  Recovery of Pacific Salmonids (*Oncorhynchus* spp.) in the Face of Climate Change: A Case Study of the Klamath River Basin, California

By

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Recovery of Pacific Salmonids (*Oncorhynchus* spp.) in the Face of Climate Change:

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**Abstract**

Climate change is predicted to alter aquatic habitats to the extent that many imperiled salmon and trout species (salmonids; *Oncorhynchus* spp.) face an escalating threat of extinction in California. This dissertation examines the impacts of climate change on salmonids from the Klamath River basin, the second largest river system in California, and now most likely the primary producer of wild salmonids in the state. The first chapter summarizes the effects of climate change on rivers within the basin, the Klamath River estuary, and coastal Pacific Ocean, as well as expected responses of different salmonid taxa. Climate change also is expected to exacerbate the negative impacts of multiple anthropogenic stressors already threatening species persistence, including dam operations, water diversions, fisheries harvest, and hatchery practices. The second chapter describes the trends of spawning adult numbers (escapement) of different taxa from several sub-basins. Trends of fall, spring and late-fall Chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*) numbers suggest that Klamath River salmonids are becoming increasingly dependent on hatchery propagation and that hatchery-produced fish are replacing wild ones. Consequently, species can become unable to endure changing environmental conditions, including those associated with climate change. The third chapter analyzes the effects of climatic forcing, habitat quality, and population dynamics on populations of four taxa. Resource management will need to address multiple factors acting on taxa at different time scales if salmonids are to persist into the next century.

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**Chapter 1** - Integrating global climate change into salmon and trout conservation:

a case study of the Klamath River, California

**Abstract**

Climate change is expected to alter all habitats (rivers, estuaries, oceans) used by anadromous fishes. For anadromous Pacific salmonids (*Oncorhynchus* spp.) effects of climate change are likely to be most strongly felt at the southern end of their range, in California. The effects should be especially severe in the Klamath River watershed, California’s second largest river, where most wild salmon and steelhead populations are in decline and river temperatures already seasonally approach lethal levels. In the river, climate change is expected to alter flow patterns, including the timing and magnitude of droughts and floods. The estuary will be impacted by more frequent and extreme tides and storms, and will experience altered salinity distribution as sea level rises. Although localized increases in ocean primary productivity may favor growth for some salmonids, benefits to populations will largely depend on movement patterns dictated by currents and prey availability. Water temperature in all three habitats is predicted to steadily increase throughout the 21st century, likely beyond salmonid tolerances in many areas. Salmonid abundance in the Klamath River basin may decrease by more than 50% by 2100, with the loss of three salmonid runs, unless climate change is actively incorporated into conservation efforts. Conservation of Klamath River salmonids will require creative, cooperative management of both the fish and their ecosystems. We recommend conservation actions that must be implemented rapidly in order to increase likelihood of salmonid persistence in the face of climate change.

**Introduction**

California marks the southern end of the range of six species of anadromous salmonids: Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), steelhead trout (*O. mykiss*) and coastal cutthroat trout (*O. clarki clarki*), with hundreds of distinct populations and runs ([Moyle 2002](#_ENREF_144)). This diversity reflects a state with over 1300 km of coastline, spanning nearly 10 degrees of latitude. Its rugged topography supports hundreds of streams and rivers, which flow into one of the most productive oceanic upwelling regions of the world. Not surprisingly, the six species, but especially Chinook and coho salmon, have supported large fisheries in the past. California is also unusual for a region with abundant salmonids in that it has a Mediterranean climate, with dry summers and wet winters, promoting strong seasonality in stream flows. The combination of climate and abundant water has made the state a highly desirable place for humans to live, so it supports a large and rapidly growing population. Human demands on the landscape have dramatically changed the availability of water to salmonids. As a result of increased water demands and degraded habitat conditions, most (65%) extant populations are in severe decline and some, such as coho salmon, are on the verge of extinction ([Moyle et al. 2008](#_ENREF_145)). Climate change is now exacerbating this situation.

The suitability of rivers in the United States for supporting salmon and trout is conservatively estimated to decrease 4-20% by 2030 and by as much as 60% by 2100 ([Eaton and Scheller 1996](#_ENREF_55)), with the greatest loss projected for California ([O'Neal 2002](#_ENREF_157), [Preston 2006](#_ENREF_163)). Because climate change is the template on which existing and future conservation actions will take place, resource managers must understand the impacts of climate change on salmonids in order for conservation to be successful ([Battin et al. 2007](#_ENREF_11), [Ficke et al. 2007](#_ENREF_61), [Schindler et al. 2008](#_ENREF_182)). Here, we briefly outline threats salmonid populations currently face in California, and review potential impacts of climate change on salmonid habitats and populations. We focus our discussion on the Klamath River in northwestern California because it is the second largest river in the state and supports or supported all six anadromous salmonid species, consisting of nine recognized taxonomic units, plus runs of five other anadromous species (Table 1.1). We compare the habitat conditions preferred by salmonids with those that are likely to result from climate change to assess likelihoods of extinction and adaptation. The Klamath River is used to illustrate how management recommendations can be implemented to promote population persistence in the face of climate change and existing stressors.

Table 1.1. Taxa (including distinct runs) of native anadromous fishes in the Klamath River basin

(Groot and Margolis 1991, Busby et al. 1996, Myers et al. 1998, Moyle 2002).

|  |  |  |  |
| --- | --- | --- | --- |
| **Species/runs** | **Spawning/rearing habitat** | **Time in freshwater (F)1, estuary (E),**  **Pacific Ocean (PO)2** | **Reproductive strategy;**  **peak spawning run** |
| Steelhead trout  (*O. mykiss)*  Winter run\*  Summer run\*\* | \*Tributary streams  \*\*Upper elevation  tributaries | Both runs =  F: Few months to 2 years  E:days to months  PO: 1 to 2 years | Both runs =  Iteroparous3;  \*November – December  \*\*April – June |
| Chinook salmon  *(O. tshawytscha)*  Fall run\*  Spring run\*\* | \*Lower elevation tributaries and  mainstem Klamath River  \*\* Tributary streams and upper elevation tributaries | Both runs =  F: Few months to 1 year  E: Days to weeks  PO: 1 to 5 years | Both runs = Semelparous4;  \*October - December  \*\* May – July |
| Coho salmon  *(O. kisutch)* | Tributary streams and upper elevation tributaries | F: One year  E: Days to months,  PO: 1 to 2 years | Semelparous;  October – November |
| Pink salmon  *(O. gorbuscha)* | Mainstem Klamath River | F: Days to weeks  E: Days to weeks  PO: 2 to 3 years | Semelparous;  September – October |
| Chum salmon  *(O. keta)* | Mainstem Klamath River | F: Days to weeks  E: Weeks to months  PO: 2 to 7 years | Semelparous;  October - December |
| Coastal cutthroat trout  *(O. clarki clarki)* | Mainstem Klamath River and lower elevation tributaries | F: Two to 3 years  E: Weeks to months  PO: Months | Iteroparous;  August - October |
| Pacific lamprey  (*Entosphenus tridentata*) | Mainstem Klamath River and tributary streams | F: Five to 7 years  E: Days  PO: 3 to 4 years | Semelparous5;  March – June |
| River lamprey  (*Lampetra ayresi*) | Tributary streams | F: Nine to 10 months  E: Weeks  PO: 3 to 4 months | Semelparous;  February – May |
| Green sturgeon  (*Acipenser medirostris*) | Mainstem Klamath River and lower Salmon River | F: Several months to 4 years  E: Months  PO: 15 to 19 years to maturity then 2 or more years | Iteroparous;  April - June |
|  |  |  |  |
|  |  |  |  |
| Table 1.1. continued |  |  |  |
| White sturgeon   1. *transmontanus)* | Mainstem Klamath River | F: Several months  E: Several months  PO: 10 to 16 years to maturity then 1 to 5 years | Iteroparous;  March – June |
| Eulachon  (*Thaleichthys pacificus*) | Lower mainstem Klamath River | F: Weeks  E: weeks,  PO: 1 to 4 years | Semelparous;  March – April |

1Time in freshwater refers to the length of time spent by juveniles rearing in freshwater

2Time in Pacific Ocean refers to the length of time spent by adults in marine habitats prior to or between spawning runs

3 Iteroparous = spawn more than once in their lifetime

4Semelparous = spawn once then die

5Small percentage of spawning adults may survive to spawn a second time

In this review, we address these issues by answering the following questions for Klamath Basin salmonids:

1. What life history and physiological characteristics make anadromous salmonids vulnerable to climate change?
2. What anthropomorphic factors increase vulnerability of anadromous salmonids to climate change?
3. What are the likely effects of climate change on salmonid habitats, especially in the Klamath River basin?
4. How are salmonids likely to respond to climate change?
5. What conservation strategies have the greatest likelihood of success in maintaining salmonids?
6. Is it really possible to save most anadromous salmonid populations, given the pessimistic scenarios presented in Salmon 2100 ([Lackey et al. 2006](#_ENREF_113))?

**Study area**

The Klamath River flows into the Pacific Ocean about 64.4 km south of the Oregon/California border, draining approximately 40,400 km2 in northern California and southern Oregon (Figure 1.1). The basin is largely forested and is recognized as one of the country’s most diverse biological areas ([Kier and Associates 1991](#_ENREF_102)).

Aquatic habitats within the basin vary greatly. The Klamath River watershed is often described as having two parts, above (upper basin) and below (lower basin) Iron Gate Dam, due to differences in hydrology, geology and climate ([Hamilton et al. 2011](#_ENREF_76)). The upper basin predominantly consists of streams that are low gradient, flowing in volcanic terrain characterized by wide valleys, large lakes, wetlands and springs (NRC 2004). Climate in the upper basin is relatively dry, similar to other high desert areas east of the Cascade Range (NRC 2004). In contrast, the lower basin is characterized by streams that are high energy and flow in steep-gradient bedrock canyons (NRC 2004). However, both the Shasta and Scott rivers, located in the lower basin, flow at least partially through wide valleys. The lower basin’s climate is variable but reflects high annual rainfall and milder temperatures (NRC 2004).

Stream flow patterns vary between the two parts of the basin. In the upper basin, stream flow is characterized by high spring flows, augmented by snowmelt, and “stable” summer base flows largely dependent on groundwater inputs ([Hamilton et al. 2011](#_ENREF_76)). In the lower basin, stream flow is characterized by high winter and spring flows, and continually decreasing base flows in the summer (Hamilton et al. 2011). Flows in the lower basin have also been altered by the presence of dams in the mainstem Klamath and Trinity rivers.

The Klamath River below Iron Gate Dam was designated in 1981 by the U.S. Congress as a Wild and Scenic River because of the value and diversity of its anadromous fisheries. However, anadromous fish populations, especially salmonids, in the Klamath River are under pressure from multiple stressors, including water diversion, dam construction and operations, sedimentation, hatchery supplementation, and habitat degradation. Abundances of some runs have declined so that they are now a mere fraction of historical levels (Hamilton et al. 2011). For example, the number of wild spring-run Chinook salmon returning to the basin in recent years has averaged about 10% of historical numbers (~ 10,000) ([Moyle et al. 2008](#_ENREF_145), [Quiñones unpublished data](#_ENREF_167)).

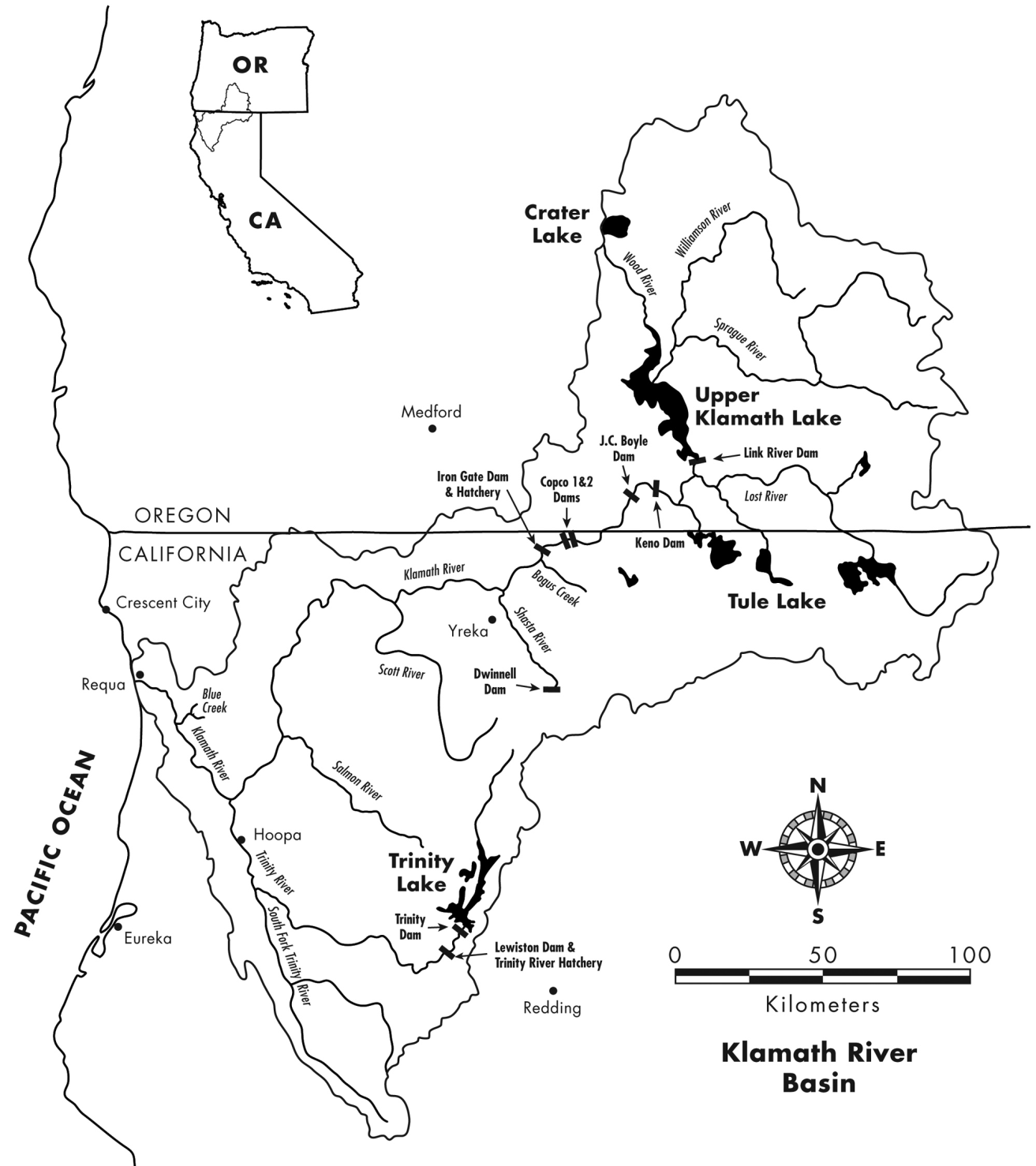


Figure 1.1. The Klamath River basin, California.

In order to alleviate conflicts over natural resource use, many stakeholders in the basin signed two agreements (Klamath Basin Restoration Agreement, Klamath Hydroelectric Settlement Agreement) in 2010. The agreements are to be implemented jointly in order to restore and maintain fisheries, while providing for the welfare and sustainability of local communities. Central to the agreements is the removal of the lower four dams on the mainstem Klamath River to provide access to an estimated 560 km of habitat currently not accessible to anadromous salmonids ([Hamilton et al. 2005](#_ENREF_77), [Huntington 2006](#_ENREF_95)). Dams have changed hydrologic patterns of the mainstem Klamath River for close to a century, although implementation of recent flow requirements may help to ameliorate some problems ([NMFS 2010](#_ENREF_155)). Comparison of mainstem flows (cubic meter per second; cms) before (1911-1917) and after (1968-2007) dam construction shows changes in the duration, timing and magnitude of monthly median flows (Figure 1.2). Monthly median flows were higher and lasted longer before dam construction, exceeding 775 cms from February to May, and peaking in April ([Quiñones 2006](#_ENREF_166)). In comparison, monthly median flows after dam construction (1968-2007) peaked in February and never exceeded 775 cms.

Figure 1.2. Comparison of Klamath River flow (cms) at Requa (gage no. 11530500; http://waterdata.usgs.gov/nwis), before (1911-1917) and after (1968-2007) construction of dams. All available data were analyzed using the Indicators of Hydrologic Alteration (IHA) model and software ([TNC 1996](#_ENREF_197)) as described in ([Magilligan and Nislow 2005](#_ENREF_125)).

1. **What life history and physiological factors make anadromous salmonids so vulnerable to climate change?**

1A. Life history factors

Anadromous Pacific salmonids have complex life histories that require a variety of environments ([Groot and Margolis 1991](#_ENREF_73), [Moyle 2002](#_ENREF_144)) (as in Table 1.2). Anadromous salmonids spawn in flowing waters from headwater creeks to rivers, rear in rivers and estuaries, and then usually spend large portions of their lives in the ocean. Adult salmonids initiate spawning migrations, from the ocean into natal rivers, in association with changes in water temperature and or river flow. Once upriver, females choose sites to build nests (redds) based on stream bed characteristics such as substrate size, flow and depth that provide good conditions for incubating embryos. Embryos incubate in redds for three to five months, with time to hatch being largely regulated by water temperature. Upon hatching (alevin stage) and absorption of the yolk sac (fry stage), juveniles rear in fresh water for a few days to 1-3 years before beginning downstream migration, often in association with increases in stream flow in spring or fall. All anadromous salmonids must undergo smoltification, a physiological process that facilitates excretion of excess salts, before they begin their oceanic existence. At this life stage, estuaries play a key role by providing habitat where food is abundant and smoltification can occur. Estuaries, located at river mouths, are areas where fresh and saltwater mix, providing habitat along a salinity gradient as fish migrate downstream. Finally, salmonids spend much of their lives in the ocean. Consequently, abundance of salmonids stocks is often strongly correlated with ocean productivity ([Mantua et al. 1997](#_ENREF_127), [Beamish et al. 1999](#_ENREF_15), [Grimes et al. 2007](#_ENREF_72)). In many years, adverse inland conditions can limit recruitment, although some compensation can occur if ocean conditions are favorable. Thus, climate change can strongly affect abundances even if only one of the three major environments (river, estuary, ocean) becomes less suitable to salmonids.

Table 1.2. Coho salmon life history, habitat used, and optimal habitat characteristics ([Groot and Margolis 1991](#_ENREF_73), [Richter and Kolmes 2005](#_ENREF_171), [Moyle et al. 2008](#_ENREF_145), [NOAA 2011](#_ENREF_156)).

|  |  |  |  |
| --- | --- | --- | --- |
| **Life history stage** | **Habitat used** | | **Optimal habitat characteristics** |
| Migrating adult  (to spawning areas) | Pacific Ocean, Estuary,  Mainstem, Tributaries | | Estuary - open river mouth, increasing flows  Tributaries - cold (~ 8-15°C), clean, flowing water with pools  Minimum water depth ~ 18 cm  Maximum water velocity ~ 2.44 m/s |
| Spawning adult | Tributaries | | Clean gravel (~ 4-14 cm in diameter)  Water velocity < 1 m/s  Minimum water depth of ~ 10 cm  Water temperature <12°C |
| Incubating embryos | Tributaries | | Intragravel flow  Low silt loading  Water temperatures 8-10°C |
| Alevin/Fry | Tributaries | | Low concentration of fine (< 3.5 mm) sediment in the gravel bed  Water temperatures <12°C |
| Table 1.2. continued | |  |  |
| Juvenile rearing | Tributaries | | Slow water habitats, especially pools  Lots of cover (e.g., fallen trees, overhanging vegetation)  Lots of food (e.g., aquatic insects)  Water temperature <15°C |
| Out-migrating juvenile | Tributaries  Mainstem,  Estuary | | Tributaries - increasing flows and temperature (but <16°C)  Mainstem – combination of slow and fast moving water  Estuary – open river mouth |
| Smoltifying juveniles | Mainstem,  Estuary | | Mainstem – cool water (<16°C), unobstructed access  Estuary – cool, productive slough habitats |
| Subadult rearing | Pacific Ocean | | Highly productive coastal habitats (strong upwelling)  Sea surface temperatures <9°C |

1B. Physiological factors

Salmonids are adapted to thrive in geologically active areas characterized by cold (usually < 18-20°C), clear water with high levels of dissolved oxygen (Moyle 2002). Temperature plays an important role during all life stages by affecting metabolic rate, growth and immune function. In general, salmonids can withstand temperatures from 0-25°C but physiological processes are typically optimal at temperatures between 4-20°C ([McEwan and Jackson 1996](#_ENREF_133), [Moyle 2002](#_ENREF_144), [Richter and Kolmes 2005](#_ENREF_171)). Prolonged exposure to temperatures above 18°C can increase the susceptibility of salmonids to disease ([Udey et al. 1975](#_ENREF_199), [McCullough 1999](#_ENREF_132), [Marcogliese 2001](#_ENREF_129), [Stocking 2006](#_ENREF_190)), and reduce or increase metabolic rates largely dependent on food availability ([Holtby et al. 1989](#_ENREF_93), [Viant et al. 2003](#_ENREF_206), [Rand et al. 2006](#_ENREF_168), [McCarthy et al. 2009](#_ENREF_131)). However, most salmonids have the ability to live in conditions in the wild that are measured as stressful in the laboratory, because they will seek out bioenergetically favorable environments (e.g., where food is abundant even if temperatures are high). Furthermore, populations in the southern part of a species’ range appear to tolerate higher temperatures than their more northern counterparts. Coho and Chinook salmon in the Klamath River seem able to withstand temperatures 2-3°C higher than those within the conventional tolerance range for each species ([Belchik 2003](#_ENREF_18), [Sutton et al. 2007](#_ENREF_193), [Strange 2010](#_ENREF_191)). Other water quality and habitat parameters, such as stream substrate composition, are also important to salmonid survival but their effects vary widely among species and are often interactive with temperature, each other, and with salmonid life histories.

1. **What anthropogenic factors increase vulnerability of anadromous salmonids to climate change?**

Salmonid populations in California, and particularly in the Klamath River, are already adversely affected by A. reduced stream flows, B. dams, C. habitat degradation and fragmentation, D. interactions hatchery-reared conspecifics, and E. overexploitation (Moyle 2002, Moyle et al. 2008). The cumulative impact from these stressors has resulted in many once-suitable aquatic habitats becoming suboptimal for salmonid survival and many populations becoming vulnerable to extinction. Climate change will exacerbate these conditions (Battin et al. 2007).

2A. Reduced stream flows

The amount of suitable freshwater habitat available to salmonids in California has been reduced by river modifications, primarily by decreasing water quantity. Diversion of surface water and pumping of groundwater for agricultural use significantly reduce the amount of water in salmonid-producing streams (Moyle 2002). Some 70-80% of the surface water stored in California is diverted for irrigated agriculture alone ([Hanak et al. 2011](#_ENREF_80)). Water diversion affects salmonids and their habitat in several, and often simultaneous, ways including dewatering of habitats, changes to temperature and flow regimes, direct mortality due to pump and screen trapping, and alterations of stream and estuarine configuration. The pumping of groundwater further reduces water quantity by dropping water tables that would normally sustain stream flow in the summer months.

In the Klamath River basin, water is diverted in both Oregon and California. The Klamath River is diverted at Keno dam to provide water for the Klamath Reclamation Project ([USDI 2011](#_ENREF_201)) and, since the construction of Lewiston Dam in 1963, up to 90% of Trinity River flow is diverted into the Sacramento River ([Trush et al. 2000](#_ENREF_198)). Diversions and groundwater pumping in the lower basin (esp. Scott and Shasta rivers) can result in low flows and dry stream reaches during the summer months ([Van Kirk and Naman 2008](#_ENREF_204)) and can disrupt salmonid movements. Low summer flows (<0.2 cm/s) in the Scott River appeared to stall fall run Chinook salmon migration for several days in 2009 by drying up stretches of the mainstem river ([Hampton 2009](#_ENREF_79)).

2B. Dams

Dam construction is one of the most obvious habitat modifications of rivers in California and on the Klamath River. Dams cause significant changes to riparian ecosystems by changing river morphology and flows. As early as the 1850s, decreases in anadromous fish abundance were associated with the presence of dams that acted as barriers to salmon returning to spawning habitats ([Groot and Margolis 1991](#_ENREF_73), [Yoshiyama et al. 1998](#_ENREF_219)). Adult salmon returning to rivers provide marine-derived nutrients to freshwater habitats, thereby increasing productivity at several trophic levels within aquatic and terrestrial habitats ([Naiman et al. 2002](#_ENREF_149), [Merz and Moyle 2006](#_ENREF_136)). Disruption of salmon migration results in decreases in the productivity of both the aquatic and terrestrial components of riparian systems ([Schindler et al. 2003](#_ENREF_183)). In addition, dams reduce exchange of nutrients, including particulate organic matter, between upstream and downstream habitats that define community composition and trophic structure ([Poff et al. 1997](#_ENREF_161)). Poff et al. ([2006](#_ENREF_162)) concluded that the interaction between hydrology and geomorphology that creates the physical environment that define river ecosystems is disrupted by dams. Reservoirs formed by dams retain sediment from inflowing streams, disrupting sediment and nutrient supply to downstream habitats ([Knighton 1998](#_ENREF_106), [Graf 2006](#_ENREF_69)). Downstream of dams, reductions in sediment supply and water quantity result in single-thread channels, changes to sediment composition, streambed cementation, channel narrowing, and beach loss ([Graf 1980](#_ENREF_68), [Magilligan and Nislow 2005](#_ENREF_125)).

Six dams currently block the mainstem Klamath River. The furthest downstream, Iron Gate Dam (rkm 306) blocks access to approximately 560 km of historical salmonid habitat ([Hamilton et al. 2005](#_ENREF_77)). Furthermore, dam operations have decreased stream flow, primarily during summer months; decreased water quality; decreased the recruitment and quality of spawning gravels; and delayed the natural temperature regime by approximately 18 days ([Bartholow 2005](#_ENREF_10), [Hamilton et al. 2011](#_ENREF_76)). The presence of dams has also resulted in toxic blooms of blue green algae (*Microcystis aeruginosa*) ([Kann and Corum 2006](#_ENREF_100), [2007](#_ENREF_101)) and increased incidence of fish disease ([Bartholomew et al. 2006](#_ENREF_9), [Foott et al. 2007](#_ENREF_63)). Dams also affect the hydrology and biology of the Shasta (Dwinnell dam) and Trinity (Lewiston and Trinity dams) rivers. Since its construction in 1928, Dwinnell dam has decreased mean annual flow to the Shasta River directly below the dam by 90% ([Vignola and Deas 2005](#_ENREF_207)). However, spring-fed tributaries ameliorate stream flow so that only about a 12% reduction is evident below the mouth of Big Springs Creek approximately 11 km downstream of the dam ([Nichols 2008](#_ENREF_151)). In the Trinity River, up to 90% of the stream flow is diverted into the Sacramento River at Lewiston dam ([USDI 2000](#_ENREF_200)).

2C. Habitat degradation and fragmentation

Habitat modifications that directly and indirectly result in salmonid declines in California include stream channel alterations; land reclamation; and impacts from livestock grazing, timber harvest and mining (Moyle 2002). The Klamath River basin has a long history of gold mining, agriculture, cattle grazing and timber harvest. Large-scale gold dredging in the lower basin has left a legacy of streams with straighter and narrower channels filled with large cobble, often resulting in reaches with subsurface flows. Mining practices have also resulted in streams that are partially disconnected from riparian ecosystems because most riparian vegetation is unable to flourish in floodplains where topsoil has been removed. The use of mercury for gold recovery has also polluted many waterways; mining debris was commonly discharged into Klamath-Trinity mountain streams until as late as the 1950s ([Alpers et al. 2005](#_ENREF_3)).

Reclamation of lands for agricultural purposes has changed the dynamics of water flow and aquifer recharge in the Klamath River basin. Drainage of wetlands for agricultural purposes has resulted in the loss of 90% of the open water and marsh habitat above Iron Gate Dam (NRC 2004) as well as wetland habitat in the Shasta and Scott rivers. Irrigation practices (surface diversion, groundwater pumping) further fragment aquatic habitat by lowering flows and or dewatering stream reaches, primarily in the summer and fall ([Van Kirk and Naman 2008](#_ENREF_204)).

2D. Interactions with hatchery-reared conspecifics

Salmonids in California are being negatively impacted by current hatchery practices. Large numbers of adult and juvenile salmon of hatchery origin overwhelm wild salmon through interbreeding, competition and disease. Interactions between hatchery and wild salmonids thus reduce the reproductive success, genetic diversity and viability of wild stocks ([Bisson et al. 2002](#_ENREF_21), [Araki et al. 2007](#_ENREF_6)). Hatchery salmon survive poorly in the wild, although if enough are produced, they can maintain fisheries, at least for a while. Furthermore, interbreeding between wild and hatchery fish may result in the loss of local adaptations ([Reisenbichler and Rubin 1999](#_ENREF_169)). After extensive review of hatchery programs, a consortium of salmon fisheries experts (Bisson et al. 2002) found no examples of wild stock survival being improved by crossbreeding with hatchery stocks. Instead, hybridization can increase disease susceptibility in wild fish (Currens et al. 1997 in Bisson et al. 2002). And, fish production in hatcheries does not necessarily increase the subsequent number of adult spawners ([Nickelson et al. 1986](#_ENREF_153)). Most hatchery programs produce populations that are increasingly more reliant on hatchery supplementation for their persistence because wild populations are less able to persist ([Levin et al. 2001](#_ENREF_120)). Populations that are largely supplemented by hatchery fish (e.g., Sacramento River fall Chinook), coupled with extensive habitat degradation and alteration, can lose the life history diversity that buffers populations from changing environmental conditions ([Lindley et al. 2009](#_ENREF_122)).

Iron Gate and Trinity River hatcheries operate on the Klamath River to mitigate for loss of habitat upstream of Iron Gate dam, on the mainstem Klamath River, and Lewiston dam, on the Trinity River. The two hatcheries release approximately 12 million juvenile salmonids (Chinook salmon, coho salmon, steelhead) into the Klamath River basin each year (Hamilton et al. 2011). Hatchery-reared fish now make up a significant portion of overall adult escapement. In any given year, approximately 32% (range 11 to 53%; Quiñones unpublished data) of fall run Chinook salmon escapement is made up of hatchery returns. A smaller portion (< 1 to 13%; Quiñones unpublished data) of hatchery-reared adults stray to spawn in neighboring streams, primarily Bogus Creek and Shasta River (S. Borok, CDFG, pers. comm. 2010). Due to supplementation programs, coho salmon runs in the basin are thought to be largely composed of hatchery fish ([Kier and Associates 1991](#_ENREF_102), [Brown et al. 1994](#_ENREF_31)).

2E. Overexploitation

Overexploitation by commercial, sports and tribal fisheries has contributed to the declines of Chinook and coho salmon in California in the past and effects of fisheries are still felt today (Moyle 2002). Through the mid-1800s and early 1900s, many of the rivers with large salmon runs in California supported cannery operations with unlimited fish catch. Not surprisingly, overharvest has been a contributing cause of the decline of salmonids in the Klamath River basin ([Kier and Associates 1991](#_ENREF_102)). From 1916-1927, an estimated 120,000-250,000 (ocean fisheries) and 35,000-70,000 (river fisheries) Klamath River fall run Chinook salmon were harvested (NRC 2004). By 1931, runs of some salmonids (i.e. spring run Chinook salmon) were considered significantly suppressed ([Snyder 1931](#_ENREF_185)). Ocean and in-river harvest can have significant impacts on escapement to specific sub-basins, perhaps altering the diversity and composition of runs to the entire Klamath River basin (Quiñones unpublished data).

1. **What are the likely effects of climate change on salmonids and their habitats, especially in the Klamath River basin?**

Climate change will further stress salmonid populations in California by altering salmonid habitat that is already adversely impacted by many other factors. Nutrient, sediment and chemical properties of aquatic habitats may change to the extent that they become unsuitable for salmonids ([Knox and Scheuring 1991](#_ENREF_109), [Van Winkle et al. 1997](#_ENREF_205), [Anderson et al. 2008](#_ENREF_4)). Here,we focus our discussion on the direct impacts that climate change will likely have on A. river, B. estuarine, and C. ocean habitats. We recognize that indirect effects can also be important (e.g. increases in fire frequency that result in increased erosion or temperatures from loss of riparian vegetation) but do not deal with them here.

3A. Effect on river habitats

Climate change has already impacted the quality (increased temperatures, changes in flow timing and magnitude) of salmonid habitat in California rivers, as a result of increases in air temperature, decreases in snowpack, and changes in precipitation patterns ([Field et al. 1999](#_ENREF_62)). Increases in air temperatures in the western United States have resulted in an estimated increase of 0.72°C in water temperatures in the last 100 years (based on conversion factors in Eaton and Scheller 1996). Although the increase in water temperature seems small, it can result in conditions that are suboptimal or lethal to salmonids already residing in the Klamath River, where summer temperatures often exceed 22°C (McCullough 1999; CDEC 2008). Water temperatures in the mainstem Klamath River are already increasing by 0.5°C per decade, likely reflecting regional increases in air temperature (Bartholow 2005). Changes in water temperature, however, vary within watersheds, depending on whether stream flows come primarily from groundwater, snowmelt or rainfall.

3A1. Groundwater

Streams fed by groundwater are generally cooler in the summer and warmer in the winter than those fed by surface runoff (e.g., snowmelt). As a result, water temperatures in the upper basin (predominantly groundwater-fed) are more likely to be buffered from climate change than those in the lower basin (predominantly snowmelt-fed). Large springs, such as those feeding streams in the Cascades, with long environmental response times, can be expected to dampen climatic temperature changes on the order of decades ([Manga 1999](#_ENREF_126)). In the Klamath basin, significant groundwater discharges flow into the Shasta River ([Nichols 2008](#_ENREF_151)) in the lower basin, and Wood River, lower Williamson River, and along the margin of the Cascade Range in the upper basin ([Gannett et al. 2010](#_ENREF_66)).

Overall, spring-fed rivers (e.g., Williamson, Wood, Shasta rivers) are expected to flow year-round due to an extended storage effect, but at reduced levels ([Thompson 2007](#_ENREF_196), [Tague et al. 2008](#_ENREF_194)). The hydrograph of spring-fed systems also is expected to reflect higher winter flows, delayed peak flows, and decreased spring and summer flows as snowmelt peaks earlier in the year and flows are mediated by geologic drainage rates ([Jefferson et al. 2007](#_ENREF_97), [Thompson 2007](#_ENREF_196), [Tague et al. 2008](#_ENREF_194)). Consequently, stream flow in spring-fed systems should be more stable (less interannual variability) than snowmelt-fed streams ([Jefferson et al. 2007](#_ENREF_97)).

3A2. Snowmelt and rainfall

Snowmelt-fed streams will be warmer and drier during the summer and fall months due to reduction in total snowpack and seasonal retention of snow ([Hayhoe et al. 2004](#_ENREF_86), [Stewart et al. 2004](#_ENREF_188), [Hamlet et al. 2005](#_ENREF_78), [Stewart et al. 2005](#_ENREF_189)). Elevations below 3000 m will suffer the most (80%) reduction in snow pack (Hayhoe et al. 2004). Snow pack (April 1) water content in the last 50 years has already significantly declined at several monitoring stations in the Klamath basin (Van Kirk and Naman 2008). Lower flows further exacerbate increasing water temperatures as river depth is often inversely related to water temperature ([Allan and Castillo 2007](#_ENREF_2)). A reduction in snowpack will have the most impacts on streams that rely on surface runoff for the bulk of their flows (e.g., Scott and Salmon rivers) when compared to spring-fed systems (e.g., Shasta River).

Climate change will alter stream flow patterns by increasing winter runoff as precipitation increasingly falls as rain rather than snow, likely decreasing spring and summer stream flow, and increasing the occurrence of winter floods and summer droughts ([Knox and Scheuring 1991](#_ENREF_109), [Field et al. 1999](#_ENREF_62), [Anderson et al. 2008](#_ENREF_4)). Earlier snowmelt and increased temperatures have already changed the timing of peak flows by 10 to 30 days (Stewart et al. 2005), with peak flows occurring earlier in more recent decades ([Cayan et al. 2001](#_ENREF_36)). In the Pacific Northwest, future peak flows are predicted to shift by 30 to 40 days (Stewart et al. 2004). If changes in flow regimes continue at the current rate, then stream flow in the Klamath River basin is expected to decrease by 10%-50% in the spring and summer, while the frequency of extreme high and low flows increases by 15%-20% ([Leung et al. 2004](#_ENREF_117), [Kim 2005](#_ENREF_103)).

3B. Effects on estuarine habitats

Climate change has already changed the size and characteristics of estuaries in the United States. A combination of melting of ice sheets and glaciers, and thermal expansion of oceans have contributed to sea level rise along the California coastline of about 0.2 m during the 20th century ([Cayan et al. 2008](#_ENREF_35)). A rise in sea level can flood estuaries so that the amount of tidal habitat is reduced by inundation and associated erosion, accompanied by increases in salinity ([Scavia et al. 2002](#_ENREF_179)). Physical processes in estuaries are also affected by changes in stream flow, directly linking climate and food web production ([Lehman 2004](#_ENREF_115)). Climate change is predicted to continue impacting the biological, physical and chemical characteristics of estuaries in the United States (Scavia et al. 2002). Not surprisingly, such effects are likely to be seen in the Klamath River estuary.

The Klamath River estuary extends upstream from the mouth of the river approximately 8 km ([Hiner and Brown 2004](#_ENREF_92)). The estuary is fairly narrow (~ 0.8 km) and habitats are predominantly sand flats with some freshwater littoral areas ([Wallace 2010](#_ENREF_209)). A relatively small amount of slough habitat is available in the south side of the estuary (Hiner and Brown 2004) and in the lower 1 km of Salt and Hunter creeks (Hiner and Brown 2004), located about 1.3 km upstream of the Klamath River mouth ([Beesley and Fiori 2007](#_ENREF_17)).

Productivity in the Klamath River estuary will likely change, reflecting changes in delivery of fresh water, sediment and nutrients caused by changes in stream flow and precipitation patterns. Projections are that sea levels may increase by at least another 0.1 m to 0.7 m by 2099, worsening the impacts from extreme tidal, storm and flooding events (Canyan et al. 2008). The rates and magnitude of salt water and fresh water mixing within estuaries will change as temperatures increase, sea level rises, and inflows become more variable. As a result, salinities are likely to vary between seasons, with concentrations highest in the summer and lowest in the winter ([Dettinger and Cayan 1995](#_ENREF_49), [Knowles and Cayan 2004](#_ENREF_107)). Decreases in fresh water delivery during the summer also may push the estuary towards eutrophication due to the accumulation of organic matter, increasing the risk of localized anoxic conditions ([Moore et al. 1997](#_ENREF_142)). Although eutrophication initially increases primary productivity, an increase in production may not cascade to fishes located higher in the food web ([Kimmerer 2002](#_ENREF_104)). In addition, sea level rise and increased rates of erosion caused by more frequent and stronger tides and storms are other agents to estuarine habitat change (Scavia et al. 2002). And, the diversity, composition and abundance of vegetation in estuaries may decrease if aquatic plant species cannot migrate inland in pace with rising sea level (Scavia et al. 2002).

3C. Effects on ocean habitats

Pacific salmon survival rates in the Pacific Ocean are associated with environmental conditions at regional scales, such as sea surface temperature, and the Pacific Decadal, El Niño Southern, and North Pacific Gyre oscillations ([Beamish 1993](#_ENREF_13), [Hare and Francis 1995](#_ENREF_82), [Mantua et al. 1997](#_ENREF_127), [Mueter et al. 2002](#_ENREF_146), [Di Lorenzo et al. 2008](#_ENREF_50)). El Niño conditions in the California current result in a decrease in zooplankton concentrations, primary prey to juvenile salmonids entering the ocean ([McGowan et al. 1998](#_ENREF_134), [Hays et al. 2005](#_ENREF_87)). However, juvenile salmon exhibit some flexibility in preferred prey during years of good and poor ocean conditions ([Brodeur et al. 2007](#_ENREF_29)). Other factors, such as seasonality of prey abundance, also play a role; smolt-to-adult survival is most strongly correlated with upwelling during the spring and fall months ([Ryding and Skalski 1999](#_ENREF_176), [Scheuerell and Williams 2005](#_ENREF_180)). Thus, the effects of changing conditions on salmon growth and survival may be patchy within the ocean ([Coronado and Hilborn 1998](#_ENREF_43)). Overall, abundances of salmonids in the ocean are predicted to shift poleward in response to decreases in prey productivity throughout the northern Pacific Ocean ([Pierce 2004](#_ENREF_160)).

Although precise effects of climate change on the coastal Pacific Ocean off California are hard to predict, some general trends appear. Changing wind patterns will likely reduce overall ocean productivity, or make it more variable, surface temperatures will increase ([Schwing et al. 2010](#_ENREF_184), [Wang et al. 2010](#_ENREF_212)), as will ocean acidity ([Hauri et al. 2009](#_ENREF_85)). Increased wind strength may favor primary productivity in the California Current ([Snyder et al. 2003](#_ENREF_186), [García-Reyes and Largier 2010](#_ENREF_67)), but benefits to higher trophic levels may be lost to advection ([Di Lorenzo et al. 2008](#_ENREF_50)), anoxic events ([Chan et al. 2008](#_ENREF_38), [Ekau et al. 2010](#_ENREF_58), [Hallegraeff 2010](#_ENREF_75)), and/or density dependent interactions in productive areas ([Ainley et al. 2009](#_ENREF_1), [Crozier et al. 2010](#_ENREF_47)). However, separate regions within the California Current system are likely to respond in different ways, with the largest reduction in productivity occurring south of Point Conception ([Checkley and Barth 2009](#_ENREF_40)). Increases in wind strength can also move areas with high productivity further offshore, while moving oxygen minimum zones inshore. Anoxic areas could be expanded by bacterial activity acting on decomposition of phytoplankton after large blooms. Productivity along the California coast may be further suppressed by the stratification of shallower waters, as reflected by an 80% decrease in zooplankton biomass ([Roemmich and McGowan 1995](#_ENREF_173)). Climate change also is likely to delay the timing of peak productivity, potentially disrupting predator-prey relationships at the time of ocean entry by juvenile salmonids ([Bograd et al. 2009](#_ENREF_22)).

1. **How are salmonids likely to respond to climate change?**

4A. Changes to river habitats

Increases in water temperatures will strongly affect the physiology and behavior of salmonids. The resulting changes in survival and reproductive success are likely to be complex and their impact on salmonid populations is unclear (Table 1.3). For example, increases in water temperatures may allow juvenile salmonids to grow faster, if food is readily available, resulting in earlier arrival to estuaries and better survival to adulthood ([Mote et al. 2003](#_ENREF_143), [Scheuerell et al. 2009](#_ENREF_181)). Increases in minimum winter temperatures ([Knowles et al. 2006](#_ENREF_108)), may also accelerate progression of embryos from incubation to hatching and emergence from stream gravels ([Murray and McPhail 1988](#_ENREF_147)), increasing the possibility that juveniles will be displaced by higher seasonal flows. For adult salmonids, metabolic costs associated with increased temperatures during upstream spawning migrations may be mitigated by shorter migrations (due to reduction in flows that offer less resistant to fish moving upstream) and more abundant food, but the benefit could be negated by an increase in the incidence of disease and a decrease in female spawner size ([Rand et al. 2006](#_ENREF_168)), which have also been shown to be correlated with warmer water temperatures ([Beacham and Murray 1993](#_ENREF_12)). Water temperatures higher than 18°C have been shown to impair salmonid growth, reproduction and survival (reviewed in Richter and Kolmes 2005) due to an increase in the metabolic costs of base functions.

Table 1.3. Maximum temperatures (°C) critical to Chinook salmon, coho salmon and steelhead trout survival at different life stages, with a brief description of their effects. Temperatures in bold are reported to result in mortality. Letters (s) and (f) denote Chinook spring and fall run, respectively. Adapted from Richter and Kolmes 2005.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  |  | **Species** |  |  |
| **Life stage** | **Chinook** | **Coho** | **Steelhead** | **Effect of exposure to maximum (near lethal) temperatures (°C)** |
| Incubation | 9-12  **14** | 11-12  **11-14** | 15-16 | Reduction in alevin survival |
| Juvenile rearing/growth | 14-20 | 15-16.5  **22-26** | 20.5-22.5  **24** | Reduction in growth, induction of heat shock proteins. Varies with food availability. |
| Smoltification | 12 (s)  17 (f)  **18** | 12-15.5 | 11-14 | Inhibits activity of gill ATPase, reduces ability to osmoregulate, loss of migratory behavior |
| Adult Migration | 19-24 | 15.6  **21-22** | 16-22  **21-22** | Stops upstream migration |
| Spawning | 14.5 | 12-20 | 13 | Reduction in spawning activity, reduction in quality of eggs |

Juvenile Klamath salmonids are able to grow in temperatures greater than 21°C, but growth, smoltification and predator avoidance can become impaired ([Marine and Cech 2004](#_ENREF_130)). Differences in critical maximum temperatures among individuals are related to the acclimation regime rather than to genetic variation ([Konecki et al. 1995](#_ENREF_110)). Therefore, salmonid developmental rates are more likely to shift (to earlier time to hatch, emergence, outmigration and ocean entry) than are genetically-based environmental tolerances. However, a shift in behavior does not guarantee that a population will persist because the reproductive success of some populations showing behavioral shifts has declined ([Bradshaw and Holzapfel 2006](#_ENREF_25)).

Changes in movement patterns are likely to govern behavioral responses of salmonid individuals to climate change, particularly in association with increases in temperature and changes in stream flow patterns. Most salmonids use temperature thresholds and changes in flow to trigger behavioral responses (Groot and Margolis 1991). Because temperature increases will hasten developmental rates and flows will peak earlier in the year, the migration patterns of Klamath salmonids will likely shift to earlier in the year. However, shifts in the timing of individual spawning migrations may be confounded by hybridization of wild stocks with hatchery stocks which also results in changes to migration timing ([Quinn et al. 2002](#_ENREF_165)). Furthermore, the photoperiod (day length) regime at a given site can influence the initiation of salmonid migrations, and may become unsynchronized with responses cued by changes in temperature ([Feder et al. 2010](#_ENREF_59)). Because day length can govern clock gene expression independently of temperature, migrations may not be initiated even when individuals are physiologically mature (Feder et al. 2010). The effects of the two most common Clock 1b alleles in Pacific salmon differ in strength and frequency depending on latitudinal location. Consequently, studies of Pacific salmon suggest that gene flow between more warm-adapted salmonids with populations closer to the poles may allow poleward populations to more readily respond to climate change (Feder et al. 2010), highlighting the importance of Klamath stocks. Another behavioral response to increased temperatures is the movement of salmonids into colder waters as a method of thermoregulation. Migrating salmonids use cold water pockets (> 3°C difference from ambient temperatures) in rivers during juvenile rearing and migration when temperatures exceed 22°C ([Nielsen et al. 1994](#_ENREF_154), [Sauter et al. 2001](#_ENREF_178), [Ebersole et al. 2003](#_ENREF_57)). Salmonids rearing in the mainstem Klamath River increasingly use thermal refuges as water temperatures increase in the summer and use thermal refuges most heavily when mainstem temperatures exceed 22°C ([Belchik 2003](#_ENREF_18), [Sutton et al. 2007](#_ENREF_193), [Strange 2010](#_ENREF_191))**.**

Changes in dispersal and survival will govern the response of salmonid populations to climate change. The reduction of suitable freshwater habitat is expected to result in a northward and or higher elevation shift in the range of cold water fishes ([Mohseni et al. 2003](#_ENREF_140), [Pierce 2004](#_ENREF_160), [Battin et al. 2007](#_ENREF_11)). As a result, salmonids in the Klamath River basin may experience local extinctions and range contractions (as in Parmesan 2006). Furthermore, genetic pleiotropic effects between dispersal and fitness traits may limit the ability of salmonids to respond to climate change (Feder et al. 2010), directly affecting the recruitment of populations throughout each species’ range. Changes in flow patterns may decrease salmonid embryo and juvenile survival. Extreme high flows can scour redds, flush juveniles out of the river system before they reach a critical size, and desynchronize juvenile arrival into the ocean with the spring phytoplankton bloom ([Mote et al. 2003](#_ENREF_143)). Fine (< 4 mm) sediment introduced by intense storm events may cap redds, preventing oxygen from reaching developing embryos and or acting as a barrier to fry emergence ([Furniss et al. 1991](#_ENREF_65)). Decreases in summer and fall flows may increase juvenile mortality through stranding, if flows go subsurface or change faster than juvenile movements allow. Changes in timing of spring and fall freshets may reduce survival of juveniles migrating from rivers into the ocean ([Lawson et al. 2004](#_ENREF_114)). Of course, salmonid survival is simultaneously affected by multiple factors. Thus, survival of juvenile Chinook salmon in the Klamath River may be positively correlated with flow but negatively correlated with high juvenile abundance, presumably due to competition between conspecifics ([Crozier and Zabel 2006](#_ENREF_45)). An increase in high flow events may reconnect the Klamath River to its floodplain, benefitting salmonid populations because highly productive floodplains can provide juvenile salmon with optimal rearing habitat ([Sommer et al. 2005](#_ENREF_187), [Feyrer et al. 2006](#_ENREF_60), [Jeffres et al. 2008](#_ENREF_98)). On the other hand, high flow events that occur too early may scour redds or carry small juveniles into the estuary before they are ready to smoltify.

Similar variable responses to changes in river flow and temperature will occur for adult salmon as well. Decreases in summer flows may increase adult survival because the metabolic cost of swimming against the current will be reduced ([Crozier and Zabel 2006](#_ENREF_45)). On the other hand, high mortality of migrating adults may occur if flows are too low and warm, halting upstream movement. Low flows were thus a major contributor to the kill of migrating salmon in the lower Klamath River in September 2002 ([Belchik et al. 2004](#_ENREF_19)). In addition, migrating adult spawners at low flows in warm water use more energy for upstream migration, resulting in pre-spawning mortality from disease, greater vulnerability to predators, and lowered egg quality.

As the flows become more variable and temperatures increase, the amount of habitat for nonnative warmwater fish species will increase concurrently with decreases in cold-water habitat ([Mohseni et al. 2003](#_ENREF_140)). Warmer conditions will favor the expansion in range of nonnative species already found in the Klamath River such as largemouth bass (*Micropterus salmoides*), black crappie (*Pomoxis nigromaculatus*), yellow perch (*Perca flavescens*), green sunfish (*Lepomis cyanellus),* and fathead minnow (*Pimephales promelas*) ([USFWS 2011](#_ENREF_202)). How strongly nonnative species will be favored is uncertain because, although numbers may increase with temperature, they may decrease with more annual variability in flows ([Marchetti and Moyle 2001](#_ENREF_128)). Accordingly, native fish numbers and reproductive success may be enhanced with a more natural flow regime, particularly in regulated rivers ([Marchetti and Moyle 2001](#_ENREF_128), [Brown and Ford 2002](#_ENREF_30)) like the Klamath River.

Responses to climate change will differ by taxa and location ([Walther et al. 2002](#_ENREF_211), [Parmesan and Yohe 2003](#_ENREF_158)). Therefore, novel interactions between Klamath River salmonids and their environment may challenge our traditional view of behaviors specific to each taxa. For example, worsening in-river conditions may lead steelhead to migrate to the ocean earlier and more often. Also, the temporal and spatial segregation of spring and fall Chinook salmon may disappear if spring Chinook salmon cannot migrate as far upstream and migration timing changes. Lastly, resistance to disease differs by species and age class, largely reflecting their location and length of exposure, so that species composition may change at different spatial scales.

4B. Changes to estuarine habitats

Estuaries are important to salmonids as habitats for rearing, smoltification and orientation for return migrations ([Groot and Margolis 1991](#_ENREF_73), [MacFarlane and Norton 2002](#_ENREF_124), [Bottom et al. 2005b](#_ENREF_24)). Juvenile salmonids use estuaries to varying degrees; Chinook salmon and steelhead can rear in estuaries for weeks to several months ([Healey 1991](#_ENREF_89), [Bottom et al. 2005a](#_ENREF_23)) while coho salmon usually reside in estuaries to a lesser extent ([Sandercock 1991](#_ENREF_177), [Miller and Sadro 2003](#_ENREF_138)). However, length of estuarine residency can vary according to temperature, stream flow, tidal cycle and condition of individual fishes at time of estuarine entrance ([Healey 1982](#_ENREF_88), [Kjelson et al. 1982](#_ENREF_105)), all factors that can be altered by climate change. This is especially true of the Klamath River estuary which is relatively small considering the size of the river.

The Klamath River estuary is confined by a canyon and so does not have extensive slough systems characteristic of most other west coast estuaries. Studies of salmonids in the estuary focused on use by juvenile Chinook salmon and concluded that most did not rear extensively in the estuary ([Sullivan 1989](#_ENREF_192), [Krakker 1991](#_ENREF_112), [Wallace and Collins 1997](#_ENREF_210)). The amount of rearing habitat available, emigration timing, and condition of salmonids entering the estuary were dependant on stream flow (Wallace and Collins 1997). Warmer temperatures in the river likely forced juvenile Chinook salmon to enter the estuary earlier, resulting in smaller sizes at ocean entry (Wallace and Collins 1997). Saltwater intrusion, and therefore salinity, was controlled by river flow and formation of a sand bar at river mouth in late summer. A layer of freshwater (1-2 m deep) was present throughout the surface of the estuary so shallow areas were primarily freshwater littoral areas. No extensive tidal flats or marshes were found (Wallace and Collins 1997).

The increase in storm surges expected with climate change may keep the mouth of the river open for longer periods than at present, potentially changing estuarine salinity and invertebrate communities. Migrating juvenile salmonids may benefit from a more open river mouth because tidal influence can reduce temperatures, decrease disease inducing conditions, and increase the forage base within the tidal influence of the lower river ([Levings et al. 1991](#_ENREF_121)). Salmonids use estuarine habitats more extensively during periods of poor ocean conditions, in order to take advantage of relatively more abundant food resources, thereby increasing the risk of predation by marine fish, mammals, and birds ([Chittenden et al. 2010b](#_ENREF_42)). Increased accessibility of the lower Klamath River may encourage more predation by seals and sea lions, particularly during high tides ([Williamson and Hillemeier 2001](#_ENREF_218)). In addition, changes in the timing of the opening of the sandbar may further disrupt migration patterns if the sandbar is not open when adults and juveniles are ready to enter or exit the system.

Overall, however, changes to the estuary are likely to have a relatively small impact on salmonid populations in the Klamath basin, because of present low use by salmonids compared to estuaries in other rivers on the California coast. Nevertheless, in some years estuarine conditions may cause high mortality in either outmigrating juveniles or entering adults.

4C. Changes to ocean habitats

The distribution of most salmonids in the Pacific Ocean will be limited to northern waters due to increases in sea surface temperatures in the south that will eventually exceed tolerance limits of most species ([Welch et al. 1998a](#_ENREF_215), [Welch et al. 1998b](#_ENREF_216)). However, ocean surface temperature effects can vary by species due to differences in timing of ocean entry and initiation of spawning migration ([Downton and Miller 1998](#_ENREF_54)). Salmonids also move between layers of colder and warmer water in the ocean on a diurnal basis as a means to reduce metabolic cost ([Walker et al. 2000](#_ENREF_208)). Furthermore, different populations of the same species may respond to ocean conditions differently depending on distribution and migration patterns ([Levin 2003](#_ENREF_118)). For example, Snake River Chinook were very productive pre-1977 while Columbia River populations were not (Levin 2003). Shifts in species distribution also can be influenced by ocean chemistry, circulation, and fishing pressure ([Harley et al. 2006](#_ENREF_83)). For example, the amount of fresh water flowing into the ocean was shown to be inversely related to survival of coho salmon in the Fraser River ([Beamish et al. 1994](#_ENREF_16)); the hypothesized mechanism behind low survival of coho was dilution of salinity in the ocean’s surface layer.

However, salmon distribution in the ocean is often most related to prey concentrations ([Walker et al. 2000](#_ENREF_208), [Koslow et al. 2002](#_ENREF_111)). The reason for this is that salmonid growth is influenced by both temperature and prey availability; growth is enhanced when temperatures are optimal and prey is readily available ([Brandt 1993](#_ENREF_26)). Consequently, growth rates may differ by species depending on oceanic migration patterns and residency. Because strong trophic linkages exist between zooplankton and fish yield ([Ware and Thomson 2005](#_ENREF_213)), desynchronization of juvenile entry into the ocean and zooplankton blooms could reduce fish recruitment ([Hays et al. 2005](#_ENREF_87)).

Based on coded wire tag recoveries, the oceanic distribution of Klamath River fall run Chinook salmon is between Cape Falcon, in Oregon, and Point Arena, in northern California ([CDFG 2001](#_ENREF_37)). However, different runs of Chinook salmon from other basins exhibit different migration patterns. Coastwide, Chinook salmon that rear in freshwater for many months (> 6) appear to travel far offshore into the central north Pacific, while Chinook salmon that rear in freshwater for a short time migrate near the coast ([Myers et al. 1998](#_ENREF_148)). Tag recoveries also suggest that most Klamath River coho salmon stay within 100 miles of the mouth of the river, moving close to shore, with very few (<1%) individuals migrating as far north as British Columbia ([Weitkamp et al. 1995](#_ENREF_214), [CDFG 2001](#_ENREF_37)). Steelhead trout from the Klamath River upon ocean entry appear to move far offshore but stay south of Cape Blanco, Oregon, although migration patterns are based on few samples ([Busby et al. 1996](#_ENREF_34)). Thus, Klamath River salmonids (together with all salmonids from California) are likely to have reduced ocean survival if predicted climate change effects on ocean conditions hold true. Given the complexity of ocean currents and their ties to world climate patterns, there is much uncertainty in these predictions, but conditions could actually become much worse than predicted.

1. **What conservation strategies have the greatest likelihood of success in maintaining salmonids?**

Conservation of salmonid abundance and diversity in the Klamath Basin will require aggressive basin-wide strategies that maintain and improve cool water habitats, while maintaining genetic and life history diversity within each species. Strategies must start with well defined principles for actions (e.g., improving habitat condition) that maximize use of limited resources in a rapidly changing environment. It may be desirable to conduct a triage exercise (as in Lackey et al. 2006) to figure out what streams, habitats, or salmonid populations will be lost no matter what we do, which will benefit most from concerted action, and which will likely be okay under continued present management. Such an exercise might show, for example, that trying to maintain salmonid rearing habitat in the mainstem Klamath River from July through September will not be possible as temperatures increase, but that improving coldwater flows in the Shasta River may have large benefits. Here, we discuss general strategies that could apply to situations where investments of time, energy, and funds are likely to make a difference in salmonid conservation.Conservation principlescan enhance salmonid recovery primarily by A. improving habitat condition, and B. enhancing genetic and life history diversity, primarily through more effective use of hatcheries.

5A. Improving habitat condition

Over the next 50 years, restoration of low elevation habitats may help mitigate the effects of climate change and enhance populations growth ([Battin et al. 2007](#_ENREF_11)). Conservation strategies that can improve habitat conditions for salmonids in the Klamath Basin in the face of climate change include:

* Protection and restoration of cold water habitats in fresh water, including habitat with groundwater inputs, at the mouth of tributaries, and within the fog belt,
* removal of migration barriers (including small and large dams, low flow and warm water barriers) to provide salmonids access to a wider range of habitats and enhance the incorporation of marine derived nutrients from decomposing carcasses throughout the stream system,
* protection and restoration of riparian buffers beside smaller order streams (1st – 3rd) where riparian vegetation can provide significant protection from solar radiation and maintain cool water temperatures, and
* reduction of fine sediment delivery (erosion) to prevent streams from becoming shallower and thus more likely to become warmer, by improving watershed management (e.g.,, reducing effects from high road density, logging, and mining).

Once conservations strategies are identified, specific conservation actions can be implemented to address these. In the Klamath River basin, cold water habitats in the fog belt, mouth of tributaries (including Blue Creek, Trinity River, Salmon River, Scott River and Shasta River) and associated with groundwater inputs (e.g., Scott River valley, Shasta River) are particularly important to salmonids in the summer months ([Belchik 2003](#_ENREF_18), [Sutton et al. 2007](#_ENREF_193), [Strange 2010](#_ENREF_191)). If the lower four dams on the mainstem Klamath River are removed, cold water habitat will also become available beneath the current location of Klamath Project reservoirs (Hamilton et al. 2011). Nevertheless, as water temperatures continue to increase, smaller streams at higher elevations may become favored by salmonids seeking cold water because lower elevations will become too warm ([Crozier et al. 2008a](#_ENREF_44)). In this case, mainstem habitats may be used primarily as migration corridors. Conservation actions should seek to provide access by removing migration barriers to cold water areas by increasing flows and removing of physical (e.g., dams, shallow water) and physiological (e.g., warm water temperatures) migration barriers. Habitat connectivity may be more important than habitat quantity or quality when populations are suppressed and habitat is fragmented ([Isaak et al. 2007](#_ENREF_96)), by allowing shifts in distribution and behavioral thermoregulation.

Conservation actions can enhance conditions for salmonids in cold water habitats (Table 1.4). Riparian vegetation should be reestablished where it has been removed. Riparian vegetation along smaller streams can cool surface waters within cold water patches by 2-4°C (Ebersole et al. 2003). The size and frequency of the thermal refugia can be enhanced by reducing water diversions, protecting springs, and removing mining from cold water habitats (Ebersole et al. 2003). The effects of groundwater pumping on base flows are often ignored and yet will become increasingly important as the amount of available surface water decreases (Mohseni et al. 2003). Managers should also consider seasonally closing cold water habitats to recreation, mining and other uses that can displace salmonids. Furthermore, activities such as grazing can degrade local riparian condition and water quality should be limited or eliminated. Because riparian vegetation can help intersect and disperse fine sediment entering streams from non-point sources, fine sediment delivery to streams can be further curtailed through outsloping and decommissioning of roads, and enforcement of Total Maximum Daily Load limits in streams flowing through both private and public lands.

Table 1.4. Examples of management actions and suggested locations that can

improve cold water conditions for salmonids in the lower Klamath River basin,

California.

|  |  |
| --- | --- |
| **Conservation action** | **Suggested locations** |
| Riparian vegetation planting | Valley portion of Scott River mainstem  Moffett Creek (Scott River) |
| Reduction of water extraction  (surface water diversion and groundwater pumping | Shasta River  Scott River  Indian Creek (Klamath River) |
| Protection of springs | Shasta River  Scott River |
| Closure to mining | Mouth of Scott River tributaries  Mouth of Salmon River tributaries  Mouth of Trinity River tributaries  Mouth of Klamath River tributaries |
| Closure to grazing  (in riparian areas) | Shasta River  Scott River headwaters  Salmon River headwaters  Trinity River headwaters  Blue Creek valley |
| Dam Removal | Dwinnell Dam (Shasta River)  Diversion dams (Little Shasta River)  Mainstem Klamath River |
| Establishment of salmonid parks  (management focused on preserving salmon and steelhead) | Blue Creek  Salmon River  Shasta River  Elk Creek (Klamath River) |

Salmonids in the Klamath River will face increasingly hostile habitat conditions unless conservation actions are implemented. Even with the uncertain effects of climate change on ocean conditions, restoration efforts can focus on improving freshwater and estuarine habitats with the goal of reestablishing healthy runs that are resilient in the face of unfavorable ocean conditions. Some actions that can immediately improve Klamath River salmonid habitat include the removal of Dwinnell Dam (Shasta River), enforcement of water diversions and groundwater pumping allocations (esp. Klamath Project, Scott River, Shasta River), and removal of the lower four dams on the Klamath River mainstem. The removal of the lower four dams should be accomplished jointly with the implementation of the Klamath Basin Restoration Agreement which provides measures (Drought Plan) for alleviating low summer flows.

5B. Enhancing genetic and life history diversity

Conservation actions that improve habitat conditions enhance genetic and life history diversity by improving salmonid health and survival. For instance, returning the hydrograph to a more natural condition may accelerate juvenile salmonid outmigration, resulting in decreased susceptibility ([Foott et al. 2007](#_ENREF_63)) and mortality ([Bartholomew et al. 2006](#_ENREF_9)) to disease, and predation ([Melnychuk et al. 2010](#_ENREF_135)) in the Klamath River mainstem. Improved connectivity to cold water habitats may also decrease infection rates because outmigrating juvenile Chinook salmon, released from Iron Gate Hatchery and captured in the mainstem Klamath River, were more resistant to disease when water temperature was below 16-17 °C ([Foott et al. 1999](#_ENREF_64)).

The ability of salmonid populations to persist in the face of climate change will largely be determined by their genetic and life history diversity. A population’s ability to respond to changing environmental conditions ([Schindler et al. 2008](#_ENREF_182)) has been defined by the magnitude of its genetic variability ([Reusch et al. 2005](#_ENREF_170)). High genetic diversity, reflected by life history diversity, can bolster species viability, even when significant numbers of individuals or populations are lost to adverse environmental conditions ([Greene et al. 2010](#_ENREF_70)). Conservation strategies that enhance genetic and life history diversity, consequently, offer the best likelihood for salmonid persistence in the face of climate change. Genetic and life history diversity closely reflect adaptations of different populations to local conditions. Therefore, habitat diversity must also be maintained in order to buffer against the effects of climate change (Crozier et al. 2008), with the emphasis of preserving a variety of habitats to foster diversity among populations ([Hilborn et al. 2003](#_ENREF_91), [Rogers and Schindler 2008](#_ENREF_175), [Schindler et al. 2008](#_ENREF_182)).

Ultimately, preservation of genetic, phenotypic and life history diversity relies on the protection of all (or most) distinct population segments, regardless of formal designation (e.g., ESU). For instance, the only viable population of spring Chinook salmon upstream of the confluence of the Klamath and Trinity rivers is not formally recognized as a separate taxon (Moyle et al. 2008). Instead, spring Chinook in this region belong to the Upper Klamath-Trinity Rivers (UKTR) Chinook salmon ESU, predominantly made up of fall run Chinook (Myers et al. 1998). The relatively much larger numbers of fall run Chinook mask the suppressed levels of spring Chinook. Spring Chinook are physiologically and behaviorally distinct from fall Chinook, in that they begin spawning migrations months before they are reproductively mature and tend to migrate further inland (Moyle 2002). Nevertheless, without formal recognition UKTR spring Chinook are not granted protection measures (e.g., Endangered Species Act) that can guard this life history variant from extinction.

5B1. Effective use of hatcheries

Perhaps the most significant conservation strategy that can enhance salmonid genetic and life history diversity is the reduction of hatchery effects on species genetic, phenotypic and life history diversity. Interactions between hatchery and wild conspecifics can reduce the abundance ([Pearsons and Temple 2010](#_ENREF_159)) and survival of wild juveniles in freshwater and estuarine habitats ([Nickelson et al. 1986](#_ENREF_153), [Levin et al. 2001](#_ENREF_120), [Levin and Williams 2002](#_ENREF_119), [Nickelson 2003](#_ENREF_152)) and reduce the reproductive success ([Bisson et al. 2002](#_ENREF_21)), fitness ([Araki et al. 2008](#_ENREF_5)), and productivity ([Buhle et al. 2009](#_ENREF_33)) of wild adults even after one generation ([Araki et al. 2007](#_ENREF_6)). Furthermore, hatchery supplementation can have negative effects on other salmonids. Pearson and Temple (2010) found that hatchery releases of Chinook and coho salmon decreased the biomass of rainbow trout over the course of nine years. And, in the ocean, releases of hatchery smolts can decrease the survival of other salmonid species (Levin et al. 2001, Levin and Williams 2002, Nickelson 2003). Increases in hatchery propagation in combination with impacts from large dams can decrease promote synchronization in species response to changing environmental conditions ([Moore et al. 2010](#_ENREF_141)).

Conservation actions that can minimize adverse hatchery effects include the relocation of hatcheries closer to river mouths and the releasing of smolts on-site to limit the amount of straying and subsequent interactions between hatchery and wild adults ([Quinn 1993](#_ENREF_164), [Buhle et al. 2009](#_ENREF_33)). However, homing behavior can be overridden by differences in habitat quality, environmental condition, genetics and/or social interactions ([Dittman and Quinn 1996](#_ENREF_52), [Dittman et al. 2010](#_ENREF_51)). Therefore, total hatchery releases should be modified so that the carrying capacity of streams is not exceeded ([Riley et al. 2009](#_ENREF_172)). Hatchery supplementation may also exceed the carrying capacity of the marine habitats, particularly in times of low ocean productivity ([Beamish et al. 1997](#_ENREF_14), [Levin et al. 2001](#_ENREF_120)), resulting in lower adult returns ([Beamish et al. 1997](#_ENREF_14), [Heard 1998](#_ENREF_90), [Kaeriyama 2004](#_ENREF_99)). Where adverse impacts outweigh benefits, hatcheries should be closed until maintenance of wild stock genetic, phenotypic and life history diversity can be ensured (as in Lackey et al. 2006). Hatcheries in the Klamath River are likely contributing to the decline of wild fall and spring Chinook salmon and summer steelhead populations (Quiñones unpublished data). Therefore, hatchery operations of these stocks should discontinue until operations can be reformed to protect wild populations.

One way around this dilemma is to exchange large-scale hatcheries for smaller conservation hatcheries, with the goal of increasing the number of wild adult returns ([Brannon et al. 2004](#_ENREF_28)). However, even small supplementation programs can have significant adverse impacts to local populations if not closely monitored. Conservation hatcheries should use locally derived broodstock, taken from a large proportion of redds ([Van Doornik et al. 2010](#_ENREF_203)) and reduce hatchery-reared adult straying by releasing at the hatchery to enhance genetic and phenotypic diversity ([Mobrand et al. 2005](#_ENREF_139)). Hatchery-reared juveniles should be released at low densities and at similar size to wild conspecifics to minimize ecological effects (Riley et al. 2009). And, hatchery rearing habitats should closely mimic natural rearing environments to prevent changes to phenotype and behavior ([Chittenden et al. 2010a](#_ENREF_41)). Nevertheless, species recovery will be enhanced more effectively through the combined effects of habitat restoration and decreased harvest levels than by curtailing hatchery operations alone (Buhle et al. 2009).

Hatchery supplementation can make wild salmonids more vulnerable to harvest levels. Harvest rates are often not sustainable by wild fish because they reflect inflated abundances due to hatchery supplementation ([Naish and Hard 2008](#_ENREF_150)). Over time, increased harvest rates lead to a replacement of wild fish by hatchery fish in mixed stock fisheries (Naish et al. 2008). Furthermore, mixed stock ocean fisheries can decrease population diversity by differentially exploiting coexisting stocks with distinct traits ([Hilborn et al. 2003](#_ENREF_91), [Hard et al. 2008](#_ENREF_81), [Schindler et al. 2008](#_ENREF_182), [Moore et al. 2010](#_ENREF_141)). Fishing may induce evolutionary changes on salmon body size, migration timing, and age of maturation, growth and fitness (reviewed in Hard et al. 2008). Recommendations to protect imperiled stocks from fishing include a reduction of fishing rates to avoid an evolutionary response, replacement of at least some mixed stock fisheries for fishing in terminal areas to protect life history traits associated with reproduction (Hard et al. 2008), and specifically targeting populations able to sustain fishing pressure. However, fisheries at terminal areas must also consider timing, location and gear type used as all of these can exert selective pressures that alter body size and migration timing (see Hard et al. 2008).

In the Klamath River basin, two hatcheries (Iron Gate and Trinity River hatcheries), supplement runs of fall Chinook, coho, and steelhead. Trinity River Hatchery also supplements a run of spring Chinook salmon. Trend analysis suggests that at least fall Chinook runs in the basin are becoming increasingly dependent on hatchery supplementation (Quiñones, unpublished data). Since 1978, adults returning to the hatcheries made up an increasingly larger proportion of basin-wide fall Chinook escapement, with the highest proportions of hatchery returns occurring since 2000. Coho salmon numbers also appear largely dependent on hatchery supplementation as wild populations are currently not viable (Hamilton et al. in progress) due to habitat degradation and overexploitation. Hatchery impacts to steelhead in the basin are unknown.

1. **Is it really possible to save most anadromous salmonid populations, given the pessimistic scenarios presented in *Salmon 2100* (Lackey et al. 2006)?**

Lackey et al. (2006) detailed challenges, including climate change, which salmon will have to overcome in order to survive this century. At the heart of the challenges salmonids face is the inability of society to reconcile the desire to preserve wild salmon with individual and collective decisions that often adversely impact aquatic habitats and biota. A primary conclusion by the authors is that recovery of wild salmon is “unlikely to happen if current trajectories in human population and development continue” (Lackey et al. 2006). In order to preserve wild salmon, they call for changes in fossil fuel consumption ([Ashley 2006](#_ENREF_7), [Hoopes 2006](#_ENREF_94)), rules of commerce ([Bailey and Boshard 2006](#_ENREF_8)), environmental laws ([Curtis and Lovell 2006](#_ENREF_48), [Lombard 2006](#_ENREF_123)), hatchery operations ([Bella 2006](#_ENREF_20), [Dose 2006](#_ENREF_53)), and predator management, including humans ([Buchal 2006](#_ENREF_32), [Michael 2006](#_ENREF_137)). Specific to the rules of commerce, they call for the elimination of incentives that result in the destruction of aquatic habitat (e.g., reclamation of wetlands, development of floodplains; Curtis and Lovell 2006) and progressive tax penalties when habitat is destroyed (Ashley 2006, Lombard 2006). They conclude that preservation of habitat is cheaper and more ecologically valuable than restoration, especially because habitat improvements cannot replace habitat loss ([Brannon 2006](#_ENREF_27), [Curtis and Lovell 2006](#_ENREF_48)). However, in some cases, streams may need to be engineered to replace lost or degraded habitat ([Bella 2006](#_ENREF_20), [Buchal 2006](#_ENREF_32)).

In California, climate change is occurring in the context of a rapidly expanding human population, likely reaching 92 million by 2100 ([Tanaka et al. 2006](#_ENREF_195)), with increasing demands for water and other natural resources. At the same time, most salmonid runs in the state are already less than 6% of their historical size ([Gresh et al. 2000](#_ENREF_71)). Under these scenarios, ecosystems that support wild salmonids must be protected along with salmonid populations themselves (Lombard 2006). In this paper, we have recommended several conservation actions that can be implemented relatively quickly in order to protect/restore salmonid habitat and populations in the Klamath River basin (Table 1.4; section 5B1). Although we understand that the causes of decline are rooted in demographic, social and economic processes ([Hartman et al. 2006](#_ENREF_84)), we believe that our recommendations can advance salmonid persistence in the face of climate change, even while broader societal changes are pursued. We follow Ashley (2006) and Wright’s (in Ashley 2006) conclusion that adverse impacts are occurring so fast, that inaction itself is a mistake. Frankly, our recommendations assume that society will make the sacrifices needed to reverse or reduce the effects of climate change. Without such sacrifices, in 100 years or less the head of the Klamath River estuary will likely be many miles upstream from its present location, most forested areas outside the fog belt (assuming the belt will still exist) will become oak stands, the Klamath River and most tributaries will be too warm to support salmonids for six months of the year, and the only salmonids left will be remnant populations of fall Chinook salmon and winter steelhead.

**Conclusion**

Climate change will likely exacerbate existing stressors as well as create new ones. With increasingly degraded conditions and longer exposure to stresses, fishes are likely to become more susceptible to factors already impacting fish health and adaptation ([Richter and Kolmes 2005](#_ENREF_171)). Although substantial uncertainties exist in predicting the effects of climate change on salmonids at the watershed level, resource management and conservation policies can still be applied to mitigate impacts of those stressors known to be impacting salmonids (Schindler et al. 2008).

Climate change is likely to increase water temperatures beyond the thermal tolerances of salmonids in many areas of the Klamath River basin, resulting in a reduction of speciesdistribution and abundance ([Ebersole et al. 2001](#_ENREF_56), [Roessig et al. 2004](#_ENREF_174)). An idea of what climatic conditions will be like in the next century can be gained by examining recent El Niño years ([Scavia et al. 2002](#_ENREF_179)), which have resulted in summer conditions that are generally warmer and drier, with low salmonid survival ([Mote et al. 2003](#_ENREF_143), [Lehodey et al. 2006](#_ENREF_116), [Wells et al. 2008](#_ENREF_217)). Such events amplify the effects of other stressors (Mote et al. 2003, Crozier et al. 2008).

Due to increases in temperatures and changes to hydrology, we can expect that the capacity of the mainstem and snowmelt-fed streams (i.e. Salmon and Scott rivers) to support rearing juvenile salmonids will decrease. Likewise, the scarcity of cool-water holding habitat will further adversely affect adult spring run Chinook salmon and summer steelhead, the most imperiled of the runs in the basin. In the Klamath River, warmer summer temperatures and lower base flows can also increase the incidence of disease (*Ceratomyxa shasta, Parvicapsula minibicornis*), increasing the risk of a fish die off as in 2002 ([Guillen 2003](#_ENREF_74), [Belchik et al. 2004](#_ENREF_19)). Because of the low quality of the habitat in the main stem during the summer and fall, even fishes using spring-fed systems like the Shasta River that migrate in the main stem will be adversely impacted by worsening conditions associated with climate change. Even with large scale restoration (e.g., dam removal), salmonids will need sufficient connectivity between spawning and rearing habitats, and migration routes in the form of suitable habitat to at least maintain base levels of recruitment. Shifts in migration timing and spawning grounds may facilitate survival under changing conditions but only if sufficient food is available at time of emergence, during rearing, and at ocean entry. Consequently, we predict that climate changes effects will reduce salmonid abundance in the Klamath basin by 25-50%, beyond declines caused by other factors, following the predictions of Chatters et al. ([Chatters et al. 1995](#_ENREF_39)) and Crozier et al. ([Crozier et al. 2008b](#_ENREF_46)) for rivers further north.

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**Chapter 2** - Escapement trends in the Klamath River: are hatchery returns

replacing wild salmonids?

**Abstract**

Hatchery supplementation can significantly influence species viability by changing genetic, phenotypic and life history diversity. For Pacific salmonids (*Oncorhynchus* spp.), interactions between hatchery-reared and wild individuals alter species’ reproductive success and ability to adapt to changing environmental conditions. We analyzed time series escapement data for seven salmonid taxa from the Klamath River basin to investigate trajectories of wild (natural escapement) and hatchery (returns to hatcheries) populations. Linear regression coupled with randomized permutations (n = 99,999) of data sets and two tailed t tests were used to detect (α = 0.05) trends over time. The taxa of interest were spring, fall, and late fall Chinook salmon (*O. tshawytscha*); coho salmon (*O. kisutch*); coastal cutthroat trout (*O. clarki clarki*); and summer and wild-hatchery hybrid steelhead trout (*O. mykiss*). Statistically significant decreases were detected for summer (Salmon River) and hybrid (Iron Gate Hatchery) steelhead. The proportion (% basinwide escapement) of fall Chinook natural escapement has also significantly decreased concurrently with significant increases in hatchery returns. In comparison, returns of Chinook (spring and fall combined) and coho to Trinity River Hatchery, fall Chinook to Iron Gate Hatchery, and fall Chinook Iron Gate Hatchery strays have significantly increased over the last three decades. Significant increases were also detected in late fall Chinook escapement to Blue Creek and spring Chinook escapement to Salmon River. However, both of these increases were found to be significantly correlated to Chinook returns to Trinity River Hatchery, suggesting at least some hatchery contribution to runs. Trends found to be statistically significant were also analyzed with Bayesian change point analysis to determine years of substantial changes in abundance and rate of change. Changes in abundances appeared related to changes in both ocean habitat conditions and hatchery practices. Our results suggest that anadromous salmonid populations in the Klamath River basin are becoming increasingly dependent on hatchery propagation. We provide empirical evidence that hatchery fish are replacing wild ones, a pattern that creates profound genetic and ecological threats to population persistence.

# Introduction

Artificial propagation of Pacific salmonids (*Oncorhynchus* spp.) can augment commercial fisheries and mitigate loss of salmonid production when fresh water habitats become inaccessible or degraded ([Lichatowich 1999](#_ENREF_65), [Brannon et al. 2004](#_ENREF_15)). In declining populations where native broodstock is used, hatchery fish may increase population sizes so that threat of inbreeding and loss of genetic diversity are minimized ([Brannon et al. 2004](#_ENREF_15), [Heggenes et al. 2006](#_ENREF_47), [Eldridge and Killebrew 2008](#_ENREF_32), [McClure et al. 2008](#_ENREF_69), [Van Doornik et al. 2010](#_ENREF_102)). Large-scale hatchery supplementation, however, can result in detrimental effects to naturally spawning populations ([Hilborn 1992](#_ENREF_48), [Fleming 1994](#_ENREF_34), [Waples 1994](#_ENREF_104), [Bisson et al. 2002](#_ENREF_13), [Buhle et al. 2009](#_ENREF_18), [Kostow 2009](#_ENREF_57)).

Hatchery-produced salmonids can differ from wild conspecifics in phenotype ([Hjort and Schreck 1982](#_ENREF_51), [Kostow 2004](#_ENREF_58), [Knudsen et al. 2006](#_ENREF_54)), fitness ([Reisenbichler and Rubin 1999](#_ENREF_92), [Araki et al. 2008](#_ENREF_5)), reproductive success ([Berejikian et al. 2001](#_ENREF_12), [McLean et al. 2004](#_ENREF_71), [Araki et al. 2007](#_ENREF_6)), physiology ([Reimers 1963](#_ENREF_91), [Brauner et al. 1994](#_ENREF_16), [Shrimpton et al. 1994](#_ENREF_95), [Chittenden et al. 2008](#_ENREF_24)), and behavior ([Fleming and Gross 1993](#_ENREF_35), [Chittenden et al. 2008](#_ENREF_24), [Chittenden et al. 2010](#_ENREF_23), [Dittman et al. 2010](#_ENREF_29), [Melnychuk et al. 2010](#_ENREF_73)). Consequently, natural spawning populations that interbreed extensively with hatchery strays may become maladapted to survival in the wild ([Chilcote et al. 1986](#_ENREF_22), [Leider et al. 1990](#_ENREF_61), [Kostow et al. 2003](#_ENREF_59), [Tymchuk et al. 2007](#_ENREF_101), [Araki et al. 2009](#_ENREF_7)). Maladaptation of wild populations coupled with ecological and behavioral interactions with hatchery fish may hinder recovery of imperiled salmonid species ([Hilborn 1992](#_ENREF_48), [NMFS 2010](#_ENREF_85)) by increasing competition ([Heard 1998](#_ENREF_45), [Levin et al. 2001](#_ENREF_64), [Kaeriyama 2004](#_ENREF_52)), predation ([Nickelson 2003](#_ENREF_84)), and/or fishing pressure ([Hard et al. 2008](#_ENREF_43)). These negative effects of hatchery fish appear to be escalating and wild populations are increasingly being replaced by their hatchery-reared counterparts or hybrids of wild-hatchery descent ([Allendorf and Leary 1988](#_ENREF_1), [Hilborn and Eggers 2000](#_ENREF_49), [Noakes et al. 2000](#_ENREF_86), [Sweeting et al. 2003](#_ENREF_99), [Zaporozhets and Zaporozhets 2004](#_ENREF_108)). Consequently, subsequent generations of wild populations become more vulnerable to extirpation and extinction ([Myers et al. 1998](#_ENREF_81), [Levin et al. 2001](#_ENREF_64), [Moore et al. 2010](#_ENREF_74)).

In California, replacement of wild runs of commercially important species (e.g., coho and Chinook salmon) has already been documented for some runs ([Weitkamp et al. 1995](#_ENREF_105), [Williams 2006](#_ENREF_107)). In the Sacramento River, historically the largest salmon producer in the state, decades of hatchery supplementation of Central Valley Chinook and related straying of adults into streams have resulted in decreasing genetic diversity so that hatchery and wild populations that are indistinguishable ([Lindley et al. 2009](#_ENREF_66)). An estimated 90% of the catch in the ocean fishery has been attributed to hatchery stock ([Barnett-Johnson et al. 2007](#_ENREF_8)). As dominance of hatchery-selected fish has increased, vulnerability of Central Valley Chinook salmon to changing environmental conditions, such as adverse ocean conditions, has also increased, likely contributing to years of dismally low adult spawner abundance (Lindley et al. 2009). Populations of coho salmon in the state also are largely dependent on artificial propagation ([Brown et al. 1994](#_ENREF_17)). Wild coho populations throughout much of the state are believed to have low viability ([CDFG 2002](#_ENREF_20), [NMFS 2010](#_ENREF_85)), sustainable only through hatchery supplementation (Weitkamp et al. 1994, Brown et al. 1994).

The Klamath River drainage is approximately 30,000 km2, located in southern Oregon and northern California (Figure 2.1). Estimates of historical abundance of all runs of salmon in the Klamath basin range from 650,000 to 1 million fish per year ([Gresh et al. 2000](#_ENREF_38)), making it the second largest producer of salmon in California. However, recent (e.g., 2009) low Chinook salmon returns to the Sacramento River may now make it the number one producer of wild salmon in the state. The Klamath River once supported 55 separate stocks of salmonids but runs of chum (*O. keta*) and pink salmon (*O. gorbuscha*) are now nearly extinct ([Nehlsen et al. 1991](#_ENREF_83), [NRC 2004](#_ENREF_87)). Klamath River coho salmon [Southern Oregon and Northern California Coasts Evolutionarily Significant Unit (ESU)] were listed under Endangered Species Acts as threatened in 1997 (62 FR 24588; Federal listing) and 2005 (state listing). Environmental groups petitioned for the listing of the basin’s spring Chinook (Upper Klamath-Trinity River ESU) in 2011 ([Diversity et al. 2011](#_ENREF_30)). Nevertheless, the Klamath River basin may represent the best opportunity for the rebuilding wild salmon populations in California because of the extensive restoration being proposed (e.g., removal of four large dams), combined with tributaries with habitat still in good condition (e.g., Blue Creek).

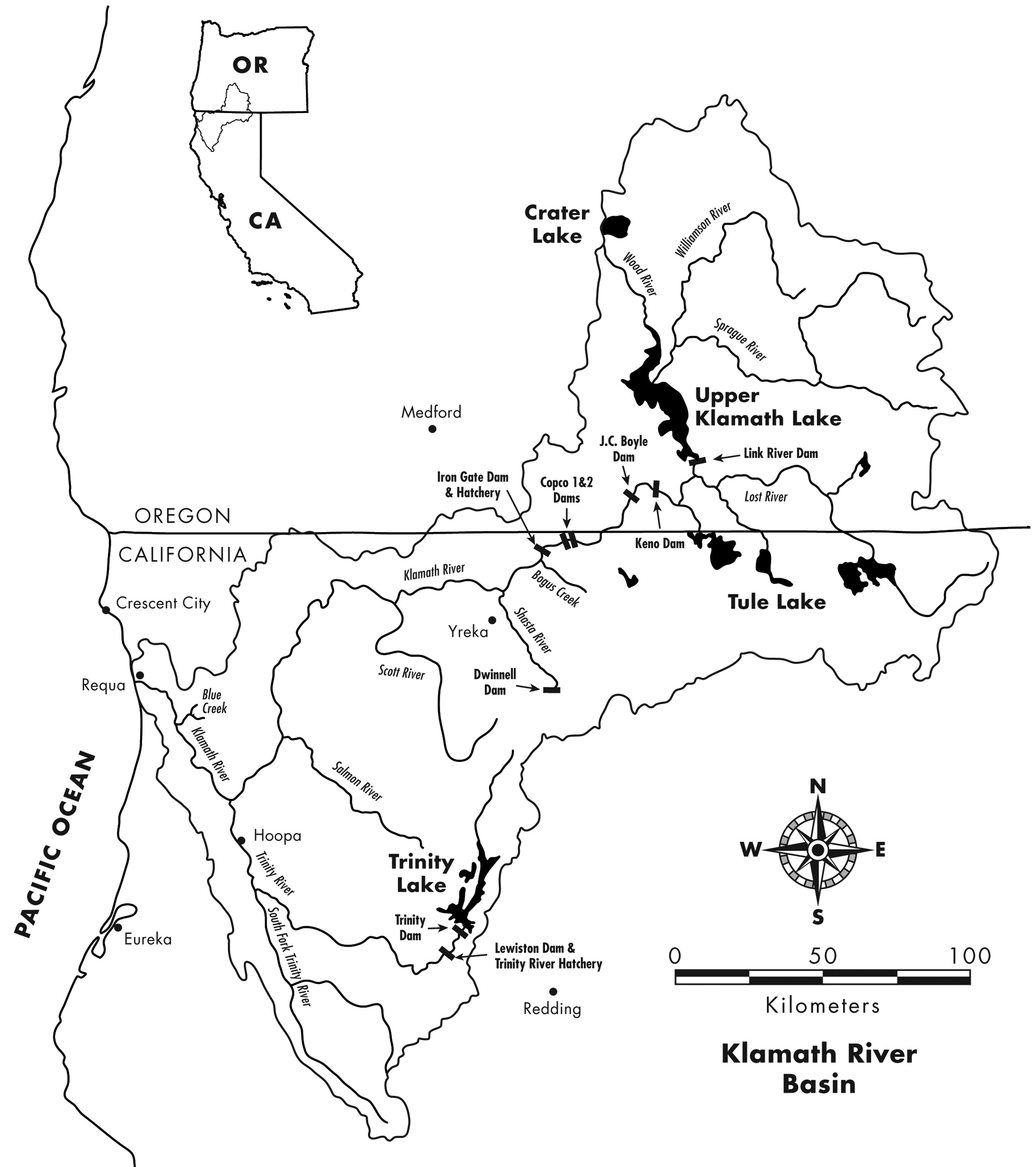


Figure 2.1. Klamath River basin, California and Oregon.

Salmonids in the Klamath River face many natural and anthropogenic stressors, including climate change, dam construction and operation, water diversion, habitat fragmentation and degradation, and impacts from hatchery supplementation ([Moyle 2002](#_ENREF_76), [Moyle et al. 2008](#_ENREF_77)). Hatchery supplementation of salmonids in the basin began in 1890 with the opening of a hatchery on Minor Creek (Trinity River; Kirk 1994 in Myers et al. 1998). Interbasin egg transfers, common before the mid-1990s, introduced broodstock from the Sacramento (Chinook), Eel (coho), Noyo (coho), Alsea (coho), Cascade (Oregon; coho), Willamette (Orego; steelhead), Washougal (Washington; steelhead) and Cowlitz (Washington, steelhead) rivers as well as Redwood Creek (Chinook) (Brown et al. 1994, Myers et al. 1998). From 1981 to 1998, up to 10 separate “major” artificial propagation efforts operated simultaneously in the basin (Myers et al. 1998).

Two hatcheries currently supplement Klamath River salmonid fisheries (Chinook, coho, steelhead): Iron Gate Hatchery (IGH, Klamath River river kilometer (rkm) 305) and Trinity River Hatchery (TRH; Trinity River rkm 250). Together the hatcheries release approximately 12 million juvenile Chinook, coho and steelhead each year ([Hamilton et al. 2011](#_ENREF_41)). Hatchery-reared adults now contribute significant numbers to spawning adults. From 1978 to 2009, 11-52% of total adult fall Chinook spawners were fish returning to the hatcheries (CDFG unpublished data). Furthermore, based on coded wire tag expansions specific to brood year, up to 13% of adults reared in IGH strayed into streams (CDFG unpublished data), primarily Bogus Creek and Shasta River which are located near the hatchery (S. Borok, CDFG, pers. comm. 2010). Coho in the basin are likely derived from hatchery sources, with very little natural production (reviewed in Weitkamp et al. 1995). In 2001, an estimated 73% of juvenile coho captured in the Klamath River estuary were classified as hatchery releases, an increase from 61% in 2000 and 34% in 1997 (CDFG 2004). Hatchery steelhead represent 20-34% of Trinity River runs but less than 8% in other parts of the basins ([Busby et al. 1994](#_ENREF_19)).

Analyses of adult spawner abundance are used to set harvest quotas ([Kope 2006](#_ENREF_55)) as well as to track demographic trends ([Routledge and Irvine 1999](#_ENREF_93)). However, analyses that do not separate trends in naturally spawning fish from trends in fish returning to hatcheries may mask declining trends in wild populations ([Wainwright and Kope 1999](#_ENREF_103), [Myers et al. 2004](#_ENREF_82), [Murdoch et al. 2010](#_ENREF_80)), the target of most conservation programs. We looked at trends in natural escapement and hatchery returns separately to determine status and trajectory of anadromous salmonid runs in the Klamath River. We recognize that natural escapement likely includes progeny of hatchery descent but estimates of hatchery contributions specific to each taxon are not available. Here, we address the following questions for seven salmonid taxa:

1. Are adult spawner numbers increasing or decreasing?
2. Do trends in natural escapement differ from trends in hatchery returns?
3. Is there evidence that wild-spawning fish are being replaced and/or supplemented by fish of hatchery origin?
4. Do trends in populations show significant changes in overall abundance or rates of change as a response, immediate or delayed, to multiple stressors?

To our knowledge, this is the most comprehensive analysis of escapement trends for Klamath River salmonids. It is designed to establish a baseline for the status of salmonids in the basin in order to evaluate effectiveness of future restoration and salmon recovery efforts.

**Methods**

Data were collected from multiple sources in order to build time series for each of the seven taxon (Table 2.1): spring, fall, and late fall Chinook salmon (*O. tshawytscha*); coho salmon (*O. kisutch*); summer and hybrid steelhead trout (*Oncorhynchus mykiss*); and coastal cutthroat trout (*O. clarki clarki*). We refer to steelhead returning to IGH as “hybrids” because the hatchery does not spawn adults of different runs separately (IGH unpublished data).

Only years with consistent sampling methods were evaluated in each time series. Therefore, not all available data were used, as reflected by the different number of years analyzed for each taxon. Escapement numbers were standardized by length (river kilometers) and type of survey when necessary in order for data to be directly comparable between years and so true trends in escapement could be discerned ([Hill and Irvine 2001](#_ENREF_50)). For example, counts of Salmon River spring Chinook and summer steelhead adults were divided by the number of river kilometers surveyed per year after removing years (e.g., 2006, 2008) with differing methods from the time series. Only summer steelhead adult numbers were included in our analysis due to the common misidentification of large resident trout as half-pounders (Quiñones unpublished observations). Half-pounders are young steelhead that return to freshwater after spending one summer in the ocean. Numbers of fall Chinook natural spawners of hatchery origin (hatchery strays) were estimated by expanding coded wire tag recoveries with production multipliers specific to brood year and tag number. However, information on tag recoveries was only available up to 2000 so the proportion of hatchery strays may be underestimated for years 2002 to 2009. Estimates of fall Chinook were taken directly from California Department of Fish and Game’s annual estimates of Chinook harvest and escapement (nrm.dfg.ca.gov/FileHandler.ashx?DocumentVersionID=48064). Although IGH has been spawning salmonids since 1962, we only incorporated data from 1967-2009 for Chinook and coho due to uncertainty whether hatchery doors were kept open throughout the entire run (K. Rushton, IGH, pers. comm. 2006). We assumed that the bias of stream surveys was the same among years and acknowledged that estimates of hatchery returns are likely more precise than those obtained through visual surveys. Nonetheless, we used the data as the only available to describe patterns of adult spawner abundance at different spatial and temporal scales.

**Time series trends**

Trends were built using data that met the following criteria as set by Biological Review Teams conducting status reviews for National Marine Fisheries Service: [1] abundance numbers were collected using the same methods for at least eight consecutive years, and [2] data sets did not contain more than 35% zero values ([Spence et al. 2005](#_ENREF_98)). Data sets were tested for autocorrelation and transformed (ln) before analysis in order to reduce the influence of outliers and increase the ability to meet distributional and variance assumptions required for linear models ([Quinn and Keough 2002](#_ENREF_90)). The percent of basinwide fall Chinook abundance made up of natural escapement was not transformed since it was a relative rather than nominal measure. Data were analyzed through linear regression of (ln) escapement vs. year. We used NCSS (v. 2004) statistical software to run all data diagnostics and fit linear regression models. Our null hypothesis was that trends did not exist (slope of trend line = 0) at a 0.05 level of significance.

Although we recognize trends in escapement may not represent trends in the population as a whole, escapement data allows monitoring of patterns that can alter genetic, phenotypic and life history (e.g., migration timing, reproductive success) diversity of the species as a whole. One drawback to using this analysis on escapement is that it assumes that harvest rate and stock productivity remain constant throughout the period of analysis ([Korman and Higgins 1997](#_ENREF_56)), an unrealistic assumption. Therefore, we used permutation tests to determine whether detected trends were real.

**Permutation tests**

Permutation tests allow for the analysis of non parametric data and have greater power than normal t tests when errors are not normal ([Anderson and Legendre 1999](#_ENREF_2), [Anderson and Robinson 2001](#_ENREF_4)). Permutation tests assume exchangeability between observations as ensured by a priori random allocation of observations. “A permutation test calculates the probability of getting a value equal to or more extreme than an observed value of a test statistic under a specified null hypothesis by recalculating the test statistic after random reordering (shuffling) of the data” (pg. 626, Anderson 2001). Manly (1997) recommended at least 1000 permutations for tests with a significance level of 0.05 (in Anderson 2001). In our case, data were shuffled 99,999 times and the p value was interpreted as the probability that an observed trend resulted from chance alone. Detailed descriptions and notations of permutation methods can be found in Anderson and Robinson (2001), and Anderson ([2001](#_ENREF_3)). We used software developed by Legendre (1999) to conduct permutation tests (http://www.bio.umontreal.ca/casgrain/en/labo/regression.html).

Table 2.1. Data used for trend analysis of salmonid escapement to the Klamath River, California.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Run/Species** | **Location** | | **Year** | **Number of years analyzed** | **Method** | **Data analyzed** | **Data source\*** |
| Fall run  Chinook salmon | Klamath River basin | | 1978-2009 | 32 | Carcass, redd, video weir and hatchery counts of adults and grilse | ln(escapement) | CDFG |
|  | Klamath River basin – natural escapement | | 1978-2009 | 32 | Carcass, redd, and video weir counts of adults and grilse | ln(escapement) | CDFG |
|  | Bogus Creek – natural escapement | | 1978-2009 | 32 | Carcass and redd counts of adults and grilse | ln(escapement) | CDFG |
|  | Salmon River – natural escapement | | 1978-2009 | 32 | Carcass and redd counts of adults and grilse | ln(escapement) | CDFG |
|  | Scott River – natural escapement | | 1978-2009 | 32 | Carcass, redd, and video weir counts of adults and grilse | ln(escapement) | CDFG |
|  | Shasta River – natural escapement | | 1978-2009 | 32 | Carcass, redd, and weir counts of adults and grilse | ln(escapement) | CDFG |
|  | Trinity River – natural escapement | | 1978-2009 | 32 | Carcass and redd counts of adults and grilse | ln(escapement) | CDFG |
|  | Klamath River basin –  % natural escapement | | 1978-2009 | 32 | Carcass and redd surveys, video weir counts of adults and grilse natural spawners | % of basin escapement as natural spawners | CDFG |
|  | Klamath River basin – hatchery strays | | 1980-2004 | 23 | Coded wire tag recoveries and production multipliers of adult and grilse natural spawners of hatchery origin | ln(escapment) | CDFG2 |
|  |  | |  |  |  |  |  |
|  |  | |  |  |  |  |  |
| Table 2.1. continued | |  |  |  |  |  |  |
|  |  | |  |  |  |  |  |
|  | Iron Gate Hatchery | | 1967-2009 | 43 | Adult and grilse returns to hatchery | ln(returns) | CDFG |
|  | Trinity River  Hatchery | | 1978-2005 | 28 | Adult and grilse returns to hatchery | ln(returns) | CDFG |
| Late fall run  Chinook Salmon | Blue Creek – natural escapement | | 1988-2009 | 20 | Stream survey peak counts of adults in reaches 1-4 | ln(escapement) | YTF |
| Spring run Chinook salmon | Salmon River – natural escapement | | 1968-2009 | 34 | 2 day snorkel survey counts of adults and grilse | ln(escapement per km) | KNF |
|  | Trinity River Hatchery | | 1980-2005 | 26 | Adult and grilse returns to hatchery | ln(returns) | USFWS |
|  | Trinity River – natural escapement | | 1978-2007 | 28 | Adult and grilse escapement to areas outside Trinity River Hatchery | ln(escapement) | CDFG3 |
| Coho  salmon | Iron Gate Hatchery | | 1967-2009 | 43 | Adult returns to hatchery | ln(returns) | IGH |
|  | Trinity River Hatchery | | 1958-2008 | 44 | Adult returns to hatchery | ln(returns) | TRH |
| Steelhead trout | Iron Gate Hatchery | | 1963-2008 | 44 | Adult (spring & fall) returns to hatchery | ln(returns) | IGH |
|  | Trinity River Hatchery | | 1958-2008 | 44 | Adult returns to hatchery | ln(returns) | TRH |
| Summer  Steelhead trout | Clear Creek- natural escapement | | 1985-2009 | 25 | 1 day snorkel survey counts of adults | ln(escapement per km) | KNF |
|  | Elk Creek – natural escapement | | 1987-2009 | 23 | 1 day snorkel survey counts of adults | ln(escapement per km) | KNF |
|  | Salmon River – natural escapement | | 1968-2009 | 34 | 2 day snorkel survey counts of adults | ln(escapement per km) | KNF |
|  |  | |  |  |  |  |  |
|  |  | |  |  |  |  |  |
|  |  | |  |  |  |  |  |
| Table 2.1. continued | |  |  |  |  |  |  |
|  | Wooley Creek – natural escapement | | 1985-  2009 | 22 | 1 day snorkel survey counts of adults | ln(escapement per km) | KNF |
| Coastal cut- throat trout | Blue Creek – natural escapement | | 1999-2009 | 9 | Stream survey peak counts of adults in reaches 1-4 | ln(escapement) | YTF |

\*CDFG = California Department of Fish and Game’s “megatable”, CDFG2 = M. Knechtle pers. comm. 2010, CDFG3 = ([Sinnen et al. 2010](#_ENREF_96)); YTF = Yurok Tribe Fisheries, KNF = Klamath National Forest, USFWS = United States Fish and Wildlife Service, IGH = Iron Gate Hatchery, TRH = Trinity River Hatchery

**Cross correlations**

Cross correlation is useful in evaluating the relationship between two time series ([Box et al. 2008](#_ENREF_14)). Because we wanted to further investigate the relationship between natural escapement and hatchery supplementation, we conducted cross correlation between pairs of time series where both natural escapement and hatchery return estimates were available for the same taxa. The pairs evaluated were:

* Total numbers of fall Chinook spawners (natural escapement + hatchery returns) in the basin vs. fall Chinook returns to both hatcheries,
* spring Chinook natural escapement to the Salmon River vs. spring Chinook returns to TRH,
* spring Chinook natural escapement to the Trinity River vs. spring Chinook returns to TRH,
* late fall Chinook natural escapement to Blue Creek vs. Chinook returns (both spring and fall runs) to TRH, and
* summer steelhead natural escapement to Salmon River vs. steelhead returns to IGH.

We also wanted to investigate whether relationships between natural escapement and hatchery returns differed by location. Therefore, cross correlations were also completed separately for fall Chinook natural escapement to Trinity, Salmon, Scott, Shasta rivers and Bogus Creek vs. fall Chinook returns to IGH and TRH. Cross correlations were completed in NCSS 2004. Pearson Correlation Coefficients were used to determine statistical significance between time series at α = 0.05 and df = n – 2.

**Bayesian change point analysis**

Time series found to have statistically significant trends (n = 8) were further analyzed to determine years with abrupt changes in abundance (step change) or with a significant rate of change (trend change). We completed Bayesian change point analysis using WinBUGS and R software as outlined in Thomson et al. (2010). First, step and trend changes between data points were assessed through piecewise linear regression models ([Denison et al. 1998](#_ENREF_27)). Second, posterior probabilities for all possible models were calculated using a Bayesian approach in reversible jump Markov chain Monte Carlo (MCMC) simulation. Our methods differed from Thomson et al. (2010) in that we allowed one change point for every 10 (rounded) years of data. Consequently, the necessary prior distributions were defined as Binomial (number of years/10, 0.5). Third, we calculated odds ratios based on a threefold increase from prior odds to underscore specific years of substantial step or trend changes ([Thomson et al. 2010](#_ENREF_100)). A prior odd is the probability of a change point occurring in any given year.

**Results**

**Time series trends and permutation tests**

Eight of the 23 time series analyzed were found to have statistically significant trends based on permutations tests (p <0.05; Table 2.2). These results are meaningful at α = 0.05 because more than 5% of the tests (n =23) completed yielded significant results. In general, hatchery returns were found to be increasing over time while most natural escapement trends decreased. For fall Chinook salmon, returns to Iron Gate Hatchery (p = <0.0002; Figure 2.2A) significantly increased as did the number of hatchery strays throughout the basin (p = 0.013; Figure 2.2B). Although no trend was detected for basin-wide adult fall Chinook spawner abundance (natural escapement + hatchery returns), the proportion (%) of natural escapement has significantly decreased (p = 0.001, r2 = 0.31, power = 0.95; Figure 2.3). Increasing trends were detected for spring Chinook salmon returning to Salmon River (p = 0.0015; Figure 2.2C), spring Chinook returning to Trinity River Hatchery (p = 0.00099; Figure 2.2D), late fall Chinook salmon returning to Blue Creek (p = 0.032; Figure 2.2E), and coho salmon returning to Trinity River Hatchery (p = <0.0001; Figure 2.2F). Decreasing trends were also detected for steelhead trout returning to Iron Gate Hatchery (p = 0.0004; Figure 2.2G) and summer steelhead trout escapement to Salmon River (p = 0.00074; Figure 2.2H). The inability of our methods to detect trends in other time series should not be interpreted as evidence of population stability but rather as indication of the limitation of our methods on time series of small sample size.

Table 2.2. Time series data tested (linear regression, two-tailed t test) for trends in escapement. Original time series data were randomized for 99,999 permutations. P values correspond to analysis of the original time series (p value reg), and permutated data (p value perm). p values, marked in bold, were found to be significant at α = 0.05.

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| **Run/**  **Species** | **Location** | | | | **Years** | **p value**  **reg** | | **r2** | | | **slope** | **intercept** | **power** | | **p value**  **perm** |
| Fall run  Chinook salmon | Klamath River  basin | | | | 1978-2009 | 0.30 | | 0.036 | | | 0.012 | -12.63 | 0.18 | | 0.30 |
|  | Klamath River basin – natural escapement | | | | 1978-2009 | 0.84 | | 0.0013 | | | 0.0024 | 6.0 | 0.05 | | 0.84 |
|  | Klamath River basin – hatchery strays | | | | 1980-2004 | **0.013** | | 0.26 | | | 0.12 | -227.35 | 0.73 | | **0.013** |
|  | Iron Gate Hatchery | | | | 1967-2009 | **<0.0001** | | 0.39 | | | 0.04 | -67.36 | 0.99 | | **<0.0002** |
|  | Trinity River  Hatchery | | | | 1978-2009 | 0.064 | | 0.13 | | | 0.036 | -63.66 | 0.46 | | 0.065 |
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| Table 2.2. continued | |  | |  | |  |  | | |  | |  |  |  | | |
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|  | Trinity River – natural escapement | | | | 1978-2009 | 0.83 | | 0.0016 | | | -0.51 | 1998.63 | 0.06 | | 0.83 |
|  | Salmon River – natural escapement | | | | 1978-2009 | 0.71 | | 0.0046 | | | -0.90 | 2000.37 | 0.06 | | 0.71 |
|  | Scott River – natural escapement | | | | 1978-2009 | 0.29 | | 0.037 | | | -2.41 | 2013.61 | 0.18 | | 0.29 |
|  | Shasta River – natural escapement | | | | 1978-2009 | 0.25 | | 0.04 | | | -2.08 | 2010.48 | 0.20 | | 0.25 |
|  | Bogus Creek– natural escapement | | | | 1978-2009 | 0.25 | | 0.04 | | | 2.23 | 1974.11 | 0.20 | | 0.25 |
| Late fall run  Chinook salmon | Blue Creek – natural escapement | | | | 1988-2009 | **0.032** | | 0.23 | | | 0.070 | -135.21 | 0.59 | | **0.032** |
| Spring run Chinook salmon | Salmon River – natural escapement | | | | 1968-2009 | **0.0013** | | 0.28 | | | 0.055 | -108.47 | 0.93 | | **0.0015** |
|  | Trinity River Hatchery | | | | 1977-2007 | **0.00087** | | 0.35 | | | 0.054 | -98.88 | 0.95 | | **0.00099** |
|  | Trinity River – natural  escapement | | | | 1978-2007 | 0.27 | | 0.047 | | | 0.023 | -37.21 | 0.19 | | 0.27 |
| Coho salmon | Iron Gate Hatchery | | | | 1967-2009 | 0.26 | | 0.030 | | | 0.013 | -19.51 | 0.20 | | 0.27 |
|  | Trinity River Hatchery | | | | 1958-2008 | **<0.0001** | | 0.47 | | | 0.09 | -169.46 | 1.0 | | **<0.0001** |
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| Steelhead trout | Iron Gate Hatchery | | | | 1963-2008 | **0.0004** | | 0.30 | | | -0.054 | 112.94 | 0.99 | | **0.0004** |
|  | Trinity River Hatchery | | | | 1958-2008 | 0.51 | | 0.010 | | | 0.010 | -64.09 | 0.77 | | 0.51 |
| Summer  steelhead trout | Clear Creek – natural escapement | | | | 1985-2009 | 0.19 | | 0.072 | | | -0.03 | 66.98 | 0.25 | | 0.19 |
|  | Elk Creek – natural escapement | | | | 1987-2009 | 0.68 | | 0.0084 | | | -0.01 | 21.80 | 0.07 | | 0.68 |
|  | Salmon River – natural escapement | | | | 1968-2009 | **0.00055** | | 0.32 | | | -0.063 | 125.62 | 0.96 | | **0.00074** |
|  | Wooley Creek – natural escapement | | | | 1985-  2009 | 0.66 | | 0.010 | | | -0.015 | 31.00 | 0.07 | | 0.65 |
| Coastal cutthroat trout | Blue Creek – natural escapement | | | | 1999-2009 | 0.10 | | 0.33 | | | 0.11 | -213.25 | 0.37 | | 0.10 |
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| **B**  **A** | | | | | | | | | |  | | | | | | | | |
| **D**  **C** | | | | | | | | | |  | | | | | | | | |

Figure 2.2. continued

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| **F**  **E** |  |
| **G**  **H** |  |

Figure 2.2. Trends in salmonid escapement for representative taxa in the Klamath River. In the upper graph, black stars represent time series data, black lines represent linear trendline (from permutations), dotted lines represent trend output, and broken lines represent intercept parameters. In the lower graphs, black bars represent posterior probabilites of step changes, gray bars represent posterior probabilites of trend changes, and the lines represent the odds ratio significant to each time series. Ch = Chinook, Sp Chinook = spring Chinook, l fall Ch = late fall Chinook, sthd = steelhead, s sthd = summer steelhead.

Figure 2. 3. Percent of basinwide fall Chinook escapement comprised of natural escapement and hatchery returns, Klamath River, California, 1978-2009.

**Cross correlations**

Several natural escapement time series were significantly correlated to hatchery returns (Table 2.3). Basinwide fall Chinook adult spawner abundance was significantly correlated to returns to both hatcheries (r(27) =0.53, p = <0.05). Fall Chinook natural escapement to Bogus Creek was significantly correlated to returns to both IGH (r(27) = 0.60, p = <0.05) and TRH (r(27) = 0.58, p = <0.05). Fall Chinook natural escapement to Salmon River was significantly correlated to returns to IGH (r(27) = 0.36, p = <0.05). Fall Chinook natural escapement to Trinity River was significantly correlated to returns to both IGH (r(27) = 0.41, p = <0.05) and TRH (r(27) = 0.72, p = <0.05). Spring Chinook natural escapement to the Salmon River was significantly correlated to spring Chinook returns to TRH (r(27) = 0.50, p = <0.05). Spring Chinook natural escapement to the Trinity River was significantly correlated to spring Chinook returns to TRH (r(23) = 0.83, p = <0.05). Late fall Chinook natural escapement to Blue Creek was significantly correlated to Chinook (spring + fall) returning to TRH (r(11) = 0.66, p = <0.05). Summer steelhead natural escapement to Salmon River was significantly correlated to steelhead returning to IGH (r(32) = 0.75, p = <0.05).

Table 2.3. Taxa and locations of abundance time series (second and third columns) paired for cross correlation analysis. Correlations [r(df-2)] in bold were found to be significant if they exceeded the corresponding minimum Pearson correlation coeficient.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Taxa** | **Location of natural escapement** | **Location of hatchery returns** | **Minimum Pearson correlation coeficient** | **r(df – 2)** |
| Fall Chinook | Klamath River basin | IGH and TRH | 0.35 | **0.53** |
|  | Bogus Creek | IGH | 0.35 | **0.60** |
|  |  | TRH | 0.35 | **0.58** |
|  | Salmon River | IGH | 0.35 | **0.36** |
|  |  | TRH | 0.35 | 0.08 |
|  | Scott River | IGH | 0.35 | 0.27 |
|  |  | TRH | 0.35 | 0.21 |
|  | Shasta River | IGH | 0.35 | 0.11 |
|  |  | TRH | 0.35 | 0.32 |
|  | Trinity River | IGH | 0.35 | **0.41** |
|  |  | TRH | 0.35 | **0.72** |
| Spring Chinook | Salmon River | TRH | 0.37 | **0.50** |
|  | Trinity River | TRH | 0.40 | **0.83** |
| Late fall Chinook | Blue Creek | TRH | 0.55 | **0.66** |
| Summer steelhead | Salmon River | IGH\*\* | 0.35 | **0.75** |

\*\*hybrids

**Bayesian change point analysis**

Significant changes to abundance (step changes) were exhibited by six of the eight time series analyzed. Fall Chinook returns to IGH experienced step changes in 1977 (decrease), 1979 (decrease), 1982 (increase), 1990 (increase), 2000 (increase) and 2004 (increase) (Figure 2.2A). Spring Chinook returns to TRH experienced step changes in 1985 (increase), 1986 (increase), 1989 (decrease), and 1990 (increase) (Figure 2.2D). Late fall Chinook escapement to Blue Creek experienced step changes in 1995 (increase) and 2004 (decrease) (Figure 2.2E). Coho returns to TRH experienced step changes in 1966 (increase), 1989 (decrease), and 1990 (decrease) (Figure 2.2F). Steelhead returns to IGH experienced step changes in 1969 (increase), 1970 (increase), 1989 (decrease), 1990 (increase), 1995 (decrease), and 2000 (increase) (Figure 2.2G). Summer steelhead escapement to Salmon River experienced step changes in 1973 (increase), 1980 (decrease), and 1990 (decrease) (Figure 2.2H). Significant trend changes were only found for one time series; steelhead returns to IGH experienced significant trend changes in 1988, 1989, 1996, and 2002 (Figure 2.2G). We interpreted the lack of significant step or trend changes as the result of steady increases in the abundance of IGH fall Chinook strays (Figure 2.2B) and Salmon River spring Chinook (Figure 2.2C).

**Discussion**

Salmonid abundances throughout the Pacific Northwest have decreased by more than 40% of historic numbers, with a decrease of more than 95% in California alone ([Gresh et al. 2000](#_ENREF_38)). Since the 1990s, researchers have identified hatchery practices as contributing to the overall decline of some wild populations ([Meffe 1992](#_ENREF_72), [Brown et al. 1994](#_ENREF_17), [Fleming 1994](#_ENREF_34), [Waples 1994](#_ENREF_104), [Reisenbichler and Rubin 1999](#_ENREF_92), [Flagg et al. 2000](#_ENREF_33), [Noakes et al. 2000](#_ENREF_86), [Levin et al. 2001](#_ENREF_64), [Levin and Williams 2002](#_ENREF_63), [Sweeting et al. 2003](#_ENREF_99)). Increasing dominance of hatchery fish in a river reduces genetic, behavioral, and life history diversity of wild populations decreasing species viability in the face of changing environmental conditions ([Greene et al. 2010](#_ENREF_37), [Schindler et al. 2010](#_ENREF_94)). Because wild populations exposed to long-term hatchery supplementation can become maladapted (as in Chicolte et al. 1986) and incapable of sustaining themselves (Lynch and O’Hely 2001), we sought to understand how trends in salmonid natural escapement and hatchery returns have changed through time in the Klamath River basin.

We found a general pattern of increasing hatchery returns with simultaneous decreasing natural escapement (2.2). Hatchery returns of fall Chinook to IGH, and spring Chinook and coho to TRH have increased significantly in the last 40+ years. Furthermore, the number of fall Chinook IGH strays spawning in rivers has also increased. In contrast, natural escapement (%) of fall Chinook salmon to the entire basin and summer steelhead to Salmon River has significantly decreased. Of particular concern are trends in steelhead populations where both returns to IGH and natural escapement of summer steelhead to Salmon River have declined. Steelhead in the basin were thought to be at a relatively low risk of extirpation when compared to other species ([Nehlsen et al. 1991](#_ENREF_83), [Busby et al. 1994](#_ENREF_19), [Moyle 2002](#_ENREF_76)). We found that recent concerns about the status of this species, particularly of the “summer” life history ([Moyle et al. 2008](#_ENREF_77)), are well founded. Interestingly, natural escapement of spring Chinook to Salmon River and late fall Chinook to Blue Creek show increasing trends. However, both of these time series show significant correlations to hatchery returns (Table 2.3), suggesting that these escapement trends reflect supplementation by hatchery strays, increasing the probability of interbreeding between hatchery and wild individuals.

Hatchery returns are likely replacing natural escapement of at least some wild populations. This pattern was most obvious for fall Chinook where the lack of a significant trend in total spawner abundance (natural escapement + hatchery returns) masked the inverse relationship of natural escapement and hatchery returns (Figure 2.3). Cross correlation results also suggested that hatchery supplementation and/or replacement may be occurring in the Salmon River, Trinity River, Bogus Creek, and Blue Creek (Table 2.3). The impact that hatchery supplementation may have on wild populations is likely underestimated because we assumed that all natural escapement consisted of wild fish from wild parentage. This is an unrealistic assumption if hatchery strays spawning in rivers are unaccounted for and are contributing genetic material to future generations (as in Araki et al. 2009). Based on the cross correlation results, hatchery strays may be reproducing in several sub-basins (Bogus Creek, Salmon River, Trinity River, Blue Creek). If this is the case, interactions between hatchery strays and wild conspecifics may be increasing the vulnerability of some taxa to extirpation and extinction (as in Levin et al. 2001). We are currently analyzing the otolith microchemistry of Chinook collected from these locations in a related study to establish the natal origin of spawning adults.

Patterns in trends likely reflected many complex and interacting factors that drive or constrain salmonid abundance. For Klamath River salmonids, overexploitation by commercial harvest, unfavorable ocean conditions and habitat degradation were proposed as constraints to species productivity ([West et al. 1989](#_ENREF_106), [Kier and Associates 1991](#_ENREF_53), [Cooperrider and Garrett 1995](#_ENREF_26), [CDFG 2003](#_ENREF_21), [NRC 2004](#_ENREF_87), [Hamilton et al. 2005](#_ENREF_42)). Commercial fishing of Chinook and coho in the Klamath River was largely unchecked prior to 1925, supporting three cannery operations in the lower river ([Snyder 1931](#_ENREF_97)). For example, a single 30 day period (September-October 1919) yielded 11,162 coho salmon in the commercial gill net fishery (Snyder 1931). However, by the late 1920s, fishing pressure was increased (from 40 to 126 boats) in response to diminished supply (Snyder 1931). Numbers of coho salmon in the basin are now less than 10% of what they were before 1920 (based on Spence et al. 2005).

Three climatic patterns have impacts on salmonid abundance in California; these are the El Niño Southern Oscillation, Pacific Decadal Oscillation, and North Pacific Gyre Oscillation ([Hare et al. 1999](#_ENREF_44), [Mueter et al. 2002](#_ENREF_79), [Levin 2003](#_ENREF_62), [Mote et al. 2003](#_ENREF_75), [Peterson and Schwing 2003](#_ENREF_89), [DiLorenzo et al. 2008](#_ENREF_28), [Cloern et al. 2010](#_ENREF_25)). Different phases of these climatic patterns increase or decrease sea surface temperatures and alter upwelling dynamics so that ocean conditions are favorable or unfavorable to salmonid survival during ocean residency. Of particular importance are unfavorable ocean conditions that limit prey availability to juvenile salmonids entering the ocean, resulting in increased mortality at this life stage and subsequent reductions in spawning adults ([Mantua et al. 1997](#_ENREF_68), [Beamish and Mahnken 2001](#_ENREF_11), [Mueter et al. 2005](#_ENREF_78)). Aquatic habitats in the Klamath basin reflect a long legacy of land use practices (e.g., mining, logging, dam construction, water diversion) that have degraded salmonid habitats ([Kier and Associates 1991](#_ENREF_53), [Moyle 2002](#_ENREF_76)). These practices resulted in the loss of habitat (kilometers of river barred by dams), increased water temperatures, embedded and/or silted spawning gravels, and lowered stream flows (Hamilton et al. 2011). Consequently, salmonids in the Klamath River may have experienced decreased survival and fluctuations in adult abundances due to all of these factors. In other rivers, hatchery supplementation has been shown to increase abundances of some populations in the short term (Beamish et al. 1997, Lynch and O’Hely 2001) but to limit a species’ ability to adapt and rebuild in the long term ([Levin and Williams 2002](#_ENREF_63), [Hard et al. 2008](#_ENREF_43), [Buhle et al. 2009](#_ENREF_18), [Moore et al. 2010](#_ENREF_74)). Events that potentially altered Klamath River salmonid productivity are summarized in Table 2.4.

Bayesian change point analysis underscored years with significant changes to abundance and/or trend for each taxon. Our interpretations discuss general patterns but recognize the complexity of interactions between factors and the likelihood of time lags in the response of adult abundances. Abundances for fall Chinook (IGH; 1982, 1990, 2000, 2004) appeared to increase in accordance with sharp decreases of IGH Chinook smolt releases [from ~10 million (1985-1988) to 5 million (1989-2009) per year, IGH unpublished data] and favorable ocean conditions in the early 2000s. The inverse relationship between hatchery releases and adult abundance likely signaled a relaxation of density dependent mortality which was high when ocean productivity was low ([Beamish and Mahnken 2001](#_ENREF_11), [Levin et al. 2001](#_ENREF_64)). In the 1980s and early 1990s, climatic patterns (e.g., PDO warm phase) resulted in unfavorable ocean conditions and poor salmon returns ([Mantua et al. 1997](#_ENREF_68), [Mantua and Hare 2002](#_ENREF_67)). Ocean conditions may also explain other increases (2000, 2004; favorable conditions) and decreases (1977, 1979; unfavorable conditions) exhibited by IGH fall Chinook. Favorable ocean conditions may also explain increases of coho (TRH) and steelhead (IGH, Salmon River) abundances during the mid 1960s to early 1970s and in 2000, years during cold PDO phases ([Mantua and Hare 2002](#_ENREF_67)). Likewise, decreases of coho and steelhead reflect unfavorable ocean conditions (warm PDO phase) in the late 1970s, mid to late 1980s and early 1990s. Steelhead IGH returns were the only taxon with trend changes (in 1988, 1989, 1996, 2002), all of which resulted in decreased abundance. Decreases in Salmon River summer steelhead may be amplified by interbreeding with IGH steelhead as suggested by cross correlation (r =0.75). Hatchery salmonids have been shown to reproduce less successfully than their wild counterparts ([Berejikian et al. 2001](#_ENREF_12), [McLean et al. 2003](#_ENREF_70), [Buhle et al. 2009](#_ENREF_18)). Consequently, when hatchery fish reproduce in the wild, they decrease the reproductive success of the naturally reproducing population ([Heath et al. 2003](#_ENREF_46), [Goodman 2005](#_ENREF_36)). Genetic analysis suggested that IGH steelhead have already interbred with steelhead in the Shasta and Scott rivers ([Pearse et al. 2007](#_ENREF_88)).

Because we dealt with escapement numbers, we considered the potential impact of commercial fishing on IGH fall Chinook abundances. Escapement by definition is the sum of fish that “escaped” being harvested and arrived into rivers and streams to spawn (www.psc.org). The Pacific Coast Salmon Fishery Management Plan established a minimum escapement of 35,000 fall Chinook natural spawners as a conservation goal ([Gutierrez 2006](#_ENREF_40)). Yet, less than 35,000 natural spawners (adults and grilse) returned to spawn in 1983 (33,310), 1984 (21,349), 1990 (16,946), 1991 (12,367), 1992 (17,171), 1993 (25,683), 1999 (28,904), 2004 (29,053) and 2005 (28,388). We expected that years when minimum escapement goals were not met would decrease basinwide spawner abundance in subsequent years. This appeared not to be the case as IGH fall abundances only significantly decreased in 1977 and 1979. Harvest numbers were not available for coho and steelhead.

Spring (TRH) and late fall (Blue Creek) Chinook abundances also seemed to reflect influences from ocean conditions and hatchery practices. Spring Chinook returns to TRH exhibited a decrease (1989) and an increase (1990) that could be explained by ocean conditions. However, other increases (1985, 1986) likely reflected the switch by the hatchery to cement raceways in the early 1980s, improving hatchery production (N. Hemphill, Trinity River Restoration Program, pers. comm. 2010) and increasing adult returns in the short term. The increase (1995) in Blue Creek late fall Chinook likely reflected the same release from density dependent factors as was seen in IGH fall Chinook due to decreases in hatchery releases. However, we hypothesize that the decrease seen in 2004 was due to the 2002 fish kill. In September of 2002, more than 30,000 fish died in the lower 58 kilometers of the Klamath River ([Guillen 2003](#_ENREF_39)). One of the runs hardest hit by this event were Chinook returning to TRH (CDFG 2003, Guillen 2003). If indeed there is a strong dependence of hatchery supplementation to Blue Creek from TRH, as suggested by cross correlation (r = 0.66), then abundances of Blue Creek late fall Chinook should have suffered a decrease in adults returning to spawn in 2004. Analysis of the age composition in runs before and after 2002 could help validate this hypothesis, because jacks (age 2 adults) would have to make up a substantial amount of the run for the decrease to be strongly expressed.

We were challenged in our interpretation of the Bayesian change point analysis in several ways. First, we were limited to the data we could find. Little data specific to the Klamath River were available prior to 1960, of the available data only a few time series were collected with standardized methods, and the majority of those data were hatchery returns. Therefore, we could not analyze previous significant changes (e.g., prior to 19th century commercial fishing) and most of the data may not reflect trends in natural escapement. Second, only major abrupt changes were captured by the analysis, ignoring incremental changes (Thomson et al. 2010) that can have significant repercussions on adult abundances (as in Busby et al. 1994). Third, our interpretation focused on large scale factors (e.g., ocean conditions) that can mask changes at the local scale (e.g., habitat degradation/restoration) which are also important in determining salmonid survival ([Ebersole et al. 2001](#_ENREF_31), [Lackey et al. 2006](#_ENREF_60), [Battin et al. 2007](#_ENREF_9)). Finally, the most realistic scenario is that all factors (e.g., hatchery supplementation, habitat degradation and ocean conditions) acted synergistically to influence the trends we described.

Hatchery supplementation is just one of the stressors acting on Klamath River salmonids (Table 2.4). However, we focused our discussion on the impacts of hatchery supplementation in order to challenge the notion that hatcheries can effectively rebuild imperiled wild populations (as in Brannon et al. 2002). Here, we propose that hatchery supplementation may be facilitating the extirpation of wild populations in parts of the Klamath River basin. Hatchery supplementation can amplify the stressors already threatening salmonid persistence. For example, an increase in hatchery propagation, coincident with the presence of large dams that homogenize aquatic habitats (Poff et al. 2007), can result in salmon populations that are less sustainable (Schindler et al. 2010), more vulnerable to extinction (Heino et al. 1997, Engen et al. 2002, Moore et al. 2010), and more susceptible to sudden changes in climate or ocean productivity ([Lindley et al. 2009](#_ENREF_66), [Beamish et al. 2011](#_ENREF_10)).

Table 2.4. Years of large scale events that likely impacted salmonid productivity in the Klamath River basin (Busby et al. 1994, USDA-FS and USDI-BLM 1994, Brown et al. 1994, Scott River watershed CRMP Committee 1995, Weitkamp et al. 1995, De la Fuente et al. 1996, De la Fuente and Elder 1998, Myers et al. 1998, NRC 2003, De la Fuente 2006, Snavely 2006, Pearse et al. 2007, Drought Monitor archive: www.drought.unl.edu/dm/archive.html, www.pmel.noaa.gov/tao/elnino.html).

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| --- | --- | --- | --- |
| **Year** | **Event** | | **Potential Effect** |
| Mid 1800s | Height of gold mining | | Change in channel structure, increased  siltation of spawning gravels, possible accretion of mercury in streams, reduction of flows |
| 1840s - present | Fire suppression | | Altered flow regimes and nutrient cycling, increased fire severity and subsequent erosion from burned areas leads to siltation of steam substrates |
| 1863 - current | Logging practices (private and federal lands) | | Increased siltation to spawning gravels, reduction in stream shading |
| 1870s – late 1880s | Height of grazing (cattle, sheep) | | Sedimentation of spawning gravels, incision of streams, reclamation of wetlands, reduction of flows |
| 1882 - 1903 | Agriculture in the upper basin begins | | Drainage of Tule Lake and Lower Klamath Lake, reduction of flows, change in flow regime of mainstem Klamath River |
| 1890s | Hatchery supplementation begins | | Introduction of broodstock from outside the basin |
| 1900s | Agriculture in the lower basin begins | | Decreased stream flow and ground water input, simplification of stream channels, removal of riparian vegetation |
| 1910s -1920s | Commercial salmon harvest | | Unlimited harvest of Chinook and coho salmon fisheries at 3 Klamath River canneries |
| 1918 | Completion of Copco 1 dam | | Separation of upper and lower basin, altered flow and nutrient cycling regimes |
| 1923-1931 | Drought conditions | | Decreased flow, increase in summer water temperatures |
|  |  | |  |
|  |  | |  |
| Table 2.4. continued | |  |  |
| 1947-1976 | Good ocean conditions for salmon growth and survival | | Cold sea-surface temperatures, high productivity in the California Current |
| 1955 | Severe flood | | Change in stream structure, decrease in riparian vegetation, pool infilling, input of large woody debris and boulders |
| 1962 | Completion of Iron Gate Dam | | Loss of approx. 560 km of spawning and rearing habitat upstream of dam |
| 1963 | Trinity Hatchery opened | | Introduction of non-native stock (e.g., coho from Eel and Noyo rivers, California, and Cascade and Alsea rivers, Oregon), decrease in run fitness, change in genetic integrity, increased competition for limited instream resources |
| 1964 | Severe flood (Biggest flood on record; ~50 year flood) | | Change in stream structure, decrease in riparian vegetation, pool infilling, input of large woody debris and boulders |
| 1965 | Iron Gate Hatchery opened | | Introduction of non-native stock (e.g., coho salmon from Cascade River, Oregon), decrease in run fitness, change in genetic integrity, increased competition for limited instream resources |
| 1974-1994 | Egg transfers from Iron Gate Hatchery to Trinity River Hatchery | | Reduction in divergence among populations (i.e. *O. mykiss*). |
| 1976-1989 | Poor ocean conditions for salmon growth and survival | | Warming of northeast Pacific Ocean (sea-surface temperatures), reduced productivity in California Current |
| 1976-1977 | Drought conditions | | Decreased flow, increase in summer water temperatures |
| 1978-1984 | IGH hatchery releases increase | | Average annual hatchery releases = >2,000,000 |
| 1985-1988 | IGH hatchery releases decrease | | Average annual hatchery releases = ~100,000 fall |
| 1986-1987 | El Niño | | Warm ocean temperatures, low flows in streams |
| 1986-1992 | Drought conditions | | Decreased flow, increase in summer water temperatures |
| 1987 | Severe forest fires | | More than 30% of some watersheds burned with high intensity, increased siltation of stream substrates |
| 1989-2009 | IGH hatchery releases increase | | Average annual hatchery releases = >5,000,000 |
| 1991-1992 | El Niño | | Warm ocean temperatures, low flows in streams |
| 1993-1994 | El Niño | | Warm ocean temperatures, low flows in streams |
|  |  | |  |
| Table 2.4. continued | |  |  |
| 1994 | Northwest Forest Plan adopted | | Increased protection of aquatic habitat within the range of the northern spotted owl |
| 1994 | Drought conditions | | Decreased flow, increase in summer water temperatures |
| 1997 | Federal listing of coho salmon | | Increased protection measures of species and designated Critical Habitat |
| 1997 | Severe flood (~ 35 year event) | | Change in stream structure, decrease in riparian vegetation, increased siltation of streams (pool infilling), input of large woody debris and boulders |
| 1997-1998 | El Niño | | Warm ocean temperatures, low flows in streams |
| 1998 | Poor ocean conditions for salmon growth and survival | | Warming of northeast Pacific Ocean (sea-surface temperatures), reduced productivity in California Current |
| 1999-2002 | Good ocean conditions for salmon growth and survival | | Cold sea-surface temperatures, high productivity in the California Current |
| 2002 | Fish die-off | | ~30,000 adults die prior to spawning (primarily Chinook salmon), expected decrease in abundance of subsequent brood year, disease monitoring intensifies |
| 2001-2005 | Drought conditions | | Decreased flow, increase in summer water temperatures |
| 2003-2005 | Poor ocean conditions for salmon growth and survival | | Warming of northeast Pacific Ocean (sea-surface temperatures), reduced productivity in California Current |
| 2004 | Blue green algae blooms | | Concerns about harmful effects from blue-green algae blooms begin to be investigated |
| 2006-2009 | Drought conditions | | Decreased flow, increase in summer water temperatures |

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**Chapter 3 -** Climatic forcing, habitat quality or population dynamics: drivers of life history variability in local populations of Pacific salmon (*Oncorhynchus* spp.)

**Abstract**

Conservation of life history diversity is essential for recovery of declining Pacific salmonid (*Oncorhynchus* spp.) populations. Life history diversity spreads the risk of extinction over multiple spatial and temporal scales, thereby increasing the probability of species persistence. Trends in salmonid abundances reflect the impact of multiple factors relating to climate, habitat quality and population characteristics. We analyzed the relationship between 10 factors and local population abundance (1968-2009) to investigate factors acting on taxa with distinct life histories from the Klamath River basin, California. The 10 factors were ocean harvest, in-river harvest, hatchery releases, hatchery returns, Pacific Decadal Oscillation, North Pacific Gyre Oscillation, El Niño Southern Oscillation, snow depth, flow and watershed disturbance. The taxa were Salmon River spring Chinook salmon, Salmon River fall Chinook salmon, Salmon River summer steelhead trout, and Scott River fall Chinook salmon. We used permutation tests of univariate correlations as a first step to identify environmental and anthropogenic factors relating to abundance of each taxon. Then we built generalized linear models (GLMs) to determine factors most influencing trends in abundance. We also included effects of density dependence within populations. Our analyses revealed that different factors acted on the abundances of taxa with different life histories. Impacts also differed in the timing of their effects. GLM results indicated that Salmon River spring Chinook salmon abundance was primarily driven by ocean harvest and ocean conditions. Salmon River fall Chinook salmon abundance was primarily driven by hatchery returns and snow depth. April 1 snow depth is indicative of instream conditions (e.g., temperature and flow) in the summer, a time particularly stressful to salmonids in the Klamath River basin. Salmon River summer steelhead trout abundance was primarily driven by ocean harvest (of fall Chinook salmon) and hatchery returns. Scott River fall Chinook salmon was solely driven by in-river harvest. All taxa exhibited strong negative density dependence. Our findings underscore the importance of understanding the factors that drive different populations of salmon and steelhead from the same basin, if life history diversity is to be preserved.

**Introduction**

Life history traits govern the likelihood of “survival and the rates of reproduction at each age in the life-span” of an organism ([Partridge and Harvey 1988](#_ENREF_81)). In a population of salmonids, diversity of life histories results in a group of individuals with various phenologies (e.g., duration of incubation, longevity of fresh water rearing, age of maturity etc.) that use a variety of rearing and migration habitats ([Lichatowich et al. 1995](#_ENREF_51)). Consideration of life history diversity is essential for the recovery of declining Pacific salmon (*Oncorhynchus* spp.) populations ([Beechie et al. 2006](#_ENREF_10)) because diverse life histories spread the risk of extinction due to catastrophic events ([Den Boer 1968](#_ENREF_26)) or long periods of unfavorable conditions ([Cole 1954](#_ENREF_21)). Populations with diverse life histories express higher stability in numbers ([Den Boer 1968](#_ENREF_26)) and probabilities of persistence ([Lichatowich et al. 1995](#_ENREF_51)), even when environmental conditions vary ([Cohen 1966](#_ENREF_19), [1968](#_ENREF_20)). Local populations strengthen species resiliency, the ability of species to replenish themselves after high mortality events, by contributing genetic and phenotypic diversity, including variable life histories, which reflect local adaptation. The decline of Pacific salmon throughout their range, in part has been a consequence of extirpation of local populations ([Schtickzelle and Quinn 2007](#_ENREF_92)) with the cumulative result of decreasing the species’ adaptive capability ([Waples et al. 2009](#_ENREF_100), [Greene et al. 2010](#_ENREF_33), [Moore et al. 2010](#_ENREF_64)). Consequently, the ability of Pacific salmon species to persist through changes expected in the future (e.g., climate change) requires protection of locally-adapted populations and their habitats ([Lackey 2003](#_ENREF_47), [Battin et al. 2007](#_ENREF_5), [Moore et al. 2010](#_ENREF_64)). Effective conservation of imperiled species should benefit from determination of multiple factors ([Pess et al. 2002](#_ENREF_83)) acting individually and collectively on abundances of taxa with different life histories. This analysis is the focus of this paper.

Both environmental and anthropogenic factors (extrinsic drivers) and internal population dynamics (intrinsic drivers) define extinction probabilities of Pacific salmon populations ([Young 1999](#_ENREF_105)). Extrinsic drivers of variability in Pacific salmon abundances include climatic forcing ([Beamish and Bouillon 1993](#_ENREF_6), [Mantua et al. 1997](#_ENREF_57), [Lehodey et al. 2006](#_ENREF_49)), fresh water habitat quality ([Bradford and Irvine 2000](#_ENREF_13), [Rosenfeld et al. 2000](#_ENREF_91), [Sharma and Hilborn 2001](#_ENREF_94), [Beechie et al. 2006](#_ENREF_10), [Isaak et al. 2007](#_ENREF_42)), and harvest by fisheries ([Nehlsen et al. 1991](#_ENREF_76), [Finney et al. 2000](#_ENREF_31), [Hard et al. 2008](#_ENREF_36)). Intrinsic drivers of variability include density-dependent effects from interactions with hatchery-produced conspecifics ([Levin et al. 2001](#_ENREF_50), [Myers et al. 2004](#_ENREF_71), [Naish et al. 2007](#_ENREF_73), [Kostow 2009](#_ENREF_46)), cohabiting juveniles ([Peterman 1984](#_ENREF_84), [Beamish and Mahnken 2001](#_ENREF_7), [Zabel et al. 2006](#_ENREF_106)), and spawning adults ([Greene and Beechie 2004](#_ENREF_32)).

Pacific salmon abundances have been linked to climatic forcing that govern ocean conditions as well as to inland hydrology (e.g., stream flow). Conditions associated with the El Niño Southern Oscillation (ENSO) usually occur every 6-18 months, primarily in the tropics, and have secondary effects in the Northern Pacific Ocean ([Wolter and Timlin 1993](#_ENREF_103)). In California, El Niño conditions result in poor ocean growth and survival of Pacific salmon ([Pearcy and Schoener 1987](#_ENREF_82), [Johnson 1988](#_ENREF_44)) and in drier, warmer conditions in rivers ([Mote et al. 2003](#_ENREF_65), [Stenseth et al. 2003](#_ENREF_95)). The Pacific Decadal Oscillation (PDO) reverses every 20-30 years and is linked primarily to sea surface temperature and height in the Northern Pacific Ocean ([Mantua et al. 1997](#_ENREF_57), [Mantua and Hare 2002](#_ENREF_56)). Warm sea surface temperatures can decrease salmon ocean survival as well as limit reproductive success ([Downton and Miller 1998](#_ENREF_28), [Hare et al. 1999](#_ENREF_37), [Peterson and Schwing 2003](#_ENREF_86)). The North Pacific Gyre Oscillation (NPGO) affects salinity and nutrient concentrations that determine plankton ecosystem dynamics in the Northern Pacific ([DiLorenzo et al. 2008](#_ENREF_27)). Fishes in the California Current, including salmon, benefit from the positive phase of NPGO that favors upwelling conditions offshore and increases prey availability ([Cloern et al. 2010](#_ENREF_18)).

The habitat requirements of Pacific salmon have been extensively studied and reviewed (e.g., Groot and Margolis 1991, Lackey et al. 2006, Moyle et al. 2008). At the most basic level, salmon need cold, clean water, so increases in water temperatures or the presence of pollutants in concentrations can impair growth, survival and/or reproduction ([Groot and Margolis 1991](#_ENREF_34), [Moyle 2002](#_ENREF_66), [Lackey et al. 2006](#_ENREF_48)). High water temperatures and high concentrations of fine sediment are two conditions most often associated with fresh water habitat degradation that reduce salmonid abundances. Exposure to high water temperatures (17 - 20°C) can limit growth ([Brett 1971](#_ENREF_14), [Thomas et al. 1986](#_ENREF_96), [Marine and Cech 2004](#_ENREF_58)), smolting capability ([Clarke and Shelbourn 1985](#_ENREF_17), [Marine and Cech 2004](#_ENREF_58)), and predator avoidance in juveniles ([Marine and Cech 2004](#_ENREF_58)), as well as spawning migrations and reproductive success in adults ([McCullough 1999](#_ENREF_61)). Increased erosion from land-use practices, and the resulting sedimentation of streams, can impair egg incubation, juvenile emergence from redds, and adult spawning migration and redd building ([Crouse et al. 1981](#_ENREF_25), [Bjornn and Reiser 1991](#_ENREF_12)).

Overexploitation in Pacific salmon fisheries has increased the risk of extinction of many species ([Nehlsen et al. 1991](#_ENREF_76)). Combined with other stressors, including land-use and climate change, overexploitation can decline numbers ([Cole 1954](#_ENREF_21), [Bradford and Irvine 2000](#_ENREF_13)) to a point where populations cannot be replenished ([Beamish et al. 2006](#_ENREF_9)). Overexploitation can also have impacts to the characteristics of the population itself by altering age structure, average body size, migration timing, and age of maturity ([Beamish et al. 2006](#_ENREF_9), [Hard et al. 2008](#_ENREF_36)). Furthermore, high harvest rates can increase the potential for bycatch of other imperiled species (e.g., steelhead trout) in both fresh water ([Raby et al. 2011](#_ENREF_90)) and marine fisheries ([Orsi and Wertheimer 1995](#_ENREF_80), [Witherell et al. 2002](#_ENREF_102), [Seeb et al. 2004](#_ENREF_93)).

Interactions among individuals in a population can also affect trends in abundance. For salmonids, these interactions result in density dependent effects that can reduce productivity over all ([Petrosky et al. 2001](#_ENREF_87)) or some ([Marschall and Crowder 1995](#_ENREF_59), [Milner et al. 2003](#_ENREF_63)) developmental stages when suitable habitat is limited. Impacts can occur between cohabitating juveniles ([Marschall and Crowder 1995](#_ENREF_59), [Azumaya and Ishida 2000](#_ENREF_4), [Milner et al. 2003](#_ENREF_63), [Zabel et al. 2006](#_ENREF_106)) and adults ([Ishida et al. 1993](#_ENREF_43), [Myers et al. 1998b](#_ENREF_72), [Myers 2001](#_ENREF_69)) or have delayed effects on later cohorts ([Myers et al. 1997](#_ENREF_70), [Bjorkstedt 2000](#_ENREF_11)). Interactions between wild and hatchery-produced salmonids are often considered separately because the introduction of hatchery fishes can artificially increase competition ([Heard 1998](#_ENREF_40), [Levin et al. 2001](#_ENREF_50), [Kaeriyama 2004](#_ENREF_45)), predation ([Nickelson 2003](#_ENREF_77)), and/or fishing pressure ([Hard et al. 2008](#_ENREF_36)) of wild stocks.

Due to the paucity of data, most studies to date have analyzed only a small number of factors at a time (e.g., land-use, climate change and fishing; Bradford and Irvine 2000). However, none of the studies distinguish drivers acting on different life histories within local populations or among populations of different locations. It is interesting to question whether different life-history taxa are influenced by the same or different extrinsic and intrinsic factors, and hence whether they are likely to have independence in their population dynamics and conservation needs. Here, we tested the effects of 10 extrinsic and intrinsic drivers, at different spatial and temporal scales, on the abundances of populations of Chinook salmon and steelhead trout with different life histories. We aimed to identify and compare factors relating to climatic forcing, habitat quality, and population dynamics that drive trends in adult spawner numbers (escapement) of four taxa. The four taxa, Salmon River spring Chinook salmon, fall Chinook salmon and summer steelhead trout, and Scott River fall Chinook salmon, were located in two adjacent, similar-sized watersheds. We hypothesized that populations primarily respond to one driver, most likely climatic forcing (i.e. ocean conditions), and that drivers would differ by life history. As the target of commercial fisheries, we hypothesized that abundances of fall Chinook would be driven by ocean harvest rates. We also hypothesized that spring Chinook and summer steelhead abundances would be driven by habitat factors (e.g., flow) because of their long residency in fresh water habitats.

**Study area and taxa**

The Klamath River, located in southern Oregon and northern California, is the second largest river system in California, draining approximately 30,000 km2 (Figure 3.1). Klamath River salmonids face many natural and human-caused stressors, including the presence of dams, habitat degradation, climate change and hatchery supplementation ([Moyle 2002](#_ENREF_66), [Moyle et al. 2008](#_ENREF_67)). Although the Klamath River once supported 55 separate taxa of salmonids, chum (*O. keta*) and pink salmon (*O. gorbuscha*) are all but extinct ([Nehlsen et al. 1991](#_ENREF_76), [NRC 2004](#_ENREF_78)) as are significant portions (~40%) of the stream-maturing taxa including spring Chinook salmon and summer steelhead trout ([Gustafson et al. 2006](#_ENREF_35)). Coho salmon (Southern Oregon and Northern California Coasts Evolutionarily Significant Unit) were listed under federal and state Endangered Species Acts in 1997 (62 FR 24588) and 2005, respectively, and are largely reliant on hatchery supplementation ([Weitkamp et al. 1995](#_ENREF_101)). Nevertheless, Klamath River stocks may represent the best opportunity for the recovery of salmonids in California because of current efforts to restore extensive areas of habitat, including the removal of four large dams.

Located in adjacent watersheds, the Salmon and Scott rivers drain about 2000 km2 and flow northwest into the Klamath River (Figure 3.1). The watersheds differ greatly in land-uses and aquatic habitat quality. The Salmon River watershed is one of the most pristine in the Klamath River basin ([Elder et al. 2002](#_ENREF_30)), although summer temperatures can exceed salmonid tolerance levels ([NCRWQCB 2005a](#_ENREF_74)). The Salmon River is distinctive in that it continues to support spring Chinook salmon and summer steelhead trout that have been extirpated from other parts of the basin (Elder et al. 2002) and large portions of the state ([Moyle et al. 2008](#_ENREF_67)). Streams in the Salmon River watershed are characterized by steep, bedrock-dominated channels. Flows are sustained by snowmelt from the Marble Mountains and Trinity Alps. The Salmon River watershed is predominately (~98%) forested lands managed by the Klamath and Six Rivers National Forests (Klamath National Forest, unpublished data). Land-uses in the watershed include timber harvest, grazing, and mining but to a lesser extent than in the Scott River watershed.

In contrast, the Scott River watershed has been significantly altered by channel straightening and drainage of wetlands ([NCRWQCB 2005b](#_ENREF_75)). High summer temperatures and fine (<4 mm) sediment loads have degraded salmonid habitats ([NCRWQCB 2005b](#_ENREF_75)). Fall Chinook salmon currently make up the only significant run of anadromous salmonids, although spring Chinook and coho salmon were once numerous ([Moyle 2002](#_ENREF_66)), and coho salmon are present in low numbers in some tributaries (Moyle et al. 2008). The mainstem river flows through a wide valley (Scott Valley) in the upper reaches and then through a bedrock-controlled canyon. Flows in the Scott River are sustained by snowmelt and groundwater inputs from the Scott Valley aquifer. However, irrigation practices exacerbate low base flows ([Drake et al. 2000](#_ENREF_29)) to the extent that long stream reaches are dry in some years (e.g., 2009). Approximately 63% of the watershed is privately owned. Primary land-uses in the watershed are agriculture, grazing, timber harvest, and mining.

**Life history and trends of selected taxa**

**Chinook salmon**

In California, Chinook salmon adults begin upstream spawning migrations from late spring through fall ([Moyle 2002](#_ENREF_66)). Most Chinook salmon express a high affinity for returning to natal streams, although straying rates can vary from 1.4% in wild fish ([Quinn et al. 1991](#_ENREF_89)) to 90% in hatchery fish ([Cramer and Chapman 2002](#_ENREF_24)) . Of all Pacific salmon, Chinook have the most varied life histories. Life histories differ in age of seaward migration, length of fresh water, estuarine, and oceanic residence, marine distribution, ocean migratory patterns, and age and season of spawning migration ([Healey and Prince 1995](#_ENREF_39), [Moyle 2002](#_ENREF_66)).

In the Klamath River, spawning migration begins as early as March (spring-run) and continues through September (fall-run) ([Myers et al. 1998a](#_ENREF_68)). Spring Chinook salmon are reproductively immature when they enter fresh water and will migrate further upstream than fall Chinook ([Moyle 2002](#_ENREF_66)). Spawning by both spring and fall Chinook salmon can start as early as late August and continue until December. Mature adults are usually two to five years old and die shortly after spawning. Currently, the only natural population of spring Chinook salmon in the Klamath River basin is thought to be in the Salmon River. Juvenile Chinook salmon predominantly (> 80%) rear in fresh water for only a few months (~5) before entering the ocean in the fall or early winter ([Olson 1996](#_ENREF_79), [Myers et al. 1998a](#_ENREF_68)). Although spring and fall Chinook salmon are not recognized as separate taxa by the National Marine Fisheries Service, most biologists treat each taxon as Distinct Population Segments due to the difference in their physiology, distribution, and behavior ([Moyle et al. 2008](#_ENREF_67)). Abundances of Salmon River and Scott River fall Chinook salmon appear to be stable, while abundances of Salmon River spring Chinook salmon appear to be increasing (Quiñones, unpublished data). However, hatchery-produced conspecifics are likely replacing the wild populations of both taxa, raising concerns about the viability and persistence of wild stocks (Quiñones, unpublished data).

**Steelhead trout**

Steelhead are the anadromous form of rainbow trout, *O. mykiss*. Two distinct life history patterns are recognized in the Klamath River basin: winter, and summer steelhead trout ([Busby et al. 1994](#_ENREF_16)). Winter steelhead trout move upstream after the onset of winter rains between November and April, shortly before spawning. Summer steelhead trout move upstream from April to June, spend the summer months in deep pools while they mature and spawn from December to April. Life histories differ in smolt age, length of marine residency, and patterns of reproduction ([Busby et al. 1994](#_ENREF_16)). Steelhead trout adults are capable of spawning once a year but often spawn every other year, up to four times. Most adults become reproductively mature from age 1 to 5 ([Busby et al. 1994](#_ENREF_16)). Juveniles will spend one to two years in cold fast-flowing perennial streams and are often associated with riffle habitats. Trends of adult Iron Gate Hatchery steelhead and Salmon River summer steelhead trout are in steep decline (Quiñones, unpublished data) and appear to be on the brink of extinction ([Moyle et al. 2008](#_ENREF_67)).

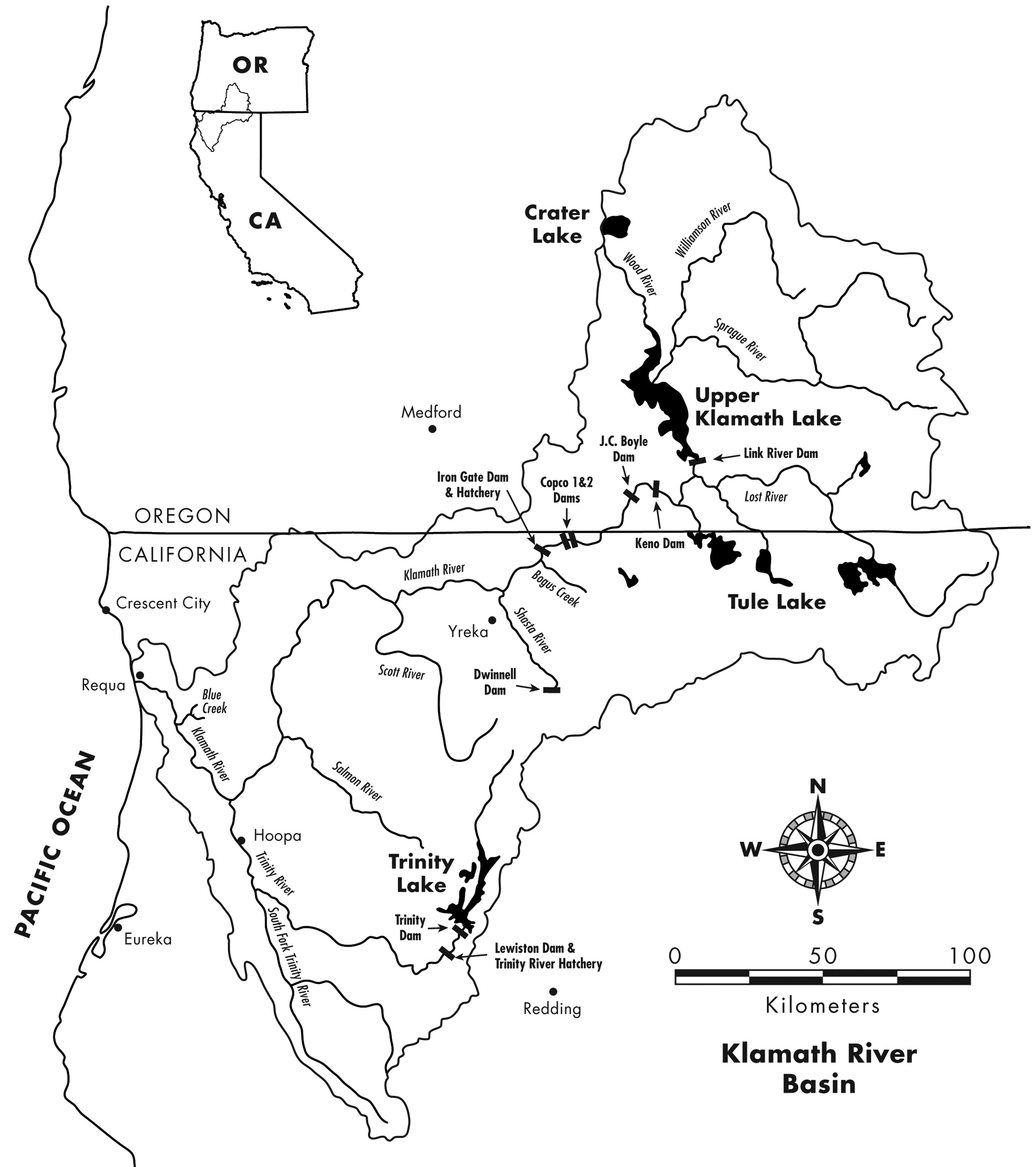


Figure 3.1. Klamath River basin, California and Oregon.

**Methods**

**Conceptual model**

To synthesize our hypotheses, we first constructed a conceptual model of variables potentially driving Pacific salmon abundances, based on peer-reviewed literature (discussed in the Introduction section; Figure 3.2). The variables were divided into three categories, those that affect internal population dynamics (population variables), climatic conditions (climate variables), and fresh water habitat quality (habitat variables). We recognize that factors interact with one another, within and among categories. Their interactions are investigated in our analysis described below. However, we organized the factors in the conceptual model to facilitate initial hypothesis generation. Population variables were factors that can directly increase or decrease salmonid abundance and therefore affect density dependent processes. Population variables were ocean harvest rate, in-river harvest numbers, Iron Gate Hatchery (IGH) juvenile releases, and IGH adult returns. Climate variables were factors that influence ocean conditions (e.g., temperature, salinity), ocean productivity (e.g., plankton concentrations) and regional weather patterns that govern precipitation and air temperatures. Climate variables were indices of the North Pacific Gyre Oscillation (NPGO), Pacific Decadal Oscillation (PDO), and El Niño Southern Oscillation (Multivariate El Niño Southern Oscillation Index; MEI). Habitat variables were factors that influence fresh water habitat quality. Habitat variables were snow depth (m), flow (cubic meters per second; cms), and Equivalent Roaded Acreage (ERA) as a surrogate for stream sedimentation. Variables are more fully described below.

Local Population Abundance

(escapement)

Population

Variables

Climate

Variables

Habitat

Variables

Figure 3.2. Conceptual model of population, climate, and habitat variables that influence patterns in adult Pacific salmon abundances (escapement). IGH = Iron Gate Hatchery, PDO = Pacific Decadal Oscillation, NPGO = North Pacific Gyre Oscillation, MEI = multivariate El Niño Southern Oscillation Index, ERA = Equivalent Roaded Acres.

**Explanatory variables**

Population variables were those that directly increased or decreased the abundance of each taxon by either introducing or removing individuals from the population (Figure 3.2). Ocean harvest rate (1981-2008) is a measure of the annual commercial harvest effort exerted specifically on Klamath River fall Chinook (ages 3 and 4; California Department of Fish and Game (CDFG), unpublished pre-season report, 2010). In-river harvest (1978-2009) is the sum number of Klamath River Chinook caught by sports and tribal fisheries annually (CDFG, unpublished data, 2010). IGH releases (1971-2009) are the total number of Chinook or steelhead juveniles (depending on time series analyzed) released each year by the hatchery (IGH, unpublished data, 2010). IGH returns (1968-2009) are the number of Chinook or steelhead adults (depending on time series analyzed) returning to the hatchery to spawn at IGH (IGH, unpublished data, 2010).

Climate variables impact the characteristics of ocean conditions, as well as inland hydrologic conditions (Figure 3.2). We chose variables that affect large-basin (NPGO) and regional spatial scales (PDO, MEI), and occur at interannual (MEI), decadal (NPGO), and interdecadal (PDO) time scales ([Mantua et al. 1997](#_ENREF_57), [Costello et al. 1998](#_ENREF_23), [DiLorenzo et al. 2008](#_ENREF_27)). Several studies have shown that ocean conditions, particularly food availability, at time of ocean entry by salmonid juveniles (critical period hypothesis) can heavily influence subsequent adult abundance ([Beamish and Mahnken 2001](#_ENREF_7)). Because we wanted to test the influence of ocean conditions at this critical period, we averaged the May and June values of the climate variables. After analyzing watershed-specific hydrographs, we concluded that May and June were the months when Klamath River salmonids most likely entered the ocean due to the timing of peak flows. The Multivariate El Niño Southern Oscillation Index (MEI; 1968-2009) incorporates data of sea-level pressure, surface wind, sea surface temperature, surface air temperature, and cloud cover associated with El Niño and La Niña events ([Wolter and Timlin 2011](#_ENREF_104)). These events usually occur every 6-18 months, primarily in the tropics, and have secondary effects in the Northern Pacific Ocean ([Trenberth 1997](#_ENREF_97)). El Niño conditions are represented by positive MEI values, while negative values represent La Niña conditions. MEI values were obtained from http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/. The Pacific Decadal Oscillation index (PDO; 1968-2009) is a measure of monthly sea surface temperature variability in the Northern Pacific Ocean ([Mantua et al. 1997](#_ENREF_57)). PDO events usually last 20-30 years. Cool PDO regimes dominated from 1890 to 1924 and from 1947 to 1976. Warm PDO regimes dominated from 1925 to 1946 and from 1977 through about 1997 ([Mantua and Hare 2002](#_ENREF_56)). PDO values were obtained from http://jisao.washington.edu/pdo/PDO.latest. The North Pacific Gyre Oscillation index (NPGO; 1968-2009) is a measure of sea surface height variability in the Northeastern Pacific Ocean and reflects changes in salinity and nutrient concentrations in the California Current ([DiLorenzo et al. 2008](#_ENREF_27)). NPGO values were obtained from http://www.o3d.org/npgo/.

Three variables with sufficient time series data were available to represent fresh water habitat quality (habitat variables; Figure 3.2). These were flow (cms), snow depth (m), and Equivalent Roaded Acreage (ERA). Flow data (1968-2009) were obtained from the California Data Exchange Center (http://cdec.water.ca.gov/; gages sfj and srs). We converted flow data from acre feet/month to cms/month then added the total amount of flow from July through September to represent base flow conditions for each year. The amount of base flow in the Salmon and Scott rivers is indicative of the amount of habitat available (e.g., by influencing wetted perimeter and depth) and is an indirect indicator of habitat quality (e.g., water temperature) during summer months, a stressful time for salmonids in the Klamath River basin (Bartholow 2005). Snow depth (m) in the Klamath River basin is routinely measured on April 1 to forecast stream flow and monitor changes in local climatic conditions (Natural Resources Conservation Service at http://www.wcc.nrcs.usda.gov/.html). We used April 1 snow depth (1986-2009) on Scott Mountain for our analysis (Andrew Reising, DWR, pers. comm. 2010). Snow melt from Scott Mountain drains into both the Salmon and Scott rivers, and so reflects the water yield potential and spring air temperatures in these watersheds. Equivalent Roaded Acreage (ERA) is an index of watershed disturbance from land-use practices such as timber harvest, wild fire, road building and restoration. The index provides an indicator of watershed conditions by comparing the watershed-specific level of disturbance with the risk of increased peak flows that result in stream channel alteration (e.g., scouring, sedimentation; D. Elder, Klamath National Forest, pers. comm. 2008). To determine ERA, disturbance values were calibrated to road acreages that would generate the same stream alterations. The channel sensitivity, soil erodibility, hydrologic response, and slope stability of each watershed is incorporated into each ERA value. We used ERA indices specific to the Salmon and Scott rivers for years 1980 to 2009 in our models. Indices were provided by the Klamath National Forest (G. Bousfield, Klamath National Forest, pers. comm., 2010).

Variables were ln-transformed when necessary to meet the assumption of normality at α = 0.1. The following variables were not transformed as they were already normally distributed: in-river harvest, snow depth, ERA, IGH releases, MEI, PDO, and NPGO. Ocean harvest rate and flow were ln-transformed once. IGH returns were ln(ln-transformed).

To determine how each variable influenced entire cohorts, variables were lagged by up to 5 years as a reflection of each taxon’s range of age at maturity, *m* (Myers et al. 1998). Variables analyzed with spring and fall Chinook data were lagged for 2 to 5 years while those analyzed with summer steelhead were lagged 2 to 4 years. With the time lags, a total of 50 (Chinook salmon) and 40 variables (steelhead trout) were considered in our analyses. Time lags are important because, although most Pacific salmon-related management (e.g., harvest quotas) is completed from one year to the next, effects from drivers are often expressed at longer time scales ([Peterman et al. 2000](#_ENREF_85), [McCann et al. 2003](#_ENREF_60)).

**Dependent variables (taxa)**

Four time series data sets, representing annual counts of different taxa were obtained from the California Department of Fish and Game (D. Chesney, pers. comm., 2010) and Klamath National Forest (R. Quiñones, unpublished data, 2010). The taxa were spring Chinook salmon, fall Chinook salmon, summer steelhead trout from the Salmon River and fall Chinook salmon from the Scott River. Spring Chinook and summer steelhead data were standardized as the number of fish per mile from annual snorkel surveys. Only adult counts were used for summer steelhead due to common misidentification of large resident trout as half-pounder steelhead (R. Quiñones, personal observations, 2001-2010). Fall Chinook data were the estimated total number of spawning adults in each river as calculated by mark-recapture carcass surveys (CDFG, unpublished data, 2010). All Chinook time series included counts of grilse, reproductively mature age 2 individuals. Time series were tested for autocorrelation and ln-transformed to meet assumptions of normality.

**General approach**

Our goal was to compare multiple variables that drive patterns in local population abundances specific to different life histories. First, we used inferential statistics (correlations) to determine variables that by themselves were significantly (p < 0.05) correlated to escapement. This was done as an initial screening exercise to avoid the problems associated with short time series and over-fitting by informational theoretical model-fitting techniques. Specifically, permutation tests were used to determine the relationship between dependent and explanatory variables. Parametric tests are robust to serial autocorrelation, which is typical of time-series data ([Manly 1991](#_ENREF_55)). The resulting test statistic is the probability that reshuffling of the data will result in a p value that is more extreme than expected under the null hypothesis ([Anderson 2001](#_ENREF_2)). We shuffled our data 99,999 times, approximately two orders of magnitude more than Manly’s (1997) recommendation of 1000 permutations at a level of significance of 0.05. Permutations were completed using software available at http://www.bio.umontreal.ca/casgrain/en/labo/regression.html (REGRESSN; Legendre 1999). The five variables most significantly correlated to each taxon’s abundance were then considered in building generalized linear models (GLMs), to reduce the problems of over-fitting of models and multicollinearity among explanatory variables.

We did not use Principle Component Analysis (PCA) to narrow down the number of explanatory variables so that clear identity of variables could be maintained within our analysis. We chose to build GLMs because it is impossible to use a probabilistic approach to fit models using multiple variables with small sample sizes. The use of GLMs avoided the problem of multiple comparisons since Akaike’s Information Criterion (AIC) is less demanding of small sample sizes ([Akaike 1978](#_ENREF_1)).

**Generalized linear models (GLMs)**

Before models were built, we set the following conditions to protect for parsimony, as recommended by Anderson (2008):

1. Only variables significantly (p <0.05) correlated to escapement and with the five highest r2 values would be used in models.
2. Variables with correlations higher than 0.5 would not be used in the same model.
3. Variables would only be kept in a model if they increased r2 values by at least 0.05, which helps to reduce problems of over-fitting of models.
4. No more than 3 (n/10) variables would be used in each model (again to reduce over-fitting of models).
5. Alternative models were identified by ΔAICc less than 2.

ΔAICc is a measure of each model relative to the one with the lowest AICc score. ΔAICc is calculated as: ΔAICc = AICc,*I* – minimum AICc.

1. When multiple models are equally preferred (lowest AICc or ΔAICc < 2) the simplest model is chosen.

Models were compared to one another by computing model weights (*wi*, Anderson 2008*)* as:

*wi* = [exp (-1/2 ΔAICc)]/[Σ exp(-1/2 ΔAICc)]. Model weights (*wi*) were interpreted as the probability that a given model has the most evidence among all candidate models considered.

**Density dependence**

Density dependence is a major driving force in recruitment of salmonid populations (e.g., Zabel et al. 2006). It is also possible that density dependence interacts with extrinsic variables to influence salmonid numbers. Density dependence was analyzed through the regressions between the difference of abundances in consecutive years (abundance at time t – abundance at time t+1) and abundance at time t. We also estimated regressions between abundances at time t and abundances lagged up to five years to investigate the occurrence of density dependence. In preliminary analyses we constructed GLMs that took the residuals of population change after density dependence acted and tested for relationships between the residuals and extrinsic factors. Such models allow for the fact that density dependence might mask the effect of other variables. The results were overwhelmingly similar to the results of the GLMs reported below that are conceptually simpler. Density-dependent variables and extrinsic effects are multicollinear in many cases and so we would not want to put them in the same GLMs. We therefore report the simpler GLM’s described below, noting that our preliminary exercise indicated a lack of complex interactions between density dependence and other explanatory variables.

**Results**

**Correlations and GLMs**

Correlations between explanatory variables and abundances (Table 3.7), as well as correlations among explanatory variables used in GLMs (Tables 3.8-3.11), are reported in the appendices. The five variables most significantly correlated to Salmon River spring Chinook salmon abundance were ocean harvest t-2 (p = 0.041, r2 = 0.18, slope = -0.32), in-river harvest t (p = 0.026, r2 = 0.17, slope = 7550.4), hatchery returns t (p = 0.0057, r2 = 0.22, slope = 0.036), MEI t-5 (p = 0.011, r2 = 0.20, slope = 0.35) and PDO t-5 (p = 0.009, r2 = 0.21, slope = 0.40). However, only two variables made up the spring Chinook GLM: ocean harvest t-2, and MEI t-5 (Table 3.1; AICc = 65.48).

Table 3.1. Generalized linear models of variables found to be significantly correlated to Salmon River spring Chinook salmon escapement. The preferred model (bold) was identified as having the fewest variables, and low ΔAIC(< 2) and high *wi* values. An asterisk (\*) identifies possible alternative models (ΔAIC 0-2).

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Variable(s)** |  |  |  | **r2** | **adj. r2** | **AICc** | **ΔAIC** | ***wi*** |
| Population Models |  |  |  |  |  |  |  |  |
| ocean harv. t-2 |  |  |  | 0.18 | 0.14 | 71.36 | 7.44 | 1.2E-02 |
| in-river harv. t |  |  |  | 0.17 | 0.14 | 89.10 | 25.18 | 1.7E-06 |
| IGH ret. t |  |  |  | 0.22 | 0.19 | 103.1 | 39.15 | 1.6E-09 |
| ocean harv. t-2 | in-river harv. t |  |  | 0.38 | 0.32 | 67.58 | 3.66 | 8.2E-02 |
| ocean harv. t-2 | IGH ret. t |  |  | 0.19 | 0.12 | 73.74 | 9.82 | 3.8E-03 |
| in-river harv. t | IGH ret. t |  |  | 0.30 | 0.25 | 86.77 | 22.85 | 5.6E-06 |
| ocean harv. t-2 | in-river harv. t | IGH ret. t |  | 0.38 | 0.29 | 70.74 | 6.82 | 1.7E-02 |
| Climate Models |  |  |  |  |  |  |  |  |
| MEI t-5 |  |  |  | 0.20 | 0.18 | 96.39 | 32.47 | 4.5E-08 |
| PDO t-5 |  |  |  | 0.21 | 0.18 | 96.17 | 32.25 | 5.1E-08 |
| MEI t-5 | PDO t-5 |  |  | 0.29 | 0.24 | 95.62 | 31.7 | 6.7E-08 |
| Combined Models |  |  |  |  |  |  |  |  |
| **ocean harv. t-2** | **MEI t-5** |  |  | **0.43** | **0.37** | **65.48** | **1.56** | **2.3E-01** |
| ocean harv. t-2 | PDO t-5 |  |  | 0.21 | 0.14 | 73.20 | 9.28 | 4.9E-03 |
| in-river harv. t | MEI t-5 |  |  | 0.36 | 0.31 | 84.33 | 20.41 | 1.9E-05 |
| in-river harv. t | PDO t-5 |  |  | 0.29 | 0.24 | 87.05 | 23.13 | 4.9E-06 |
| \*ocean harv. t-2 | in-river harv. t | MEI t-5 |  | 0.53 | 0.46 | 63.92 | 0 | 5.1E-01 |
| ocean harv. t-2 | in-river harv. t | PDO t-5 |  | 0.42 | 0.34 | 68.92 | 5 | 4.2E-02 |
| ocean harv. t-2 | in-river harv. t | MEI t-5 | PDO t-5 | 0.54 | 0.44 | 67.31 | 3.39 | 9.4E-02 |

harv. = harvest, ret. = returns

The five variables most significantly correlated to Salmon River fall Chinook salmon were hatchery returns t-4 (p = 0.021, r2 = 0.17, slope = -0.045), hatchery returns t-5 (p = 0.015, r2 = 0.18, slope = -0.049), NPGO t-4 (p = 0.0021, r2 = 0.27, slope = -0.80), ERA t (p = 0.0052, r2 = 0.24, slope = 292.5), and snow t-5 (p = 0.044, r2 = 0.22, slope = -6.01). Of these, hatchery returns t-5 and snow t-5 made up the GLM with the lowest AICc (Table 3.2; AICc = 43.74).

Table 3.2. Generalized linear models of variables found to be significantly correlated to Salmon River fall Chinook salmon escapement. The preferred model (bold) was identified as having the fewest variables, and low ΔAIC(< 2) and high *wi* values. An asterisk (\*) identifies possible alternative models (ΔAIC 0-2).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Variable(s)** |  |  | **r2** | **adj. r2** | **AICc** | **ΔAIC** | ***wi*** |
| Population Models |  |  |  |  |  |  |  |
| IGH ret. t-4 |  |  | 0.17 | 0.14 | 68.60 | 24.86 | 2.6E-06 |
| IGH ret. t-5 |  |  | 0.18 | 0.15 | 68.10 | 24.36 | 3.3E-06 |
| IGH ret. t-4 | IGH ret. t-5 |  | 0.19 | 0.13 | 70.34 | 26.6 | 1.1E-06 |
| Climate Models |  |  |  |  |  |  |  |
| NPGO t-4 |  |  | 0.27 | 0.25 | 64.34 | 20.6 | 2.1E-05 |
| Habitat Models |  |  |  |  |  |  |  |
| ERA t |  |  | 0.24 | 0.22 | 62.25 | 18.51 | 6.1E-05 |
| snow t-5 |  |  | 0.22 | 0.17 | 46.65 | 2.91 | 1.5E-01 |
| ERA t | snow t-5 |  | 0.26 | 0.17 | 48.85 | 5.11 | 5.0E-02 |
| Combined Models |  |  |  |  |  |  |  |
| IGH ret. t-5 | NPGO t-4 |  | 0.32 | 0.27 | 64.61 | 20.87 | 1.9E-05 |
| **IGH ret. t-5** | **snow t-5** |  | **0.43** | **0.36** | **43.74** | **0** | **6.4E-01** |
| IGH ret. t-5 | snow t-5 | NPGO t-4 | 0.46 | 0.36 | 46.45 | 2.71 | 1.6E-01 |

ret. = returns

The five variables most significantly correlated to Salmon River summer steelhead trout were (Chinook) ocean harvest t (p = 0.00005, r2 = 0.55, slope = 0.53), hatchery releases t (p = 0.00061, r2 = 0.37, slope = 53552), and hatchery returns t (p = 0.00001, r2 = 0.62, slope = 0.90), t-2 (p = 0.00002, r2 = 0.56, slope = 0.87), and t-3 (p = 0.00008, r2 = 0.44, slope = 0.77). Only two variables, ocean harvest t and hatchery returns t comprised the preferred model (Table 3.3; AICc = 49.41).

Table 3.3. Generalized linear models of variables found to be significantly correlated to Salmon River summer steelhead trout. The preferred model (bold) was identified as having the fewest variables, and low ΔAIC(< 2) and high *wi* values. An asterisk (\*) identifies possible alternative models (ΔAIC 0-2).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Variable(s)** |  |  | **r2** | **adj. r2** | **AICc** | **ΔAIC** | ***wi*** |
| Population Models |  |  |  |  |  |  |  |
| Chinook ocean harv. t |  |  | 0.55 | 0.53 | 61.72 | 12.31 | 2.1E-03 |
| IGH releases t |  |  | 0.37 | 0.35 | 79.60 | 30.19 | 2.7E-07 |
| IGH ret. t |  |  | 0.62 | 0.61 | 81.19 | 31.78 | 1.2E-07 |
| IGH ret. t-2 |  |  | 0.56 | 0.55 | 86.75 | 37.34 | 7.6E-09 |
| IGH ret. t-3 |  |  | 0.44 | 0.42 | 92.51 | 43.1 | 4.3E-10 |
| **Chinook ocean harv. t** | **IGH ret. t** |  | **0.75** | **0.73** | **49.41** | **0** | **9.8E-01** |
| IGH releases t | IGH ret. t |  | 0.73 | 0.71 | 57.47 | 8.06 | 1.7E-02 |
| IGH releases t | IGH ret. t-3 |  | 0.46 | 0.42 | 78.09 | 28.68 | 5.8E-07 |
| IGH releases t | IGH ret. t | IGH ret. t-3 | 0.73 | 0.70 | 60.22 | 10.81 | 4.4E-03 |
| IGH ret. t | IGH ret. t-2 |  | 0.71 | 0.69 | 74.28 | 24.87 | 3.9E-06 |
| IGH ret. t | IGH ret. t-3 |  | 0.72 | 0.70 | 71.32 | 21.91 | 1.7E-05 |
| IGH ret. t | IGH ret. t-2 | IGH ret. t-3 | 0.75 | 0.73 | 70.48 | 21.07 | 2.6E-05 |

harv. = harvest, ret. = returns

The five variables most significantly correlated to Scott River fall Chinook salmon were in-river harvest t (p = 0.019, r2 = 0.17, slope = 10772), in-river harvest t-3 (p = 0.0046, r2 = 0.27, slope = -13668), hatchery returns t-4 (p = 0.014, r2 = 0.19, slope = -0.045), NPGO t-3 (p = 0.022, r2 = 0.16, slope = -0.58), and flow t-3 (p = 0.031, r2 = 0.15, slope = 0.53). The preferred model for Scott River fall Chinook salmon contained only one variable: in-river harvest t-3 (Table 3.4; AICc = 65.11).

Table 3.4. Generalized linear models of variables found to be significantly correlated to Scott River fall Chinook salmon escapement. The preferred model (bold) was identified as having the fewest variables, and low ΔAIC(< 2) and high *wi* values. An asterisk (\*) identifies possible alternative models (ΔAIC 0-2).

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Variable(s)** |  | |  | |  | **r2** | **adj.**  **r2** | **AICc** | **ΔAIC** | | ***wi*** |
| Population Models | |  |  | |  |  |  |  |  |  | |
| in-river harv. t |  | |  | |  | 0.17 | 0.14 | 72.19 | 8.08 | 4.1E-03 | |
| **in-river harv. t-3** |  | |  | |  | **0.27** | **0.24** | **65.11** | **1** | **1.4E-01** | |
| IGH ret. t-4 |  | |  | |  | 0.19 | 0.16 | 71.47 | 7.36 | 5.9E-03 | |
| \*in-river harv. t | in-river harv. t-3 | | |  |  | 0.35 | 0.30 | 64.43 | 0.32 | 2.0E-01 | |
| in-river harv. t | IGH ret. t-4 | |  | |  | 0.31 | 0.27 | 68.69 | 4.58 | 2.4E-02 | |
| \*in-river harv. t-3 | IGH ret. t-4 | |  | |  | 0.35 | 0.30 | 64.47 | 0.36 | 2.0E-01 | |
| \*in-river harv. t | in-river harv. t-3 | | IGH ret. t-4 | |  | 0.42 | 0.35 | 64.11 | 0 | 2.4E-01 | |
| Climate Models |  | |  | |  |  |  |  |  |  | |
| NPGO t-3 |  | |  | |  | 0.16 | 0.13 | 72.55 | 8.44 | 3.5E-03 | |
| Habitat Models |  | |  | |  |  |  |  |  |  | |
| flow t-3 |  | |  | |  | 0.15 | 0.12 | 73.05 | 8.94 | 2.7E-03 | |
| Combined Models |  | |  | |  |  |  |  |  |  | |
| \*in-river harv. t | in-river harv. t-3 | | IGH ret. t-4 | | NPGO t-3 | 0.45 | 0.36 | 65.65 | 1.54 | 1.1E-01 | |
| in-river harv. t | in-river harv. t-3 | | IGH ret. t-4 | | flow t-3 | 0.44 | 0.35 | 66.31 | 2.2 | 7.8E-02 | |

ret. = returns, harv. = harvest

**Density dependence**

All four taxa showed significant (p < 0.05) negative density dependence between consecutive years (t vs. t+1, in other words, non-delayed density dependence; Figure 3.3). Abundances of Salmon River fall Chinook salmon (r2 = 0.21, p = 0.0096; Table 3.5) were significantly correlated with abundances at t-1 (delayed density dependence), while abundances of summer steelhead trout were significantly correlated with all years analyzed (r2 = 0.24-0.53, p < 0.05; Table 3.5). Neither Salmon River spring Chinook (Table 3.5) nor Scott River fall Chinook salmon (Table 3.5) abundances were significantly correlated to lagged abundances.

|  |  |
| --- | --- |
|  |  |
|  |  |

Figure 3.3. Negative (non-delayed) density dependence of Salmon River spring Chinook salmon (A), Salmon River fall Chinook salmon (B), Salmon River summer steelhead trout (C), and Scott River fall Chinook salmon (D) between years (t) and (t+1). Vertical axis is the difference between abundances of consecutive years (abundance t – abundance t+1). Horizontal axis is abundance at year (t).

Table 3.5. Delayed density dependence as revealed by regressions of Salmon

River spring Chinook salmon, Salmon River fall Chinook salmon, Salmon

River summer steelhead trout, and Scott River fall Chinook salmon

abundances at year (t) and previous consecutive five years (to t-5).

Regressions statistically significant at α = 0.05 are in bold.

|  |  |  |  |
| --- | --- | --- | --- |
| **Variables** | **slope** | **r2** | **p** |
| Salmon River spring Chinook salmon |  |  |  |
| abundance t v. abundance t-1 | 0.36 | 0.12 | 0.079 |
| abundance t v. abundance t-2 | 0.20 | 0.027 | 0.39 |
| abundance t v. abundance t-3 | -0.085 | 0.0051 | 0.73 |
| abundance t v. abundance t-4 | 0.073 | 0.0046 | 0.74 |
| abundance t v. abundance t-5 | 0.10 | 0.011 | 0.61 |
| Salmon River fall Chinook salmon |  |  |  |
| abundance t v. abundance t-1 | 0.47 | 0.21 | **0.0096** |
| abundance t v. abundance t-2 | 0.027 | 0.00069 | 0.89 |
| abundance t v. abundance t-3 | -0.11 | 0.011 | 0.60 |
| abundance t v. abundance t-4 | -0.17 | 0.031 | 0.38 |
| abundance t v. abundance t-5 | 0.022 | 0.0007 | 0.90 |
| Salmon River summer steelhead trout |  |  |  |
| abundance t v. abundance t-1 | 0.78 | 0.53 | **0.00009** |
| abundance t v. abundance t-2 | 0.83 | 0.53 | **0.00001** |
| abundance t v. abundance t-3 | 0.57 | 0.24 | **0.011** |
| abundance t v. abundance t-4 | 0.62 | 0.34 | **0.0011** |
| Scott River fall Chinook salmon |  |  |  |
| abundance t v. abundance t-1 | 0.26 | 0.069 | 0.16 |
| abundance t v. abundance t-2 | -0.16 | 0.026 | 0.39 |
| abundance t v. abundance t-2 | -0.19 | 0.036 | 0.33 |
| abundance t v. abundance t-2 | -0.16 | 0.031 | 0.38 |
| abundance t v. abundance t-2 | -0.083 | 0.013 | 0.58 |

**Discussion**

Both extrinsic and intrinsic factors appeared to drive abundance trends in Klamath River basin salmonids, and yet, the type of variables and the timing of the effects differed among taxa. This suggests that drivers of temporal change differ by both life-history taxon and location (Table 3.7). Salmon River spring Chinook salmon abundances were significantly correlated to four population (ocean harvest t-2; in-river harvest t; hatchery returns t, t-3) and two climate (MEI t-5, PDO t-5) explanatory variables. Salmon River fall Chinook salmon abundance was significantly correlated to two habitat (ERA t, snow t-5), four climate (MEI t-4; NPGO t-3, t-4, t-5), and two population (IGH returns t-4, t-5) variables. Salmon River summer steelhead trout abundance was significantly correlated to 10 population (ocean harvest t, t-2, t-3; in-river harvest t; IGH releases t, t-2; IGH returns t, t-2, t-3, t-4), three habitat (ERA t-2, t-3, t-4), and two climate (MEI t-3, PDO t-3) variables. Lastly, Scott River fall Chinook salmon abundance was significantly correlated to four population (in-river harvest t, t-3; IGH returns t-4, t-5), one climate (NPGO t-3), and one habitat (flow t-3) variable. These correlations underscore the complexity of factors determining Pacific salmon abundances. A part of this complexity comes from time lags. The results from univariate correlations allowed us to investigate the relationship between abundances and drivers that would otherwise be masked by the GLM process. Specifically, when time lags are considered there are too many possible explanatory variables and these are multicollinear, so we would have had to consider hundreds (or even more) alternative GLMs and over-fitting of models would have been likely. The use of lagged variables is important for shedding light on the magnitude of effects that variables can have on individual cohorts. For example, a significant correlation between spring Chinook abundance and ocean harvest t-2 was interpreted to mean that individuals spawning in the same year (ages 2-5) felt the effects of ocean harvest differently. Age 2 and 3 fishes in streams (escapement) likely only experienced negative impacts from ocean harvest once in their life (age – 2) because of shorter ocean residency, while age 4 and 5 fishes may have experienced negative impacts from ocean harvest twice at ages 2 and 4, and 3 and 5, respectively. Therefore, effects from variables with lags less than the age of maturity (age 5 for Chinook, age 4 for steelhead) may signal cumulative impacts to the same breeding population.

Our results challenge the notion that abundances of taxa with extended stream rearing (spring Chinook salmon, summer steelhead trout) are primarily influenced by fresh-water habitat conditions. For Salmon River spring Chinook, ocean harvest t-2 was linked to decreases (slope = -0.32; Table 3.7) in abundance while the other variables (in-river harvest t; IGH hatchery returns t, t-3; MEI t-5; PDO t-5) were linked to increases. Salmon River spring Chinook were the only taxa with a significant negative correlation to ocean harvest, suggesting that harvest practices may be disproportionally affecting this taxon. The positive correlation between in-river harvest t and abundance suggests that spawning habitat is limited in the Salmon River drainage. In-river harvest may relax competition for spawning habitat which likely benefits spring Chinook; spring Chinook spawn before fall Chinook and may therefore be at greater risk of egg mortality due to redd superimposition in areas where spawning areas overlap. Increases in abundances may also result from supplementation by hatchery strays as reflected in significant correlations between abundance and hatchery returns at t and t-3. We assumed that the fraction of hatchery strays spawning in-rivers would increase with increasing hatchery returns. The relationships between abundance (at time t) and MEI t-5 or PDO t-5 are trickier to interpret. Positive values of MEI and PDO represent ocean conditions, such as warm sea surface temperatures, that have been shown to decrease salmonid survival (Mantua et al. 1997, Hare et al. 1999, Mote et al. 2003, Peterson et al. 2003). However, El Niño conditions also cause changes to inland hydrology that alter timing of juvenile outmigration through earlier and larger spring flows (Mote et al. 2003). Earlier outmigration may enhance survival if juveniles can avoid unsuitable fresh water conditions created by El Niño events, such as lower base flows; this may explain the lagged positive correlation between abundance and MEI. It is also possible that the positive relationship is not reflective of a response to ocean conditions but rather a shift in habitat use from, for example, marine to estuarine habitats. Nevertheless, Salmon River spring Chinook abundances seem to be largely driven by events in the marine environment, contrary to our initial hypothesis, because ocean harvest t-2 and MEI t-5 were the sole components of the preferred GLM (Table 3.6).

Table 3.6. Preferred generalized linear models (GLMs) of factors influencing

abundances (escapement) of Salmon River spring Chinook salmon, Salmon River fall

Chinook salmon, Salmon River summer steelhead trout, and Scott River fall Chinook

Salmon, 1968-2009.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Variable(s)** |  | **r2** | **adj. r2** | **AICc** | ***wi*** |
| Salmon River spring Chinook salmon |  |  |  |  |  |
| ocean harvest t-2 | MEI t-5 | 0.43 | 0.37 | 65.48 | 2.3E-01 |
|  |  |  |  |  |  |
| Salmon River fall Chinook salmon |  |  |  |  |  |
| IGH returns t-5 | snow t-5 | 0.43 | 0.36 | 43.74 | 6.4E-01 |
|  |  |  |  |  |  |
| Salmon River summer steelhead |  |  |  |  |  |
| (Chinook) ocean harvest t | IGH returns t | 0.75 | 0.73 | 49.41 | 9.8E-01 |
|  |  |  |  |  |  |
| Scott River fall Chinook salmon |  |  |  |  |  |
| in-river harvest t-3 |  | 0.27 | 0.24 | 65.11 | 1.4E-01 |

Our results also challenge the notion that abundances of fall Chinook salmon, the target of commercial fisheries, are primarily influenced by harvest rates. Salmon River fall Chinook abundances seemed to be driven by events in fresh water, mainly IGH hatchery returns t-5 and snow depth t-5 (Table 3.6). However, abundances were also significantly correlated to ERA t, MEI t-4, NPGO t-3 thru 5, and IGH hatchery returns t-4 and t-5 (Table 3.7). The positive correlation between ERA t (slope = 292.53) and abundance would suggest that more watershed disturbance is better. This would only be the case if the disturbance regime (e.g., frequency, duration, magnitude) was within the historical template under which salmon evolved (Waples et al. 2009). Because the Salmon River is relatively pristine, this relationship may be a reflection of disturbances resulting in habitat improvement (e.g., spawning gravel recruitment) rather than degradation. As with Salmon River spring Chinook, the significant correlations between abundance and ocean conditions (MEI, NPGO) were unexpected. Abundances were positively correlated to MEI t-4 and negatively correlated to NPGO t-3, t-4 and t-5. As stated above, positive MEI values represent ocean conditions known to decrease salmonid survival. Values of NPGO represent ocean conditions in the opposite manner; positive values represent favorable conditions while negative values do not (Peterson et al. 2010). Due to the time lags involved, correlations between abundance and MEI and NPGO both suggest that Salmon River fall Chinook juveniles benefit from warmer, less productive ocean conditions, at least initially during May and June. Again, this relationship may reflect a shift in habitat use rather than enhanced survival in hostile ocean conditions. Juveniles may also benefit from lower April 1 snow depth (slope = -6.01, Table 3.7) if high spring flows increased mortality through the displacement of juveniles from suitable habitats ([Lytle and Poff 2004](#_ENREF_54)). Hatchery strays (IGH returns t-4: slope =-0.045; IGH returns t-5: slope = -0.049), in this case, appear to negatively impact abundance. Interbreeding between hatchery and wild conspecifics can reduce the fitness ([Araki et al. 2009](#_ENREF_3)) and resiliency ([Levin et al. 2001](#_ENREF_50), [Lynch and O'Hely 2001](#_ENREF_53), [Moore et al. 2010](#_ENREF_64)) of the population as a whole so that a reduction in abundance over the long-term could be expected.

A comparison among taxa suggests that the number of variables acting on abundance increases with increasing life history complexity. Salmon River summer steelhead trout, the taxa with the most complex life history, had the most drivers (15) acting on abundance of the four taxa (Table 3.7). However, trends seem to be primarily driven by Chinook ocean harvest t and IGH returns t (Table 3.6). Abundance was positively correlated to Chinook ocean harvest (t: slope = 0.53, t-2: slope = 0.43, t-3: slope = 0.34), IGH returns (presumably a measure of strays) (t: slope = 0.90, t-2: slope = 0.87, t-3: slope = 0.77, t-4: slope = 0.64), and IGH releases (t: slope = 53552, t-2: slope = 36489) at multiple years. Removal of Chinook adults by ocean harvest may relax competition between adult spring Chinook and summer steelhead in the summer. Both spring Chinook and summer steelhead are reproductively immature when they enter rivers ([Moyle 2002](#_ENREF_66)) and need cold pools to reside in during the summer months ([Moyle et al. 2008](#_ENREF_67)). However, Salmon River has a limited amount of cold pool habitat (Elder et al. 2002) so spring Chinook and summer steelhead may have to directly compete for their use. Exclusion of summer steelhead from pool habitat by larger and more abundant spring Chinook could result in decreases in egg survival due to increased exposure to warm temperatures ([McCullough 1999](#_ENREF_61)). This hypothesis is further supported by the positive relationship between Chinook in-river harvest at time t and summer steelhead abundance. As with Salmon River spring Chinook, a positive relationship between abundance and IGH returns may signal supplementation by hatchery strays. On the other hand, the positive relationship between abundance and IGH releases may reflect an increase in foraging opportunities for adults prior to spawning migrations. Steelhead adults in the Pacific Ocean feed primarily on squid and fish ([Burgner et al. 1992](#_ENREF_15)) and large groups of juvenile Chinook salmon, newly released from hatcheries, could offer a concentrated source of prey. The multiple correlations to lagged ERA (t-2: slope = -175.8; t-3: slope = -225.4, t-4: slope = -208.1) suggest that watershed disturbance in this case has amplified negative effects on abundance. Steelhead spend more time in fresh water than other Klamath River salmonids ([Busby et al. 1994](#_ENREF_16)) so watershed disturbance, especially activities resulting in high water temperatures, may have a strong influence on abundance. Correlations between abundance and ocean conditions, as expected, fit the critical period hypothesis ([Beamish and Mahnken 2001](#_ENREF_7)) ; warmer water (MEI t-3: slope = -0.30; PDO t-3:slope = -0.30) would be expected to reduce abundance due to increased mortality at time of juvenile ocean entry. Steelhead juveniles may be less able to shift habitat use if they are displaced or outcompeted by Chinook already present in the estuary. The Klamath River estuary is small compared to other Pacific coast estuaries, providing less rearing habitat to out-migrating salmonids ([Wallace and Collins 1997](#_ENREF_99), [Hiner 2008](#_ENREF_41)).

Although some variables are not easily controlled by resource management, the impacts of some (e.g., flow, harvest, hatchery releases/returns) can be directly alleviated by changes to current practices. Scott River fall Chinook salmon abundance was significantly correlated to four variables (Table 3.7), but only one (in-river harvest t-3) appears to drive trends in abundance (Table 3.6). As with Salmon River spring Chinook and summer steelhead, a positive correlation to in-river harvest t (slope = 10772) may signal a relaxation of competition for limited holding and/or spawning habitat. High loads of fine sediment (< 4mm) currently limit the availability of gravel beds suitable (< 20% fine sediment) for redd building in the Scott River ([NCRWQCB 2005b](#_ENREF_75)). However, in-stream harvest also had a delayed (t-3) negative impact on abundance so that benefits felt from river harvest at time t are of short duration. Like their Salmon River counterparts, Scott River fall Chinook seems to benefit from less productive ocean conditions (NPGO t-3: slope = -0.58) in May and June. We propose that this relationship reflects a shift in habitat use but recognize that other mechanisms may be at work (e.g., delayed ocean entry, reduction in predation and competition). Also like Salmon River fall Chinook, hatchery supplementation appears to have a delayed negative impact over multiple years (IGH returns t-4: slope = -0.05, IGH returns t-5: slope = -0.04). Finally, Scott River fall Chinook was the only taxon with a significant correlation to flow (t-3: slope = 0.53). The positive relationship suggests that abundance would benefit from increases in summer flows. In the Scott River, adequate instream habitat for rearing and spawning is not always achieved during low water years (e.g., 2009) because of increases in agricultural irrigation, especially in late summer ([Van Kirk and Naman 2008](#_ENREF_98)). Consequently, water use may have a negative impact on fall Chinook production.

Population abundance was strongly regulated by negative density dependence. Negative density dependence limits growth of a population by bringing it back into equilibrium with the carrying capacity of the habitat (e.g., spawning grounds). It also reflects the ability of a population to rebuild itself when carrying capacity has not been met. Salmon River fall Chinook abundance at time t was positively correlated to abundance at t-1 (slope = 0.47), likely as a result of spawning populations made up of individuals from overlapping brood classes. Correlations between abundances in subsequent years likely reflect the overlap of brood years in consecutive spawning populations due to the range of age at maturity in Chinook salmon. Steelhead life history overlaps age of maturity between spawning populations as well as rearing (fresh water residency) and migration (anadromous vs. resident forms) strategies. Consequently, Salmon River summer steelhead abundance at time t had significant correlations to abundances in all years analyzed.

Different, and often multiple, factors influence different life histories within and between locations. Therefore, resource managers need to address factors impacting taxa with specific life histories if distinctive life history patterns are to be preserved. Management actions may not be easily applied because the same factor (e.g in-river harvest) may have negative and positive linkages to the abundances of species with different life histories in different years. However, we make several general recommendations to preserve the diverse salmonids in the Klamath basin. Ocean harvest practices should be modified so that Salmon River spring Chinook salmon are not disproportionally affected. Spring and fall Chinook use different marine habitats ([Myers et al. 1998a](#_ENREF_68)) so better understanding of their migration patterns should prove helpful in reducing impacts from harvest on the imperiled spring Chinook. Salmon River fall Chinook salmon should benefit from a reduction in hatchery-produced fishes that compete for spawning and rearing habitats or reduce fitness overall. Salmon River summer steelhead trout likely would benefit from improvement in watershed condition. Because ERA is a measure linked to channel altering flows, steelhead may need more velocity refuges (e.g., floodplain habitat, deeper pools, large wood) to boost productivity. Scott River fall Chinook salmon likely would benefit from a decrease in interactions with hatchery-produced salmonids, increases in summer flows, and changes to in-river harvest. However, mitigation of in-river harvest is complicated by its seemingly positive impact on Salmon River spring Chinook, Salmon River summer steelhead, and Scott River fall Chinook life histories at time of spawning (t). Our conclusion is that these life history forms express a positive correlation with in-river harvest because spawning habitat is limiting production of juveniles. Therefore, restoration of spawning habitat may be crucial to preservation of these taxa. We also caution that, although hatchery supplementation seems to be increasing abundances of Salmon River spring Chinook salmon and summer steelhead trout, interbreeding between hatchery and wild conspecifics can increase the probability of population collapse over the long term. Interbreeding between hatchery and wild conspecifics can homogenize the genetic and phenotypic diversity of these populations, making them more vulnerable to changing environmental conditions ([Kostow 2009](#_ENREF_46), [Lindley et al. 2009](#_ENREF_52), [Moore et al. 2010](#_ENREF_64)).

We did not address climate factors (e.g., ocean conditions) in our recommendations because they are mostly beyond the influence of resource managers. A possible exception is that researchers have suggested that the carrying capacity of the Pacific Ocean for salmonids may be exceeded in years with unfavorable conditions (e.g., El Niño, negative PDO and NPGO)([Ishida et al. 1993](#_ENREF_43), [Beamish et al. 1997](#_ENREF_8), [Kaeriyama 2004](#_ENREF_45)). One way to mitigate for decreased survival in unfavorable years would be to decrease hatchery releases ([Beamish et al. 1997](#_ENREF_8)). However, resource managers can use our climate factors to understand potential impacts from climate change. There is growing evidence that the Pacific Ocean will become warmer with patchier prey distribution ([Coronado and Hilborn 1998](#_ENREF_22), [McGowan et al. 1998](#_ENREF_62), [Hays et al. 2005](#_ENREF_38)). As a result, salmonid abundances may decrease overall and distributions shift poleward ([Pierce 2004](#_ENREF_88)). Of the taxa analyzed, Salmon River summer steelhead trout may be the most adversely impacted by worsening ocean conditions. Consequently, restoration of fresh water habitat is imperative in order to boost numbers of juveniles to a level where losses in the marine environment can be sustained (Moyle et al. 2008). Furthermore, if Chinook salmon are delaying ocean entry in years with adverse ocean conditions then estuarine habitat quality and availability will also play an important role in sustaining life history diversity.

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**Appendices**

Table 3.7. Slope, r2, and p values of correlations between salmonid escapement and variables. Superscripts specify species or location

of variable. c = Chinook, s = steelhead, sal = Salmon River, sc = Scott River. For example, c,s IGH releases t specifies that Chinook

salmon or steelhead trout data were used depending on the time series being analyzed. Significant values (p < 0.05) are in bold.

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|  |  | **Salmon River**  **spring Chinook** | | | | | |  | **Salmon River**  **fall Chinook** | | | | |  | **Salmon River**  **summer steelhead** | | |  | **Scott River fall Chinook** | | | | | | | |
|  | slope | | r2 | | p | | slope | | | r2 | | | p | slope | | r2 | p | slope | | r2 | | | | | p | |
| c ocean harvest t | -0.21 | | 0.080 | | 0.17 | | -0.044 | | | 0.0017 | | | 0.84 | 0.53 | | 0.55 | **0.00005** | -0.052 | | | 0.0029 | | | | 0.79 | |
| ocean harvest t-2 | -0.32 | | 0.18 | | **0.041** | | -0.004 | | | 0.00001 | | | 0.98 | 0.43 | | 0.31 | **0.0045** | -0.21 | | 0.046 | | | | | 0.28 | |
| ocean harvest t-3 | -0.21 | | 0.053 | | 0.29 | | 0.10 | | | 0.0088 | | | 0.65 | 0.34 | | 0.18 | **0.043** | -0.078 | | | 0.0062 | | | | 0.70 | |
| ocean harvest t-4 | -0.078 | | 0.0066 | | 0.71 | | 0.23 | | | 0.046 | | | 0.31 | 0.28 | | 0.13 | 0.10 | -0.046 | | | 0.0022 | | | | 0.82 | |
| ocean harvest t-5 | -0.11 | | 0.014 | | 0.61 | | 0.39 | | | 0.13 | | | 0.088 |  | | NA |  | 0.14 | | 0.020 | | | | | 0.51 | |
| c in-river harvest t | 7550.4 | | 0.17 | | **0.026** | | 9418.7 | | | 0.11 | | | 0.057 | 7091 | | 0.16 | **0.032** | 10772 | | 0.17 | | | | | **0.019** | |
| in-river harvest t-2 | -6093.8 | | | 0.083 | 0.14 | | -572.73 | | | | 0.0004 | | 0.92 | 2106.9 | | 0.011 | 0.60 | -8605 | | 0.11 | | | | | 0.076 | |
| in-river harvest t-3 | -7004.3 | | | 0.12 | 0.088 | | -10361 | | | 0.13 | | | 0.057 | -1031 | | 0.0028 | 0.80 | -13668 | | | 0.27 | | | | **0.0046** | |
| in-river harvest t-4 | -6295.1 | | | 0.084 | 0.16 | | -8369 | | | 0.082 | | | 0.14 | -3859 | | 0.033 | 0.38 | -9014 | | 0.12 | | | | | 0.070 | |
| in-river harvest t-5 | -593.87 | | | 0.00083 | | 0.89 | -165.2 | | | 0.00003 | | | 0.98 |  | | NA |  | -2171 | | 0.0068 | | | | | 0.68 | |
| c,s IGH releases t | 950381 | | | 0.12 | 0.053 | | 1252645 | | | | | 0.10 | 0.079 | 53552 | | 0.37 | **0.00061** | 383786 | | | | 0.011 | | | 0.58 | |
| IGH releases t-2 | 91949 | | 0.0013 | | 0.85 | | 691838 | | | | 0.031 | | 0.33 | 36489 | | 0.15 | **0.0497** | -729920 | | | | 0.039 | | | 0.28 | |
| IGH releases t-3 | -251352 | | | 0.011 | 0.59 | | -140547 | | | | 0.0013 | | 0.85 | 36520 | | 0.15 | 0.052 | -1054128 | | | | | | 0.08 | | 0.11 |
| IGH releases t-4 | -282697 | | | 0.013 | 0.54 | | -409033 | | | | 0.011 | | 0.57 | 10244 | | 0.011 | 0.62 | -1011010 | | | | | | 0.07 | | 0.13 |
| IGH releases t-5 | -314286 | | | 0.013 | 0.54 | | -775843 | | | | 0.039 | | 0.28 |  | | NA |  | -450668 | | | | | 0.02 | | 0.51 | |

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| Table 3.7. continued | |  |  |  |  | |  |  |  | |  | |  | |  |  | |  |
| sa,sc ERA t | 17.14 | | 0.0017 | 0.84 | 292.53 | | 0.24 | **0.0052** | -19.30 | | 0.0024 | | 0.81 | | -42.1 | 0.0071 | | 0.64 |
| ERA t-2 | -20.24 | | 0.0025 | 0.82 | 188.12 | | 0.095 | 0.11 | -175.77 | | | 0.18 | **0.034** | | 8.74 | 0.0013 | | 0.86 |
| ERA t-3 | 27.63 | | 0.0047 | 0.75 | 134.62 | | 0.051 | 0.26 | -225.4 | 0.31 | | | **0.005** | | 29.83 | 0.015 | | 0.55 |
| ERA t-4 | 39.96 | | 0.0073 | 0.69 | 63.93 | | 0.012 | 0.60 | -208.1 | 0.26 | | | **0.013** | | 38.97 | 0.025 | | 0.45 |
| ERA t-5 | 66.36 | | 0.019 | 0.54 | 66.92 | | 0.014 | 0.58 |  | NA | | |  | | 20.67 | 0.0068 | | 0.70 |
| MEI t | 0.063 | | 0.0072 | 0.63 | 0.028 | | 0.00062 | 0.89 | -0.13 | 0.033 | | | 0.30 | | 0.015 | 0.00019 | | 0.94 |
| MEI t-2 | 0.16 | | 0.038 | 0.28 | -0.007 | | 0.00004 | 0.97 | -0.13 | 0.029 | | | 0.34 | | 0.087 | 0.0069 | | 0.65 |
| MEI t-3 | 0.23 | | 0.090 | 0.096 | 0.32 | | 0.074 | 0.14 | -0.30 | 0.19 | | | **0.014** | | 0.17 | 0.024 | | 0.40 |
| MEI t-4 | 0.20 | | 0.068 | 0.15 | 0.42 | | 0.12 | **0.0497** | -0.25 | 0.12 | | | 0.058 | | 0.26 | 0.052 | | 0.21 |
| MEI t-5 | 0.35 | | 0.20 | **0.011** | 0.31 | | 0.061 | 0.17 |  | NA | | |  | | 0.31 | 0.071 | | 0.14 |
| PDO t | 0.045 | | 0.0026 | 0.78 | 0.26 | | 0.036 | 0.29 | -0.008 | 0.00009 | | | 0.96 | | 0.19 | 0.021 | | 0.43 |
| PDO t-2 | 0.23 | | 0.070 | 0.14 | 0.044 | | 0.0012 | 0.85 | -0.26 | 0.11 | | | 0.066 | | 0.16 | 0.017 | | 0.48 |
| PDO t-3 | 0.17 | | 0.043 | 0.26 | 0.21 | | 0.024 | 0.40 | -0.30 | 0.17 | | | **0.021** | | 0.33 | 0.069 | | 0.15 |
| PDO t-4 | 0.18 | | 0.044 | 0.25 | 0.32 | | 0.055 | 0.20 | -0.25 | 0.10 | | | 0.083 | | 0.068 | 0.0029 | | 0.77 |
| PDO t-5 | 0.40 | | 0.21 | **0.009** | | 0.34 | 0.062 | 0.17 |  | NA | | |  | | 0.17 | 0.017 | | 0.48 |
| NPGO t | 0.019 | | 0.00042 | 0.91 | -0.063 | | 0.0018 | 0.82 | 0.14 | 0.028 | | | 0.35 | -0.023 | | | 0.0003 | 0.93 |
| NPGO t-2 | -0.16 | | 0.027 | 0.36 | -0.065 | | 0.0018 | 0.82 | 0.20 | 0.052 | | | 0.20 | | -0.34 | 0.053 | | 0.21 |
| NPGO t-3 | -0.053 | | 0.0038 | 0.75 | -0.56 | | 0.13 | **0.039** | 0.18 | 0.052 | | | 0.21 | | -0.58 | 0.16 | | **0.022** |
| NPGO t-4 | -0.071 | | 0.0066 | 0.67 | -0.80 | | 0.27 | **0.0021** | 0.19 | 0.055 | | | 0.21 | | -0.49 | 0.12 | | 0.056 |
| NPGO t-5 | -0.086 | | 0.010 | 0.59 | -0.59 | | 0.15 | **0.027** |  | NA | | |  | | -0.40 | 0.079 | | 0.12 |
| snow t | -4.79 | | 0.17 | 0.063 | -5.88 | | 0.16 | 0.052 | -2.38 | 0.051 | | | 0.32 | | -0.21 | 0.00026 | | 0.94 |
| snow t-2 | 2.60 | | 0.043 | 0.40 | 1.72 | | 0.014 | 0.61 | 0.35 | 0.00075 | | | 0.91 | | 4.11 | 0.091 | | 0.17 |
| snow t-3 | 4.35 | | 0.082 | 0.25 | 2.42 | | 0.028 | 0.47 | 6.65 | 0.11 | | | 0.19 | | 1.27 | 0.0093 | | 0.68 |
| snow t-4 | 4.27 | | 0.10 | 0.21 | -1.59 | | 0.015 | 0.60 | 5.16 | 0.051 | | | 0.39 | | -0.55 | 0.0023 | | 0.84 |
| snow t-5 | -1.43 | | 0.011 | 0.70 | -6.01 | | 0.22 | **0.044** |  | NA | | |  | | -4.38 | 0.14 | | 0.11 |

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| Table 3.7. continued | | | |  |  | | |  | |  | | |  | | |  | | |  | |  | | |  | | |  | |  | |  |
| sa,sc flow t | -0.023 | | | | 0.0022 | | | 0.79 | | -0.072 | | | 0.011 | | | 0.57 | | | -0.13 | | 0.079 | | | 0.11 | | | 0.44 | | 0.10 | | 0.076 |
| flow t-2 | -0.062 | | | | 0.014 | | | 0.51 | | 0.026 | | | 0.0010 | | | 0.86 | | | -0.008 | | 0.00028 | | | 0.93 | | -0.007 | | | | 0.0003 | 0.98 |
| flow t-3 | -0.021 | | | | 0.0017 | | | 0.82 | | 0.21 | | | 0.063 | | | 0.17 | | | 0.065 | | 0.020 | | | 0.44 | | | 0.53 | | 0.15 | | **0.031** |
| flow t-4 | 0.15 | | | | 0.082 | | | 0.12 | | 0.18 | | | 0.047 | | | 0.23 | | | 0.052 | | 0.011 | | | 0.58 | | | 0.40 | | 0.078 | | 0.12 |
| flow t-5 | -0.040 | | | | 0.0062 | | | 0.69 | | 0.021 | | | 0.00064 | | | 0.89 | | |  | | NA | | |  | | -0.039 | | | | 0.0007 | 0.88 |
| c,s IGH returns t | 0.036 | | | | 0.22 | | **0.0057** | | | | 0.035 | | 0.10 | | | 0.078 | | | 0.90 | | 0.62 | | | **0.00001** | | | 0.028 | | 0.073 | | 0.14 |
| IGH returns t-2 | 0.022 | | | | 0.088 | | | 0.094 | | 0.014 | | | 0.017 | | | 0.48 | | | 0.87 | | 0.56 | | | **0.00002** | | | -0.013 | | | 0.016 | 0.49 |
| IGH returns t-3 | 0.027 | | | | 0.15 | | | **0.031** | | -0.007 | | | 0.0039 | | 0.73 | | | 0.77 | | | | 0.44 | | **0.00008** | | | -0.01 | | 0.01 | | 0.58 |
| IGH returns t-4 | 0.016 | | | | 0.051 | | | 0.22 | | -0.045 | | | 0.17 | | | **0.021** | | | 0.64 | | | 0.29 | | **0.0021** | | | -0.045 | | | 0.19 | **0.014** |
| IGH returns t-5 | 0.0017 | | | | 0.00069 | | | 0.89 | | -0.049 | | | 0.18 | | | **0.015** | | |  | | | NA | |  | | | -0.04 | | 0.14 | | **0.036** |
|  | G | | | | 10.51 | | |  | |  | | | G | | | 18.61 | | |  | | | G | | 60.45 | | |  | | G | | 10.51 |
| G crit (df = 1, α=0.05) | |  | 3.8 | | |  | | |  | | |  | |  | | |  | | |  | | |  |  |  | | |  | | | |

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Table 3.8. Correlations of variables significant to spring Chinook salmon escapement (ln),

Salmon River, California.

|  |  |  |
| --- | --- | --- |
| **Variables** | **r2** | **adjusted r2** |
| ocean harvest t-2 x in-river harvest t | 0.0026 | -0.037 |
| ocean harvest t-2 x MEI t-5 | 0.0012 | -0.039 |
| ocean harvest t-2 x PDO t-5 | 0.000038 | -0.040 |
| ocean harvest t-2 x IGH returns t | 0.30 | 0.27 |
| in-river harvest t x MEI t-5 | 0.099 | 0.069 |
| in-river harvest t x PDO t-5 | 0.00023 | -0.033 |
| in-river harvest x IGH returns t | 0.057 | 0.025 |
| MEI t-5 x PDO t-5 | 0.27 | 0.25 |
| MEI t-5 x IGH returns t | 0.13 | 0.11 |
| PDO t-5 x IGH returns t | 0.18 | 0.15 |

Table 3.9. Correlations of variables significant to fall Chinook salmon escapement (ln),

Salmon River, California.

|  |  |  |
| --- | --- | --- |
| **Variables** | **r2** | **adjusted r2** |
| ERA t x NPGO t-4 | 0.089 | 0.057 |
| ERA t x snow t-5 | 0.21 | 0.16 |
| ERA t x IGH returns t-4 | 0.022 | -0.013 |
| ERA t x IGH returns t-5 | 0.018 | -0.017 |
| NPGO t-4 x snow t-5 | 0.12 | 0.066 |
| NPGO t-4 x IGH returns t-4 | 0.10 | 0.075 |
| NPGO t-4 x IGH returns t-5 | 0.13 | 0.10 |
| snow t-5 x IGH returns t-4 | 0.29 | 0.25 |
| snow t-5 x IGH returns t-5 | 0.12 | 0.072 |
| IGH returns t-4 x IGH returns t-5 | 0.37 | 0.36 |

Table 3.10. Correlations of variables significant to summer steelhead trout escapement (ln),

Salmon River, California.

|  |  |  |
| --- | --- | --- |
| **Variables** | **r2** | **adjusted r2** |
| Chinook ocean harvest t x IGH releases t | 0.50 | 0.48 |
| Chinook ocean harvest t x IGH returns t | 0.47 | 0.45 |
| Chinook ocean harvest t x IGH returns t-2 | 0.76 | 0.75 |
| Chinook ocean harvest t x IGH returns t-3 | 0.53 | 0.52 |
| IGH releases t x IGH returns t | 0.30 | 0.27 |
| IGH releases t x IGH returns t-2 | 0.65 | 0.63 |
| IGH releases t x IGH returns t-3 | 0.49 | 0.47 |
| IGH returns t x IGH returns t-2 | 0.47 | 0.45 |
| IGH returns t x IGH returns t-3 | 0.42 | 0.40 |
| IGH returns t-2 x IGH returns t-3 | 0.63 | 0.62 |

Table 3.11. Correlations of variables significant to fall Chinook salmon escapement (ln),

Scott River, California.

|  |  |  |
| --- | --- | --- |
| **Variables** | **r2** | **adjusted r2** |
| in-river harvest t x in-river harvest t-3 | 0.080 | 0.046 |
| in-river harvest t x NPGO t-3 | 0.008 | -0.025 |
| in-river harvest t x flow t-3 | 0.11 | 0.085 |
| in-river harvest x IGH returns t-4 | 0.018 | -0.015 |
| in-river harvest t-3 x NPGO t-3 | 0.13 | 0.10 |
| in-river harvest t-3 x flow t-3 | 0.081 | 0.047 |
| in-river harvest t-3 x IGH returns t-4 | 0.099 | 0.066 |
| NPGO t-3 x flow t-3 | 0.028 | 0.0017 |
| NPGO t-3 x IGH returns t-4 | 0.12 | 0.10 |
| flow t-3 x IGH returns t-4 | 0.10 | 0.078 |