs. wild studies involved steelhead, but some also involved Chinook salmon (Williamson et al. 2010, Hess et al. 2012, Anderson et al. 2013, Ford et al. 2015), and coho salmon (Theriault et al. 2010), among others. Christie et al. (2014) reviewed a number of studies and concluded that performance may decline very early during the establishment of hatchery strains and the effects superseded differences in geography, hatchery practices, and species.

An especially detailed set of studies was conducted with steelhead in the Hood River, Oregon (Araki et al. 2007, 2009; Christie et al. 2012). These studies involved following the relative viability of fish with known pedigrees (based on DNA markers) over multiple generations. The general conclusion was that even a single generation of hatchery rearing could significantly reduce the survival and reproductive success of fish in the natural environment. Because it raised concerns that the use of hatcheries in restoration efforts might have significant drawbacks (e.g., Reisenbichler and Rubin 1999, Ford 2002, McClure et al. 2008), the Hood River studies were controversial. Furthering the controversy, results by other research teams have produced different results with no or a less dramatic decline of reproductive success by hatchery fish (e.g., Hess et al. 2012, Williamson et al. 2010, Ford et al. 2015). Because these studies involved Chinook salmon rather than steelhead, and many Chinook salmon programs rear in hatcheries for a shorter time prior to release, a likely interpretation could be that the species and rearing history differences might account for the divergence in research results and that extrapolation from steelhead to Chinook salmon should be done with caution.

Salmon and steelhead hatchery programs remain a prominent component of the modern aquatic landscape in the basin. The primary purpose of these programs is to provide mitigation for the diminished production due to habitat loss and degradation. The contemporary management of hatchery programs continues to provide harvest opportunities throughout the basin, but has evolved to incorporate conservation principles and specific recovery objectives (NPPC 1999). Examples of this progression are the widely adopted recommendations from the Hatchery Scientific Review Group (HSRG) in using hatcheries to conserve or proliferate a natural population (HSRG 2009). This peer-reviewed guidance has fueled an expansion of genetic considerations in the operation, monitoring, and evaluation of hatchery programs. Further, many hatchery programs now operate under a hatchery genetic management plan, or HGMP, which are required by NOAA for hatchery program approval under the ESA. An HGMP includes identifying the purpose of the hatchery program (e.g., conservation, supplementation, harvest) and identifies risks of the hatchery programs to natural populations (NMFS 2005). Considerations in HGMPs include managing broodstock for genetic integration or segregation, promoting local adaptation, and minimizing ecological interactions between hatchery- and natural-origin fish.

Proliferation of Genetic Tools

The importance of genetic data for salmon management was largely underscored by acceptance of the stock concept and hatchery vs. wild issues. As the potential power of genetic data to answer other questions related to fisheries management gained traction, a number of important studies were published for salmon and steelhead in the basin. Most focused on the identification of stocks, patterns and quantification of genetic diversity, or a combination of these (for a review of important references see Waples et al. [2001]). Initially studies were based on protein electrophoresis (i.e., allozymes) (e.g., Phelps et al. 1994, Gustafson and Winans 1999). Allozymes provided a quality source of distinct and stable markers to identify fish stocks and detect hybridization (Milner et al. 1985, Carvalho and Hauser 1994) but often lacked the ability to distinguish fine-scale differences and required careful handling and processing of collected tissues (Brown et al. 1979, Zhivotovsky et al. 1994, Wilmot et al. 1998). In contrast, the advent of polymerase chain reaction (PCR) and DNA-based markers allowed for more accurate and precise characterization of genetic variation, particularly at fine scales (Ferguson et al. 1995).

Initially, the high cost of DNA-based technologies inhibited use of these markers by fisheries management agencies. Studies that did incorporate DNA-based markers tended to do so in tandem with existing protein data due to the wide availability of such datasets, which had been carefully standardized and subjected to quality control (Shaklee and Phelps 1990, White and Shaklee 1991, Shaklee and Bentzen 1998, Waples et al. 2001). Eventually, decreasing costs for DNA technology, as well as the development of dedicated genetic databases both specific to Pacific salmon (e.g., Seeb et al. 2007) and for genetic data in general (e.g., GenBank, the annotated collection of all publicly available DNA sequences curated by National Institutes of Health [Benson et al. 2014]) allowed for a transition away from protein-based genetic studies to those using DNA-based markers. The primary types of molecular markers applied to salmonids in the basin have included mitochondrial DNA (mtDNA) (e.g., Park et al. 1993, McCusker et al. 2000), simple sequence repeats (SSRs) such as microsatellites (μSATs) (e.g., Small et al. 1998a, Beacham et al. 2000) and single nucleotide polymorphisms (SNPs) (e.g., Aguilar and Garza 2008, Larson et al. 2014).

As with allozymes, each type of DNA marker has associated advantages and disadvantages. Mitochondrial DNA is typically inherited from the mother only. This simple inheritance and fast rate of evolution (as much as ten times faster that of nuclear DNA (Castro et al. 2010) make it a useful marker for phylogenetic studies (e.g., McVeigh and Davidson 1991, Domanico and Phillips 1995, Martin et al. 2010). While mtDNA has been used to examine population-level questions; the maternal inheritance limits the genetic information available from this marker. Simple sequence repeats, such as microsatellites, are non-coding sequences of DNA repeated in the genome that can be isolated and identified. Differences in the number of repeats tend to arise quickly, making SSRs one of the most polymorphic markers available. However, they also require considerable effort to develop and must be standardized. Single nucleotide polymorphisms (SNPs) are positions in the genome where genetic variations occur. SNPs are only informative if they vary in the groups being compared (i.e., ascertainment bias). For a review of the application of specific marker types to diagnostic and population monitoring questions see Schwartz et al. (2007).

More recently, technology has advanced to include methods such as restriction site associated DNA sequencing (i.e., RAD sequencing or genotyping by sequencing) (Miller et al. 2007, Baird et al. 2008, Davey and Blaxter 2010, Elshire et al. 2011). Studies utilizing this data can identify thousands of genetic differences, allowing for high resolution analysis of population/stock differences, hybridization, as well as candidate genes linked to functional life-history traits of interest (e.g., Hohenlohe et al. 2011, Larson et al. 2014).

Contemporary Genetic Tools in Management

As the landscape of genetic knowledge and technology has evolved, a suite of applicable genetic tools has been introduced to salmon biologists, researchers, and managers throughout the basin. These tools are typically applied to address both general and specific uncertainties and concerns in the management and recovery of populations. Perhaps the most common tool, genetic stock identification (GSI), was first applied to Pacific salmon in Milner et al. (1985) and made use of the comprehensive datasets available for Pacific salmon, combining genetic technology with the stock concept. In GSI, individuals caught in a fishery composed of mixed stocks, such as an oceanic fishery, are statistically assigned to any number of originating stocks in the genetic baseline (Milner et al. 1985, Utter and Ryman 1993). Note Utter and Ryman (1993) suggest the term mixed stock analysis (MSA) may be a more accurate description of the methodology as stocks cannot be directly identified, instead statistical associations are used to analyze the likely stock composition of a sample. The terms are generally used interchangeably to describe the same concept; we use GSI here. The GSI approach provides several advantages over traditional stock identification methodology (i.e., physical marking and tagging of individuals) including: no risk of marker loss, no alteration in fish behavior from a mark, no minimum size requirement for marking, as well as a much lower overall cost (Utter and Ryman 1993). Perhaps most importantly, GSI allows a fish to be assigned to a stock without the need for initial capture and physical marking.

GSI is contingent upon several prerequisites for application, including: 1) both the existence and characterization of genetic differences between groups, 2) reliable genetic sampling from the mixed-stock, and 3) statistical methods for estimating stock proportions based on genetic data (Utter and Ryman 1993). Due to the first requirement, the genetic data used for GSI has followed the development of contingent datasets for Pacific salmonids representing the stocks potentially sampled in the fisheries. GSI first utilized protein differences (e.g., Beacham et al. 1987, Wood et al. 1989, Shaklee et al. 1990, Winans et al. 1994, Winans et al. 2004), before incorporating DNA-based markers such as mini and microsatellites (e.g., Beacham et al. 1995, Winans et al. 1996, Small et al. 1998b, Beacham et al. 2008), mitochondrial DNA (e.g., Cronin et al. 1993, Moriya et al. 2007) and nuclear DNA sequences (e.g., Smith et al. 2005, Hess et al. 2011).

The pairing of improved statistical analyses and enhanced molecular markers has provided another important alternative to traditional marking, parentage-based tagging (PBT) (Anderson and Garza 2005). In PBT, broodstock collected for hatchery programs are genotyped. This allows subsequent progeny (returning spawners) to be assigned back to their hatchery parents through pedigree reconstruction, eliminating the need for handling and tagging of juvenile fish. Steele et al. (2013) found that fewer than 100 SNPs were needed to accurately conduct PBT, and the results were comparable in accuracy to microsatellite markers and traditional coded-wire tags for steelhead in the Snake River Basin ESU. The applicable value of PBT can be extended to support established management inferences, such as determining effective population size, calculating probabilities of inbreeding, and assessing iteroparity rates of hatchery- and natural-origin steelhead (Abadía-Cardoso et al. 2013).

Restoration and Management of a Modified River System

The current status and future direction of salmon and steelhead in the Columbia River basin is deeply complex at the biological, cultural, ecological, geographic, and political levels (for in-depth discussion see Williams [2005]). Multiple agencies and groups have a vested interest in the conservation, recovery, and sustainability of salmon and steelhead, and the approach varies by entity. For example, state agencies (Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, and Idaho Fish and Game) highlight conservation, sustainability, and harvest opportunities in their department goals and objectives statements. The Columbia River Inter-Tribal Fish Commission (representing the Yakama, Warm Springs, Umatilla, and Nez Perce Tribes) places a focus on putting fish back into rivers and protecting tribal fishing rights. Meanwhile, the US Fish and Wildlife Service and NOAA are tasked with applying the Endangered Species Act, which focuses on the protection and recovery of listed species. Further, salmon and steelhead species themselves have multifaceted and diverse life history requirements and cannot be managed under a one-size-fits-all strategy. Understanding how genetic issues fit into specific threats that vary by species, population, region, waterway (or any combination of these) will be essential in evaluating progress towards entity goals.

Studying persisting healthy stocks or successful restoration efforts may provide important clues into how to best implement future programs. One such example is the Hanford Reach stock of fall-run Chinook salmon, one of only a few truly 'robust' stocks of fall Chinook salmon in the basin (Williams et al. 2006). Chinook salmon in the Hanford Reach spawn and rear in a section of linked, free-flowing river habitat which benefits eggs, juveniles, and adults alike (Geist and Dauble 1998). Dams upstream of the reach are regulated with consideration for the specific needs of the population below (Kolar et al. 2007). Hanford Reach fall Chinook salmon are a lesson in cooperative management as this group has thrived under a collaborative effort by several stakeholders including the Bonneville Power Administration, state governments (Washington and Oregon), Public Utility Districts, Treaty Tribes, and the US Army Corps of Engineers. These agencies have developed a cooperative working strategy that considers the biological and ecological needs of salmon, despite the widely varied objectives of these entities. Cooperative management of sockeye salmon has also been implemented in the upper Columbia River, where range expansion and flow management have benefitted runs (Hyatt et al. 2015, Veale and Russelo 2016). Populations such as the Hanford Reach fall Chinook may provide important genetic metrics such as effective population size, genetic diversity, and temporal variability that might inform restoration efforts or monitoring of other populations.

The assertive use of artificial propagation and captive breeding approaches has been instrumental in preventing extinction of the Redfish Lake sockeye salmon of the Snake River (Kline and Flagg 2014). This program has demonstrated that, when sufficient resources are committed to such a program, it can preserve a valuable gene pool and preserve future options even in the face of serious habitat problems.

The use of supplementation programs to augment natural reproduction of salmon and steelhead for restoration efforts has been widely advocated in the Columbia Basin but remains a contentious subject. Such programs can have immediate benefits to population size (Hess et al. 2012, Vendetti et al. 2017) but the increases may not be sustained after the programs are phased out (Vendetti et al. 2017). These limitations may be related to continuing habitat problems or to altered productivity of the supplemented stocks, potentially due to their historic hatchery propagation (Reisenbichler and Rubin 1999). In some populations, such as Wenatchee River spring Chinook Salmon and summer steelhead, direct measures (e.g., euthanasia) are being taken to limit the proportion of hatchery-origin fish that spawn (WDFW 2010, NMFS 2013).

Another avenue to conserve and sustain natural salmon and steelhead populations is the creation and maintenance of "gene banks". Traditional gene banks are preserved gametes held in long-term storage (Thorgaard et al. 1998). These banks may provide some insurance against total stock collapse. Preservation efforts of Snake River Chinook salmon were initiated by the Nez Perce Tribe in the early 1990s (Faurot et al. 1998) and subsequently expanded to include steelhead trout (Young 2011). However, the usefulness of cryopreservation has limits. Due to preservation challenges, material for cryopreservation is almost exclusively milt from male salmon and the fertility of stored milt is lower than that of fresh material.

Another form of gene banking includes zoned portions of habitat where the release of hatchery fish is restricted, termed wild fish management zones. Similar to traditional gene banking, the goal of wild fish management zones is to preserve genetic integrity by providing protection from potential negative effects of hatchery programs (e.g., interbreeding, fitness loss, and resource competition). In Washington State, a network of wild stock gene banks have been, or are being, established for steelhead in population groups within distinct population segments defined by the ESA (see WDFW 2008). Criteria for inclusion in these areas are that the population is abundant (i.e., self-sustaining), no hatchery releases occur in or near spawning and rearing areas, and harvest is only allowed if management goals and permitting regulations are being met. Areas that lack evidence or documented history of introgression with hatchery fish may also serve as potential *defacto* gene stock gene banks. Examples of such gene banks in Idaho include spring/summer Chinook salmon in areas of the Salmon River, steelhead trout in parts of the Clearwater River (Lochsa and Selway drainages) and parts of the Salmon River (see IDFG 2012). Current state management emphasize protection and maintenance of the genetic integrity of these wild stocks (IDFG 2012).

In recent years, decreased fitness (i.e., the number of individuals that survive to reproduce) of hatchery-origin salmon (compared to natural-origin conspecifics), has been recognized as a limitation to meeting program goals. This has been partially attributed to domestication selection within the hatchery environment, which can limit performance in the natural environment (e.g., Araki et al. 2008). A great deal of research is now focused on methodologies to adapt hatchery program components to limit reductions in fitness, such as assortative mating (reviewed in Wang et al. 2002), rearing density (e.g., Banks 1994), semi-natural rearing systems (reviewed in Maynard et al. 2004), and release strategies (e.g., Johnson et al. 2015). Contemporary salmonids live in a landscape starkly different from their ancestors. This is particularly true for Pacific Northwest salmon residing within the Columbia River basin, a highly altered system and one of the most hydroelectrically-developed in world. Dams, particularly large hydropower dams, decrease the area available for spawning and rearing either through direct blockage (if no fish passage is present) or by flooding the habitat with impounded water, and also alter key river dynamics related to salmonid life history such as flow and temperature regimes (Ligon et al. 1995, Angilletta et al. 2008). Although these changes have occurred in a relatively short amount of time, a great deal of evidence exists that evolution can occur on timescales equal to or less than a single human lifetime (Grant and Grant 1995, Hendry et al. 2000, Kinnison and Hendry 2001, Quinn et al. 2001, Williams et al. 2008), demonstrating that organisms rapidly respond to environmental changes.

There is evidence that salmon are adapting, to some degree, to the altered river conditions. For example, over the past 60 years, sockeye salmon in the Columbia River have displayed a trend toward earlier upstream migration timing; with contemporary adults now migrating, on average, more than 10 days earlier than they did in the 1940s (Crozier et al. 2011). Modified life history strategies have also been demonstrated for Chinook salmon in the basin (Waples et al. 2017). Historically, all juvenile fall Chinook salmon in the Snake River migrated to the ocean as sub-yearlings. However, in the past few decades a substantial portion have shifted to a "reservoir-type" life history, wintering in lower Snake River reservoirs and then completing their migration in spring as yearlings. This life history has become so prevalent that as many as three-quarters of returning adult females are now produced from parents with the reservoir-type, yearling life history. These changes are predicted to be "anthro-evolutionary", evolutionary trajectories that have been greatly influenced by anthropogenically driven selective regimes (Waples et al. 2017).

The power of selection to drive evolution is contingent, in part, on phenotypic plasticity (i.e., flexibility) of a single genotype. Model comparisons investigating earlier migration timing for adult sockeye salmon indicate that evolutionary responses explain two-thirds of the trend, leaving only one-third to plasticity (Crozier et al. 2011). High heritability of many life history traits has been demonstrated for Pacific salmonids including growth rate (Hard 2004), maturation timing (Quinn et al. 2000), and spawn timing (Hard and Hershberger 1995, Hard 2004). These evolutionary changes may hold implications for future populations in the region. Should portions of the Columbia River system be transitioned back to a free-flowing system, either through purposeful dam removal or inevitable failure due to silting or loss of structural integrity, traits currently adaptive in the modified river system may be maladaptive in the less modified (i.e., more pristine) system. Thus, salmonids in the system may suffer from a phenomenon known as Darwinian debt (Waples et al. 2008). Darwinian debt refers to the concept that shifts toward undesirable or maladaptive traits often occur much quicker than the timescales for evolutionary recovery (Conover et al. 2009). Thus, a debt incurs and this will need to be repaid before overall fitness can be regained (Walsh et al. 2006).

There is currently significant momentum toward reintroducing salmon into regions of the basin where they have become extirpated (reviewed by Anderson et al. 2014). Examples include introductions of coho salmon into the Snake and upper Columbia rivers (Galbreath et al. 2014) and of sockeye salmon into portions of the Okanagan River basin in Canada where access to spawning areas had previously been blocked (Veale and Russelo 2016). An ambitious future goal is the reintroduction of Chinook salmon above Grand Coulee Dam (Warnock et al. 2016). Determining the best approach for donor stock selection in these situations is challenging. In some cases, such as the coho salmon, local stocks have been extirpated and more distant, lower-river stocks need to be progressively adapted during the reintroduction process. In other cases, suitable stocks from the nearest available sources may be the best alternative.

Looking Forward: Emerging Tools and Future Prospects

Future management applications are likely to incorporate new tools, particularly those developed from genetic data. The study of genetic material extracted from ancient specimens (i.e., aDNA) is now possible, permitting more direct observations of the past (Pääbo 1989, Hadly et al. 2004, Johnson et al. 2007, Ramakrishnan and Hadly 2009). A small number of studies have used aDNA to investigate demographic changes in fish species as they relate to environmental changes. However, these studies tend to focus primarily on the deep past: the Pleistocene period for Atlantic salmon (Salmo salar) (Consuegra et al. 2002) and brown trout (*S. trutta*) (Splendiani et al. 2016), as well as the upper Paleolithic period for North Iberian salmonids (*Salmo* spp.) (Turrero et al. 2012).

In a more contemporary focused study, Iwamoto et al. (2012) applied microsatellite markers to an archive of sockeye salmon scales collected in 1924 from Columbia River populations. In the ancient samples, four genetic groups were identified. Three of these four indicated genetic relationships with contemporary ESUs, two being identical and the third demonstrating similarity. However, the fourth genetic group present in the sockeye salmon populations from 1924 was absent from any contemporary populations in the basin and was considered likely to represent a now extinct Arrow Lakes (British Columbia, Canada) sockeye stock.

Another aDNA study compared genetic diversity in Chinook salmon from the Columbia River basin pre- and post-European contact (Johnson et al. 2018). The results demonstrated that over the past several thousand years, Chinook salmon from the upper-Columbia subbasin have lost more genetic diversity than those from the Snake River subbasin (which have retained most of their diversity) and that both pre- and post-contact events likely influenced the demographic history for these populations of Chinook salmon. These studies provide empirical evidence for the utility of aDNA technology in the development of genetic baselines, the identification and quantification of losses in genetic diversity, as well as for understanding extinction and management of endangered species (Nielsen and Bekkevold 2012).

Another emerging tool with applications in fisheries research is environmental DNA (eDNA). Environmental DNA, described by Ficetola et al. (2008), is the collection and amplification of DNA directly from the environment (e.g., a water sample) instead of from organisms themselves because organisms shed cells containing DNA into their environment. eDNA technology has been demonstrated as an effective way to study the distribution of fish in both freshwater and ocean systems (Dejean et al. 2011, Jerde et al. 2011, Minamoto et al. 2012, Thomsen et al. 2012, Takahara et al. 2013). Currently, the technology is generally limited to presence/absence data; however, in the case of low-density or rare species and inaccessible reaches, eDNA may be more effective than traditional methods such as electrofishing and visual surveys (Laramie et al. 2015). Within the Columbia River basin, eDNA has been empirically demonstrated to positively detect Chinook salmon within the known distribution, but the probability of detection varied by season (Laramie et al. 2015).

To date, genetic studies of salmonids have focused primarily on specific regions of DNA believed to be selectively neutral. However, decreasing costs of genetic analysis combined with increasingly advanced technology, particularly that necessary to analyze large amounts of data, has opened the door for a new era of genetic analysis, genome-wide association studies (Noor and Feder 2006, Davey et al. 2011, Roesti et al. 2014). Using this technology, researchers have successfully identified genetic variants associated with specific life-history traits, such as run-timing, for populations of salmon in the Pacific Northwest (Campbell and Narum 2008, Hess and Narum 2011). Several studies have examined the potential genetic basis of stream vs. shore spawning ecotypes in sockeye salmon (Frazer and Russello 2013, Larson et al. 2016, Nichols et al. 2016). Most recently, a distinct series of genetic variants upon which natural selection acted to produce distinct spawning behavior types in this species was identified (Veale and Russello 2017). The combination of diverse environments, homing behavior, and life history variation make salmonids an ideal candidate for wider studies of ecologically-based divergence (Dodson et al. 2013, Veale and Russello 2017). Indeed, salmonids may be taking their place among more classical examples of evolutionary model species such as the three-spined stickleback (*Gasterosteus aculeatus*) and cichlids (Cichlidae) (Hendry et al. 2000, Hendry 2001).

Summary and Conclusions

Genetic data is now broadly integrated into most management activities in the Columbia River basin. The fundamental notion of stock differences within species has been accepted and implemented. Over the past five decades, technology has advanced from comparisons of proteins to more sophisticated targeted genetic markers and gene-association studies. These advances lead one to speculate on what tools might inform management in the future. Perhaps, as processing of genetic samples continues to require less time, cost, and equipment, in-field genetic data may become a reality. Currently, genetic samples (usually in the form of a tissue sample such as a fin clip) are collected in the field. That tissue is then processed and the genotypic data analyzed post-hoc and used to inform future applications. If a genetic profile could be accessed from a fish on-site, similar to a blood glucose monitor used for humans to manage diabetes, it would allow for real-time stock identification, origin (hatchery vs. natural lineage), or specific trait identification. Armed with this information, genetic-based management actions could be applied in real time and the potential of genetic information to fully replace marks or tags could be realized. Another potential future advance may be redefinition of management units or ESUs that incorporate whole genome and/or more advanced data. Current definitions are based, in part, on any number of historical genetic studies. However, as datasets continue to be built and deeper genetic information is available, redefinition of current units may be a possibility or even a priority. No matter the specific future prospects, it is clear that genetic technology has been instrumental to our understanding of Pacific salmon in the Columbia River basin at many scales. The evolution and application of these tools is likely to continue, providing both answers to current questions as well as new questions.

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