
Impacts of Climate Change on Salmon of the Pacific Northwest

A review of the scientific literature published in 2019

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Contents

Literature Highlights.....	3
Objective and Methods	6
Physical Climate Impacts.....	8
Global and National Summaries of Climatology for 2020	8
West Coast Climate Change	9
Retrospective.....	9
Projections.....	12
California current.....	13
The "Blob"	13
Retrospectives.....	14
Projections.....	15
Biological Impacts	17
Population Trends.....	17
Vulnerability and Adaptation.....	19
Phenology	21
Life Cycle Analyses.....	21
Stage Specific Studies.....	22
Adult migration and spawning.....	22
Egg incubation	23
Juvenile rearing.....	25
Juvenile migration.....	26
Ocean rearing.....	27
Habitat.....	29
Parasites and Stressors	31
Methodology	32
Management.....	33
References.....	36

Literature Highlights

Global and national summaries of 2020 climatology—The year 2020 was another astonishingly hot year in terms of both national and global temperatures, continuing a century-long trend. It was the second hottest year in the 141-year record of global land and sea measurements (0.03°C warmer than 2019), and capped off the warmest decade on record (NOAA NCEI 2021). During 2020, records were also broken in terms of wildfire activity in the west and of declines in October sea ice extent (NOAA NCEI 2021).

Retrospective physical highlights—Shifts in the long-term characteristics of wildfires, which have become more severe, were documented in 2019. Fires were concentrated in smaller areas than occurred historically, but those fires were more severe (Haugo et al. 2019). Increased stream temperatures in the Fraser River were also documented in 2019 (increase of ~1.0°C from 1950 to 2015), with most study sites doubling the number of days over 20°C—a stressful temperature for Pacific salmon *Oncorhynchus* spp. Regarding ocean conditions, multiple papers described physical and biological characteristics of "The Blob," and synthetic reviews summarized biological thresholds for hypoxia (Chan et al. 2019) and pH (Bednarsek et al. 2019).

New local physical projections—A large set of naturalized flow projections for the entire Columbia Basin was completed by researchers at the University of Washington (Chegwiddden et al. 2019). They reported patterns similar to those of previous projections (less snow accumulation, earlier melt) but used CMIP5 instead of CMIP3 GCM projections. Hence they presented an update of the 2080 project and did a thorough job of characterizing uncertainty from different parts of the modeling chain (carbon emissions scenario vs. GCM vs. downscaling method vs. hydrological model).

Regional oceanographic models were used to explore dynamics in the Salish Sea and at the southern end of the California Current. Projections for the Salish Sea indicated higher temperatures, lower pH, and lower dissolved oxygen levels (Khangaonkar et al. 2019). In the California Current, global warming was predicted to increase ocean stratification, with less-certain impacts on the intensity of upwelling. Arellano and Rivas (2019) projected that stratification can compress the coastal zone of increased productivity, even where upwelling becomes more intense in spring.

Retrospective biological impacts—Multiple papers documented dramatic declines over decades in Atlantic salmon *Salmo salar*, including declines in effective population size throughout the range (Lehnert et al. 2019). Declines in abundance were also

reported for the southern edge of the range (Almodovar et al. 2019), along with changing age at return in the northern edge of the range (Erkinaro et al. 2019) and a reduced "portfolio effect" (higher synchrony in productivity patterns) across the range (Olmos et al. 2019). These declines in productivity and resilience continue to be well explained by sea surface temperatures and ecosystem indicators.

Climate change and anthropogenic factors continued to reduce adaptive capacity in Pacific salmon as well, through altering life history characteristics and simplifying population structure. For example, the diversity of age structure and run timing was further reduced in Central Valley (Sturrock et al. 2020) and Trinity River Chinook salmon *O. tshawytscha* (Sullivan and Hileman 2019).

Tillotson et al. (2019) describe how hatchery practices have created maladaptive selection pressures for sockeye salmon *O. nerka* migration timing in the Cedar River. Documented declines in average age and size at age of Dworshak Hatchery steelhead *O. mykiss* from the Clearwater River may be a consequence of environmental shifts in the ocean and of fisheries size selectivity (Bowersox et al. 2019). Bristol Bay sockeye spent fewer years in freshwater, but more time in the ocean, which Cline et al. (2019) attributed largely to slower ocean growth rates due to competition with hatchery fish.

Cumulative life cycle effects, including effects on adult return timing, have been linked to embryonic temperatures (Jonsson and Jonsson 2019). Such linkages indicate that impacts from climate change in early life stages can have a multitude of delayed impacts that can be difficult to predict.

Many valuable papers improved our understanding of core processes affecting salmon in all life stages, including selection vs plastic trends in phenology (Oke et al. 2019; Reed et al. 2019; Sparks et al. 2019; Thraya et al. 2019; Tillotson et al. 2019), local adaptation in physiology (Abe et al. 2019), and various processes affecting stage-specific survival. In particular, Rub et al. (2019) found a negative relationship between pinniped abundance and salmon survival through the lower Columbia River. In a step closer to understanding the direct impacts of ocean acidification for salmonids, Williams et al. (2019) showed negative impacts on olfactory function in coho salmon *O. kisutch*.

Important habitat papers include a map of historical and current tidal wetlands, demonstrating 85% loss of historical habitat across 44 estuaries in the U.S. (Brophy et al. 2019). Helaire et al. (2019) document how modern development has impacted characteristics of the lower Columbia River. Their results showed that increased channel depths and a loss of marshes have caused an increase in tides and river velocities and a decrease in baseline water height.

Projected biological impacts—Crozier et al. (2019) published a cumulative assessment of relative risks from climate change faced by evolutionarily significant units (ESUs) of salmon and distinct population segments (DPSes) of steelhead listed under the U.S. Endangered Species Act (ESA). Seven ESUs ranked *very high* in vulnerability, with five out of seven in the Central Valley and Interior Columbia recovery domains. Anthropogenic factors significantly increased climate vulnerability in these ESUs. Most of the remaining groups ranked *high* in vulnerability, with a number of chum and steelhead ranked moderate, and just Puget Sound pink salmon *O. gorbuscha* in the *low* category. Predominant threats were from increases in stream temperature, either flooding or loss of snowpack (depending on population location), sea surface temperature, and ocean acidification.

For fall Chinook salmon, challenges during adult migration through the Columbia River Basin were extensively reviewed and modeled under projected climate change scenarios (Connor et al. 2019). Snake River spring/summer Chinook and Snake River sockeye (Crozier et al. 2020) and Washington and Oregon coho (Flitcroft et al. 2019a) are predicted to encounter warmer and drier conditions in the future. Zhang et al. (2019) projected impacts of climate change on smolt migration through the Columbia and Snake Rivers for Chinook and steelhead. All papers predict substantial, negative effects from climate change for particular populations, with Snake River sockeye at extremely high risk of losing the anadromous stage.

Objective and Methods

The goal of this review was to identify literature published in 2019 that was most relevant to prediction and mitigation of climate change impacts on Columbia River Pacific salmon *Oncorhynchus* spp. listed under the U.S. Endangered Species Act. Our literature search focused on peer-reviewed scientific journals included in the *Web of Science* database, although we included highly influential reports outside that database.

We sought to capture the most relevant papers by combining climatic and salmonid terms in search criteria. This excluded studies of general principles demonstrated in other taxa or within a broader context. In total, we reviewed over 403 papers, 119 of which were included in this summary.

Literature searches were conducted in March 2020 using the Institute for Scientific Information (ISI) *Web of Science* indexing service. Each set of search criteria involved a new search, and results were compared with previous searches to identify missing topics. Specific search criteria included a publication year of 2019, plus:

- 1) A topic that contained the terms climate,¹ temperature, streamflow, flow, snowpack, precipitation, **or**² PDO, **and** a topic that contained salmon, *Oncorhynchus*, or steelhead, but **not** aquaculture or fillet
- 2) A topic that contained climate, temperature, precipitation, streamflow **or** flow **and** a topic containing "Pacific Northwest"
- 3) A topic that contained the terms marine, sea level, hyporheic, **or** groundwater **and** climate, **and** salmon, *Oncorhynchus*, **or** steelhead
- 4) Topics that contained upwelling **or** estuary **and** climate **and** Pacific
- 5) Topics that contained ocean acidification **and** salmon, *Oncorhynchus* or steelhead
- 6) Topics that contained upwelling **or** estuary **or** ocean acidification **and** California Current, Columbia River, Puget Sound or Salish Sea
- 7) A topic that contained prespawn mortality

This review is presented in two parts, with the first considering changes to physical environmental conditions that are both important to salmon and projected to change with climate. These include air temperature, precipitation, snowpack, stream

¹ The wildcard (*), was used to search using "climat*" to capture all forms of the word "climate."

² Boolean operators used in the search are shown in boldface.

flow, stream temperature, and ocean conditions. We describe projections driven by global climate model (GCM) simulations, as well as historical trends and relationships among these environmental conditions. In the second part, we summarize the literature on both retrospective and projected responses of salmon to these changes in freshwater and marine environments.

Physical Climate Impacts

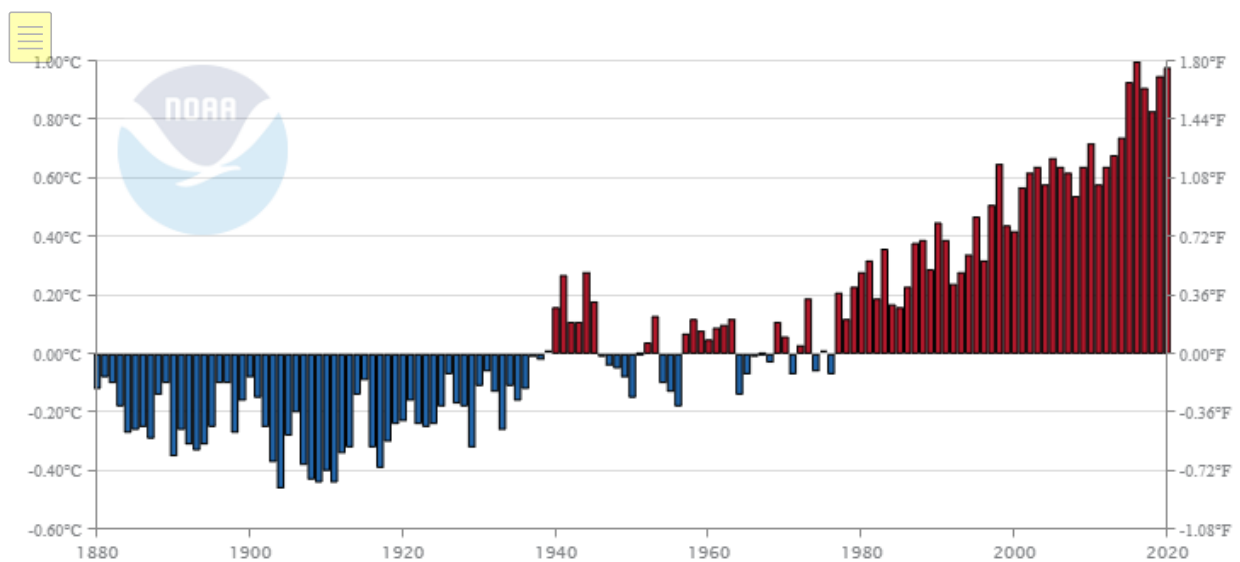
Global and National Summaries of Climatology for 2020

Signatures of climate change continue to accelerate, with 2020 breaking records among important metrics, despite a transition to La Niña conditions. As described by the NOAA National Centers for Environmental Information (NOAA NCEI 2021) in their global report, despite a slightly cooler end of the year:

The year 2020 secured the rank of second warmest year in the 141-year record, with a global land and ocean surface temperature departure from average of $+0.98^{\circ}\text{C}$ ($+1.76^{\circ}\text{F}$). This value is only 0.02°C (0.04°F) shy of tying the record high value of $+1.00^{\circ}\text{C}$ ($+1.80^{\circ}\text{F}$) set in 2016 and only 0.03°C (0.05°F) above the now third warmest year on record set in 2019.

The decadal global land and ocean surface average temperature anomaly for 2011–2020 was the warmest decade on record for the globe, with a surface global temperature of $+0.82^{\circ}\text{C}$ ($+1.48^{\circ}\text{F}$) above the 20th century average. This surpassed the previous decadal record (2001–2010) value of $+0.62^{\circ}\text{C}$ ($+1.12^{\circ}\text{F}$).

The global annual temperature has increased at an average rate of 0.08°C (0.14°F) per decade since 1880 and over twice that rate ($+0.18^{\circ}\text{C}$ / $+0.32^{\circ}\text{F}$) since 1981.



Global land and ocean temperature anomalies from January to December 1880-2020 (NOAA NCEI 2021). The figure shows a strong trend with the most negative anomalies

(coolest temperatures) between 1900 and 1920, and the most positive anomalies (warmest temperatures) since 2014.

In their national report, NCEI characterized 2020 as the most active wildfire year on record across the west, especially in California and Oregon, due to a dry winter followed by a hot, dry summer and autumn. The Pacific Northwest saw heavy precipitation, flooding, and landslides in January 2020 (NOAA NCEI 2021).

Because it is an upwelling region, warming of the surface ocean waters closest to the coast of northwestern North America had a slower warming trend than the global ocean. However, the Northeast Pacific as a whole had another year of record high heat in 2020, measured as an average over the upper 2,000 m (Cheng et al. 2021). Arctic sea ice continued to recede, with sea ice extent in October at 3.7 SD below the 1981-2010 mean. This was the lowest sea ice extent on record (NOAA NCEI 2021).

West Coast Climate Change

Retrospective

Precipitation—Cash and Burls (2019) analyzed precipitation data and North American multi-model ensemble forecasts to illuminate the relationship between El Niño events and West Coast rainfall. While they describe a statistically significant relationship between El Niño events and West Coast rainfall, they found that this relationship explained only one-third of the variability in rainfall. They noted that model forecasts do not capture variability related to variations in the 200-hPa height field, which can lead to error in predictions. However, Corringham and Cayan (2019) found that strong El Niño events were highly associated with more frequent and higher magnitude flood insurance losses in coastal Southern California and the Southwest.

Glaciers—Glaciers in the northwest create thermal and flow buffering in many streams throughout the summer once snowpack has melted. Using satellite imagery, Menounos et al. (2019) assessed glacier recession in North America outside of Alaska from 2000-2009. They found that glacier loss in British Columbia and the U.S. West Coast increased fourfold from the 2000s to the 2010s.

Forest management—Spies et al. (2019) reviewed 25 years of performance under the Northwest Forest Plan, identifying strengths and weaknesses of that framework and making recommendations. Spies et al. (2019) concluded with the following summary

statements:

1. Conservation of at-risk species within national forests is challenging in the face of threats that are beyond the control of federal managers.
2. Management efforts to promote resilience to wildfire and climate change include restoring dynamics and structure at multiple scales and revisiting reserve design.
3. Forest restoration can have an ecological and socioeconomic win-win outcome.
4. Human communities benefit from many ecosystem services beyond the supply of timber.
5. Collaboration among multiple stakeholders is essential for achieving ecological and socioeconomic goals.
6. Monitoring and adaptive management are crucial to learning about and addressing uncertainty.

Fires—Increasingly, severe wildfires resulting from climate change and land management practices threaten to impact the habitat of many salmon populations. Martinez et al. (2019) characterized fire refuges (i.e., islands that consistently remain unburned in fire-prone areas) and argued that these refuges should be incorporated into proactive land and fisheries management with climate change.

Haugo et al. (2019) compared large wildfires in the Pacific Northwest during 1984-2015 to modeled historic regimes. They found that the area burned during the study period was an order of magnitude less than that of modeled historic regimes. However, their results suggest that the severity of fires within those areas was much greater in the recent study period. They argued that restoration of natural fire regimes would involve substantially more fires of low to moderate severity.

Stream temperature and flow—Islam et al. (2019) explored how climate change has impacted stream temperatures and flow in the Fraser River. They used the Air2Stream model fit to data from 1950-2015. Results suggest that water temperatures increased during this period by an average of $\sim 1.0^{\circ}\text{C}$, leading to an approximate doubling of the number of days exceeding 20°C at most study sites. Air temperature accounted for $\sim 80\%$ of the variation in stream temperature. Consequently, as air temperatures continues to increase with climate change, their results suggested that stream temperatures in the Fraser River are likely to continue to rise.

Leach and Moore (2019) examined the potential reasons that empirically based statistical models may underestimate the impacts of climate change on stream temperature. Comparing a process-based approach to an empirical approach, the authors argued that empirical models are likely to underestimate climate impacts because they do not generally account for thermal memory, which is primarily related to snow cover.

Additionally, they suggest that groundwater may only make streams resistant to change in the short-term, as groundwater sources will also be impacted on longer time-scales.

Projections

Salish Sea—Khangaonkar et al. (2019) used the Salish Sea Model driven by downscaled outputs from the National Center for Atmospheric Research *community earth system model* to project climate impacts in the Salish Sea. Results suggest that the sea will experience increased temperatures, lower pH, and reduced levels of dissolved oxygen. However, the authors suggest that impacts in the Salish Sea will likely be less severe compared to those on the continental shelf due to strong vertical circulation of waters in the region.

Streamflow—Climate models and simulations generally agree that climate change will lead to less snow accumulation and earlier spring melt in the Pacific Northwest. However, the magnitude of predicted changes varies and is thus more uncertain.

Chegwidden et al. (2019) compared hydrological predictions in 160 different scenarios for the Columbia River Basin. Their analysis particularly explored which aspects of hydrological projections are most uncertain, and what components of the modeling chain are driving those uncertainties. Using representative concentration pathway 8.5 vs 4.5, they concluded that the choices people make affecting carbon emissions (r) have the largest impact on the extent to which snowmelt happens earlier in the spring. Their analysis assumed that the hydrologic response of a shift from snowfall to rainfall was due to rising air temperatures.

However, within a given carbon emissions scenario, certain global climate models (GCMs) tend to produce more warming than others, so specific GCMs also affected the timing of snowmelt in some cases. There was additional variation across GCMs in annual volumes of streamflow, contributing to uncertainty in how precipitation will vary in the future.

Local hydrological processes, which are represented differently by the different hydrological models, had the most influence on the lowest flows of summer. Summer flows were also sensitive to the quantity of summer precipitation, which also varied across GCMs. Thus, the choice of representative concentration pathway and global climate model had the most influence on predictions of streamflow volume and timing. However, the choice of hydrologic model was most influential on predictions of low flows.

California current

"The Blob"

Focusing on the Gulf of Alaska, Freeland and Ross (2019) asked, How unusual were ocean temperatures in the Northeast Pacific during 2014-2018? They found that conditions in the Gulf of Alaska reached over 4.5 standard deviations above normal in certain locations in 2013-2014, and anomalies over 4.0 standard deviations persisted until 2017. The authors discuss how rare such anomalies have been in the past.

The anomalous conditions of the marine heatwave led to an onshore and northward movement of warm stratified waters into the California Current ecosystem off of the West Coast. Brodeur et al. (2019a) examined how micronekton and macro zooplankton community composition and structure responded to this shift in conditions using data from fine-mesh pelagic trawl surveys off the coast of Oregon and Washington from years 2011 and 2013-2016. Their results suggest that the communities present during warm years were highly distinct during 2015 and 2016, with low plankton densities and an invertebrate composition dominated by gelatinous zooplankton.

Brodeur et al. (2019b) provide evidence that forage fish diets during this period responded by shifting to high proportions of gelatinous zooplankton, which are generally considered less nutritionally dense compared to other more commonly consumed prey. Aligned with these results, Baker et al. (2019) found evidence that sand lance *Ammodytes spp.*, a common salmon prey item, had lower condition during the warm years of "The Blob" in the Salish Sea. Brodeur et al. (2019a) warned that these results suggest the potential for a major reorganization of trophic pathways in this normally productive ecosystem.

Morgan et al. (2019) also examined ecological responses to "The Blob" in the Northern California Current. In pelagic surveys, they found that the warm "blob" period was dominated by warm-water gelatinous invertebrates and by many fish species that had previously been very rare or absent. The mix of southern and northern species may have led to novel interactions, but whether this represented an anomaly or a permanent change was unclear.

In another exploration of "The Blob's" ecological consequences, Shanks et al. (2020) described evidence that in 2015 and 2016, many coastal invertebrates failed to spawn or had reduced spawning success in sampling done near the mouth of the Coos Bay estuary in Oregon.

Retrospectives

Physical and ecological connections—Arellano-Torres et al. (2019) used sediment records to explore how marine and terrestrial productivity have been linked over the last 14,000 years in the southern California Current System.

Talloni-Alvarez et al. (2019) reviewed the current state of knowledge regarding the impacts of climate change on Canada's Pacific Ocean marine ecosystems. They describe evidence that ocean temperatures have risen, particularly off the coast of southern British Columbia. There was more uncertainty in their results regarding low dissolved oxygen and acidification. They suggest that Pacific salmon, elasmobranchs, invertebrates, and rockfishes are amongst the most vulnerable species. Finally, they argue that shifting distributions and productivity patterns may have economic impacts on some regional communities.

Waters in the California Current originate from various sources with distinct characteristics, and thus variation in the composition of source waters can impact local conditions. Bograd et al. (2019) examined a long time-series of hydrographic data off of southern California to assess variation in source water masses. Their results suggest that local water-mass structure is significantly impacted by the El Niño Southern Oscillation, with major impacts on regional biogeochemistry and ecosystem structure. These results highlighted the interconnectedness of oceanic regions.

Ocean acidification and low dissolved oxygen—Coastal upwelling ecosystems, such as those associated with the California Current, are known to be vulnerable to the effects of low dissolved oxygen (DO) and ocean acidification as a consequence of climate change. Recent marine die-offs due to hypoxia and unprecedented die-offs at shellfish farms due to acidification have inspired efforts to better understand and predict these events.

Chan et al. (2019) provide an overview of mechanisms and specific threats imposed by low DO and acidification in the California Current. They summarized some of the new research that has recently been published through the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), concluding that these efforts have helped translate the science into new management actions.

A few studies have examined how local ecological processes may interact with ocean acidification. Lowe et al. (2019) examined temporal and spatial patterns in acidification in the Salish Sea in conjunction with local physical and biological processes. In general, they found that pH and the percent of dissolved oxygen have decreased. However, they also found substantial temporal and spatial variability in measurements.

The authors suggest that their work provided evidence of the importance of local ecosystem processes in modulating ocean acidification and they argue for adopting an ecosystem-centric perspective when examining acidification and interacting stressors.

Our understanding of the vulnerability of calcifying organisms to ocean acidification would benefit from increased knowledge of critical thresholds and how these thresholds are impacted by co-occurring stressors (e.g., warming or low DO). Bednarsek et al. (2019) performed a literature review and meta-analysis to identify the impact of ocean acidification and warming on various life stages of calcifying organisms. Additionally, they identified various types of "breakpoints" representing impacts of varying severity for different life stages. They used an expert panel to assign confidence to these designations and identified remaining information gaps.

In their review, Bednarsek et al. (2019) found that an aragonite saturation range of 1.5-0.9 may represent an early warning point for lethal impacts in many species. Their meta-analysis suggests increased sensitivity of some pteropods to shell dissolution induced by ocean acidification and to survival under the combined stressors of acidification and warming. Finally, the authors identified important information gaps around the response of organisms to variability in stressors and to uncertainties in how lab results translate to population responses.

Engstrom-Ost et al. (2019) compared physiological responses to ocean temperatures and pH in copepods vs. pteropods of the California Current. Their samples were collected during the West Coast Ocean Acidification cruise of 2016. The authors found that oxidative stress was less apparent in copepods compared to pteropods. They concluded that copepods had higher adaptive potential due to exhibiting stronger vertical migration behaviors and more efficient glutathione metabolisms, whereas pteropods were more likely to experience mortality during acidic conditions.

Projections

Sea surface temperatures—Jacox et al. (2019) assessed the skill of global climate forecast systems in the North American multi model ensemble in predicting sea surface temperature variability in the California Current. They found that simple persistence forecasts had high predictive skill up to ~4 months. They also found that anomalous equatorward winds, which drive upwelling, were well forecasted during strong El Niño Southern Oscillation events (positive or negative), while the forecasts proved less useful during moderate events. The authors suggest that forecast abilities were better in the northern California Current than in the south.

Upwelling—Global warming is increasing ocean temperatures and water stratification. However, there is some evidence that global warming will intensify upwelling-favorable winds in eastern boundary upwelling systems (EBUS) which may counteract this global trend. Seabra et al. (2019) present evidence that to date, EBUS have experienced less warming than the rest of the ocean, particularly directly along the coast (more so in the Pacific than the Atlantic). This suggests the possibility that EBUS will be somewhat buffered from the impacts of global warming, at least in the short-term.

Arellano and Rivas (2019) examined the interaction between ocean stratification and the potential for increased upwelling with climate change off coastal Baja California in the southern California Current. Using a regional physical-biogeochemical coupled model nested within a global circulation model, the authors predicted the response of primary productivity by mid-century. Their model projected that increased upwelling will generally lead to higher productivity in spring, but that stratification will limit enhanced productivity to a narrow coastal zone during warm summer months.

Upwelling winds are influenced by subtropical anticyclones. Aguirre et al. (2019) used global climate simulations to track anticyclones and project changes to upwelling winds in various eastern boundary upwelling systems, including those in the California Current. Their projections suggest that upwelling winds will shift poleward in most regions, but not the north Pacific.

Hypoxic zones (areas with low oxygen) near shore are expected to expand with climate change. Dussin et al. (2019) explored the relative contribution of two factors that contribute to this effect. They found that declining oxygen in the source waters has twice the magnitude of effect than the excess nitrate concentration in those source waters. However, the two effects together produced a synergistic response, meaning that the cumulative response was larger than the sum of independent impacts of the two factors.

Biological Impacts

Population Trends

A number of papers in 2019 looked at population and demographic trends in Atlantic salmon. Atlantic salmon populations have been declining globally in the last few decades, and the southernmost populations have experienced the greatest declines. Almodovar et al. (2019) analyzed trends in Atlantic salmon in comparison to terrestrial and marine environmental variables in Spain. They describe evidence of a regime shift in biophysical conditions of feeding grounds in the North Atlantic, which occurred in 1986-1987, and which was followed by an acceleration of the anthropogenic warming trend in ocean temperatures. The authors argue that increases in river and marine temperatures and declines in the quality of marine trophic conditions since the regime shift are likely related to observed population declines.

At the northern edge of the Atlantic salmon range, populations with complex age structures (numerous age classes returning to spawn) are still present, and this diversity provides a level of population resiliency. Nonetheless, the frequency of different life history patterns (years in freshwater and at sea) has changed over 40 years. Erkinaro et al. (2019) examined shifts in maturation ages in Atlantic salmon of the Teno River in Norway/Sweden over 40 years of monitoring. Using scales to assess spawning age, they found widespread trends toward fewer years spent at sea, with females commonly spending 3-5 years at sea during the 1970s, but with most spawners now spending just 1-2 years at sea.

In alignment with these results, Olmos et al. (2019) found evidence of widespread declines in ocean age at maturity in Atlantic salmon (described in more detail in *Life Cycle Analysis* section). However, Erkinaro et al. (2019) also found an increase in the number of years spent in freshwater for northern populations, contrary to trends observed elsewhere (see Cline et al. 2019), and thus fish were not necessarily younger at spawning. Furthermore, Erkinaro et al. (2019) found that the frequency of iteroparity (repeat spawning) had increased.

Lehnert et al. (2019) reconstructed changes in effective population size (N_e) of populations of Atlantic salmon throughout its range using a genomics linkage-based method. They found evidence that N_e declined in over 60% of populations, and they associated these declines with water temperature increases. Genomic regions associated with metabolic, developmental, and physical processes demonstrated changes in diversity for declining populations. These changes were consistent with observed shifts in body

size and phenology. The authors discuss the ability of genomic methods to assess population vulnerability.

Cline et al. (2019) used a half century multivariate time-series of sockeye population data from Bristol Bay, Alaska, to examine trends in population age structure. They found evidence that as freshwater environments warmed, a higher proportion of fish began to spend one year (instead of two) in natal freshwater habitats before migrating to the ocean. However, their results also suggest that fish congruently became more likely to spend an additional year rearing in the ocean before maturation. The authors argue that this may be a consequence of the younger age of seawater migration and increasing marine competition for prey from hatchery fish utilizing the same marine habitats.

Steelhead trout *O. mykiss* exhibit significant life history variation. Bowersox et al. (2019) examined trends in the length at age and ocean-age composition of hatchery summer steelhead from Dworshak hatchery on the Clearwater River, Idaho. They found evidence that Dworshak steelhead had become younger in recent years, with length-at-age also having decreased, particularly for older ages. Samples collected from the sport and gillnet fisheries were larger and older on average compared to returns to the hatchery. The authors suggest that changes in adult age and size composition may have resulted from a combination of environmental shifts in ocean conditions and size selectivity in the fisheries.

Shuntov and Ivanov (2019) describe how recent warm ocean conditions have coincided with productive salmon fishery catches in the Russian Bering Sea and northwestern Pacific Ocean. While record catches of pink salmon from the region were the biggest contributor, they also noted high catches of chum *O. keta*, sockeye, and coho in the colder northern areas of the region. However, more southern populations in warmer areas from Sakhalin and the Kuril Islands actually underperformed recent catch projections. In support of these results, Shuntov et al. (2019) suggest that food supply for salmon in the western Bering Sea may not be a limiting factor for production, as evidenced by recent record productivity of pink salmon populations from Russia and plankton surveys.

Pink salmon, primarily from Russia, and Asian hatchery chum salmon have become extremely numerous in the North Pacific (Ruggerone and Irvine 2018). In contrast to the work of Shuntov et al. (2019) in the western Bering Sea, Batten et al. (2018) found evidence of depressed zooplankton biomass in the central and eastern Bering Sea during years of high abundance of Asian pink salmon.

In addition, research suggests that Asian salmon have impacted growth, maturation, and productivity of salmon populations from North America through

competition for prey (e.g., Frost et al. 2020; Ruggerone and Connors 2015). Why the abundance of Asian salmon appears to impact the growth productivity of North American salmon stocks while Russian stocks do not appear to suffer from density dependence in the marine environment remains a source of scientific debate. Finally, Ruggerone et al. (2019) suggest that odd-even patterns in mortality of Southern Resident Killer Whales may be related to pink salmon abundance patterns in Puget Sound.

Vulnerability and Adaptation

Crozier et al. (2019) assessed the climate vulnerability of all anadromous Pacific salmon and steelhead population units listed under the endangered species act. They used an expert based system to score the vulnerability of population units to climate change in terms of magnitude of exposure and existing adaptive potential. Populations identified as highly vulnerable to climate change impacts included Chinook in the California Central Valley, coho in California and southern Oregon, sockeye in the Snake River Basin, and spring-run Chinook in the interior Columbia and Willamette River Basins. Increases in stream temperature, sea surface temperature, and ocean acidification were the most broadly identified climate-related stressors likely to impact populations. The authors conclude that enhancing the adaptive capacity of populations is essential to mitigate climate impacts.

Anttila et al. (2019) suggested that migration conditions act as a strong selective force on cardiac capacity in sockeye salmon populations. Their study found that cardiac sarco(endo)plasmic reticulum Ca^{2+} -ATPase activity (SERCA) differed considerably across populations. They related these differences in SERCA to adult migratory experience, with populations that migrated to higher elevations and experiencing higher temperatures having larger capacities.

The dilution of adaptive traits through genetic hatchery introgression is a major concern for the conservation of wild salmon populations. Bohling et al. (2020) used genetic sequencing to compare wild coho populations in Hood Canal to a local hatchery stock. In this case, wild stocks were highly differentiated from the hatchery stock. The authors interpret this as evidence that minimal interbreeding had occurred.

While increasing temperatures with climate change may extirpate salmon populations at the southern end of their range, warming may also lead to the opportunity for range expansion at the northern extent. Carothers et al. (2019) interviewed native subsistence fishermen in the Alaskan Arctic, documenting new subsistence fisheries that are forming in the region. These results suggest that salmon may have already begun expanding their range into new northern habitats. However, in most of the study area,

such expansion had not been formally documented.

Jonsson and Jonsson (2019) reviewed how temperature exposure during embryonic development impacts later expressed life-history traits in fish. Their review described how delayed effects can be extensive, impacting growth, age at maturation, sex determination, and migration date, among other factors. They suggest that these responses likely occur through plastic epigenetic mechanisms and that these mechanisms may help salmon respond to rapid climate change.

Reed et al. (2019) estimated heritability (h^2) from a 20-year molecular dataset of Atlantic salmon. They found evidence that "sea age" was highly heritable while size at maturity was somewhat heritable, with results suggesting that these traits demonstrate high genetic correlation. However, they described evidence that size within ages was less heritable and argued that their results support the hypothesis that changes in sea age composition are more likely to reflect evolutionary responses while size-at-age responses are more likely to arise from phenotypic plasticity.

Sturrock et al. (2020) discuss how modified riverscapes and managed flows may have led to unnatural selection and a reduced portfolio effect in Chinook salmon of the California Central Valley. In particular, they discuss potential selectivity on juvenile migration timing, which is highly dependent on flow, with fish generally leaving earlier in dry/warm years (Munsch et al. 2019). Managed flows may also have led to unnatural selection on adult run-timing of Chinook in the Trinity River (Sullivan and Hileman 2019).

Similarly, Tillotson et al. (2019) described how sockeye hatchery practices in the Cedar River of Washington may have created selection pressures that contrast with natural selection by introducing environmental change in both adult and juvenile migration timing. Specifically, they suggest that the hatchery has selected for earlier spawning, despite evidence of lower survival for earlier emerging juveniles that stem from early spawners. These authors argued that there is potential for reduction in the productivity of wild populations that interbreed with these hatchery fish.

Abe et al. (2019) performed a laboratory study comparing the metabolic performance of two populations of chum salmon from geographically adjacent rivers in Japan, but whose adult migrations occurred at different times. The early migrating population was larger, migrated further, and experienced substantially warmer sea and river temperatures upon return to freshwater. Their results suggest that early -run fish had higher optimum and critical temperatures, and they discuss the mechanisms that might explain these population differences.

Phenology

Sturrock et al. (2020) focused on how unnatural flows lead to selection on run timing in Sacramento Chinook salmon, while Munsch et al. (2019) focused on the consequences of managed flow to survival in these same stocks. Munsch et al. (2019) found evidence that Sacramento Basin Chinook left freshwater earlier in spring during warm and dry stream temperatures due to high river temperatures. They suggest that this early movement can restrict the freshwater growth period. Earlier migrating fish had smaller body size, which potentially reduces marine survival.

Oke et al. (2019) examined parallel evolution of migration timing in odd- vs. even-year pink salmon of shared environments in Alaska. These populations are genetically isolated despite inhabiting the same stream environments. They describe evidence for strong determinism in migration timing, with only a minor contribution of contingency.

Sparks et al. (2019) suggest that warming will likely lead to earlier emergence times in western Alaskan sockeye. However, they note that substantial variation in emergence timing is supported by a relatively pristine habitat mosaic in this region, which may buffer negative impacts from environmental change.

Thraya et al. (2019) discussed circadian clock genes in Chinook salmon, which may impact behavior such as migration timing. These authors utilized real-time quantitative PCR (RT-qPCR) assays to examine the expression of such a clock system in target tissues. They presented evidence of a functional clock in Chinook salmon, which differed in its rhythm depending on tissue of origin.

Life Cycle Analyses

The life histories of Pacific salmon make them susceptible to impacts from across a wide range of habitats. Life cycle models provide a methodology to account for various controls on productivity throughout these habitats in a single framework. Friedman et al. (2019) developed a life cycle model for Central Valley fall Chinook salmon, a population with few remaining natural spawners. Spawning habitat of this population has lost considerable of heterogeneity compared to its historic condition. Their model suggested that the largest impacts on productivity were temperatures during egg incubation, flows during the juvenile migration, and environmentally mediated marine predation.

In their study of an Atlantic salmon population in Ireland, Honkanen et al. (2019) found that life-stage specific environmental factors explained a large percentage of variability in productivity that was unexplained by Ricker stock-recruit models, which account for density dependence. These authors interpreted their results to support both environmental factors and density dependence as important for productivity.

Olmos et al. (2019) described evidence of an increase in spatial coherence in productivity of Atlantic salmon populations using a Bayesian life cycle model (Europe and North America). Their results suggest that there has been a decline in early marine survival and a trend toward fish maturing younger with more fish returning after one year in the ocean. Similar trends toward earlier maturation have been widely described for Chinook salmon in the Pacific.

Stage Specific Studies

Adult migration and spawning

Connor et al. (2019) provided a comprehensive review of what is known regarding the influence of water temperature and flow rates on the adult migration and spawning success of Snake River fall Chinook. Informed by their literature review, these authors created models to illustrate the potential impacts of change in temperature and flow. Their results suggest that moderate increases in temperature and flow have the potential to impact productivity and diversity by increasing energetic expenditures. Connor et al. (2019) concluded that fish management actions are likely to encounter difficulty in compensating for these impacts.

Goetz and Quinn (2019) examined the movements of Chinook salmon that enter Lake Washington through navigation locks to reach spawning grounds. They found that fish arrived around periods of peak temperature, though many retreated to cooler marine waters. Once in Lake Washington, they did not find evidence that fish made much use of cooler waters below the thermocline before ascending spawning tributaries. Goetz and Quinn (2019) found that compared to sympatric sockeye, these Chinook salmon demonstrated greater temperature tolerance, but they still may need temperature refuges under future conditions. These results align with a recent study from the Snake River which suggested that sockeye in that system were also more sensitive to river temperatures compared to Chinook, despite generally migrating at warmer temperatures (Crozier et al. 2020).

Rub et al. (2019) described evidence that increases in pinniped abundance in the lower Columbia River and estuary, potentially in response to poor marine feeding

conditions, led to a decrease in upstream migration survival of tagged spring-Chinook populations. Using a mixed-effects logistic regression model for survival, they predicted a rate of decrease in survival with additional pinnipeds and described evidence that the presence of American shad, an alternate pinniped prey source, may reduce Chinook mortality.

Teffer et al. (2019) examined the impact of co-occurring thermal and fishery-related stressors on the development of infection burden in coho salmon. In their holding experiment, higher temperatures increased mortality from simulated fishery stressors in all treatments, but the impacts were stronger in females. In contrast, Whitney et al. (2019) found no evidence that fishery interactions and air exposure impacted reproductive success of steelhead caught in winter fisheries in the South Fork Clearwater River in Idaho. However, these fish were caught at cold temperatures (~2-5 °C).

Flitcroft et al. (2019a) compared temperatures and flows experienced by coho populations during their spawning migrations to projected conditions with climate change in three West Coast rivers. They projected that most fish will experience drier conditions on average during their migration if run-timing remains the same. The authors related their results to management options to mitigate impacts.

Copeland et al. (2019) described patterns of iteroparity (repeat spawning) in Snake River steelhead. Iteroparity is rare in these populations, which migrate long distances and must pass numerous hydroelectric dams to reach spawning grounds. The authors found that most iteroparous fish were female, spawned after 1 year, and skipped a year before their second spawn. They hypothesized that survival was low due to the high energetic demands of migration for these populations, considering distance, elevation, and dam passages of the migration route.

Egg incubation

How climate change will impact inter-gravel temperatures, and thus egg incubation times, is an uncertainty in climate change predictions. However, there remains a need to document present temperatures before such predictions can be made. Tuor and Shrimpton (2019) examined differences in temperature during egg development of coho salmon throughout their geographic range in British Columbia. They found that intergravel temperatures varied significantly and were generally warmer than surface waters, particularly in mid-winter. This suggested that salmon were spawning in areas of groundwater influence. In addition, they found higher variation in temperature at southern sites compared to northern sites, which often approached freezing soon after spawning. These authors propose that their results will be helpful when trying to extract incubation temperatures from surface temperatures.

Adelfio et al. (2019) examined how incubation periods of coho salmon were impacted by warm winters on the Copper River Delta in Alaska. During anomalously warm and rainy winters, which they considered a proxy for future conditions at their study sites, they found that the duration of egg incubations was reduced by almost two months on average. They found that reduced incubation periods were longer at spawning sites dependent on surface flows in comparison to those influenced by groundwater flows. Warm winters led to increased synchrony in incubation periods at study sites across the basin which the authors suggested may lead to a reduced portfolio effect and consequently reduced population stability.

However, Campbell et al. (2019) documented similar emergence times and summer growth trajectories for coho in streams geographically adjacent to the Copper River Delta and with highly distinct thermal profiles. This suggests that salmon have some ability to adjust for emergence timing through spawn timing behavior, red site selection, and genetically determined physiological factors that influence egg development rates.

Del Rio et al. (2019) conducted a lab experiment to examine the impacts of high water temperature and low dissolved oxygen on egg development and juvenile tolerances of Chinook salmon. They posited that both temperature and hypoxia are common stressors in gravel beds during incubation and may become more common with climate change. They found that rearing in low DO reduced egg survival, particularly at high temperatures, and that both factors led to increased temperature tolerances. However, they also found that while rearing in low oxygen conditions improved tolerance of hypoxia, potentially through an acclimation responses, rearing at high temperatures reduced tolerance of hypoxia.

External factors that impact the oxygen supply to eggs include dissolved oxygen concentrations and sediment porosity, and both can influence incubation survival. However, egg membrane porosity also plays a role. Bloomer et al. (2019) used electron microscopy to examine membrane thickness, porosity, and permeability to dissolved oxygen in five salmon populations of the UK. Their results demonstrated that membrane porosity was highly variable across populations, and their laboratory experiments showed that membranes with low porosity were less resistant to exposure to low-oxygen conditions. These results suggest that membrane porosity may be a mechanism through which salmon can adapt to changing conditions.

Thorn et al. (2019) examined how natural variation in the fatty acid profile and other egg characteristics influenced egg development across thermal gradients in Chinook salmon. They used fish from three populations in a common garden experiment and

found that the fatty acid profile and proximate composition of eggs was related to size at hatch and gravel departure. They posited that their study supports the hypothesis that egg nutrient composition, which likely varies as a consequence of maternal diet, is a mechanism of transgenerational impacts on offspring.

In another lab experiment, Pasquet et al. (2019) examined temperature impacts on egg malformation and death during hatching and emergence in brown trout. They found that fry that died had higher levels of yolk sac malformation, and that higher temperatures led to higher levels of other deformities, though many of these deformities were not associated with direct mortality. However, lower reproductive success is likely to result from such deformities over the long-term, despite not leading to direct mortality.

Juvenile rearing

Chittaro et al. (2019) examined habitat use and life history strategies of Snake River juvenile fall Chinook using microchemistry analyses of adult otoliths. They found that the majority of fish exhibited the yearling (vs. sub-yearling) migratory strategy and that the mainstem Snake River provided important rearing grounds for both life-history strategies. These results described spatiotemporal patterns in juvenile habitat use and may help inform the management and conservation of these populations.

Myrvold and Kennedy (2019) examined the relationship between growth, consumption, and growth efficiency in different seasons for juvenile steelhead in streams across Idaho. Surprisingly, they found that yearlings grew just as well during winter. However, subyearlings growth was better in summer. Their results suggest that winter growth was closer to total growth potential given the cooler temperatures. Food appeared to be a limiting factor for growth in all seasons, but especially during summer. They suggest that spring migration from natal streams can reduce competition during summer, when demand for food is highest.

Huey and Kingsolver (2019) used bioenergetics models to explore how food intake, activity, and temperature interact to control salmon growth. Their model demonstrated how lower food intake reduces optimal and upper thermal limits for growth. They also discuss the possibility of a "metabolic meltdown," where activity is reduced by increasing metabolic costs associated with higher temperatures, leading to reduced food intake and thus an energetic shortfall. The authors discuss key assumptions and caveats of their models in the context of climate change.

For juvenile salmon that spend one year or more in freshwater, winter periods of limited prey can create a bottleneck for survival. An improved understanding of tge constraints on overwinter survival is important, given that winter conditions will likely be

impacted by climate change. Fernandes and McMeans (2019) examined patterns in seasonal lipid storage of freshwater fishes. In a literature review, they described seasonal lipid accumulation patterns that occurred across a broad range of fish species. Their conclusions highlight how energy accumulated in the summer is important for winter survival in the many cases when food is limited.

Blair and Glover (2019) examined the impact of high temperature exposure (22°C) on the thermo-tolerance of rainbow trout fry two months later. They describe evidence that high temperature exposure reduced the ability of fish to upregulate the *hsp70b* gene, which in turn reduced their critical maximum temperature. These results demonstrate a potential sub-lethal impact of high temperature exposure that could be carried over to future life stages.

In a field study in the Eel River, California, Kelson and Carlson (2019) were surprised to find no evidence that differences in stream flow impacted growth, body condition, or migration timing of juvenile steelhead. They suggest that the muted response to interannual hydrologic variability may have been due to the high-quality habitat provided by the unimpaired, groundwater-fed tributaries to this river, which provided thermal refuge. They concluded that streams offering thermal refuge should be a high priority for conservation and restoration efforts to mitigate impacts of climate change.

Dudley (2019) applied an individual based model in a simulation to examine the impact of flow management decisions on egg incubation and juvenile rearing conditions of Chinook salmon in the Sacramento River, California. They presented evidence that temperature had the largest impact on the final -count of juvenile migrants and that flow had a major impact on red superimposition.

Juvenile migration

Henderson et al. (2019b) examined spatial variation in survival of Chinook salmon smolts migrating through the Sacramento River, California. Similar to Munsch et al. (2019), they described evidence that flow was a primary factor determining downstream survival. Henderson et al. (2019b) concluded that more information on predator densities and distributions could improve model estimates.

Similarly, in a radio tagging study Zeug et al. (2019a) found evidence that flow and fish size were related to downstream migration success of Chinook salmon in the Sacramento River. However, there was spatial variability in the magnitude of these effects, which may have been related to points of high predation. In support of the potential reintroduction of Chinook salmon into the San Joaquin River, Zeug et al.

(2019b) suggest that if fish can access them, floodplain habitats in the San Joaquin Valley could provide suitable growth conditions for such re-introductions.

Payton et al. (2019) used a novel mark/recapture technique to estimate mortality from avian predation on migrating steelhead smolts in the Columbia River. They estimated that avian predators consumed 31% of juvenile steelhead on their way to the ocean, which accounted for the majority of mortality in these river reaches. They asserted that their mark/recapture modelling approach provides a flexible framework for assessing the impact of multiple mortality factors across time or space.

Zhang et al. (2019) examined the impacts of climate change on smolt migration survival by combining statistical migration survival models with climate predictions of Columbia River conditions. They predicted declines in survival for the Lower Columbia and increases in survival for the Upper Columbia.

Woo et al. (2019) described evidence of how estuaries provide a mosaic of habitats that create a portfolio effect supporting Chinook salmon growth and survival during their smolt migration through the Nisqually River Delta, Washington. To achieve this goal they sampled the prey field in five different habitat types and compared these results to Chinook salmon diets.

Ocean rearing

Michel (2019) attempted to decoupled juvenile migration vs. marine survival for Sacramento River Chinook salmon using a "novel combination of tagging technologies." They also examined smolt-to-adult returns (SARs) in three Sacramento River populations with 20-year records. Streamflow had the biggest correlation with SARs in monitored populations, suggesting carryover impacts, but poor marine conditions were also related to lower SAR estimates. This study aligns with that of Munsch et al. (2019), which suggested that flow during juvenile rearing impacted marine survival of Sacramento Chinook by influencing the timing and condition of smolts upon marine entry.

Combining multiple modeling and analytical methods, Henderson et al. (2019a) attempted to identify marine areas with high variability in growth and to relate these areas to marine survival for Central Valley fall Chinook marked with coded wire tags. They characterized growth potential using bioenergetics models informed by temperature estimates from a physical model and secondary production from a biogeochemical model. Growth potential during the first year at sea, which they related to marine survival, was associated with upwelling, detrended sea level anomalies, and onshore/offshore currents. They also presented evidence that spatial variation in predation is important to marine survival.

The specific ocean habitat use of different salmon populations is poorly defined. Espinasse et al. (2019) used carbon and nitrogen stable isotopes derived from an extensive time-series of salmon scales (1916-2016) to examine aspects of the marine environment utilized by sockeye salmon of Rivers Inlet, British Columbia. Using previously described correlations between carbon isotopes and ocean temperatures, the authors were able to identify likely rearing areas before sampling. They argue that this method has potential to help map ocean habitat use of salmon.

Variation in marine productivity and prey quality can greatly impact the marine survival of salmon populations. Litz et al. (2019) repeatedly sampled a population of Chinook salmon and the available prey field off the coast of Oregon and Washington during two summers. In addition, they reared sub-yearlings under laboratory conditions to inform a bioenergetics model for growth. Results suggest that growth rates in the wild were more highly associated with anchovy biomass compared to other available prey species. The authors suggest that identifying factors that control the availability of important prey species such as anchovy is important to improve our understanding of salmon growth and survival during the early marine period.

Kohan et al. (2019) examined the relationship between a suite of marine variables and the size, condition, and abundance of juvenile chum captured during summer in Icy Strait, southeast Alaska. Results were in alignment with previous work suggesting that a strong Aleutian Low is related to good conditions for salmon recruitment in the region. However, the authors describe evidence of major impacts from local drivers, including freshwater discharge.

Seitz et al. (2019) performed a study using pop-up satellite tags to explore late marine mortality of Chinook salmon in the Bering Sea. They found high levels of predation on Chinook, primarily by salmon sharks as suggested by stomach temperature readings post-mortality. They used their results to suggest that the extent and impacts of late-marine mortality in these fish may be under-appreciated. Strom et al. (2019) also used pop-up satellite tags to assess adult marine mortality of Atlantic salmon from varying populations. They found that 14% of tagged fish experienced predation, with endothermic fish being the most common predators.

Shelton et al. (2019) constructed a coast-wide state-space model to estimate stock- and age-specific distributions of fall Chinook in the Pacific Ocean using data from fish tagged during 1977-1990. Results suggested that Chinook salmon ocean distributions depended strongly on region of origin and varied seasonally. Estimated survival patterns also appeared to vary substantially by region.

Williams et al. (2019) found evidence from a lab experiment that predicted levels of ocean acidification may impair olfactory function in coho salmon. Coho salmon that were exposed to elevated acidity stopped avoiding skin-extract odor that elicited an avoidance response in a control group of fish. They interpreted this behavioral shift as a consequence of disruptions in the expression of genes related to signaling from the olfactory bulb.

Habitat

Anim et al. (2019) examined tradeoffs in urban stream restoration objectives between restoring more natural flow regimes and restoring channel morphology. They examined four test scenarios comparing urban vs. natural channel morphology and hydrology on ecologically relevant metrics. They suggest that once channel morphology has been degraded, flow regimes cannot maintain natural channel hydraulics. Accordingly, they suggest that maintaining and rehabilitating channel morphology should be prioritized.

Boisjolie et al. (2019) described how variation in management standards across federal, state, and private lands creates a patchwork of habitat protections for salmon within watersheds. Due to salmon depending on connected habitats across their various life-stages, this can complicate recovery efforts. As an example, Boisjolie et al. (2019) used GIS to map and analyze habitat fragmentation in coastal coho salmon streams in Oregon. They found that watersheds with high intrinsic potential to support coho were associated with substantial gaps in protective standards. The authors discussed the implications of these results for population-scale restoration and recovery efforts.

Diversity of habitat can support population productivity and stability. Environmental variability inevitably leads to shifting periods of higher productivity in some types of habitat but lower productivity in others. Thus diversity and connectivity of habitat makes it more likely that some aspect of a watershed will be productive, no matter what the environmental conditions are.

Brennan et al. (2019) provided an in-depth illustration of how this process, which they term the "shifting habitat mosaic," can support Pacific salmon productivity. They used strontium isotope records from otoliths to track juvenile salmon movements and growth in the Nushagak River, Alaska and described spatial patterns in salmon productivity across numerous years.

Their findings suggest that productivity and habitat use varied greatly across the watershed from year-to-year and across the season as conditions changed. They argue that the connectivity of habitats within the watershed allowed fish to continually access productive habitats as conditions in previously productive habitats became less favorable. Brennan et al. (2019) posited that the shifting habitat mosaics is a central feature of ecosystem resiliency, which must be recognized and fostered in management to maintain productivity.

Flitcroft et al. (2019b) reviewed the existing literature on habitat connectivity among environments inhabited by Pacific salmon. They found the literature dominated by freshwater studies, with few articles focusing on marine or estuary habitats. They suggest that studies bridging environment types are rare, highlighting a gap in our understanding of complex habitat relationships that may impact our ability to address factors limiting productivity in conservation planning. Finally, the authors suggest the need for more interdisciplinary research teams to address this gap.

Chalifour et al. (2019) described the spatiotemporal use of habitat mosaics in the Fraser River estuary. They demonstrated that salmon used a variety of habitats types (sand flat, marsh, eelgrass) but were most common in marsh habitats. While some species were found to use multiple habitats, others were only found in a single habitat. Similar to Woo et al. (2019), the authors suggest that their findings support the importance of interconnected and diverse estuary habitats to support juvenile salmon.

Unfortunately, the extent of historical wetlands throughout the range of salmon streams has been poorly mapped. To address this gap, Brophy et al. (2019) generated maps of historical and present tidal wetlands for the entire contiguous West Coast of the United States. This effort accounted for 44 estuaries, representing the vast majority of tidal wetland habitats, and included an estimate that about 85% of historical habitat has been lost.

Given the importance of habitat connectivity, the removal of both total and partial anthropogenic barriers in less pristine streams may greatly increase watershed productivity and stability. Buddendorf et al. (2019) provide a framework for prioritizing the removal of migration barriers in restoration efforts by integrating habitat quality and river connectivity models. In a study of brown trout in Spain, Gonzalez-Ferreras et al. (2019) used a population dynamics model to simulate the population impacts of increasing habitat connectivity by removing barriers.

In a simulation modeling study, Armstrong et al. (2019) suggested how complexity in watersheds can increase interactions between salmon and wildlife. They used an example of from the Wood River Basin, Alaska, to describe how diversity of

habitat leads to spawning at different times, thus increasing the temporal availability of salmon to bear foraging. Through their modeling they suggest that watershed development would reduce habitat complexity, leading to a temporal restriction in spawning dates and thus less bear foraging, even if abundance is not changed. The authors used their results to challenge the methods of many environmental impact assessments which generally only account for changes in abundance.

Helaire et al. (2019) documented how modern development has impacted characteristics of the lower Columbia River. Their results suggest that increased channel depths and a loss of marshes have led to an increase in tides and river velocities and a decrease in baseline water height.

Martens et al. (2019) provided an assessment of stream conditions in small fish-bearing streams 18 years following passive riparian restoration. They concluded that using only passive restoration, conditions in streams are unlikely to improve salmonid production in the short-term. They suggest that second-growth forest needed more time to mature and increase light penetration into streams to support production.

In an assessment of stream conditions as a function of riparian corridor length and macroinvertebrate communities, Stanford et al. (2020) found that longer riparian corridors had higher percentages of invertebrates sensitive to disturbance, lower water temperatures, and less fine sediments. The authors suggest that restoration of long riparian corridors may be an economically efficient way to mitigate the impacts of climate change in some stream systems.

Parasites and Stressors

The myxozoan parasite *Ceratomyxa shasta* is a major contributor to mortality in salmon in the Klamath River, California. Schakau et al. (2019) suggested that dam releases can diminish the spore count of *C. shasta*. However, they argue that infection risks are likely to increase with climate change due to lower flows and higher temperatures.

Large infection burdens appear to limit some steelhead from passing hydraulically challenging river reaches. Twardek et al. (2019) assessed infection loads of steelhead in relation to migration passage of falls in the Bulkley River, British Columbia. Steelhead sampled below the falls had higher infection burdens on average compared to those sampled above, which led the authors to suggest that higher infection burdens were related to passage failure.

Hamre et al. (2019) explored how the growth rate of salmon lice *L. salmonis* is impacted by temperature. They infected Atlantic salmon with the lice and monitored their development at temperature treatments ranging 2-24°C. They found that lice developed normally from 6 to 21°C, and development rates were reduced outside this range. Results suggested that development was faster at the higher end of that range with the relationship between growth and temperature described by a second order polynomial.

In developed environments, exposure to high levels of ammonia from runoff sources such as sewage, agriculture, and industrial waste is a commonly encountered threat to fish. However, ammonia does not act in isolation, and physiological impacts can interact with other climate change effects, such as higher temperature, acidification, and lower percentages of dissolved oxygen (DO).

Franklin and Edward (2019) examined how high ammonia concentrations can interact with salinity gradients to impact fish, an issue particularly relevant to aquaculture operations in estuarine environments. Similarly, Giroux et al. (2019) examined the combined influences of exposure to high temperatures and common pyrethroid pesticides on pre-smolt Chinook salmon. They documented potential disruption of hormonal and signaling pathways in alevin and fry.

Methodology

The use of passive integrated transponder (PIT) tags to assess salmon movement and survival has become widespread. Bond et al. (2019) argued that the presence of "ghost tags," or PIT tags that remain in river systems following the death of tagged fish, could confound analyses of tag data. In a coastal California stream, they documented a substantial buildup of ghost tags that moved downstream with live fish during high flow events.

Cochran et al. (2019) compared abundance and tag-based estimates of marine survival for coho salmon across multiple years in three California streams. Abundance-based estimates tended to be higher than tag-based estimates—in some cases multiple times higher. These authors suggested that one potential cause of this discrepancy is the migration of small juveniles from the native rearing habitat before they can be enumerated by smolt trapping, which likely underestimates total population size in abundance-based estimates. Cochran et al. (2019) concluded that the two estimation methods are not comparable.

Levi et al. (2019) found that flow-collected eDNA tracked closely with the quantity of returning sockeye and coho spawners and migrating smolts. They suggested that their results support the use of eDNA methods for the enumeration of salmon, as opposed to just their presence. However, to get the most accurate results, their methods require accurate flow data. In addition, they warn that results from their method will be more robust in species with simple life histories and thus less variation in the size of individuals.

Management

Cook et al. (2019) provided a synthesis of factors that led to post-release mortality of fisheries bycatch. They described how different commercial fishing methods can lead to such mortality and outline ways in which impacts could be mitigated. These authors identified minimizing the duration of handling and good handling procedures as particularly important. They argue that trawls and hanging net fisheries are the most harmful types of fisheries, as they offer limited opportunities for minimizing impacts to bycatch.

Feddern et al. (2019) assessed selectivity in the Port Moller test fishery for sockeye salmon in Bristol Bay, Alaska. In 2011 one-half of the nets in the fishery were reduced in mesh size to limit selectivity for larger and generally older sockeye (ocean age 3). Their assessment showed that selectivity for fish of greater length was largely reduced following the mesh size change. However, they suggest that residual selectivity remained in the test fishery due to differences in girth between age classes.

In a radiotelemetry study of recreational fisheries for steelhead in the Clearwater River, Idaho, Feeken et al. (2019) present evidence of limited overlap between anglers and wild fish. They suggested that the Clearwater fishery is highly compartmentalized, allowing for recreational opportunities with minimal impact to wild populations.

Using a survey of 96 Elders, to record Traditional Ecological Knowledge, de Echeverria and Thornton (2019) examined perceived impacts of climate change in indigenous communities of British Columbia and Southeast Alaska. Their results suggest that residents of these communities have observed significant environmental and ecological changes during their lifetime, with an acceleration of changes in the last 15-20 years. The authors suggest ways that this knowledge can be used to support communities in their response to environmental change.

Portfolio effects in aggregated populations can create stability in overall abundances and thus in dependent fisheries. Weakened portfolio effects due to habitat deterioration/fragmentation or changing selection pressures from environmental change can lead to increased synchrony in populations, and thus higher overall variation in abundance. Freshwater et al. (2019) argue that declines in the portfolio effect have impacted the probability of meeting management objectives for Fraser River sockeye salmon. The authors suggest that management strategies that do not account for aggregate variability in abundance may underestimate risk.

Hayes et al. (2019) reviewed the literature on hydropeaking of reservoirs in relation to impacts on salmonids. They suggest that during migration and spawning, flows should be kept relatively stable, and flow limits should be implemented to prevent dewatering during incubation and hatching. They point out that emerging fry are particularly sensitive to flow variations, but as fish grow they become less sensitive to flow variability. Schulting et al. (2019) suggest that hydropeaking operations should ramp up more slowly to allow for macroinvertebrates to seek refugia before peak flow events.

Zarri et al. (2019) examined how environmental flows for Chinook salmon in the Sacramento River have negatively impacted sturgeon, which requires warmer water. They argue that their results highlight how it can be difficult to manage for multiple species.

Turner et al. (2019) explored how climate change may create more power generation shortfalls in the northwest due to changing hydrology impacting hydropower. They suggest that increased peak loads for daytime cooling are likely to coincide with lower summer flows, creating substantial potential for power supply shortfalls.

Commercial salmon harvest has declined due to lower abundance, but also due to lower allowable catch to protect a few intercepted populations in mixed fisheries. In an exploration of the impacts of these catch limits, Walters et al. (2019) argue that catch reductions have not helped struggling populations and that management needs better assessment of cost-benefit ratios for making regulations.

Management strategies to mitigate rising stream temperatures with climate change will be important to limit impacts on salmonids. Baker and Bonar (2019) used a pre-existing stream temperature model (stream segment temperature model) to examine how climate change will change thermal tolerance exceedance and other environmental parameters in Apache trout streams *O. apache* of Arizona. They used the modeling to discuss the potential effectiveness of various restoration options.

California Cooperative Oceanic Fisheries Investigations (CalCOFI) has generated a long-running time series of hydrographic and biological data since 1949. Gallo et al. (2019) use the CalCOFI program to examine how long-term ocean observing programs can inform ecosystem based management and the needs of stakeholders working on climate change adaptation. They suggest that the lessons learned from CalCOFI can be applied to other regional monitoring programs, including smaller scale efforts in developing countries.

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