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# Impacts of Climate Change on Salmon of the Pacific Northwest

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*A review of the scientific literature published in 2014*

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# Highlights

## Observations of Climate in 2014

The most important observations of recent climate trends reveal that 2014 was the hottest year on record globally, terrestrially, and in the ocean (Blunden and Arndt 2015). The California Current shifted from a highly productive La Niña state in 2013 to a less productive, anomalously warm state by fall 2014, with striking warm-ocean anomalies in some areas (Leising et al. 2014). The “2014 warm anomaly” or “the blob” (Bond et al. 2015) consisted of an unusually large area of warm sea surface temperatures that expanded from the Gulf of Alaska in winter to encompass most of the California Current in summer and fall 2014. Numerous unusual biological sightings indicated a year of marked climate anomalies.

At the global level, careful attention has been devoted to attribution of temperature trends to natural variability vs. increasing anthropogenic input of CO<sub>2</sub>, and a wide consensus has emerged that the latter is necessary to explain recent observations. However, attribution is notoriously difficult at the regional level, where natural variability plays a much larger role. Numerous retrospective analyses at all spatial scales have documented rising ocean temperatures. Nevertheless, a provocative analysis (Johnstone and Mantua 2014a) found that the long-term trend in sea surface temperature in the northeast Pacific is likely driven mostly by natural variability in winds. These authors did not deny that ongoing increases in CO<sub>2</sub> will raise sea surface temperatures in the future. Rather, they emphasized that natural variability extends beyond decadal patterns to include low-frequency phenomena that we cannot fully understand or predict, such as the observed trend in winds over the Pacific.

Similarly, in California over half of the state was classified as being in “extraordinary drought” status, yet the high-pressure phenomenon driving this 3-year drought appears largely due to natural variability in atmosphere-ocean dynamics (Seager et al. 2014). However, the high temperatures that exacerbated this drought are likely to have been influenced by anthropogenic factors (Funk et al. 2014; Swain et al. 2014; Wang and Schubert 2014).

A clear impact of recent ocean acidification on pteropod shell formation and survival was demonstrated by field evidence of extensive shell dissolution in undersaturated water off the coast of Washington, Oregon and California (Bednarsek et al. 2014), supported by an experimental test of causation (Busch et al. 2014). Oceanographic models continue to improve our understanding of upwelling (Jacox et al. 2014), how upwelling influences ocean acidification (Lachkar 2014), and how rising

global temperatures affect both upwelling (Sydeman et al. 2014a) and climate oscillations such as the El Niño Southern Oscillation (ENSO, Ohba et al. 2014).

## **Recent Behavioral Changes in Salmon**

Several observations have documented behavioral shifts in salmon that are likely due to warming climate trends over the past half century. In fall Chinook salmon from the Hanford Reach of the Columbia River, spawn date has shifted one week later since 1950, during a 2°C period of warming (Hayes et al. 2014). Salmon from 67 rivers on both sides of the Atlantic have shifted smolt timing approximately 2.5 days earlier/decade (Otero et al. 2014). Unusual catches of Atlantic salmon indicate range shifts in the north Atlantic have reached as far north as Svalbard (Jensen et al. 2014).

## **New Projected Responses to Climate Change**

New projections of specific impacts of climate change on salmon were conducted in the Yakima River Basin (Hardiman and Mesa 2014; Hatten et al. 2014). The ability of habitat restoration to ameliorate bass expansion and maintain Chinook habitat was explored in the John Day Basin (Lawrence et al. 2014). Even hatcheries may face shortages of cool water and undesirable consequences of rearing juveniles in warm water (Hanson and Peterson 2014).

Hydrological downscaling of climate projections for the whole Pacific Northwest have been completed (Tohver et al. 2014) in addition to more basin-specific analyses (Leibowitz et al. 2014). These and other analyses project widespread conversion of snow-dominated basins to transitional and rain-dominated basins, and increased severity of low flows due to higher summer temperatures (Sawaske and Freyberg 2014). A number of studies of stream temperature found strong bias in relation to air temperature that was not accounted for in most statistical approaches (Arismendi et al. 2014; Luce et al. 2014). Fairly complex landscape characterizations are often necessary for accurate predictions of stream temperature.

## **Continuing Research on Salmon Sensitivity and Adaptability to Climate**

Ongoing research explores the influence of temperature and flow on migration timing and growth, with population-specific responses thought to enhance stability in some metapopulations. However, studies of population abundance cycles in Fraser River sockeye suggest that such responses may be a sign of populations near threshold levels for viability, and might indicate these populations are near collapse (White et al. 2014). Analyses of the evolutionary potential of enhanced thermal tolerance produced mixed results, showing little potential plasticity in cardiac tolerance, but greater possibilities in other phenotypic aspects, such as shifts in egg size due to maternal or epigenetic effects.

Studies in 2014 elucidated more fully how disease and contaminant threats might be exacerbated by climate change. These included reviews on the temperature preferences of major salmon pathogens and thermally optimal outbreak conditions (Hanson and Peterson 2014), and on new techniques for identifying disease agents in wild salmon populations (Miller et al. 2014b). Experimental studies document a synergistic effect of temperature on heavy metal toxicity (Sappal et al. 2014) and in combinations of pesticides that are much more realistic for field conditions (Dietrich et al. 2014; Laetz et al. 2014).

Salmon marine survival continues to be analyzed in relation to major ocean indicators, showing both strong patterns and changes in these relationships over time (Litzow et al. 2014; Miller et al. 2014a; Stachura et al. 2014; Williams et al. 2014). Freshwater growth conditions affect timing of marine entry, estuary residence periods, size-selective survival in some cases, and the propensity to delay or abort the marine stage altogether, especially in steelhead.

In conclusion, new literature supports previous concerns that natural climatic variability can amplify and exacerbate long-term climate change impacts. Recent estimates of rates of climate change are similar to those previously published. Anthropogenic climate change will likely cause moderate to severe declines in most west coast 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). Salmon will adapt their behavior and possibly physiology, but these responses are unlikely to prevent long-term declines.



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# Objective and Methods

The goal of this review was to identify literature published in 2014 that is most relevant to prediction and mitigation of climate change impacts on Columbia River salmon listed under the Endangered Species Act. Because almost anything that affects salmon is 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 reports outside that database. We sought to capture the most relevant papers by combining climatic and salmonid terms in search criteria. This excluded studies of general principles demonstrated in other taxa or within a broader context. In total, we reviewed over 600 papers, 170 of which were included in this summary.

Literature searches were conducted in June 2015 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 2014, plus:

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

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

<sup>2</sup> Boolean operators used in the search are shown in boldface.



This review is presented in two major parts, with the first considering changes to the physical environmental conditions that are both important to salmon and projected to change with climate. Such conditions include air temperature, precipitation, snowpack, stream flow, stream temperature, and ocean conditions. We describe projections driven by global climate model (GCM) simulations, as well as historical trends and relationships among these environmental conditions. In the second part, we summarize the literature on responses of salmon to these environmental conditions, both projected and retrospective, in freshwater and marine environments.

# Physical Processes of Climate Change

## Annual Observations from 2014

Globally, 2014 was the hottest year on record both on land and in the ocean, according to the National Climatic Data Center annual report, *State of the Climate in 2014* (Blunden and Arndt 2015). All 10 of the warmest years on record have occurred since 1998. Compared with the 20<sup>th</sup> century average, 2014 was warmer by 0.69°C globally, 0.57°C in the ocean, and 1°C on land. This record is especially striking given the neutral conditions of El Niño Southern Oscillation (ENSO) during most of the year.

Global precipitation was average, although a long-term drought continues in the western U.S. Studies on the “hiatus,” or reduced slope of warming since 2001, indicate a variety of possible explanations, including strengthening of Pacific trade winds, which increased subsurface heat uptake, and tropical upwelling, which cools other regions (England et al. 2014).

The synthesis report of a variety of data collected throughout the California Current described general features of 2013-2014 (Leising et al. 2014). The region shifted from a highly productive La Niña state in 2013 to a warm state with some similarities to a weak El Niño state by the end of 2014. The Pacific Decadal Oscillation, North Pacific Gyre Oscillation and Multivariate ENSO Index (MEI) all changed phase in winter 2013-2014, indicating warmer conditions and reduced subarctic influences. Major regions such as the Bering Sea, Gulf of Alaska, and areas offshore from southern California, have been warmer than expected and atypical for the ENSO state; these conditions may reduce fish production.

A warm anomaly in the Northeast Pacific, termed “the blob” (Bond et al. 2015) developed during winter 2013-2014 (October through January). Within “the blob,” sea level pressure was much higher than normal, extending the 2012-2013 anomaly to new levels. Comparable anomalies have not been seen since at least the 1980s, if not 1900. February sea surface temperature in “the blob” was 2.5°C above normal, with the largest anomalies being 3 standard deviations above normal. The upwelling zone near the coast remained cool until “the blob” extended into the coastal zone in May 2014.

## National Climate Assessment

The United States Global Change Research Program completed their third national climate assessment (Melillo et al. 2014). This report reviews the ever-increasing evidence of climate warming that bears the signature of rising concentrations of greenhouse gas emissions. Extreme heat and precipitation events are increasing, summer arctic sea ice is declining sharply, and sea level is rising. These trends are expected to continue.

Within the national assessment report, regional chapters for the northwest (Mote et al. 2014) and southwest U.S. (Garfin et al. 2014) detail some of the most relevant information for anthropogenic interests as well as for Pacific salmon. As discussed in the next section, the main hydrological implications are a shift in timing of streamflow. As snowpack declines, warmer summer temperatures combined with reduced water storage will lead to lower minimum flows in summer and less water available for human needs. Widespread ecosystem shifts are expected due to disturbances from more wildfires, insect outbreaks, droughts, and tree diseases. Erosion and flooding in coastal areas are damaging infrastructure and are projected to increase.

Coastal weather can differ somewhat from region-wide projections, as explored in a study of a recent cooling trend along the central California coast (Potter 2014). Potter proposed that greater warming in the California Central Valley has increased on-shore winds along the coast, which have caused local cooling. Regional climate effects in California were also explored by Killam et al. (2014) who found that between 1925 and 2007, precipitation increased in northern and central California but decreased in southern areas. These precipitation patterns were attributed largely to the Pacific Decadal Oscillation and ENSO. Climate projections for the San Francisco Bay area forecast conditions that favor invasive fish species over native species (Quiñones and Moyle 2014), with declines exacerbated by the greater vulnerability of native species to existing anthropogenic stressors.

## Hydrological Changes in the Pacific Northwest

### Columbia Basin

The Climate Impacts Group at the University of Washington reported their analysis of projected climate impacts on hydrology throughout the Columbia Basin (Tohver et al. 2014). This analysis was based on the Global Climate Models from the

*Coupled Model Intercomparison Project, phase 3 (CMIP3)*. This work projects major shifts from snow- to rain-dominated basins: “By the 2080s for the A1B scenario, there is a complete loss of [snow-dominated] basins in the Cascades and the U.S. portion of the Rockies, and only a few rain [transitional] basins remain at the highest elevations in the U.S.”

Tohver et al. (2014) predict increasing risk of both 20-year and 100-year floods across nearly the entire Columbia River basin. This risk stems from enhanced cool-season precipitation in all basin types. Decreases in summer low flows are also projected for most of the Pacific Northwest, except the headwaters of the Columbia River. Low flows result from reduced natural storage from snowpack, reduced summer precipitation, and higher evapotranspiration from warmer summer temperatures. Rain-dominated and transitional basins show the largest effects, mainly because the most arid regions are already very dry.

Similar results were predicted in an analysis of climate change impacts on hydrological landscape classifications in Oregon (Leibowitz et al. 2014). This analysis projected a state-wide shift in areal extent of snow-dominated basins from 13 to 4-6% by the 2080s, with a similar outcome under nearly all climate scenarios. This represents a 56-68% reduction. In rain-dominated basins such as the Siletz, increased precipitation leads to higher water levels in fall and winter; however, in snow-dominated basins such as the Sandy and Middle Fork John Day, spring stream flow is altered to an extent that changes the hydrograph enormously.

A study of the Tucannon River Basin (Praskievicz and Bartlein 2014) produced a similar result, in which the current transitional regime in this basin (winter rain peak and a spring snowmelt pulse) is projected to shift to an entirely rain-dominated hydrology. Across the mountainous western United States, the most heavily snow-dominated basins will reduce the duration of snowfall (when precipitation consistently falls as snow rather than rain) from 5 months per year to 3 months per year, when comparing 1979-2012 climate with a 2036-2065 climate, averaged across 20 global climate models from the *Coupled Model Intercomparison Project, phase 5* under the Representative Concentration Pathway (RCP) 8.5 scenario (Klos et al. 2014). The geographic area over which winter (December through February) precipitation consistently falls as snow is reduced by 30%.

Earlier and more intense storms may increase flood risk substantially in the Pacific Northwest by 2040-2069, based on a regional climate model (Salathe et al. 2014). Likewise, a NOAA technical report on sea level rise and flood frequency predicts increased in flooding in California (Sweet et al. 2014).

The North Cascadia Adaptation Partnership reviews many of these same

projections for the North Cascades National Park Complex (Raymond et al. 2014). They focus on risks from road washout, which effect both humans and sediment load on fish streams, high temperature stress for fish and trees, and widespread shifts in species distributions, habitat connectivity and ecosystem structure. They recommend a path toward adaptation.

In their retrospective analyses, Sawaske and Freyberg (2014) developed a new technique for characterizing annual low flows. This technique focuses on the pattern of low flow recession during the dry season, instead of the more typical approach of absolute minimum flows. Their results reinforce previous observations of negative trends in baseflow over the past 40-80 years throughout many rain-dominated basins of coastal Washington, Oregon, and California. This approach is better able to attribute declines in baseflow due to increased evapotranspiration from higher summer air temperatures vs. those that reflect precipitation trends.

In a retrospective study of the Salmon River Basin, Idaho, Tang et al. (2014) found soil moisture (and hence drought) to be strongly correlated with the Pacific Decadal Oscillation and Atlantic Multidecadal Oscillation.

## **Puget Sound**

A model of estuary dynamics in the Snohomish River estuary, Washington, found that the extent to which salt water will intrude further upstream depends on land-use and land cover changes, and not just climate change alone (Yang et al. 2015). Climate change will cause the intrusion point to shift both up and downstream, depending on flow, whereas it shifts downstream only when changes in land cover are taken into account.

## **Fraser River**

Historical trends in temperature and flow for the Fraser River were nicely analyzed by (Riche et al. 2014). They reviewed time-series for a wide range of physical characteristics (variability and trends over the past 50 years) of the Strait of Georgia. Riche et al. (2014) found that summer temperature in the Fraser River increased markedly around 1986, although imposition of a linear regression from 1953 to 2006 indicated a trend of  $3.3 \pm 1.7^{\circ}\text{C}$  per century. Flow declined during summer but increased at other times of year, producing no net annual change but consistent with a shift to reduced input from snowmelt. They also document declines in pH in the Strait of Georgia. Similar results were shown by Kang et al. (2014), who found a decrease of 19% in the contribution of snow to runoff measured at Hope from 1949 to 2006, and no trend in precipitation forcing.

## **Stream Temperature Modeling**

An analysis of climate in the Pacific Northwest from 1901 to 2012 showed a

mean annual air temperature increase of 0.6-0.8°C, a longer freeze-free season, and increased potential drying from evapotranspiration (Abatzoglou et al. 2014b). The temperature increase was distributed across seasons with precipitation reduced in summer and fall but increased in spring, which cooled slightly. They attributed the long-term warming to rising greenhouse gases (Abatzoglou et al. 2014b).

A major hindrance in projecting salmon responses to climate change stems from the difficulty in translating projections of future air temperatures to stream temperatures. Although the physical mechanisms that govern temperature are well understood, parameterizing these physical models across a broad landscape is not feasible, and many assumptions are required to extrapolate from observed to unmeasured streams. Arismendi et al. (2014) showed that correlation methods predicting stream temperatures from air temperatures often fail, especially in regulated streams and especially when extrapolated outside the time frame during which streams were measured.

Luce et al. (2014) examined empirical relationships indicating that cold streams, specifically, were much less sensitive to air temperature than warmer streams. In the Pacific Northwest, this may represent an advantage to salmon that depend on the coldest water. Bal et al. (2014) presented improved statistical methods for translating air temperatures to stream temperatures, using time series in models that incorporated thermal oscillation at many time scales. This technique may aid water temperature forecasts in the near term. An effort to characterize the impact of urban development on stream temperature in Puget Sound, Washington (Booth et al. 2014), found that development and riparian shading had similar importance to other watershed characteristics (such as watershed area, soil composition, and lake area). Studies of the influence of cool water springs upstream of the Shasta River, California, found that input from these springs stayed cool at night, but warmed during the day to produce an oscillating pattern downstream (Nichols et al. 2014).

## **Thermal Refugia**

Thermal refugia are of particular management concern for salmonids, but they can be difficult to model when they are influenced by groundwater intrusion, which is not well mapped. In an analysis on the impact of climate change on groundwater dynamics, Kurylyl et al. (Kurylyk et al. 2014b) found complex interactions at play between groundwater exchange and aquifer dimensions. Tips for maintaining and constructing thermal refugia were presented by Kurylyl et al. (2014a).

## Forecasting

Hague and Patterson (2014) attempted to forecast near-term water temperatures for fisheries management in the Fraser River. They found that uncertainty in air temperature predictions greatly reduced the utility of sophisticated modeling approaches, such that simple historical temperature trends were equally good at 10-d forecasts. However, to forecast the most damaging extreme high water temperatures, models that included air temperature forecasts performed much better than other models (Hague and Patterson 2014).

## Ocean Conditions

### Temperature

A novel index identified by Johnstone and Mantua (2014a) links the long-term warming trend in the northeast Pacific (1900-2012) to a regional shift in winds rather than to anthropogenic climate forcing. A response (Abatzoglou et al. 2014a) questioned whether this resulted from an artifact of the sea level pressure data used, but exploration of additional datasets supported the original results (Johnstone and Mantua 2014b). A separate analysis documenting historical sea surface temperature trends around Vancouver Island found an average rate of warming of 0.9°C per century over the past 70-80 years, based on lighthouse records of temperature and salinity (Cummins and Masson 2014).

### Hypoxia

A study of dissolved oxygen concentrations in the North Pacific since 1850 (Deutsch et al. 2014) showed a decline over the 20<sup>th</sup> century that accelerated in 1990. This decline was attributed primarily to changes in tropical Pacific winds. Because the anomalies in wind patterns are not an expected effect of anthropogenic climate change, these changes were not necessarily expected to continue through the 21<sup>st</sup> century. Another study analyzing profile cores of oxygen-sensitive metals suggests that modern hypoxic conditions have not occurred in this region for hundreds to thousands of years (Erhardt et al. 2014).

### Upwelling

Upwelling is one of the most important processes determining productivity in the California Current, and one of the most difficult to model and predict under climate change scenarios. One theory states that the intensity of upwelling will increase with climate change, as the gradient increases between land and ocean temperatures.



Sydeman et al. (2014a) support this hypothesis, pointing to studies that show intensification in many upwelling systems, including the California Current. Furthermore, within each upwelling region, trends were strongest at highest latitudes, where the greatest warming is expected. The California and Humboldt Currents showed the strongest latitudinal trends in intensification.

The intensity of upwelling is important not only for local productivity, but also because it influences rates of ocean acidification. In the California Current, the volume of water undersaturated with aragonite nearly triples when wind stress doubles, in contrast to the Canary Current, which shows the opposite effect (Lachkar 2014).

However, upwelling is spatially complicated, as demonstrated in an analysis by Jacox et al. (2014). They found that within the California Current specifically, upwelling trends were positive within 50 km of the coast but were negative 50-200 m offshore, and the offshore signal was out of phase with the near-shore signal.

A long-term historical perspective was provided by Black et al. (2014) in their reanalysis of about 600 years of data for the California Current region. They showed that recent observation of winter downwelling-favorable winds was very unusual, having appeared only twice before in the historical record. These winds have made winter upwelling unusually variable in the recent past (Black et al. 2014).

## **El Niño Southern Oscillation (ENSO)**

Dynamics of the ENSO are also very difficult to model with global climate models, and different models often produce different results. Nonetheless, using the community climate system model (CCSM, version 4), Ohba et al. (2014) found that under high CO<sub>2</sub> conditions, the amplitude of ENSO was reduced due to a shallower vertical temperature gradient, with weaker upwelling in the tropical eastern Pacific.

In turn, ENSO strongly influences ocean pH. By studying time series of pH data in the tropical Pacific from 1997 to 2011, Sutton et al. (2014) found strong effects of anthropogenic CO<sub>2</sub> increases, modified by annual variation due to ENSO. Strong easterly trade winds during La Niña drive upwelling of acidic water, which affects a large area. The recent increased frequency of La Niña events accounts for some of the longer linear trend in pH (-0.0018 to -0.0026 per year).

## **Ocean Acidification**

Ocean acidification is a major concern in both the California Current and Puget Sound, although potential impacts on salmon are unclear. A new consortium, the Ocean

Margin Ecosystems Group for Acidification Studies (OMEGAS), is working to characterize physical and biological sensitivity to pH in the California Current. Work to date includes establishment of a sensor arrays and studies of key benthic invertebrates (Hofmann et al. 2014). Many of the basic processes are described by Waldbusser and Salisbury (2014).

Bednarsek (2014) documented severe damage to pteropod shell condition in the top 100 m of the California Current in 2011. Experiments by Busch (2014) demonstrated that this response directly reflects the increasing percentage of water undersaturated with respect to aragonite. Spatial and temporal characterization of current pH levels in Puget Sound were conducted by Reum et al. (2014). A nice review of research linking the impact of pCO<sub>2</sub> on physiological mechanisms to organism-level endpoints (e.g., behaviors, neurosensory capability, metabolism, etc.) found multiple pathways and physiological trade-offs occur in this process (Heuer and Grosell 2014). These complications make prediction of long-term fitness consequences difficult to predict based on short-term physiological responses to low pH.

Strong et al. (2014) present a very clear overview of ocean acidification with convenient tables linking specific mechanisms driving acidification at global to local scales (e.g., anthropogenic nutrients that enhance eutrophication) with links to local management actions that can mitigate or adapt to these drivers (e.g., pollution control). They list potential policy actions that help mitigation or adaptation at various scales, and their cost.

# Salmon Responses to Climate Change

## Projected Responses

In the 2014 literature on salmon freshwater life stages, projections of response to climate change focused on populations of the mid-Columbia Basin—specifically those of the Yakima and John Day River Basins, as well as those at the Winthrop National Fish Hatchery.

A special issue of *Climatic Change* explores the cultural importance of salmon; climate change scenarios; and responses of coho, Chinook, and steelhead in the Yakima Basin, Washington. Hatten et al. (2014) reported the most vulnerable of these salmon were Chinook and coho at the fry and juvenile stages; both species lost rearing habitat in most scenarios. A bioenergetics model of steelhead in the warmer scenarios by Hardiman and Mesa (2014) found that juvenile growth tended to increase in spring but slow in summer.

In the John Day River, Lawrence et al. (2014) explored smallmouth bass range expansions, within the context of habitat restoration and climate change scenarios. In the warm scenarios, bass tended to overlap increasingly with juvenile Chinook salmon. By the 2080s, overlap between bass and subyearling Chinook habitat in early summer could double in the North Fork John Day and quadruple in the Middle Fork. In late summer, Chinook may be thermally excluded from the Middle Fork. Restoration has the potential to reduce stream temperature, particularly in the Middle Fork, where some Chinook habitat could be maintained and overlap with bass could be reduced.

In their analysis of climate change impacts to Winthrop Hatchery fish, Hanson and Peterson (2014) found that warmer temperatures in the Wenatchee River may slightly increase stress for juveniles. Combined with summer water limitations, this warming could impede the ability of hatcheries to reach production goals without proactive management. Although the conditions modeled under the 2040s A1B emissions scenario generally fell within physiological tolerances, these authors anticipated slightly more stress and an increased probability of epizootic outbreaks.

This expectation was highlighted in a table of optimal temperature ranges and outbreak conditions for important salmon pathogens (Hanson and Peterson 2014, Table 3). Higher rearing temperatures may also increase residualism and early maturation, and may present difficulty in meeting mandated production goals. Outside the hatchery,

reduced summer flows may diminish rearing conditions. However, management solutions were suggested that could alleviate these outcomes.

A number of analyses projected responses to climate change for salmon outside the Pacific Northwest. These included coho in Alaska (Leppi et al. 2014) and chum in Japan (Kaeriyama et al. 2014), as well as non-anadromous trout in the Canadian Rockies (MacDonald et al. 2014) and central Idaho (Loinaz et al. 2014). Many places show mixed positive and negative effects, consistent with studies within the Columbia Basin. However, there was a preponderance of negative effects among these analyses, especially in the case of scour in Alaska (Leppi et al. 2014; Shanley and Albert 2014) and of temperature effects elsewhere.

Doney et al. (2014) produced a straightforward overview of general projected impacts on the world's oceans from rising greenhouse gases in the atmosphere. They explain the basic processes of acidification, deoxygenation, warming, and spatial variation in phytoplankton productivity—namely, expansion of low-productivity tropical regions with increased productivity at high latitudes. Some higher-level trophic responses were also covered.

Okey et al. (2014) summarize the history and projected impacts of climate change on Canadian Pacific ecosystems, which support Columbia River salmon during their marine migration. Their review describes the effects on marine life from changes in temperature, precipitation and hydrology, oxygen decreases, salinity and stratification, pH and sea level, and oceanographic oscillations. Okey et al. (2014) report a 1°C increase in sea-surface temperature in the Strait of Georgia during the last century and a 22% decrease in dissolved oxygen in the North Pacific over the past 50 years (at 100-400 m). They project declines in all Fraser river salmon stocks based on earlier work, with sockeye, pink, and chum declining more than coho or Chinook. They project increases in more northerly stocks and newly habitable streams in the Arctic.

## Observations of Recent Responses to Long-term Trends

The primary response expected to facilitate adaptation to climate change in salmon is a change in phenology—mainly through altered migration and spawn timing. These traits are often considered the essential characteristic that differentiates between salmon populations and that has allowed them to survive climate change in the past. Spawn timing is particularly important as the primary mechanism of reproductive isolation, which allows local adaptation and diversification within river basins. Spawn timing reflects a critical balance between egg vulnerability and adult tolerance of high summer temperatures.

Eggs have the lowest heat tolerance of any life stage (10°C lower than adults) and rely entirely on placement and timing by adults to avoid hypoxia, dewatering, scour, and heat stress. Spawn timing also determines emergence timing because developmental rates are closely tied to temperature. Thus changes in spawn date, as observed for fall Chinook in the Columbia River, are among the most important indicators of climate change. Smolt and adult migration timing are more plastic than spawn timing, but these traits also may indicate a clear response to changes in environmental conditions.

### Spawn Date

In the Hanford reach of the Columbia River, fall Chinook salmon median spawn timing shifted by one week from 1950 to 2010, the same period during which water temperature on 1 October increased by nearly 2°C (Hayes et al. 2014). This trend was consistent with the response expected from a warming water temperature cue, although causation in this case was confounded by changes in dam operation (Hayes et al. 2014).

### Smolt Date

Otero et al. (2014) analyzed variation in the dates of Atlantic salmon downstream migration for 67 rivers over the past 50 years. They found that migrations were earlier in the east than the west, but also that smolt migration timing was positively associated with increases in freshwater and sea-surface temperatures. They observed a long-term trend of advanced timing in smolt migration (2.5 d per decade), a shift in phenology that co-occurred with recent indicators of climate change, such as increased air, river, and ocean temperatures (Otero et al. 2014).

### Colonization/Range Shift

Generally, the colonization abilities of salmon are thought to be very strong. In Washington State, coho salmon quickly recolonized the upper Cedar River after a ladder was installed to allow fish passage through Landsburg Diversion Dam (Buehrens et al.

2014). In catches from the Arctic Ocean off the coast of Svalbard, (Jensen et al. 2014) found increasing proportions of Atlantic salmon. They interpreted this trend as suggestive of a general northward range shift in response to climate change, similar to that seen in other fish species.

Salmonid behavior in general is very sensitive to environmental conditions. This was clearly demonstrated in the upstream movement of rainbow trout into cutthroat trout habitat, a response driven by increasing summer temperature and declining spring precipitation (Muhlfeld et al. 2014). This invasion caused extensive hybridization, which is threatening cutthroat trout (Muhlfeld et al. 2014).

## **Salmon Sensitivity to Temperature and Flow**

### **Growth and Survival**

Smolt timing generally depends on growth conditions in freshwater. Growth, in turn, depends both on prey availability and temperature. Prey availability and temperature vary, both spatially and temporally. Furthermore, prey abundance varies with temperature, and this relationship might differ by stream. Such interactions complicate efforts to parse the net effects of warming on growth.

Thorson et al. (2014) explore this complexity under the premise that all of this localized variability essentially averages out at the population or metapopulation level—at least under the current climate. Thorson et al. (2014) analyzed temporal and spatial patterns of adult-to-parr production in 15 streams in the Snake River, Idaho. They found evidence for synchronous year effects shared by populations. They also found population effects that were consistent over time. This spatial heterogeneity in productivity reduced temporal synchrony among populations. The interaction between these factors was described in terms of the “portfolio effect” of asynchrony among populations, which stabilized the metapopulation as a whole.

Griffiths et al. (2014) also demonstrated population differences in juvenile growth response to annual variation in weather for Alaskan sockeye populations from different lakes within a watershed. Kovach et al. (2014) found similar variation in juvenile response between sockeye and coho.

Not all populations show growth responses to temperature variation, however. Chittaro et al. (2014) examined otolith rings to compare growth rates of spring/summer Chinook from four streams in the Salmon River, Idaho. Using a bioenergetics model, they showed that fish from these streams did not differ substantially in growth rate,

despite marked differences in temperature, and that this lack of variation could be explained by differences in consumption. Thus prey availability and temperature essentially cancelled each other out in terms of their influence on growth.

Explorations of brook trout in Appalachia (Petty et al. 2014) and brook charr in Maine (Kazyak et al. 2014) also explored interactions among temperature, diet, competition, and growth. A review of how competition and dominance hierarchies interact with growth potential was conducted by (Fausch 2014).

Wildfires further conflate shifts in temperature and productivity. Such fires clear riparian vegetation, which in turn raises stream temperature and causes bursts in nutrient input through erosion. Wildfires have increased in North America in recent decades, as expected from increasing summer temperatures and drought. Beakes et al. (2014) analyzed diet and bioenergetics of steelhead in a California stream and found that increased temperature following a burn was not compensated by additional prey availability; thus fire resulted in a net decline in salmon biomass in this stream (Beakes et al. 2014).

## **Thermoregulation**

A study of the behavior of juvenile steelhead on the Klamath River found that fish moved into thermal refugia when mainstem temperatures reached 22-23°C (Brewitt and Danner 2014).

## **Smolting**

The smolt life stage often proves most sensitive to climatic variation. Smolt responses to climate and growth conditions include age and timing of smoltification, and the proportion of a population that remains as parr. One important theme in 2014 was that many populations show much more diverse behavior than generally assumed. Reports of such behavior include extensive downstream movement throughout the year in juvenile coho and chinook (Shrimpton et al. 2014), widespread use of estuarine habitat over winter in coho (Craig et al. 2014; Jones et al. 2014; Neher et al. 2014), and unusual fall spawning in coastal cutthroat trout (McMillan et al. 2014).

Environmental influences on the smolt stage were described in detail for Chinook in the Stanislaus River, California by Zeug et al. (2014). They examined fish size, age and survival as a function of temperature, flow and density. Similarly, Spence and Dick (2014) found smolt migration timing related to temperature, flow, moon phase, and photoperiod for coho populations in Oregon, British Columbia and Alaska. Other authors further explored smolt physiology and cues in Atlantic salmon (Handeland et al. 2014a; Handeland et al. 2014b; Taal et al. 2014; Zydlewski et al. 2014).

A review of the literature on anadromy vs. residency produced a conceptual model of Pacific and Atlantic salmonids generally (Sloat et al. 2014), and concluded in part that freshwater growth responses related to temperature may differ considerably from those related to food availability.

An interesting variation occurs in the Klamath River, where steelhead return and spawn the same year as they migrated seaward. A study of these precocious spawners concluded that this adaptive tactic was triggered by high freshwater growth rates (Hodge et al. 2014). Sloat and Reeves (2014) reported that rates of freshwater maturation decreased inversely with temperature for steelhead reared under differing thermal regimes. Doctor et al. (2014) explored the relative contribution of genetics and plasticity to growth and maturation responses to environmental conditions by comparing two steelhead populations from Hood Canal, Washington. They found high heritabilities, and hence potential for selection, but concluded that most observed differences between populations could be explained by plastic responses. Taken together, these findings represent the potential for climate to impact the adaptive capability of steelhead.

Temperature gradients were also found to correlate with early growth rates and the frequency of migratory tactics in masu salmon (Morita et al. 2014). However, the propensity to migrate can persist in populations despite presumably very strong selection against it in the form of low marine survival (Fraser 2014). Doctor et al (2014) parsed out plastic and genetic contributions to growth rates and the propensity to smolt or mature at a given age in a controlled experiment with Washington steelhead. They found genetic differences among populations and high heritability in these traits, but also that plastic effects were sufficient to explain observed differences among Puget Sound populations.

Over much longer periods of climatic change, such as the Eocene-Oligocene transition, salmonid diversification rates were thought to be quite high, probably coinciding with changes in rates of anadromy (Macqueen and Johnston 2014). These authors attributed rapid evolution to climate change rather than whole-genome duplication.

## Estuary Usage

In 2014, several papers explored the use of estuaries, particularly by coho. Although these studies do not directly relate estuary usage to environmental conditions, they present important baseline information for planning how climate change in estuaries might ultimately influence fish behavior patterns. The amount of time spent in estuaries, and thus likely the importance of estuarine conditions, varies enormously among salmon species and populations. The use of Columbia estuary wetlands by subyearling coho has



likely been underestimated, but subyearling coho were found to utilize estuary rearing areas extensively and had high growth rates in wetland habitats (Craig et al. 2014).

Subyearling coho from the Salmon River, Oregon also displayed extensive estuary usage, including overwintering (Jones et al. 2014). Juveniles employing estuaries extensively represent a substantial proportion of the adult spawning population (20-35%), and thus play an important role in population dynamics. Similar behavior was displayed by a coho population near Homer, Alaska (Neher et al. 2014). Steelhead, on the other hand, move quickly offshore and find optimal conditions for feeding and growth in offshore rather than estuarine or near shore regions (Daly et al. 2014). Temperatures in the Columbia River estuary often exceed the lower bound of the range considered lethal for salmon (23-25°C). Roegner and Teel (2014) reported that in tidal freshwater estuarine habitats, salmon densities declined at temperatures up to 23.5°C, but negative effects on growth and condition were not apparent.

## **Migration Survival**

Both juvenile and adult salmonids must respond to environmental cues and challenges during migration. Temperature and flow characteristics each influence the ability of fish to pass a dam (Goodwin et al. 2014; Richard et al. 2014; Zabel et al. 2014). However, cumulative thermal stress was the primary predictor of migration survival in endangered Snake River sockeye adults. Crozier et al (2014) analyzed covariates of survival for migrating adult sockeye from Bonneville Dam through the Columbia and Snake Rivers to spawning grounds in the upper Salmon River. They found that survival through the Snake and Salmon Rivers was especially sensitive to temperatures experienced during migration through the hydrosystem. Cumulative temperature exposure, which reflects the daily sum of temperatures experienced over the migration from Bonneville to Lower Granite Dam, was the best predictor of survival to the spawning grounds.

In the Fraser River, Burnett et al (2014) found that after a passing a dam, adult mortality risk was greatly exacerbated by the need to employ anaerobic metabolism due to high flow or temperature or other stress. Stress may also be caused by handling from catch and release fisheries (Richard et al. 2014).

## **Disease/Temperature Interactions**

One of the primary concerns accompanying rising stream temperatures is that mortality from fish pathogens will intensify. Several review articles were published in 2014 summarizing current understanding of these dynamics. Although most such research has been done with fish in culture, Miller et al. (2014b) focused on interactions between microparasites (viruses, bacteria, myxozoans and some fungi), predators, and

wild salmon. They outlined in detail the mechanisms by which high water temperature influences disease progression, and present novel technologies currently being used to better detect and characterize disease agents, especially in the Fraser River. A second review by Burge et al. (2014) covered marine organisms more generally.

The primary immune defense against mortality from pathogens resides in the major histocompatibility complex (MHC). The diversity of alleles in this region reflects the history of selection from pathogens. A study of 27 populations of sockeye salmon in Wood River Basin, southwest Alaska (Larson et al. 2014), found that populations in different spawning habitat (beach versus stream and river) had different signatures of selection in their immune system, which presumably reflects different pathogen intensity. Beach spawners had less diversity at this locus than spawners in the other ecotypes. This might reflect the more constant temperatures at beach sites, lower spawner densities, or a number of other differences among sites. But this evidence of very fine scale differentiation in immune systems is consistent with the hope that selection via pathogens at higher temperatures will invoke a rapid evolutionary response in salmon. In a separate study in Fraser River sockeye, Chilko and Nechako fish were experimentally exposed to temperatures of 19°C. These researchers found that warm treatment induced production of heat shock proteins and elicited an elevated immune response that was quite different from fish held at cooler temperatures (Anttila et al. 2014b). This study suggested that immune responses are already differentiated among populations exposed to different swimming and temperature challenges, again supporting the potential for evolutionary responses to climate change.

Similarly, a study of three-spined stickleback resistance to *Vibrio* infection under thermal stress found negative genetic correlations in the response to stress across environments (Schade et al. 2014). Thus, tolerance to *Vibrio* infection can evolve, but fairly complex interactions between pathogen and host genotypes and temperature stress are not necessarily predicted by disease resistance at lower temperatures.

Detailed studies on *Ceratomyxa shasta* infection explored how high flows in the Klamath River in 2006 affected infection rates (Alexander et al. 2014), and the mechanism of immunity to *C. shasta* found in some strains of fish (Bjork et al. 2014). A modeling effort identified parasite concentration, water temperature, and discharge as the major predictors of mortality for both Chinook and coho salmon (Ray et al. 2014).

Additional studies examined the history of disease outbreak in Spanish hatcheries over the past two decades (Marquez et al. 2014). One finding was that the introduction of vaccines shifted the dominant pathogens, but climate warming also altered the probability of specific types of outbreaks. Pathogens with higher temperature preferences are more likely to grow in a warming climate (Marquez et al. 2014). A review of responses to an

extreme drought in the United Kingdom in 1976 shows the tremendously widespread impact of drought across terrestrial and aquatic systems, in culture and in the wild (Morley and Lewis 2014).

## **Contaminant Toxicity Increased by High Temperatures**

In addition to exacerbating disease in salmon, elevated temperatures also increase the toxicity of pesticides, and especially mixtures of pesticides. For a mixture of ethoprop and malathion, the degree of neurotoxicity in coho doubled when temperatures were increased from 12 to 18°C (Laetz et al. 2014). Similarly, in a separate study, a much lower concentration of malathion increased 50% mortality by 11.2% in Chinook salmon challenged with *Aeromonas salmonicida* at 19°C compared those similarly exposed at 11°C (Dietrich et al. 2014). A survey of the Columbia River estuary identified hotspots of sediment contamination (Counihan et al. 2014). In rainbow trout, effects from heavy metal exposure (copper) were also exacerbated by high temperature (Sappal et al. 2014).

## **Potential for Evolutionary Change in Thermal Tolerance**

To date, there is very limited evidence for evolutionary responses to recent climate change. As reviewed by Crozier and Hutchings (2014), what evidence there is appears to be related to migration timing. However, Gienapp et al. (2014) demonstrate with a theoretical model that climate change will intensify selection on consumer phenology due to differing sensitivity of traits to temperature among trophic levels.

Thermal tolerance is generally thought to have relatively little potential to evolve over ecological time frames, although extensive work is devoted to characterizing heritability, local adaptation, and genetic characteristics of traits indicative of thermal tolerance. Most studies find few genetic differences among populations in cardiac function (Anttila et al. 2014a; Munoz et al. 2014). However, thermal tolerance is strongly correlated with egg size, which is both highly heritable and a product of maternal effects. Munoz et al. (2014) suggest evolutionary rates might be accelerated by the combination of these driving factors. The role of egg size is not necessarily consistent across populations.

Temperature affects development rates and offspring size in sockeye salmon. Within these general shared patterns across an entire species, local adaptation has shaped differences in thermal response across a latitudinal gradient of sockeye (Whitney et al. 2014) and brook trout populations (Stitt et al. 2014). Similarly, critical thermal limits vary among strains of rainbow trout, although the differences are likely too small for

biological significance (Hartman and Porto 2014).

Temperature profoundly influences nearly all physiological traits, and some of these influences might not become apparent until later in the life cycle, long after exposure. For example, incubation temperature can affect future adult egg and gonad size, possibly as an epigenetic effect (Jonsson et al. 2014).

At the molecular level, studies in 2014 included the use of quantitative trait loci (QTL) to map genomic regions linked to phenotypic characteristics that moderate temperature tolerance (Everett and Seeb 2014; Jeffries et al. 2014; Meier et al. 2014; Oku et al. 2014).

Similar efforts were undertaken by Matala et al. (2014), who identified parts of the genome that respond to selection under different temperature and precipitation regimes in Columbia River steelhead.

Temperature limits might be reached through a variety of mechanisms, including tolerance of thermal-associated hypoxic conditions. Sorensen et al. (2014) suggested that the temperature dependence of anaerobic scope would be a more fruitful area of focus than the more common focus on aerobic scope in assessing the relative vulnerability of fish to a warming climate. Jorgensen et al. (2014) found cardiac impairment in adult Atlantic salmon after extended exposure to a temperatures of 19°C.

## **Salmon Sensitivity to Marine Conditions**

Literature published in 2014 regarding marine survival included general analyses of oceanographic indicators, studies of estuary and early marine survival in Chinook (Brosnan et al. 2014; Claiborne et al. 2014), later marine survival via diet comparisons (Thayer et al. 2014) and size-selective mortality in steelhead (Friedland et al. 2014b; Thompson and Beauchamp 2014).

### **Ocean Indicators**

Salmon marine survival is generally correlated with a number of ocean ecosystem indicators. Stachura et al. (2014) found relatively complex relationships between indicators of oceanographic variability and salmon temporal abundance from 1951 to 2002. However, these indicators did not fully explain shared variation in abundance observed across 34 different stocks of pink, chum, and sockeye from Asia to North America. Patterns in sea surface temperature did show some relation to population abundance, although common patterns across the majority of salmon in the North Pacific

were not strongly predicted by large-scale indices such as the Aleutian Low Index or the Pacific Decadal Oscillation (Stachura et al. 2014).

These indicators may have different effects on different stocks, or the correlations between indicators and population responses may have changed over time. Washington and British Columbia population groups had weak positive associations with warmer coastal temperatures, a finding that differs from previous analyses based on abundance and conducted over smaller spatial scales.

Litzow et al. (2014) found that 36 biological time series, including salmon, herring, shrimp, groundfish and jellyfish, from 1965 to 2008 were strongly influenced by climatic predictors, but that fishing had a very large impact on these populations as well, and commercial catch really should be included in analyses to explain decadal dynamics.

A new index of ocean conditions was developed by Sydeman et al. (2014b) to better relate ocean-climate and biological indicators. Their multivariate ocean-climate indicators (MOCI) showed that enhanced transport from the north, which carries subarctic copepods, along with intensification of upwelling off north-central California, was beneficial for salmon during 1990-2010.

Simpler use of ocean indicators is more typical in analyses presented for managers. Peterson et al. (2014) reviewed their use of physical and biological indicators in a NOAA "stop light" chart. Although these indicators have been in use for Columbia River Chinook and coho for a number of years, they have not been used for Columbia and Snake River sockeye, which have had low returns until recently. Williams et al. (2014) analyzed patterns in smolt-to-adult returns using hatchery sockeye production levels. They found that although production increases explained some of the large recent returns, most notably in 2012, high marine survival rates were a major factor throughout the time series. Indicators for sockeye survival correlated mostly with April upwelling and the Pacific Northwest Index.

Use of indicators to project salmon response to climate change is quite problematic because the importance of indicators will shift with changes in the physical dynamics they represent. For example, recent El Niño events have shifted in character from the eastern Pacific (canonical) mode to the central Pacific (Modoki) mode, as mentioned in previous reviews. The North Pacific Gyre Oscillation has also strengthened.

North Pacific Gyre Oscillation has a positive relationship with reproductive success of the Cassin's auklet, but has shifted to a negative relationship with success of Brandt's cormorant (Schmidt et al. 2014). This suggests that the mechanism of forcing

from the index through the foodweb changes over time, indicating that it is not a long-term predictor for climate change analyses. Consistent with that prediction, Miller et al. (2014a) found that the relative predictive power of climatic indices to predict Columbia River juvenile Chinook survival has shifted with time, such that the North Pacific Gyre Oscillation is now more important than the Pacific Decadal Oscillation.

Pink salmon differs from the other salmonids in its discrete 2-year life cycle. Pink broodlines are separated into “odd-year” and “even-year” spawning populations, which follow somewhat independent trajectories. Recently, odd-year populations in particular have increased in abundance, especially in the southern part of the species range (e.g., Puget Sound). Although the reasons for this are not totally clear, Irvine et al. (2014) examine numerous hypotheses and find the role of climate and of glacial refugia to be important. Population increases of pink salmon throughout the North Pacific have increased their biomass sufficiently that they have begun to dominate ecosystem processes and exert top-down control that affects many other species, such as Alaskan birds (Springer and van Vliet 2014).

Atlantic salmon are also very sensitive to growth rates driven by large-scale oceanic properties. In particular, sea surface temperature and the Atlantic Multidecadal Oscillation appear to be important for most Atlantic salmon populations, although the mechanism differs in North American and European stocks (Friedland et al. 2014a).

### **Size-Selective Mortality**

The primary mechanisms that determine marine survival usually involve either food supply or predation level. Both of these attributes contribute to the strength of size-selective mortality. Thompson and Beauchamp (2014) explored size-selective mortality at freshwater and marine life stages for steelhead from the Skagit River, Washington. They found that early growth was greatest in first-year juveniles at higher elevation, in the snow-dominant precipitation zone. Growth in the 2<sup>nd</sup> and 3<sup>rd</sup> year was not different between snow-dominant and mixed rain-snow precipitation zone. Overall, the largest smolts had the highest adult returns. They had insufficient sample size to compare survival for smolts in rain-dominant zones, but their results do suggest that expected transitions to warmer hydrological regimes might be associated with lower marine survival.

Friedland et al. (2014b) also found that growth shortly after the smolt transition was a strong predictor of survival to adulthood in British Columbia steelhead from the Keogh River from 1977 to 2005. Early marine growth was closely related to sea surface temperatures during the June-December period following ocean entry.

Claiborne et al. (2014) compared size-selective mortality between upper Columbia River summer- and fall-run Chinook collected in the Columbia River estuary vs. those captured at sea. Although they did not observe size-selective mortality, they did find that hatchery fish were relatively more abundant than wild fish in the estuary vs. ocean catches, potentially indicating lower marine survival of hatchery fish. Brosnan et al. (2014) focused on survival specifically in the Columbia River plume. They concluded that plume survival was a function of plume residence time, which in turn was a function of sea surface temperature (rather than discharge or upwelling).

Miller et al. (2014a) compared survival among years to assess the importance of early growth rates in Snake and Mid-Upper Columbia River Chinook. They found that juvenile size and marine growth were positively related to adult survival. Miller et al. (2014a) also found that size and growth were correlated with large-scale climatic indices, particularly the Pacific Decadal Oscillation and the North Pacific Gyre Oscillation, as well as biological indices, such as those described by Peterson et al. (2014). However, as mentioned above, the relative predictive power of large-scale climatic indices was not constant over the time series.

In their analysis of factors influencing survival for four Klamath Basin salmonid populations, Quinones et al. (2014) found that hatchery practices were more important than climate drivers for Klamath River fall Chinook marine survival. However, for the remaining fall and spring Chinook populations, and for the steelhead population, survival was more responsive to climate-driven factors.

## **Navigation and Survival**

Several papers have explored migration characteristics and navigational mechanisms in salmon, which may be affected by climate change if reliant on environmental cues. Byron and Burke (2014) reviewed this literature and reported these mechanisms as complex and population-specific. Burke et al. (2014) investigated observed migration patterns of juvenile spring/summer Chinook salmon in the California Current. To account for these patterns, they concluded that active spatial orientation through both a "compass sense" and landmark orientation (e.g., river mouths) would be necessary, as well as avoidance of certain oceanographic features such as strong southward currents and advection. Moreover, salmon rely on a "clock sense" to actively adjust swimming speed, in addition to direction, to compensate for varying current strength among years.

A detailed comparison of early migration characteristics by Fisher et al. (2014) revealed three basic patterns among Columbia River Chinook and coho. First, yearling smolts from the upper Columbia River spring run and Snake River spring/summer run tend to move offshore and head north very quickly upon entering the ocean. Second, subyearling smolts from summer/fall and fall runs essentially displayed the opposite pattern. They tended to move slowly northward and stay relatively close to shore. Finally, an intermediate, more diverse pattern (a wide range of latitudes and rates of movement) characterized yearling coho and Chinook smolts from the lower Columbia spring, upper Columbia summer, and upper Willamette spring runs.

These different ocean distributions exposed the various population groups to different vulnerabilities in relation to climatic differences among years. For example,



dynamics of the Columbia River plume and nearby upwelling likely affect summer/fall runs and lower Columbia runs to a greater extent than Snake River spring/summer runs. For these latter fish, conditions farther north, off Alaska might be more influential (Fisher et al. (2014).

A study of behavior in Atlantic salmon (Byron et al. 2014) found that large ocean current direction and strength had a major influence on salmon survival and growth. This influence was thought to explain some of the links between ocean indices and marine survival (Byron et al. 2014). An analysis of adult homing mechanisms for Fraser River sockeye and pink salmon found support for the use of magnetic field, as well as olfactory cues and perhaps temperature preference, to best explain fish behavior (Putman et al. 2014).

Variations in sea surface temperature do affect migration characteristics such as route selection, speed, and survival. However, Drenner et al. (2014) found that, surprisingly, adult sockeye body temperatures were not predicted by local sea surface temperatures. Their study of adult sockeye tagged with temperature loggers in the Strait of Georgia revealed highly individualized thermal histories. Fish temperatures varied from 8 to 20°C prior to Fraser River entry, indicating vertical migrations on diurnal cycles. However, whether fish surfaced during the day or night varied between years (Drenner et al. 2014).

McKinnell et al (2014) explored the very low returns of Fraser River sockeye in 2009. They found that a sequence of unfavorable conditions, from unusually high snowpack to atypical ocean conditions, affected the smolt migration, which exposed the fish to very poor growth conditions in the Strait of Georgia. However, this combination of extremes, which included sea surface temperature and pressure, wind, and precipitation, was relatively unusual.

## **Ecosystem Processes: Salmon Prey and Predators**

An understanding of salmon prey and predators is crucial for linking expected changes in physical oceanographic and atmospheric processes to salmon abundance in the future. Two reviews covered the state of our knowledge on forage fish and their predators in the California Current (Brodeur et al. 2014), and specifically in the Columbia River plume (Litz et al. 2014).

Brodeur et al. (2014) reviewed the diet of juvenile and adult coho and Chinook along with those of major competing predators. They found that primary prey of these salmon varied seasonally, but as adults they focused primarily on anchovy, herring, hake, juvenile rockfish, smelt, sardine, euphausiids, mixed crustaceans, and squid. Brodeur

et al. (2014) reported that Pacific hake might have the largest impact on forage fish due to its large biomass and high percentage of forage fish in the diet. Spiny Dogfish and Albacore had higher abundance than Chinook and coho, while their preference for forage fish was comparable to that of salmon, as were the preferences of other demersal predators such as arrowtooth flounder, Pacific halibut, Bocaccio, and Lingcod.

Thayer et al. (2014) explored variation in the ocean diets of adult Chinook salmon from central California Chinook during different ocean regimes. Specifically, they compared older data on diets from 1955 and the 1980s with data from the 2000s. They found that salmon diet composition shifted over time, but typically reflected the availability of preferred prey. Prey availability was based on catch from mid-water trawl surveys and varied in turn with sea surface temperature. Thayer et al. (2014) reported salmonid diets had shifted from juvenile rockfish, krill, herring, and squid to mostly sardine in recent years. They suggest that the change in diet might be linked to recent population crashes of California fall Chinook.

In 2013, a special issue of *Oceanography* focused on a century of research in fisheries oceanography. In this issue, Bograd et al. (2014) provide perspective on how physical drivers are linked to population dynamics and how this information can be used to adapt to climate change. This issue also revisits some long-standing analytical relationships used in fisheries oceanography. For example, Cury et al. (2014) used an expanded dataset to test density dependence implicit in standard stock-recruit models. They reported that density-dependence explained only a fraction of the variability in recruitment (5-15%), leaving much variability unexplained. Cury et al. (2014) concluded that much of the remaining variability, as Johan Hjort contended long ago, is driven by survival in very early life stages.

Llopiz et al. (2014) attributed variability in recruitment to a number of factors, including temperature, increasing concentrations of CO<sub>2</sub>, spatial variability in ocean productivity, and synergistic effects of fisheries impacts and climate change. They highlighted various survey missions and new technologies that support the development of ocean ecosystem management.

The special issue on fisheries oceanography also presents several research attempts to define indicators that will paint a picture of the entire coastal ecosystem (Boldt et al. 2014; Peterson et al. 2014). Robinson et al. (2014) suggested jellyfish as an independent indicator species of coastal ecosystem status due to its spatial, temporal, and dietary overlap with many forage fish species, including salmon.

Finally, Pinsky and Mantua (2014) reflect on current adaptation strategies to climate change for fisheries management, and Kim et al. (2014) describe the role of

intergovernmental organizations in leading this effort.

## Population Stability and Diversity

Population extinction can result from either a deterministic decline in abundance or population instability that fluctuates too close to zero. Larger fluctuations therefore generally increase extinction risk for small populations, and climate is one of the most important drivers of fluctuations in abundance. If an individual population goes extinct, sometimes it can be recolonized by other populations nearby. In this case, less synchrony among populations increases the probability that some individuals will be available to recolonize populations that blink out. Individualistic population responses to annual climate variability reduce synchrony among populations and enhance stability at the metapopulation level. Several papers studied population stability and synchrony in salmon populations along the west coast.

Kilduff et al. (2014) examined population-specific behavior in the early life stages of Chinook salmon. They evaluated relationships between growth, survival, and climate variables and found similarity among populations with similar migration histories, as demonstrated in covariability analysis. Their analysis found that life history type (subyearling vs. yearling) was more important than geography in a correlation pattern from 1980 to 2006, and that populations have become more synchronized since the 1990s. They also found co-variable survival rates among yearling Chinook from the Columbia River, Vancouver Island, and Alaska, despite previous analyses showing an inverse relationship in catch rates among these regions.

Moore et al. (2014) presented an analysis of life history diversity and population stability in steelhead from British Columbia. They found a very wide range for the ages of smolt transition and maturation, as well as for the frequency of repeat spawning. The greatest degree of synchrony was driven by year of marine migration. (Moore et al. 2014) concluded that this diversity led to reduced variability in population abundance.

Using a stochastic model, White et al. (2014) observed a contradicting pattern in stability for Fraser River sockeye: population abundance cycled among 4-year periods, driven largely by periodic predominance of 4-year-old spawners. Their model identified a suite of life history characteristics contributing to "cyclic dominance." Cycling populations were found to be near the threshold abundance for population persistence, and White et al. (2014) cautioned that such cycles could indicate a high risk of collapse. An alternative explanation for these cycles was presented through a model of predator-prey dynamics in sockeye rearing lakes (Guill et al. 2014).

Botsford et al. (2014) evaluated "cohort resonance," or a specific sensitivity to low frequencies of environmental variability, and found that salmon, with their relatively short generation time, are more vulnerable to environmental drivers than other marine fish. They suggested this vulnerability as a factor that could potentially contribute to our ability to detect responses to climate change (Botsford et al. 2014).

Salmon are important components of the California Current ecosystem, and a variety of groups track salmon abundance in relation to various ecosystem processes. A new transboundary health index for the Salish Sea was presented by (Wong and Rylko 2014), along with an observed decline in indicators for Chinook abundance.

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