Module for the Ocean Environment

Prepared for the NOAA Fisheries, Northwest Regional Office

Prepared by the Northwest Fisheries Science Center

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Contents

1. Introduction

This document is the "Module for the Ocean Environment" that has been developed to support integrated recovery plans for four anadromous species that spawn in the Snake River and its tributaries that are listed under the Federal Endangered Species Act (ESA). These species are:

- Snake River spring/summer Chinook salmon (an ESU or Evolutionarily Significant Unit)

- Snake River steelhead (a DPS or Distinct Population Segment)

- Snake River fall Chinook salmon (an ESU)

- Snake River sockeye salmon (an ESU)

Specifics on the listing of each species are provided in the individual recovery plans. The intent of the recovery plans is to identify recovery actions that will restore viability of the species, identify key information needs, define an adaptive management strategy for the plan, and describe plan implementation. In support of these recovery plans, several modules have been developed that present detailed and specific information on a particular subject to inform recovery planning (NMFS 2008; NMFS 2011).

The purpose of this Module is to use the latest science to:

1. Synthesize what we know about how each of the four listed species uses ocean ecosystems.

2. Identify major uncertainties regarding their use of the ocean environment

3. Define the role of the ocean in recovery planning and implementation of each species.

The document is organized in ten sections. Following the introduction (section one), section two discusses why the ocean should be part of recovery planning while section three provides a general description of the estuary/ocean environments salmonids occupy. Section four presents a description of the ocean life history of each listed species and section five presents a description of the ecology of the listed stocks in the estuary and ocean (e.g., growth and predator-prey interactions). Section six discusses risks to the salmon during their ocean life, including climate change; the seventh section presents key information needs. The final three sections describe recovery strategies involving the ocean, adaptive management, and implementation, respectively.

2. Why Include the Ocean as Part of Recovery Planning and Implementation

The ocean should be a part of recovery planning and implementation for listed Snake River anadromous species. In the mid-1990s, the Northwest Power and Conservation Council recognized the need to include the ocean environment in the management of Columbia River Basin salmonids. They adopted an approach to directly obtain explicit, quantitative information on marine recruitment success that could be used by salmon managers. Importantly they extended the definition of the Columbia River basin to include the North Pacific Ocean as "a geographic unit (of the Columbia River basin)" and that this "unit" should be considered in research, monitoring, and evaluation actions.

There are a number of compelling reasons why the ocean should be included in recovery planning for the listed Snake River ESUs. First, it has become increasingly clear that ocean mortality of salmon can be very high (> 95% depending on population- Bradford 1995) and highly variable. Further, variability in marine ecosystem productivity can drive much of the variability in adult salmon returns (Pearcy 1992; Welch et al. 2000; Peterson and Schwing 2003; Scheuerell and Williams 2005; Petrosky and Schaller 2010; Haeseker et al. 2012; Thomson et al. 2012; Burke et al. 2013a). For example, for Snake River yearling hatchery spring Chinook salmon, tidal freshwater/estuary/plume/ocean survival is highly correlated with the overall SAR (smolt-to-adult ratio) but not with in-river survival from outmigration year 2000 to 2009 (Figure 1). It is noteworthy for this yearling group of Chinook salmon that in-river survival varied by approximately 2.5-fold while ocean survival varied by about 25-fold. Another example of the importance of ocean conditions to the survival of Columbia River basin salmonids is provided by Williams et al. (2014) who found that changes in ocean conditions in the Northern California Current appeared to have a strong influence on variability in SARs of Columbia River sockeye salmon.
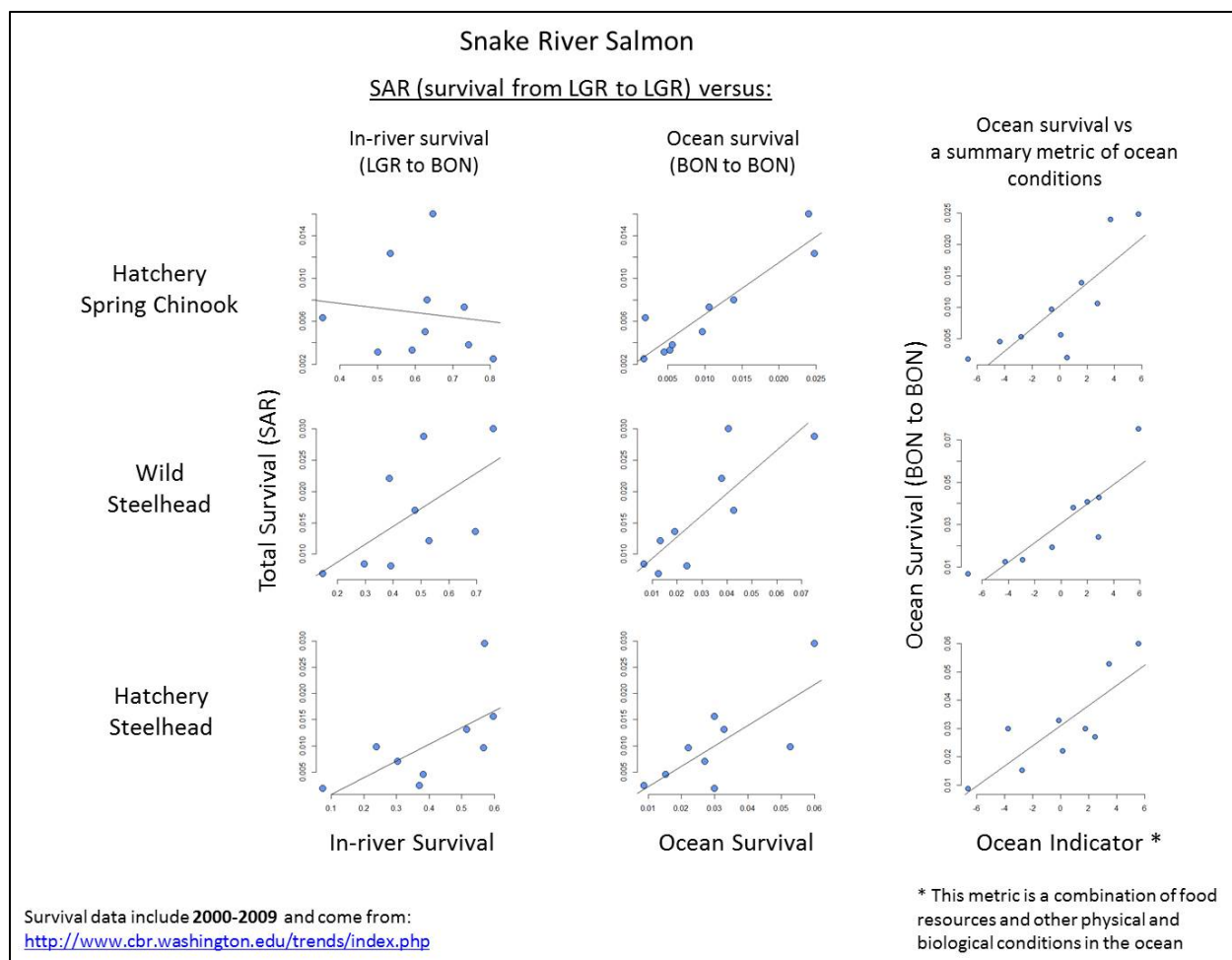
Figure 1. Smolt-to-adult survival information for several groups of Snake River salmonids during several time periods in their life histories.

Although the ocean is clearly a major driver of salmon productivity, we want to emphasize that freshwater life stages such as egg incubation or overwintering by juveniles are very important in overall productivity of salmon and steelhead (Beechie et al. 2003). One of the lessons of 100+ years of anadromous salmonid research and management is that anadromous salmon are a life cycle animal that depend on a set of inter-connected habitats that differ considerably in their characteristics (e.g., ocean vs. spawning streams) (NRC 1996). Thus, all life stages of salmon are important and cannot be discounted in recovery efforts (Bisbal and McConnaha 1998; Beechie et al. 2003; Good et al. 2007).

A second reason why the ocean should be considered in recovery planning is that the effects of variability in ocean productivity can mask, enhance, or even override underlying trends in freshwater habitat productivity and lead to a misinterpretation of the proximate causes of variability in survival or adult returns. As the ISRP stated in its review of the Ocean Synthesis report (ISRP 2012), "[t]he effectiveness of restoration as estimated from adult returns must account for all sources of mortality, including ocean mortality. Ideally, this partitioning will be accomplished for wild and hatchery stocks, in-river vs. barged, individual ESUs, and different

life histories to help determine in-river, estuarine, or ocean responses to the 4-Hs." In their 2009 Fish and Wildlife Program, the Council noted (page 31) that "……accurate monitoring and evaluation of inland efforts depends on the ability to isolate the effects of the ocean from the effects of inland actions. Without the ability to distinguish ocean effects from other effects, the Council may be tempted to correlate large salmon returns with successful mitigation practices. Likewise, poor returns of adult fish may lead the Council to abandon mitigation actions that are highly beneficial but which are overshadowed by the effects of poor ocean conditions unless the Council can determine the poor returns are in spite of, and not because of, the mitigation actions." The National Research Council (NRC 1996- page 3) also identified the potential masking effect of ocean conditions in their evaluation of the plight of anadromous salmon - "Variations in ocean conditions—especially in water temperature and currents and the associated biological communities—also contribute to the rise and fall of salmon abundance, often thwarting the interpretation of events in freshwater and surrounding terrestrial systems."

A third reason to include the ocean in recovery efforts is because there are strong atmospheric, oceanographic, and biological connections between freshwater, the estuary and the ocean. Examples of these connections are numerous. Physical connectivity includes tidal action that can push saltwater well upstream and change salinity regimes in the estuary as well as freshwater discharged into the Pacific Ocean that creates the plume environment (Horner-Devine et al. 2009). The influence of the plume is not strictly local and limited to the area near the mouth of the Columbia River but extends over broad areas off the Washington and Oregon Coasts (Hickey 1989). Another example of physical connectivity is climate-induced changes to precipitation patterns can alter the proportion of freshwater that enters the Columbia River via snow-pack vs rainfall. This change in water supply can affect what is discharged into the ocean which may change the physics and ecology of the coastal ocean environment.

Freshwater, estuary, and ocean ecosystems are also connected biologically. One example is the transport of nutrients from the ocean back to freshwater by spawning adults (NRC 1996). In addition, humans both directly and indirectly affect the performance of salmonids while they are at sea (Bisbal and McConnaha 1998). For instance, management actions in freshwater have the ability to effect fish size, timing of ocean entry, density of salmonids in the estuary and ocean, and condition of the fish which can affect growth and survival of the salmonids during later life stages (Scheuerell et al. 2009; Tomaro et al. 2012). For example, mean body size at ocean entry and early marine growth in yearling Chinook salmon are positively correlated with adult returns (Claiborne et al. 2011), body condition of sub-yearling Chinook salmon is correlated with adult returns (Miller et al. 2013), and time and size at which salmon are released from hatcheries can affect adult return rates (Bilton et al. 1982).

3. Ocean Environments and Salmon: An Overview

For purposes of this Ocean Module, we have divided the ocean environments used by salmon into the following major ecosystems: Columbia River estuary, Columbia River plume, Northern California Current, and Pacific Ocean (including the Gulf of Alaska and Bering Sea) (Figure 2). We do not include waters south of the Oregon/California border because so few Columbia River fish are found in this area. In addition, although there are species specific patterns of vertical distribution of salmon in the water column, we have not considered these here and how they may change in different ocean regions (Emmett et al. 2004).

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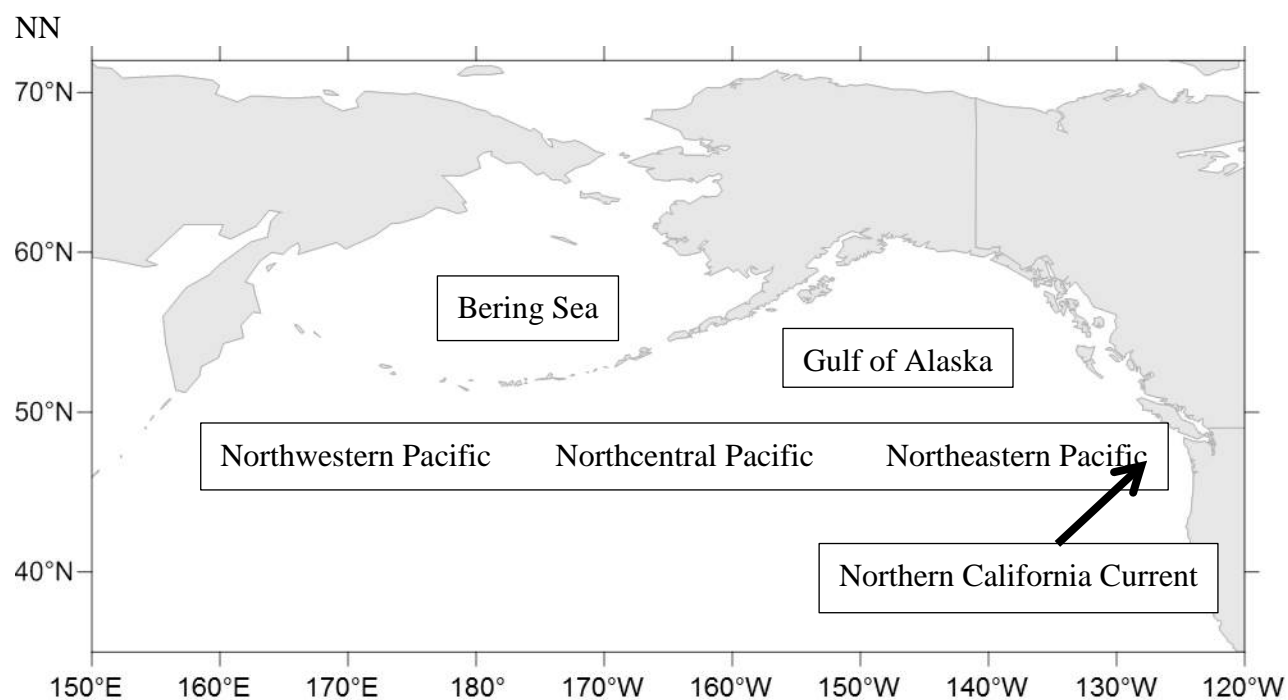
Figure 2. Map of ocean domains over which salmon and steelhead from the Columbia River Basin occur.

3.1 Columbia River Estuary

For the Ocean Module, we have defined the Columbia River estuary based upon tidal conditions. By this definition, the estuary extends 235 km (146 miles) from the river's mouth to the base of Bonneville Dam which is the upstream extent of tidal influence. It also includes tidally influenced portions of its tributary rivers, such as the lower 41 km of the Willamette River, the largest river entering the estuary.

The estuary has been considered separately in an Estuary Module from the perspective of recovery actions. However, we consider **use** of the estuary by the listed ESU's in this Module because how the fish use the estuary and what happens to them in the estuary may have a significant effect on their subsequent survival in the ocean (e.g., Weitkamp et al. In Review). Holsman et al. (2012) found a relationship between the temperature difference between the estuary and ocean that was correlated to survival of Columbia River Chinook salmon; larger temperature differences were associated with lower survival. Scheuerell et al. (2009) reported that timing of ocean entry was related to survival of Columbia River basin Chinook salmon and steelhead, with earlier migrating fish generally performing better that later migrating fish.

3.2 Columbia River Plume

From the estuary, juvenile salmonids enter the Columbia River plume, the zone where recently-discharged freshwater interacts with surrounding ocean water (Horner-Devine et al. 2009). The size, shape, volume and depth of the plume are very dynamic, even over short time scales, and are controlled by the amount of freshwater flowing out of the Columbia River, local winds, tides, and ocean currents (Hickey 1989; Jay and Smith 1990; Horner-Devine et al. 2009). In the absence of upwelling winds, the freshwater from the Columbia River moves north along the coast (Horner-Devine et al. 2009).   The plume can break apart and pieces can be found hundreds of miles from the mouth of the river (Hickey 1989). Figure 3 shows the simulated (modeled) dynamic nature of the plume over a very short time scale, six days in May 2011.
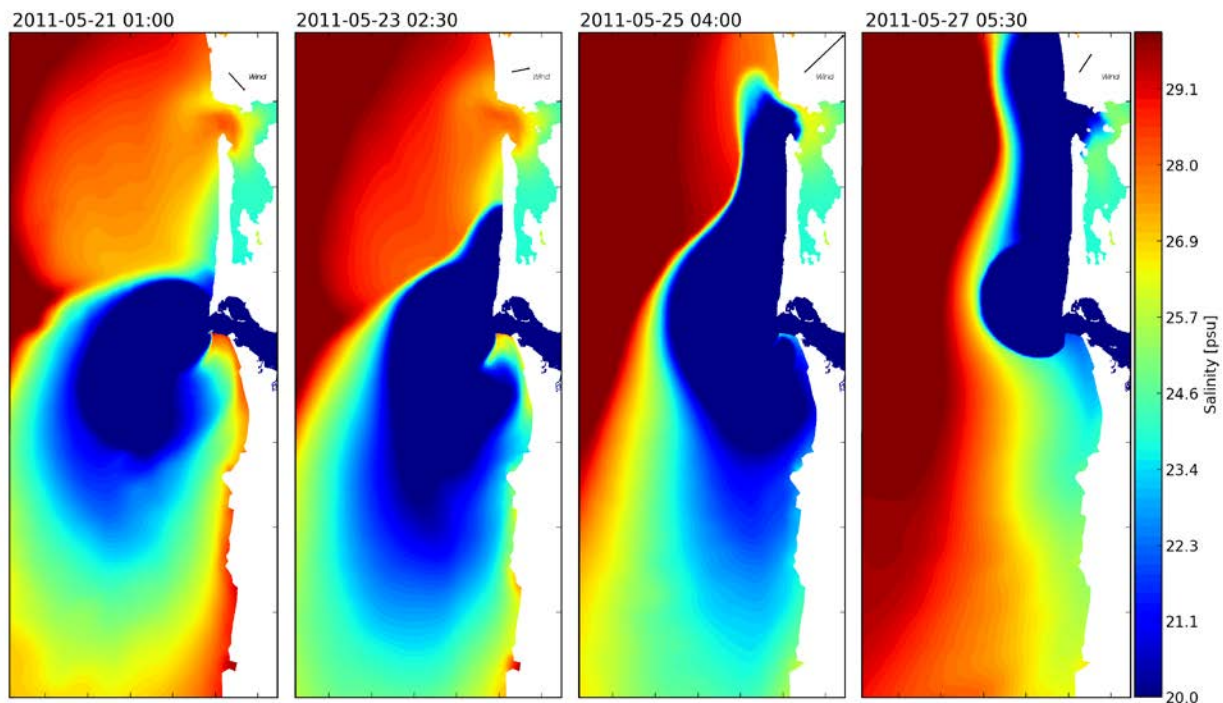
Figure 3. Changes in the location and shape of the Columbia River plume over one week in May 2011. The color scale is salinity with the freshest water in the dark blue.

3.3 Northern California Current

Once salmon leave the plume, they enter the Northern California Current (NCC). The California Current (CC) is an eastern boundary current that flows south along the coasts of Vancouver Island, Washington, Oregon, and California (Figure 4) and ends off southern Baja California. Here, we will refer to the NCC as the portion of the CC that occurs off Oregon, Washington, and Vancouver Island. In winter, southerly winds create "downwelling" conditions that result in transport of water northward and shoreward as the Davidson Current. In summer, northerly winds can transport water southward and offshore, generating "upwelling." It is this upwelling that helps make the coastal branch of the CC periodically cool, nutrient-rich, and highly productive.

A major feature of coastal areas is the continental shelf, which extends from the coastline of the continent out to the "shelf break" where the bathymetry begins to steepen rapidly. The width of the shelf varies considerably along the coast. Off of Washington, for example, the shelf is relatively flat and can be 50-80 km wide while off much of California, the shelf is steep and may be only several km wide.
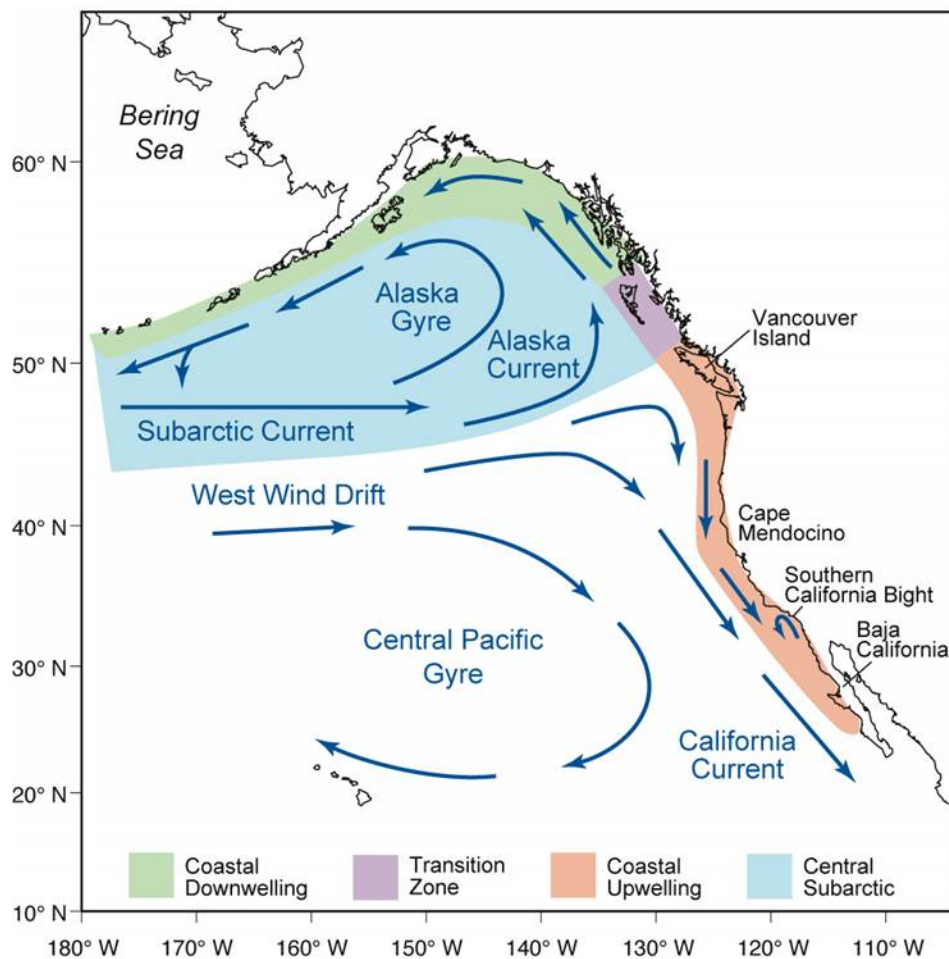
Figure 4. Schematic representation of the major current systems in the Eastern Pacific. These are the major currents salmon from the Columbia River interact with.

3.4 North Pacific Ocean

For the Ocean Module, the North Pacific will be defined as the Pacific Ocean north of approximately 45 N. This region can be loosely subdivided into the Northeastern, North Central, and Northwestern Pacific Ocean regions and the Gulf of Alaska (GOA) (Figure 2). The northern boundaries of each Pacific region are defined by land, while the southern boundaries are imprecise.

3.5. Ocean Conditions and Salmon

We define ocean conditions, in the context of salmon ecology, as that set of factors that affect ocean survival of salmonids. In general, survival in the ocean is a result of bottom up (i.e., food web related) and top down (e.g., predation) biological processes which are controlled by different types of physical/chemical processes (Figure 5). Both physical and biological processes that are important to salmon survival operate at multiple scales of space and time.
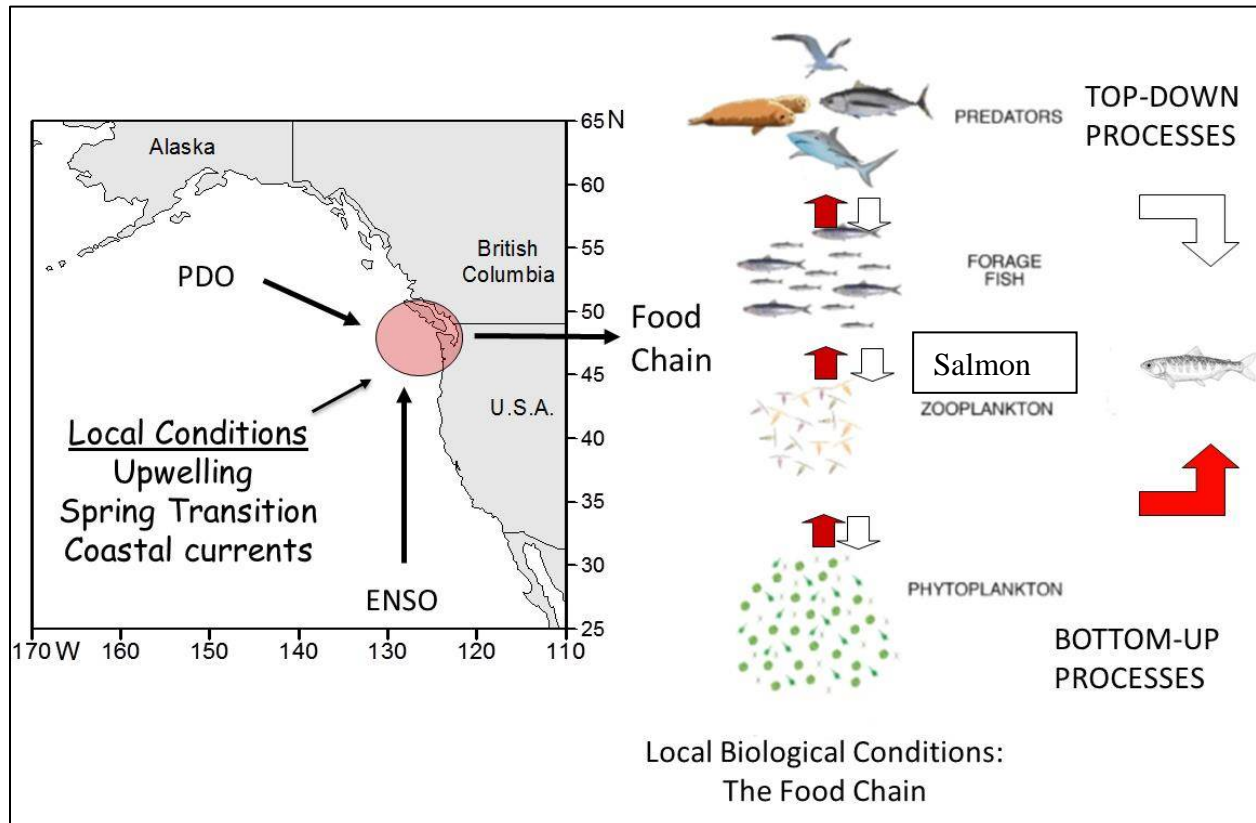
Figure 5. Schematic representation of the inter-relationships of physical and biological processes (both top down and bottom up) that affect salmon survival.

3.5.1 Physical Processes

Physical processes include climate, winds, stratification, current eddies and large-scale circulation that control to varying degrees bottom-up and top-down biological processes. In general, processes operating at larger scales constrain and at least partially regulate processes operating at smaller scales (Figure 5).

At the largest spatial scale is the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997), a very large-scale circulation pattern that results in major shifts in oceanographic conditions such as ocean temperature. The PDO index is calculated based on patterns of variation in sea surface temperature (SST) of the North Pacific Ocean from about 1900 to the present (Mantua et al. 1997). The PDO generally occurs in one of two phases with shifts in the phase of the PDO

linked with changes in salmon production (Beamish et al. 1996; Mantua et al. 1997; Francis et al. 1998; Welch et al. 2000). There is generally a warm phase and a cold phase to the PDO (Figure 6), with shifts between phases caused by changes in wind speed and direction. When winds are predominantly from the north or north-northwest in the Gulf of Alaska in winter, the ocean cools and is said to be in the "cool phase" of the PDO; this is considered to be good for Columbia River salmon (Figure 6). When winds are predominantly from the southwest, the ocean warms and is said to be in the "warm phase" of the PDO and less good for salmon from the Columbia River basin. Shifts between phases historically occurred at a frequency of decades or longer (20-30 years), but in recent years shifts between PDO phases have occurred more frequently (at about five-year intervals) (Figure 7).
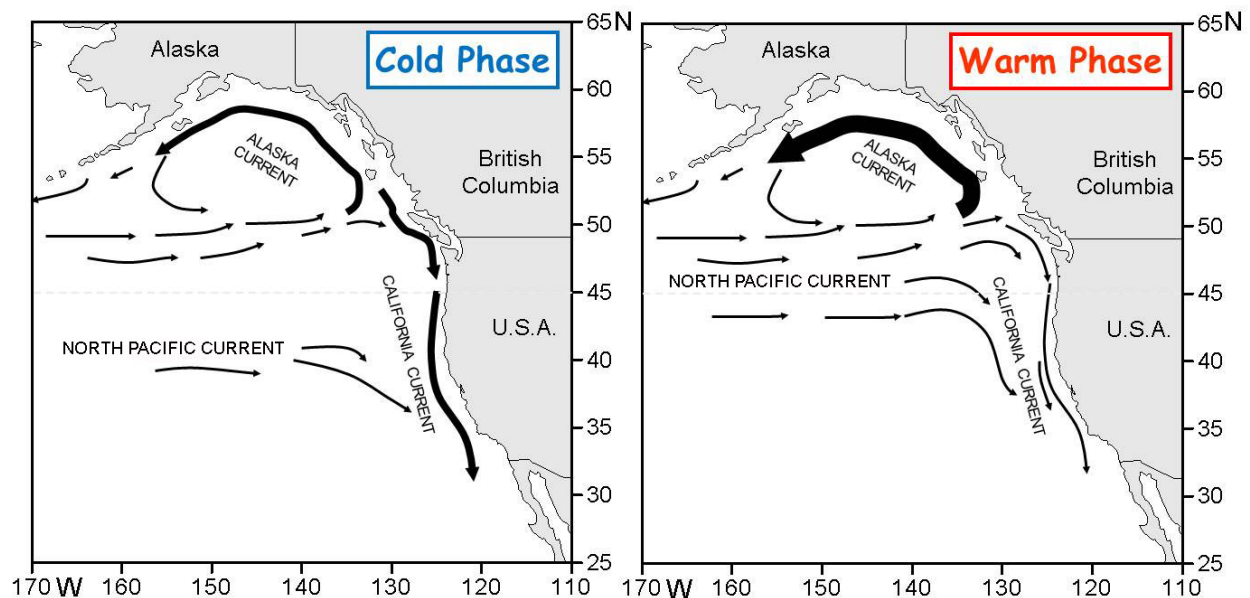
Figure 6. Illustration of how the two major phases of the PDO occur. The cold phase is the good phase for salmon while the warm phase is not as good.

Although the PDO is more-well known within the context of Pacific salmon trends, the North Pacific Gyre Oscillation (NPGO) is another wind driven, large scale circulation process. Recent studies suggest it can account for oceanographic variation not explained by the PDO such as low frequency variability in nutrients, chlorophyll and oxygen (DiLorenzo et al. 2008; Peterson et al. 2013).
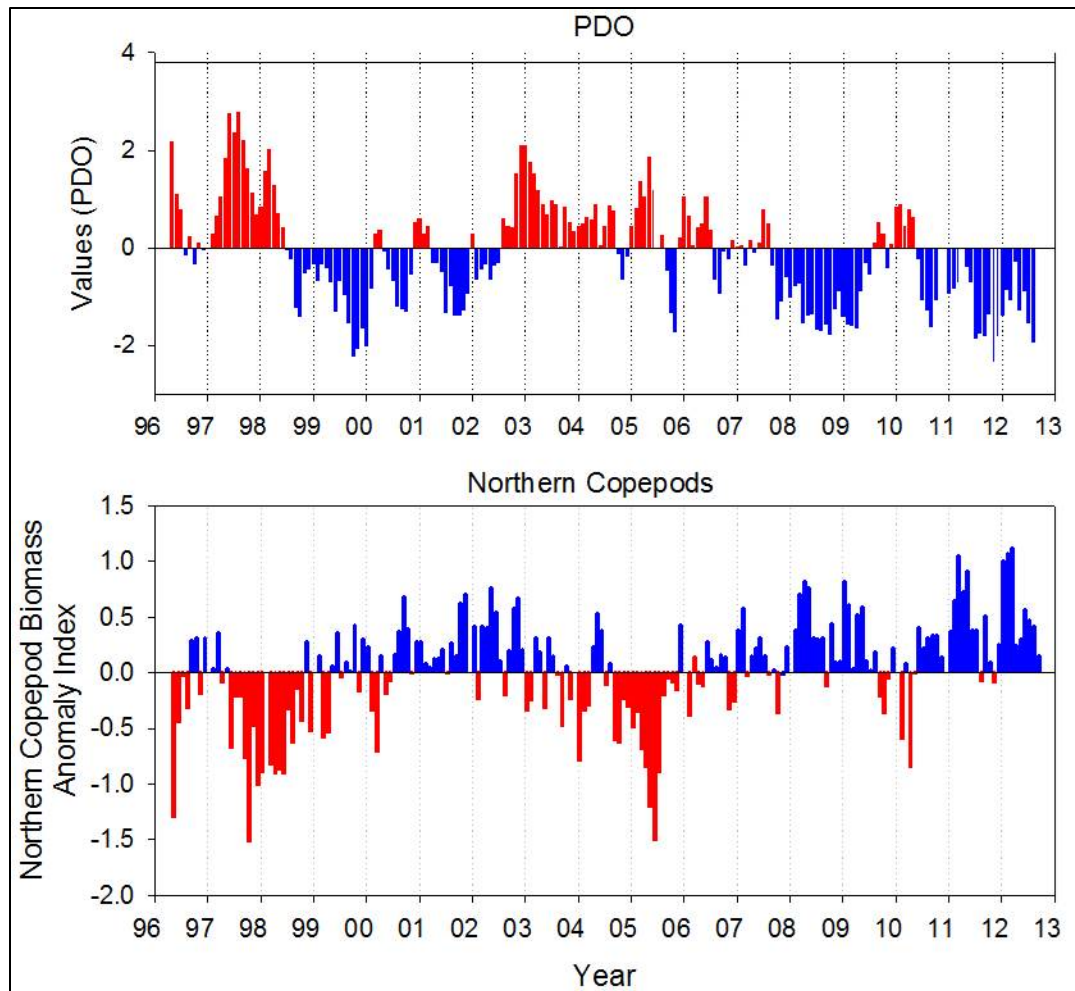
Figure 7. Fluctuations in the PDO index showing the changes from cold phase (blue) to warm phase (red) upper graph and the northern copepod index bottom graph. The upper graph illustrates how shifts between PDO phases are occurring more rapidly now. Blue in the bottom graph represents a more favorable zooplankton community for salmon. (Data Source- Bill Peterson, NWFSC, Newport, Oregon).

At a regional scale and generally operating at seasonal-to-annual temporal scales is wind-driven coastal upwelling (Hsieh et al. 1995; Macias et al. 2012). Upwelling is a dominant physical factor affecting production in coastal waters of the CC. It occurs primarily from April through September when winds blow from the north and transports nutrient rich bottom water into surface waters; this in turn fuels the rapid growth of phytoplankton resulting in high secondary productivity. The ecosystem effects of upwelling are complex, can vary spatially and temporally, depend upon the sign of the PDO, the length of the upwelling season and timing of the upwelling (e.g., Bograd et al. 2009).

Upwelling can be disrupted by El Niño events (Hsieh et al. 1995), the consequences of which are well-known and include significant reductions in biological productivity in this region. El Nino events can result in high mortality of many pelagic fishes, salmon, and seabirds. It is a disruption of the ocean-atmosphere system in the Tropical Pacific that is characterized by

unusually warm ocean temperatures in the Eastern Pacific. The opposite of El Nino events are La Niña's, which are characterized by unusually cold ocean temperatures in the Eastern Pacific. El Niño conditions generally result in warmer and more nutrient poor ocean waters throughout the eastern Pacific, and are considered 'bad' for salmon in the Pacific Northwest (Peterson et al. 2002; DiLorenzo et al. 2010; McPhayden et al. 2010). La Nina events generally produce cooler more nutrient rich water and are generally considered 'good' for salmon from this region. In recent years, the El Niño's of 1983, 1998 and 2010 have been especially strong, but impacts on salmon are also seen in weaker events such as the prolonged series of events in 1992-1996 and 2003-2006.

At smaller spatial and temporal scales (hours to weeks), a number of different physical processes occur. An example of a process occurring at a smaller scale is the Columbia River plume. Physical aspects of the plume such as volume, size and shape, are highly dynamic and can shift daily.

3.5.2. Biological Processes

Bottom up processes
Bottom-up processes are those that provide food to salmon and include both estuary and ocean food webs. In the ocean, large scale shifts in ocean food webs generally occur as a result of shifts between cold and warm phases of the PDO (Keister et al. 2011). During the cold phase of the PDO in the NCC, the amount of cold water transported from the sub-arctic domain relative to warmer waters from the subtropical domain or offshore waters of the central North Pacific Ocean appears to increase. During colder years, more lipid rich zooplankton occur in the NCC ecosystem than during warm years because they are transported south from the sub-arctic (Bi et al. 2011). This means that the food chain leading to salmon has a higher lipid content when "cold ocean conditions" prevail (Hooff and Peterson 2006). This may result in higher quality food, which may be beneficial to the salmon.

Top-Down Processes
In general, top down, biological processes that can potentially affect salmon are predation, parasites and disease. There are a wide variety of fish, birds, and mammals that prey on juvenile and adult salmon and numerous pathogens and parasites that can infect salmon. And, the magnitude of predation mortality by a predator and the effects of a pathogen or parasite are a function of a number of factors (e.g., Fresh 1997). The same large shifts in PDO can affect both predation and parasites/diseases. For example, predation on juvenile salmon by Pacific hake (*Merluccius productus)* varies inter-annually and spatially, suggesting top down control by this species is mediated in part by variation in physical conditions in the NCC.

Competition for food is another controlling biological process but is not truly a top down or bottom up process. Therefore, we have put it into its own category. Competition occurs when resources are limiting which in estuarine and marine systems is food.

4. Estuary/Ocean Life Histories of Listed Snake River Anadromous Species

In this section, we describe the ocean life history of the four listed Snake River ESUs. Our focus here is on defining when fish occur in different ocean ecosystems, where they occur, and how long they may be present in particular regions.

Ideally, we would construct ocean life histories focusing on wild (naturally spawning) fish since that is the focus of conservation and recovery efforts in the Snake River basin. However, our ability to do this is limited. First, naturally spawning fish from Snake River ESUs, especially Snake River sockeye, are at low levels of abundance. Thus, these fish are rare in samples obtained during ocean sampling. Second, there are also technical issues with identifying some Snake River ESUs in any sample of salmon. For example, there has been incomplete baseline information against which to compare unknowns for steelhead (e.g., from ocean caught fish in the NCC). Third, few naturally spawning juveniles are marked or tagged because there are considerable challenges associated with marking or tagging wild juvenile salmon including simply catching the fish to tag them. Conversely, hatchery fish can be more easily obtained and tagged. As a result, most juvenile salmonids that are marked or tagged from the listed Snake River species are the hatchery components of listed ESUs.

Given these limitations in our ability to identify wild Snake River species during their ocean life, surrogates for the wild fish are needed. The use of surrogates in species recovery planning is not without precedent but requires validation (Murphy et al. 2011). There are two possible surrogates for wild fish that can be used. First, hatchery-origin fish from the same ESUs can be used. The use of hatchery-origin fish as surrogates to draw inferences about life history and ecology of wild fish is, however, controversial (e.g., Levings et al. 1986; Fresh 1997; Weitkamp and Neely 2002). Some studies suggest that hatchery-origin and wild salmon have similar performance (e.g., survival), behavior and ecology when such factors as size can be accounted for; under these conditions, hatchery-origin fish could represent reasonable surrogates of wild fish (e.g., Sweeting and Beamish 2009; Weitkamp 2010; Daly et al. 2012; Woodson et al. 2013). Other studies suggest there can be behavioral or survival differences (e.g., differences in survival between hatchery and wild fish within an ESU) that can make use of hatchery fish as surrogates problematic (Buchanan et al. 2012).

A second surrogate for naturally spawning Snake River ESU's are more abundant ESUs from the Columbia River basin with similar life histories to Snake River ESUs. For example, Upper Columbia River summer/fall Chinook salmon can potentially be a surrogate for the Snake River fall Chinook salmon ESU while Upper Columbia River sockeye salmon can inform our understanding of the ocean life history of the Snake River sockeye salmon ESU.

Our discussion of ocean ecology of listed Snake River species will be as specific as possible with respect to species, ESU, and life history type. Life history type is an especially important determinant of many life history features such as habitat use and migration behavior. While

there are many ways salmonids can express life history diversity, we will primarily use how long fish rear in freshwater to distinguish life history types. The term yearling will refer to fish that rear for one or more years in freshwater before migrating to sea while the term sub-yearling will refer to fish that rear for less than a year in freshwater and then migrate to the ocean. Both yearling or sub-yearling life history types can occur within the same ESU (and within a population within an ESU) with the proportion of each life history type varying by species, population, and year (Fresh et al. 2005). Although the differentiation of yearling and sub-yearlings is generally associated with Chinook salmon, other species can express juvenile life history diversity as well. For example, the amount of time sockeye salmon spend in their nursery lake can vary from 1 to 3 years. In addition, while the majority of steelhead migrate to the ocean after rearing in freshwater for two years, some steelhead rear for up to five years in freshwater before migrating to the ocean (Busby et al. 1996).

One other expression of life history diversity that we will use in the Module is when adult fish enter the Columbia River. The words spring, summer, winter or fall associated with a species, ESU, or population refer to when the adult fish enter freshwater to spawn but not when they spawn. For example, spring run Chinook salmon may hold for many months in freshwater before spawning in the fall, despite entering the Columbia River from April to June.

4.1 Snake River Spring/Summer Yearling Chinook Salmon.

The Snake River spring/summer Chinook salmon ESU (abbreviated hereafter as SRSS Chinook salmon) includes all naturally spawning populations of spring/summer Chinook salmon in the mainstem Snake River and in the Tucannon River, Grande Ronde River, Imnaha River, and Salmon River sub-basins. It also includes 15 artificial propagation programs. Most juvenile Chinook salmon in this ESU rear in freshwater for about a year before migrating to sea and so are yearlings at the time they migrate. There are some sub-yearling life history types (i.e., migrating to sea in within their first year following emergence) within this ESU although their contribution to adult returns are unknown (Copeland and Vendetti 2009). In this discussion, we focus only on the yearling life history type.

4.1.1. Estuary

Detections of PIT tags from this ESU passing Bonneville Dam provide a means of estimating when fish enter the estuary. Most PIT tagged yearling SRSS Chinook salmon pass Bonneville Dam from late April through early June with most fish from this ESU passing the dam in a narrow time window that varies little between years. The average date of 50% passage (from 2003 to 2012) through Bonneville Dam was May 18 for all fish (wild fish plus hatchery-origin fish) and May 17 (range May 11 to May 22) for wild fish only (http://www.cbr.washington.edu/http://www.cbr.washington.edu/dart). The mean date for 90% of the fish (combined hatchery and wild) to pass Bonneville Dam was June 6 for these 10 years.

Available evidence suggests that the residence time of most juvenile SRSS Chinook salmon in the estuary is short and on the order of days. Weitkamp et al (2012) and Weitkamp et al. (In Review) estimated that the mean date of passage for hatchery and wild origin fish at the purse seine site at Rkm 15 using a combination of genetics analysis and tag recoveries (both PIT and CWT). Passage time at Rkm 15 was almost identical to the mean date of passage at Bonneville Dam (May 17 and 18, respectively). Based upon detections of PIT tags made in trawl collections at Rkm 70, SRSS Chinook salmon take only 1 to 2 days to migrate the 165 km from Bonneville Dam to this point in the river. McMichael et al. (2013) also reported rapid migration rates in the estuary using acoustically tagged yearling spring Chinook salmon (no stock identification was available, however); they found that most yearling Chinook salmon traveled from Rkm 153 to Rkm 8 in less than two days.

Yearling spring Chinook salmon also appear to spend only a short period of time in the "plume". McMichael et al. (2013) found that most yearling Chinook salmon (68.3%) that were tagged with acoustic transmitters (no stock origin was provided) remained in the vicinity of the river's mouth (defined as the area downstream of Rkm 8 out about 15 km from the river's mouth and north and south about 15 km) for less than a day; the average amount of time spent at the mouth of the river was 2.2 days with fish early in the year (May 5 to 18) tending to spend less time holding in this area (mean=0.7 days) compared to later in the year (mean=3.3 days) (May 19 to July 6). Another study using acoustic tags found that fish remained in the plume for an average of 7 days (Brosnan et al. 2014). This study, however, defined the plume as the Astoria-Megler Bridge (about Rkm 22.0) to nearly the mouth of Willapa Bay.

Because on average, the time spent in the estuary and plume is short, passage date at Bonneville Dam probably provides a reasonable, general estimate of ocean entry timing. Although average time spent in the estuary and plume is short, there is considerable variation in travel times and timing of estuarine and ocean entry among individual fish. For example, residence time at the mouth of river ranged from 0.1 days to 34.7 days for individual acoustically tagged yearling spring Chinook salmon (McMichael et al. 2013). Differences in ocean entry date of days to weeks for individual fish may not be unimportant and could affect their survival in the ocean (Scheuerell et al. 2009; Holsman et al. 2012).

4.1.2. NCC

Once the yearling SRSS Chinook salmon enter the NCC, they can initially disperse in any direction. An acoustic telemetry study by McMichael et al. (2013) found that yearling spring Chinook salmon (stock specific information was not provided) dispersed in all directions from the river mouth with fish early in the spring more likely to be found south of the river's mouth while later in the spring they were more likely to the north. The direction of movement once the fish leave the estuary appears to be a function of season and local environmental conditions including wind and currents (McMichael et al. 2013).

Trawl catches also suggest that yearling Chinook salmon disperse in all directions after ocean entry. In May, yearling Chinook salmon from the Columbia River (origin not known) are found in the coastal ocean off Northern Oregon and Washington, with most fish found off of Washington (Bi et al. 2007, 2008; Yu et al. 2012) (Figure 8a); few Columbia River fish move south of Newport, OR based on trawl catches conducted in this area (Brodeur et al. 2004).
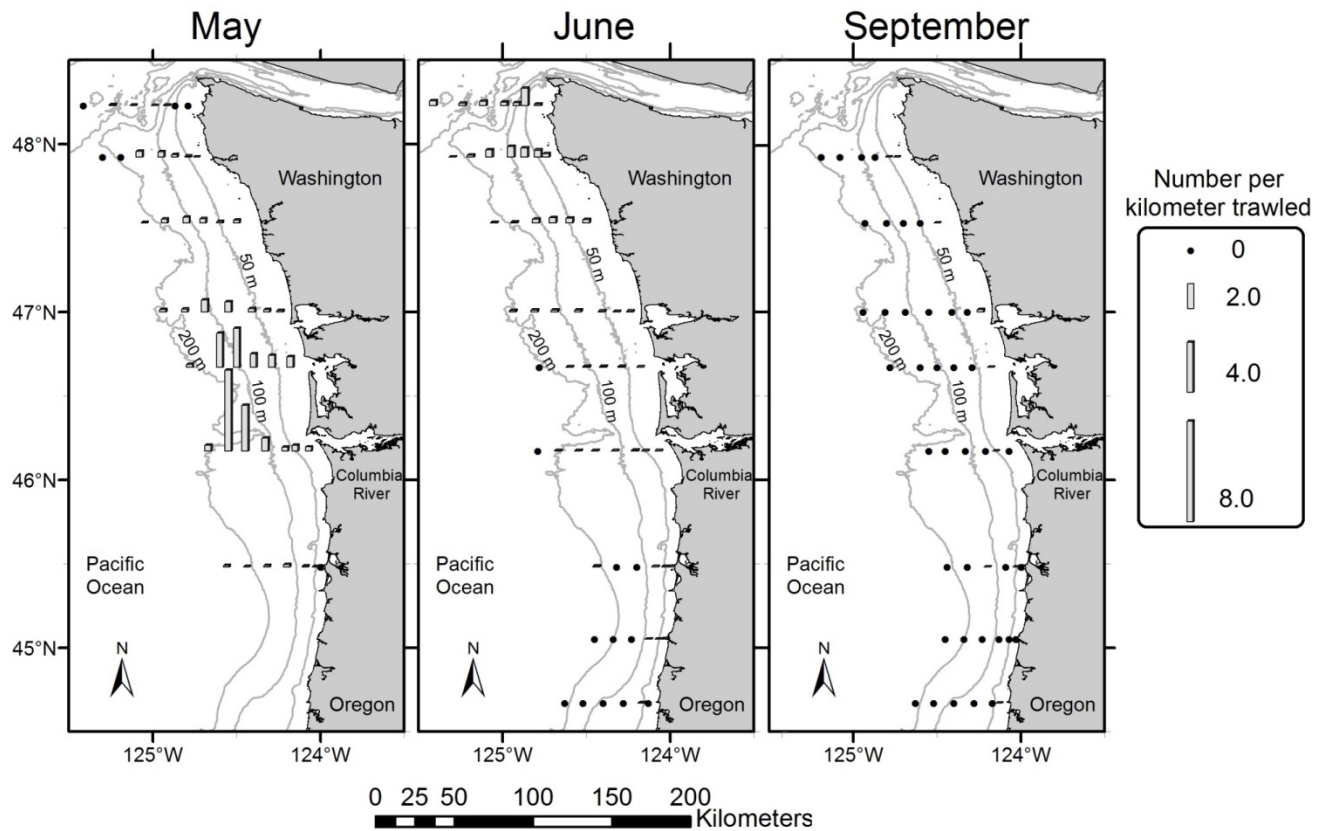
Figure 8a. Average yearling Snake River spring Chinook salmon Catch Per Unit Effort (CPUE) by station at ocean sampling stations for May 2006 – 2012 and June 1998 – 2012. (Jacobson et al. 2012)

Trawl samples collected in the NCC by US and Canadian investigators have found that in May, most yearling SRSS Chinook salmon are found on the Continental Shelf off Washington (Figure 8a. By June-July in the NCC, they are found from Northwest Washington to SE Alaska. During this time period, they occur in low numbers off Washington, and are most abundant off the WCVI and east of the Queen Charlotte Islands (Figure 8a). By September most yearling SRSS Chinook salmon have left the NCC.

It is clear from results of trawl catches that regardless of their initial dispersal behavior in the NCC, yearling SRSS Chinook salmon soon migrate northwards. Burke et al. (2013b), Yu et al. (2012), and Bi et al. (2011) used different modeling approaches to evaluate factors affecting early marine migration behavior of yearling spring Chinook salmon in the NCC. Modeling work by Yu et al. (2012) and Bi et al. (2011) suggested that environmental factors had the most influence on migration behavior while the model by Burke et al. (2013b) suggested geospatial

factors were more critical in determining migration pathway. As a result, in Burke et al.'s (2013a) model, fish could occupy sub-optimal environmental conditions.

4.1.3. North Pacific Ocean

Once SRSS Chinook salmon leave the NCC and are still in their first year of ocean life, they distribute over wide area of the NE Pacific Ocean, including along the continental shelf off Central BC, Central Alaska, SE Alaska and the GOA (Trudel et al. 2009; Tucker et al. 2011; Sharma and Quinn 2012; Fisher et al., 2014). Some yearlings from this ESU have moved as far north as Kodiak Island and can be found along coastal areas of BC and AK by the June-August time period (Trudel et al. 2009; Tucker et al. 2011; Fisher et al. 2014). During summer, Snake River yearlings are one of the most abundant stocks in the GOA. From July-September 2012, 45% of the Chinook salmon present in the GOA at this time (first ocean fish) were SRSS Chinook salmon (Teel et al. 2014). By fall and winter of their first ocean year, some SRSS Chinook salmon are still in shelf areas along the British Columbia coast (Tucker et al. 2011). By the end of their first year in the ocean (beginning of their second spring at sea), most SRSS yearlings have left the shelf (Tucker et al. 2011; Fisher et al. 2014) and are in the deeper waters of the GOA.

Fisher et al. (2014) found that dispersal or migration rates of SRSS Chinook salmon during their first year in the ocean averaged 8 km/day, one of the fastest rates for any Columbia River Chinook salmon stock. Otolith analysis suggests mean northward migration rates of interior Columbia River yearling Chinook during their first months at sea are faster during years of poor ocean conditions, suggesting juveniles may modify their migratory behavior based on ocean conditions (Jacobson et al. 2012).

Once fish enter their second year of ocean life, little is known about their ocean life history and ecology. The lack of older ages of Chinook salmon in ocean sampling (Myers et al. 1996) and lack of information on the origin of captured fish in some ocean surveys makes it impossible to conclude much about the ocean life of older SRSS Chinook salmon (e.g., 2 or 3 years at sea). For example, it is not clear if and how ocean ecology varies with age of the fish. SRSS Chinook salmon probably spend most of their ocean lives in the GOA (Myers et al. 1996) until they begin to migrate back to their stream of origin.

When fish (and from where) begin their return migrations and how this might vary with age is unclear. The life history of jack Chinook salmon (one year of ocean life before returning to spawn) is particularly relevant because jack salmon are used in forecasting adult returns of spring Chinook salmon (e.g., to Bonneville Dam). Understanding where fish that returns as "jacks" occur and when they return could help explain some of the discrepancies in forecasts made using jacks and those made using indicators of ocean conditions (Burke 2014). A modeling study by Bracis and Anderson (2013) suggested that jack Chinook salmon have a different spatial distribution in the ocean than older fish. Clairborne et al. (2011) found that age at maturity in hatchery-origin Willamette spring Chinook salmon was related to their size at release; younger returning fish were those that were larger after their first year of ocean growth.

Maturing Chinook salmon (i.e., two years or more in the ocean and destined for a spawning river) typically arrive off of coastal Washington beginning in March and April based upon fishery interceptions that have occurred in this area. It is unclear when adults first enter the estuary but spring Chinook salmon are abundant in the lower Columbia River estuary in April and May (but present in March and June as well) where they have been tagged (Wargo-Rub et al. 2011, 2012). Adult SRSS Chinook salmon tagged in the estuary took an average of 18.1 days to reach Bonneville Dam in 2011 and 15.4 days in 2010; travel times of individual fish from tagging location to Bonneville Dam ranged from 7 to 57 days (Wargo-Rub et al. 2011, 2012).

At Bonneville Dam where the fish leave the estuary, passage of SRSS Chinook salmon varies as a function of river of origin (i.e., destination in the Snake River system). From 1996 to 2001, median date of passage at Bonneville Dam ranged from April 23 for fish destined for the Tucannon River to May 29 for fish destined for the Imnaha River (Keefer et al. 2004). Keefer et al. (2004) also found that fish destined for the Clearwater drainage arrived earlier at Bonneville Dam than fish destined for the Salmon River drainage. More recently (Hess et al. (2014) found that median, annual date of passage at Bonneville Dam for 2004-2007 ranged from about April 30 to May 20 for fish destined for the Clearwater River and Lower Snake River, to about May 20 to June 10 for fish destined for the Salmon River. Median passage date can vary up to 20 days depending on the destination of the fish (Hess et al. 2014) and appears to be strongly related to discharge, with fish passing earlier at lower flows (Keefer et al. 2004).

4.1.4 Summary

Average date of estuary entry (as measured at Bonneville Dam with PIT tag data) varies little from year to year (mid-May). Based primarily upon PIT tag data, average residence time of SRSS yearling Chinook salmon in the estuary appears to be a week or less and average residence time in the plume also appears to be short and on the order of hours to days. However, there is considerable variation in residence times in different habitats and timing of estuarine and ocean entry among individual fish. Such variation may not be unimportant, as it may affect survival at later life stages and help provide resilience to the ESU (McElhaney et al. 2000; Holsman et al. 2012).

Once yearling SRSS Chinook salmon enter the NCC, they can initially disperse in any direction but they quickly begin to migrate along the coast to the north. Migration to the north appears to be controlled by a combination of environmental and geospatial factors. As the fish migrate north they distribute over a broad area of the NE Pacific Ocean, including coastal areas of Washington and British Columbia and Alaska, the continental shelf off Central BC, Central Alaska, SE Alaska and the GOA. In summer, yearlings SRRS Chinook salmon are abundant in the GOA. Some yearlings from this ESU move as far north as Kodiak Island by the June-August time period. SRSS have largely vacated coastal areas of Washington and British Columbia by September. By the end of their first year of ocean life, most fish are in the GOA. Little is known about the ocean life history of SRSS Chinook salmon after they have passed their first year in the ocean until arrive in coastal waters of Washington in March and April. Adult SRSS Chinook salmon tagged in the estuary took an average of 18.1 days to reach Bonneville Dam in 2011 and

15.4 days in 2010. Passage date of adults at Bonneville Dam varies with destination of the fish (where the fish ultimately spawn).

4.2 Snake River Steelhead

The Snake River steelhead DPS (Distinct Population Segment) occupies the Snake River Basin of southeast Washington, northeast Oregon and Idaho and includes all naturally spawning populations of steelhead in the Snake River and its tributaries. Several artificial propagation programs are considered part of the DPS as well. Snake River steelhead are known to spawn and rear in all tributaries used by Snake River spring/summer Chinook, as well as many additional tributaries.

Unlike Chinook salmon, stock specific information on steelhead after they leave the Columbia River is very limited. In part, this is because development of steelhead genetic baselines have lagged those of other species. The genetic baseline is reasonably complete in the Columbia River basin but is not yet complete outside the basin. Until the genetic baseline is in place, the origin of ocean-caught fish can only be reliably determined with the use of PIT and CWT tags, most of which are of hatchery-origin.

4.2.1 Estuary

Detections of PIT tags passing Bonneville Dam provide a means of estimating timing of estuarine entry. Based upon these PIT tag detections, the majority of Snake River steelhead pass Bonneville Dam from mid-April through early June, with most fish passing in a narrow time window that varies little between years. The average date of 50% passage (from 2003 to 2012) at Bonneville Dam was May 16 for all fish (hatchery-origin plus wild fish) and May 19 for wild fish only (HTTP://WWW.CBR.WASHINGTON.EDU/DART). The range for 50% passage of juvenile steelhead (hatchery and wild origin fish) over the 10 years was May 9 to May 31. The mean date for 90% of the Snake River steelhead (hatchery-origin plus wild fish) to pass Bonneville Dam was June 6.

Available evidence suggests that the residence time of most juvenile SR steelhead in the estuary is short and on the order of days, which suggests that passage date at Bonneville Dam for SR steelhead probably provides a reasonable, general estimate of ocean entry timing. Based upon purse seine collections in the lower estuary (sampling occurred at approximately Rkm 15), Weitkamp et al. (In Review) found that the timing of PIT tag detections of steelhead at Bonneville Dam was almost identical to the detection dates of known origin steelhead at the lower estuary purse seine site at Rkm 15 (Weitkamp et al. In Review). For example, the mean date of passage for Snake River steelhead in the lower estuary at Rkm 15 was May 21 for wild steelhead (all years combined) compared to May 19 at Bonneville Dam. Also, the average time for fish to migrate from Bonneville Dam to the trawl based PIT tag detection array at Rkm 70 was about two days and to migrate from Rkm 70 to Rkm 15 was also about two days (Weitkamp et al. In Review). Average migration rates reported by McMichael et al. (2013) for acoustically tagged steelhead (stock origin was not reported) were also very rapid as they found that most steelhead traveled from Rkm 153 to Rkm 8 in less than two days.

McMichael et al. (2013) also reported that most steelhead remained in the vicinity of the river's mouth (below Rkm 8) for only a matter of hours; 83% of the juvenile steelhead they tagged spent

less than a day near the mouth of the river. Fish tended to hold at the mouth of the river for a shorter period early in the year (Mean=0.3 days, May 5 to 18) compared to later in the year (Mean=0.8 days, May 19 to July 6).

4.2.2. NCC

After they leave the estuary, steelhead can disperse in all directions (McMichael et al. 2013) with the proportion of fish moving in any direction a function of time of year. McMichael et al. (2013) reported that in early spring most fish initially dispersed south and west while later in the spring fish mostly were dispersing north and west. The authors speculate that this difference in dispersal patterns is a function of local ocean currents. Regardless of direction the fish initially go, information from ocean trawl catches indicate steelhead migrate rapidly through the plume and near coastal region and are beyond the continental shelf in a matter of days. Daly et al. (2014) estimated that individual Columbia River steelhead were present in shelf waters for an average of 10 days (an offshore distance of about 80 km). Because of this rapid migration over shelf waters, steelhead are present in the NCC trawl catches off Washington and WCVI only in May and have completely vacated the NCC by June (Daly et al. 2014) (Figure 8b) (note that no April samples have been collected in the NCC and based upon passage data at Bonneville Dam, some steelhead are likely in the ocean in April).
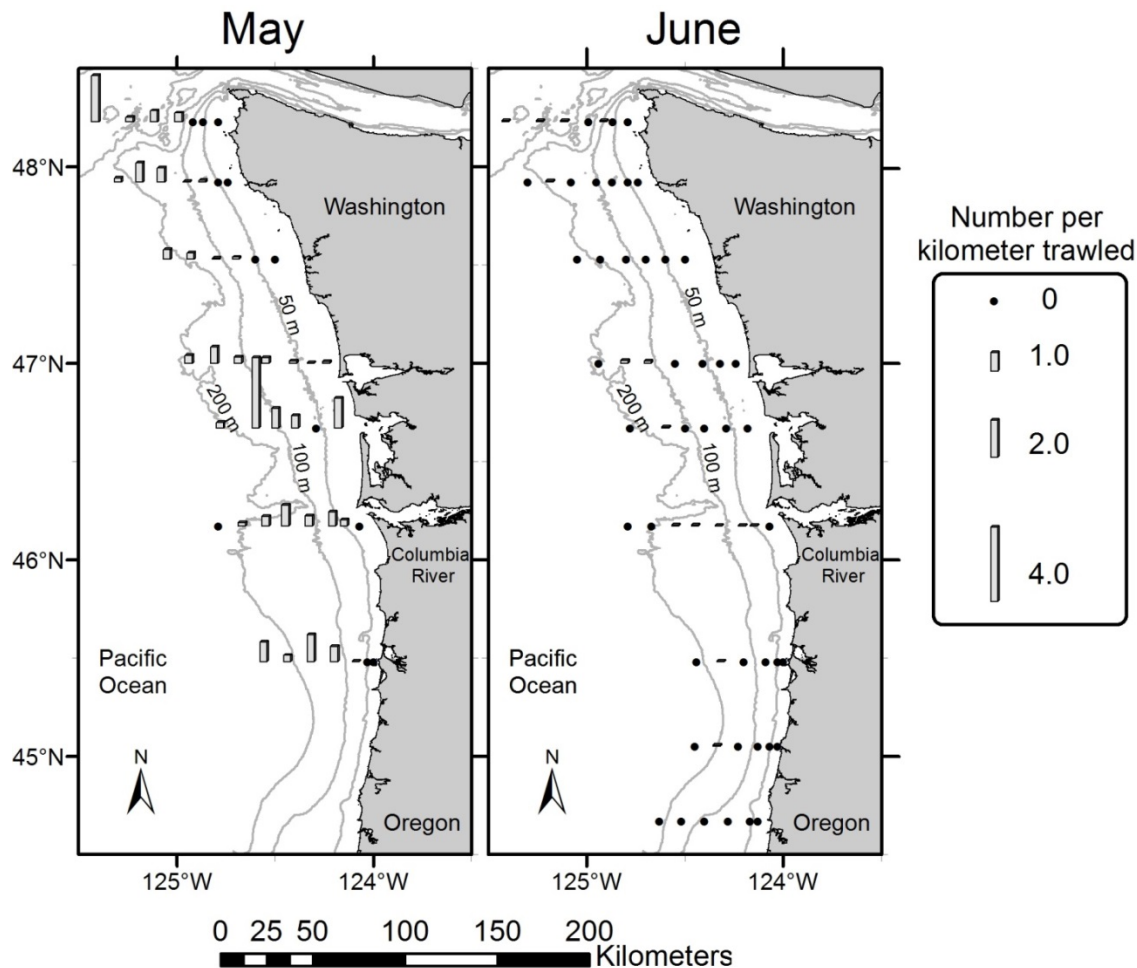
Figure 8b. Average juvenile steelhead Catch Per Unit Effort (CPUE) by station at ocean sampling stations for May 2006 – 2012 and June 1998 – 2012. (Jacobson et al. 2012).

4.2.3. North Pacific Ocean

Once the steelhead exit the coastal area, there is little known about their life in the ocean other than where they are generally found. Steelhead are the most migratory of all anadromous salmonids on the west coast of North America (Quinn and Myers 2004) and can be found over much of the North Pacific Ocean and GOA, from SE Alaska to nearly the Kuril Islands, Japan (Myers et al. 1996; Atcheson et al. 2012a). Tagged Snake River steelhead have been recovered in a broad band across the North Pacific between 40°N and 50°N latitude and from the North American Coast to 165°W (west of the date line) (Myers et al. 1996). In general, this distribution appears to be highly dependent on temperature (Welch et al. 1998; Atcheson et al. 2012a). Myers et al (1996) found 10, immature steelhead from the Columbia River in this latitude range in the western part of the Pacific Ocean. Fourteen maturing Columbia River steelhead were also reported in high seas sampling but most of these fish were caught in the eastern part of the Pacific Ocean and were north of 44°N. Forty-eight coded-wire tagged steelhead from Idaho showed this same ocean distribution with most fish found in the Pacific

Ocean between 40°N and 50°N latitude and from the North American Coast to 165°W. Recoveries of hatchery-origin Snake River steelhead (McKinnell et al. 1997) with CWTs have been made during high seas sampling. These recoveries of Snake River steelhead were made during their first two years in the ocean, primarily in the Aleutians and southern GOA. They are the dominate stock in these two areas during their first year in the ocean but not in their second year (McKinnell et al. 1997). Few steelhead have been found in the Bering Sea, probably reflecting the lack of anadromous trout (*O. mykiss* and *O. clarki*) spawning in Western Alaska.

Arrival timing of adult steelhead in coastal waters of Washington is unknown as is arrival timing and residence time in the estuary. Steelhead adults are divided into an A and B run. Both runs are summer steelhead that return in summer and spawn the following spring. B-run fish are generally 2-ocean fish from the Clearwater/Selway basin in Idaho that are larger than A-run fish which are 1-ocean and smaller. Freshwater entry is reported to be June-August for the A-run and August -November for the B-run (Busby et al. 1996). Robards and Quinn (2002) evaluated timing of passage of summer run steelhead at Bonneville Dam from 1935 to 2000 and found that passage of steelhead has been changing. They found that peak passage of the "late" portion of the run had remained about September 1 for the 60 year record of the data. However, the peak passage of the earlier portion had shifted by about 2 weeks from late July to early August (Robards and Quinn 2002). They attributed this shift to warming temperatures and reduced flows in the river over this time period.

4.2.4 Summary

Most steelhead migrate very rapidly (<5 days) through the estuary and into the ocean and are present in the immediate mouth of the river for a very short period (hours to days). Residence time at the mouth of the river is very short and increases slightly as the season progress. However, there is considerable variation in travel times and timing of estuarine and ocean entry between individual fish. For example, residence time of juvenile steelhead at the mouth of river ranged from 0.1 days to 10.8 days (McMichael et al. 2013). Differences in ocean entry date of days to weeks may not be unimportant and could affect survival of fish in the ocean (Scheuerell et al. 2009; Holsman et al. 2012).

Once steelhead leave the estuary they migrate rapidly to the west and leave the NCC off Washington by mid-June. Residence time in the NCC off of Washington appears to be around 10 days on average. Once the fish have departed coastal areas, Snake River steelhead distribute themselves in a broad band across the North Pacific, with most fish found between 40°N and 50°N latitude and from the North American Coast to 165°W (west of the date line) (Myers et al. 1996). In general, ocean distribution appears to be highly dependent on temperature. There is not much else known about ocean life of steelhead. Once fish enter the estuary, their timing of upstream migration at Bonneville Dam varies with age, size and distribution of the fish. Most wild fish pass the dam earlier than hatchery fish. The peak passage of the earlier portion of the returning steelhead has shifted by about 2 weeks from late July to early August, probably in response to warming temperatures and reduced flows in the river.

4.3 Snake River Fall Chinook Salmon

The Snake River fall Chinook salmon (SRF) ESU includes all naturally spawning fall-run Chinook salmon (adults are often referred to as "brights") in the mainstem Snake River below Hells Canyon Dam; fish spawning in the Clearwater, Tucannon, Grande Ronde, Imnaha, and Salmon rivers; and four artificial production programs. While the SRF Chinook salmon ESU is referred to as a sub-yearling group, it also contains significant numbers of yearlings. Many of the yearlings are juveniles that overwinter in the reservoirs and migrate downstream as yearlings, especially from the Clearwater River basin. Yearling migrants contribute substantially to the population as a whole in that juveniles that survive the summer and winter return at very high rates compared to the traditional sub-yearling migrants of this ESU (Connor et al. 2005). Here, we will distinguish the ocean ecology of the two life history types.

4.3.1 Estuary

For all SRF Chinook salmon (regardless of origin or life history type), the mean date for 50% of the ESU (based on PIT tag detections) to have passed Bonneville Dam over the last 10 years was June 10; for wild fish only, the mean date was July 9 (HTTP://WWW.CBR.WASHINGTON.EDU/DART). However, combining all fish oversimplifies timing of estuarine entry as the timing of passage of PIT tagged fish of this ESU at Bonneville Dam is bimodal. The peak of the first mode (10 year average), which are likely the yearlings, has been early to mid-May while the peak of the second mode, which are likely the sub-yearlings, has been late June to early July.

SRF Chinook salmon sub-yearlings and yearlings have different migration behaviors through the estuary ranging from rapid migration to extended rearing. Yearlings of this ESU migrate downstream rapidly and typically use main channels and large distributaries during their migration (Weitkamp et al. In Review). SRF yearling Chinook salmon had an average migration rate of 24.6 km/day which was more comparable with juveniles from the SRSS Chinook salmon ESU. Based upon sampling in shallow habitats such as wetlands, there is little evidence of extended rearing (weeks to months) by many SRF yearlings in the estuary.

In contrast, sub-yearlings, exhibit a diversity of migration behaviors. Like many other sub-yearling dominated ESUs (e.g., West Cascade Fall Chinook), some sub-yearlings use shallow, nearshore, and off channel areas (including wetland and floodplain areas) below Bonneville Dam for rearing and for migrating (Fresh et al. 2005). SRF Chinook salmon juveniles can be present in estuarine areas in winter, as fry in March – May, and fingerlings throughout the summer and fall (Roegner et al. 2012; Teel et al. 2014). SRF Chinook salmon sub-yearling juveniles occur in these habitats in low numbers compared to some of the other sub-yearling dominated ESUs (Teel et al. 2014).

Other sub-yearling SRF Chinook salmon make a more directed migration through the estuary and into the ocean and use main channel large distributary channels during their migration. Some of these fish can migrate rapidly through the estuary to the ocean. Of the various Columbia River basin stock groups captured in purse seining in the lower estuary at Rkm 15 for which

there was sufficient sample sizes, sub-yearling SRF Chinook salmon had the fastest average migration rate from release point to the estuary (35.2 km/day) (Weitkamp et al. In Review). The telemetry studies by McMichael et al. (2013) found that migration rate of sub-yearling Chinook salmon (all stocks considered) from Rkm 153 to Rkm 8.3 was about 70km/day, indicating they could reach the ocean from this point in the mid estuary in about 2 days. Because of the protracted time during which SRF juvenile Chinook salmon pass Bonneville Dam, the inability to determine life history type of the fish as they pass Bonneville, and the extended time some fish from this ESU spend rearing in the estuary, the date of passage at Bonneville Dam based on PIT tag detections does not represent a reasonable estimate of ocean entry time for this ESU.

Because sub-yearlings and yearlings have different habitat use patterns, an analysis of both beach seine (most representative of sub-yearlings) and purse seine (most representative of yearlings) catches is needed to derive a complete picture of timing of passage of SRF Chinook salmon through the estuary. The estuary purse seining at Rkm 15 and beach seining at several estuarine sites near the mouth of the river (Bottom et al. 2011; Roegner et al. 2012) indicates sub-yearling Chinook salmon (all Columbia River stocks combined) have a year-round presence but a broad peak of occurrence in the estuary from mid-April through July. In some years, there is no real peak or even multiple peaks in abundance, perhaps reflecting passage of different stock groups. The peak occurrence of hatchery-origin SRF Chinook yearlings in purse seine catches at Rkm 15 in the lower estuary is about May 1, which is earlier than SRSS Chinook and steelhead. The mean date of passage of identifiable sub-yearling SRF Chinook salmon at Rkm 15 is about July 15 for wild fish and June 15 for hatchery-origin fish (Weitkamp et al. In Review); this pattern more closely corresponds with the second peak of PIT tagged fish passing Bonneville Dam.

There is no data specifically on residence time of SRF sub-yearlings at the mouth of the river. The only data available is from telemetry but is not specific to stock. Sub-yearling juvenile Chinook salmon (no stock identifications were made) were present in the plume area at the mouth of the river for an average of 3.6 days, which is longer than yearling juvenile Chinook salmon. But like the other ESU's there was considerable variation between individual fish in residence time (McMichael et al. 2013).

4.3.2. NCC

Based upon McMichael et al.'s (2013) telemetry studies, initial dispersal of fish originating from this ESU varies with life history type. As we discussed for SRSS yearling Chinook salmon, yearling Chinook salmon in general (stock specific information was not provided) disperse in all directions from the river mouth with fish early in the spring more likely to be found south of the river's mouth while later in the spring, yearlings were more likely to be found to the north. Based upon telemetry studies, the initial ocean dispersal of SRF Chinook salmon sub-yearlings that enter the ocean June 19 to August 7 is primarily to the north (McMichael et al. 2013). The direction of movement of the fish after they leave the estuary was considered to be a function of season and local environmental conditions including winds and currents (McMichael et al. 2013).

Once in the NCC ecosystem, results of trawl surveys suggest that yearlings from the SRF Chinook salmon ESU do not disperse as far or as quickly from the river as do the yearlings from the SRSS Chinook salmon ESU (Trudel et al. 2009; Tucker et al. 2011; Fisher et al. 2014). In contrast, SRF Chinook salmon sub-yearlings first appear in ocean catches in June and primarily to the north of the Columbia River; some fish have reached the WCVI by June (Trudel et al. 2009) (Figure 8c). By September in the NCC, trawl catches show that SRF sub-yearlings are widely dispersed from central Oregon to WCVI (Tucker et al. 2011). By the end of their first year in the ocean, SRF sub-yearlings have not dispersed much farther to the north than the northern tip of the WCVI and thus are still in the NCC. Fisher et al. (2007) reported that sub-yearling Chinook salmon were most abundant from California to British Columbia and in shallower coastal areas during their first ocean year.
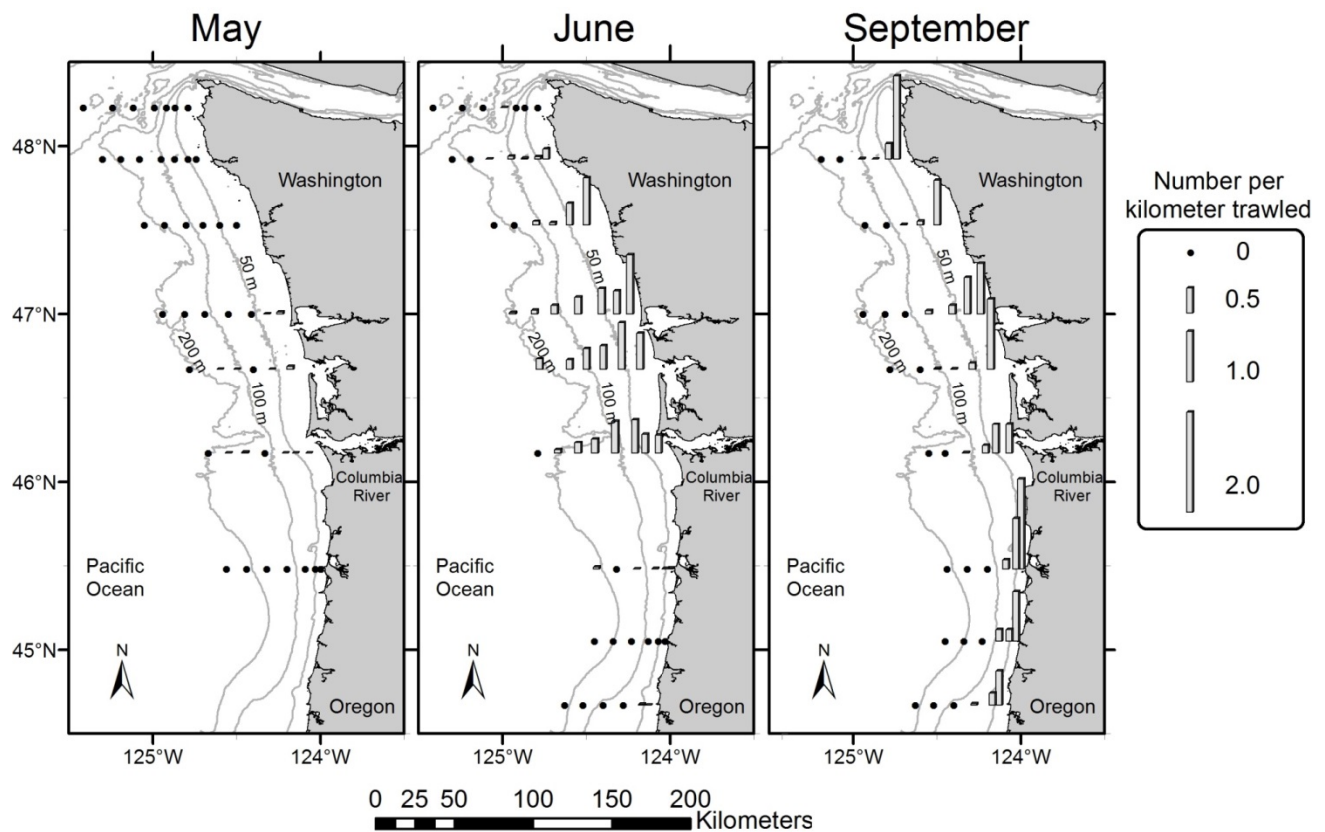
Figure 8c. Average subyearling Snake River fall Chinook salmon Catch Per Unit Effort (CPUE) by station at ocean sampling stations for May 2006 – 2012 and June 1998 – 2012. (Jacobson et al. 2012)

4.3.3 Pacific Ocean

Although some SRF yearling Chinook salmon can be found in the GOA by fall, most of these fish move only as far north as SE Alaska during their first ocean year. At the beginning of their second ocean year, most fish move off the shelf and into oceanic habitats. Sub-yearlings in general (independent of origin) migrate slower, are found closer to shore in shallower water, and do not disperse as far north as yearlings (Trudel et al. 2009; Tucker et al. 2011; Sharma and

Quinn 2012; Fisher et al. 2014) (Figure 8). Sub-yearling SRF Chinook salmon had the fastest ocean dispersal rate of any Columbia River fall Chinook stock, averaging 4 km/d (Fisher et al. 2014).

From the end of the first ocean year, and until they return to Columbia River as mature adults, there is little stock specific information on the ocean life of this ESU. An analysis by Norris et al. (2000) of ocean distribution of upriver bright (fish that spawn in the fall) stocks indicated that these stocks move further north as they get older. However, they did not distinguish Snake River fish from other stocks or sub-yearlings and yearlings.

Small numbers of maturing jack males (jack salmon are maturing male salmon that return after one year or less in the ocean which is a life history tactic common in Chinook salmon) can be found off the Washington coast in May and June of the year they enter the ocean (Beckman 2014). The ocean migration behavior of these fish is unknown.

Generally, adult fall run fish are found in the lower river in August and September with passage at Bonneville Dam occurring from mid-August to the end of September (HTTP://WWW.CBR.WASHINGTON.EDU/DART). An indication of passage timing of SRF Chinook salmon adults can be obtained from timing of the Interior Columbia River summer/fall group which includes Snake River falls (Hess et al. 2014). Median date of passage of this reporting group was mid-September from 2004-2007 (Hess et al. 2014). Passage timing of adults from the Interior Columbia River summer/fall reporting group used by Hess et al. (2014) is, however, quite broad with adults passing Bonneville from mid-June to early October. It is not clear if there is a difference in timing of adult passage through the estuary or past Bonneville Dam for SRF Chinook salmon yearlings and sub-yearlings.

4.4.4 Summary

The SRF Chinook salmon ESU is comprised of both a yearling and sub-yearling component. The estuary and ocean life history of each of these life history types is distinct. Fish from this ESU enter the estuary (based upon passage of PIT tagged fish at Bonneville Dam) in two peaks over a long time period. The peak of the first mode, which are likely the yearlings, is early to mid-May while the peak of the second mode, which is likely the sub-yearlings, has been late June to early July. In the estuary, the two life history types have distinct readience times. The yearlings spend an average of around a week (similar to yearling SRSS yearling Chinook salmon). In contrast, some sub-yearlings can rapidly migrate through the estuary while others can rear for an extended period of up to several months in the estuary. Habitat use varies with migrating fish more associated with the mainstem and larger distributaries and rearing sub-yearlings often associated with shallow water areas such as wetlands and shoreline areas.

Initial dispersal of subyearlings in the NCC is different than yearlings (in general, independent of origin) with most fish tending to move north. Yearling SRF Chinook do not move as far north as yearling SRSS Chinook salmon but by the beginning of their second year at sea they appear to move off the shelf and into the GOA. SRF Chinook salmon sub-yearlings first appear in ocean

catches in June that are primarily to the north of the Columbia River and some fish have reached the WCVI by June. By September in the NCC, trawl catches show that SRF sub-yearlings are widely dispersed from central Oregon to WCVI. By the end of their first year in the ocean, SRF sub-yearlings have not dispersed much farther to the north than the northern tip of the WCVI and thus are still in the NCC. Sub-yearlings in general (independent of origin) migrate slower, are found closer to shore in shallower water, and do not disperse as far north as yearlings. Generally, adult fall run fish are found in the lower river in August and September with passage at Bonneville Dam occurring from mid-August to the end of September. Based upon the Interior Columbia River summer/fall group which includes Snake River falls, median date of passage of this reporting group was mid-September from 2004-2007.

4.4 Snake River Sockeye Salmon

The Snake River sockeye salmon ESU is currently found only in lakes high in the Salmon River drainage of the Snake River basin, primarily in Redfish Lake. Snake River sockeye salmon are similar to many other sockeye salmon populations in that fry emerge from spawning areas and immediately move into lake habitats where they rear for 1 to 3 years. Because Snake River sockeye salmon were nearly extirpated by the mid-1990's and currently are at very low abundance levels, they are rarely detected in any ocean surveys using any sampling method. As a result, ocean migrations and distribution of this ESU are largely unknown. We have used information on sockeye salmon from other populations, including other Columbia River ESUs, to draw inferences about the estuarine and marine life history of the Snake River sockeye salmon ESU.

4.4.1. Estuary

While pre-dam reports indicate that sockeye salmon smolts passed through the lower Snake River in May and June, PIT-tagged smolts from Redfish Lake recently passed Lower Granite Dam on the lower Snake River from mid-May to mid-July. Based upon PIT tag detections at Bonneville Dam, peak passage of juvenile sockeye from this ESU at Bonneville Dam is generally in late May (HTTP://WWW.CBR.WASHINGTON.EDU/DART). This is about two weeks later than peak passage of sockeye juveniles from all populations combined (using the sockeye smolt index- HTTP://WWW.CBR.WASHINGTON.EDU/DART). Catches of sockeye salmon juveniles (origins unknown) in the estuary peak in early June, with most fish caught between May 15 and June 15 (Weitkamp et al. 2012). There is relatively little annual variation in migration timing through the estuary with peak catches occurring on June 1 in 2007, on June 5 in 2008, and on June 10 in 2010 (no real peak occurred in 2009) (Weitkamp et al. 2012). Two PIT tagged sockeye salmon migrated from Redfish Lake to the estuary purse seine sampling site (Rkm 15) in 15 and 21 days. The one fish detected at Bonneville Dam and in sampling at Rkm 15, took three days to migrate from Bonneville Dam to the lower estuary purse seine site.

4.4.2. NCC

Sockeye salmon enter the ocean and immediately began migrating north, as no sockeye from the Columbia River have been caught south of the river's mouth in 16 years of sampling in the NCC. In May and June, Columbia River sockeye salmon are most abundant off of Washington but some fish have migrated as far north as North and Central BC (Tucker et al. 2009) by June. A comparison of May, June, and September catches off of coastal Washington from 2006 to 2011 found that 65% of all sockeye caught during this time period were caught in May, 35% in June, and none in September (Teel 2013). The few fish genetically identified as from the Snake River ESU were found South of Quillayute River in May and North of Grays Harbor in June. The lack of sampling in July and August makes it problematic to determine when Columbia River sockeye salmon leave Washington coastal waters but clearly by September, all sockeye have left Washington waters.

4.4.3. North Pacific Ocean

Once Columbia River sockeye salmon leave the NCC, they likely move north into the GOA, Bering Sea, and up the coast into Alaska. By winter, sockeye salmon have clearly disappeared from coastal areas and have entered the GOA (Tucker et al. 2009). In general, maturing sockeye salmon are distributed in the GOA and into the Bering Sea but are migratory within this region (Burgner 1991; Myers et al. 1996). Water temperatures affect the distribution of fish in the GOA with warmer temperatures pushing fish further. The study by Myers et al. (1996) found six maturing sockeye salmon from the Columbia River in the GOA. In summer 2009, Beacham et al. (2011) sampled sockeye in the Bering Sea and found that most fish (86%) were of Alaska origin with the rest from British Columbia, including the Fraser system; no sockeye from the Columbia River were identified in this study.

As fish mature in the GOA and Bering Sea region, they eventually begin their return migration to their rivers of origin. The body size when sockeye salmon begin their return migration can be related to temperatures in the last months of ocean residence with warmer temperatures leading to a smaller body size (Pyper and Peterman 1999). Water temperatures affect the distribution of fish in the GOA with warmer temperatures pushing fish further north, thereby increasing the distance fish migrating south to the Columbia River have to travel. The date when sockeye salmon begin their return migration is apparently a population specific trait that is independent of where the fish are at sea (Hodgson et al. 2006). Water temperature plays an important role in determining when stocks arrive back to coastal areas near spawning rivers.

Quinn and Adams (1996) examined timing of passage of adult sockeye salmon (all stocks) at Bonneville Dam from 1949 to 1993 and concluded that timing had shifted from early July at the beginning of the time series to late June; this shift in migration timing was attributed to changes in flow and temperature regimes in the river (Quinn et al. 1997). Over the last 10 years, peak passage at Bonneville Dam of all sockeye salmon has been late June (HTTP://WWW.CBR.WASHINGTON.EDU/DART) and is consistent with the timing in the later part of the Quinn and Adams (1996) time series. More recent data shows that these trends towards shifts to earlier migration timing have continued (Crozier et al. 2008).

4.4.4. Summary

Of the four species considered in this Module, Snake River sockeye are at the lowest abundance levels and so are rarely detected in any ocean surveys using any sampling method. Based upon PIT tag detections at Bonneville Dam, peak passage of juvenile sockeye from this ESU at Bonneville Dam is generally in late May. Too few sockeye juveniles form the Snake River ESU have been sampled to draw any conclusions about length of estuary residence although there is relatively little annual variation in migration timing of juveniles (all sockeye stocks combined) through the estuary with peak catches occurring in early June.

Based upon trawl samples, sockeye juveniles from the Columbia River do not disperse south of the Columbia River and have left the NCC by September. Fish enter the GOA/Bering Sea by the end of their first ocean year. Water temperatures affect the distribution of fish in the GOA with

warmer temperatures pushing fish further north. The body size when sockeye salmon begin their return migration can be related to temperatures in the last months of ocean residence with warmer temperatures leading to a smaller body size. Water temperatures affect the distribution of fish in the GOA with warmer temperatures pushing fish further, thereby increasing the distance fish migrating south (such as to the Columbia River) have to travel. The date when sockeye salmon begin their return migration is apparently a population specific trait that is independent of where the fish are at sea. Water temperature plays an important role in determining when stocks arrive back to coastal areas near spawning rivers.

5. Ocean Ecology

This section describes ecological aspects of the ocean life of the four listed Snake River species, focusing specifically on:

1. Food habits

2. Growth

3. Ecological interactions (predation, competition, disease, and parasites)

4. Mortality

5. Habitat use

6. Habitat connectivity

Despite decades studying the ocean ecology of salmon and steelhead, there are still major gaps in our knowledge of their ocean ecology. In particular, we still have a poor understanding of the mechanisms that affect growth and survival of the fish during ocean life. This is partly due to the large size and dynamic nature of the coastal and open ocean environments, but it is also likely due to underlying differences between ESUs and DPSs, juvenile life-history strategies, species, and the experiences and biology of hatchery-origin versus natural-origin fish. We will present information in this section at the most relevant biological scale as possible (i.e., an individual Snake River ESU or DPS or particular life history type). Our goal in this section is to present the information as it exists and not to argue for a particular point of view. On some issues, this means we will present information both for and against a particular hypothesis and will use this as a way to highlight some of the Key Information Needs presented in Section 7.

5.1 Food Habits

There are few diet studies in either the estuary or ocean that are specific to ESU/DPS or life history type. In general, all three salmon species eat a mix of invertebrates and fish during their tenure in estuary and ocean habitats (e.g., LeBrasseur 1966; Brodeur 1990; Brodeur et al. 2007). Chinook salmon and steelhead are the most piscivorous and sockeye salmon the least piscivorous. While there is only limited information on the Snake River sockeye salmon ESU, sockeye diets in the ocean have been analyzed from many other sources. And, regardless of when and where sockeye are captured, they always feed almost entirely on invertebrates (Peterson et al. 1982; Burgner 1991; Healey 1991; Quinn 2005; Brodeur et al. 2007; Price et al. 2013). The species of invertebrate present in sockeye salmon stomachs depends on where and when samples are collected but krill is often a major diet item of sockeye salmon, especially in the GOA and Bering Sea (Peterson et al. 1982; Brodeur 1990; Myers et al. 1996).

In both the estuary and NCC, invertebrates tend to be more numerically dominant and more frequently occurring in juvenile Chinook salmon diets whereas fish typically represent most of the biomass of prey consumed. In the estuary *Americorophium* spp., crustaceans, and insects are the most abundant insects in juvenile Chinook salmon diets (Bottom et al. 2011; Weitkamp et al. In Review) while in the NCC, invertebrates present in juvenile Chinook salmon diets include copepods, amphipods, decapods, and euphausiids (Brodeur 1991; Daly et al. 2009, 2012). Fish found in Chinook salmon diets in the estuary and in the NCC include northern anchovy (*Engraulis mordax*), rockfish (*Sebastes* spp.), Pacific sand lance (*Ammodytes hexapterus*), and smelt (Osmeridae) (Brodeur 1991; Daley et al. 2009). In the ocean, Chinook salmon eat mostly fish and squid (*Loligo* spp.) (Brodeur 1990; Myers et al. 1996).

In estuarine and NCC habitats, steelhead have a diet that is similar to juvenile Chinook salmon but is not as heavily oriented towards fish (Brodeur 1990; Daly et al. 2014). But, similar to Chinook salmon, once steelhead leave the NCC region, their diet is comprised almost entirely of fish and squid (squid are rarely seen in diets in the NCC or off WCVI) (Brodeur 1990; Myers et al. 1996; Atcheson et al. 2012a, 2012b). Atcheson et al. (2012a) reported that steelhead diets varied by age group, region of capture and year of capture but that squid provided the highest energy content.

Diets of all three species vary in response to a number of factors associated with: 1) the prey the fish consume (e.g., prey size), 2) the fish consumers themselves (e.g., predator size), and 3) the environment (e.g., temperature). Of these, body size of the salmonid predators is especially important. Generally, predators eat larger prey as their body size increases (Fresh 1997; Duffy et al. 2010). For some salmonid species, as body size increases, the amount of fish prey consumed increases. For example, Brodeur (1991) found that Chinook salmon and steelhead ate more fish in the NCC as their body size increased. Recently, Daly et al. (2009) looked at ontogenetic shifts in diet of juvenile Chinook salmon in the NCC and found that diet shifted as a function of fish size in the size range 100 mm to 375 mm. In particular, the proportion (by weight) of fish in the diet of juvenile Chinook salmon increased as the salmon increased in size to nearly 100% of the diet (by weight) in the largest size classes examined (Daly et al. 2009).

Another factor affecting diet is prey availability, which is a function of the foraging habitat being used, time of year, year and environmental conditions (Brodeur et al. 2007; Daly et al. 2009; 2013). Due to life history and reproductive cycles of prey items, some prey may be abundant at one time of year (e.g., spring) but then all but disappear after several months. Shifts in prey availability can also occur at longer temporal scales (e.g., years to decades) to changing ocean conditions such as temperature and currents. Prey availability can also vary vertically in the water column, between day and night (due to diel vertical migration of prey species), and across the continental shelf. Shifts in diet in response to food availability can affect marine survival (Quinn 2005). Daly et al. (2013) found that winter icthyoplankton that was comprised of earlier life stages of many of the food items eaten in the spring by juvenile salmon, could help predict changes in ocean conditions and subsequent adult returns two years after the fish entered the ocean. Atcheson et al. (2012b) established that steelhead diets in the GOA and Pacific Ocean varied with ocean conditions with the amount of squid (the highest quality food item for

steelhead) that was eaten declining during warm ocean years. For Central Valley Chinook salmon, Wells et al. (2012) found that the abundance of returning adult Chinook salmon was related to condition of the juvenile Chinook salmon of the same cohort the year before they returned to the Sacramento River to spawn. The condition of these salmon was related to the proportion of krill in their diets.

Origin of the fish (hatchery vs. wild) is another factor that can potentially affect diet. There is a large amount of literature comparing diets of hatchery-origin and wild salmonids (e.g., Fresh 1997). In general, when such factors as time and fish size are accounted for, hatchery and wild origin salmon of the same species typically have similar diets during their marine life (Daly et al. 2012; Sweeting and Beamish 2009). For example, in the NCC, Daly et al. (2012) found that hatchery origin and wild juvenile Chinook salmon had similar diets during their early marine life and that both types of fish tracked seasonal and inter-annual changes in the prey base. While hatchery origin and wild Chinook salmon and steelhead had similar marine diets, wild fish consumed more food on average and were in better condition and had higher growth rates than hatchery origin salmon (Daly et al. 2012; Daly et al. 2014).

In summary, most food habits studies in the estuary and ocean are conducted at the species (e.g., sockeye vs. steelhead) level. All three salmon species eat a mix of invertebrates and fish during their tenure in estuary and ocean habitats. While there is only limited information on the Snake River sockeye salmon ESU, sockeye diets in the ocean have been analyzed from many other sources. These studies demonstrate that sockeye salmon always feed almost entirely on invertebrates with krill often a major invertebrate diet item of sockeye. In the estuary both juvenile Chinook salmon and steelhead eat a mix of different invertebrates and small fish prey. By the time Chinook salmon and steelhead are in the NCC and ocean, they eat mostly fish and some squid; squid appears to be more important in steelhead diets than in Chinook salmon. Diets of all three species vary in response to characteristics of the prey the fish consume (e.g., prey size), the fish consumers themselves (e.g., predator size), and the environment (e.g., temperature). Of these, body size of the salmonid predators is especially important with predators eating larger prey as their body size increases. Prey availability (what the salmon have to eat) is also an important factor affecting diet and can vary with the foraging habitat being used, time of year, year (e.g., reflecting El Niño's and PDO changes), and environmental conditions.

5.2. Growth

Growth is the outcome of what the fish eats (both quantity and quality), its basic physiology (e.g., metabolism), activity level, environmental conditions, genetic effects, maternal effects, and abundance and distribution of competitors. Growth is a key attribute of ocean salmon ecology since it is often strongly related to survival with high growth rates often correlated with high survival or adult return rates (Pearcy 1992; Mortensen et al. 2000; Beamish et al. 2004; Moss et al. 2005; Quinn 2005; Cross et al. 2008; Woodson et al. 2013, Friedland et al. 2014).

Growth rates vary between species, populations and life history types. For example, Figure 9 illustrates how short term growth measured with the hormone IGF-1 in May and June in the NCC can vary between stock groups. The Willamette Spring Chinook salmon grew fastest. Wells et al. (2008) examined growth rates in spatially distinct (based on their distributions along the west coast of North America) Chinook salmon populations and concluded that growth rates were strongly related to the environment the fish occupied and that this was specific to both region and life history type. In the NCC, not all yearling Chinook salmon stock groups grow at the same rates (Figure 9). Sub-yearling and yearling Chinook salmon have different growth rates during their first months in the NCC. In particular, SRSS Chinook yearlings grew more slowly than SRF yearlings while SRF sub-yearlings grew more slowly than yearling SRF (Weitkamp et al. In Review). In both May and June in the NCC off Oregon and Washington, Willamette spring Chinook salmon had the highest growth rates of any of the stocks measured (Beckman 2014; Figure 9). This may be because Willamette spring Chinook salmon typically enter marine waters nearly a month earlier than upper Columbia or Snake River stocks. The lowest percent weight gain from time of release to capture in May in the ocean was for SRSS yearling Chinook salmon (Beckman 2014).
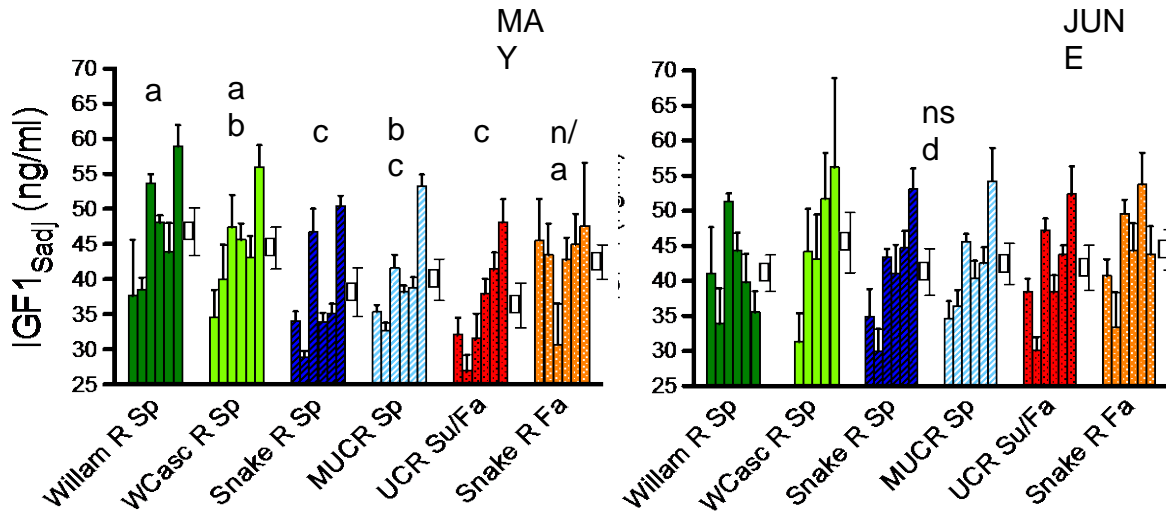
Figure 9. IGF-1$_{Sadj.}$ levels of six yearling Chinook salmon genetic stocks captured in the ocean in May and June. Individual bars show annual means of IGF-1 levels (2006-2011, left to right). Grand means of all years within a genetic stock are indicated by black triangles to the right of the bars. Error bars show standard error of the mean. Significant differences between stocks are indicated in lowercase letters above the bars (Repeated measures ANOVA; $p < 0.05$). Stocks for which n < 5 in a majority of years were not analyzed, indicated by "n/a". No significant differences are abbreviated "nsd". (Beckman 2014).
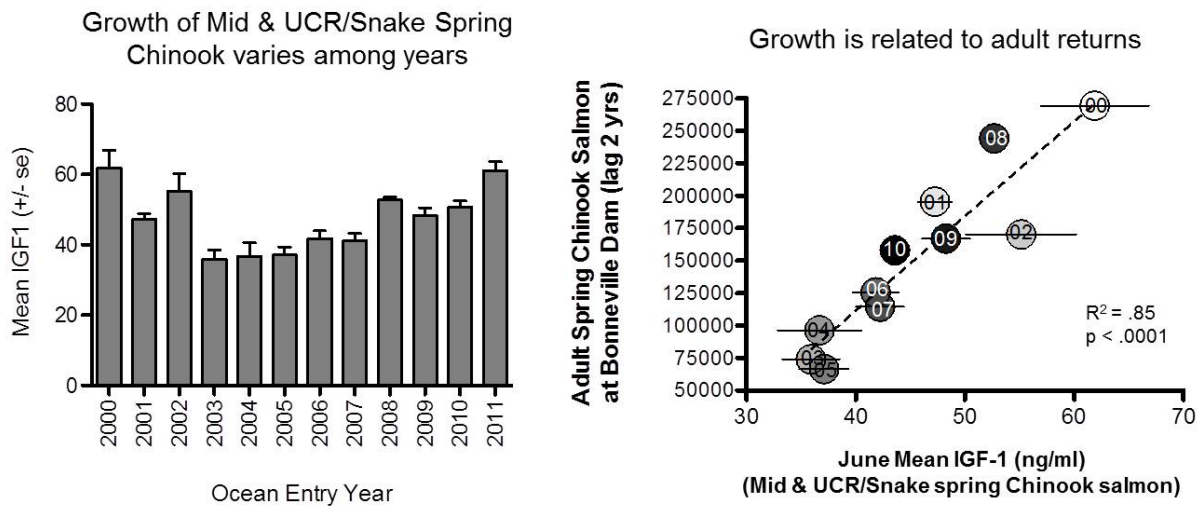
Figure 10. Growth of Spring Chinook salmon for two groups of yearling Chinook salmon from the Columbia River) using IGF-1 hormone showing variations between years and the relationship between growth and adult returns 2 years later. (Beckman 2014).

In general, growth is directly correlated to survival with higher growth rates leading to higher survival. However, the time period and location over which growth can affect salmon survival can vary between populations. Growth that occurs early in ocean life is often positively correlated to survival but the specific ocean period over which this early marine growth occurs can vary considerably between species and population (Mortensen et al. 2000; Mueter et al.

2002; Farley et al. 2007; Wells et al. 2008; MacFarlane 2010; Tomaro et al. 2012; Friedland et al. 2014). For example, Beckman (2014) found that levels of a hormone called IGF that measures growth over an 8-10 day period in May after the fish had just entered the ocean varied between years and were positively correlated to survival in two groups of yearling spring Chinook salmon originating from the Columbia River (Figure 10). Friedland et al. (2014) concluded that sustained growth during the summer and fall months after steelhead from the Keough River, British Columbia, had entered the ocean had a significant effect on survival. Woodson et al. (2013) found evidence that Central California Valley Chinook salmon experienced size and growth rate selective mortality early in their marine life near San Francisco Bay, but only during years of poor ocean conditions. Individuals that were larger and growing faster during freshwater and estuarine rearing were more likely to survive to summer and fall. Beamish et al. (2004) found that growth of Coho salmon over the late fall and winter of their first year in the ocean was related to survival to adulthood while Duffy and Beauchamp (2011) found that growth in summer in Puget Sound was strongly related to survival of Puget Sound Chinook salmon.

Higher growth rates result in greater survival as a result of several mechanisms. First, they can lead to a larger size at age which reduces vulnerability to size selective predators (Mortensen et al. 2000; Moss et al. 2005; Duffy and Beauchamp 2011; Friedland et al. 2014). Studies with a variety of salmonid stocks (including Columbia River spring Chinook salmon) have found that body size and survival are positively related (Bilton et al. 1982; Holtby et al. 1990; Henderson and Cass 1991; Mortensen et al. 2000; Duffy and Beauchamp 2011; Tomaro et al. 2012; Woodson et al. 2013). In a study of SRSS Chinook salmon by Miller et al. (2014), marine growth and size at capture were positivity correlated to survival (Miller et al. 2014). Second, in addition to reducing vulnerability to predators, a larger body size at age can increase reproductive success (e.g., through larger egg size and higher fecundity in larger females) (Quinn 2005).

Growth rates can also affect age of maturation and size at return during some specific life stages in the ocean (Clairborne et al. 2011; Martins et al. 2012). Wells et al. (2007) found that faster growth by Klamath River Chinook salmon during the year before they returned to spawn was related to earlier maturation and larger return size.

Given that growth and mortality can be related during some phases of ocean life, biological and environmental factors that reduce growth rates will be especially relevant to recovery planning (see also following section for discussion of competition effects on growth). One important environmental factor that can affect growth is changes in ocean conditions (shifts from good ocean years to bad ocean years). In general, good conditions for salmon are cooler ocean conditions (such as cool phase of the PDO) or with strong and early upwelling while poor ocean conditions for salmon occur in warmer years or in years with weak upwelling. El Nino events also result in poor ocean conditions for salmon in the NCC.

Martinson et al. (2008) found evidence of density dependent ocean growth in all life stages of Karluk Lake sockeye salmon that varied as a function of ocean conditions. Growth was

negatively related to sockeye salmon abundance during the cool regime and positively related to sockeye salmon abundance during the warm regimes. Woodson et al. (2013) found that growth rate selective mortality in Central Valley Chinook salmon only occurred during years of poor ocean conditions and not during years of good environmental conditions. In general in the NCC, food quantity and quality can be affected by large scale environmental changes such as those resulting from shifts in the PDO or upwelling. In particular, cold phases of the PDO generally lead to higher growth rates (Jacobsen et al. 2012).

Another factor that can affect growth rates is water temperatures because temperature directly affects metabolism of the fish and can affect the quantity and quality of prey available to the salmon (e.g., Mackas et al. 2007; Brodeur et al. 2008; Daly et al. 2013). Temperature affects are complex and are relevant to all ages of fish in the ocean, as Wells et al. (2007) suggested for Klamath River Chinook salmon. It is logical to assume that warmer temperatures can lead to higher growth rates of salmon because of bioenergetics issues. However, temperatures that are too warm can reduce growth rates by impacting the quantity and quality of food that is available; when temperatures reach high enough levels they can also stress the fish which can reduce growth rates (MacFarlane 2010).

The effect of higher water temperatures on growth can vary with species and life history stage (Martins et al. 2012). This is illustrated by the contrast between sockeye salmon and steelhead. In their review of climate effects on sockeye salmon growth and survival, Martins et al. (2012) found that warm water temperatures experienced by smolts in the ocean could increase growth and survival for some stocks (Alaskan) and decrease it in others (Fraser River). Hinch et al. (1995) concluded that warmer water temperatures would depress growth of Fraser River sockeye salmon by increasing metabolic costs in the warmer water temperatures and by reducing the food supply of the sockeye salmon in the areas they occupied. Friedland et al. (2014) found that the return rate of one steelhead population in Canada was negatively correlated with sea surface temperatures in the areas occupied by the steelhead. They suggested that this was due to either temperature effects on growth directly or on food webs on which the steelhead depended. The importance of temperature to steelhead growth and survival is also indicated by the work of Atcheson et al. (2012a) who found that steelhead trout in the North Pacific Ocean had a very narrow range of temperatures in which to achieve optimal growth and were thus sensitive to even small changes in temperature.

In summary, growth is a key attribute of the ocean ecology of salmon and is often strongly related to survival; high growth rates are usually correlated with high survival or adult return rates. The time period over which growth can influence survival rates can vary as a function of species, stock and life history type. The early ocean period is often a critical period for a number of salmon populations. Early ocean growth is often positively correlated to survival but the specific early ocean period over which this early marine growth occurs can vary considerably between species and population. In general, high growth rates are related to survival because they lead to a larger size at age which reduces vulnerability to size selective predators and because they can affect age of maturation and size when the fish return to spawn. Ocean conditions that affect growth can have an important effect on survival. For example, temperature

can affect growth rates by directly affecting metabolism of the fish and the quantity and quality of prey available to the salmon.

5.3. Ecological Interactions

There are three primary ecological interactions that can affect the ocean growth and survival of Chinook salmon, steelhead or sockeye salmon:

1. competition for food

2. predation

3. parasites/disease

All three are natural processes that salmon have evolved with for millennia. Of particular interest about these interactions is not that they occur, but how has our management of the system and the salmon altered these interactions and can we minimize or reduce their impacts to help recover depressed salmon populations.

5.3.1. Competition

Competition for food can be intraspecific (within a species or ESU) or interspecific (between species or ESUs); both can occur at the same time. From the perspective of this module, competition involving the Snake River ESUs can potentially occur during any space/time window after the fish pass Bonneville Dam and until they return to the river as adults and cease feeding. The main concern with competition is that it will reduce growth rates which in turn can affect size at age and survival; as noted previously, smaller fish generally survive less well than larger fish. Relationships between growth, body size/condition, survival, environmental conditions, and competition can be complex, however. For example, in a study of upper Columbia River sub-yearling Chinook salmon in the NCC, Miller et al. (2013) found (counter intuitively) that body condition declined in years that oceanographic conditions were favorable (i.e., there was abundant food). They speculated that this could have occurred for two reasons. (1) When survival was high, competition was occurring and depressing growth rates because fish (i.e., competitors) were abundant. (2) Selective mortality was greater during years of lower survival (i.e., relatively more of the smaller, slower growing individuals die in poor survival years, leaving proportionately more faster growing fish in good condition).

There is a large accumulation of evidence that demonstrates that competition involving anadromous Pacific salmonids occurs under some conditions in both estuarine and ocean ecosystems (Quinn 2005). However, most of this information on competition is not specific to the Snake River ESU's. One of the indicators of competition involving salmon in estuarine and ocean habitats is the occurrence of density dependent growth and survival for co-occurring stocks of salmonids in a particular region. Many studies of density dependent growth and survival in ocean ecosystems are typically correlative. While correlative studies suggest a relationship exists, they do not demonstrate cause and effect. In general, these types of correlative studies find that at high enough abundance/density levels in a particular region (including the estuary), growth declines (i.e., changes in growth are negatively correlated with changes in density or abundance); interspecific or intraspecific competition are the presumed

mechanism explaining the decline in growth as abundance increases (Fukuwaka and Suzuki 2000; Bugaev et al 2001; Ruggerone and Goetz 2004; Beamer et al. 2005; Ruggerone et al. 2005; Martinson et al. 2008).

Correlative studies of density-dependent growth and survival form the basis for much what we know regarding competition involving salmon in ocean habitats. In part, this reflects the fact that it is difficult to establish competition empirically because of challenges associated with measuring such things as abundance of competitors and their prey in the ocean.   Martinson et al. (2008) found evidence of density dependent ocean growth in Karluk Lake sockeye salmon that varied with climatic regime; growth was negatively related to sockeye salmon abundance during the cool regime and lower abundance levels and positively related to sockeye salmon abundance at higher abundances during the warm regimes. Brodeur et al. (1992) suggested that when ocean conditions were unfavorable during the 1983 El Nino, the amount of several key prey taxa were insufficient to sustain the total population of salmon; under these conditions of prey limitation, salmon would be competing. Using growth and abundance data, Pyper and Peterman (1999) concluded that intraspecific competition for food resources in sockeye salmon occurred in the North Pacific Ocean. Bugaev et al.'s (2001) observation that the size of sockeye salmon returning to the Ozernaya River of Russia is reduced in years when sockeye salmon are abundant in the marine environment suggests intraspecific competition was occurring in marine waters.

Much of the evidence involving density dependent effects in ocean habitats is based upon studies involving pink salmon (which are planktivorous) because they undergo large, inter-annual fluctuations in abundance. Welch and Parsons (1993) used isotope analysis and suggested that high overlap and hence competition is most likely to occur between sockeye, pink and coho salmon. Ruggerone and Goetz (2004), however, found that all 13 populations of Puget Sound Chinook salmon appeared to be affected by fluctuations in the abundance of pink salmon. Several studies suggest that sockeye salmon marine growth and survival is reduced in years of high pink salmon abundance (Bugaev et al 2001; Ruggerone et al. 2003). Atcheson et al. (2012b) found that steelhead diets in the Pacific Ocean and GOA varied with abundance of wild pink salmon stocks from Kamchatka. Indicators of good steelhead diets such as a high proportion of squid were negatively correlated with the abundance of pink salmon.

One potential source of competitors for the listed ESU's of the Snake River is the large production of hatchery fish in the Columbia River. The arrival of large numbers of fish in the estuary and NCC within narrow time windows could create conditions whereby hatchery fish might compete with and reduce growth rates of listed populations. If the overall consumptive demand (a function of both fish abundance and fish size) of hatchery fish was sufficient (i.e., how much prey do the hatchery fish eat relative to what is present), growth rates of listed populations could be reduced. This could depend upon environmental conditions, species being considered, relative amount of prey available in the environment, and habitat where the interaction occurred.

Levin et al. (2001) found a strong negative relationship between the survival of SRSS Chinook salmon and numbers of hatchery fish released, suggesting negative effects of hatchery fish were

occurring. Similar effects of hatchery fish on wild fish were suggested by Nickelson (2003) for Oregon coastal Coho salmon. Many diet studies suggest that juvenile hatchery-origin and wild salmon of the same species often have similar diets and high spatial overlap (Daly et al. 2009; Sweeting and Beamish 2009). Thus, if food was limiting in these situations, the likelihood that competition would occur is high. For example, Daly et al. (2012) evaluated a number of parameters associated with hatchery-origin and wild yearling spring Chinook salmon during early marine life to evaluate the potential for competition between these two types of fish. They found that both hatchery and wild Chinook had high dietary and spatial overlap during early marine life as well as similar growth rates. Most importantly, the overlaps in diet and spatial occurrence; size; condition; and growth appeared to change at the same time for both wild fish and hatchery-origin fish and suggested fish were responding synchronously to changes in environmental conditions.

In summary, competition can occur throughout the life cycle of salmon in estuarine and ocean habitats. One of the major indicators of competition involving salmon in estuarine and ocean habitats is the occurrence of density dependent growth and survival for co-occurring stocks of salmonids. These density dependent relationships have been established for a number salmon stocks during ocean life and often involve pink salmon because they undergo large inter-annual changes in abundance. Most evidence that density dependent relationships are occurring are correlative. In general, correlative studies have found that changes in growth are correlated with changes in density or abundance; interspecific or intraspecific competition are the presumed mechanism explaining the decline in growth. One potential source of competitors for the listed ESU's of the Snake River is the large production of hatchery fish in the Columbia River. The arrival of large numbers of fish in the estuary and NCC within narrow time windows could create conditions whereby hatchery fish might compete with and reduce growth rates of listed populations.

5.3.2. Predation

In general, although predation is considered to be a major driver of salmon mortality throughout their entire life cycle, relatively little is known about predator prey interactions in the ocean. While factors such as disease or poor feeding conditions may be the proximate cause of mortality, predation probably represents the ultimate disposal of most salmon. For example, fish that are diseased or starving are more likely to be eaten by a predator. Potential estuarine and ocean predators of salmon include many species of fish, birds, and mammals (Fresh 1997), as well as several invertebrates such as Humboldt squid (Field et al. 2013).

For Columbia River salmonids, considerable attention has focused on effects of predation by birds nesting on islands in the estuary. Caspian terns, several species of gulls, and double-crested cormorants forage on salmon smolts in the Columbia River Estuary (Collis et al. 2001). The effects of these species on anadromous salmon in the Columbia River basin has also increased in recent years as a result of the northern expansion of breeding colonies, especially Caspian terns. Ryan et al. (2003) estimated minimum predation losses in the Columbia River estuary by terns and cormorants of 11.6% for steelhead and 2.6% for yearling Chinook salmon.

Sebring et al. (2013) estimated losses of upper basin sub-yearlings (a mix of stocks including Snake River fish) to be about 2%. These percentages are not trivial and translate into millions of salmon consumed per year by birds from a single rookery.

Although tern and cormorant predation in the estuary have been a primary management concern for Columbia River origin salmon, predation by birds also occurs beyond the estuary and in the plume and ocean. Avian predation outside the estuary is not as well studied. Potential bird predators outside the estuary include common murres, rhinoceros auklets, and shearwaters (Ogi and Tsjita 1973; Lance and Thompson 2005). Near the mouth of the Columbia River, common murres and shearwaters may be especially important predators as both are very abundant during the salmon outmigration and will eat salmon. Salmon were found in 11% of the stomachs of common murres sampled (n = 30) in one year near the mouth of the Columbia River (Zamon 2013). Remains of Chinook salmon, Coho salmon, and steelhead were identified in the murres using genetic markers. Salmon have yet to be found in any of the available samples of shearwater stomachs (n = 37), but a Columbia River steelhead PIT tag was recovered from a shearwater stomach collected in 2007. Zamon (2013) found a significant linear relationship between the density of birds in May of a given year and adult returns at Bonneville Dam for Coho salmon that migrated as juveniles during that year (R_2 = 0.56; P = 0.05). No such relationship has been detected for Chinook salmon, or using bird densities in other months. Indirect evidence that avian predation might be significant near the mouth of Columbia River comes from a study of acoustically tagged fish that found that mortality rates of salmon in this region were high and residence times of the fish were short. These observations are consistent with predation, especially by birds, as the primary cause of the high mortality. Similar to any predator-prey interaction, actual predation losses are a result of the complex interactions of a number of factors such as river flow, salinity, tidal phase, and the distribution of non-salmonid prey species such as northern anchovy (Zamon et al. 2013) (Figure 11).
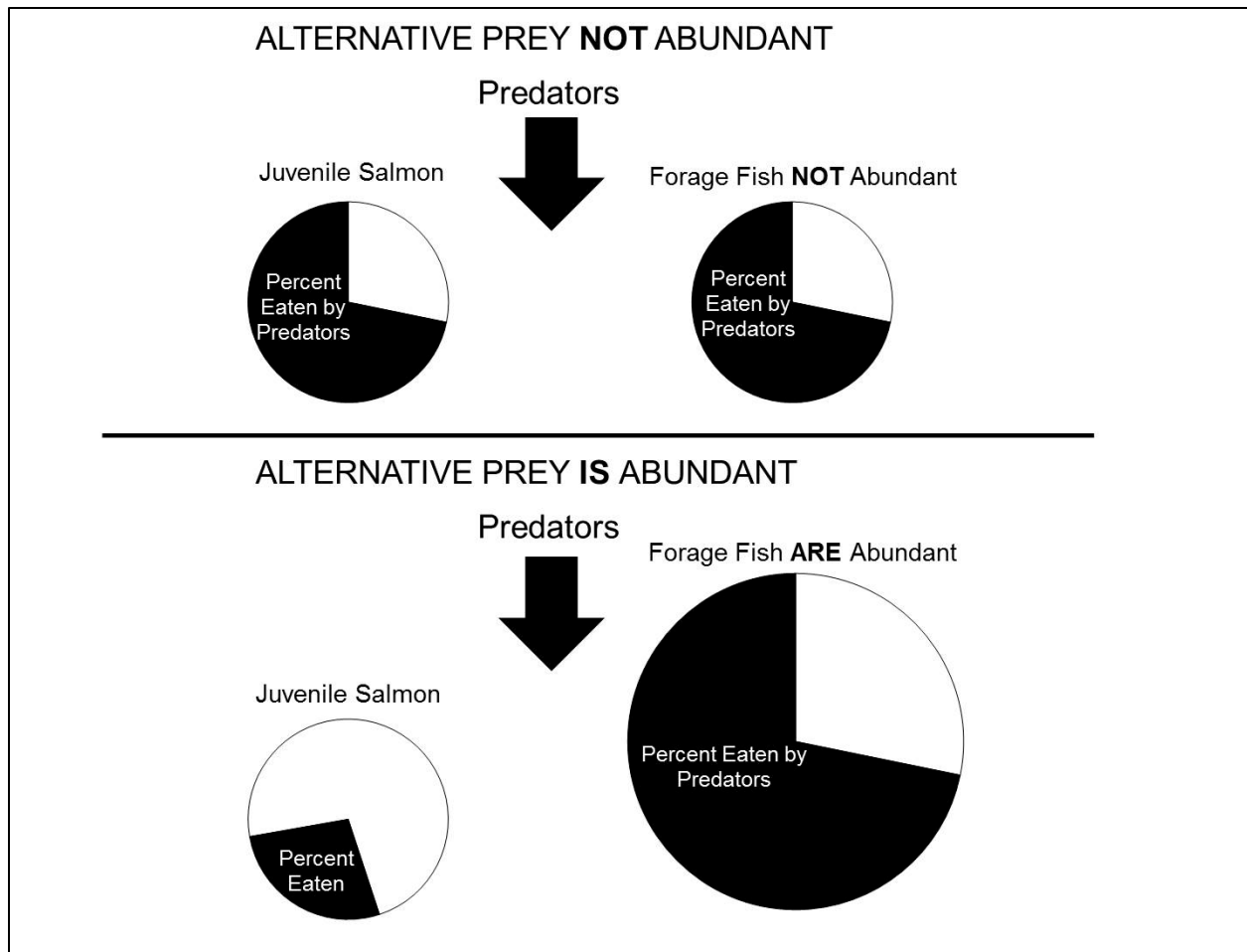
Figure 11. Conceptual diagram showing how changes in the availability of alternate prey can affect consumption of salmon by predators. (Zamon 2013).

Other than avian predators, all salmon species are preyed on at all life stages by a multitude of species such as sablefish (Sturtevant et al 2009), Pacific hake (Emmett et al. 2005), pinnipeds (McKenzie and Wynne 2008), and killer whales (Ford et al. 2006). There may be particular space/time windows, however, where predation levels are especially high. For example, Friedland et al. (2014) concluded that size mediated predation was the most likely explanation for the relationship between ocean growth of steelhead in summer and fall of their first year and their survival. Also, predation is believed to be especially high during estuarine and early marine life (Parker 1968; Pearcy 1992).

Predation rates on salmon will depend on characteristics of predators, their prey and the environment they are occupying (Fresh 1997). For example, faster growing salmon can outgrow their predators more rapidly while larger salmon have a greater chance of out swimming a predator. In the ocean, human induced climate change has the potential to affect predation losses of all populations of salmon juveniles. Environmental conditions in some years can drive predation by particular species such as Pacific hake, mackerel, and Humboldt squid in the NCC

off the coast of Washington and Oregon (Emmett et al. 2006; Emmett and Sampson 2007; Litz et al. 2011). Studies suggest that abundance of these predators is often (but not always) higher in the coastal NCC during warm years of the PDO as these predators move onto the Continental Shelf in warm years where overlap with salmon increases. In colder years, overlap is reduced and abundance of predators declines as piscivores occupy deeper habitats. Given that we can expect a greater frequency of warmer years as a result of climate change, perhaps predation will become a recurring problem, unrelated to the phase of the PDO.

Once adults enter the Columbia River estuary, predation can occur during their upstream migration. The major source of predation in the estuary is harbor seals and sea lions and while predation probably occurs in the entire lower river, it is especially high around Bonneville Dam because fish are concentrated in a smaller area and so more vulnerable to the predators. Stansell et al. (2010) estimated that pinnipeds consumed 4,000-6,000 salmonids per year in the tailrace of Bonneville dam since 2008, equivalent to 2.2 to 2.9% of the salmon run during spring (1 January to 31 May). Wargo-Rub (2011, 2012) provided estimates of adult Chinook salmon mortality during migration through the estuary to Bonneville Dam and although they did not study causes of mortality, losses are most likely due to marine mammal predation.

In summary, predation is considered to be a major driver of salmon mortality throughout their entire life cycle. However, relatively little is known about predation in the estuary and the ocean. Predation rates on salmon will depend on characteristics of predators, their prey and the environment they are occupying. Predation may be especially high during certain space/time windows such as during estuarine and early marine life. In the Columbia River estuary, for example, high predation rates by birds nesting on islands in the estuary have been documented. Factors such as disease or poor feeding conditions may be the proximate cause of mortality, but most salmon that die, probably end up being eaten by a predator. Faster growing salmon can outgrow their predators more rapidly while larger salmon have a greater chance of out swimming a predator. Human induced climate change has the potential to affect predation losses of all populations of salmon juveniles through such mechanisms as changes in temperature regimes.

5.3.3. Pathogens and Parasites

Similar to predators, pathogens can have a significant effect on the survival of juvenile salmon during their estuarine and marine residence (Jacobson et al. 2008). The outcome of an infection by a pathogen or parasite is mediated by interactions among the pathogen, its host, and the environment. A number of pathogens have been reported to affect juvenile salmon during the freshwater migration (Fryer and Sanders 1981; Bartholomew et al. 1992; Ferguson et al. 2011), but little is known about the effects of pathogens on juvenile salmon during early marine residence. The freshwater trematode, *Nanophyetus salmincola*, encysts in all tissues and organs of Pacific salmon. In the NCC, a decline of highly infected Coho salmon was observed between early and late summer (Jacobson et al. 2008). These results suggested that approximately 20% of Coho salmon mortality during the first months at sea was associated with this parasite. Abundances of this parasite are much lower in yearling and sub-yearling Chinook salmon, probably due to differences in freshwater residence and exposure to the infective stages of the

parasite. In steelhead, intensities can be similar, if not higher than in Coho salmon. Preliminary data from steelhead from the lower estuary collected in 2010 had a mean intensity of 1163 cysts in the posterior kidney (from a prevalence of 27%) (Jacobson 2014).

Renibacterium salmoninarum, the causative agent for Bacterial Kidney Disease, has been highly prevalent in Chinook salmon at hatcheries (VanderKooi and Maule 1999), and during migration through the Columbia River estuary (Elliott et al. 1997, Pascho et al. 1993). Infected yearling Chinook salmon collected off of Oregon and Washington from 1999 – 2004 had lower weight residuals (less weight than expected for size) and plasma IGF-1 than uninfected yearlings in all years except 2000 (Sandell et al. In Press). As mentioned above any factors that affect growth and condition of juvenile salmon are ultimately contributing to mortality. Chinook salmon from Snake River stocks were too few in number to analyze separately. In 2008 sample sizes of Snake River fall Chinook salmon were large enough to compare the prevalence of *R. salmoninarum* infection between June and September catches off Oregon and Washington. There was a decrease in prevalence from approximately 60% infected in June to less than 20% infected in September suggesting a loss of infected fish during the first months of ocean residence or of those fish leaving the Columbia River and estuary later in the summer (Jacobson 2014).

5.4. Mortality

In general, mortality rates of salmonids after they leave freshwater can be as high as 95% but vary considerably from year-to-year and between different populations (Parker 1968; Bradford 1995; Moss et al. 2005; Scheuerell and Williams 2005; Williams et al. 2005). Within the estuary, overall mortality rates of salmonids are unknown but an examination of avian predation losses provides some perspective on levels of mortality of salmon in this area (Table 1). Clearly, if predation from other sources were considered (e.g., pikeminnow predation below Bonneville Dam- Zimmerman 1999), mortality in the estuary would be much higher than if only avian predators are considered. Ryan et al. (2003) estimated that tern and double-crested cormorant predation from birds nesting on Rice and East Sand islands in the estuary, ranged from 11.5% to 2.6%, depending on the prey species. In a subsequent study, Sebring et al. (2013) found that predation on Upriver Bright stock groups (a mix coming from above Bonneville Dam that includes Snake River sub-yearlings), by terns and cormorants was low (about 2%). Good et al. (2007) concluded that eliminating even some of the predation mortality from Caspian tern predation in the estuary would assist recovery of Snake River steelhead trout. These benefits were comparable to reducing mortality through the hydropower system.

Table 1. Predation rates on juvenile salmon in the estuary (Zamon 2013).

Group	Caspian tern 2012	Double-crested cormorant 2012
Snake River sockeye	2.1% (1.1%-3.2%)	4.0% (2.2-6.1%)
Snake River spring/summer Chinook	2.2% (1.8%-2.7%)	4.2% (3.4%-5.2%)
Snake River fall Chinook	0.7% (0.5%-0.9%)	3.0% (2.3%-3.8%)
Snake River steelhead	10.0% (8.4%-11.9%)	5.4% (4.0%-7.0%)

Once salmonids enter the ocean, evidence suggests that natural mortality is highly variable and that early marine life is a period of critical mortality for many (but not all) salmonid stocks (Bradford 1995; Scheuerell and Williams 2005; Williams et al. 2005). By critical mortality we mean that mortality is not necessarily the highest at this time but that mortality is highly variable and thus helps set year class strength. Evidence from a wide variety of salmonid stocks, including a number from the Columbia River basin, strongly supports the hypothesis that early marine life is a critical period that can largely determine the strength of adult returns years in the future; and this critical period can range from the first weeks to months the fish are at sea (Beamish et al. 2004; Mueter et al. 2002; Farley et al. 2007; Wells et al. 2008; MacFarlane 2010; Moore et al. 2010; Duffy and Beauchamp 2011; Thomson et al. 2012; Tomaro et al. 2012; Miller et al. 2013; Burke et al. 2013a; Trudel and Hertz 2013). Thus, the condition and size of salmon as they leave the estuary and first enter the ocean may be a prime determinant of subsequent survival. What constitutes early marine life can vary with species, stock, and life history type. Using acoustically tagged fish, Brosnan et al. (2014) found that survival in the "plume" (Astoria Bridge to near the mouth of Willapa Bay) ranged from 0.13 to 0.86 for yearling Chinook salmon

of several different stocks. Because residence times in the plume were so short (an average of 7 days), they concluded that predation was the most likely mechanism explaining this loss. In contrast, Friedland et al. (2014) concluded that the period of critical mortality of Keogh River steelhead was much longer and occurred during the summer and fall of their first year in the ocean.

Most of this "early marine" mortality is thought to occur during two critical periods within the first year of ocean life. The first period is thought to be predation-based mortality that occurs during the first few weeks to months of ocean life (e.g., Brosnan et al. 2014; Friedland et al. 2014). The second period occurs during and following the first winter at sea and is thought to occur as a result of starvation (Beamish and Mahnken 2001; Moss et al. 2005). The hypothesis for the second period is that the fish have to consume enough food during their first spring and summer at sea to achieve a critical size with enough accumulated energy reserves that allows them to successfully survive the winter. Although there is strong evidence that early marine life is a critical period for survival of many salmon stocks, substantial mortality can still occur later in ocean life and more distant from the river of origin (Welch et al. 2011).

Two interrelated factors that can be important determinants of mortality are fish size and growth (Figure 12 and 13). As we noted, mortality can be a function of growth rates and size (MacFarlane 2010; Duffy and Beauchamp 2011). Faster growing fish are less likely to die than slower growing fish although this effect may vary with environmental conditions in the ocean (Woodson et al. 2013). Studies with a variety of salmonid stocks (including Columbia River spring Chinook salmon) have found that body size and survival are often positively related (Bilton et al. 1982; Holtby et al. 1990; Henderson and Cass 1991; Mortensen et al. 2000; Duffy and Beauchamp 2011; Tomaro et al. 2012; Woodson et al. 2013). In general, larger bodied fish are less likely to die than smaller bodied fish although this relationship may not be true under all ocean environmental conditions (Irvine et al. 2013). Healey (1982) showed that significant size selective mortality occurred in chum salmon during their first weeks at sea. Fish size can affect both predation- and starvation-based mortality (Willette et al. 2001).
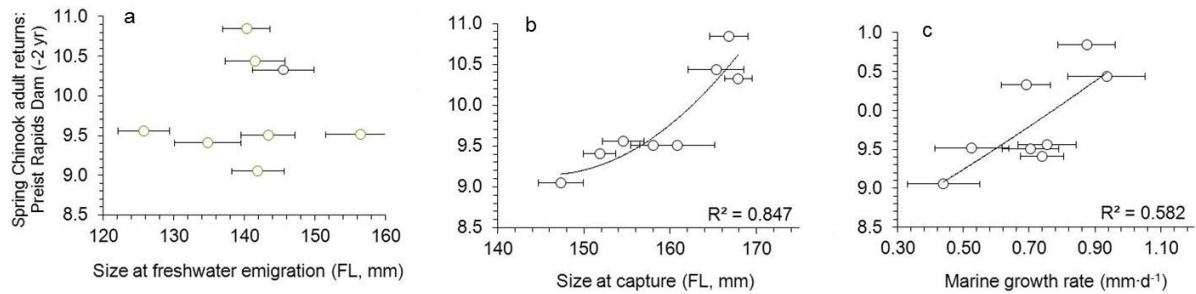
Figure 12. Relationship between adult returns and mean annual size and growth characteristics for juvenile mid-upper Columbia River spring Chinook salmon. Ln-transformed adult returns to Priest Rapids Dam (-2 yr.) versus mid-upper Columbia River mean (±SE) juvenile size at freshwater emigration (a), size at capture (b), and marine growth rate (c). Lines represent linear or polynomial fit. Juvenile collections occurred in 1999-2000, 2002-2004, and 2006-2008. (Jacobson et al. 2012)
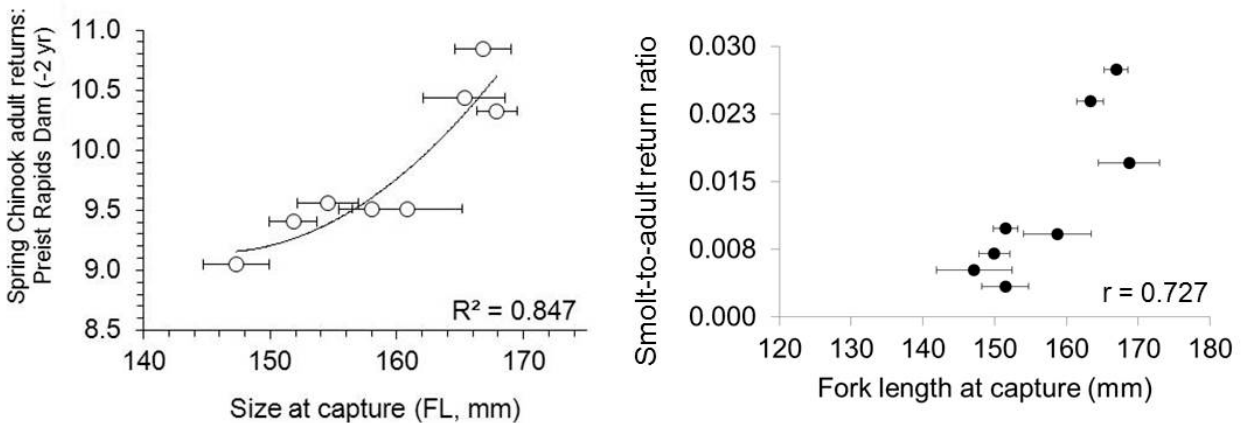
Figure 13. Relationship between Ln-transformed adult returns to Priest Rapids Dam (-2 yr) and mean annual size (±SE) at capture for juvenile mid-upper Columbia River spring Chinook salmon versus (left); and relationship between survival (back-transformed SAR) and size at capture of juvenile Snake River sp/su Chinook salmon. Juvenile collections occurred in 1999-2000, 2002-2004, and 2006-2008. (Jacobson et al. 2012).

Salmon size can be important to mortality because swimming speed is related to fish size which in turn is related to a fish's ability to evade predation. Also, high growth rates allow fish to outgrow their predators: get large enough such that predators cannot grasp, handle and eat the salmon. Thus, ocean conditions that lead to slower growth would be expected to reduce fish size and increase mortality during early marine life (Pearcy 1992; Beamish et al. 2004; Cross et al. 2008; Woodson et al. 2013).

Salmon and steelhead mortality can be affected by a number of environmental and biological factors (Fresh 1997), including factors associated with freshwater. One hypothesis is that passage through the hydroelectric dams can result in mortality that is delayed until well after the fish leave the Columbia River basin (Reichisky et al. 2014; Schaller and Petrosky 2007; Schaller et al. 2014). In addition, how the fish get to the estuary and migrate through the estuary may be important as well. In particular, some research suggests that salmon that are transported through

the hydrosystem perform less well than fish that freely migrate (e.g., Muir et al. 2006; Reichisky et al. 2014; Haeseker et al. 2012; Schaller et al. 2014). How the fish migrate through the complex system of channels in the estuary can affect survival. Harnish et al. (2012) used acoustic transmitters to evaluate mortality and travel times in different reaches for sub-yearling and yearling Chinook salmon and steelhead. They found differences in mortality were a function of pathway used; fish using the fastest pathways (the main channel) did not necessarily have the highest survival.

Interestingly, some evidence suggests flow may have an influence on marine mortality rates. Studies by Petrosky and Schaller (2010) and Haeseker et al. (2012) suggest that flow during seaward migration can affect marine survival of Snake River steelhead and SRSS Chinook salmon with lower flows correlated with reduced marine survival; however, it is not clear what the mechanism is explaining this result. Flow can also influence arrival timing in the estuary, as can transportation, which can both affect subsequent mortality (Scheuerell et al. 2009; Tomaro et al. 2012). Flow also affects plume characteristics (Burla et al. 2010) which can affect salmonid survival. Miller et al. (2013) found that returns of upper Columbia sub-yearling Chinook salmon to Priest Rapids Dam were related to plume volume at the time of emigration in most years studied.

During estuarine and marine life, fluctuations in environmental conditions can affect mortality rates. As noted previously, mortality can vary between good and bad ocean years (Cross et al. 2008; Woodson et al. 2013). In their review of climate effects on sockeye salmon growth and survival, Martins et al. (2012) found that warm temperatures could increase survival for some stocks (Alaskan) and decrease it in others (Fraser River). They speculated that temperature might be a proxy for regional mechanisms affecting marine survival (Mueter et al. 2002).

Although most studies have focused on mortality in juvenile and sub-adult life stages, adult mortality due to marine mammal predation can occur throughout ocean life and in the estuary. Wargo-Rub et al. (2012) estimated stock specific mortality of spring Chinook salmon in the lower river (to Bonneville Dam) and found that for Snake River spring Chinook salmon, survival to Bonneville Dam in 2011 was 86% for the season but varied over time with higher mortality occurring in the middle part of the run. Stansell et al. (2010) examined mortality specifically in the tailrace of Bonneville Dam and estimated that pinnipeds consumed 4,000-6,000 salmonids per year in the tailrace of Bonneville dam since 2008, equivalent to 2.2 to 2.9% of the salmon run during spring (1 January to 31 May).

In summary, salmon experience high (up to 95%) and variable mortality from the time they pass Bonneville Dam until they return as adults. Mortality rates vary as a function of species, stock, life history type, ecosystem the fish occupy, characteristics of the salmon such as fish size, and environmental characteristics. For example, warm ocean temperatures can increase survival for some sockeye stocks (Alaskan) and decrease it in other sockeye (Fraser River). Fish size and growth are often correlated with mortality with large size and fast growth related to high survival. Early marine life appears to be a critical period of mortality for many groups of salmon, especially yearling groups of Chinook salmon. By critical mortality we mean a period

where mortality is not necessarily the highest is highly variable and thus helps set year class strength. Depending on the species and origin, the period defined as early marine life can vary from the first days the fish are in the ocean to months later. Significant mortality for some species/stocks can occur, however, later in ocean life, such as for steelhead and sockeye.

5.5 Habitat Use

In the estuary, fish can potentially occupy a wide range of habitat types that range from shallow, vegetated wetland areas to the deep, more open waters of the main channels. Habitat use varies as a function of species and life history type and is strongly related to fish size; species and life history type are all interrelated, however. In general, the smaller fish (typically sub-yearling Chinook salmon) are more closely associated with either shallow open beaches or wetlands (Roegner et al. 2012) while most of the larger bodied fish (including steelhead, sockeye and yearling Chinook salmon) are associated with deeper channel areas (such as the main navigation channel). Many of the larger bodied fish appear to primarily use the lower river/estuary as a migration corridor as evidenced by their very rapid migration through the estuary. Travel times of < 7 days from Bonneville to Rkm 15 are not uncommon for steelhead and yearling spring Chinook salmon. However there is considerable variability in migration rates of individual fish and there are some yearlings found in wetland habitats. Variable migration rate and use of alternate habitats contribute to the diversity and spatial structure of the populations, which are important elements of recovery. In addition, the compressed migration window demonstrated by most yearling migrants means use of shallow water habitat may have been unappreciated when fish sampling periods and migration timing were not synchronized (Roegner et al. In Prep).

For yearling Chinook salmon and steelhead, feeding intensity (relative amount of food in stomachs) increased as the fish migrated downstream from Bonneville Dam and into the estuary (Weitkamp et al. In Review). Similarly, for steelhead, feeding intensity increased as the fish moved from the estuary and into the NCC with steelhead in the estuary consuming fewer types of prey and having less full stomachs than fish captured in the NCC (Daly et al. 2014).

The long period of residence of sub-yearling fish in the estuary and diversity of sizes that are present (Weitkamp et al. In Review) suggests the sub-yearlings in the estuary are probably a mix of fish actively migrating to the ocean and fish that are rearing for some period in shallow water habitats (Roegner et al. 2012). Sub-yearling sized Chinook salmon dominate catches in shallow, open beach areas and shallow tidal channels in different types of wetlands (Bottom et al. 2011; Roegner et al. 2010; 2012).

Within any part of the ocean, there is habitat structure with respect to such factors as depth of the bottom, distance to shore, water quality conditions (temperature and salinity), currents and eddies. How fish respond to these factors is poorly understood but depends upon their species and population, fish size, ocean entry time and other factors. Close to the estuary, the plume provides strong habitat features with respect to temperature and salinity. The potential benefits of inhabiting the plume have not been quantified for juvenile salmon, although work by Burla et al. (2010) suggests that under some conditions, the plume may benefit steelhead. We know that for spring Chinook salmon from the upper Columbia River, plume volume at the time of emigration is correlated with size at capture which is strongly related to adult returns two years later (Tomaro et al. 2012). It is not clear, however, why plume volume is important to salmon or if it is a surrogate for something else that the fish are responding to. The turbid, low-salinity water masses may provide shelter from many marine predators, aid in the physiological

transition from smolt to fully seawater adapted animal, and may create favorable feeding habitats in areas where plume water converges with shelf water to form highly dynamic turbidity fronts. Previous studies have shown that relatively high numbers of Coho and Chinook salmon smolts are present in the Columbia River plume off Oregon and Washington (Fisher and Pearcy 1995). Studies in other river plumes have demonstrated that elevated levels of potential prey items can occur in frontal regions (Grimes and Finucane, 1991; Grimes and Kingsford 1996).

Outside the plume, habitat factors that can be important to the salmon depend on species and life history. Yu et al. (2012) used a modeling approach to suggest that Chinook salmon yearling distribution (no stock assignments were done) was primarily a function of environmental factors such as temperature and chlorophyll in addition to long shore currents. They also concluded that different habitat factors affected fish north and south of the Columbia River. Although associations with habitat characteristics were probably not spurious, this approach oversimplifies the dynamics of fish in the midst of a migration. In a follow-up study, Burke et al. (2013a) used a different modeling approach and concluded that geospatial factors were more important than environmental factors. In essence, they found that fish were not selecting particular types of habitat per se but were migrating first and then responding to what they encountered second. There may be differences between the species in habitat use. Sub-yearlings may respond differently to environmental factors since they tend to not migrate as far north and are associated with the shelf area longer. Tomaro et al. (2012) showed that juvenile salmon moved slower off the coast of Washington when growth conditions were good than when they were bad.

In the North Pacific, temperature appears to be an especially important habitat factor. The importance of temperature is especially true for steelhead who have a narrow range of optimum temperatures (Atcheson et al. 2012b) and appear to be primarily restricted in the their distribution to surface waters in a narrow north-south band across the Pacific Ocean (Welch et al. 1998).

5.6 Habitat Connectivity

Although we often consider each habitat the salmon occupy in isolation, it is clear that there are physical and biological connections between habitats and the fish that occupy them. Physical connectivity includes tidal action that can push saltwater well upstream and change salinity regimes in the estuary which can have physical and biological manifestations. Freshwater discharged into the Pacific Ocean in combination with coastal winds creates the plume environment (Horner-Devine et al. 2009). The influence of the plume is not limited to the area near the mouth of the Columbia River but it can extend over broad areas off the Washington and Oregon Coasts because the plume can break apart and pieces can be found hundreds of miles from the mouth of the river (Hickey 1989). A significant portion of the plume volume (67%- Baptista 2013) is a function of river flow. The plume does not simply affect the area near the river's mouth but can affect much of coastal Washington depending on its volume, winds, and other physical factors (Hickey et al. 2009). We know that for spring Chinook salmon from the upper Columbia River, plume volume at the time of emigration is correlated with size at capture which is strongly related to adult returns two years later (Tomaro et al. 2012). Similarly, Miller et al. (2013) found that returns of a population of unlisted mid-upper Columbia sub-yearling Chinook salmon to Priest Rapids Dam were related to plume volume at emigration, in most years.

Another example of physical connectivity is climate processes such as El Nino and La Nina events and the PDO which can affect both ocean and terrestrial processes. Ocean and land temperatures can both be affected at large spatial scales by the same climate processes such as the PDO (see following section). On land, climate-induced changes can alter the proportion of freshwater that enters the Columbia River via snow-pack vs rainfall. This change in water supply can affect what is discharged into the ocean which may change the physics and ecology of the coastal ocean environment, which in turn can affect the behavior, growth, and survival of the salmon (Bisbal and McConnaha 1998; Burla et al. 2010; Miller et al. 2013).

Freshwater, estuary, and ocean ecosystems are also connected biologically. One example is the transport of nutrients from the ocean back to freshwater by spawning adults (NRC 1996). Humans both directly and indirectly affect the performance of salmonids while they are at sea (Bisbal and McConnaha 1998) by controlling fish size, timing of ocean entry, density of salmonids in the estuary and ocean, and condition of the fish. Changes in all these parameters can influence growth and survival of the salmonids during later life stages (Scheuerell et al. 2009; Tomaro et al. 2012). For example, mean body size at ocean entry and early marine growth in yearling Chinook salmon (hatchery-origin) was positively correlated with adult returns (Claiborne et al. 2011) while body condition of sub-yearling Chinook salmon has been correlated with adult returns in some Columbia River Chinook salmon (Miller et al. 2013). A number of studies have shown that manipulations of the time and size at which salmon enter the ocean (most obviously with hatchery origin fish) can affect adult return rates (Bilton et al. 1982; Holtby et al. 1990).

6. Anthropogenic Risks to Salmon During Estuarine/Ocean Life

6.1. General

Salmon populations are subject to a wide variety of risk factors that can diminish their viability or ability to persist over time. Many of these factors are naturally occurring while others result directly or indirectly from the actions of people. Further, risk factors operate at various spatial and temporal scales, can have cumulative effects, and will differ in their implications for population viability of an ESU, DPS, or population. We use the definition of viability developed by McElhaney et al. (2000) to guide recovery as encompassing four population attributes: abundance, productivity, spatial structure, and diversity.

While naturally occurring risk factors (e.g., PDO) are important determinants of population viability, we focus this discussion on anthropogenic factors. While harvest can clearly affect population viability, it's implications to listed Snake River salmonids are covered in other parts of the recovery planning process and are not considered further here. We also do not consider effects of the hatchery program as this is again part of other analyses. The effects of many potential risk factors are still not well understood. For example, while we have surveys of where toxics occur in some areas, we do not fully understand at what concentrations they are an issue for fish. We have focused much of this discussion of risk factors on climate change because of the potential of this factor to have broad scale impacts throughout the salmon life cycle and because recent analyses highlight the threat posed by climate change on our marine and estuarine ecosystems (e.g., Halpern et al. 2009).

Although our focus here is on climate change, we note that several large scale analyses of risk factors affecting salmonid populations have recently been conducted. In the estuary, Fresh et al. (2005) considered the effects of four estuarine risk factors on different Columbia River basin ESUs- flow, predation, habitat and toxics/contaminants. The estuary module further summarized the work of Fresh et al. (2005) who selected their four risk factors from a larger list because they met four criteria: 1) the factor could be linked to the hydropower system, 2) there was quantitative data, 3) a significant change in the factor was evident from historical conditions, and 4) the factor could be linked to population viability of salmonids.   Several important factors, notably temperature changes were not considered in this analysis. This analysis concluded that for yearling dominated populations, flow and habitat had a high ability to affect population viability. In contrast, none of the four factors were considered to have a high ability to affect viability of sub-yearling dominated populations (Fresh et al. 2005). More recent studies (since Fresh et al. 2005 was published) suggest that for yearling ESUs, predation by birds in the estuary may be a higher risk factor than previously considered (Sebring et al. 2013) given the high predation rates found in these studies. Habitat remains a high risk factor. Recently published studies of contaminant/toxic effects found that fish may acquire high levels of some pollutants in the upper river before they enter the estuary (Strickland et al. 2011). Johnson et al. (2013) found

the greatest uptake of pollutants in ESUs dominated by sub-yearlings, likely because individuals from these ESUs tend to have a longer residence time in the estuary.

In the California Current, analyses of risk factors have been conducted by Halpern et al. (2009) and the Integrated Ecosystem Assessment program of NOAA. None of these analyses have been specific to salmon at this time. Halpern et al. (2009) evaluated cumulative effects of 25 human activities in 19 types of marine ecosystems and concluded that factors associated with human population centers and the continental shelf were of the most concern.

6.2 Climate Change

The effects of changing climate conditions on salmon and their ecosystems, especially those associated with anthropogenic drivers, are of considerable interest to salmon managers and ecosystem scientists. In this section, we consider some of the implications of climate-driven changes occurring in the Columbia River estuary and the ocean on anadromous salmonids. Although our focus here is on effects in the ocean and estuary, the overall effect of climate change on any anadromous stock must consider all habitats and life stages simultaneously and cumulatively (Crozier et al. 2008; Healey 2011; Wainwright and Weitkamp 2013). The scope and magnitude of any affect experienced by salmon will be a function of how the climate actually changes (e.g., rate and magnitude), how these changes ultimately affect physical and biological processes, and the stock/population being considered (Tolimieri and Levin 2004). Many of these processes interact, making predicting effects of climate change especially problematic (Crozier et al. 2008).

Although there is only a limited amount of information specific to climate change effects on the Snake River ESU's (but, see Columbia River basin review by Independent Scientific Advisory Board [ISAB] 2007), there is a large and expanding literature on climate change effects in general on salmon (e.g., Schindler et al. 2008; Crozier et al. 2008) and ecosystems (e.g., see review by Griffis and Howard 2013 for a nation-wide perspective and King et al. 2011 for a 'California Current' perspective). Wainwright and Weitkamp (2013) summarized the potential physical changes that could potentially result from the effects of climate change on Oregon coast Coho salmon; although developed for Coho salmon, this synopsis provides useful guidance for considering climate change effects on Snake River salmonids. Table 2 summarizes the major physical trends in estuaries and oceans that are likely to affect Snake River salmon. There is considerable published work on the effects of climate change on salmon in freshwater environments (reviewed by ISAB 2007 and Crozier et al. 2008), and these are not detailed here. We first review effects in estuaries, then in the ocean.

6.2.1 Estuary Effects

Within the Columbia River estuary, changes in temperature, flow, and sea level (water level in the estuary) are the primary physical factors responsive to a changing climate. The water temperatures in the estuary will increase both as a result of continued increases in water temperature in the Columbia River basin and because of increases in ocean water entering the estuary. Over the last 60 years, there has been a steady increase in temperature of water entering the estuary as a result of such basin scale changes as precipitation increasingly falling as rain rather than snow in higher elevations, snow pack decreasing, peak flows increasing, and late-summer/early fall flows diminishing (ISAB 2007).

Table 2. Physical and chemical climate trends in estuaries and the ocean that may affect Snake River salmon (from ISAB 2007; Wainwright and Weitkamp 2013).

Region	Climate Trend	Certainty of Change
Estuary		
	Increasing sea level	High
	Increasing water temperature	Moderate
	Changing seasonal freshwater flows	Moderate
	Changing saltwater intrusion limit	Low
Ocean		
	Increasing water temperature	High
	Intensifying upwelling	Moderate
	Later spring transition	Low
	Intensifying stratification	Moderate
	Increasing acidity	High

Temperature changes can potentially affect all ESU's and life stages. First, we can expect changes in the amount of time juvenile salmon (primarily sub yearling Chinook salmon) occupy certain shallow water wetland habitats (i.e., tidal fluvial habitats) due to increases in temperature. What is especially critical is the amount of time temperatures will exceed sublethal and lethal thermal limits the Chinook salmon have. There are already time periods during summer and fall that juvenile salmon are not present in some estuarine habitats due to temperatures exceeding stressful thresholds. Roegner et al. (2012) found that at temperatures over 19 C, juvenile Chinook salmon tended to avoid estuarine wetlands. Thus, we can expect the duration of time juvenile salmon spend in these wetlands to decrease as temperatures increase.

Second, before temperatures exceed thermal limits, we can expect other thermal responses to occur. In particular, all species and life stages will respond bioenergetically. For example, yearling size fish will encounter elevated temperatures during their migration through the estuary that can affect their metabolic rates while sub yearling Chinook salmon can encounter elevated but not stressful temperatures in wetlands. At more modest temperature increases, growth rates of salmon may actually increase, assuming food resources do not diminish. Roegner and Teel (In Press) found that the condition of sub-yearlings was higher at summer temperatures > 19°C than during cooler temperatures in spring. High food levels may have offset the negative effects of temperature induced metabolic demands. By contrast, many salmon stocks, particularly yearling migrants, moved through the estuary before temperatures reached stressful levels. It is unclear how migration and rearing timing will adapt to changes in the estuarine temperature regime.

Third, we can expect some temperature mediated changes to occur in the food web of the estuary. There may be changes in the community structure of invertebrates available to the

salmon to feed on as well as in the plant communities in the estuary. It is not clear what these temperature related changes will be and the net effect of thermal changes on the estuarine food web. There are many uncertainties associated with this type of change such as how tolerant different organisms are to temperature changes.

The second major type of physical change that will impact the Columbia River estuary is sea level rise. As the level of the sea rises a number of changes can be expected. For example, tidal wetlands may become submerged or have longer periods of inundation than they do currently, and nearby terrestrial habitats will be flooded (Kirwan et al. 2010). In other cases, shallow water habitats such as wetlands may erode as sea levels rise. Diking and other barriers may prevent wetlands from expanding and keeping up with erosion impacts. The net effect of these processes on estuarine habitats depends on the rate of sea level rise, the rate of vegetation growth and sedimentation, and the land contours in and adjacent to the estuary (Roessig et al. 2004; Kirwan et al. 2010). The global rate of sea level rise is currently faster than the colonization rate for new wetlands (Roessig et al. 2004). The Chesapeake Bay has already experienced massive wave induced erosion of marsh areas due to a rising sea level (Stevenson et al. 2002). These types of change will clearly depend upon the rate and magnitude of sea level rise with effects varying with season and flow patterns.

The biological characteristics of affected wetlands and other shallow water habitats will be altered by climate change (Stevenson et al. 2002). Because Bonneville Dam acts as a barrier to the propagation of upstream increases in sea level, it is likely that the physical and water characteristics of the mouths of rivers below Bonneville Dam will change. Rising sea levels will push the saline portion of the estuary upstream into freshwater areas and change the location of freshwater-saltwater ecotones (Flitcroft et al. 2013). Such changes will affect how these estuarine habitats function for salmon. For example, the head of tide in tributaries to the Columbia River such as the Lewis and Cowlitz rivers will move upstream in these tributaries with accompanying changes in physical structure of the estuary (due to changes in the tidal prism) and biological characteristics of these river mouth systems. This type of change is expected to be slow as at the present rate of rise of 3 mm per year, it will be 50 years before a rise of 150 mm (6") is seen.

A third type of change that can affect salmon in the estuary (and the coastal plume) is flow-related changes below Bonneville Dam which can occur as a result of changes in precipitation patterns and water management practices. Climate forecasts for the Pacific Northwest suggest that there will be a reduction in precipitation that occurs as snowfall and an increase in rainfall, which would increase winter flow levels and diminish summer flows. Coupled with increased temperatures, such a scenario could critically limit salmon migration periods. In the estuary, there is a relationship between flow, tides, and salinity at any point. Changes in salinity (e.g., either the upstream extent of measurable salinity or the regime at any particular place) will depend on freshwater flow, tides, and basic sea level rise (polar and glacial melting). As we noted, changes in salinity or water levels in the estuary will alter the biological community structure as well as accessibility of these locations to salmon. Flow changes are also important in terms of downstream fish migration rates through the estuary. Reduced flows during the time

salmon are outmigrating, for example, could slow the downstream migration of salmon and affect their timing of ocean entry. Given the rapid migration of larger, yearling sized fish, it is not clear if flow related delays of hours or days would result in changes to growth and survival.

6.2.2. Ocean Effects

Salmon can potentially be affected by climate driven changes in the ocean's physical (e.g., temperature, circulation, stratification, upwelling), chemical (e.g., acidification, nutrient input, oxygen content), and biological (e.g., primary production, species distributions, phenology, foodweb structure, community composition and ecosystem functions/services) components and processes (Griffis and Howard 2013; Doney et al. 2014). The major physical changes in the ocean that are of concern from the perspective of climate change are higher ocean temperatures, intensified upwelling, delayed spring transition, intensified stratification, and increased ocean acidity (Wainwright and Weitkamp 2013). Although these are variables of concern, there is little direct information on if and how changes in these physical factors would impact salmon. This is due in part because global climate models continue have such coarse resolution that the California Current is not well resolved by these models, thus we cannot yet draw inferences from the global models. In addition and perhaps most importantly, the key physical drivers of productivity in the California Current, the NPGO, the PDO, the ENSO and coastal upwelling are not resolved by the current generation of climate models, so we have little idea how these drivers will change in the future. Sydeman et al. (2013) examined recent variations in the NPGO, PDO, and ENSO in relation to biological variables in the California Current. They found no changes in variability of PDO or ENSO, but an increase in variability in the NPGO, as well as an increased importance of the NPGO in explaining biological variation.

The effects of temperature changes in the ocean on salmon have received the most attention from scientists. Water temperature has a strong effect on fish physiology, development, distribution, and behavior (e.g., Marine and Cech 2004; Richter and Kolmes 2005). As ocean temperatures warm a number of things will occur that will ultimately reduce survival rates of some anadromous populations. Effects of ocean warming are suggested for a number of different salmon and steelhead stocks including Snake River steelhead and Chinook salmon (Petrosky and Schaller 2010), Fraser River sockeye salmon (Hinch et al. 1995), Central Valley Chinook salmon (MacFarlane 2010), and steelhead in general (Welch et al. 2000). In particular, we can expect metabolic rates to increase such that growth will be impacted (Hinch et al. 1995). This will also affect adult size at age and age at maturity, which in turn may have consequences for fecundity, migration ability, and ability to dig spawning redds.

One of the mechanisms by which warming water temperatures will affect salmon is by changing bioenergetics of the fish. Diet information on yearling Chinook salmon from 19 years of ocean research indicates that during warmer ocean years, juvenile salmon consume 20-29% more food than in the colder ocean years and are in significantly lower body condition (Daly and Brodeur 2014). Research also suggests that the biomass of fish prey is reduced during warmer ocean conditions at the same time that the salmon are consuming more food (Daly et al. 2013; Daly and Brodeur 2014). This food stress, along with direct effects of temperature on physiology, can shift

competitive responses and increase predation risk for salmonids (Reeves et al. 1987; Marine and Cech 2004).

Increasing ocean temperatures will also change food web relationships involving salmon, especially as ranges shift for predators, competitors, and prey (e.g. Murawski 1993; Hays et al. 2005; Cheung et al. 2009). For one, as ocean temperatures warm, the quantity and quality of salmon food will change. Locally, Francis et al. (2012) predict that changes in marine zooplankton community structure will occur as climate changes. In general, when water temperatures are warmer in the NCC (e.g., a warm phase of the PDO), food quantity and quality are diminished and salmon growth declines. Thus, one effect of warming in the NCC could be lower early marine growth of salmon which can in turn reduce survival of some ESUs. Another temperature related response associated with the food web is expected to be changes in predator distribution and abundance. For example, hake tend to be more abundant in shelf wasters when water temperatures are warmer (Emmett and Brodeur 2000). As water temperatures warm, hake may become prevalent in more years on the Shelf and increase their predation on salmon. The critical factor here is not necessarily *if* hake are on the shelf, but *when* they arrive in shelf waters relative to when juvenile salmon enter the ocean. Cleary, if juvenile salmon migrate to the ocean in late-April/early-May and if hake arrive in June, there is a mismatch which favors salmon. Global warming may result in salmon leaving the rivers earlier (because the rivers will warm faster than will the ocean) and migrating at a different rate that they did historically. The potential problems associated with 'hake-salmon' interactions may actually diminish in the future if fish enter the ocean earlier and/or migrate faster from the region.

Overall, the combination of these temperature effects will result in changes in the range of the species. Temperature is a main factor determining the northern and southern limits of fishes in the California Current (Horn and Allen 1978). Climate-driven range shifts in marine fishes have been observed (Hsieh et al. 2009) and predicted for the future (Cheung et al. 2009). Such range shifts for Pacific salmon have been observed in past periods of climate change (Ishida et al. 2009) and are occurring now (Irvine et al. 2009). For the future, Abdul-Aziz et al. (2011) illustrate this point for Pacific Northwest salmon by showing how climate scenarios can result in a dramatic contraction (30-50% by the 2080s) of the summer thermal range suitable for chum, pink, Coho, sockeye and steelhead in the marine environment. They predict an especially large contraction (86-88%) of Chinook salmon summer range under two commonly-used IPCC (2007) greenhouse gas scenarios. Previous analyses focusing on sockeye salmon (Welch et al. 1998) came to similar conclusions.

A consequence of northward shifts of suitable salmon marine habitats is that populations near the southern limit of their species' range will be more susceptible to climate change than those near the species' center of distribution. The Columbia River Basin supports the most southerly populations of sockeye salmon, which suggests that Snake River sockeye salmon may be more susceptible to these effects than either Chinook salmon or steelhead. Maintaining Snake River sockeye salmon under future climate conditions may require greater improvements in freshwater habitat and the river migration corridor than other Snake River ESUs.

Beyond water temperature, other climatological changes in the California Current are also likely to affect Snake River salmon. The timing and intensity of upwelling has an important but complex relationship to salmon production (section 3.5). There have been observed increases in upwelling intensity (Bakun 1990) and shifts in timing of spring transition and the total length of the upwelling season (Bograd et al. 2009), but analyses using climate models find little agreement on future changes in upwelling, largely because current models do not have sufficiently fine scale to resolve coastal wind and circulation processes (Diffenbaugh 2005). Upwelling of nutrient-rich water is also limited by the degree of water-column thermal stratification (Kosro et al. 2006), which is expected to increase as surface waters warm (e.g., Di Lorenzo et al. 2005). A final major issue for coastal waters is acidification as a consequence of increasing atmospheric CO_2; increasing acidity is already being observed in the California Current System (Hauri et al. 2009). Acidification will likely have little direct effect on salmon, with the exception of some possible biochemical stress (Fabry et al. 2008). However, it may have a dramatic impact on invertebrates that are important in salmon food webs (Fabry et al. 2008); the consequences for salmon depend on potentially complex shifts in prey availability and abilities of salmon to shift diets.

It should be noted, however, that biological effects of climate change, whether in estuarine or ocean environments, are extremely difficult to predict. The rapid expansion of Humboldt squid—a voracious predator-- along the West Coast of North America in recent years and their population explosion in 2009 (Field et al. 2013), remind us that although physical processes are more straightforward to predict, the response of biological systems to physical changes are much more difficult to predict.

Finally, there is a potential for complex salmon life-history changes in response to a changing climate. Many stocks of salmon have evolved to migrate long distances in the marine environment. Presumably, this is because the high metabolic cost of migration was offset by better growing conditions in more northern habitats. If productivity near the destination of a migration decreases due to an altered climate, the "expected" benefit in terms of growth may not be achieved, and the high cost of migration may not pay off in terms of an evolutionary strategy. Moreover, if warmer temperatures results in a larger predator population in northern latitudes survival for migrating individuals could decline, again resulting in long marine migrations becoming less productive.

6.2.3. Integrated Effects

So far, we have discussed a number of individual climate factors that affect salmon in certain habitats or specific parts of their life cycle. In order to fully assess the consequences of climate change, we need to consider the interactions of all the individual effects as they multiply across life stages within generations and across generations within populations (Wainwright and Weitkamp 2013). While many of the effects described above are difficult to project with much certainty, most are more likely than not to have negative effects on salmon growth and survival. Thus, the overall consequences of climate change for Snake River salmon are likely to be

negative, and will require management strategies that increase resiliency of these ESUs over the foreseeable future.

6.3. Summary

In summary, salmon populations are subject to a wide variety of risk factors during their estuarine and ocean life that can diminish their viability or ability to persist over time. Many of these factors are naturally occurring while others result directly or indirectly from the actions of people. Further, risk factors operate at various spatial and temporal scales, can have cumulative effects, and will differ in their implications for population viability of an ESU, DPS, or population. OF these risk factors, climate change effects in the estuary and ocean have received considerable attention. Within the Columbia River estuary, changes in temperature, flow, and sea level (water level in the estuary) are the primary physical factors responsive to a changing climate. In the ocean, salmon can potentially be affected by climate driven changes in the ocean's physical (e.g., temperature, circulation, stratification, upwelling), chemical (e.g., acidification, nutrient input, oxygen content), and biological (e.g., primary production, species distributions, phenology, foodweb structure, community composition and ecosystem functions/services) components and processes. Most of these risk factors are very poorly understood. Temperature changes have received the most attention. The scope and magnitude of any affect experienced by salmon will be a function of how the climate actually changes (e.g., rate and magnitude), how these changes ultimately affect physical and biological processes, and the stock/population being considered. It is important to keep in mind that the overall effect of climate change on any anadromous stock must consider all habitats and life stages simultaneously and cumulatively.

7. Ocean Ecology Snake River ESUs- Key Information Needs

From the perspective of recovery planning for listed Snake River ESUs and estuary and ocean ecology, we propose the following as key information needs:

1. Improve our ability to discriminate listed ESU's in the estuary and ocean, and detect rare stocks such as Snake River sockeye. In order to be able to understand the life history and ecology of the listed ESUs in the ocean, we have to be able to identify the origin of a fish caught anywhere in the ocean. We are limited in our ability to do this. Expected improvements in the ability to use genetic identification methods for steelhead in the ocean will improve this situation for steelhead. In several other areas, such as the Gulf of Alaska, genetic stock identification methods have only been applied recently.

2. Improve our ability to identify wild fish within listed ESUs. We are currently limited in our ability to identify the wild fish components of listed ESUs. This is due in part to the low production of the wild parts of each ESU. Clearly, this is especially true of Snake River sockeye where the number of outmigrants leaving the Central Idaho lakes is very small. A second issue in identifying wild fish since some genetic identification are not made with high certainty and adipose clip rates are always less than 100%. If Parental Based Tagging or other large-scale marking can be implemented in hatcheries in the Columbia River Basin, then our ability to discriminate hatchery-origin from wild fish would dramatically improve.

3. Better understand the role of the estuary in productivity of yearling sized fish (steelhead, Chinook salmon, sockeye salmon). In particular, for yearling sized fish, it is important to evaluate where the prey consumed by these fish are coming from. In particular, we should determine how important prey are that are exported from wetlands are to yearlings. A small sample of stomachs from these large fish has found prey derived from wetlands (Weitkamp et al. In Review), suggesting either the fish are foraging in or near wetlands or prey is being transported out into the main migratory routes.

4. Further understand density dependent growth and survival, especially as it relates to hatchery fish impacts on wild fish. Detecting density dependent effects of hatchery fish on wild fish will continue to be challenging. We suggest that some additional analytical approaches could be taken with existing information (e.g., bioenergetic analyses) to help further refine under what conditions density dependent interactions are likely occurring and how management approaches in terms of release timing can help mitigate effects.

5. Continue to study bottlenecks or critical periods in survival. Most attention has focused on early marine survival in coastal waters off the Pacific Northwest as the primary bottleneck to survival. However, there are several other spatial/temporal

windows we should consider as noted for steelhead (e.g., Friedland et al. 2014). First, we still do not fully understand mortality processes in the plume but some evidence suggests substantial mortality occurs during this period (Reichisky et al. 2013). Second, there has been almost no sampling during winter, with the exception of work by DFO off the WCVE. Winter mortality is likely critical in some years and so understanding morality processes in winter would be useful. Third, we lack an understanding of salmon ecology close to shore (within several km). Because of depth considerations for the sampling vessels, most ocean sampling work does not get close to shore. However, we know that sub-yearlings are most abundant in the most inshore stations when sampled by trawl and purse seine sets in the ocean reveal large numbers of sub-yearlings in this area. So, it seems likely that we are under-sampling the Snake River fall Chinook ESU during early ocean life in the NCC. Fourth, we should increase our understanding of mortality processes occurring in the Gulf of Alaska and North Pacific during the first summer the salmon are at sea.

6. Better understand the physical and biological relationships between the river, estuary and ocean habitats. We know there are close physical connections between the river, estuary and ocean that can affect biological processes, but these relationships can be complex and how they affect salmon survival is still unclear.

   a. We know that river flow affects plume and estuary conditions (e.g., for the estuary, salinity; for the plume, plume volume and plume surface area). Where are less clear about linkages to biological processes. In particular, one set of relationships that merits further investigation are the connections between river flow, plume, estuary, forage fish distribution and abundance and predation by birds on salmonids.

   b. Another set of relationships that merits further investigation are between time and size of ocean entry and growth and survival in the ocean. The effects on overall growth and survival of when the fish enter the ocean and their size are complex (Scheuerell et al. 2009; Muir et al. 2006; Tomaro et al. 2012) and further research is needed to resolve these issues. We know that fish size can be important to survival, but how the fish attain this size may also be important (e.g., relative amounts of growth in the estuary and ocean). An important question is do changes in growth rate, size and condition of juvenile salmon and steelhead that occur between the estuary and the NCC are related to their early marine survival.

7. Develop a better understanding of the mechanisms that link climate variability with salmon survival, especially as it relates to human caused climate change.

8. Continue to develop and refine indicators of ocean conditions that are relevant to salmon performance. This work would continue to refine the suite of ocean indicators for each stock group that provide the best predictive ability for early marine survival and adult returns and eventually transition to monitoring a core set of those indicators for each stock group. New indicators should be evaluated. This could include residence time and feeding in the estuary as predictor variables in an effort to track

the value of estuary habitat improvements on subsequent fish performance (e.g., growth and survival).

9. Determine at what time scale survival processes operate. At present, current study efforts are sufficient to understand annual patterns but we do not know if and how processes operating at finer time scales affect the salmon. But, we do not know if factors affecting survival are operating at daily, weekly or monthly scales. For example, is a delay of a day or a week entering the ocean significant (i.e., have a measurable effect on survival) for a fish that only takes five days to migrate from Bonneville Dam to the ocean? We also do not know how ocean conditions fluctuate at smaller temporal scales and if this predictable, e.g., if survival is high this week, is it also likely to be good next week or next month.

10. Determine the spatial and temporal distribution of all ESUs in the ocean following their first ocean year. Much of the focus of sampling efforts has been on the first year of ocean life when the fish are in coastal waters. We do not have a good understanding of where the fish go and how long they are present in different places after they have passed their first year at sea. As these are older and larger fish, this would likely require different types of sampling methods than have been used in coastal areas. For example, older fish of some ESU's such as the SRSS and SRF Chinook salmon ESU's might be less surface oriented. Our lack of understanding of what happens to the fish after their first year at sea is of concern because recent data strongly indicates that at least in some years and some stocks, critical mortality occurs after the fish leave the NCC (Welch et al. 2000; Burke 2013). These mortality processes are largely unstudied because of the minimal work that has occurred on older life stages.

11. Increase our understanding of anthropogenic risk factors. In general, we have little information on effects of most potential risk factors either in general (e.g., ecosystem effects) or specifically for salmonids. Several notable exceptions are effects of flow, habitat, and avian predation in the estuary. Even for climate change which is the subject of considerable interest and many studies, we lack explicit understanding of strength, magnitude, and timing of climate change effects.

12. Better understand effects of predation. Much of what we know about biological processes affecting salmon in the ocean is related to bottom-up processes or what occurs at the lower trophic levels. We have a very limited understanding of predation during ocean life both in the NCC and beyond.

8. Recovery Strategies

Most of the direct actions that will be directly taken to recover the listed Snake River ESUs will occur above Bonneville Dam. They will be designed to increase survival through the hydrosystem, improve egg-to-fry survival, improve upstream migration of adults above Bonneville Dan, and so on. Actions will of course vary by ESU and have been laid out in each recovery plan.

The overall objective of recovery efforts is to improve viability. The framework for recovering viability in listed populations was originally proposed by McElhaney et al. 2000) and the Interior Columbia River Basin Technical Recovery Team (ICTRT, see ICTRT website for further details) further developed and refined this explicitly for the listed Snake River ESUs. There are four components to viability: abundance, productivity, spatial structure and diversity. All four VSP criteria are critical to the viability of salmon populations, all are interrelated, and levels of all four attributes in aggregate define extinction risk or the likely persistence of the population or ESU. This approach to evaluating population status differs from traditional salmon management which typically assessed the status of anadromous salmonids from a production perspective using numbers of harvested fish or reproducing adults as the metric. Defining population status using the NOAA Fisheries VSP criteria incorporates a much broader view of how to define population status. This perspective recognizes that factors affecting salmon populations vary widely, so using a variety of metrics can provide insight into what types of actions are needed to help populations and ESUs recover.

Abundance is a measure of the number of members in the population (e.g., numbers of spawners or returning adults), while productivity is the rate of growth of the population over a given time interval. Productivity can also be expressed as life-stage specific survivals, since the cumulative effects of those survivals results in a population's growth rate over time. Populations that have a lot of members and a positive population growth rate are more likely to persist then populations that do not have these characteristics. Changes in abundance and productivity of a population can be measured at different and multiple time scales.

Although conservation of diversity and spatial structure are emerging paradigms in recovery and management of Pacific Salmon (McElhany et al. 2000, Waples et al. 2001), their application to salmon recovery remains a considerable challenge. Spatial structure refers to the geographic distribution of individuals in the population and the processes that generate that distribution. Salmon populations clearly exhibit complex geographic structure that can be defined at multiple spatial scales. For example, at any moment, a population can be distributed across many thousands of square miles, ranging from the headwater spawning areas to Pacific Ocean feeding grounds (Healey 1991). Within one area, such as the estuary, multiple habitat types such as deep channels, mudflats, and emergent marshes can be simultaneously occupied by members of one population. Distributing members of a population through an array of habitats helps reduce the vulnerability of the population to shifts in environmental conditions (McElhany et al. 2000). Diversity consists of the variability in life history and discrete genetic traits exhibited by

members of a population. In the ocean module and recovery plans, diversity is manifested and considered explicitly in recovery planning in a variety of ways, including differentiating yearlings from sub-yearlings and spawning timing (spring, summer, and fall). Many other traits, such as age at return, fecundity, migration behavior, and so on, follow from whether a fish is a yearling or sub-yearling and when they spawn.

8.1 Manage for Diversity

One element of viability is diversity. One of the characteristics of salmonids, but especially Chinook salmon and sockeye, is that they exhibit considerable life history diversity within a stock (Fresh et al. 2005). Clearly, a major part of this diversity is in how the fish use ocean ecosystems. For example, freshwater recovery actions should consider the mix of life history types they are generating and how they will perform in the ocean. We have shown that different life history types use the ocean differently and that ocean condition can vary greatly over the vast region salmon occupy. A year that is "good" for yearlings may not be "good" for sub-yearlings.

Another example of diversity based recovery strategies is timing of ocean entry (Scheurell et al. 2009). We know that timing of ocean entry is complex within any ESU and can vary within a year and between years. Within year variability in when the fish enter the ocean (during periods of high or low productivity) can affect their survival (Chittenden et al. 2010). While the interaction of arrival timing in the estuary and fish size can be complex (e.g., Tomaro et al. 2012), both factors can potentially affect ocean survival (e.g., Muir et al. 2006). While further research on this subject is needed, some general principles of when fish should enter the ocean should be developed.

Because of uncertainty in how ocean entry timing might affect a particular group of fish, we also suggest that fish should also be spread out within these windows, especially if ocean conditions look unfavorable, to reduce risks of competition occurring (i.e. do not put all eggs in one basked). Further, the transportation of some populations through the hydrosystem in barges makes it especially challenging to manage for some optimal range of ocean entry timing. It seems as if a bet hedging approach would be useful that recognizes that although each stock has a general time and size range when they enter the ocean, considerable variability exists within each ESU in their life history approach.

One potential opportunity to affect viability of Snake River ESU's is in how we rear and release hatchery fish because of the potential for competition between listed ESUs and hatchery fish from multiple sources. The arrival of large numbers of fish in the estuary and NCC could create conditions whereby unlisted, hatchery fish might compete with and reduce growth rates of listed populations. If the overall consumptive demand (a function of both fish abundance and fish size) of hatchery fish was sufficient (i.e., how much prey do the hatchery fish eat relative to what is present) growth rates of listed populations could be reduced. This could depend upon

environmental conditions, species being considered, relative amount of prey available in the environment, and habitat where the interaction occurred.

Given the accumulation of evidence that density dependent interactions are occurring under some circumstances, it seems that managing to reduce risks associated with the occurrence of this interaction seems prudent. For example, it seems prudent to spread out hatchery releases to reduce the likelihood of density dependent effects on naturally reproducing fish. Clearly, while this might be effective in managing density dependence in the estuary and NCC, it may be less likely to work as the fish from the Snake River mix in the ocean with stocks from other regions.

8.2 Physical and Biological Connectivity- Spatial Structure

Although we tend to examine each habitat the salmon occupy in isolation, it is clear that there are physical and biological connections between these habitats and the fish that occupy them and that management of the river and its salmon resources should account for these connections. Connectivity is one element of spatial structure (McElhaney et al. 2000). One example of connectivity between the ocean and estuary is via the plume. We know that the amount of flow can affect salinity regimes in the estuary and characteristics of the plume. Studies show that that a significant portion of plume volume (67%- Baptista 2013) is a function of river flow and that the plume does not simply affect the area near the river mouth but can affect much of coastal Washington depending on its volume, winds, and other physical factors (Hickey et al. 2009).

Characteristics of the plume can affect biological characteristics near the mouth of the river such as food webs and it can affect salmon survival. Spring Chinook salmon from the upper Columbia River, plume volume at the time of emigration is correlated with size at capture which is strongly related to adult returns two years later (Tomaro et al. 2012). Similarly, Miller et al. (2013) found that returns of a population of unlisted Upper Columbia sub-yearling Chinook salmon to Priest Rapids Dam were related to plume volume at the time of emigration in most years.

From the perspective of biological connections, it is reasonable to hypothesize that ocean growth and survival, especially in the NCC, relate to characteristics of the fish (e.g., size, timing, condition) during their estuary and plume residence. We do not fully understand these biological connections, such as how growth and fish size and condition in the estuary is related to subsequent growth in the plume and ocean. But, it seems reasonable to hypothesize that such relationships exist.

8.3 Harvest

Columbia River salmon are harvested at a number of points in their life histories with the most important U. S. fisheries targeting fish near the mouth of the river and in the river. An important part of the fishery management cycle is forecasts of the numbers of returning adults. Accurate forecasts are of course highly desirable since they can reduce risks of overharvesting and can help ensure adequate escapement to spawning grounds which is a consequence of overharvesting.

One of the more important salmon ocean science advances in recent years in the NCC, has been an increase in our understanding of the mechanisms affecting salmon ocean survival. From this mechanistic understanding of salmon ocean survival, indicators have been developed that seek to predict adult returns and survival. As illustrated by Burke et al. (2013a) these indicators can accurately forecast adult returns of some stock groups. Accurate forecasts of adult returns two years into the future can provide an early warning about when we should be concerned about low returns of stocks that comprise such a group. This could provide advance warning of at risk fisheries, where the low returns would have economic impacts on fisherman.

8.4 Improving survival in the ocean.

As we have noted, we have the ability to affect growth and survival of anadromous species in the ocean. First, a number of studies suggest that timing of ocean entry and size at ocean entry can effect growth and survival (Tomaro et al. 2012). Chittenden et al. (2010) found that timing of ocean entry of hatchery and wild Coho salmon was important to their subsequent survival with fish entering the ocean during periods of high productivity (within a year) having higher survival than those entering the ocean during periods of lower ocean productivity. Although these relationships are complex, studies suggest that in general Snake River spring Chinook and steelhead that arrive earlier in the ocean survive better. For wild fish, timing of ocean entry will be a function of when the fish begin their downstream migrations (which will depend considerably on flow) and how long it takes them which will be primarily driven by flow. However, there is considerable variability in the effects of timing between years, making it impossible (at least currently) to predict when the optimum time of ocean entry is each year. For example, in three of the four years examined by Scheuerell et al. (2009), fish that passed Bonneville Dam in early May performed best but in one year, fish that passed Bonneville in June performed best. Thus, it seems prudent with this uncertainty to ensure fish arrive in the ocean within a time frame window rather than on a particular date.

In addition, larger fish in general will perform better than smaller fish (Holtby et al. 1990) but it is clear time of ocean entry and size are related but that this relationship can be complex (e.g., Bilton et al. 1982; Beamish and Mahnken 2001). For example, in a study of hatchery-reared Coho salmon, Irvine et al. (2013) found that the effects of fish size at release varied between year and between hatchery location. In some years, being larger at release did not confer a survival advantage. It also may not the size of the fish per se but the difference in size between their arrival in the estuary and their first days/weeks in the ocean. Thus, small fish arriving in the ocean may be able to compensate for their small size if ocean conditions are favorable. In addition, the most important aspect of timing is likely not so much timing relative to calendar date but timing relative to ocean conditions such as the available food supply. Biologically important events do not occur on the same calendar date every year; thus, differences of days to weeks may be important.

Clearly, one factor that can affect survival is numbers of fish entering each ecosystem. In their comments on the Ocean Synthesis report, the ISRP suggested that "it may be worthwhile to investigate whether hatchery salmon growth and natural salmon production in freshwater can be adjusted to the extent possible, for example in the hydrosystem, to enhance survival of both hatchery and natural populations during anticipated years of poor ocean productivity." For example, during years of poor ocean productivity, adjustments might be appropriate in terms of the numbers, sizes and timing of fish entering the ocean in order to optimize their survival

9. Adapting Recovery Actions Based on Ocean Conditions

Here we discuss how we can adapt freshwater and estuary recovery actions to help reduced risks to listed ESUs using ocean information.

9.1 Forecasting

One of the more important salmon ocean science advances in recent years, especially in the NCC, has been an increase in our understanding of the mechanisms affecting ocean survival. An example of a mechanistic understanding is the linkages between the PDO, zooplankton, icthyoplankton, early marine growth, and survival. We can then use our understanding the top-down and bottom up mechanisms affecting early marine life of specific populations to develop indicators that accurately predict adult returns and survival.

Using ocean indicators for forecasting reflects a shift in application or use of ocean information. Typically, we have used ocean indicators such as PDO in correlative, retrospective types of analyses (e.g., Petrosky and Schaller 2010; Scheuerell et al. 2009); the focus has been on using, readily available off the shelf ocean indicators (i.e., off the internet) such as PDO and ocean surface temperatures, because they match with the long-term biological data (e.g., salmon abundance). However, over the last several years, it has become clear that some of these broad ocean indicators (PDO, for example) are becoming less correlative with salmon performance and that using other approaches (e.g., multivariate models) is needed.

Recently, we have begun using ocean indicators of physical and biological conditions developed from in situ sampling for forecasting survival and adult returns (Burke et al. 2013a). These indicators have been developed based upon our understanding of the mechanisms affecting early marine life. Forecasting has multiple purposes but within the context of recovery planning, forecasts can clearly be used within a harvest management context to manage both in-river and ocean fisheries. With accurate forecasting, harvest managers can decrease the risk of overharvesting and increase the probability of having adequate escapement to spawning areas.

In addition, forecasts can be used for conservation purposes. Presently, forecasts are being evaluated that use coarse scale or far field indicators like the PDO because they match the biological time series; however, "near-field" metrics may be better related to adult returns. As we have noted, in the last several years, there is evidence that the relationship between PDO and salmon performance during early marine life might be breaking down. Thus, there is a need to investigate the predictive power of the near-field metrics in the context of the early warning indicator, to understand the mechanisms underlying the statistical relationships, and to understand how these relationships vary by genetic stock group and natural versus hatchery origin. Examples here could include plume area/volume and indicators of ocean conditions that

focus on the time preceding when salmon are entering the ocean (March/April) or when they are entering the ocean (April/May).

In some cases, adult returns two years into the future can be forecast using ocean indicators. Although these forecasts are coarse in that they are not stock specific at this time, they do provide an early warning about when we should be concerned about low returns of stocks that comprise such a group. If specific stocks or groups of stocks could be identified where low returns are expected, adaptive management actions might be possible that could target stocks where low returns are expected. Examples of adaptive management actions that could be implemented would be to further restrict harvest, accelerate the timing of freshwater restoration measures, and implement captive broodstock programs.

A third application of accurate forecasts would be to incorporate the indicators that are most important (highest predictive power) in those forecasts in life cycle models. Life cycle models represent a more complete analysis of the factors affecting survival for a particular stock. The ability to accurately model the effect of future management actions in freshwater life stages depends on an adequate understanding of trends in and ties to ocean survival. Inadequate representation of variability in ocean survival can create a bias in the other stages of a life cycle model, which can lead to a misunderstanding of how both freshwater and marine habitats affect salmon.

We have found that some of the indicators we are collecting can be incorporated into life cycle models to make them more accurate because of the strong relationships between these indicators and fish survival in the ocean. Initial development of models typically relies on the longest data sets that are available. This is a weakness of some of the ocean data sets we have been collecting as they are limited to less than 15 years while other data sets such as PDO and SST are much of longer duration. It is currently unclear when the benefits of higher quality information outweigh a longer time series in terms of forecasting returns and understanding the ecology of salmon.

10. Implementation

Successful implementation of the overall recovery plans requires a process to refine direction and adjust course appropriately based upon information obtained from monitoring and research results. We have identified some of the key information needs that should be part of any research program.

10.1 Information Needs: Monitoring and Research

While the focus of recovery actions for Snake River ESU's is in freshwater and the estuary, it is very clear that we must continue to monitor and evaluate ocean conditions the fish experience in order to understand how well recovery actions are working. We must continue to provide the context for recovery actions. In the extreme, if certain freshwater recovery actions fail, we will need monitoring of ocean conditions to understand why these actions failed. We do not want to incorrectly attribute low returns to dam passage when it was in fact due to ocean effects.

Thus, we must monitor conditions of the fish themselves as well as conditions of the receiving environment (i.e. both fish and environmental indicators). While the focus regionally has been on the NCC, we must also consider information from other places the fish occupy (Gulf of Alaska).

We must also look for ways to improve collection of information. For instance, although collaboration and cooperation exists among different research groups, ocean studies of salmon ecology have not been coordinated. Studies have been organized and led in different regions by different entities, largely as a function of available funding and regional drivers of information needs. Methods have varied between regions, such as in the timing of sampling. Not all programs use the same nets sampled in the same way and not all programs have collected comparable information (e.g., the same type of growth measurement or accompanying oceanographic information). In addition, some areas and times of year have been nearly unstudied, such as the deep oceanic waters beyond the continental shelf off Oregon and Washington. Also, most marine areas have not been sampled during winter and most of the nets used to sample salmon are most effective for the smaller size classes of fish and much less effective at sampling distribution patterns of larger fish (> 1 year in the ocean).

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