Impacts of Climate Change on Salmon of the Pacific Northwest

A review of the scientific literature published in 2015

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Highlights

Physical Processes of Climate Change

Globally, nationally, and regionally, 2015 was a record-breaking climate year (Blunden and Arndt 2016). Enhanced by a strong El Niño, global annual surface temperature was the warmest ever recorded for the second year in a row, exceeding the pre-industrial average by over 1°C for the first time. New records were also set for global ocean heat content, sea level, and minimum sea ice extent.

Retrospective Climate Trends

- The North Pacific marine heatwave from 2013-2015 displayed sea surface temperature anomalies over 3 SD above normal (Bond et al. 2015). Di Lorenzo and Mantua (2016) argued that teleconnections between the North Pacific and El Niño maintained the anomalous conditions through multiple years. Climate model simulations indicate that extreme conditions such as this are likely to increase with greenhouse gas forcing.
- Historical time series data show dramatic trends in rising temperatures apparent across the conterminous U.S. (Mutiibwa et al. 2015). As new records are set, attribution of these events specifically to rising greenhouse gases has become easier statistically.
- Mera et al. (2015) linked climate change to extreme heat waves in the Central Valley, California. Analyses of the 2012-2014 California drought supported previous reports. Some aspects of the 2014 drought broke historical records (Williams et al. 2015), but extreme droughts of this or greater magnitude have been observed in the recent and ancient past, and are driven primarily by natural variability in precipitation (Diaz and Wahl 2015; Mann and Gleick 2015; Mao et al. 2015; Williams et al. 2015).
- Mao et al. (2015) found that anthropogenic warming has caused declines in snowpack and total spring runoff, which contributed to the drought and accounted for 8-27% of the drought anomaly. In brief, anthropogenic warming makes the combination of dry and warm years more likely, increasing the negative impacts of drought (Diffenbaugh et al. 2015).
- In contrast to California, the Pacific Northwest (PNW) has experienced fewer droughts due to increased precipitation (since 1979, Ficklin et al. 2015; since 1916, Mo and Lettenmaier 2015). However, not all PNW locations have exhibited these regional trends; this spatial heterogeneity is described by Duncan et al. (2015).
- Heavy snowfall has decreased in both the PNW and California (1930-2007, Kluver and Leathers 2015). Reduced snowfall has manifested in widespread glacier retreat documented in the Olympic (Riedel et al. 2015) and North Cascade mountain ranges (Marcinkowski and Peterson 2015).

Future Climate Projections

- Looking toward the future, numerous studies focused on the increasing intensity and frequency of precipitation events. Atmospheric rivers are bands of warm, wet air that cross the central Pacific Ocean and cause heavy precipitation events along the west coast of North America. Global circulation model results show that rising greenhouse gases will cause atmospheric rivers to become more intense and frequent, with maximum change affecting northern California (Gao et al. 2015; Payne and Magnusdottir 2015; Radic et al. 2015; Warner et al. 2015).
- Heavier and warmer precipitation are projected to increase rain-on-snow events, particularly at mid-elevations (Safeeq et al. 2015).
- A systematic exploration of how seasonal change in temperature and precipitation would alter runoff across the PNW revealed that the Salmon River Basin, Idaho is one of the most sensitive areas (Vano et al. 2015b). Zeroing in on the Salmon River Basin, Tennant et al. (2015) focused specifically on the snowline. An increase of 3°C would shift the snowline from 1,980 to 2,440 m. Such a shift would entail a 42% loss of area in the basin now classified as snow-dominated.
- Loss of snowpack will change the timing and quantity of runoff in the largest rivers of the PNW, which could affect hydropower production. Kao et al. (2015a) assessed power production for 132 federal dams and found a median expected loss of -2 TWh (ensemble uncertainty of +/- 9 TWh), which is 7% in annual production. In the Bonneville Power Administration study areas, annual production is projected to increase slightly, despite declines in annual runoff. This projection has an uncertainty range that includes declines in production, but does not exceed historical variability.
- While U.S. regions differ in the season during which they will be most affected, projected declines in runoff at Bonneville Power Administration installations were ~8-10% annually in the next decade, but might rebound after that. Kao et al. (2015a) projected 40-50% declines in summer runoff by 2040.
- The terrestrial landscape profoundly affects water quality and quantity in streams. Hotter, drier summers in the PNW will promote a shift to more warm-adapted vegetation, but the rate at which this occurs is modulated by fire dynamics. Existing vegetation, climate, and fire suppression efforts interact in complex ways across the region (Holmes et al. 2015; Sheehan et al. 2015; Turner et al. 2015; Vano et al. 2015b).

Upwelling Intensity and Ocean Acidification

- In the marine domain, Rykaczewski et al. (2015) and Wang et al. (2015) explored how the intensification of along-shore winds projected by global climate models (GCMs) will intensify coastal upwelling. Both studies found a latitudinal gradient in impacts, with stronger effects at higher latitudes. However, the California Current system (CCS) is more uncertain than other eastern boundary systems, partly because processes other than along-shore winds also influence upwelling (Di Lorenzo 2015; Jacox et al. 2015a). Furthermore, biological impacts depend on source water in addition to wind strength (Jacox et al. 2015b). Therefore, these results should still be considered exploratory.

- Bakun et al. (2015) discussed the potential for ocean changes to cause community shifts and predator/prey mismatches in timing, which could negatively affect salmon.
- Ocean acidification is progressing quickly, as noted in previous reviews. Aragonite undersaturation in the Bering Sea is projected to exceed historical variability by 2044, and become chronic by 2062 (Mathis et al. 2015). Takeshita et al. (2015) explored how habitats within the CCS differ in buffering capacity and hence in vulnerability to ocean acidification.

Climate Impacts to Salmon

Sockeye Run Failure Caused by High Temperatures

In early summer 2015, unprecedented high temperatures hit the lower mainstem Columbia River and tributaries (DART 2016; NOAA Fisheries 2016). Of all Redfish Lake sockeye salmon detected passing Bonneville Dam, only 4% survived to Lower Granite Dam, and none survived after temperatures exceeded 20°C at Bonneville (NOAA Fisheries 2016).

Poor Survival of Winter-run Chinook and Oregon Coho

- For Sacramento winter-run Chinook salmon, egg-to-fry survival in 2014 and 2015 was the lowest ever observed and is informally being attributed to the California drought (Martin et al. In press; Pacific Fishery Management Council 2016; Poytress 2016).
- Oregon coho returns were far below forecast in a manner consistent with low returns from previous major El Niño events and negative impacts from “the blob” (Pacific Fishery Management Council 2016). However, future analysis is necessary to formally link coho ocean survival to the recent anomalous ocean conditions.

Acidification Directly Affects Early Life Stages in Salmon

Ou et al. (2015) significantly advanced our knowledge of direct physiological impacts of lower pH on developmental stages of pink salmon. They studied acidification in freshwater, which has received less attention than ocean acidification. Their findings were consistent with negative impacts on growth observed in Atlantic salmon (Fivelstad et al. 2015). Lacking this direct evidence of negative effects of pH on early life stages in salmon, marine ecosystem models continue to project neutral or positive effects of ocean acidification on salmon (Reum et al. 2015).

Loss of Adaptive Capacity at Climatic Extremes

- Population comparisons affirmed genetic variation and local adaptation in heat tolerance for trout (Chen et al. 2015; Garvin et al. 2015; Narum and Campbell 2015) and in environmental conditions generally for Chinook salmon (Hecht et al. 2015). However, less genetic diversity was found in bull trout populations exposed to high temperatures and high winter flooding, suggesting that the ability to adapt to climate change is already being eroded (Kovach et al. 2015b).
- Because not all traits show genetic variability in heat tolerance even in the absence of strong selection on this trait, Muñoz et al. (2015a) predicted that this constraint will cause population extinction. However, Mantua et al. (2015) pointed out that behavioral plasticity might prevent exposure to the conditions explored by Muñoz et al. (2015a). Anderson et al. (2015) demonstrated that extinction risk could be minimized using conservation strategies that specifically aim to preserve existing genetic variability in thermal tolerance.
- Selective fishing on older fish is a particular concern because under climate change, evolutionary drivers might favor an older age at return, as shown in Atlantic salmon (Piou et al. 2015). Management practices that oppose adaptation to climate change undermine species resilience, causing population decline.

Exotic Predators and Prey Spread in the Columbia Basin

- Salmon populations persist by balancing growth from prey consumption with mortality from predators. In the Columbia Basin, invasive plankton species now dominate reservoirs (Emerson et al. 2015) and the estuary (Bowen et al. 2015). Chinook salmon eat these species, although they are not preferred prey (Adams et al. 2015).
- Evidence continues to show declines of native pteropods in the southern CCS due to ocean acidification (Bednarsek and Ohman 2015). Although the link between pteropod abundance and salmon survival is generally weak, Doubleday and Hopcroft (2015) found a correlation between pteropod abundance and pink salmon survival in the Gulf of Alaska.
- In freshwater, smallmouth bass is a warm-water predator expected to pose an increasing threat to Chinook salmon. Until now, mechanistic models of bass range limits have not been available; however, Lawrence et al. (2015) developed a model that can now be used to identify specific life stages that limit bass range.

Salmon Populations: Northern Advances and Southern Declines

- Some exciting changes were revealed by new observations in the Arctic: all Pacific salmon species are increasing in areas historically unfavorable for them (Logerwell et al. 2015). Phenological changes in migration (Kovach et al. 2015a; Sergeant et al. 2015; Stich et al. 2015) and spawn timing (Lyons et al. 2015) have been observed as well, but only some of these trends are in the direction expected from regional climate trends. The evidence shows that local heterogeneity can outweigh climate drivers in both the direction and rate of population response.

- Declines in Puget Sound Chinook salmon populations over 20 years reflect numerous drivers, but are attributed in part to increasing variability in stream flow by Ward et al. (2015). In southern Europe, global range limits have contracted for brown trout due in part to thermal constraints over the last century (Larios-Lopez et al. 2015).

Projected Range Contractions in the California Current System

A new bioclimatic envelope analysis of major fish distributions predicts significant range contractions and local extinctions at the southern extent of the CCS (Cheung et al. 2015). Salmon prefer colder regions of the CCS, and therefore are expected to contract their range.

NOAA Fisheries Climate Science Strategy

NOAA Fisheries released its science strategy to manage for climate change (Link et al. 2015). This strategy involves building infrastructure, tracking trends, detecting early warning signs, developing mechanistic understanding, and robust management solutions for a changing climate.

In conclusion, unprecedented heat exposures were observed in the Columbia River in 2015, along with prolonged drought in California and extraordinarily high ocean temperatures (the blob). Preliminary observations indicate severe negative consequences for endangered Redfish Lake sockeye, endangered Sacramento River winter-run Chinook and Oregon coho populations. These observations provide evidence that climate change will present enormous challenges for salmon. Climate change is advancing rapidly and will likely accelerate in coming decades (Roberts et al. 2015). New information about negative effects of freshwater acidification on salmon and loss of adaptive capacity in climate-stressed populations of bull trout increase concern about the ongoing resilience of salmon in the PNW and California.

Contents

Objective and Methods

The goal of this review was to identify literature published in 2015 that is most relevant to prediction and mitigation of climate change impacts on Columbia River salmon listed under the Endangered Species Act. Because almost anything that affects salmon is altered in some way by changes in temperature, stream flow, or marine conditions, a large amount of literature related to this topic was necessarily excluded.

In our literature search, we elected to focus on peer-reviewed scientific journals included in the *Web of Science* database, although we occasionally 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 600 papers, 170 of which were included in this summary.

Literature searches were conducted in June 2016 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 2015, plus:

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

This review is presented in two 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 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 responses of salmon to these environmental conditions, both projected and retrospective, in freshwater and marine environments.

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[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.

Physical Processes of Climate Change

Annual Observations from 2015

Globally, nationally, and regionally, 2015 was a record-breaking year in climate. At the Mauna Loa Observatory station in Hawaii, the longest-running record of atmospheric CO_2 exceeded 400 ppm for the first time, and global average concentration was 399.4 ppm. The Antarctic ozone hole was the largest observed since 1990.

Enhanced by a strong El Niño, global annual surface temperature was the warmest ever for the second year in a row, exceeding the pre-industrial average by over 1°C for the first time. Heat records were broken on every continent. In the Arctic, land surface was 2.8°C warmer than when records began in 1900. Sea ice maximum was the smallest ever recorded (7% below the 1981-2010 average), and Arctic sea surface temperatures were up to 8°C above average. New records were also set in global ocean heat content and sea level. Over 50% of the Greenland ice sheet experienced melting at the surface, with net mass loss in alpine glaciers for the 36th consecutive year. In the Northern Hemisphere, snow cover was the second lowest on record (49 years), and the permafrost reached record high elevation at 20 m.

Tropical storm activity was very high, both in terms of total number of named storms and number of most intense storms. An intensified hydrological cycle drove floods worldwide; in the U.S., May 2015 was the wettest month ever (121-year record). Nonetheless, groundwater storage was low, based on the Gravity Recovery and Climate Experiment satellite observations (14-year record), and 14% of the world experienced “severe” drought.

Retrospective Climate Trends

North Pacific Ocean: The Blob

The North Pacific marine heatwave from 2013-2015 displayed sea surface temperature anomalies over 3 SD above normal (Bond et al. 2015). Di Lorenzo and Mantua (2016) argued that teleconnections between the North Pacific and El Niño maintained the anomalous conditions through multiple years. Climate model simulations indicate that extreme conditions such as this are likely to increase with greenhouse gas forcing.

Pacific Northwest: Reduced Snowfall

A study of snowfall across the U.S. from 1930 to 2007 found that trends differed by region depending on location in relation to major storm tracks, but that the frequency of heavy (above average) snowfall has decreased in the PNW and California. Annual variation in snowfall is correlated with large-scale atmospheric circulation patterns such as the Pacific decadal oscillation (PDO) in winter, the Pacific North American pattern (PNA), and the Oceanic Niño index (ONI) in Niño region 3.4 (Kluver and Leathers 2015).

Reduced snowfall has impacted glaciers in the PNW. Glacial retreat on the Olympic Peninsula has been stunning, culminating in the loss of 82 glaciers for a reduction in combined area of 34% from 1980 to 2009 (Riedel et al. 2015). Glacial meltwater is an important contributor to streamflow during low flow periods in some basins. For example, in the Hoh Basin, up to 30% of total runoff comes from glaciers. Marcinkowski and Peterson (2015) used mountain hemlock tree rings to reconstruct increases and decreases in glacial mass from North Cascades glacier over the past 350 years. They found that recent years have shown rapid declines in glacial mass, but that glaciers in this region are not at an all-time low, which occurred in the 1940s.

They found that local glacial history was consistent with that of larger geographic regions, and reflected forcing from large-scale climate drivers such as the PDO and El Niño southern oscillation (ENSO). These long-term analyses are enormously helpful, because short-term time series often cannot detect recent trends due to high interannual variability. This problem was demonstrated by an analysis of 15 years of snowfall data in the Oregon Cascades (Kostadinov and Lookingbill 2015).

Variable Effects of Increased Temperature

Temperature patterns in the conterminous U.S. were analyzed for different metrics over various time periods, but all showed dramatically warmer temperatures in recent years, particularly in relation to extreme hot and cold events (Mutiibwa et al. 2015). In the number of days over 90°C, the frequency and area covered have dramatically increased. From 1979 to 2005, there were no years in which even 5% of the U.S. was over 90°C for extended periods. From 2006-2012, however, 5 years surpassed this record, with nearly half of the U.S. (47%) experiencing at least 90 d over 90°C in 2012. Warming occurred fastest in springtime. Spring temperatures were positively correlated with ENSO in the PNW, but the correlation coefficient was negative elsewhere in the country.

A study of recent extreme heat waves in the Central Valley in California further resolved their characteristics and attributes the increase in severity to increasing greenhouse gases (Mera et al. 2015).

As heat waves become more frequent, a particular type of drought might become more problematic; that is, flash drought caused by high temperatures as opposed to low precipitation. These flash droughts occur when soil moisture dries out very quickly because of a heat wave. Flash droughts are primarily a concern for agriculture, but will influence fish through increased irrigation demands and altered runoff patterns. Despite concern about future increases, trends during 1916-2012 show decreasing drought in the PNW, largely because of increasing precipitation (Mo and Lettenmaier 2015).

Since 1979, decreasing trends in drought were also detected using the Palmer drought severity index in the PNW (Ficklin et al. 2015). The relative importance of two alternative drivers of drought, temperature and precipitation, had similar magnitude in the PNW. The regional trend does tend to obscure spatial heterogeneity that is important for local planners. Duncan et al. (2015) showed how the regional trend played out locally across the PNW.

Stream temperatures have increased over the past half century, tracking regional climate trends. However, Reiter et al. (2015) documented that regulations imposing buffers on forest harvest have reduced the amount of stream warming in buffered areas compared to un-buffered areas.

California: Extreme Drought of 2012-2014 not Unprecedented

Analyses of the 2012-2014 California drought were consistent with previous reports. Some aspects of the 2014 drought broke historical records (Williams et al. 2015), but extreme droughts of this or greater magnitude have been observed in the recent and ancient past, and are driven primarily by natural variability in precipitation (Diaz and Wahl 2015; Mann and Gleick 2015; Mao et al. 2015; Williams et al. 2015). Nonetheless, Mao et al. (2015) found that anthropogenic warming has caused declines in snowpack and total spring runoff, which contributed to the California drought and accounted for 8-27% of the drought anomaly. In brief, anthropogenic warming makes the combination of dry and warm years more likely, increasing the negative impacts of drought (Diffenbaugh et al. 2015).

Idaho: State-wide Trends in Climate Indicators

In an effort to make climate change information more useful to a wider audience, Klos et al. (2015) assembled an interdisciplinary group to conduct a survey across Federal and State Agencies, private citizens and NGOs to identify the primary concerns about climate change impacts in Idaho. Water availability, the risk of extreme drought, changes in plant productivity and wildfire risk were the top concerns.

Based on these concerns, Klos et al. (2015) collected data on a set of biophysical indicators, such as temperature, flow/precipitation/snowpack indices, plants/salmon/bird phenologies, and forest area burned, focusing on the 1975-2010 time period. This start period was selected to avoid the significant trend over time due to the historical regime shift between PDO phases that occurred in 1976.

Ecological indicators include the date of upstream adult sockeye migration at Lower Granite Dam from 1975 to 2011. It is not clear exactly why they chose sockeye instead of more robust Chinook populations. This period includes essentially no natural anadromous run because this population was functionally extinct and reduced to captive brood stock in most of this period, and is missing data altogether for many years. They did not find a significant trend in this indicator. Other indices did show significant trends: rising mean annual air temperature, lengthening growing season, earlier dates for lilac blooming and mountain bluebird egg-laying, and more forest area burned.

Non-significant but positive trends occurred in increasing spring precipitation, earlier peak streamflow, decreased April 1 snowpack, and longer fire season. No detectable trends were found in total annual streamflow, timing of sockeye migration, mean annual stream temperature, and start of fire season. An interesting point in this paper is the comparison of the perceived importance of an indicator and how closely that indicator is linked to climate (i.e., complexity of the process involved). Water-related indices outweighed temperature-related indices likely because water is already a limiting resource in Idaho, whereas temperature is not a tightly tied to a specific human use. Fire and biological viability metrics are complicated by many influences other than climate, but are seen as potentially causing direct harm, and hence worthy of greater research to separate out different influences.

Southern California: Complex Dynamics Control Fog

Large climate drivers profoundly affect conditions in the California Current and upwelling, which in turns influences coastal fog. Fog in southern California has a complex relationship with the PDO and ENSO, showing that a historically strong correlation has disappeared in recent years (Witiw and LaDochy 2015). Other important influences on fog include pollution levels, heat island effects, and upwelling, each with waxing and waning roles in different decades, complicating any future projections.

Projected Climate Change Scenarios

Terrestrial Projections

***Increased heavy precipitation*—**Atmospheric rivers are narrow air currents that accumulate large amounts of water vapor across the Pacific Ocean and carry much of the rain that falls along the west coast of North America. Global circulation models project a northward shift in major wind patterns. Warmer air in general holds more water vapor. When these processes are combined, they have implications for the frequency and intensity of storms caused by atmospheric rivers. A series of papers that explored these dynamics appear to form a consensus on this matter (Gao et al. 2015; Payne and Magnusdottir 2015; Radic et al. 2015; Warner et al. 2015).

Schoof (2015) compiled a new set of daily precipitation projections that has been completed for the entire U.S. The number of heavy precipitation events is likely to go up along the whole coast, especially in winter. Similar to previous results, the PNW is expected to become wetter from fall through spring and possibly slightly drier in summer. Slightly shorter rainy periods are expected west of the Cascades, with little change in dry or wet spell duration in most of the interior. California is projected to have more dry days, but not a significant change in total precipitation outside the winter season (Dec-Feb). To produce these results, Schoof (2015) applied a relatively uncommon statistical downscaling method to output from Earth-system and atmosphere-ocean GCMs from the Coupled Model Intercomparison Project (CMIP5).

Increased flooding and hydrologic regime change—Winter storms cause major damage to human infrastructure and present concerns for salmon. A new set of simulated extreme runoff events examined spatial heterogeneity in risk across the PNW (Najafi and Moradkhani 2015). An ensemble average prediction was made from eight GCM/regional climate model (RCM) combinations, followed by the variable infiltration capacity (VIC) hydrological model.

The ensemble projection showed increases in extreme runoff during winter and spring in 90% of grid cells. The entire region west of the Cascades showed increased extreme runoff events from fall through spring. Snow-dominated regions such as the Salmon River Basin, the ridge of the Cascades, and the Canadian portion of the Columbia River showed more extreme events in summer.

The largest floods along the west coast are often caused by rain-on-snow events. Safeeq et al. (2015) projected a 30-40% increase in peak flows at high elevations within Washington State. Historically, most rain-on-snow events occurred in the Olympic and Cascade Mountain Ranges, as well as in the Blue Mountains. As the climate warms, areas that are now solidly snow-dominated, such as the upper Columbia River in Washington, will become more transitional and display more of these events.

Taking a different approach to identification of the PNW watersheds most sensitive to warming, Vano et al. (2015b) explored differences in runoff depending on whether warming occurred in winter or summer. In rain-dominated basins, runoff was directly dependent on precipitation in both winter and summer, and relative seasonal sensitivity did not change with climate change. With snow-dominated basins, changes in winter had a delayed effect on runoff that did not occur until the spring snowmelt.

If a basin converts from snow-dominated to transitional or from transitional to rain-dominated, winter runoff increases, and summer runoff decreases, resulting in a differential seasonal response. Vano et al. (2015b) identified watersheds that are likely to undergo a hydrological regime change with 3°C warming, based on this discrepancy. Regime-changing watersheds span the ridge of the Cascades and central Idaho.

Vano et al. (2015b) also found that the region most sensitive to both temperature and precipitation change is the Salmon River Basin. This basin had the greatest projected decline in annual runoff with warming of 1°C vs. increased runoff with a precipitation increase of 1%. The response to temperature was greater when warming was applied in summer vs. winter, whereas the response to precipitation was more sensitive in winter.

Much of the rest of Washington and Oregon and the Snake River Plain showed very little response to increased summer precipitation. Impacts from warming tend to be greater in summer, whereas the impacts from precipitation change tend to be greater in winter. Vano et al. (2015b) identified watersheds that are likely to undergo a regime change with 3°C warming, e.g., from snow-dominated to transitional, or from transitional to rain-dominated, based on the discrepancy in sensitivity to cool- vs. warm-season warming. These span the ridge of the Cascades and central Idaho.

Focusing in more detail on regime change in the Salmon River Basin, Tennant et al. (2015) show how watersheds at different elevations respond to warming. They project that a 3°C temperature increase will result in a 40% loss of snow-covered area, as the snowline increases from 1,980 to 2,440 m.

Vano et al. (2015a) conducted a separate sensitivity analysis to explore streamflow in selected basins within more specific seasonal periods. In the snow-dominated Upper Columbia Basin, they found that spring runoff (Apr-Jun) increased with up to 4°C warming because snow remained despite an earlier freshet. Summer flows (Jun-Aug) in the Willamette were much more sensitive to change in precipitation than temperature because snow had little effect in this rain-dominated basin.

In the transitional Yakima basin, irrigation demands span three seasons, impacting flows from April to September, and flows are similarly sensitive to both temperature and precipitation. Over the full range of GCM scenarios to date, declines in flow during high-demand periods are predicted in the Willamette and Yakima Basins. In the Upper Columbia Basin, increases in spring runoff are expected as more snow melts earlier in the season.

Thorne et al. (2015) used a process-based model (the basin characterization model) to (1) ask what is the magnitude of historical and projected future change in the hydrology of California's watersheds; (2) test the spatial congruence of watersheds with the most historical and future hydrologic change; and (3) identify watersheds with high levels of hydrologic change under drier and wetter future climates.

Watershed change was analyzed for climatic water deficit, April 1st snowpack, recharge, and runoff. They developed a normalized index of hydrologic change that combined the four variables, and identified which watersheds show the most spatial congruence of large historical change and continued change under the two futures. Of the top 20% of all watersheds (1028), 591 in the Sierra Nevada Mountains and Northwestern ecoregions have high spatial congruence across all time periods. Among watersheds where change accelerates in the future, but not historically, a majority are congruent between both climate models, predominantly in the Sierra Nevada, Cascade Ranges and the Northwestern ecoregions.

Hydropower production forecasts—Reduced snowpack, more intense storms and drier summers will affect hydropower generation across the country. Kao et al. (2015a) assessed power production for 132 federal dams and projected a median loss of -2 TW hours in annual power generation capacity of. At local BPA installations, the change in annual mean runoff and hence power generation was projected to decrease by 8-10% within the next decade, with impacts reduced by 2040. However, summer production was projected to drop 40-50% by 2040.

Interannual variation was similar in the projections compared to the 20-year historical baseline period (1989-2008). To generate these projections, Kao et al. (2015a) used output from the community climate system model version 3 (CCSM3) under the A1B[3] emissions scenario. They downscaled this output to 25 km resolution using the International Centre for Theoretical Physics regional climate model (RegCM2). Hydrological projections are based on the variability infiltration capacity model (VIC) and the WaterWatch runoff-based assessment approach.

Pacific Northwest Stream Flows Correlated with the PDO—One concern for salmon is that unfavorable environmental conditions can impact multiple life stages, leading to larger cumulative effects than might have been expected based on the sum of individual life-stage impacts. Large-scale climate phenomena such as the PDO were already known to correlate with terrestrial precipitation patterns, but a new study further explores the relationship of these patterns with seasonal indices of the PDO and sea-surface temperature (SST) across the U.S.

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[3] A "balanced" emissions scenario that assumes rapid economic growth and a reliance on alternate energy sources in addition to fossil fuels. See the IPCC special report *Emissions Scenarios* at www.ipcc.ch/index.htm (October 2016).

Sagarika et al. (2015) compared SST in winter with spring and summer streamflow across seasons in the PNW and found positive correlations in the PNW and negative correlations in California. These correlations were statistically significant during the cold phase of the PDO, but not the warm phase.

Increased fires promote shifts toward warmer-climate vegetation—Riparian areas are greatly influenced by vegetation in the surrounding landscape, both locally and regionally. Sheehan et al. (Sheehan et al. 2015) simulated vegetation for the Northwest U.S. using results from 20 different CMIP5 models downscaled using the multivariate adaptive constructed analogs (MACA) algorithm. They project a shift from conifer to mixed forest in the western part of the region, woodier vegetation under fire suppression scenarios in the eastern plains and plateau, and loss of subalpine communities altogether at higher elevations. Fires became much more frequent, with large fires in the western subregion driven by warmer and drier conditions. They discuss the shifts in drivers and controls on fire and vegetation throughout the region.

Zooming in on the Willamette Basin, Turner et al. (2015) projected much higher fire frequency, entailing a shift from evergreen, needle-leaf forest to a mixture containing more broadleaf trees over 20-50% of forested area. A generally more disturbed and open forest landscape is expected.

British Columbia is projected to experience a longer growing season and consequently more vegetation growth under a warmer climate, with the greatest change expected in the coastal mountains (Holmes et al. 2015).

Increasing stress on water supplies—A hotter drier climate will stress water supply for humans as well as wildlife, leading to more problems with water scarcity (Mateus et al. 2015). Mateus et al. (2015) explored the impact of climate change projections on the importance of human water demand vs. climate factors in shaping water availability across a the transitional Santiam Basin watershed in Oregon. Because agricultural and urban withdrawals are generally located at lower elevations, variation in demand has a larger impact on water scarcity at lower than higher elevations.

Vano et al. (2015a) also explored vegetation responses in the Columbia River Basin. They found that differences among basins in fire frequency changed the response to temperature and precipitation. On the Oregon and Washington coasts and in the western Cascades, vegetation changed in response to temperature increases but was fairly insensitive to precipitation changes. In contrast, vegetation in the Upper Columbia Basin was more sensitive to precipitation. Nonetheless, the majority of GCMs predicted declines in productivity in all areas for both the 4.5 and 8.5 RCP scenarios.

Similar trends projected for British Columbia and Alaska—An expert review of projected impacts from climate change in the Canadian and Alaskan coastal rainforests was conducted by Shanley et al. (Shanley et al. 2015). They used 5 GCMs and two emissions scenarios (RCP 4.5 and 8.5), downscaled by the ClimateWNA modeling software. They stratified results by alpine, subalpine, and lowland forest zones, as well as by geographic province and discuss possible implications for salmon as well as vegetation and wildlife.

Their conclusions are similar to those discussed previously—some cool, limited regions might experience higher salmon productivity, but in other regions, negative impacts are expected for more vulnerable salmon life stages. Reductions in snowmelt-dominated watersheds will expose more eggs to scour, and changes in temperature might shift migration and spawn timing. They emphasize the importance of maintaining diverse life histories for resilience to climate change.

In the Arctic, warming will occur much faster than at temperate latitudes. Nilsson et al. (2015) review the types of extreme precipitation and temperature events that will likely ensue.

Ocean Projections

Intensification of upwelling—Upwelling is a very strong correlate of early marine survival in salmon, especially for Californian stocks. Two key papers explored the implications from GCM for upwelling in the California Current. Neither study supported the Bakun (1990) hypothesis that warmer ocean-land temperature gradients would intensify upwelling. Both studies projected more intense winds at higher latitudes, but a dampened response at lower latitudes. Upwelling is therefore likely to become stronger, start earlier, and last longer in the northern CC ecosystem (Wang et al. 2015).

However, Wang et al. (2015) cautioned that projections for the California Current were more uncertain than those for other eastern boundary systems. Processes other than alongshore winds drive dynamics of the CCS, and observed decadal fluctuations in upwelling are not fully resolved by these models (Di Lorenzo 2015). Thus projections should still be considered exploratory for these very important processes.

The impact of upwelling on fish survival depends not only on intensity, but also the nutrient concentrations within upwelled water. Jacox et al. (2015b) explore how ENSO affects both vertical transport strength and nutrient supply and develops a new index of upwelling efficacy for primary productivity. They explore the teleconnections driving these responses and find similar processes at work in comparisons of ENSO and the PDO.

Jacox et al. (2015a) used a regional ocean model to evaluate the roles of wind, surface heat flux, and basin-scale climate variability in regulating the upwelled nitrate supply in the California Current. A strong positive trend in nitrate flux from 1980-2010 was driven almost exclusively by enhanced equatorward winds, negating a weak negative trend associated with increased surface heat flux.

Ocean acidification and hypoxia—Recent observational data from the Arctic Basin show that continental shelf seas in the Arctic will become undersaturated with respect to aragonite (Beaufort Sea, 2001; Chukchi Sea, 2033; Bering Sea, 2062, Mathis et al. 2015). Mean annual aragonite concentrations were evaluated at approximately 30-year intervals from north to south. However, biological impacts might occur before these threshold years. The Chukchi and Beaufort Seas are expected to pass outside the range of their respective historical variability in undersaturation by the 2020s, and the Bering Sea and Pacific-Arctic Region by ~2050.

Projected ocean acidification rates have moved from global means to subregions to individual habitats. Takeshita et al. (2015) demonstrated habitat-specific signatures of pCO_2 within the California Current. They compared surf zone, kelp forest, submarine canyon edge, and shelf break in the upper 100-m of the Southern California Bight. They found that while habitats differed in their buffering capacity, the mean and variance in pCO2 increased in all habitats, with the fastest rate of increase occurring in the deepest habitat.

Hypoxia typically accompanies low pH. At present, hypoxia occurs along the Oregon/Washington coastline seasonally, but these waters are expected to shoal, with hypoxia persistence lengthening under future climates. A study of the effects of hypoxia on local fish larvae found only small effects, although densities of larvae overall were lower under more hypoxic conditions (Johnson-Colegrove et al. 2015).

Siedlecki et al. (2015) explored the physical mechanisms that cause hypoxia along the coast, comparing the cause of local recirculation patterns within a broad area experiencing high respiration rates. They found also that the Columbia River plume lowers O_2 levels, causing a slight increase in hypoxia in areas affected by the plume. Bacterial community changes, it turns out, act as an early warning sign of impending hypoxic conditions. Spietz et al. (2015) found that bacteria community composition changes at much higher levels of dissolved oxygen than those typically causing negative impacts on fish. They studied these responses in the seasonally hypoxic area of Hood Canal, Washington.

Rising temperatures, sea level, and storminess lead to harmful algal blooms and coastal damage—Two impacts of climate change in western Washington and Oregon that are especially concerning for people are the predicted increases in harmful algal blooms and coastal damage. Moore et al. (2015b) projected a 30-day increase in the number of days favorable for harmful algal blooms in Puget Sound by 2050. This increase is driven primarily by warmer temperatures increasing the maximum growth rate of the dinoflagellate *Alexandrium*, which produces these toxic blooms. Along the outer coast, rising sea level and storm intensification will increase total water levels and erosion damage. Baron et al. (2015) and Cheng et al. (2015) focus on Tillamook County, Oregon to quantify this impact and explore a mapping technique that will be useful for coastal planners.

Climate Model Comparisons/Improvements

There is extensive work to compare modeling methods and document improvements and ongoing model development. Most of this work is beyond the scope of our review, but we note a few relevant examples. A new earth system model, BioEarth, is being developed for the Columbia Basin. BioEarth couples GCM output with a regional climate model through hydrologic impacts, dynamic vegetation, and carbon cycling. They introduce a final step involving anthropogenic feedbacks with a reservoir operations model (ColSim) and agricultural impacts using NEWS (Adam et al. 2015). This model is designed for basin-wide decision making.

Several studies documented that dynamical downscaling methods better capture spatial variation in precipitation than statistical downscaling. Jang and Kavvas (2015) dynamically downscaled all of northern California, whereas Walton et al. (2015) developed a hybrid dynamical/statistical method focused specifically on Los Angeles, CA.

Effects of Climate Change on Pacific Salmon

Historical Trends

Northward Range Shifts

Although most effects of climate change for Pacific salmon in the Northwest are negative, some environments may become newly habitable as the climate warms. Chinook and coho, in particular, are historically rare north of the Bering Strait. After a detailed habitat assessment of the western Beaufort and Chukchi Seas by Logerwell et al. (2015), evidence of a northward range expansion is now available. They report that Chinook salmon were caught in both areas, which is highly unusual. A few sockeye were also caught, presumably enroute to the Mackenzie River, where they are known to spawn. Pink and chum salmon are not unusual for this region, but they were especially abundant in the Chukchi Sea, suggesting recent warming may have been beneficial for these species.

Our ability to detect salmon range shifts, including contractions, within the PNW is limited by sampling techniques. We monitor certain populations closely, but spawner counts are labor-intensive and not possible for all populations. A systematic and broad-scale sampling regime would significantly improve our ability to detect range shifts. New methods using environmental DNA allow sampling over a large area, covering many species very quickly and inexpensively. Laramie et al. (2015) explore methodological questions about environmental DNA surveys for Chinook salmon in the Methow River Basin.

Population Declines

A population dynamics model of 21 Puget Sound Chinook salmon populations explored the importance of various factors associated with declines from 1984 to 2005. On average, these populations declined until 1995, recovered slightly, and have been relatively stable at moderately low abundance in recent years. Ward et al. (2015) developed a hierarchical Ricker stock-recruit model that included ocean covariates of the PDO and North Pacific upwelling, flow metrics (mean winter flow, flow variability, and date of peak flows), and unexplained trends.

They found the strongest estimated climatic driver was variability of winter flows. There was an additional negative trend not explained by the covariates. Whether populations increased or decreased did not differ with hydrological regime (i.e., snowmelt vs transitional vs rainfall), but about half of the populations in each category increased. Variance in population growth did not increase over time, but actually decreased slightly.

Ward et al. (2015) attributed the mechanism by which flow variability reduces population growth rate to the relationship between spawn location in fall (toward river centers under low-flow conditions) with the risk of egg scour during peak winter flows (higher in river centers). Mean flows alone did not have a negative impact, presumably because fish spawned in more protected locations outside the thalweg.

Climate change predictions do indicate a high likelihood of greater annual variability in flows (lower low flow and higher winter flow), and more intense winter storms, which would also increase the variability in winter flow. This paper suggests this variability itself might be a core problem, not just the lows and highs directly.

Pteropods are especially sensitive to ocean acidification. Work published in 2015 documents levels of shell dissolution and reduced occurrence at depth along gradients in aragonite saturation levels in the southern California Current (Bednarsek and Ohman 2015). As undersaturated water continues to shoal, habitat for pteropods is likely to be reduced. Du et al. (2015) described the phytoplankton community in northern California Current in relation to upwelling. Doubleday and Hopcroft (2015) studied the plankton community in the Gulf of Alaska and found that pteropod abundance near smolt release sites was correlated with pink salmon survival.

Phenological Trends: Migration and Spawn Timing Shifts

Shifts in migration timing continue to be observed in additional populations and species each year. Three papers on Alaskan salmon demonstrate shifts in migration timing. In southeast Alaska, pink, chum, and coho display trends toward earlier migration across various time periods, depending on the species and population (Kovach et al. 2015a). However, most southeastern Alaskan sockeye populations showed trends toward delayed migration.

Coho showed the strongest and most consistent trends across populations, with a ~2 week shift over 30-year time series. However, local factors appear to have had greater effects than the general climate trend, causing highly diverse responses across coho populations. Walsworth and Schindler (2015) analyzed a Chignik River coho population in the Aleutians that showed a significant trend toward earlier migration between 1922 and 2013. Annual variation in migration timing was also correlated with the PDO.

A study of Atlantic salmon smolt timing across sites in the Penobscot River, Maine, showed the relationship of environmental variability compared with anthropogenic factors, such as hatchery practices and dam operations. (Stich et al. 2015) found a significant temperature effect on the initiation timing of migration, where timing differed by 5 d across the thermal range observed. Both temperature and flow affected movement rate (Stich et al. 2015).

Although most research is conducted at the species level to capture individualistic climatic constraints, species interactions limit range as well. Phenological mismatch occurs when predators and prey shift their timing at different rates, disrupting the food web. Sergeant et al. (2015) found that this is not a problem for Dolly Varden in Auke Creek, Alaska, where annual variation in salmon migration timing has been tracked closely.

Long-term trends in spawn timing were also noted in Lake Trout and Yellow Perch in Lake Michigan and Lake Superior (Lyons et al. 2015). Trends in water temperature were consistent with the perch response, but the link between temperature and Lake Trout phenology was not clear.

Snake River Sockeye Salmon: Collapse of Adult Run in 2015

Severe losses of adult sockeye in summer 2015 provided a striking example of the ramifications of increased water temperatures for salmon (NOAA Fisheries 2016). Endangered Snake River sockeye, in particular, suffered considerable mortality during their upstream migration. Early in the migration season, sockeye encountered record high temperatures in the mainstem Columbia River. By the second week of July, water temperature consistently exceeded 23°C at water quality monitoring sites at Bonneville and The Dalles Dams, and 25°C in the top meter at McNary Dam. These high temperatures persisted, producing a mean July temperature of 22.4°C at both Bonneville and The Dalles. Preliminary results showed only 14% of PIT-tagged Snake River sockeye survived from Bonneville to McNary Dam, with a record low 26 out of 679 tagged fish (4%) detected at Lower Granite Dam.

Nearly all of these survivors avoided the hottest temperatures by migrating in June rather than July. Also, none of the survivors had a history of transportation during the smolt migration, which appears to have delayed effects on the adult migration upstream. Columbia River sockeye survived at a higher rate than Snake River sockeye at all temperatures, presenting interesting questions for further research.

Central Valley Winter-run Chinook Salmon: Record Low Egg-to-Fry Survival Rates in 2014

Poytress (2016) summarized historical juvenile winter-run Chinook salmon passage at Red Bluff Diversion Dam and showed that brood year 2014 represented the lowest estimate of juvenile winter Chinook production since 1996. Estimated egg-to-fry survival was 5.9% based on the fry-equivalent juvenile production index for brood-year 2014 winter Chinook. This was the lowest estimate in 18 years of monitoring.

Martin et al. (In press) tested a lab-derived relationship between incubation water temperature and winter-run Chinook salmon egg survival rates against field data and found that it significantly underestimated field-derived estimates of thermal mortality. They used a biophysical model based on mass-transfer theory to show that the discrepancy was due to the differences in water flow velocities between the lab and the field. They found support for these predictions across more than 180 fish species, suggesting that flow and temperature mediated oxygen limitation is a general mechanism underlying the thermal tolerance of embryos. They also showed that the temperature-dependent mortality rate for winter-run Chinook salmon eggs was higher in 2015 than it was in 2014 (back-to-back record high years for temperature-dependent mortality rates).

Fraser River Basin: Flow and Temperature Trends

Padilla et al. (2015) completed an updated analysis of flow and temperature in the Fraser River Basin. Interannual variability in flow during July and August increased throughout the basin from 1980 to 2005. Fall flow showed mixed responses in different sub-basins. Temperatures were most correlated with flows in July, slightly less so in August, and much less frequently in September. Variability in temperature was best predicted by whether the river was regulated.

Projected Ecological Impacts

Range Shifts of All Marine Species

When attempting to predict range shifts for a large number of species, scientists often take a bioclimatic-envelope approach. This method used climatic correlates with the present range of each species to map future ranges on an altered climate gradient. Cheung et al. (2015) projected range shifts for 28 species in the California Current by 2050 under the A2 emissions scenario using this technique. They projected high invasion rates in the northern Bering Sea, and high local extinction rates in southern California.

Cheung et al. (2015) projected range centroids would shift by a mean of 30 km/decade. Salmon are among the species with the strongest preference for cold temperatures and thus show stronger responses than average as the California Current shifts to more warm-water species. The CCS ecosystem showed a net loss of species, with local extinction rates of over 30%, especially off Baja California.

Failure of an Evolutionary Rescue Effect

Temperature affects many aspects of salmon physiology. Genetic variability in physiological tolerance of various traits might allow populations to adapt evolutionarily in response to a warming climate, facilitating persistence in a warming world. However, not all traits show variability in heat tolerance, so any one of these traits might limit adaptive potential.

In an experiment on juvenile Chinook salmon in British Columbia, Muñoz et al. (2015a) found limited variability in the upper thermal limit for heart arrhythmias. They extrapolated that this constraint would cause a 17-98% chance of “catastrophic loss” (presumably species-level extinction) by 2100. Mantua et al. (2015) responded to this paper, pointing out that behavioral plasticity would likely allow juveniles to avoid these high temperatures. Furthermore, geographic variability in temperature across the range of Chinook salmon will likely prevent extinction of the entire species. Munoz et al. (2015b) replied that physiological constraints are still highly limiting, and knowledge of evolutionary potential is crucial for understanding risks from climate change.

Genetic diversity must be present in order for populations to adapt. Selection over time tends to erode this variability, which is one reason evolutionary rates decline over time. In one concerning study, bull trout genetic diversity (i.e., allelic richness) was shown to be lower in habitats with higher temperatures and more winter flooding. These results suggest that trout populations may have less evolutionary potential to respond to further change in specific environmental characteristics (Kovach et al. 2015b).

Many salmon grow more slowly during their years at sea when the ocean is relatively warm. Piou et al. (2015) explored the consequences of poor ocean growth rates for Atlantic salmon in the context of a full population-dynamic and evolutionary model. They predicted that under several climate change scenarios, fish would mature at an older age to compensate for poor growth rates. Selection would favor an earlier threshold for maturation due to high mortality in the additional ocean year from both natural causes and fisheries. In their simulations, populations declined due to this additional mortality. Fishery selection for older salmon inhibited the adaptive response.

Vulnerability of Other Trout

Several analyses explored the vulnerability of trout species to climate change in the PNW. Bull trout in the Wenatchee River Basin were especially sensitive to habitat connectivity and wildfire size. Hence, Falke et al. (2015) concluded that land management would determine the net response to climate change. Penaluna et al. (2015) reported that coastal cutthroat trout in northwestern Oregon showed an inconsistent direction of response to climate change across streams because of complex interactions with local habitat features.

Bioenergetic models assess the amount of prey consumption necessary for fish to grow under various thermal conditions. Kao et al. (2015b) compared the energetic demands of Chinook, steelhead, and lake trout in Lakes Michigan and Huron under climate change scenarios for 2043-2070. After updating model parameters to reflect new data, they concluded that relative to the other species, Chinook salmon will need the largest increase in prey consumption (10%) to maintain positive growth rates. Other species were able to maintain current growth rates without increasing consumption.

Research on Additional Stressors

Freshwater and ocean acidification—Increasing CO_2 concentrations in both freshwater and marine environments are also an important concern, especially noteworthy because of our lack of information about the direct effects of lower pH on salmon. Community models that focus on trophic interactions in complex food webs tend to predict net positive effects on salmon (Reum et al. 2015).

However, the first study to expose extensive negative effects of exposure to projected pCO_2 levels in Pacific salmon was published this year. Ou et al. (2015) studied the effects of various levels of pCO_2, including a fluctuating treatment on developmental stages of pink salmon. They found statistically significant declines in body length, yolk conversion efficiency, and total mass in the high pCO_2 treatment compared with the control. They also found significantly inhibited predator avoidance behavior and olfaction. Fivelstad et al. (2015) described declines in specific growth rate as a function of pCO_2 in Atlantic salmon, providing additional evidence for negative effects on salmon growth.

Ocean acidification poses a direct threat to calcifying species. The consequences of decline in these species for species higher in the food web is an area of active research. Reum et al. (2015) applied a new modelling approach, *qualitative network models* to explore community responses to ocean acidification in Willapa Bay, Oregon. While this approach did not include any direct effects of acidification on salmon, Chinook salmon responded positively to the altered food webs that occurred in all of their scenarios.

Invasive species—Impacts of climate change in montane streams include not only direct physiological constraints such as those from lethal temperatures, but also more complex dynamics mediated through species interactions. Even high temperature constraints are in practice typically lower in the field than in the laboratory (Martin et al. In press). This is partly because of species interactions—namely disease agents that become more virulent and abundant at high temperatures and that may be further concentrated by low flows and fish crowding.

Changes in food webs are also a natural consequence of climate change through differences among species in physiological tolerance and bioenergetic demand. These inherent differences in species' climate niches is exacerbated by species introductions and stocking fish.

For salmon in the Columbia River Basin, threats from increasing predation by the warm water-preferring non-native, introduced smallmouth bass is a management concern. Smallmouth bass is a particular concern in the John Day River Basin, which supports a Chinook population at the upper end of the spatial distribution. This population was feeding at the maximum consumption rate expected and constitutes one of the last remaining wild populations of Chinook salmon with minimal hatchery interference. Since bass were introduced in 1971 for recreational fishing, it has been expanding its range in the basin.

Lawrence et al. (2015) helped to elucidate thermal limitations on the upstream limits of bass distribution by developing a bioenergetic model that identifies the mechanism of the range limit. Lawrence et al. (2015) identify the range limit as the point where age-0 bass cannot grow enough over summer to store sufficient reserves to survive winter, i.e., to reach a minimum size of ~55 mm. This growth limitation depends directly on temperature, because of fish bioenergetic parameters. Their model provides a more useful means for projecting bass range shifts because it can account for changes in productivity (food availability) separately from temperature changes.

Introduction of fish into fishless lakes has a different impact on the food web, and MacLennan et al. (2015) illustrated how this interspecific dynamic can also alter the impacts of rising temperatures. MacLennan et al. (2015) showed that warmer temperatures increase zooplankton biomass and species turnover in lakes stocked with rainbow trout, but not in fishless lakes. They argue that this is because trout remove large invertebrates that otherwise regulate zooplankton populations.

Several studies focused on declines in native species and preponderance of invasive species in the Columbia River Basin. The Asian calanoid copepod, *Pseudodiaptomus forbesi*, was introduced to the Columbia River estuary approximately 15 years ago. This species now dominates the late-summer zooplankton community in the estuary (Dexter et al. 2015) and in Columbia and Snake River reservoirs (Emerson et al. 2015). *P forbesi* has a diet similar to native copepods (Bowen et al. 2015). Chinook consumed *P. forbesi* at rates equal rate to that of native copepods in single-prey experiments, but preferred native copepods in multi-prey taste tests (Adams et al. 2015).

Temperature, hypoxia, contaminants and parasites—Several studies addressed interactions between multiple stressors, such as heat stress combined with hypoxia (Anttila et al. 2015) and heat stress combined with hypoxia and heavy metals (Sappal et al. 2015). Physiological processes often responded to these stressors in opposite directions; thus, the combination of stressors was sometimes less than their additive effects.

For example, warm acclimation actually reduced sensitivity to hypoxia in Atlantic salmon (Anttila et al. 2015), and the stimulatory metabolic effects of copper were counteracted by inhibitory effects of hypoxia in rainbow trout (Sappal et al. 2015). Higher temperature, however, increased sensitivity to the combination of copper and hypoxia (Sappal et al. 2015). In their review of the literature on interacting effects of combinations of elevated CO_2 (lower pH) and metals, Ivanina and Sokolova (2015) emphasized the complexity of physiological responses to multiple stressors. Nilsen et al.

(2015) demonstrated the widespread contamination of sediment in the Columbia River Basin by documenting contaminant levels in larval Pacific lamprey, which may be contributing to the decline of that species.

Parasite loads and susceptibility of fish to parasite burdens often depends on temperature, as explained in a review by Lõhmus and Björklund (2015). The complex life cycles and rapid co-evolution between many parasites and their hosts make simple projections difficult. Although very small shifts in temperature can have very large effects on fish mortality rates, as demonstrated by simple models in this paper, there are also many potential mitigating factors. Such factors include changes in other predators or hosts of the parasite or different rates of phenological change in parasite and host that could dampen these responses.

Dam and reservoirs—Dams can both increase and decrease climate change resilience. Cool-water releases from the hypolimnion level of stratified reservoirs is used to cool waters downstream from dams, which would otherwise be lethally hot for salmon (e.g., Shasta Dam and Dworshak Dam). On the other hand, dams block access to upstream habitat that might provide a thermal refuge from high summer temperatures (e.g., Willamette River, Columbia River). Quinones et al. (2015) quantify the various costs and benefits of dam removal for 24 Californian dams. They identified four dams on the Klamath River that would have the most benefit for salmon conservation.

Dams also can exacerbate thermal barriers to passage. High temperature exposure is an important problem already on the Columbia and Willamette Rivers (Keefer and Caudill 2015; Keefer et al. 2015). Keefer and Caudill (2015) describe temperature maxima inside fishways of dams and cumulative thermal exposure of migrating adult Chinook and steelhead. Keefer et al. (2015) also found that fish were exposed to extremely high temperatures in the Willamette River, a location where pre-spawn mortality is very high.

Continuing Research in Correlates of Salmon Survival

Numerous studies explored how climatic factors are correlated with marine survival of Pacific salmon. These included:

- Duration of the smolt migration for Japanese chum (Morita and Nakashima 2015)
- Ocean entry timing for Puget Sound steelhead (Moore et al. 2015a)
- North Pacific Gyre Oscillation for coho and Chinook (Kilduff et al. 2015; Mantua 2015)
- Northern copepod anomalies for Redfish Lake sockeye (Tucker et al. 2015)
- Spring phytoplankton bloom for pink salmon (Malick et al. 2015)
- Competition between pink and sockeye salmon (Ruggerone and Connors 2015).

Bakun et al. (2015) reviewed the effects of climate change on upwelling ecosystems including the California Current and considered the interactive effects of increased upwelling, stratification, current patterns and ocean acidification. They conclude that major direct effects on pelagic fishes are unlikely, but there will be a likely shift toward more subtropical marine communities along the coast. They also raise a concern about temporal food resource mismatches for salmon as a result of shifts in the seasonality of upwelling.

Other studies improved our understanding of basic ecology of juvenile Chinook and coho salmon in the California Current: location and body size (Teel et al. 2015; Weitkamp et al. 2015) and prey selection (Daly and Brodeur 2015). Daly and Brodeur (2015) describe Chinook salmon diet between 1981 and 2011. In warm years, increased consumption did not compensate fully for increased metabolic costs.

Despite eating more food that had relatively high energy density, fish were smaller and thinner in warm years, with fewer adult returns. Hertz et al. (2015) further explored salmon feeding habits with isotopic analysis, which showed results similar to those of the stomach analysis in diet breadth and diversity across different developmental stages and geographical regions. More information on juvenile Chinook salmon location and size also came to light (Teel et al. 2015; Weitkamp et al. 2015).

Numerous papers described correlations between freshwater temperature and/or flow and salmon survival. These included spawner-spawner ratios for Yukon Chinook (Neuswanger et al. 2015) and Atlantic salmon (Penaluna et al. 2015), juvenile survival in Atlantic salmon (Hvidsten et al. 2015), smolt migration survival of Sacramento River late-fall Chinook (Michel et al. 2015; Zimmerman et al. 2015), and adult pre-spawn survival of Willamette River Chinook (Benda et al. 2015; Keefer et al. 2015).

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