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# Impacts of Climate Change on Columbia River Salmon

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*A review of the scientific literature published in 2012*

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*August, 2013*

# Summary

Three major climate science reports were drafted or completed in 2012. First, a special publication of the American Meteorological Society reported that global CO<sub>2</sub> emissions had reached 9.7 Pg C in 2012, exceeding the record set in 2011 (Blunden and Arndt 2013). They reported mean atmospheric CO<sub>2</sub> concentrations at a record high of 392.6 ppm, with concentrations exceeding 400 ppm for the first time at a majority of Arctic observation stations (Blunden and Arndt 2013). Second, a number of work groups processing global climate models (GCMs) completed an array of carbon emission scenarios for the 5<sup>th</sup> assessment report from the Intergovernmental Panel on Climate Change (AR5), which is scheduled for release in fall 2013. Finally, over 300 experts completed a 3-year analytical review for *Climate Change Impacts in the United States*, the third national climate assessment report (Melillo et al. 2014) mandated by the Global Change Research Act of 1990.

Preliminary reviews of these major works indicate that for the most part, the extent and impacts of climate change predicted from our previous literature reviews are confirmed. Although some models have revised certain estimates downward, we await the full synthesis to assess changes in projections from the previous IPCC assessment report. The bulk of new literature in 2012 focused on sea level rise, sea ice extent, and glacier melting, collective weaknesses identified from 4th the IPCC assessment report.

Notable among the literature addressing these issues was a report by the National Academies, *Sea-Level Rise for the Coasts of California, Oregon, and Washington* (Committee on Sea Level Rise in California et al. 2012b), which forecasts global sea level increases of 13.5 cm by 2030 and 82.7 cm by 2100 (mean estimate). These estimates are higher than those forecast from the previous IPCC assessment report, but comparable to those from other recent estimates. However, the uncertainty range reported by NRC (2012) was much larger than those of other reports. For Oregon and Washington, projected increases in sea level from 2000 ranged -4 to 23 cm by 2030, -3 to 48 cm by 2050, and 10 to 143 cm by 2100 (Committee on Sea Level Rise in California et al. 2012a).

A special report of the IPCC provided analyses of the likelihood for climate extremes with a summary of historical and projected increases in extremely hot days, prolonged heat waves, and heavy precipitation events for global regions with and without historical data (IPCC 2012). A very likely increase in severe droughts was reported by (Dai 2012), although the major drought of the 1930s has not been exceeded to date (IPCC

2012).

Reviews of historical stream temperature trends in the Columbia River basin indicate significant warming in unregulated streams with sufficiently long time series (Arismendi et al. 2012, Isaak et al. 2012b). Isaak et al. (2012b) reported mean summer warming of up to 0.22°C per decade, although Arismendi et al. (2012) showed that certain regulated streams and short records can indicate reversed trends. One important conclusion was that temperature mitigation through controlled releases from dams can successfully lower stream temperatures (Arismendi et al. 2012, Konrad et al. 2012, Macdonald et al. 2012).

New models of streamflow and temperature across the Columbia River basin project that reductions in summer streamflow will increase stream warming to a greater degree than projected from models considering increased air temperature alone (Furey et al. 2012, Tang et al. 2012, Wu et al. 2012a). Such projections are of particular concern for snow-dominated basins such as those of the Salmon and Clearwater River.

Marine studies showed declining dissolved oxygen and expanded oxygen minimum zones off the Oregon coast (Bjorkstedt et al. 2012, Pierce et al. 2012); new models project these trends will continue, with affected areas becoming more corrosive (Bianucci and Denman 2012, Gruber et al. 2012). Gruber et al. (2012) projected aragonite undersaturation for 70% of the euphotic zone in the California Current Ecosystem (CCE) by the 2050s.

Projected impacts of climate change on salmon in 2012 are similar to those previously described. Multiple reports expanded our understanding of salmon marine distribution and its linkage to physical drivers and food web processes, specifically for Columbia River Chinook (Bi et al. 2012, Pool et al. 2012, Rupp et al. 2012, Ruzicka et al. 2012, Yu et al. 2012). Hazen et al. (2012) cautioned that climate change may lead to increased predator pressure on salmon in the California Current.

Literature in 2012 provided new insight into salmon movement through Columbia River dams during winter (Kock et al. 2012, Tiffan et al. 2012), in the estuary (Harnish et al. 2012), and in the ocean (Sharma and Quinn 2012). Multiple efforts to determine drivers of early marine survival produced somewhat contradictory results: some researchers reported a clear influence on marine survival from conditions in the mainstem Columbia River (Haeseker et al. 2012, Holsman et al. 2012), while others concluded that early marine growth was a more critical factor (Tomaro et al. 2012).

Several studies of invasive species in the Columbia River basin showed that

smallmouth bass distribution is strongly temperature dependent and that smallmouth bass is widespread in some tributaries, with negative impacts on native prey and salmon behavior (Hughes and Herlihy 2012, Kuehne et al. 2012, Lawrence et al. 2012). On a more optimistic note, evidence of rapid evolutionary response in migration timing of Alaskan pink salmon was reported (Kovach et al. 2012). In addition, an analysis of the utility of existing genetic variation for future local adaptation suggests adaptive potential in existing populations (Miller et al. 2012b). Miller et al. (2012b) showed that two somewhat distantly related populations of steelhead *O. mykiss* have evolved rapid rates of adaptation using the same conserved genetic variation. This suggests that adaptive traits by salmon might be capable of evolving faster in response to future climate warming than would generally be associated with *de novo* mutations. Similarly, successful artificial selection for heat tolerance in rainbow trout indicates that evolutionary processes can proceed quickly under the right conditions (Ojima et al. 2012, Tan et al. 2012).

In terms of climate policy, a perspective on the Columbia River Treaty by Cosenis and Williams (2012) presented a cautionary note on the success of adaptive management in the Columbia River Basin. Climate adaptation strategies are being piloted by the U.S. Forest Service with science-based partnerships (Littell et al. 2012). However, climate change remains a relatively low priority in conservation actions (Ellenwood et al. 2012). Climate science literature from 2012 provides further support for continuing temperature mitigation actions and maximal population recovery by whatever restoration actions are possible. Managers face the continuing threat of rising stream temperatures, declining summer flows, and extreme weather events, with potentially negative impacts on cold-water fish.

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# Objective and Methods

The goal of this review was to identify literature published in 2012 that is most relevant to predicting the impacts of climate change on Columbia River salmon listed under the Endangered Species Act. By necessity, a large amount of literature related to this topic was excluded: salmon are affected by almost anything related to or altered in some way by changes in temperature, stream flow, or marine conditions. Thus, we tried to identify the most directly related papers by combining climatic and salmonid terms in our literature search criteria. Many general principles of climate change that were well demonstrated for other taxa, or in a more general context, were omitted. Our review also omitted potentially relevant gray literature, mainly because the citation index we used includes only literature from peer-reviewed scientific journals. In total, we examined over 1,000 articles and papers; 224 of these were included in this review.

Our literature search was conducted using *Web of Science* in January and July 2012. Each set of search criteria involved a new search, and results were compared with previous searches to identify missing topics. Specifically, all search criteria included publication year of 2012 (PY = 2012) plus:

- 1) A topic (TS) that contained the terms **climat\***<sup>1</sup> **or** **temperature** **or** **streamflow** **or** **flow** **or** **snowpack** **or** **precipitation** **or** **PDO**<sup>2</sup> **and** a topic (TS) that contained the terms **salmon** **or** *Oncorhynchus* **or** **steelhead**
- 2) A topic (TS) that contained the terms **climat\*** **or** **temperature** **or** **precipitation** **or** **streamflow** **or** **flow** **and** a topic (TS) that contained "Pacific Northwest"
- 3) A topic (TS) that contained the terms **marine** **or** **sea level** **or** **hyporheic** **or** **groundwater** **and** a topic (TS) that contained **climat\*** **and** a topic (TS) that contained **salmon** **or** *Oncorhynchus* **or** **steelhead**;
- 4) TS = (upwelling OR estuary) AND TS = climat\* AND TS = Pacific;
- 5) FT = ("ocean acidification" OR "California current" OR "Columbia River")
- 6) TS = "prespawn mortality"

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<sup>1</sup> The wildcard (\*) was used to capture all forms of the word "climate."

<sup>2</sup> Pacific decadal oscillation

The review is organized by first considering physical environmental conditions (historical trends and relationships) and then model projections of future climate, snowpack, stream flow, temperature, ocean conditions, etc. A summary follows of the literature on ecosystem and then salmon-specific responses to these environmental drivers in freshwater and marine environments, respectively.

# Physical Processes of Climate Change

## Global Climate Analyses

### State of the Climate 2012

In their special publication, *State of the Climate 2012*, the American Meteorological Society reported global CO<sub>2</sub> emissions from fossil fuel combustion and cement production have exceeded the all-time record of  $9.5 \pm 0.5$  PgC (2011) to a new high of  $9.7 \pm 0.5$  PgC (Blunden and Arndt 2013). For the first time, atmospheric CO<sub>2</sub> exceeded 400 ppm at a majority of Arctic recording stations (Blunden and Arndt 2013)[1]. Blunden and Arndt (2013) estimated mean atmospheric CO<sub>2</sub> content at 392.6 ppm. Anthropogenic greenhouse gases together now represent a 32% increase in radiative forcing over a 1990 baseline.

The year 2012 was among the 10 warmest on record, continuing the decade-long phenomenon of above-average temperatures (all 10 warmest years occurred since 1998, Figure 1). More specifically, 2012 was 0.14–0.17°C above the 1981–2010 global average (land was 0.24°–0.29°C and the ocean was 0.10°–0.14°C above average). However, in the north and northeast Pacific Ocean, including the California Current Ecosystem (CCE), temperature was cooler than average. This was due primarily to a weak Aleutian Low pressure center, related in part to La Niña influences.

Cumulatively, Earth temperatures have been warming at a rate of 0.06°C per decade since 1880, and a more rapid 0.16°C per decade since 1970. However, there has been no trend since 2000, presumably reflecting the cooling effects of a high frequency of La Niña events in the period 1998–2012. Long-term warming trends were reflected by new records in reduced sea ice extent, Greenland ice sheet melting (97% of the ice sheet surface showed signs of melting), and permafrost warming. The hydrological cycle is also more differentiated between dry and wet locations, with dry locations becoming drier and wet locations becoming wetter. Salinity also intensified (with salty areas getting saltier, and fresh areas getting fresher).

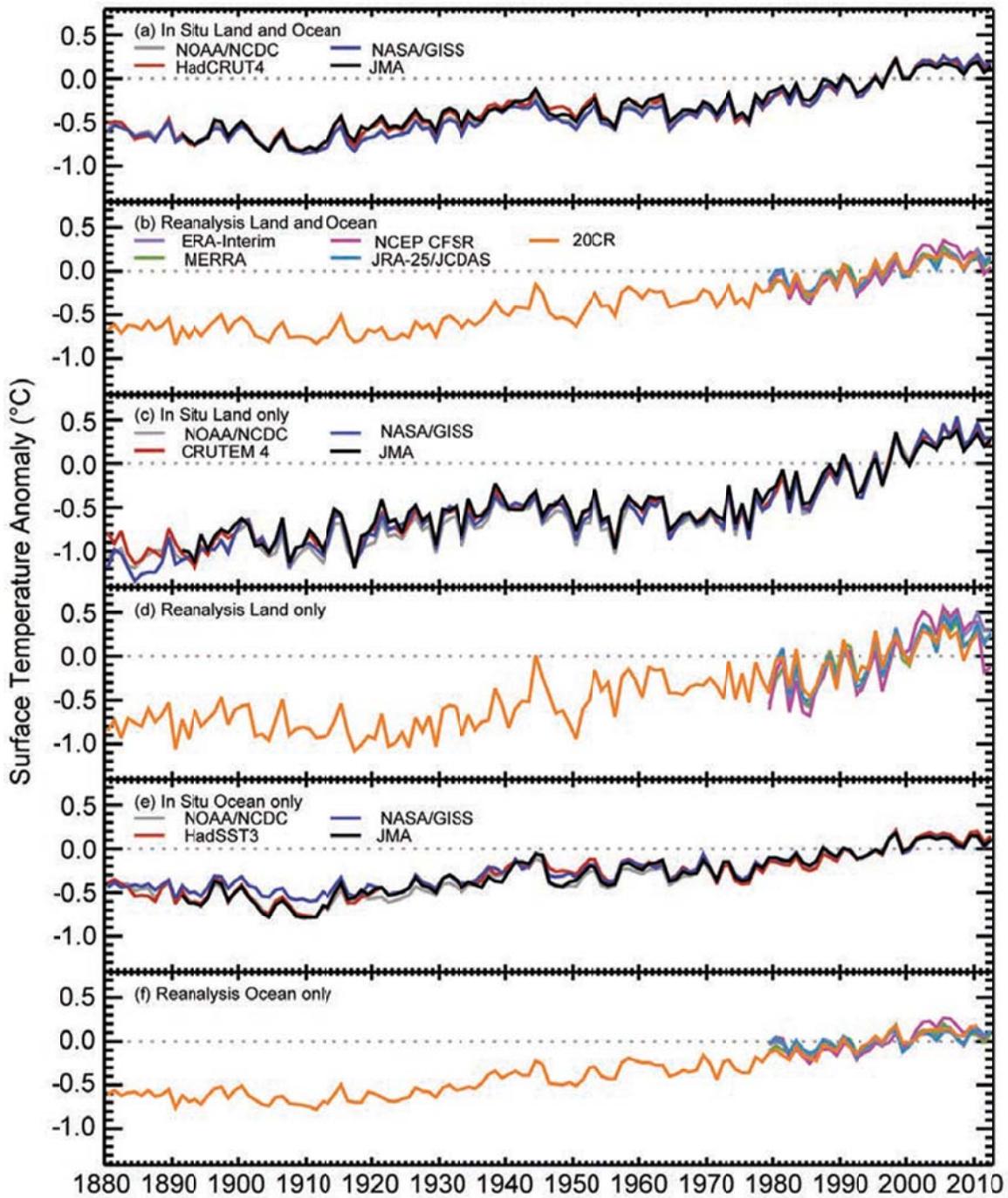


Figure 1. Global average surface temperature anomalies combining land and sea surface temperature ( $^{\circ}\text{C}$ ) during the 1881–2010 base period (Figure 2.1 in (Blunden and Arndt 2013)).

## New Analytical Methods

General Circulation Models (GCMs) are being used to produce new forecasts of climate change for the 5<sup>th</sup> IPCC Assessment Report (AR5) to be released in fall 2013. This effort is called the *Coupled Model Intercomparison Project Phase 5* (CMIP5). Chapters assessing impacts of climate change will follow in 2014. New emission scenarios called Representative Concentration Pathways (RCP) have been developed through CMIP5, and these will replace scenarios A2, A1B, B1, etc., from the 4<sup>th</sup> IPCC Assessment Report (AR4). We will wait for the AR5 synthesis to comprehensively assess changes from the AR4 projections. However, the individual reports that turned up in our review did not suggest dramatic changes in the overall projections.

## Global Climate Analyses

A major focus of climate literature in 2012 was better understanding of sea level and sea ice, which was a weakness in AR4. The National Academies produced a report on sea level rise along the Washington, Oregon, and California coasts (Committee on Sea Level Rise in California et al. 2012a). This report analyzed both the historical and projected trends for all components of sea-level rise. It concludes with projected cumulative change in global sea levels (relative to 2000) of 8-23 cm by 2030, 18-48 cm by 2050, and 50-140 cm by 2100. For the geographic region from northern California to Washington, projected rise were -4-23 cm by 2030, -3-48 cm by 2050, and 10-143 cm by 2100.

Large uncertainty in projections for the Pacific Northwest (ranging from sea level *fall* to sea level *rise*) stems from complications in predicting regional geomorphic dynamics. Terrestrial uplift along the Washington and Oregon coasts made the regional projection lower than the global projection, and could cause local sea levels to fall despite globally rising seas. However, geological tension might also cause a massive subduction zone earthquake that would suddenly lower the elevation of land along the Pacific Northwest outer coast, but raise elevations of the land in Puget Sound.

The AR4 report tracked historical global sea level increases of  $1.8 \pm 0.5$  mm per year during 1961–2003 (Solomon et al. 2007 p.48). These recent high rates might result from natural variability (especially ENSO), global warming, or both. More recent reports have produced similar estimates (Table 2.1 in the National Academy Report). For a rise of 1 m by 2100, the recent rate would have to accelerate 3 to 4 times.

Damage along the coast occurs when large storms coincide with high tides. Some climate models predict that the winter storm track will move north during the 21<sup>st</sup> century, which would increase storm impacts on the Oregon and Washington coasts.

However, the observational records (35 years) are not long enough to validate the drivers of historical trends or to clarify the role of natural interdecadal and ENSO influences (Committee on Sea Level Rise in California et al. 2012a).

In a separate paper, Boon (2012) reported accelerating sea-level rise along the Atlantic coast of the U.S. and Canada. Whether this trend will continue was not clear, but if it does, Boon (2012) projects a rise of 0.2-0.9 m above the long-term mean by 2050 in the Northeast region.

Valiela et al. (2012) documented freshening in estuarine, nearshore, and off-shore water in coastal Panama due to increased precipitation. They reported effects from freshwater added to surface waters via rain that included increased stream erosion; uprooting of stream-edge mangrove trees; increased mortality of benthic fauna; dampened upwelling of denser, nutrient-rich water; and nutrient enrichment of surface seawater.

Francis and Vavrus (2012) explained links between Arctic and mid-latitude weather and projected an increased probability of extreme weather events due to the faster rate of warming in the Arctic. Liu et al. (2012) showed how decreases in Arctic sea ice played a role in recent cold, snowy winters in Europe and the mid- and eastern US. The seasonal timing of sea ice showed strong opposing trends in both the Arctic (3 month *longer* ice-free period) and Antarctic (2 month *shorter* ice-free period). Nonetheless, it is still unclear from the new CMIP5 simulations when the Arctic will be completely ice free due to high variability in natural climate fluctuations (Stroeve et al. 2012). Glaciers and ice caps lost mass at  $148 \pm 30$  Gt/yr from 2003 to 2010, raising sea level by  $0.41 \pm 0.08$  mm/yr (Jacob et al. 2012), which is somewhat less than previously estimated.

Predicting sea level rise was a weakness of previous IPCC projections, which tended to underestimate recently observed rises. Nonetheless, in other respects, critical review showed that IPCC projections were accurate at the global scale (Rahmstorf et al. 2012). Inconsistencies between estimates of ocean heat content from different sources (Loeb et al. 2012) and heat released from warm ocean currents are being resolved (Wu et al. 2012b). Regional climate models still found local climates difficult to reproduce (Soares et al. 2012, Wehner 2013).

Using the new CMIP5 models, Gillett et al. (2012) reported results from the Canadian Earth System Model (CanESM2) with a new form of bias-correction based on regression of modeled and observed historical climates from 1851 to 2010. They confirmed the signature of greenhouse gas forcing over the historical record, as reported

in previous papers; however, their estimate of past and projected forcing was lower than other estimates. They projected an overall range for mean global warming of 1.2-4.3°C by 2100, depending on the emissions scenario.

Other authors reanalyzed the extent of historical warming. They found that the northern hemisphere warmed 1.12°C and the southern hemisphere warmed 0.84°C over the past century (Jones et al. 2012). Inputs from glaciers have been recalculated and are projected to raise sea level 148-217 mm by 2100, depending on RCP (representative concentration pathways) scenario (Marzeion et al. 2012).

## Climate Extremes

The IPCC Special Report (IPCC 2012) summarizes previous information on ENSO and other aspects of decadal variability; however, the report concludes that the impact of global warming on these patterns is still highly variable among post-AR4 models. They describe a shift toward more central rather than eastern equatorial Pacific El Niño, which we reported previously. They did not specifically focus on the PDO.

A number of authors studied ENSO in 2012 (e.g., Carre et al. 2012, Dewitte et al. 2012, Li and Ren 2012, Li et al. 2012b, Ramesh and Murtugudde 2012, Zhang et al. 2012). Most of these studies were beyond the scope of this review, except that of Zhang et al. (2012), which produced specific projections for future patterns in the frequency of El Niño events that would affect the California Current.

Zhang et al. (2012) modeled regional dynamics in the Pacific Northwest and southwest using two dynamic forecasting models: the weather research and forecasting model (driven by GCMs ECHAM5 and CCSM3) and the HadRM (driven by HADCM3). Their projections indicated that teleconnection patterns changed under future climate regimes, causing wet anomalies to dominate in both warm and cold phases of ENSO, unlike the canonical pattern associating wet conditions with cool phases, and dry conditions with warm phases.

## Pacific Northwest

### Historical Analyses

A variety of studies published in 2012 found significant trends in temperature, precipitation, and flow both within the Columbia River Basin and over broader spatial scales. In brief, studies found stream temperatures getting warmer within the Columbia River Basin (Arismendi et al. 2012, Isaak et al. 2012b) and interannual variability in stream flow increasing in the Fraser (Dery et al. 2012). In a few cases, no statistically significant trend emerged, specifically for a small set of regulated rivers (Isaak et al. 2012b), over short time-series (Arismendi et al. 2012), and for snowfall in California (Christy 2012).

***Stream temperature***—An important limitation in our description and understanding of historical trends in stream temperature is the paucity of long-term data. Arismendi et al. (2012) conducted an interesting analysis of the relationship between temperature trends over time and both the extent of the record and whether the stream was directly impacted by humans. They found significant warming trends when longer records were available—roughly 44% of streams with records prior to 1987 had significant warming trends. However, cooling trends predominated in the shorter time series, despite significant warming of air temperature in many cases. The authors noted a correlation between base flow and riparian shading with these cooling trends. Human-impacted sites showed less variability over time, likely due to flow regulation and reservoir heat storage.

Isaak et al. (2012b) also compared temperature trends between unregulated and regulated streams. They demonstrated statistically significant warming trends from 1980 to 2009 on seven unregulated Pacific Northwest streams during summer (0.22°C per decade), fall, and winter, producing an annual trend of net warming trend, despite a cooling trend in spring. Stream temperature trends were strongly correlated with air temperature, showing the expected signal from regional climate warming. Trends in 11 regulated streams were in the same direction, but were not statistically significant, indicating that modified flows, in some cases explicitly for temperature management, limits stream thermal response to climate drivers.

***Runoff***—A study of interannual variability and total runoff within the Fraser River Basin (Dery et al. 2012) found distinct trends of increasing interannual variability in spring and summer (the period of high flows) over the past 100 years. New datasets of snowfall records in California found no trend since 1878 or within the last 50 years (Christy 2012).

***Fire frequency***—Previous analyses have projected increases in fire frequency due to rising temperatures and longer fire seasons, but a new study (Holden et al. 2012) showed an added influence of the timing of snowmelt and annual streamflow. Annual area burned and severe-burn area corresponded closely to precipitation variability and total annual streamflow. Another study (Abatzoglou and Brown 2012) compared downscaling methods for future projections of wildfire danger and found a new method, the MACA (multivariate adapted constructed analogs), that outperformed other methods for the high demands of complex fire prediction.

## Projected Changes

An intensive model of stream flow and temperature in the Pacific Northwest was published in 2012 by (Wu et al. 2012a). This group used a physical model of stream temperature based on a DRTT model (dominant river-tracing-based streamflow and temperature). Averaged across the Pacific Northwest, the model projected a 3.5% *decrease* in mean annual streamflow during the 2020s, despite a net increase in annual precipitation, with *increases* thereafter of 0.6% for the 2040s and 5.5% for the 2080s. However, *summer* streamflows decreased from 19.3% in the 2020s to 30.3% in the 2080s. Wu et al. (2012a) projected increases in mean annual stream temperature from 0.55°C in the 2020s to 1.68°C in the 2080s, while mean summer stream temperatures warmed 0.92-2.10°C.

Their largest projected increases in stream temperature were for the mouth of the Columbia River, at 1.88°C for the 2020s and 4.37°C for the 2080s. Simulations indicated that projected climate change will have greater impacts on snow-dominant streams, such as those found in the upper Columbia, Salmon, and Clearwater Basins, with lower summer streamflows acting synergistically with warmer summer stream temperature changes relative to transient- and rain-dominant regimes (Wu et al. 2012a).

Donley et al. (2012) analyzed water availability for fish in the Columbia Basin by taking output from downscaled projections of the Climate Impacts Group (described in previous literature reviews) and incorporating reservoir management rules and human withdrawals for agriculture using the Water Evaluation and Planning System (WEAP). They analyzed four sub-basins (Okanogan, Methow, Wenatchee, and Yakima) under five scenarios (climate change alone, moderate or high increases in agricultural demand, and different potential conservation rules). They found potential for very serious risks to salmonids unless substantial protections are put in place and present a set of specific recommendations for each basin.

Kollat et al. (2012) modeled how human population growth and land use change would interact with climate change to dramatically increase the frequency of 100-year

floods. They found increases to flood risk of 50–60% in parts of the Pacific Northwest by 2100. Their study was for the U.S. and was not locally downscaled. However, their efforts reinforce previous results that showed the same trends but did not include the human dimensions of increases to impervious surface area and changes in runoff.

Six studies projected changes in streamflow or stream temperature at specific watersheds within the Columbia River Basin. Lutz et al. (2012) focused on the Yakima River Basin, exploring tree ring data over 366 years to characterize patterns of natural climate variability. They reconstructed five climate patterns and projected them under future climate change scenarios. These scenarios showed reductions in summer streamflow despite wetter meteorological conditions. The USGS used PRMS (precipitation runoff modeling system) to complete projections for a number of watersheds across the country, including that of the Naches River, which is a tributary to the Yakima (Markstrom et al. 2012). They predicted increased winter runoff and decreased spring and summer runoff due to shifts in precipitation falling as rain rather than snow.

Efforts to provide thermal refugia in the Snake River have relied on releases from the Dworshak Dam on the Clearwater River in Idaho. Furey et al. (2012) used a simple “conceptual” hydrological model to explore combined changes in temperature and precipitation that would cause the most substantial shifts in streamflow. They found that increased precipitation led to increased runoff if temperatures stayed constant, but that annual streamflow declined under warming scenarios.

Another sensitivity analysis of stream flow in the Salmon River Basin (Tang et al. 2012) produced similar responses with the more mechanistic VIC (variable infiltration capacity) hydrological model. In response to incremental temperature increases, Tang et al. (2012) found that:

- 1) Annual flow decreased (November to February warming increased fall flows, whereas May to July warming decreased summer flows)
- 2) For 50% of the annual flow, timing shifted 10-30 d earlier with 2°C warming, and 15-45 d earlier with 3°C warming
- 3) Flash flows increased, leading to increased bank erosion

Projecting the physical consequences of climate change in any given location is a process that involves many steps in modeling, and each step has its own uncertainties in model parameters and outcomes. Many studies include multiple GCMs and emission scenarios in their projections to represent these sources of uncertainty. Previous studies have found that sensitivity to uncertainty in different steps of the modeling process depends on such factors as the aspect of the hydrological cycle (wet or dry season) and

geographic location of interest. For example, Jung et al. (2012) focused on sensitivity differences between a rain-dominated basin and a snow-dominated basin, both in the lower Willamette Valley. They found that the snow-dominated basin was more sensitive to hydrological model parameter uncertainty because of difficulties in modeling snowmelt.

Surfleet et al. (2012) compared biases of three hydrological models (VIC, PRMS, and a site-specific GSFLOW model), in the Santiam River Basin, a tributary to the Willamette River. They found biases in the large-scale VIC model, especially at small, unregulated sites. Surfleet et al. (2012) suspected that these biases reflected unmodeled groundwater influences. Models differed in their projected flows, mostly during summer low-flow periods.

Additional studies developed detailed projections for the Boise and Spokane River Basins (Jin and Sridhar 2012), Vancouver Island (Sobie and Weaver 2012) and British Columbia headwaters (but not the Columbia River Basin, Bennett et al. 2012). In general, these studies showed similar trends in responses and the importance of spatial variation in projections as has been reported for the Columbia River Basin.

## Marine Ecosystems

A report entitled *State of the California Current 2011-2012* focused mostly on 2011 because it was written in mid-2012 (Bjorkstedt et al. 2012). This report described spring 2012 as largely ENSO-neutral, with somewhat incoherent patterns in the PDO and multi-variate ENSO index, and latitudinal variability in the timing, strength, and duration of upwelling. The northern CCE had weaker-than-average, delayed upwelling in 2011. Bjorkstedt et al. (2012) also documented declines in dissolved oxygen, nutrient-enriched water below the mixed layer, and abundant jellyfish.

**Dissolved oxygen**—Climate models predict that **dissolved oxygen** will decrease and the oxygen minimum zone (OMZ) will thicken with global warming. Pierce et al. (2012) documented both of these trends since 1960 along the Newport hydrographic line off central Oregon. They found oxygen decreasing between 100 and 550 m, the OMZ now occurs at ~800 m, and upwelled water is hypoxic on the Oregon shelf.

**Upwelling**—Analysis of historical time series found concordance of **upwelling** and the PDO, North Pacific Gyre Oscillation (NPGO) and ENSO at very low frequency especially in the southern half of the California Current Ecosystem (Macias et al. 2012b). Improved coupling of CCE with the atmosphere better reconstructs upwelling and

small-scale phenomena (Li et al. 2012a). Iles et al. (2012) concluded that “upwelling events are becoming less frequent, stronger, and longer in duration” off Oregon and California. A new sensitivity analysis that used the ROMS (regional ocean modeling system) model showed an increasing risk of coastal hypoxia and low pH off the Vancouver shelf (Bianucci and Denman 2012).

**Ocean acidification**—Literature on **ocean acidification** in 2012 focused on both physical dynamics of ocean acidification and biological sensitivities. A significant review was released by NOAA describing knowledge on this topic to date (Feely et al. 2012). Papers that focused on physical dynamics to improve our understanding of ocean acidification included several that described historical and future **patterns in pH** in the California Current. This work developed empirical relationships and described recent trends and characteristics of pH and potential drivers (Alin et al. 2012, Wootton and Pfister 2012) and reconstructed ancient time series (Honisch et al. 2012).

Wootton and Pfister (2012) found strong trends of declining pH (mean decline of -0.018 per year) in the Strait of Juan de Fuca over about 15 years, which proved more consistent with rising atmospheric CO<sub>2</sub> rather than local drivers such as upwelling. Gruber et al. (2012) reported results from a high-resolution oceanographic model of the near-shore California Current simulating the A2 and B1 climate change scenarios from the AR4. Gruber et al. (2012) projected that by the 2050s, 70% of the euphotic zone (top 60 m) of nearshore (10 km) habitat will be undersaturated ( $\Omega_{\text{arag}} < 1$ ) the entire summer, and over 50% will be undersaturated year-round, regardless of emissions scenario. No areas were similarly acidic in pre-industrial times (~1750). Sea-floor habitat grew essentially entirely undersaturated by 2025 in the simulation.

# Responses to Climate Change

## Marine Resources

Recently, numerous reviews have reported evidence for the fingerprints of climate change and projected future climate trends. These reviews include the IPCC special report on extreme events (IPCC 2012), a U.S. National Academy Report on sea level rise (Committee on Sea Level Rise in California et al. 2012a), and a Royal Society of Canada report on climate change and marine biodiversity (Hutchings et al. 2012). More fish-centric reviews of impacts of these changes are also available, especially for the UK (Cheung et al. 2012, Heath et al. 2012).

Most comprehensively, Griffis and Howard (2012), Groffman and Kareiva (2013) and Staudinger et al. (2012) contributed technical input to the 2013 *U.S. National Climate Assessment* (Melillo et al. 2014). This assessment reviewed the current state of knowledge on factors affecting oceans and freshwater resources. Doney et al. (2012) reviewed marine ecosystems globally. In the Pacific Northwest, Martins et al. (2012a) reviewed the physiological links between climate and sockeye salmon, with most data coming from the Fraser River. Rand et al. (2012) assessed sockeye extinction risk according to the International Union for the Conservation of Nature *Red List* criteria. They found that 27% of sockeye populations, mostly in British Columbia and Washington, are at very high risk of extinction, due partly to climate changes.

## Ocean Ecosystems

Several studies focused on the connection between physical drivers and plankton communities. Historical shifts in primary production pointed to important environmental drivers. Kahru et al. (2012) found that from 1996 to 2011 concentrations of chlorophyll *a* increased off central California but decreased to the north and south (the central North Pacific gyre and off southern Baja California). They associated decreased chlorophyll *a* in the North Pacific with enhanced vertical stratification, which is predicted to result from global warming, and increases in upwelling. Other authors also linked the detailed mechanisms of upwelling to primary production (Lachkar and Gruber 2012, Macias et al. 2012a), and larger-scale differences in the north and south Bering Sea (Stabeno et al. 2012).

Polovina and Woodworth (2012) found that phytoplankton cell size has been shrinking in Pacific equatorial and subtropical oceans, in addition to alternating with the ENSO cycle. Microcosm experiments indicated a shift in microzooplankton grazing rates (Chen et al. 2012). Bi et al. (2012) improved our understanding of local variation in effects of PDO on copepod communities in the California Current Ecosystem. They found these communities related in part with upwelling effects, although near-shore copepod communities were more responsive to PDO forcing than those on the shelf slope. Pirtle et al. (2012) found that marine copepod community structure was also influenced by freshwater and changing glacial melting rates.

Two studies of links between physical drivers in the ocean and lower marine trophic levels focused specifically on salmon prey items. Ruzicka et al. (2012) developed an especially relevant food-web model for Columbia River salmon. They modeled each upwelling season in the northern California Current from 2003 to 2007 and found that euphasiids were the most important link between primary productivity and fish productivity. In an alternative food-web configuration, jellyfish dominated the biomass without providing much benefit to fish; they tended to sink to the bottom, which removed nutrients from the pelagic food web.

Jellyfish are very sensitive to environmental conditions, and these relationships received increased attention in 2012 (Lebrato et al. 2012, Suchman et al. 2012). Volkov (2012) linked Arctic cold-current patterns to the mass occurrence of the large hyperiid amphipod *Themisto libellula*. This species became a major food source for salmon in the Bering Sea from 2007 to 2011. In an alternative modeling approach, Blanchard et al. (2012) employed a size-based food-web model that projected changes in potential fish production in all major ecosystems world-wide, including the Pacific Northwest.,

A study of phenological trends at four levels in the food web over 24 years in the North Sea failed to find much coherence among trophic levels (Burthe et al. 2012). Although Burthe et al. (2012) concluded a mismatch must be occurring, no adverse effects on breeding success in seabirds was apparent.

In a study of top predators in the Pacific, Hazen et al. (2012) predicted responses to climate change for 23 species. They found that sharks, loggerhead turtles and blue whales were most at risk; California sea lions, elephant seals and tuna face little change or small increases; while sooty shearwaters and albatrosses might see large gains. Hazen et al. (2012) projected greater competition among top predators in the California Current, but also higher risk of anthropogenic impacts such as shipping and fisheries bycatch. Increasing oxygen minimum zones might make prey more vulnerable to air-breathing predators.

# Impacts of Climate Change on Salmon

## Population Declines Attributed to Climatic Factors

Many salmonid populations have declined over the past century and are currently threatened with extinction. Establishing causal links between declines and climate change presents a challenge because we generally lack the spatially specific and temporally appropriate data to document direct effects of environmental driving factors. Other human impacts are additional confounding factors.

Nevertheless, inferential evidence is available from 1) concurrent changes in population and climate metrics, and 2) mechanistic models of habitat area (thermal niche models), population or individual growth models, or cumulative stress models. Several papers have taken each of these approaches.

Isaak et al. (2012a) and Zeigler et al. (2012) described recent climate changes in the Rocky Mountains within the range of several listed trout species. They identified trends in air temperature and flow and the primary climate stressors expected to affect each species. They noted that the changes observed can exacerbate management challenges by increasing the occurrence of wildfires and the movement of warm-adapted exotic species that interact with species of concern.

Connors et al. (2012) evaluated a set of hypotheses for the decline of Fraser River sockeye salmon, including sea surface temperature and interactions among drivers of decline. They concluded that sea surface temperature is a significant contributing factor, either directly or through an interaction with farmed or pink salmon. Connors et al. (2012) speculated that juvenile sockeye exposed to pathogens early in marine life may be less able to compete for resources with pink salmon later in marine life. Alternatively, reduced food availability from competition with pink salmon might lead to disease expression in sockeye that are infected but not diseased.

The antagonistic interaction between exposure to farmed salmon and oceanographic conditions during early marine life suggests that the effects of warmer sea surface temperature may be compensatory. That is, some sockeye that die because of poor ocean conditions would have died from disease, and vice versa; however, these salmon would not die as a result of both factors Connors et al. (2012 p. 310).

Transitioning to the more mechanistic quantitative models, two models involved European brown trout. In the first model, Almodevar et al. (2012) developed a habitat niche model based on presence and absence of brown trout in the Iberian Peninsula. They found that suitable habitat has already declined by 12% per decade, which corresponds to 6% decline in population size per year. Under the carbon emission scenario B2 (from AR4), they projected 50% of the habitat to be lost by the 2040s, and the population to be extinct by 2100. In the second model, Lecomte and Laplanche (2012) developed a temperature-driven growth and production model for use in future population modeling.

Piou and Prevost (2012) developed an even more sophisticated growth and production model for Atlantic salmon that includes genetic structure and microevolution. This versatile model will likely be quite useful in predicting plastic and evolutionary responses to climate change.

Other mechanistic models were more general in their application, but provided a common metric for integrating the net effect of different stressors through aerobic scope and energetic costs (Portner 2012, Sokolova et al. 2012).

Providing a larger temporal context for inferences of population decline due to warming, Turrero et al. (2012) took a paleoecological approach to evaluate fluctuations between high and low salmon abundance and climate. They identified a longer generation time (more years at sea) in Atlantic salmon and brown trout during the Upper Palaeolithic period and modeled population growth rates based on mutation rates. Turrero et al. (2012) concluded that shifts in life history were associated with a lower population growth rate.

Life-cycle modeling is a useful tool in conservation planning. Zeug et al. (2012) developed a stochastic life-cycle model for winter-run Chinook salmon in the Sacramento River, California. A sensitivity analysis revealed that a 10% change in temperature had a much larger impact on escapement than comparable changes in other inputs.

# Freshwater Processes

## Juvenile Migration

McMillan et al. (2012) found that early maturation or smolting in *O. mykiss* depended on both body size and lipid levels: fatter fish tended to mature earlier, but they were more likely to smolt under warmer temperatures. Finstad and Hein (2012) found that the propensity for Arctic char to go to sea was predicted by lake productivity (and hence growth potential) and the arduousness of the migration, suggesting locally adapted thresholds for anadromy.

Two studies found that juvenile salmon migrate downstream during winter. In the lower Snake River, juvenile fall Chinook move through the hydrosystem during winter more than previously thought (Tiffan et al. 2012). This finding has implications for dam operations, such as removal of fish screens to minimize loss in turbines. Similarly, coho moved downstream past Cowlitz Dam in winter (Kock et al. 2012). These behaviors increase as spring approaches. The effect of photoperiod and temperature on rheotactic behavior and swim speed in tanks confirms these mechanisms (Martin et al. 2012). Riley et al. (2012) found that artificial lights, such as those used at dams, can interfere with normal diel and perhaps seasonal behavior.

Migration routes through the Columbia River **estuary** vary, both between and within the main navigation channel and nearshore or side-channal areas (Harnish et al. 2012). Fish use tidal energy to facilitate migration. However, **ocean migration routes** of ocean-type (subyearling) and stream-type (yearling) Chinook are not differentiated to the extent previously thought (Sharma and Quinn 2012). Previous studies have concluded that subyearling Chinook migrate nearer to shore, while yearling Chinook undertake mid-channel migrations. Sharma and Quinn (2012) found this to be true for Chinook originating in snow-dominated rearing basins, such as the Upper Columbia, Snake, and Upper Fraser Rivers. However, subyearling and yearlings from warmer natal environments in lower rivers and coastal areas overlapped extensively in their ocean migration routes, contradicting the hypothesis.

## **Adult Migration**

Flow and temperature are regulating factors in upstream movement of salmonids. Exposure to high **temperature** is a paramount concern from California to British Columbia, as well as for Atlantic salmon (Moore et al. 2012). Moore et al. (2012) provide a conceptual overview on thermal impacts on the spawning migration. Empirical studies document actual temperatures experienced. Strange (2012) analyzed migration patterns and temperature exposure in the Klamath River in California. He tracked four run-timing groups: Klamath-Trinity spring, Trinity summer, Klamath fall and Trinity fall. Two runs avoided high temperatures by migrating before or after peak thermal maxima (the spring run and the Trinity fall run). One run avoided excessive cumulative thermal exposure by migrating very quickly (the Trinity summer run). However, the Klamath fall run stayed close to high temperature prior to migrating, which exposed them to moderately high thermal stress. The highest exposures occurred in spring-run fish that migrated slowly and hence were exposed to summer temperatures for extended periods.

In the Puntledge River on Vancouver Island, BC, a biotelemetry study used animal-borne thermal loggers to show that adult summer-run Chinook were exposed to temperatures exceeding their thermal limits and this affected their spawning migration (Hasler et al. 2012a). Cumulative thermal stress is strongly associated with mortality in early migrating adult Fraser River sockeye (Hinch et al. 2012), a stock that may also have pre-existing conditions that increase their vulnerability to thermal stress.

**Flow** is also a dominant factor controlling migration due to the energetic cost of migrating against a strong current. McElroy et al. (2012) concluded that optimal swimming path in rivers will depend on the details of complex fluvial velocity fields. Hasler et al. (2012b) used electromyogram recordings to document a large amount of individual variation in the energetic cost of swimming: this was thought to arise from variation in swimming strategies, migratory behaviors, and habitat use, in addition to river environment drivers like water temperature and velocity. Bendall et al. (2012) summarize multiple models of migration movement, including flow and olfactory signals, among other factors.

## **Direct Effects of Temperature**

Papers detailing direct effects of temperature on salmonids fell into seven broader categories:

- 1) Detailed physiology
- 2) Factors affecting maximum temperature tolerance
- 3) Thermal impacts on growth and the consequences for various growth rates
- 4) Swimming performance
- 5) Behavioral consequences of high temperature exposure, such as predator avoidance behaviors and spawn timing
- 6) Use of cool water refugia
- 7) Fish communities structured by adaptations to winter temperature

Martins et al. (2012a) reviewed the full range of climate effects on growth, phenology and survival of sockeye salmon, but 83.4% of the papers reviewed focused on temperature.

Physiological responses to thermal stress include cellular effects, hormonal responses, cardiac function, reproductive capacity, gene expression, and fatty acid production (Anderson et al. 2012a, Anderson et al. 2012b, Arts et al. 2012, Casselman et al. 2012, Jeffries et al. 2012b, Keen and Gamperl 2012, Lahnsteiner and Kletzl 2012, Lahnsteiner and Mansour 2012, LeBlanc et al. 2012, Lewis et al. 2012, Reese and Williams 2012, Tan et al. 2012)

Factors that affected survival after a high temperature challenge included maternal effects (Burt et al. 2012b) and time to spawning, or maturation status—with more mature fish having much lower survival, especially females (Jeffries et al. 2012a, Martins et al. 2012b). Size effects were somewhat contradictory, with smaller fish generally being more heat tolerant, a trend that favored jacks over older males (Clark et al. 2012). However, the effect was negligible or small in several species (Recsetar et al. 2012).

Temperature has a profound impact on growth rates, partially through altered behavior and appetite suppression (Folkedal et al. 2012a, Folkedal et al. 2012b, Hevroy et al. 2012). Atlantic salmon followed different growth trajectories after exposure to different acclimate temperatures, showing a surprising long-term effect of acclimation (Finstad and Jonsson 2012). Similarly, temperatures during development produced different reaction norms for growth in cod (Hurst et al. 2012). This interannual variation in reaction norms in cod (Hurst et al. 2012) presents a significant challenge for modeling future responses to climate based on short-term experiments without a full understanding of interacting effects.

Parra et al. (2012) found that the net effect of different temperatures on growth, combined with density effects, produced predictable spatial patterns in body size. Bioenergetic models and dynamic energy-budget models are used to model the impacts of different thermal regimes (Leach et al. 2012, Nisbet et al. 2012). These approaches have led to theories of optimal energy allocation, where the choice of storage tissue versus growth varies, depending on the length of the growing season and the severity of winter (Mogensen and Post 2012). Long-term consequences of thermal-induced differences in growth rate include reduced allocation to reproduction after compensatory growth following slow growth under cool temperatures (Lee et al. 2012).

Burt et al. (2012a) found that swimming performance in fry suffered after exposure to water temperatures of 16°C, but performance was sometimes inversely related to survival. They observed a family effect on both swimming performance and survival, where a given family might have low survival but high swimming performance. Different metrics of swimming performance showed different patterns in response to increasing temperature (Yan et al. 2012). Importantly, the maximum sustainable swim speed varied with temperature, which has implications for many studies that use this metric under novel thermal conditions.

Behavioral consequences of high temperature exposure were documented for both adults and juveniles. Adult brook trout waited to spawn, sometimes reducing net redd production during warm years, in an 11-year study in New York (Warren et al. 2012). Juvenile Chinook salmon produced stronger and more variable anti-predator behaviors in a laboratory experiment after exposure to bass (Kuehne et al. 2012). Stenhouse et al. (2012) summarized literature on coho temperature preferences, defining thermal ranges from optimal to detrimental.

Use of thermal refugia as streams warm has been difficult to predict, although several studies shed light on this behavior. Hillyard and Keeley (2012) showed that Bonneville cutthroat trout used thermal refugia more in unregulated than regulated rivers, perhaps because these refugia were more abundant and closer together. Petty et al. (2012) also reported that in response to high temperatures, brook trout moving throughout a stream network in Appalachia used refugia (dependent on cover) differentially in mainstem vs. tributary habitat. Coho salmon in the Klamath River congregated around the mouths of cool-water tributaries when mainstem temperatures approach 19°C (Sutton and Soto 2012). If the refugia exceed 23°C, they were no longer used, suggesting this temperature exceeds the maximum that can provide benefit.

Finally, Shuter et al. (2012) documents adaptations to winter temperatures that

have evolved in different fish species. They emphasized that winter is an important time of year for structuring communities—thermal adaptation is not always a response to summer maximum temperatures.

## Local Adaptation

Predicting evolutionary responses to future climate change relies on various lines of evidence that include:

- 1) Study of existing phenotypic variation among populations exposed to different environmental conditions
- 2) Genomic studies revealing genetic differences among populations that might be adaptive
- 3) Measurements of current selection under different environmental conditions within populations
- 4) Optimality models that provide the theoretical basis for predicting evolutionary responses to selection under different environmental regimes

Numerous studies measured **differences in thermal tolerance among populations**. Drinan et al. (2012a) evaluated embryonic survival, development rate, and growth rate at various temperatures in five populations of westslope cutthroat trout from Montana. Although the absolute survival at the highest temperature (14°C) was not correlated with natal stream temperature, the decline in survival from 10 to 14°C was consistent with stream rank temperature. They found that populations from warmer streams had more similar survival at 10 and 14°C than those from cooler streams. In a similar study, Colorado River cutthroat trout showed different thermal maxima (Underwood et al. 2012). However, different acclimation responses appeared to mediate this discrepancy rather than to maximize possible heat tolerance under optimal acclimation conditions. Larger fish were also less heat tolerant than smaller fish (Underwood et al. 2012). A comparison of hatchery strains of brook trout also showed genetic differences in thermal tolerance (McDermid et al. 2012).

Indirect evidence of selection based on heat tolerance comes from comparisons of natural populations exposed to different thermal regimes. However, more direct study of rapid evolution to heat tolerance comes from **artificial selection**. A strain of rainbow trout has been artificially selected for heat tolerance, and several authors have studied the physiological mechanisms of this improved heat tolerance (Ojima et al. 2012, Tan et al. 2012).

Other examples of **local adaptation** to environmental conditions, specifically **flow regime**, are fin length, body depth, body length, head shape, and eye size (Drinan et

al. 2012b, Stelkens et al. 2012). Growth thresholds that determine the probability of smolting at a given age (Sogard et al. 2012), and tolerance of hypoxia (Cote et al. 2012) also appear to be locally adapted.

Distinguishing between phenotypic plasticity and genetic roots of these differences is not easy. Limborg et al. (2012) established genetic differences among populations using genomic techniques, and secondarily associated these differences with selection. Kovach et al. (2012) tracked a change over time in a genetic marker in a population of pink salmon that he associated with direct selection on run timing. Shorter-term oscillations in selection on run timing were also detected in coho (Kodama et al. 2012).

However, Miller et al. (2012b) concluded that most local adaptation in salmon stems from standing genetic variation rather than de novo mutations. This is an important result because evolution proceeds much faster by this route. Araneda et al. (2012) used comparative genetic mapping to identify specific loci associated with spawn timing in coho.

Finally, Lof et al. (Lof et al. 2012) conducted a theoretical study of selection pressures. Their model predicted that, given plasticity and a stochastic environment, a “mismatch” in the timing of breeding and prey availability is optimal when cost of overshooting is more (or less) severe than the cost of the undershooting – in other words, when the fitness curve is asymmetric.

## Invasive Species: Smallmouth Bass and American Shad

A study of the relative abundance of alien piscivores and native prey species in seven Pacific Northwest (Hughes and Herlihy 2012) rivers found that native prey abundance was inversely related alien fish abundance. They conclude that alien piscivores are present along the entire length of the Okanogan and John Day Rivers. They suspect that declines of native prey species can be attributed to these invasions, especially those of smallmouth bass.

Lawrence et al. (2012) focused specifically on smallmouth bass invasion of the John Day River. They found extensive overlap in bass and subyearling Chinook habitat in early summer. Both species shifted upstream as temperatures warmed seasonally, but a high-gradient portion of the river might limit bass. Because temperature constituted the primary determinant of bass presence, rising stream temperatures will very likely bring more bass. Restoration activities could focus specifically on maintaining bottlenecks to discourage further upstream movement of bass.

Kuehne et al. (2012) conducted experiments to evaluate bass predation on juvenile Chinook salmon at various temperatures. They found salmon had stronger and more variable antipredator responses at warmer temperatures, which they thought might limit growth.

American shad have become the most abundant migratory species in the Columbia River. Hasselman et al. (2012) considered the potential ecological effects of shad on coastal ecosystems and salmonids.

## Diseases

The *Ceratomyxa shasta* parasite is thought to be inhibiting recovery of Chinook and coho salmon in California. Although it is not currently recognized as driving significant mortality in the Columbia River, morbidity and mortality in salmon is temperature dependent, and is likely to increase as a threat in warmer climates.

Hallett et al. (2012) tested spatial and temporal dynamics of disease progression in the Klamath River. They found that coho was more sensitive than Chinook salmon to parasite density and temperature. Ray et al. (2012) tested the effect of temperature on lethality in a laboratory study, and found a positive correlation, with higher mortality and faster progression to death at higher temperatures. In the field, parasite density varied from year to year; this also influenced the timing and magnitude of field mortality. The spatial distribution of an intermediate polychaete host for the parasite also affects parasite density, and is itself sensitive to discharge rates (Malakauskas and Wilzbach 2012). Thus these studies indicate that climate change can affect disease risk through direct temperature effects on the fish, temperature effects on parasite growth rates, and through flow effects on other hosts.

## Contaminants

Studies of the impacts of contaminants covered two focal areas. First, Elliott et al. (2012) showed that mobilization of historically stored pollutants could increase through glacial melting or intensification of flooding. Cofalla et al. (2012) focused specifically on modeling managed floods that have the potential to mobilize contaminants stored in sediment; however, the same principle of increased contamination from runoff applies to climate-change induced flood intensification.

Second, contaminant effects depend strongly on the mixture of contaminants and their interaction with temperature and salinity. Brooks et al. (2012) provide an overview of interacting effects. Others compared the toxicity of different metals with temperature (Terzi and Verep 2012) and their impact on the expression of heat shock proteins (Soyut

et al. 2012). Daley et al. (2012) studied the seasonal progression of bioamplification and depletion of persistent organic pollutants in Chinook embryos and larvae. They found that the highest concentrations of persistent organic pollutants occurred in later yolk-sac larvae, before exogenous feeding.

## Marine Processes

Studies of the effects of climate variability on salmon in their marine life stage addressed salmon spatial distribution, growth, survival, and age at maturity. Highlights for Columbia River fish include greatly improved ocean models (Gruber et al. 2012) and physical-trophic links (Pool et al. 2012, Yu et al. 2012), and mixed results on the importance of freshwater conditions for marine survival of Columbia River Chinook (Haeseker et al. 2012, Holsman et al. 2012, Tomaro et al. 2012).

## Spatial Distribution

A combination of physical drivers (upwelling, current strength, temperature) and prey availability shape salmon distribution. Several papers described predictors in the California Current to differentiate the roles of physical vs. biological processes that determine juvenile salmon distribution. Yu et al. (2012) reported that the strength of along-shore currents influences the proportion of smolts that head south versus north from the Columbia River. They identified sea surface temperature, chlorophyll *a* concentration, and copepod indices as predictors of local density for yearling Chinook north of the Columbia, but chorophyll-*a* was the only strong predictor to the south. This latter result was confirmed by Pool et al. (2012), who found coho density also related to decapod larval distribution, salinity and neuston biomass (surface plankton).

Several studies clarified variation in the habitat and migration routes of Atlantic salmon (Mork et al. 2012, Sheehan et al. 2012). These studies also found that wind forcing was a primary driving factor because salmon largely followed current strength but also had a tendency to swim toward warmer and saltier water, which likely keeps them in prey-rich areas (Mork et al. 2012).

## Growth

Studies of salmon marine growth focused on biological factors, such as maternal effects (Todd et al. 2012), prey densities (Atcheson et al. 2012a, Atcheson et al. 2012b, Dixon et al. 2012, Johnson and Schindler 2012, Sturdevant et al. 2012), and competition with other salmonids (Atcheson et al. 2012b, McKinnell and Reichardt 2012). Many studies also identified significant physical predictors of salmon growth, such as sea

surface temperature (Friedland and Todd 2012), the Northern Oscillation Index (Satterthwaite et al. 2012) or climate regime (Huusko and Hyvarinen 2012, McKinnell and Reichardt 2012, Urbach et al. 2012).

In general, these studies were consistent with earlier work showing that large-scale physical drivers set up conditions for high or low productivity, depending on location and whether currents are favorable for salmon to reach prey-rich locations. These papers provide much detail on local prey condition and preference, salmon stock-specific responses to physical drivers, and strong density-dependence, principally through competition with pink salmon.

## Age at Maturation

Long-term trends in spawner age have motivated efforts to identify the factors driving these trends. Previous studies of Altantic salmon have found a correlation between sea surface temperature and age at maturity, but the direction of this effect has not consistent. This was illustrated in studies from Norway that produced opposite results. A laboratory study showed that salmon mature earlier in response to good growth in their first year and warmer winter temperatures (Jonsson et al. 2012), and an analysis of a long-term trend toward older spawners also attributed this trend to warmer water in fall (Otero et al. 2012). However, a study with a paleological perspective showed warmer climates associated with earlier maturation and lower population growth rates (Turrero et al. 2012).

Growth conditions also influence the probability of repeat spawning: the probability of Altantic salmon repeat spawning in the Miramichi River in eastern Canada was correlated with small-fish biomass in nearby ocean waters (Chaput and Benoit 2012). However, when salmon migrated to less prey-rich areas, they were less likely to spawn multiple times.

## Marine Survival

***Ocean conditions***—The relationship between good ocean growth conditions (presence of high-quality prey) and survival is complicated. Most studies have found relationships between **physical drivers** such as upwelling, which tend to transfer nutrients predictably up the food chain, and salmon growth and survival (Beaugrand and Reid 2012, Thompson et al. 2012, Tomaro et al. 2012, Trueman et al. 2012). Correlations between physical conditions and salmon survival are generally assumed to be mediated via this mechanism, that is, high nutrient levels lead to higher primary and secondary production, followed by higher rates of survival for salmon.

For example, Rupp et al. (2012) found the 4-year average PDO to be a strong predictor of coho survival, while Miller et al. (2012a) identified more diverse physical predictors of survival, and Kaeriyama et al. (2012) identified regime shifts as drivers of ocean carrying capacity. However, McKinnell and Reichardt (2012) did not see declines in survival when growth rates declined after the 1977 regime shift, possibly because intra- or inter-specific competition reversed the relationship in some years.

**Marine predation**—Several papers argued that **predator** densities are a major driving force in long-term declines in salmon abundance. For example, Mantyniemi et al. (2012) attributed salmon declines to increasing grey seal populations at longer time scales, although interannual variation at shorter time scales responded to herring abundance. Friedland et al. (2012) reported that a combination of wind patterns affected migration routes and caused the migration of pelagic piscivores (silver and red hake, *Urophycis chuss*, spiny dogfish) to overlap with that of salmon; thus they suggested declines Gulf of Maine salmon might be driven by predation.

Holsman et al. (2012) also found predator densities to be a highly weighted predictor of smolt-to-adult survival of Columbia River Chinook salmon, along with prey density, lipid-rich copepod biomass, upwelling, temperature. They also considered freshwater predictors, including river flow, whether or not a fish had been transported through the hydrosystem, and hatchery- vs. wild-origin.

**Hypoxia**—Stauffer et al. (2012) reported on **anoxic** conditions, which resulted from strong upwelling and which combined with large populations of respiring fish to drive a major fish kill in California in 2011. Their report indicates that interactions between coincidental events are likely to drive such dramatic events in the future.

**Freshwater conditions**—A long-standing question of interest is the extent to which **freshwater conditions affect marine survival**. As mentioned above, Holsman et al. (2012) found significant effects of smolt migration conditions (especially flow and whether the fish was transported) on smolt-to-adult survival of Columbia River Chinook salmon. Haeseker et al. (2012) also analyzed survival for Columbia River Chinook. They found that spill through dams and water travel time (related to total discharge) were significant predictors of estuarine and marine survival.

However, the analysis of Tomaro et al. (2012) found neither body size at time of ocean entry nor timing of ocean entry to be correlated with adult returns in Columbia River Chinook. Rather, they found marine growth rate to be the best predictor of smolt-to-adult survival.

Two studies of Atlantic salmon did attribute long-term declines in population to smolt quality, which included both smolt timing and body condition (Russell et al. 2012, Todd et al. 2012). Todd et al. (2012) tied poor smolt condition to maternal effects of poor-condition spawners, positing a multi-generational condition cascade. On a brighter note, Melnychuk et al. (2012) found that the recent trend of increased exposure to ultraviolet radiation during the freshwater life stages (from ozone depletion) did not increase marine mortality.

## Ocean Acidification: Biological Impacts

Numerous groups continue to probe biological sensitivities and evidence of negative impacts from recent trends in ocean acidification. Here I summarize only work on pteropods and copepods because of their importance to the food chain for salmon.

First, Bednarsek et al. (2012) studied shell characteristics of pteropods in the Southern Ocean and found that the shells of these planktonic mollusks already show signs of deterioration. From a laboratory study, Comeau et al. (2012a) determined the pH levels that would erode the shells of Arctic Ocean pteropods. Comeau et al. (2012b) projected that under the A2 emissions scenario, the sea snail *Limacina helicina* would be unable to calcify shells over much of the Arctic by the end of the century.

Flynn et al. (2012) pointed out that the boundary layer around plankton has much lower pH than surrounding water, and that the ability of seawater to buffer this microenvironment effect will decrease. Lischka and Riebesell (2012) monitored conditions in Svalbard during winter and concluded that winter undersaturation, in combination with low food supply, might create a population bottleneck for Arctic pteropods.

The proportion of lipid-rich copepods in the plankton community is a strong indicator of survival for Oregon coho and Columbia River Chinook salmon (see Marine Survival above). Some copepods may be affected only subtly by direct effects of pH. For example, Weydmann et al. (2012) found no effect on egg production at higher acidities, but possible delayed or reduced success in hatching for *Calanus glacialis* (Weydmann et al. 2012). However, indirect effects of acidification via the food web present an additional threat to salmon that has not previously drawn much attention. Rossoll et al. (2012) found a decline in fatty-acid production in copepods in response to changes in their diatom prey.

In considering the biological effects of ocean acidification, an important concept is that many factors interact to drive primary productivity; climate change is very likely to enhance productivity for some factors while inhibiting the productivity of others. For

example, Gao et al. (2012) described both stimulatory and inhibitory effects of changes in photosynthetically active radiation and ultraviolet exposure. They also found that stratification, freshening, and changes in metabolic rate changed with temperature and nutrient availability. They cautioned against overinterpretation of single-factor experiments.

Several authors argued that biological stressors from multiple sources need to be considered together. These authors followed up earlier work by elaborating on the utility of “oxygen and capacity-dependent thermal tolerance” as an index that integrates disparate stressors into a physiological unit. This work reinforced the concept that interactions between pollutants, hypoxia, and thermal stress will present heightened challenges to the aerobic scope and energy budget of marine organisms.

## Conservation in Practice

Beechie et al. (2012) developed a **decision support system** to guide restoration planning that incorporates climate change. They provide a list of specific restoration actions to mitigate specific climate threats projected for the Pacific Northwest, and rank these actions for their effectiveness in ameliorating their corresponding threats.

Littell et al. (2012) described **adaptation strategies**, which were identified by science-management partnerships, and which are now being piloted by the **National Forest Service**. The strategies include increasing resilience, considering limitations, prioritizing treatments from a pragmatic point of view, adaptive management, and a focus on structure and composition as a primary goal. Mainstone et al. (2012) reviewed conservation of river flows in the UK. They recommended maintaining a natural flow regime as the best defense against climate change.

A joint adaptation strategy (National Fish Wildlife and Plants Climate Adaptation Partnership 2012) was published for a number of U.S. agencies responsible for fish and wildlife (NOAA, USFWS, and a collection of state and tribal representatives). This strategy is focused on the following seven major goals and recommendations: conserving and connecting habitat, reducing non-climate stressors, enhancing management capacity, increasing awareness and motivating action, supporting adaptive management, increasing knowledge and information, and managing species and habitats. It includes specific recommendations for cold-water fish, such as reconnecting channels with floodplains and protecting deep stream beds and riparian shade cover to limit temperature increases.

James et al. (2012) discuss **ecosystem-based management in Puget Sound**. They describe the initial framework for selecting and ranking ecosystem indicators. Konrad et al. (2012) reviewed **prescribed water releases** from dams in the Sustainable Rivers Project as a conservation strategy. They found conservation benefits from these releases, but also a need for longer-term evaluations. Macdonald et al. (2012) reviewed **water temperature management** of the Nechako River. This management technique involves forecasting meteorological conditions and responding to high air temperatures with controlled water releases to avoid critical maximum water temperature during spawning migrations. They concluded that the program successfully reduced thermal exposure of fish and prevented prespawn mortality.

Cooke et al. (2012) reviewed how science has benefitted management of Fraser River sockeye. They found that recovery from fishery capture has improved and that thermal tolerance and genomic signature could be used to predict migration success. Cosenz and Williams (2012) reviewed the history of flow management in the Columbia River and the **Columbia River Treaty**.

**Economic trade-offs**—In a case study of Shasta River management, Null and Lund (2012) optimized juvenile coho salmon migrants against cost for a diverse set of restoration options constrained by a total budget. Radeloff et al. (2012) assessed the ability of four policy scenarios to affect land-use change in the U.S. by 2051. All scenarios showed dramatic increases in urban land and loss of agricultural land, but variable increases in forest, depending on the scenario. They suggest that increasing urbanization should be taken into account when planning.

**Priority of climate change in decision-making**—Ellenwood et al. (2012) evaluated decision-making processes for three major sectors in Colorado: forests, biofuels, and grazing. Their analysis revealed that although there is interest in and discussion of climate change issues, threats from climate remain a lower priority than other issues informing these processes. From a more general perspective on climate science, Lemos et al. (2012) discussed the gap between information that scientists produce and believe to be useful vs. information that decision-makers actually use. They focused on user perceptions of how well the information fits, interplay with existing types of information, and the quality of the interaction between scientists and users. They recommended varying levels of interaction, customization of information, and repackaging of existing information to meet multiple user needs.

**General conservation principles**—To inform efforts in conserving native trout, Hakk and Williams (2012) recommended protection of genetically pure populations across the historical range, restoration of life-history diversity, and protection of large,

stronghold populations. They advised that larger populations are needed for long-term persistence. Conservation in coastal zones is complicated by multiple relevant spatial and temporal scales, spatially diffuse footprints from human action, and the potential for large consequences from small human decisions (Swaney et al. 2012)

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# Glossary

A1B, A2, B1, B2	Carbon emission scenarios from AR4
AR4	4 <sup>th</sup> IPCC Assessment Report
AOGCM	Coupled Atmosphere-Ocean General Circulation Model
AR5	5 <sup>th</sup> IPCC Assessment Report
CCE	California Current Ecosystem
CMIP3	Coupled Model Intercomparison Project Phase 3
CMIP5	Coupled Model Intercomparison Project Phase 5
ENSO	El Niño-Southern Oscillation
GCM	General Circulation Model/Global Climate Model
IPCC	Intergovernmental Panel on Climate Change
NPGO	North Pacific Gyre Oscillation
PDO	Pacific Decadal Oscillation
PgC	Petagram Carbon
RCM	Regional climate model
RCP	Representative concentration pathways (Emissions scenarios for AR5)
ROMS	Regional Ocean Modeling System
VIC	Variable infiltration capacity model
WRF	Weather Research and Forecasting model