Population Genomics for the Management of Wild Vertebrate Populations

Ashley D. Walters and Michael K. Schwartz

Abstract Management of genetic variation in natural populations is necessary to mitigate the effects of environmental change and biodiversity loss. While traditional genetic techniques have aided management of biodiversity, the rapid advancement of genomics technology has provided advancements for the field of biodiversity conservation including increased resolution and identification of adaptive loci corresponding to ecologically relevant phenotypes. In this chapter, we explore how population genomics has been implemented into wildlife management via a literature review and discussions with management and conservation agencies. We discuss the future prospects of population genomics applications in biodiversity conservation and management of wild populations. Overall, we see the potential for population genomics to improve our understanding of wild populations of fish and wildlife and have several important examples that are paving the way for the adoption of these technologies into management. However, there has been a severe lag in the implementation of population genomic data into management decisions, likely due to the length of the research cycle and the slow absorption into regulation and policy.

Keywords Biodiversity conservation · Evolutionary significant unit · Management unit · Population genomics · Wildlife management

1 Introduction and General Overview

Genetic diversity is a fundamental component of population fitness and adaptive potential (Reed and Frankham 2003; Hoffman et al. 2017); therefore, management of genetic variation in wild populations of wildlife and fish is necessary to mitigate

A. D. Walters (✉) · M. K. Schwartz
USDA Forest Service, National Genomics Center for Wildlife and Fish Conservation, Missoula, MT, USA
e-mail: ashley.walters@usda.gov

Paul Hohenlohe and Om P. Rajora (eds.), *Population Genomics: Wildlife*, Population Genomics [Om P. Rajora (Editor-in-Chief)], https://doi.org/10.1007/13836_2020_72, This is a U.S. government work and not under copyright protection in the U.S.; foreign copyright protection may apply 2020

the effects of a changing environment. Conservation genetics provides both a theoretical framework and an effective tool for addressing contemporary conservation and wildlife management issues. Traditional genetic techniques have aided management and conservation efforts on multiple fronts including biodiversity monitoring, resolving taxonomic uncertainty, wildlife forensics, and designation of conservation units. However, the rapid advancement of genomics technologies, such as the generation of large genetic marker panels and whole genome-sequencing for non-model organisms, in recent decades has provided important advancements in the field and improved traditional genetic inferences in two key areas: increased resolution and identification of ecologically important loci (Fig. 1). The population genomics approach offers a dramatic increase in the number of variable genetic markers used compared to traditional genetic methods, therefore, improving the precision of estimating diversity and population demographic parameters, connectivity, and designation of conservation units.

While genetics has provided information regarding neutral evolutionary processes for management efforts, the application of genomics increases the power to detect signatures of divergent selection and local adaptation. Preserving adaptive potential has been recognized as an important component of ensuring long-term persistence, especially in the face of global climate change (Sgró et al. 2011; Harrisson et al. 2014). From the perspective of wildlife and fisheries management, understanding how wild populations are adapted to their ecosystem can aid in a multitude of traditional wildlife management activities including translocations, reintroductions, and population augmentations as well as identification of units of conservation concern. For example, one of the first questions addressed prior to most reintroduction efforts is the assessment of the most suitable source population. Using population genomics to evaluate functional differences among populations will ultimately lead to better translocation decisions and hopefully more successful management efforts.

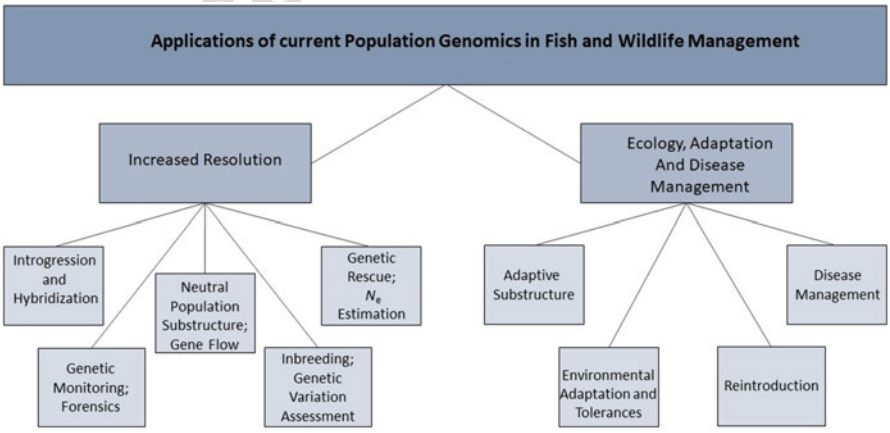

Fig. 1 Current applications for population genomics ~~for~~ fish and wildlife management

Currently, one of the most important uses of population genomics is in preserving evolutionary processes (Allendorf et al. 2010; Funk et al. 2012; Hohenlohe et al. 2019) which support future biodiversity under changing environmental conditions (Mortiz 2002). The genomics approach helps accomplish this goal by providing the enhanced power of many more loci, or by aiding in the understanding of how populations are adapted to local environments to designate conservation units (Allendorf et al. 2010; Funk et al. 2012), However, there is ongoing debate about the relative importance of neutral versus adaptive variation in the designation of conservation units (e.g., Crandall et al. 2000; Fraser and Bernatchez 2001; Pearse 2016). In a conservation context, two types of units have been defined: evolutionary significant units (ESUs) and management units (MUs; Mortiz 1994). An ESU is generally defined as a population or group of populations with high genetic and ecological distinctiveness, maximizing evolutionary potential (Fraser and Bernatchez 2001). However, MUs were originally defined as populations with significant divergence of allele frequencies at either nuclear or mitochondrial loci, regardless of their uniqueness phylogeographically. This concept thus focuses on demographic independence among populations, therefore, preserving genetic diversity of intraspecific units. Funk et al. (2012) proposed a method for identifying appropriate units for management and conservation involving three steps: (1) delineating evolutionary significant units (ESUs) using all loci, (2) recognizing management units (MUs) via non-outlier loci, and (3) identifying adaptive variation among management units through the use of outlier loci.

The identification of adaptive variation may not alter conservation and management strategies if concordant with patterns in neutral variation; however, there have been instances of incongruence between the two marker types (i.e., Pacific salmon; Prince et al. 2017; Fig. 2). The underlying controversy of a gene-targeted approach is based on the knowledge of correlative genomic variation responsible for adaptive variation and the trade-off and preservation of future adaptive potential (i.e., genomic diversity). There has been substantial argument on the prioritization of populations based on a specific allele(s) because the resulting conservation effort may reduce total genomic diversity and ultimately limit future adaptive potential (Luikart et al. 2003, 2019; Allendorf 2017; Kardos and Shafer 2018). Conservation geneticists do not advocate for managing only outlier loci, consistent with historical conservation debates over conserving allelic diversity for a set of disease resistance genes (major histocompatibility complex) known to be under selection (Vrijenhoek and Leberg 1991). In cases where only putative genetic contributions to adaptive variation can be identified without a causal mechanism, management frameworks advocate for the incorporation of additional information including neutral genetic diversity and/or important phenotypic and ecological variation (Funk et al. 2012, 2019; Schafer et al. 2015; Benestan et al. 2016; Allendorf 2017). Therefore, genomic signatures of selection are most useful in a management framework when combining variation in conservation-relevant phenotypes and loci of known function with signatures of selection (Epstein et al. 2016; Wright et al. 2017).

While the promise of genomics for conservation has been looming for a decade and has been evident in some areas of wildlife management (Schwartz et al. 2010),

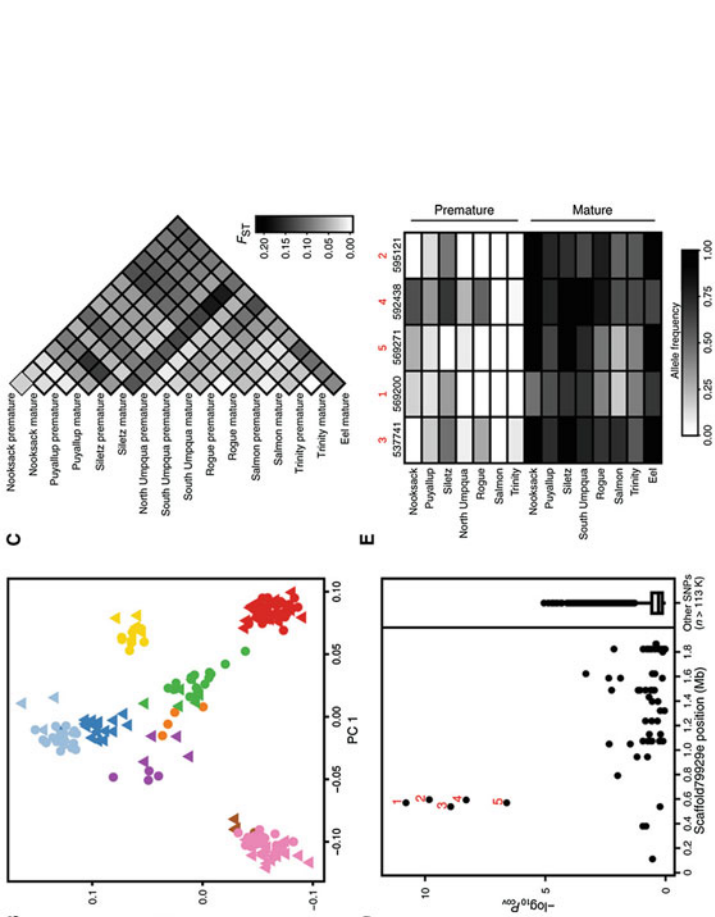

Fig. 2 Genetic and evolutionary basis of premature migration in Chinook salmon. (**a**) Map of sample locations and migration phenotypes; color indicates location and shape indicates migration category. (**b**) PCA and (**c**) pairwise F_{ST} estimates using genome-wide SNP data. (**d**) Association mapping of migration category in Chinook; red numbers indicate significant SNPs. (**e**) Allele frequency shift at significant SNPs between premature and mature migrating populations. Black numbers indicate SNP position on scaffold79929e. ~~Reproduced with permission from Prince et al. (2017)~~

we explored how population genomics has been implemented in wildlife management. We searched the literature for uses of population genomic data in wildlife and fish management. We also sent out a survey on The Ecological Society of America (ECOLOG-L) listserv to see if there were forthcoming uses of population genomic data that we missed in the literature. This allowed us to examine the extent that population genomics has been integrated into wildlife and fisheries management. ~~Below we describe the common uses of population genomic data in wildlife and fisheries management.~~

2 Applications of Population Genomics in Fish and Wildlife Management

~~Below we examine several of the areas for which genomics technology has been applied to fish and wildlife management.~~

2.1 Increased Resolution

2.1.1 Introgression/Hybridization

As exploitation of wild living resources becomes increasingly unsustainable (Hutchings 2000; Myers and Worm 2003), domestication and captive production provide an opportunity to supplement economically important populations. However, release or escape of captively bred individuals into the wild population has the potential to negatively impact genetics of wild populations. Hybridization between wild species and their domesticated relatives has been acknowledged in a variety of organisms (Randi 2008) but has been particularly common in fishes.

Management efforts may include the deliberate supplementation of wild populations with the stocking of hatchery-reared offspring (Laikre et al. 2010). Current steelhead, *Oncorhynchus mykiss*, hatchery programs in northern Puget Sound are designed as segregated programs where hatchery and wild populations are deliberately kept separate. The hatchery broodstock is restricted to hatchery-origin individuals, and the reproductive interaction between hatchery-origin and wild fish is limited. Segregated program efforts are aimed at producing a sufficient number of hatchery-origin individuals to accommodate the next generation of hatchery broodstock and support recreational harvest opportunities. Regulations require monitoring for the presence of naturally spawning hatchery fish and the reproductive interaction between hatchery-origin individuals and the wild populations. Steelhead spawning is difficult to monitor in Puget Sound because hatchery-origin and hybrid fish are morphologically indistinguishable from wild fish. Therefore, the Washington Department of Fish and Wildlife (WDFW) adopted the use of genetic tools for monitoring reproductive interaction between

hatchery-origin and wild populations; however, the effectiveness of genetic monitoring programs is dependent on the ability to differentiate hatchery-origin, hybrid, and wild fish. As a consequence of continual introductions of hatchery-origin steelhead and the cumulative effects of gene flow over time, increased resolution through a population genomics approach was required to differentiate between the origins in Puget Sound. Warheit (2014) used expressed sequence tags (ESTs) and restriction site-associated DNA sequencing (RADseq) to develop SNP panels to monitor introgression from hatchery-origin into wild steelhead populations. A total of 192 SNPs were used to genotype individuals throughout Washington state as baseline samples for genetic stock identification and genotyped in thousands of individuals annually to monitor for and quantify introgression of hatchery-origin fish into wild populations. Results suggest that segregated steelhead hatchery programs have affected the genetic structure of wild populations; however, the effects vary among river systems (Warheit 2014).

Alternatively, wild populations may accidently be exposed to escapees from farming operations with the expansion of commercial aquaculture practices, including salmon farming. Norwegian Atlantic salmon farms dominate global production with stock originating from 40 Norwegian rivers but have undergone multiple generations of domestication selection (Gjedrem 2010). As a result of captive breeding and directional selection for economically important traits, farmed and wild salmon differ in many characters. Farmed salmon display lower levels of genetic variation compared to wild populations (Skaala et al. 2004), as well as genetic differences for traits such as growth (Glover et al. 2009), physiology (Fleming et al. 2002), and behavior (Fleming and Einum 1997). In 2011, the Institute of Marine Research initiated a risk assessment of Norwegian salmon farming to evaluate the potential hazard of introgression of farmed escapees on wild salmon populations. Researchers used next-generation sequencing to discover a panel of 60 SNPs distributed across 27 of 29 chromosomes (Karlsson et al. 2011). Because of the genetic similarity between wild and farmed salmon, the genomics approach provided the resolution required to identify hatchery-informative markers. The detection of farmed escapees and the quantification of cumulative introgression are being used to address risk of continued and future genetic changes in wild Atlantic salmon populations (Taranger et al. 2014). A study of 20 Norwegian rivers utilizing the SNP panel from Karlsson et al. (2011) revealed less introgression of farmed Atlantic salmon than may be expected based upon the reported numbers of escapees observed in the populations, suggesting limited reproductive success of farmed escaped salmon in Norwegian rivers (Glover et al. 2013). These results are consistent with previous controlled experiments examining spawning success (Fleming et al. 1996, 2000).

2.1.2 Genetic Rescue

A few conservation and management efforts have applied genome-wide markers and technology to address genetic factors affecting endangered populations, such as the

loss of the genetic diversity. Genetic rescue is a conservation tool used to increase the fitness of at-risk populations by introducing new genetic variation into a population. Genomic tools can aid the identification of target populations, as well as guide management and conservation efforts (Fitzpatrick and Funk 2019). With growing knowledge of the negative effects of inbreeding depression, there is increasing interest in using genetic translocations which is expected to be most useful for small, isolated populations (Frankham 2015).

The mountain pygmy possum, *Burramys parvus*, is one of ~~the~~ Australia's most threatened marsupials. *Burramys parvus* is restricted to alpine regions of Australia, and the remaining populations are geographically isolated and genetically distinct. In 2009, the southern-most population experienced a rapid population decline. Because the population was vulnerable to extinction, a recovery program was implemented that aimed at restoration of habitat, predator control, and the introduction of males from healthy and genetically variable populations of *B. parvus*. To assess genetic diversity, individuals were genotyped using eight previously isolated microsatellite markers (Mitrovski et al. 2005), and 16 additional markers were generated with the 454 sequencing platform. Males from two source populations were introduced to the southern-most population, and alleles from introduced males became integrated into the gene pool. As a result of the introduction efforts, genetic diversity (allelic richness, heterozygosity) increased along with population size (Weeks et al. 2017).

A second example of the application of population genomics for informing reintroduction is the Burmese roofed turtle, *Batagur trivittata*, one of the world's most endangered turtles with a single wild population in Myanmar (Çilinger et al. 2017). The use of double-digest restriction site-associated DNA sequencing (ddRAD-seq) produced 1,500 genome-wide single nucleotide polymorphisms, revealing a low effective population size ($\leq$10 individuals). The most genetically diverse individuals from the captive pool were reintroduced into the wild resulting in an increase in the number of fertile eggs. Additionally, genetically diverse individuals were retained for the captive-breeding program. The use of genome-wide markers informed the genetic and demographic reinforcement of the wild population and management of captive populations.

2.1.3 Neutral Population Substructure: Population/Stock Genetic Differentiation and Conservation Units

Delineation of neutral substructure is the most common population genomics application in management and conservation. Managers have often used population genomics to track the movement and harvest of fisheries resources. One common use of the application of population genomics into resource management is genetic stock identification (GSI), an important tool for fisheries management. The efficacy of this tool is dependent upon the ability to differentiate stocks of interest; however, this can be difficult when populations are closely related. GSI uses observed allele frequencies of baseline populations sampled on the spawning grounds to infer the natal origin of fish captured in mixed-stock fisheries (Utter and Ryman 1993;

Beacham et al. 2012). Researchers used RADseq to identify 38 population informative SNPs to monitor stock composition in sockeye salmon, *Oncorhynchus nerka* (Dann et al. 2013). The use of SNPs improved accuracy in stock identification over microsatellites. The efficacy of SNPS to identify stock origin allows managers to shift fishing efforts based on return rates to stock of origin, benefiting the commercial fishery and local economy while reducing the risk of overharvest (Dann et al. 2013). Similar work has been done in Chinook salmon, *Oncorhynchus tshawytscha* (Larson et al. 2014).

Additionally, population-informative SNP panels for both chum and sockeye salmon have been used to genotype >150,000 individuals over a 3-year period along the Alaska coastline (Habicht et al. 2012; Munro et al. 2012). The Alaska Department of Fish and Game's Western Alaska Salmon Stock Identification Program (WASSIP) used this data to directly inform management decisions including allocation of resources and protecting weak stocks.

Management using a parentage-based tagging approach (PBT; Anderson and Garza 2005) involves the annual genotyping of hatchery broodstock to create a database of parental genotypes from each hatchery. Parentage analysis allows for offspring to be traced back to their parents, therefore, identifying the hatchery of origin and age. A PBT program has been implemented in the Snake River basin using <100 SNPs developed from next-generation sequencing to reconstruct pedigrees and genetically tag offspring of hatchery steelhead trout (Steele et al. 2013). The accuracy and application of SNPs for parentage analysis have resulted in the genetic tagging of approximately 95% of the steelhead and Chinook salmon in the region (Steele et al. 2013). Management agencies are continuing to genotype broodstock throughout the Snake River basin, with future efforts targeting the entire Columbia River basin.

A notable example of using population genomics to delineate fisheries conservation units is of rockfish in Puget Sound, WA, USA. In 2010, yelloweye rockfish, *Sebastes ruberrimus*, and canary rockfish, *S. pinniger*, in the inland waterways of Puget Sound were listed as threatened under the US Endangered Species Act (ESA). The definition of listable under the ESA includes taxonomically identified species and subspecies, as well as distinct population segments (DPS; USFWS-NMFS 1996). ~~These two rockfish species were designated as DPSs.~~ In order for a vertebrate population to be designated as a DPS, it must be "discrete" from other populations of the same species as well as "significant" to the remainder of the species (USFWS-NMFS 1996). Because little information was available for the rockfish species of interest in Puget Sound, the decision to designate DPSs relied heavily on evidence from other species that these populations were "discrete" taxonomic units (Drake et al. 2010). To investigate the conservation designations, researchers collaborated with recreational fishing communities to collect tissue samples from the outer coasts of the USA and Canada. Multiple analyses using RADseq (>7,000 SNPs) suggest that yelloweye rockfish in Puget Sound and British Columbia, Canada, were genetically different from coastal populations, while canary rockfish showed no genetic differentiation between the two areas (Andrews et al. 2018). For yelloweye rockfish, the genomic data support the original ESA designation with an expansion of

protected areas. Interestingly, the data for canary rockfish in Puget Sound do not support a "discrete" population, therefore, not meeting the first criterion of the ESA. Consequently, in January 2017, the National Marine Fisheries Service removed the canary rockfish from the federal list of threatened and endangered species.

2.2 *Ecological Adaptation and Disease Management*

2.2.1 Adaptive Population Substructure

Population genomics approaches can be used to identify adaptively differentiated populations (Hoban 2018; Funk et al. 2019; Razgour et al. 2018) which can be prioritized for conservation (Funk et al. 2012). One prominent example of the utility of a genomics approach for identification of adaptive substructure is life history variation in Chinook salmon. The seasonal timing of migration by adult salmonids into freshwater is a key life history trait. Chinook salmon exhibit two seasonal migration strategies, spring and fall, to spawn in freshwater. Mature migrating Chinook enter freshwater in a sexually mature state in the fall and migrate directly to spawning grounds (Quinn et al. 2015). ~~In contrast, premature migrating Chinook enter freshwater from the ocean sexually immature in the spring, migrate into the headwaters and over summer while their gonads develop before spawning in the fall~~ (Quinn et al. 2015). The storage of excess fat allows the uncoupling of migration and spawning (Hearsey and Kinziger 2015). Historically, both spring and fall types inhabited many rivers. Because premature migrating salmon spend an extended period of time in freshwater, populations have experienced a dramatic decline as a result of anthropogenic activities that affect river conditions such as logging, mining, dam construction, and water diversion (Quinn et al. 2015). In the Klamath River basin, the spring Chinook population experienced a severe decline compared to the fall Chinook. The Salmon River hosts the last remaining population of spring salmon in the Klamath River basin comprising approximately 100 individuals. However, the rapid population decline has been met with limited conservation concern. Genetic analyses find little differentiation between premature and mature migrating populations and, therefore, are generally grouped into the same ESU or DPS (Myers et al. 1998). Population genomic analysis of 301,562 SNPs identified through RADseq suggests overall genetic variation reflects geography as opposed to migration type, corresponding to the ESU designations (Prince et al. 2017). However, a single genetic locus (Greb1-Like) was associated with premature migration which has been shown to modulate diverse behavior and metabolic processes in mice (Henry et al. 2015). Further investigation of Chinook salmon suggests that less than 1% of the remaining fish carry a copy of the early migration version of the gene (Thompson et al. 2019). The results generated from the application of the genomics approach have prompted the Karuk Tribe to petition the listing of Klamath's spring Chinook as threatened or endangered under the Endangered Species Act. This proposal has been controversial because some individuals advocate for the need to

AU13

protect adaptive variation, while others are concerned about the implications of conservation decisions based on a single gene (Langin 2018).

2.2.2 Environmental Adaptation and Tolerances

Although not a vertebrate (i.e., chapter topic), researchers used RADseq to identify SNPs (>9,000) to delineate locally adapted populations of commercially important greenlip abalone, *Haliotis laevigata* (Sandoval-Castillo et al. 2018). This study incorporated genotype-environment association analyses and outlier tests to identify 8,786 putatively neutral and 323 candidate adaptive loci. Neutral genetic structure was low across the study region; however, candidate adaptive loci suggested five distinct population clusters congruent with oceanic regions with associations corresponding to differences in oxygen concentration and temperature between the regions. Additionally, 80 of the 323 candidate loci were annotated to genes whose functions putatively affect high temperature and/or low oxygen tolerance (Sandoval-Castillo et al. 2018). The results have provided a genetic baseline to develop a genetic management plan which includes a risk assessment of impacts of the commercial sea ranching and restocking activities, including policies that promote the maintenance of patterns of adaptive divergence (DoF 2016; Daume et al. 2017; Hart et al. 2017). In particular, the Abalone Aquaculture Policy's "progeny diversity strategy" recommends the use of broodstock collection and captive breeding programs based on adaptive clusters to ensure that only genetically appropriate progenies are released into the marine environment (Hart et al. 2017). AU14

2.2.3 Disease Management

The application of population genomics can provide knowledge for management and treatment of disease in wildlife species. One example is chondrodystrophy in the California condor, *Gymnogyps californianus*. Historically, the California condor was widespread throughout southern North America. However, anthropogenic activity caused a rapid decline in the population. To prevent extinction, the last wild bird was brought into captivity in 1987, resulting in a human-induced bottleneck (D'Elia et al. 2016), and the contemporary population descended from 14 individuals (USFWS 1996). The specific goal for management of the California condor population focuses on maximizing genetic diversity in captive and reintroduced populations (Ralls and Ballou 2004) which has been supported by the application of genomics methodologies. Thirty-six complete California condor genomes, representing the entire gene pool of the species, have been sequenced, which identified four million SNPs (Ryder et al. 2016). This information has provided insight into the genetic similarities among founding birds and allowed reassessment of kinship, which is now being applied to the captive propagation effort in the selection of breeding pairs. However, the captive propagation effort is hindered by the expression of chondrodystrophy, which has an autosomal recessive mode of

transmission in condors (Ralls et al. 2006). Whole genome sequencing suggests that this lethal form of dwarfism is correlated to a series of linked markers localized in a 1 Mb region of the genome, which is currently being used to detect carrier condors heterozygous for the lethal mutation (Ryder et al. 2016). This information is being incorporated into population management to reduce the risk of reproductive failure.

The Tasmanian devil (*Sarcophilus harrisii*) is the largest extant marsupial carnivore and is endemic to the island of Tasmania. In the last 20 years, the emergence of an infectious cancer, devil facial tumor disease (DFTD), has resulted in an 85% decline in the population (Hawkins et al. 2006; McCallum et al. 2007). DFTD is a transmissible cancer that spreads through physical contact during feeding and mating (Pearse and Swift 2006). In 2006, a disease-free insurance population of devils was established (Conservation Breeding Specialist Group 2008). The main goals of this program are to preserve genetic diversity, minimize inbreeding, prevent adaptation to captivity, and prevent disease (Conservation Breeding Specialist Group 2008; Lees and Andrew 2012). Whole genome sequencing has been used to understand the origins, transmission, and diversity of DFTD in Tasmanian devils (Murchison et al. 2012). Interestingly, in a single population of infected devils, a small number of individuals spontaneously recovered from the typically lethal disease. To determine if resistance to DFTD has a genetic basis, researchers sequenced the genomes of the seven individuals that recovered from DFTD infection and compared them to the genomes of six devils that succumbed to the disease (Wright et al. 2017). This genome-wide association approach identified two genomic regions where genotypes were strongly associated with disease status and associated with angiogenesis (Wright et al. 2017). The information generated from genomics techniques is being used to inform disease management, breeding programs, and reintroductions to manage genetic diversity of this endangered species.

3 Future Perspectives

The current application of population genomics to wildlife and fish management focuses on monitoring and managing existing diversity; however, there is growing interest in the application of functional genomics approaches to gain a better understanding of adaptive potential in wild populations (Corlett 2017; Connon et al. 2018; Rey et al. 2019). With the recent advances in RNA-sequencing technology allowing the application in non-model organisms (Todd et al. 2016), a population transcriptomics approach can be applied in a conservation context to identify biomarkers associated with environmental stress (Connon et al. 2018). Additionally, genomics technology can also be used to study the epigenome (i.e., epigenomics). Mutations in the epigenome are molecular changes in gene expression without altering the DNA sequence and can be involved in an organism's adaptive response to environmental change, representing the short-term interaction between organisms and their environment. The integration of epigenetics can provide insight into the physiological, biological, and ecological status of organisms and aid in the

designation of management units (Rey et al. 2019). The recent advances in genomics technology that allow the quantification of functional diversity and structure among wild populations will improve our understanding of organismal response to changing environmental conditions.

Furthermore, there is an opportunity for new genomics technology to provide the potential for genome manipulation in conservation applications (Phelps et al. 2019). Genome-editing technology refers to methods that can insert, delete, and/or replace specific regions of the genome allowing for sequence modification that can knock out the function of a gene or insertion of a specific sequence with genome edits. The most well-known genome-editing technique is CRISPR-CAS9, an RNA-guided molecule that identifies and binds to a specific region within the genome and subsequently cuts and replaces DNA (Mei et al. 2016). The promise of this tool is enhanced by its simplicity, precision, and relatively low cost (Mei et al. 2016; Phelps et al. 2019).

Genome-editing technology has the potential to aid biodiversity conservation in several ways by identifying and altering regions of the genome that may impact fitness and limit survival in wild populations. Genomic data and gene-editing technology can be used in the replacement of alleles which can assist evolution of disease resistance, remove deleterious genetic variants such as chondrodystrophy in California condors, and enhance adaptation to changing climates (i.e., facilitated adaptation; Harrisson et al. 2014). Gene-editing technology can aid in the eradication of invasive species, which are the main driver of vertebrate extinctions (e.g., Bellard et al. 2016), through gene drive methodologies. Gene drives alter Mendelian inheritance by increasing inheritability of an engineered allele to spread the desired trait throughout the population (Esvelt et al. 2014; Webber et al. 2015). For example, genome-editing techniques that alter the sex determination pathway of invasive rodents on islands aimed at producing all male offspring ultimately lead to a reduction in reproduction (Campbell et al. 2015). Additionally, gene-editing technology has the potential to aid in the resurrection of ecologically important traits (i.e., trait resurrection, modification of phenotypically relevant genes from extinct species into closely related extant taxa; Johnson et al. 2016). One notable example of trait resurrection is the alteration of genes from the extinct wooly mammoth, *Mammuthus primigenius*, in the Asian elephant, *Elephas maximum*, associated with cold temperature adaptations (Lynch et al. 2015; Shapiro 2015).

While gene-editing technology has the potential to aid in conservation and management efforts, this methodology does not come without controversy. Agencies currently lack a clear framework for implementing gene-editing approaches as conservation tools (Sandler 2019). Before implementation into conservation and management efforts of natural populations, it is imperative to evaluate practical, ethical, and legal considerations (Johnson et al. 2016; Webber et al. 2015) to reduce any unintended, irreversible consequences.

4 Conclusions

We conclude from our search of the literature and our survey that population genomics is still only partially embraced with few examples of genomic data being implemented in a management or conservation framework. The field of fisheries has been an early adopter of some genomics technologies. However, most of the advances in natural resource management have been in the use of genomics for more power and precision instead of looking at the functionality or interactions of genes and how they help organisms adapt to their environment. We had initially hoped that the lack of examples of management decisions being affected by population genomics was a function of a lag in the process. It can take time from results being obtained, to having them accepted through a peer review process, to having them adopted by management agencies to change how natural populations are conserved or managed. This may still be the case; however, our literature review and survey through ~~EcoLog~~ has led us to believe that while population genomics has an important role for wildlife management, it is still an underused tool with an important future. We predict that the next decade will see an explosion of uses of population genomic data in the management of wild populations, although as the technical details of the science becomes more specialized it will require active engagement between managers and researchers to ensure the interpretation of the science for policy is done responsibly.

References

Allendorf FW. Genetics and the conservation of natural populations: allozymes to genomes. Mol Ecol. 2017;26:420–30.

Allendorf FW, Hohenlohe PA, Luikart G. Genomics and the future of conservation genetics. Nat Rev Genet. 2010;11:697–709.

Anderson EC, Garza JC. A description of full parentage genotyping (online). Report submitted to the Pacific Salmon Commission, Vancouver, BC; 2005. Retrieved from http://swfsc.noaa.gov/publications/FED/00675.pdf.

Andrews KS, Nichols KM, Elz A, Tolimieri N, Harvey CJ, Pacunski R, Lowry D, Yamanaka KL, Tonnes DM. Cooperative research sheds light on population structure and listing status of threatened and endangered rockfish species. Conserv Genet. 2018;19:865–78.

Beacham TD, Candy JR, Wallace C, Wetklo M, Deng L, MacConnachie C. Microsatellite mixed-stock identification of Coho Salmon in British Columbia. Mar Coast Fish. 2012;4:85–100.

Bellard C, Cassey P, Blackburn TM. Alien species as a driver of recent extinctions. Biol Lett. 2016;12:20150623.

Benestan LM, Ferchaud A, Hohenlohe PA, Garner BA, Naylor GJP, Baums IB, Schwartz MK, Kelley JL, Luikart G. Conservation genomics of natural and managed populations: building a conceptual and practical framework. Mol Ecol. 2016;25:2967–77.

Campbell KJ, Beek J, Eason CT, Glen AS, Godwin J, Gould F, Holmes ND, Howald GR, Madden FM, Ponder JB, Threadgill DW, Wegmann AS, Baxter GS. The next generation of rodent eradications: innovative technologies and tools to improve species specificity and increase their feasibility on islands. Biol Conserv. 2015;185:47–58.

Çilinger FG, Rheindt FE, Garg KM, Platt K, Platt SG, Bickford DP. Conservation genomics of the endangered Burmese roofed turtle. Conserv Biol. 2017;31:1469–76.
Connon RE, Jeffries KM, Komoroske LM, Todgham AE, Fangue NA. The utility of transcriptomics in fish conservation. J Exp Biol. 2018;221:jeb148833.
Conservation Breeding Specialist Group. Tasmanian devil PHVA final report. Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group; 2008.
Corlett RT. A bigger toolbox: biotechnology in biodiversity conservation. Trends Biotechnol. 2017;35:55–65.
Crandall KA, Bininda-Emonds ORP, Mace GM, Wayne RK. Considering evolutionary processes in conservation biology. Trends Ecol Evol. 2000;15:290–5.
D'Elia J, Haig SM, Mullins TD, Miller MP. Ancient DNA reveals substantial genetic diversity in the California condor (*Gymnogyps californianus*) prior to a population bottleneck. Condor. 2016;11:703–14.
Dann TH, Habicht C, Baker TT, Seeb JE. Exploiting genetic diversity to balance conservation and harvest migratory salmon. Can J Fish Aquat Sci. 2013;70:785–93.
Daume S, Gardner C, Leporati S, Trott P. Western Australia abalone fishery MSC full assessment public certification report. SCS Global Services; 2017. p. 254.
DoF. Abalone aquaculture in Western Australia: principles and considerations relating to management of abalone aquaculture in Western Australia. Fisheries Occasional Publication 132; 2016. p. 18.
Drake JS, Berntson EA, Gustafson RG, Holmes EE, Levin PS, Tolimieri N, Waples RS, Sogard SM, Williams GD, Cope JM. Status review of five rockfish species in Puget Sound, Washington: bocaccio (*Sebastes paucispinis*), canary rockfish (*S. pinniger*), yelloweye rockfish (*S. ruberrimus*), greenstriped rockfish (*S. elongates*), and redstripe rockfish (*S. proriger*). US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service; 2010.
Epstein B, Jones M, Hamede R, Hendricks S, McCallum H, Murchison EP, Schönfeld B, Wiench C, Hohenlohe P, Storfer A. Rapid evolutionary response to transmissible cancer in Tasmanian devils. Nat Commun. 2016;7:12684.
Esvelt KM, Smidler AL, Catteruccia F, Church GM. Emerging technology: concerning RNA-guided gene drives for the alteration of wild populations. Elife. 2014;3:e03401.
Fitzpatrick SW, Funk WC. Genomics for genetic rescue. In: Population genomics. Cham: Springer; 2019.
Fleming IA, Einum S. Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. ICES J Mar Sci. 1997;54:1051–63.
Fleming IA, Jonsson B, Gross MR, Lamberg A. An experimental study of the reproductive behavior and success of farmed and wild Atlantic salmon (*Salmo salar*). J Appl Ecol. 1996;33:893–905.
Fleming IA, Hindar K, Mjølnerød IB, Jonsson B, Balstad T, Lamberg A. Lifetime success and interactions of farm salmon invading a native population. Proc Roy Soc Lond B Biol Sci. 2000;267:1517–23.
Fleming IA, Agustsson T, Finstad B, Johnsson JI, Bjornsson BT. Effects of domestication on growth physiology and endocrinology of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci. 2002;59:1323–30.
Frankham R. Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. Mol Ecol. 2015;24:2610–8.
Fraser DJ, Bernatchez L. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. Mol Ecol. 2001;10:2741–52.
Funk WC, McKay JK, Hohenlohe PA, Allendorf FW. Harnessing genomics for delineating conservation units. Trends Ecol Evol. 2012;27:489–96.
Funk WC, Forester BR, Converse SJ, Darst C, Morey S. Improving conservation policy with genomics: a guide to integrating adaptive potential into U.S. Endangered Species Act decisions for conservation practitioners and geneticists. Conserv Genet. 2019;20:115–34.
Gjedrem T. The first family based breeding program in aquaculture. Rev Aquac. 2010;2:2–15.

Glover KA, Ottera H, Olsen RE, Slinde E, Taranger GL, Skaala Ø. A comparison of farmed, wild and hybrid Atlantic salmon (*Salmo salar* L.) reared under farming conditions. Aquaculture. 2009;286:203–10.

Glover KA, Pertoldi C, Besnier F, Wennevik V, Kent M, Skaala Ø. Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. BMC Genet. 2013;14:4.

Habicht C, Munro AR, Dann TH, Eggers DM, Templin WD, Witteveen MJ, Baker TT, Howard KG, Rogers Olive SD, Liller HL, Chenoweth EL, Volk EC. Harvest and harvest rates of sockeye salmon stocks in fisheries of the Western Alaska Salmon Stock Identification Program (WASSIP), 2006–2008. Alaska Department of Fish and Game, Special Publication No. 12-24. Anchorage, AK; 2012.

Harrisson KA, Pavlova A, Telonis-Scott M, Sunnucks P. Using genomics to characterize evolutionary potential for conservation of wild populations. Evol Appl. 2014;7:1008–25.

Hart A, Strain L, Hesp A, Fisher E, Webster F, Brand-Gardner S, Walters S. Marine Stewardship Council Full Assessment Report Western Australian Abalone Managed Fishery. Perth, WA: Department of Fisheries, Western Australia; 2017.

Hawkins CE, Baars C, Hesterman H, Hocking GJ, Jones ME, Lazenby B, Mann D, Mooney N, Pemberton D, Pyecroft S, Restani M, Wiersma J. Emerging disease and population decline of an island endemic, the Tasmanian devil *Sarcophilus harrisii*. Biol Conserv. 2006;131:307–24.

Hearsey JW, Kinziger AP. Diversity in sympatric Chinook salmon runs: timing, relative fat content and maturation. Environ Biol Fishes. 2015;98:413–23.

Henry FE, Sugino K, Tozer A, Branco T, Sternson SM. Cell type-specific transcriptomics of hypothalamic energy-sensing neuron responses to weight loss. Elife. 2015;4:e09800.

Hoban S. Integrative conservation genetics: prioritizing populations using climate predictions, adaptive potential and habitat connectivity. Mol Ecol Resour. 2018;18:14–7.

Hoffman AA, Sgrò CM, Kristensen TN. Revisiting adaptive potential, population size, and conservation. Trends Ecol Evol. 2017;32:506–17.

Hohenlohe PA, Hand BK, Andrews KR, Luikart G. Population genomics provides key insights in ecology and evolution. In: Rajora OP, editor. Population genomics: concepts, approaches and applications. Cham: Springer Nature Switzerland AG; 2019. p. 483–510.

Hutchings JA. Collapse and recovery of marine fishes. Nature. 2000;406:882–5.

Johnson JA, Altwegg R, Evans DM, Ewen JG, Gordon IJ. Is there a future for genome-editing technologies in conservation? Anim Conserv. 2016;19:97–101.

Kardos M, Shafer ABA. The perils of gene-targeted conservation. Trends Ecol Evol. 2018;33:827–39.

Karlsson S, Moen T, Lien S, Glover KA, Hindar K. Generic genetic differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip. Mol Ecol Resour. 2011;11:377–87.

Laikre L, Schwartz MK, Waples RS, Ryman N, GeM Working Group. Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. Trends Ecol Evol. 2010;25:520–9.

Langin K. Salmon spawn fierce debate over protecting endangered species, thanks to a single gene. Sci News. 2018. http://www.sciencemag.org/news/2018/05/salmon-spawn-fierce-debate-over-protecting-endangered-species-thanks-single-gene.

Larson WA, Seeb JE, Pascal CE, Templin WD, Seeb LW. Single-nucleotide polymorphisms (SNPs) identified through genotyping-by-sequencing improve stock identification of Chinook salmon (*Oncorhynchus tshawytscha*) from western Alaska. Can J Fish Aquat Sci. 2014;71:698–708.

Lees C, Andrew P. The Tasmanian devil insurance meta-population: 2012 evaluation and review. Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group; 2012.

Luikart G, England PR, Tallmon D, Jordan S, Taberlet P. The power and promise of population genomics: from genotyping to genome typing. Nat Rev Genet. 2003;4:981–94.

Luikart G, Kardos M, Hand B, Rajora OP, Aitken S, Hohenlohe PA. Population genomics: advancing understanding of nature. In: Rajora OP, editor. Population genomics: concepts, approaches and applications. Cham: Spring Nature Switzerland AG; 2019. p. 3–79.
Lynch VJ, Bedoya-Reina OC, Ratan A, Sulak M, Drautz-Moses DI, Perry GH, Miller W, Schuster SC. Elephantid genomes reveal the molecular bases of wooly mammoth adaptations to the arctic. Cell Rep. 2015;12:217–8.
McCallum H, Tompkins DM, Jones M, Lachish S, Marvanek S, Lazenby B, Jocking G, Wiersma J, Hawkins CE. Distribution and impacts of Tasmanian devil facial tumor disease. Ecohealth. 2007;4:318–25.
Mei Y, Wang Y, Chen H, Sun ZS, Ju XD. Recent progress in CRISPR/Cas9 technology. J Genet Genomics. 2016;43:63–75.
Mitrovski P, Heinze DA, Guthridge K, Weeks AR. Isolation and characterization of microsatellite loci from the Australian endemic mountain pygmy-possum, *Burramys parvus* Broom. Mol Ecol Notes. 2005;5:395–7.
Moritz C. Strategies to protect biological diversity and the evolutionary processes that sustain it. Syst Biol. 2002;51:238–54.
Mortiz C. Defining 'Evolutionary Significant Units' for conservation. Trends Ecol Evol. 1994;9:373–5.
Munro AR, Habicht C, Dann TH, Eggers DM, Templin WD, Witteveen MJ, Baker TT, Howard KG, Jasper JR, Rogers Olive SD, Liller HL, Chenoweth EL, Volk EC. Harvest and harvest rates of Chum salmon stocks in fisheries of the Western Alaska Salmon Stock Identification Program (WASSIP), 2007–2009. Alaska Department of Fish and Game, Special Publication No. 12-25, Anchorage, AK; 2012.
Murchison EP, Schulz-Trieglaff OB, Ning Z, Alexandrov LB, Bauer MJ, Fu B, Hims M, Ding Z, Ivakhno S, Stewart C, Ng BL, Wong W, Aken B, White S, Alsop A, Becq J, Bignell GR, Cheetham RK, Cheng W, Connor TR, Cox AJ, Feng ZP, Gu Y, Grocock RJ, Harris SR, Khrebtukova I, Kingsbury Z, Kowarsky M, Kreiss A, Luo S, Marshall J, McBride DJ, Murray L, Pearse AM, Raine K, Rasolonjatovo I, Shaw R, Tedder P, Tregidgo C, Vilella AJ, Wedge DC, Woods GM, Gormley N, Humphray S, Schroth G, Smith G, Hall K, Searle SM, Carter NP, Papenfuss AT, Futreal PA, Campbell PJ, Yang F, Bentley DR, Evers DJ, Stratton MR. Genome sequencing and analysis of the Tasmanian devil and its transmissible cancer. Cell. 2012;148:780–91.
Myers RA, Worm B. Rapid worldwide depletion of predatory fish communities. Nature. 2003;423:280–3.
Myers JM, Kope RG, Bryant GJ, Teel D, Lierheimer LJ, Wainwright TC, Grant WS, Waknitz FW, Neely K, Lindley ST, Waples RS. Status Review of Chinook salmon from Washington, Idaho, Oregon, and California. U.S. Department of Commerce, NOAA Technical Memorandum. NMFS-NWFSC-35; 1998.
Pearse DE. Saving the spandrels? Adaptive genomic variation in conservation and fisheries management. J Fish Biol. 2016;89:2697–716.
Pearse AM, Swift K. Allograft theory: transmission of devil facial-tumour disease. Nature. 2006;439:549.
Phelps M, Seeb L, Seeb J. Transforming ecology and conservation biology through genome editing. Conserv Biol. 2019; https://doi.org/10.1111/cobi.13292.
Prince DJ, O'Rourke SM, Thompson TQ, Ali OA, Lyman HS, Saglam IK, Hotaling TJ, Spidle AP, Miller MR. The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. Evol Genet. 2017;3:e1603198.
Quinn TP, McGinnity P, Reed TE. The paradox of "premature migration" by adult anadromous salmonid fishes: patterns and hypotheses. Can J Fish Aquat Sci. 2015;73:1015–30.
Ralls K, Ballou JD. Genetic status and management of California condors. Condor. 2004;106:215–28.
Ralls K, Ballou JD, Rideout BA, Frankham R. Genetic management of chondrodystrophy in the California condor. Anim Conserv. 2006;3:145–53.

Randi E. Detecting hybridization between wild species and their domesticated relatives. Mol Ecol. 2008;17:285–93.

Razgour O, Taggart JB, Manel S, Juste J, Ibánez C, Rebelo H, Alberdi A, Jones G, Park K. An integrated framework to identify wildlife populations under threat from climate change. Mol Ecol Resour. 2018;18:18–31.

Reed DH, Frankham R. Correlation between fitness and genetic diversity. Conserv Biol. 2003;17:230–7.

Rey O, Eizaguirre C, Angers B, Baltazar-Soares M, Sagonas K, Prunier JG, Blanchet S. Linking epigenetics and biological conservation: towards a conservation epigenetics perspective. Funct Ecol. 2019:1–14.

Ryder O, Miller W, Ralls K, Ballou JD, Steiner CC, Mitelberg A, Romanov M, Chemnick LG, Mace M, Schuster S. Whole genome sequencing of California condors is now utilized for guiding genetic management. International plant and animal genome XXIV conference, San Diego, CA; 2016.

Sandler R. The ethics of genetic engineering and gene drives in conservation. Conservat Genet. 2019; https://doi.org/10.1111/cobi.13407.

Sandoval-Castillo J, Robinson NA, Hart AM, Strain LWS, Beheregaray LB. Seascape genomics reveals adaptive divergence in a connected and commercially important mollusk, the greenlip abalone (*Haliotis laevigata*), along a longitudinal environmental gradient. Mol Ecol. 2018;27:1603–20.

~~Schafer,~~ ABA, Wolf JBW, Alves PC, Bergström L, Bruford MW, Brännström I, Colling G, Dalén L, De Meester L, Ekblom R, Fawcett KD, Fior S, Hajibabaei M, Hill JA, Hoezel AR, Höglund J, Jensen EL, Krause J, Kristensen TN, Krützen M, JK MK, Norman AJ, Ogden R, Österling EM, Ouborg NJ, Piccolo J, Popović D, Primmer CR, Reed FA, Roumet M, Salmona J, Schenekar T, Schwartz MK, Segelbacher G, Senn H, Thaulow J, Valtonen M, Veale A, Vergeer P, Vijay N, Vilà C, Weissensteiner M, Wennerström L, Wheat CW, Zieliński P. Genomics and the challenging translation into conservation practice. Trends Ecol Evol. 2015;30:78–87.

Schwartz MK, McKelvey KS, Cushman SA, Luikart G. Landscape genomics: a brief perspective. In: Spatial complexity, informatics, and wildlife conservation. Tokyo: Springer; 2010. p. 165–74.

Sgró CM, Lowe AJ, Hoffmann AA. Building evolutionary resilience for conserving biodiversity under climate change. Evol Appl. 2011;4:326–37.

Shapiro B. Mammoth 2.0: will genome engineering resurrect extinct species. Genome Biol. 2015;16:228.

Skaala Ø, Hoyheim B, Glover K, Dahle G. Microsatellite analysis in domesticated and wild Atlantic salmon (*Salmo salar* L.): allelic diversity and identification of individuals. Aquaculture. 2004;240:131–43.

Steele CA, Anderson EC, Ackerman MW, Hess MA, Campbell NR, Narum SR, Campbell MR. A validation of parentage-based tagging using hatchery Steelhead in the Snake River basin. Can J Fish Aquat Sci. 2013;70:1046–54.

Taranger GL, Karlsen Ø, Bannister RJ, Glover KA, Husa V, Karlsbakk E, Kvamme BO, Boxaspen KK, Bjørn PA, Finstad B, Madhun AS, Morton HC, Svåsand T. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES J Mar Sci. 2014;72:997–1021.

Thompson TQ, Bellinger RM, O'Rourke SM, Prince DJ, Stevenson AE, Rodriques AT, Sloat MR, Speller CF, Yang DY, Butler VL, Banks MA, Miller MR. Anthropogenic habitat alteration leads to rapid loss of adaptive variation and restoration potential in wild salmon populations. Proc Natl Acad Sci U S A. 2019;116:177–86.

Todd EV, Black MA, Gemmell NJ. The power and promise of RNA-seq in ecology and evolution. Mol Ecol. 2016;25:1224–41.

USFWS. California condor recovery plan, third revision, US Fish and Wildlife Service; 1996.

USFWS-NMFS. Policy regarding the recognition of distinct vertebrate population segments under the Endangered Species Act. Fed Regist. 1996;61:4721–5.

677 Utter F, Ryman N. Genetic markers and mixed stock fisheries. Fisheries. 1993;18:11–21.
678 Verhoeven KJF, Vonholdt BM, Sork VL. Epigenetics in ecology and evolution: what we know
679 and what we need to know. Mol Ecol. 2016;25:1631–8.
680 Vrijenhoek RC, Leberg PL. Let's not throw the baby out with the bathwater: a comment
681 on management for MHC diversity in captive populations. Conserv Biol. 1991;5:252–4.
682 Warheit KI. Measuring reproductive interactions between hatchery-origin and wild
683 Steelhead (*Oncorhynchus mykiss*) from northern Puget Sound populations potentially affected
684 by segregated hatchery programs. Washington Department of Fish and Wildlife, Unpublished
685 Report, Olympia, WA; 2014.
686 Webber BL, Raghu S, Edwards OR. Is CRISPR-based gene drive a biocontrol silver bullet or
687 global conservation threat? Proc Natl Acad Sci. 2015;112:10565–7.
688 Weeks AR, Heinze D, Perrin L, Stoklosa J, Hoffmann AA, van Rooyen A, Kelly T,
689 Mansergh I. Genetic rescue increases fitness and aids rapid recovery of an endangered marsupial
690 population. Nat Commun. 2017;8:1071.
691 Wright B, Willet CE, Hamede R, Jones M, Belov K, Wade CM. Variants in the host genome
692 may inhibit tumour growth in devil facial tumours: evidence from genome-wide association.
693 Sci Rep. 2017;7:1–6.