

**Literature review for 2010 citations for BIOP:
Biological effects of climate change**

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1 Executive summary

Nationally and globally, the climate of 2010 continued trends of global warming, being one of the two warmest years on record. New analyses of observational data were generally consistent with previously reported historical trends of climate change. Climate, oceanographic, hydrologic, and stream-temperature models continue to be developed, tested, improved, and applied. Most of their assessments and projections indicated worsening physical conditions for salmon in mid-latitude regions, consistent with previous analyses: rising air temperature, moderately rising precipitation, declining snowpack, declining stream flow (partly due to water withdrawals), and rising sea surface temperature (although at reduced rates in upwelling regions). However, a few of the results could have either beneficial or negative implications for salmon. Historical analyses and predictions of net changes in primary productivity are spatially variable, and increases in the intensity of coastal upwelling (see below) could have positive or negative impacts. New studies on the biological effects of most of these processes were consistent with previous analyses, and showed that where salmon are limited by cool temperatures, warming is beneficial, at least over the short term, but in areas that are already relatively warm or where floods or low flows have negative impacts, climate change scenarios consistently project declines in salmon. In the ocean, several new studies pointed to the importance of sea surface temperature for early marine survival (as opposed to the Pacific Decadal Oscillation or smolt condition), but there were large differences among populations included in the study, and the single Columbia River population included did not show a strong ocean effect in this analysis (Sharma et al. 2009). The most geographically relevant papers include stream temperature analyses of the Boise River Basin (Isaak et al. 2010), the Wenatchee River Basin (Cristea and Burges 2010), and the Touchet Basin (Wiseman et al. 2010); and numerous climatological analyses of the Columbia Basin (see sections 4 and 5).

Several new papers documented historical and projected increases in upwelling intensity in the California Current (Bakun et al. 2010; Garcia-Reyes and Largier 2010; Wang et al. 2010). Although stronger upwelling has been positively associated with Columbia River salmon survival in the 20th century, Bakun et al. (2010) presented some possible scenarios (exacerbated by bad fisheries management) in which anoxia, toxic gas eruptions and jellyfish take over. Furthermore, although increased primary productivity predicted by some models would be expected to benefit salmon, most ecosystem models predict declines in salmon productivity south of the Arctic. Arctic conditions were expected to improve for salmon based on increased nitrate concentration (Rykaczewski and Dunne 2010), primary productivity (Kahru et al. 2010; Steinacher et al. 2010), and fisheries catches generally (Cheung et al. 2010; MacNeil et al. 2010).

A few emerging potential threats were documented for Fraser River salmon, with unknown potential for affecting Columbia River salmon. Algal blooms lowered survival of Chilko sockeye smolts (Rensel et al. 2010), and apparently increasing aggregations of sharks might be increasing predation on returning adults (Williams et al. 2010).

One other highly novel study found that gene flow increased during unfavorable river conditions, suggesting that straying might increase in response to rising temperatures (Valiente et al. 2010).

Three studies documented strong trends in salmonid phenology (one smolt-timing and two spawn-timing studies). Two of these studies also involved declining populations, and the authors suggested that part of the problem was a mismatch between rates of temperature change either in fresh- or saltwater (Kennedy and Crozier 2010) or between spring and summer (Wedekind and Kung 2010). In the 2010 BIOP we mentioned a trend toward earlier smolting in Snake River spring Chinook (Achord et al. 2007), so attention to potential phenological mismatches seem warranted. Several other studies attributed population decline more directly to environmental deterioration (Clews et al. 2010; Wiseman et al. 2010).

A large number of recent studies on Fraser River sockeye found negative impacts of high temperatures on adult migration survival and throughout the life cycle, and warned that a majority of populations within the Fraser River Basin are highly vulnerable to extinction due to climate change, based on both quantitative (Hague et al. 2011; Martins et al. 2011) and qualitative analyses (Jacob et al. 2010; McDaniels et al. 2010). McDaniels et al. (2010) considered possible management actions, but found they were limited. One study found individual variation in the use of thermal refugia during migration that depend on individual condition (Donaldson et al. 2010), while another study found that thermal refuge use corresponded to higher survival (Mathes et al. 2010). Disease morbidity and mortality is being exacerbated by warmer temperatures (Braden et al. 2010; Bradford et al. 2010; Marcos-Lopez et al. 2010) and artificial propagation (especially fish farms, Krkosek 2010; Pulkkinen et al. 2010).

Several theoretical papers described new mathematical methods of detecting impending extinction due to environmental deterioration (Drake and Griffen 2010; Ovaskainen and Meerson 2010) and elevated risks from environmental impacts at particular time scales and life stages (Worden et al. 2010).

Several studies demonstrated strong maternal effects on larval survival, compared with stronger genetic effects on juvenile growth and survival. These studies could possibly imply that negative effects of the hydrosystem could persist into the next generation, whereas evolution might modify juvenile growth and survival.

New studies provided additional details on adaptation strategies, such as those previously described in ISAB (2007), for Pacific salmon. For example, Cristea and Burges (2010) found that the cooling potential of riparian vegetation restoration is likely to postpone stressful temperatures for salmonids in Wenatchee River tributaries through the end of the century. However, vegetation restoration did not significantly reduce temperature in the mainstem Wenatchee. Such studies need to be site specific, because, for example, Null et al (2010) found that restoring and protecting cool springs was more beneficial than increasing riparian shading in the Shasta River. Several papers provided more information on adaptation strategies in general and the practical social and technical considerations for implementing them (e.g., Binder et al. 2010; Brekke et al. 2010).

In conclusion, new information from 2010 publications was generally consistent with previous analyses in reporting ongoing trends in climate consistent with climate change projections and negative implications for salmon at mid-latitudes. Modeling techniques continue to improve. A few studies focused on areas that did not receive much attention in our previous report, and thus provide new information. These areas include predicted and observed intensification of upwelling (compared with various similar and contradictory reports published previously), reduced salmon survival due to algal blooms,

climate-induced straying, and climate change-induced mismatches in phenology associated with population declines. Numerous new studies of Fraser River sockeye warn of very severe risk from climate change. Finally, several theoretical papers augment our toolbox for anticipating extinction due to environmental deterioration.

2 Table of acronyms

AO	Arctic Oscillation
BPA	Bonneville Power Administration
CCS	California Current System
ENSO	El Niño-Southern Oscillation
ESU	Evolutionarily Significant Unit
GCM	General Circulation Model
IPCC	Intergovernmental Panel on Climate Change
NPI	North Pacific Index
NPGO	North Pacific Gyre Oscillation
NO	Northern Oscillation
OA	Ocean Acidification
PDO	Pacific Decadal Oscillation
SO	Southern Oscillation or Southern Annual Mode
SST	Sea surface temperature
VIC	Variable Infiltration Capacity model
WACCA	Washington State Climate Change Assessment
WRF	Weather Research and Forecasting

3 Goals and methods of this review

The goal of this review was to identify the literature published in 2010 that is most relevant to predicting impacts of climate change on Columbia River salmon listed under the Endangered Species Act. A large amount of literature related to this topic is not included, because almost anything that affects salmon at all relates to or is altered in some way by changes in temperature, stream flow or marine conditions. We have tried to identify the most directly related papers by combining climatic and salmonid terms in the search criteria. Thus many general principles demonstrated in other taxa or with more general contexts in mind have been omitted. This review also does not include potentially relevant gray literature, because the search engine used only includes the major peer-reviewed scientific journals. Additional references were solicited from NOAA staff and independent scientists. Shallin Busch contributed the ocean acidification section. In total, the methods employed involved review of over 800 papers; 227 are included in this summary.

This search was conducted in ISI Web of Science in June, 2011. Each set of search criteria involved a new search, and results were compared with previous searches to identify missing topics. The specific search criteria all included PY=2010, plus:

- 1) TS=(climat* OR temperature OR streamflow OR flow OR snowpack OR precipitation OR PDO) AND TS=(salmon OR Oncorhynchus OR steelhead);
- 2) TS=(climat* OR Temperature OR Precipitation OR streamflow OR flow) AND TS="Pacific Northwest";
- 3) TS=(marine OR sea level OR hyporheic OR groundwater) AND TS=climat* AND TS=(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"

The review is organized by first considering physical environmental conditions (historical trends and relationships) and then projections of future climate, snowpack, stream flow, temperature, ocean conditions, etc. A summary follows of the literature on salmonid responses to these environmental conditions, progressing through the life cycle.

4 National Climate Summary of 2010

Nationally and globally, 2010 was at or near record-breaking levels in many respects, based on NOAA's Annual State of the Climate Report (Blunden et al. 2011) Strong El Niño-Southern Oscillation (ENSO), Arctic Oscillation (AO), and Southern Annular Mode (SO) conditions drove very dramatic weather events in many parts of the world, while we emitted greenhouse gases at very high levels (above the average over the past 30 years). Trends consistent with global climate change reported in the 2010 Supplemental Biological Opinion (NMFS 2010) continued: 1) 2010 was one of the two warmest years on record; 2) average global sea surface temperature was the third warmest on record and sea level continued to rise; 3) ocean salinity variations at a global scale showed intensification of the water cycle; and 4) Arctic sea ice shrank to the third smallest area on record, the Greenland ice sheet melted at the highest rate and over the largest area since at least 1958, and alpine glaciers continued to melt.

5 Historical analysis of terrestrial climate, stream flow and stream temperature in the western US and British Columbia

A number of new papers have conducted historical analyses of trends over the past half century or so in air temperature (rising), precipitation (rising), snowpack (declining) and stream flow (declining). Trends in ocean conditions and El Niño events are discussed in the ocean section. These results are generally consistent with trends described in the 2010 Biological Opinion (NMFS 2010). Further, several papers have analyzed how broad-scale climatic conditions such as the Pacific Decadal Oscillation (PDO) and ENSO drive variation in processes with significant biological implications, such as drought, forest fire, landslides, and coastal fog.

Specifically, Fu et al. (2010) showed that in Washington State from 1952 to 2002, annual mean air temperature increased 0.61°C (daily mean), 0.24°C (daily maximum), and 0.93°C (daily minimum), on average (or at a rate of 0.122, 0.048, and 0.185°C, respectively, per 10 years). Despite increasing annual precipitation, stream flow decreased at a rate of -4.88 cms/yr, with the largest effects in May and June on the west side of the Cascade Mountains. Temperature increased throughout the year (except October and December) across the state, with a small area of maximum temperature cooling in the central-eastern portion of the state. Minimum temperatures rose more than maximum temperatures. To explain the declines in streamflow, the authors suggested that human water use and increased evaporation rates due to rising temperature and more surface area exposure (e.g., from reservoirs) play important roles. Ryu et al. (2010) showed a positive relationship between a drought index based on streamflow and El Niño in the Pacific Northwest. Bumbaco and Mote (2010) studied the role of winter and summer precipitation and temperature in causing three droughts in Washington and Oregon (2001, 2003, and 2005), and found a different driver in each case (low winter

precipitation in 2001, low summer precipitation in 2003, and warm winter temperatures during key precipitation events in 2005).

Corresponding to the lower availability of water for biological processes, Meyn et al. (2010) showed that summer drought correlates strongly with the forest area burned in British Columbia. The PDO index the previous winter was related to summer drought in some areas of British Columbia, but is not a very strong driver over most of the province. Johnstone and Dawson (2010) tracked a new index of climate not mentioned in our previous report, which is the frequency of coastal fog along the California coast. They showed that fog levels are correlated with the strength of upwelling and have declined 33% from 1951 to 2008, increasing drought stress for plants.

Intense precipitation events, predicted to increase in winter with climate change, exacerbated by rain on snow events and high wind also increase the risk of landslides (Guthrie et al. 2010).

Average snow depth decreased widely across the western United States, especially at lower-elevation stations (<1000 m, Grundstein and Mote 2010). The vast majority of lower-elevation stations (80%) and a majority of mid-elevation stations (2000-3000m, 62%) showed significantly negative trends. Snow depth was strongly related to the PDO and the North Pacific Index (NPI).

Streamflow reflects both climatic factors and local habitat. For example, recent papers discussed the impact of glacier runoff and projected changes (quantified on Mt Hood by Nolin et al. 2010), and combinations of snow fall and forest integrity, whether due to harvest or fire. Specifically, Jones and Perkins (2010) studied how rain-on-snow events and harvest differentially affected different sized basins, while Eaton et al. (2010) examined changes in peak flows and the timing of the freshet, in addition to channel morphology following fire.

Wetlands are highly dynamic environments. Large scale variability in climate such as oscillations of the PDO can dramatically change local environmental conditions. After the regime shift of 1976, a wetland in southern California experienced a dramatic increase the frequency of extreme storms and floods due to a shift in the storm track across the Pacific. Zedler (2010) classified the types of events and their ecological consequences (mostly for plants) in terms of their relationships, for example, whether the ordering of events matters (e.g., river-mouth closure followed by a drought, that killed many more plants than additive effects would predict. They suggested focusing restoration actions on preparing ecosystems for likely future climates rather than restoring past communities necessarily.

6 Projected changes in terrestrial climate for the 21st century

Some of the most relevant projections of climate change conditions within the Columbia Basin were summarized in the 2010 BIOP based on reports produced for the Washington State Climate Change Assessment (WACCA), but were published in formal climate journals in 2010. In this category, Mote and Salathé (2010) described climate changes in the Pacific Northwest predicted by general circulation models produced for the Intergovernmental Panel on Climate Change (IPCC) fourth assessment report. Salathé et al. (2010) described changes predicted by the regional dynamical climate model Weather Research and Forecasting (WRF) Model. Elsner et al. (2010) summarized the

regional hydrological implications of the global model predictions, and Mantua et al. (2010) described projected increases in peak winter flows, lower late summer flows, and high summer stream temperatures that will threaten salmon. A few other sections of the WACCA report were not mentioned in the BIOP, and are summarized in this report.

Predictions of how rising greenhouse gases will affect climate depend on how functional relationships are modeled. A large body of work describes tests and improvements of the climate models, and are mostly beyond the scope of this review. It is worth noting here that work is ongoing on many aspects with especially large levels of uncertainty at the moment, such as the extent of intra-model variability compared with inter-model variability (over half of the variation between models can be explained by variation within models, Deser et al. 2010), how the global circulation models drive ENSO variability (An et al. 2010) and regional downscaling -- i.e., how to convert the large-scale global model output ($\sim 200\text{km}^2$ resolution) to the regional scale ($\sim 8\text{ km}^2$ resolution, Ainslie and Jackson 2010). There are important differences in predictions made by different downscaling approaches. Qian et al. (2010) compare predictions from two dynamical downscaling methods, a subgrid parameterization and a regional climate model. They found that both methods greatly improved the modeled snowpack compared with observations over simpler downscaling methods, but the regional model captured precipitation and snowpack along the coastal mountains much better because of the importance of mountain orientation for wind direction. This model predicted a greater change in snowpack under climate change scenarios than the subgrid approach.

Predictions of changes in snowpack are very sensitive to how temperature changes with elevation. Minder et al. (2010) clarified spatial and temporal variation in the lapse rate in the Cascades, and Minder (2010) studied the effect of different determinants of the snow melting level in physical models. Minder (2010) predicted a loss of 14.8%-18.1% of Cascade snowfall per degree of warming, assuming precipitation increases, and 19.4%-22.6% loss per degree without precipitation increases, with profound impact on accumulated snowpack.

6.1 Stream flow

Many hydrological projections are based on the Variable Infiltration Capacity model (VIC). Wenger et al. (2010) conducted a test of this model in the Pacific Northwest. They found that model predictions were relatively accurate for center of flow timing and mean annual and summer flows, and the frequency of winter floods. However, modeled frequencies of low flows and groundwater-impacted streams did not match observations closely.

Chang and Jung (2010) projected the hydrology of the Willamette River Basin. They considered predictions from 8 general circulation models (GCMs), and downscale to $1/16^{\text{th}}$ degree resolution for their hydrological model. Like previous projections, the models predicted increased winter flow, decreased summer flow, reduced snowpack, and earlier runoff. The different GCMs varied significantly in their predictions, especially later in the century. There was also substantial variation at the subbasin scale, indicating important local controls in hydrology. A new analysis by the Climate Impacts Groups for the Bonneville Power Administration (BPA) showed similar spatial variation, uncertainty, and general trends. This was a comprehensive study in draft form in 2010 (Brekke et al. 2010). It will be summarized more thoroughly in the 2011 report.

Three papers focused on changes in precipitation or hydrologic extremes. Tohver and Hamlet (2010) analyzed shifts in extreme streamflow statistics at 297 sites in the Columbia Basin, based on the Columbia Basin Climate Change Scenarios Project. First they described the same results previously reported: there was a general shift from weakly snow-dominant basins to transient basins, and from transient basins to rain-dominant basins, such that no snow-dominant sources remained in the US portion of the Columbia Basin by 2080, under the A1B scenario, and extremely few even in the highly optimistic B1 scenario. However, they found significant differences between the two downscaling methods employed in flood projections. The “hybrid delta” method predicted flooding increases throughout the Columbia Basin, whereas in Mantua et al. (2010) and the “composite delta” method, increased flooding is more spatially variable. The hybrid delta method is thought to be more accurate in this regard, reflecting the spatial distribution of warming and precipitation increases better than the composite method. Higher winter temperatures and precipitation regimes increase flooding most in transient and rain-dominant basins, but also in snow-dominant basins, despite the reduced accumulation of snowpack. Even greater increases in flooding could be caused by increasing spring storm intensity and more precipitation falling as rain rather than snow. Increased flooding in transitional and rain-dominated basins followed from increased winter precipitation. Low flow risk increased most in rain-dominant and transient basins due to rising summer temperatures and evapotranspiration rates. Snow-dominant basins, so important in the Columbia and Snake tributaries, were relatively resilient to this effect in this analysis possibly because the lowest flows tend to occur in winter, and they did not separate out summer low flows.

Rosenberg et al. (2010) examined precipitation extremes for stormwater infrastructure. They found that uncertainty in projections is too large to make engineering preparations, but that some potential outcomes could be very serious. Towler et al. (2010) similarly examined extreme precipitation events and secondary effects, in this case, turbidity, important for Portland’s water supply. They developed a technique for applying climate change scenarios to detect the impacts of predicted shifts in extreme events.

A study in California (Meyers et al. 2010) found that +2°C and +4°C climate warming and altered precipitation are likely to shift floods from spring to winter, and increase the frequency and intensity of floods. Such a change would negatively affect brook trout more than rainbow trout, which would then experience less competition from brook trout.

Another study (Moradkhani et al. 2010) explored climate change scenarios in the Tualatin River in Oregon using a different hydrological model and found that the 50-year floods and the riparian ecotone decreased in low emissions scenarios, but increased in high emissions scenarios. Thus well-established trees along the riparian corridor were flooded in the high-emission scenarios.

Some streams are currently fed by significant amounts of glacier meltwater. Nolin et al. (2010) studied a stream on Mt Hood that currently derives 41-73% of its late summer flow from glaciers. Under climate change scenarios, glaciers retreated, ultimately reducing summer flow.

7 Historical analyses and projections of ocean conditions

A number of studies published in 2010 provided insight into areas of profound importance for salmon that have been especially uncertain in prior climate change analyses. Two papers indicated that over the 20th century, upwelling in the California Current System (CCS) and the Humboldt Current System have become more intense, which is consistent with a new analysis of GCM projections that predicted it will continue to intensify with global warming. Papers focusing on historical sea surface temperatures (SST) addressed previous criticisms that observed trends are due to instrument bias, re-established the global pattern of decadal oscillations overlaid upon a background of rising SST, and documented the shifting character of El Niño events and their impact on long-term SST trends.

7.1 Upwelling

Upwelling dynamics along the Washington and Oregon coasts are a key element in Columbia River salmon marine survival and growth. The impacts of climate change on upwelling dynamics are among the most uncertain of all the predictions of climate change models. Conflicting predictions stem from 1) changes in the various driving processes that affect upwelling are expected to act in opposite directions, necessitating quantitative comparisons for determining net effects (i.e., rising SST should reduce upwelling, while increasing alongshore winds should increase upwelling) and 2) the spatial resolution of both climate models and empirical datasets have generally been too coarse to accurately capture upwelling dynamics.

Two papers published in 2010 basically supported the intensification prediction by documenting empirical trends over the 20th century, and a 3rd paper analyzed GCM reconstruction and projections of upwelling dynamics over the next century. Garcia-Reyes and Largier (2010) analyzed hourly buoy data off the California coast to describe the historical trend at an appropriate spatial and temporal scale. They found strong evidence for intensification of upwelling from 1982 to 2008, especially in central California (35°N-39°N). Specifically, they documented trends in the upwelling index (based on pressure fields), the strength of upwelling winds (based on alongshore wind speed), SST directly within the upwelling region (hence a negative trend in absolute temperature during the upwelling season), the number of days of upwelling within the season, a lengthening of the upwelling season (more days in March and October, hence earlier spring and later fall transition), and increased variability in upwelling winds (an increase in the 90th percentile and a decrease in 10% percentile), indicating stronger upwelling alternated with more relaxation in winds. They also found correlations of magnitude 0.6 or 0.7 between upwelling winds and the Northern Oscillation and the North Pacific Gyre Oscillation (NPGO), and between SST and the PDO and ENSO.

The second paper (Bakun et al. 2010) reviewed the basic argument that increasing land temperatures will intensify the pressure gradient between ocean and land, and hence intensify the alongshore wind stress, which initiates upwelling. Bakun et al. (2010) then reviewed previous tests of the hypothesis, and described a new test focusing on the relationship between water vapor and upwelling off Peru. This test showed significant correlations most of the time. Because water vapor acts as a greenhouse gas, they concluded this was consistent with a prediction of intensifying upwelling with rising

greenhouse gas concentrations. One very important point they made in this paper, however, is that intensification of upwelling is not necessarily good for fish. They described scenarios in which excessive upwelling advects zooplankton offshore too quickly for effective phytoplankton control. If omnivorous fish such as sardines are overfished or not present for some reason, there could be an ecosystem regime shift toward that currently found off Namibia, in which unconsumed phytoplankton sink and generate hypoxic zones and toxic gas eruptions, which kill fish and leave an ecosystem dominated by jellyfish.

In the third paper, Wang et al. (2010) analyzed the performance of all the major GCMs produced for the 4th IPCC assessment using a number of criteria, including PDO variation across the Pacific and upwelling near the mouth of the Columbia River. Twelve of the 23 GCMs had a reasonable representation of the PDO over the 20th century (i.e., had a spatial correlation coefficient of the first Empirical Orthogonal Function of winter SST of at least 0.7). Half of these models predicted that SST would exceed the variability of the PDO within 50 years under the A1B emissions scenario (the remainder predicted it would happen within 90 years). Averaged over 10 models, SST in the CCS was expected to increase 0.26°C per decade in the 21st century. Although the GCMs were not designed to characterize dynamics at the spatial scale of coastal upwelling, these models did remarkably well at capturing the seasonality of upwelling, even if they overestimated seasonal variation somewhat. Representation of the California Current was better than the Humboldt Current. In the CCS, 17 models predicted increases in July upwelling while only two models predicted decreases.

7.2 *Ocean temperatures*

Three studies analyzed historical trends in ocean temperatures. Carson and Harrison (2010) examined the impact of instrument bias in previously reported interdecadal trends at the ocean surface, 50m, 100m, and 300m temperatures. They found coherent signals of interdecadal variability at multiple depths, even with bias correction and comparisons of different datasets. This contrasts with recent work on the global average temperature, which showed reduced decadal variability after bias correction. Schwing et al. (2010) describe global atmospheric and oceanic teleconnections (e.g., the PDO, AO, NO, SO, and major current systems) and the major factors driving large marine ecosystems. Atmospheric teleconnections synchronize much of the decadal variability in the California and Humboldt Current Systems, as well as the Gulf of Alaska. Schwing et al. (2010) showed a persistent warming trend of 1-2°C over 100 years in SST in all large marine ecosystems, although the rate of warming was weaker in the upwelling (or downwelling) dominated coastal region. The general patterns (overall trend and decadal fluctuations) were similar to global mean surface temperature, despite some regional differences. The western Pacific showed roughly similar trends, but lags behind the eastern Pacific by about 10 years, and was driven by quite different physical processes. Thus they predicted similarities among the eastern Pacific large marine ecosystems in responses to climate change, but less so between eastern and western Pacific large marine ecosystems. Another paper (Moore et al. 2010), made a very interesting point, which is that ENSO warm water events usually only affect winter temperature in Pacific Northwest waters, while the PDO warm phase often persists through summer and fall. This has important implications for the salmonid life stage that

is affected by these events, which then has implications for impacts on population dynamics (Worden et al. 2010), as described below in the Population Dynamics Modelling Section.

Finally, Lee and McPhaden (2010) paper parsed out sea surface temperature increases in the central Pacific during El Niño events, and found that the increasing frequency and intensity of these events in this region drove most of the overall trend in sea surface temperature (SST). SST during El Niño events warmed by 0.24°C/decade, whereas SST warming in neutral and La Niña years was positive, but much smaller (0.05-0.07°C/decade) and not statistically significant over the 1982-2008 time frame. The reason for this shift in the position of the maximum warm anomaly is not known, but increasing intensity and frequency of El Niño events has been predicted to follow from rising greenhouse gases (Yeh et al. 2009), as cited in the 2010 Biological Opinion.

7.3 *Ocean acidification*

Two papers found that measured declines in pH near urban areas are faster than expected from CO₂ uptake alone and partially reflect nutrient loading (in the Hood Canal of Puget Sound, Washington, Feely et al. 2010; along the Dutch coast, Provoost et al. 2010). Wong et al. (2010) studied trends in pCO₂ in seawater along line P out from Vancouver Island, and found that it has risen in the oceanic zone at a rate of 1.36 µatm per year, tracking the atmospheric growth rate. The coastal zone pCO₂ rose at a similar rate in winter, but spring levels showed no trend.

8 Impact of stream temperature and flow on juvenile salmon

8.1 *Effects of temperature on embryo development*

There has been much concern that warmer winter temperatures will increase embryo mortality, cause earlier fry emergence, smaller fry size, and a mismatch between larval needs and food supply. In an experiment on coho survival, Lohmus et al. (2010b) found the optimal temperature for hatching and alevin survival was a relatively high 12°C; they found substantial survival (40%) still at 16°C, but very low survival at 18°C (2.5%). In a review article, Teletchea and Fontaine (2010) found a strong positive relationship between egg size and larval energy reserves, and a strong negative relationship between temperature and time to first mixed feeding (i.e., requiring external food supply) among Pacific salmon. Thus although Pacific salmon have relatively large eggs and hence more flexibility in temporally matching food availability than other fish, higher temperatures are likely to produce smaller, less flexible fry. Janhunen et al. (2010) found that alevins hatched at the higher temperature were developmentally less advanced.

If either egg or larval survival is reduced under future climatic conditions, it is theoretically possible that they might evolve in response to selection. Several studies showed that populations from different climates have locally adapted development rates and thermal tolerances. Narum et al. (2010) found evidence of selection for differing climates by comparing genetic markers in redband trout: temperature was strongly correlated with allele frequencies. And Kavanagh et al. (2010) found evidence of local

adapation to cool temperatures and reduced critical maximum temperatures in European grayling within 22 generations. However, Evans et al. (2010) and Janhunen et al. (2010) found similar results in Chinook salmon and Arctic charr, respectively, that genetic variation was relatively weak for embryo survival, but was slightly greater for larval length. Maternal effects were strong in both studies especially at the earlier developmental stages, indicating that adult migration and prespawn condition could have long-lasting effects through the next generation.

The effect of temperature during development might have more complicated effects beyond body size and emergence time. In sticklebacks, developmental temperatures and consequent compensatory growth affected skeletal and muscle morphology, with potential effects on locomotor performance (Lee et al. 2010). In zebra fish, brief exposures to cool developmental temperatures affected dorsal, anal, caudal, and pelvic fin positions, as well as gill cover and the position of the lower jaw (Georga and Koumoundouros 2010). It is not clear whether these shape changes have functional implications, but they were preserved through adulthood. Zabel et al. (2010) showed that different Chinook salmon ESU (fall vs spring/summer life history types) had different otolith/fish length relationships, demonstrating differences in morphology that are not simply explained by different growth rates. The populations do rear in very different environments, but the role of environmental temperature requires further study.

Other effects of high temperature during development include sex reversal. Magerhans and Horstgen-Schwark (2010) reported an experiment that showed that sensitivity to temperature in sex determination in rainbow trout is substantial and heritable. The initial population had a sex ratio of 51.9% female when eggs were reared at 18°C, and 49.3% female when reared at 12°C. After one generation of selection, they produced a sex ratio of either 57.6% or 44.5% female at 18°C, indicating a heritability of 0.63 for this trait. Stelkens and Wedekind (2010) reviewed the various mechanisms of sex determination and sex reversal in teleost fish.

8.2 Effects of temperature and flow on juvenile growth and survival

Many papers have continued to demonstrate strong effects of temperature and flow on juvenile salmon growth and survival. Most papers are consistent in showing improved growth when relatively cool habitat warms up: spring in Massachusetts, (Xu et al. 2010a), fall in Idaho (Jenkins and Keeley 2010); and a long-term trend of larger smolts in the Baltic (Vainikka et al. 2010). However, negative effects of warming were typical during summer (Xu et al. 2010b) and winter (Xu et al. 2010a), when consumption cannot compensate for increased metabolic demands. In northern Europe, the net effects are expected to still be positive except under the warmest climate change scenario examined (+4°C). This prediction was consistent with observations of increased size at age over 23 years in Baltic Sea Atlantic salmon, although hatchery practices and size-selective fishing also affect these populations. In more southerly locations, the negative effects were predicted to outweigh positive effects even in moderate warming scenarios (Xu et al. 2010a). Changes in growth rates might affect the timing of vulnerability to predators such as bass, which are very size selective (Christensen and Moore 2010).

Similarly, several papers showed that higher flow has positive effects when it is relatively low to start with (e.g., in spring in the heavily water-withdrawn Lemhi Creek, in fall in the more natural Marsh Creek, and higher spring flows in the Columbia for both populations of Chinook salmon (Arthaud et al. 2010), and throughout the brook trout growing season in Massachusetts, (Xu et al. 2010a), and in bringing in more insect drift to cutthroat trout in Jenkins and Keeley (2010), and increasing Atlantic salmon habitat volume (Teichert et al. 2010). However, the highest flows (floods) had negative effects (Hayes et al. 2010; Xu et al. 2010a). Hayes et al. (2010) found that relaxed density-dependent mortality over the following season compensated for the immediate negative effects on brown trout, thus there was no net effect in this case.

The rest of this section provides more detail on the papers mentioned in the previous two paragraphs. Xu et al. (2010a) tracked individual brook trout growth over an 8 year study. They found strongly interacting effects of temperature, flow, season, and density. Highest growth rates occurred in spring, and were positively correlated with temperature and flow. In the warmest season, summer, temperature was negatively correlated with growth. Flow was generally positively correlated with growth, except in winter. Furthermore, density had greater negative effects at high temperatures. Because current climate predictions indicated the greatest increases in temperature and flow are in the winter, and that flow decreases in the summer, the net prediction based on their data was a decrease in mean fish spawner size and fecundity under a moderate (1.5°C) warming scenario.

Davidson et al. (2010) studied the same study system as Xu et al. (2010a), but analyzed Atlantic salmon growth instead of brook trout growth, and included the impacts of the density of both Atlantic salmon and brook trout. Using a linear mixed model, they found that environmental effects (both temperature and discharge) were much more important than density in driving variation in growth. Warmer temperatures within a season generally had a very small negative effect, while high discharge had a strong positive effect. Interestingly, they found that more variability in temperature (the second principle component in temperature) had a negative impact at low discharge, but a positive impact at high discharge.

Habitat quality depends in part on food availability and the cost of acquiring it, which in turn depend on flow and temperature. Jenkins and Keeley (2010) found that cutthroat trout foraging location matched that predicted by the amount of energy gained (net energy intake NEI), with habitat type (pool versus riffle) and temperature explaining most of the variation among sites. Using an energetic model, they concluded that warmer temperatures will have negative effects on smaller fish, but will lengthen the growing season for larger fish.

Hayes et al. (2010) used changes in the relationship between weight and density in a New Zealand brown trout population over time to assess the impact of unusually low flows and one flood on population dynamics. They argued that although the flood caused substantial emigration or mortality, survival after the flood was higher than in other years (i.e., reduced density-dependent mortality), such that the population recovered quickly. The low-flow events had no effect on survival or biomass.

Arthaud et al. (2010) examined how well variation in flow during freshwater stages affected egg-smolt and egg-adult rates in a pristine stream (Marsh Creek, Idaho) and a stream subject to very high rates of water withdrawal (Lemhi Creek, Idaho). In

Lemhi Creek, water withdrawals are so severe that spring flows during the parr year strongly limited production and drove variation in both egg-smolt and egg-adult survival. In Marsh Creek, egg-smolt survival was correlated with parr-year August flow, but the cumulative impact on egg-adult survival was much weaker. In both populations, smolt-adult return rates were best predicted by Columbia River spring flow and ENSO.

Rising temperatures increase not only the metabolic rate of salmonids, but that of their predators, and potentially the risk from warm-adapted invasives such as bass. Christensen and Moore (2010) documented levels of bass predation on stocked rainbow trout in Twin Lakes, Washington. They found that trout sizes in fall (100-160mm) made them vulnerable to predation by large largemouth bass, but larger trout (>210mm) escaped predation. This suggests that changing growth rates due to temperature might affect not just total predation, but also the temporal period salmon are vulnerable to bass predation.

Westley et al. (2010) considered the affects of dispersal of anadromous fish through lake systems and discover a consequent lag in the community response to environmental forcing, in addition to habitat change and fishing mortality. By examining fish composition over 46 years, they found an immediate response and a 1-year time lagged response to the PDO in an upper lake where sockeye rear their first year, but just a 1-year time-lagged response in a lower lake. They emphasized these processes are important for anticipating the impact of environmental variability on community composition.

Lohmus et al. (2010a) studied variation in juvenile growth among wild-type and growth-enhanced coho salmon at 3 temperatures. They saw little evidence of compensatory growth, perhaps because fish were fed to satiation, so rank order in size was relatively consistent throughout the experiment. The fish grew more at 16°C than at 12°C, which is consistent with previous studies that found 15°C to be the optimal temperature for growth.

8.2.1 Local adaptation/genetic control in growth rates

Growth rate in general and the growth response to temperature in particular is a heritable trait, and several papers showed differences between populations consistent with a history of different selection pressures. Latitudinal gradients are especially useful for demonstrating evolutionary effects of different thermal regimes. In general, colder temperatures slow growth rate within populations, producing a latitudinal gradient of smaller size at age in cooler locations (Chavarie et al. 2010; Morita and Nagasawa 2010). However, over evolutionary time populations in cooler environments have compensated for this effect by evolving faster growth rates and better tolerance of adverse conditions at northern latitudes. Chavarie et al. (2010) demonstrated these higher growth rates in northern populations across 66 populations of lacustrine Arctic charr in eastern North America, although their anadromous forms did not showed the same strong effect. Finstad et al. (2010) showed that compared to southern Norwegian populations, northern populations of Atlantic salmon have adapted higher feeding activity and reduced metabolic expenditures to sustain them over a longer winter.

Although these patterns prove that fish evolve to different thermal regimes over long time periods, potential evolutionary responses to rapid climate change are a very

different matter. Understanding the roles of phenotypic plasticity, genetic variability, and maternal effects controlling larval survival and fry growth is key to predicting plastic and evolutionary responses to climate change. In a carefully controlled breeding design plus translocation experiment, Evans et al. (2010) quantify the strengths of these various effects in Chinook salmon from Quinsam and Big Qualicum rivers. They found that all processes were important for explaining their results, but that maternal effects were the most important process for larval survival, while additive genetic effects dominated fry survival and fry growth. These results suggest that maternal condition is very important for cross-generational effects, and that there is substantial genetic variation available for an evolutionary response to environmental change.

Van Doorslaer et al. (2010) explored rapid evolution in *Daphnia*, which are a major prey item of lake-dwelling salmonids, to increased temperature through artificial selection. They compared these newly evolved populations to *Daphnia* from a historically warmer climate. After only six months of exposure to unusually warm conditions, size at maturity had evolved. In this semi-natural experiment, the intrinsic population growth rate did not evolve. However, in a previous study (Van Doorslaer et al. 2009a) they showed the reverse effect, where population growth rate evolved but not size at maturity, demonstrating that either response is feasible, depending on ecological conditions. Furthermore, another previous study (Van Doorslaer et al. 2009b) showed that *in situ* evolution might reduce the competitive advantage and hence likelihood of invasion of more southerly, warm-adapted genotypes. Thus rapid evolution is possible, at least in *Daphnia* and perhaps other planktonic prey of salmonids, but it remains to be seen how this will pan out in natural communities and longer-lived species like salmon.

8.2.2 The timing of growth

In addition to total growth in a season being important, the rate of growth early in the season can have complex repercussions for smolting decisions, negative consequences of compensatory growth, and the ability to capitalize on ephemeral resources with large potential benefits. By manipulating the timing of food supply for California steelhead, Beakes et al. (2010) confirmed previous work indicating that the decision whether to smolt in a given year is based on growth rates the previous year, and that early size advantages are maintained over the year. Lee et al. (2010) showed that in three-spined sticklebacks, compensatory growth after cool temperature-induced slow growth negatively impacted swimming endurance, especially when it occurred near to the breeding season. Armstrong et al. (2010) found that juvenile coho salmon in the Wood River system in Alaska can only benefit from eating sockeye eggs if they are large enough to swallow them. Because growth rates are very temperature-dependent, coho juveniles in warmer streams were able to exceed the 70mm size limit necessary for eating the highly nutritious eggs. This enormous nutrient gain led to a highly non-linear response of growth rate to temperature.

8.2.3 Assessment of survival and growth risks from climate change in European salmonids

Elliott and Elliott (2010) reviewed the temperature limits for European salmonids in regard to survival, feeding and growth. They did not find evidence of local

adaptation (within species) in temperature tolerance, although there were marked differences in the upper thermal limits among species. They described the relationship between the North Atlantic Oscillation and emergence dates and adult return ages and rates. Using a growth model under climate change conditions, they predicted improved growth and earlier smolting in brown trout (age 1 instead of 2) except under the most extreme conditions ($>4^{\circ}\text{C}$), but suggested eggs of Arctic charr in some streams in southern Britain and Ireland might be at risk from high temperatures and low oxygen content. They noted several examples in which fish preferred cooler temperatures despite low oxygen levels over warmer temperatures with more oxygen, and emphasized the importance of maintaining deep pool refugia.

8.3 Behavioral and survival responses to winter conditions

Several papers described *in situ* behavioral responses to environmental conditions, especially concealment behavior and nocturnality. Winter (cold) temperatures tend to induce concealment behavior in both Grande Ronde River Chinook salmon (Van Dyke et al. 2010) and Oregon steelhead (Reeves et al. 2010), but Reeves et al. (2010) found that the response was stronger in a montane population than a coastal population. Reeves et al. (2010) also found an increase in nocturnality was more pronounced in winter in the montane population. Orpwood et al. (2010) found that riparian cover increased concealment and nocturnality in both summer and winter, regardless of food supply.

Linnansaari and Cunjak (2010) found that juvenile Atlantic salmon mortality or emigration over winter in New Brunswick, Canada was highest in early winter, before ice formation, and mortality was low during ice cover. They noted that this suggests that warmer winters that have shorter ice cover will not necessarily improve survival. Furthermore, they found that high discharge events and early maturation lowered apparent survival, although the latter might have been related to spawning-related dispersal.

One additional study (Pettersson et al. 2010) compared the suitability of different diets for aquaculture, but found that swimming ability at low temperature can be greatly impaired by an inadequate composition of fatty acids. This could have implications for wild fish if prey availability changes.

8.4 Juvenile residency, migration timing and straying responses to growth and environmental conditions

Life history diversity is a profoundly important issue in relation to environmental variability, both in facilitating a rapid response to directional environmental change and in maintaining bet-hedging strategies in case of unpredictable environmental conditions. One key trait in salmonids that is very sensitive to environmental conditions is the decision of whether to migrate to sea or not, and if they do migrate, when do they do it, and do they return to the natal rearing grounds to spawn or do they stray to a new location. Papers published in 2010 addressed all of these issues.

Johnson et al. (2010) showed that resident and migratory life-history forms of cutthroat trout were not genetically differentiated in two lower Columbia River tributaries (Abernathy Creek and the Chinook River). This study showed that resident and migratory families were not reproductively isolated, but not whether there is genetic basis to the

behavior (a genetic basis has been found with brook and rainbow trout). Thus it is still not completely resolved whether the long-term trend in these populations toward residency is an evolutionary or plastic response.

Steelhead/rainbow trout also have significant variation among populations in the probability of migrating to sea. Satterthwaite et al. (2010) built on previous models to argue that reduced smolt survival is the most important vital rate that could drive anadromous populations toward residency. The next most important rate was freshwater survival and growth.

Reed et al. (2010a) also found a strong relationship between smolt size and timing and growth opportunities. They found that sockeye salmon outplants from the same hatchery smolted earlier and at a larger size when they reared in a more productive lake, despite negative density dependence. They also had higher marine survival.

Morita and Nagasawa (2010) focused on the rate of maturation of age 0+ males and females in relation to temperature and latitude within Japan. Masu salmon matured as parr at higher rates in warmer streams, and May stream temperature was the best predictor of maturation rates across 12 populations. Furthermore, masu matured at smaller sizes in warmer streams.

8.5 *Freshwater ecosystem processes*

A variety of studies explored the effects of changes in temperature and flow on freshwater plankton communities. For example, raising the temperature reduced mean body size and prevalence of smaller phytoplankton, and total phytoplankton biomass (but not zooplankton, Yvon-Durocher et al. 2010), affected trophic dynamics (predator impact) and carrying capacities in bacteria-protist mesocosms (Beveridge et al. 2010) and increased overall productivity (Stich and Brinker 2010). Variation in the seasonality of flow (increased winter and decrease summer flow) increased phytoplankton abundance (Jones et al. 2010).

Moore and Schindler (2010) showed that insects in Alaskan streams with large salmon populations have adapted to salmon phenology by developing faster than insects in non-salmon streams so that they emerge prior to spawning, and the enormous habitat disturbance salmon create by digging redds.

McDermott et al. (2010) studied the development of hyporheic communities in recently de-glaciated streams in Alaska. These communities were negatively affected by redd-digging.

9 Environmental impacts on salmon marine stages and marine ecosystems

9.1 *Smolt timing and early ocean survival*

When salmon migrate from fresh to saltwater, they must balance the opportunities and constraints in both habitats. As discussed above, growth rates strongly influence whether and when to smolt from a freshwater perspective, and better growth might lead to earlier smolting or larger smolts (or both, e.g., Reed et al. 2010a). Similarly, some interference with the natural growth or behavioral pattern by stocking at an inappropriate

time can lead to delayed smolting (Skilbrei et al. 2010). Kennedy and Crozier (2010) showed a trend from 1978 to 2008 toward earlier smolting in wild Atlantic salmon in the River Bush, Northern Ireland. The emigration has shifted 10-14 days (depending on whether one tracks the start of the emigration or the peak emigration date), which correlates with the 5th day of river temperatures over 10°C. Nonetheless, marine survival has declined dramatically (from 30-35% early in the time series to 5-10% more recently), which the authors attributed to increasing disparity between river and ocean temperatures. Thus despite apparent tracking of some thermal cue for smolting, river temperatures still increased too fast to avoid a potentially dangerous differential (2.5°C) between river and ocean temperatures. It is not clear whether other aspects of marine conditions could be driving the population decline.

Smolt timing is well-known to be population-specific, presumably reflecting adaptation to the particular balance of trade-offs between freshwater and marine growth and survival at a given location. Spence and Hall (2010) analyzed the large scale geographic patterns in smolt timing across 53 coho populations from Alaska to central California, and found very strong geographic clustering of smolt timing, duration and variability with oceanographic zones. They suggested links to the predictability of ocean conditions. Because climate change might directly alter the timing of maximal ocean productivity and predictability, meaning specifically interannual variation in the optimal arrival time for smolts, these observations have important implications. Spence and Hall (2010) found that high latitude (mostly Alaskan) populations smolt relatively late, over a short temporal window, and with very little variability from year to year. They argued this is adaptive given the high predictability of the photoperiod-driven increases in productivity characteristic of the Arctic ocean. Southern populations (mostly Oregonian and Californian) that migrate into an ocean dominated by upwelling dynamics tend to enter earlier, but over a much larger temporal window. They argued that this is a bet-hedging strategy given the high interannual variability and unpredictability (from freshwater locations) of the spring transition. They also identified a third cluster in a transitional area mostly from British Columbia and Washington that were intermediate in smolt characteristics, and mostly migrated into buffered areas of Puget Sound and the Strait of Georgia. Although they also discussed alternative explanations and additional important factors, such as natal site elevation, migration distance, and watershed and stream size, these other factors are less likely to change with climate change.

What determines optimal ocean arrival timing is not well understood. Nonetheless, juvenile salmon survival is correlated with forage fish abundance, possibly because they provide alternative prey for predators. Zooplankton or food supply has also been identified as important. Kaltenberg et al. (2010) described the phenology and patterns of variability of forage fish and mesozooplankton populations near the Columbia River plume in 2008 and 2009. Kaltenberg et al. (2010) found a very sudden appearance in mid-May both years of large schools of forage fish which corresponded with similar sea surface temperature, salinity, and river flow (from the Columbia) each year. Zooplankton peaks occurred throughout the spring and summer as fronts passed over the sampling stations, and thus did not show strong seasonality compared with the forage fish. Litz et al. (2010) found that forage fish switched from eating mainly dinoflagellates early in 2005, during the very delayed upwelling season, to a mostly diatom-based food

source after the more normal upwelling season of 2006. They based this conclusion on lipid and fatty acid composition of the forage fish.

Chittenden et al. (2010) analyzed the survival of coho from Seymour and Quinsam Rivers, British Columbia 2007-2009, as a function of release date and marine plankton productivity. They found that coho stayed in the estuary during low marine productivity. Fish that arrived during zooplankton blooms passed quickly through the estuary and had the highest marine detection rates and smolt-adult survival (1.5-3x higher). The optimal time in both years was intermediate among the release groups.

MacFarlane (2010) measured growth in the San Francisco Bay estuary and coastal ocean over 11 cohorts. They found that the first month following ocean entry was critical for subyearling Chinook. They found very little growth accrued in the estuary, but far better growth upon arrival in the ocean. Higher salinity and lower freshwater outflow produced better growth in the estuary, while cooler temperatures, lower sea level, and greater upwelling improved growth in the ocean. They concluded that climate change conditions would yield reduced growth.

Juvenile salmon presumably do not always encounter adequate food resources. To develop a reference point for interpreting the amount of deprivation that marine fish experience, Fergusson et al. (2010) conducted a laboratory starvation experiment and compared various indices of condition with that usually observed in wild-caught Southeast Alaskan chum salmon in 2003. They found that whole body energy content, percent moisture content, and condition residuals were better indicators of starvation than weight or length, and that after 10-15 days of starvation, laboratory fish fell outside the range normally observed in wild fish.

Two studies found that sea surface temperatures during the first year in the ocean best explained adult returns. Focusing on 24 stocks of northwest Pacific Chinook salmon, Sharma and Liermann (2010) found that the PDO and ENSO indices explained much less variation in recruitment than local sea surface temperatures, which were strongly affected by the strength of upwelling and hence reflected more information about ocean productivity than basin-wide average temperatures. They simulated the effect of a 1°C change in SST, and found a 13% decline in productivity on average across populations. However, the only one population from the Columbia River was included in this analysis, Deschutes River fall Chinook, and this population showed a minimal effect of ocean predictors (SST, PDO and ENSO). Saito et al. (2010) studied the factors that best predicted smolt-adult return rates of chum salmon in Nemuro Strait in Hokkaido, Japan, 1999-2002. They found that somatic condition and growth rates during the coastal residency period (first 2-3 months in the ocean) did not predicted adult returns. Instead, sea surface temperatures during the first year (especially winter) in the ocean and the size of smolts at release best explained variation in smolt-adult returns.

Petrosky and Schaller (2010) found that warm ocean conditions in March, reduced upwelling in April, and slower river velocity (or additional trips through powerhouses at dams) during the spring migration period were the best predictors of poor ocean survival for both Chinook and steelhead. They recommended increasing spill to help compensate for lower flows and poorer ocean conditions due to climate change.

9.1.1 Algal bloom lowers survival

Although most studies of early marine survival focused on food availability and predation, algal blooms can cause high mortality in Fraser River sockeye salmon. Rensel et al. (2010) found that earlier and larger spring and early summer Fraser River flows were linked to major blooms of harmful raphidophyte flagellate *Heterosigma akashiwo* in the Strait of Georgia. Chilko sockeye salmon survival declined from 10.9% in non-bloom years to 2.7% in bloom years.

9.2 Marine habitat usage

Several studies have focused on ocean habitat usage, especially thermal preference. NOAA scientists have documented a strong aversion to temperatures over 19°C in the Columbia estuary. This is a strong limitation on habitat usage in the late summer, when juvenile salmon were once abundant (Dan Bottom, personal comm., technical reports). Peterson et al. (2010) synthesized 15 years of survey data to describe the distribution of yearling coho and Chinook salmon distribution and abundance in June and September (after leaving the estuary). The species differed in depth preference and distance offshore. Higher catches correlated positively with chlorophyll and copepod biomass in both species, and with temperature in Chinook salmon. Duffy et al. (2010) described Chinook salmon diet and habitat usage in Puget Sound. “At nearshore sites, insects (all months) and gammarid amphipods (July) were dominant prey sources, whereas in offshore diets decapods (primarily crab larvae; July) and fish (September) were most important.” They emphasized that the terrestrial sources of many of the prey items demonstrates an important link between waterfront landuse and salmon survival.

Based on trawl data, Morita et al. (2010a) found that larger and older adult sockeye, chum, and pink salmon inhabited cooler areas than smaller and younger salmon. Using this information, Morita et al. (2010b) developed a bioenergetic model explaining this pattern as a function of the optimal temperature for growth decreasing with body size, which was validated with a laboratory experiment. They concluded that the negative effects of climate warming on growth will be more severe for larger fish. Radchenko et al. (2010) described the results from surveys in the eastern Pacific, documenting the location of salmon and many other ecosystem components in 2009.

Using a combined bioenergetic-ecosystem model, Kishi et al. (2010) explained trends of declining body size in chum from 1970 to 2000 in terms of reduced densities of zooplankton and rising sea surface temperatures. They then characterized suitable potential ocean habitat for Hokkaido chum as 8-12°C in the summer and 4-6°C in the winter, based on survival studies and relationships between CPUE and SST. Using global circulation models to simulate global warming conditions, they predicted future distribution shifts: loss of habitat in the eastern North Pacific (Gulf of Alaska), and a northward shift in the Arctic Ocean. Furthermore, they predicted a lower carrying capacity in several areas. Finally, they predicted the current migration route to the Sea of Okhotsk will become unsuitable by 2050. Somewhat along similar lines, Genner et al. (2010) analyzed trends in size and abundance in the English Channel from 1911 to 2007, and found that smaller-sized fish fluctuated in abundance with temperature, showing quick responses to environmental change. Larger-sized fish, however, showed persistent

declines in the larger size classes and overall abundance, perhaps due to size-selective overharvesting.

9.3 Biological Implications of ocean acidification

Literature on how ocean acidification (OA) will affect marine species and communities is exploding, making a complete review beyond of the scope of this report. A recent meta-analysis of the impacts of OA on marine species indicated that there is significant variation in how sensitive marine species are to OA, and, if sensitive, what aspect of organismal biology changes in the face of low pH (Kroeker et al. 2010). However, in general, when all taxa are pooled, OA had negative impacts on survival, calcification, growth and reproduction (Kroeker et al. 2010). Here, we focused on laboratory experiments that explored the sensitivity of fish and salmon prey to OA.

Given the paucity of research, it is impossible to conclude whether the direct and indirect impacts of OA on salmon prey, as a whole, will be positive, negative, or neutral. Development timing of amphipods increased in response to low pH conditions, which may negatively impact population dynamics of this important food source (Egilsdottir et al. 2009; Hauton et al. 2009). Pteropod calcification rate declined with ocean pH, although pteropods can calcify below an aragonite saturation state of 1 (Comeau et al. 2010a; Comeau et al. 2009a; Comeau et al. 2009b; Comeau et al. 2010b). Pteropods in the laboratory survived without shells (Comeau et al. 2010a), though their ability to do this in the field is unknown. How OA affects pteropod population dynamics is also unknown, but energetic challenges (e.g., respiration rates) increase (Comeau et al. 2010b). A study on Antarctic krill indicated that OA is unlikely to affect the progression of early development until CO₂ levels exceed 1000ppm (effect observed at 2000ppm; Kawaguchi et al. 2011). Surface oceans may reach this level by 2100, though deep, cold water may exceed it sooner. The impact of OA on copepods varied with species and life stage, but includes evidence for increased nauplius mortality and decreased egg hatching rate (Kurihara and Ishimatsu 2008; Kurihara et al. 2004a; Kurihara et al. 2004b; Mayor et al. 2007; Pascal et al. 2010). In addition, high CO₂ levels countered some toxic effects of cadmium and copper ions on benthic copepods (Pascal et al. 2010). However, mercury and silver accumulation in *Loligo* squid paralarvae increased with CO₂ levels, which has implications for transfer of metals through food webs (Lacoue-Labarthe et al. 2011).

The role of gelatinous zooplankton in North Pacific ecosystems is steadily increasing. Analysis of time series data from the North Sea showed a negative correlation between gelatinous zooplankton and pH (Attrill and Edwards 2008; Richardson et al. 2009; Richardson and Gibbons 2008), although asexual reproduction and polyp survival in *Aurelia labiata* were not affected by OA in the laboratory (Winans and Purcell 2010).

The direct impacts of OA on salmonids are uncertain, especially because the species group spends its early life stages in fresh, not marine, waters. In the last BiOp, we reported no effect of pH 7.0 on *Salmo salar* mortality, growth, condition, metabolism, or plasma pH, hematocrit, sodium, or chloride (Fivelstad et al. 1998) and impairment of olfactory abilities in tropical clownfish (Dixson et al. 2010; Munday et al. 2009b). Recent research provides more insight on how fishes may respond (or not) to OA: 1) increased otolith size in some but not all species (Checkley Jr. et al. 2009; Franke and Clemmesen

2011; Munday et al. 2011a; Munday et al. 2011b), 2) erosion of auditory based behavior and induction of behavior linked with higher mortality due to predation in a tropical clownfish (Munday et al. 2010; Simpson et al. 2011), 3) decrease in aerobic scope in two tropical coral reef fishes (Munday et al. 2009a), 4) upregulation of some proteins in stickleback and cod and RNA expression in Atlantic herring (Franke and Clemmesen 2011), 5) no impact on early development (survival, growth, skeletal development) in a tropical damselfish and Atlantic herring (Franke and Clemmesen 2011; Munday et al. 2011a).

Two recent modeling papers explored the ecological impacts of OA and other aspects of climate change. Ainsworth et al. (2011) predicted that ocean acidification may cause salmon landings to decrease in Southeast Alaska and Prince Williams Sound food webs and increase in Northern British Columbia and Northern California Current food webs. However, when the authors applied five impacts of global change to these food webs simultaneously (primary productivity, species range shifts, zooplankton community size structure, ocean acidification, and ocean deoxygenation), projected salmon landings decreased in all locales (Ainsworth et al. 2011). Incorporating ocean acidification and ocean deoxygenation into bioclimatic envelop models for harvested fishes in the Northeast Atlantic caused 20-30% declines in projected future harvest, likely due to reduced growth performance and faster range shifts (Cheung et al. 2011). This study is informative to Pacific salmon management as it indicates how changes in physiological performance of finfishes due to ocean acidification may impact harvested populations.

9.4 *Ocean ecosystem effects*

9.4.1 Evidence of changes in Arctic marine ecosystems

Of the global reviews of documented changes in biota that appear to be responses to climate change, very few have focused on marine ecosystems. Thus the review of the “footprint” of climate change in Arctic marine biota by Wassmann et al. (2010) fills a very important hole. Wassmann reviewed 13 studies of benthos, 9 studies of fish (5 on cod, 2 on pollock, 1 each for turbot and pipefish), 7 studies of birds (5 species), 9 studies of polar bears, 2 seals and 1 whale. Responses ranged from behavioral to growth to range shifts and community reorganization (Greenland cod and shrimp). Most observations are consistent with predictions from climate change simulations: increased primary productivity, declines in endemic, ice-associated species, and invasions or increases in more temperate zone species. One study documenting a change in primary producers was Kahru et al. (2010), who showed that the annual phytoplankton bloom maximum has advanced by up to 50 days in certain areas of the Arctic, with significant trends in 11% of the Arctic Ocean, primarily reflecting the reduction in sea ice. Bloom timing has also advance in the North Pacific.

9.4.2 Ecosystem models

Several very complex models explored the ocean ecosystem dynamics of climate forcing and climate change. Popova et al. (2010) focused on the Arctic Ocean under current conditions, and found that two key processes drove variability in primary

production: the extent of winter mixing and short-wave radiation at the ocean surface, which controls phytoplankton blooms.

Two studies analyzed climate change simulations. Rykaczewski and Dunne (2010) used NOAA's Geophysical Fluid Dynamics Laboratory earth system model to study changes in nutrient supply and productivity of the California Current Ecosystem. They focused on nitrate because it is the main nutrient limiting primary production in the CCE. The model predicted a 2°C rise in ocean temperatures across the basin from 1860 to 2100 under the SRES A2 scenario. They found weaker wind-stress curl, which reduced the strength of upwelling (and downwelling, in the subtropical gyre), but other changes produced a modest increase in upwelling. They note, however, that global models might not have sufficient resolution to fully represent upwelling dynamics. Despite increased stratification, they predicted an 80% increase in nitrate concentration by 2100 in the upper 200m of the CCE, but decreases elsewhere in the Pacific. The increased nitrate concentration in the CCE comes mainly from longer transit times of deep water that are subsequently upwelled. This water is also more depleted in oxygen (18%) and more acidic (0.5 pH units). This produced a net increase in productivity of 10% in the CCE presumably benefitting surface feeding fish, but more frequent hypoxic events threatening benthic and mid-water fauna.

Steinacher et al. (2010) compared four coupled global carbon cycle-climate models that incorporated marine biogeochemical-ecosystem models. All four models predicted a decreasing trend in global net primary production and particulate organic carbon export. The models all predicted increasing temperature and stratification in all regions and increasing light in the Arctic where sea ice retreats. The high-latitude ocean retained sufficient nutrients to increase primary production and particulate organic carbon export (with increases in the Bering Sea). Nonetheless, they still projected declines in biomass throughout the north Pacific. They discussed differences among the models compared in quantitative predictions. Despite broad agreement on a regional scale, none of the models appear to do exceptionally well at modeling the coastal Pacific Northwest and Alaska (hence the upwelling-specific analyses described previously). Brown et al. (2010a) also predicted increases in primary productivity around Australia, benefitting fisheries and threatened turtles and sharks. They cautioned that the ecological benefit is sensitive to species interactions, which could reverse the benefit for some species.

Several studies in the San Francisco Bay estuary described complex physical and biological processes. MacNally et al. (2010) analyzed the factors affecting the decline of four pelagic fish in the San Francisco estuary. A combination of physical and food web driven factors suggested a diverse array of factors are responsible, but changes in freshwater flow and water clarity had strong effects. The results suggested a relatively good understanding of the ecosystem, but few management options. Cloern et al. (2010) described strong effects of the PDO and the NPGO on demersal fish, crabs and shrimp in San Francisco Bay. They emphasized the interconnectedness of the estuary in linking oceanography and watershed hydrology.

9.4.3 Seabirds, rockfish, and sharks

Several studies explored potential impacts of climate on seabird populations. Wolf et al. (2010) predicted 11-45% declines in Cassin's auklet in response to climate change. Ainley and Hyrenbach (2010) explored bottom-up and top-down drivers of a

large number of seabird species in the California Current. Black et al. (2010) analyzed ocean drivers of seabird and rockfish dynamics, emphasizing the importance of February ocean conditions.

Williams et al. (2010) documented very large aggregations of 20,000 sharks in the western Queen Charlotte Sound, British Columbia in a 2004-2006 study. Although it is not absolutely certain that this is a new phenomenon, it has not been documented until recently, and they suggested that the aggregations might be a response to rising sea temperatures. The sharks might present a “feeding gauntlet” deadly for Fraser River salmon, that typically prefer the northern migration route through Queen Charlotte Sound during warm years.

In addition to sharks, other marine fish are likely to shift their distribution in response to rising ocean temperatures. In Australia, coral reef fishes usually limited by winter temperature are predicted to survive as far south as Sydney by 2080 (Figueira and Booth 2010).

9.5 Effects on fisheries

Cheung et al. (2010) combined models that predicted increases in primary productivity with bioclimatic envelop models of species distribution to predicted the impact of climate change on fisheries catch for 1066 species of fish and invertebrates (assuming the geographic location of the fishery doesn't change). They predicted a 30–70% increase in high-latitude catches, including Alaska, a decline of about 10% in the contiguous US, and a drop of up to 40% in the tropics. MacNeil et al. (2010) similarly concluded that Arctic fisheries will benefit from invasions of southern species and increased primary productivity, while there will be species turnover in the temperate zone and significant losses in the tropics.

9.6 Review of hypotheses/frameworks for ocean climate forcing fish populations

Two papers present overviews of the prevailing physical and ecological hypotheses or conceptual frameworks currently in the literature on climate-ocean interactions. Ottersen et al. (2010) focused on three major oceanographic phenomena that drive variability in fish recruitment: temperature, mixing, and advection. They discussed the debate on bottom-up versus top-down population regulation, and trophic cascades, and the key role of forage fish as having both effects. They described immediate and delayed effects of climate, and factors that differentiate local climate drivers from large-scale climate processes such as the NAO and the PDO. They discussed direct, indirect, integrated (i.e., processes that occur over longer time scales than a particular extreme climate event) and translation (i.e., organism movement) effects of climate drivers. Any of these responses might be linear or nonlinear, at the individual or community level. They then detailed specific geographic regions and their particular climate-ecological dynamics. In the Northeast Pacific they emphasized ENSO and the PDO and biological responses. They finally discussed teleconnections and regional differences between the Atlantic and the Pacific.

Bakun (2010) reviews a number of different concepts of population regulation, such as the match-mismatch hypothesis, issues with schooling fish, and the predation

risk-nutrient level trade-off (which he calls “loopholes”). Bakun emphasized three major physical processes that provided favorable conditions for fish: nutrient enrichment through upwelling or mixing, concentration through convergence or front formation, for example, and retention processes, such as eddies. Overall this paper emphasized that oceans are complex adaptive systems, and cautioned against assuming simpler concepts from the terrestrial literature adequately capture their complexity.

10 Impact of temperature and flow on adult migrants

10.1 Migration bioenergetic cost

Upstream migrating salmon face several additional stresses due to climate change. Most importantly, rising temperatures increases the metabolic cost of swimming and holding prior to spawning. Cumulative energetic costs or acute thermal stress also increase prespawn mortality. Several papers studied the bioenergetics of migration, which are relevant for calculating these costs. Clark et al. (2010) developed a biologging tag technique for measuring energy expenditure and heart rate in actively migrating sockeye. Cook and Coughlin (2010) found that rainbow trout alter their kinematics around obstructions in the water in a way that improves their efficiency. Forgan and Forster (2010) explored the physiology of oxygen consumption in different tissues. Nadeau et al. (2010) analyzed the relative costs of swimming in the lab against low and high flows that span much of the range typical for Fraser River sockeye. They found that higher flows elevated stress, but not mortality. However, overall females had higher mortality than males. Roscoe et al. (2010) studied the behavior of natural migrants through a lake with cooler bottom water. They found that more mature females with lower energy content preferred the cooler water, while other females and males showed less preference. They posited that use of the thermal refuge slowed maturation and helped maintain energy reserves.

10.2 Migration survival and timing

Migrating upstream is an energetic and thermal bottleneck for many salmon populations. New papers clarified the role of temperature in stimulating upstream migration in a very warm river (the Klamath), and the relationship between timing, temperature, flow, and survival in the cooler Fraser River. Projections in the Fraser River of the consequences of warming over the next century are especially dire.

In the Klamath River, Strange et al. (2010) found that Chinook volitionally migrated through much warmer water than previously thought. Chinook initiated migration at 21.8-24°C. These high river temperatures produced a mean average body temperature of 21.9°C, and mean average maximum body temperature of 23.1°C over the first week of the migration. These temperatures usually cause migration blockages in the Columbia River, but apparently reflect adaptation to the much warmer conditions in the Klamath. Declining temperatures triggered migration, even when the river was still very hot. It is not known whether these fish experienced high prespawn mortality or reduced fecundity or fertility. In the Fraser River, several new papers showed a positive correlation between river temperature and mortality. MacDonald et al. (2010) developed a forecasting model for fisheries managers to facilitate real time predictions of migration

survival for various groups of populations. They found that temperature, flow, the timing of entry relative to the average for that population, and fish abundance were good predictors of migration survival. Interestingly, the best predictors did not necessarily match the *a priori* prediction based on the absolute environmental conditions. For example, temperature was an important predictor for Early Stuart sockeye, even though these fish encounter relatively lower temperatures than other fish. The authors point out that these fish still encounter high temperatures upstream, and that they might have lower thermal tolerances than other populations.

Several papers simulating future conditions in the Fraser River predicted significant declines in sockeye salmon. Hague et al. (2011) found that a 1.0 °C increase in average summer water temperature tripled the number of days per year exceeding critical salmonid thermal thresholds (i.e. 19.0 °C). Martins et al. (2011) found evidence of thermal stress-induced mortality during the migration in three of the four stock-aggregates examined. Under warming scenarios, migration survival in these stocks was projected to decline 9-16%.

Particular attention has focused on the unusual behavior among some Fraser River sockeye populations of migrating much earlier than the historical norm. The early migrants experience much higher temperatures than normally-timed fish, and have significantly lower survival. Mathes et al. (2010) found that early migrants that utilized cool lake habitat as a thermal refuge during their migration had much higher survival than fish that took the river corridor directly to spawning grounds. The early-entry river migrants accumulated extraordinarily high cumulative temperatures and none survived. The early-entry lake migrants had similar cumulative thermal exposure to normally-timed fish that stayed in the river, and similar survival. Donaldson et al. (2010) compared physiological responses to stress (gillnet capture), migration rate and survival in Adams-Shuswap and Chilko populations. The unusually early migrants of the former migrate at the same time as the normal-timed migrants of the latter population. They found delayed effects (near spawning grounds) on survival that differed between the populations. Although the two groups had similar physiological condition when they entered the river, survival among the early-entry Adams-Shuswap group correlated with migration rate (slower migrants had lower survival) and physiological condition (metabolic and osmoregulatory impairment), but not among the Chilko fish.

In the Columbia River, Jepson et al. (2010) studied the migration timing of fall Chinook. They found clear differentiation between the Upper Columbia River and Hanford Reach populations, but Deschutes, Yakima, and Snake River populations migrated throughout the season. They also found harvest was concentrated in late August and early September, and preferentially selected larger fish.

10.2.1 Traditional tribal knowledge and effects of climate change on migration survival and timing

Jacob et al. (2010) described the effects of changes in the salmon runs on native people, and the very serious long-term implications of climate change for both people and fish. Through interviews, they identified changes in salmon abundance (diminished), timing (later in summer and fall), and condition (much less healthy, both in fat content

and disease prevalence) from people's recollections of traditional conditions. They discussed potential adaptations, but predicted relatively poor prospects for both people and fish.

11 Impact of high temperatures on prespawn mortality and spawning behavior

11.1 Diseases

The prevalence and virulence of many diseases in fish are much more severe under warmer conditions, and several papers reported disease spread over recent years. Marcos-Lopez et al. (2010) reviewed the increasing risk from a number of diseases (e.g. enteric red mouth, furunculosis, proliferative kidney disease and white spot) due to climate change. The risk from some exotic pathogens that prefer cool water declines (e.g., viral haemorrhagic septicaemia (VHSV), infectious haematopoietic necrosis virus (IHNV) and spring viraemia of carp virus (SVCV), while the risk from warm-loving exotic pathogens (epizootic haematopoietic necrosis and epizootic ulcerative syndrome) increases. They recommended revising management actions to control disease to take into account changing risk levels due to climate change.

Braden et al. (2010) reported spread of proliferative kidney disease (PKD) in natural populations of pink salmon in Quinsam river, Vancouver Island. Bradford et al. (2010) reported widespread prevalence (70% of samples) of the myxozoan parasite *Parvicapsula minibicornis* throughout the Fraser River watershed, and a very advanced stage of infection in most fish on spawning grounds. Ray et al. (2010) quantified levels of *Ceratomyxa shasta* that kill juvenile Chinook salmon in the Klamath River, improving our understanding of this disease. Tonteri et al. (2010) found selection on immune related genes more common than selection on non-immune-related genes in Atlantic salmon, and that allele frequencies were related to temperature and latitude, suggesting an important role of climate in driving this selection pressure.

Although not directly related to climate change, Koel et al. (2010) reported that Great Blue herons are viable vectors of whirling disease, which affects salmonids in 25 states. Krkosek (2010) warned that sea lice are an increasing threat from farmed salmon in the Pacific, and that the abiotic and biotic factors affecting this disease are not well studied. Pulkkinen et al. (2010) found that fish farms actually select for more virulent strains of *Flavobacterium columnare*, a disease exacerbated by warmer temperatures.

11.2 Prespawn behavior and mortality

Keefer et al. (2010) documented a strong correlation between prespawn mortality in Willamette River Chinook and water temperature and fish condition. Mortality ranged from 0-90%, depending on year and release group. Fish in poor or fair condition had twice the mortality risk of fish in good condition. These fish were transported above a

dam, and thus do not represent a natural migration. Nonetheless, they do reflect a dramatic increase in risk due to high temperatures.

Young et al. (2010) found that over summer, brown trout adults in New Zealand tended to hold in deep pools, and only moved during higher flow events and cooler temperatures (below 19°C). A severe flood killed 60-70% of the tagged population.

11.2.1 A correlation between gene flow and the NAO

Valiente et al. (2010) addressed the population genetic consequences of increased male parr maturation in response to climate change. In addition to describing effects on maturation, they discovered a strong pattern in straying. Specifically, they found a strong correlation between the North Atlantic Oscillation Index and immigration from a neighboring stream. I believe that this is the first study system to document this phenomenon, and hence is especially interesting. They found that straying increased linearly when conditions in the natal stream deteriorated (became too warm). This paper is also especially notable in referring specifically to adverse conditions induced by global warming at the southern edge of a species range.

11.3 Spawning behavior

The timing of reproduction is often crucial in determining successful population growth. How climate change will affect spawn timing raises concern because of high risks of prespawn mortality with lengthening freshwater residence, extreme sensitivity of eggs to high temperature (compared to other life stages), and the potential for a mismatch between emergence suitable environmental conditions for fry. Two studies documented long-term shifts in spawn timing in freshwater fish. Wedekind and Kung (2010) showed that European grayling have advanced their spawn timing by more than 3 weeks since 1948, which they attributed to rising temperature. However, a difference between spring and summer warming rates exposed fry to inappropriate temperatures, possibly contributing to population decline. Schneider et al. (2010) showed that walleye are now spawning up to 2 weeks earlier throughout Minnesota (26 populations), with a 0.5-1 day advance for every 1 day advance in ice break up.

Several studies explored the stimulus for spawning. Wilkinson et al. (2010) experimentally manipulated temperature and photoperiod for rainbow trout, and found that under natural photoperiods, elevated winter-spring temperatures only slightly increased maturation rates. Under advanced photoperiod, temperature had a much larger relative effect, but the overall maturation rate was much lower. O'Malley et al. (2010) studied the genetic basis of variation in spawn timing. They compared geographical variation in a gene (*OtsClock1b*) associated with photoperiod among 53 populations of chum, coho and pink salmon. Combined with a previous study of Chinook salmon, they found that daylength at spawn timing explained much of the variation in allele frequencies of *OtsClock1b* in chum and Chinook, but not coho and pink salmon.

In addition to affecting juvenile survival and migration success, temperature and flow affect access to and quality of spawning sites. Taylor et al. (2010) documented the distribution of redds over 12 years in a Nova Scotia stream in relation to the timing and intensity of fall rains and beaver dams. They found that stream usage by salmon was

linearly related to precipitation, except when blocked by beaver dams. Moir and Pasternack (2010) described a strong positive relationship between substrate coarseness and faster flow in Chinook salmon spawning site selection, demonstrating interactions between habitat characteristics that are not always included in habitat suitability analysis.

12 Direct heat stress

Several papers studied direct heat stress, population variation in heat tolerance, and its genetic basis. Bellgraph et al. (2010) found that juvenile Chinook salmon survived temperatures up to 23.2°C. The fish increased swimming behavior and heart rate under higher temperatures. Brook char reduced swimming performance at temperatures over 15°C, especially in combination with ammonia (Tudorache et al. 2010). Feldhaus et al. (2010) found that redband trout amplify production of heat shock proteins (hsp70) between 19 and 22°C, indicating thermal stress. Healy et al. (2010) studied the genetic basis of variation in the heat shock response in killifish, and found a fairly complicated pattern. They concluded that variation among subspecies must be due to more than simple upregulation of a particular regulator, but involves evolution in a variety of genes. In a comprehensive review, Pankhurst and King (2010) explained the physiological processes mediating the negative effects of high temperature on reproduction.

Sublethal temperature effects interact with other stressors. Boyd et al. (2010) found higher mortality after catch-and-release under elevated temperatures in the evening in rainbow trout. A very large fish kill (25,000 carp) occurred in the St. Lawrence River in 2001, which Ouellet et al. (2010) attributed to a combination of high air temperature and low flow, which depleted oxygen in the lake. They also discussed indirect effects of long-term stress, such as immunosuppression.

Pörtner (2010) reviewed the concept of oxygen supply to the tissues being the fundamental process that determines thermal windows, and as a means for understanding the synergistic effects of multiple stressors. Ocean hypercapnia and acidification interact with warming temperature to further reduce oxygen availability. On the other hand, exposure to high CO₂ also depresses metabolic rates, which might help tolerate reduced availability of oxygen. This fundamental process is general, and hence not species-specific. Seebacher et al. (2010) made an analogous argument that the fundamental limiting factor is cellular damage from the production of reactive oxygen byproducts of metabolism.

13 Higher-level processes

13.1 Population-dynamics modeling

Key to understanding the factors regulating salmon populations (which is essential for predicting effects of climate change) is an appreciation of how different scales of variability interact with the internal periods of variation inherent in populations with overlapping generations. Worden et al. (2010) studied the frequencies of population variability as a function of 1) environmentally-induced variation in survival in the first

ocean year only, 2) environmentally-induced variation in survival in all ocean years, and 3) environmentally-induced variation in the age at reproduction. They considered these effects within the larger context of increased variability due to fishing mortality, and different censusing techniques. They found different patterns of fluctuations in all the different scenarios explored. Salmon are more sensitive to some time scales of environmental variability than others, and with fishing they are doubly sensitive to low frequency environmental variability. Long-term changes in climate could thus interact with additional fishing-induced variability to induce fluctuations that pose much greater risks of population collapse than that induced by reduced abundance alone.

Two papers focused on the mathematical properties of population decline to extinction when environmental factors are driving the decline, and provide tools for identifying this trajectory. Drake and Griffen (2010) identified an early warning signal that anticipates a tipping point, beyond which extinction is almost inevitable. The early warning signal is a “critical slowing down”. They demonstrated the statistical properties of this signal using an experimental *Daphnia* population. A reliable baseline prior to environmental degradation is crucial for successful application of this technique. Ovaskainen and Meerson (2010) reviewed recent advances in theoretical physics that characterized the properties of stochasticity useful for determining mean extinction times under various conditions.

Animals often compensate for environmental variability through phenotypic plasticity, i.e., modifying their behavior or physiology in response to environmental conditions. Reed et al. (2010b) focused on the adaptiveness of phenotypic plasticity. Specifically, they demonstrated that plasticity is only adaptive when there is a reliable cue that anticipates environmental conditions. When the cue becomes less reliable (which might result from different aspects of climate changing at different rates, for example), plasticity shifts from being adaptive to increasing population extinction risk. They emphasized that population models will need to explicitly incorporate plasticity to include this potential effect.

13.2 Population-level effects

13.2.1 Population declines attributed to climatic factors

Clews et al. (2010) studied how environmental variation correlated with population fluctuations of Atlantic salmon and brown trout in Wales from 1985 to 2004. Local catchment processes were not useful in explaining population decline, but broader scale climatic variables correlated strongly with population densities. They found that weather conditions in the previous summer explained most of the variation. Specifically, a principle component analysis showed that reductions in density were highest following hotter, sunnier, and drier conditions. Over the course of the study, summer stream temperatures were estimated to have increased by 0.5°C in headwaters and 0.6°C in larger tributaries, and in winter by 0.7°C and 1°C, respectively. This amount of warming could explain on the order of a 40% decline in density (or ~3-3.5 fewer salmon per 100m²), based on the principle component score (which also includes discharge). Winter warmed more than summer due in part to trends in the NAO, but was not strongly correlated with salmon abundance. The similarity in response between the anadromous salmon and

freshwater resident brown trout indicates that freshwater indices are either driving the declines in both species, or are correlated with ocean phenomena in salmon.

After a comprehensive physical and biological assessment, Wiseman et al. (2010) found that warm water temperature and sedimentation were the primary drivers of habitat decline in the Touchet River in Washington, contributing to contraction of spring Chinook, summer steelhead, and bull trout.

Robinson et al. (2010) reported that stressful summer temperatures (determined by cumulative degree days over 20°C measured at the bottom of an Adirondack lake) reduced stomach fullness, reproductive activity, and survival of brook trout over one year old, and especially fish over two years old. Like Crozier et al. (2010), they found a positive correlation between temperature and growth at low fish density, and a negative correlation at high fish density.

13.2.2 Expert judgment of overall risks to Fraser River sockeye

A synthetic, expert-opinion analysis of the threat of climate change over the entire life cycle of Fraser River sockeye salmon (McDaniels et al. 2010) found that the cumulative threats are very high. A substantial proportion of responses indicated the fish were highly vulnerable (the highest threat level) at all life stages except the overwintering fry stage. They identified the most vulnerable life stages to be the egg and returning adult stage for populations throughout the Fraser River drainage, especially under a +4°C warming scenario. They also considered the prospect of reducing the threat through management quite limited.

13.2.3 Paleological perspective

Finney et al. (2010) conducted a major review of the paleological literature on fluctuations in fish abundance (including salmon) over thousands of years. The most relevant topics focused on positive correlations between SST and salmon abundance in Alaska both recently and over most of the past 300 years and again over 2500 years based on sedimentary collection of marine-derived nitrogen carried into freshwater by anadromous salmon. Anomalies in the SST-salmon correlation occurred in several sections of the long-term record, which the authors attributed to changes in ocean-atmosphere circulation during these periods, producing alternate patterns of North Pacific climate variability relative to the PDO and variation in the Aleutian Low. The longer time series showed a bimodal pattern of fluctuations between low and high abundance, with high abundance during the 1250-1890 AD cooler period of the Little Ice Age. This suggests different longer term patterns than suggested from recent data. They also discussed patterns driving anchovy, sardines, and other major ecosystem players throughout the world, and synchronous shifts in all ecosystems. However, specific relationships varied across the time series between in-phase and out-of-phase correlations, indicating alternative modes of climatic forcing of ecosystem dynamics.

13.3 Trends in phenology worldwide

Worth noting here is that phenological responses to climate change have been observed across all taxa, worldwide. A new review out in 2010 (Thackeray et al. 2010) assessed 25,532 rates of phenological change for 726 UK terrestrial, freshwater, and marine taxa. Most taxa showed earlier spring phenomena at rates higher than previously reported. They separated out taxa at different trophic levels, and found that secondary consumers were responding the slowest, and hence were at most risk of a mismatch in timing between predator and prey. Because this trend was so widespread and not restricted to individual species, it highlights a growing risk of the disruption of ecosystem function and services.

14 Habitat

14.1 Stream flow habitat models

Quite a few papers used models of stream flow (or temperature, covered in the next section) to quantify habitat availability for salmonids. Hilker and Lewis (2010) developed a theoretical model of how water velocity affects potential prey populations subject to advection and diffusion downstream, and the minimum flow requirements for drift-feeders like juvenile salmon. Cover et al. (2010) examined the impact of debris flows and debris floods on headwater stream communities. They found that debris flows raised stream temperature, reduced large wood and benthic communities and most vertebrates, with the exception of rainbow trout, which were abundant in recent debris-flooded areas. Escobar-Arias and Pasternack (2010) developed a functional flows model based on shear stress dynamics to characterize fall Chinook spawning habitat; the model could be parameterized for other species. High flow events provided access to new habitat, which can have both positive and negative impacts on salmon. Access to a floodplain that contains pollutants could be detrimental for juvenile salmon. Henery et al. (2010) showed that growth was higher in free swimming Chinook that utilized the Yolo Bypass floodplain than fish that stayed in the Sacramento River, but that the fish in the floodplain accumulated 3.2% more methylmercury per day than fish in the river.

A large group of scientists worked on a new framework for assessing environmental flow needs for many streams and rivers simultaneously to foster development and implementation of environmental flow standards at the regional scale (Poff et al. 2010), and this can be a basis for initiating an adaptive management program.

14.2 Thermally-suitable habitat models and trends

Enhancing riparian vegetation is a major conservation tool recommended for reducing maximum stream temperatures. Two studies showed strong empirical effects of vegetation on stream temperature. In response to high temperature-induced disease-related fish kills, Roth et al. (2010) developed a physical model of stream temperature in Switzerland. They found that existing vegetation (mostly in-stream reeds) lowered the expected temperature by 0.7°C, but a further decrease of 1.2°C could be achieved by a mature riparian forest. Brown et al. (2010b) found that coniferous forest plantations

lowered summer temperatures in a comparison of 3 forested and 3 moorland sites in northern England.

Statistical models of stream temperature have been used to quantify habitat area that meets particular criteria for species of interest, and to track trends in habitat area over time. Larnier et al. (2010) developed and compared models to identify conditions in the Garonne River in France that are thermally stressful for salmonid migration and survival. Isaak et al. (2010) developed a spatial autocorrelation model to predicted stream temperature throughout the 2500 km² upper Boise River Basin in Idaho based on temperatures measured at particular sites. The model performed well against observed temperatures. Historical analysis showed a trend of mean basin stream temperature from 1993 to 2006 rising at a rate of 0.27°C/decade, and maximum temperatures rose by 0.34°C/decade. They detected a strong thermal signature of wildfires in the basin: stream temperatures in affected reaches rose 2-3 times more than the basin average due largely to increases in radiation. Rising temperatures shifted rainbow trout habitat to slightly higher elevations but caused 11-20% loss of bull trout habitat.

High temperature already threatens some populations in warmer climates. Null et al. (2010) explored restoration alternatives to mitigate stressful temperatures in California's Shasta River. They found that a focused on restoring and protecting cool springs provided the most benefit for salmon (much greater benefit than increasing riparian shading, for example). This conclusion might apply to regions anticipating increasing temperature stress.

14.3 Habitat projections

Wiley et al. (2010) developed a series of models to explore the effects of land cover and climate change on fish habitat in the Great Lakes. They found very significant climate change impacts, and that these impacts were very sensitive to land management. Increasing forest cover and limiting urban development had very large impacts on projected flows, temperatures, and consequently modeled fish habitat. Nonetheless, even the best-case land use scenarios involved destabilization of 57%-76% of the channel system by the end of this century due to increasing rainfall and discharge rates. Summer temperatures rose sharply, with severe consequences for cold-water fish. They projected a loss of ~74% of adult Chinook habitat (but little impact on juvenile Chinook habitat), and the reverse for steelhead: a loss of ~50% of juvenile steelhead habitat, but only ~15% loss of adult habitat. They projected large benefits of climate change for smallmouth bass and walleye.

Several papers explored the potential for riparian vegetation to mitigate future warming. Cristea and Burges (2010) explored climate change impacts in the Wenatchee watershed, a tributary to the Columbia River. They found greater potential for mitigation in smaller tributaries (-1.5°C in Icicle Creek and -2.8°C in Nason Creek) compared with the mainstem Wenatchee River (-0.3°C), due to stream width. The cooling benefit of vegetation restoration will be surpassed by climate change by the 2020s in the mainstem, but postpone stressful temperatures for salmonids in the tributaries until the end of the century, which is a significant benefit.

A study in Scotland (Hrachowitz et al. 2010) produced a comparable result. In this case, however, the highest mean weekly temperatures currently occur in small exposed streams, and these streams are projected to reach extremely stressful

temperatures for salmonids in a + 4°C climate change scenario, which raised the catchment-wide mean stream temperature by 1.4°C. They suggested that vegetation restoration would ameliorate these stresses.

Hill et al. (2010) showed that certain pristine and environmentally heterogeneous areas in northern coastal British Columbia with salmon have high potential resilience, but relatively low productivity, and hence might not be sufficient to maintain a “salmon stronghold”.

14.4 Temperature-driven air pollution

Although mountain areas often support relatively pristine habitat, they are vulnerable to transport of pollutants generated long distances away. In particular, they are especially vulnerable to chemicals that are globally distributed by atmospheric deposition in a temperature-dependent way. Persistent organic pollutants, polycyclic aromatic hydrocarbons, and organochlorine compounds are concentrated in alpine streams because of the strong temperature gradients over short distances. Jarque et al. (2010) studied the response to organochlorine compounds in brown trout from the Pyrenees to Norway. They found biologically significant concentrations of pollutants in fish muscle correlated negatively with lake temperature, but biological activity might increase their negative consequences for fish with climate change

15 Policy/human social factors

Several papers addressed policy and management issues in adapting to climate change. All emphasized the need for more applied science and dialogue between researchers, managers, and the public. Some discussed specific climatic and biological information gaps and agreement, and the need for priority setting (Wilby et al. 2010), while others focused more on human social processes (Perry et al. 2010; Slaughter et al. 2010).

More specifically, Wilby et al. (2010) claim there is a lot of confusion about how best to proceed due to uncertainty in regional climate projections, biological responses, and environmental objectives. They emphasized that certain taxonomic groups are underrepresented in baseline data and impact studies, such as macrophytes, and that whole ecosystem responses need to be understood. Environmental objectives differ across managers, the public, conservation groups, etc., who further have different time frames of concern. They argued that even standard advice, such as increasing riparian shading to lower water temperatures and reducing abstraction from river flows, needs site-specific analysis and comparison with alternative actions before implementation. They argued that information gaps include site-specific information, underrepresented taxa, ecosystem goods and services, and risks and definitions of invasive species, given recommendations for increased connectedness. Overall they recommended more applied interdisciplinary research, adaptive management and cost-benefit analysis, in addition to reevaluation of goals and priorities.

Binder et al. (2010) summarized implications for adaptation based on the Washington State Climate Change Assessment. They summarized key ingredients in

successful adaptation planning, such as political leadership, money, stakeholder engagement, actionable science, triggering extreme climatic events that motivate action and a long-term perspective. To adapt to changing water resources, they recommended expanding and diversifying water supplies, reducing demand, implementing operational changes, increasing summer drought and winter flood preparedness. To protect salmon, they recommended reducing summer stream temperatures, increasing minimum stream flows, and reducing peak winter flows by various means. They warned that these actions will involve more tradeoffs between water for fish and people.

Perry et al. (2010) emphasized that marine ecosystems and human behaviors are interconnected and showed similar features such as variability at many time scales. They suggested that fisheries focused on opportunistic species (e.g., anchovy) provide a model of flexibility that should be adopted by fisheries focussed on traditionally more stable species (e.g., cod) to adapt to increasing variability due to climate change. They cautioned that spontaneous human responses to increasing ocean variability might further de-stabilize marine ecosystem (e.g., switching to un-fished species). They recommended proactive, flexible management and communication among a broad group of stakeholders to prepare for the diversity of stresses coming to marine ecosystems.

Slaughter et al. (2010) argued that the free market (and reduced subsidies) is a better way to address over-allocation of Pacific Northwest water resources than court or regulator mandates in some respects, although both will be necessary.

The Washington State Integrated Climate Change Response Strategy: Species, Habitats and Ecosystems (Brekke et al. 2010) outlines an integrated approach to climate adaptation strategies that applies to a very wide range of ecosystems and threats. They focused on three conceptual approaches – resistance, resilience and response to facilitate natural system responses, and then building scientific and institutional readiness to support adaptation.

In their book, *Climate Savvy*, Hansen and Hoffman (2010) considered how a wide range of resource conservation issues—such as managing invasive species, harvest management, or ecological restoration—will need to change in response to climate change. Climate responses of ecosystems or organisms can be one of three types: resistance (stays the same), resilience (recovers after a disturbance), and response (e.g., movement or change). Key adaptation strategies for managing ecosystems in a changing climate included (1) protect adequate and appropriate space, (2) reduce non-climate stressors, (3) manage for uncertainty, (4) reduce local and regional climate effects, and (5) reduce the rate and extent of global climate change.

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