

Salmon Genetics and Management in the Columbia River Basin

Authors: Johnson, Bobbi M., Johnson, McLain S., and Thorgaard, Gary H.

Source: Northwest Science, 92(sp5) : 346-363

Published By: Northwest Scientific Association

URL: <https://doi.org/10.3955/046.092.0505>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Bobbi M. Johnson¹, Wenatchee Valley College, 1300 Fifth St, Wenatchee, Washington 98801

McLain S. Johnson, Washington Department of Fish and Wildlife, 3515 Highway 97A, Wenatchee, Washington 98801
and

Gary H. Thorgaard, School of Biological Sciences, Washington State University, PO Box 644236, Pullman Washington 99164-4236

Salmon Genetics and Management in the Columbia River Basin

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 km² 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-

¹Author to whom correspondence should be addressed.
Email: bobbi.johnson@wsu.edu

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

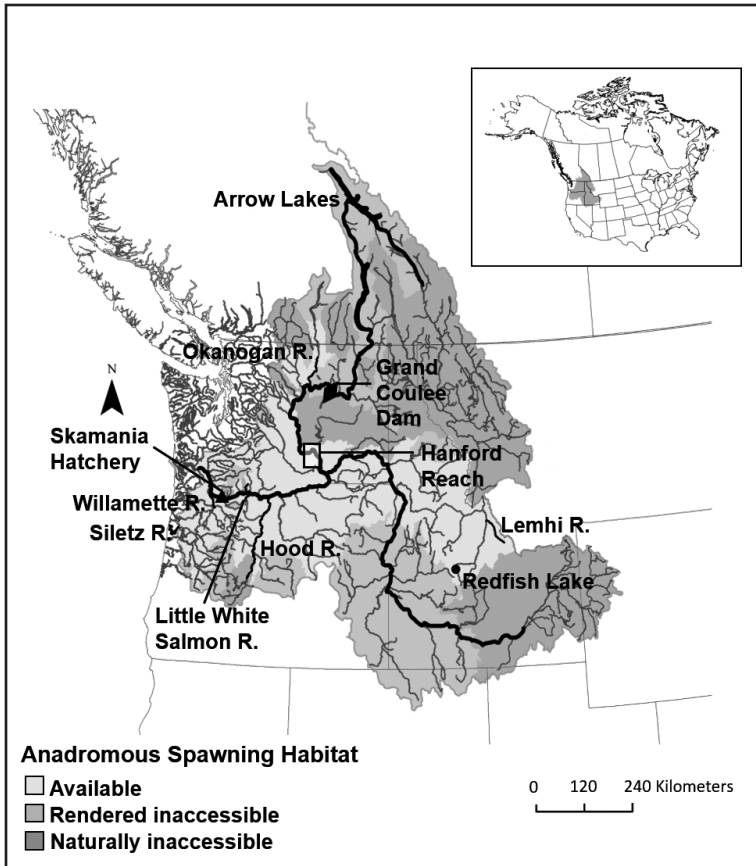


Figure 1. Map of the Columbia River Basin showing locations discussed in the manuscript. Basin (grey) is shaded to indicate areas historically (naturally) unavailable to anadromous salmon/steelhead as well as those rendered inaccessible by human influence. Habitat areas based on those developed by the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

(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 differ-

ent 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 (μ SATs) (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 than 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 mark-

ing, 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 (Abadia-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 Russello 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 Russello 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.

Acknowledgments

We thank B. Thorgaard for assistance with the figure and A. Haukenes and M. Small for their thoughtful review of an earlier version of this manuscript. We also thank C. Busack and an anonymous reviewer for their careful revision and helpful suggestions on the submitted manuscript.

Literature Cited

- Abadía-Cardoso, A., E. C. Anderson, D. E. Pearse, and J. Carlos Garza. 2013. Large-scale parentage analysis reveals reproductive patterns and heritability of spawn timing in a hatchery population of steelhead (*Oncorhynchus mykiss*). *Molecular Ecology* 22:4733-4746.
- Aguilar, A., and J. C. Garza. 2008. Isolation of 15 single nucleotide polymorphisms from coastal steelhead, *Oncorhynchus mykiss* (Salmonidae). *Molecular Ecology Resources* 8:659-662.
- Anderson, E. C., and J. C. Garza. 2005. A description of full parental genotyping. Unpublished report on file with the National Oceanic and Atmospheric Administration. Seattle, WA.
- Anderson, J. H., P. L. Faulds, W. I. Atlas, and T. P. Quinn. 2013. Reproductive success of captively bred and naturally spawned Chinook salmon colonizing newly accessible habitat. *Evolutionary Applications* 6:165-179.
- Anderson, J. H., G. R. Pess, R. W. Carmichael, M. J. Ford, T. D. Cooney, C. M. Baldwin, and M. M. McClure. 2014. Planning Pacific salmon and steelhead introductions aimed at long-term viability and recovery. *North American Journal of Fisheries Management* 34:72-93.
- Angilletta, M. J., E. A. Steel, K. K. Bartz, J. G. Kingsolver, M. D. Scheuerell, B. R. Beckman, and L. G. Crozier. 2008. Big dams and salmon evolution: changes in thermal regimes and their potential evolutionary consequences. *Evolutionary Applications* 1:286-299.
- Araki, H., B. Cooper, and M. S. Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* 318:100-103.
- Araki, H., B. A. Berejikian, M. J. Ford, and M. S. Blouin. 2008. Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications* 1:342-355.
- Araki, H., B. Cooper, and M. S. Blouin. 2009. Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. *Biology Letters* 5:621-624.
- Augerot, X., and D. N. Foley. 2005. *Atlas of Pacific Salmon*. University of California Press, Berkeley.
- Baird, N. A., P. D. Etter, T. S. Atwood, M. C. Currey, A. L. Shiver, Z. A. Lewis, E. U. Selker, W. A. Cresko, and E. A. Johnson. 2008. Rapid SNP discovery and genetic mapping using sequenced RAD markers. *PLoS One* 3:e3376.
- Banks, J. L. 1994. Raceway density and water flow as factors affecting spring Chinook Salmon (*Oncorhynchus tshawytscha*) during rearing and after release. *Aquaculture* 119:201-217.
- Beacham, T., A. Gould, R. Withler, C. Murray, and L. Barner. 1987. Biochemical genetic survey and stock identification of chum salmon (*Oncorhynchus keta*) in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1702-1713.
- Beacham, T., R. Withler, and C. Wood. 1995. Stock identification of sockeye salmon by means of minisatellite DNA variation. *North American Journal of Fisheries Management* 15:249-265.
- Beacham, T. D., R. E. Withler, and T. A. Stevens. 1996. Stock identification of Chinook salmon (*Oncorhynchus tshawytscha*) using minisatellite DNA variation. *Canadian Journal of Fisheries and Aquatic Sciences* 53:380-394.
- Beacham, T. D., I. Winther, K. L. Jonsen, M. Wetklo, L. Deng, and J. R. Candy. 2008. The application of rapid microsatellite-based stock identification to management of a Chinook salmon troll fishery off the Queen Charlotte Islands, British Columbia. *North American Journal of Fisheries Management* 28:849-855.
- Beacham, T. D., S. Pollard, and K. D. Le. 2000. Microsatellite DNA population structure and stock identification of steelhead trout (*Oncorhynchus mykiss*) in the Nass and Skeena rivers in northern British Columbia. *Marine Biotechnology* 2:587-600.
- Benson, D. A., K. Clark, I. Karsch-Mizrachi, D. J. Lipman, J. Ostell, and E. W. Sayers. 2014. GenBank. *Nucleic Acids Research* 42:D32-D37.
- Berst, A. H., and R. C. Simon. 1981. Introduction to the Proceedings of the 1980 Stock Concept International Symposium (STOCS). *Canadian Journal of Fisheries and Aquatic Sciences* 38:1457-1458.
- Booke, H. E. 1999. The stock concept revisited: perspectives on its history in fisheries. *Fisheries Research* 43:9-11.
- Brannon, E. L., M. S. Powell, T. P. Quinn, and A. Talbot. 2004. Population structure of Columbia River Basin Chinook salmon and steelhead trout. *Reviews in Fisheries Science* 12:99-232.
- Brown, W. M., M. George, and A. C. Wilson. 1979. Rapid evolution of animal mitochondrial DNA. *Proceedings of the National Academy of Sciences* 76:1967-1971.
- Buchanan, D. V., J. E. Sanders, J. L. Zinn, and J. L. Fryer. 1983. Relative susceptibility of four strains of summer steelhead to infection by *Ceratomyxa shasta*. *Transactions of the American Fisheries Society* 112:541-543.
- Campbell, N. R., and S. R. Narum. 2008. Identification of novel single-nucleotide polymorphisms in Chinook salmon and variation among life history types. *Transactions of the American Fisheries Society* 137:96-106.

- Carvalho, G., and L. Hauser. 1994. Molecular genetics and the stock concept in fisheries. *Reviews in Fish Biology and Fisheries* 4:326-350.
- Castro, J. A., A. Picornell, and M. Ramon. 2010. Mitochondrial DNA: a tool for populational genetics studies. *International Microbiology* 1:327-332.
- Chapman, D. W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth-century. *Transactions of the American Fisheries Society* 115:662-670.
- Christie, M. R., M. L. Marine, R. A. French, and M. S. Blouin. 2012. Genetic adaptation to captivity can occur in a single generation. *Proceedings of the National Academy of Sciences* 109:238-242.
- Chilcote, M. W., S. A. Leider, and J. J. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Transactions of the American Fisheries Society* 115:726-735.
- Chilcote, M. W., K. W. Goodson, and M. R. Falcy. 2011. Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences* 68:511-522.
- Chilcote, M. W., K. W. Goodson, and M. R. Falcy. 2013. Corrigendum: Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences* 70:1-3.
- Christie, M. R., M. L. Marine, R. A. French, and M. S. Blouin. 2012. Genetic adaptation to captivity can occur in a single generation. *Proceedings of the National Academy of Sciences* 109:238-242.
- Christie, M. R., M. J. Ford, and M. S. Blouin. 2014. On the reproductive success of early-generation hatchery fish in the wild. *Evolutionary Applications* 7:883-896.
- Connor, W. P., H. L. Burge, R. Waitt, and T. C. Bjornn. 2002. Juvenile life history of wild fall Chinook salmon in the Snake and Clearwater rivers. *North American Journal of Fisheries Management* 22:703-712.
- Conover, D. O., S. B. Munch, and S. A. Arnott. 2009. Reversal of evolutionary downsizing caused by selective harvest of large fish. *Proceedings of the Royal Society of London B: Biological Sciences* 276:2015-2020.
- Consuegra, S., C. García de Leániz, A. Serdio, M. González Morales, L. Straus, D. Knox, and E. Verspoor. 2002. Mitochondrial DNA variation in Pleistocene and modern Atlantic salmon from the Iberian glacial refugium. *Molecular Ecology* 11:2037-2048.
- CRITFC (Columbia River Inter-Tribal Fish Commission). 2014. Columbia Basin Passage Barriers; Columbia River Treaty. Available online at <https://www.critfc.org/tribal-treaty-fishing-rights/policy-support/columbia-river-treaty/area-blocked-salmon-columbia-basin/> (accessed 28 July 2017).
- Cronin, M. A., W. J. Spearman, R. L. Wilmot, J. C. Patton, and J. W. Bickham. 1993. Mitochondrial DNA variation in Chinook (*Oncorhynchus tshawytscha*) and chum salmon (*O. keta*) detected by restriction enzyme analysis of polymerase chain reaction (PCR) products. *Canadian Journal of Fisheries and Aquatic Sciences* 50:708-715.
- Crozier, L. G., M. D. Scheuerell, and R. W. Zabel. 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: a case study of a shift toward earlier migration date in sockeye salmon. *The American Naturalist* 178:755-773.
- Dann, T. H., C. Habicht, T. T. Baker, J. E. Seeb, and D. Fraser. 2013. Exploiting genetic diversity to balance conservation and harvest of migratory salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 70:785-793.
- Davey, J. W., and M. L. Blaxter. 2010. RADSeq: next-generation population genetics. *Briefings in Functional Genomics* 9:416-423.
- Davey, J. W., P. A. Hohenlohe, P. D. Etter, J. Q. Boone, J. M. Catchen, and M. L. Blaxter. 2011. Genome-wide genetic marker discovery and genotyping using next-generation sequencing. *Nature Reviews Genetics* 12:499-510.
- Dejean, T., A. Valentini, A. Duparc, S. Pellier-Cuit, F. Pompanon, P. Taberlet, and C. Miaud. 2011. Persistence of environmental DNA in freshwater ecosystems. *PLoS One* 6:e23398.
- Dodson, J. J., N. Aubin-Horth, V. Thériault, and D. J. Páez. 2013. The evolutionary ecology of alternative migratory tactics in salmonid fishes. *Biological Reviews* 88:602-625.
- Domanico, M. J., and R. B. Phillips. 1995. Phylogenetic analysis of Pacific salmon (genus *Oncorhynchus*) based on mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution* 4:366-371.
- Elshire, R. J., J. C. Glaubitz, Q. Sun, J. A. Poland, K. Kawamoto, E. S. Buckler, and S. E. Mitchell. 2011. A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS One* 6:e19379.
- Faurot, D., P. Kucera, R. Armstrong, and M. Blenden. 1998. Cryopreservation of Adult Male Spring and Summer Chinook Salmon Gametes in the Snake River Basin. Report DOE/BP-30423-2, Bonneville Power Administration, Portland, OR.
- Ferguson, A., J. Taggart, P. Prodöhl, O. McMeel, C. Thompson, C. Stone, P. McGinnity, and R. Hynes. 1995. The application of molecular markers to the study and conservation of fish populations, with special reference to *Salmo*. *Journal of Fish Biology* 47:103-126.
- Ficetola, G. F., C. Miaud, F. Pompanon, and P. Taberlet. 2008. Species detection using environmental DNA from water samples. *Biology Letters* 4:423-425.

- Ford, M. J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology* 16:815-825.
- Ford, M., T. N. Pearsons, and A. Murdoch. 2015. The spawning success of early maturing resident hatchery Chinook salmon in a natural river system. *Transactions of the American Fisheries Society* 144:539-548.
- Fraser, D., L. K. Weir, L. Bernatchez, M. M. Hansen, and E. B. Taylor. 2011. Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. *Heredity* 106:404-420.
- Frazer, K., and M. Russello. 2013. Lack of parallel genetic patterns underlying the repeated ecological divergence of beach and stream-spawning kokanee salmon. *Journal of Evolutionary Biology* 26:2606-2621.
- Fulton, L. A., and R. E. Pearson. 1981. Transplantation and homing experiments on salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, in the Columbia River system: fish of the 1939-44 Broods. NOAA Technical Memorandum NMFS F/NWC-12. NOAA National Marine Fisheries Service Northwest Center, Seattle, WA.
- Galbreath, P. F., M. A. Bisbee Jr., D. W. Dompier, C. M. Kamphaus, and T. H. Newsome. 2014. Extirpation and tribal reintroduction of coho salmon to the interior Columbia River Basin. *Fisheries* 39:77-87.
- Geist, D. R., and D. D. Dauble. 1998. Redd site selection and spawning habitat use by fall Chinook salmon: the importance of geomorphic features in large rivers. *Environmental Management* 22:655-669.
- Grant, P. R., and B. R. Grant. 1995. Predicting micro-evolutionary responses to directional selection on heritable variation. *Evolution* 49:241-251.
- Gustafson, R. G., and G. A. Winans. 1999. Distribution and population genetic structure of river- and sea-type sockeye salmon in western North America. *Ecology of Freshwater Fish* 8:181-193.
- Hadly, E. A., U. Ramakrishnan, Y. L. Chan, M. Van Tuinen, K. O'Keefe, P. A. Spaeth, and C. J. Conroy. 2004. Genetic response to climatic change: insights from ancient DNA and phylochronology. *PLoS Biology* 2:e290.
- Hard, J. J. 2004. Evolution of Chinook salmon life history under size-selective harvest. In A. Hendry and S. Stearns (editors), *Evolution Illuminated: Salmon and their Relatives*. Oxford University Press, New York. Pp. 315-337.
- Hard, J., and W. Hershberger. 1995. Quantitative genetic consequences of captive broodstock programs for anadromous Pacific salmon (*Oncorhynchus* spp.). In T. Flagg and C. Mahnken (editors), *An Assessment of the Status of Captive Broodstock Technology for Pacific Salmon*. Bonneville Power Administration, Portland, OR. Pp. 2-1-2-75.
- Hendry, A. P. 2001. Adaptive divergence and the evolution of reproductive isolation in the wild: an empirical demonstration using introduced sockeye salmon. *Genetica* 112-113:515-534.
- Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290:516-518.
- Hess, J., A. Matala, and S. Narum. 2011. Comparison of SNPs and microsatellites for fine-scale application of genetic stock identification of Chinook salmon in the Columbia River Basin. *Molecular Ecology Resources* 11:137-149.
- Hess, J. E., and S. R. Narum. 2011. Single-nucleotide polymorphism (SNP) loci correlated with run timing in adult Chinook salmon from the Columbia River Basin. *Transactions of the American Fisheries Society* 140:855-864.
- Hess, M. A., C. D. Rabe, J. L. Vogel, J. J. Stephenson, D. D. Nelson, and S. R. Narum. 2012. Supportive breeding boosts natural population abundance with minimal negative impacts on fitness of a wild population of Chinook salmon. *Molecular Ecology* 21:5236-5250.
- HSRG (Hatchery Scientific Review Group). 2009. Report to Congress on Columbia River Basin hatchery reform. Unpublished report on file with the Pacific Northwest Hatchery Reform Project, Seattle, WA.
- Hohenlohe, P. A., S. J. Amish, J. M. Catchen, F. W. Allendorf, and G. Luikart. 2011. Next-generation RAD sequencing identifies thousands of SNPs for assessing hybridization between rainbow and westslope cutthroat trout. *Molecular Ecology Resources* 11:117-122.
- Huntington, C., W. Nehlsen, and J. Bowers. 1996. A survey of healthy native stocks of anadromous salmonids in the Pacific Northwest and California. *Fisheries* 21:6-14.
- Hyatt, K. D., C. A. D. Alexander, and M. M. Stockwell. 2015. A decision support system for improving "fish friendly" flow compliance in the regulated Okanagan Lake and River system of British Columbia. *Canadian Water Resources Journal* 40:87-110.
- IDFG (Idaho Department of Fish and Game). 2012. Fisheries management plan 2013-2018: a comprehensive guide to managing Idaho's fisheries resources. Idaho Department of Fish and Game, Boise.
- Iwamoto, E. M., J. M. Myers, and R. G. Gustafson. 2012. Resurrecting an extinct salmon evolutionarily significant unit: archived scales, historical DNA and implications for restoration. *Molecular Ecology* 21:1567-1582.
- Jerde, C. L., A. R. Mahon, W. L. Chadderton, and D. M. Lodge. 2011. "Sight-unseen" detection of rare aquatic species using environmental DNA. *Conservation Letters* 4:150-157.

- Johnson, B. M., B. M. Kemp, and G. H. Thorgaard. 2018. Increased mitochondrial DNA diversity in ancient Columbia River basin Chinook salmon *Oncorhynchus tshawytscha*. *PLoS One* 13:0190059.
- Johnson, J. A., P. O. Dunn, and J. L. Bouzat. 2007. Effects of recent population bottlenecks on reconstructing the demographic history of prairie-chickens. *Molecular Ecology* 16:2203-2222.
- Johnson, M. S., A. R. Murdoch, and C. P. Moran. 2015. Adult survival of hatchery spring Chinook salmon released volitionally or forcibly as juveniles. *North American Journal of Aquaculture* 77:547-550.
- Kinnison, M. T., and A. P. Hendry. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* 112:145-164.
- Kline, P. A., and T. A. Flagg. 2014. Putting the Red back in Redfish Lake, 20 years of progress toward saving the Pacific Northwest's most endangered salmon population. *Fisheries* 39:488-500.
- Kolar, C. S., D. C. Chapman, W. R. Courtenay, C. M. Housel, J. D. Williams, and D. P. Jennings. 2007. Bigheaded Carps: A Biological Synopsis and Environmental Risk Assessment. American Fisheries Society, Bethesda, MD.
- Laramie, M. B., D. S. Pilliod, and C. S. Goldberg. 2015. Characterizing the distribution of an endangered salmonid using environmental DNA analysis. *Biological Conservation* 183:29-37.
- Larson, W. A., J. E. Seeb, C. E. Pascal, W. D. Templin, and L. W. Seeb. 2014. Single-nucleotide polymorphisms (SNPs) identified through genotyping-by-sequencing improve genetic stock identification of Chinook salmon (*Oncorhynchus tshawytscha*) from western Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 71:698-708.
- Larson, W. A., M. T. Limborg, G. J. McKinney, D. E. Schindler, J. E. Seeb, and L. W. Seeb. 2016. Genomic islands of divergence linked to ecotypic variation in sockeye salmon. *Molecular Ecology* 26:554-570.
- Lichatowich, J. 2001. Salmon hatcheries: Past, present and future. Alder Fork Consulting. Prepared for the Oregon Business Council. Columbia City, Oregon. Unpublished report on file with the Oregon Business Council, Portland, OR.
- Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams. *BioScience* 45:183-192.
- MacLean, J. A. and D. O. Evans. 1981. The stock concept, discreteness of fish stocks, and fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1889-1898.
- Martin, K. E., C. A. Steele, J. P. Brunelli, and G. H. Thorgaard. 2010. Mitochondrial variation and biogeographic history of Chinook salmon. *Transactions of the American Fisheries Society* 139:792-802.
- Maynard, D. J., T. A. Flagg, R. N. Iwamoto, and C. V. W. Mahnken. 2004. A review of recent studies investigating seminatural rearing strategies as a tool for increasing Pacific salmon postrelease survival. *American Fisheries Society Symposia* 44:569-590.
- McLean, J. E., P. Bentzen, and T. P. Quinn. 2003. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead (*Oncorhynchus mykiss*) through the adult stage. *Canadian Journal of Fisheries and Aquatic Sciences* 60:433-440.
- McClure, M. M., F. M. Utter, C. Baldwin, R. W. Carmichael, P. F. Hassemer, P. J. Howell, P. Spruell, T. D. Cooney, H. A. Schaller, and C. E. Petrosky. 2008. Evolutionary effects of alternative artificial propagation programs: implications for viability of endangered anadromous salmonids. *Evolutionary Applications* 1:356-375.
- McCusker, M. R., E. Parkinson, and E. B. Taylor. 2000. Mitochondrial DNA variation in rainbow trout (*Oncorhynchus mykiss*) across its native range: testing biogeographical hypotheses and their relevance to conservation. *Molecular Ecology* 9:2089-2108.
- McVeigh, H., and W. Davidson. 1991. A salmon ID phylogeny inferred from mitochondrial cytochrome b gene sequences. *Journal of Fish Biology* 39:277-282.
- Miller, M. R., J. P. Dunham, A. Amores, W. A. Cresko, and E. A. Johnson. 2007. Rapid and cost-effective polymorphism identification and genotyping using restriction site associated DNA (RAD) markers. *Genome Research* 17:240-248.
- Milner, G. B., D. J. Teel, F. M. Utter, and G. A. Winans. 1985. A genetic method of stock identification in mixed populations of Pacific salmon, *Oncorhynchus* spp. *Marine Fisheries Review* 47:1-8.
- Minamoto, T., H. Yamanaka, T. Takahara, M. N. Honjo, and Z. Kawabata. 2012. Surveillance of fish species composition using environmental DNA. *Limnology* 13:193-197.
- Moriya, S., S. Sato, T. Azumaya, O. Suzuki, S. Urawa, A. Urano, and S. Abe. 2007. Genetic stock identification of chum salmon in the Bering Sea and North Pacific Ocean using mitochondrial DNA microarray. *Marine Biotechnology* 9:179-191.
- Myers, J., G. Bryant, and J. Lynch. 1998. Factors contributing to the decline of Chinook salmon: an addendum to the 1996 west coast steelhead factors for decline report. NOAA Protected Resources Division, National Marine Fisheries Service, Portland, OR.
- National Marine Fisheries Service (NMFS). 2005. Federal register: Policy on the consideration of hatchery-origin fish in Endangered Species Act listing determinations for Pacific salmon and steelhead. National Marine Fisheries Service, National Oceanic and Atmospheric Administration (NOAA), Department of Commerce Vol. 70 No. 123:37204-37216. NMFS, Protected Resources Division, Portland, OR.

- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads - stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16:4-21.
- Nielsen, E. E., and D. Bekkevold. 2012. The memory remains: application of historical DNA for scaling biodiversity loss. *Molecular Ecology* 21:1539-1541.
- Netboy, A. 1980. The Columbia River Salmon and Steelhead Trout: Their Fight for Survival. University of Washington Press, Seattle.
- Nichols, K. M., C. C. Kozfay, and S. R. Narum. 2016. Genomic signatures among *Oncorhynchus nerka* ecotypes to inform conservation and management of endangered Sockeye Salmon. *Evolutionary Applications* 9:1285-1300.
- NMFS (National Marine Fisheries Service). 2013. Endangered Species Act (ESA) Section 7(a)(2) Biological Opinion and Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat (EFH) Consultation. On Issuance of Three Section 10(a)(1)(A) Permits for the Upper Columbia River Chiwawa River, Nason Creek, and White River Spring Chinook Salmon Hatchery Programs. NMFS Consultation Number: NWR-2013-9707. National Marine Fisheries Service, Seattle, WA.
- NOAA (National Oceanic and Atmospheric Administration). 2017. Endangered Species Act (ESA) Section 7(a)(2) Biological Opinion and Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat (EFH) Consultation. NOAA's National Marine Fisheries Service's implementation of the Mitchell Act Final Environmental Impact Statement preferred alternative and administration of Mitchell Act hatchery funding. NMFS Consultation Number: NWR-2014-697. National Oceanic and Atmospheric Administration, Seattle, WA.
- Noor, M. A., and J. L. Feder. 2006. Speciation genetics: evolving approaches. *Nature Reviews Genetics* 7:851-861.
- NPPC (Northwest Power Planning Council). 1999. Artificial Production Review: Report and Recommendations of the Northwest Power Planning Council. Northwest Power Planning Council, Portland, OR. Available online at <https://www.nwcouncil.org/reports/artificial-production-review> (accessed 01 August 2017).
- Pääbo, S. 1989. Ancient DNA: Extraction, characterization, molecular cloning, and enzymatic amplification. *Proceedings of the National Academy of Sciences* 86:1939-1943.
- Park, L. K., M. Brainard, D. Dightman, and G. A. Winans. 1993. Low levels of intraspecific variation in the mitochondrial DNA of chum salmon (*Oncorhynchus keta*). *Molecular Marine Biology and Biotechnology* 2:362-370.
- Parker, N. C., A. E. Giorgi, R. C. Heidinger, D. B. Jester Jr., E. D. Prince, and G. A. Winans (editors). 1990. Fish Marking Techniques. American Fisheries Society Symposium 7. American Fisheries Society, Bethesda, MD.
- Phelps, S., L. LeClair, S. Young, and H. Blankenship. 1994. Genetic diversity patterns of chum salmon in the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* 51:65-83.
- Quinn, T., M. Kinnison, and M. Unwin. 2001. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* 112:493-513.
- Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2000. Evolution of temporal isolation in the wild: Genetic divergence in timing of migration and breeding by introduced chinook salmon populations. *Evolution* 54:1372-1385.
- Ramakrishnan, U., and E. A. Hadly. 2009. Using phylochronology to reveal cryptic population histories: review and synthesis of 29 ancient DNA studies. *Molecular Ecology* 18:1310-1330.
- Reisenbichler, R. R. 1988. Relation between distance transferred from natal stream and recovery rate for hatchery coho salmon. *North American Journal of Fisheries Management* 8:172-174.
- Reisenbichler, R. R., and J. D. McIntyre. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada* 34:123-128.
- Reisenbichler, R. R., and S. P. Rubin. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. *International Council for the Exploration of the Seas Journal of Marine Science* 56:459-466.
- Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. In R.C. Simon and P.A. Larkin (editors), *The Stock Concept in Pacific Salmon*. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver. Pp. 19-160.
- Roesti, M., S. Gavrillets, A. P. Hendry, W. Salzburger, and D. Berner. 2014. The genomic signature of parallel adaptation from shared genetic variation. *Molecular Ecology* 23:3944-3956.
- Schwartz, M. K., G. Luikart and R. S. Waples. 2007. Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology and Evolution* 22:25-33.
- Seeb, L., A. Antonovich, M. A. Banks, T. Beacham, M. Bellinger, S. Blankenship, M. Campbell, N. Decovich, J. Garza, and C. Guthrie III. 2007. Development of a standardized DNA database for Chinook salmon. *Fisheries* 32:540-552.

- Shaklee, J., and S. Phelps. 1990. Operation of a large-scale, multiagency genetic stock identification program. *In* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, E. D. Prince, G. A. Winans (editors), *Proceeding from the International Symposium and Educational Workshop on Fish-marking Techniques*, Seattle, WA. Pp. 817-830.
- Shaklee, J. B., and P. Bentzen. 1998. Genetic identification of stocks of marine fish and shellfish. *Bulletin of Marine Science* 62:589-621.
- Shaklee, J. B., S. R. Phelps, and J. Salini. 1990. Analysis of fish stock structure and mixed-stock fisheries by the electrophoretic characterization of allelic isozymes. *In* D. H. Whitmore (editor), *Electrophoretic and Isoelectric Focusing Techniques in Fisheries Management*. CRC Press, Boca Raton, FL. Pp. 173-196.
- Simon, R. C., and P. A. Larkin (editors). 1972. *The Stock Concept in Pacific Salmon*. H. R. MacMillan Lectures in Fisheries. The University of British Columbia, Vancouver.
- Small, M., T. Beacham, R. Withler, and R. Nelson. 1998a. Discriminating coho salmon (*Oncorhynchus kisutch*) populations within the Fraser River, British Columbia, using microsatellite DNA markers. *Molecular Ecology* 7:141-155.
- Small, M. P., R. Withler and T. D. Beacham. 1998b. Population structure and stock identification of British Columbia coho salmon, *Oncorhynchus kisutch*, based on microsatellite DNA variation. *Fishery Bulletin* 96:843-858.
- Smith, C. T., W. D. Templin, J. E. Seeb, and L. W. Seeb. 2005. Single nucleotide polymorphisms provide rapid and accurate estimates of the proportions of US and Canadian Chinook salmon caught in Yukon River fisheries. *North American Journal of Fisheries Management* 25:944-953.
- Splendiani, A., T. Fioravanti, M. Giovannotti, A. Negri, P. Ruggeri, L. Olivieri, P. N. Cerioni, M. Lorenzoni, and V. C. Barucchi. 2016. The effects of paleoclimatic events on Mediterranean trout: preliminary evidences from ancient DNA. *PloS One* 11:e0157975.
- Steele, C. A., E. C. Anderson, M. W. Ackerman, M. A. Hess, N. R. Campbell, S. R. Narum, and M. R. Campbell. 2013. A validation of parentage-based tagging using hatchery steelhead in the Snake River Basin. *Canadian Journal of Fisheries and Aquatic Sciences* 70:1046-1054.
- Stouder, D. J., P. A. Bisson, and R. J. Naiman. 1997. *Pacific Salmon and Their Ecosystems: Status and Future Options*. Springer, New York.
- Takahara, T., T. Minamoto, and H. Doi. 2013. Using environmental DNA to estimate the distribution of an invasive fish species in ponds. *PloS One* 8:e56584.
- Taylor, E. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98:185-207.
- Taylor, J. E. III 1999. *Making Salmon: An Environmental History of the Northwest Fisheries Crisis*. University of Washington Press, Seattle.
- Theriault, V., G. R. Moyer, and M. A. Banks. 2010. Survival and life history characteristics among wild and hatchery coho salmon (*Oncorhynchus kisutch*) returns: how do unfed fry differ from smolt releases? *Canadian Journal of Fisheries and Aquatic Sciences* 67:486-497.
- Thomsen, P., J. Kielgast, L. L. Iversen, C. Wiuf, M. Rasmussen, M. T. P. Gilbert, L. Orlando, and E. Willerslev. 2012. Monitoring endangered freshwater biodiversity using environmental DNA. *Molecular Ecology* 21:2565-2573.
- Thorgaard, G. H., P. A. Wheeler, and J. G. Cloud. 1998. Status and potential value of sperm banking for Snake River salmon. *In* E. L. Brannon and W. C. Kinsel (editors), *Proceedings of the Columbia River Anadromous Salmonid Rehabilitation and Passage Symposium*. University of Idaho, Moscow. Pp. 51-56.
- Turrero, P., J. Horreo, and E. Garcia-Vazquez. 2012. Same old *Salmo*? Changes in life history and demographic trends of North Iberian salmonids since the Upper Palaeolithic as revealed by archaeological remains and BEAST analyses. *Molecular Ecology* 21:2318-2329.
- Utter, F. M. 1991. Biochemical genetics and fishery management: an historical perspective. *Journal of Fish Biology* 39 (Supplement A):1-20.
- Utter, F. M., F. W. Allendorf, and H. O. Hodgins. 1973. Genetic variability and relationships in Pacific salmon and related trout based on protein variations. *Systematic Zoology* 22:257-270.
- Utter, F., and N. Ryman. 1993. Genetic markers and mixed stock fisheries. *Fisheries* 18:11-21.
- Utter, F. M., D. W. Chapman, and A. R. Marshall. 1995. Genetic population structure and history of Chinook salmon of the upper Columbia River. *American Fisheries Society Symposium* 17:49-165.
- Veale, A. J., and M. A. Russello. 2016. Sockeye salmon repatriation leads to population re-establishment and rapid introgression with native kokanee. *Evolutionary Applications* 9:1301-1311.
- Veale, A. J., and M. A. Russello. 2017. An ancient selective sweep linked to reproductive life history evolution in sockeye salmon. *Scientific Reports* 7:1747.
- Venditti, D. A., R. N. Kinzer, K. A. Apperson, B. Barnett, M. Belnap, T. Copeland, M. P. Corsi, and K. Tardy. 2017. Effects of hatchery supplementation on abundance and productivity of natural-origin Chinook salmon: two decades of evaluation and implications for conservation programs. *Canadian Journal of Fisheries and Aquatic Sciences* 999:1-16.
- Walsh, M. R., S. B. Munch, S. Chiba, and D. O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecology Letters* 9:142-148.

- Wang, S., J. J. Hard, and F. Utter. 2002. Salmonid inbreeding: a review. *Reviews in Fish Biology and Fisheries* 11:301-319.
- Waples, R. S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. *Marine Fisheries Review* 53:11-22.
- Waples, R. S. 1995. Evolutionary significant units and the conservation of biological species under the Endangered Species Act. *American Fisheries Society Symposium* 17:8-27.
- Waples, R. S., O. W. Johnson, and R. P. Jones Jr. 1991. Status review for Snake River sockeye salmon. NOAA Technical Memorandum NMFS-F/NWC 195. National Marine Fisheries Service, Northwest Center, Seattle, WA.
- Waples, R. S., R. G. Gustafson, L. A. Weitkamp, J. M. Myers, O. Johnson, P. J. Busby, J. J. Hard, G. J. Bryant, F. W. Waknitz, and K. Nelly. 2001. Characterizing diversity in salmon from the Pacific Northwest. *Journal of Fish Biology* 59 (Supplement A):1-41.
- Waples, R. S., R. Zabel, M. D. Scheuerell, and B. L. Sanderson. 2008. Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia River hydropower system. *Molecular Ecology* 17:84-96.
- Waples, R. S., A. Elz, B. D. Arnsberg, J. R. Faulkner, J. J. Hard, E. Timmins-Schiffman, and L. K. Park. 2017. Human-mediated evolution in a threatened species? Juvenile life-history changes in Snake River salmon. *Evolutionary Applications* 10:667-681.
- Warnock, W. G., D. H. P. Stroud, and J. E. Merz. 2016. Donor stock selection of Chinook salmon for reintroduction to the transboundary reach of the Columbia River. *Canadian Columbia River Inter-Tribal Fisheries Commission*, Cranbrook, BC.
- WDFW (Washington Department of Fish and Wildlife). 2008. Statewide steelhead management plan: statewide policies, strategies, and actions. Washington Department of Fish and Wildlife, Olympia.
- WDFW. 2010. Spring Chinook adult management in the Wenatchee River basin. Addendum to the Wenatchee River hatchery genetic management plans. Washington Department of Fish and Wildlife, Olympia.
- White, B. A., and J. B. Shaklee. 1991. Need for replicated electrophoretic analyses in multiagency genetic stock identification (GSI) programs: examples from a pink salmon (*Oncorhynchus gorbuscha*) GSI fisheries study. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1396-1407.
- Williams, J. G., R. W. Zabel, R. S. Waples, J. A. Hutchings, and W. P. Connor. 2008. Potential for anthropogenic disturbances to influence evolutionary change in the life history of a threatened salmonid. *Evolutionary Applications* 1:271-285.
- Williams, R. N., (editor). 2005. *Return to the River: Restoring Salmon Back to the Columbia River*. Elsevier Academic Press, Burlington, MA.
- Williams, R. N., J. A. Standford, J. A. Lichatowich, W. J. Liss, C. C. Coutant, W. E. McConaha, R. R. Whitney, P. R. Mundy, P. A. Bisson, and M. S. Powell. 2006. Return to the river: strategies for salmon restoration in the Columbia River Basin. *In* R. N. Williams (editors), *Return to the River: Restoring Salmon Back to the Columbia River*. Elsevier Academic Press, Burlington, MA. Pp. 629-666.
- Williamson, K. S., A. R. Murdoch, T. N. Pearsons, E. J. Ward, and M. J. Ford. 2010. Factors influencing the relative fitness of hatchery and wild spring Chinook salmon (*Oncorhynchus tshawytscha*) in the Wenatchee River, Washington, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1840-1851.
- Wilmot, R. L., C. M. Kondzela, C. M. Guthrie, and M. M. Masuda. 1998. Genetic stock identification of chum salmon harvested incidentally in the 1994 and 1995 Bering Sea trawl fishery. *North Pacific Anadromous Fish Commission Bulletin* No. 1. Vancouver, BC.
- Winans, G. A., P. B. Aebersold, S. Urawa, and N. V. Varnavskaya. 1994. Determining continent of origin of chum salmon (*Oncorhynchus keta*) using genetic stock identification techniques: status of allozyme baseline in Asia. *Canadian Journal of Fisheries and Aquatic Sciences* 51:95-113.
- Winans, G. A., P. B. Aebersold, and R. S. Waples. 1996. Allozyme variability of *Oncorhynchus nerka* in the Pacific Northwest, with special consideration to populations of Redfish Lake, Idaho. *Transactions of the American Fisheries Society* 125:645-663.
- Winans, G. A., M. M. Paquin, D. M. Van Doornik, B. M. Baker, P. Thornton, D. Rawding, A. Marshall, P. Moran, and S. Kalinowski. 2004. Genetic stock identification of steelhead in the Columbia River Basin: an evaluation of different molecular markers. *North American Journal of Fisheries Management* 24:672-685.
- Wood, C. C., D. T. Rutherford, and S. McKinnell. 1989. Identification of sockeye salmon (*Oncorhynchus nerka*) stocks in mixed-stock fisheries in British Columbia and Southeast Alaska using biological markers. *Canadian Journal of Fisheries and Aquatic Sciences* 46:2108-2120.
- Young, W. P. 2011. Salmonid Gamete Preservation in the Snake River Basin. Annual Report 2010. Nez Perce Tribe Department of Fisheries Resources Management, Lapwai, ID.
- Zhivotovsky, L. A., A. Gharrett, A. McGregor, M. Glubokovsky, and M. W. Feldman. 1994. Gene differentiation in Pacific salmon (*Oncorhynchus* sp.): facts and models with reference to pink salmon (*O. gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 51:223-232.

Zinn, J. L., K. A. Johnson, J. E. Sanders, and J. L. Fryer.
1977. Susceptibility of salmonid species and hatch-
ery strains of Chinook salmon (*Oncorhynchus*
tshawytscha) to infections by *Ceratomyxa shasta*.
Journal of the Fisheries Research Board of Canada
34:933-936.

Received 31 July 2017

Accepted 10 July 2018