
Impacts of Climate Change on Columbia River Salmon

A review of the scientific literature published in 2013

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Summary

Climate Science Projections

A number of key new global and regional climate projections were released in 2013. Working Group I of the IPCC (Intergovernmental Panel on Climate Change) completed its contribution to the 5th IPCC Assessment Report, *Climate Change 2013: The Physical Science Basis* (IPCC 2013). Locally, two reports synthesize global modeling results for the Pacific Northwest: *Climate Change Impacts and Adaptation in Washington State* (Snover et al. 2013b), from the University of Washington Climate Impacts Group, and *Climate Variability and Change in the Past and Future* (Mote et al. 2013), from the Oregon Climate Change Research Institute.

A consequential change presented in the 5th IPCC assessment report is the introduction of four new carbon emission scenarios based on *representative concentration pathways* (RCPs 2.6, 4.5, 6, and 8.5). The lowest emissions scenario (RCP 2.6) assumes much more aggressive reductions in emissions than any previous scenario. Results from this report are very similar to those of previous reports when similar emissions scenarios are compared. However, the scenarios previously selected for downscaling by many climate modeling groups in the Pacific Northwest, including the University of Washington Climate Impacts Group, excluded the high-end emissions scenarios. Therefore, these reports reflect the mid-range of the new carbon emission scenarios (RCPs 4.5 and 6). Current downscaling efforts, such as the Integrated Scenarios of the Future Northwest Environment project, include the business-as-usual emissions scenario (RCP 8.5).

Under the RCP 8.5 scenario, Northwest air temperatures are expected to warm in all seasons, but the greatest warming is projected for summer (1.9-5.2°C in the 2041-2070 period). The range of annual warming between RCP scenarios 4.5 and 8.5 is 2.4-3.6°C. Precipitation projections across global climate models (GCMs) include both drier and wetter trends in all seasons and in annual precipitation, but most models project drier summers with the rest of the year being wetter (see Figure 2.6 in Mote et al. 2013).

At present, most of the Columbia River Basin is expected to shift to rain or mixed rain and snow by the 2080s. Peak snowmelt and peak flows in snow-dominated basins are projected to shift earlier, with some peak flows occurring in winter rather than spring. Flooding, landslide risk, and sediment flow increase due to intense winter rains. Decreased precipitation and warmer temperatures during summer lead to more extreme low flows across much of the Columbia River Basin (Hamlet et al. 2013).

A number of hydrological and temperature modeling results for individual basins within the Columbia River Basin focused on the Salmon River Basin in Idaho (Sridhar et al. 2013), the Santiam River Basin in Oregon (Surfleet and Tullos 2013b, a), and the Methow Valley in Washington (Bellmore et al. 2013). Finally, a groundwater model was developed for the Deschutes River Basin in Oregon (Waibel et al. 2013).

Retrospective Analyses

Retrospective analyses of climate trends over the past century or so in the Pacific Northwest generally identified patterns similar to those projected to result from greenhouse gas accumulation. A review of this literature for the National Climate Assessment, *Climate Variability and Change in the Past and the Future* (Mote et al. 2013), and *Technical Summary for Decision Makers* from the University of Washington Climate Impacts Group (Snover et al. 2013b), summarized the key findings. During 1895-2011, the Northwest warmed approximately 0.7°C (1.3°F) annually, with average air temperatures approximately the same in summer, but 1.1°C (2°F) higher in winter. There was no statistically significant long-term trend in precipitation (1895-2011), but analyses of shorter time-series did find trends of varying magnitude. Recent studies have found that not all streams respond to climate change in the same manner. The response depends on river management and study duration, as well as other factors.

Ocean Acidification and Hypoxia

Literature published in 2013 focused specifically on ocean acidification and hypoxia. Ocean acidification is clearly detected both on the outer coast and in Puget Sound, with acidity increases of 10-40% since 1800 (Feely et al. 2010 cited in Snover et al. 2013b). The aragonite saturation state has declined in surface water on the Oregon shelf from 1.0-4.7 in pre-industrial times to 0.66-3.9 in 2007-2011 (Harris et al. 2013). Complex trophic interactions lead to projected global ocean productivity decreases of 6.3% by the 2090s from increasing acidification, although primary production in the Arctic is expected to increase by 59% (Yool et al. 2013). A food web model of Puget Sound projected very limited impacts on salmon (Busch et al. 2013b).

In a study that focused specifically on the California Current, one group (Hauri et al. 2013) reported that aragonite undersaturation events along the shelf have quadrupled in number and lengthened in duration, and this trend will continue. Within about 20 years, the seafloor will be undersaturated most of the time, and when CO₂ levels reach 500 ppm, undersaturation will become basically permanent.

Much recent work has studied how localized levels of upwelling and productivity correlate with large-scale atmospheric processes such as the North Pacific High, North Pacific Gyre Oscillation, Pacific Decadal Oscillation, and El Niño, at both lower and higher trophic levels (Garcia-Reyes et al. 2013a; Hatch 2013; Lindegren et al. 2013). However, these dynamics are complex, and the pathways by which they influence salmon are not entirely clear and may change over time.

Estuarine habitat is likely to change with sea-level rise, and some detailed habitat mapping in 2013 helps to clarify where habitat might be gained and lost, which is crucial to long-term planning of habitat availability (Flitcroft et al. 2013).

Projected Impacts on Pacific Salmon

In general, the tenor of 2013 articles on climate change impacts to salmon is consistent with previous reports: conditions in a few cold-water locations might improve for certain life stages, but the vast majority of impacts are negative. These negative impacts are projected across Pacific salmon species, throughout the various life stages that occupy freshwater, and geographically across the west coast. Furthermore, many populations that are already highly impacted by other threats are also the most vulnerable to climate change. In 2013, two key papers quantified vulnerability or risk to specific populations: a detailed quantitative vulnerability analysis for steelhead over the entire Columbia River Basin (Wade et al. 2013), and a quantitative analysis of juvenile survival in the Lemhi River, Idaho, which compares the impact of water management options with climate change (Walters et al. 2013).

An additional qualitative analysis was conducted for Oregon coho populations (Wainwright and Weitkamp 2013), and spawn timing and juvenile growth impacts were analyzed for steelhead and Chinook salmon populations from Washington through California (Beer and Anderson 2013). Lastly, an important step in incorporating climate change into status assessments was completed for all salmonids in California (Katz et al. 2013).

Observed Impacts on Adult Migration and Spawning

Several key papers also documented challenges with the hydrosystem or for transportation relating to thermal conditions. New evidence documents temperature gradients up to 4°C within fish ladders at dams in the Columbia River that appeared to block migration by causing adult fish to reverse movement in ladders and fall back downstream (Caudill et al. 2013). Temperature-related fallback is a serious concern for fish managers under the present climate, but may become even more so when mitigating for rising river temperatures.

One mitigation strategy that has been proposed for avoiding thermal stress in rivers is to transport adult salmon upstream to spawning habitat. However, one case study showed fish failed to spawn following transportation (Mosser et al. 2013). Additional limitations might need to be placed on fisheries under warm water conditions because mortality rates are higher when temperature and handling stress interact (Gale et al. 2013). In addition to previously established influences of temperature and food availability on growth rates, some unexpected consequences of changing the thermal regime include altering sex ratios within age classes and age at maturity (Mizzau et al. 2013).

Interacting Stressors: Hypoxia, Contaminants, and Invasive Species

A significant challenge in assessing climate-change impacts is how to identify and characterize interacting stressors such as hypoxia, contaminants, and invasive species. Hypoxia, in particular, is likely to co-occur with ocean acidification and rising temperatures. The effects of hypoxia generally exacerbate thermal stress (Ellis et al. 2013), but in 2013, two review papers showed that tolerance of the two traits (as well as some others) can be correlated (Anttila et al. 2013b; Hasnain et al. 2013).

Contaminants are a persistent problem in Northwest watersheds, as elsewhere, and several studies indicate that with the projected intensification of winter storms (Conaway et al. 2013), transport of contaminants might increase. Two review papers showed that, in addition to increased contaminant loads, biological effects may grow more acute as contaminants interact with climate-related changes in factors such as temperature, flow, salinity, and pH (Hooper et al. 2013; Moe et al. 2013).

A major concern for Columbia River Basin salmon is the threat of invasions of warm-adapted species, which compete with or prey upon native salmon. American shad, brook trout, and brown trout all showed temperature-dependent responses consistent with greater future penetration across the Columbia River Basin; however, none of the work in 2013 included detailed projections for these non-native populations.

Ocean Conditions

A series of six papers report results on correlates of survival and migration characteristics for Columbia River juvenile salmon during their ocean stages (Burke et al. 2013a, b; Daly et al. 2013; Miller et al. 2013; Ralston et al. 2013; Sharma et al. 2013). These papers point to a full array of interacting physical and biological factors. Although they do not make specific projections, they do suggest salmon are highly vulnerable if ocean conditions decline systematically due to climate change.

A special issue of the journal *Conservation Biology* presented a number of papers exploring how climate change might be incorporated into decisions under the Endangered Species Act (Boughton and Pike 2013; Gregory et al. 2013; Jorgensen et al. 2013; McClure et al. 2013; Seney et al. 2013; Snover et al. 2013a; Walters et al. 2013). Generally, the uncertainty of climate projections is no longer a sufficient reason to omit them from listing and recovery planning decisions. These papers offer guidelines for progress.

In conclusion, new literature generally supports previous concerns that climate change will cause moderate to severe declines in salmon, especially when interacting factors are incorporated into the analysis (e.g., existing threats to populations, water diversion, accelerated mobilization of contaminants, hypoxia, and invasive species). Many populations are already heat stressed in either their tributary habitats or migration corridors.

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Objective and Methods

The goal of this review was to identify literature published in 2013 that is most relevant to prediction and mitigation of impacts of climate change on Columbia River salmon listed under the Endangered Species Act. Because almost anything that affects salmon is related to or 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 grey literature. 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 1,300 papers, 195 of which were included in this summary.

Literature searches were conducted January and July 2014 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. As a first step, we used specific search criteria that included a publication year of 2013, 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
- 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) A full text search that contained ocean acidification **or** California Current **or** Columbia River
- 6) 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 important to salmon and that are projected to change with the climate; for example, air temperature, precipitation, snowpack, stream

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

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

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

Physical Processes of Climate Change

In 2013, the Intergovernmental Panel on Climate Change (IPCC) completed its 5th Assessment Report (AR5) from Working Group I, *The Physical Science of Climate Change* (IPCC 2013). This contribution was based on models developed during Phase 5 of the Coupled Model Intercomparison Project (CMIP5). Projections in this report are based on new greenhouse gas emission scenarios defined in terms of representative concentration pathways (RCPs). An RCP is expressed as an increase in radiative forcing (energy from the sun absorbed by the earth) from pre-industrial values to the year 2100; RCP scenarios range 2.6-8.5 W/m². Most of these scenarios are roughly similar to those in previous reports, with one exception. The new report includes a novel, very low-emissions scenario with extremely aggressive reductions in carbon emissions and sequestration, such that emissions start declining in the 2020s (RCP 2.5). The upper emissions scenario (RCP 8.5), is approximately a “business-as-usual” scenario in which emissions continue to increase through the century, comparable to scenario A1FI in the 4th IPCC Assessment Report (AR4).

To interpret how these new results might change our understanding of climate change impacts in the Pacific Northwest, it is important to recognize that results from AR5 are very similar to those of AR4 when similar emissions scenarios are compared. However, scenarios selected from the AR4 by many climate modeling groups for downscaling in the Pacific Northwest did not include the high-end emission scenario (A1FI). Thus, downscaled models from these groups, which include those from the University of Washington Climate Impacts Group, reflect the mid-range RCP scenarios (RCPs 4.5 and 6).

Current downscaling efforts, such as the *Integrated Scenarios of the Future Northwest Environment* project do include the business-as-usual emissions scenario, RCP 8.5, as well as RCP 4.5 (which is similar to B1 from AR4). Thus projections from this effort will span a wider range of futures than those previously considered by the Climate Impacts Group (e.g., scenarios B1 and A1B or A2).

Projections for the Pacific Northwest

Climate

Two reports synthesize the new modeling results for the Pacific Northwest (Dalton et al. 2013; Snover et al. 2013b). Under emissions scenario RCP 8.5, air temperature in the Northwest is expected to increase in all seasons, but the greatest increase is projected for summer 2041-2070, at 1.9-5.2°C (3.4-9.4°F). The range of projected annual warming between RCP scenarios 4.5 and 8.5 is 2.4-3.6°C. Annual and seasonal precipitation might decrease or increase in the PNW (range 5-14%), depending on the model. However, annual changes are generally less than historical annual variation (historical SD = 14%; Mote et al. 2013); therefore, these changes will probably not be detectable for several decades at least. Most models project drier summers with the rest of the year being wetter. The driest summers were projected in models with the largest temperature increases.

Rupp et al. (2013) analyzed the performance of 41 GCMs compared to 20th century observations using a wide suite of metrics that tend to be important for impacts assessments. They ranked these models to provide a useful resource for applications in which a subset must be selected for further analysis, because not all the models can be used in impacts assessments (Rupp et al. 2013).

Across the Northern Hemisphere, the AR5 (IPCC 2013) projects the following ranges by 2081-2100, based on means of RCP scenarios 2.6-8.5: spring snow cover declines of 7-25%; glacier recessions of 15-85%; sea surface temperature increases of 1.1-3.6°C; global sea level increases of 11-38 inches; and global ocean pH decreases of 38 to 109%, which correspond to a drop in pH of 0.14-0.32.

Nationally, the climate of the United States is expected to change sufficiently that certain locations will occupy climate zones previously unknown in this country, including the “torrid” climate, which is hotter and drier than previous classifications based on the older projections. However, the overall climate type of the Pacific Northwest is not expected to change (Elguindi and Grundstein 2013).

Biases in general circulation models are corrected prior to downscaling, and thus do not affect impact assessments. However, we note that regional climate model reconstructions of 20th century climate for the Pacific Northwest tend to be wetter than observed (Kim et al. 2013). Multi-model ensembles continue to outperform individual

“best models” in general and are better tools for impact assessments (Kim et al. 2013; Snover et al. 2013a). Another assessment of regional climate modeling capability found that the weather research and forecasting (WRF) model captured temperature extremes (showing the anthropogenic warming signal) much better than precipitation extremes (Duliere et al. 2013).

Stream Temperature and Flow

To assess ecosystem responses to a changing climate and their implications for salmon, further analysis is needed of the climatic variables output from general circulation and regional climate models (GCMs and RCMs). Such analyses include hydrological and stream temperature models. A comprehensive description of stream flows across the Columbia River Basin was conducted by the Climate Impacts Group several years ago under emissions scenarios A1B and B1, and their final report was published in 2013 (Hamlet et al. 2013). Two other modeling efforts covered the entire Columbia River Basin (Beer and Anderson 2013; Wade et al. 2013), but these were focused on impacts for salmon, and thus are discussed in the salmon impacts section.

A number of hydrological and temperature modeling efforts have focused on individual subbasins within the Columbia River Basin. These subbasins include the Salmon River in Idaho (Sridhar et al. 2013), Santiam River in Oregon (Surfleet and Tullos 2013b, a), and Methow Valley in Washington (Ficklin et al. 2013). Finally, a much-needed groundwater model was developed for the Deschutes Basin in Oregon (Waibel et al. 2013). Below I summarize the scope and general results from these projects.

Flow Projections—A database of historical and projected stream flow for the Columbia River Basin, known as the 2860 Project, has been available from the Climate Impacts Group for a few years. However, the final report documenting this project and synthesizing major findings was published in 2013 (Hamlet et al. 2013). The Climate Impacts Group analyzed two emissions scenarios from the AR4 (A1B and B1). Both scenarios were modeled using 10 general circulation models from CMIP3, and both were downscaled using two different statistical methods plus a third hybrid method.

In summary, these analyses show most of the Columbia River Basin shifting to rain or mixed rain-and-snow by the 2080s. Peak snowmelt and peak flows in snow-dominated basins are projected to shift earlier, with some peak flows occurring in

winter rather than spring. Flooding, landslide risk, and sediment flows increase due to intense winter rains. Precipitation decreases in summer, and warmer summer temperatures lead to more extreme low flows across much of the basin.

Projections of Subbasin Hydrology—Sridhar, Jin, et al. (2013) used the variable infiltration capacity (VIC) hydrology model in a new model of the Salmon River Basin, Idaho. They projected peak flows 10 d earlier and total flows and snow/water equivalent reduced by 3% over the next 90 years, which could increase drought risk (Sridhar et al. 2013). Surprisingly, drought in the Klamath Basin in California was projected to decrease in severity and intensity (Madadgar and Moradkhani 2013).

In a rain-dominated basin, the Santiam River in Oregon, a new analysis using the coupled groundwater and surface water flow model (GSFLOW) also confirmed previous projections: increases in runoff during fall and winter months and decreases in runoff during spring and summer. One-hundred-year floods are projected to decrease, but changes in low flows varied by subbasin, depending on groundwater input (Surfleet and Tullos 2013a). In the McKenzie River Basin, Oregon, a 2°C increase in temperature would decrease snowpack, especially between elevations of 1000 and 2000 m, and thereby reduce water storage capacity (Sproles et al. 2013).

The most dramatic floods and avalanches often result from rain-on-snow events, which primarily threaten the transient rain and snow basins. The transient band in the Santiam River basin is projected to rise from its current intermediate elevation of 350-1100 m, into higher elevations that are snow-dominated at present (Surfleet and Tullos 2013b).

Stream Temperature Projections—A new statistical model of stream temperatures in the Methow Valley combined hydrological results from a variable infiltration capacity (VIC) model with a statistical disaggregation technique. This approach allowed a novel combination of high temporal and spatial resolution with the long time-scale projections driven by general circulation models (Caldwell et al. 2013). These results project July warming of 0.8°C (\pm 1.9°C) to 2.8°C (\pm 4.7°C) by 2080. Confidence intervals on this projection are very wide because of the statistical methods used and limited existing data, and include cooling as a possible outcome (Caldwell et al. 2013). This is much less than warming predicted for the Sierra Nevada Basin (1.0-5.5°C for the A2 scenario by 2100), particularly in the southern portion of the basin. Interestingly, this latter study also tracked dissolved oxygen, which is projected to decline 10%, and sediment, which is projected to decline 50%; either or both could stress some species (Ficklin et al. 2013).

The implications of projected climatic change for stream flow and temperature depend in part on riparian vegetation, as demonstrated by Tetzlaff et al. (2013) in an analysis of a global collection of long-term ecological research sites in the North Watch Project. The role of riparian vegetation was also illustrated in a broader study (Davis et al. 2013). Studies have addressed general changes in landscape vegetation (e.g., Albright and Peterson 2013), and one study noted that floodplain vegetation might respond more to winter and spring precipitation than summer droughts (Bollman et al. 2013). However, riparian vegetation is generally not explicitly modeled in most stream-flow projections, except to test the ability of shading to mediate temperature rises.

Groundwater—Groundwater recharge plays a crucial role in moderating both stream flow and temperature, but groundwater processes have been difficult to model in many large-scale analyses (e.g., groundwater is not modeled by VIC). Nevertheless, an important differentiation can be made between basins with short and long groundwater flow paths (i.e., the amount of time between submersion and appearance in the stream or aquifer). Short groundwater flow paths, which are typical of headwater base flows, will be more affected by seasonal change in precipitation, whereas longer processes at the regional scale might be buffered by the fact that annual precipitation is not expected to change much (Waibel et al. 2013).

Retrospective Analyses: Terrestrial and Freshwater Conditions

Although long-term trends of general warming continued in 2013, El Niño Southern Oscillation (ENSO) was in a neutral state most of the year; thus 2013 was not an extreme year compared with the last decade. The North Pacific Ocean did reach a historic high temperature in 2013 due to weakened westerly winds, and on balance, global average sea surface temperature was among the 10 highest on record (Blunden and Arndt 2014). Nonetheless, local ocean conditions were relatively cool and productive, and forage fish such as anchovy and juvenile rockfish had relatively high abundances (Wells et al. 2013; Harvey and Garfield 2014).

Notably, ENSO plays a very significant role not only in Pacific Northwest climate, but in global temperature. An analysis of the influence on global climate of temperatures in the eastern tropical Pacific indicated that the preponderance of La Niña-like conditions over the past decade can explain the recent “hiatus” in the global warming trend. Kosaka and Xie (2013) conclude this is a just a normal product of natural variability and does not indicate abatement in the general trend produced by greenhouse gas emissions.

Pacific Northwest Climate Trends

Retrospective climate analyses of the Pacific Northwest generally find the same trends over the past century or so that are projected to result from greenhouse gas accumulation. A general review of this evidence was completed by Mote et al. (2013) for the U.S. Global Change Research Program National Climate Assessment. These findings were reiterated in *Climate Change Impacts and Adaptation in Washington State* from the UW Climate Impacts Group (Snover et al. 2013b).

In summary, the Pacific Northwest has warmed approximately 0.72°C (1.3°F) from 1895 to 2011, with mean air temperatures approximately the same in summers, but higher during winters (1.1°C, 2°F). There has been no statistically significant long-term trend in precipitation during this time. However, analyses of shorter time series did find trends of varying magnitude. Studies of stream flow and snowpack are shorter in magnitude, and hence have less ability to differentiate between long-term trends and natural variability in climate (such as the PDO), although several cited below are consistent with expected changes from climate change.

The coastal ocean has changed as well. Ocean acidification has clearly been detected on both the outer coast and in Puget Sound, with acidity increases of 10-40% since 1800 (Feely et al. 2010 cited in Snover et al 2013b). Sea levels actually declined at Astoria, Oregon, by 0.1 inches/decade during 1925-2008 and by 0.7 inches/decade at Neah Bay, Washington, during 1934-2008. However, Puget Sound rose 0.8 inches/decade at Seattle during 1900-2008, and the Salish Sea rose 0.4 inches/decade at Friday Harbor during 1934-2008 (Snover et al. 2013b). Retrospective analyses of sea surface temperature showed varying trends across the California Current.

Individual studies of the general patterns reported here include the following analyses of glacial retreat, snowfall, precipitation, and stream flow and temperature.

Glacial Retreat and Snowfall—Glacial retreat in western North America over the last 100 years is unique in the climate record since the Little Ice Age, and shows a clear signal of anthropogenic forcing (Malcomb and Wiles 2013). Durre et al. (2013) analyzed an extended database of snow-depth and snowfall records to compare recent 30-year means (1981-2010) with those of an earlier 30-year period (1971-2000). The more recent "normal" period exhibited fewer days with snow on the ground, less total annual snowfall across much of the contiguous United States, and drier conditions (annually) over much of the Pacific Northwest.

Precipitation—In comparing periods without temporal overlap, 1950-1979 vs. 1980-2009, the Pacific Northwest west of the Cascade Mountain Range was drier in the recent period based on daily precipitation records. The greatest differences occurred during winters (January-March), which were ~30-40% drier. Summers (July-September) were ~30% drier across a slightly smaller spatial extent, with spring and fall showing less dramatic differences (Higgins and Kousky 2013). These patterns were especially strong during La Niña years.

However, the impact of ENSO in the Pacific Northwest may have changed in recent decades. Yu and Zou (2013) reported that a shift in the signature of recent El Niño events toward the central Pacific, compared with its more eastern-Pacific historic signature, has shifted the jetstream southward, causing drier conditions in much of the United States, including the Pacific Northwest. They suggest that this could explain the recent extended droughts. Deforestation in the Amazon has also been linked to reductions in precipitation in the Pacific Northwest and Sierra Nevada Mountains (Medvigy et al. 2013).

In a provocative study of a potential bias in our perspective on historical changes in Pacific Northwest precipitation, Luce et al. (2013) proposed that we have

systematically underestimated precipitation declines at high elevations. They contend that an elevation bias in precipitation is a predicted characteristic of weaker westerly winds, and might explain many observed trends that show declining stream flow.

Wildfires—Wildfires have profound effects on streams, driving major shifts in scouring flows and nutrient and sediment loads for up to 4 years, and affecting community composition from benthic algae to fish (Verkaik et al. 2013). But a paleoecological perspective demonstrates that wildfires can also be the driver of sudden and relatively permanent shifts in vegetation more suited to a warmer climate (Gavin et al. 2013).

Stream Flows

In an analysis that takes into account the influence of geology and drainage patterns on the response of streamflow to changes in precipitation and temperature, Safeeq et al (2013) analyzed historical patterns in streamflow from 1950-2010 across the western U.S. They identified the types of watersheds most sensitive to climate warming. Summer flows from snow-dominated watersheds with deep groundwater sources showed the strongest effects. However, spring flows were most sensitive in snow-dominated watersheds that drain rapidly.

On tribal lands in the Columbia River Basin, peak stream flows have declined and advanced to earlier in the season, November 100-year floods have increased, and low flows have intensified (Dittmer 2013). Variation in these patterns across sites within the Columbia River Basin is driven by variation in physical factors (e.g., elevation) as well as anthropogenic factors such as flow regulation. Similar to results reported last year (Isaak et al. 2012), a new study of seven basins from 1950 to 2011 compared trends in flow from above and below major dams. They found that headwater sites showed the expected signature of climate change (earlier peak flows), but no consistent shift appeared below dams (Hatcher and Jones 2013).

A majority of GCM and RCMs project that winter precipitation in the Pacific Northwest will increase and will consist of more intense precipitation events. Combined with the transition of many basins from snow-dominated to transitional or rain-dominated weather patterns, more streams will likely be exposed to winter flooding. The risk of winter flooding for salmon is largely in that eggs are scoured out of their protective nests or that shifting sediment reduces oxygen availability.

Two studies explored the risk of winter scour and flooding in the Salmon River Basin in Idaho and found relatively low risk for incubating eggs (Goode et al. 2013; McKean and Tonina 2013). Changes in streambed grain size depend crucially on sediment input, and hence could have negative or positive impacts on fish habitat (Neupane and Yager 2013). Changing flow levels also alter the relative proportion and total quantity of fish habitat, which might alter the impact of certain human actions such as adding riprap to stabilize shorelines (Jorgensen et al. 2013). Effects on stream flow represent one aspect for which evaluation of impacts under climate change might differ from those under the current climate. Such evaluations may influence regulating agencies in terms of their permitting decisions.

Stream Temperatures

A different way of thinking about warming temperatures at a given site is the elevation or latitude at which a certain thermal threshold is reached. Such a metric is useful for determining range limits and predicting range shifts. Using an analytical method, Isaak and Rieman (2013) surmised that isotherms on steep slopes (2-10% slope), such as many of the headwater streams in the Columbia Basin, will respond to a warming rate of 0.1-0.2°C/decade by shifting 0.13-1.3 km/decade, with shifts of 1.3-25 km/decade in flatter areas. Thus warming of 2°C could cause a shift of up to 143 km in a potential range limit.

All general circulation models and nearly all downscaled temperature projections anticipate a warmer climate. Because many populations of cold-water fish are already heat stressed, much research has focused on actions that can reduce local temperatures or provide thermal refugia. However, thermal refugia are generally not well characterized at present, because they often require very fine-scale thermal and groundwater maps. For the most part, such maps are not available or have not been fully analyzed. A first step toward better understanding of thermal refugia includes characterization of current spatial and temporal variability.

Thermal Refugia—A review of information on thermal refugia in the Columbia and lower Snake Rivers was produced by the U.S. Army Corps of Engineers (2013). This report 1) compared available temperatures in the mainstem and tributaries, 2) described the thermal profile of the Dworshak Reservoir and 3) described evidence of thermal refuge use from archival temperature-recording tags on individual migrating adult Chinook and steelhead. Of the seven tributaries for which they had sufficient data to compare, they found that the Clearwater River at Spalding and at Lewiston were substantially cooler than the Lower Granite pool and the Snake River at Anatone

(reflecting cooling from Dworshak), but other tributaries were fairly similar to the mainstem (Umatilla was a little cooler) or warmer. Thus the only real source of cool water identified was the Dworshak reservoir.

Modeling of thermal gradients within reservoirs in the lower Snake River found relatively shallow temperature gradients ($\sim 4^{\circ}\text{C}$ from 1 to 30 m depth) in all but the Lower Granite pool, again due to cold water from Dworshak releases. But the cold water from these releases does not have a large effect below Lower Granite Dam. Cool refugia in the reach from Bonneville to McNary Dam were identified, especially Deschutes and Little White Salmon Rivers. Studies of Chinook salmon showed that use of thermal refuge increased dramatically when mainstem temperature exceeded 21°C .

A study of the temporal characteristics of thermal refugia in Quebec found that the stability of these refugia depends on whether they are generated by groundwater input or cold-water tributary inflow. Groundwater cooling tended to follow patterns in seasonal mean discharge, whereas cold-water tributaries were more consistent from year to year (Dugdale et al. 2013). Cold-water tributaries can be predicted locally to some extent by landscape characteristics (Monk et al. 2013), as can more general hydrologic characteristics (Wigington et al. 2013). Exploring the temporal frequency of warm and cold events within streams also helps to describe thermal regimes (Arismendi et al. 2013), as does studying spatial structure in these regimes (Imholt et al. 2013b).

Aside from naturally cool tributaries, another source of cold-water input is large reservoirs. In fact, studies of historical temperature trends (Null et al. 2013) have found that water below large dams has not necessarily followed air temperature trends (unlike water above dams). Thus, managed releases of water can have a dramatic impact on thermal regime, in addition to altering the expected stream-flow responses to warming mentioned above (Hatcher and Jones 2013).

Riparian Cover—The primary mechanism of stream warming is solar radiation, which is greatly reduced by shading. Thus, a key alternative route to cooler water is to provide riparian cover, which is effective at cooling at small spatial scales (Imholt et al. 2013a; Ryan et al. 2013).

Generally stream temperature is strongly correlated with air temperature and stream flow, but a thoughtful analysis of this relationship in the Pacific Northwest was conducted by (Mayer 2012). The relationship between stream and air temperature is non-linear, with smaller increases in stream temperature at higher air temperatures. Stream temperatures often increase with urbanization, as shown in the Green-Duwamish River near Seattle, which Tan and Cherkauer (2013) attributed to modification of riparian structures and vegetation.

Projections: Ocean Conditions

A major emphasis in the 2013 literature was toward investigations of ocean acidification and hypoxia. A survey of subject-matter experts from the IPCC Working Group found consensus regarding the physical chemistry and direct impacts of ocean acidification on calcifying organisms and primary producers. However, the transfer of these impacts up the food web was more controversial (Gattuso et al. 2013). A simulation of ocean processes by Yool et al. (2013) projected a global decrease in ocean productivity of 6.3% by the 2090s, although it projected a 59% increase in primary production in the Arctic.

A major concern is the co-variation of hypoxia and high pCO₂ levels. Yool et al. (2013) found that the volume of suboxic zone (<20 mmol O₂m⁻³) increased by 12.5% globally. Coastal hypoxic zones (<70 μM, equivalent to 20-30 % air saturation) are especially vulnerable to increasing pCO₂ because of nonlinear carbon dynamics (Melzner et al. 2013). Upwelling regions, such as the California Current, are at particular risk. However, the combined ecological impacts of low O₂ and high pCO₂ are not well studied.

Similar results were apparent from a comparison of seven Earth Systems Models by Cocco et al. (2013). These models projected an increase in sea surface temperature of 2-3°C and decreases in pH and total ocean dissolved oxygen of 2-4%. Levels of dissolved oxygen in the upper mesopelagic layer (100-600 m depth) showed more complex responses, including increases and decreases, because of the sensitivity of DO levels to circulation, production, remineralization, and temperature change (Cocco et al. 2013).

Focusing specifically on the California Current, Hauri et al. (2013) found that aragonite undersaturation events along the shelf have quadrupled in number and lengthened in duration, and that this trend will continue. Without sufficient aragonite, it is very difficult for calcifying organisms to build shells. Within about 20 years, the seafloor will be undersaturated most of the time; when CO₂ levels reach 500 ppm, aragonite undersaturation will become basically permanent. Within 25 years, the saturation horizon in the central California Current will shoal into the upper 75 m.

Retrospective Analyses: the California Current

Most Pacific salmon achieve the vast majority of their growth in the ocean, and survival through this life stage is a major driver of variation in abundance for most populations. Thus, understanding the factors that determine marine growth and survival, and projecting how climate change will influence these factors, is a paramount priority.

Much recent work has focused on large-scale atmospheric processes such as the North Pacific High and North Pacific Gyre Oscillation (NPGO), and how they correlate with localized levels of upwelling and productivity at the lower trophic levels. It is important to keep in mind that nonlinearities in ecological systems can produce apparent state-transitions in marine ecosystems in response to random fluctuations in the atmosphere (Di Lorenzo and Ohman 2013).

Upwelling

Upwelling plays a crucial role in generating productivity of the California Current. Schroeder et al. (2013) found a relationship between upwelling and an index of the North Pacific High in winter, which they described as a “pre-conditioning” of the ocean that affects prey availability in spring—during the crucial early marine life stages of salmon. Understanding upwelling itself is a major challenge because it varies not just in mean values, but also in intensity, as well as in the timing of shifts between upwelling and downwelling seasons.

Using a new index that integrates these components, Bylhouwer et al. (2013) analyzed correlations between signals of the PDO and El Niño and upwelling in the California Current. They found that positive/warm phases of both large-scale processes were associated with a later onset of upwelling and a weaker and shorter upwelling season. In the southern California Current Ecosystem, Garcia-Reyes et al. (2013b) found that winter and spring winds and sea surface temperatures (and upwelling) strongly influenced success at higher trophic levels. Examples were Chinook salmon growth rates based on otolith microstructure, lay dates and reproductive success of multiple bird species, and sardine and rockfish recruitment and growth.

Hypoxia and pH

Upwelling brings to the surface deep ocean water that has not been exposed to air for extended periods and is generally diminished in oxygen. Peterson et al. (2013) found a link between the NPGO and oxygen levels in source waters upwelled in the California Current. They found that hypoxic water was more prevalent where the continental shelf is wider, covering up to 62% in some years. Dissolved oxygen and pH have been declining since 1980 in the California Undercurrent, while temperature and salinity have been increasing. Equatorial waters appear to be extending further up the coast. Also, in 2012, more acidic waters were upwelled along the coast than in 1980 (Meinvielle and Johnson 2013). Acidity also affects the aragonite saturation state, which has declined in surface water on the Oregon shelf from 1-4.7 in pre-industrial times to 0.66-3.9 in 2007-2011 (Harris et al. 2013).

Ecosystem Responses

Trends in chlorophyll levels vary across the California Current, but have been generally positive near shore over the 13 years from 1997 to 2010 (Thomas et al. 2013). Chlorophyll levels were highly correlated with the NPGO off Washington and Vancouver Island. Although I do not thoroughly review oceanographic modeling of the drivers of productivity at lower trophic levels, one that describes the influence of the PDO and NPGO on the California Current is worth mentioning (Franks et al. 2013). Other models describe dynamics for California, British Columbia, and Alaska (Coyle et al. 2013; Decima et al. 2013; Li et al. 2013).

Many fish respond to ocean/atmospheric forcing factors, including flatfish in both condition and distribution (Keller et al. 2013) and sardine and anchovy in population cycling (Lindegren et al. 2013); these responses are similar to those observed in birds (Hatch 2013). In an analysis of world fisheries catches, Cheung et al. (2013) developed a new index of the thermal preferences of the catch to determine whether there is evidence in catch data that southern species are moving northward. They found that in fact, the mean thermal preference of catch in 52 large marine ecosystems, excluding the tropics, increased 0.23°C per decade from 1970 to 2006.

Large-scale atmospheric drivers tend to cycle at longer time scales, alternating between positive and negative phases. Following these phases, several authors discussed corresponding “regime shifts” in ecological (Hatch 2013) and social-ecological systems (Perry and Masson 2013). Hatch (2013) suggested 2008 marks another regime shift in Alaska. Perry and Masson (2013) used the driver–pressure–state–impact–response

framework (used in the Integrated Ecosystem Assessment) to develop a multivariate index of regime shifts for the Strait of Georgia. Their index included a wide variety of factors, such as physical conditions, hatchery releases, and fishing effort, as well as drivers and pressures from human populations and biological indices at all trophic levels, including catch, to describe the state and impacts (Perry and Masson 2013). They identified 6 variables that acted as leading indicators of regime shift.

Although somewhat peripheral to our main topic, we also note physical analyses of the impact of Japan's Tōhoku earthquake and tsunami in 2011 on flows in the Columbia River and how the timing of the impact depended on tide height (Tolkova 2013). Increasing wave height is also shown to be a more dominant driver of coastal flooding and erosion than sea-level rise (Ruggiero 2013). Estuarine habitat is likely to change with sea level rise, and some detailed habitat mapping helps to clarify where habitat might be gained and lost, which is crucial to long-term planning of habitat availability (Flitcroft et al. 2013).

Climate Impacts on Salmon

The literature on climate impacts on salmon fall into two categories. First, retrospective analyses strive to identify the role of environmental factors in salmon biology and distribution. This background information is essential for the second category, projections affecting salmon, wherein retrospective knowledge is used to predict salmon responses to climate change in the coming decades.

Because policy decisions depend most on projected responses to future climate, I begin with a summary of work in this category. Within this body of literature, I first address *freshwater* habitat suitability and population modeling, and then focus on implications of *ocean acidification* for marine life stages. Finally, I note the potential for *range expansion* into habitats that are currently too cold or inaccessible, but might become suitable under a changing climate.

Projections Affecting Pacific Salmon

Freshwater Life Stages

A number of studies have generated quantitative and qualitative projections specific to the populations included in this Biological Opinion. Among these, the **steelhead** vulnerability assessment of Wade et al. (2013) stands out for the following qualities:

- Broad scope covering all steelhead populations in the Pacific Northwest
- Life-stage specific approach, wherein all freshwater life stages are modeled with individual tolerance criteria and spatial and temporal exposures
- Comprehensive stress index, which incorporates duration, intensity, and extremes of environmental exposure
- Population-specific vulnerability index that accounts for current population status
- Inclusion of other habitat stressors such as land use and human population density

For this study, Wade et al. (2013) produced detailed stream-flow and temperature projections. They found that historical water temperature already approaches lethal limits for adult steelhead in the Upper Snake, Rogue, Chehalis and Middle Columbia Rivers. Thus, even minor increases in thermal exposure put some of these populations above lethal limits. In future scenarios, they project the greatest temperature increases in the Upper Columbia, Lower Snake, Lower Columbia, and Upper Willamette Basins. Populations in these locations also face high habitat stress, and hence high total vulnerability scores (see Figure 6 in Wade et al. 2013). This analysis will be very useful for conservation planning.

A second analysis of steelhead focused on life history diversity in the Methow River. This analysis compared climate change with the effects of changes in temperature and food availability (Benjamin et al. 2013). Rising temperature increased growth rates, leading to smaller and younger maturation or smoltification. However, food web changes had the ability to either mediate or exacerbate the effects of temperature.

For all west coast populations of steelhead and Chinook salmon, Beer and Anderson (2013) performed quantitative projections of spawn day, egg development, and juvenile growth under climate change scenarios. They predicted that Chinook salmon would spawn later in the year, but that steelhead spawn timing would not change.

Because of counteracting impacts of increased temperature on growth, their projections showed that mid-summer weights of both species stayed the same across most of the range but increased at some high elevation and cooler sites.

Another comprehensive but qualitative analysis of full life-cycle exposure to climate change addressed Oregon Coast **coho** salmon (Wainwright and Weitkamp 2013). These authors addressed the direction and magnitude of population response to climate trends in each life stage and our certainty in that response. They found a preponderance of negative or strongly negative effects with relatively high certainty compared with neutral or positive effects, leading to a projection of population decline in most populations. A somewhat similar although simpler deduction was applied to all nine species of salmonids in the Nooksack River, Washington, where potential loss of snow and glacier melt is projected to be the primary driver of decline (Grah and Beaulieu 2013).

A model of juvenile survival for Chinook salmon in the Lemhi River compared the effects of water diversion and climate change under various management and climate scenarios (Walters et al. 2013). They found that the effects of these factors compounded: diversion alone lowered juvenile survival 42-58%, but diversion with climate change depressed survival an additional 11-39%.

Numerous additional quantitative analyses and novel approaches have been applied to a variety of trout species (Al-Chokhachy et al. 2013; Blair et al. 2013; Filipe et al. 2013; Hedger et al. 2013; Roberts et al. 2013). However, because these are not focal species for this Biological Opinion, I list only the most interesting ones: a probabilistic accounting of uncertainty for bull trout projections in the Interior Columbia River Basin (Wenger et al. 2013); a comprehensive ecological, evolutionary, and genetic model of Atlantic salmon (Piou and Prevost 2013); and a study of how carrying capacity changes with temperature in brown trout (Ayllon et al. 2013).

Of particular interest might be the release by Katz et al. (2013) of a quantitative analysis of conservation status that incorporated risk of climate change for all native salmonids in California. They found that climate change and hatchery propagation were the most pressing extinction threats, with climate change having the largest negative effect and acting on all California populations.

On a more positive, albeit limited note, Boughton and Pike (2013) showed that upstream migration in one particular steelhead population might not be very sensitive to climate warming, but that the frequency of storms could limit migration opportunity.

In summary, projections of freshwater climate impacts are consistent with those from previous analyses: a few cold-water locations showed positive responses to climate change in certain life stages, but the vast majority of impacts are negative. These negative impacts extended across salmon species, throughout the various freshwater life stages, and geographically across the West Coast. Furthermore, many populations already most impacted from other threats are also the most vulnerable to climate change.

Watershed Vulnerability Assessment

The U.S. Forest Service conducted a set of pilot vulnerability assessments of American watersheds, including two where species in this Biological Opinion reside (Umatilla and Sawtooth Basins) and summarized the general lessons learned from this process (Furniss et al. 2013). They projected a substantial loss in bull trout habitat, due to increases in winter peak flows and loss of connectivity between habitats due to high summer temperatures and reduced base-flows. Populations in 2 of the 14 subbasins assessed were considered to be at high population persistence risk by the 2040s, and in the Sawtooth Basin, 3 populations faced such risk levels by the 2080s. In the Umatilla, they estimated that about 34% of suitable bull trout habitat would be lost.

Although prospects in the Pacific Northwest are rather discouraging, we note that world-wide, salmon have successfully established new populations outside their historical range both through introduction and natural exploration (Nielsen et al. 2013). Some barriers to migration might continue to separate populations, such as the barrier of northern Quebec between North American and European Atlantic salmon. But recolonization after natural disturbances is generally swift (Milner et al. 2013).

Ocean Life Stages

An analysis of cumulative and interacting effects of tidal power development and climate change on ESA-listed species in Puget Sound, Washington (Busch et al. 2013a) found that salmon showed interactive effects from these two stressors. Although some species showed little direct impacts from climate change (e.g., steelhead), the combined effects of changing foodweb and tidal power produced very high risk to these populations.

Migration Pathways—Climate change will affect many aspects of marine life, including growth, survival, and behavior. Marine migrations are currently little understood. In a review of the impacts of climate change on marine migratory species, Anderson et al. (2013) described the relevant physical changes and current knowledge about fidelity to foraging and breeding habitats and migration corridors and bioclimate envelop models of current distributions, and phenology. They then developed an individual-based model for a generalized response to climate change based on phenology-mediated growth, survival, and reproduction. Using this model, they projected population growth, extinction risk, and adaptation mechanisms.

Anderson et al. (2013) concluded that the size of the bioclimate envelop is very important for population fate, and more specialized species are at greater risk. Genetic adaptation might be too slow to prevent phenological mismatch with prey, and rescue by phenotypic plasticity depends on whether the cue for the behavioral response tracks climate change, i.e., whether the existing reaction norm will successfully track future bioclimate envelops.

However, it is not clear to what extent individual species traits will be important in determining responses to climate change. A comparison of observed shifts in ranges across marine species with local climate changes found that variation in local climate explained more than species traits (Pinsky et al. 2013). Increasing variability in certain atmospheric indices, such as the NPGO, also seems to be correlated with increasing influence on a number of ecosystem components from krill to seabirds (Sydeman et al. 2013) in recent decades. But the extent to which these patterns will continue is unknown.

Ocean Acidification—In 2013, extensive work focused on ocean acidification and interactions with hypoxia. Generally these publications show substantial resilience to direct effects of ocean acidification at higher trophic levels, especially for fish important for fisheries such as walleye pollock (Hurst et al. 2013) and cod (Frommel et al. 2013; Maneja et al. 2013a; Maneja et al. 2013b). However, hypoxia effects at lower trophic levels are highly idiosyncratic, which makes projecting cumulative food-web responses very challenging.

An elegant demonstration of these complexities can be found in the scenarios compared by Busch et al. (2013b) using a food web model of Puget Sound. Using the *Ecopath with Ecosim* model, they examined varying numbers of functional groups that were negatively affected by ocean acidification, from one to all heterotrophic calcifying groups. Scenarios either increased or decreased fisheries yield, because impacts at different levels of the food chain sometimes cancelled each other out. Ultimately, most impacts on fisheries stemmed from direct rather than indirect effects. Thus, modeled

impacts on salmon were relatively small, with less than a 5% change in yield in all scenarios except one, in which ocean acidification affected only macrozooplankton.

Our understanding of sensitivity to ocean acidification is growing quickly. A meta-analysis of 228 studies reported that 100 new species have been studied recently (Kroeker et al. 2013). In general, heavily calcified organisms, including calcified algae, corals, mollusks, and the larval stages of echinoderms, are the most negatively impacted, whereas crustaceans, fish, fleshy algae, seagrasses, and diatoms are less affected or even benefit from acidification. The diversity of individual species and life-stage sensitivities indicates that evolution of tolerance to ocean acidification is possible and perhaps likely in some species (Kelly and Hofmann 2013; Kelly et al. 2013).

Effects of ocean acidification on fish often involve olfactory ability, in some cases impairing behavior (Leduc et al. 2013; Lonnstedt et al. 2013) and in other cases improving hearing (Bignami et al. 2013). These results bear relevance to otolith studies in which bone growth is used as an indicator of body size. Ocean acidification might interact with toxicants, both in terms of the carbon balance and fish responses (Nikinmaa 2013) and might also affect virus-host interactions, though current studies mostly involve phytoplankton (e.g., Carreira et al. 2013).

Retrospective Analyses: Environmental Influences on Salmon

Migration Behavior and Survival

Temperature-Related Migration Blockage—Most Pacific salmon reproduce only once in their lifetime, and historically, survival during the upstream migration has been high. Reducing anthropogenic hindrances during this stage is crucial for recovery. Thermal barriers to migration have probably always characterized migrations for some stocks (e.g., Okanogan sockeye and Klamath River Chinook). However, modern structures and water withdrawals that cause temperatures to shoot near or past lethal limits may create serious thermal barriers for many more stocks, and addressing this problem is a high priority for salmon managers.

Several papers in 2013 documented this problem, and in some cases, the failure of transportation to mitigate the problem. In the Columbia River, temperature gradients over 4°C within fish ladders at dams were associated with fallbacks and passage delays during adult migrations (Caudill et al. 2013). In Butte Creek, California, transportation of fish that had stopped migrating did not result in successful spawning (Mosser et al. 2013).

Changes in Migration Behavior—Extensive work with Atlantic salmon continues to show high sensitivity to environmental conditions in both juvenile behavior (Heggenes et al. 2013; Roy et al. 2013) and smolt stages (Handeland et al. 2013; Lacroix 2013; Lefevre et al. 2013). Marine migratory behavior is affected by smolt timing and marine water temperature. In one case, late smolt arrival coincided with a ring of warm marine water around the Bay of Fundy. This resulted in prolonged residency in the bay, where high predation apparently caused a near failure of cohort survival (Lacroix 2013).

Although not necessarily related to environmental conditions, a useful study of spring/summer Chinook salmon in the Columbia River Basin showed that within a population, the *order* of migration timing is age-structured (Bracis and Anderson 2013). They showed that within a population, the oldest fish migrate first and the youngest last. This analysis could help understand constraints on adult distribution and ability to stay within productive areas of the ocean in the year of adult return under future conditions.

Enhanced Vulnerability to Fisheries—Temperature interacts with other stressors. Of particular concern is the stress from fisheries during the upstream migration. A review across species found widespread evidence that mortality after catch and release is elevated at higher temperatures, even when those temperatures are within the normal tolerance range (Gale et al. 2013). Consistent with this general review, a specific study on Atlantic salmon documented a negative interaction between temperature and stress from catch-release handling (Richard et al. 2013). However, pink and chum salmon seem to be more resilient to handling stress on the spawning grounds than other species (Raby et al. 2013).

Growth and Sensitivity to Environmental Conditions

Most Pacific salmon have variable life histories that depend largely on growth opportunity. Recent studies have related residency in steelhead (Berejikian et al. 2013) and unusual yearling life history in fall Chinook salmon (Hegg et al. 2013) to water temperature and flow. In these relationships, the mechanistic driver was thought to be related to lipid, as has been shown for Atlantic salmon (Jonsson et al. 2013). Temperature may affect lipid reserves, which dropped after exposure to high thermal stress in steelhead (Kammerer and Heppell 2013a) and redband trout (Kammerer and Heppell 2013b), as indicated by production of heat shock protein. At higher temperatures, steelhead grow less and produce more heat shock protein (Kammerer and Heppell 2013a).

An analysis of Willamette Chinook salmon (Johnson and Friesen 2013) found no change in mean age at maturity, despite changes in environmental conditions over 17 years. However, these researchers did detect a relationship between adult body size and the Pacific Decadal Oscillation. Because growth rates have different consequences for age at return for males vs. females, relative sizes of fish on the spawning grounds might shift in a warmer climate. In a recent study on Chinook salmon, Mizzau et al. (2013) found that at 15°C compared with 10°C, sexual-size dimorphism was biased toward males in juveniles, whereas it was biased toward females in mature adults. The head start in male growth apparently caused earlier maturation, which led to reproduction with larger, older females.

An interesting paper related multi-species fish responses to a severity index representing flow extremes in Ontario (Jones and Petreman 2013). They found that across species, low-flow events depressed young-of-the-year growth while high-flow events increased growth; likewise, abundance was depressed by low-flow events but augmented by high-flow events.

Habitat Preference

Much behavior is mediated by thermal conditions in combination with other habitat factors, and I briefly visit a few of the studies relevant to salmonids. In general, this literature is consistent with our previous understanding of salmon behavior and optimal growth conditions. For example, steelhead in California minimize activity under warmer conditions and avoid pools over 30°C (Sloat and Osterback 2013). One interesting study demonstrated a correlation between boldness and stress, such as that induced by hypoxia or temperature (Frost et al. 2013). This suggests indirect mechanisms that alter the impact of stress on growth rate. An overview of winter behavior outlines some potentially relevant insights for detailed behavior models (Weber et al. 2013).

Evolutionary Response to Thermal Environments: Migration Timing

Migration timing is strongly related to environmental covariates, but these responses can be plastic (i.e., immediate behavioral responses to the environment) or genetic (i.e., determined by selection in previous generations). Kovach et al. (2013b) show how a suite of juvenile and adult stages in five salmon species have changed with climate in Auke Creek, Alaska. Evolutionary responses in migration phenology in pink salmon were recently linked to natural selection (Kovach et al. 2012), but further study of this population has shown they did not lose genetic variation despite the rapid shift in gene frequencies (Kovach et al. 2013a).

A second study on this same population trend found that early and late-migrating phenotypes have essentially come to different solutions in the survival trade-off between the freshwater vs. marine life stages (Gharrett et al. 2013). Gharrett et al. (2013) argued that embryos from early migrating adults had lower freshwater survival but high early marine survival: these embryos face harsh winter conditions and the effects of ongoing spawning, but they arrived earlier in the ocean under better feeding conditions. Late-migrating adults, on the other hand, produce offspring with better early growth in freshwater but poorer marine survival. In salmon, this type of divergent selection with alternate solutions to a common problem (maximizing lifetime fitness) gives rise to much phenotypic and genetic diversity.

Local Adaptation in Egg Size and Survival, Redd Depth, and Heat Shock Proteins

Many aspects of thermal tolerance and preference have a genetic basis and are local adaptations to specific habitats and life histories. However, these traits are also extremely sensitive to acclimation, timing, and maternal conditions, which are very difficult to control for in population comparisons, but which might explain some of the patterns described here. Nonetheless, egg-size/temperature relationships differ among populations in the direction expected from local adaptation (Braun et al. 2013).

Populations of Fraser River sockeye salmon historically exposed to warmer incubation regimes produced larger eggs than expected from a single egg-size/temperature relationship for all populations; this might reflect compensation for the warmer environment through local adaptation. Fraser River sockeye also may have evolved thermal reaction norms to match river conditions during the migration season (Whitney et al. 2013). Another study of Fraser River sockeye found that aerobic scope and cardiac performance was consistent with local adaptation across populations with migrations of varying timing and difficulty (Eliason et al. 2013).

Whitney et al. (2013) also found that populations that experience higher egg incubation temperatures have right-shifted thermal reaction norms. However, Chen et al. (2013) showed patterns among Fraser River sockeye populations that indicated upper temperature tolerance in eggs varied with age at measurement. These results suggest that temperature tolerance at a single point in time might not be a robust test of local adaptation. This study also found differences in heart rates across populations, and concluded they had evidence for thermal adaptation (Chen et al. 2013). Another purported adaptation to incubation conditions involved female redd depth in brown trout (Riedl and Peter 2013), where variation along an elevation gradient in Switzerland was thought to reflect adaptation to scour risk.

Expression of heat shock proteins is consistent with individual population exposure to high temperatures in redband trout, but there is an interesting trade-off between the benefit of expressing these proteins in response to short-term vs. long-term exposure. In the short term, elevation heat shock proteins are beneficial. However, chronic production of these proteins has negative consequences, so over evolutionary time, selection works to reduce their expression (Narum et al. 2013). It is important to keep in mind that similar phenotypic responses to temperature and other stressors might reflect very different physiological processes (Wellband and Heath 2013a, b).

Thermal preferences are not always genetically determined. A study of ecotype by population growth and thermal preference in lake trout found that acclimation explained more variation than population growth, indicating a plastic response to early growth conditions (McDermid et al. 2013).

Many adaptations to climate have a genetic basis. However, these adaptations evolve relatively quickly, as shown by the high relatedness within basins among populations of different life history types, compared with between-basin divergence (Moran et al. 2013). Population genetics presents powerful tools for deciphering local adaptation, and great advances are being made in identifying genes subject to natural selection (Vincent et al. 2013). For example, differentiation at three circadian-clock genes was associated with differences in run-timing of spring vs. fall Chinook in Feather River, California (O'Malley et al. 2013).

Interacting Stressors: Hypoxia, Contaminants, and Disease

Methods of Analyses

A popular conceptual model for integrating the impact of multiple stressors is the theory of oxygen and capacity limited thermal tolerance (so-called OCLTT). This theory relates thermal exposure to aerobic scope, which in turn affects the performance measures typically used to indicate fitness. In 2013, this theory came under fire (Clark et al. 2013). However, the criticisms of this approach were less applicable to upstream-migrating salmon than to salmon in other contexts, and upstream migration is the primary context in which we have referred to OCLTT in these reports (see also the general defense by Farrell 2013). The effects of hypoxia generally exacerbate temperature stress (e.g., in brook char, Ellis et al. 2013), but tolerance of the two traits can be correlated. For example, enhanced tolerance of hypoxia was observed in strain of genetically selected, fast-growing rainbow trout compared to a slow-growing strain (Roze et al. 2013).

Anttila et al. presented two studies (2013a, 2013b) reviewing the evidence for a correlation between thermal tolerance and hypoxia tolerance, and found a positive correlation between these traits. They concluded that their findings supported the OCLTT theory. However, Hasnain et al. (2013) presented a broader review of traits related to thermal adaptation. These included metrics of growth (optimal growth temperature, final temperature preferendum), survival (upper incipient lethal temperature, critical thermal maximum), and reproduction (optimum spawning temperature, optimum egg development temperature). Growth, survival, and reproduction metrics were evaluated across 173 North American freshwater fish species, and results showed that all of these traits were highly correlated, with a strong phylogenetic component.

An emerging new technique is metabolomics, in which low molecular mass metabolites within the cell, tissue, or biofluid of an organism are analyzed in response to an external stressor (Lankadurai et al. 2013). This technique might lead to growth in the study of interactions among stressors. Dolomatov et al. (2013) summarize much of the physiology of temperature regulation.

Contaminants

Contaminants are a persistent problem in Northwest watersheds, as elsewhere. This threat may grow more acute as contaminants interact with factors that change with climate, such as flow, salinity, or pH. Attempts to attribute fish decline to effects of contaminants is often difficult, as shown in a case study of Fraser River sockeye salmon (Ross et al. 2013). The complexity of such interactions was reviewed by Hooper et al. (2013) and Moe et al. (2013), with the latter presenting a framework for solving the problem. For example, many climate models predict an increase in severe storm events in the Pacific Northwest. Extreme flows are associated with such events, and these flows have both direct and indirect effects.

Extreme flows carry most of the toxic sediment that arrives in an estuary from contaminated areas within a steep coastal basin in San Lorenzo, California (Conaway et al. 2013). The impact of contaminant pulses, such as those carrying polycyclic aromatic hydrocarbons, can increase at higher temperature (Brinkmann et al. 2013). Despite concern that the toxicity of insecticides in estuaries might intensify under increasing salinity, one study showed little effect (Riar et al. 2013). Aluminum is more toxic in more acidic water, and a study of migrating Atlantic salmon smolts found that at low exposures, the toxic effect of aluminum was delayed at times until the fish entered marine water (Thorstad et al. 2013).

Fish Pathogens

Some **diseases** are affected by flow and temperature regimes, either through pathogen growth rates, vector dynamics, or virulence/resistance by the fish. *Ceratomyxa shasta*, a parasite common from the Columbia to Klamath Rivers, is sensitive to temperature at all stages of transmission. Ongoing work examines relationships between transmission of this parasite and water velocity and temperature (Ray and Bartholomew 2013). The parasite-host relationship involves co-evolution, as shown for the evolution of oligochete resistance to the myxozoan parasite that causes whirling disease in the Colorado River (Nehring et al. 2013). **Proliferative kidney disease** is also more difficult for brown trout to completely expel under warmer conditions (Schmidt-Posthaus et al. 2013).

Invasive Species

A major concern for Columbia River Basin salmon is the threat of invasion by warm-adapted species that compete with or prey upon native salmon. **American shad** has come to dominate the anadromous fish migration in the lower Columbia River. The incursion of shad upstream past McNary Dam is correlated with higher water temperatures and lower levels of flow. The conditions projected with climate change (warmer summer temperature and lower summer flows) are consistent with further penetration of the upper Columbia River by American shad (Hinrichsen et al. 2013). **Brook trout** has also invaded much of the Columbia Basin. Studies in both the Canadian Rockies (Warnock and Rasmussen 2013) and in Vermont (Butryn et al. 2013), found that brook trout more readily invaded warmer streams. **Brown trout** are not a recognized threat at this point in the Columbia River Basin, but numerous studies have documented their habitat preferences and invasion behavior (see especially Labonne et al. 2013), and they are probably selectively preferred under warmer conditions.

Marine Survival and Behavior

Numerous papers analyzed the relationships between early marine conditions and adult returns for Columbia River salmon. Daly et al. (2013) found that larval fish biomass in the winter prior to smolt arrival was a good predictor of salmon survival. In a separate study, juvenile rockfish survival (a favored prey species) was correlated with sea level anomalies (Ralston et al. 2013). Miller et al. (2013) found that fish condition in September (but not June) and Columbia River plume volume explained most of the variation in adult returns. Burke et al. (2013b) found that a large suite of variables was necessary to explain adult returns. Sharma et al. (2013) related the spatial scale of ocean covariation to adult returns and found that a spatial scale of 350-450 km best represented the correlation structures. These relationships point to large-scale driving factors in the Pacific Ocean that synchronize responses from many populations.

In their study of geographic patterns, rather than survival, Burke et al. (2013a) explored decision rules that can explain marine distributions and found that geographic rather than environmental factors apparently controlled migration. These results suggest that fish might hazard highly unsuitable conditions to reach their goal. Hypoxia, in particular, is increasing along the Oregon coast, challenging the tolerance of many invertebrates, although some were resistant (Eerkes-Medrano et al. 2013).

One report published in 2013 for a stock outside the Columbia Basin was noteworthy: a modeling effort by Dorner et al. (2013) found that detection of oceanographic drivers using a Ricker function on catch data can be extremely difficult. They concluded that it is unlikely that modeling efforts at present can accurately represent such marine drivers or manage them for climatic effects.

Climate is clearly important in driving survival during both the freshwater and marine life stages of Pacific salmon, and co-variations in survival are observed over large spatial scales (Sharma et al. 2013). Nevertheless, climate over the past 500 years did not synchronize population dynamics across 20 populations of sockeye salmon in Alaska (Rogers et al. 2013).

Climate Change and Endangered Species

A series of papers in a special issue of *Conservation Biology* considers how climate change affects ESA decisions. The Special Issue addresses a range of issues from climate science to biology to policy focus. Starting with the climate science, Snover et al. (2013a) offer guidance for choosing climate change scenarios and clarification of irreducible uncertainty. One piece of advice from this paper is that climate scientists, biologists and policy makers should work together early in the process for the best outcome. Although not in the special issue, a separate paper finds a successful approach taken by NOAA's Regional Integrated Sciences and Assessments (RISAs) program in disseminating information and promoting scientist/client interaction and application of the information (Kirchhoff 2013).

The Special Issue in *Conservation Biology* also addresses more conceptual biological issues, such as clarification of the breadth of the conceptual model needed to encompass the full range of climate impacts (not just lethal maximum temperatures) and the imperative of considering long term (100 year) climate projections in setting goals for proactive actions and necessary levels of population protection (McClure et al. 2013). Although not part of this special issue, another paper fills out many of these steps in a framework document that includes a case study on salmon in the Pacific Northwest (Wilsey et al. 2013).

Other papers in the Special Issue address the policy decision making process, including an overview of ESA processes (Seney et al. 2013) and explication of a decision focused approach (Gregory et al. 2013), similar to the adaptation turning point approach mentioned above.

Our literature search was designed to identify cutting-edge experimental and analytical science relevant to understanding the impacts of climate change on Pacific salmon. As such, it does not cover most policy documents or practical approaches to decision-making, which are typically not published in peer-review scientific journals. Nonetheless the smattering of papers from this literature may be useful to mention.

A crucial question for reintroduction or restoration programs is whether climate change will make a given habitat unsuitable, regardless of habitat restoration actions. This question is addressed in a case study of prospects for reintroduction of Atlantic

salmon to the Rhine River, where (Bolscher et al. 2013) propose a five-step process to determine adaptation turning points. These steps are

- 1) Describe the system of interest and scope of the project
- 2) Identify potential key impacts of climate change,
- 3) Identify the socio-political objectives of concern
- 4) Determine adaptation turning points, such as when critical thermal maxima are likely to be exceeded, and
- 5) Develop alternate adaptation strategies, i.e., actions to postpone or avoid turning points.

Obstacles to applying these frameworks often involve institutional and operational issues, including competing demands for a shared resource, and effective communication between climate information and water managers. A study of hotspots of water quality vulnerability in the Columbia River Basin lays out some areas of concern when human interests are considered alongside biological interests in an integrated water supply, demand, quality assessment (Chang et al. 2013).

Options for responding to ocean acidification are especially sparse. To address this deficiency, Bille et al. (2013) review four categories of management responses: preventing ocean acidification; strengthening ecosystem resilience; adapting human activities; and repairing damages.

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Glossary

A1B, A2, B1	Carbon emission scenarios from AR4
AR4	4 th IPCC Assessment Report
AR5	5 th IPCC Assessment Report
CMIP3	Coupled Model Intercomparison Project Phase 3
CMIP5	Coupled Model Intercomparison Project Phase 5
ENSO	El Niño-Southern Oscillation
GCM	Global Climate Model
IPCC	Intergovernmental Panel on Climate Change
NPGO	North Pacific Gyre Oscillation
PDO	Pacific Decadal Oscillation
RCM	Regional climate model
RCP	Representative concentration pathways (Emissions scenarios for AR5)
VIC	Variable infiltration capacity model