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Review

A Comprehensive Review of the Impacts of Climate Change on Salmon: Strengths and Weaknesses of the Literature by Life Stage

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Abstract: As we confront novel environmental challenges, a full understanding of the physical and biological processes that govern species responses to climate change will help maintain biodiversity and support conservation measures that are more robust to irreducible uncertainty. However, climate impacts are so complex, and the literature on salmon and trout is so vast that researchers and decision makers scramble to make sense of it all. Therefore, we conducted a systematic literature review of climate impacts on salmon and anadromous trout as a resource for stakeholders, managers, and researchers. We reviewed studies published from 2010 to 2021 that address climate impacts on these fish and organized them in a database of 1169 physical and 1853 biological papers. Papers are labeled with keywords across eight categories related to subject matter and study methods. We compared the literature by biological process and life stage and used these comparisons to assess strengths and weaknesses. We then summarized expected phenotypic and genetic responses and management actions by life stage. Overall, we found the largest research gaps related to species interactions, behavioral responses, and effects that carry over across life stages. With this collection of the literature, we can better apply scarce conservation resources, fill knowledge gaps, and make informed decisions that do not ignore uncertainty.

Keywords: anadromous fish; ecological responses to climate change; future projections; global change; ocean; freshwater

Key Contribution: This paper summarizes an enormous literature across sub-disciplines revealing the intricacy and complexity of climate impacts on anadromous salmon and trout. Highlighting strengths and weaknesses of each life stage, we provide useful information for decision makers on what to expect with climate change, and what tools are at their disposal for saving these iconic species.

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Citation: Crozier, L.G.; Siegel, J.E. A Comprehensive Review of the Impacts of Climate Change on Salmon: Strengths and Weaknesses of the Literature by Life Stage. *Fishes* **2023**, *8*, 319. https://doi.org/10.3390/fishes8060319

Academic Editor: Bror Jonsson

Received: 5 May 2023
Revised: 14 June 2023
Accepted: 14 June 2023
Published: 16 June 2023

1. Introduction

Across the globe, climate change is forcing species to respond to unprecedented conditions. Pressures from climate change are overlaid on numerous other stressors, such as habitat degradation, resource exploitation, and depleted genetic diversity, which have already reduced the natural resilience of many native species [1–3]. Mass mortality events are increasingly attributed to warming temperatures [4,5]. Climate-driven extirpations, range shifts, and changes in phenology and productivity are reported at increasing rates every year [6–8].

The ability to predict the biological consequences of climate allows for proactive planning, which greatly reduces the risk of not meeting societal goals such as ecological, economic or social stability [9]. Quantitative projections of the biological consequences of climate change often rely on broad-scale statistical models that include relatively few predictor variables (e.g., [10,11]). This modelling approach assumes stationarity in the underlying correlation structure of relevant factors, creating a risk of model failure should the ecosystem shift. Predicting responses under conditions that are far outside our historical reference period is likely to be more accurate when it is grounded in more mechanistic understanding of how different biological processes interact [12–14].

Anticipating future change and reducing the extinction risk depends on untangling a web of physiological, ecological, and evolutionary responses [15]. Although our understanding of these complex and interacting processes will never be complete, it is worth considering how to assess our distance from this goal by quantitatively examining the areas of research in well-studied taxonomic groups. By synthesizing what is understood about climate impacts on anadromous salmon and trout (*Oncorhynchus* and *Salmo* spp.) with supporting information from other trout and charr (*Salvelinus* spp.), we show how research can be organized by biological process to evaluate data gaps in order to focus future research and management actions most effectively.

Warming temperatures have been strongly associated with mass mortality events in both cold-water and warm-water inland fish populations [4]. In Atlantic salmon (*Salmo salar*), declines have been attributed to climate change [16–18], with fisheries also to blame [19]. In Pacific salmon (*Oncorhynchus* spp.), large mortality events of critically endangered populations [20–22] and population declines [23–25] have been attributed, in part, to climatic conditions that are becoming more frequent with climate change [26–33]. Preserving these ecologically, economically and culturally significant species will require a rapid change in our current trajectory.

Anadromous salmon and trout face especially complex threats because their life history exposes them to a diverse set of interacting stressors in terrestrial/freshwater systems as well as the marine environment (Figure 1, and e.g., [33,34]). Furthermore, these fishes need to match migration timing with distinct seasonal patterns in biotic and abiotic conditions through diverse habitats. Populations will evolve genetically in both adaptive and maladaptive directions [35], but historical and ongoing declines in genetic diversity [3] and habitat quality and accessibility have greatly reduced the natural adaptive capacity of these fishes. Thus, a primary question facing managers is how to prioritize conservation actions to improve their adaptive capacity.

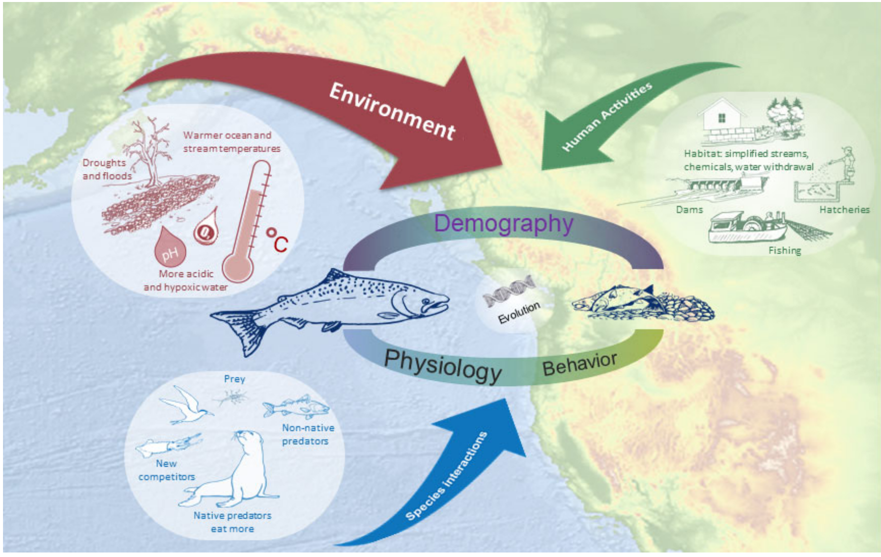

Figure 1. Multiple biological processes shape the impact of climate change on salmon. The primary factors that were represented as drivers are highlighted with arrows and icons. Additional processes are emphasized within the salmon life cycle. Process font size roughly represents the relative frequency of different processes among either drivers or responses in our review. The map shows the western U.S. and Canada and part of the marine migration range of PNW populations of *Onchorynchus*.

A vast and growing body of literature exists on climate impacts to salmon and trout, but the breadth and scope of this collection makes it difficult to evaluate and use. We reviewed and categorized a selection of relevant studies to provide a practical resource for both researchers and conservation decision makers. We included research from around the world, although we focused most on papers that were relevant to threatened and endangered salmon populations in the Columbia River Basin, located in the U.S. Pacific Northwest (PNW).

As a product of this review we provide (1) a categorized, searchable database of the literature as a resource for scientists and managers; (2) a synthesis of the main areas of research on climate impacts on salmon and trout by process and life stage, with relative data strengths and weaknesses identified and with summaries of expected phenotypic or genetic changes and areas of management evaluated for each stage; (3) a summary of future projections that identify phenomena established in the general literature but not included in the projections available for management decisions; and (4) recommendations that address management priorities, research gaps, and dealing with uncertainty.

2. Methods

2.1. Study Region

The Columbia Basin covers 668,000 km^2 and drains more water into the Pacific Ocean than any other river in North or South America. It straddles British Columbia, Canada and seven U.S. states, although much of the upper Columbia and Snake River Basins are inaccessible to anadromous fish due to impassable mainstem dams in Washington and Idaho. Human development has led to extirpation in an estimated 179 of 290 historical populations (62%) of salmon and steelhead trout in the Columbia Basin [36]. Of the remaining populations, five Pacific salmon species, as well as steelhead, include one or more stocks listed as threatened or endangered under the U.S. Endangered Species Act [37]. Some of these listed stocks complete arduous freshwater migrations, migrating distances of up to 1400 km and scaling extraordinary vertical ascents over 2000 m [38].

2.2. Literature Collection

For the overall dataset, we synthesized and augmented results from annual literature reviews conducted since 2010. These reviews were intended to identify new scientific findings relevant to the prediction and mitigation of climate change impacts on federally protected salmon and steelhead (*Oncorhynchus* spp.) from the Columbia River Basin [39–48]. For each annual review, our search focused on peer-reviewed scientific journals included in the *Web of Science* Core Collection database.

We conducted four searches of this database using publication year and (Boolean operators used in the search are shown in boldface) salmon, *Oncorhynchus*, or steelhead, and (1) prespawn mortality, (2) ocean acidification, (3) climate(the wildcard (*) was used to search using “climat*” to capture all forms of the word “climate”), temperature, streamflow, flow, snowpack, precipitation, or PDO, (4) marine, sea level, hyporheic, or groundwater and climate. Additional searches involved physical/climatic terms and geographic terms, without the biological requirement. The physical/climatic terms were: climate, temperature, streamflow, flow, snowpack, precipitation, PDO, marine, sea level, hyporheic, groundwater, upwelling, estuary or ocean acidification. Geographic terms were: Pacific Northwest, Pacific, California Current, Columbia River, Puget Sound or Salish Sea.

We supplemented these results with technical reports from state or federal agencies involving Columbia and Snake River populations. Combined, the number of physical and biological study was reduced to 3022 papers (1169 physical, 1853 biological) that are listed in our database (Data S1). For this synthesis, we quantified characteristics using only the 1853 papers that were primarily relevant to biological impacts on salmon, although we briefly summarize the most pertinent physical results.

2.3. Classification Strategy

We assigned 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*, *sub-region*, *study type*, *study duration*, *drivers* and *responses* (see Supplementary File S1: Table S1 Description of the criteria used to assign each label). A *driver* represented a natural or anthropogenic explanatory variable, i.e., a factor represented as potentially forcing change on salmon. The *response* was defined as biological outcomes measured or described in salmon as the outcome of an explanatory variable, such as a change in survival or behavior (loosely based on definitions suggested by [49]). Where appropriate, papers were assigned multiple labels within a category (e.g., multiple species studied).

In addition to these categorical labels, we also identified papers by biological process. To predict and prevent the most damaging aspects of climate change, Urban et al. [15] identified six biological processes which should be accounted for in projection modeling: *environmental conditions*, *physiology*, *demography*, *species interactions*, *dispersal and evolution*. It is important to consider all processes, because any one of them could alter the net response to a changing climate. As described below, we refined the definitions of these processes somewhat to reflect topics that are most relevant for salmon. To explore how frequently each process is documented in the salmon literature, we grouped *drivers* and *responses* into these process categories as shown in Table 1.

In general, *environmental* process papers were those focused on environmental conditions as drivers and how they interact to affect the other five processes. Climate indices were often used to represent combinations of physical drivers that are difficult to separate empirically. *Physiology* studies focused on condition metrics, growth, maturation, performance, and morphology; *demography* papers focused on population dynamics, life history and phenology; and *species interactions* papers focused on ecosystem indices, salmon prey, competitors, predators, and dynamics associated with disease. Ecosystem indices may not always reflect direct species interactions, but do reflect some cumulative properties of multiple species. Because the region of primary interest is nested within the larger range of salmon species, and salmon are largely identified by watershed, the *dispersal* process referred mostly to changes in habitat use and migration behavior, and less often to dispersal outside the current range, although colonization was also discussed [50].

The *evolution* process label was assigned to any paper that used evolutionary methods of 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 non-genetic mechanisms. We indicated these papers in the database so that they can be excluded from analyses if desired. Finally, we added a *management* category, which consists of papers that directly addressed anthropogenic actions that are actively managed, such as fisheries, restoration actions, and the impact of changes in salmon as a resource for communities.

2.4. Synthesis

While physical climate change papers were not the main focus of this review, we first provided a summary of the observed and expected physical consequences of climate change. Next, we categorized the research highlights by individual life stage and full life cycle (population-level) analyses. We organized papers by life stage because of the distinctiveness of research for each and to emphasize the biological and management needs for each part of the life cycle. For each life stage, we characterized focal areas of research by clarifying the main drivers and responses examined. We also looked at the number or percentage of papers within each life stage that were assigned a given label and compared these values with the respective values for the relevant label across the database as a whole and across all categories to examine the relative frequency of different topics in research. We then highlighted papers that projected future biological responses to climate changes. Note that papers often addressed multiple life stages, and thus were considered in all of the stages that received particular attention or analysis.

Table 1. Biological processes, labels and their definitions that were assigned to papers within the driver and response categories. Each label was considered either a driver or a response, and they are ordered as such in the table. Methods papers were not assigned to a biological process.

Process		Definition
	Driver	
Environment	Acidity	Ocean and freshwater acidification
	Climate indices	Large-scale climate indices (PDO, ENSO)
	Contaminants	Contaminants such as heavy metals and PCBs
	Dissolved oxygen	Dissolved oxygen concentrations, hypoxic waters
	Environment	Other environmental drivers (e.g., salinity, upwelling)
	Flow	Freshwater flow levels
	Habitat	Physical habitat characteristics
	Marine temp	Marine water temperatures
	Freshwater temp	Freshwater water temperatures
Species interactions	Density food	Density, competition, and food availability
	Disease	Impacts of disease
	Ecosystem	Relevant ecosystem interactions not focused on salmon
	Invasives	Invasive species competing or preying on salmon
	Predators	Salmon predators
	Prey	Salmon prey
Evolution	Genetics	Genetically derived traits or genetic diversity
Management	Fisheries	Impacts from fisheries
	Management	Management levers (e.g., flow, hatchery, policy, framework)
	Restoration	Habitat restoration as a driver
	Methods	Methodologies for science or management
	Response	
Physiology	Growth	Salmon growth
	Immune	Immune system responses
	Maturation	Sexual maturation
	Morphology	Physical morphology
	Performance	Fish performance metrics (e.g., swim speed)
	Physiology/condition	Internal physiological responses/fish condition metrics
Demography	Carryover	Carryover impacts from one life stage to another
	Life history	Life history changes, often demographic
	Mortality	Mortality rates
	Phenology	Timing of life history events (e.g., spawning, migration)
	Population resiliency	Resilience of entire populations
	Productivity	Population productivity
Dispersal	Behavior	Changes in behavior
	Habitat distribution	Distribution within available habitat
Species interactions	Diet	Diet composition as a response
Evolution	Genetic adaptation	Change in genotype or adaptive response (phenotype)
Management	Livelihood	Human economic or subsistence

Finally, we provide a synthesis of the strengths and weaknesses of the literature by life stage. Particular areas of research or types of study that were more heavily represented quantitatively within the reviewed literature were defined as candidate strengths, and those less represented were defined as candidate weaknesses. However, numerical representation is not equal to depth of understanding. We therefore refined this list to more specific study areas using our judgment to ensure that identified strengths were relatively well studied and understood, while weaknesses represented gaps in the scientific knowledge that limit our ability to manage for and predict the consequences of climate change's impacts on Pacific salmon. Note that some of these results are based on the frequencies of representation across categories in our database not detailed in the main text, but are reported in Supplementary File S1: Quantitative analysis of categories across the entire database.

While we provide a large number of references in this review, in the interest of space we did not cite all of the supporting literature, but rather offer the database itself for additional references on each topic. Here, we prioritize some of the lesser-known topics to draw attention to them, while avoiding repetition of widely known information.

3. Results

3.1. Observed and Projected Physical Impacts of Climate Change

3.1.1. Global

Historical trends and projected future trajectories of climate change are summarized at the global and regional scales in the Sixth Assessment Report (AR6) of the Intergovernmental Panel on Climate Change [51] and the most recent Synthesis *Report*. This assessment report contains the most recent, authoritative, and comprehensive summary of our global knowledge on climate impacts and represents a monumental achievement. Over 234 authors and 517 contributing authors from 66 nations contributed to the report and its conclusion that "it is unequivocal that human influence has warmed the atmosphere, ocean and land. Widespread and rapid changes in the atmosphere, ocean, cryosphere and biosphere have occurred." (IPCC 2021; Summary for Policymakers. Pages 3–32).

The AR6 documents numerous observed changes; here we list just a few examples.

- Global surface temperature in the last decade (2011–2020) was 1.09 °C higher than in 1850–1900
- Due to human influences, global average land precipitation has increased, changing near-surface salinity
- Glaciers have been retreating, Arctic sea ice in September has decreased about 40% from 1979–1988 to 2010–2019, and spring snow cover has decreased in the northern hemisphere.
- The global upper ocean (0–700 m) has warmed, the ocean surface is more acidic, oxygen levels have dropped in many upper ocean regions since the mid-20th century, and the global mean sea level has increased by 0.2 m between 1901 and 2018, and at a rate twice as fast as the long-term average from 2006 to 2018.
- Human influence is the main driver of more frequent and more intense terrestrial and marine heat waves, and concurrent events among heatwaves, droughts, wildfires and flooding.

All of these trends are expected to continue and intensify over the next century globally and in the Pacific Northwest (PNW). Here, we provide a summary of specific studies addressing the essential physical environmental changes expected in the PNW and California Current.

As climate science has progressed, analytical tools have been developed to quantitatively attribute extreme events to climate change. For example, the American Meteorological Society (AMS) now publishes an annual special report documenting the causes of extreme climate events around the world (e.g., [52]).

Scientists have long predicted that climate change would create meteorological and oceanographic conditions outside the range of our historic records. However, the AMS special report of 2016 was the "first of these reports to find that some extreme events were not possible in a preindustrial climate" [52]. Specific events identified included the North Pacific marine heat wave known as the Blob, which had major impacts on regional marine mammal, bird, and fish populations, including salmon [52].

Anthropogenic climate change has already impacted the northwestern U.S., and observations of change have been consistent with past projections [53,54]. In Washington [55] and Idaho [56], average temperatures have risen by about 1.1 °C since 1900, while in Oregon, warming has been more extreme at, 1.4 °C [57]. In addition, the seasonal duration of the freeze-free season has declined, and potential evapotranspiration has increased, leading to larger water deficits [58].

Temperature increases have been observed throughout the year, while precipitation increases have been seen primarily in spring, while showing mixed trends during other parts of the year. As new temperature records are set, studies in North America have increasingly attributed changes to increases in atmospheric greenhouse gases [58–60].

3.1.2. Freshwater Impacts

As air temperatures have increased, the spring snowpack has declined throughout the western U.S. during the 20th century [61–64]. Heavy snowfall events have also decreased in frequency in the PNW and California in the period of 1930–2007, [65]. With snowpack decline and warmer air temperatures, glaciers have retreated in North America [66] and in the PNW specifically [67–69]. The snowpack has also begun to melt earlier in the year, and peak stream flows during spring have congruently shifted timing [62,70,71], although water management has compensated for this change in some managed river reaches [72,73]. These factors have combined to make summer drought and low flow conditions more common [70,74]. Declines in summer precipitation have led to lower minimum streamflows, and long-term trends in low flow extremes have occurred throughout the West [75–77]. Shifts in the timing of and extremes of the hydrological cycle have implications for fish behavior, growth rates, and risk of mortality from stranding or overcrowding.

These regime changes have led to a higher frequency of forest fires [78], although poor forest management has contributed to this problem [79]. Forest fires are a dynamic part of the natural landscape, and have complex effects on streams. Initially, there is often sediment input from erosion, and fish passage may be blocked. Over time, the sediment is redistributed and can lead to an increase in nutrients in the stream, boosting productivity. Long-term effects depend on overall landscape processes. from Stream temperatures, which are impacted by climate conditions via solar radiation, precipitation, and snowpack accumulation/melt, have also increased [80]. Higher temperatures are associated with lower oxygen concentration, which can lead to hypoxic conditions. These increases are expected to continue alongside increasing air temperature, declining snowpacks, and decreasing canopy cover from land use and forest fires [31,71,81].

3.1.3. Marine Impacts

Oceans have absorbed much of the heat created by human-produced greenhouse gases, leading to a steep and persistent upward trend in global ocean temperatures [82]. Chen et al. [82] reported increases from the sea surface to the 2000 m depth since 1985, with record temperatures in 2020, although increases in ocean temperatures have generally been more extreme at the surface [83]. In the North Pacific, sea surface temperatures also increased during the 20th century [84–86]. However, these increases may be partly a consequence of regional shifts in wind as opposed to direct forcing from increases in air temperature [84,87].

While higher surface temperatures are mitigated by the upwelling of cold, deep sea waters, warming of ~0.7 °C has occurred since 1900 in PNW coastal areas [88]. Acidic (low pH) and hypoxic (low oxygen) waters commonly occur in coastal waters of the California Current as a consequence of upwelling. However, research suggests that increases in ocean acidification from the uptake of atmospheric CO_2 have increased the spatial extent of acidic and poorly oxygenated waters [89]. Combined with recent increases in upwelling, acidic and hypoxic waters have impacted nearshore areas in particular [90]. Trends in ocean acidification consistent with increases in atmospheric CO_2 have been documented in Puget Sound and the Strait of Georgia, which are isolated from upwelling dynamics [71,91].

A large body of research has focused on the causes and impacts of a major marine heatwave in the North Pacific Ocean known colloquially as the Blob. The Blob persisted from 2014 to 2016, when sea surface temperature anomalies were observed to exceed 3 standard deviations (~4.5 °C) above normal [92,93]. Its development was attributed to multiple co-occurring natural drivers exacerbated by global warming [94]. Persistence of the Blob may have been maintained for multiple years through teleconnections between the North Pacific and El Niño [95].

Novel environmental conditions during this anomalous marine heatwave led to numerous ecological disturbances in the California Current, including a historically unique community composition, including plankton, pyrosomes, crabs, and fish that are generally observed in more southern oceans [96–98]. In addition, the lower energy content in the plankton community had cascading trophic impacts that resulted in seabird die-offs [5,99], reduced pelagic fish conditions [100–102], and shifts in fish species distributions and spawn timings [99,103].

Climate model simulations indicate that extreme conditions such as those experienced during the 2014–2016 marine heatwave are likely to occur more frequently as climate change progresses [95]. Consistent with this prediction, anomalously warm ocean conditions returned to the North Pacific in 2019–2020 [83].

3.2. Life-Stage Specific Research

Salmon and trout spawn in freshwater streams. Generally, spawning occurs in fall or spring, eggs incubate over the following weeks to months, and then emerge from the gravel. In anadromous populations, the freshwater rearing stage lasts until juveniles migrate to the ocean, which is the smolt stage. They then rear in the ocean until they return to spawn. The duration of these stages is extremely variable, across both species and populations in species with longer life spans. For example, pink salmon (*O. gorbuscha*) has a relatively fixed life span of 2 years, of which only a few weeks are spent in freshwater. Coho most frequently lives for about 3 years, divided approximately in half between freshwater and ocean stages. Chum (*O. keta*) lives longer, but spends less time in freshwater.

The remaining salmon species can spend many years in freshwater. *O mykiss* and *O. nerka* have fully freshwater resident forms (rainbow trout and kokanee, respectively). These forms retain the ability to resume anadromy under appropriate conditions. In fact, it is often difficult to distinguish resident and anadromous contributions to reproduction in some populations, which raises challenges for population dynamics modeling.

Salmon life stages are associated with distinct physical and biological needs, and will likely respond differently to future climate forcing. Furthermore, life stages may occur in completely different spatial regions, require different methods of study, and are tractable for answering different questions. We compared the relative frequency of papers studying different life stages. The juvenile rearing stages in freshwater (33%) and saltwater (28%) were the stages that were addressed most commonly. Migration stages were highlighted in 10% and 14% of the papers for the downstream and upstream directions, respectively. Egg, spawning and population level analyses constituted 6%, 7%, and 9% of the database, respectively. In all stages, environmental factors were the most prevalent driver, but the relative proportion of species interactions (more common in marine studies) and drivers affected by human activities (more common in upstream migration and population-level analyses) depended on the life stage (Figure 2). Among responses, demographic processes were generally most prevalent, but the relative proportion of physiological and behavioral processes varied by life stage (Figure 2).

Study types also varied across life stages (Figure 3). The egg stage was most often studied experimentally. Field studies were most prevalent in research on the two migration stages and the spawning stage. The fewest models, reviews, and projections were performed on the egg and migratory stages. The marine stage had the highest percentage of reviews and meta-analyses, whereas theoretical work and projections of future salmon responses to climate change were most often completed at the population level.

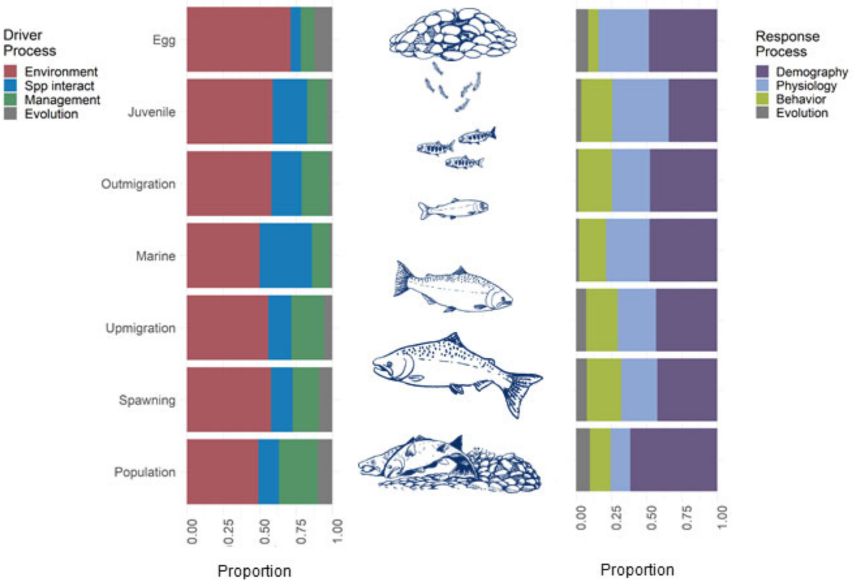

Figure 2. Barcharts show the relative frequency of papers addressing each process among drivers (**left**) and responses (**right**) for each life stage.

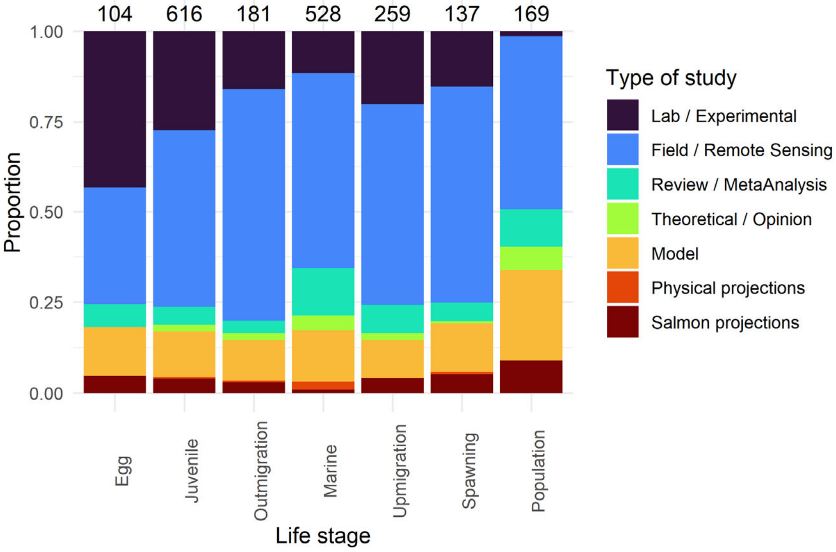

Figure 3. Relative proportion of papers on each life stage that involved different types of studies. The absolute number of papers represented in each column is at the top. The juvenile stage refers to the freshwater rearing portion of the life cycle.

3.2.1. Egg Incubation

Salmon lay eggs in gravel nests, called redds. Incubation periods are as short as a few weeks for low-elevation species, especially pink, chum, fall Chinook, and coho. Incubation may continue for as long as six months in the higher elevation redds of spring Chinook, sockeye, and steelhead. Redds may be laid in very shallow water by beach spawning pink and kokanee, or submerged up to 10 m by summer and fall Chinook [104]. Eggs are also buried within an individual redd at variable depths, which are usually deeper for larger spawners.

Adult female behavior and competition dynamics determines where, when, and how redds are buried, which largely determining the environmental experience of the eggs. After spawning, females will often protect redds from superimposition until they die. However, variability in the river environment over the incubation period plays a large role in determining which spawning habitats are most productive and the rate of development, which determines when alevins emerge from the gravel.

Drivers:

The components of climate change that are most likely to affect egg incubation directly are changes in stream and groundwater temperatures and flow (see Supplementary File S1: Table S2 for stage-specific values for all labels). Temperature affects survival when lethal limits are exceeded, but also governs egg development times, egg viability, and sublethal effects that carry over into subsequent life stages. A higher percentage of papers included temperature as a driver in this stage than in any other (61%, Supplementary File S1: Table S2). Changes in flow, which were examined in 29% of the studies, can affect the risk of dewatering, the deposition rate of fine sediment that can suffocate eggs, and the risk of redds being dislodged as a result of scouring during high-flow events.

Responses:

Deposition of fine sediment on redds reduces the availability of oxygen to embryos. During different stages of embryo development, salmon demonstrate variation in sensitivity to the combined impacts of temperature and hypoxia on mortality and growth [105]. Beyond high flows, increased sedimentation can also occur as a consequence of habitat disturbances from natural events, such as wildfires [106], and from anthropogenic activities, such as forestry or land development [107].

Eggs require more oxygen at higher temperatures, and in some cases oxygen limitation may reduce survival at temperatures that would otherwise not be lethal [21]. Tolerance of hypoxia and high temperature are also genetically linked, and hence display correlations both phylogenetically and within organisms with some overlapping physiological mechanisms [108]. Although relatively rare compared with other life stages, declines in population productivity have been linked to climate effects specifically in the egg stage [23,109,110].

Laboratory experiments on early life stages have been common in the hatchery and aquaculture industries, and these industries also facilitate easier access to fish for more general ecology studies. Thus, extensive laboratory work over decades has informed our understanding of the functional response of embryos to various temperatures and levels of dissolved oxygen (53% of all papers in the egg stage). Many of these studies were transgenerational, tracking eggs from spawners to the juvenile stage. Intergenerational studies improved our understanding of the heritability of traits and evolutionary mechanisms in the egg stage (16% of all papers covering egg stage included genetics as a driver, compared with 8% across all life stages). In particular, there is evidence that egg size, thermal tolerance, and development rates have a heritable component, suggesting the possibility for genetic adaptation of these traits [111–118].

Projections:

Projections specific to the egg stage focused on increasing flood intensity, which will likely increase mortality, and rising temperatures, which will hasten emergence timing or increase mortality [119–124]. These estimates are difficult to field test, and the egg stage is often nested within assessments of spawner-to-juvenile productivity. These projections accounted for direct mortality based on observed correlations, and some accounted for a change in incubation timing that would carry over into the next life stage [124]. Neither carryover effects nor processes other than flow and temperature were included in these projections.

3.2.2. Juvenile Freshwater Rearing and Migration

Juvenile salmon freshwater rearing may continue for days to years, varying at the species, population, and individual level. In the Pacific Northwest, Chinook and steelhead exhibit the widest range of freshwater behavior. At the southern edge of the Chinook range, for example, some adults spawn in late fall or winter, and their offspring migrate the following spring. At the northern edge of the range in Alaska, adult Chinook usually spawns in summer, but smolts may not migrate until spring up to two years later. Steelhead and Atlantic salmon can also spend over two years in freshwater before migrating to the ocean, with substantial variation in life history patterns across and within populations [125–127]. Differences in juvenile age at migration, the seasonal timing of migration, and the rate of travel from their natal habitat to the ocean are largely driven by growth rates and habitat conditions interacting with evolved thresholds for behavioral and physiological changes. In the Pacific Northwest, many freshwater habitats are heavily impounded and degraded by human activities. Habitat loss and degradation (which include both biotic and abiotic components) and management actions to mitigate them are therefore a core area of research in the juvenile life stage.

Drivers:

Salmon behavior, growth, and development rates are extremely plastic and respond quickly to habitat conditions. Habitat suitability played a role in a higher fraction of studies in the juvenile rearing (27%) and migration (32%) stages than in any other life stage. Habitat quality depends on many factors, including all components of water quality (especially temperature, flow, and contaminants), as well as biotic conditions.

Physical conditions affect general biotic conditions, including salmon prey, which then affects salmon. For example, the abundance, biomass, mean body size, and carrying capacity of macroinvertebrate and planktonic prey species have each been shown to respond to changes in river temperature and flow [128–130]. The physical changes therefore affect salmon through both direct and indirect pathways.

Variation in flow impacts habitat suitability by altering current speeds and water availability through the inundation of floodplains. Wildfires also can increase summer stream temperatures through the removal of shading from riparian vegetation and can increase productivity through bursts in nutrient inputs from erosion. However, increased prey fueled by extra nutrients may not be enough to compensate for higher salmon metabolic needs at higher temperatures. For steelhead in a California stream, fire resulted in a net decline in salmon biomass [131].

Species interactions as a driver have received substantial attention in juvenile freshwater (35%) and marine stages (52%) because of the intense competition for food and risk of predation in these stages (Figure 4). These studies examined disease (94 papers), predators (96 papers) and competition, mostly with invasive species (32 papers) and among trout [132]. In the Pacific Northwest, the invasive species studied included zooplankton in the lower Columbia River and multiple reservoirs [133–135].

Although the full implications of these invasions are not known, some feeding experiments show that Chinook salmon and other predators ate the Asian calanoid copepod *Pseudodiaptomus forbesi*. However, in other experiments, these fish preferred native prey [135]. Peak abundance of the invasive zooplankton occurred during periods of peak water temperature, especially in late summer and early fall [133,134].

Invasive American shad (*Alosa sapidissima*) interact with salmon as prey and competitors [136–138]. More generally, a depleted prey base was correlated with the abundance of nonnative fish across seven streams [139]. Additional studies addressed competition among trout species [132].

Changes in growth rate may alter the window of time during which juvenile salmon are vulnerable to size-selective predators such as bass [140]. Smallmouth bass also interacts with salmon at multiple trophic levels, mostly as predators, and are expected to increase their range and abundance in a warmer climate [141–143]. Kuehne, et al. [144] suggested that salmon expend extra energy on predator avoidance at warmer temperatures, further reducing growth.

Responses:

The juvenile life stage was the only stage during in which a higher proportion of papers described a physiological response process (49%) than a demographic response process (42%). This ordering largely reflected the importance of growth rates (26%) as a focus of research in this stage. Behavioral responses have also been closely monitored, especially habitat use (20% of juvenile papers) and migration timing (29% of juvenile migration papers), due to the relative ease of studying freshwater rearing streams. In the rearing and migration stage, adequate numbers of study fish can be sampled using smolt traps and fish can be individually tagged and followed by remote electronic detection.

Behavioral studies have focused on food and growth constraints, movement out of natal areas, interactions with other species, and behavior around dams. Juvenile salmon behaviorally thermoregulate to best take advantage of the amount of available food. For example, in a controlled study, Boltana and Sanhueza [145] found that juvenile Atlantic salmon reared with access to a larger range of temperatures within which they could self-regulate had higher growth, survival, and muscle growth compared to fish raised in a more restricted range of temperatures. Like adults, juvenile salmon use cold-water thermal refuges when temperatures are above optimum. However, food resources may become scarce in refuge habitat as densities increase [146].

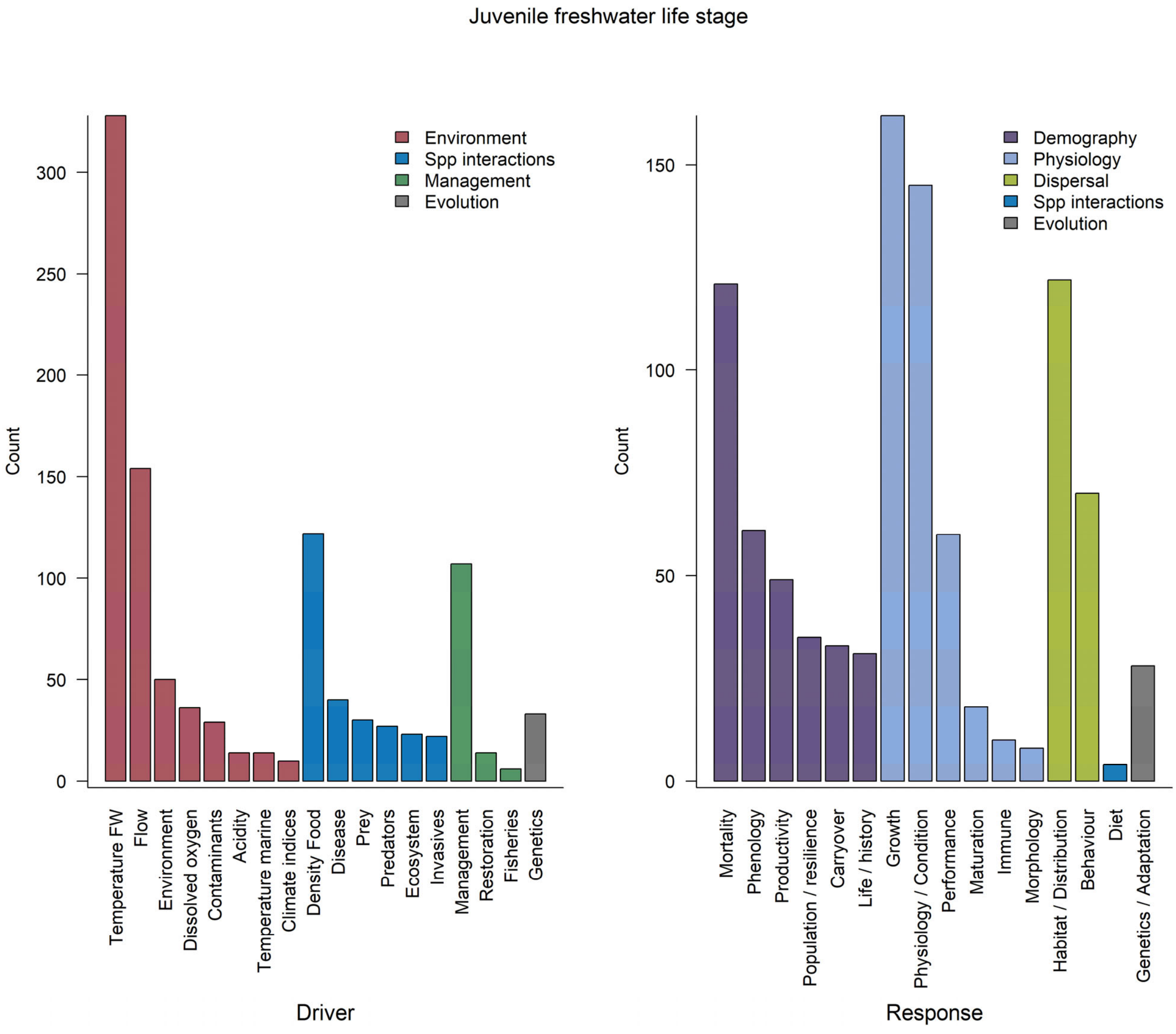

Figure 4. The number of papers covering the juvenile life stage that compared each type of driver (**left**) and each type of response (**right**). Colors reflect the process associated with each label.

Projections:

More work on projecting climate change effects has been completed for the juvenile stage than any other, and many of these juvenile-specific projections are included in full life cycle models. In the PNW, projections using future scenarios for temperature and flow were estimated for the juvenile production of coastal coho [147], dam passage of coho in the Cowlitz River [148], and trout production in northwestern Oregon [149]. In the Columbia Basin, models have estimated steelhead growth in the Yakima Basin [150], smolt survival for Chinook and steelhead in the mainstem Columbia River [151] and Lemhi River [152].

Smallmouth bass are expected to further invade the John Day River [153], and disease risks will likely increase for hatcheries in the upper Columbia [154]. The projection model for early salmon life history with the greatest geographic scope was developed by Beer and Anderson [155] for the whole western U.S. This model predicted higher rates of growth for fish in the coolest streams, but lower rates for fish in warmer streams in the Columbia Basin and California Central Valley leading to smaller sizes at marine entry and thus lower survival. Furthermore, steelhead were predicted to spawn earlier due to their spring spawning behavior, while fall-spawning Chinook are predicted to spawn later at many sites.

3.2.3. Marine Stage

The marine life stage is where explosive growth differentiates anadromous from resident life history types. Salmon smolts enter the marine stage after leaving natal freshwater streams and remain in this stage until they return as adults to spawn in freshwater. Due to the difficulty of directly studying salmon in the ocean, a large proportion of studies on this stage rely on data from freshwater adult returns.

Most of the directly observed information about this life stage comes from oceanic research cruises and fisheries catches. Marine residency may last less than one year, particularly in hatchery fish, but typically lasts 1–3 years for Chinook and coho salmon. Historically, six- and seven-year old Chinook spawners were not uncommon, but now they are extremely rare. Males often return at a younger age than females and make up a higher fraction of the resident component in species that express both anadromous and resident life histories. This difference between males and females is thought to be a consequence of the higher energetic requirements to produce eggs versus sperm; thus, larger size is more directly related to reproductive success in females than in males. Mortality in the marine stage is largely driven by predation and directed salmon fisheries, plus non-targeted catches in other fisheries.

Drivers:

Salmon marine survival is generally correlated with overall ocean productivity. Productivity in the California Current is fueled by cold, nutrient-rich upwelled, deep water, and cooler surface water flowing predominantly from the north, as opposed to warmer water from the south and west. The relative contributions of these different water sources are driven by seasonal and inter-annual wind patterns. Seasonally, the California Current is more productive after the spring transition in wind direction.

At the annual and decadal scale, the Pacific Decadal Oscillation, the North Pacific Gyre Oscillation, and the El Niño Southern Oscillation all affect the strength of currents from north, south or west, feeding the California Current. The complexity of these phenomena and how they interact with the food web explain the high representation (Figure 5) of large-scale climate (14%) and ecosystem (27%) indices over an exclusive reliance on temperature (32% included temperature but not a climate index).

Correlations between salmon productivity and specific ocean indices are typically strong, although their strength varies between species and life history types [156–163]. How climate change will affect drivers of natural ocean variability, on the other hand, is much less certain compared with the data available on climate drivers of freshwater conditions [51,84,164–166]. Moreover, statistical correlations with climate indices tend to break down over time [167–170], which necessitates a more mechanistic understanding to support robust projections with climate change.

Other environmental drivers, such as pH, oxygen, and contaminants, are generally modeled as indirect effects on salmon through ecosystem models [171–173]. There are a few studies on the direct effects of pH on salmon physiology, specifically of pH effects on olfactory systems and the ability to respond to predators [174–176]. Conversely, other work demonstrates that salmon have a relatively higher resilience to changes in pH than other fish [177].

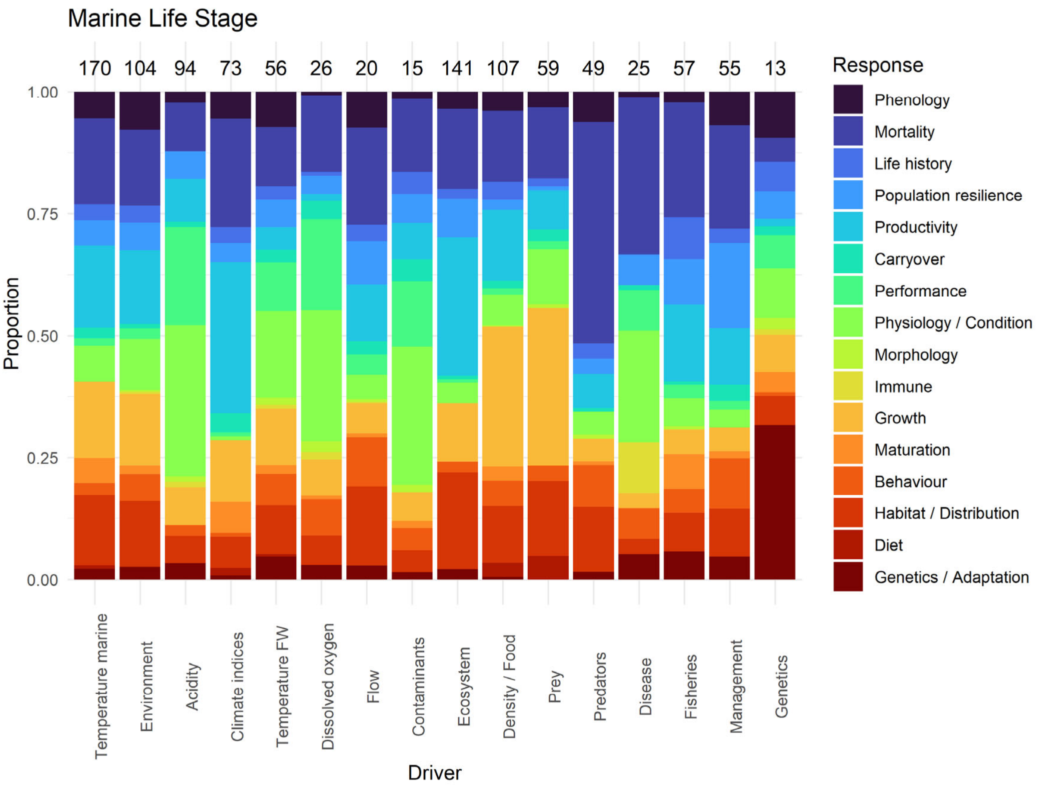

Figure 5. Proportion of papers within the marine life stage that compared each type of driver (x-axis) with each type of response (colors). The absolute number of papers represented in each column is provided at the top.

Forage and groundfish are important as salmon prey when they are small, then competitors and predators as they grow, depending on their spatial and temporal overlap with salmon. However, in California, the excess consumption of anchovy due to lack of other prey in recent years has led to a thiamine deficiency, causing reproductive failure in critically endangered winter-run Chinook salmon [178]. Large schools of forage fish also attract predators, which might then increase or decrease predation on salmon [179,180]. Forage, hake, and groundfish are economically valuable, and thus are the subject of research, monitoring, and climate projections in their own right, which is important for understanding future intersections with salmon [181–183]. Some reviews cover the state of our knowledge on forage fish and their predators in the California Current [184] and specifically in the Columbia River plume [185,186].

End-to-end models attempt to link atmospheric and physical drivers through ocean ecosystem processes all the way to the top predators and fisheries. End-to-end models for the California Current have explored many different aspects of productivity for the food web and fisheries, but relatively few of these models have explicitly focused on salmon. Some examples of Pacific salmon-relevant results include an analysis of the sensitivity of local fish productivity to upwelling intensity [187] and a study on the detrimental effects on salmon from increasing competition from jellyfish [188], which is relevant because jellyfish are generally more tolerant of warmer, more acidic and nutrient-poor conditions associated with climate change and human impacts [189–192]. Another mechanistic approach to modeling the ocean stage is to embed individual based models or models of intermediate complexity into a regional ocean model. This approach has been applied primarily to the southern California Current to understand environmental drivers in salmon prey (krill) [193], salmon growth [194], and salmon predators (sea lions) [195].

Responses:

Largely for the purposes of distributing ocean catch among countries, efforts have evolved to clarify the ocean distribution of salmon. Migration pathways have been revealed by the retrieval of coded wire, acoustic, and passive integrated transponder tags, supplemented by the genetic stock identification of untagged fish. Ocean migration routes of Chinook salmon reflect patterns of both life history (ocean-type subyearling vs stream-type yearling) and population [159,196–198]. Yearling migrants from the interior Columbia and Fraser Basins generally migrate in May and June and move quickly northward along an offshore route. However, subyearling and yearling migrants from warmer natal environments in lower rivers and coastal areas remain in nearshore areas and in the California Current for much longer periods.

Carryover effects from freshwater have received particular attention. A long-standing question of interest is to what extent freshwater conditions affect marine survival, and how management can improve the deleterious consequences of carryover effects. Ocean arrival timing, body size, flow rate and passage route through dams, and wild vs. hatchery origin have often been tested as predictors of marine survival [199,200]. Contaminant exposure in freshwater [201,202], especially aluminum [203], also can reduce marine survival. However, freshwater contaminants have rarely been included in carryover-effect projection studies of Pacific salmon.

Many different toxins are present during harmful algal blooms, and these blooms are increasing worldwide [204,205]. Several fish kills of farmed salmon have been attributed to harmful algal blooms, or red tides [206–208]. Nonetheless, most wild salmon appear to be relatively resilient to domoic acid, the most notorious product of red tides in the California Current [209]. Domoic acid produces amnesic shellfish poison, which is retained in shellfish that feed on contaminated algae, and which then has fatal effects on marine mammals and seabirds that prey on poisoned shellfish [210,211]. The neurotoxin saxitoxin, which causes paralytic shellfish poisoning, is also expected to increase with climate change [212,213]. Saxitoxin negatively impacts a variety of fish, including Atlantic salmon and rainbow trout [214], and it has been isolated from naturally migrating Japanese chum [215].

Understanding species interactions has been especially challenging in the marine life stage. Individual tracking studies can clarify when and where ocean mortality occurs (e.g., before or after good growth), but these studies are rare compared with studies of freshwater movement. Nonetheless, they have produced valuable information on where ocean mortality occurs [216,217] and in some cases, information about the specific predator from depth- or temperature-recording tags. Characteristic body temperatures in different species can be strong identifiers, as can as behaviors such as diving to preferred depths or haul-outs onto land, when tag data can be recovered after predation occurs [218].

Correlations between prey abundance, salmon growth, and salmon survival have been inconsistent across populations and over time. Several papers studying California fall Chinook have described a correspondence between prey abundance and salmon survival [219–221]. Similarly, Columbia River studies have found strong correlations between climate variables, salmon diet or size, and adult returns [222–227].

However, patterns in early marine size and survival do not necessarily match. Inconsistent patterns in growth and early ocean survival (e.g., [228]) have been attributed to higher size-selective mortality in years with lower survival [222,229,230], or alternatively, higher energetic demands in a warmer ocean that ultimately lead to mortality despite better growth conditions [231,232].

Some of the most important trends over time for the marine stage occurred in age at maturation and size at age. Comparisons between Paleolithic and present-day Atlantic salmon showed that spending two and three years at sea was much more common historically than it is now [233], and this trend has continued recently [125,234]. Age at maturity has a strong genetic basis in Atlantic salmon, and is associated with a single locus with a large effect [235]. The strong fishery-induced selection for this trait has been attributed to both indirect effects stemming from harvest of salmon prey and direct effects relating to the harvest of larger salmon [236,237].

In Pacific salmon, declining age at maturation and size of older salmon have also been widespread [238,239]. While fishing is likely to be responsible for some of this trend [240], additional factors are also involved. Warming environmental conditions are also associated with younger age at maturity across many diverse taxa independently from fisheries [241]. Larger smolts at marine entry and faster growing fish in the marine stage generally mature after fewer years in the ocean, explaining another component of the observed trends [125,242].

An additional factor may be changes in predation pressure. Long-term trends of increasing density in marine mammal populations have been blamed for lowering salmon survival in the California Current [243], in Puget Sound [158–160,244,245] and in Europe [246]. Killer whales in particular favor larger Chinook salmon [238,247]. Salmon sharks have also been identified as late-ocean stage predators that could be driving down the average age at return [218,248].

Projections:

Our database included 29 papers that provided projections for salmon or ecosystem components on which they depend. The salmon-focused papers used a number of different approaches to capture ecological mechanisms. For example, temperature indices were used as a covariate in regression models predicting survival [27,249], as a driver of bioenergetic consumption rates that predict growth rates [250], or as a correlate of observed spatial distributions [10,251–254].

Many food web models include salmon as a functional group and predict changes in biomass as they respond to changes in bottom-up and top-down interactions [171,173,255–258]. A few models focused on particular predators that might be directly relevant for salmon [259,260] and their prey, often with a focus on the impacts of ocean acidification [261–265]. There is also a large body of work on lower-trophic-level responses to climate change.

3.2.4. Adult Migration and Spawning

Salmon are considered upstream migrants from the time they enter freshwater until they reach potential spawning grounds. The relative importance of the migration stages (upstream and downstream) differs greatly between coastal populations in undammed rivers and interior populations. Pacific Northwest interior populations migrate past up to nine hydroelectric projects. Thus migration can take just a few days for coastal populations or an entire year for some interior steelhead. Fish may interrupt upstream movement and “hold” or linger downstream of or at spawning grounds for hours, days or months.

The environmental characteristics of the system determine the run type and species that may be present in a given watershed. Salmon typically consume little to no food during their upstream migration and spawning stages, so their bioenergetic reserves are limited by their condition upon entering freshwater. The physiological demands of migration therefore range from relatively unimportant to prohibitive. Anthropogenic barriers to migration have been devastating for some populations and are a major focus of research and management.

Drivers:

Temperature and flow are the main environmental determinants of the timing and success of upstream migration and spawning. Physiological responses to high temperature and flow, fisheries handling, and other stressors have been extensively examined in cardiac tissue because of the importance of this organ during strenuous exertion.

Genetic variation has also been examined in traits such as aerobic scope and optimal swim temperature and speed [266], with such examinations contributing to the relatively large proportion of studies that include evolutionary processes (11%). Once salmon reach holding areas, they may face density-dependent mortality related to multiple stressors, such as temperature, oxygen levels, parasite loads, contaminants, and disease transmission rates [28,267–269]. Bioenergetic constraints driven largely by temperature often co-occur with low flows, a combination that stresses fish physiologically through low dissolved oxygen and crowding. Crowding also tends to amplify the spread and virulence of diseases [270]. Thus, fish exposure to both pathogens and parasites is extended at a time when their vulnerability is already increased because of other stressors. A higher proportion of research focused on the upstream migration stage assessed disease agents as a driver (16%) compared to any other life stage.

Upstream migration studies also constituted the majority of papers in the species interactions process. In the spawning stage, the density of conspecifics (11%) was the most-studied driver within this process. A small number of studies investigated other species that track migrating salmon (predator/prey) [271–274], injuries associated with escape from a predator or fishing net [275], and potential for migration interference by other species such as invasive American shad [137,138,276].

Responses:

Relative to other life stages, migration and spawning had the highest proportion of papers studying behavior (25%) and particularly effects on mortality and evolutionary processes (e.g., selection on run timing or migration rate). Temperature and flow change systematically by season and location and have large impacts on behaviors such as the timing of freshwater entry and migration speed, including the tendency to stop migrating or stray into a temporary habitat. These response processes have a profound impact on the cumulative bioenergetic cost of adult migration, and greatly affect fecundity and carryover effects on life stage in the subsequent generation (maternal effects on eggs).

A large body of work tracking individual fish in the Columbia River has provided detailed information on behavior and survival, largely in relation to dams and use of thermal refuges. Holding in thermal refuges can increase risks from disease [277] and capture in fisheries [278]. Population differences in the use of thermal refuges during migration are thought to reflect the environmental conditions encountered, namely the relative availability of cool habitat, as well as the amount of time available before spawning, or the urgency of reaching upriver sites [279–286]. For example, sumer-run steelhead make extensive use of cool habitats that are beyond the migration route to spawning areas ("overshoot") because they do not need to spawn until the following spring [282,287].

Studies of carryover effects from previous life stages on spawning success include examinations of origin (hatchery vs. wild) and smolt age [288], juvenile experience during migration and river environment [289–291], and the upstream migration experience through dams [268,292]. For Atlantic salmon ocean conditions have been included in carryover effect studies [17,293], including from the marine to the subsequent generation egg stage [117,293]. A few studies described how the placement and density of redds varied with environmental conditions, having carryover effects for egg survival and development time [155,294].

Projections:

The projected impacts of climate change on the adult stage frequently found the most severe effects were from stressful temperatures that either lowered aerobic scope during migration or increased mortality during migration or holding [27–31,295]. Changes in flow are expected to result from shifts in precipitation during the adult migration period via changes in the frequency of storms, which in part determine the adult migration window [296,297]. Anthropogenic actions could either exacerbate or mitigate these impacts in flow-limited and flooded systems [123,296,298,299].

Populations differ in their exposure and their projected responses to climate change depending on spatial and temporal factors. While increases in water temperature are generally thought to increase migration stress in most PNW populations, some may experience positive effects, such as improved spawning habitat due to changing fire frequency [294] or the increased use of habitats that were previously below the optimum [300,301].

3.2.5. Population-Level Analyses

Papers focusing on population responses (as opposed to those focusing on individual life-stages) were largely represented by three types of studies: time series analyses of spawner abundance; productivity in terms of smolt or adult recruits per spawner; or the cumulative effects of stage-specific characteristics, such as survival, growth, and migration timing. Therefore, most papers given the *population* label had demographic response variables (85 vs. 46% across the database as a whole; Supplementary File S1: Figure S1) and were more likely than average to use a modeling approach, which tracked population abundance or life history characteristics as a function of environmental factors (31 vs. 16% of whole database).

Of the 19 studies that projected future salmon abundance over the entire life cycle, 58% based them on estimates of habitat suitability or carrying capacity, 21% involved population dynamics models with environmental drivers, while 21% involved qualitative assessments of risk across the full life cycle. Another set of papers examined population dynamics from a theoretical perspective or assessed the ability to detect climate-driven changes using simulation studies (Supplementary File S1: Table S2).

Species interactions were represented in 20% of the papers with the population label. Freshwater species interactions focused largely on non-native trout species affecting native trout [32,302,303] or showed declines in prey availability associated with the presence of non-native fish [304,305]. Marine species interactions included indices of ecosystem condition, generally assumed to drive prey availability [306–308], predators [109], and competition among salmon species [309,310].

Drivers:

The drivers that emerged as most important to salmon populations depended on the modeling approach used. Papers seemed to fall into one of two general categories. The first school of thought argues that the spatial and temporal scale of the most important drivers should match the scale of variation in salmon productivity. These studies focused on characterizing the temporal and spatial correlation structure across many populations. They often found that populations with different freshwater conditions, life histories, and individual management impacts showed similar interannual variation or long-term trends, in either adult recruits per spawner or population abundance. They concluded that the primary driver regulating productivity is operates at an oceanographic regional scale, as typically captured by broad-scale climate indices [309,311,312].

The second modeling approach that encompassed many of the papers in our review focused on freshwater drivers. These papers were usually associated with individual populations for which habitat condition, smolt counts, or other stage-survival estimates were available. These populations were often of concern in a freshwater management decision that needed quantitative support. Life cycle models have been built using a range of approaches, from habitat capacity [313,314] to integrated population models [315]. Some of these approaches incorporated drivers that influence freshwater stages only or that use freshwater indices in addition to marine indices.

Overall, freshwater temperature and flow were the most common individual factors driving population responses (included in 33% and 30% of studies, respectively, followed by habitat (25%). Ocean temperatures and climate indices were included in 14 and 12% of the papers, respectively. Other environmental factors usually included other marine indices (e.g., sea ice melt date, upwelling indices, and salinity) and accounted for an additional 11% of papers.

Responses:

A number of modeling studies tracked changes in population abundance and the likelihood of extinction, as well as changes in life history characteristics, especially body size and age at migration/maturation [238,239,316]. Studies also identified changes in phenology [317], effective population size [318], and genetic variation for particular traits [319,320]. Theoretical papers primarily focused on extinction probability and consistency in abundance (stability). Using this approach, several demonstrated that larger population aggregates are more stable than individual populations, called the "portfolio effect" [321,322].

Projections:

Four out of the nineteen papers that were considered projections were vulnerability assessments that used a variety of qualitative and quantitative methods [305,323–325]. Six papers focused on inland trout species [32,149,326–329], while nine focused on salmon. Quantitative projection models for anadromous species captured Atlantic salmon [330,331], masou salmon (*O. masou*) [332], coho salmon (*O. kisutch*) [314,333], steelhead trout [314,334], and most frequently, Chinook salmon [27,314,335,336].

Climate drivers in these projections focused mostly on freshwater temperatures and flows and their associated effects on habitat; only occasionally did they include climate change in both the freshwater and marine stages [27,327,330]. The salmon models accounted for changes in various processes affecting growth and survival implicitly, using correlations with total production or carrying capacities. Models that focused on Atlantic salmon addressed more processes explicitly, including competition with invasive species and evolution [327,330,331].

3.3. Strengths, Weakness, Expected Responses and Management Opportunities

Life stages differed in both the types of studies that predominated, and the specific emphasis of research. In this section, we identify and summarize the strengths and weaknesses of information on each life stage that affects our ability to understand climate change impacts. We also summarize management actions addressed in each life stage and any expected phenotypic or genetic changes based on the studied responses to environmental drivers (Table 2).

Table 2. Comparison across life stages of strengths, weaknesses, the predominant expected form of phenotypic change or genetic adaptation to climate change, and the most prevalent management actions addressed for that life stage.

Strength	Weakness	Expected Change	Management Options
	Population level		
Population-scale demographic processes; carryover effects in life history	Missing processes, esp. evolution and species interactions; carryover effects (other than life history); disease	Smaller, younger, fewer spawners; higher pathogen loads	Fisheries, flow management, dams, habitat restoration, forest management, stocking, invasive species management
	Egg stage		
Mechanistic understanding, evolutionary processes	Carryover effects in projection models; micro-climatic habitat projections	Egg size, emergence timing, alevin condition, epigenetic effects	Flow management, contaminants, adult condition, habitat condition
	Juvenile stage		
Widest understanding, adaptive management and hypothesis testing	Species interactions; carryover effects from eggs; data-poor watersheds (validate remote data)	Life history strategy (timing and growth rate, size and age at migration, migration timing)	Habitat; contaminants; disease; invasive species; dams; juvenile transportation; management of forests, fires, and flows
	Marine stage		
Many populations; broad spatial and temporal scales of analysis	Experiments and direct observations; behavior; species interactions; projections grounded in mechanistic understanding	Age and size at maturation; health of adult migrants	Fisheries targeting salmon, forage fish, groundfish, and predators; estuary and bottom habitat; contaminants and pathogens; hatcheries and aquaculture
	Adult stage		
Individual behavior, physiology	Less- studied systems outside main rivers; carryover effects from the ocean	Timing, condition, disease tolerance, prespawn mortality, spawn behavior	Fisheries; migration barriers; dam operations; influences on temperature; flow management; fish transportation; marine mammal predators; hatcheries; contaminant and disease reduction

3.3.1. Egg Incubation

Strengths. The primary strength of research focused on egg incubation is a mechanistic understanding of the physiological and evolutionary processes of egg development. For example, Pankhurst and Munday [337] reviewed a set of these physiological mechanisms in detail. They explain how temperature impacts egg development in particular, but also discussed how other stressors such as O_2 and pCO_2 during spawning and the early life stages affect eggs and later life stages. If environmental conditions actually experienced by the egg are known, this baseline knowledge can support predictions of development rates, emergence timing and condition, and survival.

Weaknesses. Despite the large number of experimental studies on egg development and survival, field tests of predictions for naturally deposited eggs are relatively difficult to preform. The non-destructive monitoring of egg survival and condition in the field is challenging, as is the attainment of physical measurements and the hydrological modeling of in situ subsurface flows and temperatures. Lack of field studies creates a weakness in the ability to relate laboratory results to population consequences. For example, in one of the few studies that measured subsurface conditions, Tuor and Shrimpton [338] suggest that there are systematic discrepancies between surface and inter-gravel temperatures across latitudinal and longitudinal gradients. These discrepancies presumably reflected differences in groundwater intrusion, a variable typically not accounted for in landscape-level models.

Furthermore, stream bed habitats are highly dynamic and can be altered suddenly by flooding, sediment deposition, or water diversion, causing radically different survival from year to year despite similar precipitation [339]. Mating behavior can also be more influential than physical characteristics [339]. Therefore, population level projections extrapolated from mechanistic knowledge of egg temperature and oxygen requirements, and even egg-box survival, require field-based corrections.

Individual and interannual variation in adult site selection and redd-building behavior can drastically alter population-level consequences for egg survival. In some cases, such behavior has produced less ecological variation in emergence timing and survival than expected from thermal differences between streams alone [122,340,341]. Finally, a number of research papers on the egg stage documented carryover effects from maternal condition/behavior on egg survival and from egg development to later life stages. However, these epigenetic effects are still poorly understood and can be difficult to assess at the population-level. These complications were largely ignored in the few projections studies for this life stage.

Expected change. Climate impacts acting on the egg stage are expected to cause phenotypic changes throughout the life cycle due to carryover effects. The high number of multi-generational egg studies allows for the assessment of carryover effects, which were more commonly studied in the egg stage than any other (16 vs, 2% across all other life stages). Carryover effects during the egg stage were studied both from the previous stage (spawner-to-egg), and to subsequent stages (egg-to-juvenile or later stages).

Non-genetic carryover effects from spawner to egg are known as maternal effects. In early development, maternal effects typically have large impacts compared with the influence of additive and non-additive genetic variation [342–344]. Various mechanisms were proposed for this, especially hormone-mediated and energetic processes, but increasing work is focusing on DNA methylation and epigenetic mechanisms [343,345–347]. Toxicants can also influence methylation state, and therefore epigenetic dynamics [348]. Other forms of adult stress, such as from migration exposure to fisheries and environmental conditions, can reduce the aerobic scope and other indices of performance in offspring through various mechanisms associated with maternal effects [349].

Factors such as organic pollutants, which affect eggs during incubation [350], can continue to affect later life stages. Alevins that hatch earlier due to higher temperatures tend to be less developmentally advanced, have lower energetic stores [344], and exhibit reduced burst swimming performance [351]. They also exhibit reduced growth rates, altered behavior [352] and higher rates of malformations [353]. These factors all likely reduce their probability of survival as juveniles. However, perhaps counterbalancing some of these effects, incubation temperatures have also been related to diverse traits such as future adult egg and gonad size, growth rate, age at maturation, and adult migration timing in Atlantic salmon [354,355]. These responses appear to occur through plastic epigenetic mechanisms, and the patterns revealed in a review by Jonsson and Jonsson [354] seemed to be adaptive, such that they may help salmon respond to climate change.

Management. Management actions that affected the egg stage included improving flow and thermal regimes by altering dam operations [100,356–360]. Habitat restoration options [361,362] included removing barriers to historic habitat, augmenting gravel for spawning, and reintroductions to newly accessible or restored habitats.

3.3.2. Juvenile Freshwater Rearing and Migration

Strengths. Research on the juvenile stage reflects a vast body of field work and in-stream monitoring that has been conducted using a wide range of sampling techniques. The freshwater juvenile life stage was the most heavily represented in our database, with 616 papers (33%, Figure 4). Advances in tagging technology have produced abundant data on individual size, movement, and mortality, spanning demographic, physiological and behavioral processes.

Spatial analyses of patterns in freshwater temperature and flow are also relatively abundant compared to the spatial analysis of marine conditions ([29], e.g., [323,363–365]). Physiological tolerances are relatively well defined due largely to the feasibility of obtaining and holding young salmon, although some important gaps remain [366]. Many restoration activities have been implemented to improve rearing habitat, although monitoring of their effectiveness is relatively infrequent. Benefits from restoration are difficult to quantify in part because location-specific changes interact with processes in other life stages through carryover effects, and benefits at the population-level can be difficult to detect. Nonetheless, intensively monitored watersheds offer standout examples of tests of restoration effectiveness [367,368].

Weaknesses. Given the consideration of growth rate as a primary constraint in the juvenile life stage, a major weakness for this stage is presented by the lack of existing projections for bottom-up food-web processes. Projections of competitors and predators, particularly from invasive or warm-adapted species, were also sparse compared to ecosystem modelling approaches in the marine environment. There were a few studies on abundant invasive species such as smallmouth bass *Micropterus dolomieu* [369], largemouth bass *Micropterus salmoides* [370] and American shad *Alosa sapidissima* [136,138], but the broader extent of the potential impacts from range shifts is largely unknown.

Although we expect that increases in water temperature and declines in summer flow will further restrict habitat suitability in many places that are already capacity-limited (e.g., [371]), most research does not account for additional processes, such as changes in prey quality. As water temperatures increase, salmon metabolic rates rise exponentially. Therefore, if salmon are to maintain current growth rates, then prey quality or availability must increase in tandem with temperature (e.g., [372,373]). Temperature directly impacts the metabolic, developmental and population growth rates of prey with consequences for potential prey abundance and quality (e.g., [374]). Furthermore, invertebrate species distributions are changing in complex ways at the same time as salmonid habitat availability is being altered by changing environmental conditions and other anthropogenic impacts (e.g., [375,376]). However, no projection studies in our database attempted to quantify these responses in prey as drivers of a response in salmon.

Systematic patterns in smolt timing, age, body size, and habitat requirements are relatively well characterized in relation to environmental conditions in the Columbia Basin. Many of these factors are included in a few projection models (e.g., [155,377]), but this was uncommon in the literature. There remains an ongoing need to account for how these patterns will be altered with climate change [378]. Specific gaps include the need to separate density-dependent from density-independent drivers of life history strategy, and how changes in juvenile strategy will affect marine survival. There is also a need to extrapolate this information to less well-studied streams, to validate habitat metrics for carrying capacities, to study changes in prey, and to examine interactions with competitors and predators (e.g., [370]).

Expected change. Expected climate responses in the juvenile stage include changes in the phenology of growth, size at age and stage, timing of fry, parr and smolt movement and specific habitat use (e.g., [33,155]). There are significant anthropogenic constraints on behavioral adaptation for many populations due to habitat simplification, which limits heterogeneity in stream habitats, barriers to migration such as road culverts, as well as a lack of physical habitats that are currently unoccupied to move into. Diverse stream habitats are needed for thermoregulation and optimal swimming strategies (e.g., [145,379,380]). The relative importance of density-dependent (e.g., growth driven) and density-independent (e.g., flow driven) triggers for fry and parr movement are not completely understood, but both are important.

Smolt migration timing has a strong plastic (e.g., [381]) and genetic ([382], e.g., [383]) control. At least one recent study has demonstrated rapid genetic adaptation in response to selection on smolt timing [384]. The genetic basis of migration timing is related to growth potential because the threshold body size that triggers migration differs across streams [385]. Thermal tolerance may also be related to growth potential [386]. 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 the overall rates of evolution [387].

Management. An extensive body of work on projecting habitat conditions takes into account the extent to which management actions can mitigate further habitat deterioration due to climate change [362], (e.g., [388]). Decision trees have been developed to help managers determine which habitat actions are most likely to ameliorate particular types of climate impacts (e.g., [123,389]). Explicitly modeled actions in climate change projections involved flow regulation [151,152,390–393]; dam passage [148]; riparian vegetation [153]; and, less frequently, forest management [149].

3.3.3. Marine Stage

Strengths. Research addressing the marine stage is strengthened by broad spatial scales and multi-population and ecosystem perspectives. An additional strength is the long time series of historical ocean catch data, which clearly demonstrate the enormous implications of past climate change for salmon population abundance. This attribute helps to differentiate robust, large-scale patterns in the data from idiosyncrasies amongst individual populations.

Weaknesses. A primary weakness of the existing literature on the marine life stage is the lack of direct observations and experimental manipulation due to the difficulty of such studies in the marine environment. As a result, our mechanistic understanding of the processes restricting productivity is limited and researchers are forced to conjecture based on indirect evidence. For example, one might conclude through indirect evidence that the dominant mode of climate sensitivity during this stage is unlikely to be exceedance of physiological tolerances or starvation. First, the ranges of potential physiological stressors typically encountered in the ocean, such as temperature and pH, are far narrower than those encountered in freshwater. Second, for the majority of Columbia River salmon populations, most interannual variation in survival is established during their first summer in the ocean [394], when growth rates are high compared to those in freshwater, even in "bad ocean" years [231].

With starvation and exposure being considered unlikely major drivers of marine mortality, the primary mechanism of marine mortality is assumed to be predation. However, it is not clear exactly why predation would be higher in a warmer ocean. One possibility is that it is mediated through behavioral responses of multiple species. For example, seabirds in California alter their foraging locations in response to changes in primary prey, which leads to greater overlap with and consumption of salmon in warmer years [230]. However, an analogous mechanism has not been identified for Columbia River populations, despite several studies exploring the role of freshwater plume size and interactions with forage fish and predators (e.g., [179]]. Therefore, we conclude that the most significant weakness in the body of knowledge regarding the marine stage is in our understanding of species interactions.

The few direct observations that exist of the marine stage come primarily from ocean fisheries, which are supplemented by a handful of dedicated surveys that collect information on size and diet of multiple species. These data generally account for a small proportion of individuals and are limited in their spatial and temporal distribution across the ocean, limiting conclusions that can be drawn from analyses. Although some effort have been devoted to tracking individually tagged fish through parts of their marine migration [395], the majority of the ocean stage is not studied directly. Therefore, most climate-focused studies on this stage rely on estimates of survival from juvenile to adult stages based on counts in freshwater.

Large-scale climate indices often account for greater variation than more mechanistic indicators of specific interactions [394]. This is likely because many species respond in their own way to these large-scale shifts in ocean conditions, and various combinations of these behavior sets affect salmon survival. Consequently, predictive models of these processes are often correlative instead of mechanistic, making them more likely to break down over time [167,169,396–398].

Individual-based models, which have been developed for Chinook salmon from the Columbia River [399,400] and forage fish in the California Current [195], hold promise for exploring hypotheses relating to more complex species interactions, and assessing their support in the data. However, the open habitat and scale of the marine ecosystem creates complex interactions that are difficult to model, especially combined with intersecting migrations of forage fish, larger predatory fish, seabirds and marine mammals. This inherent complexity creates major challenges for modeling in a non-stationary climate [167,398].

Expected change. Ocean migration routes presumably affect marine survival and are highly heritable, based on different survival rates for different populations, and present relatively little interannual variation [159,196,401]. However, we have no information either on how optimal migration routes might change with climate change nor on the genetic basis of this trait. Therefore, we cannot yet model how quickly this trait might respond to selection due to climate change. Other potentially heritable traits that could respond to selection, but are also highly plastic, are age at return and growth rates. Anticipating how sex-linked age at return responds to selection has received attention in the context of fishery-induced selection [402]. Responses to climate change are thus largely expected to consist of more widespread reductions in survival, in population abundance, and in age and size at return. These are the responses observed during anomalously warm ocean years, which are expected to develop more frequently with climate change [403].

Management. The area of management most frequently quantified in the marine environment was fisheries, and 11% of papers on the marine stage addressed impacts of fisheries in some way. Additional management actions addressed included hatchery production, farmed salmon, aquaculture, modification of shorelines, and nearshore and ocean-bottom habitat restoration, as well as planning and characterizing the efficacy of marine protected areas.

3.3.4. Adult Migration and Spawning

Strengths. The strength of the body adult migration literature is that individual migration histories are extremely well documented in certain systems. These studies are often in larger migration corridors where future projections of temperature and flow are relatively robust (e.g., [26,404]). Systems such as the Columbia River have large fisheries and dams at which adults can be enumerated, and these tend to have the most adult monitoring. However, smaller streams and un-dammed rivers have much less individual data.

Population estimates in such systems, if made at all, often come from spawning ground or carcass surveys, which are less precise, particularly in terms of timing. Although our search criteria focused on the Columbia River and thus did not capture all papers on smaller streams, 65% of papers on upstream migration were based in three major river systems: the Columbia, the Fraser, and the Sacramento. In comparison, the percentage based on these systems was only 29% of the dataset as a whole. The spawning stage, similarly, had a large quantity of redd survey data, adult counts, and descriptions of habitat needs. Management of the adult life stage benefits from the ability to restore migration corridors and to use management levers through fisheries and dams. Field studies have excellent spatial and temporal data coverage.

Weaknesses. Weaknesses in projections for the adult stage stem largely from a poor ability to account for carryover effects. Specific gaps include carryover effects from the ocean stage; behavioral responses to novel conditions in both migration and spawning, especially in smaller streams; and evolutionary responses to increased disease pressures. Uncertainty in predicting responses at the spawning stage relate to the behavioral responses of adults in site selection, stress tolerance, and the consequences of sublethal stressors, such as the need to increase endurance when confronted with higher bioenergetic costs. Our knowledge of behavioral responses is based almost entirely on correlations in field data rather than experimental manipulations. Therefore, it is difficult to extrapolate beyond observed conditions and separate effects from different environmental drivers that tend to co-vary (e.g., temperature and flow).

Expected change. The primary means of adaptation in the adult stage that was reported was a change in run and spawn timing through both plastic and genetic change [405,406]. Genetic mechanisms governing phenology are especially well studied in this stage [407–410]. Additional studies have characterized historical adaptation to physiological challenges, such as evolution in aerobic scope and cardiac performance [411–418]. However, no future projections were available for physiological adaptations in this stage.

Phenological traits are both highly plastic and strongly heritable and thus extremely likely to change [383,406]. Temperature, flow, and photoperiod (as an index of date) are the primary cues thought to drive plastic responses in phenology, with flow being the strongest cue for migration timing [27,296], and temperature being the primary factor driving spawn timing [155]. Shifts in habitat use, where possible, are also likely through a plastic response [294,419].

Management. A relatively large proportion of studies on adult migration involved management (31%). The majority of management options involved hydrosystem and flow management, fisheries, and influences on temperature. Many studies demonstrated carryover effects (9%) from hatchery practices or juvenile transportation on adult survival, homing, and overall fitness, demonstrating potential ways to improve management (e.g.,[289]). Adult transportation to spawning grounds is also employed for endangered Snake River sockeye, threatened Willamette River Chinook and other populations that spawn upstream of impassable barriers; the success of these programs is highly variable [268,420,421].

3.3.5. Population-Level Analyses

Strengths. Ultimately, the primary concern of most salmon researchers is the risk of population decline or extirpation with climate change. The strength of population-level analyses is that they often directly address our primary concern, which is extinction risk. They also have the potential to include any stage-specific issues that have been studied within a more holistic perspective. A few studies included multiple processes of concern in population dynamic models, such as the combination of evolutionary, behavioral, and demographic processes [330,331]; but such an interdisciplinary approach was rare overall. Population models most often accounted for change in multiple processes affecting growth and survival implicitly, using correlations with total production or carrying capacities. Modeling studies that focused on Atlantic salmon more frequently explicitly addressed multiple processes, including competition with invasive species and evolution [327,330,331].

Weaknesses. A weakness in population-level studies for salmon (but not trout), is species interactions, as well as the absence of information on evolution in disease tolerance and carryover effects other than life history characteristics. Population dynamics models are potentially an appropriate tool for integrating cumulative effects across life stages and interactions among processes, in their respective modes of impact on population viability. However, modeling approaches are still very heterogeneous and face technical challenges. For example, the data and processing requirements can be high for integrated population models. On the other hand, combining results from different studies can lose track of correlated effects and cumulative uncertainty across life stages. While these difficulties can be overcome, they are current hindrances to date.

Carryover effects [422], in particular, involve influences on one life stage that may not directly induce mortality in the observed life stage but do induce mortality or loss of fecundity in later stages. For example, fish may survive poor juvenile growth in freshwater but experience higher predation upon marine entry as a result. Adults returning in poor condition may have low disease resistance and depleted energetic reserves with which to migrate, compete, and produce eggs; thus, despite surviving the marine environment, their reproductive success is limited. These effects were not addressed in any of the projections in our database. Delayed effects of passage through dams, on the other hand, were widely discussed, with radically divergent conclusions.

Expected change. Many population models documented historical changes in abundance and likelihood of extinction, as well as changes in life history characteristics, with climate variability. For some of the reasons described above, body size and age at migration/maturation [238,239,316] may continue to decline, while phenology [317], effective population size [318], and genetic variation for particular traits [319,320] continue to reflect climate trends.

We found 19 projection papers at the population level. Climate drivers in these projections focused mostly on freshwater temperatures and flows and associated effects on freshwater habitat; only occasionally did they include climate change quantitatively in both freshwater and marine stages [27,330,331], but qualitative summaries generally addressed both environments [33,34]. Considering threats in both environments increased the overall estimated vulnerability of anadromous populations [325,423–425].

Management. Human impacts that were modeled as drivers included fisheries as the largest single factor (35%), as well as flow regulation [330,426–428]; dam removal [332]; habitat restoration [336]; forest management, including harvest and wildfire control [149,429]; stocking [430]; and the control of invasive species [328]. Across the broader category of 448 papers assigned to management drivers in general, rather than just those that we associated with the population level, fisheries, habitat, and dams/flow management each accounted for similar proportions (~25%), with hatcheries/fish farms/stocking activities, policy/framework analysis and 'other' each accounting for about 9%. This consistency in frequency indicates a fairly even representation across sectors as major impacts on salmon and trout.

4. Discussion

In cataloging 1853 studies and reviewing several hundred additional studies published recently, we have comprehensively explored the impacts of climate change on anadromous salmon and trout. Their most generally expected responses to climate change are shown in Figure 6. This synthesis showcases salmon as a case study where an extensive body of knowledge is ready for integration into better-informed projections of population and species responses to climate. Skillful incorporation of this information should ensure a robust characterization of likely biological responses and facilitate management that is more effective and better able to anticipate changing conditions.

Even so, the complexity of the salmon life cycle causes particular challenges in predicting climate impacts. Our review identified extensive laboratory and experimental work, which has elucidated many of the physiological processes that shape functional relationships and provide mechanistic understanding. Unfortunately, these relationships and mechanisms can rarely be scaled up to population-level responses directly because of the complex processes and heterogeneous environmental conditions involved across the salmon life cycle. Furthermore, within an individual study, they are usually considered in either freshwater or marine environments, but not both. We found only one modelling team in our review that explicitly accounted for evolutionary, demographic, and physiological processes across multiple life stages: the individual-based demo-genetic model of Atlantic salmon growth and maturation [330,331]. Consequently, managers and scientists have generally depended on population-specific correlations to account for missing parameters, processes, and life stages, and have frequently ignored life stages that lie outside their management domain.

Within the literature, we observed a highly heterogeneous representation of processes across the life cycle, reflecting the different environments and priorities of research groups. Although the number of papers counted in each category did not perfectly reflect the understanding of each topic, they provided an index of the relative attention devoted to different topic areas. The most mechanistic and physiologically grounded studies, where genetic understanding was best developed, focused on early life stages. As the spatial and temporal scales of salmon life stages expanded, mechanistic relationships became less common, while correlations with synoptic indices of environmental and ecological conditions became more common.

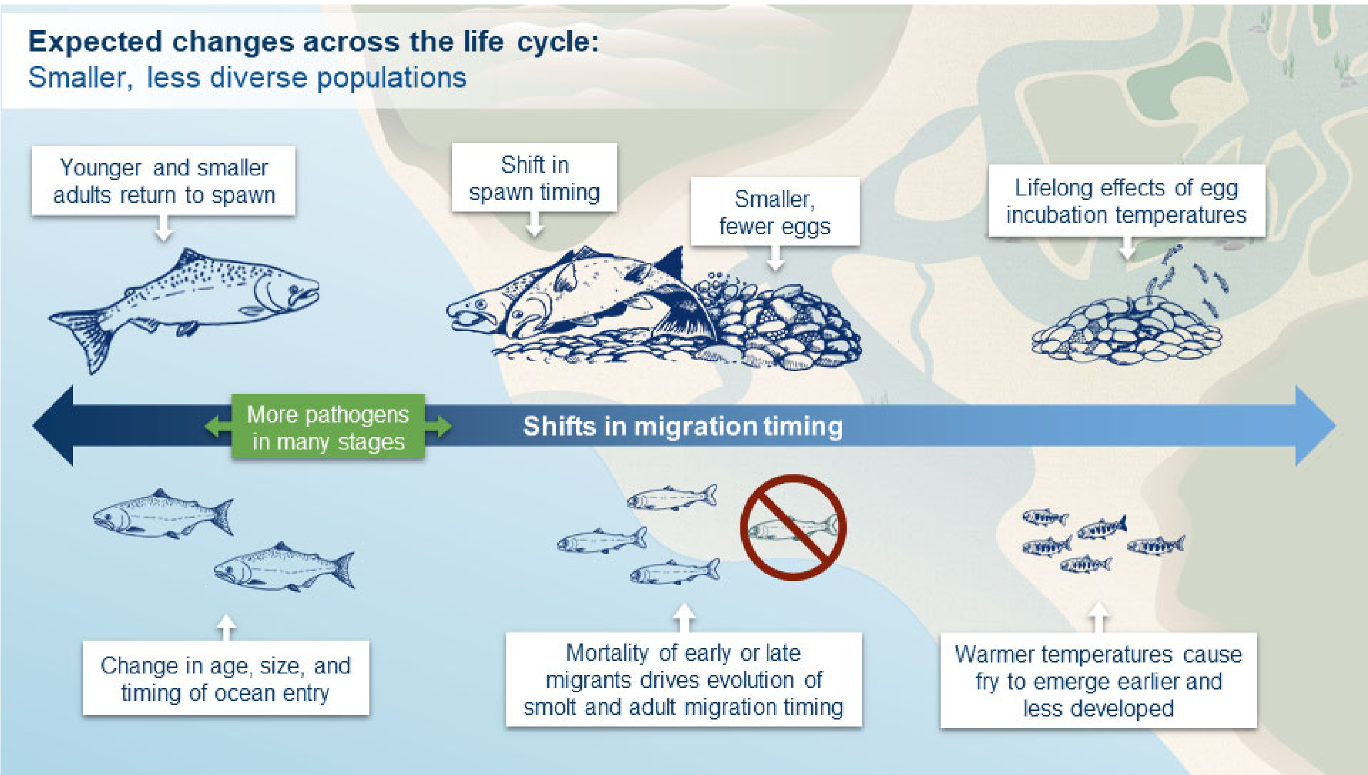

Figure 6. Some of the observed and expected changes in salmon. General shifts in growth and developmental rates lead to behavioral changes. Shifts in migration and spawn timing, as well as in the age and size at maturity, result from both plastic and evolutionary dynamics. Increased prevalence of disease, epigenetic and other carryover effects are less certain.

By synthesizing the rich body of research on different life stages and accounting for process representation explicitly, more of the existing literature can be marshalled toward effective action. The aim is to inform a more holistic approach that considers the whole salmon life cycle. Through this lens research can be refocused on applying new technologies and methodologies to previously intractable questions, and projection modeling can more efficiently address missing processes and other uncertainties. In addition, management can use available resources to the greatest effect by addressing population-limiting factors more directly. Considering this vast body of research, we propose the following path forward for salmon conservation.

(1) Capitalizing on the strengths of research in each life stage: we should use these studies to prioritize actions that reduce human impacts on freshwater and coastal ecosystems with the goal of maximizing the number, diversity, and health of wild smolts and spawners.

Using the breadth of available science, we can target resources toward addressing the factors that most constrain population growth as well as behavioral and genetic diversity. This recommendation is driven by the dominant role of human impacts in freshwater, our corresponding ability to reduce these impacts (dependent on political will), and the strong indication that many freshwater impacts carry over to affect marine survival [431]. For example, improved water quality and reduced burdens from pathogens and contaminants can greatly improve survival in later life stages. Increasing life history diversity through expanding freshwater habitat diversity can also dampen population volatility, which reduces the risk of extinction. In a future climate, productivity may be reduced as a consequence of a warmer and less productive marine environment [432]. In this case, a restored, functional freshwater environment may be the difference between depressed productivity and extinction [433].

Local human activities as well as climate change have significantly reduced ecosystem services and functions around the world ([166], Report sections 4.3.2, 4.3.3, 5.3, 5.4.1, 6.4.2), and the northern California Current is heavily impacted by coastal land and marine activities [434]. The impacts analyzed by Halpern et al. [434] included fishery removals, habitat destruction from fishing, aquaculture, ship traffic and ballast water releases (related to invasive species transport), ocean- and land-based pollution, nutrient and sediment inputs. A similar analysis found that numerous human pressures have increased steadily since the 1980s. Increased pressures included finfish and shellfish aquaculture, seafood demand, fisheries removals, coastal engineering, dredging, freshwater and sediment retention, while those that decreased included oil and gas activities, bottom structures, and light pollution (Figure S27 in [435]). Widespread loss and degradation of estuary habitats [436,437], destructive demersal fishing [438], high nutrient inputs, fishery removals, and aquaculture [435] have had widespread cumulative impacts on salmon and ecosystem capacity.

Nonetheless, freshwater restoration actions can be better targeted and might have more immediate effects because their outcomes have already been researched so extensively. The effects of freshwater habitat conditions on growth, survival, and movement are relatively well understood and sufficiently influential that many recommendations for habitat restoration and flow management can be considered as minimum requirements for persistent salmon populations. These are areas of strength in the literature (Supplementary File S1: Table S2). Because some information is available on nearly all processes, resource decisions can at least qualitatively incorporate potential risk from the less well-studied processes.

Habitat restoration is a tool immediately available to managers with guidance specifically designed to increase resiliency and adaptive capacity in the face of climate change [123,388,439–441]. In many watersheds, degraded, blocked, and disconnected habitats have lowered salmon carrying capacities and homogenized remaining habitat. These losses substantially increase population vulnerability to fluctuations from annual environmental extremes, such as a flood or drought [442]. Restored habitat complexity can augment food webs and is generally beneficial for maximizing growth, as fish use different habitats at different times for different needs such as feeding, digesting, and avoiding predators [380,443]. Thus, well-designed habitat restoration can support a wider diversity of salmon life histories, which could slow the process of reinforce diminishing genetic heterogeneity [444,445]. Population and full life cycle models or methods of similar scope are necessary to verify that population-level benefits are likely [446]. An example of a qualitative framework with specific management recommendations by life stage was completed for Fraser River sockeye salmon [33]. These recommendations can be modified for other species in other locations, ensuring that the full life cycle is considered.

To effectively mitigate long-term climate impacts, habitat must be restored systematically on a larger scale than has been implemented in the past. To support anadromous salmon metapopulations, basin-wide actions are necessary. However, such wide-scale actions face challenges. Region-wide quantification of threats and benefits are needed to guide restoration in the future, but such quantification is often limited to particular components of the environment (e.g., [323,447,448]) because of the difficulty in acquiring data appropriate for larger spatial scales. Perhaps more importantly, putting water back in streams requires whole-basin planning and multi-sector cooperation (e.g., [449]). In the western U.S. and many other places globally, declines in dry season flows are already creating intense competition among users, such as agriculture, urban, recreational and energy sectors. Restored riparian zones, wetlands, and floodplains will not only help salmon populations, but retain runoff, which will increase summer water supplies, providing benefits and security to both humans and wildlife. To understand and ensure these benefits, participation by stakeholders in developing these plans is essential for success [441].

(2) Research should continue to focus on identified gaps in knowledge and model parameters, which limit our ability to predict and counteract climate impacts. Targeting these weaknesses will help managers avoid surprises.

Several knowledge gaps that limit the effectiveness of conservation, management and modeling efforts were identified in our review. The marine life stage was identified as having the largest uncertainty in the mechanistic controls which drive productivity. In particular, new research is needed to improve our understanding of the factors responsible for lower survival in the marine stage during warmer years. The primary research goal should be to identify additional marine management actions, with the secondary goal of improving forecasts of short- and long-term prospects for decision makers. Paleontological, as well as recent studies, have shown that major fluctuations in salmon populations track changes in the marine climate [450]. Therefore, an exclusive focus on freshwater options is unlikely to prevent devastating climate impacts on salmon.

Overall, very few studies addressed more than one or two processes as drivers over the entire life cycle. This general deficit made it difficult to assess the potential influence of less-studied factors and interactions. The magnitude of such influence may be large, judging from analyses that explicitly specify unexplained variation. Random effects that reflect un-modelled processes are typically very large in state space models that estimate process and observation errors explicitly [315,451]. This suggests that there are major factors driving variation in population productivity that we are currently not able to account for.

Our understanding of carryover effects, species interactions, functional relationships, and genetic constraints and opportunities emerged as weaknesses from our analysis. How productivity is impacted by the interacting factors of density, prey, and predators, and how these relationships are modulated by environmental variability remain areas of uncertainty across multiple life stages. As models identify particular parameters or functional relationships that are especially impactful for the focal species, more data are needed to clarify these relationships. These models will require more targeted data collection to fill research gaps, such as those laid out by Wells et al. [452] for the marine stage. These are areas where new technologies and methodological approaches can reduce earlier constraints on research to help overcome the challenges of studying the ocean environment.

New technologies are greatly improving our ability to detect species interactions and habitat use in both freshwater and marine environments. For example, environmental DNA (eDNA) and rapid genetic screening techniques can provide highly targeted information more efficiently and with less handling stress and mortality than traditional survey methods. These and other types of data can be collected by autonomous vehicles, filling holes between (but not replacing) ship-based surveys. These methods provide data in key areas, including population abundance [453], the presence of invasive species [454–456], a history of thermal stress [457], habitat issues such as barriers to passage [458], and community composition [459]. While these techniques have limitations [460], we predict that new genetic approaches will change our entire perspective on freshwater and marine communities and the spatial and temporal overlap among species.

Similarly, new methods of examining satellite data and crowd sourcing drone imagery are available. These techniques can map and track changes in habitat and ecological characteristics, including functional groups at lower trophic levels [461], and could dramatically improve the spatial and temporal resolution of field surveys. New animal tracking technology and video analysis tools are also rapidly improving our ability to record species interaction events and movements. Many new tools and approaches are being coordinated by Global Ocean Observing System (http://goosocean.org, accessed on 1 May 2023) to combine information from different research networks and platforms for a truly global perspective.

Systems-oriented approaches to analyses of community resilience can help to pinpoint communities wherein species interactions are especially important. Naman et al. [462] used a food-web perspective to help address critical riverine management questions. In addition to capacity and productivity questions, Naman et al. [462] pointed out that the introduction of invasive species, as well as the extirpation of native species, can have cascading effects on focal populations and ecosystem processes.

Because the primary tool for anticipating future responses to climate change is the projection model, we discuss factors limiting the utility of projection modeling here. A goal of predictive modeling should be to better identify factors that could cause populations to decline so that management efforts on the ground can be better targeted. To this end a rigorous sensitivity analyses of plausible alternative functional relationships and the full range of reasonable parameter values within a given functional form, followed by real-world testing of model predictions needs to be instituted [463]. Sensitivity analyses should explicitly characterize both the relative uncertainty in different parameters or functional relationships and the biological impact across this range of uncertainty [463]. Our goal should be to more accurately reflect uncertainty in these areas, and then (e.g., [464]) target research on areas with the largest potential effects, given the expected trends in climate. Qualitative network models [465–467] are another way to represent relationships that might not be resolvable empirically or that change frequently. This approach explores a very wide range of parameter combinations more efficiently than fully quantitative models, and in some cases may more honestly reflect our level of uncertainty. Decision makers could then more effectively manage risk.

The ideal approach for salmon would be similar to recommendations for marine science in general in the context of climate change. As detailed by Tommasi et al. [468], we advocate an iterative process of model development and data collection to advance a variety of approaches, including single-species, multi-species, and ecosystem-based models and research in each of the empirical areas mentioned above [469]. Salmon are highly sensitive to lower trophic level processes, so better understanding of climate impacts on prey is essential and requires more study. Still, predators account for most salmon mortality in both freshwater and marine environments. Thus, we need to go beyond the single-species perspective to multi-species experiments and models to probe deeper into how climate drivers affect species interactions and community dynamics.

(3) Characterizing uncertainty in climate impact projections requires implementing an ensemble modeling approach. A number of models with different assumptions should be used to simulate future conditions, and mechanistic and statistical models should be updated frequently to incorporate different biological processes and new environmental correlations.

As climate change progresses, and we encounter unprecedented conditions in the atmosphere and ocean, statistical correlations will break down, and model uncertainty will grow. Statistical methods can help extend our knowledge from intensively studied populations to locations with sparse data. However, we must recognize the risk in depending on retrospective correlations for climate change projections: correlations are likely to break down in a non-stationary climate as ecological relationships and animal behaviors shift in response to novel conditions. Novel conditions are already occurring, as demonstrated by the unprecedented warm waters of the Blob that lasted in the North Pacific from 2014 to 2016 [470]. Warm events have occurred repeatedly since the Blob [471], and the frequency of these events is expected to increase [403] and to co-occur with terrestrial droughts in "compound extremes" [472]. Species distribution models trained on data from previous years did not always predict responses to the heatwave well [181]. In future projections, novel conditions constitute from 50% (2060s) to 100% (2090s) of the California Current in an average year under high carbon emission scenarios [473], presenting profound challenges for our modeling tools [474].

Mechanistic models are expected to have longer forecast horizons and perform better at intermediate to long time-scales, assuming the mechanistic drivers are modeled correctly [13]. Exploration of forecast skill in population dynamic modeling is rarely done because short-term uncertainty is expected to be extremely high. However, such analyses would help to clarify the strengths and weaknesses of different modeling approaches. We also need to think carefully about processes that are often ignored: species interactions, changes in behavior, and evolutionary dynamics. These areas need systematic scoping to identify populations and locations where they could alter future outcomes for focal species.

Nonetheless, for short-term forecasting, statistical models will likely continue to have the greatest forecast skill, despite the risk of correlations breaking down over time. Frequent updating of statistical correlations, combined with careful and informed interpretation and forecast skill assessment, can mitigate this risk by recognizing when relationships have broken down and replacing outdated variables with new covariates that better represent the challenges salmon are facing in new environmental conditions. This process in and of itself can lead to greater mechanistic understanding.

In addition, any projection of future conditions should be compared systematically and quantitatively with other projections. Model ensemble averages have been shown to produce better predictions than individual models when rigorously tested. Ensembles also allow for explicit accounting of the uncertainty attributed to model type. Ensemble modeling is necessary to account for the high level of uncertainty in biological as well as physical processes. Such uncertainty follows from weak mechanistic understanding in many research areas combined with limited representation of the full range of biological processes known to affect species responses to climate change. The ensemble approach has been formalized in climate and weather forecasting communities, where a wide range of models are continually under development and regularly compared [51].

In the stock assessment and ecosystem modeling communities, global efforts have been initiated to systematically compare outputs from different models, given a shared set of scenarios within the current climate (e.g., Fisheries and Marine Ecosystem Model Intercomparison Project, FISHMIP [475] and Center for the Advancement of Population Assessment Methodology, CAPAM). Future projections have used a multi-model approach for groundfish [476] and forage fish [477]. However, this practice is not widely established in most ecological applications, despite an urgent need for robust marine planning [9].

In summary, the vast resources that have been devoted to salmon research can be marshalled more effectively by using the strengths of the existing body of knowledge to guide effective management and conservation, address areas of scientific weakness, acknowledge our current level of uncertainty, and more accurately represent the array of potential future conditions. We encourage the community to actively plan for a future of surprises and invoke informed proactive actions to adapt to climate change.

5. Conclusions

The rich literature studying salmon and trout provides a valuable case study demonstrating the complexity of climate impacts on biological systems. Information across biological processes can be marshalled to provide robust projections of responses to climate change. We are at a nexus in which an exquisitely valuable and sensitive taxonomic group is on the brink of catastrophic change. We have an impressive array of knowledge, but widescale cooperation is essential to overcome the enormous challenge of filling knowledge gaps and forestalling the worst outcomes for this resource and the communities who depend on them. Only by combining our collective wisdom and energy can we prevent the loss of this flexible and adaptable set of species while maintaining and augmenting the freshwater and marine ecosystems on which they depend.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes8060319/s1, Supplementary File S1: Quantitative analysis of categories across the entire database; Supplementary File S1: Table S1. Description of the criteria used to assign each label; Supplementary File S1: Table S2. The number of papers assigned to each label across the database as a whole and within each life stage; Supplementary File S1: Figure S1. Panel plots for each life stage and label, showing the number and percentage of papers in each label; Supplementary File S2: Complete list of studies used in the quantification of categories and the labels assigned to each citation; Code File S1: R code example for reading data file; Data S1: csv file with data for use with R code.

Author Contributions: L.G.C. and J.E.S. designed the study. The literature was searched and compiled by L.G.C. from 2010 to 2016 and by both authors from 2017 to 2021. Both authors designed the categories. J.E.S. assigned the labels and categories. Both authors contributed text and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: All citations analyzed are provided in Supplementary File S2.

Acknowledgments: We would like to thank NOAA Fisheries West Coast Region Adaptive Management Implementation Plan team for supporting and reviewing the annual literature reviews since 2010, and providing much useful feedback over the years. Blane Bellerud provided salmon images and icon, and Su Kim helped with design in Figures 1, 2 and 6. We also thank Aimee Fullerton, Jeff Jorgensen, Peter Kiffney, Mark Urban, and Beth Sanderson for reading various drafts and providing helpful direction and reviews.

Conflicts of Interest: The authors declare no conflict of interest.

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