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From threats to solutions: A literature review of climate adaptation in anadromous salmon and trout

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Abstract

Understanding the evolutionary responses of anadromous salmon and trout to climate change is critical for effective conservation planning. In this study, we conducted a comprehensive review of literature published from 2010 to 2020 to synthesize current knowledge on climate impacts to these fish populations. Specifically, we focused on 199 papers that explored evolutionary processes in response to changing environmental conditions. Our analysis revealed several key themes, including the interwoven influences of climate and human activities on genetic variation, phenotypic traits, and population dynamics. We found that geographic patterns in genetic diversity are closely linked to climatic gradients, highlighting the importance to conservation strategies of variation in existing adaptive capacity. Additionally, temporal trends in phenology, maturation age, and fecundity indicate ongoing evolutionary and plastic responses to climate change. Importantly, human activities were identified as significant drivers of maladaptation in anadromous salmon and trout populations. We emphasize the need for targeted monitoring of specific evolutionary processes to mitigate the loss of genetic diversity and enhance adaptive capacity. Our study underscores the importance of identifying and protecting areas of high genetic diversity and rare genes, particularly in regions projected to experience rapid climatic shifts. In conclusion, our findings identify strengths and gaps in the research investigating the role of evolutionary dynamics in the face of climate change. By capitalizing on new tools for sequencing, genomic analysis, and automated field data collection, we can establish baselines for tracking evolutionary responses to climate change. Better integration of evolutionary processes into projections of future climate impacts will lead to more effective strategies to ensure the long-term resilience of these iconic fish species and other wildlife.

KEYWORDS
anadromous fish, evolutionary responses to climate change, freshwater, future projections, genetic approaches, global change, ocean

INTRODUCTION

Climate change is forcing species to respond to unprecedented environmental conditions across the globe, dramatically escalating extinction rates and conservation concerns (Barbarossa et al., 2021; Roman-Palacios & Wiens, 2020; Smith et al., 2023; Wiens, 2016). Because climate impacts are so widespread, and mitigation needs far exceed conservation resources, a major challenge today is how to prioritize conservation actions. Relative risk to different taxa depends on a multitude of stressors affecting them and is influenced by the interactions among physiological, ecological, and evolutionary processes. However, the majority of literature on climate impacts focuses on physiological and ecological dynamics, with only 11% addressing evolutionary processes (Crozier & Siegel, 2023).

The importance of evolutionary dynamics is recognized in climate vulnerability assessments, where adaptive capacity is valued as a key component in defining vulnerability (Foden et al., 2013; Nicotra et al., 2015). However, data are typically insufficient to assess large-scale adaptive capacity, and we lack consensus on how to measure it (Lankford et al., 2014; Wade et al., 2017). Perhaps more concerning, as the climate crisis receives increasing public attention, genetic interventions such as assisted migration are accelerating without adequate research on optimal strategies and outcomes (Fenu et al., 2023). Moreover, genetic engineering is becoming readily available and is frequently advocated, despite acknowledgments that we have no way to fully prevent undesirable outcomes (Hedrick et al., 2013; Torda & Quigley, 2022). Overconfidence in our ability to predict the most important individual genes or traits could well be counterproductive (Kardos et al., 2021).

Our overall aim was to help decision-makers and the public in targeting data collection and research toward the most useful and effective projects. To this end, we attempt to provide easier access to literature that explores (1) the genetic landscape that shapes adaptive potential, (2) current trends in climate-sensitive phenotypic traits that are closely related to fitness, and (3) human impacts on adaptive potential (Carroll et al., 2014). Our analysis was designed to help discern these trends and issues and to clarify the scope over which evolutionary analyses are being applied in climate-impact studies. Toward this goal, we examined the literature addressing climate impacts on a well-studied focal group of species, anadromous salmon and trout (*Oncorhynchus* and *Salmo* spp.), with supporting information from studies of other trout and char (*Salvelinus* spp.).

Genetic work in this group has expanded rapidly over three decades for both conservation and commercial applications (Tkach & Watson, 2023). For example, population genetic analyses in western regions were needed in the 1990s to define distinct population segments for protection under the U.S. Endangered Species Act (ESA, Waples, 1991), and to establish captive broodstock programs to save populations that were functionally extinct (Kline et al., 2019). Additional sequencing work developed stock identification tools to guide mixed-stock fisheries and other conservation projects (Matala et al., 2014; Waples, Punt, et al., 2008). Extensive research has also been done for aquaculture, especially in Atlantic salmon (Davidson et al., 1989; Li & Wang, 2017). Currently, whole genome sequences are publicly available for Atlantic salmon (*Salmo salar*) (Lien et al., 2016), steelhead/rainbow trout (*Oncorhynchus mykiss*) (Salem et al., 2022), and Chinook salmon (*Oncorhynchus tshawytscha*) (Narum et al., 2018).

Local adaptation is common in these fishes, with some species swimming over 1000 km through freshwater during both the juvenile and adult migrations to utilize spawning habitat distant from the ocean. Anadromous species face especially complex conservation threats because their life history exposes them to a diverse set of interacting stressors in both terrestrial/freshwater systems and the marine environment (Figure 1) (Crozier et al., 2008; Healey, 2011; Wainwright & Weitkamp, 2013). However, their remarkable adaptive capacity has been greatly reduced, largely owing to blocked migration routes, habitat degradation, fisheries, and hatchery practices (Gustafson et al., 2007; NRC, 1996). Looking forward, we expect that populations will evolve in both adaptive and maladaptive directions in response to modern climate change (McGaughran et al., 2021). Thus, a primary question facing managers is how to preserve and augment the adaptive capacity of these species.

A vast and rapidly growing body of literature characterizes climate impacts on salmon and trout. In fact, the breadth and scope of this work makes it cumbersome for conservation practitioners to evaluate and use. To increase usability, we collated and categorized a selection of relevant studies to provide a resource for researchers and wildlands decision-makers. We included research from around the world, although we focused most on papers relevant to wild anadromous salmon and steelhead trout populations in the Columbia River Basin, a 668,000-km^2 drainage area located in the U.S. Pacific Northwest. This region supports six species of Pacific salmon (*Onchorynchus* spp.) including 13 distinct population segments that are threatened or endangered (NOAA Fisheries, 2022). An initial description of the database was published by Crozier and Siegel (2023). Here, we analyze 199 papers that specifically focused on evolutionary processes (e.g., changes in gene frequencies, drivers of natural selection, or genetic attributes of fitness associated with climate), elaborating on topics that were less prominent when considering the database as a whole.

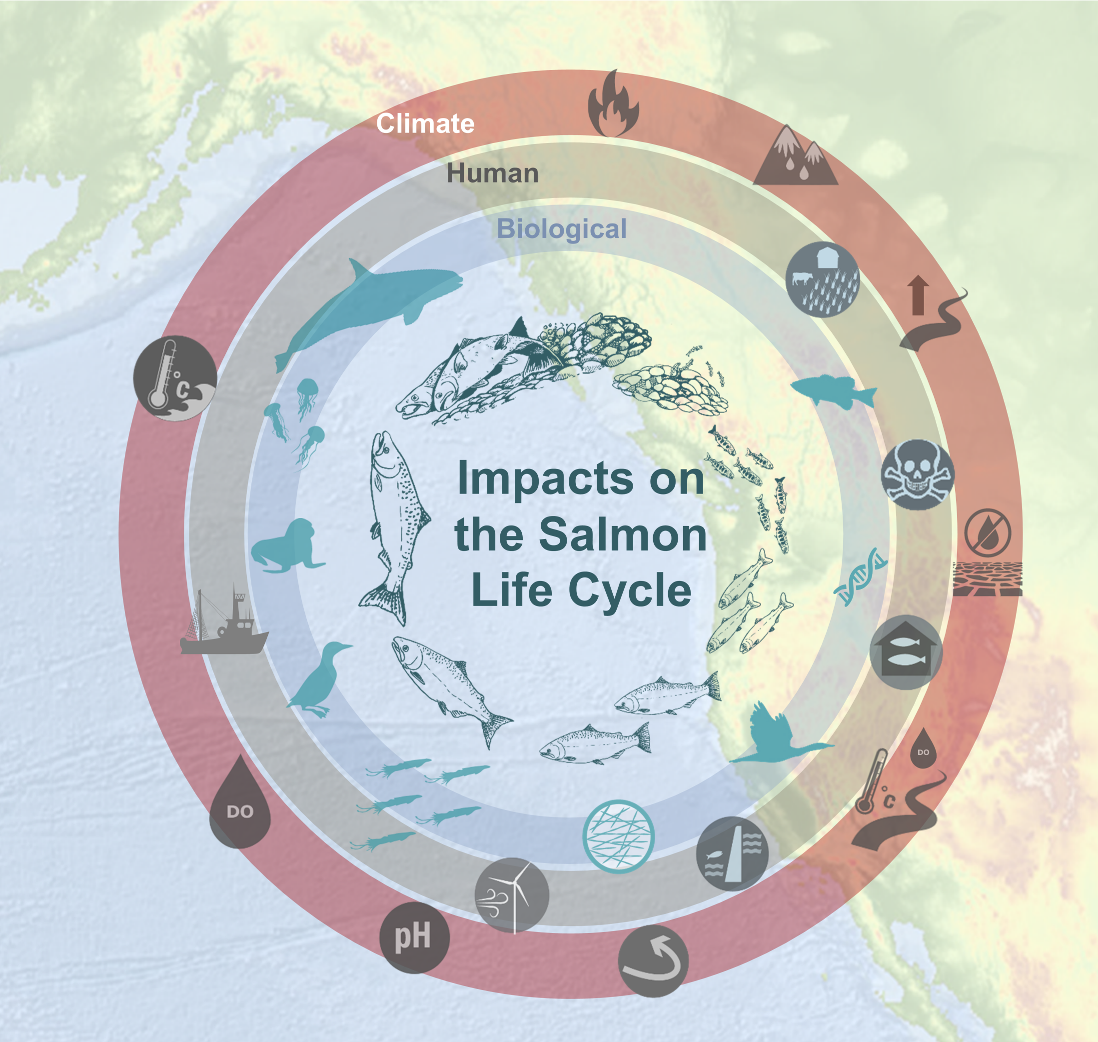

FIGURE 1 A selection of climatic, anthropogenic, and ecological factors potentially imposing selective pressures on anadromous salmon and trout. Icons in the climate ring represent changes in wildfire intensity and frequency; snow accumulation and the timing of snowmelt; increased flooding and drought; rising stream temperatures and decreased oxygen in freshwater; altered currents and coastal upwelling; decreased oxygen, increased acidity, and rising temperatures in the ocean. Anthropogenic impacts include many kinds of landscape modification, agricultural runoff, toxic chemicals, fish hatcheries, dams, seawall and stream-hardening structures, estuary and coastal activities, wind energy development on land and offshore, and fishing. Ecological factors include changes in prey, competitors and predators, as well as harmful algal blooms and diseases. The inner circle shows the salmon life cycle. Artwork by NOAA Fisheries.

Our objectives for this review were to (1) classify and quantify attributes of the literature that explicitly addressed climate impacts on this group of fish, (2) summarize dominant themes in this literature, and (3) recommend priorities for conservation decision-makers.

DESCRIPTION OF THE LITERATURE SURVEYED

Literature collection

Our database consisted of papers collected originally to inform adaptive management of the Columbia River Federal Power System from 2010 to 2020, an approach required to comply with federal consultations for the ESA (NOAA Fisheries, 2008, 2010). We initiated these reviews to identify new scientific findings relevant to the prediction and mitigation of climate change impacts on federally protected salmon and steelhead. Literature prior to 2010 had been summarized in earlier consultations (NOAA Fisheries, 2008, 2010).

For each annual review, we emphasized peer-reviewed scientific journals included in the *Web of Science* Core Collection database. We conducted searches of this database using combinations of taxonomic (salmon, *Oncorhynchus*, or steelhead) and climatic terms (climate, temperature, streamflow, flow, snowpack, precipitation, Pacific Decadal

Oscillation, marine, sea level, hyporheic, groundwater, or ocean acidification). The list of climatic terms indicates the environmental factors that we considered most likely to invoke responses to climate change which we consider to be climate impacts. We supplemented these results with technical reports from state and federal agencies involving Columbia and Snake River populations. The results were first reduced to 1853 papers deemed most relevant for all biological impacts of climate change (Crozier & Siegel, 2023). We included experimental, field, and modeling studies, as well as reviews, meta-analyses, and opinion pieces.

Literature classification

To classify our dataset, we began by assigning labels within a set of eight categories to all papers based on the primary focus of the study. These categories included *species*, *life stage*, *region*, *subregion*, *study type*, *study duration*, *drivers*, and *responses* (Appendix S1: Table S1). A *driver* was defined as a natural or anthropogenic explanatory variable; these included factors represented as potentially forcing change on salmon or trout and preexisting conditions within the population, such as genetic variation prior to some perturbation. A *response* was defined as a biological outcome measured or described in salmon or trout as the outcome of an explanatory variable (loosely based on definitions suggested by Oesterwind et al., 2016). For example, current genetic variation across spatial gradients was interpreted by the author as a response to past climatic and other pressures, such as recolonization after the last glacial maximum or climatically driven fluctuations in population size. Where appropriate, papers were assigned multiple labels within a category (e.g., when multiple species were studied).

We assigned all of the drivers and responses to the set of biological process categories identified by Urban et al. (2016) as being necessary to consider in concert in order to predict and prevent the most damaging aspects of climate change. These categories were *evolution*, *physiology*, *demography*, *species interactions*, *dispersal*, and *environmental conditions*.

Evolutionary processes address, in a broad sense, the ability of a species to adapt genetically to a changing environment. They may involve potential responses to natural and artificial selection, the ability to avoid inbreeding and genetic drift, specific genes associated with particular environmental stressors, and plasticity in phenotypic characteristics of a particular genotype. Physiological processes govern growth, development through life stages, movement, reproduction, and survival. Demographic processes address birth, death, and migration; the schedule and timing of life cycle events; and investments in reproduction. Species interactions involve data on interaction types, strengths, and spatiotemporal variation. The dispersal category includes colonizations and subsequent range shifts, but here we focus most on shifts in local habitat use. The environmental category refers to aspects of the environment that are measured to characterize climate and habitat variation.

We grouped *drivers* and *responses* into these process categories as shown in Appendix S1: Table S1. Using the assigned labels, we isolated the subset that included either *genetics* as a driver, or *genetics and adaptation* as a response. Both of these labels were associated with the *evolution* process, which was meant to include any paper that used evolutionary methods in their analysis (e.g., genetic assays, common garden or phylogenetically driven comparisons, estimates of selection). A few papers with this label used more general concepts of adaptation through nongenetic mechanisms. The papers quantified in this section can be found at https://connect.fisheries.noaa.gov/ClimateSalmonLiterature/, by selecting "Yes" in the Evolution selection box.

Because all of the six biological processes interact in biological systems, we looked specifically at the overlap between papers in the *evolution* category and those in other process categories. We also compared the relative frequency with which specific topics were addressed within the subset of evolutionary papers compared with the database as a whole. This step was designed to identify potential opportunities for additional integration of evolutionary processes into the larger study of climate impacts.

Literature quantification

The species and regions covered in our review are shown in Figure 2. Atlantic and Pacific salmon species were similarly represented. See Appendix S1: Table S2 for the numerical summary, and Appendix S1: Table S3 for the list of citations that were quantified. The species most frequently studied was steelhead/rainbow trout (23% of studies), followed by Chinook salmon and Atlantic salmon (19% and 15%, respectively). Also represented were sockeye salmon, coho salmon, and brown trout (6%–7% each), along with pink salmon, chum salmon, and cutthroat trout (3.5%–4.5% each). Rainbow trout/steelhead and Atlantic salmon were comparatively better represented within the evolutionary literature than within other processes, with a respective 23% and 15% of studies focusing on evolution, compared with their representations of 14% and 13% in the remainder of the database.

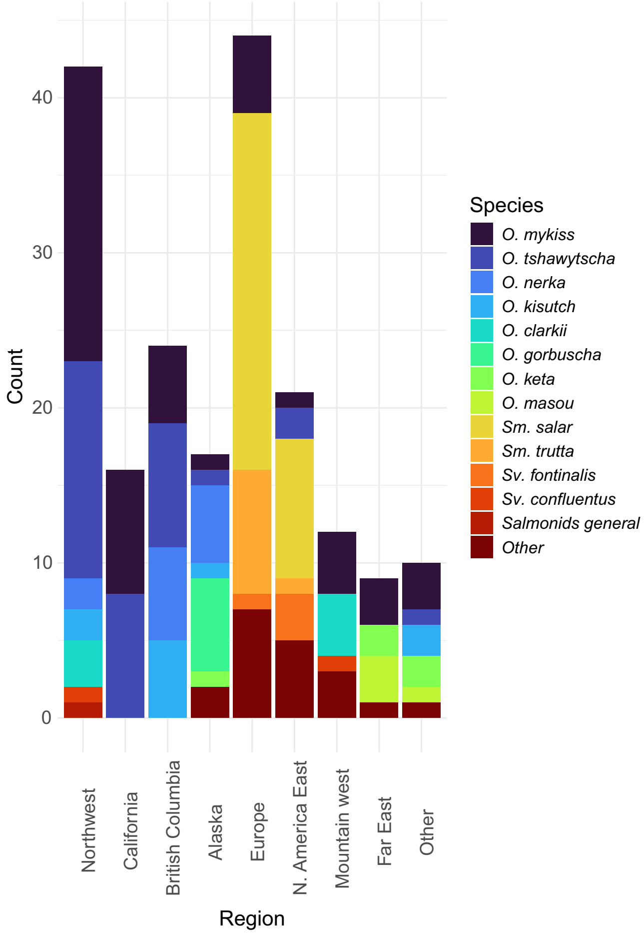

FIGURE 2 Count of papers within each geographical region (*x*-axis) and by species (colors). N. America East, eastern North America; O., *Oncorhynchus*; Sm., *Salmo*; Sv., *Salvelinus*. Far East includes Russia and Japan. See Appendix S1: Table S1 for region descriptions.

Rainbow trout and Atlantic salmon are intensively cultivated and therefore often studied within the context of artificial selection, epigenetic controls, and genetic engineering. These two species also have good reference genomes (Lien et al., 2016; Pearse et al., 2019), as does Chinook salmon (Christensen et al., 2018), which greatly facilitates genome mapping. One particular subspecies, landlocked redband trout (*O. mykiss gairdneri*), displayed especially extensive local climate adaptation, which facilitated mapping between genetic characteristics and environmental gradients (e.g., Chen et al., 2018; Chen & Narum, 2021; Garvin et al., 2015; Narum & Campbell, 2015).

Among these studies, the regions addressed most frequently were Europe (20%, 41 papers) and the Pacific Northwest (20%, 40 papers; Figure 2). Western Atlantic populations from Canada and the United States were reflected in about 11% (21) of the papers, while northeastern Pacific populations from California, British Columbia, and Alaska were each addressed in 8%–11% (16–21) of the papers. Pacific salmon and trout have been introduced or used in aquaculture in many other locations, and studies from these places can reveal how they respond and adapt to new environmental conditions (7 papers were from South America, Asia, or Australia/New Zealand).

The drivers that were most frequently studied were genetic characteristics (in 70% of evolutionary studies), not surprisingly, followed by temperature (in 40% of the evolutionary studies; Figure 3; Appendix S1: Table S2), then by habitat type (20%), with much less quantification of the role of flow or other environmental factors (each 8.5% or less). Similar attention was given to fisheries and hatcheries in driving responses (5%). Policy considerations or general conservation recommendations appeared in about 3% of papers, with a similar number attending to issues involving flow or dams. The species interactions process largely addressed pathogens, hybridization, and prey availability, and these topics were covered in 22 papers (11%).

Among response metrics, genetic characteristics again dominated (72%), followed by physiological (19%) and phenological traits (18%; Figure 3). Many traits had similar levels of representation, including the set related to performance, life history, habitat use/distribution, growth, population resilience, and mortality (10%–11%). Immune responses had a higher rank order in evolutionary studies than nonevolutionary studies, but they still represented only about 3% of studies.

Comparing evolutionary papers to the database overall, genetics, phenology, and life history were more frequently studied as responses in an evolutionary context, whereas migration behavior and habitat use, as well as productivity and mortality, were less frequently studied (Figure 4).

DOMINANT THEMES AND MAJOR AREAS OF RESEARCH

To communicate focal areas of study and results from this body of work, we describe first the aspects of genetic variability and epigenetic processes that were most frequently examined. These included descriptions of neutral and adaptive genetic variation, studies on relationships between genotypes and climate-sensitive phenotypes, and some of the controls on the transcription of these genes, particularly levels of DNA methylation. The spatial patterns of genetic variability are relevant for understanding historical adaptation to environmental conditions, as well as for providing a baseline of genetic diversity for future evolution.

The next set of topics studied more frequently within an evolutionary context than the literature at large

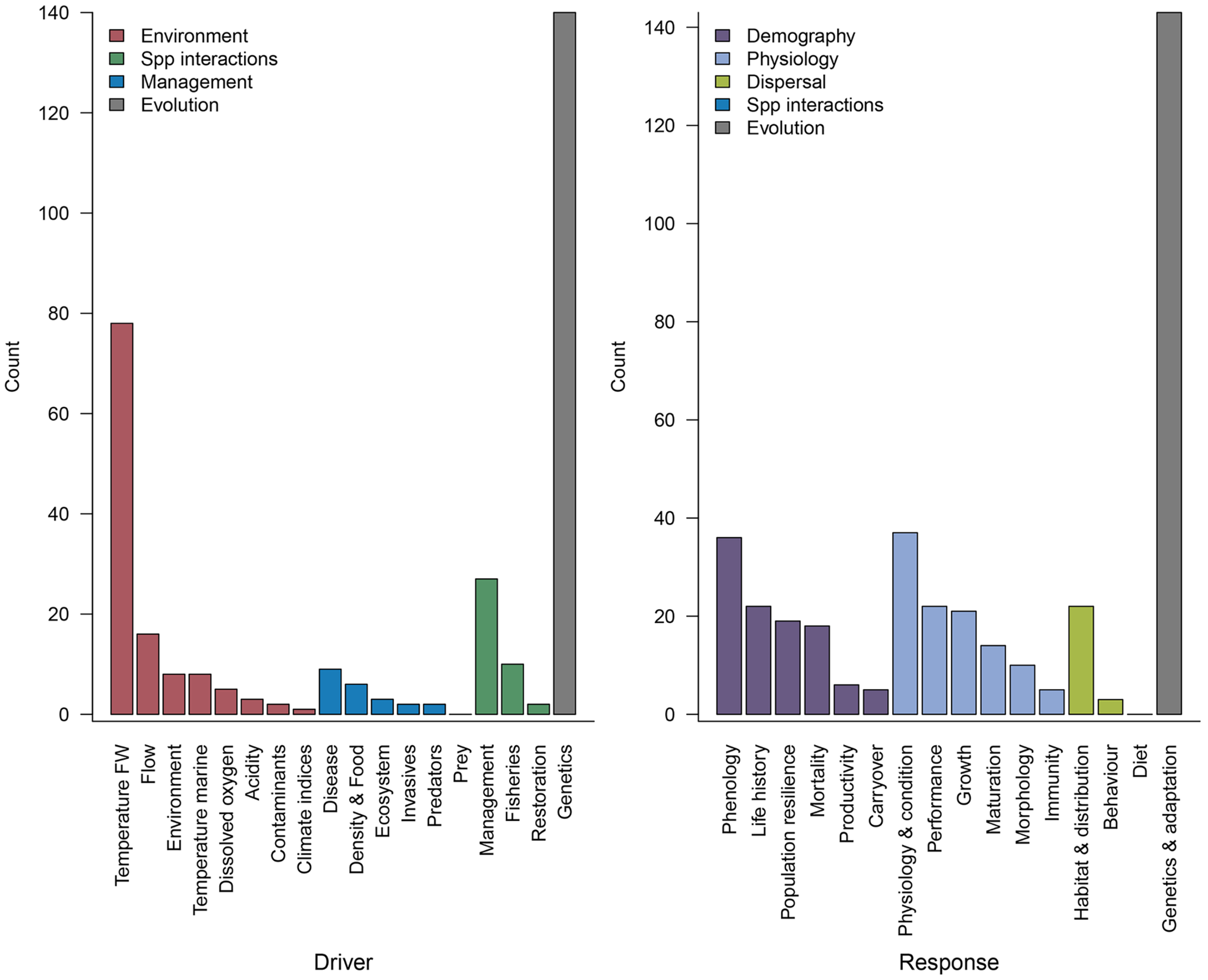

FIGURE 3 Counts of papers within each *process driver* and *process response*, showing the counts of individual drivers and responses, colored by process. See Appendix S1: Table S1 for a definition of all categories. FW, freshwater.

addressed shifts in phenology and life history over time (Figure 4). The primary driver for many of these recent changes was anthropogenic, so we also review the literature discussing human activities that impose selection on salmon and trout and that have implications for their resilience to climate change. Finally, we describe the quantitative projections of evolutionary change in our database that explore future climate scenarios and identify some important gaps in this type of study.

Genetic and epigenetic variation related to climate

Major areas of study or themes within the reviewed body of literature included (1) the structure of existing genetic variation and gradients in diversity assessed by neutral genetic markers, (2) adaptive genetic variation related to climate, (3) experimental studies and artificial selection on climate-sensitive traits, and (4) epigenetic processes.

Spatial patterns in neutral genetic variation

Genetic diversity consists of the total genetic variation within a population or species and is generally correlated with the ability to respond adaptively to any change, including climate change. Genetic variation is considered *neutral* if it does not directly affect fitness, or the likelihood of passing genes to the next generation; and *adaptive* if it produces an advantage for survival or reproduction. Importantly, variation that is neutral in one context might be adaptive in another, so these assignments can change over space or time.

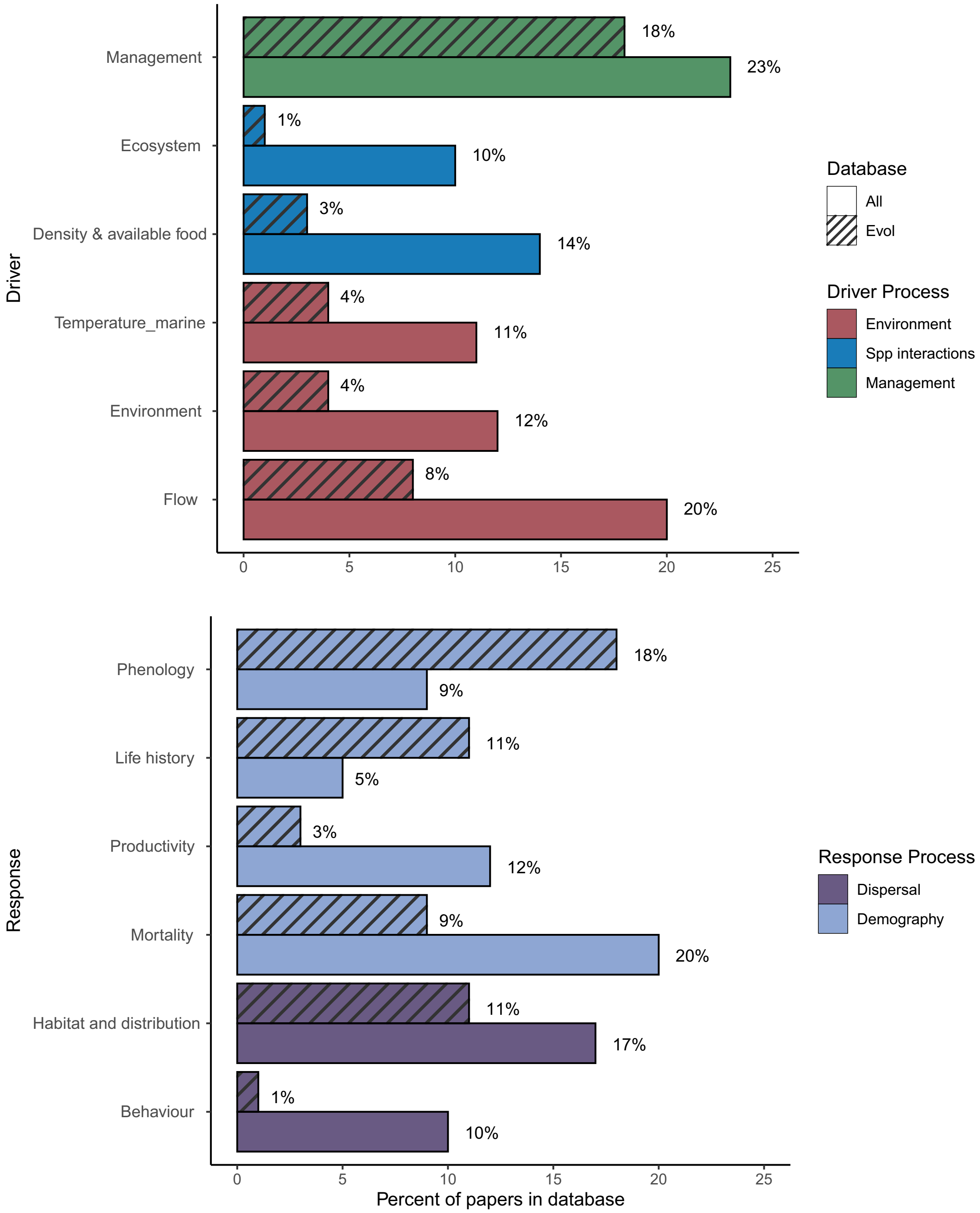

FIGURE 4 Select drivers and responses that differed in their relative representation within the overall database (All) compared with their relative representation within the evolutionary subset of papers (Evol). Factors shown differed by at least 5%, whereas other factors appeared in more similar proportions in the two datasets. Genetics as driver and Genetics and Adaptation as response are not shown because they were used to define the evolutionary subset.

Furthermore, it is impossible to know in advance whether some particular gene might be adaptive in the future. Therefore, any patterns in purportedly neutral genetic diversity are potentially relevant to climate vulnerability (e.g., Abadia-Cardoso et al., 2016; Scribner et al., 2017; Valiente et al., 2010). Rather than attempt an exhaustive summary of the enormous literature in this field, our search isolated studies that directly associated their results with climate. This focus revealed spatial and temporal patterns in both neutral and purportedly adaptive genetic variation.

Spatial gradients in genetic diversity can be correlated with the severity of exposure from climate change, suggesting that knowledge of these gradients could be useful in conservation prioritization. In North America, a set of studies examining the full geographic range of coho salmon (Rondeau et al., 2023; Rougemont et al., 2020, 2022) found that genetic heterozygosity is higher in southern than in northern populations (e.g., California vs. Alaska). This general pattern was attributed to the locations of glacial refugia during the last ice age and the process of range expansion after glacial retreat ~11,000 years ago, in which small founder populations were responsible for recolonization of northern sites. The rate of climate change is much faster at higher than at lower latitudes, exposing less diverse populations to a higher rate of change.

In contrast to these studies in North America, Horreo et al. (2019) found that genetic diversity of Atlantic salmon in Europe was consistently lower at lower latitudes. They proposed that this pattern resulted from a negative correlation between genetic diversity and sea surface temperature. The cline in diversity was not correlated with anthropogenic habitat disturbance in southern populations. Regardless of the mechanism that originally created the spatial patterns, a reduction in genetic diversity may heighten future risk in a rapidly changing environment by limiting the potential for further adaptation and increasing the risk of inbreeding depression and loss of fitness. Therefore, protection of existing areas of higher diversity is an important component of a climate-resilient conservation strategy.

At the much smaller spatial scale of watersheds within the Columbia Basin, Kovach et al. (2015) studied bull trout (*Salvelinus confluentus*) populations in locations predicted to experience relatively stronger changes in temperature and flow due to climate change. They found that these trout had lower allelic richness and genetic heterogeneity than other populations. The less diverse populations were more exposed to climate change due to anthropogenic reductions in habitat complexity, as well as being at lower elevations, both of which led to warmer temperatures and higher risk of flooding. Since vulnerability is often defined as the combination of exposure and adaptive capacity, these populations were more vulnerable in both dimensions.

Overlaid on the glacial impacts to population structure, we can see signals of pressure from modern human development. Recent declines in southern coho populations have reduced the number of rare alleles to frequencies below all other populations examined, indicating ongoing depletion of their genetic diversity (Rougemont et al., 2020). Frequency of rare alleles is a different metric of genetic diversity than heterozygosity, and may be more sensitive to population bottlenecks. Whether lost rare alleles will be important for climate adaptation is unknown. However, in many southern populations, physiological tolerances are approaching critical limits, and rare alleles could harbor important adaptive variation (e.g., Abadia-Cardoso et al., 2016).

Spatial patterns in adaptive genetic variation in climate-sensitive traits

Although markers of neutral genetic diversity may be positively correlated with beneficial genetic variation in future climates, we can assert the utility of genetic variation more directly when it is shown to be adaptively related to climate. The subdiscipline of landscape or riverscape genomics correlates genetic structure with environmental variables, often to identify candidate loci that may be responsible for local adaptation to climate (e.g., Alshwairikh et al., 2021; Hand et al., 2016; Hecht et al., 2015; Matala et al., 2014; Vincent et al., 2013).

Many of the papers used landscape genomics to infer that freshwater climate indices, usually precipitation and temperature, as well as migration distance, can be strongly associated with genomic variation. Marine conditions have not yet been examined extensively. However, Dallaire et al. (2021) found genetic patterns in Arctic char that were more consistent with local sea surface temperatures than with terrestrial conditions. These patterns are thought to represent adaptive genomic divergence rather than drift, and landscape genomics studies can help in identifying the genetic basis of traits that respond to climatic drivers (Alshwairikh et al., 2021; Dallaire et al., 2021; De Mita et al., 2013; Hecht et al., 2015; Horreo et al., 2019; Narum et al., 2018).

Other important spatial trends in purportedly adaptive genetic variation appear to reflect climate-related selection for disease resistance. The proximate reason that many salmon die under warm, low-flow conditions is often related to disease (Belchik et al., 2004; Borgwardt et al., 2020; Morley & Lewis, 2014; Ouellet et al., 2010). In both Atlantic and Pacific salmon, latitudinal clines in variability have been observed at genes of the major histocompatibility complex (MHC) (Dionne et al., 2007; Limborg et al., 2012). These clines are thought to reflect diversifying selection pressure from pathogens, which is stronger in warmer environments. Smaller scale temporal patterns in allele frequency are also consistent with selection for disease resistance (Dionne et al., 2009).

Positive correlations between pathogen burdens and water temperature have been documented (Dionne et al., 2009). Additional work with sockeye salmon has revealed that MHC differentiation was tied to spawning habitat (e.g., stream vs. beach), and thus reflected strong selection that varied at fine spatial scales (Larson et al., 2014) and by life stage (de Eyto et al., 2011).

Resistance to specific pathogens, such as the myxozoan parasite *Ceratonova shasta* (formerly *Ceratomyxa*), varies greatly across populations coincident with exposure (Bjork et al., 2014), also indicating strong selection on the immune system.

However, to detect ongoing evolution in these traits is difficult because it requires active screening over multiple generations. Immunological and genetic material degrades quickly under ambient conditions, so tissues collected for other reasons generally cannot be used to assess disease resistance. Thus, we have little information on the strength of selection and current rates of evolution in response to increasing pressures from pathogens range-wide, which may explain the dearth of future projections in this area.

Experimental work on genotype-to-phenotype relationships

More direct measurements of evolutionary potential in response to climate change come from laboratory and breeding experiments that studied local adaptation to climate-sensitive traits, such as temperature-dependent aerobic scope (Verhille et al., 2016), developmental rates (Meier et al., 2014; Whitney et al., 2014), disease resistance (Wellband & Heath, 2013), and spawn timing (O'Malley et al., 2010).

Studies of local adaptation in traits such as heat tolerance have been extensive in landlocked populations, such as redband trout (Chen & Narum, 2021; Crichigno et al., 2018; Garvin et al., 2015; Narum et al., 2013; Narum & Campbell, 2015; Verhille et al., 2016) and Lahontan cutthroat trout (*O. mykiss henshawi*) (Amish et al., 2019). Examples from anadromous populations focused mostly on sockeye salmon in the Fraser River. In these populations, local adaptation has been reported in optimal temperatures for embryonic survival (Whitney et al., 2013) and for cardiac performance during adult migration (Eliason et al., 2017; Eliason & Farrell, 2016). More broadly, biomarkers in sockeye and Chinook salmon have been developed to detect stress from high temperature (Akbarzadeh et al., 2018; Anttila et al., 2014) and hypoxia (Akbarzadeh et al., 2020), and these could be used to track increasing selection pressure from climate change.

Artificial selection for enhanced heat tolerance has been successful for laboratory strains of rainbow trout (Crichigno & Cussac, 2019; Ojima et al., 2012; Tan et al., 2012), but anadromous populations may not respond to chronic temperature stress in freshwater through physiological adaptation because of opposing demands in the ocean. Observations indicate that migratory salmon and trout typically respond to different freshwater temperatures through behavioral rather than physiological traits (Crozier et al., 2011; Hodgson & Quinn, 2002; Muñoz et al., 2015; Reed et al., 2011).

Epigenetic processes and other carryover effects

Many traits that carry over from one generation to the next are not encoded in DNA sequences, although careful experimentation is needed to separate genetic from epigenetic processes. A set of studies using typical genetic methods elucidated epigenetic mechanisms that play a substantial role in responses to climate. Nongenetic carryover effects from spawner to egg typically have large impacts compared with the influence of additive and nonadditive genetic variation (Evans et al., 2010; Janhunen et al., 2010; Venney et al., 2020). Adult stressors, such as exposure to fishing gear and adverse environmental conditions during migration, can lead to reduced aerobic scope and other indices of performance in offspring (Banet et al., 2019). Effects of conditions experienced by eggs during incubation can also carry over to subsequent life stages. For example, eggs can accumulate organic pollutants to toxic levels that may reduce growth and survival in later life stages (Daley et al., 2012). Incubation temperatures, in particular, have profound effects on later life stages, resulting in either increased or reduced fitness, depending on the temperature range studied (Burgerhout et al., 2017; Hurst et al., 2012; Jonsson et al., 2014; Jonsson & Jonsson, 2019).

Various mechanisms have been proposed for these carryover effects, especially hormone-mediated and energetic processes, but effort is increasingly focused on the role of DNA methylation and other epigenetic mechanisms in plastic responses (Eirin-Lopez & Putnam, 2019; Gavery & Roberts, 2017; Le Luyer et al., 2017; Venney et al., 2020). Epigenetic processes influence which genes are turned on and off. For example, the addition of a methyl group to one of the four bases within the genome, or to nucleosomes (around which DNA is wrapped), can turn off a gene. Toxicants can also influence epigenetic dynamics (Bollati & Baccarelli, 2010), as can climatic conditions. Incubation temperatures, for example, were related by epigenetic mechanisms to such diverse traits as future adult egg and gonad size, growth rate, age at maturation, and adult migration timing in Atlantic salmon (Jonsson et al., 2014; Jonsson & Jonsson, 2019).

In their review, Jonsson and Jonsson (2019) summarized evidence that increased DNA methylation is associated with reduced gene activity and also with lower temperatures. Although stressful temperatures typically reduce fitness, epigenetic processes appear to be adaptive in direction across a broad range of temperatures, an outcome usually called acclimatization.

Fitness is presumably increased in warmer environments through a variety of processes (Eirin-Lopez & Putnam, 2019), including epigenetically enhanced growth rates in Atlantic salmon (Burgerhout et al., 2017), induced maturation in Atlantic salmon parr (Morán & Pérez-Figueroa, 2011), and differentiation of anadromous and resident life history types in steelhead/rainbow trout (Baerwald et al., 2016). Although the consequences are not totally clear, DNA methylation patterns were shown to differ between hatchery-reared and wild steelhead trout (Gavery et al., 2019). Direct manipulation of "epigenetic memory" through environmental conditions is being used in aquaculture to produce desired phenotypes and avoid undesired traits (Gavery & Roberts, 2017; Liu et al., 2022).

Temporal trends in phenotypic variation

Many phenotypic traits that strongly affect individual fitness and population viability are determined by an interaction between genetic and nongenetic processes. To determine the exact role of evolutionary processes can be challenging, but will be helped by tracking major phenotypic trends.

Run and spawn timing

Shifts in run and spawn timing have occurred in response to both natural and anthropogenic selection (see Crozier & Hutchings, 2014 for a review). Kovach et al. (2012) documented rapid evolution in response to a change in environmental conditions in pink salmon from Alaska, for which 32 years of genetic data were available (17 generations). Specifically, the frequency of a genetic marker for late migration timing declined with a 2-week advance in adult migration timing, whereas there was essentially no change at other neutral loci. The proximate driver of selection appeared to be lower survival of late migrating fry in the ocean stage, rather than direct selection during the adult stage (Manhard et al., 2017, 2018).

The availability of a long series of genetic data for demonstrating an evolutionary response, as in the above example, is very rare. In most cases, inferences must be drawn between evidence of climatically driven selection and a phenotypic response (e.g., Crozier et al., 2011). Hatcheries have also driven selection through preferential collection of fish for broodstock from the early portion of a run. This can select for earlier run and spawn timing, which may be maladaptive for natural populations (Quinn et al., 2002; Tillotson et al., 2019; Vainikka et al., 2010). In other cases, human alteration to natural flow regimes has driven selection on run timing (Sturrock et al., 2020; Sullivan & Hileman, 2019; Thompson et al., 2019; Waples et al., 2017).

Smolt migration timing has strong plastic (e.g., Teichert et al., 2020) and genetic controls (Spence & Dick, 2014; e.g., Carlson & Seamons, 2008). At least one study demonstrated rapid genetic adaptation in response to selection on smolt migration timing (Manhard et al., 2017). This phenological trait is linked to physiological attributes involved in the cue to initiate the parr–smolt transformation, such as threshold body size and condition level, where lower thresholds suffice in streams with lower growth rates (Debes et al., 2020).

Lower growth rates can stem from either reduced food supply or cooler temperatures (e.g., Chittaro et al., 2014; Jenkins & Keeley, 2010). It is difficult to fully quantify food availability, but differences in thermal performance curves have been associated with differences in threshold smolt body sizes (Debes et al., 2021). Many genes and physiological traits are involved in thermal tolerance, and some of these traits, such as cardiac arrhythmic temperature, have much less variation than others and may constrain overall rates of evolution (Muñoz et al., 2015).

Many phenological traits are highly adapted to local climate and typically have high heritability (Carlson & Seamons, 2008; Hess & Narum, 2011; O'Malley et al., 2010, 2013; Thompson et al., 2020). However, their genetic architecture varies from traits that are highly polygenic to complex phenotypes that respond strongly to a single gene (sometimes called *genes of large effect*). For example, the clock genes, *OtsClock1a* and *OtsClock1b*, were highly influential in spawn timing (O'Malley et al., 2010), whereas multiple loci are likely to control other physiological traits such as musculature, immunological traits (Hess & Narum, 2011; O'Malley et al., 2013), and factors regulating growth (Debes et al., 2020, 2021).

Early-run populations tend to be among the most vulnerable in terms of both historical threats (Gustafson et al., 2007) and vulnerability to climate change (Crozier et al., 2019). Spring-run Chinook salmon and summer-run steelhead life histories often involve long-distance adult migrations to habitat that is at high elevation, where prolonged snow seasons and cool groundwater historically maintained cold-water habitat. These locations may be accessible only during certain times of the year. Adults fast and hold in deep, cool pools until they spawn in fall (Chinook) or spring (steelhead). This life history type is particularly impacted by migration blockage (dams) due to the high elevation locations of their spawning sites. In addition, these populations are exposed to widespread anthropogenic alterations in habitat, temperatures and flows, as well as fishing pressure, during their long summer holding period.

In contrast, fall-run Chinook and winter-run steelhead spend less time in freshwater and spawn at lower elevations in larger rivers, where they are less vulnerable to some of these pressures. Consequently, a much higher percentage of spring-run Chinook and summer-run steelhead conservation units are threatened or endangered than fall-run Chinook or winter-run steelhead.

In spring-run Chinook and summer-run steelhead, early adult migration timing has apparently evolved only once in each species, and this trait was then shared across all populations that display the early migration phenotype (Hess et al., 2016; Micheletti et al., 2018; Narum et al., 2018; Prince et al., 2017). If these specific alleles are lost, the entire life history type may disappear, even if suitable habitat eventually is made available (Thompson et al., 2019).

Age and size at maturity

In recent decades, strong trends toward younger ages at maturity and smaller sizes of older fish have been reported in Pacific salmon and steelhead (Freshwater et al., 2022; Losee et al., 2019; Ohlberger et al., 2018; Oke et al., 2020). Age at maturation in Atlantic salmon and trout has changed as well, but with conflicting trends between sexes (Czorlich et al., 2018) and by stock origin (Turrero et al., 2012; Erkinaro et al., 2019 vs. Besnier et al., 2024). In many studies, proportions of both older age classes and size at age tend to be lower, despite contrasting patterns in freshwater residence. For example, some Alaskan sockeye now spend fewer years in freshwater (Cline et al., 2019), whereas Finnish Atlantic salmon often spend more (Erkinaro et al., 2019).

There is a strong correlation between body size and fecundity, particularly for females, so age at maturation reflects a trade-off between additional growth and the risk of mortality during that extra year in the ocean. The declines in fecundity expected with trends in body size (on the order of 16%) have now been validated in Pacific Northwest Chinook salmon (Malick et al., 2023). If survival to maturity had also increased, then declines in fecundity might not pose a risk for population viability. However, total marine survival has also declined in many wild and hatchery Chinook and steelhead populations all along the West Coast (Ford, 2022; Welch et al., 2020), and for wild Chinook and steelhead in Puget Sound (Losee et al., 2019).

Younger age at maturation can reflect (1) an increase in the propensity to mature at a younger age due to a plastic response to improved freshwater and ocean growth conditions, (2) an increase in the propensity to mature at a younger age due to an evolutionary response to increased mortality of older fish, or (3) no change in the propensity to mature at a younger age, but higher realized return rates in younger fish because of higher mortality in older age classes. There is evidence supporting all of these processes, and different populations may be responding to distinct combinations of pressures.

Higher feeding rates in hatcheries are well established as plastic drivers of younger age at return (e.g., Chen et al., 2023; Gallinat et al., 2023; Harstad et al., 2023; McPhee et al., 2024). If growth in the ocean is also higher in a warmer environment, then climate effects could also drive earlier maturation. There is evidence for higher growth rates in recent years for some Pacific salmon populations (Siegel et al., 2017). However, poorer ocean growth rates are more often cited, particularly in Atlantic salmon, where they have been attributed to reduced prey availability and later maturation ages (e.g., Czorlich et al., 2022).

Warmer temperatures affect growth rate through both a change in prey communities and increased bioenergetic costs. Prey communities exhibit their own spatial and demographic responses to environmental change, but they also may be reduced by increased predator consumption (e.g., by hatchery fish), as argued by Cline et al. (2019), or overfishing (e.g., Czorlich et al., 2022; Hjermann et al., 2004). Hatchery fish now constitute at least 40% of the salmon biomass in the North Pacific (Ruggerone & Irvine, 2018) and much higher percentages in the California Current, where competitive interactions could decrease fitness in wild fish (Connors et al., 2020; McMillan et al., 2023; Ohlberger et al., 2022).

Selection results from a shift in the balance between the benefit of increased fecundity from spawning at a larger size and the mortality risk of remaining in the ocean longer. The discovery in Atlantic salmon of a particular allele with a large effect on maturation age, which is closely related to fitness, has greatly enhanced the ability to detect genetic change as a driver of this trait (Åsheim et al., 2023; Czorlich et al., 2018). Although the explanatory power of two genes (vgll3 and six6) has declined over time, they demonstrate the power of genotype-environment interactions for maturation timing (Besnier et al., 2024; Raunsgard et al., 2024).

The risk of mortality is expected to be higher in an ocean that is more acidic, less oxygenated, and warmer, all conditions expected to result from anthropogenic climate change (Waples & Audzijonyte, 2016). Other changes in the ocean community also affect mortality rates (Kendall et al., 2020; Manishin et al., 2021). Numbers of marine mammals have increased dramatically since their protection in the 1970s (Chasco et al., 2017; Ohlberger et al., 2018), likely increasing predation on salmon (Wargo Rub et al., 2019). Most of those species do not specialize on salmon (Adams et al., 2016; Szoboszlai et al., 2015), except in some cases during juvenile (Moore & Berejikian, 2022) or adult migration (Sorel et al., 2021). Nevertheless, resident (as opposed to offshore and transient) killer whales (*Orcinus orca*) preferentially prey on larger Chinook salmon (Hanson et al., 2021), a tendency that directly imposes selection for earlier maturation (Ohlberger et al., 2019). Marine mammals do not appear to be a major driver of recent declines in Atlantic salmon populations (Almodovar et al., 2019; Dadswell et al., 2022; Mills et al., 2013; Olmos et al., 2020).

Ocean fisheries increase selective pressure toward earlier maturation by increasing the mortality risk of longer ocean residency (Audzijonyte et al., 2013). Harvesting techniques that selectively capture larger fish in terminal fisheries also drive evolution toward smaller adults. In cases where early growth rates are slower and mortality rates are relatively low, the adaptive response would be to remain in the ocean another year to reach a threshold size for reproduction. However, model results show that size-selective harvest undermines this adaptive response, threatening the persistence of populations adapting to climate change (Ayllón et al., 2021).

Smaller, younger adults are expected as the third of "three universal responses to climate warming," a widespread ecological theory with the first response being poleward range shifts and the second, changes in phenology (Daufresne et al., 2009). A variety of mechanisms may underlie this macroecological observation, but for aquatic species, the primary explanation relates to metabolic responses to temperature from early life stages onward.

At the bottom of the food web, organisms with smaller body sizes or lower lipid stores provide less ecotrophic efficiency in warmer environments, which can result in reduced body size of predators up the trophic ladder (Daufresne et al., 2009). Studies investigating body-size change in the context of climate warming have most often attributed this response to a change in food availability or quality (Gardner et al., 2011, tab. 1). However, alternative explanations have been advanced based either on experimental studies, where earlier maturation can occur without a change in metabolic rate (Wootton et al., 2022), or on bioenergetic models, where trade-offs exist between energy allocation and growth, reproduction, and reserves (Audzijonyte et al., 2022). A variety of nonclimatic drivers are likely to be involved in a given situation; however, a "faster life history" has been observed in warmer conditions in 332 Indo-Pacific fishes (Wang et al., 2020); Atlantic Bluefin tuna (Andrews et al., 2023); Indian shad (Ahammad et al., 2021); four Lake Erie fishes (Gíslason et al., 2021); European hake in the Mediterranean (Legaki et al., 2024); and in controlled environments or experiments with Eurasian perch (Niu et al., 2023), bluegill sunfish (White et al., 2020), and zebrafish (Wootton et al., 2022). Thus, it appears likely that climatic drivers are contributing to these recent widespread trends.

Human influences on (mal)adaptation

Fisheries and other human actions were considered drivers of evolutionary processes in 18% of the studies (Figure 3; Appendix S1: Table S2). The most common actors were fisheries, hatcheries, and habitat effects, including dams. In some cases, the direction of anthropogenic selection was the same as that of climate selection, whereas in others they push in opposite directions. We consider human influences to be maladaptive in a changing climate when they push a trait in the opposite direction from the way in which the optimum phenotype is shifting due to climate change. They may also be maladaptive in the sense of reducing adaptive capacity if they reduce the ability of the population to respond to natural selection from climate change (see Crespi, 2000 for additional definitions). More specifically, even when the direction of anthropogenic trait change is adaptive, it often reduces future adaptability (Derry et al., 2019) by depleting genetic variation, reducing the total effective population size, and reducing stability from phenotypic variability (e.g., overlapping age classes) (Munsch et al., 2022; Waples & Audzijonyte, 2016). These pressures therefore produce smaller, less diverse, and less stable populations over the long term. The term (mal) adaptation (sensu Derry et al., 2019) accounts for the full range of potential impacts on fitness, from positive to negative.

Fisheries-induced evolution

Selection by fisheries may be in the same or opposite direction from the optimal phenotype in a warming environment. Fisheries-induced evolution has been documented extensively (Allendorf & Hard, 2009; Hard et al., 2008) and provides insight into potential rates of rapid adaptation to climate change (e.g., Audzijonyte et al., 2013). Fisheries generally remove larger individuals and thus select for smaller, more rapidly maturing populations. A warmer environment also tends to favor these traits through both plastic and genetic mechanisms (Waples & Audzijonyte, 2016), and disentangling the causes of these phenotypic changes can be challenging (Morita & Fukuwaka, 2007; Siegel et al., 2018; Tillotson et al., 2021). In the case of early maturation, effects from human activities and natural pressures may be similar in direction.

However, when growth rates decline in a warmer environment, a longer ocean-rearing period is needed to reach body sizes associated with sufficiently high fecundity to maintain populations at their replacement rate. Therefore, fishing pressure toward earlier maturation directly increases extinction risk (Ayllón et al., 2021; Piou & Prevost, 2013). Ayllón et al. (2021) modeled size-selective harvest and fisheries-induced phenotypic changes exacerbated by climate impacts; they found a direct threat to simulated populations of brown trout in Spain. Piou et al. (2015) found similar results in a population model of Atlantic salmon in France. In addition, like other anthropogenic impacts, fishery-induced evolution also reduces natural resilience to climate change through demographic processes and by limiting general adaptive potential.

Hatchery-induced evolution

Hatchery and stocking practices have often introduced nonlocal genotypes into a watershed (Almodovar et al., 2020; Ostergren et al., 2021). Such introductions are likely to undermine local adaptation to climate and other site-specific conditions unless broodstock is collected from carefully matched habitats. Even when local broodstock is used, selection for traits that are beneficial in hatcheries or to humans, combined with relaxation from natural selection and unintentional effects of relatively small breeding populations, can lead to many potential genetic impacts on wild fish (Naish et al., 2007; Tave & Hutson, 2019).

Domestication selection alters developmental traits, often favoring rapid growth and maturation, as well as behavioral traits that increase vulnerability to predation (Debes & Hutchings, 2014), immunological traits (López et al., 2019), and morphological traits such as eye size (Perry et al., 2021). Many of these effects contribute to a general reduction in fitness in the wild (e.g., Baskett & Waples, 2013; Christie et al., 2014).

Preferential breeding of fish with particular phenotypes is likely in hatchery programs unless extensive protocols are in place to avoid these outcomes. The number of hatchery fish spawned is far lower than the number that return. Thus, for hatchery populations, the number of fish that effectively transmit their genes to the next generation is typically lower by an order of magnitude or more compared with naturally spawning populations (Christie et al., 2012). Consequently, hatchery programs can impose strong selection. An efficient method of collecting broodstock is to focus on a particular part of the larger run, which can then impose selection on migration and spawn timing, sometimes in directions that are contrary to what would be optimal for spawning in the wild (Morita, 2019; Tillotson & Quinn, 2018).

For example, Austin et al. (2021) described a wild population of Chinook salmon in the Pacific Northwest that has been spawning up to one-half day later per year over 2–6 decades. At the same time, a nearby spawning group influenced by hatchery strays had shifted its spawn timing in the opposite direction. These fish are now spawning earlier, coincident with trends in egg collection time at the hatchery. This pressure from hatchery practices exposes fish in the river to increasingly stressful summer temperatures, inhibiting their natural ability to adapt to climate change.

Another strong selective force with an anthropogenic signature is the overall prevalence, specific types, and virulence of diseases. There are a wide variety of mechanisms by which hatchery operations can increase the incidence and severity of infectious disease, including (1) the introduction of exotic pathogens, (2) amplification of endemic pathogens, (3) genetic effects on disease resistance of wild stocks, and (4) introduction of pollutants or stressors that alter disease ecology (Naish & Hard, 2008).

The introduction of exotic pathogens is the easiest mechanism to attribute to human translocations of fish or fish food. For example, whirling disease, caused by the parasite *Myxobolus cereralis* that was introduced from Europe in the 1950s, caused extreme declines in wild rainbow trout in the western United States (Hedrick et al., 1998). Similarly, the trematode parasite *Gyrodactylus salaris* was transported via aquaculture operations to Norway, where it has severely reduced wild Atlantic salmon populations (Johnsen & Jensen, 1986). Nonetheless, most diseases that are regularly documented in hatchery fish stem from endemic pathogens (Naish et al., 2007). In addition to spreading pathogens such as sea lice and *C. shasta* (Robinson et al., 2020), artificial propagation programs can select for pathogens more fatal to fish. At fish farms, Pulkkinen et al. (2010) found active selection for more virulent strains of *Flavobacterium columnare*, a disease exacerbated by warmer temperatures (Wakabayashi, 1991).

Genetic effects on disease resistance are not well monitored, and could act either through introducing different strains of a pathogen or by flooding natural populations with disease-susceptible fish, undermining natural resistance in the spawning population. Trade-offs have been documented between increased resistance to one disease associated with loss of resistance to another (Naish et al., 2007), so selection for diseases that proliferate in hatcheries could reduce natural resilience to other diseases in the wild.

Population responses to dams and water management

Another anthropogenic influence that has dramatically changed the evolutionary status of anadromous fish populations in particular is the construction of dams and water withdrawals that alter natural flows and migration pathways (Waples, Zabel, et al., 2008). Complete blockage of migration to historical spawning sites has not only extirpated many populations (Gustafson et al., 2007), it has also obscured the realization of anadromous life history in populations that remained landlocked (Fraik et al., 2021; Pearse & Campbell, 2018). When dams blocking migration have been removed, dormant life history types have reemerged (Quinn et al., 2017).

More subtle changes to migration timing have also occurred. For example, mismatches between water releases and historical salmon migration times have selected against natural fry migration times in the San Joaquin River in California (Sturrock et al., 2020). The construction of reservoirs and retention of cold water has favored a yearling smolt life history in Snake River Fall Chinook, which may or may not have existed historically. This change in behavior could have been caused by both slower growth rates due to lower temperatures and reduced survival of subyearling smolts through the hydrosystem (Waples et al., 2017; Williams et al., 2008). Resulting changes in juvenile migration timing can create mismatches between arrival in marine environments and prey availability.

In a third example, managed flows in the Trinity River in California have led to shifts in run timing and greater overlap between spring- and fall-run Chinook migrations, as both adjust to pulse flows in early spring (Sullivan & Hileman, 2019). Greater temporal overlap can lead to genetic mixing of populations that were historically separate, but more likely will lead to the loss of historical variation in migration timing. Similarly, changes in flow management as well as warming temperatures have driven changes in sockeye run timing in the Columbia River (Crozier et al., 2011). Although all of these responses are likely to have substantial plastic elements, there are indications of evolutionary responses at play (Crozier et al., 2011; Williams et al., 2008).

Projected evolutionary response to climate change

Studies that presented future climate projections and salmon or trout responses constituted a small proportion of papers in our database, especially within the subcategory of evolutionary process (only 2.5%). Nonetheless, climate-induced population extirpations or contractions could result in the loss of much genetic variation. Human-imposed maladaptation may escalate these losses, further reduce the likelihood of persistence, and misrepresent population vulnerability. These consequences were demonstrated in three case studies showing the role that evolutionary processes can play in future projections of population processes.

Processes modeled in these three projections were constraints on evolution in heat tolerance of cardiac traits, shifts in run timing, and changes in growth and age at maturation. While only a few populations were modeled, widely observed trends have been consistent with these projections. These trends include shifts in phenology (Madsen et al., 2020), declines in effective population size (Lehnert et al., 2019), declines in body size, and changes in age at migration/maturation, with earlier versus later predictions for Pacific versus Atlantic populations, respectively (Ohlberger et al., 2018; Oke et al., 2020; Olmos et al., 2019).

In our first example, Muñoz et al. (2015) predicted that in juvenile salmon, many aspects of thermal performance associated with cardiac function could evolve quickly in response to a 4°C temperature increase. However, they also found that a lack of plasticity or genetic variation in arrhythmic temperature, another cardiac trait, would limit successful adaptation in this scenario. Their study demonstrated that physiological traits are highly variable in their potential to evolve with climate change, and illustrates the risk in assuming that selection on a single trait can be isolated from constraints in other traits. In this case, a faster evolutionary response would have been assumed if arrhythmic temperature had not been included in the study design.

In our second example, Reed et al. (2011) modeled population dynamic responses to warming river temperatures. They found that the risk of extinction for Fraser River sockeye was greatly reduced when run timing was allowed to evolve (Reed et al., 2011). Under reasonable assumptions of heritability and plasticity, the adult migration advanced by about 10 days with 2°C of warming. The frequency at which simulated populations declined to the quasi-extinction threshold was 83% less likely in scenarios where migration timing evolved than in those that did not include evolution in the model. This model directly addressed plasticity, a factor that can make modeling salmon responses more complex.

Reed et al. (2010) also revealed trade-offs between plasticity and natural selection, which resulted in different population trajectories, depending on the reliability of the environmental cue that triggered the plasticity.

They showed that as cues become less reliable, the responses exhibited by fish may become less adaptive. Some individual climate indices are projected to become more variable in climate models (van der Wiel & Bintanja, 2021). Not only that, but correlations among climate variables are widely expected to change (Black et al., 2018; Litzow et al., 2020; Smith et al., 2022), generating increasingly novel environmental conditions.

Novel conditions are already occurring, as demonstrated by the unprecedented warm waters seen during the North Pacific marine heatwave of 2014 to 2016 (Jacox et al., 2016), and by repeated warming events that have occurred since (Thompson et al., 2022). These events are expected to occur in the future with increasing frequency (Frölicher et al., 2018) and with co-occurring terrestrial droughts in "compound extremes" (Shi et al., 2021). In projections for the 2060s to the 2090s under high carbon scenarios, novel conditions will exist 50% to 100% of the California Current in an average year (Smith et al., 2022). Such conditions will present profound challenges for responses in plastic traits that evolved in a different climate.

Our third example considered the entire life cycle of Atlantic salmon in the individual-based evolutionary population dynamic model of Piou and Prevost (2012). Their model was developed to examine harvest selection on body size, given other climate-driven constraints. They examined stressors to multiple life stages, such as increased river temperature, decreased river flow, and slower oceanic growth (Piou & Prevost, 2013). The potential to respond genetically and behaviorally was included, with fish maturing in freshwater or at different ocean ages.

This study found that evolutionary and plastic responses could push in opposite directions for a given trait and that reduced oceanic growth was the most significant threat to this population. Reduced growth rate due to the warmer ocean led to prolonged ocean residency, which was associated with a higher mortality rate overall and fewer anadromous adults returning to fresh water. Furthermore, returning adults had a higher proportion of multiple sea winter age classes, which were more vulnerable to the fishery. Adding another population stressor, selective fishing, resulted in sex-specific impacts and hurt females more than males because they mature at a later age (Piou et al., 2015).

A similar analysis drew parallel conclusions regarding the importance of avoiding overexploitation through size-selective harvest regulations to account for climate-induced changes (Ayllón et al., 2021). This ecogenetic approach presents a highly flexible demonstration of the complexity of interrelated stressors and potential responses confronting salmon.

Gaps in projections

From our perspective, there was a conspicuous absence of studies that projected evolutionary adaptation to disease and contaminants. Disease risk is likely to increase with climate change for multiple reasons. First, pathogens with higher temperature preferences are more likely to grow in a warming climate (Marquez et al., 2014). Parasite loads and susceptibility of fish to parasites often increase with temperature (Lõhmus & Björklund, 2015) and other stressors: sea lice (e.g., Hamre et al., 2019; Vehanen et al., 2020) and proliferative kidney disease (e.g., Ros et al., 2022) are particularly well-documented examples. Proliferative kidney disease, which is specifically exacerbated by warming and hatcheries, has been associated with population declines of brown trout (Ros et al., 2021) and is now an emerging threat in Alaska (Gorgoglione et al., 2020).

Second, transmission rates through disease vectors often increase with higher temperatures and lower flows, both of which are expected to occur more frequently with climate change. Invertebrate hosts of the parasites *C. shasta* and *Parvicapsula minibicornis*, for example, are strongly affected by temperature and flow (Alexander et al., 2014; Hallett et al., 2012; Malakauskas & Wilzbach, 2012). Accordingly, different Chinook populations throughout the West Coast show variation in resistance to *C. shasta* (Bartholomew, 1998; Bjork et al., 2014). Likewise, juvenile sockeye populations within the Fraser River Basin exhibit distinct parasite infection profiles associated with rearing location (Mahony et al., 2017).

Miller et al. (2014) completed a review of emerging pathogens in wild salmon and the modern technologies used to help identify them. Risk from a substantial number of pathogens is expected to increase due to climate change, although risk from some pathogens that prefer cool water will decline (Miller et al., 2014). Most of this research is in freshwater. However, infectious diseases are also common in marine environments, where they are not as well understood and are harder to manage (Burge et al., 2014). Disease in the marine environment is an area that has received little research, but presents an emerging threat to both wild and cultured salmonids.

Although pollution is widely recognized as a current threat to wildlife, the impending amplification of this threat due to climate change is less commonly appreciated. In a review of new and emerging threats to biodiversity, Reid et al. (2019) identified new contaminants, engineered nanomaterials, and microplastic pollution as three of 10 top categories of concern. Through changes in precipitation, wind, glaciation, temperature, and ocean acidification, climate change will exacerbate exposure to many contaminants, including pesticides, hydrocarbons, metals, and a wide array of other common chemicals (Hooper et al., 2013).

The combination of increased temperature, hypoxia, and acidity in particular will increase the biological impacts of contaminants to which populations are already exposed. Amplified biological effects include altered expression of heat shock proteins (Soyut et al., 2012) and disruption of hormonal signaling, development, and fertility (Forbes et al., 2019), with more severe effects of metals in an acidic environment (Hoglund et al., 2020; Maguire et al., 2020). Toxic chemicals can also reduce resistance to pathogens (Dietrich et al., 2014), which are themselves a greater threat in warmer conditions. Exposure to contaminants may initially be sublethal, but the impacts stemming from reduced performance can carry over from one life stage to the next. Genetic variability in susceptibility to contaminants could be present and evolve (Laporte et al., 2016), but was not described in studies that met our search criteria.

SUMMARY AND RECOMMENDED PRIORITIES FOR CONSERVATION

In this review, we synthesized the main areas of research that addressed evolutionary processes in assessing the impact of climate variability and climate change on anadromous salmon and trout. We focused on studies relevant to the persistence of wild populations. Evidence of recent evolutionary responses to climate change was concentrated primarily on phenological traits, particularly smolt and adult migration timing and spawning. Many additional life history, physiological, and morphological traits reflect historical adaptations to climate, and are likely under selection by ongoing climate change. However, extensive plasticity and anthropogenic selection are also driving rapid changes in these traits, reducing the detectability of a signal from climate change.

These results are consistent with a recent meta-analysis across taxa by Grainger and Levine (2022). They synthesized research on rapid evolution in life history traits in response to three drivers: warming, predation, and competition. They found significant evidence of predation/harvest effects on adults, driving a shift toward smaller body size, but relatively weak support for evolutionary responses to warming and competition. The multiple influences on these traits could be additive (Ayllón et al., 2021) and thus result in additional loss of the genetic variation needed to respond to further warming. Anthropogenic influences on genetic variation that strongly oppose natural evolution in response to climate change can put populations at grave risk (Piou & Prevost, 2013).

Major developments in the research we examined included the discovery that genes with large effects on run timing may have evolved only once and could easily be lost by extirpation of the few remaining populations that harbor these alleles (Prince et al., 2017; Thompson et al., 2019). Preserving these populations should be a high priority because this particular life history trait would be unlikely to evolve again. Additional work on the dominance characteristics of this locus is needed. Nevertheless, current data suggest that where the spring-run phenotype has been extirpated, restoration attempts based on colonists from fall-run populations that have lost this allele are unlikely to be successful (Ford et al., 2020).

At the other extreme of specificity, seemingly ubiquitous spatial patterns in genetic variation throughout the genome are geographically correlated with environmental conditions. Therefore, a wide variety of genes will presumably be affected by climate change. This expectation is consistent with the nearly universal impact of environmental conditions on physiological processes and a high frequency of polygenic traits.

Markedly few studies explored the evolutionary consequences of future climate projections directly. Those that did emphasized the complexity of pressure and response interactions. For example, we saw conflicting trends in different cardiac traits (Muñoz et al., 2015), multiple and sometimes counteracting selective forces (e.g., natural and anthropogenic selection on body size) (Ayllón et al., 2021; Bowerman et al., 2021), and plastic versus genetic responses that characterize so many crucial traits involving climate response (Piou et al., 2015; Reed et al., 2011). Thus, although it is relatively straightforward to demonstrate that selection is strong, and evolutionary responses to climate have shaped existing populations, it may not be possible to predict the net responses to all pressures that will drive evolution in the future, particularly for anadromous fish.

Therefore, we caution that directed evolution through genetic manipulation, or exclusive focus on a small number of traits and pressures could imperil wild fish. Instead, we recommend accelerating research on (1) reducing anthropogenic maladaptation and (2) preserving genetic heterogeneity that is essential for salmon and trout to survive climate change. These are two important ways that evolutionary considerations can shape these conservation priorities.

Actions to reduce anthropogenic maladaptation

Most studies analyzing anthropogenic impacts found strong influences on neutral and adaptive genetic diversity.

Fishing, hatchery production, stocking of fish in streams, and fish farming can have numerous evolutionary implications, as can habitat alterations to water flow, temperature, and landscape connectivity (Figure 5) (Williams et al., 2008). Anthropogenic activities can directly increase exposure to climate impacts by intensifying environmental stresses such as warming streams, amplifying extreme high and low flows, altering the hydrograph, and degrading habitat heterogeneity and refuges. They can also escalate ecological pressures such as increased pathogen virulence (Pulkkinen et al., 2010) or prevalence (Robinson et al., 2020; Stige et al., 2021), and reduced resilience to ocean warming (Shephard & Gargan, 2021). Generally, these influences reduce adaptive capacity by lowering effective population sizes and total genetic diversity. In addition, humans often intensify selection on particular phenotypes. The direction of this selection might be toward or away from the optimum in a future climate, but even intentional conservation strategies can lower fitness in the short or long term, damaging climate resilience (Derry et al., 2019).

While many of these negative impacts have been widely recognized, their increased importance with climate change is not frequently pointed out. Compounding pressures driving smaller body size, food scarcity due to rapid growth by stocked fish, and land use exacerbating habitat degradation are accelerating problems. The role of climate change in amplifying pressures from diseases has received even less attention, as evidenced by the absence of papers projecting specific evolutionary consequences to immune systems.

Because of the outsized role of humans in exacerbating these problems, many solutions have also been developed. Thanks to intensive research, the importance of temperature and flow is sufficiently understood in some cases to inform water management that can effectively limit the spread of disease within rivers (e.g., *C. shasta* in the Klamath River). Likewise, some dams are now managed with the explicit goal of reducing mortality from pathogens (Alama-Bermejo et al., 2022; Mauduit et al., 2022; Robinson et al., 2022). A hatchery and genetics management plan (HGMP) is required to complete the permitting process when a hatchery operates within the habitat of ESA-listed fish, with the explicit goal of reducing negative impacts on wild fish (Hatchery Scientific Review Group, 2015; Naish et al., 2007). Additional protocols have been recommended to reduce the risks from hatcheries (Anderson et al., 2020; Baskett & Waples, 2013)

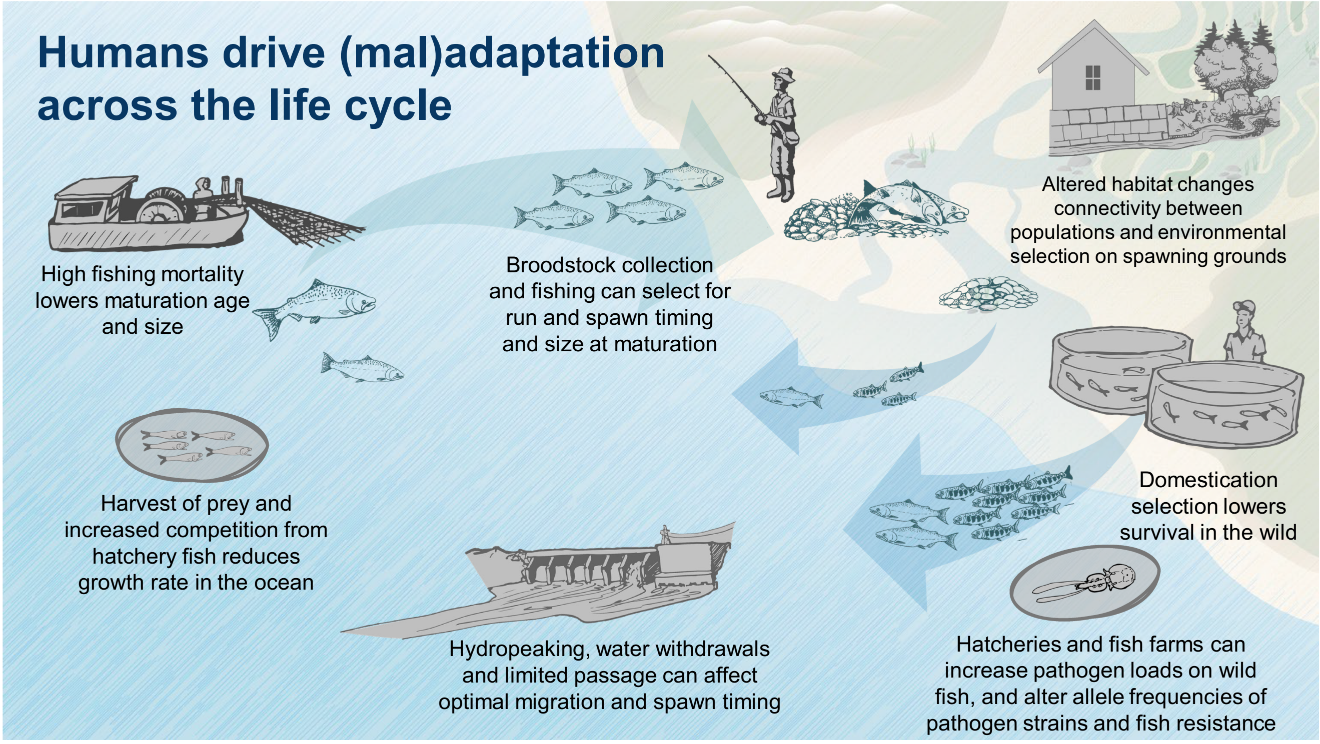

FIGURE 5 Human activities can drive evolutionary change at many life stages. This change could be adaptive if anthropogenic and climatic selection push a trait in the same direction, or maladaptive if they push in opposite directions. Local circumstances determine the direction of selection so (mal)adaptation refers to the full range between adaptive and maladaptive change (sensu Derry et al., 2019). Acknowledging a wide range of possibilities, we highlight here the more commonly observed trends. Drawings were prepared by Blane Bellerud (NOAA Fisheries).

and aquaculture (Tave & Hutson, 2019). Genomic monitoring and scientifically based breeding programs can minimize inbreeding and loss of fish health (Waters et al., 2020). Finally, new genomic methods can more efficiently detect domestication selection (Waters et al., 2018). Still, cumulative risks from hatcheries remain very difficult or impossible to fully assess (Anderson et al., 2020).

Finally, management can foster natural adaptive capacity or facilitate adaptation (Meek et al., 2023; Tkach & Watson, 2023; Willi et al., 2022). Genetic rescue is already practiced through maintenance of captive broodstock for critically endangered populations such as Snake River sockeye (Kline et al., 2019) and Central Valley winter-run Chinook (NMFS, 2014). A stellar achievement of this effort has been to maintain as much as possible of the very sparse original genetic variation (Kalinowski et al., 2012). However, during the period that Snake River sockeye was in captivity or landlocked, adult migration timing did not evolve in response to changed temperature and flow in the same way as other historically co-migrating wild sockeye populations (Crozier et al., 2011; Quinn & Adams, 1996). As we enter a period when more critically endangered populations might be brought into captivity, hatchery managers might face the question of whether to impose some form of climate selection to improve fitness in the future, when these populations might be reintroduced into the wild.

Experimental translocations provide useful information regarding whether transplanted populations will interbreed with local remnant stocks (Weise et al., 2020). Other management actions that can increase adaptive capacity include promotion of habitat connectivity, restoration of estuary and stream habitats, conservation of microclimatic refuges, and promotion of intraspecific diversity (Beever et al., 2016; Mawdsley et al., 2009).

Direct methods to foster adaptation include genetic engineering (Cong et al., 2013; Edvardsen et al., 2014; Esvelt et al., 2014; Komor et al., 2017), artificial selection (Gallardo-Hidalgo et al., 2021), assisted gene flow, and managed relocation (Aitken & Whitlock, 2013; Weise et al., 2020). Some research is devoted to manipulating epigenetic marks in cultured shellfish (Gavery & Roberts, 2017) and salmon (e.g., Liu et al., 2022; Wellband et al., 2021; Zhang et al., 2023). Certain adaptations, such as higher thermal tolerance, offer apparent advantages for aquaculture. However, these methods present many risks for wild populations. Genetic engineering through gene drives, for example, uses inexpensive, widely available technology to spread targeted genes throughout a population quickly, despite any fitness disadvantage that it might entail (Champer et al., 2016). In fact, these methods are largely used in biocontrol of pests, especially mosquitos, and therefore often deliberately spread debilitating genes.

Gene editing is one of many alternatives being considered by conservation biologists (e.g., Anthony et al., 2020; Phelps et al., 2020) because the risks of inaction seem intolerable (Derry et al., 2019; Piaggio et al., 2017). Habitats where widespread dispersal is uncontrolled, such as marine environments, have been called too risky for gene drive technology (Courtier-Orgogozo et al., 2020). Yet, genome editing is still being advocated by marine ecologists, along with other uses of inexpensive and rapid techniques (especially using clustered regularly interspaced short palindromic repeats CRISPR) to advance genomic work in wild populations (Phelps et al., 2020).

Perhaps most importantly, there exists the critical risk that edited genes will spread to nontarget populations and species (Courtier-Orgogozo et al., 2020; Webber et al., 2015) or have negative effects in less-studied life stages. Although the intention might be to advance putatively adaptive genes, such as heat tolerant lines of rainbow trout, gene editing is likely to have unintended consequences that could be detrimental to wild populations (Hedrick et al., 2013; Thomas et al., 2013).

More generally, an exclusive focus on any particular genotype presumed to be advantageous could instead undermine conservation goals through inbreeding depression and loss of adaptive potential or merely by diverting effort and resources away from more beneficial broad-scale actions (Kardos et al., 2021; Kardos & Shafer, 2018). We simply do not have nearly enough understanding of genetic mechanisms or selective factors to rule out the possibility of catastrophic unintended consequences.

Identify and protect pearls and hotspots in existing genetic variation and manage them to maximize genetic diversity

Certain genes have been identified that have a large impact on traits important in determining survival and reproductive success, such as those driving early migration timing in Chinook salmon and steelhead and sex-determined age at return in Atlantic salmon. These advances demonstrate the importance of continuing to identify such genes and ensuring their persistence. Populations that harbor unique alleles of particular importance might be considered genetic *pearls*.

Furthermore, the widespread loss of genetic diversity in areas of high human density and high climate exposure (Kovach et al., 2015) suggests that habitats supporting *hotspots* of diversity and rare alleles should be prioritized for protection. On the other side of the diversity continuum, screening more widely for inbreeding depression could raise alerts for populations at greater risk than recognized based on demographics alone.

Identifying these pearls and hotspots requires broad genetic screening, which has historically been impractical. However, advances in technology such as rapid screening and sequencing techniques can greatly accelerate our ability to identify specific components of existing diversity. High-throughput screening for genotypes, combined with whole-genome sequencing, are especially important for detecting cryptic variation, rapid evolution in disease resistance, and an understanding of the causal variants that underlie statistical correlations between genetic markers and environmental conditions. Available methods and their applications are reviewed by Meek et al. (2023) and Li and Wang (2017).

Additional genetic methods are being developed to look retrospectively at past evolution. The "resurrection approach," for example, revives ancestors from stored propagules or eggs and compares their traits with those of contemporaries (Franks et al., 2018). Discovery of "lost" genetic variation could be especially useful where entire life history types have disappeared, such as early-run sockeye in the upper Columbia River (Iwamoto et al., 2012).

We must be careful to avoid exclusive focus on adaptation to freshwater habitats: there could also be cryptic pearls of adaptive variation that influence marine survival. During the recent eastern Pacific warming trend, marine survival dropped to precipitously low levels in many Chinook, sockeye, and steelhead populations (Welch et al., 2020). There could be adaptive genetic variation for marine survival that is being lost. We have almost no understanding of selective forces in the ocean.

Mortality during ocean rearing is high, but the exact sources of mortality are likely variable and generally not well understood. The ocean stage is relatively long and unpredictable compared with freshwater stages, ocean communities are heterogenous, and interactions with other fish are patchy and hard to document. Nonetheless, based on the relatively consistent and distinct spatial patterns in ocean catch of different populations from year to year, we assume that ocean migration routes are strongly heritable (Seeb et al., 2011; Sharma & Quinn, 2012; Shelton et al., 2019). No doubt, many other genetically or epigenetically determined traits influence marine survival as well (Eirin-Lopez & Putnam, 2019).

New research tools are needed to identify these mechanisms. For example, autonomous underwater vehicles (AUVs) can collect genetic samples (eDNA) alongside other tracking devices. These vehicles may someday be capable of continuous monitoring of marine communities and perhaps even selection events. Traditional evolutionary studies could also focus more on selection during the marine stage. As the ocean grows increasingly crowded with offshore wind development and aquaculture, better information on how these new anthropogenic stressors might drive selection on salmon and trout would be extremely valuable.

Although many genotypic and phenotypic traits have the potential to respond rapidly to climate change based on both heritability (Carlson & Seamons, 2008) and selection, actual rates of evolution are surprisingly slow (Merilä et al., 2001). Constraints to rapid adaptation are not fully understood (Gomulkiewicz & Houle, 2009; Merilä, 2012), but some involve variation in effect size and dominance of different alleles, which can greatly alter long-term responses to selection (Kardos & Luikart, 2021). Therefore, we caution that rapid adaptation to climate change is unlikely to save salmon without substantial parallel work to rehabilitate habitats in tributaries (Battin et al., 2007; Cordoleani et al., 2024; Justice et al., 2017) and estuaries (Hodgson et al., 2020). Comprehensive reviews of historical habitats across large spatial areas (Beechie et al., 2021; Bond et al., 2019; Brophy et al., 2019), combined with an analysis of the evolutionary consequences of specific lost habitats (McClure et al., 2008), provide context for the scale of the problem we face. Actions need to be completed across entire watersheds to substantively increase salmon abundance (Roni et al., 2010). Fortunately, well-informed guidance is available to help prioritize restoration efforts that maximize the benefit of actions given limited resources (Ebersole et al., 2020; Ettinger et al., 2021; Herbold et al., 2018; Timpane-Padgham et al., 2017).

An especially relevant constraint to rapid adaptation occurs in species that are anadromous or have complex life histories. Namely, different selection pressures over the life cycle can slow evolution on a single trait. This occurs especially when there are extensive genetic correlations among multiple traits and with carryover effects between environments (Gallardo-Hidalgo et al., 2021; Lin et al., 2017). For example, the need for strong muscle performance in a cooler ocean might outweigh the benefit of physiological adaptation to warmer freshwater conditions. Evolutionary theory informs these theoretical relationships, but empirical estimates are exceedingly rare.

Nonetheless, some characteristics of climate change may accelerate rates of evolution. Higher temperatures increase rates of mutation and recombination and shorten generation times, all of which could increase evolutionary potential (McGaughran et al., 2021). Small, isolated populations that characterize most threatened and endangered species are prone to genetic drift and have little resistance to rapid genetic change, for better or worse.

Finally, salmon and trout are not the only species that will evolve in response to climate change. Smaller organisms, such as prey and pathogens, often have shorter generation times and larger population sizes, and thus might respond more quickly to environmental change (Van Doorslaer et al., 2010). They would then impose various selection pressures on salmon and trout that could drive unanticipated evolutionary responses.

CONCLUSION

Our analysis documented extensive work linking climate to genotypes and important trends in climate-sensitive phenotypes. We have also shown that human activities often undermine desperately needed natural adaptive capacity. Strong selection is coming, and it inherently reduces diversity by causing high mortality in less-fit genotypes. For populations to persist, they need as much genetic variation as possible, especially in traits that are adaptive to future climates. We cannot accurately predict winners and losers in future climate scenarios, so spreading specific genes that are presumed to be adaptive is likely to be counterproductive (Kardos et al., 2021). However, evolutionary studies are greatly needed to identify (1) *hotspots* of high diversity, particularly in locations that seem to be climatically analogous to predicted future conditions; and (2) *pearls* of valuable, rare genes that are at great risk of being lost due to human activities.

Increased genetic screening is also needed to track the loss of genetic diversity and current evolution in response to climate drivers, especially during the marine life stage. Maintenance of habitat heterogeneity and diverse microclimates also supports genetic variation and population stability. Finally, we must apply additional pressure to reduce activities that are driving traits in the opposite direction of those under natural selection.

AUTHOR CONTRIBUTIONS

Lisa G. Crozier and Jared E. Siegel designed the study. Literature was searched and compiled by Lisa G. Crozier from 2010 to 2016, and by both authors from 2017 to 2021. Both authors designed the categories. Jared E. Siegel assigned the labels and categories. Both authors contributed text and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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