Impacts of Climate Change on Salmon of the Pacific Northwest

A review of the scientific literature published in 2018

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Highlights

Long-term trends in warming have continued at global, national and regional scales. Globally, 2014-2018 were the 5 warmest years on record both on land and in the ocean (2018 was 4th). Recent events, including the 2013-2016 marine heatwave (Jacox et al. 2018a), have now been attributed directly to anthropogenic warming in the annual special issue on extreme events (Herring et al. 2018). Unprecedented phenomena occurred during the recent marine heatwave, including a range expansion of a subtropical crab (Sadowski et al. 2018), shifts in pelagic fish (Auth et al. 2018), die-offs of Cassin's auklets (Jones et al. 2018b).

Major product releases included the 4th National Climate Assessment and the River Management Joint Operating Committee projections of naturalized stream flows for Columbia River Basin (RMJOC 2018). We now have very high confidence that anthropogenic effects are evident and will profoundly affect our region. Projections are similar to previous analyses, and confidence has increased: air temperatures will increase, snowpack will decline, with greatest effects on streamflow in the Snake River Basin (see also Ahmadalipour et al. 2018; Jiang et al. 2018). Hydrological models predict increasing extremes in both high and low streamflow in the western U.S. (Naz et al. 2018) generally and the Blue Mountains in the Snake River Basin specifically (Clifton et al. 2018). Stream flows and temperature will be affected by impacts of climate change on agriculture and forests. Stream temperature projections for the PNW explored the western U.S. as a whole (Isaak et al. 2018b), focusing on thermal refuges (Krosby et al. 2018), and most specifically on tailwater temperatures (Jager et al. 2018).

A crucial intermediate stage between streams and oceans is the estuary stage. A new study projects nearly complete loss of existing tidal wetlands along the U.S. West Coast, due to sea level rise (Thorne et al. 2018). California and Oregon showed the greatest threat to tidal wetlands (100%), while 68% of Washington tidal wetlands are expected to be submerged. Coastal development and steep topography prevent horizontal migration of most wetlands, causing the net contraction of this crucial habitat.

For salmon, correlations between freshwater and marine survival have important consequences for population dynamics. Synchrony between terrestrial and marine environmental conditions (e.g., coastal upwelling, precipitation and river discharge) has increased in spatial scale causing the highest levels of synchrony in the last 250 years (Black et al. 2018). Salmon productivity (recruits/spawner) has also become more synchronized across 24 wild Chinook populations from Oregon to the Yukon (Dorner et al. 2018). Contrary to previous summaries which found that northern and southern stocks

had inverse responses to ocean temperatures, the current analysis found positive pairwise correlations between nearly all stocks. Although a few populations tended to be less correlated with others, there was no latitudinal trend in correlations.

Chinook salmon from California to Alaska, like other species, are maturing younger and smaller than they did historically, with stronger trends in the northern stocks (Ohlberger et al. 2018b). Siegel et al. (2018) attributed younger maturation in certain Alaskan Chinook salmon to faster growth in the second ocean year, with both genetic and environmental drivers. Climate change might select for later upstream migration timing in Snake River fall Chinook (Plumb 2018), although selective fishing can depresses heterogeneity in run timing and thus reduce resilience to climate change (Tillotson and Quinn 2018). There is some evidence of recent biological and human adaptation to climate change (Miller et al. 2018), but mostly papers documented historical adaptations to climate. Future adaptive potential is limited by loss of genetic diversity, such as that documented between ancient and modern Chinook in mid-Columbia River and Snake River Basin (Johnson et al. 2018).

New projections of sea surface temperature were released in 2018 indicating that the California Current will be 3°C warmer during 2070-2099 compared with 1976-2005 (Alexander et al. 2018), and the coolest year will be warmer than the warmest year in recent history. Rather than adapt in place, widespread poleward distribution shifts are expected (Morley et al. 2018).

Projections of more intense upwelling due to stronger alongshore winds were made by Xiu et al. (2018), and due to a positive correlation with SST (Addison et al. 2018). De-oxygenization and ocean acidification of marine waters are important concerns, and were reviewed and modeled by numerous authors, including the additive and interacting effects of multiple stressors. A rare review of effects of acidification on freshwater biota will be useful in accounting for full life cycle effects on salmon (Hasler et al. 2018). However, a study of Atlantic salmon found that early marine growth was not reduced in a high CO₂ treatment (McCormick and Regish 2018). Numerous papers focused on how physical characteristics retain upwelled water, setting up areas of especially high productivity, and recommended protecting these habitats proactively (Barcelo et al. 2018; Cox et al. 2018; Fiechter et al. 2018; Shanks and Morgan 2018). A simplified food web model used threshold generalized additive models to explore how bottom-up and top-down regulation may alternate in the southern California Current Ecosystem under different climatic conditions (Lindegren et al. 2018).

A climate vulnerability assessment of 1,074 marine species found 157 species as highly vulnerable, but only a few species-specific results are available (Jones and Cheung 2018). Salmon have declined globally, and analyses attempting to explain these trends have pointed to complex drivers in Atlantic salmon (Soto et al. 2018) and Puget Sound salmon (Sobocinski et al. 2018). One paper specifically attributed climate change to declines at the southern range edge in Spain via water temperatures (Nicola et al. 2018). However, earlier river ice retreat (Cunningham et al. 2018) and warmer ocean temperatures may improve survival to maturity for Chinook salmon at the northern extent of their range in the Yukon River (Cunningham et al. 2018; Siegel et al. 2018), though concerns over the impacts of declines in average size and age-at-maturity remain for these populations. Specific studies of high winter flows found a negative effect on pink salmon (Milner et al. 2018) and brook trout (Blum et al. 2018). Low flows were found to constrain Olympic Peninsula coho (Ohlberger et al. 2018a). The timing of smolt migration timing in Atlantic salmon in Nova Scotia suggested higher temperatures would lead to earlier emigration through energy depletion, which could create a mismatch with ocean conditions (Strople et al. 2018) (or poorer marine survival due to size-selective mortality). Interactions between temperature and other stressors, e.g., from fisheries, tagging, or hatchery fish, greatly increased mortality. Thermal refuge use was tracked in Columbia River Chinook and steelhead, showing large differences among runs (Keefer et al. 2018).

The importance of habitat complexity with climate change is receiving more attention (e.g., Herbold et al. 2018) but an interesting new study documented a systematic relationship in England for 430 climate-threatened and range-declining species. They found that the buffering effect of microclimatic variation was greater in the regions that experienced the greatest warming, where local extirpation was reduced by 9-12% (Suggitt et al. 2018).

In sum, updated projections of change are similar to or greater than previous projections. We are increasingly confident in our projections because every year brings stronger validation of previous predictions in both physical and biological realms. Retaining and restoring habitat complexity, access to climate refuges (both flow and temperature), and improving growth opportunity in both freshwater and marine environments are strongly advocated in the recent literature.

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Objective and Methods

The goal of this review was to identify literature published in 2018 that is most relevant to prediction and mitigation of climate change impacts on Columbia River Pacific salmon *Oncorhynchus* spp. listed under the 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 512 papers, 233 of which were included in this summary.

Literature searches were conducted in March 2019 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. We used specific search criteria that included a publication year of 2018, plus:

- A topic that contained the terms climate,¹ temperature, streamflow, flow, snowpack, precipitation, or² 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 major parts, with the first considering changes to the physical environmental conditions that are both important to salmon and projected to change with climate. Such conditions include air temperature, precipitation, snowpack, stream flow, stream temperature, and ocean conditions. We describe projections driven

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.

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 Changes in Climate and Ocean Conditions

Global climate change

Retrospective

Global annual mean surface temperatures have exceeded the long-term average (1880-2018) every year since 1977, according to the National Centers for Environmental Information (NCEI 2018). The years from 2014 to 2018 were the five warmest on record, and in 2018, global annual mean surface temperatures were the fourth warmest on record: both land and ocean temperatures met this criterion, as did the combination of the two (Blunden and Arndt 2019). The long-term increase in global temperature has been 0.07°C/decade from 1880 to 2018 and a faster 0.17°C/decade since 1970 (NCEI 2018).

In 2018 the Bulletin of the American Meteorological Society published a special issue, *Explaining Extreme Events of 2016 from a Climate Perspective* (Herring et al. 2018). While scientists have long predicted that climate change would create climatic conditions beyond the realm of natural variability, this issue was the first to include manuscripts concluding that some extreme events during 2016 would not have been "possible in pre-industrial times." Specific events identified included record global temperatures, a heat wave in Asia, and the North Pacific marine heat wave known as the "Blob." Further identification of unprecedented events caused by global warming is likely to become common in coming years.

Fine-tuning and updating climate models is an ongoing process. Laloyaux et al. (2018) provided a coupled reanalysis of atmospheric, ocean, land, ocean wave, and sea ice conditions during the 20th century from a climate model ensemble. Compared to previous reanalysis efforts, their dynamical model and data assimilation systems were updated to better account for radiative forcing and the observing system. The updated reanalysis shows improvements over previous efforts, particularly in the representation of atmosphere-ocean heat fluxes and mean sea level pressure.

Decadal-scale climate variability patterns can affect global estimates of surface temperature and thus obscure the signal of climate change. Chen and Tung (2018) utilized an empirical orthogonal function analysis in an attempt to describe the influence of large-scale climate indices on estimates of global temperature. Results suggest that the Pacific Ocean effects these estimates primarily on interannual time scales through the El Nino-Southern Oscillation (ENSO) pattern, while the Atlantic contributes strongly to global means through the Atlantic Multidecadal Oscillation.

Projections

Alexander et al. (2018) assessed projected changes in sea surface temperature in large marine ecosystems of the northern hemisphere utilizing an ensemble of global climate models. Utilizing the RCP 8.5 "business as usual" scenario for greenhouse gases, they compared a 1976-2005 baseline period to projected change through the 21st century. While substantial differences in predictions existed between models, there was general agreement in predicting positive trends in mean temperature. Changes in mean temperature were predicted to supersede historical interannual variability, with SSTs always being warmer during 2070–2099 than during the warmest baseline year in most regions. Trends were generally strongest in the summer. Ensemble model means suggest average increases of about 3°C in the California Current Ecosystem during 2070-2099 compared to the baseline period.

Coastal zones around the world are threatened by runoff, which can lead to influxes of nutrients, metals, and organic pollutants. The impacts of pollutants often interact with temperature and thus may worsen with climate change. Lu et al. (2018) provided a global-scale review of threats to coastal zones as a consequence of climate change. Coasts of the western Atlantic and eastern Pacific were hotspots for industrial pollution and degradation related to semi-closed seas which retain water. Northern California also showed high increases in some pollutants. More active management may be necessary to limit the effects of climate change interacting with pollutants.

Climate change may increase plant growth and farm productivity at higher latitudes where the growing season is generally limited by temperature. However, the ability of plants to take advantage of warmer conditions may be limited in some cases by seasonal water availability. Isaac-Renton et al. (2018) suggested that northern boreal forests at the edge of their range may not increase in growth as a response to anthropogenic warming due to a lack of physiological adaptation to drier conditions.

Monitoring and modeling

Climate change is leading to dramatic changes in the arctic environment; however, year-round monitoring is limited in the region due to the challenging environment, and this restricts our understanding of impacts. Hauri et al. (2018) described the Chukchi Ecosystem Observatory off the coast of northwestern Alaska, one of the few year-round moored monitoring arrays in the arctic. Data from this observatory were combined with ship-based observations to produce a time-series of change in seasonal sea ice, water temperature, and ecosystem responses.

National climate change

Retrospective

In 2018, the National Centers for Environmental Information reported that in the U.S., land surface temperatures in 2018 were 0.83°C warmer than the long-term average from 1880 to 2018 ((NCEI 2018). Since 1970, annual mean land temperatures in the U.S. have warmed faster than the global average, at a rate of 0.28°C/decade.

The U.S. Global Change Research Program published Volume I of its *Fourth National Climate Assessment* (NCA4) in 2017. This volume catalogues observed changes in climate and future projections (USGCRP 2017). Volume II of NCA4 was published in 2018 and catalogues the numerous ways in which environmental change brought on by climate change threatens health and economic prosperity in the U.S. (USGCRP 2018). This second volume of the NCA4 is an extensive report covering a wide range of likely economic and ecological climate impacts at national and regional scales, as well as ways to reduce impacts through adaptation measures and emission reductions. Chapter 7 describes the risk of climate change to ecosystems and ecosystem services such as fisheries (Carter et al. 2018).

An increased frequency of extreme weather events is one predicted consequence of climate change. Armal et al. (2018) identified trends in extreme rainfall events in the contiguous U.S. Using information from 1,244 rainfall stations, they found statistically significant trends in 742 stations, with almost all trends toward a higher frequency of extreme rain events. They concluded that most of these trends could be largely explained by anthropogenic changes in air temperature (n = 409), while others, including those in the west and northwest, (n = 293) were better explained by a combination of anthropogenic changes in air temperature and large-scale climate signals such as El Niño and the Pacific Decadal Oscillation.

Climate change is often described in terms of changing average conditions; however, climate change will also impact the variability of conditions, which may have equal or greater importance to ecosystems. Previous research has shown that productive winter upwelling conditions in the California Current are set up by the North Pacific High (NPH), and that these conditions are negatively correlated with precipitation and river flow in the west. Black et al. (2018) demonstrated that as variability in the NPH has increased, terrestrial and marine conditions have become more synchronized across larger spatial scales. Higher levels of environmental synchrony could lead to increased levels of synchrony in the life histories of Pacific salmon populations if selection for life history strategies is constricted. For example, Dorner et al. (2018) demonstrate that productivity of Chinook salmon has become more synchronized across the species range, particularly on the regional scale. Lower levels of diversity have been shown to generally reduce overall population productivity and viability (Schindler et al. 2015).

Projections

As demonstrated by Armal et al. (2018), extreme rainfall events have already increased in the U.S. Naz et al. (2018) predicted future climate change impacts on extreme hydrological events at 138 headwater subbasins upstream from 33 reservoirs across the nation from 2011 to 2050. They utilized the variable infiltration capacity (VIC) hydrologic model forced by a downscaled and bias-corrected ensemble of climate models informed by the RCP 8.5 emissions scenario. Results suggested wide-scale increases in the frequency of high streamflow in the central U.S. and of low streamflow in the western U.S. Frequencies of high and low streamflow are likely to increase in the majority of subbasins upstream from hydropower and flood control reservoirs, providing future challenges for water management.

Tidal wetlands are important rearing habitat for juvenile salmon and help to ameliorate economic damage from storm surges. Sea level rise threatens to submerge tidal wetlands on U.S. coasts. Thorne et al. (2018) predicted that all or nearly all existing high and middle marsh habitats along the West Coast are likely to be lost by 2110, across conservative to higher sea level rise scenarios. California and Oregon showed the greatest threat to tidal wetlands (100%), while 68% of Washington tidal wetlands are expected to be submerged. Coastal development and steep topography prevent horizontal migration of most wetlands, causing the net contraction of this crucial habitat.

Climate change will alter the extent and distribution of agricultural land in the U.S. Mu et al. (2018) projected that crop land will expand across the northern and interior western U.S., while decreasing in the south, though the extent of change depends on the modeling scenario.

Monitoring and modeling

Water managers and ecologists are interested in the ability to predict future hydrologic conditions with climate change. However, confidence in the prediction of hydrologic metrics depends on the ability of models to describe hydrologic processes in a changing environment. Ekstrom et al. (2018) discussed the need to evaluate the validity of model inputs used to produce climate change projections of hydrological metrics under future conditions. Specifically, they aim to raise awareness regarding issues with input metric formulation, input data, and the context of management decisions.

West Coast climate change

Retrospective

In the northwestern U.S. mean annual temperatures were substantially cooler in 2018 than in the record warm year of 2015, although the mean in 2018 was still 1.06°C higher than the long-term average of 1880-2018 (NCEI 2018). Since 1970, change in mean annual temperature in the northwestern U.S. has occurred at a rate similar to that of the entire country, increasing 0.27°C/decade and remaining above the long-term average in all but two years since 1986.

Multi-year droughts, and generally drier summer conditions, are predicted to become more common in the western U.S. with climate change. Deitch et al. (2018) examined how a multi-year drought from 2012 to 2015 affected discharge and stream connectivity in a salmon-bearing coastal system in California. Each year of the drought saw progressively lower streamflows and increasing channel disconnection, with flows in 2015 at only 10-20% of 2012 levels. Additionally, discharge in the year following the drought was lower than would have been expected based on precipitation only, suggesting a lagged effect of drought on stream flow.

Projections

The River Management Joint Operating Committee³ commissioned a climate change study for the Columbia Basin which was published in 2018 (RMJOC 2018). Results of this study demonstrated that air temperatures in the basin have already warmed ~1.5°F since the 1970s and are predicted to increase another ~3-10°F by the 2070s, depending on future emissions. There is more uncertainty in predictions for precipitation; however, most models suggest that winters will become wetter while summers will generally become drier. Snowpack decline is predicted to continue, with an earlier spring transition leading to generally higher streamflows in fall and winter with lower flows in summer and late spring. The greatest changes in streamflow are predicted to occur in the Snake River Basin, though there are high levels of uncertainty in predictions for this region. In California the frequency of extreme dry and wet conditions is also predicted to increase (Swain et al. 2018).

Ishida et al. (2018) projected the effect of climate change on snowpack accumulation in watersheds of the Sierra Nevada mountains of northern California. They simulated 21st century conditions forced by two global climate models (ECHAM5 and CCSM3) and four emission scenarios (A1B, A1FI, A2, and B1) downscaled to a 9-km

³ The River Management Joint Operating Committee is comprised of staff from the Bureau of Reclamation, U.S. Army Corps of Engineers, and Bonneville Power Administration.

resolution utilizing a regional model. While the magnitude of trends depended on the emission scenario, extensive declines in snowpack were predicted in all the ensemble-average results. Declines are likely to have environmental impacts, as well as effects on drinking water, irrigation, flood control, and hydropower generation.

Ahmadalipour et al. (2018) examined sources of uncertainty between climate change projections from ten CMIP5 global climate models and two downscaling procedures for the Columbia River Basin. A historical period of 1970-2000 was simulated and a future period of 2010-2099 was projected under RCP 4.5 and RCP 8.5. Historical comparisons suggested that Bayesian model averaging (BMA) was more accurate than individual models. Increases in annual precipitation and temperature across the basin were projected to varying degrees by BMA, and uncertainty associated with the choice of GCM was the main contributor to total uncertainty. Uncertainty associated with the downscaling method is important, particularly for summer projections (representing ~10-20% of total uncertainty). Uncertainty associated with emissions scenarios (RCP 4.5 or 8.5) grew as projections progressed further into the future.

Jiang et al. (2018) examined the consistency of climate projections downscaled for the Pacific Northwest. They found differences in temperature predictions between downscaling methods, particularly for coastal and high-elevation areas. Precipitation predictions also varied for high-elevation areas, rain shadows, and other arid areas. The authors provide guidance for selecting datasets for climate change impact studies in the Pacific Northwest.

Water availability and competition

A number of papers examined the potential effects of climate change on agriculture in the northwest. Some crops, such as dryland cereal grains, are expected to become more productive, yet competition for water is likely to increase due to lower summer flows and increased evapotranspiration. This competition will likely challenge water management efforts to balance agricultural vs. environmental needs. Addressing these challenges while maintaining productivity and sustainability will require transdisciplinary efforts and stakeholder involvement (Eigenbrode et al. 2018).

Cooper et al. (2018) examined whether the magnitude of low river flows in the western U.S., which generally occur in September or October, are driven more by summer conditions or the prior winter's precipitation. They found that while low flows were more sensitive to summer evaporative demand than to winter precipitation, interannual variability in winter precipitation was greater. Malek et al. (2018b) predicted that summer evapotranspiration is likely to increase in conjunction with declines in snowpack and increased variability in winter precipitation. Their results suggest that low

summer flows are likely to become lower, more variable, and less predictable.

As climate change reduces summer water availability, it may become increasingly important to secure environmental flows to support imperiled salmon populations. The *Columbia Basin Water Transactions Program* is a flow-restoration partnership that has been operating since 2002. McCoy et al. (2018) described a framework for tracking the implementation and effects of water transactions within the program. They suggest that better understanding of program efficacy can inform future flow-restoration and adaptive management efforts.

Water-intensive agricultural production may face the largest challenges under future conditions. For example, Houston et al. (2018) examined potential strategies to make specialty fruit agriculture more resistant to warmer and drier summers. Neibergs et al. (2018) explored the potential for increased cattle production costs. However, warming temperatures in the Pacific Northwest may lead to increased productivity of grain farms (Karimi et al. 2018; Rajagopalan et al. 2018).

Malek et al. (2018a) performed an economic analysis to determine if irrigators should adopt more efficient technologies to minimize the impacts of projected drier summers. They used a large-scale, grid-based modeling framework that mechanistically simulated hydrologic and agricultural processes to estimate economic tradeoffs in the Yakima River Basin in Washington. Results suggest that investing in more efficient irrigation technologies can provide economic benefit to farmers under the expected conditions of climate change. However, the authors warn that under extreme climate scenarios, more efficient technologies do not provide economic benefit because of reduced productivity. In a survey of wheat farmers in the northwest, only 18-28% of respondents planned to take moderate- to large-scale actions in response to predicted climate change (Roesch-McNally 2018).

The effect of climate change on ground water availability is likely to be uneven. Sridhar et al. (2018) coupled a surface-flow model with a ground-flow model to improve predictions of surface water availability with climate change in the Snake River Basin. Combining the VIC and MODFLOW models (VIC-MF), they predicted flow for 1986-2042. Comparisons with historical data show improved performance of the combined model over the VIC model alone. Projections using RCP 4.5 and 8.5 emission scenarios suggested an increase in water table heights in downstream areas of the basin and a decrease in upstream areas. Such assessments will help stakeholders manage water supplies more sustainably.

Forests

Climate change will impact forests of the western U.S., which dominate the landscape of many watersheds in the region. Forests are already showing evidence of increased drought severity, forest fire, and insect outbreak. Additionally, climate change will affect tree reproduction, growth, and phenology, which will lead to spatial shifts in vegetation. Halofsky et al. (2018b) projected that the largest changes will occur at low- and high-elevation forests, with expansion of low-elevation dry forests and diminishing high-elevation cold forests and subalpine habitats. Halofsky et al. (2018a) also assessed climate adaptation strategies for forest management in the region.

Forest fires affect salmon streams by altering sediment load, channel structure, and stream temperature through the removal of canopy. Holden et al. (2018) examined environmental factors contributing to observed increases in the extent of forest fires throughout the western U.S. They found strong correlations between the number of dry-season rainy days and the annual extent of forest fires, as well as a significant decline in the number of dry-season rainy days over the study period (1984-2015). Consequently, predicted decreases in dry-season precipitation, combined with increases in air temperature, will likely contribute to the existing trend to of more extensive and severe forests fires.

Beyond environmental factors, management practices have left forests more dense and less diverse, which increases vulnerability to fire damage. Attempting to restore forest composition to a state more similar to historical conditions would likely increase fire resiliency, though methods to do so are often contentious (Johnston et al. 2018).

Agne et al. (2018) reviewed literature on insect outbreaks and other pathogens affecting coastal Douglas-fir forests in the Pacific Northwest and examined how future climate change may influence disturbance ecology. They suggest that Douglas-fir beetle and black stain root disease could become more prevalent with climate change, while other pathogens will be more affected by management practices. Agne et al. (Agne et al. 2018) also suggested that due to complex interacting effects of disturbance and disease, climate impacts will differ by region and forest type.

Stream Temperature and Flow

Factors affecting stream temperature

As described above, wildfires are increasing in frequency and intensity throughout the west as a consequence of climate change. Wildfires have been shown to lead to higher stream temperatures through combustion heat as well as through increased levels of solar radiation from loss of riparian canopy. Koontz et al. (2018) showed that streams are generally warmer following a burn event and that the strength of this effect depends on the size of the burned area. However, David et al. (2018) reported that wildfire smoke can have a cooling effect. They quantified wildfire smoke utilizing high-resolution satellite imagery and quantified its effect on stream temperature in the lower Klamath River Basin in Northern California, utilizing linear mixed-effect models. Results suggested that dense smoke significantly reduced stream temperature, likely through the vectors of reduced solar radiation and lower air temperatures.

One use of stream temperature models is to identify the best ways to ameliorate the effects of climate change with habitat restoration or preservation. The potential role of riparian vegetation in mitigating the effects of climate change has been increasingly recognized in the literature. Fabris et al. (2018) utilized a physical stream temperature model to incorporate simulations of run-off that could affect juvenile Atlantic salmon. Simulations included heat-transfer estimates to examine the effect of riparian stream shading during the low-flow season of a Scottish stream. Results suggest that riparian vegetation moderates both nighttime cooling and daytime warming rates and thus restricts daily temperature oscillations.

Isaak et al. (2018a) sought to identify variation in seasonal patterns of stream temperature across heterogeneous landscapes. They used principal component analysis to analyze stream temperature regimes in relation to an extensive list of metrics for streams in the mountains of Idaho. Four principle components accounted for 93.4% of the total variation in streamflow. The first was associated with magnitude and variability and the second with winter length and intensity. Daily variation in stream temperature was much smaller in winter than in summer. Knowledge of such patterns can improve our understanding of climate impacts on habitat diversity and can improve predictions of location-specific climate impacts on stream residents.

Heatwaves are expected to increase in duration, frequency, and intensity with climate change. Piccolroaz et al. (2018) explored the effect of three historical heatwaves on stream temperature in different types of rivers (regulated, lowland, and snow-fed) in Switzerland. Lowland rivers were particularly sensitive to heatwaves, while snow-fed and regulated streams demonstrated muted responses.

Winfree et al. (2018) examined landscape influences on stream temperature in streams from Southeast Alaska. Utilizing regression and time-series analyses, they found summer temperatures higher and water temperatures more sensitive to air temperatures in watersheds with lakes. Winter temperatures were warmer in watersheds with higher forest coverage and more lakes, and mean temperature ranges were much wider in summer (4.0-17.2°C) than in winter (0.5-3.5°C).

Zheng et al. (2018) combined long-term measurements of rainfall, snow, and streamflow in six Western U.S watersheds. They found that peak streamflow was most affected by peak snow accumulation, snow-free days, and the speed of snowmelt. Anomalies in streamflow were related to variation in anomalies of snow accumulation. For interior basins, the majority of stream flow originated as snowpack, while for coastal basins, stream flows were more driven by rainfall. Such baseline data on how these processes contribute to river flow are needed to gauge potential impacts on water supply from predicted snowpack decline and changing rainfall patterns.

Modeling

Most statistical stream temperature models depend primarily on the relationship between air and water temperatures. However, due to a number of factors, including the high heat capacity of water and the mediating influence of ground-water sources, the effect of air temperature on stream temperature generally lags and varies spatially, depending on stream characteristics. Culler et al. (2018) explored variability in the sensitivity of stream temperature to air temperature and how sensitivity changed with stream order and discharge in an uninhabited New Hampshire watershed. Results demonstrated that changes in stream temperature lagged behind those in air temperature, that stream temperature changes were generally lower in magnitude than those of air temperature, and that smaller headwater streams were generally less sensitive to air temperature but more sensitive to discharge than other streams. The authors discuss how such modeling can help predict the effects of various restoration scenarios.

Jackson et al. (2018) developed a statistical model for spatiotemporal stream temperature estimates across Scotland. Their approach was novel in that it incorporated methodology for both temporal and spatial autocorrelations while predicting daily estimates of maximum stream temperature. Temporal autocorrelation was modeled within sites and spatial autocorrelation was modeled at the regional and river network scale. Interactions between some variables were considered to help describe variation in effects across time and space. Their models produced accurate and precise predictions were, despite the lofty goal of predicting continuous daily estimates across an entire region. Solar radiation is a major driver of stream temperature; thus, riparian shading can greatly reduce maximum water temperature. Loicq et al. (2018) used data derived from light detection and ranging (LiDAR) to estimate the effects of riparian shading on solar radiation at a fine scale. Shading data was incorporated into a one-dimensional stream temperature model fit to the Loir River in France. Results suggested that riparian vegetation can lead to a cooling effect of multiple degrees, particularly in smaller channels. Seixas et al. (2018) also used LiDAR data to examine the effect of riparian shading on stream temperature in the Chehalis River Basin in Washington State. They developed a tree-growth model and incorporated the effects of tree growth into a pre-existing model predicting stream temperature changes with climate change through 2080. Results suggested that increases in canopy cover can considerably mitigate increases in stream temperature, particularly in smaller channels.

Watson and Chang (2018) tested the utility of distance-weighted variables to examine the effects of landscape characteristics on a set of stream temperature metrics. Fitting models to a number of watersheds in the Portland-Vancouver metropolitan area, the authors found mixed support for distance-weighted variables over simple surface area proportions, depending on the metric being predicted. Models of mean daily range in stream temperature were improved using distance-weighted variables, while those for seven-day moving average daily maximum temperature were not.

Projections

Jager et al. (2018) assessed how climate change might increase the risk of violating thermal and flow thresholds below dams in the Pacific Northwest. They modeled tailwater temperature and flow informed by downscaled CMIP5 climate projections and found that with climate change, thermal and flow thresholds were exceeded with increasing regularity throughout the region.

Isaak et al. (2018b) examined recent trends in stream temperature across the Western U.S. using a large regional dataset. Stream warming trends paralleled changes in air temperature and were pervasive during the low-water warm seasons of 1996-2015 (0.18-0.35°C/decade) and 1976-2015 (0.14-0.27°C/decade). Their results show how continued warming will likely effect the cumulative temperature exposure of migrating sockeye salmon *O. nerka* and the availability of suitable habitat for brown trout *Salmo trutta* and rainbow trout *O. mykiss*. Isaak et al. (Isaak et al. 2018b) concluded that most stream habitats will likely remain suitable for salmonids in the near future, with some becoming too warm.

Streams with intact riparian corridors and that lie in mountainous terrain are likely to be more resilient to changes in air temperature. These areas may provide refuge from climate change for a number of species, including Pacific salmon. Krosby et al. (2018) identified potential stream refugia throughout the Pacific Northwest based on a suite of features thought to reflect the ability of streams to serve as such refuges. Analyzed features include large temperature gradients, high canopy cover, large relative stream width, low exposure to solar radiation, and low levels of human modification. They created an index of refuge potential for all streams in the region, with mountain area streams scoring highest. Flat lowland areas, which commonly contain migration corridors, were generally scored lowest, and thus were prioritized for conservation and restoration.

Fullerton et al. (2018) utilized remotely sensed high-resolution water temperature information to describe fine-grained thermal heterogeneity in numerous streams of the Pacific Northwest and California. Heterogeneities in the water column are difficult to capture without spatially continuous data. Results demonstrated diversity between river systems in the expression of thermal heterogeneity. Within-river patterns in heterogeneity were predicted to shift with climate change in many rivers. Such shifts may affect cool patches in streams, which presently serve as thermal refuges for migrating salmon.

Clifton et al. (2018) predicted effects of climate change on the semi-arid Blue Mountains in northeastern Oregon. Their predictions mirrored those for other parts of the Pacific Northwest: warmer temperatures will reduce snowpack, which will result in generally higher winter flows and lower summer flows. Additionally, higher predicted peak flows will increase erosion and scour. Reduced availability of water in the summer will effect aquatic ecosystems and restrict water supplies for agriculture, municipal consumption, and livestock grazing. The authors argue that proactive adaptation measures such as road design and water management should be implemented.

Frans et al. (2018) applied a glacio-hydrological model to predict mass change in glaciers and resulting changes to river discharge from 1960 to 2099. Results suggested that the rate of glacial decline will increase, with mixed changes in summer runoff. In high-elevation basins, glacial melt will ameliorate declines in snowpack until the later 21st century, when glaciers become too small to make up the difference. However, lower elevation basins will see continued declines in summer streamflow as a consequence of both small glacier decline and reduced snowpack.

A few papers from regions outside the U.S. examined predicted future stream temperatures in relation to fish populations. Vigliano et al. (2018) explored present habitat use of salmonids and perch in relation to thermal habitat and food availability in northern Patagonia. They examined projected changes in habitat availability as a consequence of climate model predictions informed by emission scenarios RCP 4.5 and 8.5 through the 21st century. Fish did not use all thermally suitable habitat available, and often used habitat outside of their defined thermal niches. Food availability appeared to drive habitat use. This study shows how complex interactions between physical and biological conditions will determine salmonid response to environmental change.

Dugdale et al. (2018) utilized a deterministic, processed-based model to examine potential effects of climate change on stream temperature in the lower St John River in eastern Canada. Following calibration of the model to historic conditions, they projected 21st century stream temperatures forced by meteorological conditions from a regional climate model. Results suggested increases in temperature of approximately ~1°C by 2070-2074 and more by the end of the century. The authors suggest that these changes are likely to hinder Atlantic salmon but help striped bass.

California Current

Retrospective

Harvey et al. (2018) reported the status of a comprehensive suite of ocean ecosystem indicators in the California Current Ecosystem during 2017. They describe 2017 as a transition year between the marine heat wave of 2013-2016, including the strong El Niño of 2015-2016, and more "normal" ocean conditions. Indicators of temperature circulation along the West Coast, abundance of forage fish, squid, and krill species, and growth of California Sea Lion *Zalophus californianus* pups were closer to long-term averages. However, anomalously warm water masses persisted in 2017, along with anomalously high abundance of southern copepods and pyrosomes. Ocean catches of juvenile salmon were also low in 2017.

A number of papers focused on how local topographic features and circulation patterns influence spatial patterns of productivity in the California Current. Fiechter et al. (2018) utilized a physical-biogeochemical model for retrospective analysis of alongshore phytoplankton variability in the California Current during 1988–2010. Results suggest that while strong upwelling generally occurs near major topographic features, high concentrations of phytoplankton only occur when local circulation patterns lead to retention of upwelled nutrients on the shelf.

Barcelo et al. (2018) utilized information from marine surveys in the northern California Current (1990-2015) to identify places where species richness and community persistence remains high despite environmental fluctuations. They identified a refuge off the southern coast of Washington, suggesting that upwelling regions with retentive topographic features, such as wide continental shelves, can function as marine refuges. Identification of marine refuges could become increasingly important as a management tool to support resiliency with climate change.

Larvae in coastal upwelling ecosystems are highly vulnerable to offshore transport, and thus depend on the above described retentive areas. Larval and phytoplankton subsidies to intertidal zones may be in-part controlled by surf-zone hydrodynamics as opposed to upwelling processes (Shanks and Morgan 2018). Drake et al. (2018) described how active shoreward swimming boosts the nearshore larval supply in the California Current.

Non-mobile marine species with higher temperature tolerances and/or greater dispersal ability may be better able to adapt to changing climate conditions. Sorte et al. (2018) evaluated a biophysical process in mussels that could support persistence in the face of changing conditions, either by promoting poleward dispersal or by increasing the prevalence of more thermal-tolerant phenotypes. They utilized intensive field observations from 2014 to 2015 with coastal circulation models. Poleward dispersal was found to increase under downwelling conditions, and thermal tolerance was higher in cohorts that experienced higher variability in temperature during dispersal. Consequently, climate-driven changes in wind patterns, which will affect upwelling currents, will likely have indirect impacts on species adaptability.

To facilitate conservation and management of continental shelf ecosystems, Cox et al. (2018) provide a synthesis of the key habitats preferred by foraging marine mammals and seabirds. Important habitats include shelf-edge fronts, upwelling and tidal-mixing fronts, offshore banks, regions of stratification, and topographically complex coastal areas with strong tidal currents. The importance of these habitat features is related to their ability to create densities of prey in a predictable manner, or related to making prey accessible to predators, thus increase foraging efficiency. Future conservation should aim to protect the viability of such habitats.

Coastal upwelling fronts are generally considered bio-aggregators across trophic levels, leading them to be important feeding grounds. However, how plantivorous fish interact with marine fronts has received little attention. As marine fronts also tend to be places with strong environmental gradients (e.g., temperature and salinity), Sato et al. (2018) hypothesized that the physiological tolerance of species would likely have a larger impact on their distributions than the distributions of zooplankton prey. Fish distributions were consistently found offshore of the front in warmer waters, while zooplankton concentrations were generally highest around the 200 m isobath regardless of the position of the front. These results suggest that the upwelling front acts as a barrier to prey access for many mid-trophic level fish species and the location of the front largely determines the amount of overlap between prey and predators.

Marine sources of upwelled, nutrient-rich water and the fate of organic matter after upwelling are not well understood. High-resolution models suggest that the majority of deep-water nutrients originate offshore, outside of the California Current (Frischknecht et al. 2018). Not all upwelled nutrients are utilized by the nearshore ecosystem; thus inorganic and organic nutrients are transported back offshore, supporting the open ocean ecosystem and contributing to carbon sequestration in that environment. Examining sediment deposition in Monterey Bay, Castro et al. (2018) found that about 4-5% of primary productivity was transferred to the deep ocean. In a study of the southern California Current, Stephens et al. (2018) found that in some cases, as much carbon accumulated in sinking sources as in non-sinking reservoirs that may be transported to the open ocean. Their results aligned with those of Frischknecht et al. (2018) in suggesting that coastal upwelling may be an efficient CO₂ sequestering process.

Our understanding of ecological processes in the California Current was challenged by two papers in 2018. Hogle et al. (2018) provided evidence that iron may limit phytoplankton productivity in subsurface chlorophyll-maximum layers, where the limiting factors were generally thought to be light availability and nitrate flux. Phytoplankton had robust responses to increased iron or iron + light treatments in experimental incubations. Based on proxy estimations, diatoms in the California Current may be persistently iron deficient during spring and summer growing seasons and the prevalence of iron deficiency may have increased in recent decades. Hogle et al. (Hogle et al. 2018) suggested that iron-limited productivity may be common in upwelling zones worldwide.

In the Northeast Pacific Ocean, productivity has generally been considered to be regulated by bottom-up processes. However, Lindegren et al. (2018) explored the dynamics and relative importance between bottom-up and top-down forces during variable conditions in the southern California Current using a generalized food web model. While bottom-up forces were found to be primary, the authors describe an alternative mode of regulation represented by interacting bottom-up and top-down regulation. Biota were shown to respond distinctly to El Niño events based on the signal of the Pacific Decadal Oscillation. Results suggest that pelagic fish may be more sensitive to exploitation during El Niño events.

Improvements in estimates of consumption by predators and the dynamics of prey switching can lead to more effective understanding and management of ecosystem dynamics in the California Current. Warzybok et al. (2018) developed a bioenergetics model describing the prey requirements of common bird predator species and projected variability in avian consumption of common forage fish species. They suggested that increased consumption of forage fish by predators such as seabirds may contribute to stress on commercially important stocks.

In central California, sea lion diets changed substantially with environmental variability, largely in proportion to prey availability (Robinson et al. 2018). However, some predator species may respond to environmental change in unexpected ways. For example, Schmidt et al. (2018) utilized a theoretical model to assess the response of Brandt's cormorant *Phalacrocorax penicillatus* to increase or decrease in the frequency of ENSO oscillations. They predicted that an increase in ENSO variability would lead to higher adult abundance and a reduced probability of extinction.

The extent of climate warming that has already occurred may have had positive effects on productivity in the Humboldt Current System off the coast of Peru by leading to increases in coastal upwelling of nutrients (Salvatteci et al. 2018).

Projections

Addison et al. (2018) explored patterns in upwelling-driven marine productivity during the Holocene utilizing sediment cores. Due to correspondence between sea surface temperature records and the increase in magnitude of late Holocene upwelling off of northern California, the authors suggested that warming in the California Current may be conducive to upwelling intensification. However, they warn that the relationship between SST and upwelling may not hold, considering that the mechanisms forcing variability in SST may differ in the future with climate change.

Modeling performed by Xiu et al. (2018) also suggests that climate change will lead to an intensification of upwelling due to stronger alongshore winds. Xiu et al. (2018) also suggest that climate change will increase water stratification in the California Current while enhancing nutrient flux from the deep source waters. They describe the difficulty in predicting ecosystem responses to predicted physical changes due to a range of co-occurring processes at different scales.

"The Blob"

A number of papers addressed causes and impacts of the marine heat wave known as The *Blob*, which appeared in the North Pacific Ocean between 2014 and 2016, and which significantly impacted many marine species and fisheries. Several of these papers were included in a special issue of the Bulletin of the American Meteorological Society, *Explaining Extreme Events of 2016 from a Climate Perspective* (Herring et al. 2018). One contribution attributed origins of the *Blob* to a confluence of multiple co-occurring natural drivers whose effects were likely exacerbated by anthropogenic warming (Jacox et al. (2018a).

A contribution from Du and Peterson (2018) compared phytoplankton communities sampled in the northern California Current in 2011-2013 to those sampled during the *Blob* period of 2014-2015. They described three phytoplankton community compositions utilizing cluster analysis. The first, based on samples taken during the upwelling season, was characterized by high abundance and diversity of diatoms. The second was a pre-upwelling/relaxation community characterized by low abundance and diversity of diatoms and dinoflagellates. The third was based on samples taken during the warm anomaly with reduced diatom abundance and diversity but high dinoflagellate diversity. Warm-water anomalies during the *Blob* period appear to have led to range expansion into northern California for the subtropical crab *Portunus xantusii* (Sadowski et al. 2018). This species was never detected in regional surveys before 2016.

Auth et al. (2018) documented shifts in the timing and spawning locations of pelagic fish stocks in the northern California Current based on larval sampling during the peak of warm conditions in 2015-2016. They documented the highest larval abundances and earliest spawn timing, along with northerly shifts in distribution for a number of species. Results demonstrated that for numerous ecologically and commercially important fish species, spawning phenology and distribution dramatically shifted in response to the *Blob*. These authors suggest that the *Blob* marine heat wave could be an indication of future conditions under projected climate change.

Jones et al. (2018b) investigated causes of the unprecedented die-off of Cassin's Auklets *Ptychoramphus aleuticus*, a small zooplankton-eating seabird, throughout the California Current ecosystem in 2014-2015. They presented evidence that the die-off was a consequence of warm-water anomalies during the *Blob* period, which led to a higher prevalence of lipid-poor zooplankton species. This investigation provided an example of how a higher frequency of marine heat waves may have complex impacts on future food webs and ecosystem structures.

Morrow et al. (2018) compared productivity, grazing, and carbon export processes between conditions in the southern California Current during the warm-water anomalies of 2014-2015 vs. the El Niño of 2015-2016. The relationship between carbon export and controlling processes was similar during both periods. However, during the anomalously warm years, net primary production was lower under similar light and nutrient conditions, and mass-specific grazing rates were reduced at low-to-moderate chlorophyll levels. Morrow et al. (Morrow et al. 2018) proposed further study to determine whether these changes were due to species composition differences or other causes. Vazquez-Cuervo and Gomez-Valdes (2018) explored variability in salinity anomalies of the southern California Current Ecosystem during the *Blob* period. They aimed to determine the utility of using remote sensing data from the Soil Moisture Active Passive (SMAP) Mission, which has previously been used to estimate marine surface salinities, by comparing SMAP with in-situ data from the California Cooperative Oceanic Fisheries Investigations (CalCOFI). These authors suggest that observed differences between SMAP and CalCOFI were consistent with previously described increases in stratification during 2015 and changes in the mixed layer depth. SMAP observed fresher-than-normal anomalies down to the coast of Baja California.

Modeling and monitoring

Jacox et al. (2018b) presented new marine indices, which aim to more accurately estimate upwelling strength and nutrient concentrations of upwelled waters in the California Current. They contend that these new indices, which are available from 1988 to present, will provide monitoring value and increase our understanding of the impacts of upwelling on the California Current Ecosystem.

Flexas et al. (2018) presented a method to optimize sampling of ocean fronts utilizing autonomous gliders combined with Regional Ocean Modeling System (ROMS) model output. Model output was used to direct gliders to areas with high environmental gradients, while the gliders simultaneously validated model output.

Chao et al. (2018) assessed the accuracy and precision of a near-real-time, three-dimensional modeling system for the California coastal ocean. Their system is composed of a Regional Ocean Modeling System forced by the North American Mesoscale Forecast System. Validated against independent observations, respective temperature and salinity values showed root mean squared differences of 0.7-0.92°C and 0.13-0.17. Validation of depth-averaged currents derived from spray gliders demonstrated a largely accurate reproduction of seasonal variations in flow patterns.

Similarly, Zaba et al. (2018) examined the ability of data-constrained state space estimates of the California Current to reproduce its physical features as measured by the California Underwater Glider Network. The authors suggest that state space estimates captured patterns observed by gliders, including mean states, annual cycles, and interannual variability.

Productive regions represent a small fraction of ocean waters but account for a disproportionate amount of productivity and biogeochemical processes. However, the range of chlorophyll concentrations in productive regions can be difficult to model. Consequently, chlorophyll concentrations are poorly represented in the global earth

system models often utilized to project climate change impacts on marine ecosystems. Van Oostende et al. (2018) combined downscaling with the integration of a biogeochemical model that included three size-classes of phytoplankton linked to higher trophic levels. They successfully reproduced high chlorophyll concentrations in a model of upwelling areas in the California Current. The biogeochemical component allowed the model to better capture coastal hypoxia along the continental shelf and likely improved the representation of ecological dynamics.

Complex interactions between river currents and tidal flows largely determine the dynamic extent of usable salmonid habitat and are difficult to model. Sandbach et al. (2018) described current and sediment transport patterns in the Columbia River estuary utilizing a shallow-water model informed by field measurements. Results demonstrated the complexity of interactions between tidal, fluvial, and topographic influences in determining how habitat changes over time.

Acidification and Dissolved Oxygen

Retrospective

Substantial natural variation in oceanic carbon chemistry and limitations in baseline information make it difficult to isolate anomalies in ocean acidification. To better understand the dynamics of ocean acidification, increases in scale are needed for temporal and spatial estimates of marine inorganic carbon concentrations. To address this need regionally off the coast of Northern California, Davis et al. (2018b) developed an empirical model based on existing hydrographic measurements to estimate spatial and temporal patterns of Aragonite concentration. Their results demonstrated lower aragonite concentrations at depth during anomalous the warm conditions of 2014-2015 and highlighted the connection between low aragonite concentrations and upwelled waters.

In a similar study focused on the Pacific Northwest, Fassbender et al. (2018) combined data from a variety of sources to analyze temporal and spatial patterns in ocean carbon chemistry. Results suggest that organisms living in inlet harbors, including the Salish Sea and Hood Canal, are exposed to larger seasonal changes in acidity than those living in open ocean environments. Inlet waters may have lower buffering capacities, making them less efficient at absorbing carbon and thus more sensitive to ocean acidification.

El Niño–Southern Oscillations (ENSO) have been shown to be related to the biogeochemical and physical properties of waters in coastal upwelling regions. Turi et al. (2018) utilized a global climate model to investigate the influence of ENSO oscillations

on oxygen content and acidity in the California Current. Oxygen responded most strongly offshore, while the response of pH was limited to coastal areas. Results suggest that oxygen in surface waters responds to variability in temperature which affects solubility while pH is driven by dissolved inorganic carbon, which is determined by upwelling. These results highlight the effects that ENSO oscillations can have on the California Current in addition to the effects of climate change.

Levin (2018) provides an extensive review of literature related to ocean deoxygenation, including its causes and ecological effects. She suggests that declines in ocean oxygen over the past century are well documented and understood to be a consequence of the effects of climate warming on solubility, stratification, and possibly respiration. Deoxygenation trends have been stronger in some regions, including the North Pacific, and tend to be most severe in mid-shelf waters. Many other natural and anthropogenic factors can exacerbate the effects of deoxygenation. Ocean deoxygenation is complex, depending on physical, biogeochemical, and ecological process. Consequently, accurate modeling and forecasting will require interdisciplinary efforts.

Projections

Marine uptake of anthropogenic carbon dioxide mitigates global warming, but leads to ocean acidification. Eastern boundary upwelling systems are likely to be particularly sensitive to ocean acidification due to the naturally occurring upwelling of relatively acidic waters. Franco et al. (2018) utilized the Regional Ocean Modeling System to explore past and future changes in pH and CaCO³ concentrations in the Humboldt Current System off the coast of South America. Results suggest that climate change will lead to year-round under saturation of calcite by the end of the century if climate change continues unabated.

Palter and Trossman (2018) utilized models to predict how changes in ocean circulation may affect deoxygenation with increased atmospheric CO_2 concentrations. While results suggested that global warming will cause widespread deoxygenation, shifts in ocean currents were expected to moderate oxygen loss to some extent. Dissolved oxygen declines were predicted to occur primarily due to changes in mixing and O_2 solubility, particularly in the Southern Ocean. While ocean circulation is predicted to slow increasing the residence time of deep sea water, this slowing is predicted to have only a small effect due to low metabolic rates at depth.

Ecological impacts

Ocean acidification is a global phenomenon overlaid by pronounced regional variability and modulated by local physics, chemistry, and biology. Recognition of the multifaceted nature of acidification and its interplay with other ocean drivers has led to

international and regional initiatives to establish observation networks and develop unifying principles for biological responses. Threats presented by ocean acidification to ecosystem services and the socio-economic consequences, are becoming increasingly apparent and quantifiable. To address the challenges of a future ocean acidification, Hurd et al. (2018) argue that we need better experimental designs and more rigorous testing of adaptation capabilities and mitigation/intervention strategies.

Jones et al. (2018a) assessed vulnerability to ocean acidification for species in the nearshore environment of Olympic National Park, Washington. They used available experimental evidence combined with expert opinion to assess vulnerability in 700 marine invertebrate and algal species. Results reinforced the paradigm that shell-forming organisms in the intertidal zone are most sensitive to ocean acidification, but also highlighted knowledge gaps.

Past research has suggested that bacteria on molluscan shell surfaces could damage the periostracum, a thin organic coating, making shells more prone to dissolution. Bausch et al. (2018) examined the influence of bacteria on shell dissolution in gastropod larvae and pteropods under the conditions of ocean acidification. In general, antibiotics were found to reduce shell dissolution in gastropod larvae, but not in adult pteropods. Results suggest that the effects of bacteria on the resistance to shell dissolution may differ between organism and life-stages.

Bednarsek et al. (2018) provided new insight into the physiological responses of pteropods to multiple stressors and how these stressors may limit tolerance. In 2016, the combination of a marine heat wave and El Niño event exposed pteropods in the California Current to co-occurring high temperatures, low aragonite concentrations and pH levels, and deoxygenation. Bednarsek et al. (2018) utilized oxidative stress biomarkers to analyze the cellular status and antioxidant defenses of pteropods. Results suggested that temperature and aragonite concentrations were the most important variables in determining biological response. Some physiological responses to multiple stressors were determined to be additive, while others demonstrated interactions. The accumulation of oxidative damage under combined high temperature and low aragonite conditions/pH conditions necessitated metabolic compensation, suggesting energetic trade-offs under such conditions.

In examining the effects of ocean acidification on zooplankton, most experiments focus on single species. These experiments have shown that ocean acidification can greatly affect development, physiology, and skeletal mineralization. However, impacts to individual species may also change trophic interactions alter ecosystem equilibrium. In an experimental setting Hammill et al. (2018) examined the effects of ocean acidification on interactions between a cubozoan predator and its zooplankton prey, including

Copepoda, Pleocyemata, Dendrobranchiata, and Amphipoda. The combined effects of predation pressure with ocean acidification had a larger impact on prey species than would have been predicted by additive effects alone. These results suggests that the ecological consequences of ocean acidification are likely to be larger and more complicated than indicated by single-species experiments.

In a lab experiment, Coll-Llado et al. (2018) found that gilthead sea bream larvae exposed to low pH conditions (pH7.3) were more likely to incur calcite growth on their otoliths, as opposed to the normal formation with aragonite crystals. They observed higher otolith growth rates in more acidic treatments. This may affect fish hearing, orientation, and balance.

In another experimental study, Gilmore et al. (2018) tested the effects of prolonged hypoxia exposure on juvenile golden perch *Macquaria ambigua ambigua* and silver perch *Bidyanus bidyanus*. Golden perch demonstrated a substantially higher tolerance and ability to acclimate to hypoxia exposure in comparison to silver perch. The distinct response of these two related species demonstrates our lack of understanding of how individual species will respond to an increase in freshwater hypoxic conditions with climate change.

Gomez et al. (2018) explored the physiological response to acidification of a deep-sea coral present in the California Current Ecosystem, *L. pertusa*, by examining calcification and feeding behavior under varying aragonite concentrations. While feeding rates did not change among treatments, *L. pertusa* was found to exhibit net calcification in favorable conditions and net dissolution in unfavorable conditions. Results suggest an increasing frequency of suboptimal conditions in the California Current could threaten the persistence of this species.

Compared to the effects of acidification on marine ecosystems, little attention has been paid to the effects on freshwater biota. Hasler et al. (2018) reviewed the existing literature on the effects of weak acidification on freshwater ecosystems. Most recent studies focused on the physiological responses of fish at the organism level. Many animals exhibited reduced growth rates, while primary producers generally demonstrated increased growth. The authors describe a need for more studies to focus on the potential for weak acidification to effect freshwater biota, particularly its effects on community structure and ecological regimes.

Biological Responses of Salmonids to Climate Change

Large-Scale Ecosystem Impacts

Global warming and anthropogenic loss of biodiversity represent profound threats to ecosystem functionality. These two factors are often examined in isolation, but likely have interacting effects on ecosystem function. Garcia et al. (2018) examined how changes in temperature and biodiversity affect ecosystem function utilizing an experiment with microbes. Their results suggest that under thermal stress, more diverse ecosystems maintained higher functionality. These results imply that the extensive loss of biodiversity already experienced has left global ecosystems with less resiliency to absorb the impacts of climate change.

Pelletier and Coltman (2018) argue that the most pervasive anthropogenic threats to biodiversity include over-exploitation, habitat change, climate change, invasive species, and pollution. They describe how these influences can effect population genetic variability and consequently induce microevolution in wild populations. They review recent studies that explore the effects of such influences on biodiversity and call for a better predictive framework that integrates microevolution to anthropogenic forces in forecasting population status with climate change.

While climate change studies often focus on means and variability, climatic conditions are generally autocorrelated. For example, residuals of the warming trend of mean global air temperatures are autocorrelated due to the effects of multi-year indices, such as the El Niño–Southern Oscillation and the Atlantic Multidecadal Oscillation (Chen and Tung 2018), which influence global mean temperatures. Paleo-climate records suggest that the strength of this "climate memory" can change substantially over time. Van der Bolt et al. (2018) demonstrate that intensifications in climate memory, which leads to longer durations of anomalous conditions, increases the probability of ecosystems and populations passing critical tipping points.

Extreme weather events can also trigger ecosystem responses in conjunction with gradual climate change. Harris et al. (2018) use examples from Australian biota to demonstrate this phenomenon, which they described as a "press-pull" framework. While Australian biota is adapted to high levels of climate variability, recent directional changed combined with extreme events has led to sudden population collapses and shifts into novel ecological relationships.

While the impacts of climate change are broad, there is limited information on the biological sensitivity of many species and uncertainty in projections of physical change. Consequently, many climate vulnerability assessments are limited in geographic range and in the number of taxa assessed. Jones and Cheung (2018) developed a modeling approach utilizing fuzzy logic to account for exposure and biological traits in a vulnerability assessment of 1,074 marine species. They identified 157 species as highly vulnerable and another 294 as being at high risk.

Plasticity and Adaptation

In a literature review of studies documenting adaptation to climate change in marine systems, Miller et al. (2018) found ample evidence that marine species are adapting by adjusting the distribution and timing of biological events. Most marine species will likely continue moving poleward with continued climate change, and the amount of movement will depend on the extent of future anthropogenic forcing (Morley et al. 2018). Salmon may be able to adjust the timing of life history events such as spawning, juvenile migration, and marine rearing distribution. However, anadromous species may be generally more vulnerable to environmental change than marine species due to the dependence on native rivers.

Miller et al. (2018) found that documentation of adaptation through evolutionary processes was more limited than range and phonological shifts. This may be because genetic evolution is more difficult to demonstrate than changes in the distribution and timing of life history events. While direct documentation of evolutionary responses to climate change is limited, there are many reports of genetic adaptation across salmonid populations, in particular those that experience distinct temperature regimes. These studies indicate that genetic adaptation to increasing temperature has happened in the past and thus may be possible in the future. To assess this potential, and especially how quickly it might happen, we need to identify physiological mechanisms by which it might occur, their functional limitations, and where genetic diversity in these traits exists.

Chen et al. (2018b) studied adaptive divergence in cardiac function of redband trout *O. mykiss gairdneri* populations from geographically diverse Idaho streams. They demonstrated that fish from warmer streams had higher maximum heart rates and higher rate-limiting temperatures. Genomic mapping suggested evidence of selection for thermal tolerance, and genetic loci potentially important for thermal adaptation were identified.

Christensen et al. (2018) examined genetic variation in single nucleotide polymorphisms of Arctic char from Greenland, which is experiencing rapid environmental changes. They combined current samples with those taken in the 1950s-1960s to investigate variation in spatial and temporal genetic structure among geographically distinct populations. Substantially more genetic variation was observed between populations than across time periods within populations. They suggested that potential for adaptive responses exists, but long generation times may limit the ability of populations to track rapid environmental change, and low stray rates may further limit genetic adaptation.

Cook et al. (2018) examined variation in routine metabolic rates of brook trout *Salvelinus fontinalis* embryos and alevins exposed to different temperatures. Variation in metabolic rates was compared across family and population levels. Family was the more important variable in predicting metabolic rates, though population differences were also observed. Such variation may indicate adaptive potential to respond to predicted warming scenarios.

Cultured rainbow trout in Patogonia are being challenged by warming water temperatures. Prior experiments with other cultured trout stocks suggest potential for improvement in thermal performance. Crichigno et al. (2018) hypothesized that differences exist in thermal tolerance between different hatchery stocks and a wild introduced river population. In an experimental setting, they demonstrated differences in growth, condition, and temperature tolerance. They suggest that thermal performance of a hatchery stock could be improved by cross-breading with the studied wild stock.

Recent studies have linked factors such as temperature, stream gradient, and river confluences to explain levels of genetic variability within a stream network. Such studies, which can be termed "riverscape genetics," have the potential to enhance our understanding of the influence of habitat heterogeneity on gene flow and genetic structure. However, a lack of consistency in methodology has made comparisons difficult. Davis et al. (2018a) described potential uses and proposed a workflow for such comparisons.

Sylvester et al. (2018) examined the population structure of Atlantic salmon Salmo salar from Labrador, Canada, and its relationship with landscape characteristics utilizing microsatellites and single nucleotide polymorphisms. Genetic differentiation was found between coastal populations and those that migrated through a large marine fjord. Multivariate machine-learning techniques were used to identify warm temperature extremes and annual temperature range as the factors most related to this observed genetic variation. Sylvester et al. (Sylvester et al. 2018) suggest that their methodology shows fine-scale population structure across an environmental gradient at the northern extent of a species range and that it could be useful in predicting population responses to climate change.

Conditions are warming more rapidly in the Arctic than at lower latitudes, causing migratory salmonids to encounter warm, physically challenging river conditions more frequently in this region. In a field and laboratory experiment, Gilbert and Tierney (2018) showed that warm water has more detrimental impacts on critical swimming speeds and repeat critical swimming performance in an arctic salmonid, Arctic char, compared to a temperate salmonid, rainbow trout. Thus climate change may favor the poleward expansion of more temperate species.

The ability of organisms to genetically adapt to climate change depends on how selection on multiple traits interact, and whether those traits are linked genetically. Upper thermal limits and hypoxia tolerance are likely to be important traits in determining the effects of climate change on fish populations. Healy et al. (2018) compared genetic diversity associated with thermal and hypoxia tolerance in two sub-species of Atlantic killifish, *Fundulus heteroclitus*, which have previously been shown to differ in these traits. Single nucleotide polymorphisms (SNPs) were found related to each trait independently, but none were shared between both traits. These results suggest that, at least in Atlantic killifish, thermal and hypoxia tolerance are genetically independent traits.

Another potential limitation in the ability of salmon populations to adapt to climate change is the reduced level of existing genetic diversity compared to historic levels. Johnson et al. (2018) compared genetic variation in Chinook salmon from the Columbia River Basin between contemporary and ancient samples. A total of 84 samples determined to be Chinook salmon were collected from vertebrae found in ancient middens and compared to 379 contemporary samples. Results suggest a decline in genetic diversity, as demonstrated by a loss of mitochondrial haplotypes as well as reductions in haplotype and nucleotide diversity. Genetic losses in this comparison appeared larger for Chinook from the mid-Columbia than those from the Snake River Basin.

Mapping of trait-associated loci can reveal potential genetic regions involved in fitness-related traits. Watson and Chang (2018) analyzed data from adult Chinook salmon to identify loci associated with six life history traits. They then determined how two alternative captive rearing approaches affected variation at these loci. Loci associated with adult migration timing, length and weight at return, age at maturity, spawn timing, and daily growth were identified. Divergence in these loci suggested that these traits, in particular return and spawn timing, may have responded to domestication selection.

Pink salmon in Auke Creek, Alaska demonstrates distinct spawning types, with returns of an "early migrating" segment in August and a "late-migrating" segment in September. Manhard et al. (2018a) cross-bred early migrating with late-migrating pink salmon and monitored survival and migration timing of the offspring. Cross-bred fish had intermediate run-timing, demonstrating that for this trait, genetic effects are additive and natural selection may have favored a bimodal pattern. This study provides an example of how artificial mixing of different genotypes can be maladaptive.

Martinez et al. (2018) examined patterns in genetic diversity across 463 fish species. Their analysis compared estimates of genetic diversity, as measured by mean heterozygosity and mean rarefied number of alleles per locus, with habitat associations, conservation status, and other life-history characteristics. They found that marine fishes demonstrated higher genetic diversity than freshwater fishes. Their results suggest that age at maturity and fecundity were negatively associated with genetic diversity in both marine and freshwater species.

Environmental rescue represents a situation where adaptive evolution prevents the extinction of a population facing environmental stress. Models of evolutionary rescue can be used to predict stress levels where extinction becomes likely or when resistance to new conditions are likely to develop (Anciaux et al. 2018).

However, Becker et al. (2018) argued that the ability of populations/species to adapt genetically will likely provide an uneven buffer against extinction threat, depending on standing genetic variation and demographic effects. They warned of costs associated with genetic adaptation, such as reduced resiliency to other stressors. Accordingly, the ability of organisms to respond with genetic adaption is likely to vary substantially among populations and across species.

Straying within metapopulations can promote stability and evolutionary rescue. However, it can also introduce maladapted individuals that may lower overall fitness. Yeakel et al. (2018) applied an existing eco-evolutionary model of two locally adapted populations to examine the potential effects of density-dependent straying. Results suggested that low levels of straying support a robust metapopulation, but that this strength is eroded at higher levels of straying.

Thorn and Morbey (2018) reared Chinook salmon from introduced Great Lakes populations to evaluate the effects of egg size on variation in early life history traits. They reared fish at a range of temperatures measuring a number of fitness-related traits during development. In fitness-related traits, much variation between populations was found related to egg size. However, the importance of egg size was diminished at higher temperatures, suggesting important impacts from other factors. Results suggest that egg size is important in determining phenotypes among and within populations and may provide an important mechanism through which salmonids can adapt to climate change.

In an evaluation of transgenerational phenotype effects, Wong et al. (2018) used purple sea urchins *Strongylocentrotus purpuratus* conditioned to pCO₂ concentrations and temperatures representative of conditions in the California Current. They utilized RNA-seq and comparative transciptomics to show that the conditioning of adults affected the gene expression of progeny during early development. Results suggest that transgenerational plasticity may contribute to the ability of species to adapt to environmental change.

Understanding past evolution can inform predictions of evolutionary change in response to a warming climate. Franks et al. (2018) reviewed the "resurrection approach," which revives ancestors from stored propagules or eggs and compares their traits to that of contemporaries. They explore the limitations of this approach, and discuss its usefulness in documenting evolution in populations and in guiding conservation and management efforts.

Phenology

Emergence timing

Temperature plays a major role in the speed of egg development. Beer and Steel (2018) examined the effects of temperature variability on egg development and emergence timing of Chinook salmon. A mechanistic model was utilized to illuminate lab results and predict emergence timing in a natural river system. Interannual water temperature regimes and spawning date described the most variability in natural emergence timing. However, temperature variability, as well as family lineage, egg size, individual spawn timing, and spawning cue, had smaller but significant effects.

Fuhrman et al. (2018) also investigated the effect of stream temperature on emergence timing in Chinook salmon, in this case utilizing a common garden experiment. Their results demonstrate that warmer thermal regimes caused earlier emergence at lower cumulative temperatures. Similar to the findings of Beer and Steel (2018), a family effect on emergence timing and development was also described. Creating population-specific reaction norms for emergence timing may help predict the effects of changing stream temperature on this trait.

Juvenile migration timing

There is concern that for some salmon populations, climate change may drive mismatches between juvenile arrival timing and prey availability in the marine environment. However, phenological diversity can contribute to metapopulation-level resilience by reducing the risk of a complete mismatch. Carr-Harris et al. (2018) explored phenological diversity of marine migration timing in relation to zooplankton prey for sockeye salmon *O. nerka* from the Skeena River of Canada. They found that sockeye migrated over a period of more than 50 d. Populations from higher elevation and further inland streams arrived in the estuary later, and different populations encountered distinct prey fields. They recommended that managers maintain and augment such life-history diversity.

Age at maturation

Age at maturity has been shown to reflect both genetics and plasticity, such that faster growing individuals generally mature earlier. A better understanding of the genetic architecture related to age at maturity would help illuminate the potential for ongoing evolution in this trait. Age at maturity in Atlantic salmon has been associated with a single locus and is thus ideal for studying genetic adaptation. Many populations of Atlantic salmon have demonstrated substantial declines in average age at maturation in recent decades. Czorlich et al. (2018) demonstrate a decline in the expression of an allele associated with late maturity in an Atlantic salmon population. Due to sex-specific selection, this genetic change led to a phenotypic change only in males.

Mean size and age at maturation have declined in Chinook salmon across its range in North America. This is a concern due to the value of large Chinook salmon in commercial and subsistence fisheries and because smaller size, particularly of females, may lead to reduced population productivity. Using long-term datasets for Chinook salmon from California to Alaska, Ohlberger et al. (2018b) examined these size trends and identified potential causes. Results suggest that hatchery fish in particular have become smaller and younger throughout the West Coast, and that proportions of older fish have declined in most regions. However, they note that in older fish, negative size trends were minimal at the southern extent of the species range. These authors identified selective harvest, hatchery practices, interspecific-species competition, changes in climate, and changes in late marine predation as potential causes of demographic change.

Siegel et al. (2018) explored declines in size and age at maturation in two populations from western Alaska utilizing multidimensional probabilistic maturation reaction norms that accounted for growth history. Growth data was informed by retrospective scale analysis, and population data was informed by run-reconstructions accounting for harvest. Models accounting for growth history universally outperformed size-at-age models, suggesting that growth during particular life stages had disproportionate effects on maturation age. Faster growth during the second marine rearing year was most strongly associated with earlier maturation. Changes in maturation reaction norms suggest a genetic basis of declines in age, potentially through selective exploitation or environmental selection. These results highlight concern for climate effects on salmon rearing conditions in the Bering Sea, where ecosystem productivity depends upon sea ice coverage which is predicted to continue to decline rapidly.

Adult migration and spawn timing

A substantial body of research has focused on potential fisheries selection for earlier age at maturation. However, Tillotson and Quinn (2018) point out that selection on migration and spawn timing may also be an important impact of fisheries. There is substantial potential for such selection because exploitation of returning adults is often temporally disproportionate. Tillotson and Quinn (2018) describe how temporally selective fishing practices can ultimately limit breeding periods and reduce phenotypic diversity, thus depressing productivity and resilience to climate change.

Utilizing a simulation, Plumb (2018) explored the potential effects of rising stream temperature on selection for migration timing in adult Snake River fall-run Chinook. These fish undergo long migrations at temperatures well above optimum for Chinook salmon. Early arriving fish tend to experience the highest temperatures. Use of cold-water tributaries can mitigate the effects of warm water temperatures to some extent. However, results from these simulations suggest that increases in temperature will select against early migrants, potentially truncating the onset of the run.

Physiological Studies

Akbarzadeh et al. (2018) reviewed functional genomic studies to identify thermally sensitive biomarkers that could be utilized to test for physiological signs of thermal stress from non-lethal samples of gill tissue. They combined a literature search and a comparison of microarray datasets with other sources to develop quantitative reverse transcription PCR assays for identified genes in Chinook and sockeye salmon. Activity of these genes at different levels of thermal stress was compared, and a subset of candidate genes were identified as consistent markers of thermal stress. The authors suggest that while individual genes may be activated by other processes, the ability to detect expression of the identified genes in concert may provide a reliable means of detecting thermal stress using non-lethal field samples.

In a lab study, Arevalo et al. (2018) examined the effect of temperature and food

availability on the growth of brown trout directly after emergence. The authors also identified gene expression for proteins related to energy metabolism. Emerged fish were exposed at 8 and 11°C treatments and subsequently fed ad libitum, starved, or fed ad libitum after being starved. Starved fish lost less mass at the lower temperature treatment while fed fish demonstrated marginally higher growth at 11°C. An over-expression of proteasome and autophagy-related genes in starved fish was identified.

Physiological performance peaks within a specific temperature range, which varies by species. Preferred temperatures are generally estimated from laboratory experiments; however, they remain unknown for many less-studied fish species. Hasnain et al. (2018) presented a statistical method (Bayesian phylogenetic regression) to estimate temperature parameters using relationships between metrics and genetic relatedness. Incorporating taxonomic family relatedness was found to improve estimation accuracy.

Salmon may be at a higher risk of physiological effects from ocean acidification than other marine species due to their need to acclimate rapidly between freshwater and saltwater habitats. McCormick and Regish (2018) examined the effect of ocean acidification on salinity tolerance and early marine growth in Atlantic salmon smolts. They did not find effects on salinity tolerance between treatments (610 vs. 1010 μ atm CO²) and actually found higher growth in the more acidic treatment. This study indicates that elevated CO² is not likely to affect osmoregulation negatively.

While salinity tolerance may not be strongly impaired by acidification, increased temperatures may be detrimental more detrimental. Vargas-Chacoff et al. (2018) examined how salinity tolerance was affected by the interaction between temperature and salinity in Atlantic salmon smolts. Fish were exposed to quick changes in temperature in freshwater and seawater with and without prior acclimation. The authors found that high temperature resulted in poor ion regulation in saltwater, while no temperature effect was observed in freshwater. At 24°C, all fish exposed to saltwater died, demonstrating low levels of osmoregulatory activity. These results suggest that osmoregulation is effected by temperature and that there is a temperature threshold for osmoregulatory failure in saltwater.

Changes in marine temperature are likely to have a number of physiological consequences beyond changes in metabolic rate. For example, in a study of small planktivorous fish, Gliwicz et al. (2018) found that higher ambient temperatures increased the distance at which fish reacted to prey. Numerous fish species (including many tuna and sharks) demonstrate regional endothermy, which in many cases augments eyesight by warming the retinas. However, Gliwicz et al. (2018) suggest that ambient temperatures can have a similar effect on fish that do not demonstrate this trait.

Climate change is likely to reduce the availability of biologically essential omega-3 fatty acids produced by phytoplankton in marine ecosystems. Loss of these lipids may induce cascading trophic effects, with distinct impacts on different species depending on compensatory mechanisms (Gourtay et al. 2018). Reproduction rates of many marine fish species are also likely to be altered with temperature (Veilleux et al. 2018). The ecological consequences of these effects and their interactions add complexity to predictions of climate change impacts in marine ecosystems.

Population Trends

Dorner et al. (2018) examined environmental factors affecting productivity of Chinook salmon from Oregon to Alaska. Utilizing dynamic factor analysis, they found that trends in productivity were related to the North Pacific Gyre Oscillation and reported that Chinook productivity has become more synchronous across populations in recent years, particularly within regions. Synchronization has been reported in other Pacific salmon species and may decrease overall resilience. Such observations may be in part a consequence of increasing synchronization of terrestrial and marine conditions across larger spatial scales, as reported by see Black et al. (2018 in National Climate Change section).

Chinook salmon at the northern extent of its range have declined in abundance and size in recent decades, although the drivers of these declines are unclear. Cunningham et al. (2018) constructed a stage-structured assessment model to examine the role of various hypothesized marine and freshwater factors in determining population dynamics of Yukon River Chinook. Important factors influencing productivity included late timing of the annual ice retreat, cold Bering Sea temperatures, and high levels of intraspecific competition at sea. Density dependence was detected in freshwater, but not in marine environments. Overall, results suggest that mortality at sea was the primary driver of population dynamics for these fish.

Sobocinski et al. (2018) examined a broad suite of drivers affecting populations of coho salmon *O. kisutch*, Chinook salmon, and steelhead from Puget Sound and the Strait of Georgia. They utilized qualitative network modelling, a tool to help conceptualize complex and interrelated networks of variables, to simulate perturbations and estimate their influence over a 40-year period. Their network included environmental and oceanographic drivers, primary production variables, food-web variables, and anthropogenic impacts. Results suggest that anthropogenic impacts had the biggest influence on survival and abundance.

McCarthy et al. (2018) provided perspective on pre-historic trends of sockeye salmon abundance from populations in Alaska. They utilized stable isotope data (δ^{15} N) from sediment cores taken from Russian Lake in the Kenai River watershed and compared them to records from the same periods previously taken from Kodiak Island. Results suggest that abundance has oscillated over time and was particularly diminished during a 650-year period of glacial advance from 100 BCE to 550 CE at both locations. Glacial advances may have simultaneously affected spawning and rearing habitats in each location while creating unfavorable cold conditions for nearshore marine rearing.

A number of papers explored environmental influences on demographic trends in Atlantic salmon. Rougemont and Bernatchez (2018) examined the demographic history of Atlantic salmon across its entire range using admixture graphs, geo-genetic maps and approximate Bayesian computation. They compared patterns in genetic differentiation for population groupings from North America and Eurasia. Results suggest that the demographic history of Atlantic salmon has been determined by multiple secondary contacts between and within populations from the North American and European continents.

In more recent history, Atlantic salmon has demonstrated synchronous declines in abundance across its range in Eurasia and North America. Declines have occurred despite a reduction in fisheries and improvements to many river habitats, implying a possible marine mechanism, which remains unclear. Utilizing stable isotope data from salmon from the St. John River in Canada, Soto et al. (2018) present evidence that salmon spending one year in the ocean before maturing had reared in different places than those spending multiple years. Nevertheless, declines were synchronous in both groups. The authors suggest that declines in St. John River salmon are more likely to be a consequence of conditions during the initial post-smolt period, when both groups experienced similar conditions.

In a tagging study of wild reared Atlantic salmon from Scotland, Armstrong et al. (2018) examined population trends as well as the effects of size, condition, and migration timing on survival to adulthood. Larger fish in better condition had higher return rates, while later-migrating juveniles had lower return rates. Over the years assessed (1999-2014), an increase was seen in the proportion of fish returning after two or more years at sea, along with an increase in smolt-to-adult survival. Possible explanations for demographic changes are discussed.

Nicola et al. (2018) analyzed historic trends in abundance for Atlantic salmon from populations in Spain at the southern extent of the species range. These populations have experienced large declines and are likely at high risk from global warming due to their depressed state and relatively warm-water habitats. This study compared long-term fishery trends (1949-2013) to temperature and hydrological data. While other significant factors were found, time-series models suggested that increases in stream and marine temperature were the primary factors driving declining abundance and that rising temperatures may have suppressed recovery from a fisheries-induced collapse in the 1970s. These results highlight concern for the sustainability of these populations, given the likely persistence of warming water temperatures.

Stage-Specific Ecological Studies

Freshwater rearing

Winter represents the egg incubation period for many salmonid species; thus, increases in egg scour as a consequence of winter pulse flows is a concern. However, spring and fall low flow conditions can be detrimental to spawning and rearing respectively. Accordingly, studies exploring how populations respond to variability in freshwater flows are necessary to predict the consequences of environmental change.

Blum et al. (2018) examined a 28-year record of brook trout to assess how flow extremes and other environmental variables relate to young-of-year abundance. Using mixed models, they found that covariates accounting for extreme flow conditions were better predictors of abundance than mean conditions. Specifically, extreme high winter flow was found to have a negative effect on young-of-year abundance. Habitat preservation and restoration can help maintain and increase population resiliency to variable flow conditions as the frequency of extreme winter hydrological events increases.

Extreme hydrological events are also likely to impact the macroinvertebrate communities that rearing juvenile salmon depend on. Milner et al. (2018) demonstrated that a major winter flood reset the invertebrate community in a long-studied river ecosystem. This community had not recovered by the time of another flood 9 years later. Accordingly, higher frequencies of flooding may have lasting impacts on the productivity of invertebrate communities, which will in turn affect rearing salmon. Milner et al. (2018) also described direct effects of winter flooding on pink salmon *O. gorbuscha* escapement, presumably through egg scour mortality. These results demonstrate some ways in which climate change is likely to affect salmon productivity beyond direct temperature effects.

Anderson and Topping (2018) used data from long-term spawning surveys and monitoring at a juvenile trap to explore factors influencing freshwater productivity of Chinook salmon in the Green River, Washington State. As is common in Puget Sound populations, Green River Chinook juveniles demonstrated distinct pulses in downstream movement, including movement at the fry and parr stages. Abundance of late migrating parr had been previously shown to be density dependent based on number of spawners, while early migrating fry were density independent. As observed by Blum et al. (2018), total juvenile production was found to decrease with larger peak flows during winter, potentially due to redd scour. However, parr productivity was greater in years with higher spring flows. Anderson and Topping (2018) suggest that greater productivity was likely due to increased access to rearing habitat and higher survival of downstream migrants due to higher spring flow conditions. This study suggests that restoration of juvenile habitat could increase parr productivity by alleviating density dependence.

Phillis et al. (2018) utilized otolith-derived isotope ratios to reconstruct juvenile habitat use by endangered Sacramento River winter Chinook that survived to adulthood. Results suggest that about half of surviving adults reared in non-natal habitats *not* designated as critical under the Endangered Species Act. For these fish, growth and size at migration were similar to those of fish that reared in natal habitats. This study shows how salmon populations can rely on diverse and dispersed habitats if they are accessible.

Designing successful restoration projects depends on understanding habitat preferences of species. Favrot et al. (2018) investigated micro-habitat use by Catherine Creek Chinook salmon during fall and winter using a mixed-effects logistic regression resource selection function model. Micro-habitat use shifted between seasons, with silty areas further from the bank used more in winter. Woody debris was utilized more frequently in low gradient reaches. Deep-water areas supporting slow currents near cover were densely occupied in moderate-gradient reaches, while areas of moderate depth with slow currents adjacent to bank cover were most occupied in low-gradient reaches.

Stream temperature directly effects metabolic processes in ectotherms such as Pacific salmon. Myrvold and Kennedy (2018) described how climate change may lead to increased density dependence in rearing juvenile salmonids. However, the ecological impacts of increased stream temperature on salmon will also depend on changes in food availability, which will determine if salmon can compensate for increased metabolic rates. Using observations from a large database of macroinvetebrates from streams in Idaho, Richards et al. (2018) presented information on threshold change points for over 400 macroinvertebrate taxa and provide a list of ecosystem indicator taxa.

Goertler et al. (2018a) provide an example of how food availability can change with climate. They compared how juvenile Chinook diets responded to flooding vs. draught conditions in the Yolo Bypass, one of the last remaining large floodplain habitats in the Sacramento River watershed. The authors found that Chinook salmon primarily consumed aquatic–riparian insects during flooding and zooplankton during drought conditions. Salmon caught during draught conditions consumed more, presumably to offset higher metabolic costs. Beyond providing increased rearing habitat and prey consumption, Goertler et al. (2018b) suggest that complicated floodplain environments such as the Yolo Bypass support resiliency by promoting population phenotypic and life history diversity.

Manhard et al. (2018b) performed a meta-analysis to estimate mass and temperature-dependent parameters of juvenile coho *kisutch*. Growth observations from ten distinct populations were used to inform an allometric model which incorporated the Ratkowsky growth model. Parameters were scaled relative to ration, and the model had skill in predicting growth of coho salmon from tributaries and constructed ponds. The authors suggest that due to their simplicity, such models are useful for describing growth in freshwater fish populations.

In salmon populations, variation in life history trait expression is often analyzed in relation to environmental variability. Yet strong ecological links between species often produce distinct effects. Bailey et al. (2018) examined how size, age, and abundance of steelhead smolts from the Koegh River in Canada were affected by weather, pink salmon abundance, experimental nutrient addition, and density-dependent processes. Warmer temperatures and nutrient additions were related to larger smolts. An independent effect of pink spawning abundance was found on steelhead smolt age and productivity, suggesting a linkage between the two species that may affect rearing in conjunction with environmental variability and management actions.

Hatchery fish often have lower survival and spawning success than their wild counterparts, and one explanation is that selective forces in hatcheries may be maladaptive to natural environments (Tillotson and Quinn 2018). Fenkes et al. (2018) suggest that exposing juvenile fish to variable flow conditions, can lead to more robust and faster-growing individuals. Further advancement in modifying hatchery environments to mimic wild environments could potentially reduce the gap in success between hatchery and wild origin individuals.

Harstad et al. (2018) assessed the effect of rearing conditions on the survival and demographics of stream-type Chinook salmon at four hatcheries in the upper Columbia River. They compared rearing programs that utilized surface water and natural thermal regimes with those that utilized groundwater sources and restricted temperature variability. Fish that overwintered in colder surface water had reduced growth and mini-jack rates, but substantially higher smolt-to-adult survival, and smaller juveniles tended to mature at later ages. In alignment with Fenkes et al. (2018), they conclude by suggesting that hatchery conditions that more resemble natural thermal regimes are likely to produce later-maturing, larger adults with higher smolt-to-adult survival.

Many coho salmon populations thrive in intermittent streams and may be especially vulnerable to more frequent draught conditions caused by climate change. Obedzinski et al. (2018) examined variability of coho survival in intermittent California streams utilizing a mark/recapture method. They found that survival in individual stream sections was related to streamflow and duration of disconnection. However, despite these impacts, juvenile fish were often able to survive in disconnected pools. Factors affecting survival in such conditions have been little studied.

Larsen and Woelfle-Erskine (2018) evaluated the effects of groundwater on survival in disconnected pools based on snorkel surveys combined with environmental monitoring. They found that pools in which fish congregated had groundwater influence with relatively high oxygen content and that fish persisted in only these pools. Accordingly, how groundwater fluxes will change with climate change may be important for these populations.

Hwan et al. (2018) compared survival during wet vs. dry years for young-of-year steelhead and coho salmon during the summer dry season in an intermittent California coastal stream. Results were generally consistent with those from the studies discussed above, suggesting higher survival during wet years with survival decreasing at the end of summer due to longer periods of disconnection. They estimated somewhat higher survival rates for coho in comparison to steelhead. Results show the connection between annual precipitation and summer survival while demonstrating that juvenile salmonids are fairly resistant to drought conditions. However, potential carryover effects on survival to adulthood due to reduced growth and poor condition remains a concern.

Ohlberger et al. (2018a) examined the effects of past and projected flow extremes and flow variability on the productivity of coastal coho populations from the Olympic Peninsula. Using a stage-based life-cycle model, the authors show evidence that productivity depends on river-flow characteristics and is limited by low minimum summer flows in particular. As low summer flows are predicted to become more severe with climate change, productivity in these populations is expected to decline.

The most severe effects of climate change on Pacific salmon are likely to occur at the southern edge of their range, where temperatures above thermal optimum are already common. Assessments of how these species respond to environmental variability at the limit of their range can help inform prediction of climate impacts. Basic et al. (2018) assessed environmental drivers of European grayling *Thymallus thymallus* recruitment in England at the southern extent of the species' range. Recruitment increased at higher rearing temperatures up to about the mean (13.5°C) before declining at higher temperatures. Low flows during rearing were also associated with poor recruitment.

Beyond climate change, expanding urbanization threatens many salmon populations by destroying habitat, altering temperature and flow regimes, and increasing exposure to contaminants. Spanjer et al. (2018) used a bioenergetics model to examine effects on juvenile salmon growth from temperature differences related to urbanization in Pacific Northwest streams. Urban streams tended to be warmer with earlier emergence dates and faster early season growth. However, fish in urban streams experienced increased stress and lower growth efficiencies later in the season.

Juvenile migration

Temperature has been shown to influence stress responses in fish. However, data is lacking on specific responses by different salmon species at distinct life history stages. Madaro et al. (2018) acclimated Atlantic salmon smolts to temperatures of 4, 8, 12 and 17°C before exposing them to an acute stressor for 60 seconds. Oxygen consumption rates and cortisol production were measured before and after the stressor period and compared between temperatures. Amplitude of the max cortisol response and peak oxygen uptake both increased exponentially with temperature, while time to recovery decreased. This research demonstrates how salmon are particularly vulnerable to hypoxic conditions when stressed at high temperature.

Bassett et al. (2018) examined spatial and temporal differences in the physiological development of seawater tolerance in Fraser River sockeye salmon smolts. Four populations were sampled at different times to characterize smolt transformation. As expected, pre-migratory fish had low levels of gill Na+–K+-ATPase (NKA) activity. Some populations demonstrated high gill NKA activity upon initiation of downstream migration from rearing lakes, while other did not. Variable gill NKA activity was found at the onset of migration, with no relationship to distance from the ocean.

Buchanan et al. (2018) examined patterns of survival in acoustic-tagged juvenile fall Chinook migrating through the San Joaquin Delta. Since 2002, survival has been low in this reach, which is heavily channelized and impacted by flow regulation. Estimated survival from this study ranged 0-0.05, with low river flows during most years from 2010 2015. However, during the high flow year of 2011, survival was still only 0.02, demonstrating that higher flows alone did not alleviate high mortality. Of fish that survived migration to the delta, nearly half were salvaged from water export facilities and transported downstream for release below the delta.

Perry et al. (2018) examined the interacting influences of tides and river flows on survival, travel times, and routing of juvenile late-fall Chinook salmon through the Sacramento–San Joaquin River Delta. Using a Bayesian modeling framework, they found travel time inversely related to flow throughout the delta. Survival was positively related to flow only in reaches that transitioned from bidirectional tidal flows to unidirectional flow under high flow conditions.

Chittaro et al. (2018) examined variability in estimates of somatic growth rate derived from otoliths of juvenile Chinook salmon migrating in the Columbia River estuary. During the eight-year period examined, they found that growth rates decreased later in spring and as fish approached the ocean and increased with fish length. The authors argue that growth could be improved with estuary habitat restoration which would likely benefit marine survival.

For migratory species, experiences in one habitat may impact survival in the next habitat through what are termed "carryover effects." For example, Jonsson and Jonsson (2018) showed that egg incubation temperature affected timing of the homing migration for Atlantic salmon in Norway. A failure to account for carryover effects can lead to an incomplete assessment of the true consequences of management actions and environmental variability. Gosselin et al. (2018) examined carryover effects on Snake River Chinook salmon from a juvenile transport program which aims to increase survival through the Columbia/Snake River hydropower system. Benefits of transportation were shown to depend on day of the year, hatchery/wild origin, and environmental variables. This information can be used to inform transportation protocols to maximize the benefits of survival to maturity.

Larger smolt size is thought to increase early marine survival due to size-dependent predation. However, the magnitude of this effect likely varies substantially across populations and with environmental variability and rearing experience. Studies examining this relationship are often context-dependent and anecdotal due to data limitations. Gregory et al. (2018) described a flexible framework to examine how extrinsic factors may affect the relationship between body size and marine survival. Their approach is applicable in a wide range of data scenarios. Specifically, they suggest that use of state-space models would improve the generality and robustness of findings over more commonly used methods.

Timing of ocean-entry with favorable ocean conditions can be a major determinant of marine survival in salmon. In Bras d'Or Lake, an inland sea in Nova Scotia, residence time of Atlantic salmon smolts are highly variable and related to body condition. Strople et al. (2018) examined the relationship between bioenergetics and migration strategy in Atlantic salmon smolts vs. the potential effects of warmer temperatures on energetic requirements. Bioenergetic simulation results suggested higher temperatures would result in faster depletion of energy, which would lead more smolts to leave the Bras d'Or earlier. This change in marine entry timing could create a mismatch with ocean conditions.

Tiffan et al. (2018) examined the influence of water velocity and physiological development stage on the migration of fall Chinook juveniles through free-flowing reaches of the Clearwater River and impounded reaches of the Snake River. Radio tagging results suggested that water velocity was a larger determinant of downstream movement than stage of physiological development. Movement slowed to match water velocities in impounded reaches, suggesting a low behavioral disposition to move downstream. These results contrast with those from a previous study of Snake River fish. The authors suggest that the behavioral difference observed was likely due to a more advanced smolt transition in Snake vs. Clearwater fish, as demonstrated by higher levels of gill Na+/K+-ATPase activity.

Osterback et al. (2018) examined how drought conditions effected the ecology of juvenile coho and steelhead in the coastal lagoon of Scott Creek, a heavily studied watershed in central California. In the drought year of 2015, a seasonal sandbar at the mouth of the lagoon formed two months earlier than normal, trapping salmon for an additional 7 months. Salmon trapped in the lagoon through summer faced periods of high water temperature and low dissolved oxygen concentration. Steelhead grew more than coho during this period, and both species repeatedly moved between the lagoon and cooler lower mainstem, which was interpreted as temperature-regulating behavior.

Marine rearing

Size-selective mortality upon marine entry has long been hypothesized as a critical process affecting the productivity of salmon populations. However, the strength of size-selectivity may depend on environmental variability and is likely not consistent across populations. Gamble et al. (2018) examined patterns in size-selective mortality in Puget Sound Chinook by comparing estuary, nearshore, and offshore samples. Fork lengths were back-calculated using retrospective scale analysis. These authors did not find any evidence of size-selective mortality during the study years (2014 and 2015). These results suggest that size-selective mortality upon marine entry may not always be the primary force of early marine mortality that it is often assumed to be.

Juvenile salmon migrants that encounter high-quality feeding conditions upon marine arrival are likely to have higher survival, and such conditions may help smaller fish erase size differences that can lead to size-selective mortality. Friedman et al. (2018) examined variables that affect assemblages of salmon forage taxa during marine entry of Chinook salmon off the U.S. West Coast from California to Washington. Forage taxa were sampled during the spring 2011-2015, and abundance and distribution of forage communities were identified. These authors identified longitudinal gradients with four distinct multi-species assemblages. They found that spatial distribution of assemblages were related to previously observed spatial covariation in population survival, suggesting that ocean dynamics of prey species play a major role in salmon population dynamics.

Jensen et al. (2018) provided evidence that increased marine growth leads to increased survival of Arctic char *Salvelinus alpinus* and brown trout in Norway. Utilizing a 25-year time series from the River Halselva, these authors found correlation between the two species in total growth, growth rates, duration at sea, and survival. As generalist feeders, these species may be good indicators of ecosystem productivity in the local fjord ecosystem.

Productive nearshore habitat can impact early marine survival of salmon by increasing the availability of shelter and food. Kennedy et al. (2018) examined the use of eelgrass habitats by juvenile chum salmon *O. keta* on Vancouver Island in British Columbia. They used stable isotope analyses to compare estimates of overall prey availability to salmon consumption and found evidence that eelgrass invertebrates made up roughly 80% of chum salmon diets.

Using a multiple model approach, Henderson et al. (2018) aimed to identify coastal marine regions with high growth potential for Central Valley fall Chinook juveniles during their first spring/summer at sea and to relate spatial variability in growth potential to ocean conditions. Growth patterns were associated with upwelling, sea level anomalies, and onshore/offshore currents, and the authors were able to predict survival with environmental data. They suggested that survival following marine entry was likely mediated by an interaction between environmentally dependent growth conditions and spatial shifts in predators.

Chittenden et al. (2018) explored the potential for changes in marine food availability to explain recent declines in abundance of Chinook salmon populations in the Salish Sea. Smolt diet was analyzed in conjunction with zooplankton sampling. Hatchery fish were large and consumed larger prey, spending very little time in the estuary and bay, and onset of piscivory occurred at ~74 mm, less than the average fork length of hatchery fish. The larger size of hatchery smolts may have been disadvantageous if it caused them to leave sheltered habitats prematurely due to energetic needs. Jellyfish and harmful algae blooms within zooplankton masses also may have affected juvenile access to food sources.

Ecosystem shifts in response to environmental change will also affect the behavior of salmon predators. For example, Abrahms et al. (2018) found that in elephant seals, site fidelity for foraging grounds was weaker in anomalous climate years. This result suggests that predator movements may become less predictable as the environment changes.

Kaplan et al. (2018) examined how the abundance of Pacific sardine *Sardinops* sagax impacts predators in the California Current Ecosystem by combining three ecosystem models. They predicted that species such as the brown pelican *Pelecanus* occidentalis, which are heavily dependent on sardine, are moderately to highly susceptible to fluctuations in forage fish populations. Some discrepancies between models were identified and discussed.

Models examining the biological effects of climate rarely allow for non-stationary relationships between environmental variables and biological responses. However, Litzow et al. (2018) demonstrated that relationships between Pacific salmon abundance and climate variables shifted during 1965-2012 in the Gulf of Alaska. In particular, they noted that the relative importance of major marine indices shifted around 1988-1989. These authors suggest that regression models assuming stationary climate-salmon relationships are inadequate over multi-decadal time series. Their results demonstrate the ability of models that relax this assumption to better describe temporal patterns in productivity.

Adult migration and spawning

Fish that survive traumatic events, such as fishery encounters or predation escapes, are thought to have reduced reproductive success. Injuries, stress, and the energetic expenditure stemming from such events can decrease disease resistance and increase the risk of migration/pre-spawn mortality. Bass et al. (2018a) examined fisheries-related incidental mortality in Fraser River sockeye salmon that encountered gill-nets. Fish with visible gillnet wounds had estimated migration mortality rates that were 16% higher overall and 18% higher in females. Accounting for gillnet injury rates, the authors estimated a 3.8-9.9% decline in migration success. It is probable that the decline in successful spawning was likely higher than this. This study represents the importance of accounting for carryover effects on reproductive success. Bass et al. (2018b) also presented evidence that release after capture in gill-nets may be more detrimental to migrating sockeye than release after capture in beach seines.

Migration stressors such as high river temperatures, fishery interactions, and predator encounters likely influence susceptibility to pathogens. To explore how these stressors impact the survival of migrating adults, Teffer et al. (2018) conducted simultaneous holding and telemetry studies with Chilliwack River Chinook salmon from British Columbia. High temperatures reduced survival of laboratory fish but did not increase infection burdens from simulated gillnetting. However, gillnetting reduced migration rates and final travel distances while increasing infection rates of tagged fish. Little research has examined how steelhead respond to catch-and-release fishery encounters, despite steelhead being a popular sport fish. Twardek et al. (2018) used nonlethal blood sampling and radio telemetry to examine the post-release effects of catch-and-release encounters. Steelhead exposed to air had greater impairment and moved downstream following encounters, though there were no observable differences in movement following two weeks. However, higher blood lactate levels in angled fish suggested a lasting stress response, and stress responses were elevated at higher temperatures. Results suggest that anglers should limit air exposure and minimize handling, particularly when water temperatures are warm.

Naughton et al. (2018a) performed a field experiment to test how radio-tagging contributed to increased prespawn mortality in adult Chinook salmon. They suggest that while detrimental effects of radio tagging on survival and pre-spawn mortality appeared small in their analysis, potential tag effects should be accounted for in tag studies.

Bowerman et al. (2018) examined rates of prespawn mortality in female Willamette River Chinook salmon in relation to origin and environmental variables. Annual prespawn mortality was highly variable (1-100%) over a 14-year study and was strongly related to maximum water temperatures and percent hatchery origin. High temperatures (>20°C) combined with higher percent hatchery origin (>80%) consistently led to prespawn mortality rates above 80%.

Minke-Martin et al. (2018) examined the relative influence of physiological condition and migratory experience on survival and egg retention on Fraser River sockeye salmon using archival temperature loggers and radio tags. Fish were tracked to natal lakes following passage through a hydroelectric dam. Fish with lower plasma glucose levels were more likely to reach spawning grounds, and spawners arriving earlier experienced more ideal temperatures and demonstrated greater longevity on spawning beds. Higher dam discharge was associated with more egg retention and shorter longevity, but not lower migration survival, demonstrating a delayed carryover effect.

Use of temperature refugia may help salmonids mitigate the effects of increasing river temperatures in migratory corridors. Keefer et al. (2018) utilized a combination of radio telemetry and archival temperature loggers to track the spatially explicit thermal histories of Columbia River Chinook salmon and steelhead during their spawning migrations. Spring and most summer-run Chinook migrated before peak temperature periods and demonstrated little evidence of prolonged use of thermal refugia. In contrast, many fall-run Chinook and steelhead demonstrated frequent use of thermal refugia near tributary confluences. Steelhead often utilized refugia for extended periods, sometimes lasting weeks.

Frechette et al. (2018) examined behavioral thermoregulation by adult Atlantic salmon from the Quebec River in Canada utilizing infrared remote sensing, temperature monitoring, and acoustic telemetry. At temperatures of 17-19°C and above, adults engaged in thermoregulation, maintaining body temperatures of 16-20°C through the utilization of cool-water refugia. Deep, stable, and stratified pools were utilized by numerous individuals simultaneously. Low flows combined with high temperatures can limit access between refugia in this system.

Lennox et al. (2018) examined the potential bioenergetics consequences of increasing river temperature on the spawning migration and success of Atlantic salmon in Norway. They utilized archival temperature loggers to describe the temperature experience of fish and created bioenergetics models accounting for temperature, body size, and activity levels. Unlike Keefer et al. (2018), these authors found little evidence of refuge use, possibly because migration temperatures in the study watershed were lower than those in the Columbia River, reaching a maximum of ~18°C. While models demonstrate that increases in temperature would increase the energetic cost of migration, results suggest that swimming speed and size are also important. Lennox et al. (Lennox et al. 2018) suggest that smaller individuals are likely to be more sensitive to changes in temperature.

Spawning migration movements of salmonids are not always unidirectional, and variable movement can complicate estimates of survival and escapement. Mann and Snow (2018) used radio telemetry to examine movement patterns of summer Chinook salmon approaching Wells Dam on the upper Columbia River. While fish tagged at Wells Dam were primarily from upstream rivers (Okanagon and Methow), a significant proportion were from downstream populations. Combined with fallback, this may have led to overestimation of passage rates at Wells Dam in past years.

Impoundments and diversions can affect the composition of river water from natal spawning tributaries, which provide cues that salmon rely on for homing. In a radio telemetry study of sockeye salmon in British Columbia, Middleton et al. (2018) found evidence that fish delayed migration at a powerhouse on the Fraser River fed by waters from a native spawning tributary. The powerhouse was located below the confluence with the native spawning river, and the mix of source water may have caused a delay in the arrival to the spawning grounds.

Habitat

Retrospective

In addition to direct impacts on native species, climate change will alter the suitability of conditions for invasive species, affecting competition. McCann et al. (2018) found that as a consequence of increasing stream temperatures, invasive sea lamprey in Great Lakes tributaries migrated earlier, likely to improve conditions for growth and survival. However, these temperature increases are unlikely to limit their distribution (McCann et al. 2018).

As stream temperatures increase, many native salmonids face increased competition with more warm-water tolerant invasive species. For example, Howell (2018) examined how temperature relates to distribution patterns of native bull trout and invasive brook trout in the Powder River Basin of eastern Oregon. Areas with only brook trout had substantially higher maximum summer stream temperatures, suggesting the potential for future range expansion of this invasive species with climate change.

Identifying how changes in flow will affect the available habitat of salmon is important for predicting the effects of management actions and climate change. Nahorniak et al. (2018) generated over 2200 hydraulic models for more than 900 individual river reaches in Pacific Northwest salmon streams. Hydraulic models were utilized to generate estimates of depth and velocity throughout reaches related to habitat suitability indices for Pacific salmon species. These authors concluded that while a few sources of error were identified, overall, their automated hydraulic model generation process met the precision and accuracy requirements of habitat suitability models.

While many studies have examined the ecological importance of habitat complexity to rearing salmon, few have directly connected watershed-level habitat complexity to productivity. Hall et al. (2018) combined habitat status and population monitoring data from large Puget Sound rivers to explore the relationship between Chinook salmon productivity and basin-wide productivity. Habitat diversity was summarized with principle component analysis. Juvenile productivity was positively related to habitat complexity and negatively related to spawner density, suggesting density dependent mechanisms. Productivity varied less in watersheds with higher habitat complexity. This approach may be useful to track long-term effects of habitat changes and restoration activities.

Changes in flow regimes may alter the amount of habitat available for spawning. This in turn could lead to a restriction in the distribution of juveniles, further decreasing productivity through density dependence. Parry et al. (2018) examined redd distributions of Atlantic salmon in relation to flow in the Frome River, UK, from 1980 to 2015. Their results suggest that during low-flow years, salmon access to the upper river was restricted, and redd densities were more aggregated in lower reaches.

Restoration

Pacific Salmon in California are at the southern end of their range and utilize wide-ranging strategies to survive the variable climate of this region. Land use changes since the 1800s have reduced the availability of diverse habitats, leading to depressed productivity, distribution, and phenotypic/genetic diversity. With climate change, increasing temperatures and more frequent droughts further threaten these populations. Herbold et al. (2018) argue that the best way to re-develop the productivity and resilience of these populations is to restore habitat diversity, reconnect migratory corridors, and target management to replenish genetic and phenotypic diversity.

Like salmon, other species threatened by climate change can benefit from increased habitat diversity. Suggitt et al. (2018) utilized distribution data for 430 climate-threatened and range-declining species to examine how habitat heterogeneity related to population declines. Their results suggest that population impacts were reduced in areas where topography creates greater variation in microclimates. The population buffering provided by this habitat diversity was found to be generally strongest for species most sensitive to warming and in areas where warming was strongest.

Due to limited resources, it is important to implement restoration projects that effectively target limitations on population productivity and sustainability, and assessment tools can be useful in guiding such projects. Roni et al. (2018) reviewed various assessment tools, including (1) life cycle and fish-habitat models, (2) watershed assessment methods and techniques, (3) reach assessments, (4) prioritization tools, and (5) common monitoring methods. While no single assessment methodology addresses all the steps necessary to develop and implement restoration projects, these authors provide guidance for selecting situationally appropriate assessment tools.

As lowland reaches of rivers warm, efforts have increased to restore access to historical habitats truncated by dam construction. These habitats are often the coolest and most temperature-buffered within a watershed. Accordingly, restoring access may represent one of the best management options to increase population resiliency in the face climate change. In many such places, remnant populations of rainbow trout have persisted in upstream habitats that supported anadromous steelhead populations before the erection of migration barriers. Pearse and Campbell (2018) surveyed the genetic variation of such populations in the upper Tuolumne and Merced Rivers in and around Yosemite National Park. Their results demonstrate that despite extensive stocking of rainbow trout, these populations retained largely indigenous ancestry and adaptive genomic variation associated with anadromy. Accordingly, such resident trout populations could contribute to the recovery of steelhead populations following the restoration of migratory routes.

Trap-and-haul programs have become a common mitigation strategy to provide access to cold-water refugia upstream from impoundments. However, Naughton et al. (2018b) suggest that better protocols are needed to maximize the effectiveness of such programs. They used radio-telemetry to compare adults released into a cold-water reservoir vs. those released directly into tributaries of the relatively warm South Santiam River in Oregon. The majority of reservoir releases moved into tributaries but experienced lower cumulative temperatures than the tributary releases. However, about 14% of reservoir releases fell back over the dam versus only 1% of tributary releases. The authors suggest that when designing protocols for such programs, survival benefits from cooler reservoir temperatures should be compared against the risk of fallback and homing errors.

Ecologically functional estuaries are important transition environments for many juvenile salmon before they enter the open ocean. Healthy rearing habitat in estuaries provide growth opportunities for juveniles to increase size exposing themselves to marine predators. Davis et al. (2018c) presented results from 3 years of post-restoration monitoring, including data on habitat availability, invertebrate biomass, and abundance in juvenile Chinook salmon from a Puget Sound estuary. Three years following dike removal, productivity of restored mudflats reached levels comparable to references sites and growth rates were also similar between site groups. Woo et al. (2018) also provided an analysis of food availability in restored river deltas in Puget Sound, Washington. Their results also suggest that restored environments connected to existing productive habitat can help support salmon growth and survival within a few years of flow reconnection.

Disease/contaminant susceptibility

Climate change is likely to alter the susceptibility of organisms to ecotoxicological risks. Accordingly, understanding climate interaction with pollutants is important in assessing the impacts of climate change on marine ecosystems. Alava et al. (2018) utilized an ecosystem model to examine the effects of climate change on the bioaccumulation of organic mercury (MeHg) and polychlorinated biophenyls (PCBs) in the Northwestern Pacific marine food web. They estimated respective increases of 8 and 3% in the bio-accumulation of MeHg and PCBs by 2100 under a high emissions scenario. Proportional increases in the bioaccumulation of MeHg were predicted to be about 10% higher in mid-trophic level species, such as Chinook salmon, in comparison to top predators.

Chen et al. (2018a) examined migrating juvenile steelhead in the Puget Sound region for *Nanophyetus salmincola* parasite loads and for the presence of persistent organic pollutants (POPs). Parasite loads and POP concentrations were higher in fish migrating from southern Puget Sound in comparison to the northern parts of the sound. Potential negative impacts of high *N. salmincola* and POP levels early marine survival were demonstrated for one population from the southern part of Puget Sound.

Most existing studies suggest that the impacts of climate stressors will be additive, including increasing temperatures, deoxygenation, acidification, and contaminants. However, the potential for interactions remains largely unexplored. Sampaio et al. (2018) analyzed the effects of warming and acidification on the accumulation of mercury in the organs of meagre *Argyrosomus regius*. While Hg accumulation increased under a warming scenario, co-occurring acidification was found to dampen Hg accumulation and reduce contamination-elicited oxidative stress. Results suggest that this species may be able to tolerate future ocean conditions, though more research is needed to better understand the range of potential responses to multiple stressors.

Stewart et al. (2018) examined the effects of increased temperature on the immune defenses of fish. Using controlled experiments with three-spined stickleback exposed to three common parasites, they examined the effects of realistic warming on resiliency to infection. Increased temperatures were found to alter rates of infection and disease progression in an infection-specific manner. Effects on the immunocompetence of individuals were found to be similar in magnitude to thermal effects. This finding may suggest a level of adaptability in populations and demonstrates the difficulty in projecting infectious disease impacts from temperature data alone.

Many salmon-bearing watersheds are heavily managed through dam operations. Consequently, understanding the effects of dam operations on abiotic and biotic factors is important for successful management. The Klamath River is managed to limit infectious disease rates, specifically from *Ceratonova Shasta*, a myxosporean parasite that becomes more virulent at high densities and that has caused significant mortality events.

Javaheri et al. (2018) proposed that management in the Klamath River would benefit from better knowledge of "water age," defined as the travel time required for a parcel of water released from the dam to reach a specific location. This would allow for better predictions of how water releases affect parasite density and water temperature in specific reaches. To this end, Javaheri et al. (2018) performed a sensitivity analysis of water age and temperature to hydrologic and meteorological variables. Results suggest that flow rate and bottom roughness were the most influential parameters on water age.

Increasing frequencies of disease in marine organisms has co-occurred with climate change, suggesting a link with increasing temperatures. The documentation of genome-wide gene expression has created an unprecedented opportunity to examine the response of molecular regulation mechanism to environmental variability. Yue et al. (2018) performed a comprehensive transcriptomic analysis by RNA-seq and a proteomic analysis to explore potential mechanisms linking thermal stress and depressed disease resistance in the turbot *Scophthalmus maximus*. Results suggest that prolonged oxidative stress and metabolic disorder at higher temperatures might contribute to epizootics.

Management

Fisheries

Salmon management has generally been unable to recover depressed wild populations, despite increasing knowledge of salmon ecology. Gayeski et al. (2018) argue that management must become more place-based to achieve recovery goals in the face of continued habitat degradation and climate change. They identify a number of place-based management policies, including locating fisheries closer to rivers where the catch of individual populations can be better regulated, requiring fishing gear that allows for high rates of survival for released non-target fish, and frequently allowing escapement to exceed maximum sustainable yield. These authors provide examples of management in places where such policies are being implemented.

Dam and water management

Natural flow regimes, with their seasonal components, are thought to drive physical and biological processes in flood plains, thus preserving the functionality and productivity of riverine habitats. Hayes et al. (2018) present a functional flood-plain approach to flow management which emulates natural flows, including seasonal variability and peak flows. Such an approach can help managers protect the functionality of river floodplains in regulated systems.

Choi et al. (2018) examined how base flow relates to habitat suitability for fish located in Ungcheon Stream, both upstream and downstream of Boryeong Dam in the Republic of Korea. They combined hydrologic and hydraulic simulations with habitat

suitability index models to relate flow to habitat suitability for key species. Levels of base flow were found to significantly affect habitat suitability. These authors suggest a "building block approach" to restore aquatic habitat by modifying dam operations to represent a more natural flow regime.

Sundt-Hansen et al. (2018) utilized an individual-based model to examine and potentially mitigate the effects of climate change on Atlantic salmon through changes in dam management on the River Mandalselva in Norway. Their predictions utilized a range of potential future temperature and discharge scenarios based on global climate models. Abundance decreased in all future scenarios; however, the models suggested potential mitigation of these decreases by altering flow releases. In particular, they suggested increasing the minimum permitted discharge level.

Environmental flow assessments generally involve attempts to determine conditions beneficial for a number of species and life stages. However, flow requirements can conflict among different species and life stages and are often poorly quantified. Millidine et al. (2018) investigated and discussed the various effects of flow regulation on Atlantic salmon fry utilizing saturation stocking and electrofishing combined with hydraulic and habitat models.

Nguyen et al. (2018) reviewed ecological models used to assess impacts of water management on biological communities. They provided a summary of inputs, approaches, output variables, and ecosystem interactions described in models within the current body of literature. Their review suggests that a common limitation is the inability to separate dam-related impacts from other anthropogenic impacts. They highlight the potential for the integration of modelling techniques with remote sensing data to characterize habitat. This approach may improve the ability to predict biological responses to water management decisions.

Despite its position upstream from four dams and downstream from ten, the short, free-flowing Hanford Reach of the Columbia River supports one of the most productive fall Chinook salmon populations in the basin. Langshaw et al. (2018) suggest that hydrological management may have contributed to this productivity, potentially through actions that increased available habitat during spawning periods; increased egg survival by mitigating redd scour, desiccation, and sedimentation; and increased food availability.

Dam operations often lead to large and abrupt changes in river flow. Song et al. (2018) examined the influence of variation in flow on thermal and biogeochemical dynamics in the hyporheic zone of the Hanford Reach using a two-dimensional thermo-hydro-biogeochemical model that accounted for aerobic respiration.

High-frequency fluctuations in flow had strong thermal and biogeochemical effects during low-flow periods in fall and winter. Flow fluctuation enhanced biogeochemical process rates due to increasing nutrient and oxygen supply. This study provides a basis for examining the localized ecological effects of flow management.

Dam operations can artificially reduce downstream temperatures by releasing deep water from reservoirs and increasing flows during low-flow periods. This practice can be beneficial to cold-water obligate species and may help mitigate the effects of climate change in these habitats. Benjankar et al. (2018) utilized an integrated modeling framework to suggest that, given the expected effects of climate change, reservoir management will be more beneficial than unregulated flows for bull trout in the South Fork Boise River of Idaho.

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