

Effects of Climate Change on Oregon Coast Coho Salmon: Habitat and Life-Cycle Interactions

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Abstract

Coho salmon (*Oncorhynchus kisutch*) populations that spawn in the coastal rivers of Oregon, U.S.A., formerly supported robust fisheries but are now listed as a "threatened species" under the U.S. Endangered Species Act. Climate change is an increasing concern in salmon conservation, and we assess the effects of climate change on sustainability of this population group. Four distinct habitats are important to different life-history stages of coho salmon: terrestrial forests, freshwater rivers and lakes, estuaries, and the ocean. Each of these habitats is affected by multiple aspects of climate change, resulting in a complex web of pathways influencing sustainability. We summarize regional climate change studies to predict future climate patterns affecting these habitats, identify the ecological pathways by which these patterns affect coho salmon, and review coho salmon ecology to assess the likely direction and magnitude of population response. Despite substantial uncertainties in specific effects and variations in effects among populations, the preponderance of negative effects throughout the life cycle indicates a significant climate-driven risk to future sustainability of these populations. We recommend that management policies for all four habitats focus on maximizing resilience to the effects of climate change as it interacts with other natural and anthropogenic changes.

Keywords: climate change effects; life-cycle assessment; habitat; Pacific salmon; conservation

Introduction

Recent climate change has had widespread ecological effects, including changes in phenology, trophic interactions, range limits, extinctions, and genetic adaptations (Parmesan 2006). In this context, anadromous salmon present a unique combination of life history patterns, and face effects from climate-driven changes in land, river, lake, estuary, and ocean habitats. Beginning in the late 1980s (Regier et al. 1990 and associated papers; special issue of Fisheries 1990. vol. 15 no. 11) numerous papers have been written about climate effects on fish; those specifically relating to Pacific salmon (Oncorhynchus spp.) have recently been reviewed (Battin et al. 2007, Schindler et al. 2008, Crozier et al. 2008a). These studies have identified a number of common mechanisms by which climate influences salmon sustainability, including effects on physiological heat tolerance and metabolic costs, disease resistance, seasonal timing of important life-history events, growth and

¹Author to whom correspondence should be addressed. Email: thomas.wainwright@noaa.gov development rates, freshwater habitat structure, and the structure of ecosystems on which salmon depend. These individual effects accumulate across the life cycle and across generations, and may be synergistic (Francis and Mantua 2003, Mote et al. 2003, Independent Scientific Advisory Board 2007). Despite this extensive literature, we found no comprehensive and integrated analyses of climate effects across the entire life cycle and range of habitats vital to salmon life-histories for any single species or stock.

Coho salmon (*Oncorhynchus kisutch*) is an anadromous species that ranges around the north Pacific rim from central California to northern Korea (Sandercock 1991). Within the species, coho salmon that breed along the Oregon Coast from the Columbia River (46°12'N) south to Cape Blanco (42°50'N) form a distinct population group (Weitkamp et al. 1995). Oregon Coast coho salmon display substantial population substructure, with 21 independent populations grouped into 5 biogeographic strata that represent regional-scale diversity (Figure 1; Lawson et al. 2007). Historically, Oregon Coast coho salmon

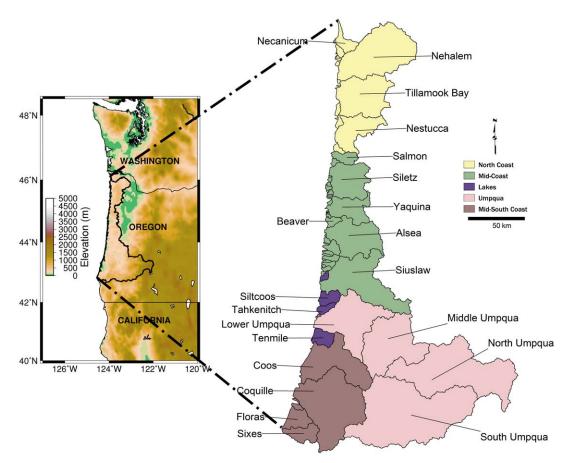


Figure 1. Geographic location (inset) and range of Oregon Coast coho salmon, identifying 21 major independent populations. Shading identifies five biogeographic strata (regional scale diversity units) that include both the independent populations and smaller coastal watersheds. Based on Lawson et al. (2007).

supported important marine and freshwater fisheries, but substantial population declines have greatly reduced abundance (Lichatowich 1989, Weitkamp et al. 1995), and they are presently listed as a "threatened species" under the U.S. Endangered Species Act (ESA). Past reviews of the status of Oregon Coast coho salmon (Weitkamp et al. 1995, Lawson 2005, Wainwright et al. 2008) have recognized climate change as a risk factor, but were not able to address this issue in depth; this analysis was conducted as part of an ESA status update to remedy that omission.

Oregon Coast coho salmon inhabit rivers in this region that drain the west side of the Coast Range, which is relatively low (peaks at 500-1300 m) and narrow with rivers typically less than

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75 km in length; an exception is the Umpqua River, which bisects the Coast Range to drain the southern Oregon Cascade Mountains with higher peaks (1000-3400 m) than the Coast Range. The Oregon Coast receives high rainfall (120-240 cm annually) but has moderate air temperatures throughout the year, resulting in low snowfall in winter (30-60 cm annually) and winter and summer stream temperatures of 4-8 °C, and 15-21 °C, respectively. Seasonal river flows in this region are characterized by a single peak in December or January and relatively low flow in summer and fall. The Umpqua River, with its much larger basin extending into the snowy Cascade Mountains, also has a single winter peak in flow but more extended flow in spring due to snow melt (Weitkamp et al. 1995).

Coho salmon occupy several distinct habitats in their life cycle (Sandercock 1991). Spawning occurs and eggs develop in freshwater habitats, where juveniles typically develop through summer and the following winter before migrating downstream to estuaries and then coastal ocean habitats. A large portion of Oregon coho remain along the Oregon, Washington and Vancouver Island coasts throughout their first summer at sea, while a faster-migrating component of the population may reach the Gulf of Alaska by late summer (Pearcy 1992, Morris et al. 2007). The first few weeks or months of ocean residency are believed to be critical to overall marine survival (Pearcy 2002, Van Doornik et al. 2007), therefore our analysis of marine impacts is focused on the northern California Current. After growing in the ocean for up to 18 months, maturing fish return to freshwater to spawn and die.

Here, we provide an analysis of the potential impact of climate change across the Oregon Coast coho salmon life cycle. Although qualitative in nature, we provide the first comprehensive climate-change assessment for a specific Pacific salmon stock.

Approach

To understand the risks to salmon populations associated with climate change, it is necessary to integrate across habitats and through the entire salmon life cycle (Figure 2). Coho salmon reside sequentially in freshwater, estuary, and ocean habitats; forest habitats are also essential to coho salmon because they influence the quality of freshwater habitats (Cederholm and Reid 1987).

Climate conditions affect each of these habitats and affect different portions of the life cycle through different pathways (Figure 2). This results in a complex set of potential effects. In linking the complexities of the global climate system across local land- and ocean-scape processes to the complexities of ecosystems, some uncertainty is unavoidable, and it is likely that the detailed response of individual species is unknowable (Perry and McKinnell. 2005). While models of the physical characteristics of climate change at a variety of scales are improving rapidly (Solomon et al. 2007), climate models are limited by lack of data at appropriate scales and good methods for downscaling global results to local habitats (Salathé 2005, Mantua et al. 2010). Also, there are

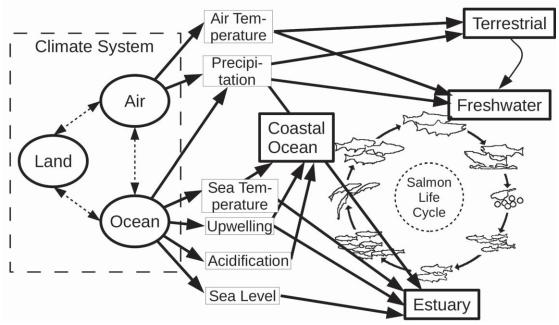


Figure 2. Conceptual diagram of multiple pathways by which climate influences the salmon life cycle. The climate system affects four habitats (terrestrial, freshwater, estuary, and coastal ocean) vital to salmon life stages, which in turn influence salmon reproduction, growth, and mortality.

difficulties in linking physical climate to biological response because of ecosystem complexity and limited understanding of aquatic ecosystems (Roessig et al. 2004). Accurately predicting the response of salmon to climate change would require reliable models of climate and biological response across a variety of habitats and ecosystems along with interactions with other factors. While models of physiological and organismal response to individual climate factors are being developed and are likely to provide predictive capabilities in the near term, integrative models predicting ecosystem-level changes to the whole suite of climate effects are unlikely to be available in the near future. For this reason, the analysis we present here is qualitative: we only assess the direction and magnitude of coho salmon population response.

Our approach consisted of three sequential steps. First, we summarized past and projected trends in climate patterns across habitats important to the various life stages of Oregon Coast coho. Second, we identified the pathways by which those trends are likely to affect coho salmon and their habitats. Finally, we assessed the direction and magnitude of coho salmon population response and the degree of certainty of that response.

Our assessment is based on a review of relevant literature regarding both regional climate changes (past observations and future projections) and biological response to these changes. Our review emphasizes peer-reviewed journal articles and books, but in a few places we had to rely on government and university reports. Few of these studies specifically address conditions on the Oregon Coast, but we assume that the general patterns of change noted for the Pacific Northwest region as a whole will apply. Individual studies presented projections for a range of future time spans; we focus on the more certain near-term results, extending only to the middle of this century (ca. 2050).

In summarizing effects, we classified the certainty of both future regional climate patterns and the effects of these patterns on Oregon Coast coho salmon into three categories: high certainty (greater than about 80% chance of occurrence), moderate certainty (around 50% to 80% chance of occurrence), and low certainty (less than about 50% chance of occurrence). These classifications are strictly our judgment, informed by the pertinent literature. In making these judgments, we considered the stated degree of certainty in forecast studies (where reported), the degree of consensus among multiple studies, the similarity of the study domain to the Oregon Coast region, and (for biological studies) the ecological similarity of the species studied to coho salmon.

Results

We first review past and future changes in the physical and chemical environment, then discuss how these changes are likely to affect biological processes that determine the sustainability of Oregon coast coho salmon populations. Both physical changes and biological responses are summarized in Table 1.

Physical and Chemical Setting

For the Pacific Northwest, observed and projected climate change patterns have been recently reviewed (e.g., Karl et al. 2009, Mote and Salathé 2010); we simply highlight items of importance to salmon. For salmon, the most important climate variables are air temperature, precipitation, snow pack, stream flow, stream temperature, sea level, sea temperature, upwelling, and ocean acidity.

Air Temperature-Numerous studies have documented an increase in air temperature over the last century, with expectations for continued increases in air temperature into the future (e.g., Solomon et al. 2007). For the Pacific Northwest as a whole, average surface air temperature in the Pacific Northwest has increased by approximately 0.8 °C over the past century (Karl et al. 2009). Average temperature in Oregon west of the Cascade Mountains increased more than global average temperatures during the 20th Century, with more moderate increases (0.5 to 1.0 °C over the century) close to the coast; increases were greatest in the winter (January-March), with a winter trend of 1.8 °C per century west of the Cascade crest (Mote 2003b). For the future, Leung et al. (2004) project an average increase in temperature of 1.0 to 2.5 °C

					Rang on O	Range of Effects on Oregon Coast	ects oast		
Type	Physical/Chemical Pattern	of Change	Process Affecting Salmon	;	- 10		+	‡	of Effect
Terrestrial	Warmer, drier summers	Moderate	Increased fires, increased tree stress $\&$ disease affect LWD ¹ , sediment supplies,	×	×	×			Low
	Reduced snow pack, warmer winters	High	riparian zone structure Increased growth of higher elevation forests affect LWD ¹ , sediment, riparian zone structure			X	X		Low
Freshwater	Reduced summer flow Earlier peak flow	High High	Less accessible summer rearing habitat Potential migration timing mismatch	\mathbf{X}^2	××	×			Moderate Moderate
	Increased floods	Moderate	Redd disruption, juvenile displacement, sediment dynamics	\mathbf{X}^2	Х	×	×		Moderate
	Higher summer stream temperature	Moderate	Thermal stress, restricted habitat availability, increased susceptibility to disease, parasites, and predators	X	×				Moderate
	Higher winter stream temperature	Low	Increased fry growth, shorter incubation				Х	Х	Low
Estuarine	Higher sea level Higher water temperature	High Moderate	Reduced availability of wetland habitats Thermal stress, increased susceptibility to disease. parasties and predators	××	××				Moderate Moderate
	(Combined effects)		Changing estuarine ecosystem composition and structure	Х	X	×	X	X	Low
Marine	Higher ocean temperature	High	Thermal stress, shifts in migration, range shifts, susceptibility to disease, parasites and predators	×	X				Moderate
	Intensified upwelling	Moderate	Increased nutrients (food supply), coastal cooling, ecosystem shifts; increased offshore transport			Х	X	x	Low
	Delayed spring transition	Low	Food timing mismatch with outmigrants, ecosystem shifts		Х	×			Low
	Intensified stratification	Moderate	Reduced food supply, change in habitat	х	Х				Low
	Increased acidity	High	Disruption of food supply, ecosystem shifts	Х	Х				Moderate
	(Combined effects)		Changing composition and structure of ecosystem; changing food supply and predation	Х	×	Х	X	×	Low

TABLE 1. Summary of climate patterns and their effects on Oregon Coast coho salmon. Effect ratings are: ++, strongly positive; +, positive; 0, neutral; -, negative, - -, strongly

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 1 Large woody debris. 2 Strong negative effects are for the snow-fed portions of the Umpqua Basin only.

by mid-century for the western U.S., while Mote et al. (2008b) predict that average warming over the next 50 years will be about 0.1 to 0.6 °C per decade, resulting in an increase of 0.9 to 2.9 °C by the 2040s; they also predict that future warming will be greater during the summer than the winter.

Precipitation—During the last century, trends in precipitation at stations in western Oregon were predominantly positive, but modest (up to 50% increase in 100 years) (Mote 2003b). Changes in the frequency of precipitation extremes have been observed during the last century (Rosenberg et al. 2010, Mass et al. 2011), but the direction of these trends varies geographically and few are statistically significant at the 95% level. During the next century, mean change in average annual precipitation is likely to be near zero, with a range of -11% to +12% by the 2040s, tending to decrease in summer (June-July-August; -30 to +17%) and increase in winter (December-January-February; -13 to +27%) (Mote et al. 2008b). Climate models also predict increased variability in precipitation resulting in more extreme rainfall events by the middle of this century (Mote et al. 2008b, Rosenberg et al. 2010).

Snow Pack and Stream Flow-Changes in temperature and precipitation combine to affect changes in snow pack and seasonal stream flow. Measured snow pack declined by more than 40% at most measuring stations in western Oregon over the 1950-2000 period (Mote 2003a). A more localized study for the Cascade Mountains extended the snow pack time series back to the 1930s using stream flow, temperature, and precipitation records to reconstruct likely stream flow (Stoelinga et al. 2010); they concluded that spring snow pack in the Cascade Mountains as a whole has declined by about 16% over the past 75 years (2% per decade). The differences between these reports result from three factors: the specific geographic area studied, the starting year of the time series, and the methods used to adjust for decadal-scale climate fluctuations. While the magnitude of estimated trends differ, both studies conclude that spring snow pack has been declining in the region, and these observed trends are most likely not an artifact of decadal-scale climate fluctuations (Hamlet et al. 2005, Mote et al. 2005, Mote 2006). Mote (2003a) notes that snow pack declines are largely temperature driven, with the rate of decline in snow pack strongly related to elevation, with the most rapid declines at elevations below 1800 m.

A few studies have examined trends in stream flow for the past century. Lins and Slack (1999) found coherent downward trends in maximum, median, and minimum daily flow for Pacific Northwest streams over a variety of time periods during the 20th century, suggesting decreasing flows in all seasons. Using similar data for the period 1949-2006, Luce and Holden (2009) found a consistent pattern of declining trends in stream flow in western Washington and Oregon streams, with flows in dry years declining more rapidly than those in average or wet years. Twentieth-century warming trends resulted in substantial changes in flood risk in the western U.S., although the direction of that change varied by characteristics of the river basins (Hamlet and Lettenmaier 2007). There has also been a significant shift toward earlier peak flows throughout the western U.S., which is attributable to climate forcing (Hidalgo et al. 2009).

In the future, increased winter temperatures in the mountains are predicted to result in increased winter rainfall and decreased snowfall, with mountain snow pack expected to decline by anywhere from 11% to 21% (Casola et al. 2009) to as much as 70% (Leung et al. 2004, Payne et al. 2004) by mid-century. These changes are expected to result in increased winter flooding (including more frequent rain-on-snow events), earlier peak runoff, and reduced runoff and soil moisture in summer (Leung et al. 2004, Chang and Jung 2010). These trends will likely be strongest for snow-fed streams, and thus are most relevant to the Umpqua River basin. For the predominantly rain-fed and mixed rain/snow-fed coastal rivers, the shift in peak flow timing is not expected to be substantial, but there is an expectation of greater winter flooding and lower summer flows (Mote et al. 2003, Hamlet and Lettenmaier 2007, Chang and Jung 2010, Mantua et al. 2010).

Stream Temperature—There are few studies that directly address climate-driven trends in stream

temperature. The combination of warmer air, reduced spring/summer snow pack, and reduced summer precipitation can be expected to raise future stream temperatures, but other factors will influence the magnitude of the response. A study in Washington found that reduced summer flow was a larger influence on stream temperatures than was increased air temperature, and also found that riparian vegetation buffers could prevent projected temperature increases (Cristea and Burges 2009). Increases in stream water temperature would also have direct effects on other aspects of water quality by enhancing biochemical and physiological rates and reducing the capacity of water to hold dissolved oxygen (Lettenmaier et al. 2008).

Sea Level-Local sea level changes result from a combination of global average sea level and changes in coastal elevation due to local tectonic activity. Global average sea level rose about 20 cm over the past century, with the rate increasing over the past 15 years (Bindoff et al. 2007, Karl et al. 2009). However, the rate of change varied substantially by region and had considerable decadal-scale variability (Bindoff et al. 2007). Recent projections (Solomon et al. 2007) suggest an increase of 20 to 60 cm over the next century, but do not include recent new information on the dynamics of ice melt-models accounting for this information suggest sea level rise of up to 0.4 to 1.5 m this century (Rahmstorf 2007). For the Washington Coast, Mote et al. (2008a) estimated that sea level increase by 2100 will range from 15 cm to 1.25 m; we can expect a similar rise on the Oregon Coast, with higher rise in northern Oregon, an area with more rapid coastal subsidence (Verdonck 2006).

Sea Temperature—While it is well known that the global oceans on average are warming (Bindoff et al. 2007), patterns of warming vary by region, and few studies have examined physical climate change in Pacific Northwest coastal waters. Regional temperature trends in the North Pacific are difficult to discern because they are confounded with interannual and decadal-scale fluctuations related to the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (Bindoff et al. 2007). Two studies along the U. S. West Coast specifically examined sea temperature trends. In one, sea-surface temperature (SST) for the Pacific Northwest coastal ocean is projected to increase by about 1.5 °C by the 2040s, although the included models did not accurately reproduce observed SST for the late 20th century (Mote et al. 2008b). A similar study off of southern and central California projects SST increases ranging from 0.3 to 0.8 °C by the 2040s, but the trend varies with depth, season and location (Auad et al. 2006).

Upwelling—The timing of the onset of winddriven coastal upwelling in spring and its intensity over the upwelling season are critical factors in the productivity and structure of the California Current ecosystem (Checkley and Barth 2009, Chavez and Messié 2009). Bakun (1990) first proposed that climate change would cause an intensification of upwelling in the California Current, due to increased contrast between oceanic and continental temperatures. He documented an increase in upwelling-favorable winds during the period from 1945-1975 in all of the eastern boundary currents of the world, including the California Current, consistent with this theory.

Some recent modeling exercises and analyses of upwelling data support Bakun's hypothesis and suggest that upwelling is continuing to intensify. In an analysis of upwelling records from years 1967-2008, Bograd et al. (2009) found a trend towards later onset and a shorter upwelling season in the northern California Current, with a delay of 1 day per year in spring transition date at 48°N. Snyder et al. (2003) used a regional climate model to predict the effects of increased CO₂ on upwelling intensity and duration off the coast of California and found intensified upwelling and a shift in the onset of upwelling. In the northern California Current, they project decreased upwelling in April-June and increased upwelling in July-October, with an onset of upwelling up to a month later than at present. In contrast, neither Mote and Mantua (2002) nor Diffenbaugh (2005) found substantial changes in coastal upwelling timing or intensity under global warming scenarios using large scale general circulation models. However, Diffenbaugh (2005) cautioned that these large-scale models do not reliably resolve fine-scale upwelling processes, and that small changes that are difficult to detect with these models may still have important dynamical and ecological consequences, as will be discussed later.

Upwelling is affected by water-column thermal stratification to the extent that strong vertical stratification can limit upwelling of nutrient-rich cold water (Kosro et al. 2006). Historical increases in surface temperature and stratification in the southern California Current have been reported (Roemmich and McGowan 1995, Bograd and Lynn 2003, Palacios et al. 2004, Di Lorenzo et al. 2005). One modeling study concluded that increases in wind strength would be sufficient to overcome this stratification and maintain upwelling in the southern California Current (Auad et al. 2006). Unfortunately, no similar studies have been conducted for the northern California Current, but we may expect a similar response to warming throughout the California Current system (McGowan et al. 1998).

Ocean Acidity-Increasing atmospheric CO₂ is absorbed by the surface layers of the ocean, leading to increased acidity and decreased concentration of carbonate in the ocean (Bindoff et al. 2007, Fabry et al. 2008). Based on both observations and retrospective modeling of the California Current, Hauri et al. (2009) concluded that mean pH declined by about 0.1 unit since pre-industrial times. In the California Current, intensified upwelling may also increase the effects of ocean acidification. Feely et al. (2008) determined that recently upwelled water sampled in 2007 was both under-saturated in aragonite (a form of calcium carbonate) and acidic (pH < 7.75), or "corrosive" to calcium carbonate. This water would normally remain at depth but intense upwelling off southern Oregon and northern California brought it to the surface.

Processes Affecting Oregon Coast Coho Salmon

The effects of physical and chemical changes described above can influence salmon during all life history stages (Figure 2). Although our analysis is conducted habitat-by-habitat, we first describe the fundamental effects of changing temperature on fish because they apply to salmon in all habitats; we then discuss other effects by habitat.

Common Temperature Effects-Water temperature can have a pronounced effect on fish physiology, growth, and development rate (Marine and Cech 2004, Richter and Kolmes 2005). The major effects of warmer water are increased physiological stress and reduced growth as temperatures approach upper thermal limits (Marine and Cech 2004), although in some situations warmer temperatures can lead to faster growth, shorter egg incubation time, and earlier maturation (Beckman et al. 1998). Temperature also can determine the distribution of coho (Welsh et al. 2001) and other salmon (Keleher and Rahel 1996, Jonsson and Jonsson 2009), with possible reductions in total habitat available, as well as shifts toward cooler habitats under rising temperatures (Mohseni et al. 2003). Warmer temperatures have also been found to affect the timing, speed and success of adult upstream migration (Goniea et al. 2006, Farrell et al. 2008). Temperature also mediates interactions with other species that have different thermal tolerance, and higher temperatures can shift competitive advantage (Reeves et al. 1987) and increase predation risk for salmonids by slowing their response to predators (Marine and Cech 2004) and increasing predator bioenergetic demand (Vigg et al. 1991, Petersen and Kitchell 2001). Other effects of higher temperatures include increased disease and parasite susceptibility (Marcogliese 2008), changes in migration timing (Crozier et al. 2008a), and increasing abundance of more heat tolerant species, including warm-water predators (Independent Scientific Advisory Board 2007).

Terrestrial Habitats—Coastal forests are important to coho salmon, to the extent that the southern limit of coho salmon distribution corresponds to the southern limit of the Coast Range Ecoregion characterized by Sitka spruce and coast redwood forests (Weitkamp et al. 1995). Forests determine the quality of freshwater habitats through three processes: (1) by regulating dynamics of erosion and landslides that affect stream sediments, (2) through tree fall that influences the structure of pools used by juvenile salmon, and (3) by regulating water runoff and water quality including light, temperature and nutrients (Cederholm and Reid 1987, Ball et al. 2010).

Climate change will have a number of effects on forests in the Pacific Northwest. Some of these will occur only over long time spans and will have little effect within the time frame of this assessment; these include decreased tree growth at low elevations due to reduced summer precipitation, increased growth at higher elevations due to longer growing seasons and higher concentrations of CO₂, upward expansion of tree lines, and shifts in species distributions and forest community composition (Mote et al. 2003, McKenney et al. 2007, Latta et al. 2010). Other changes are expected to be more rapid, and may have significant effects by mid-century. Higher air temperatures and reduced summer precipitation will likely increase frequency of forest fires (Kitzberger et al. 2007, Keeton et al. 2007), although this effect may be small for the Oregon Coast Range (Westerling et al. 2006, Waring et al. 2011). Increased fire frequency would likely increase sediment runoff into streams, which could degrade spawning and rearing habitat. Other effects include increased frequency of damaging insect outbreaks (Williams and Liebhold 2002, Hicke et al. 2006). Temperature and water deficit increases have already led to increased mortality of trees in the western U.S., which could lead to substantial changes in forest structure (van Mantgem et al. 2009). These changes in "disturbance regimes" could lead to more rapid changes in forests through influences on growth, productivity and mortality (Franklin et al. 1991). The effect of such changes on salmon are indirect and will vary by elevation, forest type, and local conditions. This makes it difficult to predict the response of Oregon Coast coho salmon to these changes. For these reasons, we rated the certainty of terrestrial effects on coho salmon as "low."

Freshwater Habitats—Coho salmon typically spend about half of their life in freshwater (Sandercock 1991), and more than half of egg-to-adult mortality occurs in freshwater (Bradford 1995, Quinn 2005). Annual variation in freshwater survival is largely driven by climate-related environmental factors such as water temperature and flow (Lawson et al. 2004), so climate change effects on freshwater habitats are expected to have a significant effect on coho salmon populations.

The predicted physical changes of reduced summer stream flow, earlier spring peak flow, increased flood frequency, and higher stream temperatures (Table 1) will all have effects on salmon (Independent Scientific Advisory Board 2007). Some of these effects have well-understood relationships to salmon reproduction and survival. In particular for juvenile coho salmon, summer water temperature, flow and availability of pools are critical aspects of habitat (Reeves et al. 1989, Beechie et al. 1994). The geographic patterns of these changes will also likely affect the local distributions of fish within river basins, by increasing survival in some habitats and decreasing survival in others (e.g., Shuter and Post 1990).

Reduced summer stream flows will affect the availability of summer rearing habitat, especially in combination with warmer temperatures (Independent Scientific Advisory Board 2007, Mantua et al. 2010), as well as reducing parr survival and increasing development rates (Morrison et al. 2002, Crozier and Zabel 2006, Crozier et al. 2008a). Availability of both summer and winter rearing habitats can be limiting factors for Oregon Coast coho salmon (Reeves et al. 1989, Nickelson et al. 1992), thus decreased availability or quality of summer habitat is likely to reduce coho salmon freshwater productivity.

In snow-fed streams of the Umpqua River basin, earlier spring peak flows may reduce spawning success as a result of earlier dewatering of redds (Independent Scientific Advisory Board 2007), and may also affect the timing of smolt outmigration, which could result in a temporal mismatch between ocean entry and marine food availability (Taylor 2008, Crozier et al. 2008a). This shift in flow timing is unlikely to be significant in rain-fed streams (Mote et al. 2003).

Increased winter flood frequency and intensity may increase egg and fry mortality through scouring and increased sediment transport, and parr-to-smolt mortality due to displacement from appropriate habitats (Independent Scientific Advisory Board 2007, Mantua et al. 2010). In contrast, it may improve reproduction in subsequent years through gravel deposition and flushing of fine sediments (Swanson et al. 1998). The balance of these effects is likely to depend on local geology, topography, and vegetation (Swanson et al. 1998).

As reviewed under "Common Temperature Effects" above, increases in stream temperature can be expected to have a pronounced effect on fish physiology, growth, and distribution of coho salmon, with range shifts toward cooler (e.g. higher elevation) habitats to be expected. Within the range of Oregon Coast coho salmon, 43% of available stream habitat has already been identified as having summer temperatures exceeding tolerance limits for salmon, and this fraction exceeds 70% in the Umpqua River basin (Table 2) (Oregon Department of Environmental Quality 2007). Given this high proportion of streams that are already temperature-impaired, we can expect future reductions in available freshwater rearing habitat as average water temperatures increase, especially in the Umpqua River basin. However, an analysis of coho salmon habitats suggests that summer rearing habitat is not presently the main limit on capacity for most coastal coho salmon populations (Oregon Department of Fish and Wildlife 2005). Accordingly, currently abundant summer habitat may serve to buffer the effects of increased temperatures on this habitat type. While most studies have focused on negative effects of peak summer temperatures, Mantua et al. (2010) speculate that increasing winter temperatures could be beneficial to some salmon populations

TABLE 2. Percent of coastal coho salmon stream habitat that are temperature impaired (i.e., that exceed Oregon standards for summer water temperature for salmon), by biogeographic stratum. Based on data from Oregon Department of Environmental Quality (2007).

Stratum	Total Habitat Miles	Impaired Miles	Impaired Percent	
Lakes	239	14	6%	
Mid-Coast	2017	607	30%	
Mid-South Coast	1193	426	36%	
North Coast	1466	471	32%	
Umpqua	2009	1430	71%	
TOTAL	6924	2948	43%	

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(particularly those at higher elevations) due to increased fry growth. No studies have assessed climate-driven trends in winter stream temperature in the Pacific Northwest, so the potential magnitude of this effect cannot be evaluated.

Estuarine Habitats—Although only a small portion of their total life cycle is spent in estuaries, estuaries are important to salmon (Simenstad et al. 2000, Magnusson and Hilborn 2003), and Oregon coast coho utilize estuaries for juvenile rearing (Cornwell et al. 2001, Miller and Sadro 2003, Koski 2009). Of the 21 major independent Oregon Coast coho salmon populations (Figure 1), only the lake populations (Siltcoos, Tahkenitch, and Tenmile) lack extensive estuaries (Adamus et al. 2005). Estuaries are influenced by conditions in both freshwater and ocean habitats, including freshwater flow patterns, stream temperature, sea level rise, sea surface temperature, patterns of upwelling, and ocean acidity.

As in other habitats, warming is expected and will have a number of effects. Temperaturemediated shifts in species distributions will result in changes in community species composition (Kennedy 1990, Roessig et al. 2004) away from the historical template; the net effect of this on salmon is difficult to predict. Warming in estuaries can also be expected to have similar effects on coho salmon as in other habitats: increased physiological stress and increased susceptibility to disease, parasites, and predation (see "Common Temperature Effects").

Changes in the amount and timing of freshwater input (including nutrients and sediments) will likely result in changes in estuarine circulation and biological productivity (Scavia et al. 2002). Combined effects of freshwater flow and temperature will alter estuarine mixing, residence time, and eutrophication (Scavia et al. 2002).

Estuaries will be affected directly by sea-level rise (Kirwan et al. 2010). As sea level rises, terrestrial habitats will be flooded and tidal wetlands will be submerged; the net effect on wetland habitats depends on the rate of sea-level rise relative to the rates of marsh plant growth and sedimentation (Morris et al. 2002, Kirwan et al. 2010) and the physiography of the estuarine basin (Kennedy 1990, Roessig et al. 2004). The global rate of sea-level rise is currently faster than plants can colonize new wetland habitats (Roessig et al. 2004), and will be higher for much of the Oregon coast due to coastal subsidence (Verdonck 2006). Whether upland areas will be flooded also depends on human uses of the upland habitats and related diking and shore protection structures. Considering rates of sea level rise and the widespread presence of dikes that would restrict estuary expansion, in most Oregon estuaries there is likely to be a near-term loss of wetland habitats for coho salmon. Sea level rise will also result in greater intrusion of marine water into estuaries, resulting in an overall increase in salinity, which will also contribute to changes in estuarine communities (Kennedy 1990).

Ocean Habitats—Coho salmon spend about half of their life in the ocean, typically entering marine waters from late April through early June (Weitkamp et al. 1995, Morris et al. 2007) and residing in local waters off the coasts of Washington and Oregon throughout that summer (Morris et al. 2007, Van Doornik et al. 2007). This suggests that conditions in the northern California Current during the first ocean summer would be the most important determinants of marine growth and survival of Oregon Coast coho, and that region is our focus.

Coho salmon marine mortality is both high and variable (Bradford 1995, Coronado and Hilborn 1998), and there is a strong potential for climate change in marine environments to influence the long term outlook for Oregon Coast coho. Salmon will experience effects of changes in temperature (Welch et al. 1995, Cole 2000), upwelling (Nickelson 1986, Fisher and Pearcy 1988), and acidification (Fabry et al. 2008). But the ocean environment is dynamic, complex and more difficult to observe than freshwater and estuary habitats, which makes understanding of climate effects on salmon during ocean residence more difficult (Harley et al. 2006).

Temperature increases are the most commonly noted marine effect of climate change, and there has been substantial literature discussing temperature effects on marine fish in general (Pepin 1991, Cheung et al. 2009) and coho salmon in particular (Nickelson 1986, Cole 2000). Increases in temperature are expected to have similar effects to those described in freshwater and estuarine habitats, including increased physiological stress and reduced growth, and increased disease, predation and parasite susceptibility (see "Common Temperature Effects"). Beyond these general effects, temperature is a significant determinant of the latitudinal distribution of marine fishes in the California Current (Horn and Allen 1978), and recent shifts in distributions of larval fishes has been demonstrated (Hsieh et al. 2009). Pacific salmon have historically exhibited distribution shifts with large-scale changes in climate (Ishida et al. 2001, Ishida et al. 2009), and such shifts are occurring now (Irvine et al. 2009). Projected rates of distribution change for a variety of marine fishes range from 30 to 130 km/decade towards the pole and 3.5 m/decade to deeper waters (Cheung et al. 2009). Such changes in distribution, combined with shifts in primary production, is projected to result in major changes in global distribution of fish and fisheries (Cheung et al. 2010).

Distribution shifts are not uniform among species, with the result that community structure will change over time, with likely changes in predatorprey relationships (Murawski 1993, Cheung et al. 2009), which could lead to increasing predation on Oregon Coast salmon. A number of recent observations support this. Piscivorous predators such as Pacific hake (Merluccius productus) are generally most abundant in the Northern California Current in warm years (Emmett et al. 2006), and would be expected to increase in abundance if coastal temperatures increase. As an extreme example, during the 1997-98 El Niño, several species of warm-water predatory fishes invaded Oregon waters (Pearcy 2002, Emmett et al. 2006). Similarly, the predatory Humboldt squid (Dosidicus gigas) recently expanded its range along the West Coast of North America, which apparently includes a summer feeding migration to the northern California Current (Zeidberg and Robison 2007, Field et al. 2012). This species was first reported off the Oregon coast during the 1997-98 El Niño (Pearcy 2002), and was caught as far north as Southeast Alaska in the warm years of 2004 and 2005 (Wing 2006). It became extremely abundant in the northern California Current during summer 2009 (Litz et al. 2011), only to return to extremely low abundances in summers of 2010-2012 (M. Litz, Oregon State University, pers. comm). Prey consumed by these squid is predominantly pelagic fishes, including juvenile salmon (Field et al. 2012).

Upwelling is a major factor driving biological productivity and structuring ecosystems in the California Current, and upwelling intensity and phenology influences coho salmon populations (Scarnecchia 1981, Nickelson 1986, Fisher and Pearcy 1988, Koslow et al. 2002). How future changes in upwelling will impact marine ecosystems supporting Oregon Coast coho salmon is extremely difficult to predict because our current understanding of the mechanisms linking physical climate change to marine ecosystems is extremely limited (Schwing et al. 2006). Intensified upwelling should generally enhance primary productivity, but it is not clear that such production would be available to mid-trophic fishes such as salmon (Bakun 1990). The date of onset of upwelling (spring transition) is also an important predictor of salmon survival, with earlier transition dates corresponding to better survival (Koslow et al. 2002, Logerwell et al. 2003), so the recent observed delay in spring transition is a concern.

Stratification also can directly affect coho salmon. In general, warming of the ocean's upper layers will lead to greater stratification, reducing the delivery of deep nutrients into the near-surface photic zone when upwelling occurs (Overland et al. 2009, Hoegh-Guldberg and Bruno 2010). Roemmich and McGowan (1995) noted a declining trend in zooplankton abundance in the southern California Current between 1951 and 1993, which they attribute to increased stratification that suppressed nutrient flow into surface layers. Higher marine salmon survival is correlated with weaker stratification (Hobday and Boehlert 2001, Koslow et al. 2002); as a consequence, the expected intensification of stratification would have a negative effect on coho salmon.

Acidification has been shown to affect organisms directly, and these effects are likely to transfer throughout the ecosystem (Fabry et al. 2008, Doney et al. 2009, National Research Council 2010). The California Current is particularly prone to coastal acidification from upwelled water (Feely et al. 2008). Acidification may have strong negative effects on some coho food items, such as pteropods; however, marine juvenile coho salmon are fairly omnivorous (Brodeur et al. 2007, Daly et al. 2009), so might be less affected by acidification than are more specialized predators. Acidification will also likely result in some direct biochemical stress on fishes (Fabry et al. 2008), but there are no published studies of these effects specific to salmon.

Interactions and Life-cycle Integration

While many of the predicted individual effects of climate change on Oregon Coast coho salmon are weak or are uncertain, it is in combination that they determine cumulative impacts. There are two aspects to combining effects: interactions among effects within habitats and the accumulation of those effects across habitats within the life-cycle and across generations.

Interactions Within Habitats-Synergistic interactions among stressors make prediction of impacts difficult and single-factor studies will often under-predict impacts (Fabry et al. 2008, Perry et al. 2009). If only a few well-measured stressors are considered, it may be possible to develop quantitative measures of combined effects (e.g., Crozier et al. 2008b). However, considering only the direct effects of a few factors does not tell the whole story. Physical and chemical changes will affect not only salmon, but also all other species in the local ecosystems. It is likely that the largest influence of climate change on Oregon Coast coho salmon will be through effects on ecosystem structure and the balance of flows through food webs (Harley et al. 2006). The complexity of estuarine and ocean ecosystems makes assessment of the magnitude (and even of the direction) of climate effects on any particular species difficult (Perry and McKinnell 2005, Harley et al. 2006, Brown et al. 2009). For example, in estuaries the combined effects of warming, changes in freshwater hydrology, sea level rise, and coastal upwelling are likely to result in substantial changes in estuarine productivity and community structure (Kennedy 1990, Scavia et al. 2002), which are likely to affect survival of coho salmon rearing or migrating in estuaries. Whether that influence will be positive or negative is unclear.

Given such uncertainty, past events may provide insights into future ecosystem conditions. The northern California Current has alternated between "warm" and "cool" phases, which are characterized by noticeable ecosystem shifts (Peterson and Schwing 2003, Brodeur et al. 2005, Emmett et al. 2006). These phases are related to phases of both the Pacific Decadal Oscillation and the El Niño Southern Oscillation. Coho salmon marine survival and abundance is higher during the cool phase than during the warm phase (Johnson 1988, Logerwell et al. 2003, Rupp et al. 2011). Climate models suggest that conditions similar to recent warm-phase periods will be more frequent in the future (Schwing et al. 2006, Wang et al. 2009), so observed responses to warm-phase conditions can provide an analogy for future conditions. Two recent short-term warming events provide examples of possible effects of long-term climate change. In 1988-89, a strong El Niño affected marine ecosystems in this region (Pearcy 2002, Peterson et al. 2002, Zamon and Welch 2005). More recently, a strong warm-water event occurred in summer 2005 that also had implications for the entire marine ecosystem (Schwing et al. 2006, Bograd et al. 2009). These events changed zooplankton community structure (Peterson et al. 2002, Zamon and Welch 2005, Mackas et al. 2006), led to record low rockfish recruitment and a lack of other small pelagic species that are important prey for coho salmon (Brodeur et al. 2006), brought in warm-water predators (Pearcy 2002), and led to a breeding failure in sea birds (Sydeman et al. 2006) and the nearly complete loss of juvenile Sacramento River fall Chinook salmon that year (Lindley et al. 2009). If these events are similar to likely future conditions, it would indicate substantial risks to sustainability of Oregon Coast coho salmon.

Life-Cycle Accumulation—Estimating the accumulated impact of climate change across the salmon life cycle depends on two important factors (Paulik 1973): First, that the combined effects across life stages are the product (rather than the sum) of the individual stage effects, and, second, that these effects also multiply across generations. This means that small changes at any life stage can result in quite large changes over multiple generations. Furthermore, because spawning and the freshwater juvenile phase are strongly limited by habitat capacity, while later stages (e.g., marine phase) are less so, climate-driven changes can have different consequences for different life stages. Changes in forests and freshwater habitats will mostly affect habitat capacity, as will summer low flows and high temperatures by restricting the amount of accessible habitat. In the long term, these habitat-capacity effects will change the overall maximum abundance of populations. In contrast, factors such as ambient temperature and food supply affect individual growth, thus influencing life history traits including adult body size, fecundity, migration timing and maturation rates (Mangel 1994), as well as having direct influence on survival.

In Table 3, we summarize the number of climate change effects for specific habitats by level of certainty and by direction and magnitude of the effect. While there are some expected positive

TABLE 3. Summary of the numbers of potential effects (see Table 1) categorized by direction and magnitude of effect and by level of certainty. Values in parentheses apply to snow-fed river basins.

		Direction and Magnitude of Effect					
	Certainty		-	0	+	++	
Freshwa	ater & Terrestrial						
	Low	1	1	2	2	1	
	Moderate	1 (3)	4	2	1	0	
Estuarir	ie						
	Low	1	1	1	1	1	
	Moderate	2	2	0	0	0	
Marine							
	Low	2	3	3	2	2	
	Moderate	2	2	0	0	0	
OVERA	LL						
	Low	4	5	6	5	4	
	Moderate	5 (7)	8	2	1	0	
	TOTAL	9 (11)	13	8	6	4	

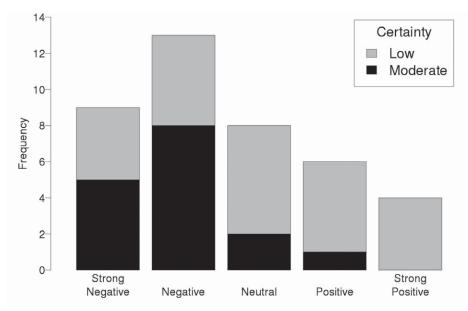


Figure 3. Summary of the overall frequency of positive and negative effects, by certainty categories. Data from Table 3.

effects, negative effects predominate for each life history stage. When summed across all habitats (Figure 3), it is apparent that negative effects are both more frequent and of greater certainty than positive effects - all but one (increased floods) of the positive effects are of low certainty. Because individual life-stage effects are multiplicative, the predominantly negative effects seen in Table 3 would thus be expected to substantially affect both the capacity and productivity of the Oregon Coast coho populations, resulting in reduced numbers, reduced capacity to support harvest, and reduced resilience to environmental fluctuations or other anthropogenic threats. Climate change may therefore increase local population extinction risk in habitats most affected by climate change, which could reduce overall diversity and longterm resilience (Gustafson et al. 2007, Williams et al. 2009).

Discussion

Differences Among Populations

Due to differences in local climate and geomorphology among the many river basins along the Oregon Coast and spatial variation in physical forcing of coastal waters, it is likely that individual populations will be affected by climate change in different ways. We have already noted some differences between populations that reside in Coast Range drainages that are predominantly rain-fed and those in the Umpqua River basin which includes snow-fed tributaries in the Cascade Range. This results in substantial differences in seasonal hydrography, and makes the Umpqua Basin more vulnerable to decreases in winter snow pack and resulting reductions in summer stream flow and increases in summer stream temperatures.

As another example, basins with large estuaries are likely to receive more influence from sea level rise than those with small estuaries. In particular, the Nehalem, Yaquina, Alsea, Siuslaw, Umpqua, Coos and Tillamook Bay populations have the largest estuaries and are most likely to have estuarine ecosystems altered by sea level rise; this includes changes in food webs and displacement of salt marshes, with potentially negative consequences for all coho salmon that use estuaries as a migration corridor, but especially alternate life history forms which rely on extended estuarine rearing (Miller and Sadro 2003, Koski 2009, Bennett et al. 2011).

The three populations in the Lakes biogeographic stratum have large dune-bound lakes that support a numerically important but fairly unusual coho salmon life history type characterized by extended lake rearing prior to ocean entry (McGie 1979). Climate change will likely uniquely influence these populations because of their unusual reliance on lake habitats. Due to their shallow depth and limited shading from riparian vegetation, water temperatures in these lakes may rise at greater rates than will those in flowing streams. Exotic warm-water fishes have already severely reduced summer rearing of juvenile coho salmon in these lakes (Gray 2005) and, as water temperatures increase, these warm-water exotics will likely increase in abundance relative to juvenile coho salmon, as well as having increased rates of predation on salmon (Vigg et al. 1991). Alternate life history types, such as those associated with extended lake or estuarine rearing, provide an important component of the species diversity with which to guard against an uncertain future. The life history types that will be successful in the future is neither static nor predictable, therefore maintaining or promoting existing diversity is essential for continued existence of populations into the future (Bottom et al. 2009, Schindler et al. 2010).

Finally, there is spatial variability in the response of the coastal ocean to climate change which would differentially affect populations. For example, variability in the onset and intensity of upwelling (Bograd et al. 2009) has been greatest in the northern portion of the coast, and less variable (i.e., more predictable) to the south. Also, Feely et al. (2008) documented that acidic waters were closest to the surface in regions with the most intense upwelling-northern California and southern Oregon, as far north as 44°N (approximately the Siuslaw River). In combination, these factors indicate that changes in the coastal ecosystem will vary along the Oregon coast. Given the importance of conditions immediately following ocean entry for salmon survival, this means we can expect differences in population response between the northern and southern coastal populations.

Sources of Uncertainty

It is unsatisfying when we are unable to make clear, quantitative predictions on an important topic. However, there are limitations in our understanding of processes, in our ability to gather sufficient data as the basis for predictions, and in the inherent predictability of the processes themselves. These limitations are particularly true for the complex interactions between climate change and salmon populations (Mote et al. 2003). In summarizing both the physical/chemical changes and biological responses above, we have tried to accurately reflect the uncertainties in individual factors, but there are other important unknowns.

One of these involves the inherent plasticity of organisms, reflected in their ability to acclimate and adapt to changes. Like other Pacific salmon, coho salmon are a cold-water species; therefore expected warming of their habitats will likely not be beneficial. Two obvious ways that coho salmon can adjust for increasing temperatures are shifting range (moving to cooler waters) or through behavioral or genetic adaptations. Freshwater range shifts can be local, such as shift to cooler headwater reaches within a basin, or, at a larger scale, production may shift to more favorable river systems. However, most rivers and streams from central California to central Alaska area already occupied by salmonids, so opportunities for colonization are limited. In the ocean, changing migratory patterns could allow Oregon Coast coho salmon to occupy cooler water with productive habitats (Welch et al. 1995, Welch et al. 1998). Many Oregon Coast coho salmon already migrate northwards to Alaska during their first summer in the ocean (Morris et al. 2007), but it is unclear how quickly their migration patterns would adapt because their marine distributions, like those of Chinook salmon (Weitkamp 2010), are surprisingly rigid (Weitkamp 2012). For example, Oregon Coast coho salmon that entered the ocean during the strong 1982-83 El Niño event had extremely low survival and adults returning in 1983 were anomalously small (Johnson 1988), but marine distribution patterns were very similar to other years examined (Weitkamp and Neely 2002; L.A. Weitkamp, unpublished data). This apparent lack

of migrational response to poor ocean conditions suggests that Oregon Coast coho salmon may be slow to adapt to changing geographic distribution of ocean conditions.

The most relevant behavioral or genetic response to climate change is phenological shifts, such as shifting spawn timing or downstream and upstream migration timing (Crozier et al. 2008a). Such shifts could result in resource mis-matches at a number of life-history stages, resulting in evolutionary tradeoffs that could constrain adaptation for changes at any particular life stage. Shifting freshwater migration timing, shifting ocean ranges, and shifting upwelling phenology all could lead to growth and survival limitations (Beamish and Mahnken 2001). It is easy to imagine disastrous consequences, but more difficult to actually predict the long-term likelihood in the face of adaptation and life-history variation. Salmon have been observed to adapt rapidly to new habitats in some situations (Hendry et al. 2000, Quinn et al. 2001), but success is not readily predictable.

Managing for Climate Change

A key consideration in defining a "threatened species" under the U.S. Endangered Species Act is a determination of whether the population segment is "…likely to become endangered within the foreseeable future…". This focus on future conditions makes policy and management response to future trends in climate and other conditions a key consideration in conserving Oregon Coast coho and other Pacific salmon.

In the absence of a global solution to limit climate change, resource managers will need to plan for the expected biological response to changing conditions by these populations. Unfortunately, the number of realistic options available to managers to counter the potentially negative effects of climate change across all stages of the salmon life cycle are extremely limited. One feasible option is to promote the natural resilience of Pacific salmon, which have evolved complex life histories in response to naturally dynamic ecosystems and generally have a large capacity to adapt to changing conditions (Healey 2009, Waples et al. 2009). The evolutionary response of Pacific salmon to climate change is one of the least understood aspects of their biology, and depends on factors including population size and productivity, population genetic diversity, heritability of traits, and the rate and selective pressure of particular elements of climate change (Naish and Hard 2008). Therefore, by maintaining a diverse population structure the whole population or species could benefit from a stabilizing "portfolio effect" (Schindler et al. 2010), preventing major fluctuations (and possible extinction) of the population/species as a whole. Furthermore, managing habitat processes so that they are resilient to increasingly variable disturbance regimes (i.e., "self-repair"-Bottom et al. 2009) would help ensure that habitats do not exceed the levels of variation under which salmon have evolved (Bisson et al. 2009, Waples et al. 2009).

Specific recommendations for freshwater habitats include maintaining natural flow regimes, improving water quality in degraded areas, protecting and restoring riparian and floodplain vegetation, maintaining channel and floodplain dynamics, maintaining upland watershed processes, and protecting cold-water refuges (Cristea and Burges 2009, Hixon et al. 2010). In addition, harvest and artificial-production policies should incorporate a resilience-based perspective, including efforts to conserve small populations, sustain and increase life-history diversity, allow higher and more variable spawning escapement, and reduce mixed-stock fisheries in favor of locally-targeted harvest (Healey 2009). Many of these approaches have already been initiated for the conservation of Oregon coast coho (Oregon Department of Fish and Wildlife 2007). Whether these actions will provide adequate defense for salmon in the face of climate change is uncertain, but the long history of salmon declines and extinctions indicates that current conditions and recent management practices are unlikely to reliably sustain populations into the foreseeable future.

Conclusions

Our analysis suggests that, while there may be some favorable influences, the net effect of climate change is likely to be unfavorable for Oregon Coast coho salmon at all stages of their life cycle. Despite large uncertainties surrounding specific effects at individual life stages, expectations for increasing stream and ocean temperatures, drier summers, higher incidence of flooding, and altered estuarine and marine habitats, lead us to expect increasingly frequent years when survival is depressed, resulting in overall population declines. In the face of climate change and other humandriven and natural stressors, it is important that management for this species focus on improving resilience of both populations and the habitats on which they depend. This will require a shift in policies toward managing diversity of habitats

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and fish populations and an integrated perspective linking resilience in ecological and human systems; without this shift, the future does not look bright for these salmon.

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