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A Landscape Approach to Determining and Predicting Juvenile Coho Salmon (*Oncorhynchus kisutch*) Movement Timing and Growth Patterns Prior to Ocean Entry

by

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Thesis Committee:
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Abstract

Coho salmon (*Oncorhynchus kisutch*) rely on unique habitats during the winter season, which may dictate how much individuals may growth and when migration from freshwater rearing habitat to the ocean occurs. Here I analyze movement timing and growth patterns for coho salmon through a field-based study and a literature review. For the field portion, I examined hatchery-stocked juvenile coho salmon across four stream basins in the Russian River watershed, California to determine the relative importance of climate, landscape, and fish size metrics in predicting movement and growth patterns over a winter rearing and spring smolt outmigration time period (December 2014 – June 2015). I observed three unique movement strategies: winter parr movement, spring smolt movement, and inter-tributary movement. Movement was predicted in relation to daily temperature and precipitation, followed by in-stream and upslope basin conditions in random forest modeling. Specifically, fish that moved later were associated with basins that contained higher productivity and low-gradient floodplain habitats, while fish that moved earlier came from streams that lacked invertebrate prey and had limited low-gradient rearing habitat. Fish size and timing of movement were the primary predictors of growth, with relatively larger fish in the spring growing faster than fish that were relatively smaller prior to winter. These relationships suggest that hatchery-release fish are still highly influenced by environmental conditions once released, especially in terms of initial seasonal movement, and that watershed conditions should be considered when utilizing hatchery-rearing programs to supplement wild fish populations.

In North America, coho salmon populations are distributed from Alaska through California, and may exhibit unique movement and growth patterns in relationship to population-scale vulnerability (Endangered Species Act listing), basin area, and availability and types of rearing habitat. For the second part of my thesis, I conducted a literature review to assess what factors are commonly considered in predicting movement and growth patterns for these fish, as well as the types (season and life stage) and number of movement strategies reported. Eighteen studies were summarized, of which sixteen identified unique movement strategies, ranging from one to four. Despite a wide range of basin areas and latitudes, winter parr and spring smolt movements were commonly observed, with authors primarily relating these behaviors to in-stream habitat and fish size metrics. Additionally, growth was linked positively and primarily with off-channel winter rearing, which may outweigh the importance of fish size in predicting growth when high quality rearing habitats are available during the winter season.

Recognizing movement timing diversity and its drivers can help recover threatened coho salmon populations. More widely distributed populations may have unique phenotypic expressions based on localized genetic and environmental interactions, increasing diversity and overall stability across the population, a concept known as the portfolio effect. Understanding fish-habitat relationships can aid recovery efforts by providing a framework of climatic and watershed conditions that support unique behaviors, even in already severely limited populations.

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Chapter 1 : Introduction

Freshwater ecosystems support unique and diverse ecological communities as well as provide a multitude of ecosystems services. Human communities rely on freshwater systems to provide drinking and irrigation water, flood buffering, and habitat for commercial fish species while terrestrial and aquatic communities benefit from freshwater food, shelter, and nutrient cycling. However, freshwater systems are some of the most threatened ecosystems globally (Dudgeon et al. 2006), and a disproportionately large number of aquatic species are considered vulnerable or imperiled (Strayer and Dudgeon 2010). In the United States alone, 47% of rivers and streams are considered impaired or threatened (United States Environmental Protection Agency 2009), which impacts wildlife by reducing quality habitat and increasing competition for limited resources.

Conserving and restoring freshwater habitat requires an understanding of the spatial- and temporal-scale of influences on physical habitat characteristics (Roni et al. 2008, Bernhardt and Palmer 2011). Large-scale processes, like climate and geologic patterns, influence stream valley gradients and vegetation communities, which in turn influence stream habitat, forming a hierarchical ecosystem structure (Frissell et al. 1986, Montgomery 1999). In-stream habitat patch types and connectivity evolve constantly too, due to seasonal patterns in precipitation and temperature, as well as disturbance events like floods and droughts. These factors affect stream flow regimes, and thus habitat quality and connectivity, establishing shifting habitat mosaics across watersheds (Stanford et al. 2005).

Habitat connectivity is especially important for highly mobile lotic fish, which must access different habitats to complete their life histories (Schlosser and Angermeier 1995, Fausch et al. 2002). This is especially true for Pacific salmon (*Oncorhynchus* spp.), which evolved and adapted to the highly dynamic Pacific coastal watersheds, where tectonic activity, fires, landslides, and seasonal climate and productivity patterns all influenced population phenotypic trait persistence (Waples et al. 2008). Natural watershed barriers led to isolation, and the strong tendency of salmon spawners to home to natal streams continually reinforces local adaptations, including timing of spawn and smolt outmigration (Quinn 2005, Waples et al. 2008). Local adaptations extend across a wide geographic range as well. Anadromous Pacific salmon populations occur across the North Pacific from Japan, across Russia, and down western North America. The wide range of marine and freshwater productivities encountered further increases the life history diversity of salmonids (National Research Council 1996, Quinn 2005).

Most Pacific salmon species are anadromous, meaning juvenile fish hatch and rear in freshwater prior to migrating to the ocean, where they grow and mature before returning to stream habitat to spawn (Groot et al. 1995, Quinn 2005). Life history variation occurs among Pacific salmon species due to different life stage residency periods, spatial locations of juvenile rearing, timing of outmigration to the ocean, and spawn timing and size of returning adults (Waples et al. 2001). Life stage transitions are related to fish size and fitness, which in turn are determined by energy available for growth (Dodson et al. 2013, Sloat et al. 2014). Growth is determined by metabolic rate and activity costs, which are governed by temperature, prey caloric quality, and activity demands (Hansen et al. 1993, Sloat et al. 2014). Specific to juvenile salmon, foraging and swimming energetic costs are important, and differ based on stream velocity, competition, and predator and prey densities (Fausch 1984, Nielsen 1992, Rosenfeld et al. 2005). Consequently, long-distance movement is influenced by environmental conditions, as individuals maximize their ability to compete for limited resources and reach maturation condition and size, rather than being simply a genetic-controlled response (Olsson et al. 2006).

Freshwater habitat degradation often results in loss of unique habitat types, with low and high gradient streams disproportionately degraded in freshwater systems, reducing estuary, floodplain and ephemeral stream quantity and quality (McClure et al. 2008). Pacific salmon that rely on freshwater habitat for extensive time periods are also disproportionately endangered and threatened compared to salmon that spend more time in marine environments (National Research Council 1996). Climate change is predicted to alter natural stream flow and thermal regimes, further degrading and disconnecting freshwater systems (Meyer et al. 1999, Gibson et al. 2005).

Multiple studies have documented the importance of low and high gradient habitat to juvenile salmonids due to the unique thermal, stream flow, and foraging opportunities that exist there compared to main channel streams. Floodplains provide warmer temperatures, slower stream flows, and greater growth opportunities for fish than main channel stream habitat during winter storm inundation due to their low slope and wetland and riparian forest communities (Sommer et al. 2001, Bellmore et al. 2013). Estuaries are often highly productive environments in comparison to streams because warmer estuary temperatures provide high quality growth opportunities for juvenile salmonids (Satterthwaite et al. 2012, Craig et al. 2014). Ephemeral, upper watershed tributaries can also provide high quality habitat to juvenile salmonids when seasonally connected, potentially because of lower resource competition (Wigington et al. 2006).

Life history diversity can increase population resiliency through greater phenotypic trait expression. This is due to greater variation among sub-populations within a population leading to more stability in the overall population, or the portfolio effect (Doak et al. 1998, Tilman et al. 1998). For instance, high annual variability in spawn timing among the many Bristol Bay, Alaska sockeye salmon populations led to a high degree of stability across this large system (Schindler et al. 2010). Greater variability in spatial and temporal habitat use can improve population stability by reducing the impact of localized environmental and biological stressors, like droughts, landslides, or density-dependent factors. Life history diversity relies in part on habitat heterogeneity and the persistence of populations that utilize these unique habitats (Hilborn et al. 2003, Beechie et al. 2006, Waples et al. 2009). Life history diversity is already at risk for Pacific salmon: it is estimated that between 16 and 40% of historical populations are lost across the North American range, especially in interior and southern basins (National Research Council 1996, Gustafson et al. 2007). Additionally, it is estimated that these local population extinctions have resulted in between a 15 and 33% decline in phenotypic diversity, quantified as habitat, life history, and genetic variability (Gustafson et al. 2007).

Increased stability due to life history diversity in spawning adult salmon is well documented in pristine populations (Greene et al. 2010, Schindler et al. 2010) as well as the loss of stability in vulnerable populations (Moore et al. 2010, Carlson et al. 2011). Juvenile life history diversity is also of concern however because most juvenile Pacific salmon rely on freshwater habitat for growth prior to marine residency, and thus population success. Diversity in spatial and temporal habitat use by juvenile fish is especially important for coho salmon (*O. kisutch*), which rely on freshwater and estuarine habitat for one to two years prior to their marine life stage (Shapovalov and Taft 1954, Sandercock 1991). Anthropogenic impacts, including freshwater habitat degradation, have already extirpated or reduced coho salmon populations (Brown et al. 1994, Gustafson et al. 2007). Due to their extensive population loss and lengthy freshwater rearing, many monitoring and restoration activities are focused on coho salmon recovery. This recovery infrastructure and life history strategy make coho salmon an excellent case study to analyze how freshwater habitat distribution relates to population dynamics.

I have two main objectives with this thesis. First, through a field-based study, I will analyze pre-smolt outmigration movement and growth patterns in a southern, hatchery-stocked coho salmon population, examining how these patterns relate to fish size and stream landscape characteristics (Chapter Two). Second, I will consider similarities and differences among coho salmon populations with regards to movement, growth, and their biological and environmental drivers through a literature review (Chapter Three). This literature review will synthesize our understanding of winter and spring pre-smolt migration movement and growth patterns for coho salmon across their

North American range, as well as consider future research and management actions to conserve and support juvenile movement and growth diversity.

Chapter 2 : Landscape and fish size predictors of juvenile coho salmon (*Oncorhynchus kisutch*) movement timing and growth

Introduction

Highly mobile populations pose unique problems for conservation and habitat restoration planning, due to the importance of multiple habitats and connections over the life span of these species. This is true for Pacific salmon (*Oncorhynchus* spp.), a highly mobile fish genus that relies upon freshwater, estuary, and marine habitat to complete their anadromous life history (Groot et al. 1995, Quinn 2005). Mobility across freshwater systems is especially important due to the diversity of habitat types and connections utilized by Pacific salmon over their residency and to complete their life cycle. Many Pacific salmon species, especially in the interior and southern extents of their range, are listed under the Endangered Species Act, some for more than twenty years. Freshwater habitat degradation is considered one of the main reasons for these population declines and lack of recovery (Nehlsen et al. 1991, National Research Council 1996).

Despite a solid understanding in the scientific community of the importance of habitat complexity to Pacific salmon survival, the study of temporal and spatial diversity of habitat use by these fish is still a work in progress. Temporal diversity in habitat use is well documented for spawning Pacific salmon (Greene et al. 2010, Schindler et al. 2010). However, spatial and temporal habitat use by juvenile salmon is also of concern because of the reliance of most species on freshwater rearing habitat prior to marine residency, as well as the importance of freshwater growth to marine survival and reproductive success (Holtby et al. 1990, Quinn 2005). Furthermore, spatial and temporal variability in timing of movement and fish size traits supports life history diversity in Pacific salmon (Waples 1991). Understanding drivers of life history diversity can also improve fishery management: conserving habitats that support diverse phenotypic expressions can increase the ability of a population to persist, a concept known as phenotypic management (Watters et al. 2003).

Coho salmon (*Oncorhynchus kisutch*) in particular rely heavily on freshwater habitat because of their one to two-year residency prior to ocean migration (Shapovalov and Taft 1954, Sandercock 1991). This extended freshwater residency can increase the vulnerability of this species to freshwater habitat loss and degradation, which is evident in the federal Endangered Species Act listing of the four southern evolutionary significant units (ESU) (Brown et al. 1994, National Research Council 1996, Gustafson et al. 2007). It is well understood that, following emergence, juvenile fish (parr) rely upon cold-water, pool habitat to survive through the dry, summer seasons (Sandercock 1991, Nickelson et al. 1992, Reeves et al. 2011). However, winter-rearing strategies are more complicated. Rain events reconnect previously isolated or dry ephemeral streams and lateral floodplain zones, increasing habitat availability, growth, and survival benefits from different habitat types. This is evident in the winter movement of juvenile coho salmon to estuaries, floodplains, and non-natal streams during the winter season (Ebersole et al. 2006, Koski 2009, Bennett et al. 2014). The reasons for these movements may be the increased potential for growth and survival associated with these low velocity, high productivity habitats (Tschaplinski and Hartman 1983, Ebersole et al. 2006, Reeves et al. 2011) or predator avoidance (Dionne and Dodson 2002).

The mechanisms that govern where and when juvenile coho movements occur are still unclear. Multiple studies have shown that timing of winter and spring movements correlate with fish size prior to the winter, with smaller fish more likely to migrate out of freshwater rearing habitat during the winter and larger fish more likely to wait until the spring to move downstream as smolts (Roni et al. 2012, Rebenack et al. 2015). This may be partly explained by competitive ability: larger individuals can outcompete smaller fish for limited rearing and foraging habitat, decreasing growth potential of smaller fish (Tschaplinski and Hartman 1983, Sandercock 1991, Nielsen 1992).

Rearing habitat may influence both fish size and timing of movement. Multiple studies have observed relatively greater survival and growth of juvenile coho salmon in rearing habitats that provide lower velocity flow, greater productivity, and complex shelter in the form of vegetation, large wood, and undercut banks (Peterson 1982, Tschaplinski and Hartman 1983, Fausch 1984). Moreover, coho salmon preferentially select these habitat types when available during the winter, including upstream migration to small tributaries, side channels, ponds, and alcove habitats (Ebersole et al. 2006, Bennett et al. 2011).

It is well documented that juvenile coho salmon in wild, northern populations exhibit multiple movement strategies within a population prior to smolt outmigration, and that fish size and winter habitat availability may influence timing of movement. However, there is limited research in the southern extent of the coho salmon range where populations are already diminished and supported by hatchery-rearing programs. Southern coho salmon populations may display different movement strategies: estuary rearing likely offers different growth potential because of seasonal estuary closures (lagoons) (Emmett et al. 2000, Hayes et al. 2008), while stream temperatures are typically warmer, potentially leading to faster growth and earlier maturation and migration in comparison to northern populations (Morita and Nagasawa 2010, Beacham et al. 2014). Stream productivity is likely more limited as well, since salmon spawner biomass is typically lower in southern latitudes where population abundances are reduced below historical numbers, reducing marine nutrient loading and egg consumption opportunities for growing juvenile fish (Naiman et al. 2002, Hicks et al. 2005, Bentley et al. 2015). Additionally, hatchery-reared populations may exhibit less size variability than wild fish, since spawning location and limited summer habitat can strongly influence pre-winter juvenile distribution and size (Ebersole et al. 2009a, Flitcroft et al. 2014). Studies on other Pacific salmon species have also noted variability in timing of outmigration corresponding to variability in stream flow regimes (Zimmerman et al. 2015) and fish size at timing of outmigration associated with latitude (Freshwater et al. 2016). Thus, a better understanding of juvenile coho populations across their entire range is warranted.

In this study I attempt to identify juvenile coho salmon winter-rearing strategies in a southern, endangered hatchery-stocked population, as well as determine the importance of environmental conditions and fish size to coho salmon growth and movement timing through the winter and spring seasons, prior to smolt outmigration. To address this gap in our knowledge, a broodstock-reared population was studied in the Russian River, California, the largest remaining watershed in the southern regional Central California Coast Coho Evolutionary Significant Unit (ESU). Understanding the mechanisms influencing growth rates and movement in hatchery populations and human-impacted watersheds could help prioritize habitat restoration efforts aimed at salmon population recovery.

Climate change in western North America is expected to increase temperatures and alter stream flow regimes (Stewart et al. 2004). Specific to California, temperatures and precipitation intensity are predicted to increase, leading to more flood and drought occurrences (Pierce et al. 2013a, 2013b). My study took place during a severe drought, and habitat quality and connectivity may have been reduced in comparison to average rainfall years. This could limit coho salmon movement strategies by reducing habitat connectivity, providing a model of fish responses to future conditions. It is important to understand behavior of coho salmon already experiencing these conditions in order to apply this knowledge to more northerly, intact populations as well as future recovery and restoration management decision making.

To address these questions, movement data for a hatchery-reared coho salmon population in the Russian River watershed were analyzed for the 2014-2015 winter through spring season, covering potential early winter emigration and spring smolt outmigration from the stocking streams. Two main questions were addressed: 1) Are multiple movement seasons evident for coho salmon parr and smolts in a southern, endangered population; and 2) Are individual movement patterns related to fish size metrics, in-stream habitat quality, and landscape characteristics? Previous work has documented early winter pre-smolt movement when off-channel habitat and in-stream habitat quality are low, likely due to limited rearing and growth opportunities

(Tschaplinski and Hartman 1983, Bennett et al. 2011). Later spring emigration timing has also been associated with higher quality rearing habitat, or greater growth potential (Quinn and Peterson 1996, Bennett et al. 2011). Watershed characteristics can influence in-stream habitat quality as well, with low-gradient, forested and wetland systems more likely to support salmon-rearing habitat (Sharma and Hilborn 2001, Ward et al. 2012). Therefore, I hypothesize that low quality streams (e.g., high gradient, limited vegetation, low productivity with limited prey abundance, and low in-stream habitat variability) and limited rearing habitat will reduce fish rearing and growth opportunities, and lead to earlier, pre-smolt winter movement and lower growth of smolt emigrants. I predict that streams with high quality and abundant rearing habitat (e.g., low gradient, high vegetation coverage, productive, and high in-stream habitat variability) will lead to more growth opportunities across the stream length, supporting later, spring smolt movement patterns and greater growth of smolt emigrants. Incorporating variables that represent fish competitive ability and habitat quality may help address our limited understanding of the interactive effects of habitat quality, location within a watershed, and fish size on spatial and temporal distribution of juvenile coho salmon.

Methods

Study Area

The Russian River watershed (3850 km^2), located in Mendocino and Sonoma Counties in Northern California, drains into the Pacific Ocean (Figure 2.1) (mouth of Russian River at 38° 27’2”N and 123° 7’46” W). The watershed has a Mediterranean climate, with the majority of precipitation occurring as rainfall during the winter season, primarily from October through March. Winter stream flows increase during initial precipitation events, and summer flows are maintained from groundwater sources and dam releases on the two main rivers, the Russian River and Dry Creek (Steiner Environmental Consulting 1996, National Marine Fisheries Service 2008). Coho salmon habitat is limited primarily to lower watershed, small, tributary streams due to the dominance of warm-water predator species and increased summer flows in the main stem, riverine habitats (Steiner Environmental Consulting 1996, National Marine Fisheries Service 2008). The watershed includes agriculture, a history of timber harvest, rural, and urban development land uses, as well as a variety of remaining natural ecosystems, including coastal redwood forests, oak woodlands, and seasonal marshes (Steiner Environmental Consulting 1996, Opperman et al. 2005).

Coho Salmon

The Russian River Coho Salmon Captive Broodstock Program (RRCSCBP) has raised and released juvenile coho salmon across the lower watershed since 2004, with the goal of increasing population numbers and spatial dispersion for this federally endangered species (FISHPRO 2004, National Marine Fisheries Service 2012). All biological data were collected under Section 10(a)(1)(A) Endangered Species Act permit 10094 and California Department of Fish and Wildlife, Scientific Collecting Permit 2043. Four streams that are part of this program are monitored using Passive Integrated Transponder (PIT) tags (Biomark, Boise, Idaho, FDX HPT12, 12.5-mm long) and stationary antenna systems: Dutch Bill Creek (DUT), Green Valley Creek (GRE), Mill Creek (MIL), and Willow Creek (WIL) (Figure 2.1). Hatchery-reared juvenile coho salmon were released into streams in June 2014 (WIL) and December 2014 (DUT, GRE, MIL). Prior to release, ~15 % of each stream release group were randomly selected, anesthetized with Tricaine Methanesulfonate (MS-222), PIT-tagged, weighed (g), and measured for length (mm) at the hatchery. PIT-tagged individuals were reared in common tanks at the hatchery and are presumed to have similar growth and survival rates compared to all untagged fish in their respective release groups. Additionally, fish were monitored for tag loss prior to release and genetic diversity was maximized across streams by integrating multiple genetic lineages per release group (Mariska Obedzinski, personal communication). PIT technology is regularly used in studies of fish ecology because of the accurate information it can provide on individual growth, survival, and movement in small streams (Zydlewski et al. 2001, Gibbons and Andrews 2004, Achord et al. 2011).

Fish size was compared among study stream release groups to determine the degree of similarity (Table 2.1). Prior to comparisons, two fish were removed because they represented large outliers, based on their relative length and weight. All data were $\log_{10}$-transformed to improve distribution, although heteroscedasticity was a problem for all variables when data were assessed using Bartlett's test for equal variance. To address heteroscedasticity, the non-parametric Welch's *F*-test was used to compare multiple study stream release group fish sizes, followed by a Games-Howell post-hoc test, which addresses multiple pairwise comparisons when sample sizes and variances are unequal

(Zimmerman and Zumbo 1993). Fish size variables included pre-winter absolute fish length (fork length, FL), relative fork length (individual fork length in comparison to mean fork length per release group), and Condition factor (K), which was calculated as (pre-winter wet weight * 100) / (pre-winter absolute fork length) (Weatherley and Rogers 1978). Pre-winter absolute fork length and pre-winter Condition were significantly different among all study stream release groups, likely due to the earlier release of WIL fish (FL: $F_{3, 4034}=3222.00$, $p < 0.001$; K: $F_{3, 4306}=32.73$, $p < 0.001$). To address differences in absolute fork lengths, relative fork lengths were used to standardize fish size across the study streams for analyses (i.e., pre-winter relative fork length: $F_{3, 4057}=0.00$, $p = 1.00$). This suggests that relative distribution of fork lengths is comparable among the streams. Therefore, relative fork length was used in analysis rather than pre-winter absolute fork length, although absolute values were used to calculate individual growth rates. Despite observing significantly different Condition factor among the four study streams, this variable was still used as a predictor variable because of its potential importance in explaining fitness, growth, and behavior (Bentley and Schindler 2013, Sloat et al. 2014).

PIT-tagged coho salmon movement patterns were monitored using stationary PIT antenna arrays that collected data continuously throughout the study period, although detections were limited periodically due to equipment malfunctions (Appendix A). All antenna sites consisted of paired antennas that covered a stream cross-section in a high velocity, shallow riffle habitat, with the exception of the GRE upstream site which was a single antenna (Figure 2.2). Riffle habitats were selected to increase detection efficiency due to shallower water depths and to detect coho salmon moving through a habitat rather than remaining fairly stationary for extended periods, which typically occurs in slower flowing pool habitats (Mariska Obedzinski, personal communication).

Fish movement was analyzed based on individual movement day past each antenna site. Three of the four study streams included two antenna sites, so movement was recorded for an individual at both an upstream site and a downstream site (GRE, MIL, and WIL), but at DUT movement was recorded at only the downstream site (Figure 2.2). Timing of movement was calculated as movement day for each individual fish past an antenna site, beginning at day one for all upstream detection sites and a separate day one for all downstream detections. Day one movement is therefore standardized across all streams and represents the first day a fish was detected at any site after all fish were stocked (10 December 2014 for all upstream and downstream sites). Some fish moved prior to all fish being stocked in the study streams; these fish were removed from analyses. Multiple fish could have a movement day value of one, but not all streams necessarily have fish that moved this first day. Movement is also assumed to be downstream, based on comparisons among upstream and downstream detection site timing when both sites were available per stream. Data on timing of movement had unequal variance and sample sizes among study streams. This led to the use of the non-parametric Welch's *F*-test and the post-hoc Games-Howell test, which are both robust to unequal variances and sample sizes, although less-so for non-normal distributions (Zimmerman 2012).

Three of the four study streams had fish detected that were released in other stream basins in the watershed. These fish were not included in the analysis of timing of movement due to the limited sample size for this inter-stream movement group. Instead, timing of movement and fish size for these individuals were compared as a group (*inter*-stream movement) in comparison to all other study fish (*intra*-stream movement). Because no release stream PIT-tag detection days were available for the inter-stream fish, the earliest detection date was used to calculate movement day for these fish, since this would be the closest detection to when they began their winter movement (i.e., closest date to when they left the stream in which they were stocked). This is not the case for the inter-stream movement data, however, because this day is the first day they were detected moving upstream into a study stream.

All four study streams had downstream migrant smolt traps to capture fish during their spring outmigration. Downstream migrant smolt traps were installed in lower stream habitat in each of the four streams once winter flows subsided enough for safe trapping conditions and until stream flows were too low to capture fish or no more fish were trapped per stream (March - June 2015). All traps were located in close proximity to the downstream detection site in each study stream, except in the case of WIL, which had a trap located at the upstream detection site. Traps were checked at least daily, and all coho salmon were measured prior to release downstream. Following removal from the trap, all coho salmon were relocated to buckets with stream water and aerators to supply oxygen. All coho salmon ≥55 mm in length were anesthetized with MS-222, scanned for PIT tags (Avid, Norco, California, Power Tracker V), weighed, measured for absolute fork length, and then allowed to recover in another aerated bucket prior to release. Daily growth rates were calculated as the change in individual fork length between hatchery release and smolt trap recapture divided by the number of days between release and recapture. Individual relative spring fork lengths were also calculated, based on the mean fork length at recapture for each study stream. Overwinter growth rates were calculated for individuals released in December 2014, but growth rates for WIL fish encompassed both the summer and winter seasons due to their June 2014 release.

Food Availability and In-Stream Habitat

Food availability and in-stream habitat complexity and diversity can influence fish growth and movement patterns prior to smoltification (Quinn and Peterson 1996, Rosenfeld et al. 2005). To incorporate these potential factors I estimated macroinvertebrate abundance and in-stream habitat metrics for each study stream. Sampling was conducted in March 2015 following winter flow peaks, to represent spring-time productivity and growth potential peaks for invertebrates as well as physical habitat diversity and quality at the midpoint during the movement study season and the beginning of the spring recapture measurement season (i.e., end point of growth rate estimate). Four in-stream sampling sites were selected along a longitudinal gradient within each of the study streams (Figure 2.2). Sites were randomly generated within four equal length stream segments of the main channel habitat for each study stream. Some sites were adjusted due to lack of access to stream sections, but all reaches were at least 1.4 km apart to minimize spatial autocorrelation. In the three streams with multiple PIT antenna arrays, sites were dispersed so that they were located both downstream and upstream of PIT detection arrays.

Riffle habitats are often important prey feeding sources for juvenile salmonids because they provide drift supply to downstream pools where fish often feed (Rosenfeld and Raeburn 2009). To represent these supply habitats to pool-rearing fish, three riffle or glide habitat units separated by pool habitat were selected within each sampling site in March 2015, based on standard stream habitat type classifications (Bisson et al. 1982). Within each site, sampled habitat units were separated by at least one slow-flowing unit and their spatial location was recorded with a Garmin eTrex 20 GPS unit at the downstream end.

Habitat units were sampled for benthic macroinvertebrates across multiple microhabitat patches to represent variation in substrate, flow, and depth variability (Figure 2.2). A single cross-section within each habitat unit was sampled at three points, representing both slower flowing, wetted edges of the unit and the fast flowing thalweg to capture potential within patch differences in stream velocity, which can impact physical and community stream characteristics (Frissell et al. 1986). When the thalweg was located at a habitat edge, the center was sampled in addition to the edges. Sampling was performed using standard kick net and laboratory procedures for benthic invertebrate stream sampling (Carter and Resh 2001). A D-frame kick net with a 500-µm net was held downstream from the sampled substrate for 60 seconds while the sampler gently disturbed the substrate from the surface to a depth of ~10-cm by cleaning all substrate and vegetation within the approximate square area of the D-frame kick-net. The kick-net was rinsed into a 500-µm sieve and large debris was cleaned and removed. The three kick net samples were composited into a single sample per habitat unit and preserved at a final concentration of 70% ethanol, except for the WIL sample sites, which were stored in 70% isopropyl alcohol and transferred to 70% ethanol within 90 days.

Preserved macroinvertebrate samples were sorted under a minimum of 10x magnification in the lab using a two-phase sampling method, in which large, rare species were removed first from a sample and then the remaining sample was subsampled until a minimum of 300 individuals were selected. This subsampling technique reduces variability in species richness, while maximizing sampling efficiency with dense samples (Vinson and Hawkins 1996). Subsampling was performed using a Caton subsampler, in which grids were randomly selected and individuals were enumerated until the minimum number of individuals were selected and entire grid cells were sorted. Abundance was estimated for the entire sample when a subset of all grid cells were sampled.

Average wetted and bankfull width was calculated for each unit based on current, wetted conditions and bankfull channel characteristics, including observed changes in slope, sediment, and vegetation structure. Habitat shelter quality was calculated as well based on California Department of Fish and Wildlife habitat metrics designed for salmonid monitoring, including habitat quality rankings and percent coverage of refuge (Flosi et al. 2010) (Appendix B). Variables utilized in analysis included mean shelter, as well as coefficients of variation of shelter and channel widths, which represent the degree of habitat heterogeneity across the study streams (Appendix B).

Landscape Influences

Riparian and basin land use variables were calculated and extracted using geographic information systems (ArcGIS 10.2) and Geospatial Modeling Environment software (Beyer 2012, ESRI 2013) (Appendix B). National Elevation Data at the 10-m scale was used to calculate streamlines, watershed boundaries, and slope (U.S. Geological Survey 2000). Basins were delineated based on the mouth of each study stream (basin mouth), which was further separated into the downstream basins (i.e., upslope of each downstream antenna detection site), and upstream basins (i.e., upslope of each upstream antenna detection site). Land cover data were obtained from the 30-m scale National Land Cover Database (U.S. Geological Survey 2014) and were used to calculate percent coverage of vegetation and development activities. To examine basin and riparian influences on fish behavior, environmental data were extracted at multiple spatial scales: basin-scale (basin mouth, downstream, or upstream), 120-m riparian stream buffer, 60-m riparian stream buffer, and 30-m riparian stream buffer, as well as stream-scale slope, which represents the near-stream topology since data were extracted from the 10-m scale DEM derived streamline. To address the influence of travel distance through streams and to the ocean, stream distances ('as the fish swims') were calculated from each detection site as well as the basin stream mouths. Drainage density was calculated as well, which can represent the degree of habitat heterogeneity in basin, due to larger drainage density value associations with greater confluence density and slope gradients through a basin (Benda et al. 2004).

Basin-scale Topographic Wetness Index (TWI) and Slope Position Classification (SPC) were also calculated based on relative slope positions per upstream and downstream basin (Beven and Kirkby 1979, Weiss 2001) (Appendix B). Topographic Wetness Index indicates the soil moisture content based on the potential for water pooling or flowing downslope, which can represent the degree of stream channel flooding (Beven and Kirkby 1979). The range of values calculated were scaled to an index ranging from 1 (low soil moisture and high water run-off potential) to 10 (high soil moisture and water pooling potential). Slope Position Classification was calculated using a 250-m and 500-m circular neighborhood around each 10-m elevation pixel, classifying basin areas into ridge, upper slope, middle slope, flat slope, lower slope, and valley types (Jenness 2006). Slope Position Classifications represent valley and stream channel characteristics, with constrained stream sections less likely to provide slow velocity, pool habitat than wider valley, low-gradient stream segments (Montgomery and Buffington 1997, Weiss 2001). Classifications were then compared to measured bankfull measurements conducted during in-stream data collection to determine accuracy of classifications.

Precipitation and temperature may catalyze initial winter movement of juvenile coho salmon (Hartman et al. 1982) and temperature is an important control of metabolic rates and growth (Sloat et al. 2014). To address these climate cues, air temperature and precipitation data were downloaded from the Parameter-Elevation Regressions on Independent Slope Model (PRISM) Climate Group (PRISM Climate Group 2004). Daily and two-week averages of total precipitation and mean temperature data were extracted for each PIT detection site for the entire movement study period, including the month prior to fish movement (November 2014 – June 2015). Previous studies have observed correlations between fish movement and daily streamflow patterns and seasonal temperature variation (Bustard and Narver 1975, Tschaplinski and Hartman 1983). Two-week averages of precipitation and temperature data were highly correlated with daily values, so only daily values were used in analyses. Precipitation data were used in place of stream flow data, and when combined with other flow-related variables, such as upslope characteristics, drainage density, and vegetation, can provide an effective understanding of in-stream flow conditions (Poff and Zimmerman 2010, Price 2011). Daily precipitation and temperature values were then joined to each fish movement date, to compare individual movement patterns to local climatic conditions.

Statistical Analysis

All analyses were conducted using R version 3.2.2 (R Core Team 2015) with the MASS and RandomForest packages. Due to the high number of landscape and in-stream variables, principal component analysis (PCA) was used to reduce watershed data dimensionality based on relative importance as well as similarity among variables. Variables were identified by type (geomorphology, in-stream habitat, vegetation, and agriculture and development) and summarized as means and standard deviations or coefficients of variation to quantify average conditions and variability among basins (basin summaries available in Appendix B). Basin scales (basin mouth, downstream basin, upstream basin) and riparian scales (120-m, 60-m, 30-m, and near-stream scales) were analyzed simultaneously to explore differences among basin types. Relative importance of variables were similar in PCA analyses that included both basin and riparian-scale values compared to analyses including just basin-scale values (Appendix C). Therefore, basin-scale data were used in all further analyses. To incorporate variation in watershed-scale conditions in further analyses, I extracted the site scores along principal component (PC) 1 and 2 for each stream basin, which were used in modeling fish movement and growth (below). The small number of study streams precluded the direct use of landscape variables in fish movement and growth models.

Fish size analyses were conducted for the subset of individuals detected within each study stream release group. These additional tests were used to determine if fish size patterns were similar to release group comparisons prior to winter movement. As with the release group comparisons, pre-winter absolute fork length, relative length, Condition factor, and growth rates were compared among streams using Welch's *F*-test and the post-hoc Games-Howell test. When variables met assumptions of normality and equal variance, parametric ANOVA or *t*-tests were used.

The power of landscape, climate, and fish size variables to predict timing of movement and individual growth rates were analyzed using random forest models. Random forest modeling is well suited to large, non-parametric data sets that include both categorical and numerical variables that may be highly correlated, which was the case with this data set (Breiman 2001, Cutler et al. 2007). Model explanatory power is determined by averaging many regression tree outputs into a single forest. Each tree is built by randomly selecting two-thirds of the data set to assess predictive power of each variable to the response (out of bag error) while the remaining one-third of data is used to assess the accuracy of this tree in predicting the response (Breiman 2001). Because accuracy and predictive relationships are relative to the variables included in the model, random forests determine the relative importance of variables in reducing overall model predictive error, rather than the significance of individual variables. Model explanatory success is based on the Pseudo R^2, which was calculated as 1 – the mean square error across all trees in the model divided by the variance in the response. Predictor variable importance is based on the mean percent decrease in overall model accuracy in predicting the response with the removal of that single predictor, which was calculated based on the out-of-bag error rate. Variable importance scores were then standardized (variable importance/standard deviation) to determine relative importance among the predictor variables. Relationships between individual predictor variables and the response were also visualized using partial dependence plots, which depict the impact of one predictor on the response if all other predictors are held constant. Only non-watershed variables were visualized with partial dependence plots (temperature, precipitation, movement, fish size) since limited replication of study streams did not allow for one-on-one visualization of PC components with fish movement and growth.

Because detection rates (and potentially survival) differed among upstream and downstream detection sites as well as at spring smolt traps, random forest models had different sample sizes. However, the same fish could be represented in multiple models if detected at upstream and downstream detection sites and at spring smolt traps. Although random forest models allow for multi-collinearity, correlation among variables was assessed using Pearson's correlation. All models included correlations < 0.66 except for the downstream detection site model, which included highly correlated (>0.99) principal coordinates among the basins. These correlated variables were left in the model to determine the relative importance of different catchments on fish behavior. Random forest models included $\log_{10}$-transformed fish size variables for consistency with other analyses. All models had 3000 trees, which stabilized tree error.

Results

Movement patterns were documented using PIT detection site data in the four study streams from December 10, 2014 through the end of smolt migration for the year (June 18, 2014). A total of 1779 individual juvenile coho salmon were detected moving through the four study streams, of which 1291 individuals were detected moving past one of the three upstream detection sites, 1246 were detected moving past one of the four downstream detection sites, and 758 individuals were detected at both upstream and downstream sites per stream (Table 2.3). Similar to release group comparisons, detected individuals pre-winter absolute fork length ($F_{3,\,499}$=448.12, $p < 0.001$) and Condition factor ($F_{3,\,422}$=3.94, $p = 0.009$) differed significantly among study streams (Figure 2.3a, b). Pre-winter relative fork lengths were also differed significantly, with WIL having a lower relative fork length for detected individuals ($F_{3,\,498}$=4.27, $p = 0.005$); however, the median values were much more similar for relative fork lengths compared to absolute fork lengths (Figure 2.3c).

Observed movement patterns across the watershed exhibited a generally bimodal distribution, with fish movement past both upstream and downstream detection sites occurring during the winter (December 2014 – February 2015) or the spring (March 2015 – June 2015) (Figure 2.4). Movement timing among streams also differed significantly for both upstream ($F_{2,\,332}$=8.66, $p < 0.001$) and downstream sites ($F_{3,\,244}$=356.86, $p <$ 0.001) (Figure 2.5). Some inter-stream movement was documented, with fish stocked in other watershed streams observed in DUT (32 fish, which originated from three other streams), GRE (2 fish, originated from two other streams), and MIL (8 fish, originated from four other streams). All inter-stream detections occurred at downstream detection sites, and no inter-stream movement was documented for WIL. Significant differences were observed for movement timing between inter-stream and intra-stream fish groups ($F_{1,\,51}$=315.91, $p < 0.001$), with inter-stream fish moving significantly earlier during the study period (Figure 2.6). No significant difference existed in pre-winter relative fork lengths between fish making inter-stream and intra-stream movements ($F_{1,\,1823}$=0.03, p =0.865).

A subset of 219 individuals were recaptured in spring to calculate spring recapture absolute fork lengths, spring relative fork lengths, and growth rates over in the four streams from March 11 to June 11, 2015 (Table 2.4). Similar to release groups, pre-winter absolute fork length of this subset was differed significantly among study streams ($F_{3,105}$=201.31, p <0.001). Spring recapture absolute lengths were significantly different among streams ($F_{3,\,274}$ = 48.15, $p < 0.001$) except for DUT and MIL (Figure 2.7a); however no significant differences in spring relative fork length distributions of these fish were found among the streams ($F_{3,274}$ = 0.59, p = 0.620) (Figure 2.7b). Growth rates differed significantly among study streams ($F_{3,105}$=3.40, p = 0.021) (Figure 2.7c), where

MIL fish had a significantly greater growth rate than DUT fish (Games-Howell post-hoc test $p = 0.019$); no differences existed among all other stream pairwise comparisons (Figure 2.7c).

To understand potential differences in landscape and in-stream habitat characteristics among study stream basins, principal components analysis (PCA) was used to assess dissimilarities among basin types, study streams, and the importance of variables in explaining these differences. The first two axes of the PCA explained 77.5% of the total variation across the study basins, with PC 1 explaining 58.5% of the total variance and PC 2 explaining 19.0% of the total variance (Figure 2.8, Appendix C). PC I was primarily explained by coniferous forest coverage, basin-scale geomorphology (slope characteristics), development, agriculture, herbaceous vegetation, and invertebrate abundance (Appendix C). PC II was primarily explained by wetland coverage, drainage density, in-stream physical habitat parameters, and deciduous and mixed forest coverage (Appendix C).

Study streams were closely clustered among basin types, although PC I was primarily positively related to the GRE study basins while PC II was positively associated with MIL and negatively associated with DUT and WIL (Figure 2.8). The GRE basin was positively associated with development and agricultural land cover, non-forested vegetation, invertebrate abundance, and low gradient habitat and high surface water pooling potential (high TWI) values while negatively associated with high slope and coniferous forest coverage. The downstream basin type for GRE was more strongly positively influenced by low gradient and development characteristics than the upstream basin. The MIL basin was positively associated with non-coniferous forest coverage and in-stream physical habitat variation, as well as negatively associated drainage density and wetland coverage. The DUT basin was primarily associated with high gradient variables, although both DUT basin types were closely grouped at the center of the PCA model. The WIL basin was positively associated with drainage density and wetland coverage, especially the downstream basin type. The WIL basin was also negatively associated with in-stream physical habitat variation and deciduous and mixed forest coverage.

Relationships among fish movement and growth response variables and watershed, climate, and fish size predictors were modeled to understand potential interactions and directional relationships (Table 2.5). Eighty percent of total variation in movement past the upstream detection sites were captured by the random forest model, with precipitation, temperature, and watershed conditions providing explanatory power (n = 1291, mean square residuals = 538.3) (Figure 2.9, Appendix D). Daily temperature and precipitation, and stream basin PC 2 and PC 1 explained the majority of the variation, followed by fish size metrics (Figure 2.9, Appendix D). Earlier fish movement occurred during cooler winter temperatures and greater precipitation events while fish size had a limited influence on upstream movement (Figure 2.10). The importance of PC 1 and PC 2 may explain the significantly earlier movement time of fish past the upstream detection sites in GRE and MIL in comparison to WIL (Figure 2.5a). The downstream and entire GRE basins were positively associated with PC 1, which was characterized by greater development, agriculture, higher invertebrate productivity, and lower slope gradient. Earlier movement from GRE may be related to high productivity and availability of low gradient habitat downstream in comparison to upstream habitats. Earlier movement from MIL may be because of similar patterns: the upstream MIL basin was positively associated with PC 2, which was characterized by in-stream habitat variability and deciduous forest coverage, which are not indicative of preferred off-channel winter rearing habitat features. The upstream WIL basin was more closely clustered with stream flow dissipation and off-channel rearing features, such as wetlands and high drainage density, potentially reducing the impact of high-velocity flows from precipitation events on fish movement in this stream (Figure 2.8).

Movement past the downstream detection sites were affected by movement past the upstream sites and downstream daily temperature and precipitation, followed by upstream daily temperature, PC 2 and PC 1 metrics for all basins, with 73.9% of total movement day variance explained (n = 758, mean square residuals = 128.0) (Figure 2.11, Appendix D). Fish that moved earlier past upstream detection sites were more likely to move earlier past downstream sites as well (Figure 2.12). Temperature and precipitation had limited effect on movement timing in comparison to the upstream movement model (Figure 2.12). The importance of PC 2 and PC 1 may again explain later movement past the downstream detection sites in GRE and WIL and the earlier movement of fish out of DUT and MIL basins (Figure 2.5b). GRE was associated with high productivity and low gradients in its lower basin, potentially supporting more growth and foraging benefits and later movement from this stream basin (Figure 2.8). WIL was also associated with beneficial winter rearing habitat, with drainage density and wetland coverage describing this basin on the PC 2 axis (Figure 2.8). DUT and MIL may have earlier fish movement patterns because of the association of lower MIL with forest coverage and in-stream physical habitat heterogeneity, which are not likely supporting features of floodplain rearing. DUT had the earliest movement timing of the streams, which may be because of the clustering of this basin along gradient features in the PCA analysis (Figure 2.8). Condition factor was removed from this model because it had a negative variable importance score, and reduced model accuracy when included.

Growth rate models captured 70.8% of total variation in the data set, with fish size metrics influencing growth more so than basin characteristics (n = 219, mean square residuals = 6.78×10^{-8}). Pre-winter relative fork length was the most important predictor of growth, followed by spring relative fork length, downstream movement day, and PC 2 and 1 from the downstream basins (Figure 2.13, Appendix D). Pre-winter relative fork length and downstream movement day were inversely related to growth, meaning larger fish and fish that moved later in the season grew more slowly (Figure 2.14). However, fish that had a higher relative length in the spring grew more quickly, suggesting that pre-winter fish size may not determine smolt size alone (Figure 2.14).

Discussion

Due to diminished population abundances, hatchery stocking and stream restoration are common strategies utilized to support Pacific salmon recovery efforts (Fraser 2008, Roni et al. 2008, Araki and Schmid 2010, Ogston et al. 2015). One important aspect of recovery is conservation of life history diversity, including timing of movement of juvenile fish (Waples 1991). This study identified multiple movement strategies of juvenile coho salmon from four streams in the Russian River watershed, as well as the importance of temperature and precipitation patterns, landscape characteristics, and fish size in influencing growth and timing of movement.

Movement

Three winter-rearing strategies were observed through monitoring of PIT-tagged coho salmon in the Russian River watershed from December 2014 through June 2015: 1) winter movement after stocking from the hatchery; 2) rearing in streams until the spring season when smolt migration occurred; and 3) a small subset of inter-tributary movers, with fish stocked in non-study streams moving into and back out of three of the four study streams. Variation in movement was primarily explained by temperature and precipitation events, but watershed variables were the next most important (Figure 2.9 and Figure 2.11). Fish size was outweighed by these coarser-scale variables, with limited power in predicting movement past both upstream and downstream detection sites.

The importance of watershed variables may indicate landscape interactions with precipitation, temperature, and stream productivity. PC 2 was primarily described winter habitat quantity and quality characteristics, due to the association of wetland, drainage density, in-stream habitat variability, and deciduous forest variables (Figure 2.8). High drainage density is associated with greater habitat heterogeneity and valley floor area (Benda et al. 2004), features indicative of preferred juvenile coho salmon winter habitats, such as wetland and pool features (Reeves et al. 2011). PC 1 was primarily described stream productivity characteristics, with a positive association of development, agriculture, and invertebrate abundance, and negative association with coniferous forest (Figure 2.8). These variables may influence stream temperatures (limited winter canopy from low coniferous forest coverage) as well as nutrient levels from development and agriculture run-off, potentially increasing invertebrate abundances (reviewed in Allan 2004). Additionally, deciduous forests are linked to high terrestrial prey inputs in small streams (Baxter et al. 2005) as well as potential nutrient resources from nitrogen-fixing alder species (Bisson et al. 2009). Productivity and complex habitats may influence how coho salmon respond to winter disturbance events, such as floods. Warmer waters may increase growth opportunities due to positive associations between water temperatures and fish metabolic rates, further improving the quality of winter rearing habitats in these low canopy basins when high water velocities are not a limiting factor. These foraging and rearing benefits may delay timing of movement.

Juvenile coho winter movement tends to coincide with increased stream flows (Bramblett et al. 2002, Miller and Sadro 2003, Roni et al. 2012, Jones et al. 2014), decreasing water temperatures (Tschaplinski and Hartman 1983), and reduced habitat complexity (Tschaplinski and Hartman 1983, Roni et al. 2012). The importance of low temperatures and high precipitation intensity for early movement past upstream detection sites in my study follows these previously documented stream flow patterns, especially when channel complexity is considered (i.e., PC 2 watershed variables). For instance, precipitation may have less intense or delayed effects on stream flow conditions in systems with greater drainage densities, low-gradient habitats, and in the presence of channel roughness characteristics, such as forest land and varied in-stream channel widths, which are usually formed by large wood and boulder structures (Bisson et al. 1982). DUT and MIL both had significantly earlier movement past downstream detection sites in comparison to GRE and WIL. This may be due to the association of GRE and WIL with low gradient, wetlands, herbaceous vegetation, and high invertebrate abundances (Figure 2.8). MIL and DUT were more associated with high gradients throughout the basins, based on greater slopes and the presence of ridge lines ((Figure 2.8). Therefore, large rain events may cause greater velocity stream flows, due to lack of dissipation across wide and rough channels and floodplain features in these two streams (Montgomery 1999). These patterns all support my hypothesis of greater off-channel habitat quantity leading to delayed movements, leading to more spring smolt migrants than early winter movers.

The importance of in-stream habitat variability may influence fish movement and growth opportunities. Although fish left MIL on average earlier than GRE and WIL for downstream detection sites, MIL fish still left significantly later than DUT and at comparable times to fish from GRE for upstream detection sites (Figure 2.5). Habitat heterogeneity in MIL may provide more refuge and foraging opportunities for fish, delaying movements. In-stream habitat heterogeneity is linked to greater pool-riffle ratios, leading to more prey drift to downstream feeding salmon (Rosenfeld and Raeburn 2009) and pool habitat, an important feature when off-channel rearing is limited. These characteristics all support the original hypothesis of greater winter habitat quality leading to later movement for fish past both upstream and downstream detection sites.

Fish that moved between streams (inter-stream) moved significantly earlier than fish that stayed in their stocked stream (intra-stream) in this study, which may be explained by winter habitat characteristics and interactions with climate conditions. On average, inter-stream fish moved 54 days earlier than intra-stream fish (Figure 2.6). Inter-stream fish may leave their stocking streams actively searching for better habitat during initial winter storm events, which primarily occurred in the first sixty days of the study, when larger rain events occurred and prior to the majority of spring fish movement (Figure 2.4). Over 95% (42/43) of the individuals detected in the inter-stream movement group were stocked downstream of the study streams in which they were detected, suggesting active, upstream swimming during the winter season. Active swimming may mean that individuals preferentially sought habitats that improved their ability to compete and survive, such as foraging and rearing space. No significant differences were observed when fish size or precipitation on movement day were compared between inter- and intra-stream movers, suggesting other drivers may be important, such as differences in habitat between stocked-streams and streams to which fish moved. Five of the seven fish that moved into Mill Creek were stocked into Dry Creek that fall, a higher order stream that Mill Creek feeds into, with controlled dam-release flows. Fish may leave Dry Creek for Mill Creek because it is a smaller system, potentially providing more sheltered habitat from high velocity stream flows. These patterns support delayed movement associated with higher quality winter rearing habitat, but further work considering habitat differences between streams that fish leave and streams that fish move into may provide more context on fish-habitat relationships during the winter season.

Pre-winter relative fork length and Condition factor were not important in predicting movement patterns. This contradicts previous studies, which found that smaller wild coho salmon were more likely to leave streams during the winter (Bennett et al. 2011, Roni et al. 2012). However, the relationship between pre-winter fish size and movement can also vary by year, suggesting that shifts in habitat conditions and growth potential are an important driver of when fish move out of freshwater habitat (Pess et al. 2011, Rebenack et al. 2015). When fish move to habitats that have greater growth potential than their previous habitat, fish size can also have limited predictive power of this behavior (Quinn and Peterson 1996, Jones et al. 2014). Variability in fish size in my study may also be low in comparison to analyses with wild fish since hatchery fish in three of the four study streams only experienced one season of environmental selection (winter). Wild coho must also survive in streams from the spring through fall seasons, and habitat unit, stream reach, and basin conditions can strongly influence fish size and survival to the onset of winter (Ebersole et al. 2009a). Fish in Willow Creek had a more narrow range and significantly smaller detected pre-winter relative fork lengths in this study (Figure 3c). This may be explained by summer habitat limitations, potentially reducing growth potential and thus the range of relative lengths in comparison to more recently hatchery-released fish in the three other streams. Greater variability in lengths may have been observed if all fish reared through the study streams in the summer across a gradient of habitat qualities, as observed in previous work (Ebersole et al. 2009a). Homogeneity in fish size may limit my ability to judge the importance of fish length and Condition on behavior, or the ability to capture its importance in this study.

Later seasonal movement by fish (spring smolt movers) may be in response to different cues than early winter movers despite originating from the same hatchery release groups. Spring movement past upstream detection sites was associated with increased temperatures and periods of lower precipitation intensity, indicative of more stable stream flow and thermal conditions. Others have hypothesized that smolt movement may be strongly influenced by photoperiod and temperature cues rather than simply stream flow conditions (Quinn 2005, Roni et al. 2012). This may be the case for the hatchery-stocked fish in this study, since their peak spring movement timing is comparable to previous years in these streams (California Sea Grant, unpublished data). Temperature and precipitation may have been less important in predicting movement past downstream detection sites due to warmer than average drought conditions that prevailed over the period of my study or the importance of photoperiod over temperature and streamflow on catalyzing spring smolt movement. Reduced variation due to drought would limit the range of thermal conditions individuals experienced through the winter and spring seasons, potentially limiting its effect on spring smolt movement and movement past the lower watershed, downstream detection sites.

Growth

Understanding drivers of growth is essential if we are to improve freshwater survival of coho salmon (Ebersole et al. 2009b, Roni et al. 2012). Unlike timing of movement, growth appeared to be primarily influenced by fish size metrics, suggesting that the same abiotic and biotic drivers do not directly affect both movement and growth.

Growth appeared to outweigh initial size at stocking in determining spring fork lengths: growth rates were greater for fish that were relatively larger than other spring movers when recaptured in the spring. Size-dependent mortality may influence this observed relationship: fish detected in spring were significantly larger at release (pre-winter measurements) compared to their original release group ($F_{1,2911}$=38.50*,* p <0.001). This suggests that smaller fish were less likely to be detected or survive the winter. However, small fish size prior to the winter is not always associated with smaller smolt sizes, since winter rearing habitat that has high growth potential can outweigh pre-winter fish length (Quinn and Peterson 1996, Miller and Sadro 2003, Ebersole et al. 2009b). This could be the case in my study: greater growth potential for smaller fish that did survive to be detected may allow them to outpace fish that were initially larger, leading to relatively smaller stocked fish being relatively larger smolts in the spring. This suggests that habitat is more important than fish relative length beyond a certain minimum value prior to the winter season, in terms of predicting growth and relative size for spring smolts.

Implications

This study demonstrates the importance of understanding both watershed conditions and fish size for salmon recovery efforts involving broodstock programs. Further research that expands the spatial scale of hatchery-stocked streams to establish a larger environmental gradient could improve our understanding of fish-habitat relationships in hatchery-influenced systems. By occurring during an extreme drought, this study may represent future conditions in this watershed as well as ones that more northern populations may face. Rainfall and temperature patterns may become increasingly important in predicting when fish move and from where. Furthermore, coarse-scale patterns (watershed conditions) were more important than fish size in predicting timing of movement. Connectivity and habitat quality across streams and within streams is an essential consideration for determining the ability of fish to respond to winter stream environments.

Hatchery programs may be able to better mimic wild coho salmon population life histories by diversifying spatial and temporal stocking. Releasing fish into streams throughout the watershed and across different seasons prior to smolt outmigration could increase portfolio effects by increasing variability in movement through streams and potentially entry into the ocean as well (Doak et al. 1998, Tilman et al. 1998). For instance, the range of dates over which fished moved may be reduced if fish were only stocked in streams that supported early winter movement (e.g., Dutch Bill) or streams that supported later season movement (Willow, Green Valley). Supporting stream populations and the habitats that they rely on can diversify behavior across a watershed, and in turn increase population resiliency (Hilborn et al. 2003).

Watershed management must continue to focus on large-scale processes when considering conservation and recovery goals for highly mobile fish species (Fausch et al. 2002). After climate and movement variables, watershed variables linked to winter habitat quality and quantity were the most important in predicting movement past upstream and downstream detection sites. Maintaining these connections and diverse habitat features may allow for continued support of diverse life history strategies, even for endangered fish during drought years. Supporting diverse habitats and phenotypes allows phenotypic management to be incorporated into population recovery efforts, increasing the likelihood of population persistence despite unknown future environmental conditions (Watters et al. 2003). In the case of coho salmon, early winter movement strategies may allow individuals to increase their growth potential by moving to other stream habitats that provide additional rearing opportunities. This may allow fish that are smaller at the onset of winter to grow enough to outpace fish that were initially larger, potentially increasing survival probability of these larger smolts (Quinn and Peterson 1996, Ebersole et al. 2009b). The importance of these early movers is also evident at the spawning stage, with early juvenile movers supplementing returning spawning populations (Jones et al. 2014, Bennett et al. 2014). Recognizing these patterns and their drivers is the first step in phenotypic management, and should be continually studied when population resiliency is reduced or threatened, as in the case of many Pacific salmon populations.

Tables

Table 2.1. Summary statistics for release groups per study stream, including mean and standard deviation of pre-winter fish size variables. All measurements were completed at the hatchery during the measurement date range. Release date is when fish were released into each study stream. K = (pre-winter wet weight (g) * 100) / (pre-winter absolute fork length (mm)) (Weatherley and Rogers 1978). MN = Mean, SD = Standard Deviation, FL = fork length, K = Condition factor, DUT = Dutch Bill Creek, GRE = Green Valley Creek, MIL = Mill Creek, WIL = Willow Creek.

Study Stream	PIT-tagged Fish Released (total release size)	Measurement Date Range	Release Date	MN Release FL +/- SD (mm)	MN Release Relative FL +/- SD	MN Release Weight +/- SD (g)	MN Release K +/- SD
DUT	1821 (12164)	9/22/14 - 9/24/14	12/4/14	82 +/- 10	0.0 +/- 0.12	6.9 +/- 2.5	0.0012 +/- 0.0
GRE	1514 (10088)	10/14/14 - 10/15/14	12/9/14	85 +/- 10	0.0 +/- 0.12	7.6 +/- 2.9	0.0012 +/- 0.0
MIL	2718 (18173)	9/8/14 - 9/15/14	12/2/14 - 12/3/14	80 +/- 10	0.0 +/- 0.12	6.4 +/- 2.5	0.0012 +/- 0.0
WIL	2254 (15393)	5/23/14 - 6/4/14	6/11/14	66 +/- 5	0.0 +/- 0.075	3.4 +/- 0.87	0.0012 +/- 0.0

Table 2.2. Summary statistics by landscape and in-stream variable type across all basin types (n = 11). Methods in Appendix B. SPC = Slope Position Classification, TWI = Topographic Wetness Index, SD = standard deviation, BMI = benthic macroinvertebrate abundance, Dev. = Development, CV = coefficient of variation.

Variable	Minimum	Maximum	Median
Basin Area and Distance			
Basin Area (km^2)	17.6	98.1	30.6
Stream Length (km)	25.6	136	41.9
Distance to ocean (km)	4.35	59.2	37.3
Distance to stream mouth (km)	0	9.98	0.680
Geomorphology			
Drainage density	0.0013	0.0015	0.0014
Relief ratio	0.043	0.213	0.061
Mean % Slope	14.4	40.8	31.6
SPC Valley (%)	39.6	47.9	46.8
SPC Low Slope (%)	1.04	4.97	1.47
SPC Flat Slope (%)	0.010	6.14	0.270
SPC Middle Slope (%)	2.14	3.19	2.74
SPC Upper Slope (%)	1.03	3.91	1.42
SPC Ridge (%)	42.2	50.3	48.2
Mean TWI (%)	2.23	2.65	2.37
SD TWI (%)	0.523	0.593	0.543
Vegetation			
Mean Canopy Cover (%)	27.3	71.1	58.9
Barren Land (%)	0	0.124	0
Deciduous Forest (%)	0.464	3.70	1.65
Conifer Forest (%)	18.7	80.2	63.4
Herbaceous (%)	3.10	39.4	15.3
Herbaceous Wetland (%)	0	0.289	0
Mixed Forest (%)	3.02	12.6	5.84
Shrub (%)	6.06	14.6	12.05
Wooded Wetland (%)	0	2.57	0.350
Development and Agriculture			
Impervious (%)	0.034	2.12	0.119
Cultivated Crops (%)	0	5.07	0
Dev. High (%)	0	0.159	0
Dev. Low (%)	0	2.03	0.020
Dev. Medium (%)	0	0.853	0
Dev. Open (%)	1.99	10.74	3.77
In-stream habitat			
Mean BMI	498	3717	834
SD BMI	372	1892	607
CV Bankfull Width	0.958	16.5	4.23
CV Shelter	0.698	1.61	0.990
CV Wetted:Bankfull Width	0.896	11.5	3.03
CV Wetted Width	1.74	6.47	3.06
Mean Shelter	6.50	51.7	21.6

Table 2.3. Summary statistics for the subset of fish detected per release group, where fish size variables are from pre-winter measurements. All detected individuals were measured at the hatchery prior to release into each study stream. No upstream detections are recorded for DUT since only one PIT antenna site was present. MN = Mean, SD = Standard Deviation, FL = fork length, K = Condition factor, Det. = Detection, DUT = Dutch Bill Creek, GRE = Green Valley Creek, MIL = Mill Creek, WIL = Willow Creek.

Study Stream	PIT-tagged fish detected	Mean FL +/- SD (mm)	MN Relative FL +/- SD	MN Weight +/- SD (g)	MN K +/- SD	Mean US Det. Day +/- SD (n)	Mean DS Det. Day +/- SD (n)
DUT	284	83 +/- 10	0.013 +/- 0.12	7.2 +/- 2.7	0.0012 +/- 0.0	--	53 +/- 52 (284)
GRE	649	86 +/- 10	0.014 +/- 0.12	8.1 +/- 2.9	0.0012 +/- 0.0	122 +/- 60 (630)	152 +/- 16 (295)
MIL	737	81 +/- 10	0.0070 +/- 0.12	6.6 +/- 2.5	0.0012 +/- 0.0	124 +/- 43 (559)	123 +/- 44 (618)
WIL	109	65 +/- 4	-0.013 +/- 0.065	3.2 +/- 0.8	0.0012 +/- 0.0	138 +/- 33 (102)	151 +/- 14 (49)

Table 2.4. Summary statistics for the subset of fish recaptured at spring migrant traps per original release group. All pre-winter measurements were taken at the hatchery prior to release in each study stream and all spring measurements took place at the spring migrant smolt traps. PW = pre-winter measurement, MN = Mean, SD = Standard Deviation, FL = fork length, Weight = WT, K = Condition factor, Rel. = Relative, GR = growth rate, DUT = Dutch Bill Creek, GRE = Green Valley Creek, MIL = Mill Creek, WIL = Willow Creek.

Study Stream	PIT-tagged fish recaptured	Recapture date range	MN PW FL +/- SD (mm)	MN PW Relative FL +/- SD	MN PW K +/- SD	MN PW Weight +/- SD (g)	MN Spring Relative FL +/- SD	MN Spring FL +/- SD (mm)	MN Growth Rate +/- SD (mm/day)
DUT	31	3/24/15 - 4/27/15	85 +/- 8.8	0.034 +/- 0.11	0.0012 +/- 0.0	7.9 +/- 2.6	-0.0018 +/- 0.07	108 +/- 7.7	0.00116 +/- 0.0
GRE	80	3/29/15 - 6/11/15	90 +/- 11	0.060 +/- 0.13	0.0012 +/- 0.0	9.3 +/- 3.3	0.0028 +/- 0.08	118 +/- 9.1	0.0013 +/- 0.0
MIL	82	3/11/15 - 5/6/15	82 +/- 9.2	0.028 +/- 0.12	0.0012 +/- 0.0	7.0 +/- 2.3	-0.013 +/- 0.09	112 +/- 10.0	0.0014 +/- 0.0
WIL	85	4/14/15 - 5/30/15	66 +/- 4.3	-0.0055 +/- 0.066	0.0012 +/- 0.0	3.3 +/- 0.8	0.0000 +/- 0.09	101 +/- 8.6	0.0013 +/- 0.0

Table 2.5. Random forest regression model summaries.

Response variable	**Percent Variance explained (Pseudo R^2)**	**Sample size**	**Mean square residuals**
Upstream detection site movement day	80.0	1291	538.3
Downstream detection site movement day	73.9	758	128.0
Growth rate	70.8	219	6.78×10^{-8}

Figures

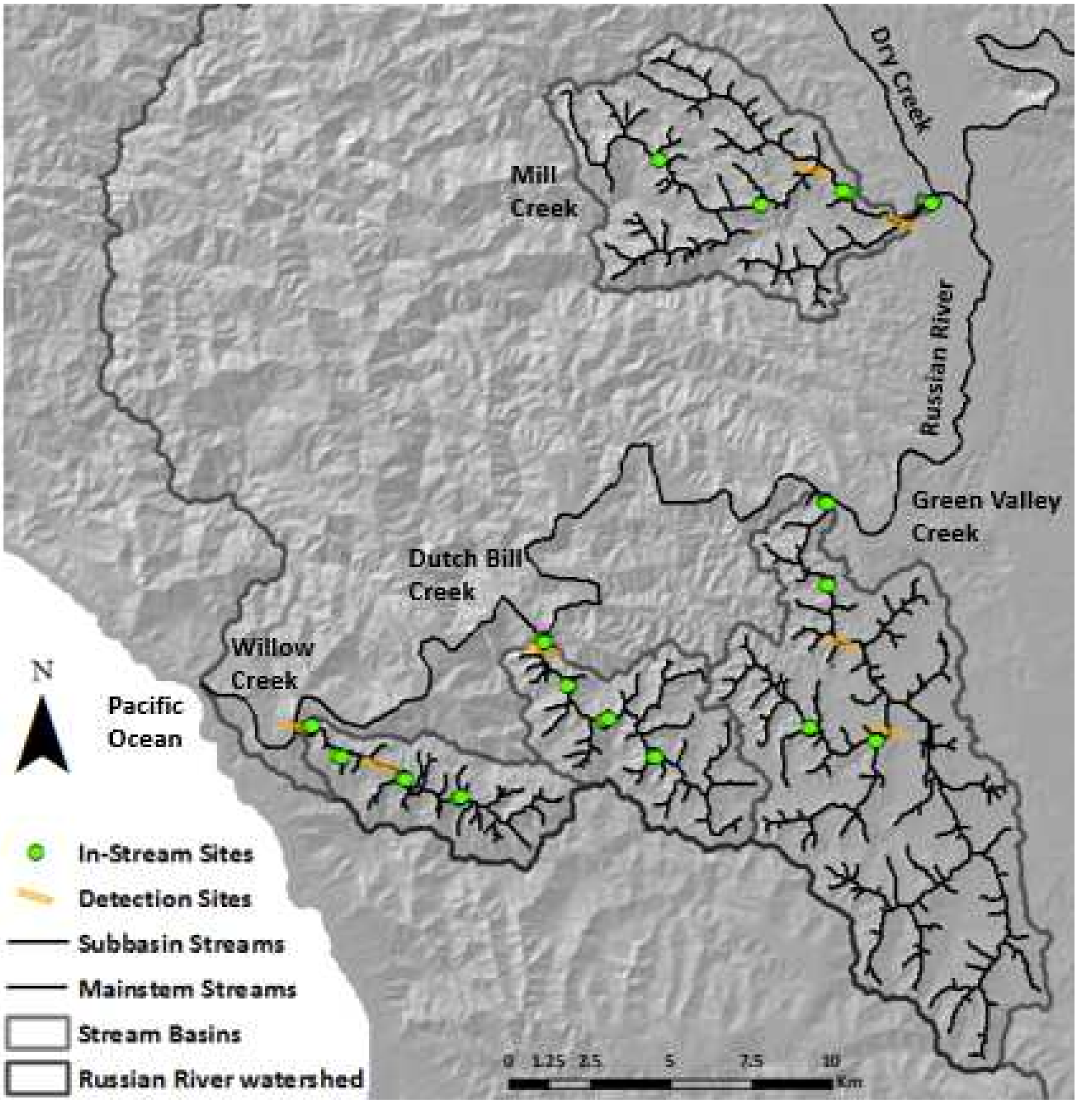

Figure 2.1. The four study stream basins in the Russian River watershed, northern California. Upslope influences on detection sites are delineated per upstream and downstream detection site. Main stem tributaries (Dry Creek and Russian River) are labeled.

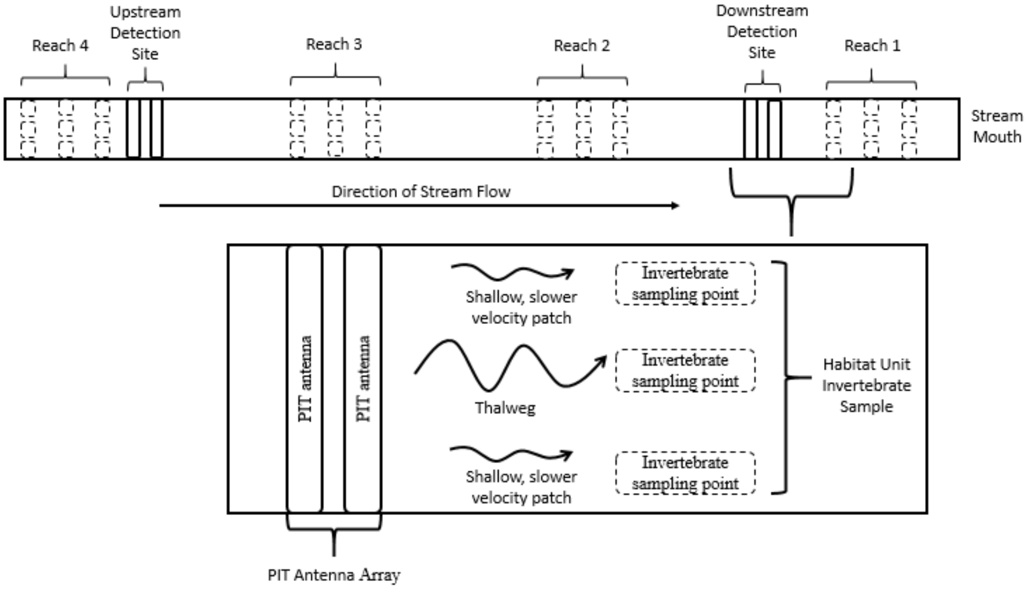

Figure 2.2. Diagram of PIT detection and in-stream sampling reach distribution across a stream. Paired antennas improve detection efficiency per site, and were used as the site design for all but one site in this study, the GRE upstream basin detection site. Macroinvertebrate and in-stream physical habitat measurements were composited per habitat unit and across four reaches per study stream to represent microhabitat and reach-scale variability. Physical habitat metrics were collected to represent the whole habitat unit, and were thus not collected only at microhabitat sampling points.

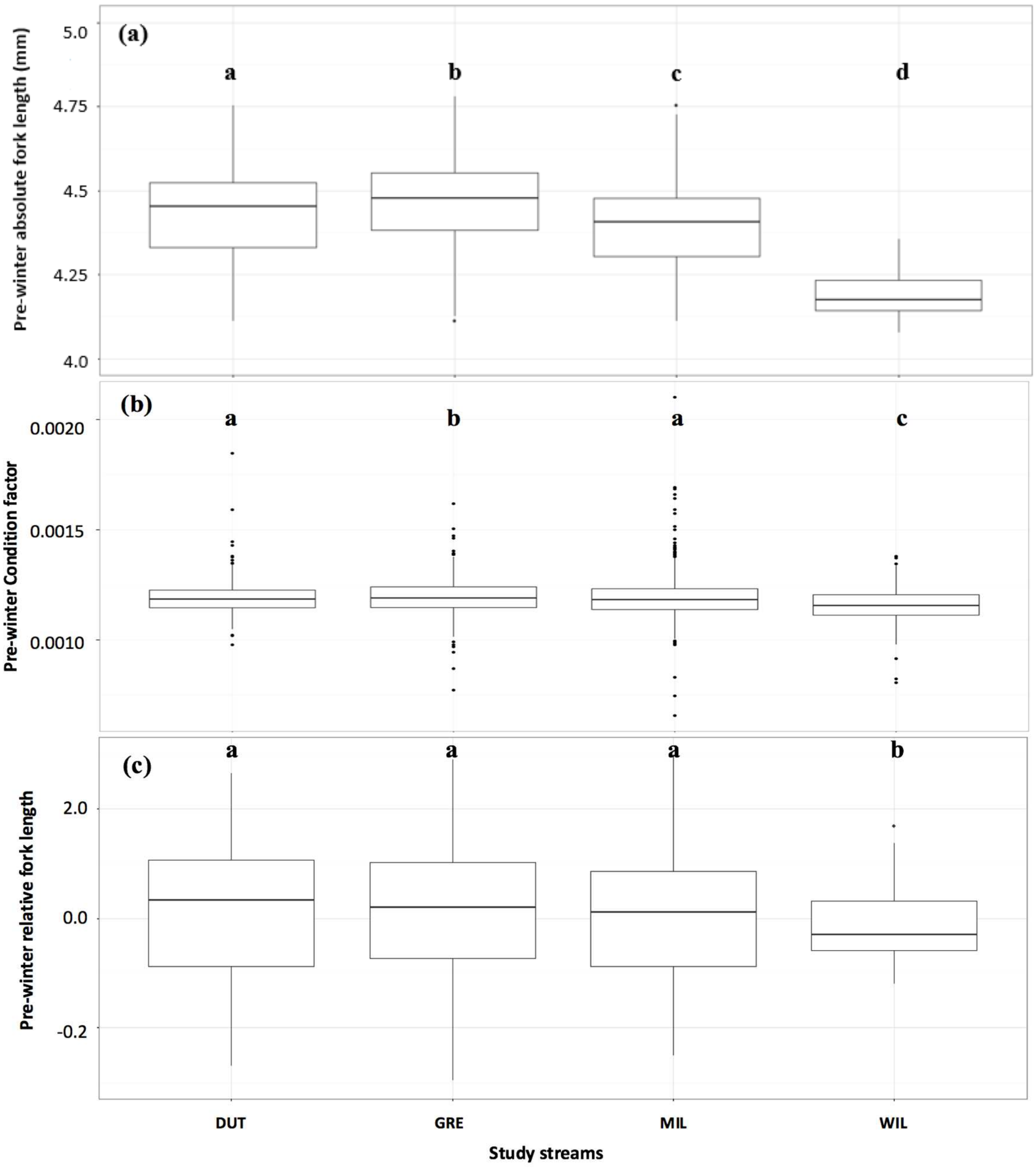

Figure 2.3. Distribution of all detected individuals pre-winter (a) absolute fork length ($\log_{10}$-transformed), (b) pre-winter Condition factor, and (c) pre-winter relative fork length (n = 1779) among the four study streams. Boxplots denote the median value with the box limits extending to the upper (75th percentile) and lower (25th percentile) quartiles. Whiskers extend 1.5 times beyond the interquartile distance of the median, with observations beyond these extents represented as open circles. Letters above study streams represent significantly different pairwise comparisons ($p < 0.05$).

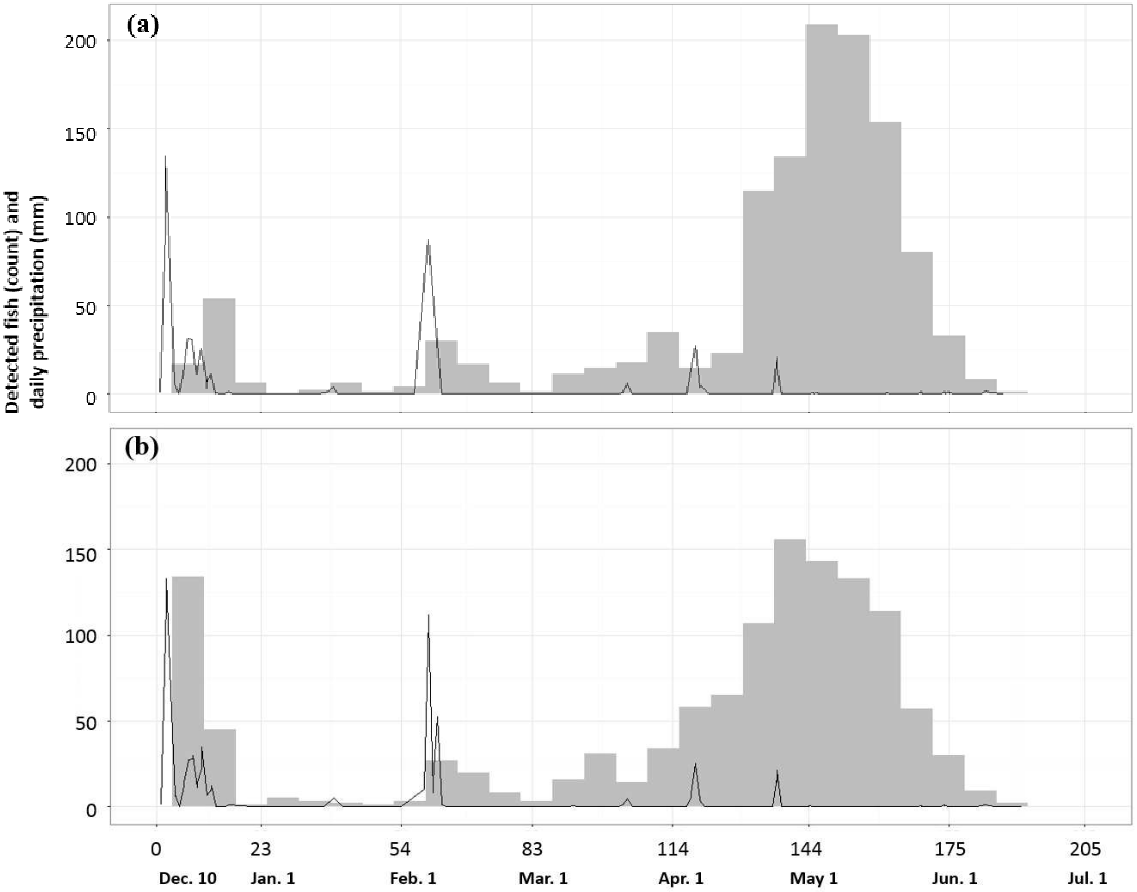

Figure 2.4. Individual fish movement day past (a) upstream detection sites (n =1291) and (b) downstream detection sites (n=1246). Counts are grouped by week-long intervals (gray bars), with day 1 occurring on December 10, 2015 (month included below movement days). Total daily precipitation (mm) per movement day is included for reference (black line).

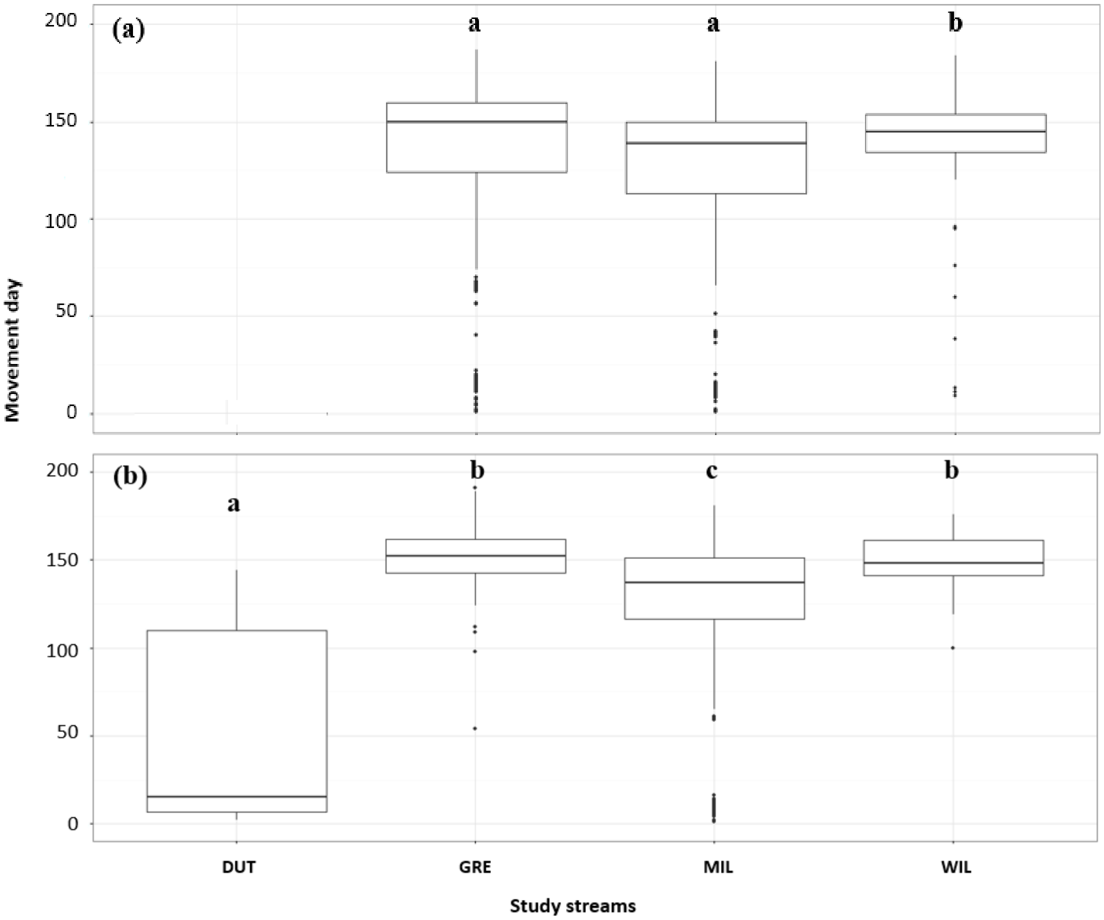

Figure 2.5. Individual fish movement day past (a) upstream detection sites (three streams, n =1291) and (b) downstream detection sites (four streams, n = 1246). Box and whiskers as in Figure 3. Letters above study streams represent significantly different pairwise comparisons (*p* < 0.05).

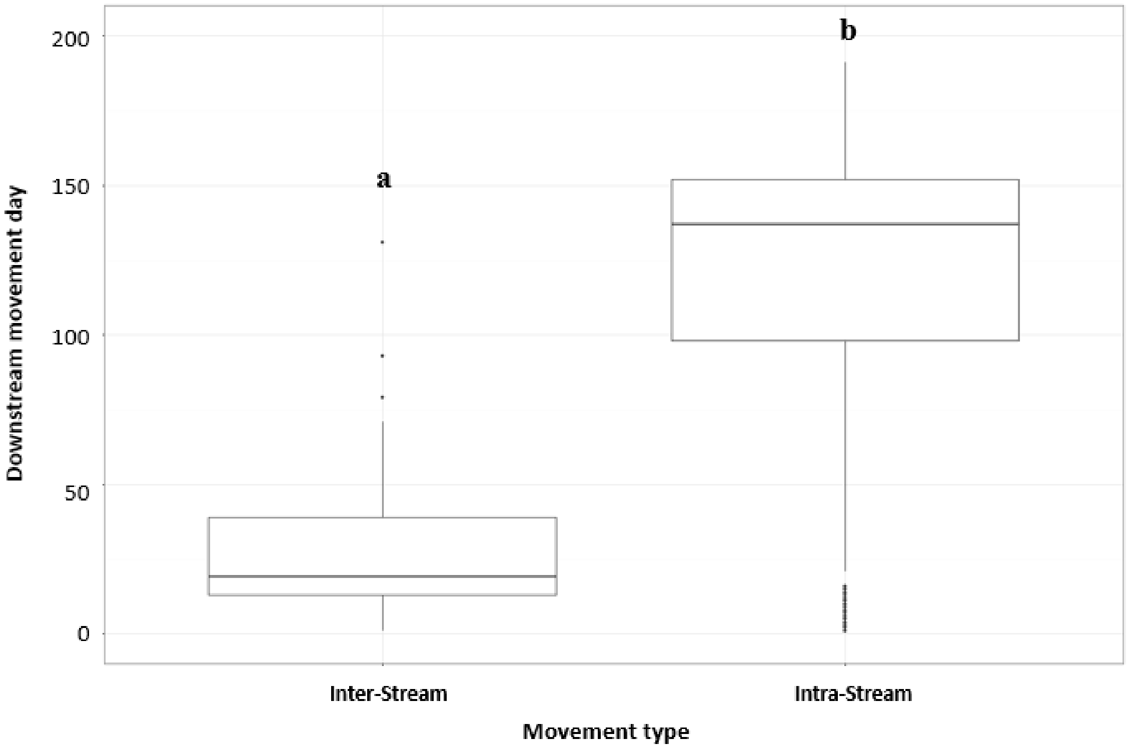

Figure 2.6. Individual movement day past downstream detection sites for inter-stream detected fish (three streams, n = 42) and intra-stream detected fish (four streams, n = 1246). Movement day is the maximum movement day past downstream detection sites for intra-stream group, and minimum movement day past downstream detection sites for inter-stream groups. Box and whiskers as in Figure 3. Letters above study streams represent significantly different pairwise comparisons ($p < 0.05$).

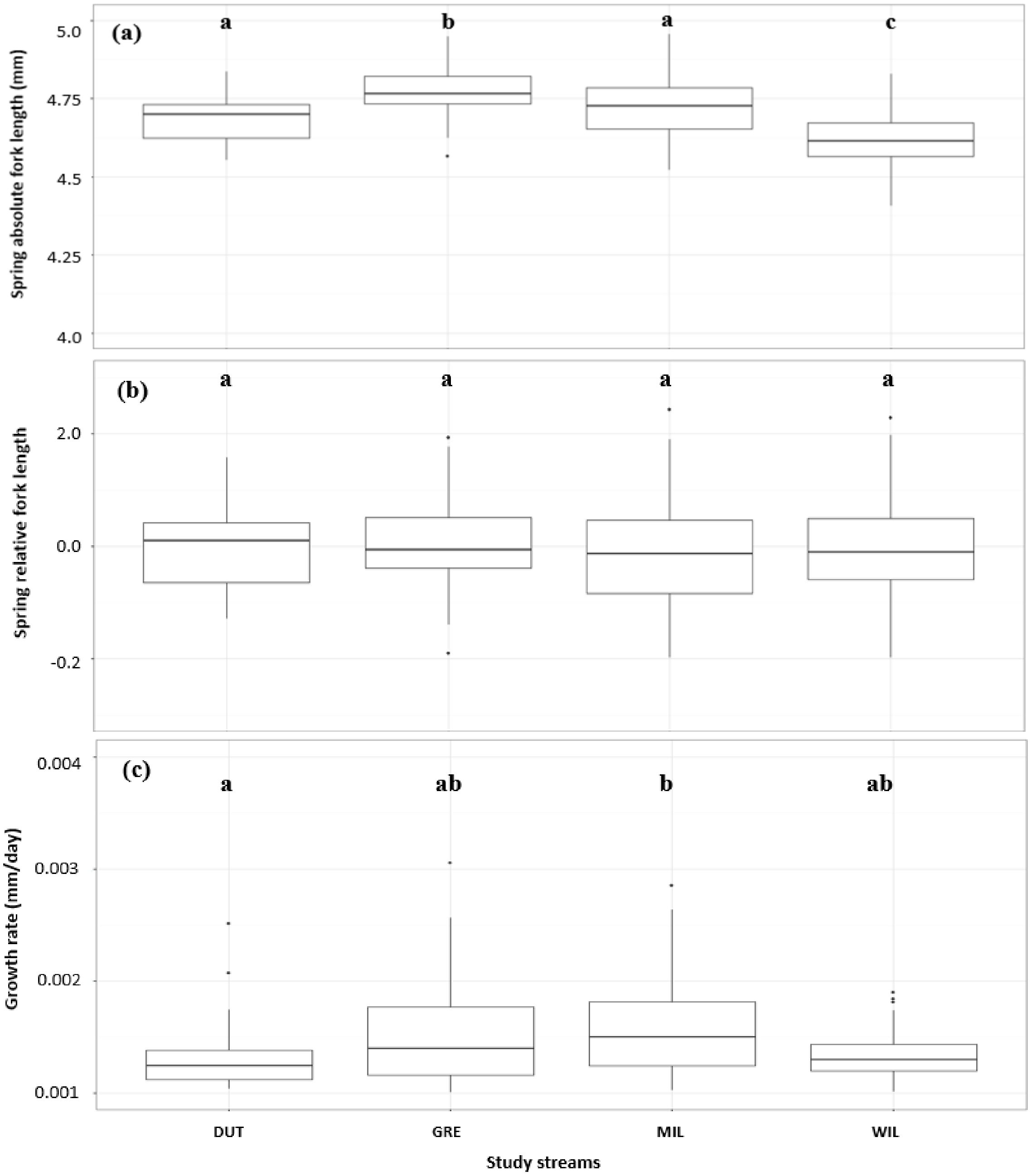

Figure 2.7. Distribution of (a) absolute fork length (log10-transformed), (b) relative fork length, and (c) growth rate (n = 219) of all spring recaptured individuals among the four study streams. Box and whiskers as in Figure 3. Letters above study streams represent significantly different pairwise comparisons ($p < 0.05$).

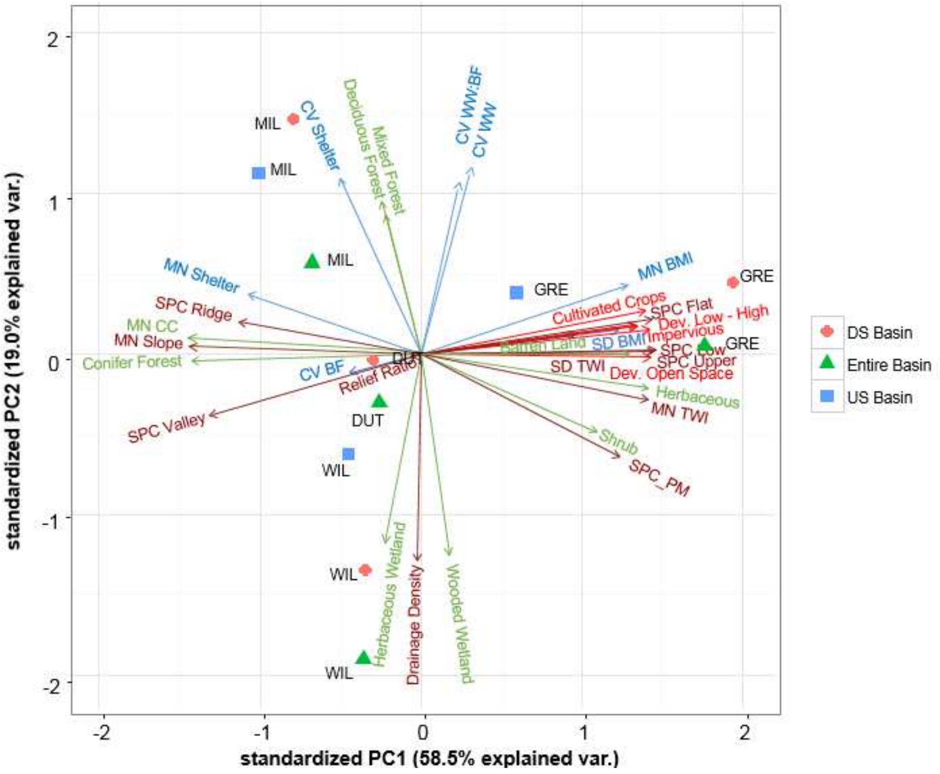

Figure 2.8. PCA for all basin-scale landscape variables across the three basin types. Site scores are indicated by symbols representing basin type (circle = downstream, triangle = entire basin, square=upstream) and stream name. In-stream variable labels and vectors are in blue, vegetation in green, geomorphology in brown, and agriculture and development in red. Full variable descriptions in Appendix B. Abbreviations for in-stream variables on figure are: mean benthic invertebrate abundance (MN BMI), standard deviation of mean benthic invertebrate abundance (SD BMI), mean in-stream shelter rating (MN Shelter), coefficient of variation of mean in-stream shelter rating (CV Shelter), coefficient of variation in wetted width (CV WW), coefficient of variation in bankfull width (CV BF), coefficient of variation in ratio of wetted width to bankfull width (CV WW:BF). Abbreviations for vegetation on figure are mean % coverage of: canopy coverage (MN CC), conifer trees (Conifer Forest), deciduous trees (Deciduous Forest), mixed trees (Mixed Forest), herbaceous plants (Herbaceous), shrub and scrub (Shrub), wooded wetlands (Wooded Wetland), herbaceous wetlands (Herbaceous Wetland), bare ground (Barren Land). Abbreviations for geomorphology variables on figure are: Slope (MN Slope, Slope Position Classification Valley (SPC Valley), Low Slope (SPC Low), Flat Slope (SPC Flat), Middle Slope (SPC Mid), Upper Slope (SPC Upper), Ridge (SPC Ridge), Mean Basin Topographic Wetness Index (MN TWI), Standard Deviation of Mean Topographic Wetness Index (SD TWI). Abbreviations for agriculture and development variables on figure are % cover: open space development (Dev. Open Space), low intensity development (Dev. Low), medium intensity development (Dev. Med), high intensity development (Dev. High), cropland (Cultivated Crops), and impervious surface (Impervious).

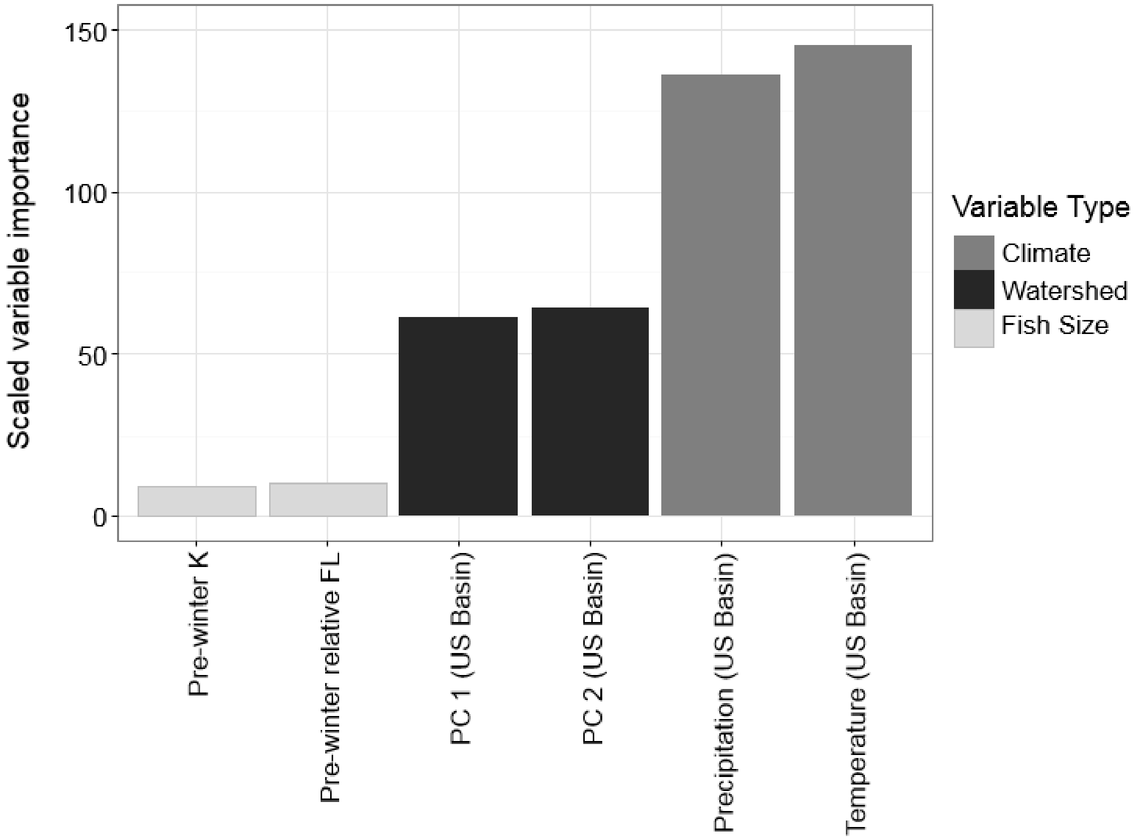

Figure 2.9. Variable importance values for upstream movement day random forest model (n = 1291). Variable importance is scaled (mean decrease in model accuracy percentage/standard deviation). Variable name is listed on the x-axis with variable types included on the right-hand side. Variable names included basin type when multiple basins are included in the model for that variable. K = Condition factor, FL=fork length, US=upstream, DS=downstream, PC = principal component.

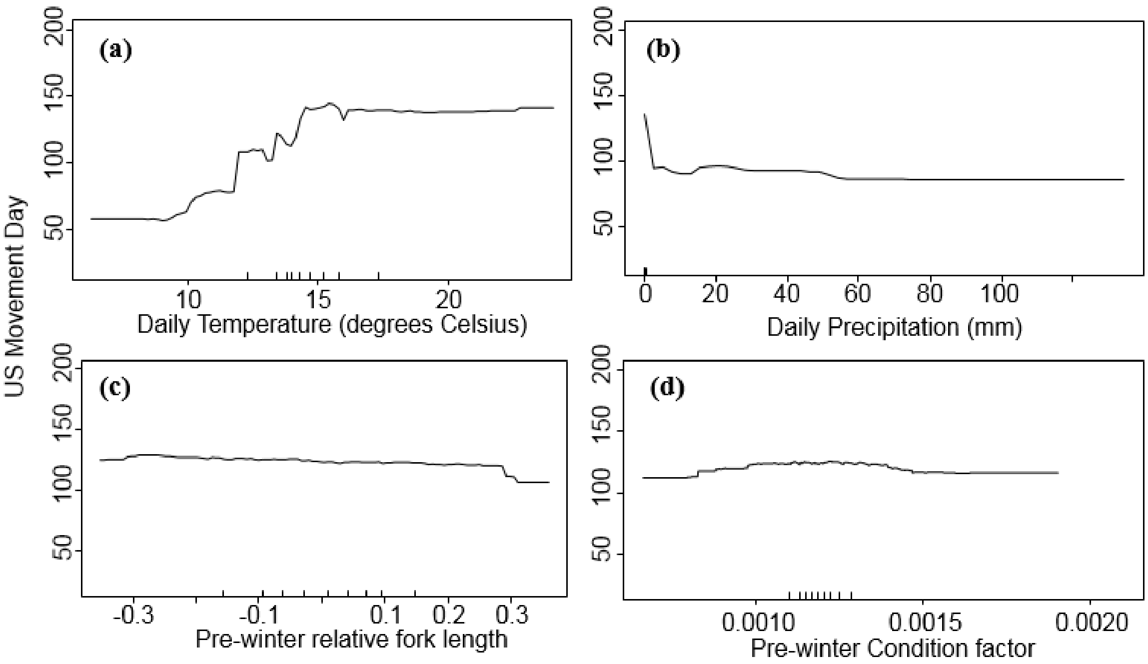

Figure 2.10. Partial dependence plot for upstream movement day versus the four most important non-watershed variables (n=1291). a) Upstream daily temperature (degrees Celsius), b) Upstream basin daily precipitation (mm), c) Pre-winter relative fork length, d) Pre-winter Condition factor. Partial dependence plots depict the impact of one predictor on the response if all other predictors are held constant.

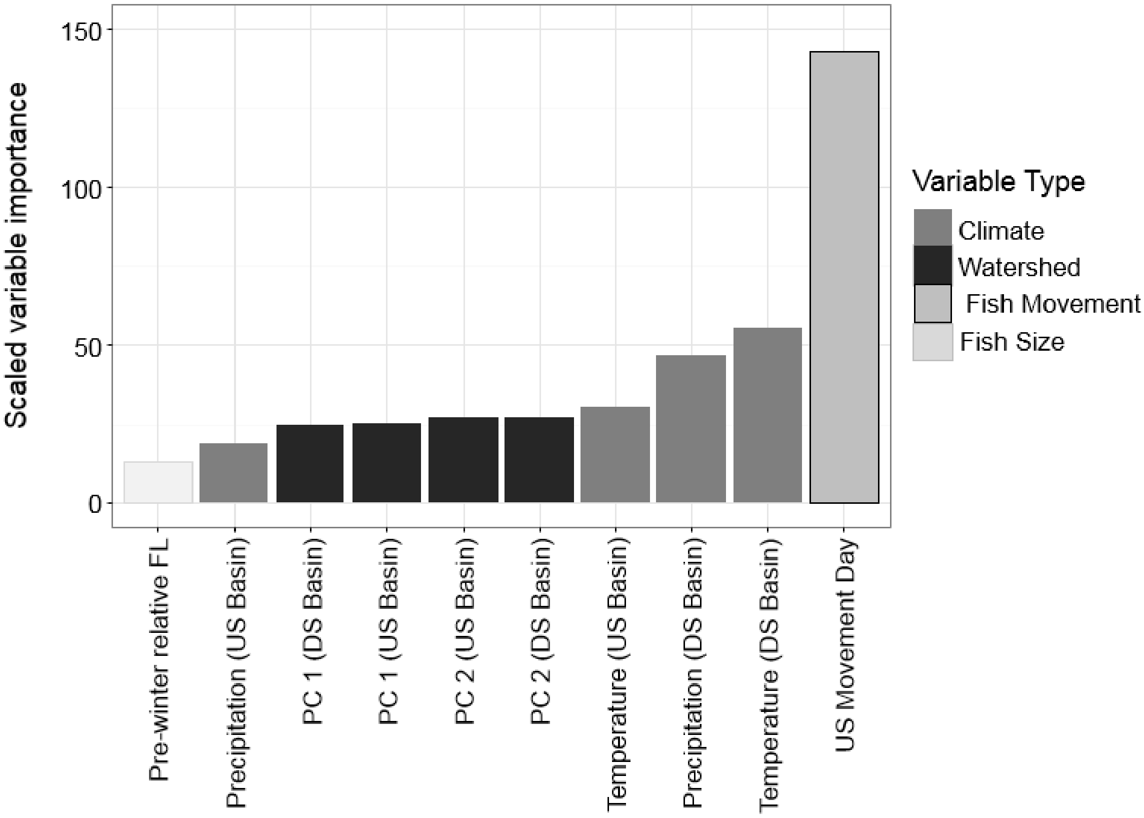

Figure 2.11. Variable importance values downstream movement random forest model (n = 758). Variable importance is scaled (mean decrease in model accuracy percentage/standard deviation). Variable names are listed on the x-axis with variable types included on the right-hand side. Variable names included basin type when multiple basins are included in the model for that variable. FL=fork length, K = Condition factor, US=upstream, DS=downstream, PC = principal component.

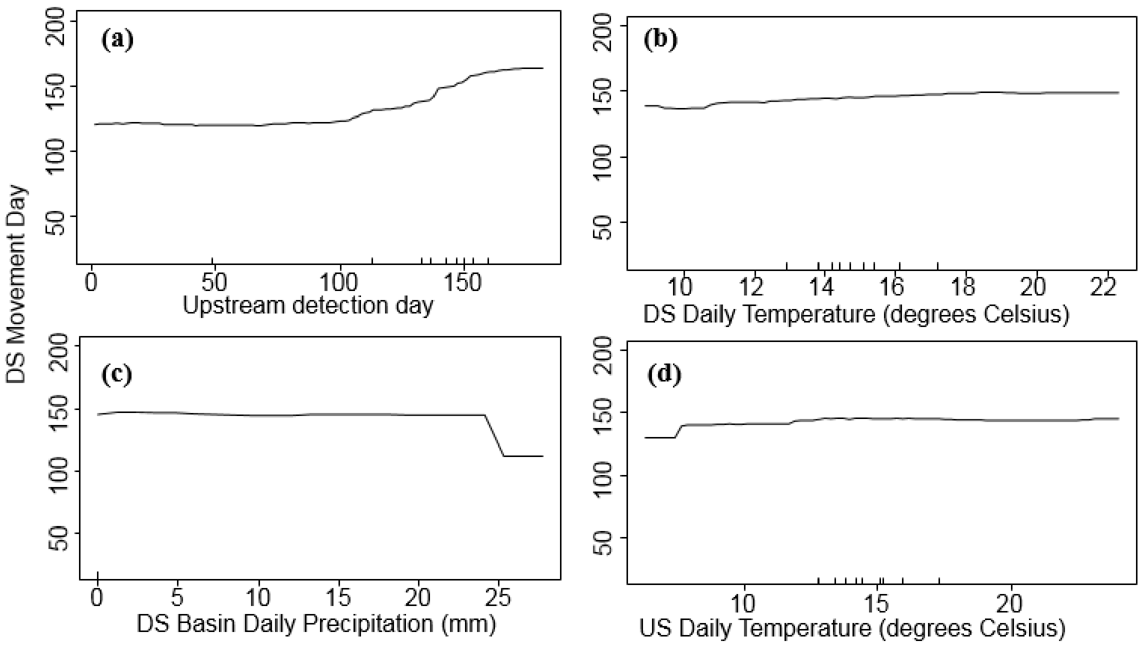

Figure 2.12. Partial dependence plot for downstream movement day versus the most important variable (a) through the fourth most important variable (d) (n=758), where a) Upstream movement day, b) Daily downstream basin temperature (degrees Celsius), c) Daily Downstream basin precipitation (mm), d) Daily Upstream basin temperature (degrees Celsius). Partial dependence plots depict the impact of one predictor on the response if all other predictors are held constant.

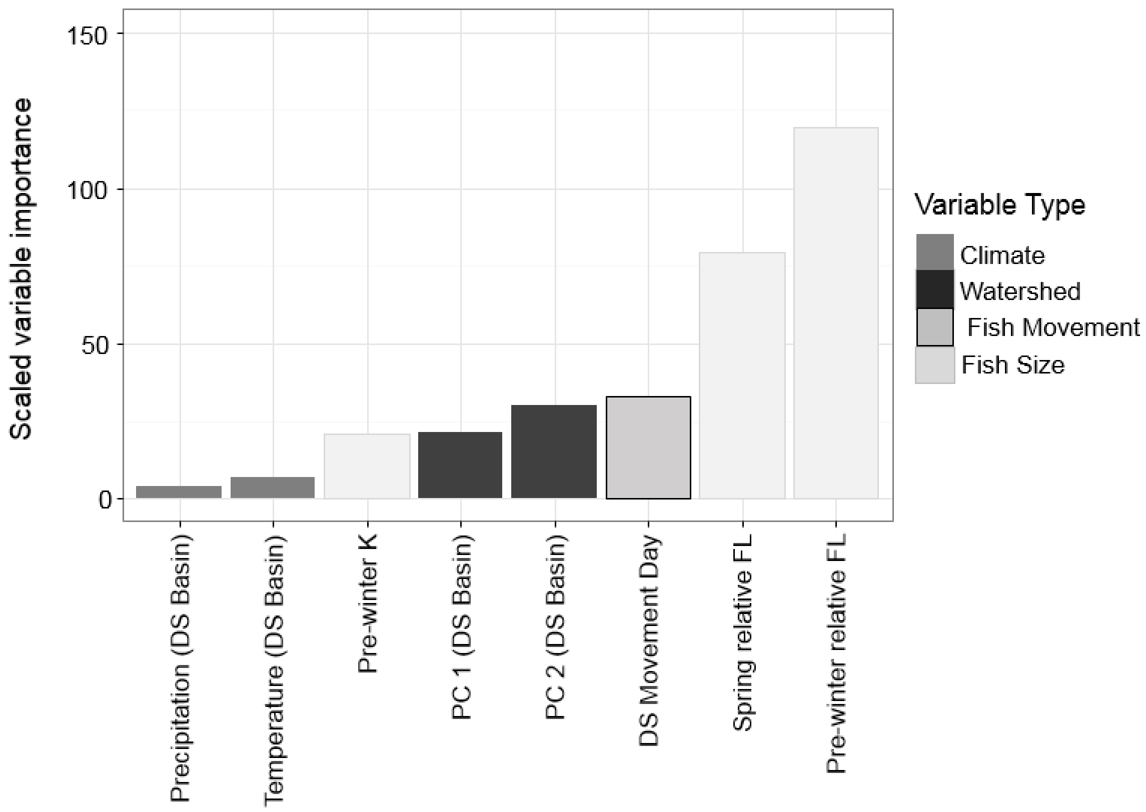

Figure 2.13. Variable importance values for the growth rate random forest model (n = 219). Variable importance is scaled (mean decrease in model accuracy percentage/standard deviation). Variable names are listed on the x-axis with variable types included on the right-hand side. Variable names included basin type when multiple basins are included in the model for that variable. FL=fork length, K = Condition factor, US=upstream, DS=downstream, PC = principal component.

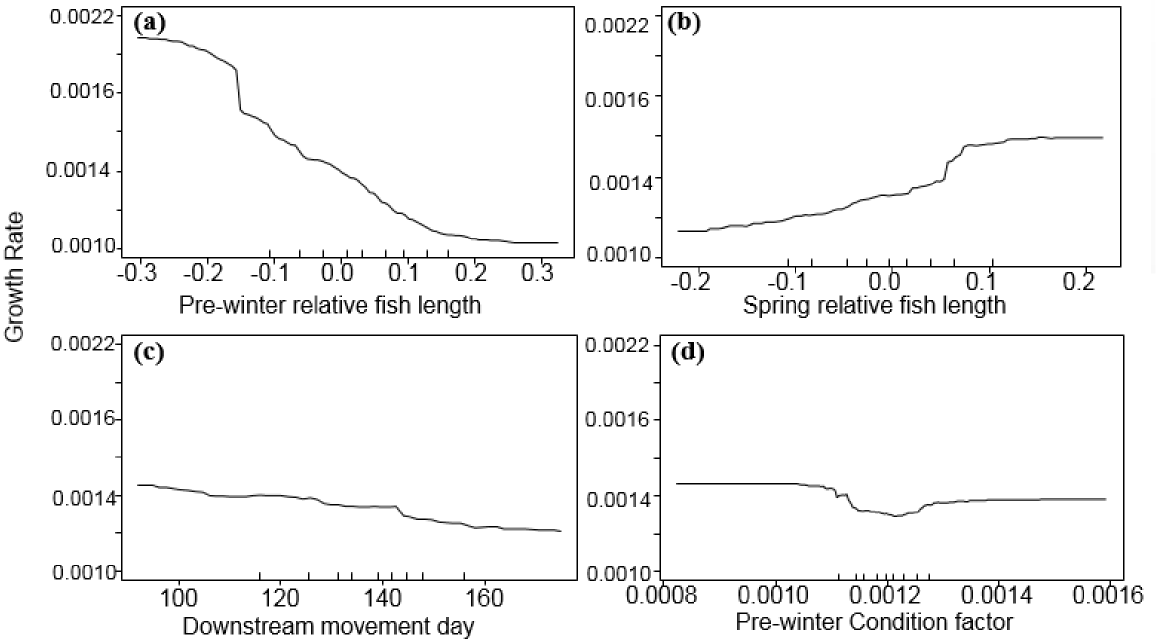

Figure 2.14. Partial dependence plot for growth rate (mm/day) versus the most important variable (a) through the fourth most important variable (d) (n=219), where a) pre-winter relative fork length (mm), b) spring relative fork length (mm), c) downstream movement day, and d) pre-winter Condition factor (ratio of forklength (mm) to body weight (g).

Chapter 3 : Documenting diversity: Evidence of multiple life history strategies across the North American range of coho salmon (*Oncorhynchus kisutch*)

Introduction

Conservation and recovery actions require an understanding life history strategies, including ecosystem-scale interactions among species of concern and their environment. The expression of a species life history reflects the interplay between genetically-based traits, the environment, and phenotypic plasticity in trait expression (Waples et al. 2001). Unique life history strategies occur when variation in timing of movement, fish size, and maturation exist within specific populations and species (Waples 1991). Life histories of Pacific salmon (*Oncorhynchus* spp.) are especially complex because of their anadromous life cycle, and reliance upon marine, estuary, and freshwater systems (Groot et al. 1995, Quinn 2005). Salmon ecology is extensively studied because of its commercial and cultural importance, as well as the decline of many populations, and their subsequent listings under the US Federal Endangered Species Act (ESA) (National Research Council 1996).

Phenotypic expression of Pacific salmon traits can be highly localized because of the association of populations with specific watersheds. Speciation occurred across the dynamic watersheds that drain into the Pacific Ocean, with surviving populations adapted to the seasonal shifts of river and estuary ecosystems (Waples et al. 2008). This evolution, in combination with the strong homing tendency of salmon, has led to highly diverse, localized life history strategies, including seasonal freshwater habitat shifts, and flexible timing of maturation and migration (Taylor 1991, Waples et al. 2001, Quinn

2005). For instance, studies have noted that variability in smolt size and timing of emigration are correlated with latitude in sockeye salmon (*O. nerka*) (Freshwater et al. 2016) and with spawning abundance and flow regimes in Chinook salmon (*O. tshawytscha*) (Beechie et al. 2006, Zimmerman et al. 2015).

One component of salmon life history that is essential to population recovery is the process of smolt outmigration, which represents the cumulative freshwater rearing of individuals prior to their adult, marine residency. Coho salmon (*O. kisutch*) have the longest freshwater residency of the anadromous Pacific salmon, spending one to two years in freshwater (Shapovalov and Taft 1954, Sandercock 1991). Coho salmon rearing shifts seasonally as well, with fish relying on cold, main channel pools during the summer months and inundated floodplain channels, ponds, and ephemeral upper watershed tributaries during winter floods (Tschaplinski and Hartman 1983, Nickelson et al. 1992). These unique movement strategies during the winter can result in differential outmigration timing and smolt size because of variability in growth potential in these different rearing and foraging habitats (Craig et al. 2014, Rebenack et al. 2015), as well as varied smolt survival to spawning age (Jones et al. 2014, Bennett et al. 2014).

Growth potential is an important aspect of freshwater rearing because of its strong association with survival to smolt life stages (Quinn and Peterson 1996, Ebersole et al. 2006). Juvenile salmon growth potential is dependent upon energy requirements for other needs, such as foraging, predator avoidance, and competition for resources (Fausch 1984, Nielsen 1992). Energy allotments are strongly dependent upon the quality of habitat and population density, since these control resource availability. It is well established that juvenile coho salmon prefer low-velocity, cold water pools with abundant invertebrate drift and complex shelter structures, including large wood, undercut banks, vegetation, and boulders (Bustard and Narver 1975, Tschaplinski and Hartman 1983, Roni and Quinn 2001, Rosenfeld et al. 2005). However, competition for these habitats can be especially high during the winter season, when high quality refugia are limited by increased stream flows in main channel pools and lack of floodplain habitat because of degraded conditions that reduce connectivity (Nickelson et al. 1992).

At larger spatial scales, temperature and flow regimes can strongly influence growth potential and habitat quality. Seasonal precipitation and temperature interact and affect habitat connectivity, controlling fish growth and movement across watersheds. Landscape characteristics mediate fish growth by providing complex floodplain shelter, food resources, and temperature moderation (Tockner et al. 2000, Wipfli and Baxter 2010). Riverine landscapes change drastically across seasons, especially in regions with highly seasonal precipitation patterns, such as the west coast of North America. Winter rains and spring snowmelt can change watershed habitat quality by reconnecting floodplains and ephemeral, headwater streams, as well as decreasing temperatures and increasing stream flows.

When the effects of large-scale landscape patterns on in-stream habitat (e.g., shelter complexity), food availability, and fish population density are considered, a more complete understanding of the underlying basis of life history variability is possible. Understanding these relationships for coho salmon prior to outmigration to the ocean is important because limited survival and growth during this stage can have population-scale impacts. Salmon-habitat interactions are extensively studied because of the loss of populations and subsequent habitat restoration efforts (Roni et al. 2008, Bisson et al. 2009). Multiple studies have documented patterns in movement and growth of coho salmon, but these studies are restricted to specific basins or regions. Understanding patterns across the wide range of coho salmon may improve our ability to compare and differentiate among the drivers of juvenile movement and growth patterns.

In this literature review I synthesize published literature on coho salmon movement and growth patterns prior to smolt outmigration. Comparisons will be made among identified unique pre-smolt movement behaviors as well as the influences of landscape and fish size on observed movement and growth patterns. Conclusions will be drawn regarding which variables most commonly influence movement and growth, differences in population diversity, knowledge gaps, and how current knowledge and future research can address recovery and conservation efforts focused on coho salmon across North America.

Methods

I used the online reference database Web of Science to review papers published from the beginning of the database (~1900) through 4 April 2016. This limited my potential sources to peer-reviewed, scientific publications and excluded the gray literature. My study is not an exhaustive list of all research conducted on coho salmon juvenile behavior prior to smolt migration; laboratory experiments, literature on behavior in specific habitat patches, gray literature, and studies comparing abundance or smolt biomass were excluded when growth and movement timing were not considered across a watershed. Search criteria included species, life stage, and response terminology: “coho salmon”, “smolt”, “parr”, “juvenile”, “migration”, “emigration”, “movement”, “winter”, and “spring”. Additional references were located based on citations from articles returned during Web of Science searches.

Data collected from studies included river mouth latitude, basin area, land use, ESA population status, study years, and the abiotic and biotic variables considered in evaluating influences on coho movement and growth. Not all of these parameters were found directly from reviewed articles (e.g., land use, population status). These incomplete records were supplemented by information from references within the articles as well as federal reports defining metapopulations (Evolutionary Significant Unit, ESU), geographic ranges, and ESA listing status. When multiple basins or populations were included in a publication, basin characteristics were averaged and population status was based on the most vulnerable listing (e.g., Threatened when one population is a Species of Concern and another is Threatened). These basin-scale and metapopulation-scale variables were noted to determine how life history diversity may be related to how vulnerable a population is (ESA listing) or the watershed size and location may be correlated to movement and growth diversity across the North American range of coho salmon, or species-scale diversity. Length of study was also noted to consider how potential for inter-annual variability (i.e., variable results among study years) within a single study may impact noted growth and movement patterns.

Spatial as well as temporal rearing and movement diversity were considered, including pre-smolt movement by fry (initial free-swimming life stage), parr (free-swimming, less than one year of age), age-1 smolts, and age-2 smolts (where longer freshwater rearing occurs in northern populations) (Sandercock 1991, Quinn 2005). Movement is defined as seasonal passage from one habitat type to another, i.e., spring smolt outmigration or parr leaving their natal stream during the winter. Seasonality of movement strategies were classified based on the season of final timing of outmigration for an individual, so spring for all individuals that ultimately left freshwater rearing habitat during the spring season and as a fall or winter if individuals did not return to freshwater after this outmigration season.

The number of unique movement strategies were tabulated and related to rearing habitat types in each reviewed study. This was to consider potential correlations between habitat types and movement diversity per basin, or phenotypic plasticity within a watershed population related to habitat. Strategies were tabulated if noted as unique from other strategies observed in a reviewed study. For example, two spring smolt strategies were counted if a study observed that outmigrating spring smolts either reared in their natal stream during the winter or reared in estuarine habitat during the winter, but then moved back upstream into freshwater before outmigrating as a spring smolt. Rearing habitat types were based on study classifications (tributary, pond/lake, estuary, or main-stem habitat). Since many studies compared main stem rearing to some other rearing location, tributary, pond/lake, and estuary rearing were also standardized as off-channel to compare to main channel (i.e., the main stem rearing fish).

My main objective was to consider commonalities as well as potential gaps in our understanding of movement and growth patterns. Therefore, the following influential factors were noted as being present or absent in study designs: 1) climate-driven processes (precipitation, stream flow, temperature, or larger-scale climatic cycles), 2) density-dependence (relative fish length or number of fish per habitat unit of measure), 3) landscape influences (riparian or upslope conditions, migration distance), 4) in-stream physical habitat metrics (habitat complexity, volume, rearing habitat type), and 5) food availability (macroinvertebrate abundance and biomass, spawner density, or primary productivity estimates).

Directional relationships that were reported for predictors and response variables in each study were also tabulated to determine similarities among studies. Directional (positive, negative) statistical significance was noted for predictor variables, as well as non-significant relationships. These directional effects were defined as positive when an increase in quantity or quality of a variable was significantly correlated with either a delay in timing of movement (spring-smolt) or an increase in growth. Directional effects were defined as negative when an increase in quantity or quality of a variable was significantly correlated with earlier movement (pre-spring smolt movement) or lower growth, and defined as neutral when no statistically significant correlation was observed. Some studies measured both movement and growth patterns while others only considered one. Additionally, growth was indirectly considered in some studies by comparing pre-winter and spring fish sizes. These were categorized as growth measurements in my study (i.e., larger smolts were categorized as having positive growth in comparison to smaller smolts within a single study).

Pacific salmon population resilience is influenced by genetic and environmental interactions, since individuals can adapt to local environments through their phenotypic expression. This phenotypic plasticity allows individuals to adapt to resource availability. Supporting the phenotypic diversity that results from individual phenotypic plasticity is essential to population resiliency, because of the localized adaptations of individuals allow populations to respond to dynamic environments (Healey 2009, Waples et al. 2009). To address these interactions, principal components analysis (PCA) was used to assess similarity among study watershed and population characteristics, by reducing these multivariate aspects to two-dimensional, measureable space (Table 3.1). Essentially, the aim was to examine if watershed and population characteristics are correlated with significant trends in coho movement patterns and growth. Not all studies analyzed with PCA included the same predictor variables, so separate PCAs were run on a subset of studies to compare the relationship of movement strategy and diversity to rearing habitat type (16 studies) and the statistical effect of pre-movement individual fork length on fish growth (five studies). When studies found inter-annual variability in predictive relationships for fork length, data were included separately in PCA to capture variation in fish size within basins.

Results

Eighteen studies from eighteen different coastal basins from southeast Alaska through northern California (59 to 40º N latitude) were analyzed for relationships between climate, watershed, and fish size on movement and growth patterns (Table 3.2, Figure 3.1, Appendix E). Studies primarily occurred in the last ten years, although long-term winter movement patterns were also documented during the 1970s and 1980s. Ten studies included ≥3 years of field data collection, representing potential inter-annual variability in watershed and fish patterns. Twelve of the studies occurred in basins <200 km^2 and all occurred within close proximity to the coast, with five studies including estuarine habitat. Population status followed a latitudinal trend, with northern populations unlisted, followed by increasing listings of Species of Concern, and Threatened populations in more southerly populations (Table 3.2). Three studies in Alaska and British Columbia also described age-1 versus age-2 smolt outmigrations, which were noted separately from spring smolt outmigration strategies (Appendix E).

Commonalities in movement strategies and potential factors existed across studies. The majority included fish size, in-stream physical habitat, and landscape predictor variables in their analyses, while only four specifically included density-dependent processes and only three considered food availability (Table 3.3). Rearing habitat type (main stem, off-channel ponds, lakes, or tributary streams, estuary) (n = 6) and pre-movement fish length (n = 8) were the most common reported statistics, and were used in summary data comparisons. Multiple movement patterns were evident even in southern, threatened populations as well as in small, coastal basins with limited estuary habitat and larger basins with extensive estuary zones (Appendix E). The number of movement strategies was also correlated with rearing habitat types: up to four strategies were documented for studies considering estuary rearing, three movement strategies were found in studies considering tributary and pond and lake rearing, while two movement strategies on average were noted for studies in which only main channel rearing was considered (Table 3.4).

Studies that reported drivers of movement patterns had varied directional relationships, with climate-driven and fish size variables having positive, negative, or neutral effects on movement (Figure 3.2, Appendix E). This means that these abiotic and biotic drivers can both be associated with later fish movement, earlier fish movement, or have no measurable effect on fish movement, depending upon the study basin, season, or year (Figure 3.2, Appendix E). In-stream habitat and landscape variables were significant predictors of the timing of movement, but were reported as both positive and negative drivers of movement, depending upon the study system (Figure 3.2). Drivers of fish movement were explored across both coarse and fine-spatial scales, with climate-driven, landscape, in-stream habitat, and fish size metrics all commonly considered, although density and stream productivity considerations were less well reported (Figure 3.2).

Drivers of growth were primarily reported for finer-scale variables, such as in-stream habitat and fish size metrics over climate and stream productivity variables (Figure 3.3). In-stream habitat type and quality metrics were highly positively associated with growth, meaning higher quality habitat was correlated with greater growth across reviewed studies. In fact, all studies that considered impacts of rearing habitat on fish growth found that off-channel rearing was positively associated with growth, whether or not rearing habitat types were ephemeral streams, side channels, ponds, lakes, or estuaries (Appendix E). By contrast, fish size had a variable influence on growth, with positive, negative, and no effect on growth all reported (Figure 3.3). Landscape variables, primarily migration distance, were most commonly negatively associated with growth, suggesting watershed location was important to growth potential (Figure 3.3). Inverse relationships between watershed location and growth suggested that lower watershed locations were more often associated with greater growth than upper watershed fish location.

The correlation of basin and population characteristics with movement timing and growth were explored using principal component analysis (PCA). The first model considered the type of and number of movement strategies per basin, and how off-channel rearing habitat types, population ESA status, length of study, and basin location may be related across the range of coho salmon (Figure 3.4, Appendix C). The first two PCA axes explained 43.4% of the total variation across studies, with PC 1 explaining 24.2% and PC 2 explaining 19.2% of total variance. Winter parr and spring smolt movement strategies were the primary variables influencing PC 1, with winter and parr movement strategy components negatively associated with PC 1 and spring and smolt movement strategy components positively associated with PC 1. PC 2 was primarily influenced by population and basin characteristics, with positive association for basin latitude and non-listed ESA status, and a negative association with Threatened ESA status and number of rearing strategies. Rearing habitat type differed along a latitudinal and basin area gradient as well, with main channel rearing primarily noted in northern latitude and large basins and estuary rearing primarily noted in southern, smaller basins.

The second PCA model assessed the effect of fish size on growth, with 92.3% of the total variation explained by population and basin characteristics, as well as rearing location (Figure 3.5, Appendix C). PC 1 explained the majority of variance, 66.4%, and was primarily positively influenced by main-channel rearing, basin area, and Threatened ESA listing, and negatively influenced by basin latitude and Species of Concern ESA listing. PC 2 was primarily positively influenced by fish fork length and negatively influenced by the length of the study, suggesting inter-annual variability may influence the reported effect of fish size on growth. This ordination suggests that the influence of fish size on growth is not correlated to population status (e.g. vulnerable, or Threatened, populations exhibit similar patterns in growth as less vulnerable, or unlisted populations), basin area, or location across the range of coho salmon and could also vary across study years. Instead, finer-scale variables may be more important in predicting growth, such as seasonal shifts in habitat quality, density-dependent patterns, and climate cycles.

Discussion

Commonalities and Gaps in Knowledge

Multiple movement strategies prior to smolt ocean outmigration were evident across the range of coho salmon, including winter downstream movement into lower freshwater habitats and estuaries, and upstream movement into headwater streams, which were distinctly separated from peak outmigration by smolts during the spring. Although factors related to early movement varied, multiple studies found a correlation between increased stream flow and initial fall movement by parr, with variation in this relationship occurring among seasons and study years (Tschaplinski and Hartman 1983, Miller and Sadro 2003, Roni et al. 2012, Jones et al. 2014). Growth potential may influence early movement as well; smaller fish were more likely to move earlier than larger fish, and early movers that reared in floodplain, estuary, and headwater stream habitats were often reported to grow more than main channel stream rearing fish (Thedinga et al. 1994, Bennett et al. 2011, Roni et al. 2012).

Coarse-scale and fine-scale variables were commonly considered in movement studies, including stream flow patterns, migration distances, and rearing habitat types (main channel versus tributary, estuary, or floodplain habitats) (Figure 3.2). However, comparisons among studies may be improved by providing metrics that represent the quality or relative abundance of rearing habitat types. Many studies included qualitative descriptors of watershed conditions, but pool frequencies, shelter quality, or relative abundance of specific habitat types may improve our ability to compare fish responses to watershed conditions across species' ranges, rather than within specific basins. Population or fish community densities were not commonly considered, despite established understandings of the importance of density-dependent growth and mortality even in salmon populations with low abundances (Walters et al. 2013) as well as resource partitioning that can occur among competitive Pacific salmon species (Reeves et al. 2011). Effects of productivity on fish behavior were also lacking. Food web considerations may illustrate additional ecosystem-scale patterns that are not always evident from studying population and abiotic patterns alone (Naiman et al. 2012). Considering these density-dependent factors may add to our understanding of drivers of growth, since fine-scale variables like in-stream habitat were considered more frequently than population, community, or watershed considerations (Figure 3.3) and may illustrate commonalities in growth potential – habitat patterns not gleaned from coarse-scale correlations alone (Figure 3.5).

Patterns in Movement Strategies

Timing of movement (winter versus spring) was more important in differentiating study results than population or basin-specific characteristics (Figure 3.4). The significance of this is that movement occurred across multiple coho salmon populations, regardless of vulnerability (ESA listing) and basin size and location. This suggests that factors other than rearing habitat type alone influenced fish movement timing, and that movement diversity is a species-scale pattern rather than simply a population-scale pattern. Although not one specific rearing habitat type was associated with a particular movement strategy, the availability of some type of non-main channel habitat was associated with spring smolt movement, suggesting movement strategies were associated with habitat quality (Figure 3.2). For example, density-dependent processes or genetics may explain diversity in the timing of movements rather than basin-level physical habitat or population abundance characteristics as evidenced by the prevalence of movement diversity across the range of coho salmon. Winter movement has been considered a response of less fit individuals to either competition or inability to avoid winter flood conditions, and these individuals were often considered lost from the population (Koski 2009). This may explain why off-channel rearing was associated with spring smolt movement rather than winter-parr movement strategies in the studies reviewed (Appendix E). However, winter movement strategies may provide a population benefit by producing larger smolts (Ebersole et al. 2009b) and by winter movers contributing to returning adult spawner populations (Jones et al. 2014, Bennett et al. 2014).

Although most studies reported two distinct movement strategies, more were reported for studies in southern latitudes and when non-main channel habitats were available (Table 3.4 and Figure 3.3). This suggests that rearing habitat diversity may be important in determining how many additional movement strategies beyond winter parr and spring smolt movement are supported in a watershed. For instance, studies in Oregon reported spring and summer downstream movement to estuaries and winter inter-stream movement by juvenile coho salmon in addition to downstream winter parr and spring smolt strategies (Miller and Sadro 2003, Ebersole et al. 2006, Craig et al. 2014, Jones et al. 2014). This could also be a study design effect: basin areas were smaller in studies from southern latitudes, which may support more efficient data collection because they had narrower stream channels and shorter streams than large river basins in British Columbia and Alaska.

Patterns in Growth

No single driver of growth was evident within or across studies. Positive relationships between growth and initial fish fork length were not observed in ordination analysis, and the effect of fish size also changed with study length, suggesting inter-annual variability (Figure 3.5). Inconsistency in predictors of growth may have to do with finer-scale variables than were captured in this review, such as relative abundance and quality of rearing habitat within reviewed studies. For instance, studies comparing growth in main- versus off-channel habitat in the same basin observed greater growth in off-channel habitat as well as opposing relationships between growth and rearing habitat spatial location within a watershed and growth (Quinn and Peterson 1996, Roni et al. 2012, Rebenack et al. 2015). This suggests that winter habitat may be more important in predicting smolt survival and size than summer conditions, at least when high quality winter rearing habitat is available, regardless of its location within a watershed. This also provides an explanation for early movement to high quality rearing habitats, even when they were located upstream or in estuaries, where predation risk can increase and additional energy is required to offset costs of swimming. Greater growth associated with high risk habitats may represent an alternative to more evolutionarily conservative bet-hedging strategies of lower mortality risk, but lower growth associated with extended freshwater rearing. This more conservative behavior may support population persistence by reducing risk, but it also reduces variability within the population (Slatkin 1974, Wilbur and Rudolf 2006).

Growth is a complex variable, influenced by thermal conditions, energetic needs, and food availability, which can all shift quickly and frequently in stream systems. Fish can respond quickly to these changing conditions, with juvenile coho salmon observed rearing and foraging in unique thermal patches to increase their growth potential in

Alaska (Armstrong and Schindler 2013) as well as increasing growth by feeding in higher velocity riffle habitat with greater prey densities (Rosenfeld and Raeburn 2009). Understanding spatial and temporal productivity gradients throughout watersheds may improve our understanding of growth in relationship to rearing habitat and its location within the watershed, two important drivers of growth in this review. Additional understanding of these relationships could potentially help explain the inter-annual variability observed in some studies included in this review (Appendix E).

Implications

Although many individual studies exist that assess juvenile coho salmon movement diversity and growth benefits from different habitat types, commonalities and gaps have not yet been assessed across the wide geographic range of this vulnerable and important species. This review included eighteen studies to assess drivers of diversity in timing of movement and growth to help address this knowledge gap. Although this is a relatively small sample size with limited repeatability in statistically considered variables, this review can help determine next steps forward in coho salmon recovery and habitat restoration efforts. Small sample sizes may over-emphasize observed similarities, such as the greater number of movement strategies associated with estuary habitat availability (Table 3.4). Many of these study basins included land use activities that degrade freshwater habitat and can harm populations, such as timber harvest and stream flow controls. However, most studies included land use only in basin descriptions rather than analyses. These similar landscape influences can reduce watershed habitat heterogeneity, leading to lower life history diversity and greater similarity across the study range, as already observed in studies of variability in the timing of return to spawn (Schindler et al. 2010, Moore et al. 2010). Land use has been linked to spatial diversity in spawning abundances (Pess et al. 2002, Andrew and Wulder 2011), so quantifying landscape impacts on juvenile fish behavior may provide additional context to observed life history diversity.

Despite degraded watersheds and vulnerable populations, at least two movement strategies were reported in all cases. This could be a publication bias or evidence that even highly impacted watersheds and populations support life history diversity in pre-smolt behavior. Conserving this diversity could help buffer fragile populations against disturbance. This goal could be achieved by preserving and restoring non-main channel rearing habitat connectivity during the winter season, such as estuary and off-channel pond and lake habitats, all of which were associated with distinct movement strategies and increased growth in this review. These are also highly vulnerable habitat types, due to the disproportionate loss of estuarine and floodplain habitats across the range of coho salmon (McClure et al. 2008). When these habitats are restored, Pacific salmon can adapt quickly to newly available habitats, increasing spatial and temporal distribution and resiliency of these populations (Bottom et al. 2005, Anderson et al. 2008).

Inter-annual patterns in movement and growth suggest that long-term monitoring is essential to understand population benefits of multiple rearing strategies by coho salmon. In one study, estuary rearing was associated with positive growth in comparison to stream-rearing fish during one year but negative growth in another year (Rebenack et al. 2015). The positive relationship between growth and survival may buffer populations against poor conditions in the long-term, even when growth benefits are only occasionally obtained from certain habitat types (Holtby et al. 1990, Quinn and Peterson 1996, Ebersole et al. 2006). In order to determine seasonal habitat and fish size associations with long term population benefits, studies need to be conducted over multiple study years.

Conserving life history variability where present, and restoring patterns that support it when absent or reduced, could increase the stability and resiliency of coho salmon populations. Watershed connectivity and habitat quality can inform potential distribution of juvenile coho salmon, and how this may affect timing of movements, smolt size, and ultimately survival. Although watersheds are unique across the wide geographic range of coho salmon, mapping and quantifying the current and historical non-main channel rearing options for coho salmon, whether they are ephemeral streams, ponds, lakes, or estuaries, could help prioritize restoration and conservation efforts. Estuaries were associated with the greatest diversity in timing of movements, and efforts to understand and protect these dynamic habitats may provide the greatest benefit to juvenile coho salmon.

Tables

Table 3.1. Variable descriptions utilized in principle component analysis (PCA). Not all variables used in all analyses: rearing habitat effect used separately from pre-winter fork length effect. Binary variables are based on whether or not that study included that variable. Effects are based on significance of variable: positive effect (1), negative effect (0), or no significant effect (0.5) on response variable.

Variable	Variable Type	Description
Basin latitude	Numeric	Latitude at basin mouth (Decimal Degrees)
Basin area	Numeric	Drainage area (km^2) as reported or found for the study area; averaged when multiple basins analyzed in a literature study.
Population status	Binary (presence/ absence)	Not listed or listed status for population ESU under ESA (Threatened and Species of Concern). Maximum listing used when multiple populations analyzed in a literature study.
Off-channel type	Binary (presence/ absence)	Main channel (only rearing habitat considered), tributary (to main channel), pond or lake, estuary.
Movement strategy	Binary (presence/ absence)	Unique life stage-movement season and life stage identified.
Number of movement strategies	Numeric	Number of unique life stage-movement seasons identified per study.
Pre-winter fork length effect	Ordinal	Significance of pre-winter fork length on movement strategy: 0 = negative influence; 0.5 = non-significant influence; 1 = positive influence. Positive influence equates to later movement timing associated with longer pre-winter fork length, negative influence equates to earlier movement timing associated with shorter pre-winter fork length, and non-significant influence means no effect of pre-winter fork length detected on movement timing.

Table 3.2. Summary of study locations, population characteristics, and study timelines, organized north to south based on basin mouth latitude (n = 18). Study years listed are for the beginning year (fall) rather than the end of a study year (spring). If multiple basins were included in a study, latitude and basin area values listed are the mean, and population status is for the most vulnerable population. Land use includes historical and current practices. Precip = Precipitation, R = Rain, SN = Snowmelt, GL = glacier-melt, Pop. = Population, NL = Not listed, SC = Species of Concern, Th = Threatened.

Latitude (°N)	Basin name	Basin area (km^2)	Land use	Precip type	Pop. status	Study years	Reference
59.45	Situk River, AK	200	Commercial harvest	R, SN	NL	1990	(Thedinga et al. 1994)
58.28	Taku River, AK	16000	Commercial harvest	GL	NL	1987	(Murphy et al. 1997)
55.82	Staney Creek, AK	164	Timber harvest	R, SN	NL	1996	(Bramblett et al. 2002)
50.70	Keogh River, BC	129	Logging, nutrient treatments, hatchery steelhead rearing, commercial harvest	R, SN	NL	1977 - 1986	(Irvine et al. 1989)
49.14	Chilliwack River, BC	1230	Logging, floodplain habitat restoration	R, SN	NL	2006	(Rosenfeld et al. 2008)
48.90	Carnation Creek, BC	10	Timber harvest	R, SN	NL	1972 - 1980	(Tschaplinski and Hartman 1983)
48.17	East Twin River, WA	35	Timber harvest, restoration	R	SC	2004, 2005	(Bennett et al. 2011)
48.17	East Twin and West Twin Rivers, WA	35, 33	Timber harvest, restoration	R	SC	2005 - 2008	(Roni et al. 2012)
48.05	Skagit, Stillaguamish, Quillayute, and Hoh River, WA	2774	Wilderness recreation, timber harvest, agriculture, rural residential	R	SC	1987 - 2000	(Roni et al. 2006)
47.66	Big Beef Creek, WA	38	Timber harvest, fishway at upper watershed lake, wetlands, streams	R	SC	1990, 1991	(Quinn and Peterson 1996)
47.50	Cedar River, WA	487	Dam, fish ladder, habitat restoration	R	SC	2006 - 2008	(Pess et al. 2011)

Latitude (°N)	Basin name	Basin area (km^2)	Land use	Precip type	Pop. status	Study years	Reference
46.33	Grays River, WA	321	Dyking and development of wetlands and estuary habitat; timber harvest, coho hatchery	R	Th	2008 - 2010	(Craig et al. 2014)
45.05	Salmon River, OR	195	Agriculture, grazing, water diversion, tidal channel and marsh restoration	R	Th	2008 - 2011	(Jones et al. 2014)
43.92	West Fork Smith River, OR	69	Timber harvest, roads, splash dams	R	Th	2002	(Ebersole et al. 2006a)
43.81	West Fork Smith River, OR	69	Timber harvest, roads, splash dams	R	Th	2003 - 2005	(Ebersole et al. 2009)
43.32	South Slough, OR	78	NA	R	Th	1999, 2000	(Miller and Sadro 2003)
40.79	Freshwater Creek, CA	92	Timber harvest, agriculture, residential land use, restored tidal marshland	R	Th	2010 - 2012	(Rebenack et al. 2015)

Table 3.3. Potential drivers of movement and/or growth patterns considered per study. X's equate to yes and blank cells equate to no, studies organized north to south based on basin mouth latitude, as in Table 3.2 (n = 18).

Climate -Driven	Density	In-stream Habitat	Landscape	Fish Size	Productivity	Reference
X			X	X		(Thedinga et al. 1994b)
X				X		(Murphy et al. 1997)
		X		X		(Bramblett et al. 2002)
		X		X		(Irvine and Ward 1989)
		X		X	X	(Rosenfeld et al. 2008)
X				X		(Hartman et al. 1982)
X		X	X			(Tschaplinski and Hartman 1983b)
				X		(Bennett et al. 2011)
	X	X	X	X		(Roni et al. 2012)
	X	X		X		(Roni et al. 2006)
		X	X	X		(Quinn and Peterson 1996)
	X	X	X	X		(Pess et al. 2011)
		X				(Craig et al. 2014)
		X	X	X		(Jones et al. 2014)
X	X	X	X	X	X	(Ebersole et al. 2006a)
X		X	X	X	X	(Ebersole et al. 2009)
X		X	X	X		(Miller and Sadro 2003)
X		X	X	X		(Rebenack et al. 2015)

Table 3.4. Rearing habitat types documented per movement study, with mean and standard deviation of noted unique juvenile life histories leading to smolt outmigration (n = 17).

Rearing habitat type	Number of studies	Mean number of movement strategies (±standard deviation)
Estuary	5	4 (+/- 0.5)
Main Channel	5	2 (+/- 1.0)
Pond/Lake	4	3 (+/- 1.0)
Tributary	3	3 (+/- 0.5)

Figures

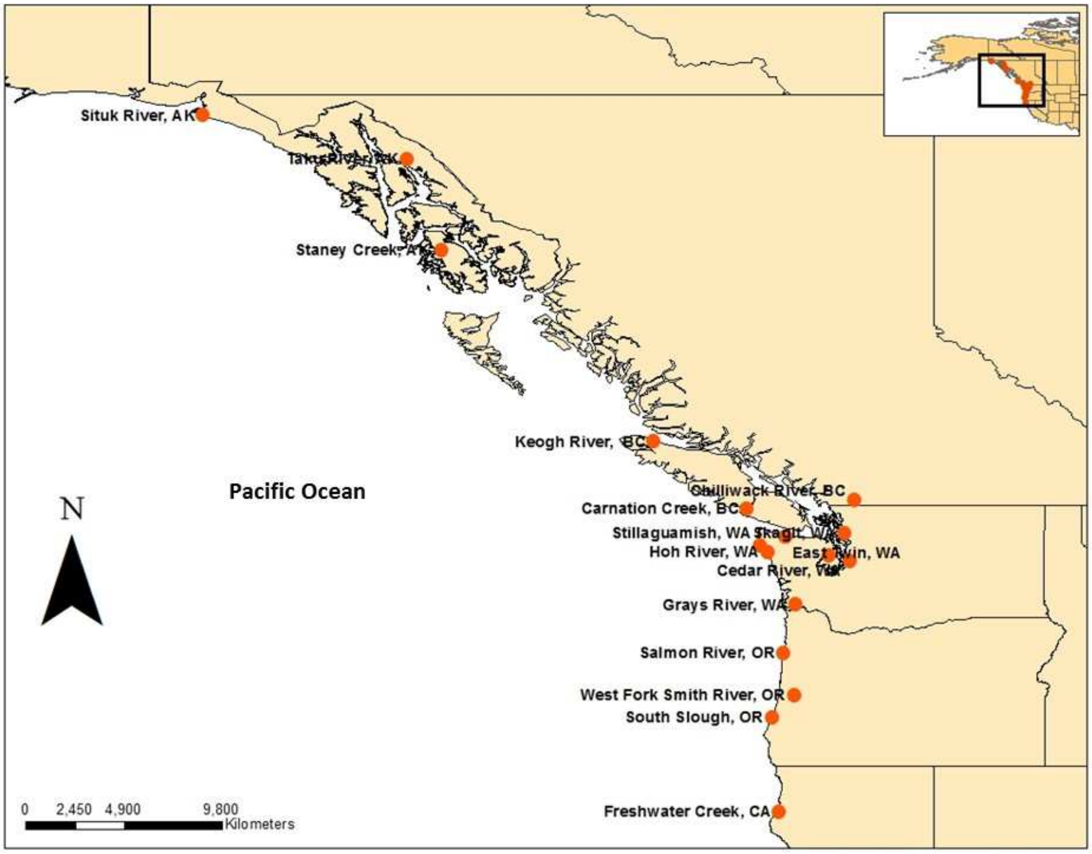

Figure 3.1. Basin mouth locations and names of the reviewed studies (n = 18).

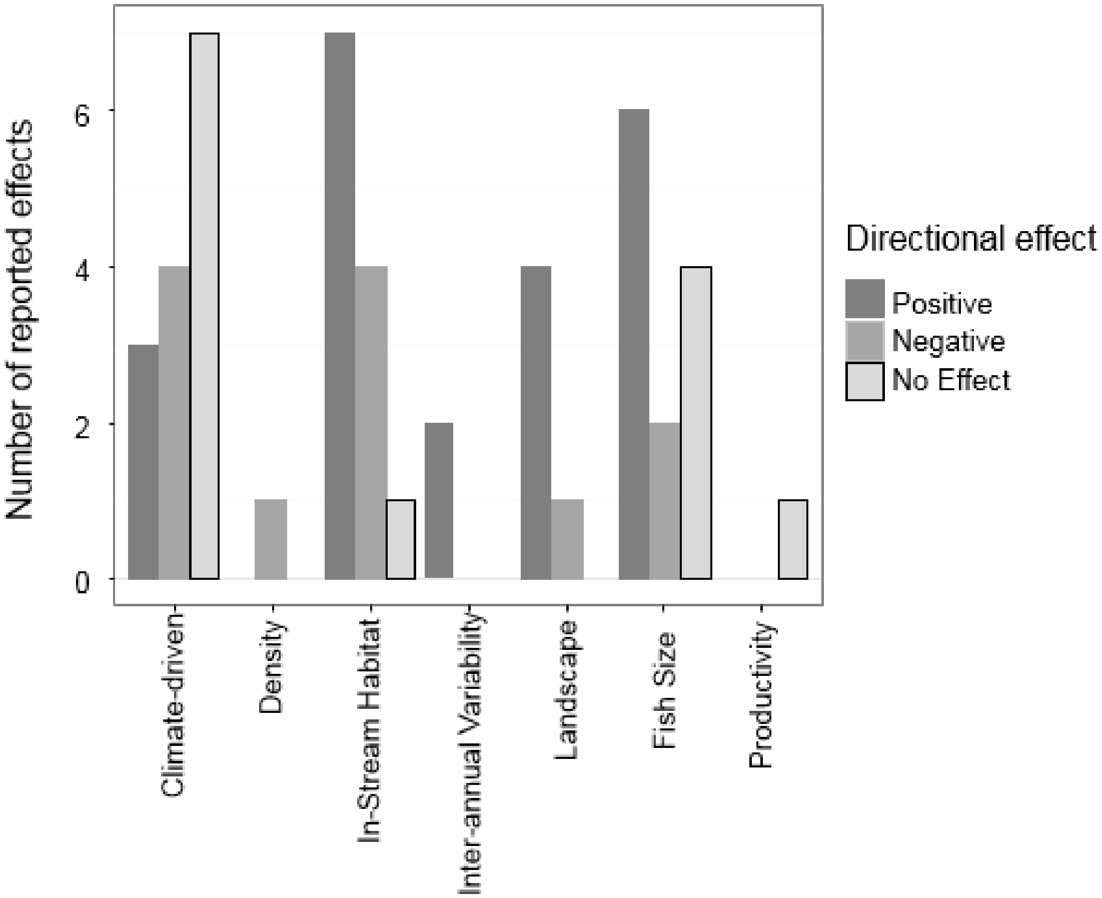

Figure 3.2. Directional effects noted across studies for environmental, fish size, and population effects on movement timing. Effect indicates a significant relationship from a reviewed study ($p < 0.05$). A positive effect on movement indicates that as a predictor variable increases in quantity or quality, it is associated with an increase in movement timing, or later (spring) season movement. A negative effect on movement indicates that as a predictor variable increases in quantity or quality, it is associated with a decrease in movement timing, or earlier (winter) seasonal movement (n = 16).

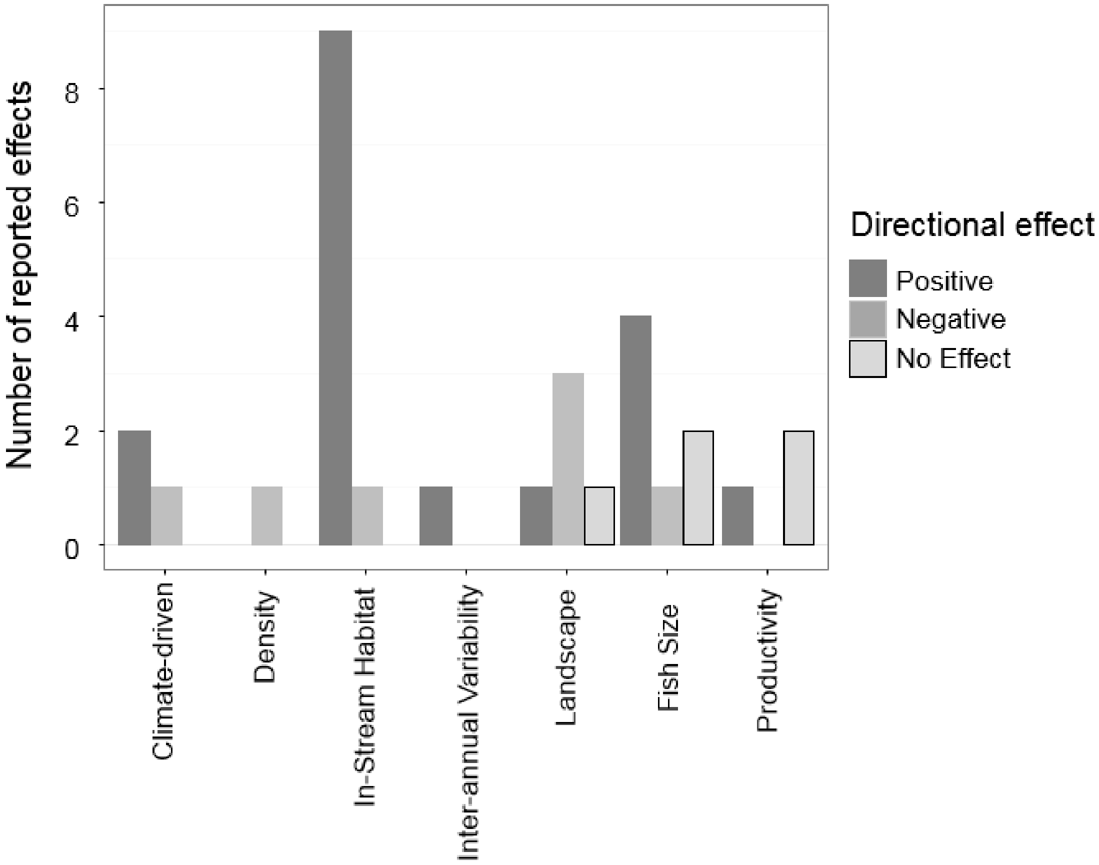

Figure 3.3. Directional effects noted across studies for environmental variables, fish size, and population effects on growth. Effect indicates a significant relationship from a reviewed study (*p* < 0.05). A positive effect on growth indicates that as a predictor variable increases in quantity or quality, it is associated with an increase in growth. A negative effect on growth indicates that as a predictor variable increases in quantity or quality, it is associated with a decrease in growth (n = 16).

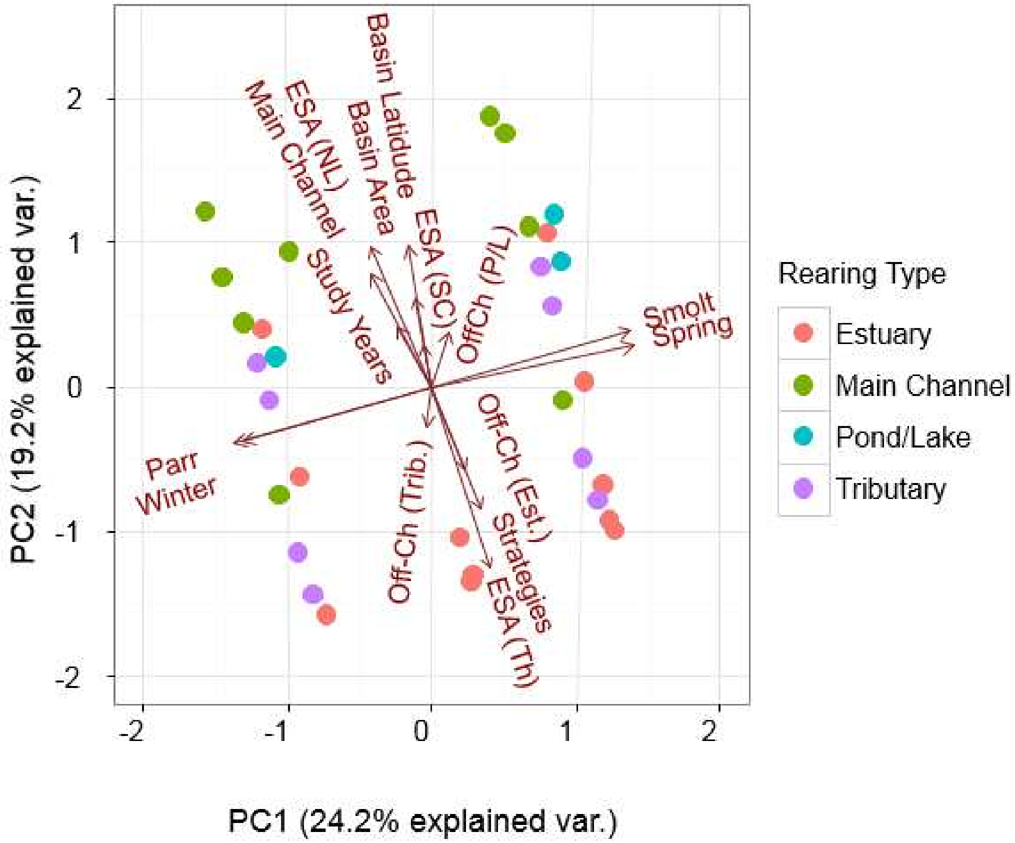

Figure 3.4. Standardized PCA results for habitat effect on movement strategy (n = 16). Studies are grouped by non-main channel rearing habitat type (main channel when no non-main channel rearing identified). Shortened vector names are Off-Ch = Off-Channel habitat, ESA = Endangered Species Act listing, NL = ESA Not Listed, SC = ESA Species of Concern, Th = ESA Threatened, Strategies = number of unique movement strategies per study, Main Channel = Main-channel rearing, Trib = tributary-rearing, P/L = pond or lake rearing.

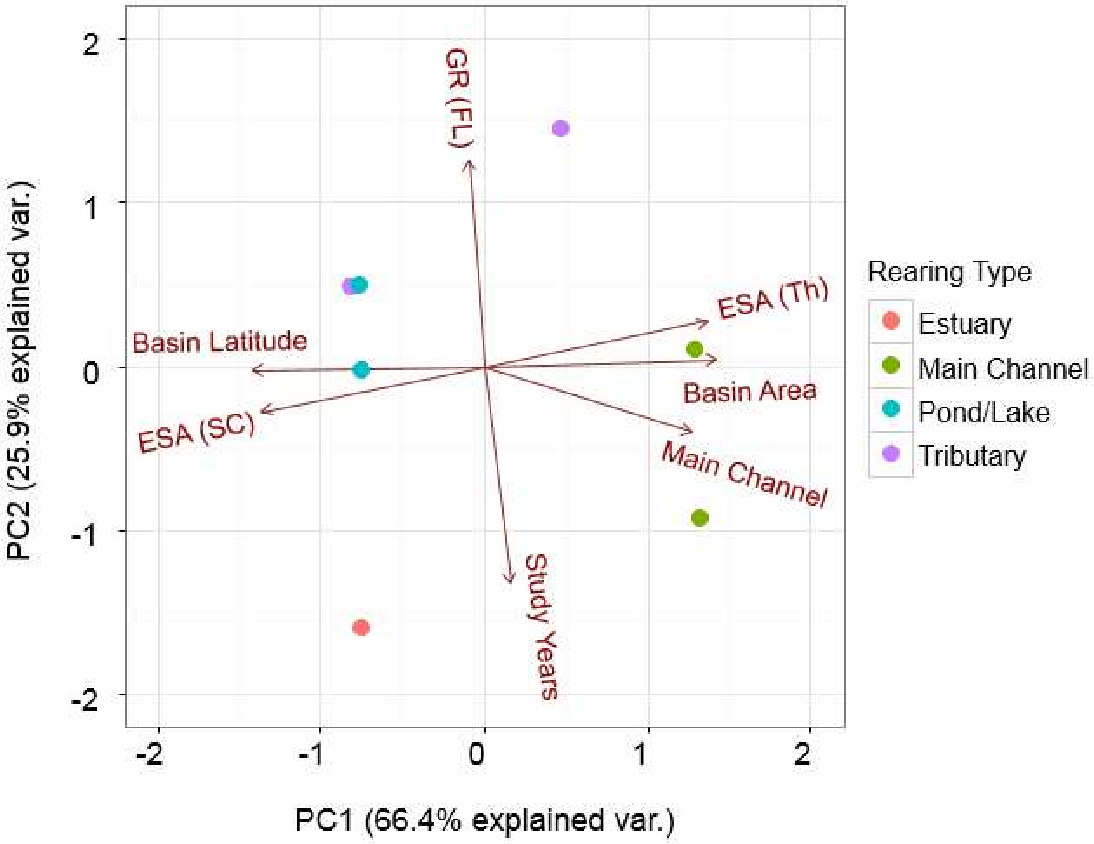

Figure 3.5. Standardized PCA results for initial fish fork length statistical effect on growth (n = 8). Studies are grouped by non-main channel rearing habitat type (main channel when no non-main channel rearing identified). Shortened vector names are ESA = Endangered Species Act listing, SC = ESA Species of Concern, Th = ESA Threatened, Main Channel = Main-channel rearing, GR = Growth rate, FL = fish fork length.

Chapter 4 : Conclusions

Coho salmon depend upon freshwater rearing for one to two years prior to smolt outmigration to the ocean. During this extensive juvenile rearing period, fish must navigate dynamic watershed conditions, including winter flooding, which can both reconnect high quality rearing habitat that provides ample shelter and foraging opportunities, as well as decrease the quality of main channel habitat due to high velocity storm conditions. I examined fish-habitat relationships through an observational study of hatchery-released coho salmon movement in a southern, drought-stricken watershed as well as through a literature review of movement and growth studies on coho salmon in watersheds across their North American range.

Diversity in movement behavior is evident across the entire range of coho salmon, including more vulnerable populations experiencing extreme drought conditions. The observational portion (Chapter 2) identified three unique movement strategies that increase distribution of fish temporally (winter downstream movement versus spring downstream movement) as well as spatially (inter-stream movement and lower and upper stream segregation). This variability was observed despite limited freshwater rearing for these hatchery-released fish as well as drought conditions limiting habitat connectivity. Continual support of movement diversity must therefore consider watershed conditions as well as habitat interactions with precipitation and thermal regimes, which are expected to increase in intensity with climate change. Restoring and conserving non-main channel habitat, such as wetlands and low-gradient stream habitats, may aid in supporting juvenile movement diversity. This is based on the importance of these watershed features as well as the association of off-channel rearing habitat types with fish behavior in both the observational study (Chapter 2) and literature review, which also considered the role of small tributaries and estuarine habitats (Chapter 3). Furthermore, quality of in-stream habitat may also be important, especially when off-channel habitat is limited. This is evident in the delayed movement timing from Mill Creek despite limited off-channel features (Chapter 2) as well as the importance of tributary streams when ponds, lakes, and estuaries were not used or available by fish in studies included in my review (Chapter 3).

Growth pattern analyses suggest that two factors are at play: how big a fish is prior to the winter and the growth potential of its winter rearing habitat. Although little variability in fish size existed in the fish that comprised my sample from the Russian River, evidence from the literature supports the importance of winter growth on spring smolt size (Quinn and Peterson 1996, Ebersole et al. 2006). Growth potential can shift seasonally as well, due to thermal conditions, stream velocity, and dynamics of prey availability among different habitat types across watersheds (Satterthwaite et al. 2012). It is therefore essential to provide connectivity across watersheds, allowing fish to utilize inter-stream movement and downstream movement during the winter season. These movement strategies may be alternatives to the bet hedging strategy of remaining within stocking or rearing habitat during the winter season. Winter movement may increase growth capabilities, by allowing fish to grow more than in their stocking or summer rearing location, although at the risk of greater predation during movement and reduced growth from increased swimming energetic costs or limited foraging in newly found habitats. However, if individuals that move survive, this behavior could increase population stability by increasing the spatial and temporal template on which the population functions.

Seasonal and inter-annual shifts in fish behavior emphasize the importance of quantifying fish-habitat interactions beyond single seasons and study years. Multiple reviewed studies observed inter-annual variability in fish size and growth and movement patterns, suggesting that long-term monitoring is essential to long-term recovery goals. Mapping utilized habitats and their association with growth across multiple years could help prioritize watershed conservation strategies, by preserving and restoring habitats associated with unique, life history patterns. My observational study in the Russian River took place during an extreme drought in California, and therefore may provide a portrait of future conditions across the range of coho salmon. Based on this study, I suggest that management strategies should continue to focus on providing low-velocity winter refuges, since infrequent, but high intensity precipitation events, such as the ones during the 2014 – 2015 winter, may become the new normal. Initial fish movement was associated with these rain events, including upstream inter-stream movement, suggesting fish are actively searching for higher quality habitat during winter flood events. Not all streams necessarily need to provide the same habitat types though, because juvenile fish are capable of extensive migrations across stream networks. Additionally, streams that provide unique habitats may increase population stability by allowing fish to distribute themselves across watersheds rather than all fish responding to the same environmental conditions within a specific stream.

Pacific salmon recovery efforts are often supported by freshwater restoration projects, which may be lacking in terms of addressing the large temporal and spatial scales of population patterns and watershed processes (Bernhardt and Palmer 2011, Naiman et al. 2012). Long-term persistence of salmon populations is often dependent on the ability of a population to withstand disturbances, which can improve when greater phenotypic diversity is present (Watters et al. 2003, Schindler et al. 2010). Diversity in the timing of movement could increase population persistence by spatially and temporally distributing rearing and outmigration timing by juvenile fish. This is evident even in endangered populations, with significantly different movement times across different streams despite similar fish sizes. Improving juvenile salmon resilience to changing conditions may increase when diverse stream systems and connections are supported through conservation and restoration efforts. Not all streams necessarily need to provide low gradient, floodplain-rearing habitat for coho salmon, but connections to streams, lakes, and estuaries that do provide these benefits can allow fish to move and potentially grow more than in lower quality winter rearing areas. Movement behavior is even evident in hatchery-reared populations, further supporting the importance of understanding habitat impacts on fish, and the important role these early movers have in shaping decision making. This study provides evidence that low gradient and productive stream habitats supporting delayed movement timing, and high gradient habitats supporting earlier movement timing. Future work could evaluate relocation habitat types and conditions as well as habitat differences between streams for the inter-stream detected fish group. These additional considerations could help address the population benefits of early movement strategies, since other work has documented spawning success by these individuals, but not necessarily where they are rearing after leaving study streams (Jones et al. 2014, Bennett et al. 2014).

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Appendix A: PIT antenna site design and detection metrics

Table A1. PIT detection site description and sample size of PIT tagged individual fish. Number of detected fish is the total number of unique fish detected per detection site and release group size is the total number of PIT tagged individuals released per study stream. Some fish were detected at multiple detection sites per stream. Detection limitations mean partial to no detection capability at a site, due to equipment malfunctions.

Study stream	Detection site	Array type	Detections limited	Number of fish detected	Distance to stream mouth (m)	Release group size
DUT	Downstream detection site	Paired antennas	N/A	337	680	2830
GRE	Downstream detection site	Paired antennas	1/15/15-1/21/15; 5/5/15-6/4/15	411	6300	2778
	Upstream detection site	Single antenna	N/A	983	9980	
MIL	Downstream detection site	Paired antennas	N/A	702	2000	3724
	Upstream detection site	Paired antennas	2/5/15 – 2/9/15; 4/9/15-4/14/15	674	6100	
WIL	Downstream detection site	Paired antennas	12/1/14-12/30/14	49	410	2255
	Upstream detection site	Paired antennas		102	3700	

Appendix B: Landscape and in-stream habitat methods and data summaries

Table B1. Shelter rating categories, based on California salmonid stream habitat restoration manual (Flosi et al. 2010). Shelter ratings were calculated by estimating the shelter rating value and then multiplying it by percent coverage, forming a shelter index on a scale from 0 to 500.

Shelter Rating: Pool shelter is the product of shelter complexity and percent shelter cover.

Shelter rating values are:

> **Value 1:** Unit has no shelter
> **Value 2:** Unit is lacking significant shelter and complexity. Unit has no LWD. Unit contains at least one of the following features in limited availability: SWD, Boulders, root masses, undercut bank, submerged vegetation, bubble curtain.
> **Value 3:** Unit generally provides shelter, but lacks complexity, containing at least two of the following features in limited availability: LWD, SWD, Boulders, root masses, undercut bank, submerged vegetation, bubble curtain.
> **Value 4:** Unit provides quality shelter from at least three of the following complex features: >1 LWD, > 2 SWD, undercut bank, large root mass, extensive aquatic vegetation/ submerged branches, >4 undercut boulders.
> **Value 5:** Unit has excellent shelter with at least four complex shelter features (each available in extensive amounts). Unit must include >2 LWD and numerous SWD. Unit is difficult to navigate and survey.

In-stream Shelter Percent Cover: A measure of the area of the unit occupied by in-stream shelter as observed from an overhead view.

Table B2. Landscape and in-stream variables used in predictive models to determine landscape influences on fish movement and growth patterns. Variables used in statistical analysis have their abbreviated, dataset name included in parentheses.

Variable	Units	Source	Method
Basin Characteristics			
Stream lines	m	DEM derived	Calculated using ArcGIS Hydrology tool set
Basin area	m^2	DEM derived	Calculated using ArcGIS watershed delineation tool. Delineated as upslope influence per PIT antenna site and stream mouth.
Riparian buffers	m^2	DEM derived	Calculated using ArcGIS buffer tool at 30, 60, and 120 meter extents around the streamlines per basin.
Stream name	categorical	USGS Geographic Names Information System	Release stream for each hatchery release group.
Basin name	categorical	USGS Geographic Names Information System	Release stream mouth, downstream detection site, or upstream detection site.
Stream length	m	DEM derived	Length of stream habitat calculated using ArcGIS Hydrology tool set.
Drainage density	m	DEM derived	Stream length/basin area
Relief ratio	m	DEM derived	Distance between minimum and maximum elevation point per basin.
Distance to ocean	m	DEM derived	Length of each basin mouth to the ocean.
Distance to stream mouth	m	DEM derived	Length of each basin mouth to the mouth of overall basin.
Mean slope (MN Slope)	percent	DEM derived	Percent slope calculated from DEM layers in ArcGIS.
Maximum near stream slope	percent	DEM derived	Maximum percent slope calculated from DEM layers in ArcGIS per basin streamline. Considered near-stream rather than stream because of the 10-meter scale accuracy of DEM layers.
Mean canopy coverage (MN CC)	percent	National Land Cover Database 2011	Mean canopy coverage calculated per basin and riparian buffer area.
Mean impervious surface	percent	National Land Cover Database 2011	Mean percent impervious surface calculated per basin and riparian buffer area (Impervious).

Variable	Units	Source	Method
Land use type	percent	National Land Cover Database 2011	Land cover classifications calculated per basin and riparian buffer area (Dev. Open, Dev. Low, Dev. Med., Dev. High, Cultivated Crops, Barren Land, Conifer Forest, Deciduous Forest, Mixed Forest, Shrub, Herbaceous, Herbaceous Wetland, Wooded Wetland)
Topographic Wetness Index (TWI), mean and standard deviation (MN TWI, SD TWI)	index	DEM derived	1 - 10 scaled index representing soil moisture conditions (1 = high run-off potential, 10 = high pooling potential) (Beven and Kirkby 1979).
Slope Position classification (SPC)	percent	DEM derived	Basin-scale percent coverage per six classification of slope types (Weiss 2001). Classifications are Valley, Lower Slope (lower), Flat Slope (flat), Middle Slope (middle), Upper slope (Upper), and Ridge.
In-Stream Habitat			
Macroinvertebrate abundance, mean and standard deviation (MN BMI, SD BMI)	count	field collected, laboratory estimated	Mean benthic abundance per habitat basin.
Shelter rating: mean and coefficient of variation (MN Shelter, CV Shelter)	index	field measurement.	Calculated using the California Fish and Wildlife salmonid habitat protocol (Flosi et al. 2010).
In-Stream Habitat			
Wetted width, bankfull width,	proportion	field measurement	Variation in mean habitat unit width measurements (m) among each study stream (m).
Coefficient of variation (CV WW, CV BF, CV), Wetted Width: bankfull width, coefficient of variation (CV WW:BF)	proportion	field measurement	Variation in habitat unit ratio of mean bankfull width to mean wetted width (m).

Table B3. Summary of basin characteristics for each study stream. DS=downstream, US=upstream.

Study Stream	Basin type	Basin area (km^2)	Stream length (km)	Basin Mouth: distance to Ocean (km)	Basin Mouth: distance to stream mouth (km)
DUT	DS Basin	30.6	41.9	17.3	0.68
	Entire Basin	30.9	42.7	16.6	0.00
GRE	DS Basin	87.1	119.2	43.6	6.30
	Entire Basin	98.1	136.4	37.3	0.00
	US Basin	25.7	36.0	47.2	9.98
MIL	DS Basin	56.7	77.3	55.1	2.00
	Entire Basin	57.1	79.2	53.1	0.00
	US Basin	29.8	38.9	59.2	6.10
WIL	DS Basin	22.1	32.0	4.76	0.41
	Entire Basin	22.1	33.6	4.35	0.00
	US Basin	17.6	25.6	8.05	3.70

Table B4. Summary of geomorphology data for study basins (n = 11). MN = mean, SD = standard deviation, TWI = Topographic Wetness Index, DS=downstream, US=upstream. Valley, Low Slope, Flat Slope, Middle Slope, Upper Slope, and Ridge are percent coverage classifications.

Study Stream	Basin type	Drainage Density	Relief Ratio	MN % Slope	Valley	Low Slope	Flat Slope	Middle Slope	Upper Slope	Ridge	MN TWI	SD of TWI
DUT	DS Basin	0.00137	0.213	32.102	43.9	1.39	0.31	2.54	1.50	50.3	2.34	0.526
	Entire Basin	0.00138	0.119	32.126	44.0	1.40	0.31	2.54	1.50	50.2	2.34	0.527
GRE	DS Basin	0.00137	0.050	14.436	39.6	4.97	6.14	3.19	3.91	42.2	2.65	0.578
	Entire Basin	0.00139	0.045	16.681	41.0	4.53	5.49	3.03	3.58	42.4	2.61	0.593
	US Basin	0.00140	0.043	21.360	41.7	2.23	1.41	2.94	2.25	49.5	2.51	0.573
MIL	DS Basin	0.00136	0.061	38.047	46.9	1.12	0.03	2.27	1.13	48.5	2.24	0.535
	Entire Basin	0.00139	0.056	37.793	46.8	1.18	0.27	2.27	1.26	48.2	2.25	0.543
	US Basin	0.00130	0.076	40.771	47.2	1.04	0.01	2.14	1.03	48.6	2.23	0.524
WIL	DS Basin	0.00145	0.061	30.895	47.9	1.47	0.11	2.77	1.42	46.4	2.38	0.547
	Entire Basin	0.00152	0.061	30.875	47.9	1.47	0.11	2.77	1.42	46.3	2.39	0.548
	US Basin	0.00145	0.091	31.551	46.9	1.50	0.12	2.74	1.37	47.4	2.37	0.523

Table B5. Summary of in-stream data for study basins (n = 11). MN = mean, SD = standard deviation, BMI = benthic macroinvertebrate abundance, CV = coefficient of variation, DS=downstream, US=upstream.

Study Stream	Basin type	MN BMI	SD BMI	MN shelter rating	CV, shelter rating	CV, Wetted Width (m)	CV, Bankfull Width (m)	CV, Wetted Width: Bankfull Width
DUT	DS Basin	1017	1164	35	1	2.8	3.0	3.0
	Entire Basin	849	1038	27	1	1.7	2.4	2.8
GRE	DS Basin	3717	1528	7	1	6.5	5.9	5.1
	Entire Basin	2920	1892	19	1	3.1	2.1	3.3
	US Basin	3717	1528	7	1	6.5	5.9	5.1
MIL	DS Basin	633	454	51	2	5.4	4.2	11.5
	Entire Basin	834	579	45	1	3.8	2.1	1.9
	US Basin	538	372	52	2	6.3	4.5	3.2
WIL	DS Basin	498	456	22	1	2.3	12.4	2.6
	Entire Basin	498	456	22	1	1.9	1.0	0.9
	US Basin	508	607	16	1	2.5	16.5	2.9

Table B6. Summary of vegetation coverage for study basins. All values are percent coverage (n = 11). DS=downstream, US=upstream.

Study Stream	Basin type	MN Canopy	Deciduous forest	Conifer forest	Mixed forest	Shrub/ Scrub	Herbaceous	Wooded wetland	Herbaceous wetland	Barren surface
DUT	DS Basin	60.4	0.5	67.0	3.0	13.0	10.4	0.227	0.000	0.000
	Entire Basin	60.5	0.5	66.8	3.0	12.9	10.3	0.350	0.000	0.124
GRE	DS Basin	27.3	1.7	18.7	5.8	14.6	39.4	0.936	0.007	0.123
	Entire Basin	30.7	2.1	22.5	6.1	13.8	36.1	0.846	0.006	0.098
	US Basin	46.1	1.6	44.8	7.5	13.8	23.6	0.203	0.000	0.122
MIL	DS Basin	63.5	3.7	63.9	12.6	8.7	8.7	0.000	0.000	0.088
	Entire Basin	63.1	3.7	63.4	12.6	8.7	8.7	0.000	0.000	0.000
	US Basin	71.1	2.8	80.2	5.9	6.1	3.1	0.000	0.000	0.000
WIL	DS Basin	54.7	1.3	59.1	4.8	12.0	16.3	2.564	0.265	0.000
	Entire Basin	54.7	1.3	59.0	4.8	12.0	16.2	2.569	0.289	0.000
	US Basin	58.9	0.9	68.0	3.7	7.7	15.3	0.612	0.000	0.000

Table B7. Summary agriculture and development for study basins. All values are percent coverage (n = 11). DS=downstream, US=upstream.

Study Stream	Basin type	MN Impervious surface	Developed open space	Low development intensity	Medium development intensity	High development intensity	Cropland
DUT	DS Basin	0.25	5.30	0.177	0.115	0.000	0.000
	Entire Basin	0.30	5.59	0.242	0.117	0.000	0.000
GRE	DS Basin	2.08	10.66	2.029	0.761	0.154	5.071
	Entire Basin	2.12	10.74	2.024	0.853	0.159	4.506
	US Basin	0.41	6.90	0.035	0.028	0.000	1.314
MIL	DS Basin	0.07	2.37	0.011	0.000	0.000	0.000
	Entire Basin	0.08	2.40	0.017	0.000	0.000	0.550
	US Basin	0.03	1.99	0.000	0.000	0.000	0.000
WIL	DS Basin	0.12	3.66	0.020	0.000	0.000	0.000
	Entire Basin	0.12	3.70	0.020	0.000	0.000	0.000
	US Basin	0.09	3.77	0.000	0.000	0.000	0.000

Appendix C: PCA supporting data for Chapter 2 and Chapter 3 results

Table C1. PCA loading values (eigenvectors) model with basin and riparian-scale variables from Chapter 2 watershed analysis. Includes basin and in-stream watershed characteristics (n = 11). Scale denoted in parentheses for predictor variables: Basin = full basin-scale, 120 = 120-m riparian scale, 60 = 60-m riparian scale, 30 = 30-m riparian scale, stream = near-stream scale (10-m).

Predictor Variable	PC1	PC2
Geomorphology		
Barren Land	0.089	-0.004
Barren Land (120)	0.085	-0.014
Drainage Density	-0.019	0.182
Max. Slope (Stream)	-0.113	-0.046
Min. Slope (Stream)	-0.079	-0.132
MN Slope	-0.123	-0.072
MN Slope (120)	-0.118	-0.090
MN Slope (30)	-0.118	-0.082
MN Slope (60)	-0.117	-0.091
MN Slope (Stream)	-0.118	0.003
MN TWI	0.122	0.082
Relief Ratio	-0.040	0.006
SD TWI	0.118	0.024
SPC Flat Slope	0.131	0.003
SPC Low Slope	0.131	0.024
SPC Middle Slope	0.102	0.131
SPC Ridge	-0.100	-0.067
SPC Upper Slope	0.132	0.023
SPC Valley	-0.121	0.028
Vegetation		
Conifer Forest	-0.129	-0.030
Conifer Forest (120)	-0.129	0.025
Conifer Forest (30)	-0.127	0.031
Conifer Forest (60)	-0.128	0.031
Conifer Forest (Stream)	-0.127	0.033
Deciduous Forest	-0.005	-0.167
Deciduous Forest (120)	0.001	-0.194
Deciduous Forest (30)	0.023	-0.167
Deciduous Forest (60)	0.014	-0.180
Deciduous Forest (Stream)	0.022	-0.162
Herbaceous	0.125	0.063
Herbaceous (120)	0.131	0.016
Herbaceous (30)	0.130	0.007
Herbaceous (60)	0.130	0.016
Herbaceous (Stream)	0.130	0.006
Herbaceous Wetland	-0.034	0.183
Herbaceous Wetland (120)	-0.034	0.183
Herbaceous Wetland (30)	-0.036	0.181
Herbaceous Wetland (60)	-0.035	0.182

Predictor Variable	PC1	PC2
Herbaceous Wetland (Stream)	-0.036	0.180
Mixed Forest	-0.005	-0.167
Mixed Forest (120)	0.017	-0.171
Mixed Forest (30)	0.040	-0.172
Mixed Forest (60)	0.029	-0.176
Mixed Forest (Stream)	0.051	-0.163
MN CC	-0.127	-0.060
MN CC (120)	-0.131	-0.027
MN CC (30)	-0.129	-0.027
MN CC (60)	-0.129	-0.030
MN CC (Stream)	-0.129	-0.026
Shrub	0.094	0.093
Shrub (120)	0.118	-0.047
Shrub (30)	0.109	-0.083
Shrub (60)	0.111	-0.081
Shrub (Stream)	0.106	-0.076
Wooded Wetland	0.000	0.208
Wooded Wetland (120)	0.002	0.209
Wooded Wetland (30)	0.008	0.212
Wooded Wetland (60)	0.003	0.211
Wooded Wetland (Stream)	0.018	0.211
Development and Agriculture		
Cultivated Crops	0.130	-0.006
Cultivated Crops (120)	0.128	-0.025
Cultivated Crops (30)	0.126	-0.032
Cultivated Crops (60)	0.126	-0.033
Cultivated Crops (Stream)	0.123	-0.039
Dev. High	0.126	0.006
Dev. High (120)	0.126	0.006
Dev. High (30)	0.125	0.006
Dev. High (60)	0.125	0.006
Dev. High (Stream)	0.125	0.006
Dev. Low	0.127	0.007
Dev. Low (120)	0.119	0.011
Dev. Low (30)	0.120	0.014
Dev. Low (60)	0.113	0.015
Dev. Low (Stream)	0.098	0.016
Dev. Med (120)	0.124	0.006
Dev. Med (30)	0.120	0.006
Dev. Med (60)	0.121	0.006
Dev. Med (Stream)	0.115	0.007
Dev. Medium	0.127	0.005
Dev. Open	0.129	0.037
Dev. Open (120)	0.095	-0.060
Dev. Open (30)	0.064	-0.159
Dev. Open (60)	0.065	-0.135
Dev. Open (Stream)	0.073	-0.144
Impervious	0.130	0.008
Impervious (120)	0.128	0.009
Impervious (30)	0.128	-0.018
Impervious (60)	0.127	-0.007

Predictor Variable	**PC1**	**PC2**
Impervious (Stream)	0.125	-0.006
In-Stream Habitat		
CV BF	-0.029	0.079
CV Shelter	-0.036	-0.146
CV WW	0.038	-0.134
CV WW:BF	0.012	-0.135
MN BMI	0.117	-0.020
MN Shelter	-0.077	-0.144
SD BMI	0.119	-0.007

Table C2. PCA loading values (eigenvectors) model with basin-scale variables only from Chapter 2 watershed analysis. Includes basin and in-stream watershed characteristics (n = 11).

Predictor Variable	**PC1**	**PC2**
Geomorphology		
Barren Land	0.1465	0.0297
Drainage Density	0.0003	-0.3685
MN Slope	-0.2212	0.0613
MN TWI	0.2215	-0.0738
Relief Ratio	-0.0691	-0.0515
SPC Flat Slope	0.2193	0.0778
SPC Low Slope	0.2233	0.0403
SPC Middle Slope	0.1979	-0.1767
SPC Ridge	-0.1766	0.0405
SPC Upper Slope	0.2262	0.0378
SPC Valley	-0.2007	-0.1086
Vegetation		
Conifer Forest	-0.2216	-0.0146
Deciduous Forest	-0.0400	0.3008
Herbaceous	0.2228	-0.0410
Herbaceous Wetland	-0.0303	-0.3216
Mixed Forest	-0.0380	0.2710
MN CC	-0.2245	0.0358
Shrub	0.1703	-0.1344
Wooded Wetland	0.0323	-0.3478
Development and Agriculture		
Cultivated Crops	0.2173	0.0918
Dev. High	0.2090	0.0720
Dev. Low	0.2103	0.0677
Dev. Medium	0.2098	0.0665
Dev. Open	0.2227	-0.0001
Impervious	0.2181	0.0647
In-Stream Habitat		
CV BF	-0.0234	-0.1379
CV Shelter	-0.0853	0.3141
CV WW	0.0476	0.3203
CV WW:BF	0.0010	0.2795
MN BMI	0.1988	0.1034
MN Shelter	-0.1613	0.2217
SD BMI	0.1995	0.0534
SD TWI	0.2028	0.0190

Table C3. PCA loading values (eigenvectors) model for Chapter 3 analysis of habitat effect on movement strategy across literature reviewed studies (n = 16). Shortened variable names are ESA = Endangered Species Act listing, Strategies = number of unique movement strategies per study.

Variable	**PC1**	**PC2**
Basin Latitude (°N)	-0.0569	0.3821
Basin Area (km^2)	-0.0237	0.1134
Not Listed (ESA)	-0.1488	0.3801
Species of Concern (ESA)	-0.0413	0.2414
Threatened (ESA)	0.1402	-0.4933
Study Years	-0.0818	0.1642
Strategies	0.1166	-0.3329
Main Channel Rearing	-0.1470	0.3063
Tributary Rearing	-0.0117	-0.1076
Estuary Rearing	0.0803	-0.2255
Pond/Lake Rearing	0.0393	0.1479
Parr	-0.4781	-0.1529
Smolt	0.4781	0.1529
Spring	0.4868	0.1112
Winter	-0.4567	-0.1484

Table C4. PCA loading values (eigenvectors) model for Chapter 3 analysis of initial fish fork length statistical effect on growth across literature reviewed studies (n = 8). ESA = Endangered Species Act listing.

Variable	**PC1**	**PC2**
Basin Latitude (°N)	-0.4629	-0.0106
Basin Area (km^2)	0.4631	0.0236
Species of Concern (ESA)	-0.4452	-0.1442
Threatened (ESA)	0.4452	0.1442
Study Years	0.0515	-0.6930
Main Channel Rearing	0.4137	-0.2104
Initial fork length effect on growth rate	-0.0326	0.6582

Appendix D: Random forest model supporting data

Table D1. Variable importance scores for all predictor variables in the three random forest models. Basin type included in parentheses after variable name for in-stream and landscape variables. Importance scores are mean decrease in model accuracy per variable per model, divided by the standard deviation among trees in mean decreasing model accuracy.

Predictor Variable	**Mean Decrease in Model Accuracy (%)**	**Variable Type**
Model: Upstream movement day		
Temperature (US Basin)	145.33	Climate
Precipitation (US Basin)	136.12	Climate
PC 2 (US Basin)	64.11	Watershed
PC 1 (US Basin)	61.23	Watershed
Pre-winter relative FL	10.50	Fish Size
Pre-winter K	9.03	Fish Size
Model: Downstream movement day		
US Movement Day	141.91	Fish Movement
Temperature (DS Basin)	54.34	Climate
Precipitation (DS Basin)	45.78	Climate
Temperature (US Basin)	29.33	Climate
PC 2 (DS Basin)	26.10	Watershed
PC 2 (US Basin)	25.87	Watershed
PC 1 (US Basin)	24.26	Watershed
PC 1 (DS Basin)	23.79	Watershed
Precipitation (US Basin)	18.04	Climate
Pre-winter relative FL	11.89	Fish Size
Model: Growth rate		
Pre-winter relative FL	118.23	Fish Size
Spring relative FL	78.14	Fish Size
DS Movement Day	32.07	Fish Size
PC 2 (DS Basin)	29.19	Watershed
PC 1 (DS Basin)	20.70	Watershed
Pre-winter K	19.88	Fish Size
Temperature (DS Basin)	5.73	Climate
Precipitation (DS Basin)	3.38	Climate

Appendix E: Directional classification supporting data

Table E1. Influential factors analyzed for influence on pre-smolt outmigration and growth of coho salmon. Positive and negative relationships were statistically significant in the studies while non-relationships were not found to be statistically significant by the authors. Positive relationships were noted when an increase in factor quantity or quality corresponded with later timing of movement (spring movement) or greater growth rate and negative relationships were noted when an increase in factor quantity or quality corresponded with an earlier timing of movement (pre-spring movement) or lower growth rate. Inner-seasonal variations in relationships between factors and movement and growth responses were noted by multiple directional relationship symbols.

Unique pre-smolt and smolt movement strategies	Influential movement factors (+/-/≠)	Influential growth factors (+/-/≠)	Reference
Age-1 smolts early in the summer and then late in the summer ; age-2 smolts early in the summer	Distance to ocean (+), age (+), fish length (+), distance to ocean*age (-)	N/A	(Thedinga et al. 1994)
N/A	age (-), streamflow (+ for age-0 and age-1, ≠ for age-2), size (- for age-0), estuary rearing limited for age-0	N/A	(Murphy et al. 1997)
movement into small-tributary habitat in the spring and remaining until the following fall; fall migrations between small-tributary habitat and main-stream habitat (occasionally multiple times during the season), overwintering in small-tributary habitat	small-tributary rearing (+)	N/A	(Bramblett et al. 2002)
Fall/winter age-0; age-1 early spring – summer; age-2, early spring	Lake-rearing*age (-), stream-rearing*age (+), age (+), growth (-)	Lake-rearing (+), stream-rearing (-)	(Irvine et al. 1989)
N/A	Stream-type rearing (-), pond-type rearing (+), off-channel habitat area (+)	Stream-type rearing (-), Pond-type rearing (+), density (-)	(Rosenfeld et al. 2008)
Summer parr and winter parr	Streamflow (+/≠), temperature (-/≠)	N/A	(Hartman et al. 1982)

Unique pre-smolt and smolt movement strategies	Influential movement factors (+/-/≠)	Influential growth factors (+/-/≠)	Reference
winter movers and non-movers	Streamflow (+/≠), temperature (-/≠), in-stream cover volume (+), pool depth (+), bank cover area (-)	N/A	(Tschaplinski and Hartman 1983)
Fall/winter and spring migration	Pre-winter fish length (+), main-channel rearing (-), tributary rearing (+), pre-winter fish condition (≠)	pre-winter fish condition (≠), pre-winter fish length (+), tributary rearing (+), main-channel rearing (-)	(Bennett et al. 2011)
Fall/winter, fall estuary and overwinter freshwater, inter-stream movement, and spring migration	Stream flow (+/≠), temperature (+/≠), pre-winter length (+), distance to ocean (+), pre-winter habitat depth (+), pre-winter density (-)	pre-winter relative length (-), pre-winter habitat depth (-), year, distance to ocean (≠)	(Roni et al. 2012)
N/A	N/A	Pond-rearing (+), stream-type (-), density (-), distance to ocean (-)	(Roni et al. 2006)
N/A	Smolt size (≠), lake rearing (+), distance to ocean (+)	Lake rearing (+), pre-winter fish size for stream-fish (+), pre-winter fish size for lake-fish (≠)	(Quinn and Peterson 1996)
fall/winter and spring migration	Pre-winter fish length (+ 2007 and 2008, but ≠ in 2006), in-stream habitat (≠), study year (movement timings variable by year), density (≠)	Distance to ocean (+), study year (growth variable across years)	(Pess et al. 2011)
Spring smolt migrants; fry estuary migrants (rear in estuary spring – summer); fry freshwater migrants (rear in downstream freshwater habitat spring – summer); parr migrants (migrate downstream in summer and may utilize estuary pre-smolt)	N/A	Length of estuary rearing (+), restored emergent and main stem wetland rearing (+) in comparison to forested wetland rearing	(Craig et al. 2014)
Spring smolt migration, summer estuary rearing and spring smolt migration, fall/winter estuary rearing and spring smolt outmigration, summer estuary rearing, winter freshwater rearing, spring smolt outmigration	Stream flow (+/≠) pre-winter fish size (≠)	Distance to ocean (-), estuary rearing (+), freshwater rearing (-)	(Jones et al. 2014)

Unique pre-smolt and smolt movement strategies	**Influential movement factors (+/-/≠)**	**Influential growth factors (+/-/≠)**	**Reference**
Natal stream reach, non-natal stream , mobile (multiple streams)	Distance to non-natal stream (-)	pre-winter fish weight (+), movement to intermittent upper watershed tributary (+), streamflow (-), stream temperature (+), spawning density (+)	(Ebersole et al. 2006a)
Fall/winter (small number, personal observation) and spring smolt migration	Distance to ocean (+)	Pre-winter fish length (+), temperature (+), intermittent tributary rearing (+), main-channel rearing (-), percent bedrock (≠), black spot present (≠), spawner biomass (≠), deciduous riparian canopy cover (≠), distance to ocean (-)	(Ebersole et al. 2009)
Fall/winter to estuary, fall estuary and freshwater overwinter, spring migration	Stream flow (+/≠), distance to ocean (+), salinity (+)	Estuary ecotone rearing (+), upper watershed freshwater rearing (-), distance to ocean (+)	(Miller and Sadro 2003)
Fall/winter and spring smolt migration	Fall/winter movement and stream flow (+), pre-winter fish length*year (+/-), distance to ocean (-)	Movement season (+/-)	(Rebenack et al. 2015)