

Early marine migratory patterns and the factors that promote resident type behavior of Chinook salmon, *Oncorhynchus tshawytscha*, in Puget Sound, Washington.

Joshua Chamberlin

A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington

2009

Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

University of Washington
Graduate School

This is to certify that I have examined this copy of a master's thesis by

Joshua Chamberlin

and have found that it is complete and satisfactory in all respects,
and that any and all revisions required by the final
examining committee have been made.

Committee Members:

Thomas Quinn

Tim Essington

John Ferguson

Kate Myers

Date: _____

In presenting this thesis in partial fulfillment of the requirements for a master's degree at the University of Washington, I agree that the Library shall make its copies freely available for inspection. I further agree that extensive copying of this thesis is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Any other reproduction for any purposes or by any means shall not be allowed without my permission.

Signature _____

Date _____

Table of Contents

	Page
List of Figures.....	ii
List of Tables.....	iii
General Introduction.....	1
Chapter One: The influence of hatchery rearing strategies on the resident-type behavior of Chinook salmon, <i>Oncorhynchus tshawytscha</i> , in Puget Sound, WA.....	5
Introduction.....	5
Methods.....	9
General Dataset Criteria.....	9
Relative Contributions.....	11
Data Analysis.....	12
Results.....	14
Discussion.....	16
Chapter Two: Migratory behavior of yearling Chinook salmon, <i>Oncorhynchus tshawytscha</i> , during their first summer in the marine waters of Hood Canal, WA.....	29
Introduction.....	29
Methods.....	32
Study site.....	32
Tagging and Tag Characteristics.....	33
Receivers.....	34
Data Analysis.....	35
Results.....	39
Discussion.....	43
General Conclusions.....	58
References.....	60

List of Figures

Figure Number	Page
Fig. 1.1. Map of Puget Sound with designated PSC Regions	25
Fig. 1.2. Scatterplot of size at release and day of release by age class.....	26
Fig. 1.3. Interaction effect between release region and weight at release	27
Fig. 1.4. Box and whisker plot of proportion resident for age-0 and age-1 fish across all years for each release region	28
Fig. 2.1. Map of Hood Canal with receiver locations and release site	51
Fig. 2.2. Histogram of elapsed time between detections	52
Fig. 2.3. Proportion of fish detected throughout the study area by week.....	53
Fig. 2.4. Temporal fish displacement throughout Hood Canal	54
Fig. 2.5. Number of detections on specific receivers by distance from release site.....	55
Fig. 2.6. Circular histogram for time of day when movements occurred	56
Fig. 2.7. Normalized difference of inactivity per fish at each receiver	57

List of Tables

Table Number	Page
Table 1.1. List of hatcheries, number of years of data, and number of releases	23
Table 1.2. Comparison of models and model scores (QAIC)	24
Table 1.3. Model coefficients and standard error for best fit model	25
Table 2.1. Movement metrics across all tide stages and between movement directions	50

Acknowledgements

The work presented in this thesis is the result of input and ideas from several individuals who all deserve credit for the final product. Without collaboration and cooperation along the way this work would not have been possible.

I would first like to thank NOAA Fisheries Northwest Fisheries Science Center Fish Ecology division for providing funding for me and the work I have done throughout the entire project. Next I would like to thank my advisor, Tom Quinn, for his unbelievable support during my time at SAFS. His ideas, input, attentiveness, and creativity have helped shape this work and he has taught me how to better myself as a scientist and a colleague. I would also like to thank the rest of my committee; Tim Essington for his insightfulness and willingness to explain complex topics, John Ferguson for his detailed comments and helpful suggestions, and Kate Myers for her candidness and editorial input.

Kurt Fresh and Anna Kagley from the Northwest Fisheries Science Center provided incredible help conceptualizing ideas and working in the field. I would also like to acknowledge Greg Bargmann and Debbie Farrer for their contributions to the telemetry work in Hood Canal as well as all of those who helped out at Hoodsport Hatchery.

I can't say enough about the group of people in the Quinn lab both past and present. You all listened to me a number of times and always had incredible feedback and support. Finally I would like to thank my family and friends for all their support throughout this process: mom, dad, jessica, and many, many others.

General Introduction

Migration is a fundamental component of the life history and ecology of many animal species across numerous taxa . In fishes, the spatial extent and duration of migrations can vary depending on species and environment (Harden Jones 1968; Lucas and Baras 2001; Northcote 1978). Some species migrate thousands of kilometers (Rooper et al. 2008) whereas other migrate only hundreds of meters (Massicotte et al. 2008). Furthermore, migrations occur at various temporal and spatial scales; some species migrating only once in each animal's lifetime whereas others migrate annually or at irregular intervals. In addition to variation in migration patterns among species, there can also be considerable variation in migratory behavior among populations within species (Quinn and Brodeur 1991). Studies on geographically separate populations of fishes reveal differences in the tendency to migrate, and on the routes and the spatial and temporal extent of migrations (e.g, in salmonids:Quinn 2005; Quinn and Myers 2004). Moreover, partial and differential migrations represent alternative patterns of migratory behavior that may be expressed by individuals within a specific population (Dingle 1996). Within a partially migratory population, some individuals do not migrate but instead remain resident in their natal habitat (Jonsson and Jonsson 1993). For example, coastal cutthroat trout (*Oncorhynchus clarki clarki*) along the west coast of North America can have anadromous and freshwater resident individuals within a given population (Zydlewski et al. 2009). Differential migration refers to an exclusively migratory population

where the extent of migration varies among individuals. While partial migration suggests a distinct difference in migratory preference, populations with differential migration strategies likely represent a continuum of migratory behaviors.

Complex migrations across highly variable environments may also cause significant behavioral differences among populations and individuals. Shifts in habitat characteristics, both physical and biological, can cause species to interact differently with their surroundings, with consequences for their migratory behavior. For example, Ramenofsky et al. (2008) saw increased locomotive activity of captive white-crowned sparrows (*Zonotrichia leucophrys*) when food resources were limited and illumination was increased. For fishes, such habitat shifts or changes could dramatically affect local distributions. Kallio-Nyberg et al. (1999) found that Atlantic salmon (*Salmo salar*) distributions were contracted in years when forage fish abundance was high. Understanding how individuals interact with their environment may explain specific differences in migratory behavior.

Pacific salmon (*Oncorhynchus* spp.) undergo significant migrations throughout their anadromous life cycle, most of which occurs in the marine environment (Quinn and Myers 2004). Significant life history diversity within the genus is linked to the considerable differences in migratory behavior among the species. The extent of migrations of each species is strongly driven by age at maturity. For example, pink salmon (*O. gorbuscha*) consistently migrate to freshwater to spawn after one year at sea whereas sockeye salmon (*O. nerka*) typically spend two or three years at sea and travel farther from their natal location. In addition to absolute distance, the species

also differ in their use of marine habitats. Coho salmon, *O. kisutch*, and Chinook salmon, *O. tshawytscha*, are associated with coastal habitats to a much greater extent than pink, sockeye, and chum, *O. keta*, salmon (Groot and Margolis 1991).

Chinook salmon are a particularly diverse species in terms of their life history and migration patterns, influenced by a complex blend of genetic and environmental factors (Healey 1991; Quinn 2005). They exhibit two distinct juvenile life histories: stream-type and ocean-type (Healey 1983). Stream-type fish spend a full year growing in streams before migrating to sea whereas ocean-type migrate to sea in their first year of life, typically at a smaller size and later in the spring than the older stream-type fish. The two life history types vary in several other ways including their marine distributions; stream-type individuals are typically distributed offshore whereas ocean-type individuals are distributed along the coast (Healey 1983).

Puget Sound is a highly glaciated, semi-enclosed, estuarine basin. Several major sills and constriction points between and among the numerous islands and fjords make Puget Sound a highly complex system, presenting alternative rearing and migration options for salmon produced in the adjacent watersheds. Puget Sound populations of Chinook salmon are predominantly ocean-type fish. Adults return in the late summer or early fall to spawn and juveniles typically migrate out of their natal streams and leave Puget Sound in May and June of their first year of life. However, Puget Sound has supported a winter fishery for Chinook salmon for many years, indicating that there is a “resident” component of the local populations.

The work presented herein explores the resident-type Chinook salmon in Puget Sound at two distinct levels: population and individual. At the population level, we used coded wire tag data from multiple years to test the hypothesized effect of several factors on the relative proportion of fish that contributed to the resident population. Our analysis at the individual level evaluated the specific movement behavior of resident fish during their first months in the marine environment, using ultrasonic transmitters and receivers to detect movements. Together, these analyses provide a framework for understanding long term trends and patterns in what influences a resident-type behavior for fish in Puget Sound and the specific movement patterns of resident-type fish during the early marine phase of their migration.

Chapter One: The influence of hatchery rearing strategies on the resident-type behavior of Chinook salmon, *Oncorhynchus tshawytscha*, in Puget Sound, Washington.

Introduction

Migrations occur over various spatial and temporal scales. Some species migrate on an annual basis between feeding and breeding grounds (“iteroparous migrants”) and others display a more protracted, “round trip” migration that may last an entire lifetime (“ontogenetic” or “life-long migrants”; Dingle 1996; Dingle and Drake 2007; Ramenofsky and Wingfield 2007). Migratory behavior is generally viewed as an adaptation to availability and changing location of resources (Dingle 1996; Dingle and Drake 2007). Thus migrations typically occur as programmed responses to predictable (e.g., seasonal), or facultative responses to unpredictable changes in the environment (MacCall 1990; Ramenofsky and Wingfield 2007). Organisms commonly migrate to areas where conditions are ideal for breeding, or where they can exploit a local food source (Northcote 1978). While the ecological basis for broad scale patterns (breeding and feeding migrations) may be evident, the basis for variation in migratory behavior among individuals within populations is much less clear (Secor 1999). Drake et al. (1995) developed a conceptual model showing the components and processes of migration. Features of the environment, including depletion of resources by the population itself, can affect the likelihood and extent of migration by the population. In addition to this population perspective, migration can also be viewed from the standpoint of individuals, each of which has

combinations of behavior, physiology, morphology, and life history that influence migration. Understanding the effects of various conditions experienced at the individual level may help to explain variation in specific migratory patterns.

Pacific salmon (*Oncorhynchus* spp.) display temporally and spatially variable migrations. The combination of anadromy and semelparity causes each species to experience drastically different conditions throughout their range along their “life-long” migration from freshwater to the ocean, and back, depending upon the population’s location of origin and life history characteristics. For example, populations of Chinook salmon, *O. tshawytscha*, that enter the Bering Sea at the northern end of their range experience very different conditions than southern populations entering the Pacific Ocean off central California. Furthermore, populations may enter the marine environment at the same location yet exhibit different migratory patterns, suggesting that genetic background and juvenile life history traits can influence migratory behavior. Weitkamp and Neely (2002) found that separate populations of coho salmon (*O. kisutch*) from the Columbia River system had very different marine migration patterns even though they entered the ocean at the same location.

Chinook salmon are a particularly diverse species in terms of their life history and migration patterns, influenced by a complex blend of genetic and environmental controls (Healey 1991; Quinn 2005). They exhibit two distinct juvenile life histories: stream-type and ocean-type (Healey 1983). Stream-type fish rear for a full year in freshwater before entering the marine environment in their second spring as yearlings

whereas ocean-type Chinook salmon migrate to the ocean during their first spring or summer as sub-yearlings. Stream-type populations dominate in the northern part of the species' range (Alaska and northern British Columbia) and in interior (high elevation) populations in large rivers such as the Fraser and Columbia rivers, whereas the ocean-type life history is more prevalent in the southern portion of the range (Washington, Oregon, and California) and especially in coastal populations (Healey 1983; Taylor 1990). The extent to which the differences between these two life history types reflect genetic adaptations or phenotypically plastic responses to growing conditions is a subject of considerable controversy. The distinction between the types has been supported by molecular genetic evidence (Waples et al. 2004) and experiments involving the heritability of specific traits (Clarke et al. 1992; Clarke et al. 1994; Taylor 1989). In contrast, Brannon et al. (2004) emphasized the influence of temperature and growth on life history characteristics, and the diversification of Chinook salmon transplanted to New Zealand also suggests significant phenotypic plasticity (Quinn et al. 2001).

Stream-type and ocean-type Chinook salmon also vary in the extent of their marine migrations. Healey (1983) found that stream-type individuals were more often distributed offshore whereas ocean-type fish tended to remain in protected inland and coastal areas. Further analysis by Sharma (2009) has largely corroborated this observation, though this dichotomy is more evident in some populations than others. However, it is not clear to what extent ocean migration patterns reflect genetic programming (Kallio-Nyberg et al. 1999) or plastic responses to size at seawater

entry, and stream and ocean type Chinook salmon differ in both respects. In addition, differences in juvenile size and growth rate can affect seaward migration rates (Beckman et al. 1998; Giorgi et al. 1997). For example, Ewing et al. (1984) reported that Chinook salmon from the Deschutes River migrated faster when they were released at larger size and/or later in the year. When coupled with the geographic differences in location where fish enter the ocean, variations in growth rate and size could influence the duration of marine residency (Quinn et al. 2004; Vollestad et al. 2004).

Puget Sound is a large, semi-enclosed basin supporting a number of Chinook salmon populations representing primarily ocean-type and, to a lesser extent, stream-type life history patterns (Beechie et al. 2006) (Figure 1.1). The highly mixed, semi-estuarine waters of Puget Sound are an important migratory corridor and rearing ground during early life history stages (Duffy et al. 2005; Greene et al. 2005). Stream-type fish typically enter Puget Sound between March and April and generally move quickly through the estuarine environment whereas ocean-type fish enter Puget Sound between May and June after spending a few months rearing in streams and estuaries (Simenstad et al. 1981). After leaving their natal rivers most Puget Sound Chinook salmon migrate to the coast of the Pacific Ocean to rear (Quinn et al. 2005). However, the inside waters of Puget Sound have supported a year-round commercial and recreational fishery for salmon since the late 19th century, suggesting that a significant resident population exists (Haw et al. 1967; Pressey 1953). While the presence of resident fish has been recognized for many years by management agencies, local

fishermen, and tribes, the factors promoting resident-type behavior, as opposed to migration to the Pacific Ocean, remain unknown.

Using coded wire tag recovery data (Johnson 1990) from Puget Sound hatchery releases, we evaluated the effects of specific factors on the proportion of hatchery-reared Chinook salmon exhibiting resident-type behavior in Puget Sound. Specifically we applied generalized linear mixed models to identify the potential effects of four factors on subsequent migratory behavior: 1) release region, 2) size (weight) at release, 3) day of the year when the fish were released, and 4) age class (i.e., yearling or sub-yearling). We hypothesized that the proportion of a cohort that displayed resident behavior was positively related to 1) distance from the Pacific Ocean, 2) body size at release, 3) date of release, and 4) age at release.

Methods

General Dataset Criteria

All data for analysis were acquired via the Regional Mark Processing Center (RMPC) CWT Database (www.rmhc.org). The CWT database houses all release and recovery information of the numerous CWT programs (Jefferts et al. 1963; Johnson 1990) along the west coast of the United States and British Columbia. Hatchery releases were grouped by region as defined by the Pacific Salmon Commission (Fig 1.1). Five regions were used for analysis: South Puget Sound, Middle Puget Sound, Nooksack River, Hood Canal, and the Strait of Juan de Fuca. All populations within these regions are included in the Puget Sound Evolutionary Significant Unit (Myers et

al. 1998), and thus represent a generally similar genetic lineage. We did not include fish from the Stillaguamish and Skagit rivers in northern Puget Sound because they lacked sufficient release and recovery data for the period of interest. Cohorts were assigned an age class (yearling or sub-yearling) based on the elapsed time between spawning date and release day (number of days since January 1 of the year of release). Size at release was recorded in the CWT database as the mean weight per fish (g) for the release group. Analysis was restricted to releases between 1972 and 1993 because significant changes in fishing regulations precluded comparable analysis after 1993. Prior to 1994, all marine areas of Puget Sound and the Strait of Juan de Fuca were open year round for Chinook salmon angling. Beginning in 1994, the Washington Department of Fish and Wildlife closed regions within Puget Sound to Chinook salmon fishing for varying periods among years, precluding our use of data from this period. We excluded data prior to 1972 because the number of tagged hatchery groups was too limited.

The data included releases from federal, state, University of Washington, and tribal rearing facilities with consistent release data throughout the analysis period (Table 1.1). Local sport fishing cooperative programs were not included due to their inconsistency and relatively small numbers of fish released, nor were releases that deviated from the normal release procedures or standards (i.e. reported disease, premature release caused by flooding, and unusual experimental treatments). The data were limited to release groups of fall-run Chinook salmon because this run, which is based on the timing of adult returns to freshwater, accounted for approximately 94%

of all Chinook salmon released into Puget Sound from 1972-1993. They are primarily ocean-type fish (i.e., sub-yearling migrants) and so a full year of rearing would be inconsistent with their typical life history.

Recovery data were collected for tag codes defined by the above criteria. Over 95% of all CWT recoveries of Chinook salmon within Puget Sound and the Strait of Juan de Fuca were from sport fishermen, so we restricted our analysis to these data. Specific fish, or CWT recoveries, were considered resident if they were recovered within Puget Sound from November to March, inclusive. Puget Sound, in this context, was defined as the area south of Admiralty Inlet including Hood Canal and the Whidbey Basin (Fig 1.1). Resident fish might be caught throughout the year, but limiting recoveries to the November-March period excluded adults returning from the ocean in the summer to spawn in the fall. Thus our data were conservative with respect to the true proportion of salmon from each cohort that expressed a resident behavior. Fishing effort within Puget Sound and the coastal areas of Washington, Oregon, Alaska, and British Columbia was not equal among years or regions. Thus, we did not attempt to estimate the absolute proportion of salmon smolts that resided within Puget Sound as sub-adults. Rather, we were interested in the relative effects of different rearing factors on resident behavior. Our analysis assumed that fish from different hatcheries and release groups were equally vulnerable to fishing in all respects other than their spatial distribution. This assumption is difficult to test but seems plausible. We defined Puget Sound releases as those occurring in marine areas

6-13 and resident recoveries as fish recovered in marine areas 8-13 (WDFW Recreational Salmon Fishing Catch Record Areas).

Relative Contributions

To determine the effect of each rearing factor on residency, we calculated the relative contribution of each release group to the resident population using methods similar to Weitkamp and Neely (2002) and Adlerstein et al. (2007). The relative contribution of each release group provided an index of residency which was used as the response variable for our analyses. Each index of residency (R_{iy}) was established for each cohort using the following equation:

$$R_{iy} = r_{ips} / r_{itot} \quad (\text{Equation 1})$$

where r_{ips} is the number of resident recoveries within Puget Sound, and r_{itot} is the total number of recoveries of the cohort from all areas (coast-wide).

Data Analysis

Generalized linear models (GLM) are typically applied to data not normally distributed and are commonly used to analyze fishery catch data, including CWT recovery data (Cormack and Skalski 1992; Pascual 1993; Venables and Dichmont 2004). GLM's accommodate non-normal data in two ways: 1) the response can come from a variety of exponential family distributions (i.e. Poisson, Binomial, Gamma, etc.) and 2) the mean of the response is related to the linear form of the predictors via a link function (McCullagh and Nedler 1989; Nedler and Wedderburn 1972). We used generalized linear mixed models (GLMM: Venables and Dichmont 2004), which are

an extension of the typical GLM that accounts for potential correlations between observations. Release year was chosen as the random effect since inter-annual variability in specific contribution was assumed to exist and to affect all release groups within the same year equally, but we had no specific hypothesis with respect to year. Grouping by year enabled us to make direct comparisons of each particular fixed effect within a given year. The proportion of fish from a specific release group found in the resident population was used as the response variable so we modeled our data using a binomial distribution. The canonical link for the binomial distribution was the *logit* function. Models were setup as follows:

$$\mathbf{Logit}(Y) = \log(\mu / 1 - \mu) = \eta \quad (\text{Equation 2})$$

and

$$\eta = X\beta + Z\zeta \quad (\text{Equation 3})$$

where μ is the mean of the response, η is the linear form of the predictors, and $X\beta$ and $Z\zeta$ represent the matrices of observations for the fixed and random effects and their corresponding coefficients respectively. All analyses were performed using the *lme4* package (Bates et al. 2008) in the R Statistical Environment (R Development Core Team 2008). Explanatory variables were both categorical (release region and age class) and continuous (release day and weight). The continuous variables were not transformed prior to analysis. Model fit was based on maximum likelihood statistics using the negative log likelihood method for choosing models with the best fit of the observed data. Models were compared using the quasi-Akaike Information Criteria

(QAIC) method (Burnham and Anderson 1998). QAIC is calculated the same as AIC but is corrected for overdispersed data (Faraway 2006).

Finally, it was necessary to address the potential auto correlation between age class and both weight at release and day of release. In general, age-1 fish are larger than age-0 fish (Fig 1.2), though variation among hatchery releases caused significant overlap. For example, if age-0 fish were released at the same size as age-1 fish, they would have to be released later in the year. Likewise, fish of the different age classes released on the same day of the year would differ significantly in size. Therefore, we chose to include all three factors as separate variables for our analyses.

Results

A total of 226 release groups from 28 hatcheries throughout the five regions of Puget Sound were considered for analysis (Table 1.1). Hatcheries included in the analysis accounted for ~88% of fall run Chinook salmon CWT releases into Puget Sound between 1972 and 1993, and within each region the releases accounted for from 67% (Nooksack River) to 98% (Strait of Juan de Fuca) of all tagged Chinook salmon released during the study period. Approximately 79% of all releases (n=179) were age-0 fish, and the remaining 21% (n=47) were age-1 fish. Of the age-0 releases, most were from Middle Puget Sound hatcheries (30%; n=60), and 40% (n=19) of the age-1 fish were from South Puget Sound hatcheries. Across all regions of Puget Sound age-0 fish were smaller and released later in the year (mean = 9.14 g and day 147) in all years than age-1 fish (mean= 67.99 g and day 96, Fig 2). Age-1 fish released from

hatcheries in the South Puget Sound region ($n = 19$) were the largest (mean = 72.69 g) and were released earlier in the year (mean release day = 89) whereas releases from the Middle Puget Sound region ($n = 4$) were the smallest (mean = 52.08 g) and those from the Juan de Fuca region ($n = 7$) were released the latest (mean release day = 118).

For all fish combined over all years, 30% displayed a resident behavior based on the date and location where they were caught. Fish released as age-1 fish had a slightly higher relative contribution (34%) than age-0 fish (29%). The general trend in resident proportion across all regions and age classes displayed a period of higher residency in the mid- to late-1970's, followed by a period of lower residency proportions in the mid- to late-1980's and a trend of increasing resident behavior into the early 1990's. However, the level of residency varied by region; Hood Canal releases had the highest contribution (mean = 0.304) and Nooksack River had the lowest overall contribution (mean = 0.141) for all releases and years.

A total of 13 models were used to test for the effect of specific rearing practices on relative contribution of resident-type fish (Table 1.2). Release region was the best single parameter model (n_4 ; QAIC = 286.68; $-\loglik = -1270$) and accounted for 40% of the total variation among release groups, whereas weight at release, day of release, and age class each had minimal effects on residence behavior. However, when combined with release region, the model likelihoods were improved substantially by including these factors. The overall best model included the interaction between release region and weight at release which showed a positive effect of weight across all regions (n_{12} , QAIC = 260.34, $-\loglik = -1102$) (Table 1.3).

Model coefficients represent effects relative to the Hood Canal region, which had a nearly uniform contribution across all size classes compared to other regions (Fig 1.3). The largest effects from the interaction between weight at release and release region were seen in the Middle Puget Sound and Juan de Fuca regions where both regions showed a roughly 40% increase in predicted relative contribution as fish were released at larger sizes. Releases from hatcheries within the Middle Puget Sound region had the highest overall predicted contribution and showed a significant increase with fish weight (Fig. 1.3).

Discussion

Our results indicated that there were substantial proportions of Puget Sound fall Chinook salmon displaying resident behavior, as indicated by the date and location of catch, and that the relative contribution of resident-type fish from hatchery releases within Puget Sound was strongly influenced by the region where the release took place. While relative proportions varied from year to year, releases within the Middle Puget Sound, South Puget Sound, and Hood Canal regions were generally higher than those from the Strait of Juan de Fuca and Nooksack River regions (Fig 1.4). Size also played an important role; in general, the relative contribution from age-1 fish was greater than age-0 fish, but the magnitude of the effect varied among regions. Our best fit model predicted that release groups of smaller fish (age-0) from a particular region could contribute more to the resident population than release of larger fish (age-1) from other regions. This suggests that hatchery location rather than rearing

practices can have the dominant effect on Chinook salmon remaining as residents in Puget Sound.

Current Chinook salmon hatchery practices in Puget Sound are based on the premise that larger fish contribute more to the resident population and thus harvest within Puget Sound. Contribution to Puget Sound fisheries involves survival as well as migration. Appleby and Doty (1995) found higher survival rates for large Chinook salmon entering Puget Sound, although the year to year variation was great. Likewise, Quinn et al. (2005) found that the Chinook salmon released from the University of Washington hatchery were larger and had higher survival rates than those from the Soos Creek hatchery, in the same region.. However, there was considerable variation in survival among years, and neither hatchery showed a positive relationship between inter-annual variation in smolt size and marine survival. Thus the effect of size on survival seems to be weak. Our models used relative proportions and were therefore not biased with respect to differences in survival for a particular release groups.

Interactions between release region and size at release were apparent from our analysis of all areas of the Puget Sound, except for Hood Canal. Our overall results indicated that larger fish were more likely to become residents but a large yearling from the Nooksack River region was less likely to become a resident than a smaller sub-yearling released from the Middle Puget Sound region. Adopting a region-specific program could maximize the return both biologically and economically, since age-0 fish are less costly to rear than age-1 fish.

Neither day of release or age class seemed to influence the propensity of Chinook salmon to display resident-type behavior. A “delayed release” program is also currently used by fisheries managers to supplement the resident population of coho salmon in Puget Sound, where hatchery reared coho salmon are transferred to saltwater net pens near their typical release period and held for an additional 1-3 months. Rensel et al. (1988) examined data from the first few years of the program and reported that coho salmon released from net pens made a larger contribution to Puget Sound fisheries, especially in the south Puget Sound region. The results of our analyses for Chinook salmon are contrary to those for coho salmon and suggest that further scrutiny of the release strategies may be warranted.

Weight at release, day of release, and age class are inherently related and therefore interpretation of the model results is challenging. Age class likely incorporates the weight at release variable because age-1 fish were, on average, larger than age-0 fish. However, age-0 fish released later in the year, may be the same size as age-1 fish released early the following year, reflecting differences in growth rates between specific release groups that may be attributable to conditions not tested in our study (e.g. diet, water temperature, genetics, etc.). Similarly, day of release may incorporate age class, and thus weight at release, as the average day of release for age-0 fish (day 147) was significantly later than that of age-1 fish (day 96). However, several groups of age-1 and age-0 were released on the same days of the year (day 89-162) yet fish differed significantly in size. To test for the correlative effects between release day and age class we combined the individual predictors into a single rearing

day variable and revisited the analyses. The rearing day variable did not improve the fit of the models, which included the individual predictors, and therefore weight at release was interpreted as the single most important factor influencing a resident-type behavior after accounting for release region

Our results are consistent with several other studies regarding the effect of origin on distribution of Chinook and coho salmon. Moring (1976) found that the majority of recoveries of yearling Chinook salmon within two years of release into Puget Sound occurred in the region of release. Weitkamp and Neely (2002) showed that the distribution of coho salmon along the US west coast depended upon the geographic origin of the fish (i.e., most fish released in Oregon were caught there) but that fish released within the same river (e.g., Colombia River) could have different distribution patterns. Similar population-specific migration patterns have been observed in Atlantic salmon in the Baltic Sea (Jutla et al. 2003; Kallio-Nyberg et al. 2000; Kallio-Nyberg et al. 1999) and the Bay of Fundy (Lacroix 2008; Lacroix and Knox 2005; Lacroix and McCurdy 1996; Lacroix et al. 2004), which are also semi-enclosed marine basins.

There are several potential explanations for the differences in migratory patterns among regions. The importance of release region suggests a substantial localized effect in each particular region of Puget Sound. First, physical oceanographic properties including tidal currents and exchange rates can affect fish migration (Lacroix and Knox 2005; Lacroix and McCurdy 1996; McMahon and Holtby 1992). In areas where tidal currents are stronger, migrating fish may adjust

their behavior to take advantage of direction and magnitude of currents. For example, LaCroix and McCurdy (1996) found that most Atlantic salmon smolts migrated on the ebb tide and held position on the flood tides suggesting a passive component to their active migration when currents were favorable. Tidal currents and exchange rates in south Puget Sound and Hood Canal, and to a lesser extent middle Puget Sound, are smaller than those found in the north basin and the Strait of Juan de Fuca (Babson et al. 2005; Mofjeld and Larsen 1984). Fish released in these areas may be influenced less by tidal currents and therefore remain for a longer period of time.

Second, the spatial and temporal variability in prey items may also affect the migratory behavior of fish (Emmett et al. 2006). When food sources are abundant during early migratory periods, out-migrating fish may adjust their migratory patterns to take advantage of available food resources. Atlantic salmon in the Baltic Sea migrated shorter distances when herring biomass was greater in the areas near their river of origin (Kallio-Nyberg et al. 1999). Thus, salmon encountering favorable conditions upon entering Puget Sound may have a higher likelihood of remaining resident. However, Rice (2007) found evidence that forage fish abundance and general fish diversity increased from south to north within Puget Sound, and therefore less favorable conditions for salmon may exist in areas deeper within the Puget Sound basin (e.g. South Puget Sound and Hood Canal). It is likely that environmental conditions and/or oceanographic processes influence prey distribution and may have an indirect impact on migratory fish.

Third, geographic differences between regions could affect the distribution of salmon simply because fish enter the marine environment at different distances from the ocean. By definition a resident fish remains in Puget Sound as opposed to migrating to the ocean. However, not all regions are equidistant to the point of entry to the ocean. The areas with the lowest overall contribution rates (Strait of Juan de Fuca and Nooksack River) are closest to the Pacific Ocean and have the fewest alternative routes available to juvenile salmon (Fig 1.1). Fish entering marine waters in these areas are outside the main basin of Puget Sound and may be more likely to migrate directly to the ocean or north into the Strait of Georgia. In contrast, the areas with higher overall contributions are located farther south within Puget Sound and fish entering at these points have several route options and a greater distance to travel before they leave Puget Sound as we defined it

The apparent influence of geographic region may be partly confounded by our definition of a resident fish. Of the five regions we used for analyses, only three (Hood Canal, Middle Puget Sound, and South Puget Sound) release fish in the area where a resident capture is defined. However, fish released from all regions included some that were identified as residents, indicating that releases from areas outside the resident area still contributed to the resident population. Furthermore, our definition of residence is quite coarse and does not provide information on movement at the individual level. Geographic differences may also incorporate genetic differences for some populations of salmon (Kallio-Nyberg et al. 2004; Kallio-Nyberg et al. 1999). We were not able to draw any conclusions about genetic effects because our analysis

was limited to hatchery-reared fish in Puget Sound where broodstock transfers have been common among various facilities, greatly complicating such analyses.

Finally, smolt size may also affect migration behavior. Several studies have assessed the effects of smolt size on seaward migration in the freshwater systems (Beckman et al. 1998; Ewing et al. 1984; Giorgi et al. 1997). In general, larger smolts migrate faster and earlier than smaller individuals. However, little work has explored the effect of smolt size on early marine migration patterns. In the Baltic Sea, larger Atlantic salmon smolts migrated shorter distances than smaller smolts (Juttila et al. 2003; Kallio-Nyberg et al. 1999; Saloniemi et al. 2004). Likewise, larger Chinook salmon smolts were more often found in the inside waters throughout southeast Alaska (Orsi and Jaenicke 1996).

While our results indicate an effect of rearing on migration pattern it was fairly subtle suggesting that the effect upon migration was a matter of degree, rather than a shift from one state to another. Specific migration patterns are likely due to a combination of several factors including habitat quality, environmental variation, and genetic diversity. Pacific salmon display significant plasticity in the migratory behavior and the actual mechanism for such diversity remains unclear.

Table 1.1. List of hatcheries, years of release data, number of releases, and counts of CWT fish by region. Number of releases and count of CWT fish are separated by age class.

REGION	Hatchery	Years	AGE-0		AGE-1		TOTAL	
			Releases	CWT fish	Releases	CWT fish	Releases	CWT fish
Hood Canal								
	Enetai	4	4	35,369	-	-	4	35,369
	George Adams	5	7	66,443	-	-	7	66,443
	Hoodsport	15	16	8,855	7	35,587	23	1,231,137
	Sund Rocks	3	-	-	5	14,276	5	14,276
	<i>total</i>		27	-	12	-	39	1,347,225
Juan de Fuca								
	Dungeness River	3	3	77,418	-	-	3	77,418
	Elwha River	13	20	1,639,845	3	144,957	23	1,784,802
	Hoko Falls	6	6	920,228	-	-	6	920,228
	<i>total</i>		29	2,637,491	3	144,957	32	2,782,448
Middle PS								
	Grovers Creek	10	10	1,667,801	-	-	10	1,667,801
	Icy Creek	3	1	50,854	3	144,533	4	195,387
	Issaquah Creek	5	5	723,563	-	-	5	723,653
	Portage Bay	12	20	1,231,467	-	-	20	1,231,467
	Soos Creek	17	19	3,001,210	2	48,400	21	3,049,610
	Voights Creek	4	6	286,853	-	-	6	286,853
	<i>total</i>		50	5,243,093	2	48,400	52	5,291,583
Nooksack								
	Glenwood Springs	3	2	93,000	1	21,300	3	114,300
	Kendall Creek	4	6	380,724	1	18,092	7	398,816
	Lummi River	8	10	720,600	2	50,439	12	771,039
	Samish River	12	12	2,120,272	-	-	12	2,120,272
	Skookum Creek	2	2	113,417	-	-	2	113,417
	<i>total</i>		30	3,335,013	3	68,531	33	3,403,544
South PS								
	Capitol Lake	7	3	549,110	4	268,991	7	818,101
	Fox Island Net Pens	5	2	4,927	6	133,698	8	182,969
	Garrison Creek	4	10	702,717	-	-	10	702,717
	Hupp Springs	2	-	-	2	8,894	2	8,894
	Kalama Creek	7	9	1,246,815	-	-	9	1,246,815
	Minter Creek	3	5	373,574	3	79,046	8	452,620
	Nisqually River	1	1	155,943	-	-	1	155,943
	S.Sound Net Pens	5	4	121,687	4	536,934	8	658,621
	<i>total</i>		19	1,898,019	7	615,980	26	2,513,999
TOTAL			183	16,292,692	43	1,505,147	226	19,028,968

Table 1.2. Comparison of models and predictors. Model selection used the adjusted AIC (QAIC) method to select the best model.

Model	Predictor(s)	log(L)	K	QAIC	Δ QAIC
n1	Region	-1270	5	286.68	26.34
n2	Day	-1847	1	403.48	143.14
n3	Age	-1969	2	431.87	171.53
n4	Weight	-1965	1	429.00	168.66
n5	Region,Day	-1193	6	272.03	11.69
n6	Region,Age	-1183	7	271.87	11.53
n7	Region,Weight	-1163	6	267.54	7.20
n8	Day,Age	-1847	3	407.48	147.14
n9	Region,Day,Age	-1172	8	271.49	11.15
n10	Region:Day	-1168	11	274.62	14.28
n11	Region:Age	-1112	12	264.51	4.17
n12	Region:Weight	-1102	11	260.34	0.00
n13	Region,Weight,Age	-1162	9	269.32	8.98

Table 1.3. Model coefficients and standard error for best fit model. All coefficients are relative to the Hood Canal region.

	Coeff.	S.E.
Intercept	-1.3837	0.0134
JUAN	-0.5851	0.0049
MPS	0.0957	0.0031
NOOK	-0.8965	0.0032
SPS	0.0211	0.0036
Weight	0.0003	0.00004
JUAN:Weight	0.01199	0.00008
MPS:Weight	0.0134	0.0001
NOOK:Weight	0.0088	0.00006
SPS:Weight	0.0055	0.00005

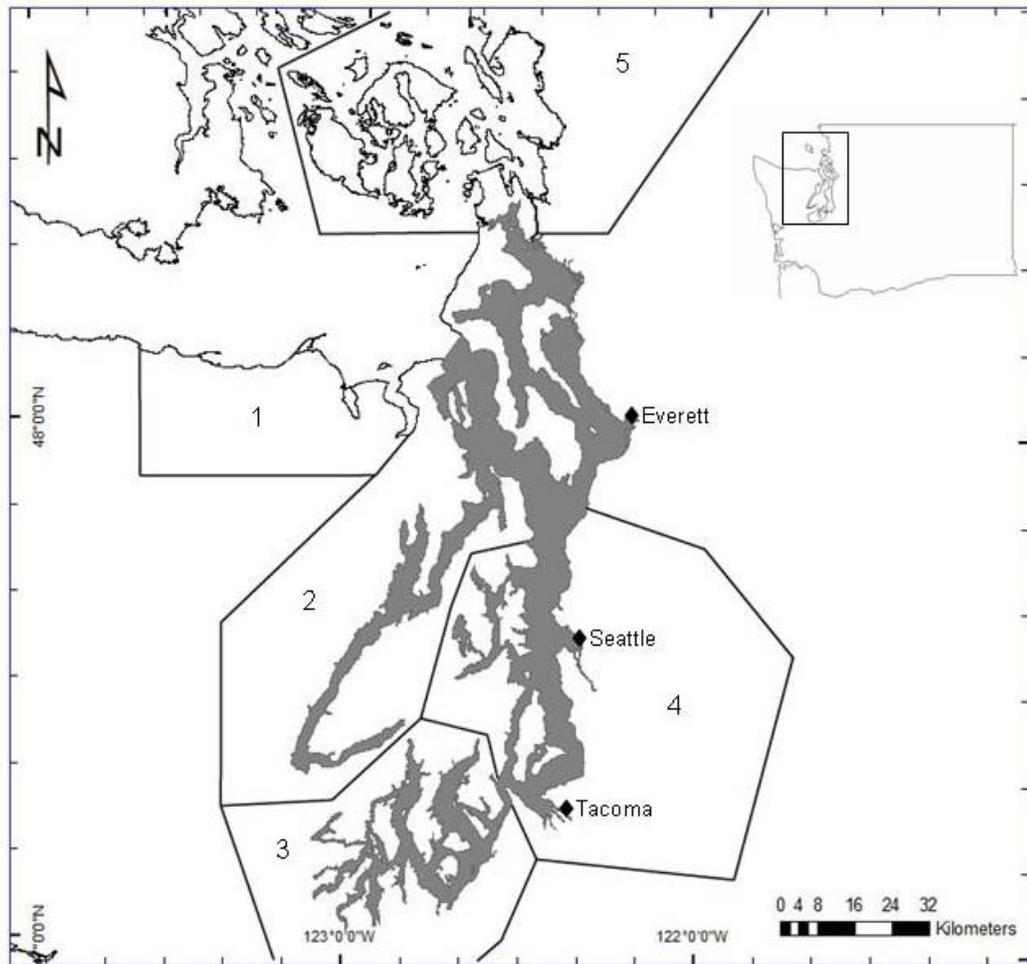


Figure 1.1. Map of study area indicating the regions used for analysis. 1) Strait of Juan de Fuca, 2) Hood Canal, 3) South Puget Sound, 4) Middle Puget Sound, 5) Nooksack (including San Juan Islands). Shaded region represents the areas of Puget Sound where CWT recoveries between November and March were considered resident.

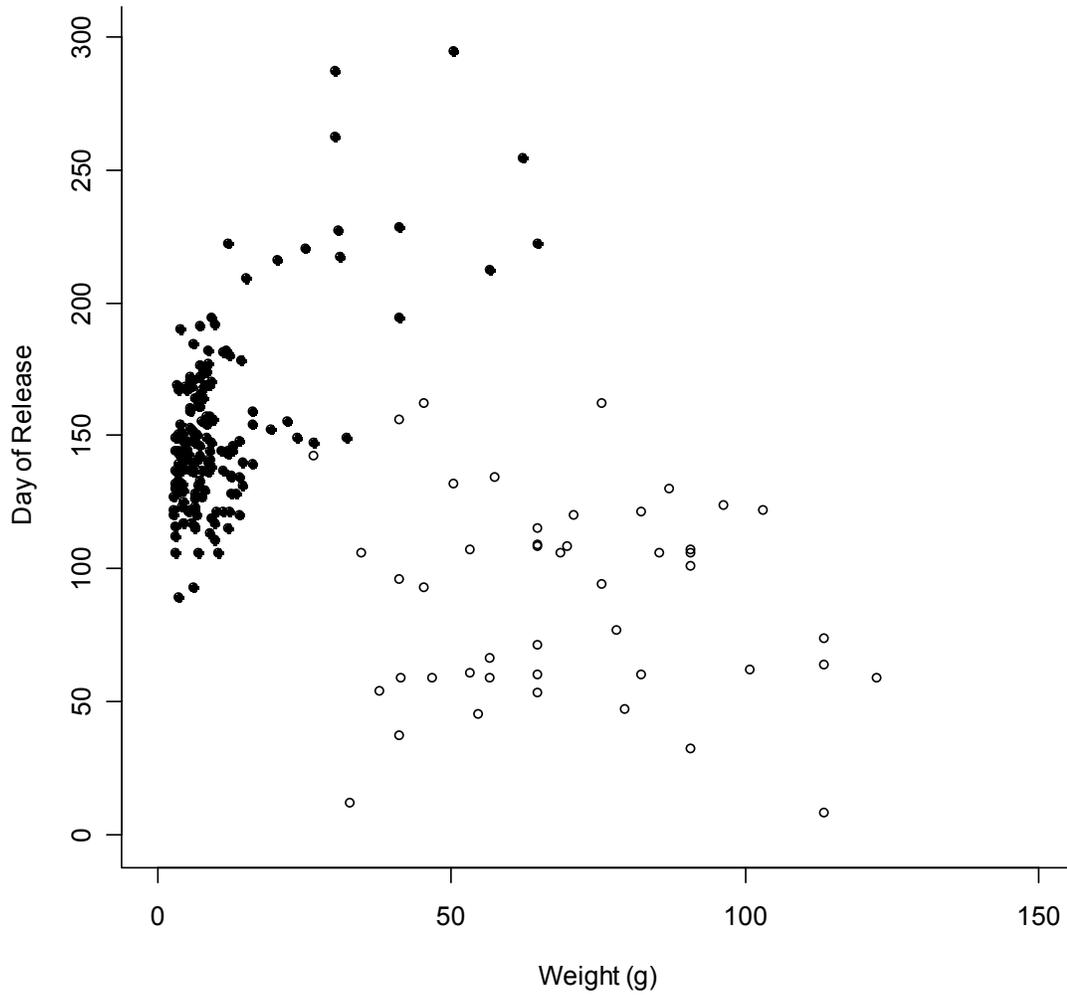


Figure 1.2. Scatterplot of the relationship between day of release and weight at release for age-0 (filled circles) and age-1 (open circles) fish from all regions across all years.

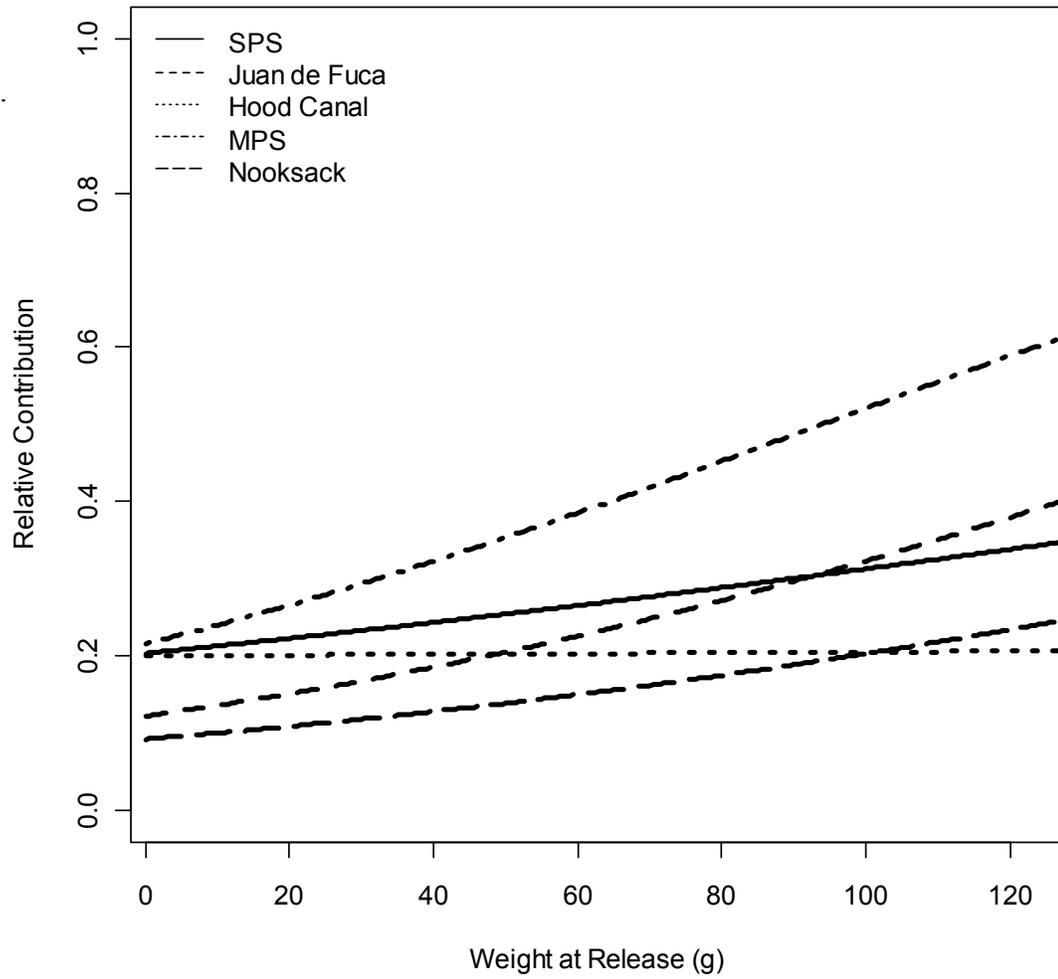


Figure 1.3. Interaction effect between release region and weight at release. Plot shows predicted contribution as a function of size at release for each region. Predicted contributions were calculated using the best-fit model coefficients.

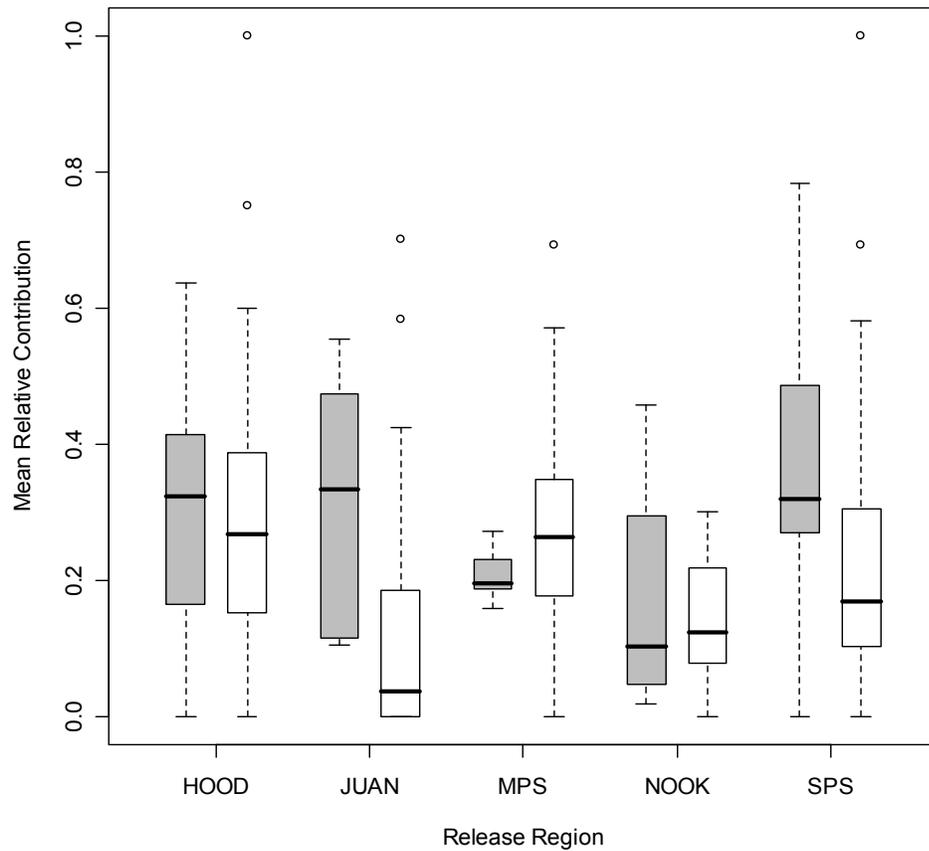


Figure 1.4. Box and whisker plot of mean relative contribution for age-0 (white boxes) and age-1 (shaded boxes) across all years for each release region. Dark lines within boxes represent the median for each region/age class. Dotted lines extend to the upper and lower extremes of each data class. Open circles represent outliers in the data

Chapter Two: Migratory behavior of yearling Chinook salmon (*Oncorhynchus tshawytscha*) during their first summer in the marine waters of Hood Canal, Washington

Introduction

Migration is a fundamental component of the life history and ecology of many animal species across numerous taxa (Dingle 1996). The spatial extent and duration of migrations can vary depending on species and environment (Harden Jones 1968; Lucas and Baras 2001; Northcote 1978). Some species migrate thousands of kilometers (Rooker et al. 2008) whereas others migrate only hundreds of meters (Massicotte et al. 2008). Furthermore, migrations occur at various temporal scales, with some species migrating only once in each animal's lifetime and others migrating annually to the same location (e.g. breeding migrations).

Complex interactions between the physical and biological features of the environment (temperature, prey, etc.), the internal state of the animal (hormone levels, stored energy, etc.) and genotype combine to affect migratory behavior. For fishes, such habitat shifts or changes could dramatically affect local distributions and there are numerous examples of environmental influences on migration (Leggett 1977). . Kallio-Nyberg et al. (1999) found that Atlantic salmon (*Salmo salar*) distributions were contracted in years when forage fish abundance was high. Understanding how the behavior of individuals is affected by these internal and external factors is a major challenge for research on migratory behavior.

Pacific salmon (*Oncorhynchus* spp.) undergo significant migrations throughout their anadromous life cycle, most of which occurs in the marine environment (Quinn and Myers 2004). Significant life history diversity within the genus is linked to the considerable differences in migratory behavior among the species. Chinook salmon (*O. tshawytscha*), in particular, demonstrate a wide range of migratory patterns. Ocean-type Chinook salmon (i.e., those migrating to sea as sub-yearlings) are generally found in the southern portion of the species' range, and are commonly associated with coastal habitats throughout their ocean migration. In contrast, stream type individuals migrate to sea as yearlings, typically at a larger size but earlier in the spring than ocean-type fish, and distribute farther offshore at sea (Healey 1983; Sharma 2009).

Puget Sound is located near the geographic center of the distribution of Chinook salmon along the west coast of North America (Healey 1983), where the ocean-type life history predominates but some stream-type fish are found (Myers et al. 1998). In addition to the two common marine distribution patterns of these life history types (i.e., coastal and open ocean), some individuals display a third marine pattern: resident behavior. Such individuals remain within Puget Sound instead of migrating to the ocean after leaving freshwater. These resident fish have been an important component of a large recreational fishery in the region (Haw et al. 1967; Pressey 1953) yet their movements within Puget Sound are largely unknown.

Many studies have contributed to our understanding of the general patterns of migration and distribution of the Pacific salmon (Groot and Margolis 1991; Quinn

2005). However, most of this work and especially that on the early marine period has provided a limited level of detail on the movements of individuals because the methods involved catch per unit of effort (Hartt et al. 1986), mark-recapture (Pearcy and Fisher 1988; Weitkamp and Neely 2002) or genetic analysis (Van Doornik et al. 2007). In contrast, relatively little has been done to evaluate migratory behavior of individuals, especially during the early marine phase. Telemetry is a commonly used research tool for evaluating and describing fish behavior, including home ranges, movement rates, daily activity patterns, and stage-specific survival. Telemetry allows researchers to gather information on individuals of a population over a variety of spatial and temporal scales. Many marine species have been studied using acoustic telemetry (Andrews et al. 2007; Dewar et al. 2008; Mitamura et al. 2009; Welch et al. 2002), including salmonids (Kallio-Nyberg et al. 2007; Lacroix et al. 2004; Melnychuk et al. 2007; Quinn et al. 1989).

While the early marine migratory period is a critical life stages for juvenile salmon (Beamish and Mahnken 2001), little is known about specific behaviors during this period. High mortality during this period has been observed and can strongly affect adult returns (Greene and Beechie 2004), but cause and effect relationships are difficult to define. Thus, understanding behavior during the early marine life stage may provide critical information regarding habitat use, distributions, and survival, may reveal potentially alternative migratory strategies.

For this study we used acoustic telemetry to evaluate the migratory behavior of individual yearling Chinook salmon in Hood Canal, Washington. Yearling releases

from the Hoodspout hatchery are part of the state's Recreational Fisheries Enhancement Program and are intended to augment the resident population. Our primary objective was to quantitatively describe the movements of these salmon during their initial period in marine habitat after release, contrasting a series of predictions based on the hypothesis that they would show resident behavior against predictions that would be consistent with migration to the ocean. We hypothesized that fish exhibiting resident behavior would remain in Hood Canal for the duration of the study, would show movement rates at or below speeds observed for migratory species, not direct their movements toward the ocean, and would remain at fixed locations for long periods of time. In contrast, fish displaying migratory behavior would be expected to leave Hood Canal within a time period appropriate for their length-specific swimming capacity, would move rapidly, primarily towards the outlet to the open water, and would not remain long at habitats within the fjord. This study focuses on individual behavior of resident type fish and builds upon previous work conducted on the regional scale regarding resident type behavior of Chinook salmon in Puget Sound.

Methods

Study Site

Hood Canal is a relatively long (62 km), narrow (maximum width = 4 km) fjord in western Puget Sound (Fig. 2.1). The canal connects to greater Puget Sound at its northern extent, 18 km south of Admiralty Inlet. The west side of the canal is

characterized by relatively large, shallow sills created by rivers draining the leeward Olympic Mountains, followed by a highly incised mid-channel region (max depth = 150 m) sloping gently upward to the eastern shoreline. The depth and habitat complexity of Hood Canal varies significantly from north to south. The northern end of Hood Canal has a long, narrow entrance, and there is a large sill located at the entrance to Dabob Bay. Tidal currents and exchange rates are far greater in the northern end of the canal than the southern end, which becomes shallow near the terminus.

Tagging and Tag Characteristics

Sixty yearling Chinook salmon smolts were tagged for this study. The fish were reared at the Washington Department of Fish and Wildlife hatchery in Hoodport as part of the yearling release program implemented by the Recreational Fisheries Enhancement Group. Yearling fish are spawned in the fall, emerge as fry in the spring and are reared for a full year before being released the next spring. The range of fish sizes was fairly narrow due to common rearing conditions experienced in the hatchery environment (mean fork length = 212 mm (range from 192 mm to 233 mm); mean weight = 100.8 g (range from 70 g to 150 g)).

All fish were tagged with Vemco V7-2L coded transmitters (7 x 18 mm; 1.7 g in air; AMIRIX Inc.), which randomly transmit unique identification codes at 69 kHz. Each code was transmitted approximately once a minute (ranged from 30 to 90 s) which resulted in a tag life of 150 days after initial activation on 7 May 2008.

Transmitter range was approximately 400 m, though detection is affected by water conditions (salinity, temperature, etc.) sea surface conditions (wind, wave activity, etc.), signal noise in the water column (boat activity, sonar, etc.) and the proximity of the transmitter or the receiver to the surface or substrate.

Transmitters were surgically implanted into the peritoneal cavity of each fish. Prior to surgery, the fish was anesthetized with MS-222, measured, and weighed. The fish was then placed on the surgery platform made from closed cell foam and coated in Stress-Coat (Aquarium Pharmaceuticals) to alleviate additional stress. A tube was placed into the mouth of the fish to continuously irrigate the gills with a 50:50 mixture of fresh water and anesthetic. An incision was made on the ventral side of the fish just forward of the base of the pelvic fin, the transmitter was inserted and situated along the ventral line, and the incision was closed with three surgeon stitches using dissolvable suture material. The fish was then placed into a 100 L tank with oxygenated water for observation until it recovered equilibrium and resumed normal swimming. After recovery the fish were returned to the hatchery pond, and held and monitored for an additional 48 h before being released with other untagged fish representing normal production from the hatchery. No mortalities were recorded prior to release.

Receivers

A network of 58 Vemco VR2 receivers was arranged throughout Hood Canal (Fig. 2.1) to passively detect the movement of tagged fish. Forty six receivers were

placed along the nearshore areas of the canal and three were attached to buoys in the central channel. In addition, nine receivers were placed along the entire span of the Hood Canal Bridge (Fig. 2.1) at the north end of the canal. The bridge array provided complete coverage of the exit point for the study area because the detection ranges of the receivers overlapped. Receivers were deployed in April (prior to tagging) and most were retrieved in late August of 2008. Because of the retrieval of many of the receivers and the anticipated termination of the battery life of the transmitters, the study effectively ended on 19 August 2008. Additional arrays, maintained by the Pacific Ocean Shelf Tracking project (Welch et al. 2002), were located outside the study area and provided coverage of the outlet of Puget Sound and the Strait of Juan de Fuca (Fig. 2.1).

Data Analysis

Fish were detected on receivers between 9 May and 19 August 2008.

Although our primary goal was to study movement patterns, the detections indicated a fish was alive and allowed us to generate weekly survival estimates. Fish not detected in a given week but detected in subsequent weeks were included in the detection estimates of previous weeks. Fish detections for the final week of the study were estimated by expanding the number of observed detections for the final week by a factor equal to the mean detection probability of all weeks throughout the entire study.

Analysis of fish movement from detection data required us to define what constituted a movement event. The fish could be moving or not moving during

periods when they were not detected but we had no information at such times.

However, the last detection on a receiver in a given period of time constituted a movement because the fish left the detection range of the receiver. Likewise, the first detection on a receiver at a given time was also considered a movement. We tallied these “first” and “last” detections for analysis of temporal patterns of movement, and movement rate. Consecutive detections on different receivers were interpreted as clear indications of fish movement. However, consecutive detections on the same receiver were more difficult to interpret. It was possible for a fish to “drift” in and out of the detection range of a particular receiver without engaging in a directed movement. For example, if the fish was at the periphery of the receiver’s range, very subtle movements or even shifts in detection range due to environmental conditions might cause it to be undetected for a few minutes even though it did not actually move any substantial distance. To eliminate such false activity records, we disregarded breaks in detection at a given receiver of less than 60 minutes. For example, if a fish was detected for 2 h at a receiver, then not detected for 10 min, and then detected again for another 2 h before leaving for several days, we considered this to be a pattern of continuous residence of 4 h and 10 min. However, if it left for 2 h and then returned, we tallied the first and last detections as movements. This “60 minute cut-off rule” was based on inspection of frequency histograms of elapsed time intervals between detections for the entire dataset (Fig 2.2).

The spatial and temporal displacement of fish as a group throughout the study period was measured as the proportion of the total number of fish present in a given

week detected on each particular receiver. Fish could be heard on multiple receivers in each week and displacement measured the spread of the entire tagged group throughout the study area. In addition to this characterization of the dispersal of the group, several metrics were used to describe individual movement. For this analysis, we used only movements that occurred within a 24 h period to avoid analysis of fish undetected for so long that movement estimates were meaningless. We determined the straight-line distance between the locations of receivers with consecutive detections and calculated movement rate as km-day^{-1} for each fish. Multiple detections for single fish in a given day were added together and scaled appropriately. Distance per movement was calculated using the same method and averaged over all movements for a particular fish. While these metrics under-estimate actual swimming speed because fish likely did not swim in a straight line, they provide useful estimates of travel rate for comparison with other migratory species in the region and salmonids elsewhere.

Rate of movement was also calculated as body lengths per second for comparison to tide stage and direction. Rates were calculated on an individual basis using fork length at time of tagging. Fish presumably grew over the study period but we used this value for overall estimation purposes. Movement rates were compared to tide stage (ebb, flood, high slack, and low slack) during the period which the movement occurred. Predicted tide height, tide stage, and times for Seabeck WA were used for all analyses with tidal data because this location is central within the study area and represented tide heights and times throughout Hood Canal with little

variation (± 0.1 m and ± 5 mins, respectively). On ebb tides the current flows out of the canal whereas on flood tides the dominant current direction is into the canal. Slack tides were defined as the 1 hr period before and after each high and low tide. Currents during the slack were considered neutral.

To analyze the overall direction of movement by fish throughout the study period we assigned each movement as directed “in” or “out” of the study area. The study area is roughly aligned on a north/south axis with the exit at the northern end, opening into greater Puget Sound and eventually the Pacific Ocean. Directions were determined by calculating the difference in latitude between the receivers with consecutive detections. If the value was positive it indicated a “out”, or northward movement. Likewise, if the value was negative it indicated an “in”, or southward movement away from the exit point of the study area. For this analysis, detections within Dabob Bay were removed due to the position of the bay relative to the rest of the study area (Fig. 2.1). Direction of movement was compared to all other movement metrics as well as tidal flow and direction for the entire study period.

Analyses of diel activity patterns were conducted using the Rayleigh test of uniformity for circular data (Mardia 1972). Movement data were binned by hour of the day for analysis. Sunrise and sunset times throughout the study period changed by less than 1 hr and therefore periods of daylight were defined as the elapsed time between sunrise and sunset of the shortest day (6:00 and 20:30 respectively).

Results

Sixty yearling Chinook were implanted with acoustics transmitters. However, only 58 fish were released from the hatchery because two fish were lost the night prior to release to otter predation. Of the 58 fish released into Hood Canal, 41 (70.6%) were detected during the study period and 18 fish (31%) were still being detected within the study area at the end of the study period (15 weeks). The largest decrease in number of fish detected (presumably a result of mortality because migration from the study area was known – see below) occurred in the first three weeks of the study period (Fig. 2.3). The number of fish detected continued to decrease until week 8 at which point it remained constant (~40%) until week 12. The number detected dropped over the last three weeks of the study to 29%. Fish initially detected did not differ in size from those not detected (ANOVA; $F=0.189$, $p=0.665$) nor was there a difference in size between fish that were initially detected and those that survived throughout the entire study period ($F=0.152$, $p=0.698$).

A total of 49,278 detections were recorded throughout the study period on 46 of the 48 receivers. A total of 6,928 detections (12.7%) were characterized as fish movements. Movement throughout the canal was generally diffused rather than directed (Fig 2.4). Initially, fish were detected at receivers near the release site and slowly dispersed in both directions. The number fish detected and the number of detections per unit of time decreased over the summer while the number of receivers where detections occurred increased. Likewise, the number of detections and the

number of fish detected decreased with distance from the release point (Fig 2.5). Most detections (59%) occurred on receivers within 15 km of the release site and 33% of all detections were on receivers < 7 km from the release site. The highest number of fish detected on a single receiver was 27 (66%) located 1.6 km north of the release site. Only nine fish (27%) had more than a single detection on receivers > 40 km from the release point. Fifteen fish (30%) were detected south of the release point, accounting for 11% of all detections, including each of the first 14 weeks of the study. By week 6, fish had spread throughout the entire study area and had been detected on all receivers. After week 6, fish were detected at receivers from the release point to the Hood Canal Bridge for the remainder of the study period. Through week 14 fish were still being detected at receivers south of the release site, and by the end of the study period all detections were occurring > 40 km from the release site.

Eight fish were detected at or beyond the Hood Canal bridge, but seven of these were later detected within Hood Canal. Three of the fish were detected on multiple occasions at the bridge. The majority of detections at or beyond the bridge occurred in July (72%), but fish were detected at or beyond the bridge in each month of the study period. The number of fish detected and total detections on bridge receivers was not uniform ($\chi^2=26.35$; $p < 0.001$). The receivers on the western side of the bridge had the fewest number of detections (11) and detected the fewest fish (2), whereas the receiver in the center of the bridge and those immediately east of the center had the most detections (43) and detected the most fish (6).

Greater than 60% of movement detections represented localized activity where fish were detected on the same receiver with more than 60 minutes between detections without being detected on another receiver. The mean distance between movements was 3.2 km (sd = 3.3 km) based on movements inferred from detections on different receivers. The maximum distance between detections was 30.4 km, nearly half the length of the study area. The mean distance traveled per day was 16.8 km (sd = 12.9 km), with a maximum distance per day of 50 km. The distance traveled per day by individual fish did not change significantly over the course of the study period (Kruskal-Wallis, $\chi^2 = 5.77$, $p = 0.123$). However, the distance between detections varied over time and on average was approximately 3 km for May, June, and July, whereas movements in August were significantly higher (mean = 4.5 km; Kruskal-Wallis, $\chi^2 = 18.310$, $p = 0.0003$) and the variation was much greater.

Movement rates were calculated from detections as a standardized body length per second ($\text{BL} \cdot \text{s}^{-1}$) or approximately $20 \text{ cm} \cdot \text{s}^{-1}$, based upon mean size of tagged individuals. The total number of movements per fish ranged between 6 and 243 (median = 20). The overall mean rate of movement for all fish throughout the study period was $0.86 \text{ BL} \cdot \text{sec}^{-1}$ (SD = $0.72 \text{ BL} \cdot \text{sec}^{-1}$). The mean rate of movement per fish ranged between 0.44 and $1.52 \text{ BL} \cdot \text{sec}^{-1}$, with a maximum of $2.88 \text{ BL} \cdot \text{sec}^{-1}$. Movement rates did not change significantly as the study period progressed (Kruskal-Wallis, $\chi^2 = 5.762$, $p = 0.123$).

Differences in diurnal movement behavior were small. The majority of the overall movements occurred during daylight hours (60%); however, the hourly

distribution of movements throughout the entire 24 hour period was uniform (Rayleigh's $z_{0.05,6329}=0.0046$, $p=0.875$; Fig. 2.6). The changes in diel activity across months were not significant (χ^2 ; $p=0.21$). Rate of movement ($t_{\text{stat}} = 0.22$, $p= 0.82$) and distance per movement ($t_{\text{stat}} = -1.49$, $p = 0.14$) were not statistically different for day and night periods.

Tide stage had a mixed affect on movement metrics. The proportion of movements occurring in each tide stage was not different from the proportion of time represented by each tide stage ($\chi^2 = 0.158$, $p = 0.691$). A total of 782 movements occurred during the ebb tide and 733 during the flood stage. Of the movements that occurred during the ebb tide, 471 (60%) occurred during the day. The same pattern was evident in movements during the flood tide; however, the proportion was slightly greater (535 movements; 73%). The mean movement rates for ebb and flood tide stages were 0.74 and 0.68 BL•sec⁻¹ respectively (Welch t-test, $p=0.20$). Movement direction was determined for all movements between receivers. Of the 1,515 movements that occurred within a 24 hr period, 789 (52%) were moving “in” and 726 (48%) were moving “out” of the study area. The rate of movements “Out” of the study area were significantly greater than movements “IN” during the ebb tide (Table 2.1). Movement rates in both directions during the flood and slack tide stages were not statistically different. Differences between distances per movement in both directions were statistically significant for all tide stages (Table 2.1), where mean distance per movement directed “out” of the study area were consistently higher than “in” movements.

The majority of all detections recorded throughout the study period were during periods of inactivity. Fish were considered inactive if consecutive detections were recorded within 60 min. on a single receiver. The median period of inactivity per fish was 1.25 d and ranged from 0.02 to 7.12 d. The mean time per fish spent near a specific receiver generally decreased with distance from released point (Fig 2.7). Locations of inactivity followed general dispersal trends for movements. Receivers where the greatest amount of inactivity per fish occurred were located at 8.0 km, 17.0 km, and 32.9 km from the release point. Over the entire study period, inactivity was focused around receivers within 6-17 km from the release site. More fish were inactive around receivers in this portion of Hood Canal was higher than at receivers in the remainder of the study area (mean = 19.5 vs. 6 fish). Fish settled at receivers further from the release point as the study progressed. Inactivity was limited near receivers greater than 42 km from the release site.

Discussion

Eighteen of 41 fish were still within the study area 100 days after release, indicating some level of residency for yearling Chinook salmon in Hood Canal. Analysis of coded wire tagging data from Puget Sound hatcheries indicated that about 24% of the Chinook salmon smolts released in Hood Canal were caught in recreational fisheries as residents (Chapter 1). Thus, our results are similar (31%) and even slightly higher than estimated from previous analyses of CWT data. The difference

could be the result of environmental factors not tested for or taken in to account and/or the disparity between sample sizes.

Catches of hatchery reared juvenile Chinook salmon throughout nearshore sites in Puget Sound show peaks in late May and June, approximately 30 days after release from their respective hatcheries (Duffy et al. 2005). Duffy et al. (2005) also estimated that residence times for CWT Chinook salmon released into Puget Sound ranged from 5 to 130 d, although the majority of fish resided within the area for only 10-35 d. Our results indicate that 31% of the tagged fish remained within Hood Canal for at least 100 d suggesting an increased level of residency for this particular release.

Detection data from Hood Canal suggest a significant pattern of residency, where of the 41 fish detected during the study, only 8 were detected leaving the study area, and of these, 7 were later detected back within the study area. Furthermore, none of the fish detected leaving Hood Canal were detected on the POST arrays, suggesting they did not emigrate out of Puget Sound via Admiralty Inlet or the Strait of Juan de Fuca (Fig 2.1). This behavior may not be unique to Chinook salmon, as Thorstad et al. (2007) also found similar patterns of residency for Atlantic salmon (*Salmo salar*) in a Norwegian fjord system, and that several post-smolts returned to receivers 9.5 km from the release site after being detected 37 km away.

The general displacement of fish throughout our study suggests that although fish spread away from the release point, most remained in Hood Canal throughout the summers. Fish gradually dispersed throughout the length of the canal over the entire study period, but were concentrated within 10 km of the release site for the first three

weeks of the study. In subsequent weeks, the mean distance from release point of all detections moved further away and the variation in number of fish detected at each receiver increased. While we expected to see fish move northward toward the exit of the canal, we were surprised to see continuous use of areas south of the release point, especially given the recent concern with water quality issues in this portion of Hood Canal (Palsson et al. 2008). At the end of the study period the center of fish activity had shifted considerably more north than in previous weeks, although activity was still present on several receivers near the release point. Our results were similar to results of studies in the Strait of Georgia and suggested coho and Chinook salmon may have similar periods of residency in these two inland seas (Beamish et al. 2008)Chittenden et al. 2009).

The relatively long periods of inactivity observed for fish in our study also suggests some resident behavior. If fish were undergoing a directed migration out of the study area and presumably to the ocean, we would expect to have observed very little inactivity and that most fish would be detected at a given receiver for only short periods of time (i.e., they were passing by *en route* to sea). However, all test fish remained inactive for some period of time. Specific locations of inactivity appeared to be associated with certain nearshore habitats and were not uniform across receivers, suggesting the residency behavior was specific to habitat types. Receivers with the least amount of inactivity were located in the mid channel area of the Canal, indicating fish in open water were undergoing a more directed movement. In contrast, the highest amount of inactivity occurred at receivers located 8.0, 17.0, and 32.9 km from

the release point and in areas characterized by freshwater input, a relatively protected shoreline, and shallow river or stream delta habitat. The Hamma Hamma River (17.0 km from release point) has a large, shallow delta that extends roughly 750 m from the shoreline (Fig.1). Both Stavis Bay (32.9 km) and Dewatto River (8.0 km) have similar shallow deltas. It has been suggested that differences in migration timing for salmonids could be affected by growth and physiological condition (Beamish and Mahnken 2001). Puget Sound estuaries play an important role in the early life history of salmon throughout the region by providing increased opportunity for growth and gradual transitions from freshwater to marine environments (Simenstad et al. 1981). Hood Canal has few true estuaries due to the steep bathymetry and close proximity to high gradient stream/streams, and the delta habitats likely provide the most preferable conditions for growth and physiological changes in the areas.

The mean rate of movement by fish in this study (0.86 BL s^{-1}) was similar to rates in other studies of salmonids in the region, and also to theoretical predictions. Hatchery and wild coho salmon released into the Campbell River (BC) moved at 0.31 and 0.67 BL/sec respectively (Chittenden et al. 2008). Sockeye salmon smolts in the Fraser River system traveled between 0.46 and 1.8 BL/sec (Welch et al. 2009), but moved faster in marine waters ($\sim 1.5 \text{ BL/sec}$). The vast majority of movement rates (97%) observed in our study were below 1.5 BL/sec and may be indicative of a behavior not directed toward immediate ocean migration. Ware (1978) reported that the optimal cruising speed and the optimal foraging speed are similar for pelagic fishes, and are a function of length raised to the power of 0.04. For fish in the size

range of ours, this would mean that optimal speeds may be slightly over 1 length/sec (27 cm/ s^{-1} for a fish 20 cm long). If we calculate daily travel distance from our observed movement rates, they would range from 7.7 to 26.3 km/day. The Hood Canal Bridge array is located 64 km from the release point, and fish could conceivably exit the study area in 2.4 to 8.1 days based on calculated movement rates. However, fish remained in the study area for 100+ d, again indicating a resident rather than a migratory behavior.

Tide stage and direction had no apparent affect on the proportion of movements during our study, as the total number of detected movement events during each tidal cycle (ebb, flood, low slack, and high slack) was in direct proportion to the amount of time in each tide stage during the period of study. Direction of movement was also independent of tide stage, and fish appeared to move both with and against tidal flow. These findings are different than results of similar studies on Atlantic salmon in northeastern Canada, where post-smolts tended to move out of coastal habitats on ebb tides and commonly oriented themselves against flood tide currents (Hedger et al. 2008; Lacroix and McCurdy 1996; Lacroix et al. 2004), suggesting the post-smolts adopted a highly oriented seaward migration strategy. In contrast, fish in our study displayed resident behaviors as mean movement rates during each tide cycle were nearly identical. However, we did observe that movement rates in the “out” direction were higher than rates in the “in” direction during ebb tides. This difference may have been due to some passive component of movement due to tidal currents. However, our estimates of movement rate did not include the affect of current velocity

or direction on movement rate and we cannot draw any conclusions on the actual mechanisms which may have resulted in the observed difference in rates between the “in” and “out” periods.

Diel patterns in migratory behavior were indiscernible for this particular study. Movements occurred during all hours of the day and night. Statistical tests revealed uniform distribution of movements at all hours. Fish movement metrics did not differ between day and night periods. Candy and Quinn (1999) found that adult Chinook salmon in Johnstone Strait moved faster on average during the day than during the night. However, diel patterns in fish behavior may be associated more with vertical movements as a function of predation and/or predator avoidance.

The receiver array across the extent of Hood Canal Bridge provided complete coverage of the exit point from the study area, and this enabled us to estimate survival of the tagged fish during the study period. Of the 58 tagged fish that were released, 18 were still moving and apparently alive after 115 d in Hood Canal. Our estimates of apparent survival were slightly higher than on other studies for salmon in the region. Observed mortality for juvenile coho salmon in the Strait of Georgia was estimated at nearly 90% through mid September in 2006 (Beamish et al. 2008). However, Chittenden et al. (2009) saw roughly 30% mortality in acoustic tagged coho salmon in the same region. The largest drop in survival occurred during the first week after release. Nearly 30% of tagged fish were never detected and therefore assumed to be mortalities. Effects of handling and tagging may have played a major role in this sudden loss. However, the ratio of tag weight to body weight for fish tagged in our

study was well within the recommended limits suggested by other studies on Chinook salmon smolt conducted in the lab (Hall et al. 2009).

The results of this study present significant, parallel lines of evidence that juvenile Chinook salmon released from one hatchery displayed an alternative, and “resident” migratory strategy during the early phase of the marine component of their life cycle. However, it is difficult to interpret the extent to which differences persist or the mechanism(s) that may cause the perceived differences in migratory behavior. The migratory strategies for Chinook salmon in this region likely represent a continuum of behaviors, rather than one distinct migratory pattern and are likely the product of complex interactions between individuals and their environment.

Table 2.1. Movement metrics across all tide stages and between movement directions. Welch two sample t-test was used for comparison between directions and Kruskal Wallace rank sum test for comparison across tide stage. P values in bold are significant at alpha = 0.05).

	Moves	BL/sec	Distance/move
EBB		0.744	4.25
In	277	0.688	3.824
Out	233	0.811	4.769
	<i>(p value)</i>	(0.032)	(0.04)
FLOOD		0.686	4.760
In	260	0.686	4.083
Out	233	0.686	5.531
	<i>(p value)</i>	<i>(0.494)</i>	(0.013)
SLACK		0.744	4.240
In	252	0.686	3.540
Out	260	0.800	4.929
	<i>(p value)</i>	<i>(0.077)</i>	(0.002)
total	1515	<i>(0.161)</i>	(<0.0001)

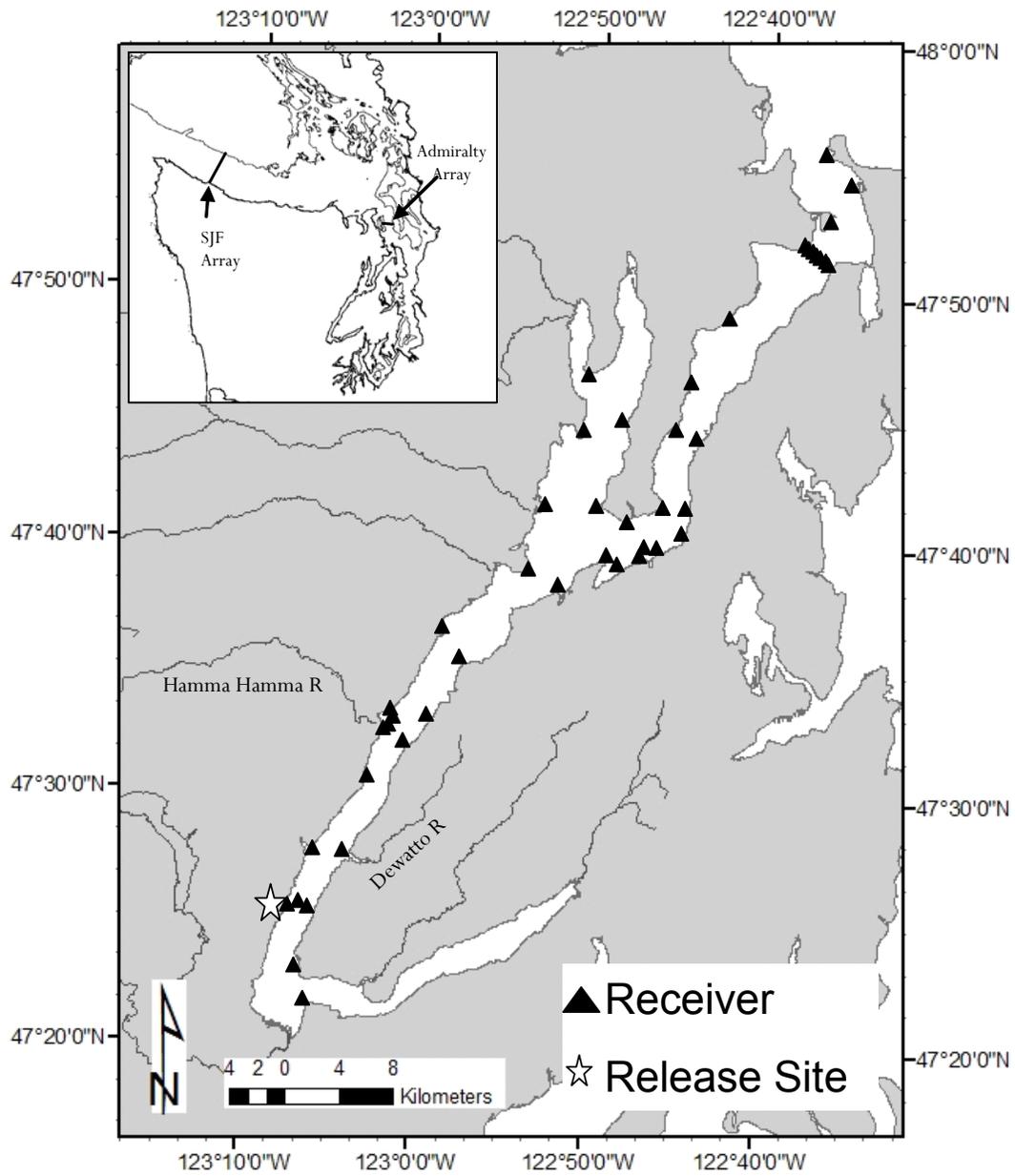


Figure 2.1. Map of Hood Canal with receiver locations and release site. Inset shows additional receiver arrays outside the study area where fish could be detected.

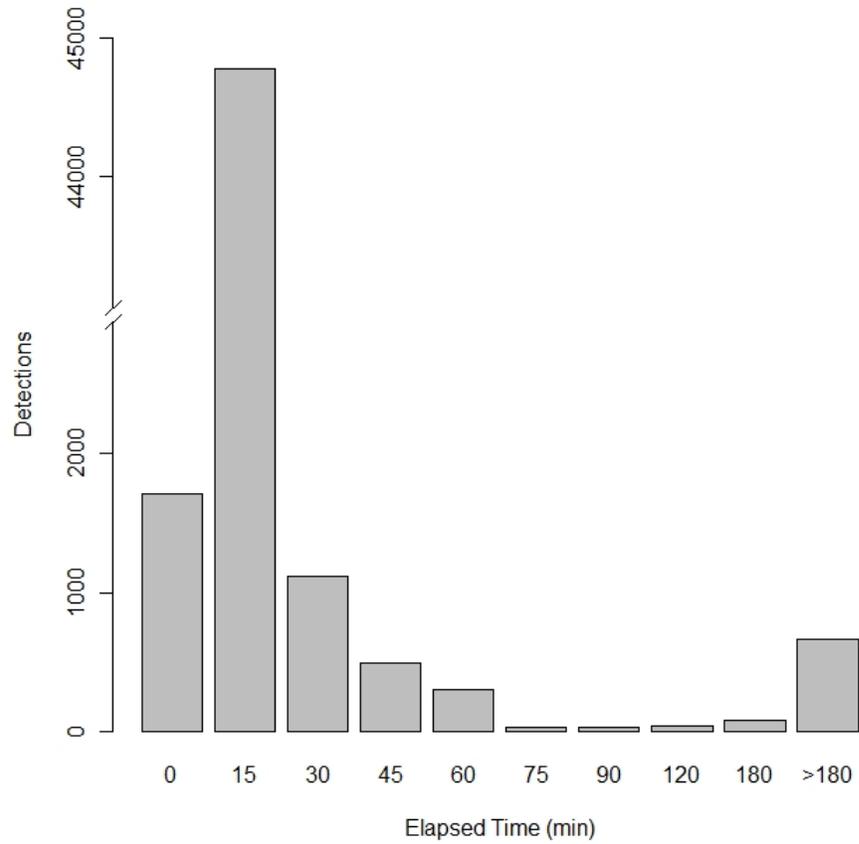


Figure 2.2. Frequency histogram used to determine “60 minute” rule for movement detections. Data are binned by elapsed time between consecutive detections. Data are represented on broken y-axis for visualization.

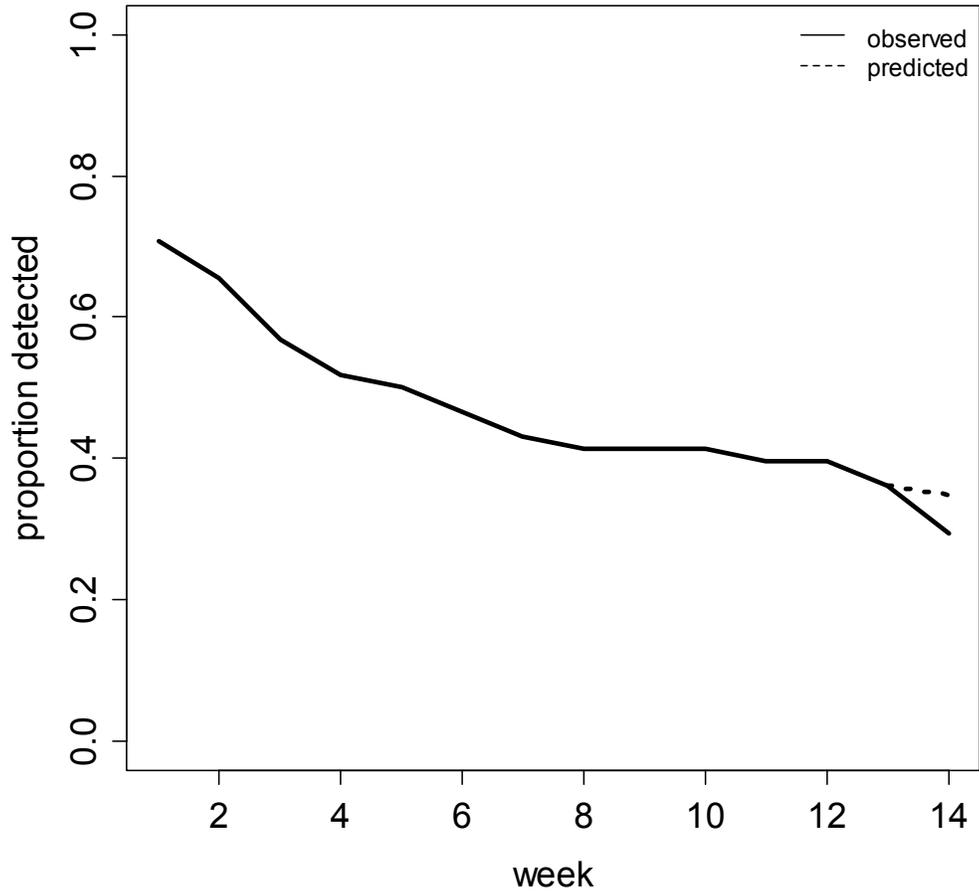


Figure 2.3. Proportion of fish detected by week throughout the study period. Solid line represents observed survival. Dashed line indicates predicted survival based upon detection efficiency throughout the entire study.

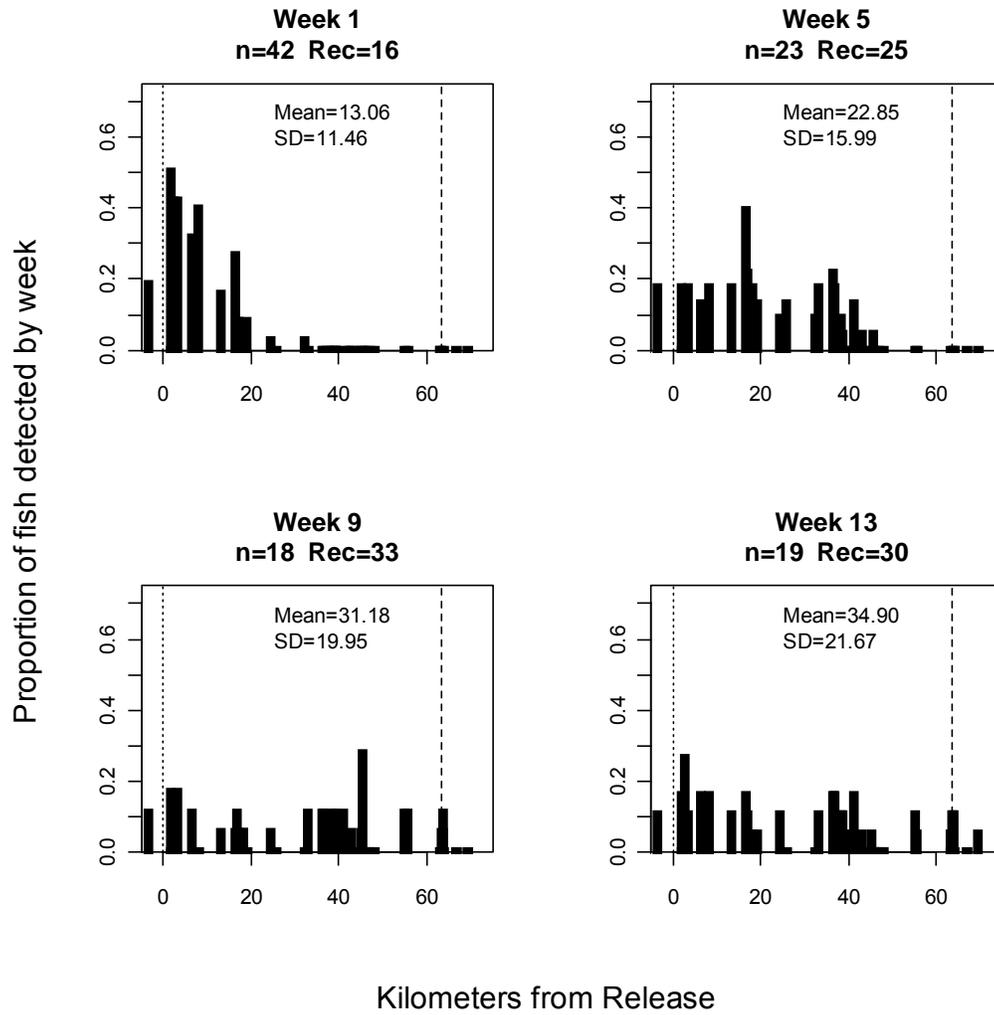


Figure 2.4. Weekly displacement of fish throughout the study period. Dotted line represent release point and dashed line represents receiver array at Hood Canal Bridge.

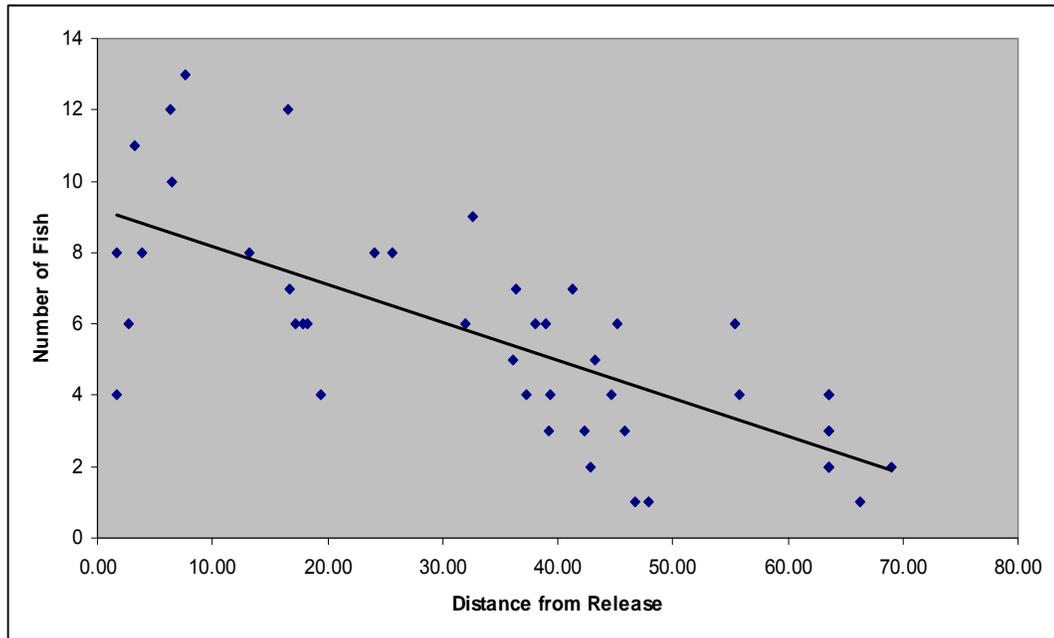


Figure 2.5. Relationship between distance from release point and the number of fish detected at specific receivers.

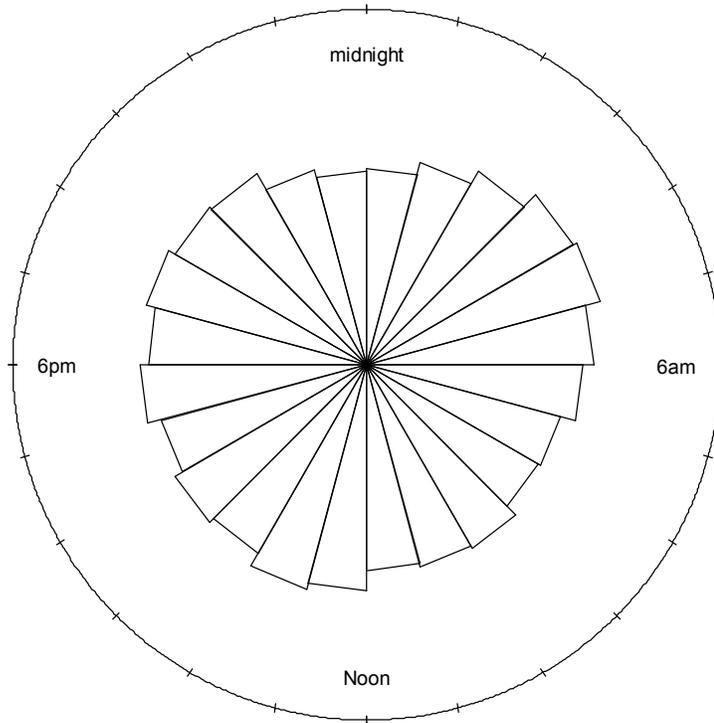


Figure 2.6. Circular histogram for time of day when fish movements occurred. Data are for all fish movements throughout the study period. Rayleigh test of uniformity (Rayleigh's $Z_{0.05,6329}=0.0046$, $p=0.875$).

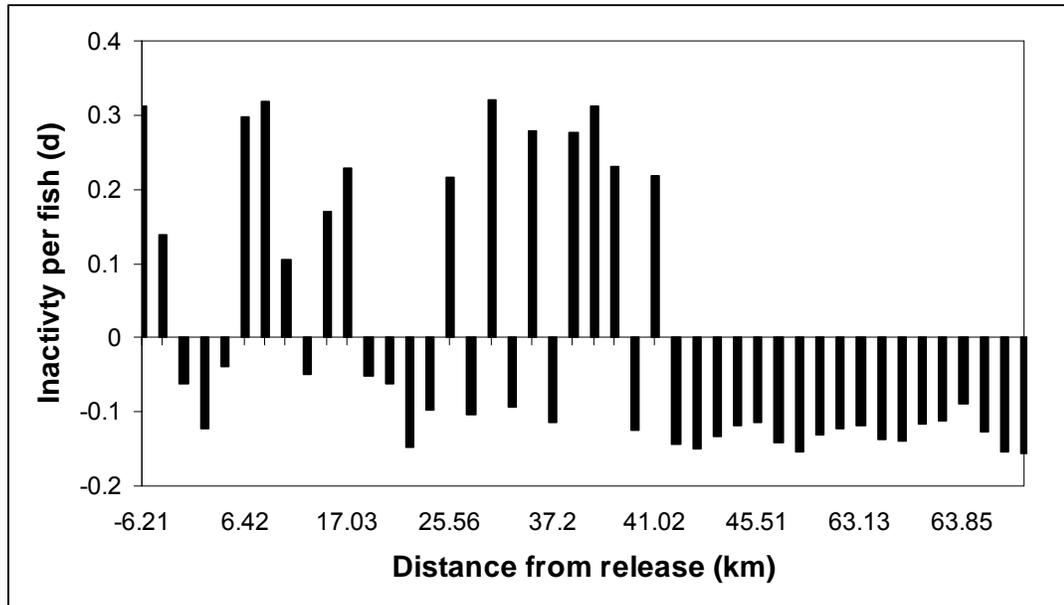


Figure 2.7. Periods of inactivity per fish for specific receivers located throughout the study area. Receivers are arranged by distance from release point. Data are normalized to the mean period of inactivity per fish for all receivers.

General Conclusions

The results of this study present several lines of evidence that support the existence of resident-type Chinook salmon in Puget Sound. This work has described the influence of several factors upon a resident-type migration strategy and evaluated the specific movement behaviors of such individuals.

The coded wire tag analysis revealed a clearly significant effect of the geographic region where fish enter the marine environment upon the proportion of fish from a particular release group that remained resident. Puget Sound is a highly complex and highly variable environment. Our results indicate that certain areas within the basin may be more suitable as fish habitat than others and that certain physical habitat characteristics may encourage fish to employ an alternative migration strategy. Furthermore, the size of a particular fish upon entry into marine waters also affected residency though the magnitude of the effect was not constant among regions. Identifying factors that potentially promote a resident-type strategy for Chinook salmon could be informative for future management decisions regarding Puget Sound fisheries.

The results from the telemetry research provided evidence across several metrics that much of the observed behavior within a particular region was indicative of a resident fish. Fish moved considerably slower than other migratory species, consistently moved against tidal currents, were inactive for significant periods of time in particular habitats, and remained in the study area for >100 days after release. Understanding behavior during the early marine migratory period is crucial for salmon

recovery and identifying critical habitat and could provide useful information for restoration efforts.

While this work has identified factors related to a resident migration and the specific behaviors associated with such a strategy, it is important to note that the relationship between resident and migrant is not clearly defined. Instead, it should be represented as a continuum of behaviors and strategies that are likely the result of several complex interactions at the individual (genetic) and environmental (physical habitat) levels and that further research is needed to completely understand the specific mechanism(s).

References

- Adlerstein, S. A., E. S. Rutherford, D. Clapp, J. A. Clevenger, and J. E. Johnson. 2007. Estimating seasonal movements of Chinook salmon in Lake Huron from efficiency analysis of coded wire tag recoveries in recreational fisheries. *North American Journal of Fisheries Management* 27(3):792-803.
- Andrews, K. S., P. S. Levin, S. L. Katz, D. Farrer, V. F. Gallucci, and G. Bargmann. 2007. Acoustic monitoring of sixgill shark movements in Puget Sound: evidence for localized movement. *Canadian Journal of Zoology* 85(11):1136-1142.
- Appleby, A. E., and D. C. Doty. 1995. Status and trends in the survival and distribution of resident coho and Chinook salmon in Puget Sound, Washington. Washington Department of Fish and Wildlife.
- Babson, A. L., M. Kawase, and P. MacCready. 2005. Seasonal and interannual variability in the circulation of Puget Sound: a box model study. *Atmosphere and Ocean* 44:29-45.
- Bates, D., M. Maechler, and B. Dai. 2008. lme4: Linear mixed-effects models using Eigen and S4 classes.
- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49(1-4):423-437.
- Beamish, R. J., R. M. Sweeting, K. L. Lange, and C. M. Neville. 2008. Changes in the population ecology of hatchery and wild coho salmon in the Strait of Georgia. *Transactions of the American Fisheries Society* 137(2):503-520.
- Beckman, B. R., D. A. Larsen, B. Lee-Pawlak, and W. W. Dickhoff. 1998. Relation of fish size and growth rate to migration of spring Chinook salmon smolts. *North American Journal of Fisheries Management* 18:537-546.
- Beechie, T., E. Buhle, M. Ruckleshaus, A. Fullerton, and L. Holsinger. 2006. Hydrologic regime and the conservation of salmon life history diversity. *Biological Conservation* 130:560-572.
- Brannon, E. L., M. S. Powell, T. P. Quinn, and A. Talbot. 2004. Population structure of Columbia River basin Chinook salmon and steelhead trout. *Reviews in Fisheries Science* 12:99-232.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference : a practical information-theoretic approach. Springer, New York.
- Candy, J. R., and T. P. Quinn. 1999. Behavior of adult chinook salmon (*Oncorhynchus tshawytscha*) in British Columbia coastal waters determined from ultrasonic telemetry. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 77(7):1161-1169.

- Chittenden, C., K. Butterworth, K. Cubitt, M. Jacobs, A. Ladouceur, D. Welch, and R. McKinley. 2009. Maximum tag to body size ratios for an endangered coho salmon (*O.kisutch*) stock based on physiology and performance. *Environmental Biology of Fishes* 84(1):129-140.
- Chittenden, C. M., S. Sura, K. G. Butterworth, K. F. Cubitt, N. P. Manel-La, S. Balfry, F. Okland, and R. S. McKinley. 2008. Riverine, estuarine and marine migratory behaviour and physiology of wild and hatchery-reared coho salmon *Oncorhynchus kisutch* (Walbaum) smolts descending the Campbell River, BC, Canada. *Journal of Fish Biology* 72(3):614-628.
- Clarke, W. C., R. E. Withler, and J. E. Shelbourn. 1992. Genetic control of juvenile life history pattern in Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 49:2300-2306.
- Clarke, W. C., R. E. Withler, and J. E. Shelbourn. 1994. Inheritance of smolting phenotypes in backcrosses of hybrid stream x ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). *Estuaries* 17:13-25.
- Cormack, R. M., and J. R. Skalski. 1992. Analysis of coded wire tag returns from commercial catches. *Canadian Journal of Fisheries and Aquatic Sciences* 49(9):1816-1825.
- Dewar, H., P. Mous, M. Domeier, A. Muljadi, J. Pet, and J. Whitty. 2008. Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. *Marine Biology* 155(2):121-133.
- Dingle, H. 1996. *Migration: The Biology of Life on the Move*. Oxford University Press, Oxford (United Kingdom).
- Dingle, H., and V. A. Drake. 2007. What Is Migration? *BioScience*. 57(2):113-122.
- Drake, V. A., A.G. Gatehouse, and R. A. Farrow. 1995. Insect migration: A holistic conceptual model. Pages 427-457 in V.A. Drake, and A. G. Gatehouse, editors. *Insect migration: tracking resources through space and time*. Cambridge University Press, Cambridge, United Kingdom.
- Duffy, E. J., D. A. Beauchamp, and R. M. Buckley. 2005. Early marine life history of juvenile Pacific salmon in two regions of Puget Sound. *Estuarine Coastal and Shelf Science* 64(1):94-107.
- Emmett, R. L., G. K. Krutzikowsky, and P. Bentley. 2006. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998-2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids. *Progress in Oceanography* 68:1-26.
- Ewing, R. D., C. E. Hart, C. A. Fustish, and G. Concannon. 1984. Effects of size and time of release on seaward migration of spring Chinook salmon, *Oncorhynchus tshawytscha*. *Fishery Bulletin* 82(1):157-164.
- Faraway, J. J. 2006. *Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models*. Chapman and Hall/CRC, Boca Raton, FL.
- Giorgi, A. E., T. W. Hillman, J. R. Stevenson, S. G. Hays, and C. M. Peven. 1997. Factors that influence the downstream migration rates of juvenile salmon and

- steelhead through the hydroelectric system in the mid-Columbia River basin. *North American Journal of Fisheries Management* 17:268-282.
- Greene, C. M., and T. J. Beechie. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 61(4):590-602.
- Greene, C. M., D. W. Jensen, G. R. Pess, E. A. Steele, and E. Beamer. 2005. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates in the Skagit River, Washington. *Transactions of the American Fisheries Society* 134:1562-1581.
- Groot, C., and L. Margolis. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver.
- Hall, J. E., J. Chamberlin, A. N. Kagley, C. Greene, and K. L. Fresh. 2009. Effects of gastric and surgical insertions of dummy ultrasonic transmitters on juvenile Chinook salmon in seawater. *Transactions of the American Fisheries Society* 138(1):52-57.
- Harden Jones, F. R. 1968. Fish migration. St. Martin's Press, New York.
- Hartt, A. C., M. B. Dell, and C. International North Pacific Fisheries. 1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. International North Pacific Fisheries Commission, Vancouver.
- Haw, F., H. O. Wendler, and G. Deschamps. 1967. Development of Washington state salmon sport fishery through 1964. Washington Department of Fisheries, Research Bulletin 7.
- Healey, M. C. 1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type Chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Field-Naturalist* 97(4):427-433.
- Healey, M. C. 1991. Life history of Chinook salmon: *Oncorhynchus tshawytscha*. C. Groot, and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver, BC.
- Hedger, R. D., F. Martin, D. Hatin, F. Caron, F. G. Whoriskey, and J. J. Dodson. 2008. Active migration of wild Atlantic salmon *Salmo salar* smolt through a coastal embayment. *Marine Ecology-Progress Series* 355:235-246.
- Jefferts, K. B., P. K. Bergman, and H. F. Fiscus. 1963. A coded wire identification system for macro-organisms. *Nature* 198:460-462.
- Johnson, J. K. 1990. Regional overview of coded-wire tagging of anadromous salmon and steelhead in northwest America. *American Fisheries Society Symposium* 7:782-816.
- Jonsson, B., and N. Jonsson. 1993. PARTIAL MIGRATION - NICHE SHIFT VERSUS SEXUAL-MATURATION IN FISHES. *Reviews in Fish Biology and Fisheries* 3(4):348-365.
- Jutila, E., E. Jokikokko, I. Kallio-Nyberg, I. Saloniemi, and P. Pasanen. 2003. Differences in sea migration between wild and reared Atlantic salmon (*Salmo salar L.*) in the Baltic Sea. *Fisheries Research* 60(2-3):333-343.

- Kallio-Nyberg, I., E. Jutila, I. Saloniemi, and E. Jokikokko. 2004. Association between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simojoki River in the Baltic Sea. *Journal of Fish Biology* 65(1):122-134.
- Kallio-Nyberg, I., M. L. Koljonen, and I. Saloniemi. 2000. Effect of maternal and paternal line on spatial and temporal marine distribution in Atlantic salmon. *Animal Behaviour* 60:377-384.
- Kallio-Nyberg, I., H. Peltonen, and H. Rita. 1999. Effects of stock-specific and environmental factors on the feeding migration of Atlantic salmon (*Salmo salar*) in the Baltic Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 56(5):853-861.
- Kallio-Nyberg, I., I. Saloniemi, E. Jutila, and A. Saura. 2007. Effects of marine conditions, fishing, and smolt traits on the survival of tagged, hatchery-reared sea trout (*Salmo trutta trutta*) in the Baltic Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 64(9):1183-1198.
- Lacroix, G. L. 2008. Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the Bay of Fundy, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 65(9):2063-2079.
- Lacroix, G. L., and D. Knox. 2005. Distribution of Atlantic salmon (*Salmo salar*) postsmolts of different origins in the Bay of Fundy and Gulf of Maine and evaluation of factors affecting migration, growth, and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 62(6):1363-1376.
- Lacroix, G. L., and P. McCurdy. 1996. Migratory behaviour of post-smolt Atlantic salmon during initial stages of seaward migration. *Journal of Fish Biology* 49(6):1086-1101.
- Lacroix, G. L., P. McCurdy, and D. Knox. 2004. Migration of Atlantic salmon postsmolts in relation to habitat use in a coastal system. *Transactions of the American Fisheries Society* 133(6):1455-1471.
- Leggett, W. C. 1977. The ecology of fish migrations. *Annual Review of Ecology and Systematics* 8:285-308.
- Lucas, M. C., and E. Baras. 2001. *Migration of freshwater fishes*. Blackwell Science, Oxford; Malden, MA.
- MacCall, A. D. 1990. *Dynamic geography of marine fish populations*. Washington Sea Grant Program : Distributed by University of Washington Press, Seattle.
- Mardia, K. V. 1972. *Statistics of directional data*. Academic Press, London; New York.
- Massicotte, R., P. Magnan, and B. Angers. 2008. Intralacustrine site fidelity and nonrandom mating in the littoral-spawning northern redbelly dace (*Phoxinus eos*). *Canadian Journal of Fisheries and Aquatic Sciences* 65(9):2016-2025.
- McCullagh, P., and J. Nedler. 1989. *Generalized linear models* (2 ed.). London: Chapman & Hall.
- McMahon, T. E., and L. B. Holtby. 1992. Behavior, habitat use, and movements of coho salmon (*Oncorhynchus kisutch*) smolts during seaward migration. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1478-1485.

- Melnychuk, M. C., D. W. Welch, C. J. Walters, and V. Christensen. 2007. Riverine and early ocean migration and mortality patterns of juvenile steelhead trout (*Oncorhynchus mykiss*) from the Cheakamus River, British Columbia. Pages 55-65 in.
- Mitamura, H., K. Uchida, Y. Miyamoto, N. Arai, T. Kakihara, T. Yokota, J. Okuyama, Y. Kawabata, and T. Yasuda. 2009. Preliminary study on homing, site fidelity, and diel movement of black rockfish *Sebastes inermis* measured by acoustic telemetry. *Fisheries Science* 75(5):1133-1140.
- Mofjeld, H. O., and L. H. Larsen. 1984. Tides and tidal currents of the inland waters of western Washington. NOAA Technical Memorandum, ERL PMEL-56, Seattle, WA.
- Moring, J. R. 1976. Contributions of delayed-release, pen-cultured Chinook salmon to the sport fishery in Puget Sound, Washington. *The Progressive Fish Culturist* 38(1):36-39.
- Myers, J. M., R. G. Cope, G. J. Bryant, D. Teel, L. J. Lierheimer, T. C. Wainwright, W. S. Grant, F. W. Waknitz, K. Neely, S. T. Linley, and R. S. Waples. 1998. Status review of Chinook salmon from Washington, Idaho, Oregon and California. . National Oceanic and Atmospheric Administration, National Marine Fisheries Service, NMFS-NWFSC-35, Seattle, WA.
- Nedler, J. A., and R. Wedderburn. 1972. Generalized linear models. *Journal of the Royal Statistical Society Series a-General* 135(3):370-384.
- Northcote, T. G. 1978. Migratory strategies and production in freshwater fishes. Blackwell Scientific Publications, Oxford, London, etc.
- Orsi, J. A., and H. W. Jaenicke. 1996. Marine distribution and origin of prerecruit Chinook salmon, *Oncorhynchus tshawytscha*, in southeastern Alaska. *Fishery Bulletin* 94(3):482-497.
- Palsson, W. A., R. E. Pacunski, T. R. Parra, and J. Beam. 2008. The effects of hypoxia on marine fish populations in southern Hood Canal, Washington. Pages 255-280 in K. D. McLaughlin, editor. American Fisheries Society Symposium. Amer Fisheries Soc.
- Pascual, M. A. 1993. The estimation of salmon population parameters from coded wire tag data.
- Pearcy, W. G., and J. P. Fisher. 1988. Migrations of coho salmon, *Oncorhynchus kisutch*, during their 1st summer in the ocean. *Fishery Bulletin* 86(2):173-195.
- Pressey, R. T. 1953. The sport fishery for salmon on Puget Sound. Washington Department of Fisheries, Fisheries Research Papers 1:33-48.
- Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. American Fisheries Society, Bethesda, Md.
- Quinn, T. P., and R. D. Brodeur. 1991. Intra-specific variations in the movement patterns of marine animals. *American Zoologist* 31(1):231-241.
- Quinn, T. P., B. R. Dickerson, and L. A. Vollestad. 2005. Marine survival and distribution patterns of two Puget Sound hatchery populations of coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) salmon. *Fisheries Research* 76:209-220.

- Quinn, T. P., M. T. Kinnison, and M. J. Unwin. 2001. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* 112/113:493-513.
- Quinn, T. P., and K. W. Myers. 2004. Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. *Reviews in Fish Biology and Fisheries* 14(4):421-442.
- Quinn, T. P., B. A. Terhart, and C. Groot. 1989. Migratory orientation and vertical movements of homing adult sockeye salmon, *Oncorhynchus nerka*, in coastal waters. *Animal Behaviour* 37:587-599.
- Quinn, T. P., L. A. Vollestad, J. Peterson, and V. Gallucci. 2004. Influences of fresh water and marine growth on the egg size-egg number tradeoff in coho and Chinook salmon. *Transactions of the American Fisheries Society* 133:55-65.
- Ramenofsky, M., R. Agatsuma, and T. Ramfar. 2008. Environmental conditions affect the behavior of captive, migratory white-crowned sparrows. *Condor* 110(4):658-671.
- Ramenofsky, M., and J. C. Wingfield. 2007. Regulation of migration. *Bioscience* 57(2):135-143.
- Rensel, J. E., R. P. Harris, and T. J. Tynan. 1988. Fishery contribution and spawning escapement of coho salmon in net-pens in southern Puget Sound, Washington. *North American Journal of Fisheries Management* 8:359-366.
- Rice, C. A. 2007. Evaluating the biological condition of Puget Sound. Ph.D Dissertation. University of Washington, Seattle.
- Rooker, J. R., D. H. Secor, G. De Metro, R. Schloesser, B. A. Block, and J. D. Neilson. 2008. Natal Homing and Connectivity in Atlantic Bluefin Tuna Populations. *Science* 322(5902):742-744.
- Saloniemi, I., E. Jokikokko, I. Kallio-Nyberg, E. Jutila, and P. Pasanen. 2004. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. *ICES Journal of Marine Science* 61(5):782-787.
- Secor, D. H. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fisheries Research* 43(1-3):13-34.
- Sharma, R. 2009. Investigating relationships between the environment, recruitment, survival, maturation and distribution of Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*), and its implications on management. Ph.D Dissertation. University of Washington, Seattle.
- Simenstad, C. A., K. L. Fresh, and E. O. Salo. 1981. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon - an unappreciated function. *Estuaries* 4(3):285-286.
- Taylor, E. B. 1989. Precocial male maturation in laboratory-reared populations of Chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Journal of Zoology* 67:1665-1669.
- Taylor, E. B. 1990. Environmental correlates of life-history variation in juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *Journal of Fish Biology* 37:1-17.

- Thorstad, E. B., F. Okland, B. Finstad, R. Sivertsgard, N. Plantalech, P. A. Bjorn, and R. S. McKinley. 2007. Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. *Hydrobiologia*:99-107.
- Van Doornik, D. M., D. J. Teel, D. R. Kuligowski, C. A. Morgan, and E. Casillas. 2007. Genetic analyses provide insight into the early ocean stock distribution and survival of juvenile coho salmon off the coasts of Washington and Oregon. *North American Journal of Fisheries Management* 27(1):220-237.
- Venables, W. N., and C. M. Dichmont. 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries Research* 70(2-3):319-337.
- Vollestad, L. A., J. Peterson, and T. P. Quinn. 2004. Effects of fresh water and marine growth rates on early maturity in male coho and Chinook salmon. *Transactions of the American Fisheries Society* 133:495-503.
- Waples, R. S., D. J. Teel, J. M. Myers, and A. R. Marshall. 2004. Life-history divergence in Chinook salmon: historic contingency and parallel evolution. *Evolution* 58:386-403.
- Ware, D. M. 1978. Bioenergetics of pelagic fish - theoretical change in swimming speed and ration with body size. *Journal of the Fisheries Research Board of Canada* 35(2):220-228.
- Weitkamp, L., and K. Neely. 2002. Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. *Canadian Journal of Fisheries and Aquatic Sciences* 59(7):1100-1115.
- Welch, D. W., G. W. Boehlert, and B. R. Ward. 2002. POST - the Pacific Ocean salmon tracking project. *Oceanologica Acta* 25(5):243-253.
- Welch, D. W., M. C. Melnychuk, E. R. Rechisky, A. D. Porter, M. C. Jacobs, A. Ladouceur, R. S. McKinley, and G. D. Jackson. 2009. Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. *Canadian Journal of Fisheries and Aquatic Sciences* 66(5):736-750.
- Zydlewski, G. B., J. Zydlewski, and J. Johnson. 2009. Patterns of migration and residency in coastal cutthroat trout *Oncorhynchus clarkii clarkii* from two tributaries of the lower Columbia River. *Journal of Fish Biology* 75(1):203-222.