MIGRATION AND SURVIVAL OF JUVENILE SPRING CHINOOK AND SOCKEYE SALMON DETERMINED BY A LARGE-SCALE TELEMETRY ARRAY

by

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Abstract

This thesis documents the use a large-scale acoustic telemetry array to track hatchery-reared salmon smolts during their seaward migration, presents estimates of early marine survival, and describes migration behaviour in the ocean of two species of Pacific salmon from the Columbia and Fraser River basins.

In the Columbia River basin, it is hypothesized that seaward migrating Snake River spring Chinook salmon suffer from “delayed mortality” due to passage through eight hydropower dams or “differential delayed mortality” from transportation via barge around the dams. I tested these hypotheses by comparing survival of in-river migrating smolts from the Snake River basin to 1) a Yakima River population that migrated past only four dams and 2) a Snake River group that was transported around all dams. Early marine survival estimates of non-transported Snake and Yakima smolts from the mouth of the Columbia River to Vancouver Island (a 485 km, one month journey) was equal in both 2006 and 2008 (2007 estimates were not available), which contradicts the delayed mortality theory. Early marine survival for the transported groups was slightly higher than for the in-river migrants, again contradicting the differential delayed mortality theory. These measurements form the first direct experimental test of key theories concerning juvenile fish survival in the coastal ocean.

Cultus Lake sockeye salmon are a genetically unique population from the Fraser River basin and are now endangered due to the very low return of adults in recent years. Mean survivorship of smolts (2004-7) from release to the northern Strait of Georgia ranged from 10-50%, while survivorship to the final sub-array in Queen Charlotte Strait ranged from 7-28%. Cultus Lake smolts displayed four migratory behaviours: northward migration to enter the Pacific Ocean via Queen Charlotte Strait; westward migration through the Strait of Juan de Fuca; migration into Howe Sound before continued the migration north; and migration upstream into Cultus Lake. These are the first direct observations of movement and survival for Fraser River sockeye salmon smolts. The availability of early marine survival data fills key knowledge gaps and as well as permitting direct testing of important salmon conservation hypotheses and rapid scientific advance.

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Dale Webber from Vemco informed me of the POST project when it was at its infancy. I think I thank Dale for encouraging me to relocate from the Bahamas to Canada.

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Dedication

In memory of my beloved Grandmother, Marion McGilvray
You will be missed.

Co-authorship Statement

For the duration of my PhD program I worked with David Welch, who appears as second author for Chapters 2-5 (Columbia River spring Chinook salmon survival). Dr. Welch had envisioned an experiment to test delayed mortality hypotheses of Snake River spring Chinook salmon in the Columbia River basin using the POST array. For several years we worked to make the experimental design successful. Specifically, for Chapters 2-5, I identified the appropriate spring Chinook salmon populations to be used in the analyses, I coordinated with state and tribal fishery agencies in the U.S. on smolt transfer, holding and tagging logistics, I performed the research, tagged salmon smolts, deployed and recovered some of telemetry equipment, analyzed the data, and prepared the manuscripts.

Chapter 6 (survival and migration of Cultus Lake sockeye salmon) was truly a collaborative effort involving Kintama Research staff, particularly Aswea Porter and David Welch, and my previous lab-mate Mike Melnychuk, who's Ph.D. research at UBC focused on survival of Fraser and Squamish river salmon smolts. For the duration of the study (2004-7) I contributed to design of the research program, fish tagging, equipment deployment and recovery, mobile tracking in Cultus Lake and the Vedder and Fraser rivers, data analysis, and preparation of the manuscript.

1 General Introduction

1.1 Conservation of depleted species

As the human population swells and the need for and exploitation of natural resources continues to increase, our "ecological footprint" (Wackernagel and Rees 1996) continues to expand. Human activities and development have altered much of the landscape, and have encroached upon freshwater and marine environments as well. As a result, many species and populations of plants and animals, both terrestrial and aquatic, have been severely negatively impacted and are greatly depleted relative to historical levels. In Canada and the United States, wildlife are protected by the federal government under the Species at Risk Act (SARA), or the Endangered Species Act (ESA), respectively. Both of these acts are charged with identifying, protecting, recovering, and managing endangered or threatened species. Population monitoring is an integral part of developing recovery strategies and determining critical habitats. These assessments provide the best available science to resource managers.

Pacific salmon are highly migratory and utilize freshwater rivers, streams and lakes to spawn and rear, as well as estuarine and marine habitats to forage and mature before returning to the their natal streams. The anadromous life history of Pacific salmonids makes them particularly vulnerable because they rely on a wide spectrum of habitats for survival, and these habitats, in most cases, have been significantly altered. Rivers and streams have been physically disturbed by the development of roads, infrastructure, dams, and irrigation channels. These physical changes alter water levels, water flow and may affect habitats upstream and downstream of the disturbance (Mallik and Richardson 2009). They have been chemically altered by point source and non point source pollution. Even the vast oceans have been affected by human activity; increasing global demand for fossil fuels has lead to increased atmospheric carbon dioxide and sea surface temperatures that could have major direct and indirect effects on salmon populations of the Pacific Northwest (Ashley 2006).

1.2 *Marine survival of juvenile salmonids*

Substantial mortality occurs during the 2-3 year marine life history stage of migratory salmonids (Bradford 1995). The estimated proportion of total integrated mortality is significantly higher in the ocean when compared to mortality during the juvenile outmigration or the adult migration upstream for spring Chinook salmon *Oncorhynchus tshawytscha* (also called yearling or stream-type) from the Columbia River basin (Buchanan et al. 2007, Figure 1.1). Much of this mortality occurs soon after ocean entry (Pearcy 1992), and a second phase of juvenile mortality may occur several months later if smolts do not attain favourable size during their first summer in the ocean (Beamish and Mahnken 2001). Mortality in the ocean is driven largely by predation, while size at ocean entry (larger smolts generally have higher survival), timing of ocean entry, and rearing history (wild fish tend to return at higher rates than hatchery raised) are all factors that contribute to variation in juvenile mortality rates (Quinn et al. 2002).

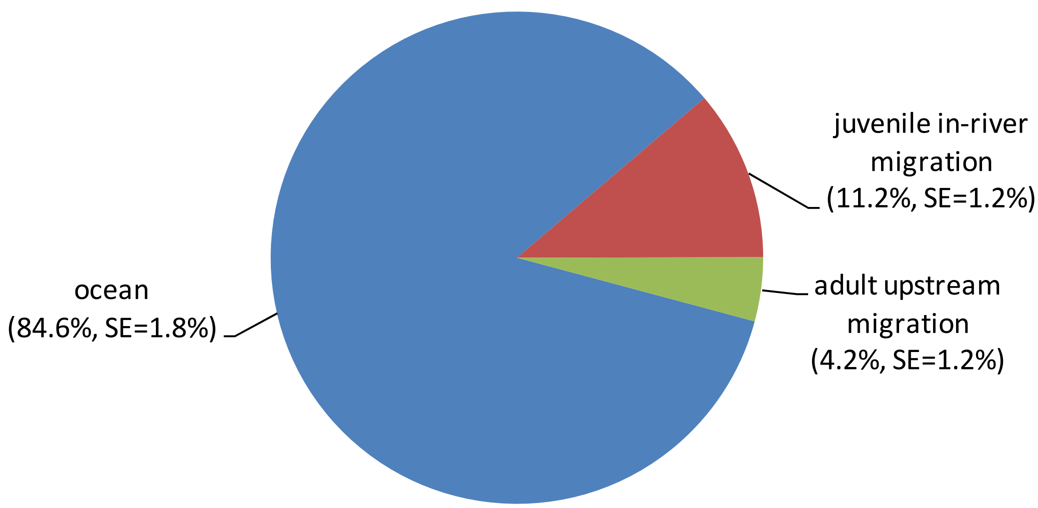

Figure 1.1. The estimated proportion of total integrated mortality accounted for by the juvenile in-river migration, ocean life stages and adult upstream migration for spring Chinook from the Clearwater River (Columbia River Basin, USA), 1999 to 2003 with standard error (SE). From Buchannan et al. 2007.

Changes in ocean and atmospheric conditions also have profound effects on salmon production in the Pacific basin. Long-term data sets of ocean climate conditions, including sea surface temperature, show fluctuations that occur on decadal or interdecadal timescales. These fluctuations correlate with trends in Pacific salmon productivity (Mantua et al. 1997; Welch et al. 1998) as well as zooplankton species distribution and abundance (Mackas et al. 2007). Interspecific competition for these food resources may be an important factor affecting salmon populations (Ruggerone and Nielsen 2004), therefore resource availability influenced by ocean climate likely determines early marine growth and success of salmon smolts after ocean entry.

Although there are reliable estimates of adult return rates for many populations of Pacific salmon, it has not been possible to partition marine survival into specific life history stages. Despite the extensive amount of research that has been conducted on the early marine life history of juvenile salmonids around the Pacific Rim region (Symons 2003) data on survival, fine-scale ocean distribution and behaviour after seaward migration from their rivers is largely lacking. Most often, survival is determined from the ratio of tagged smolts to returning adults; however, this measure of survival incorporates juvenile freshwater survival during downstream migration, juvenile marine survival, immature and adult survival.

Most of what is known about ocean migration and distribution during the early marine life history of juvenile salmon originating from North America is based on tag returns during labor intensive inshore and offshore trawl or seine surveys (Beamish et al. 2000; Brodeur et al. 2004; e.g., Hartt and Dell 1986; Meyers et al. 1996). Tags returns from juveniles offer a snapshot of the migration patterns. Catches during large scale sampling studies in the Pacific Northwest have suggested that most juvenile salmon remain on or near the continental shelf during their northward migration. Such information has been used to reconstruct migration routes and ocean distribution of juvenile salmon subsequent to their entry into seawater (French et al. 1976; Groot and Cooke 1987; Hartt and Dell 1986; Walter et al. 1997).

Advances in tagging and telemetry technology have allowed direct observation of juvenile salmon during their seaward migration. These observations are valuable and necessary, but often stop at the river mouth due to logistic constraints. For example, Schreck et al. (2006) used radio telemetry to estimate freshwater and estuarine components of survival of juvenile salmon smolts during their seaward migration; however; radio signals attenuate in deep or higher saline waters, and therefore radio tracking fish in the open ocean is not possible. In recent years acoustic transmitters have become compact enough to enable tagging of small marine animals (Voegeli et al. 1998), as well as many juvenile fish species including juvenile salmonids, and underwater automated acoustic receivers have become commercial available. These advances in acoustic tracking make it potentially possible to partition marine survival into specific marine life history phases, or regions, after seaward migration from natal rivers. Quantifying early marine survival with acoustic technology is just one of the technological methods that may have large implications for the future sustainability of Pacific salmon (Knudsen and Doyle 2006).

1.3 Threatened salmon in the Pacific Northwest

Many populations of Pacific salmon are in decline, or have declined to extirpation, particularly in southern regions of their range (Gresh et al. 2000). The next two sections provide a brief history of the decline of the two populations studied in this thesis.

1.4 Spring Chinook salmon, Snake River basin, USA

Hydropower development in the Columbia River began in the 1930s, and by 1975 eight major dams extended from the confluence of the Clearwater and Snake rivers to the lower Columbia River (and many more were constructed in the upper reaches of the Snake and Columbia). Coincident with the completion of the dams, there was substantial loss of habitat, increased hatchery production, and a period of poor ocean conditions. In the mid-1970s the number of adult spring Chinook salmon (who's progeny migrate to sea after rearing for more than one year in freshwater) returning to the Snake River decreased dramatically (Schaller et al. 1999), and in 1992 the Snake River spring/summer Chinook salmon evolutionarily significant unit (ESU), a distinct population of Chinook salmon, was listed as "threatened" under the U.S. Endangered Species Act despite two decades of fish passage improvements and mitigation programs intended to improve survival.

Although other factors have affected salmon survival, the level of impact of hydropower development on the survival of juvenile salmon has been, and remains, a contentious issue. To assess the impact of the dams the U.S. National Marine Fisheries Service (NMFS) created the Plan for Analyzing and Testing Hypotheses (PATH) in 1995, which recruited a multi-agency panel of approximately 30 scientists intended to provide information on the impact of the Federal

Columbia River Power System (FCRPS) on juvenile salmon survival. Their findings however, were not consistent with the findings from NMFS biologists working independently of PATH.

Scientists from the NMFS Northwest Fisheries Science Center concluded that variability in ocean climate caused regional differences in productivity (Levin 2003) and even if the dams were breached and 100% of the juvenile fish survived to reproduce, the declining trend would continue if restoration efforts were focused only in freshwater (Kareiva et al. 2000). PATH scientists such as Petrosky et al. (2001) ruled out the freshwater spawning and rearing stage as a source of decreased survival and Deriso et al. (2001) found that recruitment decreased as a result of dam passage. Peters and Marmorek (2001) reported modeling framework and decision analysis models which showed that the drawdown of the four Snake River dams was the most robust action in terms of recovery goals. Therefore, after five years of hypothesis testing, there was still no consensus about the major causes of mortality, and after several revisions of the NMFS FCRPS Biological Opinion, litigation is still ongoing.

Research on salmon passage and survival in the river continues as well. To estimate survival of seaward migrating salmonids through the Columbia River hydrosystem (the series of eight dams), passive integrated transponder (PIT) tags (Prentice et al. 1990) are implanted into millions of wild and hatchery salmon smolts prior to or during migration each year which are subsequently detected by antennas at dam bypasses (Skalski et al. 1998). Direct mortality at the dams has decreased to only a few percent at each dam, and this is due to improvements of fish passage in the hydrosystem (Ferguson et al. 2007; Muir et al. 2001; Williams and Matthews 1995). There are two hypotheses however, regarding additional mortality of Snake River spring Chinook salmon caused by the hydrosystem that cannot be tested with the PIT tag system or modeled without early marine survival data:

1) For seaward migrating smolts from the Snake River, extra, latent or delayed mortality may occur in the estuary or after ocean entry as a result of migrating through the heavily impounded Snake and Columbia River system. This is thought to occur as a result of higher accumulated stress resulting from passing through four dams in the lower Snake River as well as four dams in the lower Columbia River (Budy et al. 2002; Independent Scientific Advisory Board 2007; Schaller et al. 1999; Schaller and Petrosky 2007; Wilson 2003). Delayed

hydrosystem mortality was hypothesized to occur because survival from seaward migration until adult return is substantially lower for Snake River spring Chinook salmon relative to mainstem Columbia River populations (Berggren et al. 2006).

2) One management strategy employed in the basin to mitigate for salmon losses at the Snake River (a tributary of the Columbia River) dams is the salmon transportation program, which transports migrating salmon smolts from bypass collectors at the Snake River dams and McNary dam in the lower Columbia River and transports them via barge to a release site in the lower Columbia River below Bonneville Dam, the final dam that smolts must pass during their seaward migration to the ocean. Despite a survival rate of near 100% to the lower river (on the barge), the transportation program has not consistently resulted in a larger proportion of transported smolts returning to the Snake River as adults when compared to smolts that migrated the length of the river and through the eight dams (Ward et al. 1997; Williams et al. 2005) indicating a failure of the transportation program to increase adult return rates to a sustainable level. The failure of transported smolts to return at higher rates is attributed to transportation-induced differential delayed mortality. In recent years however, the transportation program has shown improvements in relative survival of transported spring Chinook salmon (Buchanan et al. 2007; Schaller et al. 2007).

Although more than a billion dollars has been spent on migratory salmonid research in the Columbia River basin there is still a lack of knowledge on early marine survival of Snake River spring Chinook salmon, and still no consensus regarding principal causes of mortality. Increased research and awareness about climate-induced changes in salmon survival and physical oceanographic conditions that affect population variations (such as Scheuerell and Williams (2005), and Botsford and Lawrence (2002) , respectively) has demonstrated the need to incorporate ocean survival data into the management of Pacific salmon.

1.5 Cultus Lake sockeye salmon, Fraser River, Canada

Cultus Lake sockeye salmon (*Oncorhynchus nerka*) are a genetically unique population that has been studied since the 1920s. Most of the earlier work was carried out by R.E. Foerster and W.E. Ricker and focused on life history research and ecological experimentation, with an emphasis on juvenile sockeye salmon predator control in Cultus Lake. More than a half century later the number of Cultus Lake sockeye salmon returning to spawn suddenly plummeted to fewer than 100 beginning in the early 1990s. This resulted in an emergency assessment by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2002 that found the population to be "endangered". Predation on juveniles within the lake still remains a concern, as well as invasive aquatic plants (which provide cover for predators), however, COSEWIC (2003) listed the three primary causes of decline as overfishing and incidental harvest, high pre-spawning mortality, and low marine survival.

Cultus Lake sockeye salmon are incidentally harvested in the late run mixed stock Fraser River sockeye salmon fishery, therefore it is not possible to prevent capture of Cultus Lake sockeye salmon unless commercial, recreational, and First Nations late run fisheries are closed. Because of social and economic repercussions resulting from closure of the fishery, the fishery has remained open, and Cultus Lake sockeye have not been listed under the federal Species at Risk Act (SARA). Although since the assessment of Cultus Lake sockeye salmon by COSEWIC there has been a renewed interest in Cultus Lake sockeye salmon research to identify and evaluate management options (Amos 2008; Bradford et al. 2007; Pestes et al. 2008; Shortreed 2007).

In addition to losses in the mixed stock fishery, there has also been unusually high pre-spawning mortality in adult late run sockeye salmon prematurely migrating up-river to the spawning grounds since 1995 (Cooke et al. 2004). English et al. (2005) also found that in-river survival of late run fish radio tracked in the Fraser River was significantly lower than summer run fish during the same year. As a result of the incidental harvest and high pre-spawning mortality, the number of Cultus Lake sockeye salmon reaching the spawning grounds has been severely depressed in recent years.

The marine distribution and survival of Cultus Lake sockeye salmon is listed as one of the knowledge gaps by the Cultus Sockeye Recovery Team (2005): "*survival and distribution of Cultus sockeye in the Fraser River and near-shore marine areas have not been documented, nor has the distribution of the population in the North Pacific Ocean*". Groot and Cooke (1987) reconstructed migration routes of Fraser River sockeye salmon which demonstrated that most smolts concentrate around the Gulf Islands or swim into Howe Sound before exiting the Georgia Basin through the northern route through Johnstone Strait or through the Strait of Juan de Fuca to the south. Peterman et al. (1994) modelled sockeye salmon smolts movement in the Strait of Georgia and found that the most influential physical factor determining migratory route in the southern Strait of Georgia was wind-generated surface currents. These studies provided preliminary information and a potential mechanism which may determine sockeye salmon smolt movements; however marine distribution and preferred migratory route to the Pacific Ocean is unknown for the Cultus Lake sockeye salmon population.

Poor adult in-river survival has contributed to the decline of Cultus Lake sockeye, but what is not known is why marine survival has decreased dramatically over the past decade (COSEWIC 2003). Unlike the Columbia River there is no large scale PIT tag system in place for measuring in-river juvenile survival during the seaward migration (although the distance from Cultus Lake to the mouth of the Fraser River is only 100 km). If most mortality occurs within the first several months after salmon leave their rearing grounds, then it is likely that much of the mortality is occurring in the Strait of Georgia.

1.6 The Pacific Ocean Shelf Tracking array (POST)

The data collected for this thesis were obtained from the POST array. The POST acoustic array is a large-scale telemetry network designed to track highly migratory marine animals that utilize the continental shelf as a migration corridor (Welch et al. 2002). This network of stationary acoustic receivers is primarily intended to intercept tagged juvenile Pacific salmon during their early marine life history phase. Since acoustic transmitter size has significantly decreased over the past several years, and acoustic signals can propagate in both fresh and salt water, the use of acoustic technology for tracking salmon smolts in both freshwater and ocean habitats is becoming more prevalent (Chittenden et al. 2008; Lacroix et al. 2004; Melnychuk et al. 2007; Welch et al. 2004).

Presently the array extends from California to Alaska (Figure 1.2) with an emphasis in southern British Columbia (Georgia Basin) and the Columbia River. For this thesis, data were collected from sub-arrays between Oregon and southeast Alaska. There are six major marine acoustic detection sub-arrays between the Columbia River and southeast Alaska. Each of these sub-arrays is comprised of up to 45 individual stationary acoustic receivers (or transducers), which are deployed every ~800 m across the sea floor so that an “acoustic curtain” upwards of 34 km is created.

Figure 1.2. Map of the Pacific Ocean Shelf Tracking (POST) array. Red bars and dots indicate individual sub-arrays. POST map courtesy of the POST Project 2009.

The sub-arrays in the Georgia Basin area are deployed in the Strait of Juan de Fuca, Strait of Georgia, Queen Charlotte Strait, and Lippy Point on the northwest coast of Vancouver Island (Figure 1.2). The lines within the Straits extend from the mainland (either British Columbia or Washington) to Vancouver Island. Provided 100% of the equipment is recovered from depth (up to 300 m) it is possible to achieve near perfect detection of tagged salmon smolts swimming overhead. Sub-arrays at Lippy Point, Willapa Bay (WA), and Graves Harbor (AK) extend to the shelf break (~200 m isobath). In addition to the six major marine sub-arrays, multiple sub-arrays were also deployed within Howe Sound, the Fraser River, and the Columbia River.

Uniquely coded transmitters (Vemco, Halifax, Nova Scotia) are implanted into smolts so that individual fish can be cross-referenced with the tagging data and identified when they are detected on the acoustic receivers. (Surgical details are provided in Chapter 2 of this thesis.) The expected battery life of the transmitters depends on the programming of the tag and the goals of the study. For this study the battery life was ~4.5 months as a result of using a relatively long transmission interval (up to one minute) to prolong battery life. The long transmission interval also reduced the probability of two ID codes transmitting simultaneously, and thus causing a tag collision which can not be decoded by the acoustic receiver. Larger smolts may carry transmitters that are capable of measuring and transmitting pressure (depth) and/or temperature data or they may carry transmitters that can be programmed to “sleep” for a specified period of time (e.g. to conserve battery power and to allow tracking the smolt when it returns as an adult several years later). This type of transmitter was used on Cultus Lake sockeye salmon (Chapter 6 of this thesis). Detection data are collected periodically and uploaded to a master database which can be accessed via the POST web portal (http://www.postcoml.org).

1.7 Estimating survival from telemetry data

Acoustic detection data from migrating salmon smolts are analogous to a mark-recapture tagging study. Although smolts are not captured physically, the data from the tag which they carry are captured when smolts are within range of an acoustic receiver. Because smolts are detected on multiple sequential sub-arrays during their migration, and they are individually identifiable by their tag code, it is possible to estimate survival of the population of tagged fish, and the detection rates of all but the last sub-array passed by the fish.

Estimates of survival probability (Φ), detection probability (p), and their associated variances were calculated using the Cormack-Jolly-Seber (CJS) model for live recaptured animals implemented in *Program MARK* (White and Burnham 1999). This model jointly estimates survival and detection within a likelihood framework. Model assumptions are discussed in Chapters 1 and 4 of this thesis.

Capture (detection) histories for each individual were formed and the fully time-varying CJS model (survival and detection probability for each release group and each treatment type) was used to assess goodness of fit (GOF) to the data within Program MARK. If there was overdispersion in the data it was corrected to yield an overdispersion factor, $\hat{c}$. In general, if $\hat{c}$ is greater than 1 then the resulting standard errors on the estimates are inflated (multiplied) by the $\hat{c}$ value. A logit link function was used in survival models, which constrained the parameter estimates and their 95% upper and lower confidence limits to [0,1].

Survivorship was calculated by multiplying survival from release by sequential survival probabilities estimated in each migration segment (e.g., $\phi_1\phi_2\phi_3$, etc.). The variance was calculated for each survivorship estimate using the programming language R (R Development Core Team 2008) and the Delta Method:

$$\widehat{var(Y)} = \left(\frac{\partial(\hat{Y})}{\partial\hat{\varphi}}\right) \cdot \hat{\Sigma} \cdot \left(\frac{\partial(\hat{Y})}{\partial\hat{\varphi}}\right)^{\mathrm{T}}$$

Where *Y* is the product of the survival estimates, the first term is a row vector containing the partial derivatives of Y with respect to each of the survival parameters, the middle term is the variance-covariance matrix from the model output, and the last term is the transpose of the row vector. We then calculated the standard error, $SE = \sqrt{\widehat{var(Y)}}$, and the 95% confidence interval, $95\%\ CI = Y \pm 1.96 \cdot SE$.

Candidate models/hypotheses were formed and an information theoretic approach, i.e. Akaike's Information Criterion (AIC), was used to select the most parsimonious model. In general, the model with the lowest AIC value (which accounts for the number of model parameters) has more support in the data, and if the ΔAIC of the other candidate models is much greater than 2, then these models (i.e. hypotheses) have little or no support (Burnham and Anderson 2002).

1.8 Thesis objectives

The aim of this thesis is to provide some of the first direct estimates of early marine survival and to describe migration characteristics of depleted populations of two species of Pacific salmon originating from different river basins in the Pacific Northwest of North America, using a large scale acoustic telemetry array. The majority of this thesis reports results from experiments carried out from 2006-8 on seaward migrating spring Chinook salmon from the Columbia River, USA, (Chapters 2-5) and Chapter 6 reports survival and migration behaviour of seaward migrating Cultus Lake sockeye salmon from the Fraser River in British Columbia, Canada, studied from 2004-7. For the spring Chinook salmon studies, three treatment groups were used in a nested experimental design: 1) smolts from a tributary of the Snake River were tagged and released from the hatchery and migrated the length of the river to the Pacific Ocean, 2) a second group from the same hatchery was tagged and then transported to below the final dam in the Columbia River, 3) smolts from the Yakima River, a tributary of the mid-Columbia River, were tagged and released from their hatchery to migrate to the ocean. Smolts released from the Snake River hatchery (#1) are compared to transported smolts (#2) in Chapter 5, and to Yakima Riversmolts (#3) in Chapters 3 and 4. For Cultus Lake sockeye salmon, only one treatment group was released in each year.

Chapter 1 described the stocks used in the study, the Pacific Ocean Shelf Tracking (POST) acoustic tracking array that made the study possible and the general statistical methods used for estimation of survival rates over different parts of the early ocean migration. Chapter 2 details the surgical procedure for implanting transmitters into salmon smolts, and describes tag effects as they relate to survival, growth and tag retention, and implications of tag loss or tag induced mortality on survival estimates. Chapter 3 is a brief chapter that focuses only on 2006 estuarine and early marine survival estimates of Columbia River spring Chinook salmon and emphasizes the effectiveness and availability of a large scale telemetry array to estimate early marine survival. This chapter was published as a “Rapid Communication” in the Canadian Journal of Fisheries and Aquatic Sciences, which had a strict size limit. Therefore, I was not able to elaborate on the results in the discussion. Chapter 4, however, goes into much more detail of in-river and early marine survival and describes migration characteristics of the two populations of in-river migrating Columbia River spring Chinook salmon tracked in 2006-9, and tests the hypothesis that there is delayed, hydrosystem-induced delayed mortality. Chapter 5 tests the hypothesis that there is post-Bonneville differential delayed mortality, by comparing early marine survival of Snake River spring Chinook salmon that were either transported or migrated in the river. This chapter also presents early marine migration characteristics of both groups. Chapter 6 presents river and early marine survival estimates for Cultus Lake sockeye salmon, as well as detailed migration characteristics of smolts travelling through Howe Sound and the Strait of Georgia. Chapter 7 summarizes the significance of my thesis and discusses future research and applications of early marine survival data.

Overall, my thesis demonstrates the utility of a large-scale acoustic array for obtaining mark-recapture (detection) data which can be used to estimate early marine survival and describes migratory behaviour of salmon smolts. These data are critical for directly testing hypotheses related to the short to medium term effects of hydropower operations in the Columbia River and for filling knowledge gaps to facilitate recovery of depleted populations.

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2 Surgical Implantation of Acoustic Tags: Influence of Tag Loss and Tag-induced Mortality on Free-ranging and Hatchery-held Spring Chinook Salmon (*O. tschawtscha*) Smolts[1]

2.1 Introduction

Pacific salmon researchers have acknowledged for decades that most of the mortality experienced by salmon occurs during the first several months at sea (seeQuinn 2005); however, tracking juvenile salmon through rivers and into the ocean has only recently been accomplished (Chittenden et al. 2008; Lacroix et al. 2004a; Melnychuk et al. 2007; Rechisky et al. 2009; Welch et al. 2008) due to the development of stationary acoustic receivers and the miniaturization of acoustic transmitters (see review by Heupel et al. 2006; Voegeli et al. 1998). Thus, it is possible to measure survival of individually identifiable fish and to test hypotheses regarding their ocean survival during the critical months after ocean entry.

To measure survival with acoustic tags it is necessary to surgically implant the transmitter into the abdominal cavity of a fish, as external methods of attachment are unlikely to be successful, and tag loss will confound estimates of survival (i.e., tag loss is assumed to be mortality). The surgical procedure or the tag itself, however, may potentially alter behavior, growth, or survival if the size of the tag exceeds biological limits (Chittenden et al. 2009; Lacroix et al. 2004b; Welch et al. 2007). If transmitters cause mortality or are expelled by the animal, then the results may not be representative of the untagged population. It is thus important to quantify the effects of tag implantation on growth and survival.

Tag effect studies have been conducted on numerous species and with several internal tag types (coded wire tags, passive integrated transponder [PIT] tags, radio transmitters, acoustic transmitters). The results obtained from these studies are dependent on the specifics of transmitter size and fish size (often expressed as percent body mass or tag burden), and

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morphology of the study species as well as the study duration. For example, Lacroix et al. (2004b) specifically recommended that transmitter weight not exceed 8% of body weight for Atlantic salmon *Salmo salar* measuring 14-15 cm and tagged for several months. These specifications, however, may not be applicable to other species and thus it is important to quantify tag effects for individual tagging studies particularly if the study focuses on survival.

Pacific salmon from the Columbia River basin (northwestern USA) are often the subject of tag effects studies due to their conservation status (13 of 16 salmonid populations from the Columbia River Basin are listed under the *U.S. Endangered Species Act*), and thus extensive research on salmon survival takes place within the basin (Independent Scientific Review Panel/Independent Scientific Advisory Board 2009). Passive Integrated Transponder tags are the primary method of measuring survival in the Columbia River Basin (Faulkner et al. 2007) because they are small, light, and inexpensive, and have little or negligible effect on survival (Prentice et al. 1987); however, the use of radio transmitters (Adams et al. 1998a; Adams et al. 1998b; Hockersmith et al. 2003; Martinelli et al. 1998), and acoustic transmitters have become more common with the advent of smaller transmitters (Anglea et al. 2004; Brown et al. 2006).

Tag effects studies are generally conducted in controlled environments where predation or prey capture is not a factor and fish are held in artificial conditions and fed to satiation every day. While captive studies do not incorporate stresses encountered by fish in the wild, they are the most practical method currently available for measuring changes in growth, and for monitoring survival and tag retention. If a captive study and a field study are conducted concurrently (on the same population within the same year) then the specific results from the captive study can then be extrapolated to help assess the potential negative impact of tag implantation on the release group used in field studies. If the captive tag study yields no tag effects or tag loss, then the field study may be impacted minimally by tag implantation effects; however, if captive studies reveal significant mortality or tag loss, then field study results may be severely compromised and at a minimum should be adjusted for negative tag effects (e.g., field estimates of survival could be corrected upwards to compensate for tag loss). The adjustments based on captive studies may, however, underestimate mortality and tag loss in the wild, as migrating smolts must contend with predation, prey acquisition, and other stressors such as dam passage.

Short-term tag effects may be measured in the river by using a paired release strategy to compare migration behavior or survival of a tagged group to a control group. Hockersmith et al. (2003) used this strategy in the Columbia River to compare survival and migration rate of radio transmitter tagged and PIT tagged yearling Chinook salmon *Oncorhynchus tshawytscha* and found no initial differences between treatments, though they did detect a decrease in survival for transmitter tagged fish tracked to more distant sites in the river. This reduced survival, however, may have been influenced by the presence of the radio tag antenna trailing behind the fish which could become entangled, biofouled, or infected (Adams et al. 1998b; Jepsen et al. 2002). Martinelli et al. (1998) compared different methods of implantation of radio transmitters in subyearling Chinook salmon and also found no difference in migration time for fish tracked for fewer than five days.

To date, medium and long term tag effects studies are completely lacking for the ocean phase of the life history due to logistical difficulties. To address this issue we: (1) conducted captive studies to quantify tag effects in two populations of juvenile spring Chinook salmon from the Columbia River Basin implanted with dummy acoustic transmitters (DATs); to do so, we measured and compared growth, survival, and tag loss of DAT tagged fish to a control group tagged with PIT tags (which is the generally accepted method for analyzing in-river survival of juvenile salmon); (2) concurrently, we released spring Chinook salmon from these two populations tagged with live acoustic transmitters and estimated their survival during the seaward migration (Chapter 4 of this thesis); to examine size effects on fish survival, we compared survival by size class and statistical survival models to determine if survival is positively associated with size at tagging; (3) we then adjusted estimated survival probabilities of migrating smolts for tag loss and tag mortality that was quantified in captivity; and (4) additionally, we compared our acoustic tag survival estimates of migrating smolts to PIT tags survival estimates estimated independently for both populations in both years of the study.

2.2 Methods

In 2006 and 2008, we conducted captive tagging studies with two populations of hatchery spring Chinook salmon to quantify acoustic tag retention and the effect of transmitter implantation on survival and growth (Table 2.1). For the study, we used two different size acoustic transmitters; in 2006 smolts were tagged with 9 mm DATs, and in 2008 smaller 7 mm DATs were used. Additionally, we released acoustic tagged smolts from both populations in both years with live 7 mm and 9 mm transmitters, respectively, (Table 2.2) and estimated river and early ocean survival using the Pacific Ocean Shelf Tracking (POST) array (Welch et al. 2002). Smolts used in our study were obtained from Dworshak National Fish Hatchery (NFH; Ahsahka, ID) on the Clearwater River (a tributary of the Snake River) and Cle Elum Supplementation and Research Facility (CESRF; Cle Elum, WA) on the Yakima River (a tributary of the Columbia River).

2.2.1 Study/release sites

For logistical reasons, all Dworshak hatchery spring Chinook salmon were tagged at Kooskia NFH. Smolts were transferred from Dworshak NFH to Kooskia NFH in early March 2006 and in February/March 2008. In 2006 captive tag effects studies were conducted at Kooskia NFH; however, in 2008 smolts were transferred back to Dworshak NFH (one week after tagging) for tag effect studies (the transfer back to Dworshak NFH was necessary because of limited availability of tanks at Kooskia NFH). In both years in-river (IR) migrating fish used in field studies were released from Kooskia NFH (60 km upstream of Dworshak NFH; Figure 2.1).

In 2006 and 2008, spring Chinook salmon released from CESRF acclimation sites in the upper Yakima River were recaptured in the lower river at the Chandler Juvenile Monitoring Facility (CJMF) downstream of Prosser Dam and used in our captive and field studies. We chose to recapture fish downstream at CJMF because fish mortality from the acclimation sites to CJMF (~200 km) was as high as 80% in recent years (Yakama Nation 2008). All tagging and captive tag studies took place at Prosser Hatchery, Prosser, WA, which is directly adjacent to CJMF. In both years IR fish used in field studies were released into the Yakima River from the CJMF (Figure 2.1).

2.2.2 Tags and tagging

We used Vemco (Halifax, Nova Scotia) V9-6L acoustic transmitters (9 mm x 21 mm, 3.1 g in air, 69 kHz) and V7-2L transmitters (7 mm x 20 mm, 1.6 g in air, 69 kHz) to estimate survival of migrating fish in 2006 and 2008, respectively (Table 2.2). The larger, more powerful V9 transmitter has a detection radius ≤400 m, while the smaller V7 tag has a detection radius ≤300 m; however, detection range is location and time-dependent, and may vary with freshwater/estuarine/ocean conditions, local topography, river flow, and weather conditions. Each transmitter was uniquely coded so that individual fish were identified when detected by river and ocean receivers along their migration route. For captive tag effects studies, we used DATs that were identical in volume, weight, and shape to live transmitters used in respective years. Dummy acoustic tags were also embedded with a PIT tag (12.5 mm x 2.07 mm, 0.1 g) at our request by the manufacturer, and all control fish were implanted with a PIT tag; therefore, each individual could be identified throughout the tag effects study (unless a tag was lost). DAT tagged fish and control fish were held in the same tank. We did not include a non-tagged group because it was necessary to identify all individuals for growth analyses.

We specified a minimum size limit of 140 mm fork length (FL) for smolts implanted with a 9 mm acoustic or dummy tag, and a minimum size of 130 mm FL for the 7 mm tag. The mean tag to body weight ratio for Yakima River smolts implanted with live 9 mm transmitters was similar to the ratio of smolts implanted with DATs (7.4% and 7.7%, respectively, Table 2.3); however, Dworshak smolts implanted with live 9 mm transmitters and released, were slightly smaller on average than the hatchery-held DAT tagged smolts, and the mean tag to body weight ratio was thus slightly higher for IR smolts (IR=9.3%, captive smolts=7.6%; Table 2.3). Although the mean tag to body weight ratio was higher for IR smolts, there were DAT tagged representatives within each size class (Figure 2.2). The mean tag weight to body weight ratio for fish implanted with live 7 mm transmitters was similar to the ratio for smolts implanted with DATs for both Yakima (5.8% and 5.9%, respectively) and Dworshak populations (4.5% and 4.2%, respectively; Table 2.3).

Surgical procedures used to implant acoustic transmitters were reviewed annually by institutional animal care committees and met or exceeded the Canadian Council on Animal Care standards (www.ccac.ca). The same surgical protocol was used in 2006 and 2008 for fish tagged with live and dummy acoustic transmitters and PIT tags. Portable self-sustaining surgical units are assembled on site, and fish surgery was carried out by highly experienced, veterinarian-trained staff. Fish were not fed for 24 h prior to surgery. Fish were dip netted from their holding tank and lightly anaesthetized, or sedated, with a low dose (20 ppm) of Tricaine Methane Sulphonate (MS-222) to reduce stress from handling. A mucous protectant (Vidalife) was added to all water baths and contact surfaces, and surgeons wore latex or nitril gloves while handling fish to reduce scale and mucous loss. All water baths were aerated, and dissolved oxygen (DO) and temperature were monitored approximately every three minutes. Fish were taken from the sedation bath once there was slight loss of equilibrium and were anesthetized one at a time in 70 ppm of MS-222. Induction time to total loss of equilibrium, loss of reflex reactivity, and slow and irregular opercular motion was <5 min. Each individual was removed from the induction bath, fork length was measured to the nearest mm and weight was measured to the nearest tenth of a gram. The fish was then placed ventral side up into a v-shaped trough and a maintenance dose of anesthetic (50 ppm) was pumped through the fish's mouth and over the gills. Tags were disinfected in an iodine solution (Ovadine) and rinsed in distilled water. An incision was made at the ventral midline midway between the pelvic and pectoral fins with a #12 curved blade on #3 scalpel and the tag was gently inserted through the incision into the peritoneal cavity. The transmitter was set in place directly below the incision with the tip of the scalpel blade. For IR fish used in field studies, a PIT tag was inserted through the incision prior to transmitter insertion. This was to ensure that IR fish were not collected at Snake and Columbia River dams for transport to the lower Columbia River. Two surgical-grade stainless steel cutting needle drivers and sterile, absorbable Monocryl 4-0 violet sutures with a swaged on reverse cutting needle (14 mm) were then used to set and tie sutures using a surgeon's knot covered by a square knot. Sutures were carefully tied to achieve edge apposition (i.e., no overlap of the incision edges). For a 9 mm live or dummy transmitter, the incision was 10-12 mm in length and was closed with two interrupted sutures; for a 7 mm live or dummy transmitter the incision was 7-8 mm and was closed with one suture; for PIT tagged control fish in the captive, tag effects study, a 2mm incision was made and no sutures were used. Two sets of instruments were rotated during surgeries so that one set soaked in the disinfectant solution (Ovadine and distilled water) during surgery. Instruments were rinsed with distilled water before use. Surgery time was <2 min for a 9 mm tag and about 1 min for a 7 mm tag. Immediately following surgery, fish were placed into a recovery bath and monitored. Within minutes fish regained equilibrium and reactivity; after several more minutes of recovery, fish were transferred into either the captive study holding tank or one of the field study tanks. At both hatcheries, captive fish were held in partially shaded outdoor tanks. Well water at Prosser Hatchery ranged from 13 to 16 °C, recirculated well water at Kooskia NFH was 11°C, and river water from the North Fork of the Clearwater River at Dworshak NFH increased from 4°C to 10 °C as the captive study progressed.

To reduce bias during tagging (i.e., to reduce the chance that a surgeon might take more care in tagging a fish bound for the tagging study) DAT tagged fish were randomly tagged during the tagging of acoustic tagged fish intended for release. The surgeon was aware of the fate of the fish since transmitter identification must be verified before insertion (i.e., we could not conduct a truly blind study); however, intermingling dummy tagging with live acoustic tagging was intended to reduce any involuntary bias. Within each year, the same surgeons tagged all treatment groups at both hatcheries.

2.2.3 Captive study

Tanks were monitored daily for dead fish or expelled tags, and fork length and weight were recorded 1-3 times post-surgery (depending on the length of the study). All weights were adjusted by subtracting the average weight of the dummy tags. Tag retention was calculated each day as:

$$\frac{\text{N tags intact}}{\text{N tags implanted} - \text{N mortalities of tagged fish}}$$

and survival was calculated as:

$$\frac{\text{N live fish}}{\text{N fish initially tagged.}}$$

The percent of tags available for detection (K, i.e., live fish with tags) was calculated as:

$$\frac{\text{N tags implanted} - \text{N mortalities of tagged fish} - \text{N tags expelled}}{\text{N tags implanted.}}$$

Sample size. Approximately 100 DAT tagged fish and 100 PIT tagged fish were tagged at each hatchery in each year. Mean fork lengths and mean weights were similar for both treatments (Table 2.1).

Duration. In 2006 the Dworshak captive tag study took place at Kooskia NFH from May 31 to Nov 17 (24 weeks) and fish were measured at weeks 5, 11, and 24. The study was terminated and fish were euthanized with a lethal dose of MS-222 after the final measurement during week 24. In 2008 the captive tag study took place from April 22 to Oct 3, 2008 (23 weeks). Approximately one week after tagging, the fish were transferred from Kooskia NFH back to Dworshak NFH for the duration of the study; mortality after transfer was zero. Fish were measured at weeks 7 and 23. During week 23, a dead DAT fish was found with fresh water fungus *Saprolignia* spp. In the following days, four PIT tagged and four DAT tagged smolts succumbed to the fungus, therefore we took final measurements and terminated the study before the fungus spread to all of the captive fish.

The Yakima River spring Chinook salmon captive tag study in 2006 took place at Prosser Hatchery from May 27 to Aug 21 (12 weeks) and fish were measured at weeks 6 and 12. In early September, a major mortality event occurred due to a disease outbreak at the hatchery which killed approximately 60% of the study fish and therefore the tag study was effectively terminated after measurements were taken on Aug 21, 2006. In 2008 the tag study took place from May 7 to June 13 (5 weeks) and fish were measured at week 5. The study was inadvertently terminated during week 5 after nearly all of the fish died (DAT and PIT tagged) the day after we obtained growth measurements. Several of the fish that died just prior to this major mortality event were examined by a fish pathologist (Eric Pelton, U.S. Fish and Wildlife) because there had been a decline in survival of both DAT and PIT tagged fish during week 5 (prior to week 5 survival was 98% for DAT tagged fish and 100% for PIT tagged fish). There was no indication of disease or stress, however, and therefore we do not know the cause of the mass mortality that subsequently occurred the day after our growth measurements were collected.

2.2.4 Field study

Sample size. In each year, at each hatchery, ~400 fish were tagged with live acoustic transmitters and were released into their respective rivers as the IR groups (Table 2.2). We attempted to match mean sizes between both hatcheries; however, we were somewhat limited in size availability because we were collecting Yakima Riversmolts at CJMF as they migrated through. Therefore the mean FL of Dworshak smolts was approximately 10 mm smaller than the mean FL of Yakima River smolts in 2006 and 6 mm larger in 2008.

Release timing. Dworshak smolts were released in the Snake River basin 349 km upstream of the confluence of the Snake and Columbia rivers (RKm 522). We released Yakima smolts into the Yakima River, 76 km upstream of the confluence to the Columbia River (RKm 539), several weeks after the Dworshak smolts were released in order to have both populations arrive at the Columbia River mouth simultaneously so that they encountered similar ocean conditions.

Array Location. The POST array is composed of individual Vemco omni-directional acoustic receivers (VR2s or VR3s) anchored to the river or ocean floor to form a component line or an "acoustic curtain" at each sub-array (Welch et al. 2002) and extends ~2,300 km from the Snake River to southeast Alaska (Figure 2.1). Each receiver records the date, time, and identification of uniquely coded acoustic tags passing near it. Oceanic receivers of the POST array at Willapa Bay (southern WA), Lippy Point (northwest Vancouver Island, BC), and Graves Harbor (southeast AK) were deployed approximately every 800 m and extend from near-shore to the edge of the continental shelf, a distance of up to 30 km.

Component sub-arrays relative to this study were deployed within the Columbia River at McGowan's Channel (10 km below Bonneville Dam), in Lake Celilo (7 km below John Day Dam in 2006, and above and below John Day Dam in 2008), and in Lake Wallula (21 km below the confluence of the upper Columbia and Snake rivers). In the Snake River, receivers were installed in Lake Bryan (14 km below Lower Granite Dam; total distance from the ocean was 681 km). At each of these locations, receivers were deployed across the river as paired lines to evaluate the detection probability for each of the pairs, and to provide a survival measurement below four of the major hydroelectric dams. In-river receivers were deployed every 100-200 meters to ensure high transmitter detection rates in the fast flowing rivers. In 2007 an additional line of receivers was deployed at the Astoria Bridge, 22 km from the mouth of the Columbia River. Therefore survival was estimated to an additional point near the river mouth in 2008, but not in 2006.

2.2.5 Data analyses

Captive Studies. All data analyses for captive studies were performed in the statistical programming language R (R Development Core Team 2008). We used chi-squared tests of homogeneity to test the null hypothesis that survival of PIT tagged fish is equal to survival of DAT tagged fish. This null hypothesis was tested for each population at those times when growth was measured. For example, in 2006 we compared the survival of each treatment group (PIT and DAT) of the Dworshak population at weeks 5, 11, and 24, and for the Yakima population we compared survival at weeks 6 and 12. In 2008 it was only necessary to make a statistical comparison for Yakima smolts (at week 5), as no mortality occurred in DAT tagged Dworshak smolts. In the case where the expected cell count was less than five, we estimated the p-value using a Monte Carlo simulation. This simulation is based on 2000 replicates, and as a result the degrees of freedom are reported as NA. We repeated this procedure with the tag retention data using the null hypothesis that tag retention of PIT tagged fish was equal to tag retention of DAT tagged fish; however, we only tested the 2006 data as there was no PIT tag or DAT tag loss in either population in 2008.

To determine whether DAT tag loss or mortality was a function of FL we used logistic regression analyses with tag retention or survival as the dichotomous response variable (1= tag retained/survived, 0=tag lost/died) and fork length at tagging as the continuous independent variable. As mortality was low or zero for Dworshak smolts implanted with either 9 mm or 7 mm DATs, respectively, and tag loss was zero for 7 mm DATs for both populations, we only conducted three logistic regression analyses for Yakima River smolts: (1) survival (with 9 mm DAT intact at death) as a function of FL; (2) retention of 9 mm DATs as a function of FL; and (3) survival with 7 mm DATs as a function of FL. A Wald X^2 test was used to assess significance of the FL coefficient.

We used t-tests to compare fork length and weight of PIT tagged to DAT tagged smolts after each measurement was obtained. ANCOVA analyses were used to compare specific growth rate. Specific growth rate (SGR, % weight/week) of PIT tagged and DAT tagged fish was calculated for each interval: from initial tagging to the second measurement, from the second measurement to the third measurement, etc. SGR in weight was calculated as: $SGR=100\ [(\ln(W_2)-\ln(W_1))/(t_2-t_1)]$, where W_2 is the weight at time t_2 and W_1 is the weight at time t_1. For the first interval we compared SGR of the two treatment groups with initial fork length as the covariate; for subsequent intervals we used the fork length from the previous measurement as the covariate.

In 2008 it was obvious at week 23 that a small percentage of the Dworshak smolts had become sexually mature males (13% DAT, 5% PIT). These precocious males were noticeably smaller, were olive green in color (not silvery smolts) and were swollen with milt. These fish were excluded from the 2008 growth analyses as they were not representative of a typical spring Chinook salmon smolt, and were unmistakable outliers in the study.

Field Studies. Estimates of smolt survival (Φ) and detection probability (*p*) for each recapture occasion, i.e., acoustic detection line, in 2006 and 2008 were calculated using the Cormack-Jolly-Seber (CJS) model for live recaptured animals implemented in Program MARK (White and Burnham 1999). This model jointly estimates survival and detection within a likelihood framework. For in-river lines, we recognized basic CJS model assumptions (equal survival probability, equal recapture probability, no tag loss, and instantaneous sampling); however, for oceanic lines that are not bounded on the offshore end (continental slope), we required two additional assumptions: (1) as fish migrate they cross over the acoustic detection lines that span the length of the continental shelf; and (2) the majority of the fish departing the Columbia River swim north. These assumptions are supported by evidence from numerous ocean sampling programs (Bi et al. 2007; Brodeur et al. 2004; e.g., Fisher and Pearcy 1995). To estimate overdispersion in the data we used a median $\hat{c}$ procedure (White and Burnham 1999) to test the goodness of fit (GOF) of our global model ($\Phi_{population*line}\ p_{population*line,}$ where line =acoustic detection site) and then corrected for this overdispersion across all candidate models.

Survival probabilities in both years were estimated to detection sites within the Columbia River and to an ocean detection site adjacent to Willapa Bay. Smolts were detected north of Willapa Bay at Lippy Point (both populations) and in Alaska (Dworshak only, in both years); however, it was not possible to estimate survival to Lippy Point with the CJS model due to small sample size on the Alaska detection line. Therefore, in order to examine medium term tag effects, we present the percent of fish detected at Lippy Point, which represents the minimum survival of migrating fish and likely underestimates survival to this site.

Because of the low number of fish detected at Vancouver Island and Alaska, we included in our models two additional treatment groups (each N=100) of spring Chinook salmon smolts from Dworshak NFH, tagged with the same acoustic tag (V9 in 2006, V7 in 2008), that were released below Bonneville Dam during the spring seaward migration, in order to better quantify the detection probability of the Willapa Bay detection line, and thus, reduce the uncertainty around the survival estimates. (These two additional treatment groups were used in our transportation survival study which is reported in Chapter 5.) The survival estimate of the transported group was modeled independently from the IR treatment groups. Recapture parameters were modeled independently for each treatment group except at Willapa Bay where all treatment groups (Yakima, Snake IR and transported Snake Chinook salmon smolts) were pooled.

To test the hypothesis that smaller fish have lower survival due to tag burden, we followed a similar procedure as described above, except we modeled each population of spring Chinook salmon separately and then compared the global CJS survival model ($\Phi_{line}\ p_{line}$) to an additive model that included fork length as a covariate ($\Phi_{line + FL}\ p_{line}$), as well as a model that included the interaction between acoustic detection site and FL ($\Phi_{line * FL}\ p_{line}$). We used Akaike's Information Criterion (AIC) values to rank the performance of the models. In general, the model with the lowest AIC value (which accounts for the number of model parameters, n_{pars}) has more support in the data, and if the ΔAIC of the other candidate models is greater than 2, then these models (i.e., hypotheses) have little or no support. If the additive model has more support given the data (i.e., ΔAIC <2) then there is evidence that FL had a constant additive effect on survival at each detection site. If the interaction model has more support then the effect of FL varies at each detection site.

Comparison with PIT Tag studies. We obtained PIT tag survival estimates for seaward migrating Dworshak (Steve Smith, National Oceanic and Atmospheric Administration (NOAA), pers. Comm.; Faulkner et al. 2008) and Yakima (David Lind, Yakama Nation, pers. Comm.) spring Chinook salmon to compare with our estimates of IR survival using 9 mm and 7 mm acoustic tags in 2006 and 2008, respectively. Passive integrated transponder tagged Dworshak smolts were released at Dworshak NFH and survival was estimated to several dams in the lower Snake and Columbia rivers to as far as Bonneville Dam (577 km). Acoustic tagged smolts were released at Kooskia NFH and survival was estimated to four (2006) or five (2008) detection sites in the lower Snake and Columbia rivers and to coastal Washington (adjacent to Willapa Bay, 911 km). PIT tagged Yakima smolts were released from acclimation sites in the upper Yakima River; however, survival estimates were calculated only for those fish that were recaptured and released at CJMF. Survival was estimated to two dams in the lower Columbia River- McNary Dam and John Day Dam (268 km). Survival estimates for acoustic tagged Yakima smolts were from release at CJMF to three (2006) or four (2008) river detection sites and to Willapa Bay (655km).

To statistically compare survival rates (S/km) we regressed the log-transformed cumulative survival estimates at the j-th detection site, $\ln(S_{i,j}) = bd_{i,j}$, for each of the i-th populations against migration distance from the respective release sites, $d_{i,j}$, resulting in a survival rate per km, b_i. To estimate the uncertainty in the estimated regression coefficients (b_i) we used a Monte Carlo procedure to randomly generate 10,000 individual survival estimates at each of the detection sites for each population *i* (in each year) using the estimated survival proportions, $S_{i,j}$, and associated estimated variances that define the parameters of the binomial distribution. We then took the 10,000 sets of generated survival estimates with distance for each population, and calculated the log-transformed regression estimates to empirically define the distribution of survival rates, b_i, for each population. The null hypothesis that the survival rate of acoustic tagged smolts is equal to that of the PIT tagged smolts is equivalent to assuming that on average the difference in the regression coefficients, $b_{DAT} - b_{PIT}$, is zero. We tested this null hypothesis by evaluating whether the central 95% of the 10,000 survival rate differences included zero.

Survival estimates of IR spring Chinook salmon corrected for tag loss in captive studies. To correct for tag loss and mortality, we calculated the percent of tagged animals available for detection on day *i*, K_i, from the proportion of fish that were alive and retaining tags in captivity. We then used K_i to provide an estimate of survival in free-ranging smolts adjusted to account for tag loss and mortality due to surgical implantation of tags:

$$S_K(t, j) = \frac{\text{estimated survival to detection site j}}{\text{K for the median day of arrival, t, to detection site J}}$$

For example, the median time to arrival at Willapa Bay for IR Dworshak smolts in 2006 was 24 days, and so we calculated K on day 24 of the captive survival study and divided the IR survival estimate at Willapa Bay by $K_{t=24}$ to obtain S_K.

2.3 Results

2.3.1 Tag effects- Captive studies

2.3.1.1 Tag retention

9 mm DATs. One hundred percent of PIT tagged and 95% of DAT tagged Dworshak fish retained their tags for the duration of the tag study in 2006 (24 weeks, Figure 2.3, Table 2.4). At weeks 5 and 11, there were no significant differences in tag retention of PIT tagged and DAT tagged smolts; however, at week 24 DAT tag loss was significantly greater than PIT tag loss (Table 2.4a). The initial fork lengths of the four fish that expelled tags were distributed across the size range of DAT tagged fish (Figure 2.2); too few tags were expelled to warrant a significance test of whether some size classes had greater tag expulsion.

One hundred percent of PIT tagged and 83% of DAT tagged Yakima fish retained their tags for the duration of the study (12 weeks; Figure 2.3). Tag loss was significantly greater for DAT tagged smolts at week 6 and week 12 (Table 2.4a). We believe that tag loss was greater in DAT tagged Yakima smolts because the sutures (most of which were present after 86 days) were observed tearing through the skin and muscle toward the incision (Figure 2.5b, c); Dworshak smolts also retained their sutures for several months; however, tearing was not observed (Figure 2.5a). The sutures, when completely ripped out, left a large open wound where the tag could be expelled. Often times the incision itself was well healed or completely healed but the sutures prevented complete recovery from the surgery. In some cases the sutures were observed to have ripped toward the incision and completely out of the body but the DAT tag was still intact. Tag retention was not a function of initial FL (Wald X^2= 0.603, df = 99, p = 0.547), therefore tag loss was not limited to smaller individuals (Figure 2.2).

7 mm DATs. Retention of PIT tags and 7 mm DATs was 100% for the duration of the study for both Dworshak (23 weeks) and Yakima smolts (5 weeks; Figure 2.4).

2.3.1.2 Captive survival

9 mm DATs. Approximately one month into the Dworshak tag study, fish were treated with chloramine-T due to an *Ichthyophthirius* spp. ("ich") outbreak at Kooskia NFH. The death of 12 DAT tagged fish and eight PIT tagged fish was attributed to ich and/or treatment. Following the ich outbreak only one DAT tagged fish and two PIT tagged fish died during the remainder of the study (a total of 170 days). Total survival of DAT tagged fish was 87%, and survival excluding the mortalities associated with chloramine-T treatment was 99%. Survival of PIT tagged fish was similar; total survival was 90% and survival excluding chloramine-T mortalities was 98%. Since the ich parasite cannot survive in seawater and in-river migrants were released from the hatchery before the outbreak, it is likely that in-river migrants were not affected. At weeks five, 11, and 24 there were no significant differences in survival of PIT tagged and DAT tagged smolts (Table 2.4b; Figure 2.3). As only one fish died after the ich outbreak, a significance test for survival as a function of FL was not warranted.

Eighty four percent of DAT tagged and 96% of PIT tagged Yakima fish survived to day 86 (the final day of the study). At week 6, there was no significant difference in survival of PIT tagged and DAT tagged smolts; however, at week 12 survival of PIT tag smolt was significantly greater than DAT tagged smolts (Table 2.4b; Figure 2.3). As mortality was not limited to smaller individuals, survival was not a function of initial FL (Wald X^2= -0.309, df = 99, p = 0.757, Figure 2.2). Mortality of some DAT tagged fish may be attributed to the suture wound.

7 mm DATs. Survival of PIT tagged and DAT tagged Dworshak smolts was 100% up to day 108 of the study. On day 108, one PIT tagged fish was found dead with no obvious cause of mortality. On day 159, a dead DAT fish was found with fresh water fungus *Saprolignia* spp. In the following days, four PIT tagged and four DAT tagged smolts succumbed to the fungus. At that point we terminated the tag study as it was obvious that the fungus was spreading throughout the fish in the tank and the tag study results would be compromised. Prior to the occurrence of the fungus (day 159), survival was 100% for DAT tagged fish and 99% for PIT tagged fish. Had these fish had the opportunity to migrate they would have reached the ocean in several weeks (median day of arrival of IR smolts to the ocean was 35 days), and thus would likely not have been affected by this freshwater pathogen.

Survival of Yakima smolts to day 31 was 98% for DAT tagged and 100% for PIT tagged fish. From day 32 to day 37, nine DAT tagged and four PIT tagged fish died. Although more DAT tagged fish died during the final week the difference was not significant (Table 2.4b). Because the study was inadvertently terminated on day 38 (see Methods) we were not able to monitor fish in captivity beyond five weeks. Survival was not a function of initial fork length (Wald X^2= 1.075, df = 99, p = 0.283; Figure 2.2), therefore mortality was not limited to smaller individuals.

2.3.1.3 Growth

9 mm DATs. The initial mean fork length (mm) and weight (g) of PIT tagged and 9 mm DAT tagged Dworshak smolts were not significantly different (Table 2.4c,d, Figure 2.6). At five weeks post-surgery the mean fork length and mean weight of PIT tagged smolts were significantly greater than DAT tagged fish. At 11 and 24 weeks post-surgery the mean fork length and weight of PIT tagged smolts remained significantly greater than DAT tagged fish.

The specific growth rates (% weight/week) of PIT tagged smolts were significantly greater than DAT tagged smolts from week 0 to week 5 when we accounted for initial fork length (Table 2.4e). During this initial five week period PIT tagged fish grew 2.2%/week more than DAT tagged fish. From week 5 to the final week of the study (week 24), however, specific growth rate was not statistically distinguishable for the two treatments, demonstrating that DAT tagged smolts grew at the same rate as PIT tagged smolts and that recovery from an initial set back in growth (due to the DAT or the surgery, or the cumulative effects of both) occurred within five weeks post-surgery.

The initial mean fork length and weight of PIT tagged and DAT tagged Yakima smolts were not significantly different; however, by week 6 PIT tagged fish were significantly larger than DAT tagged fish (Table 2.4c, d, Figure 2.6). At week 12 this difference was still significant.

The specific growth rates of PIT tagged smolts were significantly greater than DAT tagged smolts from week 0 to week 6 when we accounted for initial fork length (Table 2.4e). During this initial six week period, PIT tagged fish grew 1.3%/week more than DAT tagged fish. From week six to the final week of the study (week 12), PIT tagged fish grew 0.58%/week more than the DAT tagged fish; however, this was not a significant difference for the two treatment groups. Therefore, Dworshak and Yakima fish tagged with a 9 mm DAT suffered an initial growth set back due either to the DAT or the surgery, or the cumulative effects of both, but this effect did not persist beyond the first growth measurements at weeks 5 and 6, respectively.

7 mm DATs. The initial mean fork length and weight of PIT tagged and 7 mm DAT tagged Dworshak smolts were not significantly different (Table 2.4c, d, Figure 2.7). The mean fork length and weight of PIT tagged smolts seven and 23 weeks post-surgery also were not significantly greater than DAT tagged fish (Table 2.4c, d). Therefore, the 7 mm DAT did not have an initial impact on fork length or weight, as was observed for the 9 mm tag (which was implanted into slightly larger fish).

The specific growth rate analyses indicated that PIT tagged Dworshak fish grew 0.52%/week more than DAT tagged fish during the first seven weeks, which was significantly greater (Table 2.4e), despite the non-significant finding for the fork length and weight comparisons during the same time interval. From week 7 to week 23, however, specific growth rates were not statistically distinguishable for the two treatments, and both groups grew at approximately the same rate; thus recovery from the initial set back in growth occurred in less than seven weeks post-surgery.

The initial mean fork length and weight of PIT tagged and DAT tagged Yakima smolts were not significantly different (Table 2.4c, d, Figure 2.7). The mean fork length and weight of PIT tagged smolts five weeks post surgery also were not significantly greater than DAT tagged fish.

The specific growth rate analyses indicated that PIT tagged Yakima fish grew 0.48%/week more than DAT tagged fish during the first five weeks, which was significantly greater, despite the non-significant finding for the fork length and weight comparison during the same time interval (Table 2.4e). As the study ran for only five weeks, we were unable to monitor growth for a second interval. However, compared to the 9 mm tag, the initial set back in growth rate was not as large for the 7 mm tag (1.3% vs. 0.48%).

2.3.2 Tag effects- Field studies

In 2006 and 2008, Columbia River basin spring Chinook salmon smolts were tagged with 9 mm (minimum size 140 mm FL) and 7 mm (minimum size 130 mm FL) acoustic tags, respectively, released into the river, and tracked as far north as Alaska. Although smolts were detected on the Vancouver Island line (at Lippy Point), survivorship for these IR groups was estimated to coastal Washington (the Willapa Bay detection site, Figure 2.8). To determine if tags may have affected survival we: (1) plotted the estimated survival of 5 mm size classes at each detection site for each population in each year for a visual comparison of survival by size; (2) used initial fork length as an individual covariate within a linear model framework in *Program MARK* to statistically test the hypothesis that smaller fish have lower survival due to tag burden; and (3) compared our in-river survival estimates obtained with acoustic tags to other studies that obtained survival estimates with PIT tags.

2.3.2.1 Survival by size class

9 mm transmitter. Survival of Dworshak IR smolts tagged with 9 mm transmitters was variable across all size classes at each detection site, and smaller size classes did not appear to have lower survival (Figure 2.9). Similarly, survival of Yakima IR smolts was variable across all size classes at each detection site as well (Figure 2.9). The smallest Yakima smolts size class had the lowest survival; however, it was made up of only six fish. It is possible that fish at the lower limit of our size requirements of 140 mm may have suffered from tag induced mortality (Welch et al. 2007); however, it is difficult to draw conclusions about this size class because of the low sample size. If smaller fish had reduced survival then we would have expected survival to increase with increasing body size, however, the largest groups did not have the highest survival. Thus, the 9 mm acoustic transmitter did not appear to differentially affect survival over the size range tested.

7 mm transmitter. Survival of Dworshak IR smolts tagged with 7 mm transmitters was variable across all size classes at each detection site (i.e., there was no general trend in survival), with the exception that the largest size class (155-159 mm) appeared to have consistently higher survival than all other size classes (Figure 2.10). Survival of Yakima IR smolts was variable across all size classes at each detection site; however, the largest Yakima size class had the lowest survival, in contrast to Dworshak. The sample size of the largest Yakima size class was low, however, and therefore it is difficult to draw conclusions about this size class. In general, survival did not increase with increasing body size, and thus the 7 mm acoustic transmitter did not appear to differentially affect survival across the size range tested.

2.3.2.2 Fork length as a covariate in survival models

To test the hypothesis that smaller IR fish have lower survival due to tag burden we used an information theoretic approach to compare the fully time-varying CJS survival models to additive and interaction models that included fork length as a covariate.

9 mm transmitters. For Dworshak IR smolts, the most parsimonious survival model was the fully time (i.e., line) varying CJS model (Table 2.5). The ΔAIC of the additive model with fork length as a covariate was ~2, and the deviances of the models were nearly identical which implies that there was no difference in the models. For Yakima IR smolts, there was some support for the additive survival model with fork length as a covariate (ΔAIC=0.83); however, the most parsimonious model was the fully time varying CJS model. Therefore there is no support that smaller smolts suffered higher mortality.

7 mm transmitters. For Dworshak smolts implanted with 7 mm transmitters, the most parsimonious survival model was the additive model with fork length as a covariate, which provided support that as fork length increased survival increased; however, Figure 2.10 demonstrates that the largest size class had consistently higher survival, and therefore we re-ran the analysis and excluded smolts that were 155-159 mm FL to determine if size was a factor across all of the other sizes (from 130-154 mm FL). When we excluded the largest size class, the fully time varying CJS model was the most parsimonious model (Table 2.5). The AIC of the additive model with fork length as a covariate was <2, and the deviances of the models were nearly identical which implies that there was no additional support for a model with FL as a covariate.

For Yakima IR smolts, there was little support for the additive model with fork length as a covariate; the most parsimonious model was the fully time varying CJS model (Table 2.5). There is no statistical support that smaller smolts suffered higher mortality.

2.3.2.3 Comparative survival of in river migrants using acoustic tags and PIT tags

9 mm transmitter. Survival of acoustic tagged smolts was similar to PIT tagged smolt survival (Figure 2.8). We compared our Dworshak spring Chinook salmon acoustic survival rate (S/km) to the Pacific Ocean with NOAA's PIT tag survival rate from Dworshak NFH to Bonneville Dam in 2006. We chose to compare survival rate rather than survivorship estimates because distances to detection sites for each tag type vary, but we present the estimates of apparent survivorship in parentheses to inform the interpretation. We found no difference in estimated survival rate ($p>0.05$; Figure 2.8) between acoustically tagged smolts to the Pacific Ocean (survivorship to Willapa Bay, 911 km from the release site, was 27.5%, SE=6.9%) and PIT tagged smolts to Bonneville Dam (survivorship from release, a distance of 577 km, was 40.8%, SE=6.1%). Due to tag limitations we could only tag smolts >140 mm FL (i.e., we could not tag the entire size range) and our release dates were during the latter part of the spring Chinook salmon migration. Further, we released Dworshak smolts from Kooskia Hatchery 60 km upstream (purely for logistical reasons); however, comparing results from the two studies provided a second approach to assessing the reasonableness of our survival estimates by assessing whether our acoustically tagged smolts had lower survival than smolts tagged with PIT tags, a much smaller tag.

PIT tag survival estimates of Yakima spring Chinook salmon released from Cle Elum Hatchery and recaptured at CJFM in Prosser, WA, were available to McNary Dam and John Day Dam in the lower Columbia River. Although survival of PIT tagged fish could only be estimated to as far as John Day Dam (survivorship to John Day, 268 km from the release site, was 51.8%, SE= 4.3%,) the estimated survival rate calculated from acoustic tag estimates for the entire lower Columbia River and into the ocean (survivorship to Willapa Bay, 655 km from release, was 27.9%, SE=7.0%,) is consistent with the estimated PIT tag survival rate to John Day Dam ($p>0.05$; Figure 2.8).

7 mm transmitter. We compared our Dworshak spring Chinook salmon acoustic survival estimates to the river mouth and to Willapa Bay (survivorship to Willapa Bay was 11.8%, SE=2.1%) to NOAA's PIT tag survival estimates in the river to as far as Bonneville Dam (survivorship to Bonneville Dam was 29.7%, SE=5.0%) in 2008 and found no difference in estimated survival rate (p>0.05; Figure 2.8). Because we used the smaller 7 mm tag we were able to tag smolts as small as 130 mm FL, and we were able to tag and release fish approximately one week earlier than in 2006. Therefore our release dates coincided with the peak of the Snake River spring Chinook salmon run but were still several weeks after NOAA PIT tagged smolts were released from Dworshak NFH.

PIT tag survival estimates for Yakima River spring Chinook salmon were available to McNary Dam and John Day Dam in 2008. The estimated survival rate from release to John Day Dam (survivorship was 66.7%, SE=5.5%) was not significantly different than the estimated survival rate of acoustic tagged Yakima River spring Chinook salmon smolts from release to Willapa Bay (survivorship of acoustic tagged smolts to Willapa Bay was 17.3%, SE= 2.6%; p>0.05; Figure 2.8).

2.3.2.4 Survival estimates of IR spring Chinook salmon corrected for tag loss in captive studies

How much does tag loss and mortality due to the surgical procedure affect survival estimates for IR smolts? All estimates of K (live, tagged animals in the captive study) were >98% at the time when migrating IR smolts would have passed the Willapa Bay detection line. K was greater than >97% when Dworshak smolts migrated passed Lippy Point (in 2006 and 2008), and 85% when Yakima smolts passed Lippy Point in 2006 (in 2008 the Yakima tag study was only held for five weeks which was insufficient time to estimates K to Lippy Point). In general, the difference between adjusted and unadjusted survival estimates is negligible and well within the 95% confidence interval of the unadjusted survival estimates for both populations in both years (Figure 2.11). Dworshak smolts had zero mortality and tag loss in captivity within the first month in 2006 and 2008, and thus the survivorship estimates to Willapa Bay are not altered (28.5% in 2006, 11.8% in 2008). Beyond one month there was minor tag loss and mortality of captive Dworshak smolts in 2006 and therefore minimum survival of migrating smolts would increase 2%, from 1.49 to 1.52% at the Lippy Point detections site. In 2008 there was no tag loss or mortality in captive smolts at the time when migrating smolts were passing Lippy Point and no adjustment is necessary (minimum survival to Lippy Point was 3.1%).

For Yakima smolts in 2006 and 2008, the percent of fish available for detection based on captive studies was 99% at Willapa Bay. If we account for this slight reduction in detectability, survivorship would increase from 27.9% to 28.1% at Willapa Bay in 2006, and from 17.4% to 17.6% in 2008. Although combined tag loss and mortality was 15% after 45 days in captivity for Yakima smolts in 2006, the minimum survival of free ranging smolts to Lippy Point would only increase from 0.7% to 0.8% (we could not assess medium term tag loss for Yakima smolts in 2008).

2.4 Discussion

Overall, short term (<1 month) mortality and tag loss following surgical implantation was minimal for 9 mm dummy acoustic transmitters implanted into smolts ≥140 mm FL and weighing 5.2-10.4% of the body weight. The short term effects of the smaller 7 mm transmitter on tag retention and mortality were negligible for smolts ≥130 mm FL implanted with 7 mm dummy transmitters, and weighing 2.8-7.6% of the weight of the fish. Therefore, estimates of survival of migrating smolts over long distances and up to one month are reasonable within these size limitations.

Medium term (30-90 d) mortality and tag loss was minimal for Dworshak smolts tagged with both transmitter sizes. Yakima smolts tagged with 9 mm transmitters were more susceptible to medium term tag loss, but nearly three months post-implantation 84% of the tags were still retained. We believe that the 16% tag loss may have been due to the sutures tearing through the skin, leaving a large open wound through which the transmitter could escape. While conducting surgeries we noticed that the skin and musculature of the body wall of Yakima smolts was much thinner and more delicate than what we observed in the more robust Dworshak population, and this may have made fish more susceptible to chafing by the sutures. Further, we noted that 60% of the Yakima DAT tagged fish had one suture that had either ripped out or was visibly ripping through the skin 86 days post-surgery. Tag loss and mortality, however, were not a function of size (i.e., smaller fish no more susceptible than larger fish), and damage did not appear to be caused by the transmitter pushing against sutures (see Figures 2.5 b, c).

Water temperature may contribute to the more fragile skin of the Yakima smolts, as Dworshak smolts were held in colder water than Yakima smolts and showed only minor medium term effects from the 9 mm tag. Both populations were, however, held at water temperatures that were comparable to their respective river temperatures; therefore it is possible that the Yakima River population has inherently more delicate skin. It has been demonstrated that fish implanted with transmitters have significantly higher occurrence of tag loss at higher temperatures (Bunnell and Isely 1999; Knights and Lasee 1996). In bluegills *Lepomis macrochirus,* transmitters were expelled through necrotic muscle tissue for fish held at 20°C (Knights and Lasee 1996), and in rainbow trout *O. mykiss* held at the same temperature, transmitters were expelled through the incision (Bunnell and Isely 1999). There is, however, contrasting evidence that fish held in warmer water heal faster after injury (Anderson and Roberts 1975). As we observed transmitter expulsion at the torn suture site, it is difficult to discern whether warmer temperatures caused the musculature to become more delicate and susceptible to chafing by sutures.

Ideally, the use of a more rapidly dissolving suture would likely address this issue, but commercially available absorbable sutures are designed for use in mammals. In mammals, these sutures rapidly lose their strength; however, the sutures do not readily degrade in fish held in cold water. Had the sutures degraded as desired, the tearing we observed in Yakima River fish would likely not have occurred and tag loss would have been lower. This does not appear to be a common problem among researchers that use surgical implantation as a method of transmitter attachment (Wagner and Cooke 2005). We suspect that the wound caused by the sutures may have also contributed to mortalities, as we witnessed several fish with the pyloric caeca or liver protruding through the wound. We also witnessed several live fish that had lost transmitters and had well healed wounds where the transmitter exited; therefore, transmitter expulsion did not always kill the fish.

We were unable to assess medium or long term tag effects of the 7 mm transmitter on Yakima smolts, as the tag study was inadvertently terminated on day 37. Although survival and tag retention was >98% for the first month of the study, nine DAT and four PIT tagged fish died during the last week. Because PIT tagged fish also died in the final days of the study we hesitate to attribute the death of DAT tagged fish (in the last five days) to the transmitters or the surgical procedure. On the final day of the study, we also observed potential tag expulsion. Unlike the 9 mm DAT, tag expulsion of the 7 mm DAT in Yakima smolts was beginning to occur at a location away from the incision site (a pore had started to form in the body wall). This mechanism of tag expulsion has previously been reported by Lucas (1989), Moore et al. (1990), Welch et al. (2007), and others (see Jepsen et al. 2002). Unfortunately we were unable to quantify tag loss through the body wall in 2008 to compare to the 2006 tag study results.

Although we were not able to observe medium/long term tag effects, there is support that 7 mm transmitters had less of an effect on the Yakima River population than 9 mm transmitters. For example, the mean FL of PIT tagged and 9 mm DAT tagged fish differed significantly after six weeks, whereas mean FL five weeks post-implantation with the 7 mm tag was not significantly different. Further evidence that 7 mm transmitters had less of an effect is reflected in the growth rates; during the first interval after tagging, PIT tagged smolts grew 1.3% per week more than 9 mm DAT tagged smolts and only 0.48% per week more than 7 mm DAT tagged fish.

In Dworshak smolts tagged with both tag types, growth rate rebounded for DAT tagged fish after an initial period of slower growth following surgery. An initial period of impaired growth followed by growth at the same rate as control fish was also observed in fall Chinook salmon smolts implanted with radio transmitters that weighed up to 5.5% of the body weight of the fish (Adams et al. 1998a). Tag loss may thus have the potential to have some relatively small effects on long term tracking studies (>3 months), when we consider only tag effects in captivity. It is possible that tag loss and mortality are higher in the wild, but the contribution of this source of error needs to be put in perspective relative to the size of the survival decline being measured in free-ranging smolts. Our results indicate that short or medium-term studies would be minimally affected by tag loss or tag induced mortality even for Yakima smolts tagged with 9 mm transmitters.

We found no strong evidence for a relationship between size and survival for IR smolts. Survival by 5 mm size class was variable for both transmitter types and for both populations and there was little support for survival models that incorporated body length as a covariate.

There was only one exception to this general observation that did show some evidence for larger tagged smolts surviving better: in Dworshak smolts implanted with 7 mm tags in 2008, the largest size class (155-159 mm FL) had higher survival than all other size classes. The survival model results were consistent with this finding: when we included body size as a covariate and used all size classes tagged, this model had more support; however, when we excluded fish in the 155 to 159 mm FL size range, there was little support for the fork length model. This indicates that size did not affect survival of fish between 130 and 154 mm FL.

This survival difference (the largest size class with the highest survival) appeared to develop in the first migration interval between the release site and Lake Bryan (downstream of Lower Granite Dam) and persisted as fish migrated downstream. It is possible that larger fish escaped post-release predation or migrated more quickly resulting in higher survival; however, we did not see this trend in 2006 with the 9 mm tag where the largest smolts had the lowest survival in the same migration segment. In summary, only one of four comparisons showed evidence for larger fish having improved survival, and this result was restricted to the largest size class tagged. We thus have little evidence that the surgically implanted tags of the size we used were imposing a substantial burden on smolts above our specified size thresholds.

Although captive fish do not encounter the stressors that IR fish must contend with in the wild, captive studies are the most practical method available for quantifying tag loss and mortality following surgical implantation of a transmitter. We used captive fish data to infer tag loss and tag mortality in actively migrating smolts and found that survival estimates of IR smolts to Willapa Bay (40 km north of the Columbia River mouth) were unlikely to be affected by tag loss or tag mortality because tag retention and survival of captive groups was near 100% during the first month. Nearly all (96% in 2006 and 92% in 2008) of the Yakima smolts had migrated rapidly down the river and across the Willapa Bay line by day 30. Dworshak fish had farther to travel to reach the Willapa Bay line; however, by day 45 most fish had passed Willapa Bay (97% in 2006 and 88% in 2008).

In 2006 by day 60, all Dworshak fish had passed Lippy Point on northern Vancouver Island. The proportion of live, tagged, captive fish was 95% at day 45 and day 60, indicating that only 5% of IR fish may not have been available for detection (combined smolt mortality and tag loss) at both ocean lines. In 2008 by day 70, 88% of Dworshak smolts had reached Lippy Point, and 100% of the captive fish were alive and tagged; therefore, all fish migrating past these detections site were presumably detectable.

In 2006 two Yakima fish were detected at Lippy Point and had passed by day 50. The proportion of live, tagged, captive fish was 85% at day 50, indicating that 15% of IR fish may not have been available for detection at Lippy Point. In 2008 the mean travel time of Yakima smolts to Lippy Point was 56 days; however, we are unable to estimate potential nondetection since the captive tag study was terminated on day 37.

While it was not possible to directly measure tag loss or tag-induced mortality in free ranging salmon smolts (i.e., IR), it was possible to further assess tag effects by comparing the survival estimates for IR fish with that of PIT tagged smolts. As PIT tags have become the standard method for measuring salmon survival in the Columbia River, it is reasonable to compare acoustic tag performance to PIT tag performance. For instance, a short term comparative survival study that used acoustic tags (similar in size to the 7 mm tag) and PIT tags found no difference in survival through a major hydropower dam in the Columbia River(Steig et al. 2005). The authors also noted that the sample size of PIT tagged fish used to achieve the same precision was two orders of magnitude greater than acoustic tagged fish (90000 vs. ~800). Therefore, for our study, we used PIT tag survival estimates estimated independently for the same populations in the same migration year (see Methods). Although release times and mean fish size were not identical for the two groups, the PIT tag estimates offer an alternative method for estimating survival within the Snake and Columbia rivers using a much smaller tag that does not require surgical implantation (PIT tags are generally injected using a large-gauge hypodermic needle). We can thus use PIT tags as a benchmark of survival using very small tags. As our estimated decline in smolt survival with distance are consistent with the decline in survival of PIT tagged smolts with distance (see Figure 2.8), the negative effects of surgical implantation of our tags appear to be very minimal in IR smolts, at least to the last dam where PIT tag-based estimates of survival can be obtained for Dworshak smolts (Bonneville) and to John Day Dam for Yakima smolts. Below Bonneville Dam, no comparison of PIT and acoustic tagged smolts is possible, but the smooth decline in survival obtained with acoustic tags with distance downstream of Bonneville Dam does not suggest that there was a sudden decrease in survival for acoustically tagged smolts.

Other means of quantifying tag effects include measures of swimming performance, predator avoidance, and physiological indices. Swimming performance (critical swim speed, U_{crit}) has been tested in several species of salmonids and results indicate that juvenile salmon tagged with acoustic transmitters (representing various tag burdens) are capable of attaining U_{crit} values comparable to control groups (Moore et al. (1990), species: Atlantic salmon, tag burden: ~2.2% of fish weight; Brown et al. (2006) fall Chinook salmon, 10.7%; Anglea et al. (2004) juvenile fall Chinook salmon, 6.7%; Chittenden et al. (2009), coho *O. kisutch*, 8%). Predator avoidance experiments were also conducted by Anglea et al. (2004) which demonstrated that juvenile fall Chinook salmon tagged with acoustic transmitters and exposed to adult rainbow trout were not consumed in significantly higher proportions than the untagged control group. Adams et al. (1998b), however, found that juvenile fall Chinook salmon of similar size, implanted with radio transmitters resulting in similar body burden by weight, were eaten by smallmouth bass *Micropterus dolomieu* in greater numbers. These contrasting results could be due to different experimental design, different predators, or the presence of the 31cm antenna trailing behind the radio tagged fish in Adams et al. (1998b), which may have aided in prey detection and subsequent capture.

To measure physiological response to surgery and tag presence, blood samples of tagged and control fish are often taken following a specified period of time (e.g., soon after tagging and at the end of a study) or post-exercise. Hematocrit level is a common metric used to evaluate stress response, and several studies have shown that after 2-3 weeks hematocrit levels of tagged juvenile salmon were within normal ranges found in salmonids and were comparable to control fish (Chittenden et al. 2009; Martinelli et al. 1998; Moore et al. 1990). As the smolts tagged in these studies had similar tag burdens to smolts presented in this study, these earlier studies suggest that stress due to tagging may subside within several weeks after surgery.

The use of different acoustic tags represents a trade-off between biological and technical limitations on any telemetry system designed to study fish movements and survival. Generally speaking, smaller tags impose less of a burden on the animal that they are implanted in, but smaller tags are also harder to detect, for several reasons: (1) smaller transducers will not as efficiently convert electrical power from the battery into sound waves at the frequencies of primary interest for marine telemetry systems (as they are farther off-resonance), so the acoustic power output (loudness) will drop; and (2) smaller tags necessarily have smaller batteries, which means that tag lifespan is also reduced relative to what could be obtained with a tag containing larger batteries, unless transmission frequency is reduced to compensate.

Reducing the tag size makes it harder to detect tags and also tags are detectable for a shorter period of time. To achieve the same probability of detecting the passage of a tagged fish means that additional economic investments must be made in receivers to use in constructing the individual sub-arrays forming the telemetry system in order to compensate for the reduced signal strength (range) of the tags. Similarly, smaller tags place greater physical limits on the geographic range that migrating salmon smolts can be successfully studied over. Our current results indicate that dummy V7 and V9 Vemco acoustic tags do not have a substantial influence on survival rates for free-ranging or hatchery-reared smolts ≥130 and ≥140 mm, respectively, relative to the other sources of mortality, and that these tags can be used in studies potentially lasting for five months or more in duration. Similar survival trials have shown that salmon smolts down to 100 mm FL (Chittenden et al 2008) can be tagged with Vemco V6-sized tags; this, combined with our results, suggests that telemetry arrays capable of effectively measuring salmon survival are now technically feasible for many stocks and species of wild Pacific salmon, and not just for hatchery smolts ≥130 mm FL. However, consideration of the increased cost of such systems means that researchers need to carefully design these systems in order to make them as economical as possible.

In conclusion, tagging salmon smolts to measure survival beyond rivers and into the ocean requires both successful surgical implantation of transmitters and medium to long-term (>1 month) retention of tags. A critical requirement is that the combined effect of surgery and tag size does not affect growth and survival. We used multiple approaches to quantify the effect of tag implantation on survival for Columbia River spring Chinook salmon smolts, including captive smolt studies at hatcheries, a comparison of the statistical fit of an alternative survival model

(FL as an individual covariate) for free-ranging smolts, and a comparison with independent survival estimates obtained from PIT tags. Overall, tagging effects were minimal for the size range of fish that we tagged (7 mm tag: $\geq$ 130 mm; 9 mm tag: $\geq$ 140 mm). We also found that different populations within the same river basin may not have a completely equal response to tag implantation, with the Yakima smolts having a greater incidence of sutures tearing through the skin and subsequent tag loss over time. Finally, adjusted survival estimates (S_K) for IR smolts to reflect tag loss and smolt mortality observed in captive populations are well within the 95% confidence intervals of unadjusted survival estimates, indicating that these sources of uncertainty are likely very small relative to the overall mortality we have measured.

Our results indicate that acoustic telemetry appears to be a reliable method for measuring survival of free-ranging smolts and testing alternative hypotheses concerning the cause of the poor ocean survival of some populations of smolts originating from the Columbia River basin (Schaller et al. 1999). Measurement of Chinook salmon smolt movement or survival over periods of many months appears to be quite feasible when smolts are implanted with 9 mm transmitters <11.5% of body weight and 7 mm transmitters <7.3% of body weight. While movement measurements do not require precise estimation of the proportion of tagged animals reaching a sub-array, the more demanding task of estimating smolt survival over time periods up to at least three months post-surgery appears to be feasible, with estimates of survival apparently not substantially compromised by tagging-induced mortality or tag loss, compared to the smaller PIT tag. Future, long-term, survival studies (> six months) that are intended to quantify ocean survival beyond the three-month time period should also include long-term tag retention studies in hatcheries to establish whether smolt survival and tag retention on longer time scales is also feasible; recent work on coho salmon (Chittenden et al. 2009) indicates that high survival and tag retention out to at least 8 months post-surgery is feasible.

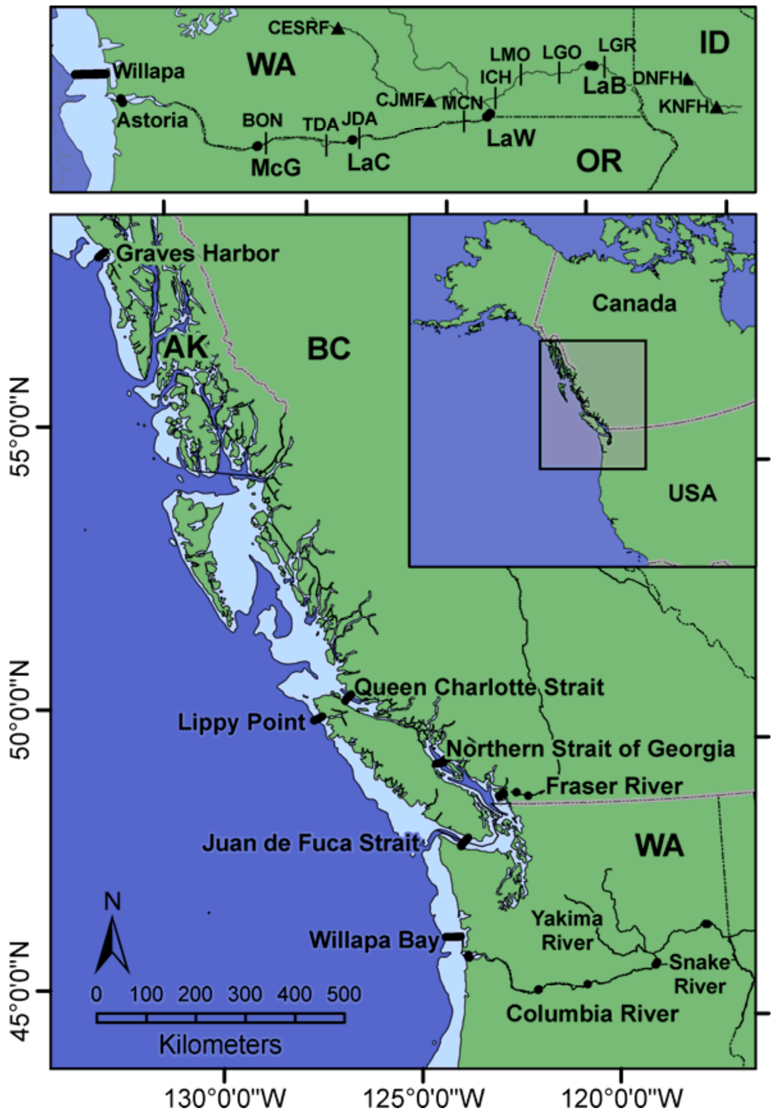

Figure 2.1. Pacific Ocean Shelf Tracking (POST) acoustic array. Acoustic tagged smolts were detected in the Columbia River Basin and at ocean sites at Willapa Bay, Lippy Point and Graves Harbor. The inset shows the location of the hatcheries (DNFH=Dworshak National Fish Hatchery, CESRF=Cle Elum Supplementation and Research Facility), release sites (CJMF=Chandler Juvenile Monitoring Facility, KNFH=Kooskia National Fish Hatchery); acoustic detection sites (McG=McGowan's Channel (10 km below Bonneville Dam), LaC=Lake Celilo (7 km below John Day Dam), LaW=Lake Wallula (10 km below the confluence of the Snake and Columbia rivers), LaB=Lake Bryan (14 km below Lower Granite Dam); and dams (BON=Bonneville, TDA=The Dalles, JDA=John Day, MCN=McNary, ICH=Ice Harbor, LMO=Lower Monumental, LGO=Little Goose, LGR=Lower Granite) within the Yakima, lower Snake and Columbia rivers. The continental shelf (depths <200 m) is shaded.

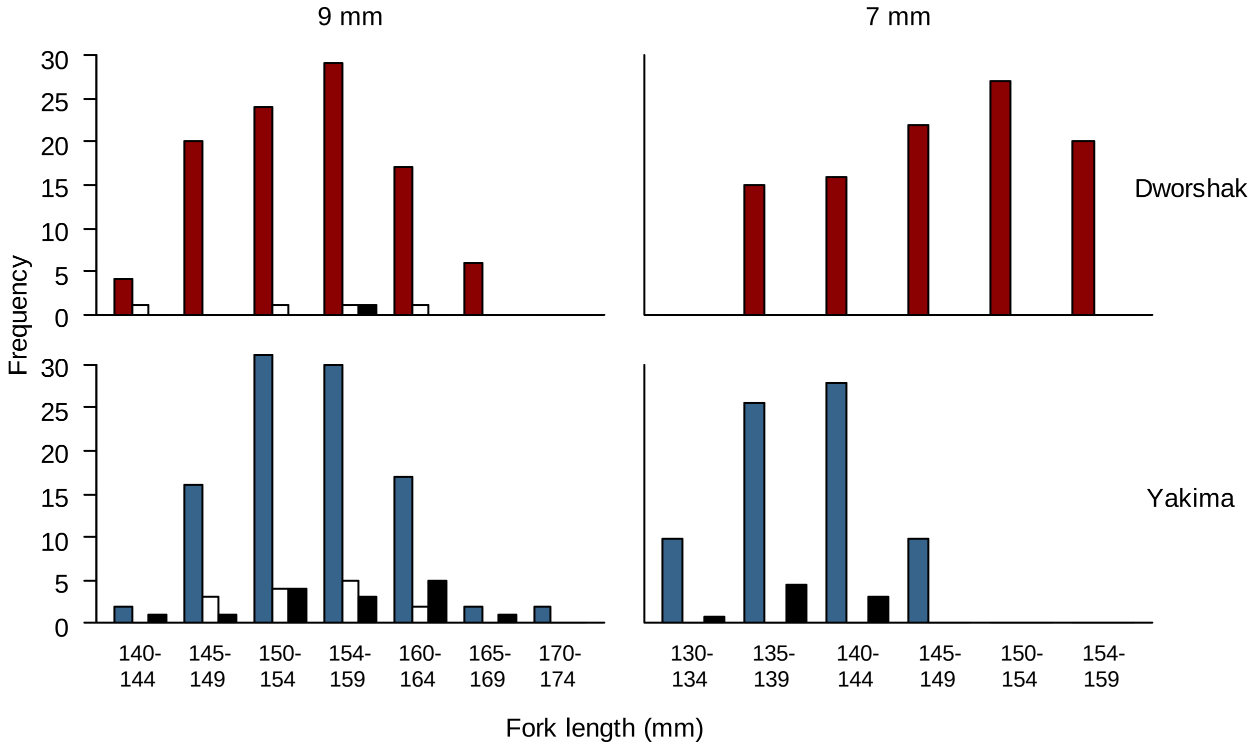

Figure 2.2. Size distribution of Dworshak (red bars) and Yakima (blue bars) spring Chinook salmon tagged with 9 mm and 7 mm dummy acoustic transmitters (2006 and 2008, respectively), initial size of smolts that expelled tags (white bars), and initial size of fish that died during the tag study (black bars). Dworshak mortalities exclude deaths due to “ich” (a freshwater parasite) in 2006 and precocial male maturation in 2008. There was no tag loss in 2008.

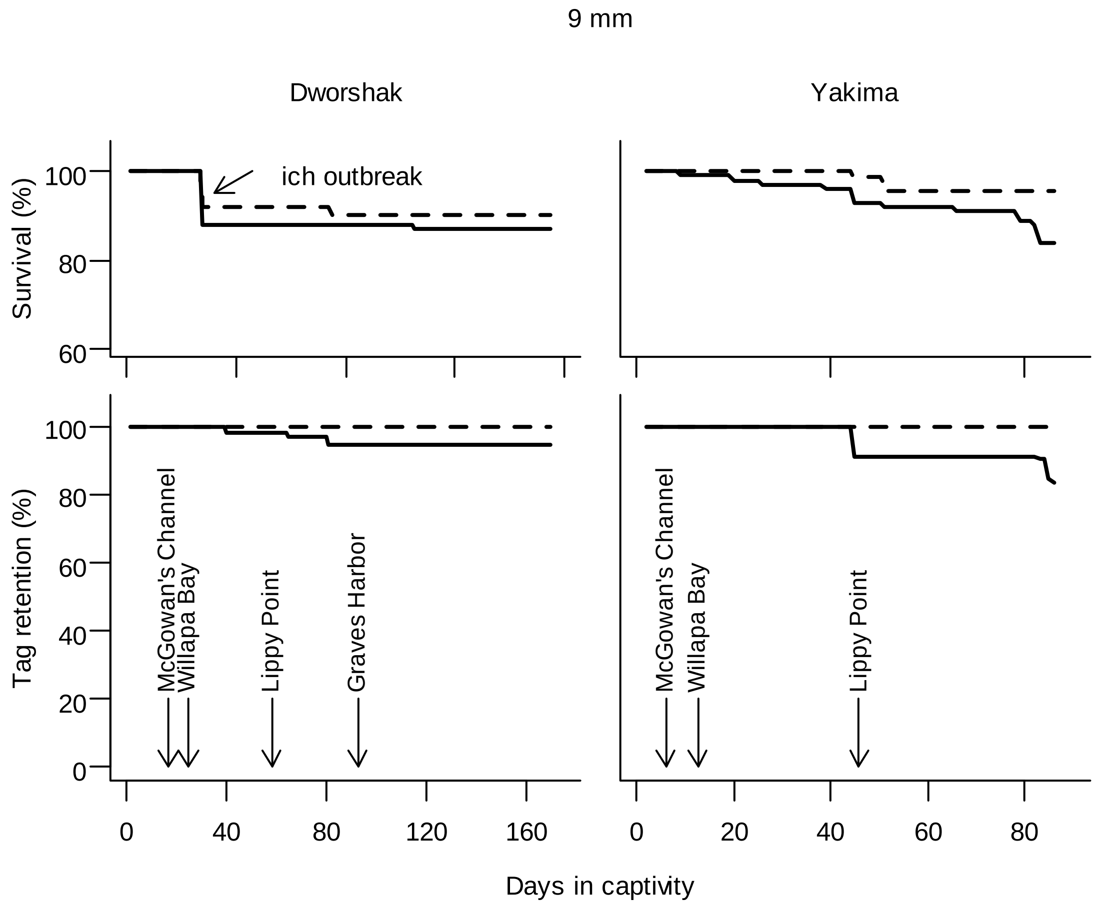

Figure 2.3. Tag retention and survival for Dworshak and Yakima spring Chinook salmon tagged with 9 mm dummy acoustic transmitters (solid lines) and passive integrated transponder tags (dashed lines) in 2006. The arrows on the tag retention plots are reference points that indicate the mean day of arrival of in-river migrants to each of the acoustic detection lines. Yakima River smolts were not detected at Graves Harbor. Note the y-axis scale on the survival plot does not go to zero.

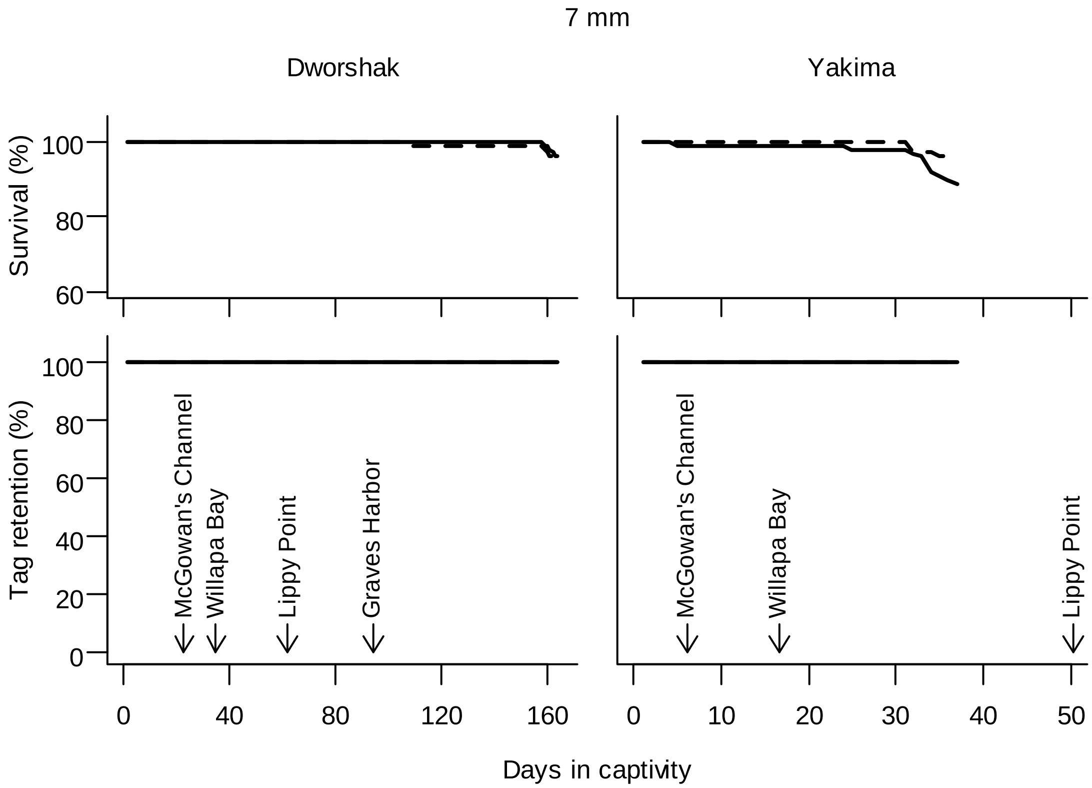

Figure 2.4. Tag retention and survival for Dworshak and Yakima spring Chinook salmon tagged with 7 mm dummy acoustic transmitters (solid lines) and passive integrated transponder tags (dashed lines) in 2008. The arrows on the tag retention plots are reference points that indicate the mean day of arrival of in-river migrants to each of the acoustic detection lines. Yakima River smolts were not detected at Graves Harbor. Note the y-axis scale on the survival plot does not go to zero.

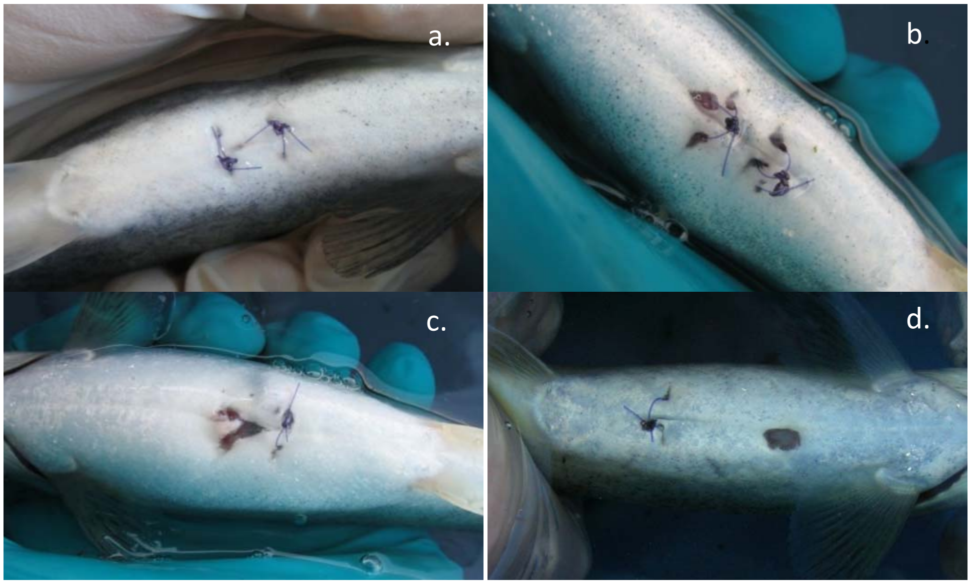

Figure 2.5. Post-surgery healing. a. Typical Dworshak spring Chinook salmon smolt 11 weeks post-surgery with healed incision and 9 mm dummy acoustic transmitter (DAT) and sutures still intact, b. After 12 weeks in captivity, Yakima Chinook salmon implanted with a 9 mm DAT have a completely healed incision, although sutures have not dissolved and are tearing through the skin of some fish, c. Yakima River spring Chinook salmon 12 weeks post-surgery with sutures torn to incision leaving wound for 9 mm transmitter to exit. The relatively delicate skin of Yakima Chinook salmon may be an intrinsic trait; however, suture tearing may be attributed to warmer water temperatures experienced at Prosser Hatchery. As Yakima smolts migrated into the ocean only days after release, they would have experienced cooler water temperatures within weeks of surgery. As well, it is likely that tag loss would have been minimal during the time when fish migrated over the array (see Figure 3), d. Yakima River spring Chinook salmon implanted with a 7 mm DAT five weeks post-surgery; this fish is forming a pore anterior of the surgery site in which to potentially expel the transmitter. (Suture tearing and tag expulsion did not occur in Dworshak fish.)

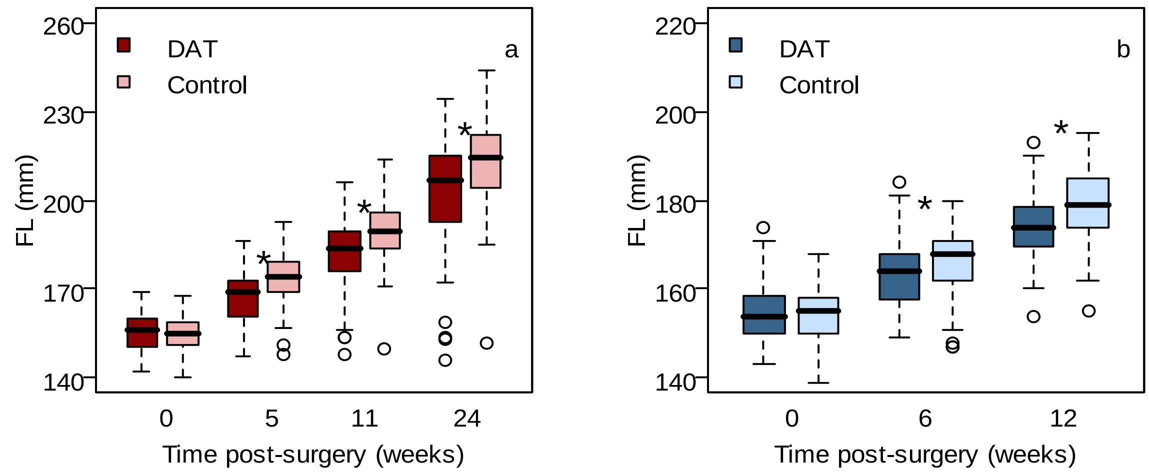

Figure 2.6. Boxplots (median, quartiles, and 95% confidence interval) of fork length (FL) for Dworshak (a) and Yakima (b) spring Chinook salmon tagged with 9 mm dummy acoustic transmitters (DAT) and passive integrated transponder tags (Control) in 2006. Asterisks indicate a difference at a 0.05 level of significance. Open circles represent precocious fish that were not included in the analysis. Boxplots of weight are not shown, but see Table 2.4d.

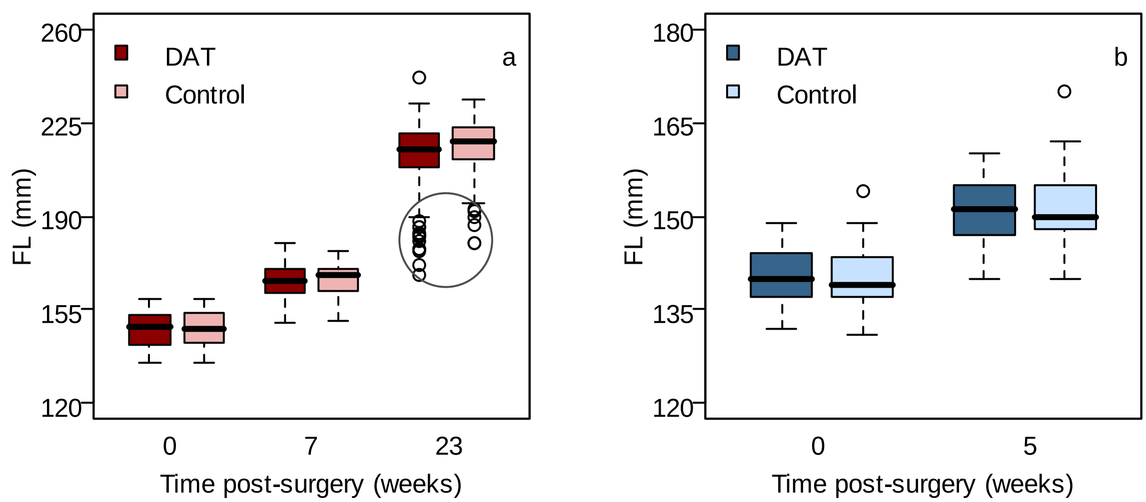

Figure 2.7. Boxplots (median, quartiles, and 95% confidence interval) of fork length (FL) for Dworshak (a) and Yakima (b) spring Chinook salmon tagged with 7 mm dummy acoustic transmitters (DAT) and passive integrated transponder tags (Control) in 2008. There was no significant difference in FL of DAT and control groups for either population during the study. The circle in (a) shows the FL's of precocial males which were excluded from the significance test. Open circles represent precocious fish that were not included in the analysis. Boxplots of weight are not shown, but see Table 2.4d.

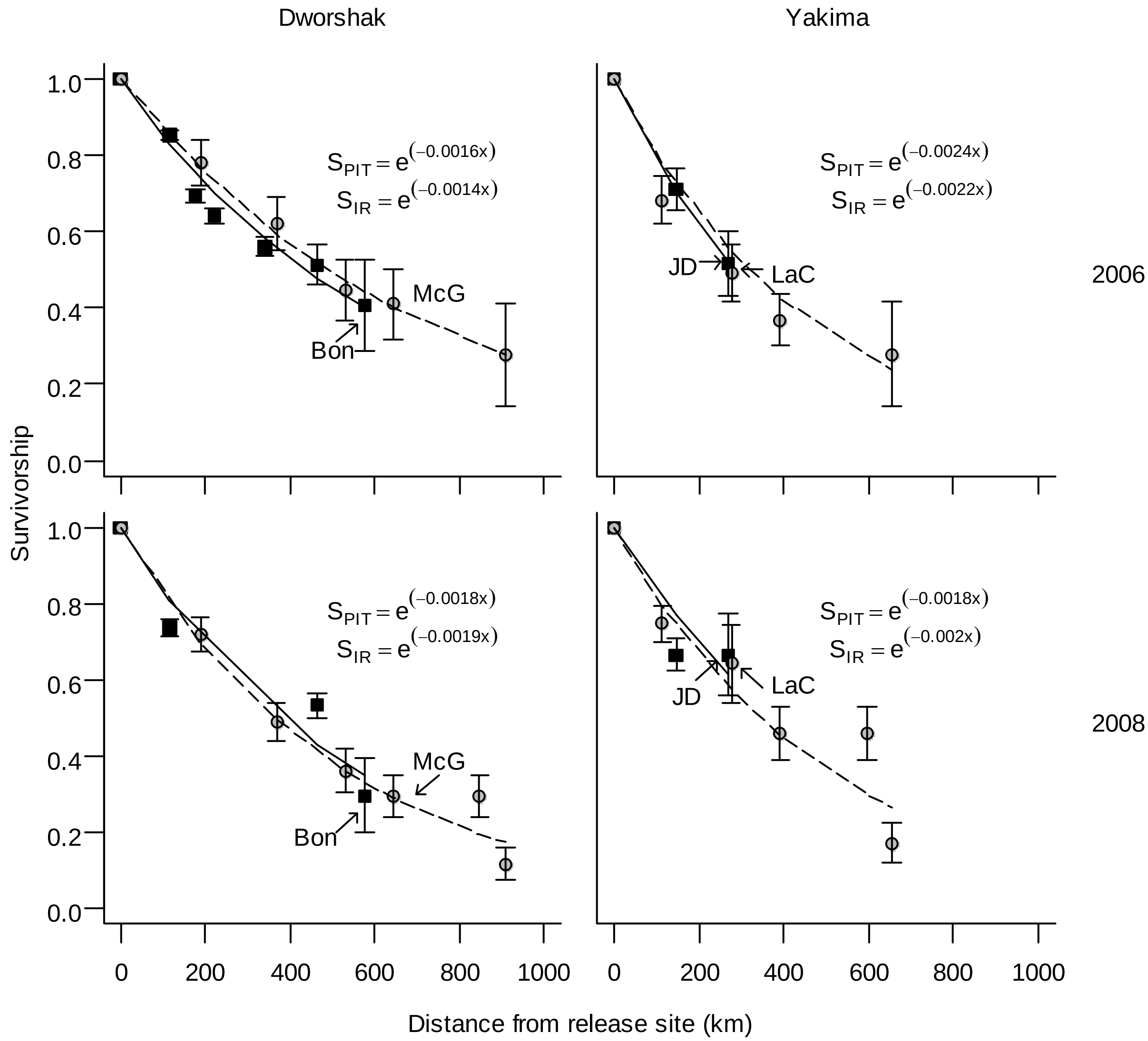

Figure 2.8. Survivorship of Dworshak and Yakima spring Chinook salmon in 2006 and 2008. Survivorship of acoustic tagged smolts (grey circles, dashed line) was estimated to coastal Washington (Willapa Bay). Survivorship of passive integrated transponder (PIT) tagged smolts (black squares, solid line) was estimated to Bonneville Dam (Bon) and John Day (JD) for Dworshak and Yakima smolts, respectively. Survivorship curves are calculated by fitting the log-transformed regression $S(x)=e^{-bx}$, where x is distance from release site. (PIT tag survival estimates for Dworshak are from Steve Smith at NOAA/National Marine Fisheries Service/Northwest Fisheries Science Center and Faulkner et al. 2008, and Yakima PIT tag estimates are from David Lind at Yakama Fisheries). IR =in-river treatment groups presented in this study, McG=McGowan's Channel (10 km downstream of Bon), LaC=Lake Celilo (7 km downstream of JD). Error bars are 95% confidence intervals.

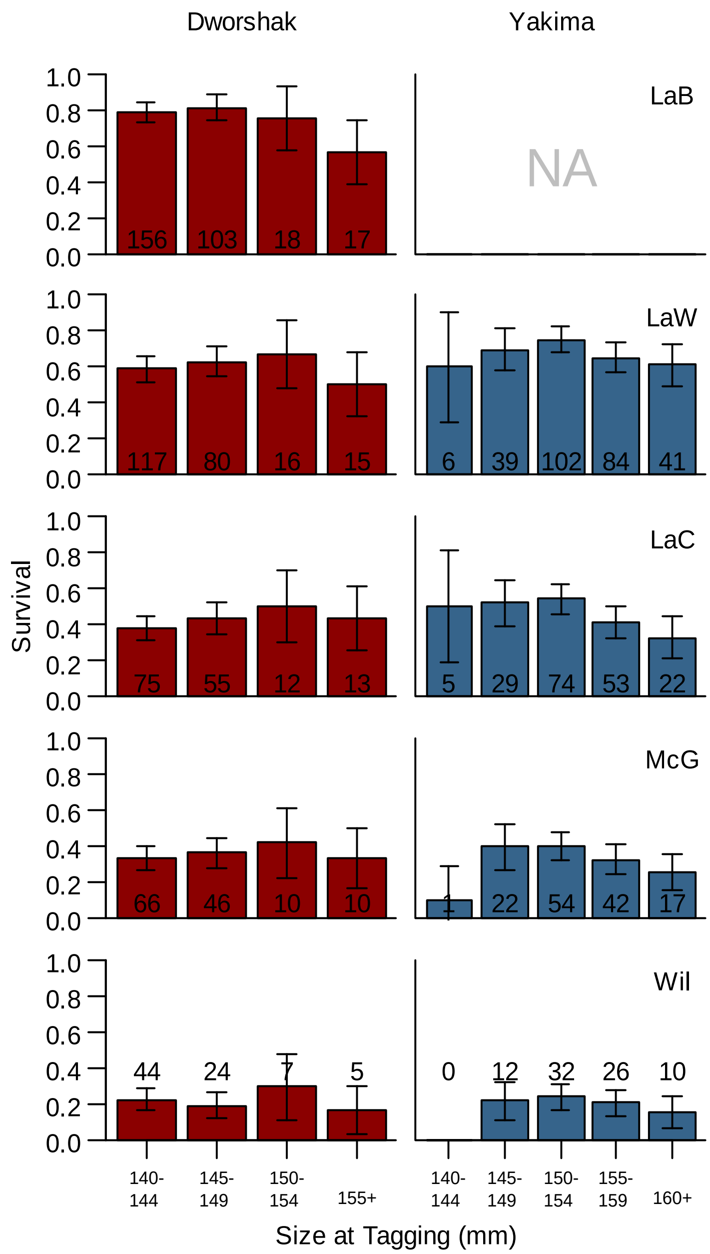

Figure 2.9. Survival in 2006 by size class (fork length) of migrating Dworshak (red) and Yakima (blue) spring Chinook salmon tagged with 9 mm acoustic transmitters. The numbers on or above the bars indicate the estimated number of fish detected within each size class at each detection site. LaB=Lake Bryan, LaW=Lake Wallula, LaC=Lake Celilo, McG=McGowan's Channel, Wil=Willapa Bay. Error bars are 95% confidence intervals.

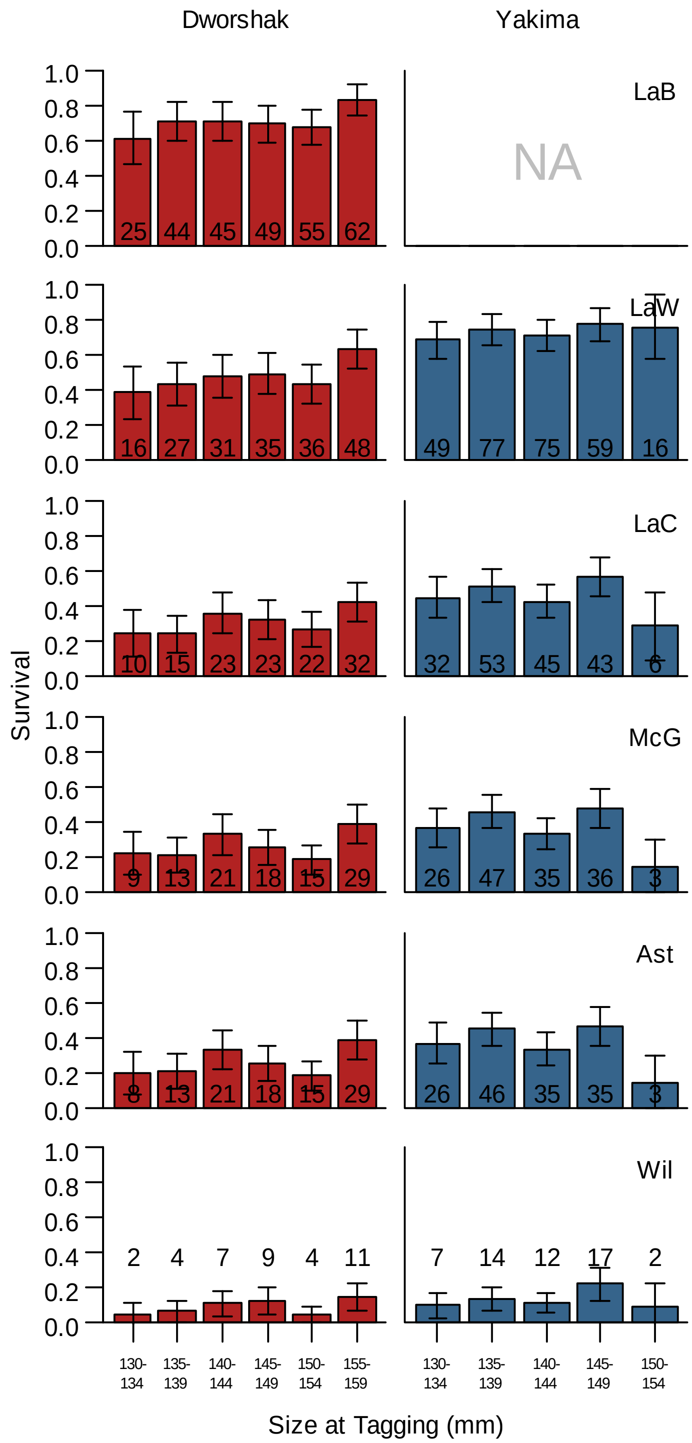

Figure 2.10. Survival in 2008 by size class (fork length) of migrating Dworshak (red) and Yakima (blue) spring Chinook salmon tagged with 7 mm acoustic transmitters. The numbers on or above the bars indicate the estimated number of fish detected within each size class at each detection site. LaB=Lake Bryan, LaW=Lake Wallula, LaC=Lake Celilo, McG=McGowan's Channel, Ast=Astoria Bridge, Wil=Willapa Bay. Error bars are 95% confidence intervals.

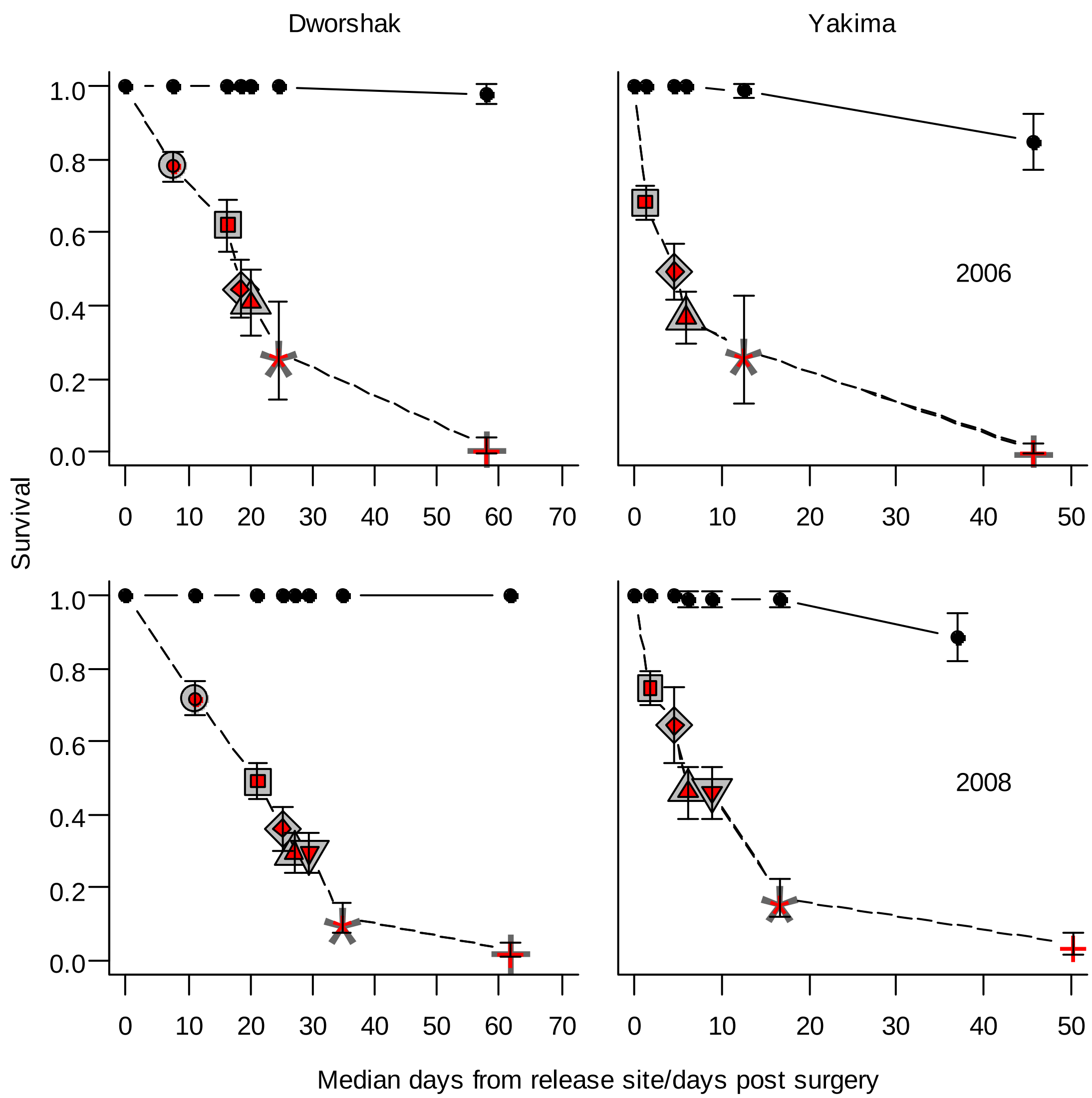

Figure 2.11. Proportion of tagged animals available for detection from the captive tag study (K; black circles), estimated in river survival with 95% confidence intervals (red symbols), and estimated IR survival corrected for tag effects (SK, larger, grey symbols). The correction for potential mortality and tag loss as a result of surgical implantation had no material effect on the measured survival of free-ranging smolts. Note that the corrected survival falls almost perfectly on top of the survival estimates. ○=Lake Bryan, □=Lake Wallula, ◇=Lake Celilo, △= McGowan's Channel, ▽=Astoria Bridge, * =Willapa Bay, + =Lippy Point.

Table 2.1. Tagging summary for captive spring Chinook salmon smolts tagged with 9 mm dummy acoustic transmitters (DATs) in 2006, and 7 mm DATs in 2008. Dworshak smolts were transferred and tagged at Kooskia National Fish Hatchery (NFH). In 2006 the tag study was conducted at Kooskia NFH; however, in 2008 the smolts were transferred back to Dworshak NFH for the remainder of the tag study. Cle Elum smolts were captured at the Chandler Juvenile Monitoring Facility and held at Prosser Hatchery. (FL= fork length, g=grams)

9 mm

Tributary (Hatchery)	Study Site	Tag Type	# Tagged	Mean size at tagging (mm FL; range)	Mean weight at tagging (g; range)
Snake (Dworshak)	Kooskia NFH	DAT	100	154.5 (142-169)	41.7 (31.0-57.5)
Snake (Dworshak)	Kooskia NFH	PIT tag	100	154.8 (140-168)	41.9 (28.4-60.2)
Yakima (Cle Elum)	Prosser Hatchery	DAT	100	154.8 (143-174)	41.4 (29.9-59.6)
Yakima (Cle Elum)	Prosser Hatchery	PIT tag	92	154.4 (139-170)	40.7 (23.7-60.4)

7 mm

Tributary (Hatchery)	Study Site	Tag Type	# Tagged	Mean size at tagging (mm FL; range)	Mean weight at tagging (g; range)
Snake (Dworshak)	Dworshak NFH	DAT	100	148.2 (135-159)	39.1 (25.8-57.1)
Snake (Dworshak)	Dworshak NFH	PIT tag	100	148.1 (135-159)	38.2 (25.5-58.0)
Yakima (Cle Elum)	Prosser Hatchery	DAT	97	139.9 (132-149)	27.3 (21.1-34.4)
Yakima (Cle Elum)	Prosser Hatchery	PIT tag	100	140.2 (131-154)	27.3 (20.5-35.4)

Table 2.2. Tagging summary for seaward migrating spring Chinook salmon smolts tagged with 9 mm acoustic transmitters in 2006 and 7 mm transmitters in 2008. Dworshak smolts were transferred to and then tagged and released at Kooskia National Fish Hatchery (NFH) (60 km upstream of Dworshak NFH). Cle Elum smolts were captured and released at Chandler Juvenile Monitoring Facility (CJMF). (FL= fork length, g=grams)

9 mm

Tributary (Hatchery)	Release Date	# Tagged	Mean size at tagging (mm FL; range)	Mean weight at tagging (g; range)	Release Site
Snake (Dworshak)	1-May	198	146.9 (140-208)	35.2 (26.9-117.5)	Kooskia NFH
Snake (Dworshak)	8-May	198	145.6 (140-192)	34.0 (27.4-83.7)	Kooskia NFH
Yakima (Cle Elum)	30-May	199	154.5 (140-173)	43.2 (30.0-64.2)	CJMF
Yakima (Cle Elum)	6-Jun	199	154.5 (140-168)	41.9(28.8-59.2)	CJMF

7 mm

Tributary (Hatchery)	Release Date	# Tagged	Mean size at tagging (mm FL; range)	Mean weight at tagging (g; range)	Release Site
Snake (Dworshak)	25-Apr	197	146.2 (130-159)	37.5 (23.3-55.5)	Kooskia NFH
Snake (Dworshak)	2-May	198	146.3 (131-159)	37.3 (23.9-52.7)	Kooskia NFH
Yakima (Cle Elum)	15-May	189	140.3 (129-158)	28.1 (22.0-10.9)	CJMF
Yakima (Cle Elum)	21-May	189	140.4 (131-157)	28.1 (22.1-37.2)	CJMF

Table 2.3. Tag burden (%) of spring Chinook salmon smolts implanted with 9 mm and 7 mm dummy acoustic transmitters (DAT) used in captive tag effects studies, and 9 mm and 7 mm live transmitters used to estimate in-river (IR) survival estimates; mean (range).

	9 mm		7 mm	
Tag Group	Tag weight : Body weight	Tag length : Fork length	Tag weight : Body weight	Tag length : Fork length
Dworshak DAT	7.6 (5.4-10.0)	13.6 (12.4-14.8)	4.2 (2.8-6.2)	13.5 (12.6-14.8)
Yakima DAT	7.7 (5.2-10.4)	13.6 (12.1-14.7)	5.9 (4.7-7.6)	14.3 (13.4-15.2)
Dworshak IR	9.3 (2.6-11.5)	14.4 (10.1-15.0)	4.5 (2.9-6.9)	13.7 (12.6-15.4)
Yakima IR	7.4 (4.8-10.8)	13.6 (12.1-15.0)	5.8 (3.9-7.3)	14.3 (12.7-15.5)

Table 2.4. Summary of statistical analyses used in the captive tag study. Significant p-values are represented by bold type. Degrees of freedom (d.f.) for the X2 tests for tag retention and survival are not available (NA) because p-values were estimated with a Monte Carlo simulation when some cells contained fewer than five data points. DAT=dummy acoustic tag, PIT=passive integrated transponder tag. (* excludes precocial males)

a. Tag Retention	Tag Size	Population	Time since Tagging	DAT	PIT	X^2	d.f.	p
	9 mm	Dworshak	week 5	0.98	1	2.1	NA	0.25
			week 11	0.97	1	3.2	NA	0.13
			week 24	**0.95**	**1**	**5.3**	**NA**	**0.03**
		Yakima	week 6	**0.91**	**1**	**7.5**	**NA**	**0.007**
			week 12	**0.83**	**1**	**9**	**NA**	**0.002**
	7 mm	Dworshak	week 7	no tag loss				
			week 23	no tag loss				
		Yakima	week 5	no tag loss				

b. Survival	Tag Size	Population	Time since Tagging	DAT	PIT	X^2	d.f.	p
	9 mm	Dworshak	week 5	0.88	0.93	1.5	NA	0.35
			week 11	0.88	0.91	0.48	NA	0.64
			week 24	0.87	0.90	0.44	NA	0.65
		Yakima	week 6	**0.93**	**0.99**	**4.2**	**NA**	**0.07**
			week 12	**0.84**	**0.96**	**8.8**	**NA**	**0.005**
	7 mm	Dworshak	week 7	no mortality				
			week 23	no mortality				
		Yakima	week 5	0.89	0.96	3.8	NA	0.06

Table 2.4 cont. Summary of statistical analyses used in the captive tag study. Significant p-values are represented by bold type.

c. Fork Length (mm)

Tag Size	Population	Time since Tagging	DAT mean (SD)	PIT mean (SD)	t	d.f.	p
9 mm	Dworshak	week 0	155.3 (6.5)	155.2 (5.6)	0.07	158	0.94
		week 5	**167.6 (8.8)**	**173.8 (7.8)**	**4.8**	**159**	**<0.001**
		week 11	**182.1 (11.4)**	**189.6 (9.9)**	**4.6**	**157**	**<0.001**
		week 24	**202.8 (17.9)**	**212.9 (14.7)**	**3.9**	**153**	**<0.001**
	Yakima	week 0	154.6 (5.9)	154.2 (5.9)	0.41	147	0.68
		week 6	**163.5 (7.5)**	**166 (7.6)**	**2.2**	**148**	**0.03**
		week 12	**174.2 (7.8)**	**178.8 (7.7)**	**3.7**	**148**	**<0.001**
7 mm	Dworshak	week 0	148.3 (5.8)	147.9 (6.9)	0.33	195	0.74
		week 7	165.1 (6.3)	166.6 (5.6)	1.7	192	0.08
		week 23*	215.9 (9.5)	217.3 (8.9)	0.9	165	0.35
		week 0	139.9 (4.5)	139.9 (4.7)	0.03	177	0.98
	Yakima	week 5	150.5 (5.1)	151.2 (5.3)	0.9	177	0.36

Table 2.4 cont. Summary of statistical analyses used in the captive tag study. Significant p-values are represented by bold type.

d. Weight (g)

Tag Size	Population	Time since Tagging	DAT mean (SD)	PIT mean (SD)	t	d.f.	p
9 mm	Dworshak	week 0	42.2 (6.4)	42.3 (5.8)	0.1	161	0.91
		week 5	**59.7 (13.2)**	**67.6 (12.1)**	**4.1**	**161**	**<0.001**
		week 11	**72.6 (15.4)**	**81.2 (14.2)**	**3.7**	**161**	**<0.001**
		week 24	**93.6 (23.9)**	**107.2 (21.4)**	**3.8**	**160**	**<0.001**
	Yakima	week 0	41.2 (6.1)	40.5 (5.9)	0.72	140	0.47
		week 6	**51.1 (8.8)**	**54.4 (8.0)**	**2.3**	**137**	**0.02**
		week 12	**68.7 (11.8)**	**75.2 (11.1)**	**3.4**	**139**	**<0.001**
7 mm	Dworshak	week 0	39.2 (6.6)	38.1 (6.8)	1.15	195	0.25
		week 7	55.1 (8.2)	55.6 (8.3)	0.48	195	0.63
		week 23*	114 (18.4)	115.3 (16.2)	0.53	165	0.59
	Yakima	week 0	27.4 (2.9)	27.2 (3.3)	0.52	178	0.60
		week 5	37.6 (4.6)	38.2 (5.2)	0.84	178	0.40

Table 2.4 cont. Summary of statistical analyses used in the captive tag study. Significant p-values are represented by bold type.

e. Specific Growth Rate (% g/week)	Tag Size	Population	Time	DAT mean (SD)	PIT mean (SD)	F	d.f.	p
	9 mm	Dworshak	week 0 to week 5	**5.84 (2.6)**	**8.12 (2.2)**	**37.5**	**165**	**<0.001**
			week 5 to week 11	3.28 (1.7)	3.09 (1.7)	0.19	165	0.65
			week 11 to week 24	1.85 (1.2)	2.13 (0.74)	0.028	165	0.86
		Yakima	week 0 to week 6	**3.33 (0.91)**	**4.61 (1.06)**	**62.3**	**144**	**<0.001**
			week 6 to week 12	4.99 (2.02)	5.48 (1.62)	3.73	144	0.055
	7 mm	Dworshak	week 0 to week 7	**4.87 (1.2)**	**5.45 (1.2)**	**13.19**	**169**	**<0.001**
			week 7 to week 23*	4.59 (0.91)	4.57 (0.88)	0.16	169	0.69
		Yakima	week 0 to week 5	**6.16 (1.3)**	**6.65 (1.6)**	**4.81**	**178**	**0.029**

Table 2.5. Model selection for fork length (FL) analyses using Akaike's Information Criterion (AIC). QAICc=quasi-AIC corrected for overdispersion and effective sample size. Φ=survival probability, line=acoustic detection site. Recapture parameters were held constant for all models ($p_{population*line}$).

2006

	Model	QAICc	ΔQAICc	Num. Par	QDeviance
Snake	Φ_{line}	592.37	0	11	570.14
	$\Phi_{line + FL}$	594.35	1.98	12	570.08
	$\Phi_{line * FL}$	600.97	6.62	17	566.44
Yakima	Φ_{line}	1281.24	0	9	1263.06
	$\Phi_{line + FL}$	1282.07	0.83	10	1261.85
	$\Phi_{line * FL}$	1282.71	0.65	14	1254.30

2008

	Model	AICc	ΔAICc	Num. Par	Deviance
Snake	$\Phi_{line + FL}$	1765.71	0	14	1737.31
	Φ_{line}	1769.53	3.82	13	1743.18
	$\Phi_{line * FL}$	1775.38	5.86	20	1734.59
Snake (FL=130-154)	Φ_{line}	1381.77	0	13	1355.32
	$\Phi_{line + FL}$	1383.56	1.79	14	1355.05
	$\Phi_{line * FL}$	1388.66	5.10	20	1347.62
Yakima	Φ_{line}	1683.99	0	11	1661.70
	$\Phi_{line + FL}$	1685.12	1.13	12	1660.78
	$\Phi_{line * FL}$	1687.51	2.39	17	1652.84

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3 Experimental Measurement of Hydrosystem-induced Delayed Mortality in Juvenile Columbia River Spring Chinook Salmon Using a Large-scale Acoustic Array[2]

3.1 Introduction

Out-migrating Snake River Chinook salmon (*Oncorhynchus tshawytscha*) smolts must pass four major hydro dams in the Snake River and four in the lower Columbia River before reaching the Pacific Ocean. Although direct mortality at the dams has decreased in recent years (Muir et al. 2001), subsequent survival from seaward migration until adult return is substantially lower for wild and hatchery Snake River spring Chinook salmon relative to some mainstem Columbia River populations (Berggren et al. 2008; Yakama Nation 2008). It has thus been hypothesized that delayed mortality may occur after passage out of the hydropower system (i.e. the impounded section of the rivers) due to the cumulative stress caused by dam passage. (e.g., Budy et al. 2002; Schaller and Petrosky 2007). Therefore, to quantify delayed or indirect effects of dam passage, survival must be measured downstream of the final dam and preferably beyond fresh water.

The Pacific Ocean Shelf Tracking (POST) array (Welch et al. 2002) is a potentially continental-scale marine tracking array composed of individual acoustic receivers anchored to the ocean floor in a precise geometry. Each receiver records the date and time of uniquely coded acoustic tags passing nearby. In this study, cross-shelf ocean detection lines were located off southeast Alaska, British Columbia (around Vancouver Island), and Washington (40 km north of the Columbia River mouth), as well as in the Columbia and Snake rivers (Figure 3.1). The potential tracking distance from the Snake River detection site to southeast Alaska was ~2,300 km.

In 2006 we used the POST array to test the hypothesis that greater mortality is expressed in a population of hatchery-origin Snake River spring Chinook salmon smolts after migrating

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through the impounded section of the river (eight dams) than that of a downstream population from the Yakima River (a tributary of the mid-Columbia River) that migrates through only the four lower Columbia River dams. Smolt to adult return rates (SAR) of the Snake River population (Berggren et al. 2008) averaged only one-fifth that of the Yakima River population (Yakama Nation 2008) for fish released between 1999-2005 and preliminary adult returns from the 2006 release year were consistent with prior years (SAR_{Yakima}=2.7%, B. Bosch, Yakima-Klickitat Fisheries Project, Yakima, WA, personal communication, 2008; SAR_{Snake}=0.38%, (Berggren et al. 2008), providing a comparative test of whether this differential mortality develops shortly after they passed out of the hydrosystem. Our results provide the first estimates of survival and distribution in the ocean and substantially extend the period of life history during which is it possible to test whether delayed mortality occurs in juvenile salmon (Figure 3.1).

3.2 Methods

3.2.1 Populations used in the study

The Snake River population of spring Chinook salmon used in this study was reared at the Dworshak National Fish Hatchery (DNFH), on the Clearwater River (a tributary of the Snake River). Dworshak NFH Spring Chinook salmon from the Clearwater River are not a component of the Snake River evolutionary significant unit (ESU); however their survival is routinely compared with other populations in the Snake River basin as well as downstream Columbia River populations (see Berggren et al. 2008). Of the Snake River populations, Dworshak generally has the lowest SARs (Berggren et al. 2008) and therefore the difference in survival estimates should be particularly pronounced when compared to a population from outside of the Snake River basin. For logistical ease, Dworshak fish were transferred, tagged, and released at Kooskia NFH (60 km upstream of DNFH); distance to the Columbia River mouth is 870 km.

The Yakima River population was reared at the Cle Elum Supplementation and Research Facility (CESRF) on the Yakima River. Migrating hatchery spring Chinook salmon released from CESRF acclimation sites were collected from the lower Yakima River at the Chandler Juvenile Monitoring Facility (CJMF; 194-249 km from the acclimation sites) and held for tagging. We collected fish at CJMF because mortality in the Yakima River has been as high as 80% in recent years (Yakama Nation 2008). Fish released from CJMF migrated 76 km down the Yakima River to enter the Columbia River just upstream from the Snake-Columbia River confluence; distance to the Columbia River mouth is 615 km. Thus, both the Snake and Yakima River populations shared a common migration path that passed through the four lower Columbia River dams before reaching the ocean listening line at Willapa Bay, a total distance of 910 and 655 km, respectively.

3.2.2 Tagging

We surgically implanted 794 smolts (two release groups of approximately 200 at each hatchery) with individually identifiable Vemco V9-6L acoustic transmitters (9 x 20 mm, 3.1 g in air, 2 g in water; Shad Bay, Nova Scotia, Canada). The tags were programmed to transmit a unique code at a mean interval of 60 seconds and the rated battery life of the tag (4 months) was intended to exceed the likely migration time to the POST sub-array in Alaska. A passive integrated transponder (PIT) tag was placed in the body cavity (through the incision) to ensure that tagged smolts were diverted back into the river at the dam bypass facilities. We set a minimum body size requirement of 140 mm fork length (FL) which meant that only the upper portion of the smolt size distribution could be tagged. The mean percent body weight of the transmitters was 8.3% (range=2.6-11.5%). The surgical procedure used to implant acoustic transmitters was approved by the Vancouver Island University Animal Care Committee.

3.2.3 Array location

Component sub-arrays were deployed within the Columbia River at McGowan's Channel at river kilometer (rkm) 224 (10 km below Bonneville Dam), in Lake Celilo at rkm 340 (7 km below John Day Dam), and in Lake Wallula at rkm 502 (21 km below the confluence of the upper Columbia and Snake rivers; Figure 3.1). In the Snake River, receivers were installed in Lake Bryan at Snake River rkm 159 (14 km below Lower Granite Dam; total distance from the ocean was 681 km). At each of these locations, receivers were deployed as paired lines, to assist in evaluating detection probability and to provide a survival measurement below three of the major hydroelectric dams.

Oceanic components of the POST array at Willapa Bay (southern WA), Lippy Point (northwest Vancouver Island, BC), and Graves Harbor (southeast AK) were deployed as single lines and extended from near-shore to the edge of the continental shelf (200 m depth), a distance of up to 30 km (Figure 3.1).

3.2.4 Survival analysis

Estimates of smolt survival (Φ) and detection probability (*p*) at each detection site were calculated using the Cormack-Jolly-Seber (CJS) model for live recaptured animals implemented in Program MARK (White and Burnham 1999). This model jointly estimates survival and detection within a likelihood framework. Because sample size beyond Willapa Bay was low it was not possible to reliably estimate survival to British Columbia or Alaska. Therefore, we mainly focus on estimates of survival and detection to the ocean line at Willapa Bay.

For in-river lines, we recognized basic CJS model assumptions (equal survival probability, equal recapture probability, no tag loss, and instantaneous sampling); however, for oceanic lines that are not bounded on the offshore end (continental slope), we required two additional assumptions; 1) as fish migrate they cross over the acoustic detection lines that span the length of the continental shelf and 2) the majority of the fish departing the Columbia River swim north. These assumptions are supported by evidence from numerous ocean sampling programs (Bi et al. 2007; Brodeur et al. 2004; e.g., Fisher and Pearcy 1995).

To estimate overdispersion in the data we used a median $\hat{c}$ procedure (White and Burnham 1999) to test the goodness of fit (GOF) of our global model ($\Phi_{population*line}$ $p_{population*line}$) and then corrected for this overdispersion ($\hat{c}$=2.1) across all candidate models. We hypothesized that distance and number of dams within a migration segment (Table 3.1) may affect survival so we modeled multiplicative effects of each external covariate ($\Phi_{population\ *\ distance}$; $\Phi_{population*\ dam\ number}$), as well as their interaction ($\Phi_{population\ *\ distance\ *\ dam\ number}$) in addition to the fully varying CJS global model. Because of the low number of fish detected at Vancouver Island and Alaska, we included in our models two additional treatment groups (each N=100) of spring Chinook salmon smolts from Dworshak NFH, tagged with the same acoustic tag, that were released below Bonneville Dam during the spring seaward migration in order to better quantify the detection probability of the Willapa Bay detection line. The survival estimate of this group was modeled in the same way across models ($\Phi_{group\ *line}$) and did not influence survival estimates for run-of-river smolts. Recapture parameters were modeled to vary with population and line except at Willapa Bay where all populations were pooled.

We used an information theoretic approach, i.e. Akaike's Information Criterion (AIC), to select the most parsimonious model. In general, the model with the lowest AIC value (which accounts for the number of model parameters, n_{pars}) has more support in the data, and if the ΔAIC of the other candidate models is greater than 2, then these models (i.e. hypotheses) have little or no support. We report survival estimates from the model which had the most support.

3.2.5 Cross-shelf distribution

For each population we used a X^2 goodness of fit test to determine if the cross-shelf ocean distribution adjacent to Willapa Bay was significantly different from the null hypothesis of a uniform distribution. To perform the tests we counted the number of unique ID codes detected at each of the 40 receivers for each population. If a fish was detected at more than one receiver a proportion was allocated to the receiver, e.g. if an ID code was detected on two receivers, each receiver was assigned a value of 0.5. If a receiver was displaced during the migration (e.g. by fishing activity) then that receiver was omitted from the data set (30 active receivers were used in the final analysis). To meet the requirements of the X^2 test we pooled data into 15 groups.

3.3 Results

3.3.1 Survival

The most parsimonious model based on an information theoretic approach was the model which constrained survival solely as a function of distance travelled ($\Phi_{population\ *\ distance,}$ AIC=1677.0, n_{pars}=14). Although this model had considerably more support than the global model ($\Phi_{population\ *\ line}$, AIC=1687.7, ΔAIC=10.7, n_{pars}=21), the added effect of distance on survival was negative for Dworshak smolts (Φ/km=0.9993) as expected, but positive for the Yakima River population (Φ/km=1.0007). This was a surprising result for the Yakima River population but was likely caused by low survival in the lower Yakima River (the shortest migration segment which also lacked dams), combined with higher survival in the lower Columbia River and ocean (the longest segment). The model which constrained survival as a function of dam number also had support in the data ($\Phi_{population * dam number}$, AIC=1677.2, ΔAIC=0.2, n_{pars}=14); however, the rate of survival per dam was slightly >1 for both populations indicating that there was no negative survival effect due to the number of dams passed in a migration segment. The lack of effect of the number of dams passed on direct in-river survival may be a reflection of the improvements of fish passage in the hydrosystem (Muir et al. 2001), so that any remaining negative effect of the dams may be too small to be measurable once the effect of distance is accounted for. There was little support for a model including an interaction between number of dams within a migration segment and distance travelled ($\Phi_{population * distance * dam number}$, AIC=1680.5, ΔAIC=3.5, n_{pars}=16).

Survival of Snake River smolts ranged between 74-82% for individual river segments and between 70-78% for Yakima smolts (Table 3.1). Survivorship of Snake and Yakima smolts to McGowan's Channel, located just below Bonneville Dam (the final dam) was 40% and 36%, respectively. There was no detectable difference in survivorship from release to Willapa Bay between populations (S_{Snake}=29%, S_{Yakima}=28%, Table 3.1), and the mean time for smolts to reach this line after passing Bonneville Dam was ~five days for both. Therefore delayed mortality was not evident after several days in the coastal ocean at a point located 274 km beyond the hydrosystem. Although we tagged only larger individuals, and migration time was delayed by several weeks relative to untagged runs, these survivorship estimates were very similar to independent PIT tag estimates of survival of Dworshak (see Welch et al. 2008) and Yakima (D. Lind, Yakima-Klickitat Fisheries Project, Yakima, WA, personal communication, 2007) spring Chinook salmon in 2006.

Tagged Chinook salmon were also detected on acoustic lines on the west coast of Vancouver Island and Alaska. The large distance between ocean detection sites (~500 km and 1000 km, respectively), the relatively low numbers detected on these lines, and the fact that the detected smolts arrived at both locations within two days of line deployment prevented us from reliably estimating survival to these locations. However, the detection of four Snake and two Yakima smolts on the Vancouver Island line, some 1,500 km distant from the release site (30 days travel time from Willapa Bay for both populations), and the detection of two Snake

River smolts on the Alaska line (and none from the Yakima River population), some 2,500 km from the release site is inconsistent with the delayed mortality hypothesis.

3.3.2 Coastal ocean distribution

The cross-shelf distribution of the Snake River population was significantly different from the null hypothesis of a uniform distribution (X^2 Goodness of fit test; $p < 0.01$), while the Yakima River population was not ($p=0.57$; Figure 3.1a, b) with the Snake River population more concentrated on the offshore portion of the line.

3.4 Discussion

3.4.1 Study limitations

1) We were limited to tagging smolts > 140 mm FL, 2) tagged fish were released 2-4 weeks after the main hatchery releases, 3) tagged smolts were detected on the outermost receiver at Willapa Bay, suggesting that some smolts may migrate beyond the offshore extent of the sub-array, and 4) arrival to the first ocean line was not simultaneous for the two populations despite our attempts to do so. Future work should address these limitations by using smaller tags, extending the marine components of the array farther offshore (to depths ≥200 m), and by modifying release strategies to better synchronize release dates and arrival times in the ocean.

3.4.2 Conclusions

Lower river and early marine survival data for Columbia River basin Chinook salmon is essential for assessing the hypothesized delayed effects of dam passage on smolt survival. In this study we found no evidence that delayed mortality was expressed by Snake River smolts (>140 mm FL) by the time they had reached the first ocean sub-array, some 274 km from Bonneville dam, when compared with a size-matched group from the Yakima River population. This result is based on the assumption that smolts turn north after ocean entry, and is supported by the high proportion of smolts detected on the Willapa Bay line subsequent to passing the detection line below Bonneville Dam. The mean time of arrival from below Bonneville Dam to Willapa Bay (five days) puts an initial lower limit on the period when differential mortality may be expressed in these populations. Our results imply that if delayed mortality causes the disparity in adult return rates of hatchery-origin Snake River spring Chinook salmon, it is at a time and place more distant from the Columbia River; however, it is plausible that delayed mortality may operate on smaller fish (<140 mm FL) that were not tested here. Our result that the number of dams passed within a migration segment did not affect survival also supports the findings that direct in-river mortality of salmon smolts has decreased in recent decades (Muir et al. 2001), possibly to the level of an undammed river (Welch et al. 2008). We note that our study was not designed to measure very small effects on mortality, as it was focused on making the first large-scale measurements of migratory survival for salmon. It is not correct to conclude that the dams play no role in affecting survival, simply that any contributory effect appears to be small.

The differing marine distributions of the two populations at Willapa Bay provides a potential mechanism in support of the alternative hypothesis that populations from the same river basin can have different responses to ocean conditions (e.g., Levin 2003). It remains unclear whether the entire size range of these two populations, as well as wild smolts, have similar survival and behavior as the smolts reported here. The technical development of the POST array allowed us to make a direct scientific test of a key hypothesis concerning delayed mortality of a population of Snake River spring Chinook salmon in the ocean. As such, it marks an important scientific milestone. Advances in the array design, however, will allow us to study marine survival over the complete size range of naturally occurring spring Chinook smolts, as well as other endangered populations of salmon originating from the Columbia River basin.

Figure 3.1. Map of the Pacific Ocean Shelf Tracking (POST) acoustic array and distribution of spring Chinook smolts on the continental shelf. Panel (a) shows the 2006 POST acoustic array (black dots and thick black lines). The continental shelf (depths <200m) is shaded. Panel (b) shows the location of the release sites (CJMF=Chandler Juvenile Monitoring Facility, KNFH=Kooskia National Fish Hatchery), detection sites (McG=McGowan's Channel, LaC=Lake Celilo, LaW=Lake Wallula, LaB=Lake Bryan); and dams (BON=Bonneville, TDA=The Dalles, JDA=John Day, MCN=McNary, ICH=Ice Harbor, LMO=Lower Monumental, LGO=Little Goose, LGR=Lower Granite) within the Yakima, lower Snake and Columbia rivers. Pie shapes represent the proportion of fish surviving to each detection site (Dworshak=black, Yakima=grey). Panel (c) and (d) show the cross shelf distribution of Snake River and Yakima River smolts on the Willapa Bay line, respectively. Numbers above the bars represent the percentage of time the receiver was oper operational during the migration.

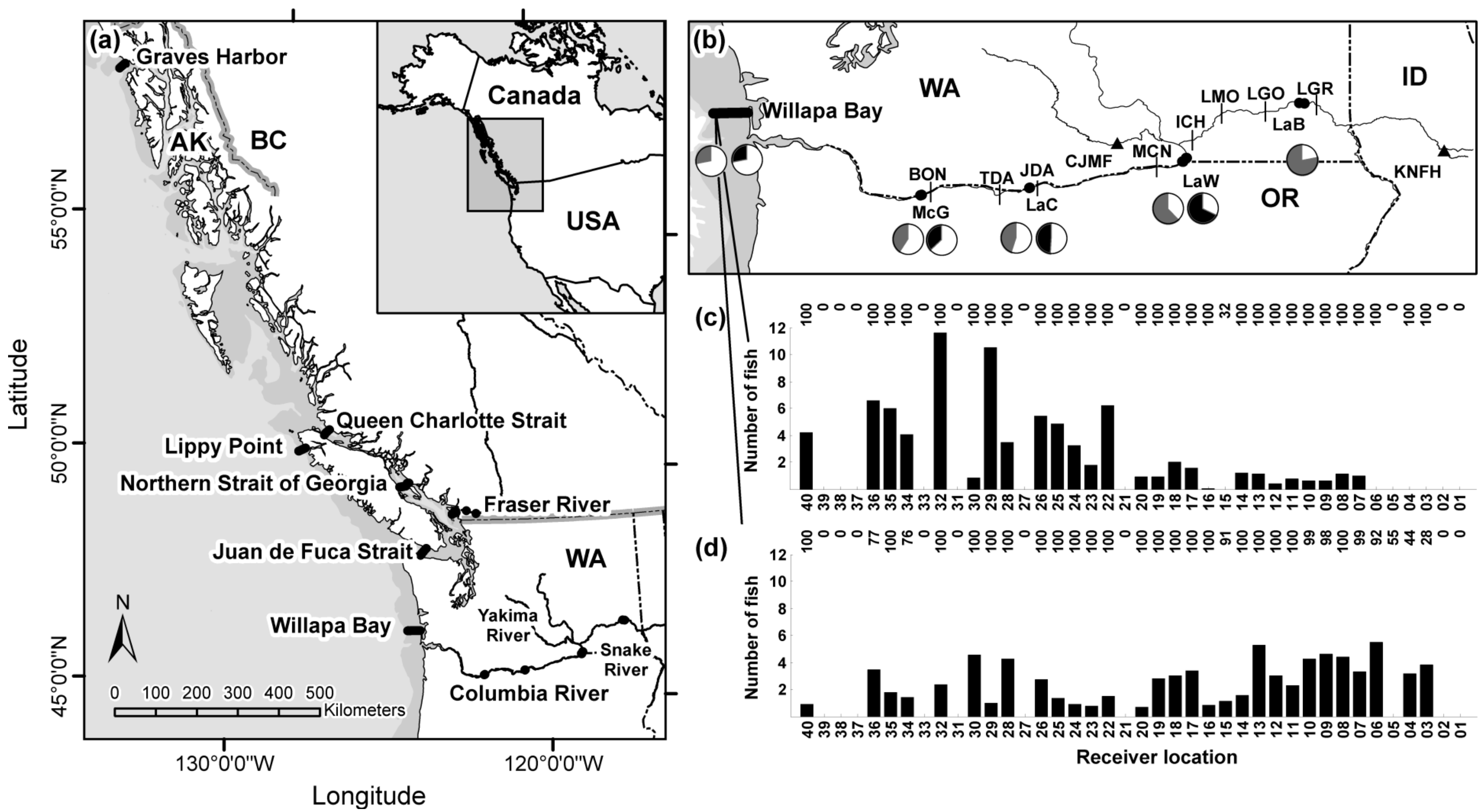
(a)
Graves Harbor
AK
BC
Canada
USA
Queen Charlotte Strait
Lippy Point
Northern Strait of Georgia
Fraser River
Juan de Fuca Strait
WA
Willapa Bay
Yakima River
Snake River
Columbia River
N
0 100 200 300 400 500
Kilometers
55°0'0"N
50°0'0"N
45°0'0"N
130°0'0"W
120°0'0"W
Latitude
Longitude
(b)
WA
Willapa Bay
ID
OR
BON
McG
TDA
JDA
LaC
CJMF
MCN
LaW
ICH
LMO
LGO
LGR
LaB
KNFH
(c)
100 0 0 0 100 100 100 0 100 0 100 100 100 0 100 100 100 100 100 0 100 100 100 100 100 32 100 100 100 100 100 100 100 100 100 0 100 100 0 0
(d)
100 0 0 0 77 100 76 0 100 0 100 100 100 0 100 100 100 100 100 0 100 100 100 100 100 91 100 100 100 100 99 98 100 99 92 55 44 28 0 0
Number of fish
40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21 20 19 18 17 16 15 14 13 12 11 10 09 08 07 06 05 04 03 02 01
Receiver location

Table 3.1. Mean survival for Snake River (Dworshak) and Yakima (CESRF) spring Chinook salmon implanted with V9-6L acoustic transmitters and PIT tags in 2006. Segment distance to the first detection site is measured from release location; all others are measured from previous detection site (LaB=Lake Bryan, LaW=Lake Wallula, LaC=Lake Celilo, McG=McGowan's Channel, WiB=Willapa Bay; see Methods for site details). Survival estimates are ± SE; NA= not applicable. Snake River smolts were released on May 1 (N=198; mean FL=146.9 mm, range=140-208 mm), and May 8 (N=198; 145.6 140-192); Yakima River smolts released on May 30 (N=199; 154.5, 140-173) and June 6 (N=199; 154.5, 140-168). The two release dates for Yakima smolts were chosen in an attempt to have their arrival at Bonneville Dam coincide with the Snake River release groups. Yakima smolts entered the Columbia River upstream of confluence with the Snake and therefore were not detected on the Lake Bryan line in the Snake River.

	Snake						Yakima					
Detection site	Segment distance (km)	Dams passed/ segment	Est. n	Survival probability	Cumulative survival	Detection probability	Segment distance (km)	Dams passed/ segment	Est. n	Survival probability	Cumulative survival	Detection probability
LaB	189	1	308	0.78 ± 0.02	0.78 ± 0.02	0.97 ± 0.02	NA	NA	NA	NA	NA	NA
LaW	179	3	245	0.78 ± 0.02	0.61 ± 0.03	0.92 ± 0.03	113	0	258	0.70 ± 0.03	0.70 ± 0.03	1.00 ± 0
LaC	162	2	176	0.79 ± 0.02	0.48 ± 0.04	0.56 ± 0.06	162	2	186	0.72± 0.03	0.51 ± 0.03	0.77 ± 0.05
McG	116	2	162	0.82 ± 0.06	0.40 ± 0.05	0.72 ± 0.07	116	2	139	0.70 ± 0.02	0.36± 0.04	0.86 ± 0.05
WiB	263	0	109	0.74 ± 0.08	0.29 ± 0.04	0.69 ± 0.08	263	0	106	0.78 ± 0.10	0.28± 0.05	0.69 ± 0.08

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4 Comparative Early Ocean Survival and Migration Behaviour of Juvenile Spring Chinook Salmon Migrating from Two Tributaries of the Columbia River[3]

4.1 Introduction

Little is known about the fate of Pacific salmon smolts immediately following ocean entry. Mortality rate is highest during this life history phase (Beamish et al. 2004; Buchanan et al. 2007; Quinn 2005), however it is unclear precisely when and where in the ocean most of this mortality occurs and to what extent migration behaviour may influence survival. For seaward migrating smolts from the Snake River, a tributary of the Columbia River, extra or latent mortality after ocean entry may occur as a result of migrating through the heavily impounded Snake and Columbia River system. This is thought to occur as a result of higher accumulated stress resulting from passing through four dams in the lower Snake River as well as four dams in the lower Columbia River (Budy et al. 2002; Independent Scientific Advisory Board 2007; Schaller et al. 1999; Schaller and Petrosky 2007; Wilson 2003). Delayed mortality can be most simply defined as indirect mortality caused by passage through the hydropower dams, which does not occur while the smolts migrate down-river (i.e. direct mortality), but which is instead manifested at some later time. Given such mortality, differential survival of smolts originating from different tributaries is not detectable during their migration through the impounded rivers within the Columbia River basin (the hydrosystem), but must be measured downstream of the final dam and preferably beyond fresh water.

Delayed hydrosystem mortality was hypothesized to occur because survival from seaward migration until adult return is substantially lower for Snake River spring Chinook salmon relative to mainstem Columbia River populations (Berggren et al. 2006). Smolts migrate through the dams by going over the dam in spillways, through turbines, or through an intricate bypass system, all of which may be more stressful than migrating down an unimpounded river (Budy et al. 2002). The marine phase, however, may also result in differential survival of Snake River

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stocks. Populations may migrate at different times or to different parts of the ocean thereby exposing them to different conditions, or they may migrate concurrently but may respond differentially to ocean conditions; or their freshwater experience may be different (Levin 2003). There is some support based on coded wire tag returns from spring Chinook salmon from various Columbia River ESU's (evolutionarily significant units) that ocean distributions are different and therefore ocean conditions could have different effects on populations originating from the same river basin (Zabel and Williams 2000). These two potential mechanisms of mortality- stressful freshwater experience subsequently manifesting itself as mortality in the ocean, and the direct effects of the ocean on survival- are confounded when analyzing adult return rates and thus require more direct measurements of survival during ocean migration to allow clearer discrimination.

There is a growing consensus about the need for direct assessment of early marine survival to quantify variability in salmon survival after passage beyond the hydrosystem (Brodeur et al. 2000; Deriso et al. 2001; Kareiva et al. 2000; Peters and Marmorek 2001; Scheuerell and Williams 2005). This would also avoid the current approach of treating the marine life history phase of salmon as a "black box" (Brodeur et al. 2000), where past investigations on Columbia and Snake River spring Chinook salmon have assumed that there is a common ocean effect on juvenile survival (Budy et al. 2002; Budy and Schaller 2007; Petrosky et al. 2001).

In 2006, the Pacific Ocean Shelf Tracking (POST) array (Welch et al. 2002 www.postcoml.org), which is based on the use of acoustic frequencies (rather than radio frequencies), was expanded to include sub-arrays within the Columbia and Snake rivers and across the continental shelf off Willapa Bay, Washington. Additional POST cross-shelf detection lines located farther north off Vancouver Island (British Columbia), southeast Alaska, and across all approaches to the Strait of Georgia were available to detect tagged smolts moving along their migration route in the ocean, providing a potential measure of survival up to 2500 km from their release site in the Snake River.

We used detections from the array in 2006, 2007 and 2008 to estimate and compare the survival of Snake and Yakima River spring Chinook salmon migrating down-river and along the continental shelf. Snake River smolts migrate farther to the Columbia River mouth and through twice the number of dams. Smolt to adult survival rates for the Yakima River population (Bosch and Fast 2006) averaged four times higher than the Snake River population (Berggren et al. 2006) for fish released between 1999-2005, suggesting that the different rates of survival may be related to their prior hydrosystem experience. Here we use the POST array to test the hypothesis that greater mortality is expressed in Snake River smolts after migrating through the hydrosystem. Our results substantially extend the period of life history during which is it possible to address whether delayed mortality occurs in juvenile salmon from the Columbia River basin and is the first study to describe migration behavior in the ocean.

4.2 Methods

4.2.1 Populations studied

The Snake River population of spring Chinook salmon used in this study was reared at the Dworshak National Fish Hatchery (NFH), on the Clearwater River (a tributary of the Snake River). Dworshak NFH spring Chinook salmon are not a component of the threatened Snake River evolutionarily significant unit (ESU); however, their survival is routinely compared with other populations in the Snake River basin as well as downstream Columbia River populations (see Berggren et al. 2008). Of the Snake River populations that have been studied, Dworshak generally has the lowest smolt-to-adult return rates (SARs). For release years 1999-2006 the mean SAR was 0.5% (Berggren et al. 2008).

To test the delayed mortality hypothesis it was necessary to select a hatchery Chinook salmon population from the mid/lower Columbia River that has demonstrated higher adult return rates and navigates fewer dams than the Snake River stock. If the Snake River population had significantly lower survival below Bonneville Dam, this difference could be attributed to delayed hydrosystem mortality caused by passage through four additional dams in the Snake River. The Yakima River population was reared at the Cle Elum Supplementation and Research Facility (CESRF) on the upper Yakima River. This is a mid-Columbia River population and presently this ESU is not listed under the United States ESA. The Yakima/Klickitat Fisheries Program established the CESRF facility in 1997 to enhance production of spring Chinook salmon in the Yakima River basin in order to increase harvest and augment the natural population. The research facility (also referred to as Cle Elum hatchery) spawns returning wild spring Chinook salmon captured at Roza Dam (a barrier to migrating fish) on the Yakima River. Eggs are incubated at the Cle Elum hatchery and fry are transferred to acclimation sites in winter, approximately one year after emergence. There are three acclimation sites which represent areas where historical spawning occurred; two are located on the Yakima River north and south of the hatchery (Easton and Clark Flats, respectively) and one is located on a tributary of the Yakima River (Jack Creek). If differential or latent mortality risk is acquired while Snake River fish migrate in river we would expect to see lower survival at river and marine detection sites than that of the lower/mid Columbia stock. Alternatively, if the Snake River stock does not suffer differential mortality from dam passage we would expect to find similar daily survival rates for both stocks through the hydropower system and during early marine life.

4.2.2 Tag and release sites

Several months prior to tagging, Dworshak smolts were transferred to Kooskia NFH (60 km upstream of Dworshak NFH) and were held at a constant water temperature that facilitated smolt growth (~12 °C). (At Dworshak hatchery, winter water temperature is only a few degrees above freezing, therefore smolt growth during this time is typically minimal.) It was necessary to rear fish in relatively warmer water to ensure that tagged fish met minimum body size requirements for acoustic tagging (see below). In addition to optimal water temperatures, Kooskia NFH provided access to numerous holding tanks required for the experimental design. Fish were released from Kooskia NFH into Clear Creek which runs successively into the Clearwater River, the Snake River, the Columbia River, and finally into the Pacific Ocean. Distance from release to the Columbia River mouth is 870 km.

Yakima River hatchery spring Chinook salmon smolts were volitionally released from CESRF acclimation sites from March 15 to May 31. Migrating smolts were then collected from the lower Yakima River at the Chandler Juvenile Monitoring Facility (CJMF; 194-249 km from the acclimation sites) and held for tagging. We collected fish at CJMF because mortality in the Yakima River has been as high as 80% in recent years (Yakama Nation 2008). Fish released from CJMF migrated 76 km down the Yakima River to enter the Columbia River just upstream from the Snake-Columbia River confluence; distance to the Columbia River mouth is 615 km. Thus, both the Snake and Yakima River populations shared a common migration path that passed through the four lower Columbia River dams before reaching the ocean listening line at Willapa Bay, a total distance of 910 and 655 km, respectively.

Within each population the two release groups were released from their hatchery one week apart (Table 4.1). As Dworshak smolts migrated an additional 250 km, the release times for tagged fish were scheduled such that the smolts from both populations would arrive in the area of common migration (at the confluence of the Columbia and Snake rivers) on approximately the same date, and therefore timing of ocean entry (and presumably ocean conditions) would be similar. Therefore, tagged Dworshak smolts were released 3-4 weeks earlier than Yakima smolts to allow time to migrate down the lower Snake River. In general, Dworshak smolts were released in late April and early May, and Yakima smolts were released mid-late May and early June (Table 4.1).

The spill management program in the Columbia River Basin regulates the volume of water that flows over the spillways of the lower Snake and Columbia River dams during spring and summer, providing an alternate route for seaward migrating ESA listed salmonids that might otherwise migrate through the turbines. Migration over the dams in the spill also permits more fish to migrate in the river thereby decreasing the proportion of fish that are collected at and transported from Snake River dams. As transportation studies have not conclusively or consistently resulted in higher adult returns of ESA listed salmonids to the Snake River (see Chapter 5), the spill program aims to keep fish in the river while maintaining safe levels of total dissolved gas caused by spill. Therefore, spill was occurring at the four lower Snake River dams and the four lower Columbia River dams throughout our study periods in spring and summer of 2006-8.

4.2.3 Tag specs and surgical protocol

In each year of the study we surgically implanted 704 to 794 yearling Chinook salmon smolts with individually identifiable 69 kHz Vemco acoustic transmitters (Shad Bay, Nova Scotia, Canada). At each of the two hatcheries we tagged two release groups of approximately 175-200 fish (Table 4.1). In 2006 and 2007, smolts were implanted with V9-6L acoustic transmitters

(9 x 20 mm, 3.1 g in air, 2 g in water) which were programmed to transmit a unique code at a mean interval of 90 seconds. In 2008, smolts were implanted with a slightly smaller transmitter, the V7-2L (7 mm x 20 mm, 1.6 g in air, 0.75 g in water), which transmitted a unique code at a mean interval of 60 seconds. The rated battery life of both tag types tags was intended to exceed the migration time to the POST sub-array in Alaska (>90 days). In general, the larger, more powerful V9-6L transmitter has a detection radius ≤400 m, while the smaller V7-2L tag has a detection radius ≤300 m. The transmission interval of the V7-2L was faster or more frequent than the programming in previous years to compensate for the reduced detection radius and to prevent a significant decrease in detection probability.

Therefore although the acoustic output of the V7-2L is weaker than the V9-6L, the advantage of using the smaller tag is the ability to tag smaller fish; in 2006 and 2007, we set a minimum body size requirement of 140 mm fork length (FL) based on previous surgical trials (Welch et al. 2007), and in 2008 we set a minimum of 130 mm FL. The tag effects study in Chapter 2 demonstrated that tag retention and survival in captivity was high for both tag types; however, the minimum size threshold prevented us from tagging the entire size distribution. We estimate that we tagged the upper 18% of the size distribution of Yakima smolts passing through the Chandler Juvenile Monitoring Facility in 2006, and tagged the upper 73% in 2008. Size at release of Dworshak smolts released from Dworshak hatchery was unavailable in 2006, as the hatchery did not measure individual fish lengths prior to release. In 2008, a sample of individual fork lengths were taken, and we estimated that we tagged the upper 10% of the smolt size distribution; therefore in 2006, we can deduce that we tagged less than 10% of the size distribution since our minimum size was larger.

Surgical procedures used to implant acoustic transmitters were reviewed annually by institutional animal care committees and met or exceeded the Canadian Council on Animal Care standards (www.ccac.ca). The same surgical protocol was used in all years for both treatment types; a detailed description is given in Chapter 2 (Rechisky and Welch (2009)). In general, portable self-sustaining surgical units were assembled on site, and fish surgery was carried out by highly experienced, veterinarian-trained staff. Fish were anesthetised one at a time in 70 ppm of Tricaine Methane Sulphonate (MS-222). Fork length was measured to the nearest mm and weight was measured to the nearest tenth of a gram. The fish was then placed ventral side up into a v-shaped trough and a maintenance dose of anaesthetic (50 ppm) was pumped through the fish's mouth and over the gills. An incision was made at the ventral midline midway between the pelvic and pectoral fins and the tag was gently inserted through the incision into the peritoneal cavity. For a 9 mm transmitter, the incision was 10-12 mm in length and was closed with two interrupted sutures; for a 7 mm transmitter the incision was 7-8 mm and was closed with one suture. Surgery time was <2 min for a 9 mm tag and about 1 min for a 7 mm tag. Immediately following surgery, fish were placed into a recovery bath and monitored. Within minutes fish regained equilibrium and reactivity.

In addition to the acoustic transmitter, a passive integrated transponder (PIT) tag was placed in the body cavity (through the incision) of all acoustic tagged smolts. Juvenile spring Chinook salmon are collected at Snake River dam bypass facilities and transported via truck or barge to below Bonneville Dam during the spring seaward migration. By default, non-PIT tagged smolts that pass through the bypass are transported; smolts implanted with PIT tags are returned to the river unless selected for transportation via the separation-by-code procedure. Therefore, all acoustic tagged fish were also PIT tagged to be consistent; however the purpose of the PIT tag was to ensure that tagged IR smolts were diverted back into the river at the dam bypass facilities and not collected for transport to below Bonneville Dam, the last dam in the system. All POST PIT tag codes and release information were uploaded to the PIT Tag Information System (PTAGIS) database maintained by the Pacific States Marine Fisheries Commission (PSMFC, Portland, Oregon; http://www.ptagis.org).

4.2.4 Acoustic array location

The Pacific Ocean Shelf Tracking array is comprised of individual acoustic receiver units (Vemco model VR2 or VR3-UWM) which are typically deployed in a line (also called a sub-array) across a river, a strait, or the continental shelf. In the ocean, the units were deployed approximately every 800 m, however, in rivers the spacing between adjacent receivers was typically much less as the transmitter detection radius typically decreases with increasing water velocity. During this study the POST array extended from the Columbia River basin (WA, OR, ID) to southeast Alaska, including multiple sub-arrays in the southern British Columbia region. The location of the sub-arrays relative to this study are described below.

Within the Columbia River basin component sub-arrays were deployed in the Snake River in Lake Bryan at Snake River rkm 159 (14 km below Lower Granite Dam; total distance from the ocean was 681 km). Within the Columbia River sub-arrays were deployed in Lake Wallula at rkm 502 (21 km below the confluence of the upper Columbia and Snake rivers), in Lake Celilo at rkm 340 (7 km below John Day Dam), and at McGowan's Channel at river kilometer (rkm) 224 (10 km below Bonneville Dam; Figure 4.1). At each of these locations, receivers were deployed as paired lines, to assist in evaluating detection probability and to provide a survival measurement below three of the major hydroelectric dams. In 2007 an additional sub-array was deployed at the Astoria Bridge in the Columbia River estuary, 23 km from the river mouth. This sub-array was deployed as one line; however the receiver spacing was greatly reduced in order to provide a reliable estimate of detection probability (and hence survival) to the river mouth.

Marine components of the POST array at Willapa Bay (southern WA), Lippy Point (northwest Vancouver Island, BC), and Graves Harbor (southeast AK) were deployed as single lines and extended from near-shore to the edge of the continental shelf (200 m depth), a distance of up to 30 km (Figure 4.1). The Willapa Bay detection site is located 40 km north of the mouth of the Columbia River, adjacent to Willapa Bay, WA.; Lippy Point is located 525 km north of the Columbia River mouth and Graves Harbor is an additional 1105 km to the north. The total distance from the release site in the Clearwater River to Graves Harbor, AK is 2500 km.

4.2.5 Survival estimate analyses

All acoustic detection data from the array were first screened for logical occurrence in space and time, and single detections were discarded if they were inconsistent with the detection sequence. In-river fish were defined as any fish migrating in the river regardless of whether they went through the bypasses, over the dams in the spill, or through the turbines. We did not include Snake River Chinook smolts that were inadvertently transported from lower Snake River dam bypass facilities and released below Bonneville Dam.

Estimates of survival (Φ), detection probability (*p*), and their associated variances were calculated in each year using the Cormack-Jolly-Seber (CJS) model for live recaptured animals implemented in Program MARK (White and Burnham 1999). This model jointly estimates survival and detection within a likelihood framework. For in-river lines, we recognized basic CJS model assumptions (equal survival probability, equal recapture probability, no tag loss, and instantaneous sampling); however, for marine lines that are not bounded on the offshore end (continental slope), we required two additional assumptions; 1) as fish migrate along the coast they cross over the acoustic detection lines that span the length of the continental shelf to 200m, and 2) the majority of the fish departing the Columbia River swim north. These assumptions are supported by evidence from numerous ocean sampling programs that confirm that juvenile spring Chinook salmon remain almost entirely on the continental shelf and primarily migrate north upon leaving the river (Beamish et al. 2005; Bi et al. 2007; Brodeur et al. 2004; Fisher and Pearcy 1995).

Capture (detection) histories for each individual were formed and the fully time varying CJS model (survival and detection probability for each release group and each treatment type) was used to assess goodness of fit (GOF) to the data with the bootstrap GOF test within Program MARK. If there was overdispersion in the data it was corrected by dividing the model deviance by the mean expected deviance (from 1000 bootstrapped simulations) to yield an overdispersion factor, $\hat{c}$. In general, if $\hat{c}$ is greater than 1 then the resulting standard errors on the estimates are inflated (multiplied) by the $\hat{c}$ value. In 2006 the $\hat{c}$ overdispersion factor was 1.74 and thus the survival model was correct for overdispersion. In 2007 and 2008 there was no overdispersion ($\hat{c}$=1). We specified a logit link function for our survival models, which constrains the parameter estimates and their 95% upper and lower confidence limits to [0,1]. As most parameter estimates did not occur at the boundary, the back transformed confidence limits were often sufficient; however when parameter estimates were at the boundary, or very close to 0 or 1, the SE was often very close to 0. To produce confidence limits based on the likelihood function, we used the profile likelihood method for estimating confidence limits. The resulting confidence limits are asymmetrical, yet bounded by [0,1].

To produce estimates of survival we reduced (pooled) the release groups which resulted in one survival estimate for each population at each detection site. There were several reasons to pool the release groups; 1) pooling release groups increased sample size which resulted in a more precise estimate of survival, 2) the second IR group in 2006 and 2008 migrated rapidly downstream to “catch up” with the first release group therefore both release groups experienced similar conditions in the lower Columbia River and ocean, 3) the pooled survival estimates were used to estimate survival ratios of the two populations from a common detection site.

As survival estimates are dependent on detection rates, we estimated the detection probability at Willapa Bay by pooling all fish detected at that site and subsequent sites to produce the most precise detection probability. Therefore the survival estimates were unique for each population; however we modeled only one detection probability for Willapa Bay. Furthermore, because of the low number of fish detected at Vancouver Island and Alaska, we included in our models two additional transported groups (each N=100) of Dworshak spring Chinook salmon smolts that were tagged with the same acoustic tag, and released below Bonneville Dam, in order to better quantify the detection probability of the Willapa Bay detection line. (These two additional groups were used in the transportation survival study in described in Chapter 5 of this thesis.)

Although several fish were detected in Alaska, too few were detected to provide adequate information about the detection rate of the northwestern Vancouver Island acoustic sub-array (the CJS model calculates detection probability using the proportion of undetected fish that are recorded at more distant sites). Therefore, to estimate survival we assumed that the detection probability of the Lippy Point line was equal to the detection probability of the Willapa Bay line. We did this for several reasons: 1) all marine acoustic receiver nodes are deployed at equal or approximately equal spacing intervals, 2) rigorous analyses of detection probability for lines that are fully in tact, bounded by landmasses, and have ample detections beyond the line in question (which renders them estimable) have revealed that detection rates of POST lines in the ocean are remarkably consistent across multiple sites and over multiple years (~92% for V9 transmitters and ~73% for V7 transmitters at three sites in four years; M. Melnychuck, UBC PhD dissertation, 2009), 3) the distribution of fish across the acoustic line at Lippy Point is centered on the inner to middle continental shelf, therefore it appears that fish were confined to the shelf (see Figure 4.5 a and b), 3) if estimates at Lippy Point are biased they will be equally biased for both treatment types, 4) the estimated detection probability at Willapa Bay is consistent with other POST sub-arrays. In 2006 the detection probability at Willapa Bay was 69%. This estimate, however, accounts for 25% loss of the line (either by fishers or failure). If the inherent detection rate was 92% and gear loss was 25% then the expected detection rate is 69% (0.92*0.75) which is the same as the direct estimated detection probability. The detection probability in 2008 was 74%, which is consistent with the average detection probability of V7 transmitters on bounded lines (gear loss in 2008 was only 2%), and 5) we have no reason to believe that the acoustic environment at Lippy Point would be significantly different from that at Willapa Bay or other POST detection sites in the ocean.

To calculate survivorship we simply multiplied survival from release by sequential survival probabilities estimated in each migration segment (e.g., $\phi_1\phi_2\phi_3$, etc.). We derived the variance for each survivorship estimate using the programming language R with the Delta Method:

$$\widehat{var(Y)} = \left(\frac{\partial(\hat{Y})}{\partial\hat{\varphi}}\right) \cdot \hat{\Sigma} \cdot \left(\frac{\partial(\hat{Y})}{\partial\hat{\varphi}}\right)^{\mathrm{T}}$$

Where *Y* is the product of the survival estimates, the first term is a row vector containing the partial derivatives of Y with respect to each of the survival parameters, the middle term is the variance-covariance matrix from the model output, and the last term is the transpose of the row vector. We then calculated the standard error, $SE = \sqrt{\widehat{var(Y)}}$, and the 95% confidence interval, 95% $CI = Y \pm 1.96 \cdot SE$.

4.2.6 Survival models and model selection

In each year we modeled a suite of seven survival-related hypotheses. We hypothesized that individual covariates such as fork length, as well as external covariates such as the number of dams passed within a migration segment, the distance and mean travel time travelled in a migration segment, may differentially affect survival. The seven models/hypotheses were as follows:

1. Survival varies within each migration segment.
2. Survival is a function of FL. We hypothesize that larger smolts have higher survival.
3. Survival is a function of distance. We expect an inverse relationship: survival declines with increasing distance.
4. Survival is a function of mean travel time. As travel time increases, smolts may be more susceptible to predation and therefore survival may decrease. Travel time in the river is determined by river water velocity as well as distance.
5. Survival is a function of the additive effects of distance and dams. If we account for distance, does the number of dams influence survival?
6. Survival is a function of the interaction of distance and dams.
7. Survival is a function of the additive effect of FL within each migration segment. Survival varies by line and is a function of FL.

We used an information theoretic approach, i.e. Akaike's Information Criterion (AIC), to select the most parsimonious model. In general, the model with the lowest AIC value (which accounts for the number of model parameters, n_{pars}) has more support in the data, and if the ΔAIC of the other candidate models is greater than 2, then these models (i.e. hypotheses) have little or no support. We report survival estimates from the model which had the most support.

4.2.7 Survival ratios

To compare survivorship of Dworshak and Yakima smolts in the common area of the migration we calculated survivorship ratios ($S_{Dworshak}/S_{Yakima}$) and statistically tested whether the ratios were different from 1. If delayed mortality is experienced by the Dworshak population, we would expect the survival ratios to be significantly less than 1 downstream of the hydrosystem. If ratios are greater than 1, the Dworshak population had higher survival. We first multiplied segment specific survival probabilities in the common migration pathway to obtain cumulative survival estimates conditional on survival from Lake Wallula to McGowan's Channel (Bonneville Dam, SR_{hydro}), and from McGowan's Channel to three detection sites downstream of the hydrosystem: 1) Astoria (SR_{Ast}; 2007 and 2008), 2) Willapa Bay (SR_{WiB}), and 3) northwestern Vancouver Island (SR_{LIP}). Survival from Lake Wallula to Bonneville Dam is the area of common migration in the lower Columbia River hydrosystem. McGowan's Channel to Astoria includes the estuary. Survivorship estimates to Willapa Bay include the estuary and the plume; and survivorship to Lippy Point includes the estuary, the plume and early ocean survival.

We used one-sided z-tests (on the log scale) to test whether survival ratios were less than 1 at the 5% significance level using the test statistic:

$$z = \frac{\ln(\widehat{SR}) - 0}{\widehat{SE}\ ln(\widehat{SR})}$$

where $\widehat{SR}$ is the maximum likelihood estimate of SR_{hydro}, SR_{Ast}, SR_{WiB} or SR_{LIP}, where appropriate, and $\widehat{SE}$ $\ln(\widehat{SR})$ $=(\widehat{SE}\ (\widehat{SR}))/(\widehat{SR})$. The standard error of the survival ratio was derived using the delta method. If survival probabilities are estimated independently during the CJS estimation process then covariance is zero, however because we pooled data to estimate detection probabilities at ocean detection sites, we used the variance-covariance matrices from the CJS model output to estimate $\widehat{SE}\ (\widehat{SR})$.

4.2.8 Survival rate

To account for the effect of migration distance on survival and to illustrate potential differences in post-release survival, we assumed the exponential survival model $S_{i,j} = e^{bd_{i,j}}$ and regressed the log-transformed cumulative survival estimates at the j-th detection site, $\ln(S_{i,j}) = bd_{i,j}$, for each of the i-th populations against migration distance from the respective release sites, $d_{i,j}$, resulting in a decrease in survival rate per km, *b* (i.e., minus an instantaneous mortality rate b per mile). To isolate migration segments where differences in survival rate may vary, we partitioned this total migration distance into several parts: 1) release to the first detection site (Lake Bryan for Dworshak and Lake Wallula for Yakima), 2) Lake Wallula to Lake Celilo, 3) Lake Celilo to McGowan's Channel, 4) McGowan's Channel to Willapa Bay in 2006 and 5) McGowan's Channel to the Astoria Bridge and 6) Astoria Bridge to Willapa Bay in 2008. For Yakima smolts the first segment from release to Lake Wallula includes a small stretch of the Yakima River and mid Columbia River (113 km total); Snake River smolts migrated through a small stretch of the Clearwater River followed by a longer route in the lower Snake River (190 km total). The segments from Lake Wallula to Willapa Bay include the common migration corridor of the entire lower Columbia River, the estuary, and 40 km of ocean (542 km from Lake Wallula).

To estimate the uncertainty in the estimated regression coefficients we used a Monte Carlo procedure to randomly generate 10,000 individual survival estimates at each of the detection sites for each stock using the estimated survival proportions, $S_{i,j}$, and associated variances to define the parameters of the binomial sampling distribution leading to uncertainty in the survival values. We then took the 10,000 sets of generated survival estimates for each population, and calculated the log-transformed regression estimates to empirically define the distribution of minus mortality rates, b_i, for each population.

The null hypothesis that the survival rate of Snake River smolts is equal to that of the Yakima River smolts is equivalent to assuming that on average the difference in the regression coefficients, $b_1 - b_2$, is zero. We tested this null hypothesis for each of the simulated migration segments by evaluating whether the central 95% of the 10,000 survival rate differences included zero.

4.2.9 Cross shelf distribution

As smolts migrated along the continental shelf, their position was recorded on discrete sections of the sub-arrays. We used these data to compare spatial distributions of the two populations by assessing whether cross-shelf ocean distribution may be different for two populations of the same species which originated from different tributaries within the same river basin. In each year we used a X^2 test of homogeneity to test the null hypothesis that the proportion of Dworshak smolts detected across the Willapa Bay sub-array was similar to the proportion of Yakima smolts. To perform the tests we counted the number of unique ID codes for each population detected at each of the acoustic receivers deployed at Willapa Bay. (In 2006, 40 receivers were deployed; in 2007 five additional receivers were deployed on the west end of the sub-array nearest the continental slope.) If a fish was detected at more than one receiver a proportion was allocated to the receiver, e.g. if an ID code was detected on two receivers, each receiver was assigned a value of 0.5. If a receiver was displaced during the time when fish were migrating past the receiver (e.g. by fishing activity) then that receiver was omitted from the data set. To satisfy the requirements of the X^2 test (expected frequency count >5 per category) it was necessary to pool across receivers. In 2006, 10 of 40 receivers were lost to or displaced by commercial fishing gear, and we pooled data by every second receiver, therefore the data were pooled into 15 groups. In 2007 and 2008, receiver recovery was higher, however survival to Willapa Bay was lower and therefore there were fewer detections. As a result it was necessary to pool receivers into groups of five to satisfy the X^2 requirements, which resulted in nine categories.

As survival in the ocean from Willapa Bay to Lippy Point was low, the relatively low number of detections at Lippy Point prevented us from testing the distribution of the two populations at this more distant site.

4.2.10 Travel time and migration rate

For each release group of each population we calculated segment specific mean travel time (days) to each detection site, and cumulative mean travel time (days) from release to all subsequent detection sites. Additionally, we calculated segment specific mean migration rate over ground (km/day) to each detection site, and cumulative mean migration rate over ground (km/day) from release to all subsequent detection sites. For these calculations we took the time of the first detection from the subsequent site and subtracted it from the last detection time from the previous site resulting in the shortest possible time interval between detection sites. Fish that were not detected at both sites were not included in the calculations.

These movement data presented us with a unique opportunity to test the hypothesis that larger fish swim faster in the ocean. Even over the relatively small range of body sizes of smolts that were tagged (130-208 mm FL), we might expect to find that larger smolts swim faster in the coastal ocean. We performed an analysis of covariance (ANCOVA) using a linear model in the programming language R (R Development Core Team 2008) to test whether migration rate (MR) from Willapa Bay to Lippy Point (dependent variable) was a function of FL (predictor variable). We included in the model an additional variable to account for the effect of tag type (or year, 9 mm tags were used in 2006 and 7 mm tags were used in 2008), and the interaction between FL and tag type (MR~FL+tag type+FL*tag type). Migration rate data were available for 2006 and 2008; however no smolts were detected at Lippy Point in 2007.

4.3 Results

Following release from the hatchery, a proportion of Dworshak spring Chinook salmon from the Snake River basin was detected on the sub-array in the Snake River below Lower Granite dam, and on all sub-arrays in the lower Columbia River. In 2007 and 2008 smolts were also detected on the newly deployed sub-array in the Columbia River estuary near the river mouth (Astoria Bridge). Upon entry into the Pacific Ocean, smolts were detected on the ocean sub-array at Willapa Bay, and in 2006 and 2008 Snake River smolts were detected at Lippy Point (NW Vancouver Island) and at Graves Harbor (SE Alaska; one smolt was detected in 2006 and two smolts were detected in 2008). No fish were detected beyond Willapa Bay in 2007. The total tracking distance from release to the detection site in Alaska was 2500 km.

Spring Chinook salmon released from the lower Yakima River were detected at all lower Columbia River detection sites and on two of the ocean sub-arrays at Willapa Bay and Lippy Point, except in 2007 when no smolts were detected at Lippy Point. Yakima smolts were not detected on the Alaska sub-array. The total tracking distance from release to Lippy Point was 1140 km.

In 2007 a relatively low proportion of smolts was detected on the POST array when compared to other years of the study and when compared to independent estimates of survival from other studies in the same year. The low apparent survival or non-detection of smolts from both populations was possibly associated with over handling during tagging resulting in unusually high post-release mortality. We present results from the 2007 study, however, we make no attempt to draw conclusions regarding survival during this year. Distribution and rate of movement data are presented, but are limited due to low survival in 2007.

4.3.1 Model selection

In each year and for each population of spring Chinook salmon we modeled seven hypotheses regarding survival using the CJS mark-recapture model (fully time varying estimates of ϕ and p) and variants thereof (Table 4.2). In 2006 the most parsimonious model based on an information theoretic approach from our set of candidate models constrained survival as a function of mean travel time (ϕ_{TT} p_t). The slope parameters for travel time were significantly less than 0 (on the logit scale) for both populations indicating that survivorship decreased with increasing travel time. This model had the majority of the QAICc weight (0.6); however, there was also support for the fully time varying CJS model (ϕ_t p_t) as well. The ΔQAICc of this model was 1.5 and the QAICc weight was 0.29, indicating that this model was supported by the data as well (Table 4.2). All other candidate models including distance and dam number in a migration segment had very little or zero weight.

In 2007, the model which had that most support was the fully time varying CJS model (QAICc weight=0.88; Table 4.2b). It is not surprising that hypotheses/models concerning FL and travel time, etc., were not supported by the data given that apparent survival was unusually low following release. The fully time varying model fits the data best because it allowed ϕ and p to vary in each migration segment, whereas the other candidate models constrained these parameters too much to represent the poor survival immediately after release.

In 2008, the most parsimonious model was a time varying model with the additive effect of FL (ϕ_{t+FL} p_t; Table 4.2c). Although this model had most the AICc weight (0.77), the slope of the FL parameter was only significantly different from zero for the Dworshak population. As discussed in Chapter 2, this model had the most support when we included all sizes; however, when we removed the largest size class (155-159 mm FL) the slope of the FL parameter for Dworshak smolts was no longer significant and thus, the FL model was no longer the highest ranking model. The fully time varying CJS model was a competing model that also had weight (AICc weight= 0.23), however including the effect of FL marginally improved fit of the model. All other models had zero weight indicating that travel time, distance, dams were not useful predictors of survival in 2008.

4.3.2 Estimates of survival

Estimated survival probabilities for Dworshak smolts from release at Kooskia hatchery to the first detection site in Lake Bryan (below Lower Granite Dam) was 0.75 (SE=0.02) in 2006, 0.19 (SE=0.03) in 2007, and 0.71 (SE=0.02) in 2008 (Table 4.3). Survivorship from release to McGowan's Channel (the hydrosystem) was 0.4 (SE=0.04) in 2006, 0.08 (SE=0.02) in 2007, and 0.28 (SE=0.03) in 2008. Survivorship from release to Lippy Point (assuming detection probability was similar to Willapa Bay) was 0.03 (SE=0.01) in 2006 and in 2008 (Table 4.4, Figure 4.2). In 2007 no smolts were detected at Lippy Point.

Estimated survival probabilities for Yakima smolts from release at Chandler Juvenile Monitoring Facility to the first detection site in Lake Wallula (below the confluence of the Snake and Columbia rivers) were 0.73 (SE=0.02) in 2006, 0.32 (SE=0.03) in 2007, and 0.76 (SE=0.03) in 2008. Survivorship from release to McGowan's Channel (the hydrosystem) was 0.37 (SE=0.03) in 2006, 0.11 (SE=0.02) in 2007, and 0.48 (SE=0.04) in 2008. Survivorship from release to Lippy Point (assuming detection probability was similar to Willapa Bay) was 0.01 (SE=0.01) in 2006 and 0.05 (SE=0.02) in 2008 (Table 4.4, Figure 4.2). In 2007 no smolts were detected at Lippy Point.

To illustrate differences in freshwater migration survival and marine migration survival, we categorized migration segments into zones with similar hydrographic conditions (2006 and 2008 only). Survival from release to McGowan's Channel (below Bonneville Dam, the final dam that smolts encounter) is the hydrosystem; survival from McGowan's Channel to the Astoria Bridge is considered the estuary; survival from the Astoria Bridge to Willapa Bay encompasses the Columbia River mouth and plume in the ocean; and from Willapa Bay to Lippy Point is considered ocean shelf. In 2006 the Astoria Bridge sub-array was not yet deployed therefore we could not delineate between estuary and plume survival in that year.

In 2006, survival in the estuary and plume (Dworshak S_{e+p}=0.78, SE=0.02; Yakima S_{e+p}= 0.63, SE=0.03) was significantly higher than survival in the hydrosystem and in the ocean for both populations, and ocean survival (Dworshak S_{ocean}=0.08, SE=0.04; Yakima S_{ocean}=0.05, SE=0.04) was considerably lower in than in the hydrosystem ((Dworshak S_{hydro}=0.4, SE=0.04; Yakima S_{hydro}= 0.37; SE=0.03; Figure 4.3, Tables 4.3 and 4.4). In 2008, estimated survival in the estuary was 1.0 (for both populations) which was much higher than survival in any other zone. Survival in the hydrosystem, plume and ocean was similar for the Dworshak population (S_{hydro}=0.28, SE=0.03; S_{plume}=0.38, SE=0.07; S_{ocean}=0.24, SE=0.08); however hydrosystem survival of Yakima smolts (S_{hydro}=0.48, SE=0.04) was marginally higher than survival in the plume (S_{plume}=0.39, SE=0.06), and considerably higher than survival in the ocean (S_{ocean}=0.27, SE=0.07).

If we consider mean travel time in each zone, daily survival rate ($S^{1/t}$) in the estuary and plume combined was highest relative to the hydrosystem and ocean in 2006 for both populations (Dworshak S/d_{e+p}=0.953, Yakima S/d_{e+p}=0.912; Figure 4.3). Smolts from both populations migrated rapidly through the estuary and plume, a distance of 264 km, in five days on average (Tables 4.5 and 4.6). For Dworshak smolts in 2006, survival/day was lowest in the coastal ocean (Dworshak S/d_{ocean}=0.924), and for Yakima smolts survival/day was lowest in the hydrosystem (Yakima S/d_{hydro}=0.830). In 2008, survival/day was highest in the estuary for both populations (Dworshak $S/d_{estuary}$=1, Yakima $S/d_{estuary}$=1). Smolts moved through the estuary in only 2.5 days. Daily survival was similar in the hydrosystem and in the plume, and for both populations. In 2008 ocean daily survival was markedly higher than in 2006, particularly for the Yakima River population. In general, the estuary may be the safest part of the smolt migration, and inter-annual variability in ocean conditions may lead to small changes in daily survival rate that may translate into substantial changes in survival during early ocean migration.

4.3.3 Survival ratios

To assess whether Dworshak smolts have poorer survival due to delayed mortality from dam passage we compared survival of Dworshak and Yakima smolts in the common area of the migration by calculating survivorship ratios ($S_{Dworshak}/S_{Yakima}$) from Lake Wallula to McGowan's Channel (Bonneville Dam; SR_{hydro}) and from McGowan's Channel to three subsequent detection sites: 1) Astoria (SR_{Ast}; 2007 and 2008), 2) Willapa Bay (SR_{WiB}), and 3) northwestern Vancouver Island (SR_{LIP}). In 2006, survival ratios were significantly greater than 1 at the 5% significance level in the hydrosystem (SR_{hydro} =1.41, SE=0.11, z=4.34, p<0.001), and from McGowan's Channel to Willapa Bay (SR_{WiB} =1.24, SE=0.07, z=4.07, p<0.001), indicating that Dworshak smolts actually had higher survival in the hydrosystem after passing four dams, as well as higher survival in the estuary and plume, after passing eight dams (Table 4.7). The survival ratio to Lippy Point was not significantly different from 1 (SR_{LIP} =2.17, SE=2.07, z=0.809, p=0.209), and this was due to high variance around the survival estimates to this distant location. In 2008, the survival ratio estimated for the hydrosystem did not exceed 1 but was not significantly less than 1 at the 5% significance level (SR_{hydro}=0.93, SE=0.11, z=-0.603, p=0.274), nor was it significantly lower from McGowan's Channel to the Astoria Bridge (SR_{Ast} =1.0, SE=0, z=0.005, p=0.5), Willapa Bay (SR_{WiB} =0.99, SE=0.23, z=-0.021, p=0.492), or Lippy Point (SR_{LIP} =0.88, SE=0.4, z=-0.268, p=0.397). Therefore, Dworshak smolts did not suffer from delayed mortality when compared to a population from the mid-Columbia River.

4.3.4 Survival rate

Appendix C shows the distribution of per km instantaneous mortality rates (b) of seaward migrating juvenile spring Chinook salmon in 2006, 2007, and 2008. In general, Dworshak smolts had lower post-release mortality than Yakima smolts; however this was only significant in 2006. In 2007 post-release mortality was high for both populations, and thus the difference was not significant when comparing populations. Not surprisingly, mortality per km in 2007 was significantly higher than mortality rates in 2006 and 2008. There was no significant difference in mortality rates in all other migration segments in all years.

4.3.5 Detection probability, p

In 2006 and 2007 smolts were tagged with 9 mm transmitters; in 2008 smolts were tagged with a smaller 7 mm transmitter with a lower output, and therefore we anticipated that detection probabilities would be affected by the decrease in detection radius. (The tradeoff was that we were able to tag smaller smolts.) The estimated detection probability of Dworshak smolts in the Snake River below Lower Granite Dam was >0.96 in all years (Table 4.8). Below the confluence of the Snake and Columbia rivers the detection probability of Dworshak smolts in Lake Wallula was >0.93 in all years, and >0.96 for Yakima smolts. At these sites, the river is broader, and river velocity is slower relative to sites further downstream, which facilitated higher detection probabilities. Further downstream, in Lake Celilo (LaC) and McGowan's Channel (McG), detection probabilities varied; they were highest in 2007 (Dworshak p_{LaC} =0.92, p_{McG}=0.79; Yakima p_{LaC}=0.97, p_{McG}=0.97), intermediate in 2006 (Dworshak p_{LaC} =0.56, p_{McG}=0.70; Yakima p_{LaC}=0.78, p_{McG}=0.84), and lowest in 2008 (Dworshak p_{LaC} =0.51, p_{McG}=0.15; Yakima p_{LaC}=0.33, p_{McG}=0.10) for both populations. Although relatively few fish were detected overall in 2007, the detection probability was likely highest due to lower river flows in that year. The poor detection probabilities in 2008 were likely a function of above average river flow (DeHart 2009) combined with decreased detection range of the 7 mm transmitters. At the Astoria Bridge sub-array (2007 and 2008), 200 km downstream of McGowan's Channel, the spacing interval of the acoustic receivers was greatly reduced to ensure high detection rates. As a result, detection probabilities remained high in 2007 (>0.83), and in 2008 there was a marked improvement over the Lake Celilo and McGowan's Channel detection sites, (>0.75; Table 4.8). As this detection site was nearest the river mouth it was critical to detect most of the tagged, migrating smolts so that in-river detection rates and survival could be accurately estimated, particularly in 2008 when smaller tags were used.

Detection rates in the ocean at Willapa Bay accurately reflected the amount of gear loss in 2006. That is, in 2006, 25% (10 of 40) of the acoustic receivers were removed or shifted out of place by commercial fishing gear, and as a result the detection probability in 2006 was 0.69 (Table 4.8). In 2008, 98% of the receivers were retained on the 34 km long sub-array; however the reduced power of the 7 mm transmitters resulted in a reduced detection probability. The estimated detection probability in 2008 was consistent with detection probabilities of 7 mm transmitters on POST sub-arrays in the Strait of Georgia, British Columbia (M. Melnychuck, pers. comm.).

The Lippy Point sub-array extended 18 km to the edge of the continental shelf and remained completely intact in all years; however, it was not possible to estimate detection probability because only one fish in 2006 and two fish in 2008 were detected at the subsequent detection site in Alaska. To estimate survival probabilities to this line we assumed that the detection probability at Lippy Point was equal to that at Willapa Bay in our mark-recapture models in each year. Similarly, in 2007, no smolts were detected on the Lippy Point sub-array, so it was not possible to estimate the detection probability at Willapa Bay. Therefore we assumed that the probability was the same as in 2006 when gear loss was comparable.

4.3.6 Cross-shelf distribution

In each year we used a X^2 test of homogeneity to test the null hypothesis that the proportion of Dworshak smolts detected across the Willapa Bay sub-array was similar to the proportion of Yakima smolts. In 2006, the distribution of Dworshak smolts was significantly different from the distribution of Yakima smolts (X^2=47.57, *d.f.*=14 , p<0.0001). As shown in Figure 4.4, Dworshak smolts were distributed on the outer half of the continental shelf, while Yakima smolts were distributed across the entire array but with a concentration on the inner portion of the sub-array. In 2007, fewer smolts were detected on the sub-array but both populations were distributed across the length of the sub-array (Figure 4.4). There was no significant difference in the distributions (X^2=2.94, *d.f.*=8 , p=0.938); however the lack of fish surviving to the array may obscure any differences in distribution. In 2008, both populations were distributed towards the outer half of the continental shelf, and their distributions were not significantly different (X^2=5.48, *d.f.*=8 , *p*=0.706, Figure 4.4).

The distribution of smolts on the Lippy Point sub-array was confined to the inner section in 2006, and was more widely distributed in 2008 for both populations. Too few fish survived to Lippy Point to perform a statistical test on the distribution, but for illustrative purposes we present histograms in Figure 4.5. In 2007, no smolts were detected on this sub-array.

4.3.7 Travel time and migration rate

Segment specific mean travel time, cumulative mean travel time, segment specific mean migration rate, and cumulative mean migration rate tables are presented in Appendices 1 and 2. Segment specific mean travel time in the river and the ocean is also shown in Figure 4.7. In general, travel time between successive detection sites in the Columbia River was less than five days (Figure 4.7). Travel time of Dworshak smolts from release to McGowan's Channel (647 km) ranged from 17.1-22.8 days. Travel time of Yakima smolts from release to McGowan's Channel (391 km) ranged from 5.3-7.7 days. Travel times of both populations decreased when river flow was fastest in 2006. Travel time in the ocean from Willapa Bay to Lippy Point (485 km) was approximately one month for both populations in 2006 and 2008. Segment specific travel time from Lippy Point to Graves Harbor (1105 km) could only be calculated from one individual in 2006; travel time for this fish was 38.4 days. Across all years, a total of three Dworshak smolts was detected on the Graves Harbor sub-array; travel time from release was approximately three months (90.2, 93.9, 94.5 days).

There was a tendency for larger fish to travel faster in the ocean from Willapa Bay to Lippy Point (485 km) in 2008 (7 mm transmitters), contrary to 2006 (9 mm transmitters) when there was a tendency for smaller smolts to migrate faster (Figure 4.6). Thus, there was a significant interaction between FL and year in our ANCOVA model that included both years (t=2.71, p=0.015) and therefore we analyzed the effect of FL for each year separately. In 2006, however, there were only four fish (two Dworshak, two Yakima) that were detected at both Willapa Bay and Lippy Point. Although several more fish were detected at the Lippy Point sub-array (but not detected at Willapa Bay), we could not calculate a migration rate for fish that were not detected at both locations, therefore they could not be used in the analysis.

In 2006 the FL coefficient was not statistically significant, indicating that FL was not a good predictor of migration rate in that year. In 2008, FL was a significant variable for predicting rate of movement (p=0.002). The coefficient for FL was 0.408 (SE=0.108) indicating that for every mm of fish length the migration rate increased 0.408 km/d, or for every cm of length migration rate increased by 4.1 km/day (Figure 4.6).

4.4 Discussion

Riverine and early marine survival data for Columbia River basin Chinook salmon are essential for delineating and assessing the effects of impounded rivers and the impact of the marine environment on salmon survival. Early marine migration data are also valuable in that we can test hypotheses regarding smolt behavior in the ocean, and compare survival of smolts with varying freshwater migration histories. As well, these data can be useful for examining survival model assumptions. We tagged and released >2200 yearling Chinook salmon to estimate juvenile survival in the river and in the ocean. Additionally, we documented some of the most extensive observations of marine migration patterns and behavior of salmon smolts in the open ocean using a large scale acoustic telemetry array.

4.4.1 Model selection

We tested several hypotheses regarding smolt survival, including the effect of distance and dam number in relation to migration segment, travel time, and body size (FL). In 2006, travel time was the best predictor of survival. Smith et al. (2003) found some evidence that reduced river flow increases travel time of subyearling Chinook salmon smolts, however water velocity and turbulence provide cues to migrating salmon which may have the most influence on travel time while migrating in river (Tiffan et al. 2009). In 2007, survival declined dramatically after release, therefore when we constrained survival to include effects of distance, dams, etc, such simple models did not perform well. As expected, the most parsimonious model in 2007 was the fully time varying CJS model, which did not constrain for any of the factors above. In general, survival data reported from the 2007 seaward migration is not representative of the population and should be treated as such. We reported 2007 data to demonstrate the contrasting survival estimates compared to other years; however migration behavior data (migration rate, cross-shelf distribution) may still provide insight into smolt behavior. In 2008, the model that constrained survival as a function of FL was the most parsimonious model, and indicated that larger smolts had higher survival. This result however, only applied to Dworshak smolts; it was not observed in Yakima smolts. Further, the apparent effect of FL did not apply when we removed the largest size group (155-159 mm FL) from the model (see Chapter 2), therefore the largest size group survived better than smolts that ranged between 130-154 mm FL, however within the latter size group there was no significant positive correlation between body size and survival. In 2006 and 2008 the full CJS model (ϕ_t p_t) was a competing candidate model within the set of hypotheses tested indicating that travel time and FL were not dominant predictors of survival. Models which included distance and number of dams in a migration segment resulted in little or no support in the data. The lack of estimated effect of the number of dams passed on direct in-river survival may be a reflection of the improvements of fish passage in the hydrosystem (Ferguson et al. 2007; Muir et al. 2001; Williams and Matthews 1995). Any remaining negative effect of the dams may be too small to be measurable once the effect of travel time and body size is accounted for.

4.4.2 Survival in the hydrosystem

Additionally, we compared our survival estimates to independent PIT tag estimates of survival for the same populations in the same years in order to verify our survival estimates. Typically, our release dates were two to four weeks after PIT tagged smolts were released, and our minimum size requirement prevented us from tagging the smaller individuals; however comparing survival of acoustic tagged smolts that underwent surgery to a group tagged with a smaller tag and a using a less invasive procedure allowed us to ground truth our estimates. As our survival estimates extended into the ocean, it was only possible to compare PIT tag estimates to just below Bonneville Dam in McGowan's Channel for Dworshak smolts and to John Day Dam for Yakima smolts. In 2006 the PIT tag survival estimate of spring Chinook salmon smolts released from Dworshak NFH to Bonneville Dam (hydrosystem survival) was 0.408 (SE=0.061; S. Smith, NOAA, pers. comm.), which was similar to our acoustic tag estimate of 0.40

(SE=0.04) to McGowan's Channel. Similarly in 2008, survival of PIT tagged Dworshak smolts was 0.297 (SE=0.059; S. Smith, NOAA, personal comm.) and survival of acoustic tagged smolts was 0.28 (SE=0.03). Survival of PIT tagged Yakima smolts released from Chandler Juvenile Monitoring Facility to John Day Dam was 0.519 (SE=0.043; D. Lind, Yakama Fisheries, personal comm.) in 2006, which was similar to the acoustic survival estimate 0.51 (SE=0.03) estimated from the same release site to Lake Celilo just below John Day Dam. In 2008, survival of PIT tagged Yakima smolts was 0.674 (SE=0.055), and survival of acoustic tagged smolts was 0.66 (SE=0.05). Therefore our estimates of survival in the hydrosystem are remarkably similar to PIT tag estimates despite differences in release dates, body size and release location (Dworshak only).

4.4.3 Survival in the estuary

Downstream of the hydrosystem, survival in the estuary from McGowan's Channel to the Astoria Bridge was 100% for both populations in 2008, and despite initial losses following release, survival in the estuary was >89% in 2007. In 2006, we could not delineate between survival in the estuary and the plume, however survival from McGowan's Channel to Willapa Bay was relatively high. High survival estimates below the hydrosystem and in the upper estuary are consistent with survival estimates reported for spring Chinook salmon in other telemetry studies. Schreck et al. (2006) conducted radiotelemetry studies from 1995-98 and found that overall mortality of in-river smolts and transported smolts from release into the bypass system of Bonneville Dam and downstream of Bonneville Dam, respectively, was low (11-17%) and that most of this mortality was due to avian predation which occurred in the lower estuary between rkm 0-46. More recently, Eder et al. (Eder et al. 2009) used acoustic transmitters to estimate river and estuary survival of spring Chinook smolts released at Lower Granite Dam. Survival in 2008 in the lower river and estuary, from rkm 202 to 35.6, was 0.969 (SE=0.016). Therefore, our survival estimates of 100% downstream of Bonneville Dam appear reasonable.

4.4.4 Early marine survival

Survival in the plume in 2008 was relatively low (~38% for both populations) compared to combined survival in the estuary and plume in 2006 (73-78%). Early marine survival however, was low in 2006 (5-8%) and high in 2008 (24-27%). Survival estimates in the ocean (Willapa Bay to Lippy Point) are based on the assumption that the detection probability of the Lippy Point sub-array was similar to Willapa Bay. As this is the first study to assess early marine survival of Columbia River Chinook salmon in the open ocean, there are no studies in which to compare our survival estimates. There are however, annual estimates of ocean ecosystem indicators produced by NOAA intended to predict conditions for salmon survival. These indicators range from "good" to "intermediate" to "poor" and include local biological indicators, local and regional physical indicators, and large scale ocean and atmospheric indicators (http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/g-forecast.cfm#Table1). In 2006, ocean conditions were deemed intermediate-poor for juvenile salmon entering the ocean. The period of poor ocean conditions ended in 2007, and in 2008 ocean conditions were deemed good for juvenile salmon survival. The rating of the indicators is consistent with our preliminary early marine survival estimates; survival in 2006 was poor compared to good survival in 2008. Thus, our early marine survival estimates may be a useful method for ground truthing predicted ocean conditions for juvenile salmon.

4.4.5 Delayed mortality of Snake River spring Chinook salmon

In this study we found no evidence that delayed mortality was expressed by Snake River smolts (>130 mm FL) by the time they had reached ocean sub-arrays on the Washington and Vancouver Island coasts, some 274 km and 749 km from Bonneville dam, when compared with a size-matched group from the Yakima River population. Survival ratios in 2006 indicated that Dworshak smolts actually had significantly higher survival than Yakima smolts from McGowan's Channel to Willapa Bay, and in 2008 the survival ratio for this migration segment was not significantly different from 1 indicating that survival was not greater for Yakima smolts. We estimated survival ratios from McGowan's Channel to Lippy Point, however low sample size at this distant detection site resulted in large standard errors, therefore results were non-significant, as expected.

Tagged Chinook salmon were also detected on the acoustic sub-array in Alaska. The low numbers detected on this sub-array (~1000 km north of Lippy Point), prevented us from estimating survival to this location; however, the detection of two Snake River smolts on the Alaska line in 2006 and 1 in 2008 (and none from the Yakima population), some 2,500 km from the release site is inconsistent with the delayed mortality hypothesis. Quite possibly many Columbia River Chinook salmon do not migrate as far north as the array in Alaska, rearing instead in areas such as fjords in northern British Columbia so lack of detections in Alaska is not good evidence of poor survival after passing the Lippy Point sub-array.

4.4.6 Assessing additional model assumptions

Survival estimates presented in this chapter are based on the assumption that smolts turn north after ocean entry, and is supported by the high proportion of smolts detected on the Willapa Bay line subsequent to passing the detection line below Bonneville Dam or at the Astoria Bridge. Preliminary data from 2009 also demonstrate that smolts primarily migrate north. Prior to the 2009 seaward migration an acoustic sub-array was deployed south of the Columbia River mouth; only two smolts (of 1400 released upriver) were detected.

This result is also based on the assumption that smolts are confined to the continental shelf. Peak smolt detections at Willapa Bay were centered on-shelf for both populations with declining detections farther offshore. In 2006 there was some evidence of smolts migrating beyond the offshore limit of the marine listening lines, with the acoustic receiver farthest offshore at Willapa Bay (31 km from shore) recording multiple detections of a Snake River smolt and one detection of a Yakima River smolt (this animal was also heard farther landward). In an attempt to detect all smolts passing this sub-array, it was extended beyond the shelf by five acoustic receivers (3 km) before the seaward migration in 2007. In 2007, four smolts were detected on the farthest receiver (3 Dworshak andoneYakima), though all were heard farther landward as well. In 2008 four unique tag codes were detected (two Dworshak, two Yakima) on the farthest functioning receiver (receiver 44; receiver 45 was not operational in 2008). Farther north, the distribution of Columbia River smolts on the Lippy Point sub-array was confined to the shelf. In 2006 all smolts were detected on the inner half of the array. In 2008 the distribution extended beyond the mid-shelf area; however only one Yakima smolt was detected on the farthest receiver but this smolt was also detected farther landward. The smolt migration may thus extend further out into the slope region at Willapa Bay, beyond the 200m isobaths, particularly in years when the Columbia River plume spreads far offshore.

A largely shelf-bound distribution is consistent with distributional patterns reported by numerous investigators (Bi et al. 2007; Brodeur et al. 2004; Fisher and Pearcy 1995). If tagged smolts were not detected due to straying off of the shelf then we would have expected survival estimates be much lower due to non-detection. Survival from Bonneville Dam to Willapa Bay, a 264 km migration through the estuary and plume, was 78% for Dworshak smolts and 63% for Yakima smolts. In 2008, survival in this same migration corridor was lower, 38% for Dworshak and 39% for Yakima, however subsequent high survival in the ocean to Lippy Point provides evidence that smolts migrated north and remained primarily on the shelf.

4.4.7 Survival rate

Although Yakima smolts travelled a shorter distance to the ocean (and thus were exposed to in-river mortality agents for a shorter period of time), survival to McGowan's Channel and Willapa Bay was similar for both populations in 2006. Thus, when scaled by distance traveled, overall survival rate was lower for Yakima smolts (Figure 4.2). When we partitioned the migration route however, we found that the increased mortality of Yakima River Chinook salmon occurs in the 113 km undammed stretch between the release site and the first detection site in Lake Wallula (Appendix Figure C.1). Below Lake Wallula, in the region of common migration, mortality rates were not significantly different for the two populations (Appendix Figure C.1, C.2, C.3). In 2008, mortality rate to the first detection site was once again greater for Yakima smolts, although the difference was not significant (Appendix Figure C.3), and as in 2006 mortality rates in the region of common migration were similar beyond this point.

High mortality of Yakima smolts measured during the first migration segment may be caused by the thriving small mouth bass population introduced to the Yakima River (Fritts and Pearsons 2004); however, spring Chinook smolts are generally large enough to escape predation risk from these predators (Fritts and Pearsons 2006). The occurrence of non-anadromous precocious males or "minijacks" may be responsible for the initial low survival estimate (Larsen et al. 2004); however we saw no evidence of repeated downstream-upstream migrations in the months following release. It is possible that avian predation in the Yakima and the mid-Columbia River contributed to post-release mortality. The area near the Chandler Juvenile Monitoring Facility (where fish were released) is considered a “hotspot” for predatory birds (Bosch and Fast 2006). We also have evidence of Caspian tern predation in the mid-Columbia, as 15 POST tags were recovered from the tern colony on Crescent Island (17 km upstream of the Lake Wallula detection site, but below the confluence of the Snake and Columbia rivers) in 2006, 12 of which were identified as tags from Yakima smolts. In contrast, only two tags were found at this bird colony in 2008 (but the tags were not identifiable).

4.4.8 Marine migration characteristics

Larger smolts migrated significantly faster from Willapa Bay to Lippy Point in 2008; however, FL was not a good predictor of migration rate in 2006. The difference between years may be related to the size of the tag, which was larger in 2006; however sample size was very low in 2006 and therefore to compare across years may be futile.

The cross-shelf distribution of the Snake River population was significantly different from the Yakima River population in 2006 with the Snake River population more concentrated on the offshore portion of the line. The differing marine distributions of the two populations at Willapa Bay in 2006 provides a potential mechanism in support of the hypothesis that populations from the same river basin can have different responses to ocean conditions (e.g., Levin 2003). In 2006, however, our release dates were not as synchronous as we intended. Dworshak smolts migrated more rapidly than down the Snake and Columbia rivers (this was attributed to above average river flows), passing through Lake Wallula in mid-May and reaching the Washington coast by the end of the month. Most Yakima smolts migrated through Lake Wallula during the first week of June and entered the ocean during the second week of June. Consequently, Dworshak smolts entered the ocean approximately two weeks earlier than Yakima smolts, which may have exposed them to different plume conditions caused by changes in the direction of local winds that alter the distribution of the plume within a few days time (Garcia Berdeal et al. 2000). Thus, the distribution of Dworshak smolts in 2006 may have been attributed to timing of ocean entry and plume dynamics that ushered smolts farther offshore. In 2008, both populations entered the ocean in early June and their distributions were not significantly different. This supports the suggestion that plume condition may affect distribution of smolts on the shelf at Willapa Bay; however more data is necessary to evaluate this hypothesis.

4.4.9 Study limitations

1) We were limited to tagging smolts ≥140 mm FL in 2006 and ≥130 mm FL in 2008, 2) tagged fish were released 2-4 weeks after the main hatchery releases, 3) tagged smolts were detected on the outermost receiver at Willapa Bay, suggesting that some smolts may migrate beyond the offshore extent of the sub-array, possible due to varying plume conditions. Future work should address these limitations by using smaller tags and further extending the marine components of the array farther offshore. Advances in the array design, and smaller tags, will allow us to study marine survival over the complete size range of naturally occurring spring Chinook smolts, as well as other endangered populations of salmon originating from the Columbia River basin.

4.4.10 Conclusions

Data on early marine migration for Columbia River basin Chinook salmon is essential for assessing marine survival and behavior, and the effects of the hydrosystem on smolt survival. Determining when and where mortality occurs during the early ocean migration may reveal how populations from the same river basin can have different responses to ocean conditions (Levin 2003). Despite significant increases in direct hydrosystem survival in recent years (Muir et al. 2001; Williams et al. 2001), the average survival of Yakima River hatchery spring Chinook salmon from smolt seaward migration until adult return from the ocean was consistently greater than that of Dworshak (Snake River) hatchery spring Chinook salmon over the past several years (Berggren et al. 2006; Bosch and Fast 2006). Using the POST array, we estimated freshwater and early marine survival of Snake and Yakima River spring Chinook salmon to a location on the continental shelf 749 km beyond Bonneville Dam, the final dam in the Columbia River, and tracked smolts as far as Alaska. Travel times and rate of movement through the Columbia River were rapid (relative to ocean rates from Willapa Bay to Lippy Point) and this is attributed to water velocity. There was some evidence of delayed migration in the Willapa Bay line area, however travel times to this ocean line from within the river indicate that most smolts from both populations migrated north, consistent with evidence from marine surveys (Bi et al. 2007; Emmett and Brodeur 2000; Fisher and Pearcy 1995), and at similar speeds.

Our results imply that if delayed mortality causes the disparity in adult return rates of hatchery-origin Snake River spring Chinook salmon, it is at a time and place more distant from the Columbia River; however, it is plausible that delayed mortality may operate on smaller fish (<130 mm FL) that were not tested here. It remains unclear whether the entire size ranges of these two populations, as well as wild smolts, have similar survival and behavior as the smolts reported here.

Exploring recovery and management options including dam breaching, transportation of smolts to bypass the hydrosystem, habitat restoration, and potentially estuary and early marine enhancement also requires comparative early marine survival information to guide policy decisions. Our use of the POST array allows us to extend research on ESA listed species into the ocean, where much of the mortality may to be expressed. Our results suggest that the ocean plays a critical role in the early life history of migrating juvenile salmon. Greater consideration should be given to the marine portion of smolt migration in the management and conservation of Columbia River salmon stocks.

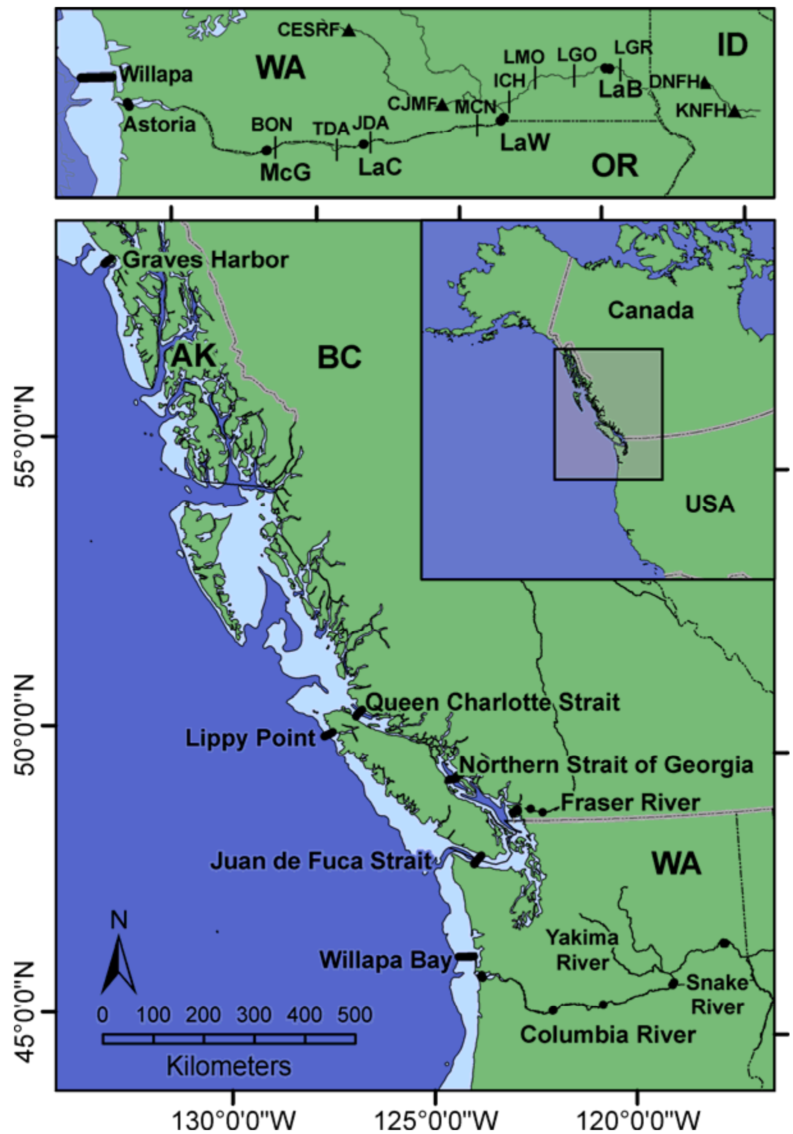


Figure 4.1. Map of the Pacific Ocean Shelf Tracking (POST) acoustic array. The inset shows the location of the hatchery sites (CESRF=Cle Elum Supplementation and Research Facility; DNFH=Dworshak National Fish Hatchery), release sites (CJMF=Chandler Juvenile Monitoring Facility, KNFH=Kooskia National Fish Hatchery); detection sites (LaB=Lake Bryan, LaW=Lake Wallula, La=Lake Celilo, McG= McGowan's Channel); and dams (BON=Bonneville, TDA=The Dalles, JDA=John Day, MCN=McNary, ICH=Ice Harbor, LMO=Lower Monumental, LGO=Little Goose, LGR=Lower Granite) within the Yakima, lower Snake and Columbia rivers. The continental shelf (depths <200m) is shaded.

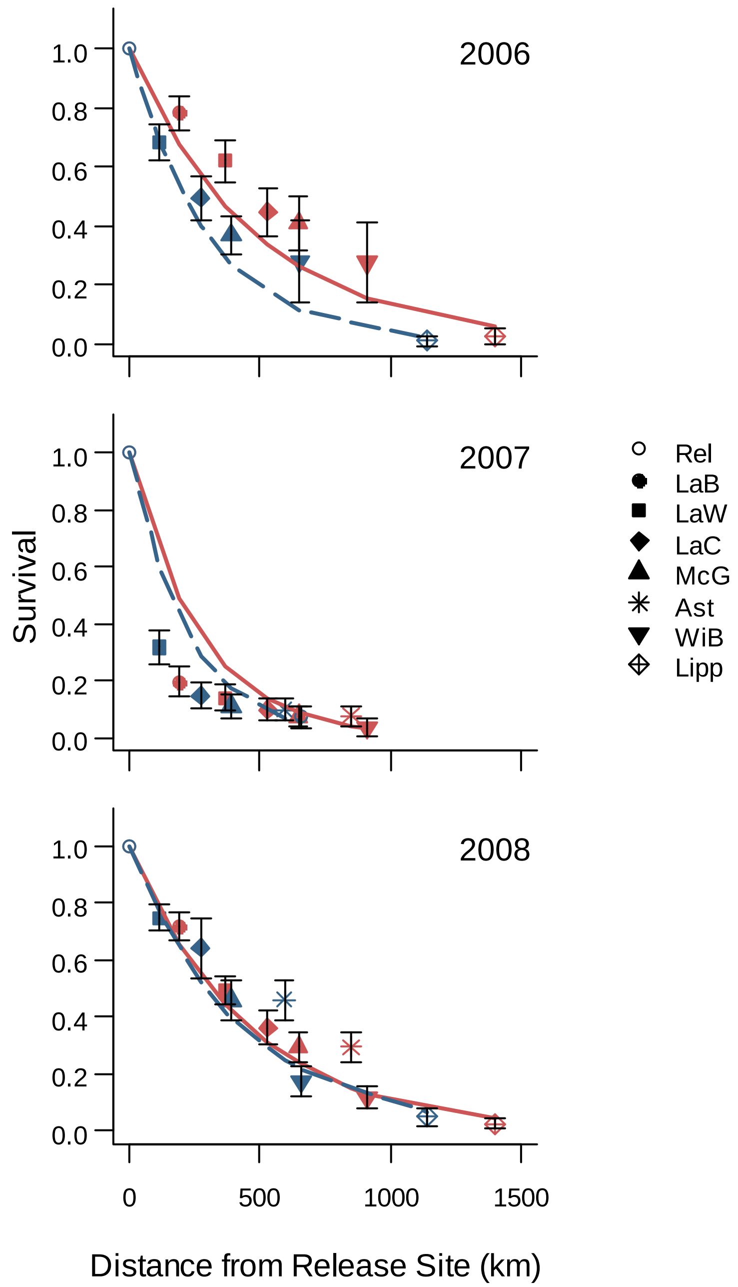


Figure 4.2. Survivorship of spring Chinook salmon smolts to Lippy Point on the northwestern end of Vancouver Island in 2006, 2007 and 2008. Dworshak smolts (red, solid line) were released from Kooskia National Fish Hatchery in the Snake River basin. Yakima River smolts (blue, dashed line) were released from the Chandler Juvenile Monitoring Facility in the Yakima River basin. (Rel=release, LaB-Lake Bryan, LaW=Lake Wallula, LaC=Lake Celilo, McG=McGowan's Channel, Ast=Astoria Bridge, WiB=Willapa Bay, Lipp=Lippy Point). The Astoria Bridge receivers were deployed in 2007 and 2008.

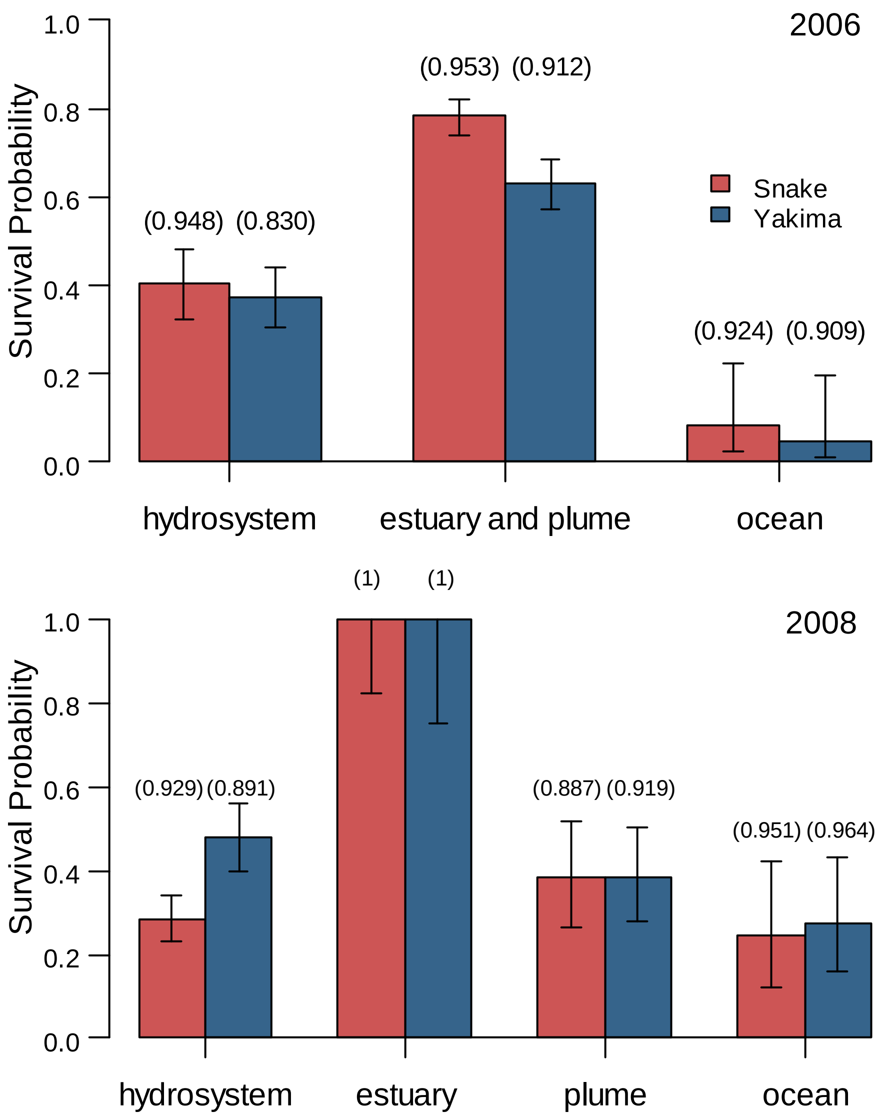
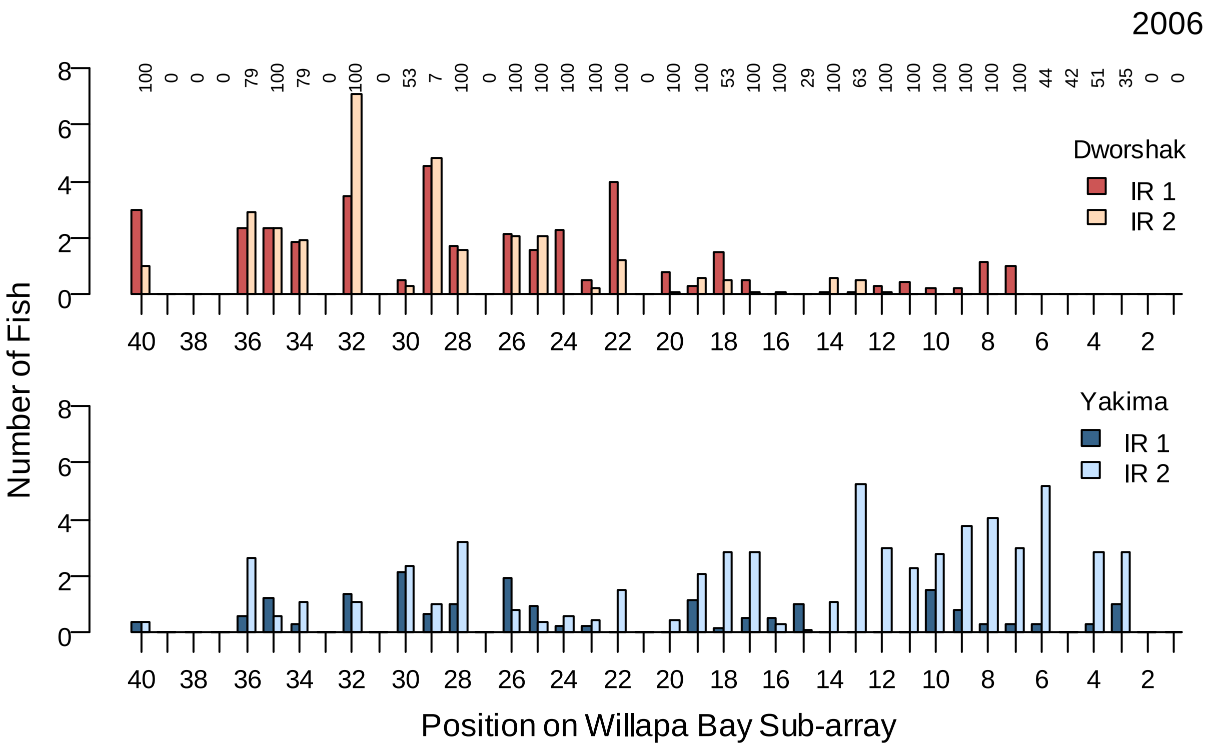
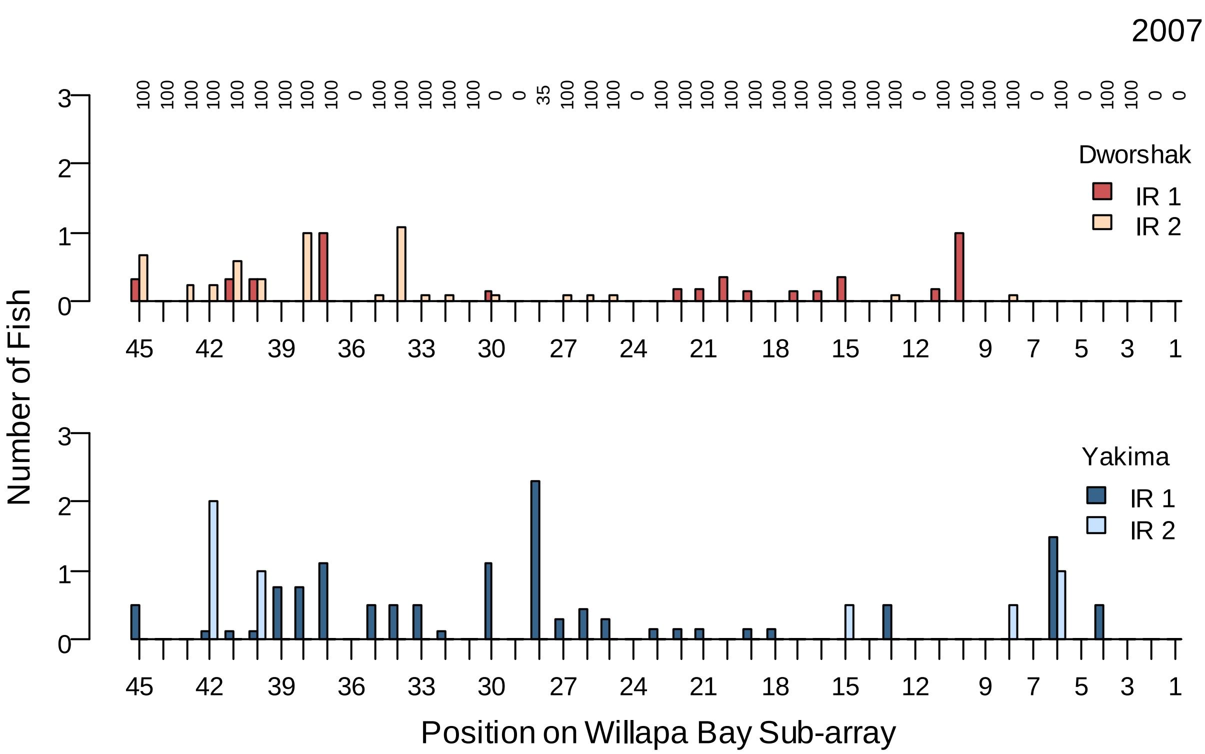


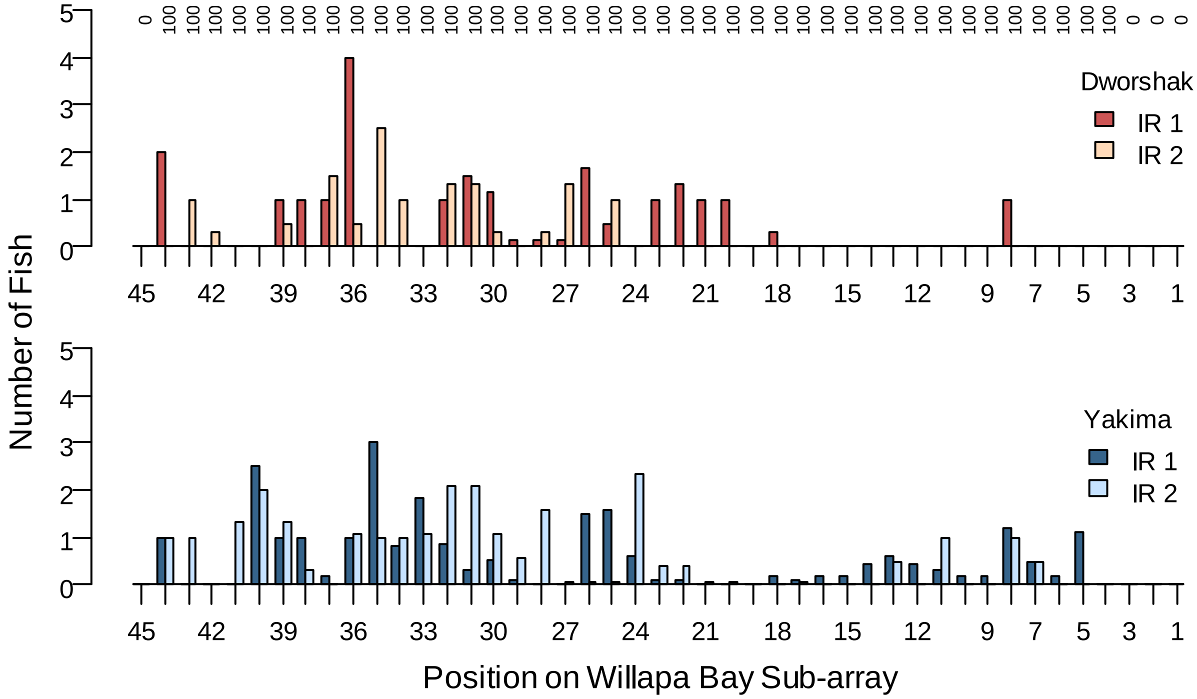
Figure 4.3. Dworshak (red) and Yakima (blue) Spring Chinook salmon survival estimates in four migration zones in 2006 and 2008. Numbers in parentheses above bars indicate mean survival per day.

Figure 4.4. Cross-shelf distribution of Dworshak and Yakima spring Chinook salmon smolts off of southern Washington at Willapa Bay in 2006, 2007, and 2008. Two release groups from each population were released in-river (IR) to freely migrate to the ocean. Position 1 on the x-axis represents the eastern-most acoustic receiver nearest shore. A total of 40 receivers (VR2's and VR3's) was deployed in 2006. In 2007, five receivers were added on the offshore portion of the sub-array. In 2008, receiver 45 was not operational; therefore the sub-array was effectively 44 receivers in length. If a fish was detected at more than one receiver a proportion was allocated to the receiver, e.g. if an ID code was detected on two receivers, each receiver was assigned a value of 0.5. The values above the bars indicate the proportion of time that the receiver was operation during the migration.


2006
100 0 0 0 79 100 79 0 100 0 53 7 100 0 100 100 100 100 100 0 100 100 53 100 100 29 100 63 100 100 100 100 100 100 44 42 51 35 0 0
Dworshak
IR 1
IR 2
Yakima
IR 1
IR 2
Number of Fish
0 2 4 6 8
40 38 36 34 32 30 28 26 24 22 20 18 16 14 12 10 8 6 4 2
Position on Willapa Bay Sub-array

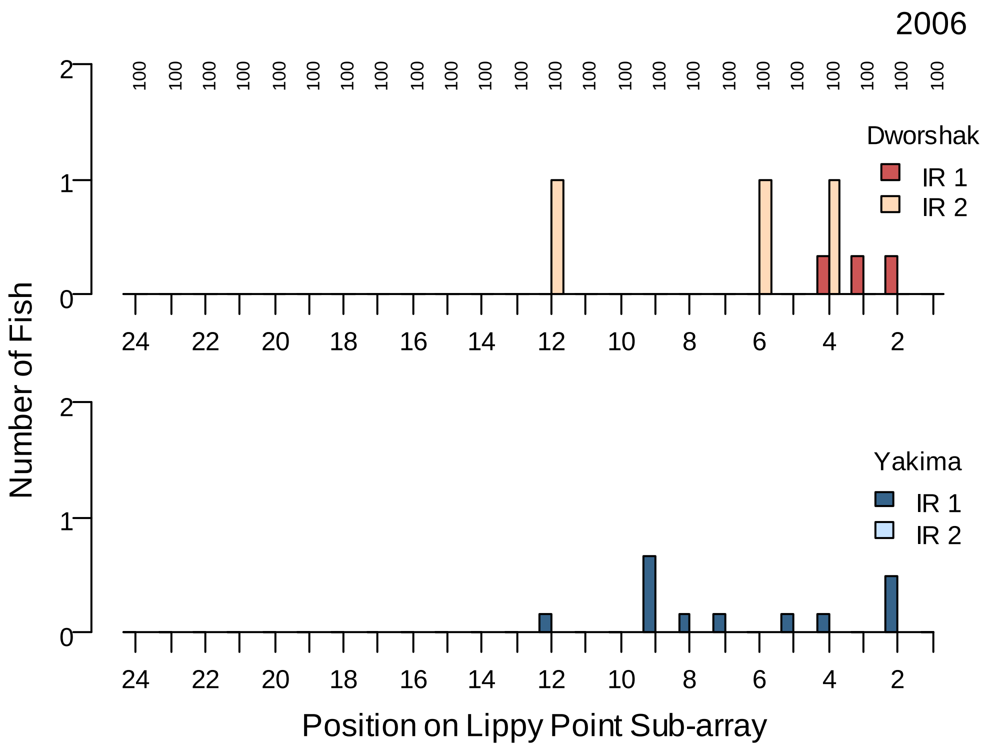

2007
100 100 100 100 100 100 100 100 100 0 100 100 100 100 100 0 0 35 100 100 100 0 100 100 100 100 100 100 100 100 100 100 0 100 100 100 100 0 100 0 100 100 0 0
Dworshak
IR 1
IR 2
Yakima
IR 1
IR 2
Number of Fish
0 1 2 3
45 42 39 36 33 30 27 24 21 18 15 12 9 7 5 3 1
Position on Willapa Bay Sub-array

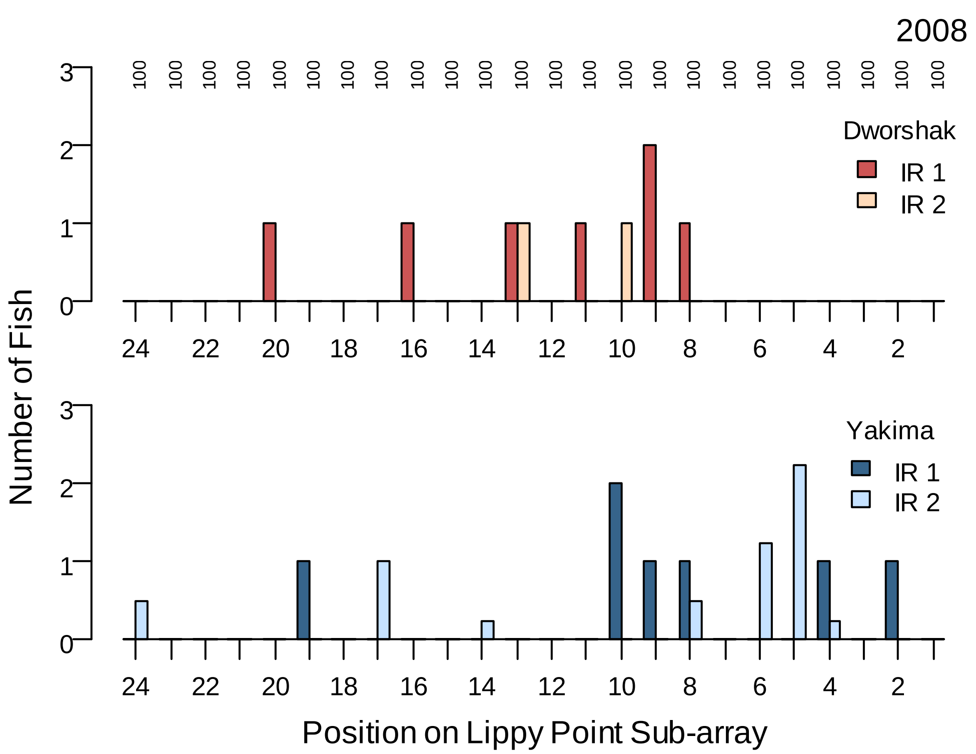
2008



Number of Fish
Dworshak
IR 1
IR 2
Yakima
IR 1
IR 2
Position on Willapa Bay Sub-array

Figure 4.5. Cross-shelf distribution of Dworshak and Yakima spring Chinook salmon smolts at Lippy Point on northwestern Vancouver Island in 2006 and 2008. Two release groups from each population were released in-river (IR) to freely migrate to the ocean. No smolts were detected at Lippy Point in 2007. Position 1 on the x-axis represents the eastern-most acoustic receiver nearest shore. A total of 24 receivers (VR2's and VR3's) was deployed in 2006. If a fish was detected at more than one receiver a proportion was allocated to the receiver, e.g. if an ID code was detected on two receivers, each receiver was assigned a value of 0.5. The values above the bars indicate the proportion of time that the receiver was operation during the migration.


2006
Dworshak
IR 1
IR 2
Yakima
IR 1
IR 2
Number of Fish
Position on Lippy Point Sub-array


2008
Dworshak
IR 1
IR 2
Yakima
IR 1
IR 2
Number of Fish
Position on Lippy Point Sub-array

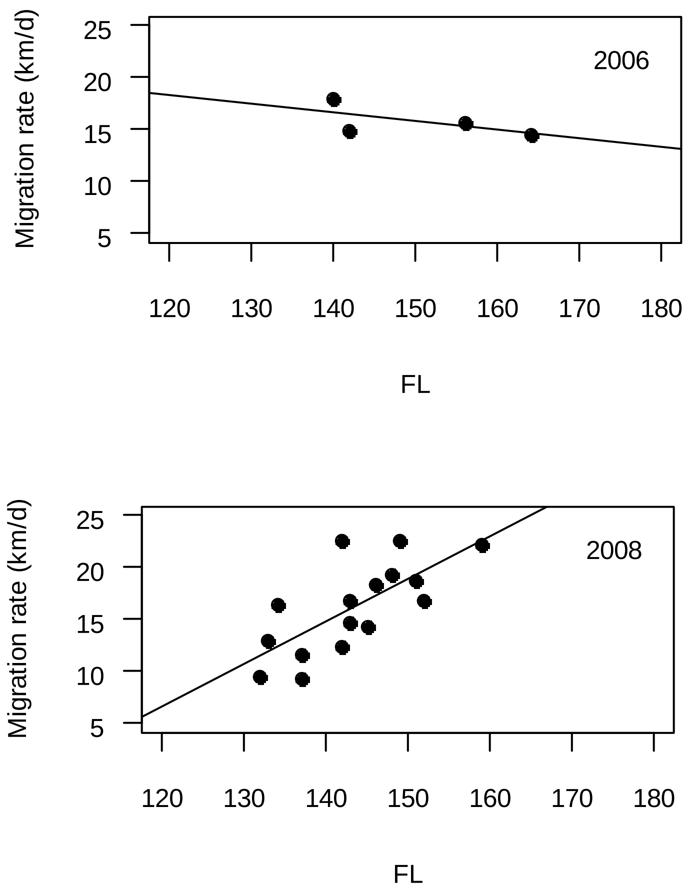


Figure 4.6. Migration rate vs. fork length (FL) of spring Chinook salmon smolts (Dworshak and Yakima smolts combined). In 2006 smolts were tagged with 9 mm transmitters. In 2008 smolts were tagged with 7 mm transmitters. In 2008 increasing FL was a significant predictor of migration rate.

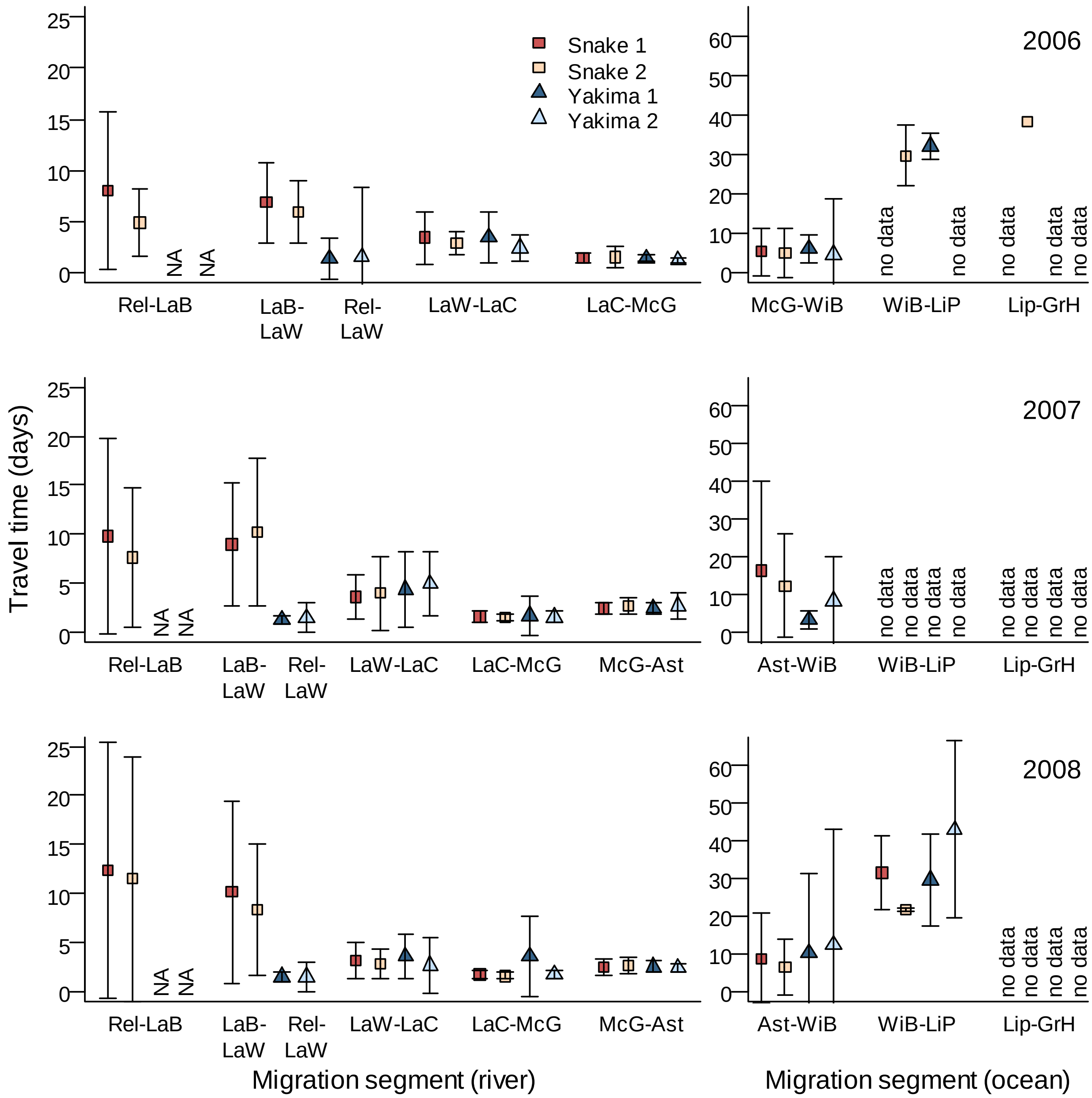


Figure 4.7. Segment specific travel time of Dworshak and Yakima spring Chinook salmon smolts in the Columbia River hydrosystem and Pacific Ocean in 2006, 2007 and 2008. Error bars represent standard deviation. Note the different scale of the y-axes for river and ocean travel times.

Table 4.1. Tagging summary for seaward migrating spring Chinook smolts tagged with 9mm (3.1 grams in air) acoustic transmitters in 2006 and 2007, and 7mm (1.6 grams in air) transmitters in 2008. (FL= fork length, g=grams, IR=in-river).

	Treatment Group	Release Date	# Tagged	Mean size at tagging (mm FL; range)	Mean weight at tagging (g; range)
2006	Snake IR	1-May	198	146.9 (140-208)	35.2 (26.9-117.5)
		8-May	198	145.6 (140-192)	34.0 (27.4-83.7)
	Yakima IR	30-May	199	154.5 (140-173)	43.2 (30.0-64.2)
		6-Jun	199	154.5 (140-168)	41.9(28.8-59.2)
2007	Snake IR	7-May	175	149.1 (141-173)	39.7 (30.1-60.6)
		14-May	174	149.0 (140-166)	39.5 (32.2-55.4)
	Yakima IR	28-May	188	155.1 (141-195)	46.3 (31.4-97.7)
		3-Jun	167	153.6 (140-180)	44.6 (32.2-79.4)
2008	Snake IR	25-Apr	197	146.2 (130-159)	37.5 (23.3-55.5)
		2-May	198	146.3 (131-159)	37.3 (23.9-52.7)
	Yakima IR	15-May	189	140.3 (129-158)	28.1 (22.0-10.9)
		21-May	189	140.4 (131-157)	28.1 (22.1-37.2)

Table 4.2. Model selection for Columbia River spring Chinook salmon survival analyses using Akaike's Information Criterion (AIC). Φ=survival probability, p=recapture probability, TT=travel time, t=time-varying (or detection line-varying), FL=fork length, dist=distance within a migration segment, QAICc=quasi-AIC corrected for overdispersion and effective sample size. Recapture parameters were held constant for all models.

2006

Model	QAICc	ΔQAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance
$\phi_{TT}\ p_t$	1686.2	0	0.607	1	14	1658.0
$\phi_t\ p_t$	1687.7	1.5	0.288	0.474	21	1645.3
$\phi_{t+FL}\ p_t$	1691.0	4.8	0.054	0.089	23	1644.6
$\phi_{dist}\ p_t$	1692.5	6.3	0.026	0.043	14	1664.3
$\phi_{dist+dam}\ p_t$	1693.0	6.9	0.020	0.032	16	1660.8
$\phi_{dist*dam}\ p_t$	1695.8	9.6	0.005	0.008	18	1659.5
$\phi_{FL}\ p_t$	1763.3	77.1	0	0	14	1735.1

2007

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance
$\phi_t\ p_t$	1269.5	0.0	0.876	1	22	1224.8
$\phi_{t+FL}\ p_t$	1273.4	3.9	0.124	0.141	24	1224.6
$\phi_{dist+dam}\ p_t$	1343.7	74.2	0	0	19	1305.2
$\phi_{TT}\ p_t$	1374.0	104.5	0	0	15	1343.7
$\phi_{dist*dam}\ p_t$	1377.8	108.3	0	0	17	1343.4
$\phi_{dist}\ p_t$	1390.6	121.1	0	0	15	1360.3
$\phi_{FL}\ p_t$	1416.1	146.6	0	0	15	1385.8

2008

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
$\phi_{t+FL}\ p_t$	4030.5	0.0	0.768	1	26	3977.9
$\phi_t\ p_t$	4032.9	2.4	0.232	0.302	24	3984.4
$\phi_{TT}\ p_t$	4059.4	28.9	0	0	17	4025.1
$\phi_{dist*dam}\ p_t$	4064.6	34.1	0	0	21	4022.2
$\phi_{dist+dam}\ p_t$	4066.6	36.1	0	0	19	4028.3
$\phi_{dist}\ p_t$	4088.7	58.2	0	0	17	4054.5
$\phi_{FL}\ p_t$	4108.6	78.1	0	0	17	4074.3

Table 4.3. Segment specific survival probabilities of Dworshak and Yakima yearling Chinook salmon released from Kooskia National Fish Hatchery, Kooskia, ID, and Chandler Juvenile Monitoring Facility, Prosser, WA, respectively. Standard errors are in parentheses.

Detection site	Dworshak					Yakima				
	Segment distance (km)	Dams passed/ segment	Survival Probability			Segment distance (km)	Dams passed/ segment	Survival Probability		
			2006	2007	2008			2006	2007	2008
LaB	189	1	0.75 (0.02)	0.19 (0.03)	0.71 (0.02)	NA	NA	NA	NA	NA
LaW	179	3	0.75 (0.02)	0.72 (0.07)	0.68 (0.03)	113	0	0.73 (0.02)	0.32 (0.03)	0.76 (0.03)
LaC	162	2	0.83 (0.02)	0.71 (0.09)	0.73 (0.05)	162	2	0.69 (0.02)	0.46 (0.06)	0.87 (0.07)
McG	116	2	0.86 (0.02)	0.77 (0.1)	0.81 (0.07)	116	2	0.74 (0.02)	0.75 (0.08)	0.73 (0.07)
Ast	201	0	(a)	1 (0)	1 (0)	201	0	(a)	0.89 (0.08)	1 (0)
WiB	63	0	0.78 (0.02)	0.48 (0.16)	0.38 (0.07)	63	0	0.63 (0.03)	0.73 (0.15)	0.39 (0.06)
Lip	485	0	0.08 (0.04)	0 (0)	0.24 (0.08)	485	0	0.05 (0.04)	0 (0)	0.27 (0.07)

(a) The sub-array at the Astoria Bridge was not deployed in 2006

Table 4.4. Survivorship from release of Dworshak and Yakima yearling Chinook salmon released from Kooskia National Fish Hatchery, Kooskia, ID, and Chandler Juvenile Monitoring Facility, Prosser, WA, respectively. Standard errors are in parentheses. Distance is cumulative from the release site.

	Dworshak				Yakima			
		Survivorship				Survivorship		
Detection site	Distance (km)	2006	2007	2008	Distance (km)	2006	2007	2008
LaB	190	0.75 (0.02)	0.19 (0.03)	0.71 (0.02)	NA	NA	NA	NA
LaW	369	0.56 (0.03)	0.14 (0.02)	0.48 (0.03)	113	0.73 (0.02)	0.32 (0.03)	0.76 (0.03)
LaC	531	0.47 (0.04)	0.1 (0.02)	0.35 (0.03)	275	0.51 (0.03)	0.15 (0.02)	0.66 (0.05)
McG	647	0.4 (0.04)	0.08 (0.02)	0.28 (0.03)	391	0.37 (0.03)	0.11 (0.02)	0.48 (0.04)
Ast	848	(a)	0.08 (0.02)	0.28 (0.03)	592	(a)	0.1 (0.02)	0.48 (0.04)
WiB	911	0.32 (0.04)	0.04 (0.01)	0.11 (0.02)	655	0.23 (0.03)	0.07 (0.02)	0.18 (0.03)
Lip	1396	0.03 (0.01)	0 (0)	0.03 (0.01)	1140	0.01 (0.01)	0 (0)	0.05 (0.02)

(a) The sub-array at the Astoria Bridge was not deployed in 2006

Table 4.5. Estimated Dworshak to Yakima spring Chinook salmon survival ratios. Survival ratios are from Lake Wallula (LaW) to McGowan's Channel (McG) 10 km below Bonneville Dam (hydro), from McG to Astoria (Ast), McG to Willapa Bay (WiB), and McG to north western Vancouver Island (LIP). Values in parentheses are standard errors. NA=not applicable. Significant values less than 1 would support delayed mortality of Dworshak smolts relative to Yakima smolts, however one sided z-tests at the 5% significance level (in bold) indicate that Dworshak smolts had higher survival. In 2007, post release mortality was anomalously high, and subsequent survival to LIP was 0.

Migration segment	Surv ratio	SE	Z-statistic	p-value
2006				
Hydro	**1.41**	0.11	4.35	**<0.0001**
Ast	NA	NA	NA	NA
WiB	**1.24**	0.07	4.07	**<0.0001**
LiP	2.17	2.07	0.81	0.209
2007				
Migration segment	Surv ratio	SE	Z-statistic	p-value
Hydro	**1.57**	0.36	1.94	**0.026**
Ast	1.12	0.09	1.34	0.090
WiB	0.74	0.29	-0.77	0.221
LiP	no data	no data	no data	no data
2008				
Migration segment	Surv ratio	SE	Z-statistic	p-value
Hydro	0.93	0.11	-0.60	0.274
Ast	1.00	0.00	0.01	0.500
WiB	1.00	0.23	-0.02	0.492
LiP	0.88	0.40	-0.27	0.397

Table 4.6. Detection probability of Snake and Yakima spring Chinook salmon smolts on POST sub-arrays in the Columbia River basin (LaB-Lake Bryan, LaW=Lake Wallula, LaC=Lake Celilo, McG=McGowan's Channel, Ast=Astoria Bridge) and Pacific Ocean (WiB=Willapa Bay, Lip=Lippy Point).

	Snake			Yakima		
Detection Site	2006	2007	2008	2006	2007	2008
LaB	0.97 (0.02)	0.96 (0.04)	0.96 (0.01)	NA	NA	NA
LaW	0.93 (0.03)	0.94 (0.05)	0.98 (0.01)	1.0 (0)	1.0 (0)	0.96 (0.02)
LaC	0.56 (0.06)	0.92 (0.06)	0.51 (0.05)	0.78 (0.05)	0.97 (0.03)	0.33 (0.04)
McG	0.70 (0.07)	0.79 (0.1)	0.15 (0.03)	0.84 (0.06)	0.97 (0.04)	0.1 (0.02)
Ast	(a)	0.83 (0.1)	0.81 (0.06)	(a)	0.94 (0.07)	0.75 (0.05)
WiB [(d)]	0.69 (0.07)		0.74 (0.07)	0.69 (0.07)		0.74 (0.07)
Lip	(b)	(c)	(b)	(b)	(c)	(b)

(a) The sub-array at the Astoria Bridge was not deployed in 2006

(b) The detection probability at Lippy Point was assumed to be equivalent to WiB

(c) No smolts were detected; detection probability was not estimable

(d) Populations were pooled during the estimation process

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5 Early Marine Survival of Transported and In-River Migrant Hatchery Snake River Spring Chinook Salmon Smolts: Does Transportation Reduce Survival?[4]

5.1 Introduction

Quantifying early marine survival of endangered salmon smolts is critical for effectively managing and rebuilding salmon stocks from the Columbia River basin which declined in the last century due to over-harvesting and hydroelectric dam construction (Raymond 1988). One management strategy employed in the basin to mitigate for salmon losses at the Snake River (a tributary of the Columbia River) dams is the salmon transportation program, which transports migrating salmon smolts from bypass collectors at the Snake River dams and McNary Dam in the lower Columbia River and transports them via barge to a release site in the lower Columbia River below Bonneville Dam, the final dam that smolts must pass during their seaward migration to the ocean. Direct mortality at the dams has been reduced in recent years (Ferguson et al. 2007; Muir et al. 2001). As a result, survival of spring (also called yearling or stream-type) Chinook salmon smolts *Oncorhynchus tshawytscha* migrating through the hydrosystem, from Lower Granite Dam to Bonneville Dam, is typically ~50% (Faulkner et al. 2009, Table 43). Survival in the transportation barge during the ~36 hour, 460 km ride to below Bonneville Dam is near 100%.

Despite two-fold greater survival during the seaward migration, the transportation program has not consistently resulted in a larger proportion of transported smolts returning to the Snake River as adults when compared to smolts that migrated the length of the river and through eight dams (Ward et al. 1997; Williams et al. 2005). Although transportation was already in effect for over two decades, Snake River spring Chinook salmon were nevertheless listed as threatened on the U.S. endangered species list in 1992, indicating a failure of the transportation program to increase adult return rates to a sustainable level. In recent years however, the transportation program has shown improvements in relative survival of

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transported spring Chinook salmon (Buchanan et al. 2007, Table G.15; Schaller et al. 2007, Table 3.2). Nevertheless, the threatened status was reaffirmed in 2005 (http://www.nmfs.noaa.gov/pr/species/esa/).

Transportation studies have been ongoing since the 1970s, shortly after the transportation program was established by the U.S. National Marine Fisheries Service (NMFS) (e.g., Ebel et al. 1973; Ebel 1970; McCabe et al. 1979; Trefethen and Ebel 1973). Prior to the ESA listing of Snake River spring Chinook salmon it had been recognized that transportation may result in delayed or differential mortality due to the transportation process (Ebel 1980). Coded wire tags and thermal brands were used to evaluate survival of returning adults early on (e.g., Bugert and Mendel 1997; Chapman et al. 1997), and with the development of the passive integrated transponder (PIT) tag in the early 1990's (Prentice et al. 1990) and the growing use of small radio tags (e.g., Schreck et al. 2006), biologists were able to more accurately estimate survival of seaward migrating smolts in the river and survival of adults back to the Snake River.

Recent studies have found that differential delayed mortality of spring Chinook salmon could be related to stress associated with transportation with steelhead *O. mykiss* (Congleton et al. 2000), differential size at release and timing of ocean entry (Muir et al. 2006) , impaired homing abilities and straying to other spawning rivers within the basin (Keefer et al. 2008), and/or increased susceptibility to disease transmission in the transportation barge (Eder et al. 2009).

Other studies have found contrary evidence that transportation of spring Chinook salmon smolts with increasing densities of juvenile steelhead did not result in lower smolts to adult return (SAR) rates (Wagner et al. 2004), and that transported smolts may be less susceptible to pathogens (Arkoosh et al. 2006), that transportation had little or no effects on auditory and olfactory systems of smolts, respectively (Halvorsen et al. 2009), and that the SAR of transported smolts was higher than smolts migrating seaward in the river through dam bypasses (Sandford and Smith 2002). Therefore various studies have investigated potential mechanisms that may lead to differential mortality, while others have attempted to estimate the magnitude of differential mortality using smolt to adult return rates (SAR).

Two metrics are typically used to evaluate the success of the transportation program: the transport to in-river (T/I) ratio, and post-Bonneville differential delayed mortality ratio, (D). T/I compares the ratio of the SAR to Lower Granite Dam (LGR) of transported smolts, SAR_{TR}, to the SAR of in-river migrants, SAR_{IR}, migrating as smolts from LGR and returning as adults to LGR (Figure 5.1). If the T/I ratio is > 1 then transportation provides a benefit by increasing adult returns in a greater proportion than if they are left to volitionally migrate downstream. D is the ratio of the SAR of transported smolts released below Bonneville Dam and returning to LGR to the SAR of in-river migrants estimated from Bonneville Dam to adult return to LGR (Buchanan et al. 2007; Schaller et al. 2007; Figure 5.1). If D is >1 then transported smolts returned in a higher proportion than in river migrants.

Excluding 2001, the geometric mean of the system-wide T/I estimates for hatchery-reared spring Chinook salmon from the Snake River Basin was 1.15 (SE=0.03) for release years 1997 through 2003 (Buchanan et al. 2007) indicating a benefit for transported smolts. The geometric mean of the D estimates for hatchery-reared spring Chinook salmon from the Snake River Basin for these years was 1.00 (SE=0.09) indicating that differential delayed mortality did not occur (Buchanan et al. 2007). Dworshak hatchery-specific estimates of T/I are similar from 1997 to 2004, excluding 2001 (geometric mean T/I=1.08, 90% CI=0.63-1.85), however D was lower (geometric mean=0.62, 90% CI=0.33-1.20) than the aggregate Snake River estimate indicating delayed mortality of transported smolts (Schaller et al. 2007). Both of these indirect estimations, however, rely on adult fish returning to spawn 2-3 years after migrating from the river as smolts, and any difference in survival between groups is attributed to their treatment as smolts.

The recent development of acoustic tags small enough to implant into salmon smolts provides a technique for estimating salmon survival during their seaward migration in the river below the hydrosystem (Clemens et al. 2009; McMichael et al. 2010; Rechisky et al. 2009), as well as in the ocean (Chittenden et al. 2008; Melnychuk et al. 2007; Rechisky et al. 2009). Like the development of the PIT tag system, acoustic tags can further aid in determination of whether differential mortality occurs soon after release from the barge, and if so, to what extent. PIT tag studies have demonstrated that spring Chinook salmon transported as smolts may or may not return in higher proportions compared to non-transported smolts; however, early maring survival and adult marine survival are confounded in estimates of SAR because SARs are estimated 2-3 year after salmon migrate to the ocean. The advantage to using acoustic tags is that survival can be measured during the seaward migration below the hydrosystem and during early marine life.

No direct comparison of early marine mortality of transported and non-transported salmon smolts has previously been possible because the technology to do so did not exist or it was considered logistically infeasible to track small salmon smolts in the vast expanse of the Pacific continental shelf. Partly to address these critical conservation questions, a prototype continental-scale telemetry array, the Pacific Ocean Shelf Tracking array (POST; Welch et al. 2002) was designed and deployed to address these issues.

Using the acoustic array, we estimated in-river and early marine survival of yearling Chinook salmon smolts released from a hatchery in the Snake River basin and compared that to the survival of a group from the same hatchery that was transported 650 km downstream via barge and released approximately ~10 km downstream of Bonneville Dam. We present the first estimates of survival in the estuary, plume, and along the continental shelf for salmon smolts migrating from the Columbia River. Additionally we calculated a T/I ratio to Willapa Bay, WA, and Lippy Point on Vancouver Island, BC, (T/I_{WIB} and T/I_{LIP}, respectively). For our study, the T/I ratio is the ratio of the survival of transported smolts (S_{TR}) released in the lower Columbia River at McGowan's Channel (MCG, 10 km below Bonneville Dam) to coastal ocean detection sites located 40 km (WIB) and 525 km (LIP) north of the mouth of the Columbia River to the juvenile survival of in-river migrants (S_{IR}) released at Kooskia National Fish Hatchery (NFH) to WIB and LIP. D to Willapa Bay and Lippy Point (D_{WIL} and D_{LIP}, respectively) is the ratio of juvenile survival of transported smolts from MCG to WIL, and MCG to LIP to the juvenile survival of in-river migrants from below Bonneville Dam to WIL and LIP.

In addition to estimating early ocean survival of in-river and transported smolts we also report the first direct measurements of the coastal migration characteristics (rate of movement, travel time and the cross-shelf distribution) of Snake River spring Chinook salmon during their migration north along the continental shelf.

5.2 *Methods*

5.2.1 Smolt acquisition and tagging

We tagged spring Chinook salmon smolts reared at the Dworshak National Fish Hatchery (NFH), on the Clearwater River (a tributary of the Snake River). Dworshak NFH is located above the four lower Snake River dams (as well as the four lower Columbia River dams) and thus, Dworshak smolts have the potential to be diverted to barges and transported to below Bonneville Dam from the three Snake River dams where transportation occurs, as well as McNary Dam in the lower Columbia River. Annual PIT tag estimates of survival (in-river juvenile survival and SARs) are estimated by the National Oceanographic and Atmospheric Administration (NOAA; Seattle, WA), as well as the Fish Passage Centre (Portland, OR); Snake River spring Chinook smolt to adult return rates are low [<1% in recent years; (Berggren et al. 2006)].

Because of tank limitations at Dworshak Hatchery, each year approximately 1,500 Spring Chinook smolts from Dworshak NFH were transferred to Kooskia NFH (60 km upstream of Dworshak NFH) on to three months prior to tagging. Additionally, river and hatchery water temperatures at Dworshak NFH in the winter and early spring are low, generally ranging between 4-10 °C, and therefore fish growth is minimal. Water temperature at Kooskia NFH was several degrees warmer (12-13 °C), which facilitated more rapid growth necessary to attain minimum body size requirements necessary for tagging (see below). Although the smolts were reared in slightly warmer water for up to several months before tagging, it was necessary to retain the fish for several weeks beyond the typical hatchery release date (April 1) to ensure that a sufficient number of smolts exceeded the minimum size requirements that were set for tagging. As a result of the transfer and holding time, in-river smolts migrated an additional 60 km down the Clearwater River and three to six weeks later than conventionally released Dworshak and Kooskia spring Chinook smolts. Nevertheless, in 2006 and 2008 >99% of acoustic tagged smolts passed Lower Granite Dam (the first dam smolts encounter in the Snake River) during the latter part of the peak passage of all migrating spring Chinook salmon from the Snake River. In 2007 99% of the first release group passed during the peak of the migration; however river flows decreased thereafter, and the second release group passed Lower Granite

Dam during the extreme tail end of the distribution of Snake River Spring Chinook salmon passage times (www.fpc.org; Faulkner et al. 2009).

In 2006 and 2007 we used individually identifiable Vemco (Shad Bay, Nova Scotia, Canada) V9-6L coded acoustic transmitters (9 x 21 mm, 3.1 g in air, 2 g in water) and in 2008 we used a smaller V7-2L transmitter (7 mm x 20 mm, 1.6 g in air, 0.75 g in water). We set minimum body size requirements based on our previous tag effect studies (Welch et al. 2007) of 140 mm fork length (FL) for the V9-6L tag, and 130 mm FL for the V7-2L tag. Assessments of tag effects for smolts held over several months in hatcheries demonstrated that tag retention and survival in captivity was high for both tag types (Chapter 2 in this thesis); however, this size threshold meant that we could only tag the upper size distribution. Based on FL samples taken at the hatchery, we estimate that we tagged the upper 10% of the smolt size distribution in 2008. Size at release of Dworshak smolts released from Dworshak hatchery was unavailable in 2006, as the hatchery did not measure individual fish lengths prior to release. Therefore in 2006, we can deduce that we tagged less than 10% of the size distribution since our minimum size at tagging was larger.

We attempted to size match tagged fish within and between treatment groups in each year. In 2007 and 2008, mean FL and range was similar for both in-river release groups, and in-river groups were similar to both transported groups; however in 2006 we had an insufficient number of larger smolts (150-159 mm) available for tagging in the in-river groups and therefore the transported groups were 9 mm larger than in-river groups on average (Table 5.1). In 2006 the transmitters weighed 5.6-10.9% of the fish body weight in air for transported fish, and 2.6-11.5% for in-river fish. Body burden was similar in 2007; tags weighed 5.5-10.5% of transported smolt weight and 5.1-10.3% of in-river smolt weight in 2007. In 2008 a smaller tag was used (as well as smaller fish) and the body burden was 3.1-6.1% for transported fish and 2.9-6.9% for in-river fish.

Tags used in this study were programmed to transmit a unique code at 69 kHz using several different mean transmission intervals, all of which provided an operational lifespan long enough to cover the observed duration of the migration to the Alaska sub-array (three months) and to prevent tag transmission collisions. (Multiple code transmission intervals were used to provide calibration data on relative performance of this first generation array, but are irrelevant to this study because equal proportions of these tags were used in each experimental release group). The larger, more powerful V9-6L transmitter used in 2006-07 had a greater detection radius (≤400 m) than the smaller V7 tag used in 2008 (≤300 m); however, our data indicate that the detection range is location and time-dependent, and varies with freshwater, estuarine, and ocean conditions, as well as local topography, river flow, and weather conditions.

Surgical procedures used to implant acoustic transmitters were reviewed annually by institutional animal care committees and met or exceeded the Canadian Council on Animal Care standards (www.ccac.ca). The same surgical protocol was used in all years for both treatment types; a detailed description is provided in Chapter 2 of this thesis. In brief, portable surgical units are assembled on site, and fish surgery was carried out by experienced, veterinarian-trained staff. Fish were anaesthetised individually in 70 ppm Tricaine Methane Sulphonate (MS-222) buffered with 140 ppm $NaHCO_3$). Fork length was measured to the nearest mm and weight was measured to the nearest tenth of a gram. The fish was then placed ventral side up into a v-shaped trough and a maintenance dose of buffered anaesthetic (50 ppm) was pumped through the fish's mouth and over the gills. An incision was made at the ventral midline midway between the pelvic and pectoral fins and each smolt was double tagged by placing a PIT and acoustic tag through the incision into the peritoneal cavity. For a 9 mm transmitter, the incision was 10-12 mm in length and was closed with two interrupted sutures; for a 7 mm transmitter the incision was 7-8 mm and was typically closed with one suture. Surgery time was <2 min for a 9 mm tag and about 1 min for a 7 mm tag. Immediately following surgery, fish were placed into a recovery bath and monitored. Within minutes fish regained equilibrium and reactivity.

Hatchery and wild juvenile spring Chinook salmon are collected at Snake River dam bypass facilities and transported via barge to below Bonneville Dam during the spring seaward migration if they do not migrate over the dam with the spill or through the turbines. By default, non-PIT tagged smolts that pass through the bypass are transported; smolts implanted with PIT tags are returned to the river unless selected for transportation via the separation-by-code procedure. We PIT tagged all acoustic tagged smolts and provided the PIT tag data to the PIT Tag Information System (PTAGIS) database maintained by the Pacific States Marine Fisheries

Commission (PSMFC, Portland, Oregon; http://www.ptagis.org) to ensure that tagged in-river smolts were diverted back into the river at the dam bypass facilities and not collected for transportation.

In 2006 and 2007 tagging of in-river smolts took place in April and early May. In-river smolts were released on May 1 and 8 in 2006, and May 7 and 14 in 2007 (Table 5.1). Transported smolts were tagged from May 30 to June 1 in 2006, and May 31 and June 1 in 2007. In 2006 they were transported on June 6 and 14, and in 2007 they were transported on June 5 and 11. In 2008 all tagging took place from April 19-24. Because we used a smaller transmitter we were able to tag smaller fish and thus, the holding period was shorter and the release dates were earlier than previous years. Hence, in-river fish were released on April 25 and May 2, and smolts were transported on May 17 and 23. These holding periods for the transported smolts were not consistent with the conventional practice of transporting migrating smolts immediately upon arrival at Snake River dams. Our extended holding period at the hatchery (3-5 weeks) was instituted so that the release of the transported fish would coincide with the time of arrival of the in-river migrants that migrated 650 km to below Bonneville Dam, so that both groups were exposed to common environmental effects in the ocean.

In each year approximately 600 smolts were implanted with acoustic transmitters, however in 2007 sample sizes were slightly smaller for in-river groups (Table 5.1). Approximately 400 were in-river smolts (two release groups of ~200) and approximately 200 were transported (two transported groups of ~100). We released twice as many in-river smolts because survival of Snake River yearling Chinook salmon from the Snake River Trap to Bonneville Dam from 1999 to 2005 (excluding the drought year 2001) was 49% (Faulkner et al. 2009). Therefore, we expected approximately 100 smolts from each in-river release group to survive to below Bonneville Dam, where groups of 100 transported smolts were released from the barges, thus approximately balancing the study design. The in-river groups were released into Clear Creek which flows successively into the Clearwater, Snake, and Columbia rivers (Figure 5.1). Distance to the Columbia River mouth is 870 km.

Tagged smolts were apparently overhandled prior to surgery in 2007 due to exceptionally small fish sizes at the time of tagging, associated with poor growth the previous winter. Although it is unclear whether the stress from repeated handling or exposure to MS-222 caused the problem (Porter et al; 2007 BPA Report), poor initial survival shortly after release precludes the use of these data for most practical purposes. We report them here for completeness because of the importance of our general findings for addressing the policy questions concerning the role of the transport program for improving salmon conservation.

5.2.2 Transportation of acoustic tagged smolts

Fish were held at Kooskia NFH until run-of-river groups were estimated to have reached Bonneville Dam; this was done to insure that timing of ocean entry, and thus ocean conditions, were similar for both transported and in-river migrant smolts. Transported groups were transferred directly from Kooskia NFH to the Army Corp of Engineers fish transportation barge at Lower Granite Dam via truck. The transport truck was equipped with a 1,200 l capacity tank, which was aerated with oxygen. Temperature and dissolved oxygen were monitored during the three hour ride from Kooskia, ID to Lower Granite Dam. In all years smolts were loaded onto the barge by 11:00, and the barge departed shortly thereafter. If necessary, fish were acclimatized to the water in the barge if the water temperature in the barge was >2 °C different from the water in the truck tank. Barge transport time to below Bonneville Dam (a distance of 470 km) was approximately 34 hours. Smolts were released from the barge in the evenings between 19:20-22:30. Distance to the Columbia River mouth was 222-227 km, depending upon which of the four nearby release sites the transported fish were released. Because transported fish were released downstream of Bonneville Dam they were not detected on acoustic sub-arrays in Lake Bryan (Snake River), below the confluence of the Columbia and the Snake River (Lake Wallula, above McNary Dam), or on the John Day array.

Survival during truck transport was 100% except for the second in-river group in 2007 when one tagged fish was injured during netting from the tank to the truck. This fish was removed from the study. Observers on the barges reported no mortalities in any years of the study.

5.2.3 POST array elements and location

The POST acoustic receiver array is comprised of individual Vemco acoustic receivers (models VR2 or VR3 UWM) anchored to the seabed of the continental shelf along the Pacific northwest to form a series of acoustic listening lines or sub-arrays (www.postcoml.org; Welch, et al. 2002). Each receiver records the date and time of uniquely coded acoustic transmitters passing near the receiver. Prior to 2006 the array extended from coastal Washington to southern British Columbia and up to southeast Alaska (Figure 5.2). In 2006, permanent receivers were also deployed to form four permanent sub-arrays within the Snake and Columbia rivers; therefore the tracking distance of the POST array extended from the Snake River release sites to the continental shelf at Graves Harbor, AK, a distance of 2,500 km (Figure 5.2).

Marine components of the POST array adjacent to Willapa Bay (southern WA), Lippy Point (northwest Vancouver Island, BC), and Graves Harbor (southeast AK) extend from near-shore to the edge of the continental shelf (~ 200m isobath), a distance of up to 34 km. Acoustic receivers on these open ended arrays were deployed perpendicular to the coast at approximately every 800 m. In southern British Columbia, acoustic sub-arrays located across the Strait of Juan de Fuca, Strait of Georgia, Howe Sound, Queen Charlotte Strait and in the Fraser River are bound by landmasses on either end. The longest sub-array was the southern WA site at Willapa Bay which consisted of 40 receivers in 2006, and was extended offshore to 45 receivers in 2007-08.

Component sub-arrays within the Columbia River were deployed as paired lines (with ~200 m spacing), to ensure high detection probability and to provide in-river survival measurements below three of the major hydroelectric dams. Detection sites were located across McGowan's Channel at river kilometer (rkm) 224 (10 km below the Bonneville Dam), across Lake Wallula at rkm 502 (in the NcNary Dam reservoir, 21 km below the confluence of the upper Columbia and Snake rivers). In 2006 acoustic receivers were deployed in Lake Celilo at rkm 340 (7 km below the John Day Dam); however, in early 2008 part of the sub-array was displaced by sturgeon fishermen. Therefore, prior to the seaward migration in 2008, an additional sub-array was deployed across the reservoir above John Day Dam (at rkm 351). Data from the remaining acoustic receivers below John Day Dam and the new sub-array above the dam were pooled because of their close geographic proximity to form the John Day acoustic detection site (not to be confused with the PIT tag detection site at the dam itself). The two lines were also combined for data analyses since the distance between the lines was minimal and juvenile survival through the dam was high (Faulkner et al. 2009). In the Snake River, receivers were installed in Lake Bryan at Snake River rkm 159 (14 km below Lower Granite Dam; total distance from the ocean was 681 km). In 2007 an additional sub-array was deploy across the estuary on the Astoria Bridge (23 km from the Columbia River mouth). This array was not deployed as paired lines; instead, receivers were fixed to each of the bridge pylons and therefore receiver spacing ranged between 50-100 m ensuring that detection rates would be high. The addition of the Astoria sub-array allowed us to partition survival in two critical areas: the estuary and the ocean plume. For this study the estuary is defined as the tidal area ranging from Bonneville Dam to the Astoria Bridge, and the plume is defined as the area from the Astoria Bridge to the Willapa Bay sub-array. We assumed that smolts did not migrate south of the Columbia River, an assumption supported by the 2009 field study, which recorded only three of 1,600 smolts released at a cross-shelf sub-array located at Cascade Head, Oregon, south of the Columbia River mouth.

5.2.4 Data analysis

All acoustic detection data from the array were first screened for logical occurrence in space and time, and single tag detections on a sub-array were discarded if they were inconsistent with the detection sequence. In-river fish were defined as any fish migrating in the river, regardless of their specific route through the dams (bypasses, over the dams in the spill, or through the turbines), which was not monitored in this study. We did not include Snake River Chinook salmon smolts that were inadvertently transported from lower Snake River dam bypass facilities and released below Bonneville Dam.

5.2.4.1 Estimates of Survival

Estimates of survival and detection probability were calculated in each year using the Cormack-Jolly-Seber (CJS) model for live recaptured animals implemented in Program MARK (White and Burnham 1999). This model jointly estimates survival and detection within a likelihood framework. The CJS model calculates detection probability using the proportion of undetected fish that are recorded at more distant sites. For in-river sub-arrays, we recognized basic CJS model assumptions (equal survival probability, equal recapture probability, no tag loss, and instantaneous sampling); however, for continental shelf lines that are not bounded on the offshore end (continental slope), we required two additional assumptions; 1) as fish migrate along the coast they cross over the acoustic detection lines that span the length of the continental shelf to 200m, and 2) the majority of the fish departing the Columbia River swim north. These assumptions are supported by evidence from numerous ocean sampling programs that confirm that juvenile spring Chinook salmon remain almost entirely on the continental shelf and primarily migrate north upon leaving the river (Beamish et al. 2005; Bi et al. 2007; Brodeur et al. 2004; Fisher and Pearcy 1995).

Capture (detection) histories for each individual were formed and the fully time varying CJS model (survival and detection probability for each release group and each treatment type) was used to assess goodness of fit (GOF) to the data with the bootstrap GOF test within Program MARK. If there was overdispersion in the data it was corrected by dividing the model deviance by the mean expected deviance (from 1000 bootstrapped simulations) to yield an overdispersion factor, $\hat{c}$. In general, if $\hat{c}$ is greater than 1 then the resulting standard errors on the estimates are inflated by the $\hat{c}$ value. In 2006 the $\hat{c}$ overdispersion factor was 1.74 and thus the survival model was corrected for overdispersion. In 2007 and 2008 there was no overdispersion ($\hat{c}$=1). To produce estimates of survival we reduced (pooled) the release groups which resulted in one survival estimate for each treatment type at each detection site. There were several reasons to pool the release groups; 1) pooling release groups increased sample size which resulted in a more precise estimate of survival, 2) the second in-river group in 2006 and 2008 migrated rapidly downstream and largely “caught up” with the first release group; therefore both release groups experienced similar conditions in the lower Columbia River and ocean, 3) the pooled survival estimates were used to estimate D and TIR at Willapa Bay and northwestern Vancouver Island.

To calculate survivorship from release, we multiplied segment specific survival probabilities and used the Delta Method to calculate the variance around the resulting cumulative survival estimates. To compare survivorship of transported and in-river migrant smolts in the unimpounded section of the river and ocean, we only considered survival from McGowan's Channel and beyond for in-river migrant smolts. Therefore we compared the segment specific survival from McGowan's Channel (below Bonneville Dam) to Willapa Bay in 2006, and from McGowan's Channel to Astoria in 2007 and 2008, and multiplied that by subsequent segment survival estimates. This was similar to calculating survival from release, but we disregarded mortality occurring upstream for in-river smolts, and therefore isolated survival in the common migration pathway of all smolts. Transported smolts were released from the barge near the detection site in McGowan's Channel downstream of Bonneville Dam, therefore survival of transported smolts at McGowan's Channel was assumed to be 1.

As survival estimates are dependent on detection rates, we estimated the detection probability at Willapa Bay by pooling all fish detected at that site, as smolt mortality prior to reaching Willapa Bay substantially reduces the number of tagged smolts available upon which to base the estimation of the detection probability. The survival estimates were unique for each treatment group (in-river migrant and transported), however we modeled only one aggregate detection probability for Willapa Bay. We also included in our models two additional in-river groups (each N=200) of spring Chinook salmon smolts migrating from the Yakima River, tagged with the same acoustic tag, that were released at the Chandler Juvenile Monitoring Facility on the lower Yakima River during the spring seaward migration, in order to better quantify the detection probability of the Willapa Bay detection line. (These two additional in-river groups were used in our comparative survival study from 2006-8 which is reported in Chapter 4 of this thesis).

Although several fish were detected in Alaska, too few were detected to provide adequate information about the detection rate of the northwestern Vancouver Island acoustic sub-array (N_{2006}=2 in-river migrants; N_{2007}=0; N_{2008}=1 in-river migrant). Therefore, to estimate survival we assumed that the detection probability of the Lippy Point line was equal to the detection probability of the Willapa Bay line. We did this for several reasons: 1) all marine acoustic receiver nodes are deployed at approximately equal spacing intervals, 2) CJS analyses of detection probability for fully intact lines, bounded by landmasses, and with ample detections beyond the line in question (which renders them estimable) have revealed that detection rates of POST sub-arrays are very consistent across multiple sites and over multiple years (~92% for V9 transmitters and ~73% for V7 transmitters at three sites in four years; M. Melnychuck, personal comm.), 3) the distribution of smolts across the acoustic line at Lippy Point is centered on the inner to middle continental shelf, therefore it appears that fish were confined to the shelf (Figure 5.7), 3) if estimates at Lippy Point are biased they will be equally biased for both treatment types, 4) the estimated detection probability at Willapa Bay is consistent with other POST sub-arrays. In 2006 the detection probability at Willapa Bay was 69%. This estimate, however, accounts for 25% loss of the equipment at Willapa Bay (largely to commercial fishing activities). If the inherent detection rate for V9 tags is 92% and gear loss was 25% then the expected detection rate is 69% (0.92*0.75), the same as our estimated detection probability of 69%. The detection probability in 2008 was 74%, which is consistent with the average detection probability of V7 transmitters on bounded lines (gear loss at Lippy Point in 2008 was only 2%), and 5) we have no reason to believe that the acoustic environment at Lippy Point would be significantly different than that at Willapa Bay or other POST detection sites in the ocean.

5.2.4.2 Transportation-in river (T/I) survival ratio from release to Willapa Bay and Lippy Point.

For consistency we have adopted the same notation as Buchanan et al. (2007). For this study, the transportation-in river ratio is defined as the ratio of survivorship of transported smolts to in-river migrant smolts from the release sites (Kooskia NFH or below Bonneville Dam) to the Willapa Bay ocean detection site (T/I_{WIB}) and to the continental shelf off north western Vancouver Island at Lippy Point (T/I_{LIP}). Transported smolts were released in McGowan's Channel (below Bonneville Dam) therefore survival through the impounded section of the river (the area which was bypassed) was assumed to be 100% since mortality on the barge was zero. As a result, transported smolts have a significant initial survival advantage as they did not incur mortality during the downstream migration (see Table 5.4 for in-river mortality of in-river smolts). To test if transportation confers higher survival in the ocean (whether this survival advantage persists) we used one-sided z-tests to test whether values of T/I were greater than 1 at the 5% significance level using the same test statistic as Buchanan et al. (2007):

$$z = \frac{\ln(\hat{R})}{\widehat{SE}\left(\hat{R}\right)/\hat{R}}$$

where $\hat{R}$ is the maximum likelihood estimate of T/I_{WIB} or T/I_{LIP}, where appropriate. To compute $\hat{R}$ and $\widehat{SE}\left(\hat{R}\right)$ we reparameterized the survival models within Program MARK to estimate T/I ratios and their associated standard errors. The distance from McGowan's Channel to the Willapa Bay detection site was 264 km (which includes the lower Columbia River, the estuary and the plume), therefore we expected transported smolts to have higher survival than in-river smolts (i.e., T/I>1) given that in-river smolts must travel 3.5x the distance and require several additional weeks of travel compared to their counterparts on the barge. The distance from McGowan's Channel to Lippy Point was an additional 525 km of coastal ocean; therefore, if exposure to mortality was similar for both treatment types then we would expect higher survival of transported smolts to persist.

5.2.4.3 Differential post-Bonneville mortality (D) survival ratio to Willapa Bay and Lippy Point.

We defined the differential post-Bonneville mortality (D) survival ratio as the ratio of survivorship of transported smolts to IR smolts from McGowan's Channel (4 km below Bonneville Dam) to (a) the Willapa Bay sub-array (D_{WIB}) and (b) Lippy Point sub-array (D_{LIP}). We did this by estimating D for IR smolts conditional on surviving to reach Bonneville Dam. We thus compared survival for a common migration pathway for two groups with different travel experiences in the river. To test if transportation conferred higher survival for smolts not migrating through the eight dams in the hydrosystem, we used one-sided z-tests to test whether values of D were greater than 1 at the 5% significance level using the same test statistic as Buchanan et al. (Buchanan et al. 2007):

$$z = \frac{\ln(\hat{D})}{\widehat{SE}\left(\hat{D}\right)/\hat{D}}$$

where $\hat{D}$ is the maximum likelihood estimate of D_{WIB} or D_{LIP}, where appropriate. To compute $\hat{D}$ and $\widehat{SE}\left(\hat{D}\right)$ we reparameterized the survival models within Program MARK to estimate D ratios and their associated standard errors. If D was significantly greater than 1 then the survival of transported smolts downstream of Bonneville Dam was greater than that of smolts that had initially survived in-river migration through the lower Snake and Columbia River hydrosystem to reach Bonneville.

5.2.4.4 Post-Release Mortality

To compare post-release mortality for IR and transported smolts we examined the mortality rate per km in the first migration segment following release, when smolts typically experience short term elevated levels of mortality (Brown and Day 2002). In-river smolts were released into the Clearwater River (a tributary of the Snake River), and migrated 190 km and through one dam (Lower Granite Dam) in the first migration segment before being detected on the Lake Bryan sub-array in the Snake River. Transported smolts were released into the upper reaches of the estuary below Bonneville Dam. In 2006 the first migration segment for transported smolts was from McGowan's Channel to Willapa Bay (264 km), and in 2007 and 2008 the first detection site following release was at the Astoria Bridge (201 km from McGowan's Channel).

To statistically compare mortality per km, we assumed the exponential survival model $S_{i,j} = e^{bd_{i,j}}$ and regressed the log-transformed cumulative survival estimates at the j-th detection site, $\ln(S_{i,j}) = bd_{i,j}$, for each of the i-th populations against migration distance from the respective release sites, $d_{i,j}$, resulting in a decrease in survival rate per km, b (i.e., minus an instantaneous mortality rate b per mile). To assess uncertainty in the estimated regression coefficients we used a Monte Carlo procedure to randomly generate 10,000 individual survival estimates at each of the detection sites for each stock using the estimated survival proportions, $S_{i,j}$, and associated variances to define the parameters of the binomial sampling distribution leading to uncertainty in the survival values. We then took the 10,000 sets of generated survival estimates for each population, and calculated the log-transformed regression estimates to empirically define the distribution of minus instantaneous mortality rates, b_i per time or distance in an exponential survival model $S=e^{bx}$ (x=distance or time) for each population.

The null hypothesis that the survival rate of Snake River smolts is equal to that of the Yakima River smolts is equivalent to assuming that on average the difference in the regression coefficients, $b_1 - b_2$, is zero. We tested this null hypothesis for each of the simulated migration segments by evaluating whether the central 95% of the 10,000 survival rate differences included zero.

5.2.5 Travel time and rate of movement

For each in-river release group we calculated segment specific mean travel times (days) and migration rate (km/d) to McGowan's Channel, Astoria Bridge (2007, 2008), Willapa Bay, Lippy Point, and Graves Harbor. We also calculated cumulative mean travel time (days) and migration rate (km/d) from release to McGowan's Channel and to all subsequent detection sites. For transported smolts we calculated mean travel times and migration rates to the Astoria Bridge and subsequent detection site. To calculate migration rate we took the time of the first detection from the subsequent site and subtracted it from the last detection time from the previous site resulting in the shortest possible time interval between detection sites. Fish that were not detected at both sites were not included in the calculations.

We performed an analysis of covariance (ANCOVA) using a linear model in the programming language R (R Development Core Team 2008) to test whether rate of movement from Willapa Bay to Lippy Point (dependent variable) was a function of FL (predictor variable). We included in the model an additional variable to account for the effect of tag type (or year, 9 mm tags were used in 2006 and 7 mm tags were used in 2008), and the interaction between FL and tag type (ROM~FL+tag type+FL*tag type). Movement rate data were available for 2006 and 2008; however only one transported smolts was detected at Lippy Point in 2007, therefore we did not include 2007 data in the analysis.

5.3 Results

5.3.1 In-river survivorship

Hydrosystem survival of in-river migrating Dworshak spring Chinook salmon smolts released from Kooskia NFH to McGowan's Channel (below Bonneville Dam) was 0.41 (SE=0.09) in 2006 and 0.30 (SE=0.06) in 2008 (Table 5.2). Our results are comparable to independent estimates of PIT tag survival of Dworshak spring Chinook salmon released from Dworshak hatchery in 2006 (0.408, SE=0.06) and 2008 (0.297, SE=0.059; S. Smith, NOAA, pers. comm.; Faulkner et al. 2007; Faulkner et al. 2009).

In 2007 post-release survival to Lake Bryan (below Lower Granite Dam in the Snake River) was unusually low, only 0.19 (SE=0.05), and likewise survivorship to McGowan's Channel was only 0.08 (SE=0.04). Our 2007 survival estimates were inconsistent with survival estimates reported from NOAA PIT tag studies in 2007 of ~0.49%. It is unclear why post-release survival was low following release; we speculate that overhandling prior to surgery may have reduced survival (see Methods). We present 2007 results for completeness, but caution that these results are not representative of Dworshak spring Chinook salmon survival.

5.3.2 Estuary and plume survival

In 2006 we estimated survival of in-river migrating smolts from below Bonneville Dam to the coastal ocean (Willapa Bay) sub-array, therefore survival in the estuary and the plume are not separately estimable. The addition of the Astoria sub-array in 2007 enabled us to partition survival into two distinct and critical segments: the estuary and the ocean plume. In 2007 and in 2008 survival from below Bonneville Dam to the Astoria Bridge of in-river migrants was 1.0 (SE=0), indicating very high survival in the 200 km stretch of estuary below Bonneville Dam. Subsequent survival from Astoria to Willapa Bay (through the plume), a distance of only 63 km, was 0.50 (SE=0.14) in 2007, and 0.39 (SE=0.07) in 2008 indicating that more than half of the smolts died once they reached the ocean (Table 5.3). In 2006 combined survival through the estuary and plume of in-river migrants was 0.67 (SE=0.17) which implies that survival upon ocean entry may have been higher.

Transported spring Chinook salmon smolts were released from the barge into McGowan's Channel 8-12 km below Bonneville Dam. Survival in the estuary was 0.69 (SE=0.04) in 2007 and 0.77 (SE=0.05) in 2008. Similar to in-river smolts, survival of transported smolts in the plume was relatively low; 0.34 (SE= 0.05) in 2007, and 0.51 (SE=0.07) in 2008. In 2006 combined survival through the estuary and the plume was 0.54 (SE=0.12).

5.3.3 Coastal ocean survival

Estimated survival along the continental shelf from Willapa Bay to Lippy Point, a distance of 485 km, was low for all smolts (Table 5.4). In 2006 ocean survival of transported smolts was 0.14 (SE= 0.06), and survival for in-river migrant smolts was only 0.05 (SE= 0.04). In 2008 survival was higher for both groups but markedly better for in-river smolts compared to 2006 (in-river= 0.26, SE= 0.08; transported= 0.23, SE= 0.06), consistent with the substantially better coastal ocean conditions measured in 2008 (http://www.nwfsc.noaa.gov/research/divisions/fed /oeip/g-forecast.cfm#Table1).

5.3.4 Survivorship from release to Willapa Bay and Lippy Point

When cumulative survival from release is considered, survival of transported smolts was ≥2x the survival of IR smolts, simply because IR smolts travelled an additional 647 km through the Snake and Columbia rivers before reaching the lower river and coastal ocean sub-arrays.

5.3.4.1 Transportation-in river (T/I) survival ratio

As expected, results from z-tests of the transportation to in-river ratio from release to Willapa Bay (T/I_{WIB}) and Lippy Point (T/I_{LIP}) indicate that transported smolts had statistically higher survival to both ocean locations in all years (Table 5.5). The T/I_{WIB} ratios from 2006-8 ranged between 1.95-6.44 and all were significantly greater than 1 indicating that transported smolts had 2-6.4 times higher survival to Willapa Bay (Table 5.5). The T/I_{WIB} ratio of 6.4 (SE=2.35) however, was due to particularly high post-release mortality of in-river smolts in 2007, therefore survival of transported smolts was essentially 2-3.3 times higher than in-river smolts if 2007 is excluded.

As smolts migrated north the survival difference persisted; the T/I_{LIP} ratios were 5.15 (SE=3.91) in 2006 and 2.87 (SE=1.22) in 2008 and thus survival of transported smolts was 2.9-5.2 x higher than in-river smolts. These results were not surprising since in-river smolts travelled farther and for a longer period of time (2-3 weeks more); however, the disparity in ocean survival estimates in 2006, and thus the very high T/I_{LIP} ratio, many be attributed to differences in timing of ocean entry.

5.3.5 Post Bonneville survivorship to Willapa Bay and Lippy Point

Pooled survivorship of in-river smolts from below Bonneville Dam to Willapa Bay was 0.67 (SE=0.17) in 2006, and 0.48 (SE=0.13) in 2007 and 0.40 (0.07) in 2008. Post-Bonneville survivorship to Lippy Point was 0.04 (SE=0.03) in 2006, and 0.10 (SE=0.03) in 2008. (Survivorship to Lippy Point was not estimable in 2007.)

Pooled survivorship of transported smolts from below Bonneville Dam to Willapa Bay was 0.54 (SE=0.12) in 2006, and 0.23 (SE=0.04) in 2007 and 0.39 (SE=0.05) in 2008 (Table 5.4). The 2007 estimate reflects the high post-release mortality that was also observed in in-river smolts, therefore survival in this migration segment may not be representative of the population in that year. Post-Bonneville survivorship to Lippy Point was 0.08 (SE=0.03) in 2006 and 0.09 (SE=0.03) in 2008. (Survivorship to Lippy Point was not estimable in 2007.) As the distance travelled was the same for both treatment types it was possible to directly compare survival to the ocean detection sub-arrays, 264 km and 787 km beyond the hydrosystem, respectively.

5.3.5.1 Differential post-Bonneville mortality (D) survival ratio

In 2006 Z-tests indicated that transported smolts did not have significantly lower survival from below Bonneville Dam to Willapa Bay than in-river smolts (D_{WIB}=0.8, SE=0.14; Table 5.5). In 2008 transported smolts had slightly lower survival than in-river smolts to Willapa Bay, although the difference was not significant (D_{WIB}=0.91, SE=0.17). D_{LIP} was 2.1 (SE=1.6) in 2006 indicating that transported smolts had higher survival to Lippy Point, however this difference was not significant. In 2008 transported smolts had lower survival than in-river smolts to Lippy Point (D_{LIP} =0.79, SE=0.33), but again this difference was not significant. Because mortality in the ocean was high, sample size was small at this more distant sub-array, and therefore we did not have the statistical power to find a difference. The point estimates, however, demonstrate the variability in ocean survival. No smolts were detected entering the Strait of Juan de Fuca.

5.3.6 Post-release mortality

We calculated the mortality rate per km in the first migration segment for in-river and transported smolts in order to compare post-release mortality of smolts released from the hatchery to smolts released from the transportation barge below Bonneville Dam. We used a Monte Carlo procedure to statistically compare mortality rates since distance travelled was different for each treatment type. In 2006 and 2008 there was no statistical difference in post release mortality (Appendix C, Figure C.4; $p>0.05$), indicating that smolts from both treatment types suffer losses following release but that the degree of mortality was similar for fish released in different environments. We did not conduct the analysis for 2007 data because of unusually high post-release mortality of in-river smolts.

5.3.7 Timing of ocean entry

In all years an attempt was made to release transported fish below Bonneville Dam at approximately the time when in-river fish were passing Bonneville Dam. The assumption was that if the rate of movement from Bonneville Dam to the ocean is similar for both treatments, then smolts would enter the ocean at approximately the same date, and would therefore experience similar ocean conditions. We did not attempt to transport and release smolts during the time when Dworshak smolts are typically transported and released from the barges, and therefore our transportation release dates were generally later than what is typically observed for Dworshak spring Chinook salmon.

In 2006 we estimated the arrival of in-river smolts at Bonneville Dam prior to tagging and release based on historical run times from the past decade and scheduled the release of transported fish accordingly. In that year, however, river flow was the highest it had been in a decade and therefore in-river smolt rate of movement was much faster than we had anticipated. As a result, transported fish were released 2-3 weeks after the passage of in-river smolts at Bonneville Dam and therefore subsequent arrival to the ocean detection sub-array adjacent to Willapa Bay was mismatched. The peak arrival of both in-river groups was on May 25, despite one week difference in release dates, and peak passage of the transported groups was on June 13 and June 20 (Figure 5.5).

In 2007 we estimated in-river run time to Bonneville Dam based on historical run times, and we monitored in-river fish passage through the preceding dams in the hydrosystem with PTAGIS. As a result, timing of ocean entry (passage at the Astoria Bridge detection sub-array) was more similar for in-river and transported groups; however, high post-release mortality of in-river smolts resulted in very few fish surviving to the ocean. Those in-river fish that were detected at the Astoria Bridge sub-array were detected in low numbers (only one or two fish per day) and over a period of two to three weeks, therefore a peak was not discernable.

Transported fish arrived in greater numbers and were detected on the Astoria sub-array in two distinct groups (Figure 5.5).

In 2008 we estimated in-river arrival at Bonneville Dam by monitoring smolt movements through preceding dams in the hydrosystem with PTAGIS. We were also able to transport smolts to the barge using a stand-by procedure, as opposed to setting a firm transport date. The resulting time of ocean entry was ideal; however because the in-river smolts travelled 850 km to the Astoria Bridge sub-array, the distributions of in-river release groups were quite protracted by the time they reach the ocean. As in 2006, the second in-river release group was detected on the sub-array at the same time as the first release group (despite a one week delay in release timing), between May 15 and June 16. Conversely, the transported smolts, which travelled only 200 km, arrived in two distinct groups on May 20 and May 26 (Figure 5.5). Nevertheless, ocean conditions were likely very similar for transported and in-river groups.

5.3.8 Distribution on the ocean lines

In all years, for both ocean detection sites, horizontal distribution across the continental shelf was similar for in-river and transported groups (Figures 5.6 and 5.7). In 2007 transported fish were distributed across the Willapa Bay sub-array. Smolts that had previously migrated in the river were detected across much of the array, however no fish were detected inshore (the inner 25% of the sub-array). The in-river group, however, was likely underrepresented because of high post-release mortality and subsequent low number of fish surviving to the ocean.

5.3.9 Travel time and rate of movement

Cumulative travel time and segment specific travel time in the estuary and ocean are presented in Tables 5.6 and 5.7, respectively. For in-river smolts, cumulative travel time from release to McGowan's Channel was fastest in 2006 (mean=17.1 days, s.d.=4.7) when river flows were highest. In 2006 and 2008 it took approximately two months for smolts to reach Lippy Point from the Snake River basin, a distance of almost 1400 km. Transported fish took almost 40 days to reach this site (from release), and for both treatment groups in all years segment specific travel time from Willapa Bay to Lippy point was remarkably consistent-approximately one month. Also notable, is the travel time of in-river smolts to Graves Harbor in AK. Although only three fish have been detected at this sub-array to date, travel times to this detection site, 2501 km from release, were 90.2, 93.9, and 94.5 days, and all originated from different in-river release groups.

Segment specific rate of movement from the estuary to the ocean is presented in Table 5.8. Rate of movement for in-river and transported smolts was rapid in the estuary in 2007 and 2008 (McGowan's Channel to Astoria) particularly in 2008 when mean rates reached 80.7 km/day (SD=12.4) for in-river smolts and 87.7 km/day (SD =21.3) for transported smolts. Once smolts entered the ocean and were no longer under the influence of river flow, rate of movement slowed considerably and movement rates became more consistent across groups. Rate of movement in the ocean ranged between 16.5 km/day (SD=2.2) to 22.8 km/day (SD=1.7) for all release groups (excluding 2007).

There was a tendency for larger fish to travel faster from Willapa Bay to Lippy Point (485 km; Figure 5.8), however FL was not a significant predictor of migration rate (p=0.113).

5.4 Discussion

Consistent with hypotheses regarding high mortality within the first several months at sea (see Quinn 2005), we found that in-river migrating yearling Chinook salmon tagged with acoustic transmitters had the lowest survival during their first month in the ocean relative to their migration in the river and estuary. Survival in the impounded section of the river basin was 30-40% (excluding 2007, see Results), and subsequent survival through the estuary was near 100%; however, of the surviving fish, most died before reaching the detection sub-array off the northwestern coast of Vancouver Island. Transported smolts that were released below Bonneville Dam into the upper reaches of the estuary suffered losses of up to 31% in the same area where in-river smolts had very little mortality. This initial mortality however, was comparable to the mortality experienced by our acoustic tagged in-river group after release from Kooskia hatchery to below Lower granite Dam in 2006 (0.75, SE=0.02) and 2008 (0.71, SE=0.02), as well as production spring Chinook salmon smolts released from Kooskia hatchery and detected at Lower Granite Dam in 2006 (0.716, SE=0.041) and 2008 (0.624, SE=0.020), demonstrating that there may be an initial period of high post-release predation on hatchery smolts, and that less fit or less predator wary smolts are culled upon release into a unfamiliar environment. Once transported smolts migrated through the upper estuary (2-3 days) they were exposed to increased mortality at the river mouth and plume (where more than 50% of the fish perished), which may be partly due to avian predators from colonies located just inside the river mouth (Collis et al. 2002; Roby et al. 2002; Schreck et al. 2006). Along the shelf, from the south coast of Washington (Willapa Bay) to the north coast of Vancouver Island (Lippy Point), mortality ranged between 86-95% in 2006 and 74-77% in 2008.

Early marine survival estimates for both treatment types were poor in 2006 and improved in 2008. These results are consistent with annual estimates of ocean ecosystem indicators produced by NOAA intended to predict conditions for salmon survival. These indicators range from "good" to "intermediate" to "poor" and include local biological indicators, local and regional physical indicators, and large scale ocean and atmospheric indicators (http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/g-forecast.cfm#Table1). In 2006, ocean conditions were deemed intermediate-poor for juvenile salmon entering the ocean. The period of poor ocean conditions ended in 2007, and in 2008 ocean conditions were deemed good for juvenile salmon survival. Thus, our data support oceanographic indicators of relative salmon survival, and estimates of early marine survival may be used to corroborate future indicator predictions.

If we consider T/I values to Lippy Point, transported smolts had 3-5x higher survival; however, in-river smolts had been migrating several weeks longer than transported smolts so one would expect the transported smolts to have higher cumulative survival to Lippy Point.

To test the hypothesis that transported smolts suffer from differential delayed mortality, we compared survival of in-river and transported groups from below Bonneville Dam to two ocean detection sub-arrays. Relative survival of transported smolts, D_{WIL}, was lower to the detection site at Willapa Bay in 2006 (264 km), but this finding was not significant. In addition to possible stress related effects (e.g., Congleton et al. 2000; Eder et al. 2009) this difference in survival could be attributed to 1) expected post-release mortality of the transported group below Bonneville Dam, or 2) timing of ocean entry. We transported smolts directly from the hatchery to the transportation barge; therefore it is feasible that post-release mortality was elevated because fish did not migrate in the river and experience culling upon release from the hatchery. Although we attempted to artificially induce simultaneous arrival to the ocean, in-river smolts entered the ocean 2-3 weeks prior to transported smolts which may have exposed them to different plume conditions which can change within a few days (Garcia Berdeal et al. 2000); therefore the survival difference may be confounded with differential migration timing and variable ocean conditions. As the Astoria Bridge sub-array was not deployed in 2006, it was not possible to partition the estuary from the plume.

In 2008 relative survival of transported and in-river smolts to Willapa Bay was similar. In 2008 the distribution of arrival times of in-river migrant to the Willapa Bay sub-array was greatly protracted, while the majority of transported smolts migrated across the Willapa Bay sub-array within several days. The migration timing overlapped, however, and therefore smolts likely encountered similar ocean conditions. There was evidence of post-release mortality of transported smolts to the Astoria sub-array, but survival of in-river smolts was lower in the plume and therefore cumulative survival to Willapa Bay was similar for both treatment types.

Estimates of D_{LIP}, 750 km from the detection site below Bonneville Dam, were variable and transported smolt survival did not differ significantly from 1 in 2006 or 2008. Therefore we did not see a delayed mortality effect one month after smolts have entered the ocean. The number of fish surviving to this detection site was low and variance on these estimated ratios for Lippy Point were high, so there was little power to detect a significant difference.

Transported smolts experienced more mortality from Bonneville Dam to Willapa Bay and Astoria in 2006 and 2008, respectively, than did in-river migrants. This initial mortality experienced by the transported smolts after release from the barge may be typical of post-release mortality that is experienced by many hatchery reared fish upon release directly from a hatchery (Brown and Day 2002). This difference may partially explain differential mortality that is not related to the transportation.

Subsequent early marine survival was low for both groups regardless of release site in the river; however in 2006 early marine survival of transported smolts was double that of in-river smolts, but comparable in 2008. The estimated D for Dworshak hatchery spring Chinook salmon seaward migrating in 2006 and returning in 2008 and 2009 estimated by the Comparative

Survival Study was 0.57 (upper limit of 90% confidence interval=.81) indicating that transported smolts had a significantly lower smolt to adult return rate from Bonneville Dam to adult return to Lower Granite Dam (Tuomikoski et al. 2009). Although there are several caveats to our study, including smolts size, release date and location, the discrepancy could also be due to differences in marine survival beyond the Lippy Point sub-array. In 2006 two smolts that had previously migrated in the river and zero transported smolts were detected on the Alaska array at Graves Harbor. While we recognize that we can not draw conclusions from such scare data, detecting only in-river smolts could be a preliminary indication of better survival of in-river fish, or it could indicate that transported smolts did not migrated past the AK sub-array but took up residence somewhere between Vancouver Island and southeast AK. Another potential factor that may contribute to a low D is straying of transported smolts returning as adults to the Snake River. Earlier studies reported that straying was not a factor (e.g., Ebel et al. 1973; Slatick et al. 1975) however more recent studies have found that straying can be up to 10% greater for transported fish than for in-river fish (Bugert and Mendel 1997; Keefer et al. 2008).

Horizontal distributions of smolts in the ocean at Willapa Bay and NW Vancouver Island were very similar despite the difference in migration history. In 2006 there was evidence that smolts may have migrated along the outer edge of the shelf and may have gone undetected; therefore the sub-array was extended an additional 5 km in 2007. In 2007 and 2008 smolts were detected on the outermost receiver once again (34 km offshore), however it was clear that the majority of the fish were migrating between 20-30 km offshore and within the boundaries of the receivers. At the Lippy Point sub-array, they showed a similar pattern in 2006 slightly inshore, and in 2008 both groups were more centrally located across the shelf. As the shelf is narrower and the array contains fewer receivers, it is obvious from the horizontal distribution that spring Chinook salmon smolts remain closer to the Vancouver Island shore. In 2006 all smolts remained within 15 km of shore, and in 2008 all smolts were detected within 20 km from shore.

Travel time and rate of movement in the river was likely regulated by river flow. In 2006 the transported groups migrated slightly slower from below Bonneville Dam to the ocean and this was likely because transported fish were released later than in-river smolts when the river flows were lower and river velocities were correspondingly lower. In 2008 migration timing was more similar and likewise, travel time for transported and in-river groups was the same from Bonneville Dam to Astoria (2.6 days). Travel time in the ocean from Willapa Bay to Lippy Point was remarkably stable across years, treatment types and release groups. Interestingly, cumulative travel time of in-river smolts in 2007 and 2008 was similar to McGowan's Channel, Astoria, and Willapa Bay despite high post-release mortality in 2007. Even more surprising was that in-river fish from three separate release groups were detected in Alaska between 90.2 and 94.5 days.

In conclusion, because the technology to estimate survival of juvenile salmonids in the ocean did not exist until recently, it was necessary to estimate the ratio of PIT tagged smolt to adult survival, which compares survival after 2-3 years at sea and may mask differential mortality that may occur after release. By evaluating juvenile survival soon after ocean entry it is possible to examine the magnitude of D in the first month of ocean life, when differential effects of transport are more likely to be expressed, rather than examining survival over the full 2-3 year period before the smolts return as adults. This approach also potentially reduces the time needed to test transportation strategies, as it is possible to establish early ocean survival rates within a few weeks of smolt passage, and these measurements are not confounded with survival variations later in the life history. As survivorship from release below Bonneville Dam to Lippy Point for both treatment types in all years was less than 10%, with highest mortality occurring in the ocean, this should further raise concerns about the effect of early marine survival on rebuilding populations of yearling Chinook salmon which was emphasized by Kareiva et al. (2000), as well as implementing management plans that consider the marine ecosystem (Bisbal and Mcconnaha 1998).

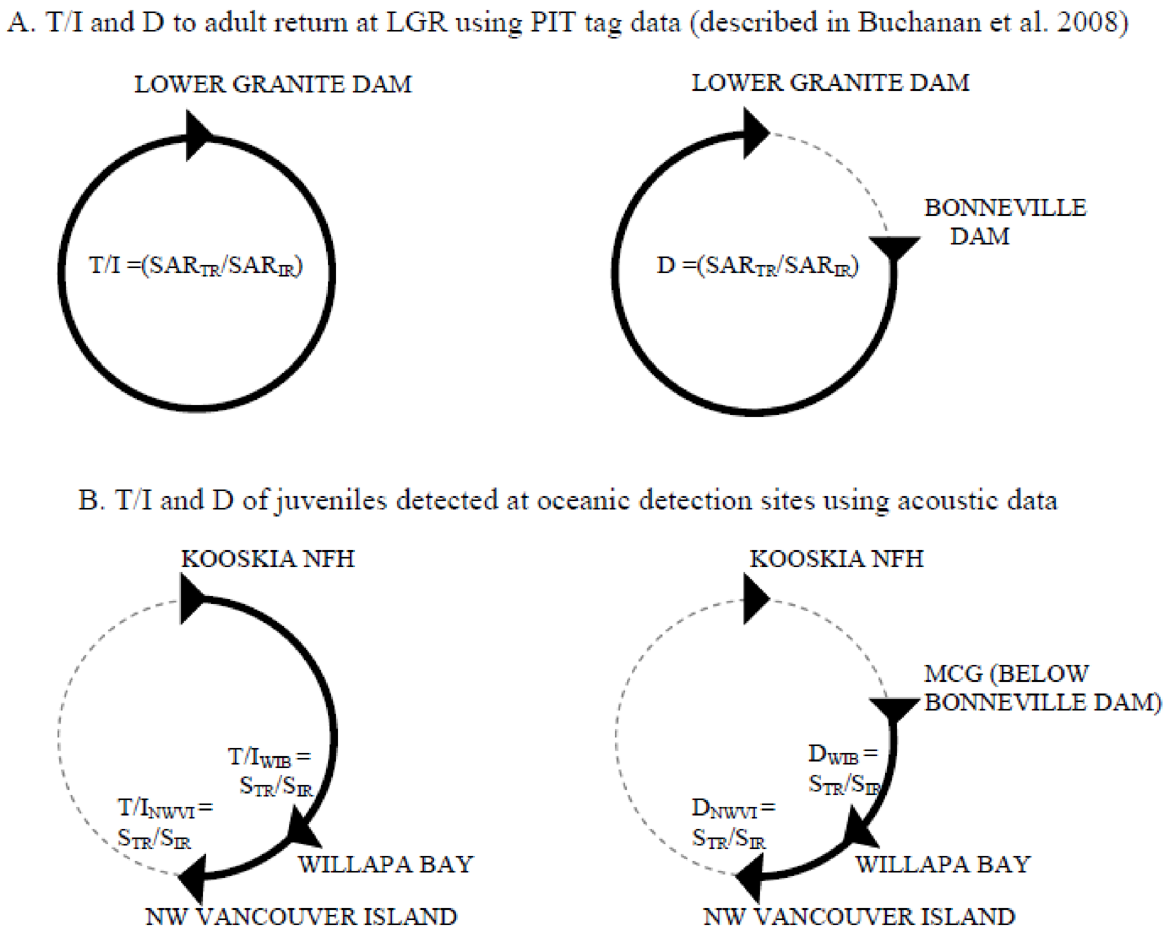

Figure 5.1. Schematic of components used in transportation to in-river survival ratios (T/I) and post-Bonneville differential delayed mortality ratios (D). A) T/I and D estimated with PIT tag data. T/I is the ratio of the smolt to adult return rate (SAR) to Lower Granite Dam (LGR) of transported smolts (SAR_{TR}, assumes survival in the barge from LGR to release below Bonneville Dam is 100%) to SAR of in-river migrants (SAR_{IR}) migrating as smolts from LGR and returning as adults to LGR. D is the ratio of the SAR of transported smolts released below Bonneville Dam and returning to LGR to the SAR of in-river migrants estimated from Bonneville Dam to adult return to LGR. B. T/I to Willapa Bay and Lippy Point on Vancouver Island (TIR_{WIB} and TIR_{LIP}, respectively), are the ratios of juvenile survival of transported smolts (S_{TR}) released in the Lower Columbia River (McGowan's Channel, MCG, 10 km below Bonneville Dam; survival during transport was 1) to marine detection sites 40 km (WIB) and 525 km (LIP) north of the mouth of the Columbia River to the juvenile survival of in-river migrants (S_{IR}) released at Kooskia National Fish Hatchery (NFH) to WIB and LIP. D to Willapa Bay and Lippy Point (D_{WIL} and D_{LIP}, respectively) is the ratio of juvenile survival of transported smolts from MCG to WIL and LIP to the juvenile survival of in-river migrants from below Bonneville Dam to the same sites. Bold lines indicate the portion of the life cycle that is included in the T/I and D estimates.

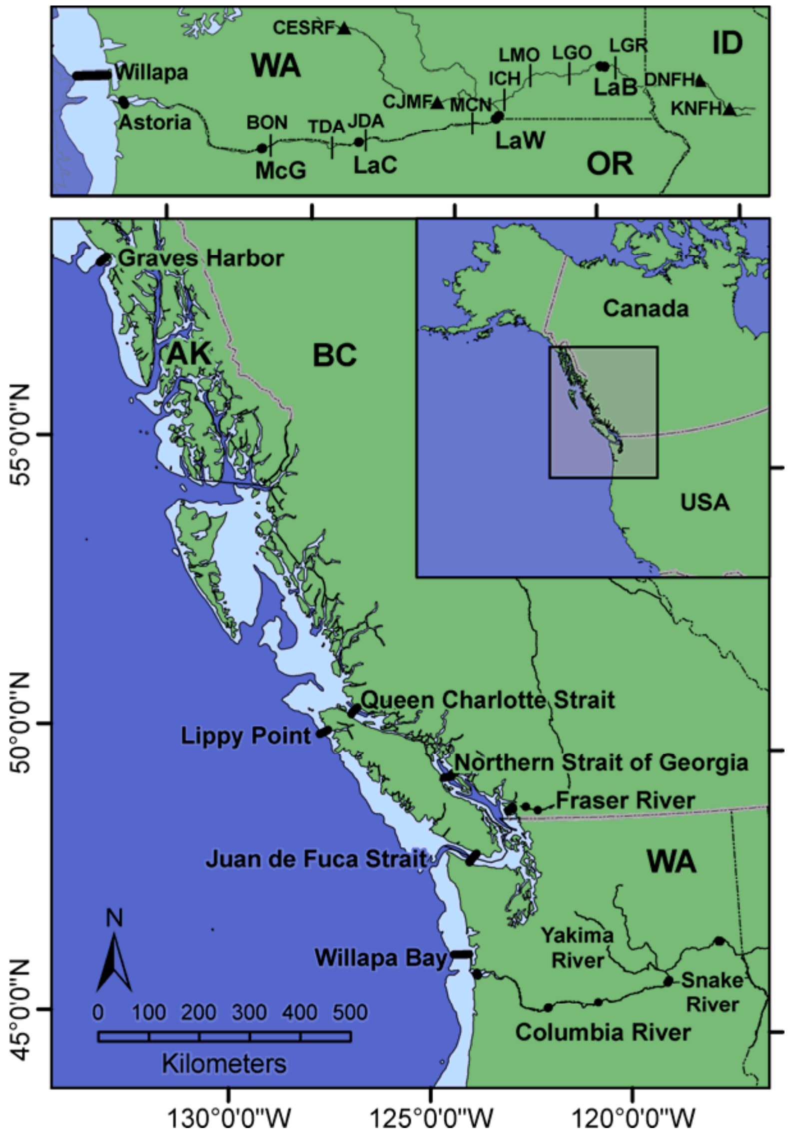

Figure 5.2. Pacific Ocean Shelf Tracking (POST) acoustic array. The inset shows the location of the in-river release site (KNFH=Kooskia National Fish Hatchery); detection sites (LaB=Lake Bryan, LaW=Lake Wallula, La=Lake Celilo, McG= McGowan's Channel) and dams (BON=Bonneville, TDA=The Dalles, JDA=John Day, MCN=McNary, ICH=Ice Harbor, LMO=Lower Monumental, LGO=Little Goose, LGR=Lower Granite) within the lower Snake and Columbia rivers. The continental shelf (depths <200m) is shaded. Transported fish were release at McG.

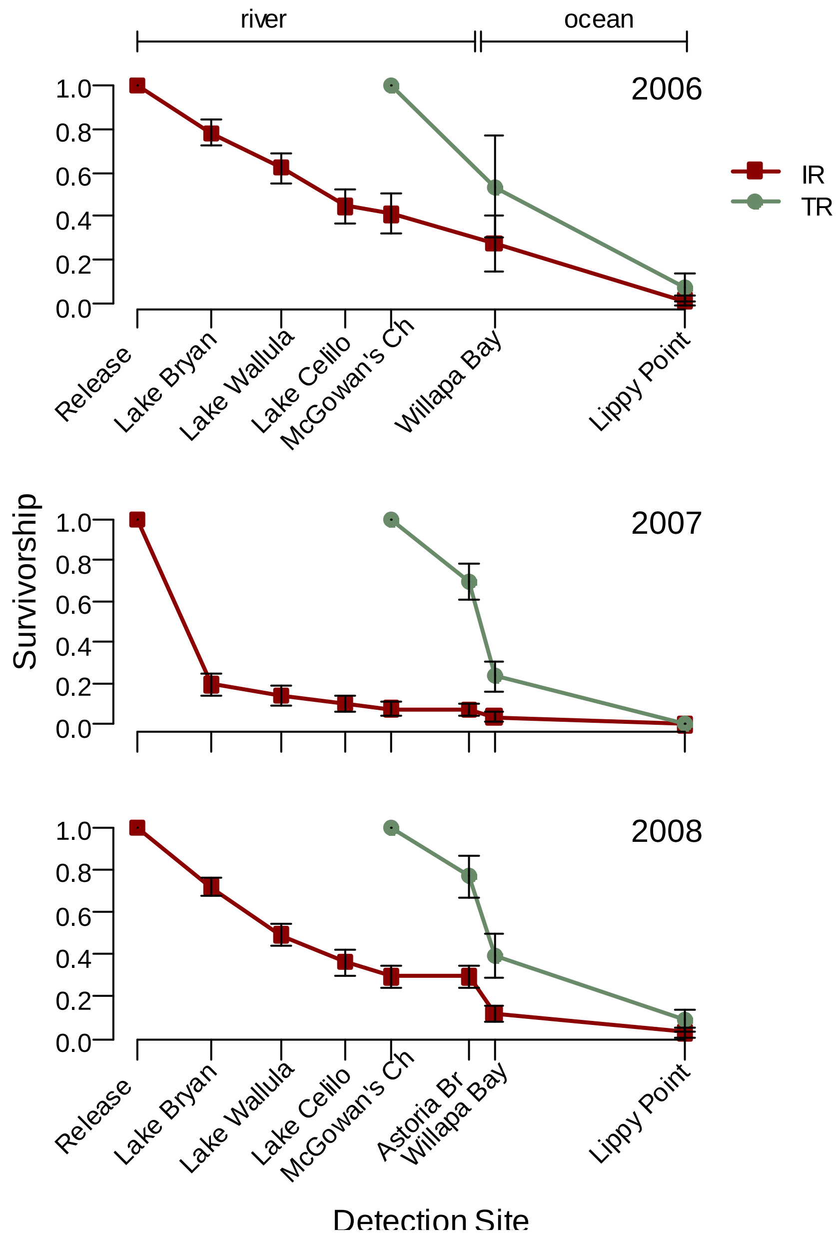

Figure 5.3. Survivorship of in-river (IR) and transported (TR) Dworshak spring Chinook salmon smolts from release in 2006, 2007 and 2008. IR smolts were released from Kooskia Hatchery in the Snake River basin. TR smolts were released at the McGowan's Channel detection site below Bonneville Dam. Error bars are 95% CIs. To calculate survival to Lippy Point we assumed the detection probability of the Lippy Point sub-array was equal to the more southerly Willap Bay sub-array. This likely overestimates coastal ocean survival, as a smaller proportion of receivers was typically lost to fishing activity on the Lippy Point sub-array.

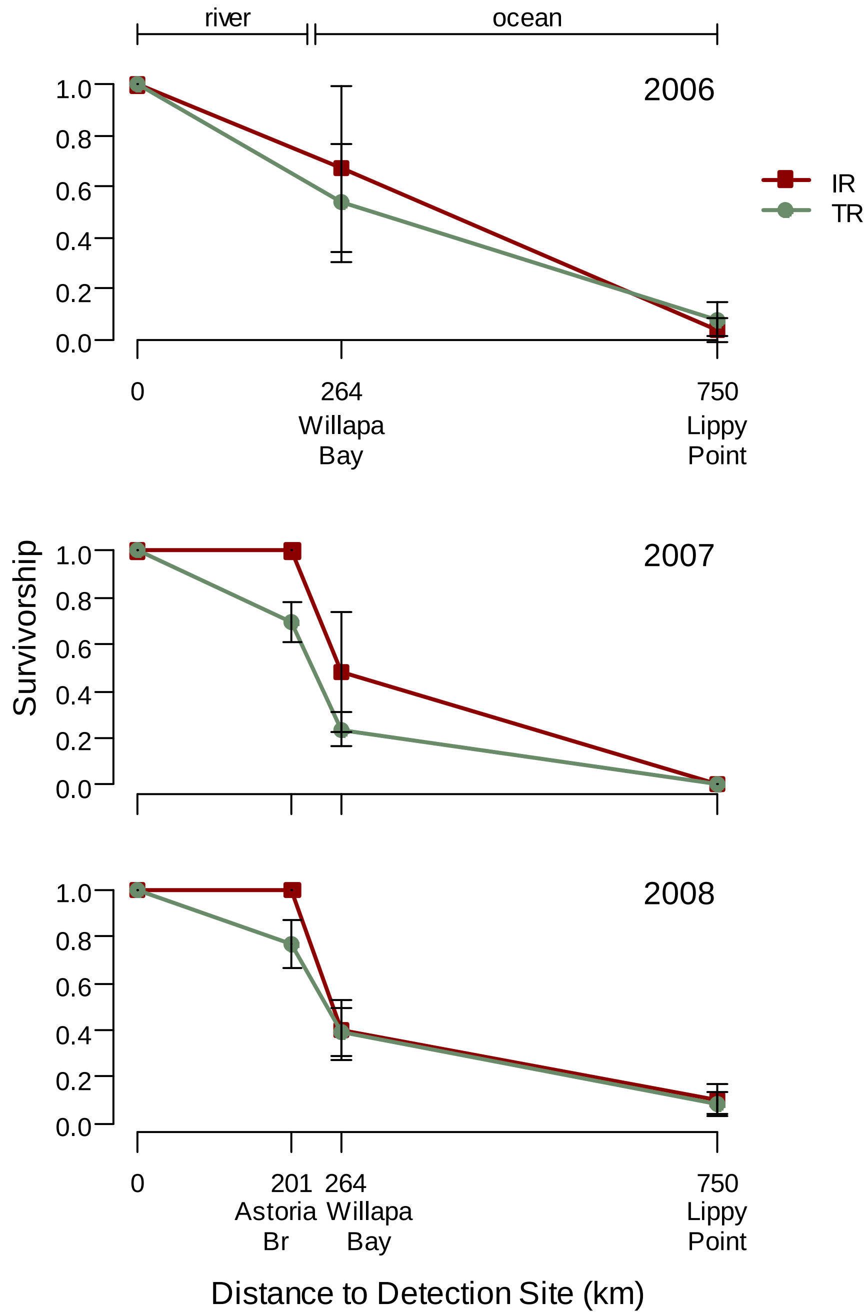

Figure 5.4. Conditional survivorship of in-river (IR) and transported (TR) Dworshak spring Chinook salmon smolts from McGowan's Channel (10 km below Bonneville Dam) in 2006, 2007 and 2008. Error bars are 95% CI's. To calculate survival to Lippy Point in 2006 and 2008 we assumed the detection probability of the Lippy Point line sub-array equal to the more southerly Willapa Bay sub-array. To calculate survival to Willapa Bay in 2007 we assumed the detection probability of the line was equal to the estimated detection probability in 2006. Only one transported fish was detected on the Lippy Point line in 2007.

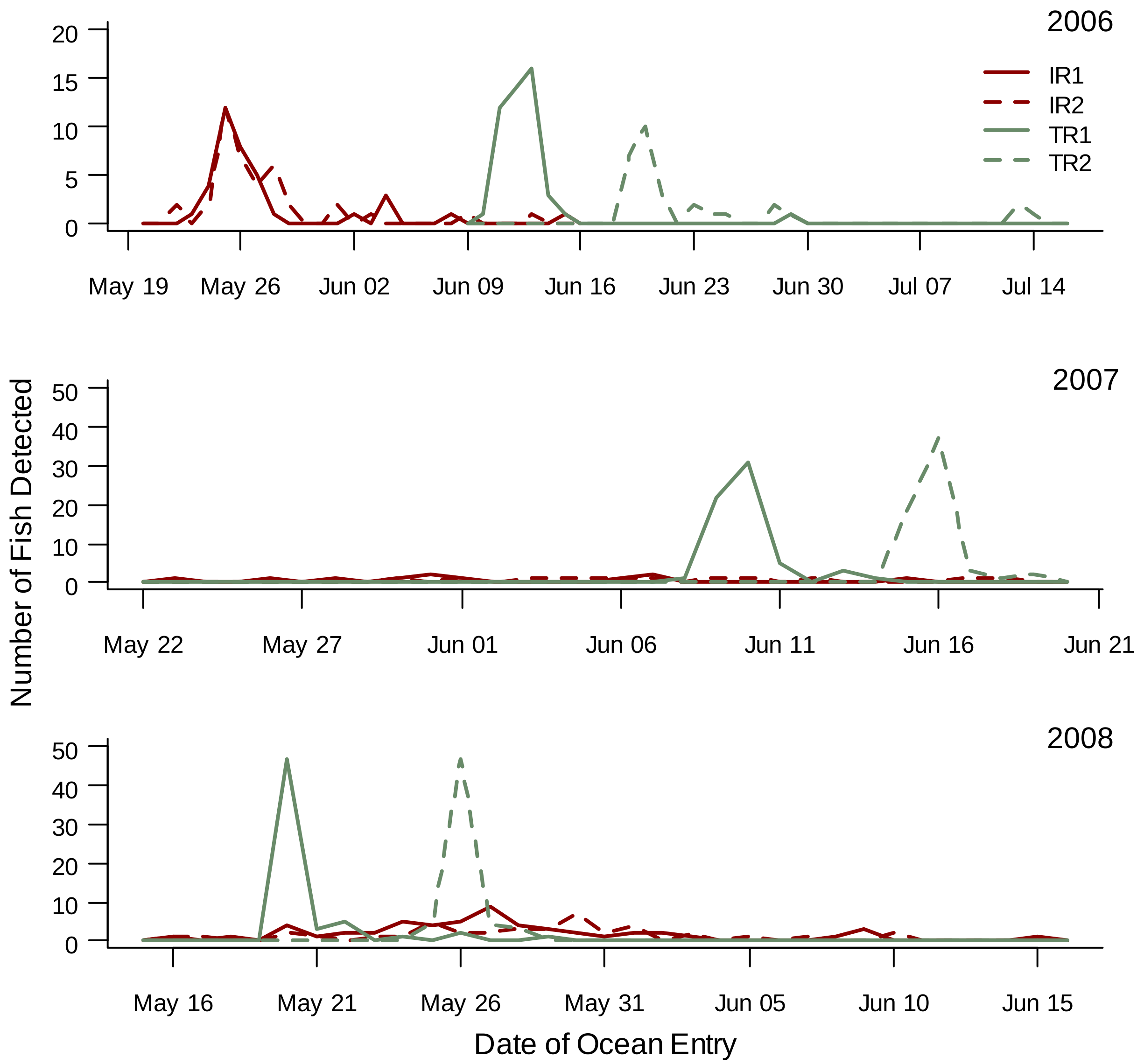

Figure 5.5. Timing of ocean entry of two release groups of in-river (IR) and transported (TR) Dworshak spring Chinook salmon smolts in 2006, 2007 and 2008. Timing of ocean entry was determined by detections on the Willapa Bay sub-array in 2006 (40 km north of the Columbia River mouth) and the Astoria Bridge 2007-08 (23 km up the Columbia River).

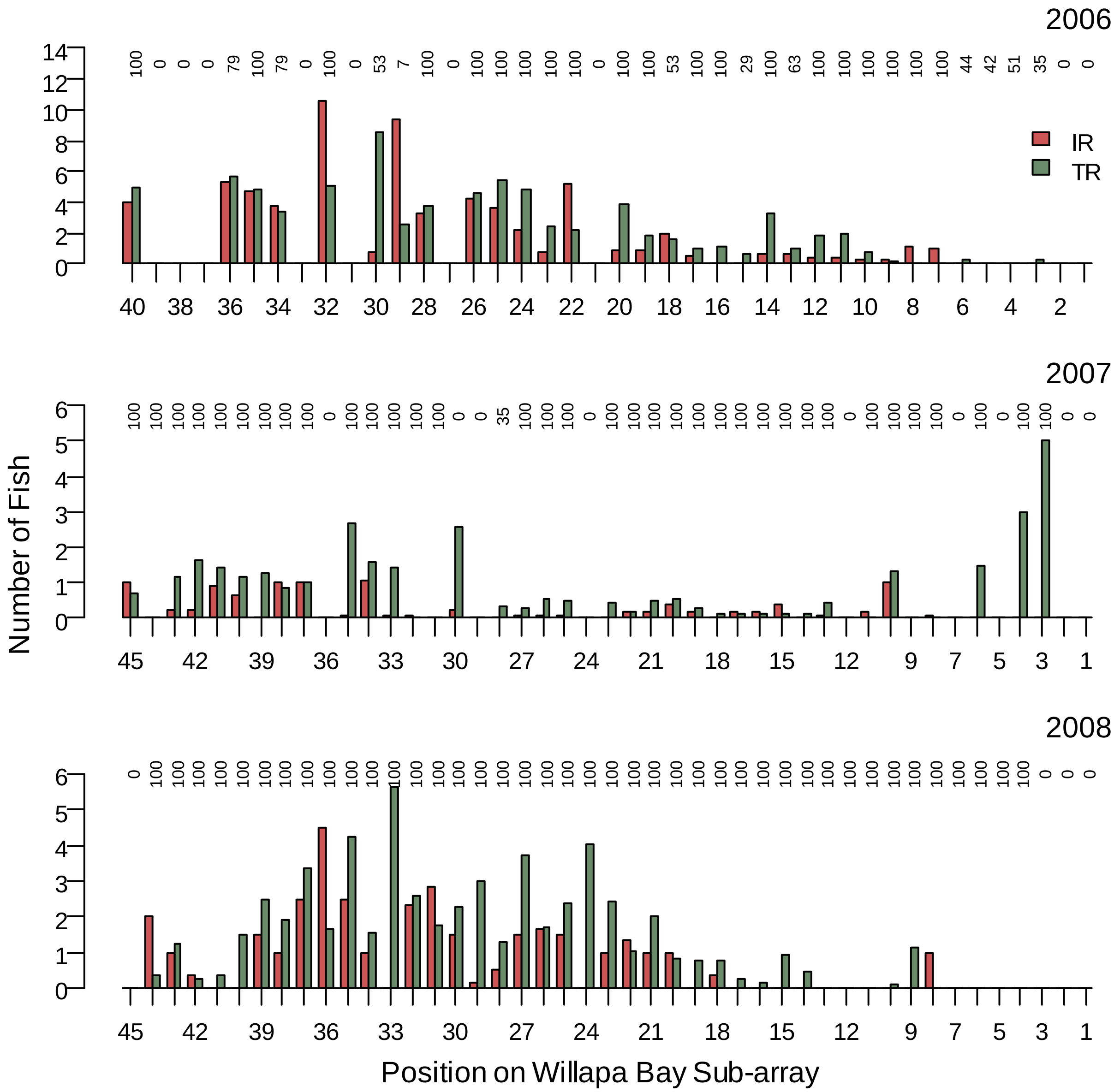

Figure 5.6. Cross-shelf distribution of in-river (IR) and transported (TR) Dworshak spring Chinook salmon smolts off of southern Washington at Willapa Bay in 2006, 2007, and 2008. If a fish was detected at more than one receiver a proportion was allocated to the receiver, e.g. if an ID code was detected on two receivers, each receiver was assigned a value of 0.5. Position 1 on the x-axis represents the eastern-most acoustic receiver nearest shore. A total of 40 receivers (VR2's and VR3's) was deployed in 2006. In 2007, five receivers were added on the offshore portion of the sub-array. In 2008, receiver 45 was not operational; therefore the sub-array was effectively 44 receivers in length. The values above the bars indicate the proportion of time that the receiver was operation during the migration.

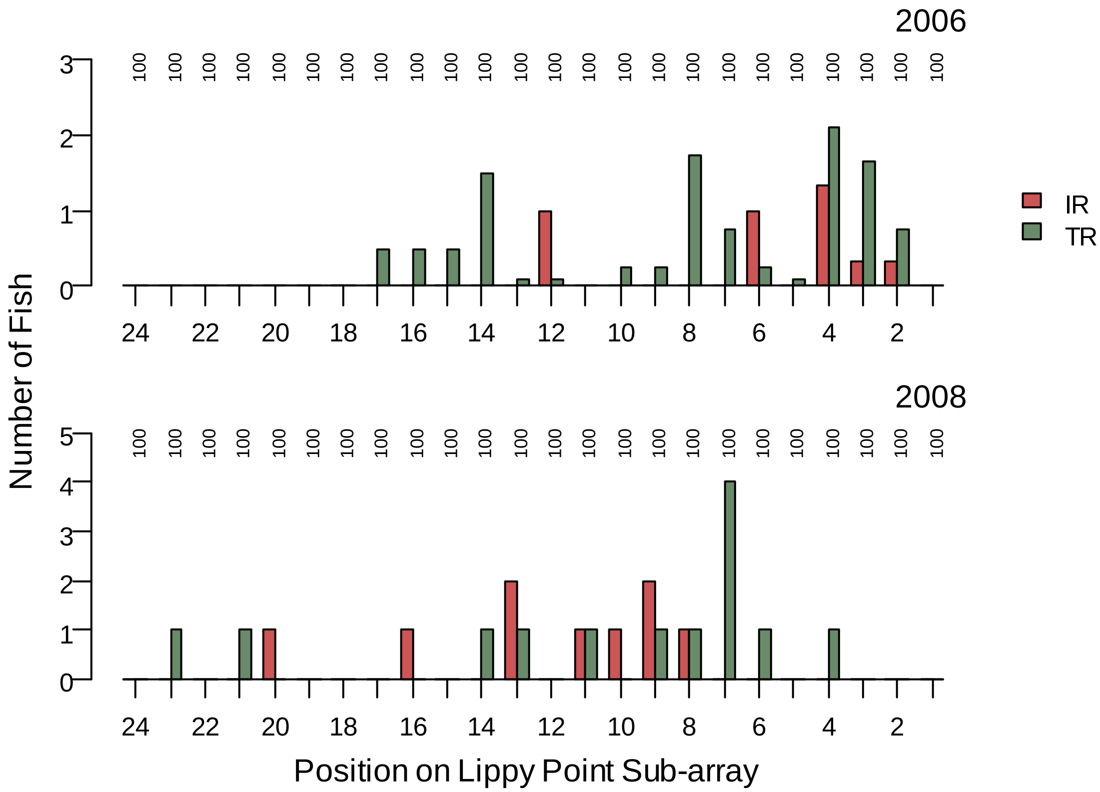

Figure 5.7. Cross-shelf distribution of in-river (IR) and transported (TR) Dworshak spring Chinook salmon smolts at Lippy Point on northwestern Vancouver Island in 2006 and 2008. Position 1 on the x-axis represents the eastern-most acoustic receiver nearest shore. A total of 24 receivers (VR2's and VR3's) was deployed in 2006. No smolts were detected at Lippy Point in 2007. If a fish was detected at more than one receiver a proportion was allocated to the receiver, e.g., if an ID code was detected on two receivers, each receiver was assigned a value of 0.5. The values above the bars indicate the proportion of time that the receiver was operation during the migration.

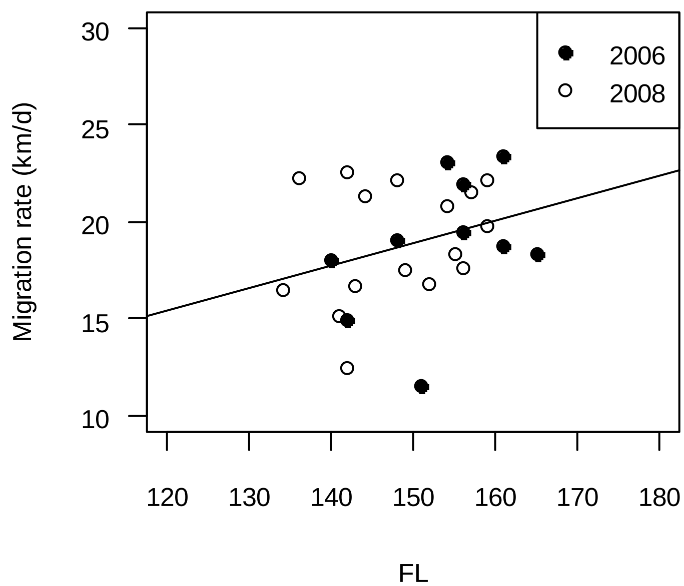

Figure 5.8. Migration rate vs. FL of Dworshak spring Chinook salmon smolts in 2006 and 2008 (in-river and transported smolts combined). Although there was a tendency for larger fish to travel faster from Willapa Bay to Lippy Point (485 km), FL was not a significant predictor of migration rate (p=0.113). Only one smolt was detected at Lippy Point in 2007 and was not included in the analysis.

Table 5.1. Summary of Dworshak-origin spring Chinook salmon tagging. In 2006-07 smolts were implanted with 9 mm acoustic transmitters; in 2008 smolts were implanted with 7 mm transmitters. All smolts were also PIT tagged. IR fish were released at Kooskia NFH; transported fish were released below Bonneville Dam. (IR=in-river, TR=transported, FL= fork length, g=grams)

Release Group	Release Date	# Tagged	Mean size at tagging (mm FL; range)	Mean weight at tagging (g; range)
2006				
IR 1	1-May	198	146.9 (140-208)	35.2 (26.9-117.5)
IR 2	8-May	198	145.6 (140-192)	34.0 (27.4-83.7)
TR 1	6-Jun	102	154.5 (141-168)	42.5 (30.8-55.3)
TR 2	14-Jun	101	154.6 (140-168)	41.9 (28.5-55.5)
2007				
IR 1	7-May	175	149.1 (141-173)	39.7 (30.1-60.6)
IR 2	14-May	174	149.0 (140-166)	39.5 (32.2-55.4)
TR 1	5-Jun	99	148.8 (140-166)	37.3 (30.9-56.6)
TR 2	11-Jun	99	148.4 (141-163)	36.5 (29.5-54)
2008				
IR 1	25-Apr	197	146.2 (130-159)	37.5 (23.3-55.5)
IR 2	2-May	198	146.3 (131-159)	37.3 (23.9-52.7)
TR 1	17-May	100	149.4 (135-159)	39.9 (26.5-52.3)
TR 2	23-May	99	148.3 (131-158)	39.3 (26.2-51.8)

Table 5.2. Survivorship (SE) from release of in-river (IR) and transported Dworshak spring Chinook salmon smolts. IR fish were released at Kooskia NFH; transported fish were released below Bonneville Dam.

Year	Treatment	Detection Site			
		McGowan's Channel (647/NA)	Astoria Bridge (848/201)	Willapa Bay (911/264)	Lippy Point (1396/749)
2006	IR	0.41 (0.05)	(b)	0.28 (0.07)	0.015 (0.01)
	Transported	1.0 [(a)]	(b)	0.54 (0.23)	0.077 (0.034)
2007	IR	0.08 (0.02)	0.07 (0.01)	0.04 (0.01)	(c)
	Transported	1.0 [(a)]	0.69 (0.04)	0.23 (0.04)	(c)
2008	IR	0.3 (0.03)	0.3 (0.03)	0.12 (0.02)	0.031 (0.01)
	Transported	1.0 [(a)]	0.77 (0.05)	0.39 (0.5)	0.088 (0.03)

(a) No mortality was observed during transportation, therefore survival assumed to be 1.
(b) Astoria Bridge sub-array not deployed in 2006.
(c) Survival not estimable.

Table 5.3. Survivorship (SE) of in-river (IR) and transported spring Chinook salmon smolts from McGowan's Channel (below Bonneville Dam).

Year	Treatment	Detection Site		
		Astoria Bridge (201)	Willapa Bay (264)	Lippy Point (749)
2006	IR	(a)	0.67 (0.17)	0.036 (0.025)
	Transported	(a)	0.54 (0.12)	0.077 (0.034)
2007	IR	1.0 (0)	0.48 (0.13)	(b)
	Transported	0.69 (0.04)	0.23 (0.04)	(b)
2008	IR	1.0 (0)	0.4 (0.07)	0.1 (0.03)
	Transported	0.77 (0.05)	0.39 (0.05)	0.088 (0.03)

(a) Not deployed in 2006
(b) Survival not estimable in 2007

Table 5.4. Segment survival (SE) of in-river (IR) and transported Dworshak spring Chinook salmon smolts. IR fish were released at Kooskia NFH; transported fish were released below Bonneville Dam.

Year	Treatment	Migration Segment (km)			
		Estuary (201)	Plume (63)	Estuary + Plume (264)	Ocean (485)
2006	IR	(a)	(a)	0.67 (0.17)	0.05 (0.04)
	Transported	(a)	(a)	0.54 (0.12)	0.14 (0.06)
2007	IR	1 (0)	0.5 (0.14)	0.48 (0.26)	(b)
	Transported	0.69 (0.04)	0.34 (0.05)	0.23 (0.04)	(b)
2008	IR	1 (0)	0.39 (0.07)	0.40 (0.13)	0.26 (0.08)
	Transported	0.77 (0.05)	0.51 (0.07)	0.39 (0.11)	0.23 (0.06)

(a) the Astoria Bridge acoustic detection line was not deployed in 2006

(b) Survival was not estimable to this site in 2007

Table 5.5. Transport to in-river (T/I) and differential delayed mortality (D) ratios. T/I ratios (SE) to Willapa Bay and Lippy Point on Vancouver Island (TIR_{WIB} and TIR_{LIP}, respectively), are the ratios of juvenile survival of transported smolts (S_{TR}) released in the Lower Columbia River (McGowan's Channel, MCG, 10 km below Bonneville Dam; survival during transport was 1) to marine detection sites 40 km (WIB) and 525 km (LIP) north of the mouth of the Columbia River to the juvenile survival of in-river migrants (S_{IR}) released at Kooskia National Fish Hatchery (NFH) to WIB and LIP. D (SE) to Willapa Bay and Lippy Point (D_{WIL} and D_{LIP}, respectively) is the ratio of juvenile survival of transported smolts from MCG to WIL and LIP to the juvenile survival of in-river migrants from below Bonneville Dam to the same sites. Bold indicates ratios significantly different from 1.

	TIR_{WIL}	Z statistic	p-value	TIR_{LIP}	Z statistic	p-value
2006	1.95 (0.35)	3.716	**<0.0001**	5.15 (3.91)	2.158	**0.015**
2007	6.44 (2.35)	5.100	**<0.0001**	NA	NA	NA
2008	3.30 (0.63)	6.253	**<0.0001**	2.87 (1.22)	2.480	**0.007**

	D_{WIL}	Z statistic	p-value	D_{LIP}	Z statistic	p-value
2006	0.80 (0.14)	-1.285	0.099	2.11 (1.60)	0.984	0.164
2007	0.49 (0.16)	-2.251	**0.012**	NA	NA	NA
2008	0.91 (0.17)	-0.495	0.312	0.79 (0.33)	-0.547	0.291

Table 5.6. Mean Travel time from release to sub-arrays (days, st. dev.). Dworshak in-river (IR) smolts were released at Kooskia Hatchery (870 km from Columbia River mouth). Transported Dworshak fish (TR) were released from the barge below Bonneville Dam near McGowan's Channel (at river km 224-228). The Astoria Bridge detection site was first deployed in 2007. Parentheses below detection sites indicate cumulative distance (km) from release site (IR/transported).

		Detection Sub-array				
Year	Release Group	McGowan's Channel (647/0)	Astoria Bridge (848/201)	Willapa Bay, WA (911/264)	Lippy Point, BC (1396/749)	Grave's Harbor, AK (2501/1854)
2006	IR 1	19.6 (4.4)		26.2 (4.8)	57.9 [(a)]	94.5 [(a)]
	IR 2	14.1 (3.0)		19.0 (4.2)	52.9 (1.8)	90.2 [(a)]
	Pooled Mean	17.1 (4.7)		22.4 (5.8)	54.2 (2.9)	92.3 ± 3
	TR 1			4.8 (2.7)	30.7 (7.9)	no data
	TR 2			8.0 (7.3)	64.0 (6.0)	no data
	Pooled Mean			6.0 (5.2)	39.8 (17.1)	
2007	IR 1	22.1 (5.5)	25.5 (6.6)	38.1 (9.4)	no data	no data
	IR 2	22.3 (5.9)	24.4 (6.0)	34.3 (10.4)	no data	no data
	Pooled Mean	22.2 (5.6)	24.9 (6.2)	36.2 (9.6)		
	TR 1		3.5 (1.1)	6.2 (2.6)	38.7 [(a)]	no data
	TR 2		3.2 (0.8)	11.5 (5.7)	no data	no data
	Pooled Mean		3.3 (1.0)	8.4 (4.9)		
2008	IR 1	25.2 (4.5)	31.8 (5.9)	39.4 (6.8)	66.0 (9.2)	93.9[(a)]
	IR 2	20.8 (8.6)	26.1 (5.6)	32.3 (5.6)	54.7 (0.3)	no data
	Pooled Mean	22.8 (7.1)	29.3 (6.4)	36.7 (7.2)	63.5 (9.4)	
	TR 1		2.8 (1.8)	12.0 (5.2)	41.1 (4.5)	no data
	TR 2		2.3 (0.6)	11.5 (3.5)	36.3 (4.2)	no data
	Pooled Mean		2.6 (1.3)	11.8 (4.4)	38.5 (4.8)	

(a) calculated from only one individual.

Table 5.7. Segment specific travel times (days; st. dev.) of in-river (IR) and transported (TR) Dworshak spring Chinook salmon smolts. Parentheses below segments indicate segment distances (km). See Table 5.6 for details.

		Migration Segment				
Year	Release Group	McGowan's Channel-Willapa Bay (264)	McGowan's Channel-Astoria Bridge (201)	Astoria Bridge-Willapa Bay (63)	Willapa Bay-Lippy Point (485)	Lippy Point-Graves Harbor (1105)
2006	IR 1	5.3 (3.1)			(b)	(b)
	IR 2	4.8 (3.2)			29.6 (3.9)	38.4 (a)
	Pooled Mean	5.1 (3.1)				
	TR 1	5.9 (5.2)			23.6 (2.3)	no data
	TR 2	6.2 (5.4)			42.3[a]	no data
	Pooled Mean	6.0 (5.2)			26.3 (7.4)	
2007	IR 1		2.4 (0.3)	16.2 (12.2)	no data	no data
	IR 2		2.6 (0.4)	12.3 (7.0)	no data	no data
	Pooled Mean		2.5 (0.4)	14.3 (9.5)		
	TR 1		3.5 (1.1)	2.8 (2.4)	33.9[a]	no data
	TR 2		3.2 (0.8)	8.5 (5.6)	no data	no data
	Pooled Mean		3.3 (1.0)	5.3 (5.0)		
2008	IR 1		2.5 (0.4)	8.7 (6.1)	31.6 (5.0)	(b)
	IR 2		2.7 (0.5)	6.5 (3.8)	21.7 (0.3)	no data
	Pooled Mean		2.6 (0.4)	8.0 (5.5)	28.3 (6.4)	
	TR 1		2.8 (1.8)	8.9 (5.5)	26.9 (3.6)	no data
	TR 2		2.3 (0.6)	9.2 (3.9)	23.2 (1.9)	no data
	Pooled Mean		2.6 (1.3)	9.0 (4.8)	25.0 (3.3)	

(a) calculated from only one individual.
(b) not detected at the previous detection site, therefore not calculable.

Table 5.8. Segment-specific rate of movement (km/day; st. dev.) of in-river (IR) and transported (TR) Dworshak spring Chinook salmon smolts in 2006, 2007 and 2008. See Table 5.6 for details. Parentheses below detection sites indicate segment distances (km).

		Migration Segment				
Year	Release Group	McGowan's Channel-Willapa Bay (264)	McGowan's Channel-Astoria (201)	Astoria-Willapa Bay (63)	Willapa Bay-Lippy Point (485)	Lippy Point-Graves Harbor (1105)
2006	IR 1	62.3 (24.6)			(b)	(b)
	IR 2	67.1 (23.2)			16.5 (2.2)	28.8 (a)
	Pooled Mean	64.7 (23.8)				
	TR 1	57.8 (19.4)			22.4 (2.2)	no data
	TR 2	55.4 (19.4)			12.4[(a)]	no data
	Pooled Mean	56.9 (19.3)			21.0 (4.3)	
2007	IR 1		84.5 (10.4)	6.6 (5.4)	no data	no data
	IR 2		77.8 (11.2)	6.4 (3.2)	no data	no data
	Pooled Mean		80.8 (11.1)	6.5 (4.1)		
	TR 1		62.7 (17.0)	33.9 (19.7)	7.8[(a)]	no data
	TR 2		64.9 (11.2)	12.5 (9.2)	no data	no data
	Pooled Mean		63.8 (14.5)	24.7 (19.1)		
2008	IR 1		83.9 (12.2)	10.7 (6.9)	15.6 (2.1)	(b)
	IR 2		77.0 (12.4)	12.6 (6.7)	22.3 (0.3)	no data
	Pooled Mean		80.7 (12.4)	11.4 (6.8)	17.8 (3.8)	
	TR 1		84.5 (24.3)	10.9 (7.6)	19.8 (2.6)	no data
	TR 2		90.9 (17.3)	8.7 (5.8)	22.8 (1.7)	no data
	Pooled Mean		87.7 (21.3)	9.9 (6.9)	21.3 (2.6)	

(a) Calculated from only one individual.
(b) Not detected at the previous detection site, therefore not calculable.

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6 Freshwater and Marine Migration and Survival of Endangered Cultus Lake Sockeye Salmon Smolts Using POST, A large-scale Acoustic Telemetry Array[5]

6.1 Introduction

The management and conservation of salmon populations would be aided by a better understanding of the marine life history phase (e.g., English 2008; Lacroix 2008; McKinnell et al. 2001). The early marine stage is poorly studied relative to both the initial freshwater life history phases (egg to fry, fry to smolt) and the very late marine and freshwater life history phases of returning adults (e.g., Groot and Margolis 1991). Although there are many estimates of overall survival for Pacific salmon stocks based on outmigrating smolt numbers and the subsequent level of adult return some years later, it has not been possible to directly study survival at discrete periods during the marine portion of their life history. It is therefore difficult to pinpoint where major periods of mortality occur or understand their cause. Such information is necessary for understanding population dynamics and for making informed decisions for assisting the rebuilding of threatened and endangered populations of salmon.

The development and continued miniaturization of uniquely-coded acoustic tags in the last decade holds the promise of allowing major advances in marine research. (Heupel et al. 2006; Voegeli et al. 1998, 2001). Unlike radio waves, sound transmits effectively in both fresh and saline waters. Acoustic receivers can be arranged in line arrays or “curtains” (e.g. Lacroix and Voegeli 2000; Lacroix et al. 2005) placed in selected locations along potential migratory routes. In this way, it is possible both to track individuals seamlessly between the fresh and marine environments and to partition survival in order to understand where episodes of mortality occur.

This technology has formed the basis of the Pacific Ocean Shelf Tracking Project (POST) for tracking both juvenile (Melnychuk et al. 2007; Welch et al. 2003, 2004) and adult (e.g., Cooke et al. 2008) salmon as well as other species (Lindley et al. 2008; Welch et al. 2006). The POST

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array is intended as a permanent continental-scale telemetry research platform for the entire west coast of North America, including major rivers. The component listening "curtains" (or sub-arrays) use Vemco VR-2 or VR-3 passive acoustic receivers in precise geometries to enable a nearly complete census of acoustically-tagged salmon as they cross each successive curtain. Although centered along the shelf in southern British Columbia waters, the array currently extends almost 900 km up the Columbia-Snake River in the United States, and spans over 2,500 km in geographic extent from the Columbia River to Graves Harbor, southeast Alaska (Haggan et al. 2008).

In this study, we used the POST array to study the migratory behaviour and survival of Cultus Lake sockeye salmon smolts over the four year period 2004-2007. This sockeye salmon population is genetically unique and has been studied since the 1920s (Ricker 2006). Between the 1920s and the 1960s, the number of returning adult Cultus sockeye salmon averaged around 20,000. However, a rapid decline in the number of adult sockeye salmon returning to spawn in the 1990s reduced the population to fewer than 100 (decreasing by 92% between 1991 and 2002; English et al. 2008), triggering a recommendation for an emergency listing of the population as endangered by the Committee on the Status of Endangered Wildlife in Canada in 2002 (COSEWIC 2003). Although the federal government accepted the evidence, legal listing as endangered was not made because of the impact the decision would have on commercial fisheries of other stocks of Fraser sockeye. (Cultus Lake sockeye salmon are incidentally harvested during the late-run Fraser River sockeye salmon fishery and fisheries closures would lead to economic losses estimated to be on the order of $200M; Government of Canada 2005).

What is unclear is why marine survival decreased dramatically in the 1990s. COSEWIC (2003) listed the three primary causes of sockeye salmon decline as overfishing and incidental harvest, high pre-spawning mortality, and low marine survival. Poor marine survival seems to be a feature shared by a number of salmonid stocks and other species in south and central coast BC waters (English et al. 2008) and the cause clearly warrants further investigation. The Cultus Sockeye Recovery Team states that "*survival and distribution of Cultus sockeye in the Fraser River and near-shore marine areas have not been documented, thus resulting in a* *knowledge gap for this specific stock*" (Cultus Sockeye Recovery Team 2005). It was thus of interest to explore how tracking migrating Cultus Lake sockeye salmon smolts using the POST array might help to fill gaps in our understanding about where possible survival "bottlenecks" might occur.

The objectives of our study were to estimate survival and migratory behaviour of Cultus Lake sockeye salmon smolts within the Fraser River and along their initial coastal migration. This work builds on our existing understanding from earlier investigations into the migration of Fraser River sockeye salmon (Groot and Cooke 1987; Groot and Quinn 1987; Groot et al. 1989).

6.2 Methods

6.2.1 Study site

Cultus Lake drains into the lower Fraser River via Sweltzer Creek, Vedder River, and Sumas River (Fig. 1). The total distance from the release site at the lake outflow to the mouth of the Fraser River is 100 km. Mean annual discharge of the Fraser River, which drains into the Strait of Georgia, is 3,600 $m^3 \bullet s^{-1}$, with highest flows peaking in late June. Exit routes to the Pacific Ocean from the Strait of Georgia include Johnstone Strait and Queen Charlotte Strait to the north, and the Strait of Juan de Fuca to the south (Fig. 1).

6.2.2 Smolt release groups

Hatchery-reared 1½-yr old sockeye salmon smolts were surgically implanted with acoustic transmitters prior to release in 2004-2007. All smolts were from Cultus Lake stock. Those tagged in 2004, 2005, and 2007 were reared from wild adult returns. The fish tagged in 2006 were from more complex origins because only 10 females were available for broodstock, which were taken from a total return of only 60 adults in the 2004 brood year. These smolts were produced from wild x wild parents (85%) or a mixture of hatchery-produced, naturally-returning parents (one or both parents; 15%). Some of the 2006 matings also used cryo-preserved sperm taken from wild adult males in 2002.

In 2004 (n=100), sockeye smolts were reared at Rosewall Creek Hatchery on Vancouver Island, tagged, and then transported by helicopter to Cultus Lake for release. In 2005 (n=376), 2006 (n=200), and 2007 (n=200), smolts were tagged at Inch Creek Hatchery (located near

Cultus Lake) and then transported by truck to Cultus Lake for release. In all years but 2005, tagged fish were released in Sweltzer Creek at the outflow from Cultus Lake. A fence in Sweltzer Creek upstream of the release site was in place each year until about June 1 to reduce the frequency of upstream movement into the lake. In 2005, fish were released in June after the fence had been removed and therefore they were released approximately 500 m downstream of the standard release site.

Average fork length of all Cultus Lake hatchery smolts tagged over the four years of the study ranged from 159-189 mm (Table 6.1). It should be noted that these hatchery-reared smolts were considerably larger than typical wild smolts (ca. 100 mm), but currently available acoustic tags are too large for use in wild sockeye salmon smolts.

6.2.3 Tag characteristics

Tags were programmed to transmit their acoustic codes at 69 KHz with a 30-90 sec random time interval between successive transmissions (average 60 sec). In 2004, we implanted Vemco V9-6L tags which had projected life spans of >4 months. In 2005, we used a combination of V9-6L, V9-1L, and V9-2L tags (Table 6.1). The latter two models have an extended battery life owing to their larger size. We programmed a “sleep” period that began on July 22 (V9-1L) or Dec. 1, 2005 (V9-2L); during this time acoustic transmission was terminated in order to reserve power for the 2007 return migration of any surviving adults. These tags were programmed to re-activate and begin transmission again on 30 June 2007, prior to the historic arrival time in the Strait of Georgia. The tags had sufficient projected reserve battery power to allow transmission to continue until at least September 15, 2007, after the time of expected adult entry into the Fraser River. The larger tags were implanted into larger smolts (see Table 6.1). In 2006 and 2007, we used all V9-1L tags with 41-45 days of active transmission after release until their programmed sleep periods began on June 1-4 2006 or June 27-28 2007. The 2006 tags were programmed to reactivate between April 18 and July 4, 2008 while the 2007 tags should reactivate on July 26, 2009.

Tag lengths ranged between 10.0-16.7% of body length (mean ratios: V9-6L, 12.5%; V9-1L, 13.3%; V9-2L, 15.5%) and tag mass ranged between 2.4-9.6% of body mass (mean ratios: V9-6L, 5.5%; V9-1L, 5.1%; V9-2L, 5.9%). Tag:body size ratios of nearly all fish were below recommended limits for juvenile salmonids of 16% of length and 8% of weight (Lacroix et al. 2004).

6.2.4 Surgical techniques

Acoustic tags were surgically implanted into smolts following standard protocols (Welch et al. 2007). Smolts were sedated with 1 ppm metomidate HCl (Aquacalm™) for a minimum of 10 minutes, then 3-4 minutes prior to surgery they were brought under full anaesthesia using 70 ppm Tricaine methane Sulphonate (MS-222) mixed with a 140 ppm $NaHCO_3$ buffer. Gills were continuously irrigated during surgery using a purpose-built surgical table with re-circulating water bath containing 50 ppm MS-222 (100 ppm $NaHCO_3$) flowing into the mouth. A tag was inserted into the abdominal cavity through a mid-ventral line incision, which was closed using 2-3 polydioxanone monofilament sutures. Fish were then transferred to a recovery tank. Water baths were continually monitored for temperature and dissolved oxygen. All water baths were changed as needed to maintain dissolved oxygen levels between 8-11 ppm and to maintain water temperatures within 2°C of ambient hatchery tank water. A water conditioner and mucous-protectant (Vidalife™) was used in all water baths.

Animal care protocols were reviewed and approved annually by institutional animal care committees prior to all field work. Sockeye salmon smolts used in this study were surgically implanted at least two days prior to release to allow time for recovery from the anaesthetic and to monitor fish for signs of mortality, tag shedding, and abnormal swimming behaviour. No mortalities were observed. The 2005 release of tagged smolts was several weeks later than other years (Table 6.1) because an electrical failure at the hatchery resulted in the death of almost all surgically implanted smolts prior to their release. Logistical constraints resulted in the subsequent surgery and release of different fish much later (early June, 2005) than originally planned (Kintama Research 2005).

6.2.5 Hydrophone receiver deployments

Acoustic receivers were installed as single or paired units in the lower Fraser River at several locations downstream of the Sumas River confluence. Locations varied between years, with three lines and six receivers in 2004, two lines and four receivers in 2005, three lines (six sub-lines) and 12 receivers in 2006, and four lines (7 sub-lines) and 14 receivers in 2007 (Fig. 1). Receivers in the Fraser River were generally mounted about 1-1.5 m above the river bed.

Ocean detections were recorded in the northern Strait of Georgia (NSOG), Queen Charlotte Strait (QCS), and the Strait of Juan de Fuca (JDF; Fig. 1). Two acoustic sub-arrays were also deployed in Howe Sound (HS), a coastal fjord 30 km north of the Fraser River mouth. In 2004 and 2005, Vemco VR2 receivers were used to construct all listening lines using a receiver geometry calculated to provide a high probability of detection of any passing tagged smolts. These units were deployed in the spring and recovered in the fall at least 110 days after Cultus Lake sockeye salmon smolts were released, well after the time that smolts were detected crossing ocean lines of receivers. In 2006, VR2 units on NSOG, QCS and JDF lines initially deployed in the spring were replaced with permanent, year-round VR3 receiver lines during summer 2006. They were uploaded twice in 2007, once in the spring and once in the fall after outmigration. The NSOG and QCS lines remained relatively intact over the course of the study with <10% loss of receivers per year, even when the more fragile VR2 deployment methodology was used. However, the JDF line was subjected to extensive shrimp bottom trawling and subsequent gear loss in 2004, with one third of receivers not recovered. In other years receiver loss was <10% on the JDF line.

6.2.6 Freshwater mobile tracking

To assess the potential for smolts to residualize in freshwater rather than migrate out to sea, we surveyed the number and location of smolts tagged with V9-2L or V9-6L tags in Cultus Lake, the Vedder and Sumas rivers, and Sweltzer Creek for two days in late July 2005 (Kintama Research 2005). We conducted two similar additional surveys in August 2007 to detect any 'sleeper' tags (from residualized or dead fish) that were released in 2005 and turned back on in 2007 (Kintama Research 2008). The 2005 census would not have detected any of the V9-1L 'sleeper' tags released that year as the survey was conducted four days after the tags would have turned off. Similarly, the 2007 survey would not have detected any tags released in 2007 as these surveys occurred during programmed sleep periods of tags.

On the first survey day of each year we used a VR-2 deployed for 6-10 min at 31 fixed stations spaced approximately 500 m apart, covering approximately 95% of the Cultus Lake area. Two days later in 2005, a VEMCO VR-28 mobile receiver was used to listen for tags while conducting sampling transects, covering approximately 60% of the lake area. In 2007, one week after the first survey, we resampled the 31 fixed stations with a VR-2 and VR-60 mobile receiver.

Additionally, a network of eight VR-2 receivers was deployed between Oct. 2006-Oct. 2007 in Cultus Lake for a separate, unrelated study (C. Tovey, Fisheries & Oceans Canada, unpublished data). These receivers detected several 2005 tags which had likely never left the lake and which began transmitting again about June 30 2007 following their sleep period, and also detected several 2007 tags from fish that had either residualized, died, or extruded tags in the lake (see results).

To look for possible mortality locations in the first segment of the migration downstream of Sweltzer Creek (before the stationary Fraser River array), we spent one day in 2005 and two days in 2007 sampling in the rivers that connect Cultus Lake with the Fraser River. We walked along a 6 km stretch of the Vedder River downstream of the confluence with Sweltzer Creek and lowered a VR-2 receiver in the river at 19 stations, each separated by 200-500 m. In 2007, 600 m of Sweltzer Creek from the Vedder confluence upstream was also sampled. In the lower Vedder Canal, Sumas River, and approximately 2 km of the Fraser River downstream of the Sumas confluence, deeper water permitted tracking by boat. In 2005, we towed a VR-2 receiver and drifted or trolled across these areas, with a single pass sufficient in the narrow Vedder and Sumas rivers and making three transects in the wider Fraser River section. In 2007, 15 fixed stations in the Vedder Canal and Sumas River were each sampled twice, one week apart.

6.2.7 Data analysis

We compiled a database of detections from the stationary receivers consisting of the dates, times and geographical locations where each tag was detected. First, we identified and excluded any detections likely to be false (due to aliasing or tag collisions). Detections were excluded as false if they were detected only once on a line within a 30 min interval, had one or more other tags heard on the same receiver around the time of the suspect detection, and did not have supporting detections from other time periods or lines. Supporting detections are defined as a temporally consistent sequence of detections from release along the migration path. This screening excluded a small number of sporadic detections (0.03%) and the vast majority of the retained data consisted of multiple detections closely spaced in time on a given receiver or sub-array. After eliminating suspect detections, we used these filtered data to estimate survival and detection probabilities, migration routes, and travel times and rates of tagged smolts.

Estimation of survival and detection probabilities are described in the next section (see below). To identify possible migratory pathways along the shelf or within the channel, we plotted the number of fish that were heard at each position on the line of acoustic receivers. Because individual fish are usually heard at more than one position on a line, we allocated a proportion of each fish to each of the receivers on which it was detected (i.e. if a fish was heard at three positions, each unit was allocated 0.33 of a fish). We used a $\chi 2$ Goodness of Fit to test if fish were distributed uniformly across the major ocean lines (i.e. each receiver as a separate category). We then grouped fish detected on adjacent receivers to identify broader migratory routes and increase the power of the test. Because the NSOG line is divided by an island, we grouped the fish heard on this line into east or west (i.e. two categories). The QCS line is not divided by an island; in order to avoid arbitrarily defining east and west, we ran a series of $\chi 2$ tests in which we grouped neighbouring receivers over an increasingly larger spatial extent (i.e. fewer categories in each test) up to a maximum of five receivers per group (representing ~4 km wide potential migration routes). When the number of receivers per group did not divide evenly, we dropped the receivers on the ends preferentially. We filled in gaps from lost receivers using arithmetic progression from neighbouring units. To test if individuals maintained a preferred migratory route between the NSOG line and the QCS line (240 km to the north), we ran a correlation analysis using the average distance from the mainland that each smolt was detected on each line. Travel times in each segment were measured as the difference between travel times from release until the first detection of a tag on a line, for successive lines. Travel times from release to the mouth of the Fraser River and from the river mouth to the ocean lines were estimated using the furthest downstream line in the Fraser River each year. The segment distances used in travel rate estimation were measured with mapping software as shortest-route distances between lines of receivers excluding land masses.

6.2.8 Survival rate estimation

We used the fully time varying Cormack-Jolly-Seber model (CJS) for live recaptures and variants thereof to simultaneously estimate survival (ϕ) and detection (p) probabilities in each segment of the migration. To do so, we first determined the detection history of individual fish at each receiver (i.e., "re-capture") line along the migration path. Sockeye salmon smolts were detected on 2-4 detection lines in the Fraser River (depending on year), and then two lines in the ocean (NSOG and QCS) for a total of five, six or seven detection sites. Only two fish in 2005 and six fish in 2007 were detected on the JDF line, but these were pooled with the QCS detections for the final digit of the CJS tag capture histories to represent exit from the Strait of Georgia system.

The final survival probability is confounded with detection probability at the final line (QCS/JDF), essentially because there is no more distant location where the ratio of detected to undetected tags can be assessed. To isolate these factors, we estimated an overall detection probability for the NSOG line (p_{NSOG}) across all four years of the study and assumed this value for the QCS and JDF lines in all years. This approach is reasonable because all three lines had similar receiver geometry during the study period. We used a shorter, 3-digit capture history involving release, NSOG "recapture", and QCS "recapture" to more accurately estimate the mean and variance of p_{NSOG}. This estimate of p is the fraction of smolts detected on the QCS line that were also detected on NSOG. Our estimate of p_{NSOG} was for V9 tags from all populations of salmon smolts tagged under POST in 2004-2007 that crossed this line, not just Cultus Lake sockeye. This pooling was done because sample sizes of some populations crossing ocean lines were small and thus population-specific p estimates were highly variable. No consistent seasonality pattern was observed in population-specific p_{NSOG} estimates when compared with their average run timing across this line, so pooling was justified. Further, model selection criteria showed 99.9% support, as measured by Akaike weights, for a model in which species, populations, and years were pooled in a set of four other models involving less pooling of species, population, and year-specific estimates of $p_{\text{NSOG.}}$ With years pooled, a single estimate of p_{NSOG} was generated and then applied to QCS and JDF as a fixed value in each year. To avoid underestimating uncertainty in the survival estimate for the final migration segment due to fixing this value, survival rates were also calculated by fixing the detection probabilities of QCS and JDF at the lower and upper 95% confidence limits of p_{NSOG}; this bounded a range of uncertainty for the final stage survival estimate and thus the total migration survivorship estimates (Fig. 2).

After assuming fixed values for the final stage detection probabilities, we used the full capture histories in a CJS live recaptures-only model implemented with Program MARK (White and Burnham 1999) through RMark (Laake and Rexstad 2007) to estimate ϕ in river and ocean segments as well as *p* on river lines in each year. Our approach involved two main steps:

(i) To determine whether survival was on average best described as a function of body size, migration distance and/or average travel time, we tested several candidate models. We first combined all four years in a capture history dataset and assigned 'year' as a group covariate. Combining years allowed us to constrain the slope of survival vs. one such covariate to be consistent among years (while permitting intercepts to differ). For example, we constrained the relative survival difference of a big smolt and a small smolt to be equal among years in logit space, even though particular body sizes or overall survival at a particular body size could differ among years.

We considered eight candidate models (Table 6.2) using this combined dataset. Detection probabilities in all models were line-specific and year-specific, $p_{(time*year)}$, where the 'time' factor represents re-capture locations at receiver lines. One survival model was the classic time-varying CJS model, $\phi_{(time*group)}$, with separate segment-specific survival estimates for each of the four years. Another model incorporated the additive effect of body size as an individual covariate into the CJS model. The other six models involved minimum migration distance or average travel time group covariates to replace the freely-varying segment-specific estimates. These constrained models, some of which included body size as a covariate, involved fewer parameters. Some allowed for separate effects of in-river and ocean segments of distance or travel time on survival, and others were further constrained without this multiplicative habitat effect. We estimated a variance inflation factor ($\hat{c}$) to compensate for overdispersion, or extra-binomial variation, in estimated probabilities (Burnham et al. 1987). We estimated $\hat{c}$ (=1.3325) using the deviance ratio method in MARK's goodness-of-fit bootstrapping routine assuming the general CJS model, $\phi_{(time*year)}p_{(time*year)}$, QAIC$_c$ values, corrected for extra-binomial variation and sample sizes, were computed for model comparison.

(ii) Once we determined the best-supported models on average from the eight models described above, we analyzed the four years independently so that we could estimate the extra-binomial variation, $\hat{c}$, for each year of the study. By estimating $\hat{c}$ annually the variance around each of the estimated probabilities is specific to the variation observed within that year (and not all years combined). Using the bootstrapping routine again, we estimated $\hat{c}$ for the fully time varying CJS models as 1.73, 0.59, 1.44, and 1.28 in 2004-2007, respectively. The $\hat{c}$ value estimated at <1 in 2005 was set to 1 (Cooch and White 2007). These $\hat{c}$ values were used to expand standard errors of real parameter estimates and values in the variance-covariance matrix.

The top two candidate models had almost equal support and together had nearly 100% of the support within the set of eight models considered, and therefore we considered only these two models for each individual year. We computed model-averaged parameter estimates for ϕ and *p* at each segment or detection station for that year. For each sequential receiver station, we calculated survivorship from release to that point as the product of segment-specific ϕ estimates. We used the Delta method to calculate the variance of this product.

6.3 Results

6.3.1 Survival estimates

6.3.1.1 Model selection

Of the eight survival models evaluated across all years, the strongest support was found for two models: the fully time varying CJS model (with year- and segment-specific estimates); and the fully time varying CJS model that incorporated body size as an individual covariate (Table 6.2). These two models had essentially equal support, as seen in their Akaike weights. These models differed by a single parameter, so the small difference in AIC suggests little support for the larger model overall. However, when analyzed separately 2004 and 2006 had somewhat more support for the model incorporating body size (ΔQAICc > 3), so these models were both used for averaging the year-specific estimates. The six models with migration distance or average travel time constraints had fewer parameters but had much poorer fits (as measured by the overall likelihood of each model), so had little support from the data within the model set.

6.3.1.2 Survival probability estimates

With each year analyzed separately, the model-averaged estimates of the top two models in Table 6.2 show decreasing survivorship over the first 500 km of the juvenile salmon migration (Fig. 3). The "low *p*" (or "high *p*") estimates reported in Fig. 2 show the estimated survivorship to exit from the Strait of Georgia system assuming that the value of p_{QCS} is set to the lower (or upper) 95% confidence interval of p_{NSOG} rather than the mean estimate (see Methods). Since this bounded range of survivorship estimates is relatively small (compared to yearly differences, for example), and since much mortality occurred before the final segment, our survivorship estimates appear to be fairly robust to uncertainty in p_{QCS}.

The 2005 cohort stands out with markedly lower mean survival (0.12) compared to the other years, especially in the freshwater component of the migration where survival was less than one-third that of the other years (0.5-0.7). Taken across all years, mean survivorship to the northern Strait of Georgia ranged from 0.1-0.5, while survivorship to the final line in Queen Charlotte Strait ranged from 0.07-0.28 (Fig. 3).

Survivorship to the outer lines was probably underestimated in 2006 and possibly in 2007. Smolt tags in 2006 were programmed to shut off from June 1-4 (and to begin re-transmitting two years later during the adult return migration), but some surviving out-bound smolts may not have crossed the QCS line before the tag's transmissions were stopped. The mean date of first crossing the QCS line was May 25 02:16, but a few fish (n=3) were still detected on June 1-2. The likelihood that a few fish crossed the line after their tags were turned off is also supported by the date of crossing the NSOG line: the mean crossing date was May 8 10:52 for fish that were detected on QCS (n=30), and May 10 23:11 for fish not detected on QCS (n=24). Individuals late in crossing the NSOG line thus also tended to be the individuals not detected on QCS. Similarly, tags in 2007 were programmed to shut off around June 27-28, and a few fish were still detected on the QCS line June 20-25. Thus, some slower moving smolts could have crossed the QCS line undetected; four of the five tags last detected on the NSOG line (between June 10-17) were not detected on the QCS line. However, the potential effect of a premature shut-down of active transmission is likely to have little effect on the overall estimate of survival to QCS, as the majority of detected animals reached the QCS line at least two days prior to tag shut-down (27 of 30 detected survivors in 2006; 43 of 44 detected survivors in 2007).

Segment-specific survival estimates (Fig. 4) provide a way to directly assess Cultus Lake smolt survival in various segments of their migration path. The markedly lower freshwater survival in 2005 stands out. However, the 2005 cohort had relatively high marine survival indicating that the reduced survival observed in freshwater did not persist in the ocean. The Fraser-to-NSOG segment survival for 2006 indicated significantly lower marine survival (despite high freshwater survival that year) compared to both the 2005 and 2007 cohorts. There were no marked trends in marine survival within the NSOG-to-QCS segment other than the slightly lower (and more uncertain) value measured in 2004, and there was considerable overlap in all 95% confidence intervals.

Our reported survival estimates depend on the simultaneously estimated detection probabilities at the various sub-arrays (or listening lines) that we deployed. Detection probabilities on individual receiver lines in the Fraser River (p_i) ranged from 14-98% across all years (average of 64%). Taking the product of (1-p_i) for all Fraser River lines in each year results in the probability of a smolt crossing all Fraser lines without being detected (Melnychuk et al. 2007). This value is the non-detection rate for the Fraser River sub-array as a whole, and ranged from 0.7%, 23%, 0.03% and 7.8% in 2004-2007, respectively; thus, in most years, aggregated detection probabilities for the lower Fraser River sub-array exceeded 90%. Detection probabilities on the NSOG line averaged 90% (range 85%-93%). As discussed earlier, this value was assumed for the QCS/JDF lines as the geometry of these sub-arrays is very similar.

6.3.2 Migration behaviour

Cultus Lake sockeye salmon displayed four predominant migratory behaviours (Table 6.3). Northward migration in the ocean was the most common behaviour observed, which accounted for 9.8-34.5% of all released fish each year. These fish migrated quickly out of the Fraser River and then had a directed migration crossing the NSOG and QCS lines. Migration north but first entering Howe Sound prior to heading across the two northern lines of NSOG and QCS occurred in 1.6-9% of all released fish each year. Only eight fish, two (0.5% of released fish) in 2005 and six (3% of released fish) in 2007 were ever detected swimming south from the Fraser River (Table 6.3). However, it should be noted that one-third of the receivers on the JDF line were lost in 2004 so it is possible that some fish migrated south through these gaps and were not detected in 2004. Two of the six fish crossing the JDF line in 2007 were also detected later on the Lippy Point line (Figure 6.1). There was some evidence of fish milling within the Fraser River and in the vicinity of ocean lines (Table 6.3).

Some tagged fish moved upstream after release in Sweltzer Creek into Cultus Lake (Tables 3, 4) during both of the years where freshwater surveys were conducted (4.5% in 2005 and 6.0% in 2007). After this initial upstream movement, fish could have remained within Cultus Lake without migrating out of freshwater, died in the lake, or shed their tags in the lake. Four of the 12 fish detected in the 2007 surveys were detected at the same stations as in 2005, which suggests these were probably tags lying on the lake bottom. It is unclear whether the tags only detected on a single survey were present in moving (and therefore surviving) sockeye, but this seems likely for at least some tags.

6.3.2.1 Distribution across receiver curtains

Because POST lines in the Strait of Georgia are bordered by land on both sides and because detection probabilities were high in all years, it was possible to explore the distribution of migrating smolts at sea and establish whether fish had preferred "migration highways". Smolts crossing the NSOG line (Fig. 5) showed a marked preference for the mainland route east of Texada Island in 2004 and 2006 ($p<0.001$) when compared to a uniform distribution across all receivers on the line (i.e. each receiver treated as a separate category in the χ^2 analysis). This preference was not evident in 2005 and 2007 ($p>0.37$). When fish were grouped according to whether they migrated on the east versus the west side of Texada Island (two categories; Texada Island splits the NSOG line into two sections), they showed a significant preference for the eastern channel (all years analyzed separately $p\leq0.001$).

The distribution of smolts crossing the QCS line (Fig. 6) was not significantly different from uniform when each receiver was treated as a separate category in the $\chi 2$ analysis (2005-2007 years tested separately $p>0.24$; 2004 insufficient data). However, when the detections on neighbouring receivers were aggregated together (ie extending the spatial area and reducing the number of categories), the $\chi 2$ tests became increasingly significant as the area of aggregation increased (Fig. 7). Fish showed significant preference for the eastern side of the Strait in 2004, 2006, and 2007 ($p=0.04$, $p<0.001$, $p=0.002$ respectively over a 3.2 km extent) and near-significant selection for the eastern-central channel in 2005 ($p=0.11$).

A correlation analysis showed no relationship between where individuals crossed the NSOG line (estimated as the average distance from the B.C. mainland) and where they crossed the QCS line 240 km to the north (r^2=0.04-0.2; 2004-2007).

6.3.2.2 Travel rate and swimming speeds

Cultus Lake smolts exited the Fraser River in <6 days. The later-released fish in 2005 and 2007 travelled faster, with mean times to the river mouth of 4.1 and 4.0 days, respectively. The earlier-released fish in 2004 and 2006 took slightly longer to reach the river mouth (5.6 and 5.0 days, respectively). There was no clear pattern with release date and time taken to exit the Strait of Georgia across the QCS line. Average times from release to reaching the QCS line ranged between 25.6 to 34.1 days.

Travel rate was variable among years and for different sections of the migration route, with mean values ranging between 5-30 km•d^{-1} (Fig. 8; 0.46-1.8 body lengths per second (BL•s^{-1})). Fish tagged in 2004 had the slowest migration rate in the Fraser River with a mean speed of 15.5 km•d^{-1}. However, these fish had the fastest mean swimming rate in the marine sections when swimming directly to both the NSOG and QCS lines. The 2007 cohort had the fastest rate of movement out of the Fraser River (25.8 km•d^{-1}) but relatively slow rates in the ocean segment from the river to mouth to either HS or NSOG. In most years, travel rates in the NSOG to QSC segment were faster than in other segments, around 26 km•d^{-1}.

6.4 Discussion

6.4.1 Survival

A significant constraint on salmon conservation and management is our poor understanding of mortality during different life history stages after leaving freshwater. Poor marine survival has been implicated for the drastic decline of many salmon (Beamish et al. 2004; English et al. 2008; McKinnell et al. 2001) and steelhead (Ward 2000; Welch et al. 2000) stocks in southern BC. This study presents a first step in monitoring both freshwater and early marine survival of endangered Cultus Lake sockeye salmon during the initial stages of migration.

Survival rates during the freshwater migration phase were relatively stable among the years studied, at 50-70% of migrating smolts (except 2005, when survival was <20%, possibly due to the very late release). However, given the relatively short distances that must be travelled to the mouth of the Fraser River (≤100 km), the short duration of the freshwater migration, and the absence of obvious impediments to travel, such as dams, the specific survival levels observed are surprisingly low. Our results do seem consistent with freshwater survival estimates for other west coast salmon populations [Keogh R steelhead: 75% (Welch et al. 2004); Cheakamus R steelhead: 80% (Melnychuk et al. 2007); Thompson R steelhead: 30%; Thompson River Chinook salmon: 23%; Snake River Steelhead: 18%; Snake River Chinook salmon: 25% (Welch et al. 2008)]. As the higher survival estimates are seen for smolts travelling much shorter distances to the sea (0.3~16 km), and the lower survival estimates are for smolts travelling much farther to the sea (300-900 km), the Cultus sockeye salmon results generally fall in the middle of this range.

Several factors may have caused the high freshwater mortality observed in 2005. First, these hatchery-reared fish were released much later than in other years because a power failure killed almost all of the smolts that were originally implanted (Kintama Research 2005). Later release times have been associated with poorer survival in other studies (Bilton et al. 1982), and the lower water levels in Sweltzer Creek during June compared to May may make the fish more susceptible to predators. (Three smolts were observed being taken immediately by birds post-release that year.) Second, a fence normally sited in Sweltzer Creek to reduce the frequency of fish migrating back up into Cultus Lake was removed on 1 June 2005, which meant some smolts could have migrated back upstream (however, the 2005 lake survey revealed similar levels of residualization as in 2007 when the fence was in place).

Marine survival rates were also stable across years (including 2005), and were consistent with survival estimates for the nearby Cheakamus R steelhead (Melnychuk et al. 2007). The 2005 sockeye salmon smolt outmigration year resulted in exceptionally poor adult returns coastwide in 2007 (DFO 2008**);** however, our results for 2005 do not show a substantial difference between years in early ocean survival in the Strait of Georgia (SOG), and which is consistent with independent information provided by a DFO SOG trawl survey for juvenile salmon (DFO 2008; p. 13). This could be explained by several possibilities: first, the SOG may have been insulated from events occurring more broadly on the west coast and thus higher mortality at sea could have occurred later, beyond the SOG. Second, the low abundances of salmon smolts in the ocean in these other regions could also have been the result of poor downstream survival in other natal rivers. Third, the relatively high survival of Cultus Lake sockeye salmon smolts through the Strait of Georgia system in 2005 may have been the result of the fittest individuals surviving the high freshwater mortality phase and thus migrating through the Strait of Georgia with relatively high survival.

Overall, survivals showed a relatively steady attrition with distance and do not indicate particular areas of higher mortality at the spatial resolution of this study. Unfortunately, we have no comparable data on baseline survival rates for the earlier period of much better adult returns that occurred prior to the deployment of POST in 2004.

It should be noted that the survival estimates presented here using the pilot phase of the POST array may not accurately represent survival in the overall Cultus Lake sockeye salmon population. We sampled smolts that were about 50% longer than wild free-ranging smolts in order to accommodate the V9 acoustic tags that the "1st generation" POST array was originally designed around in 2003. As salmon survival scales positively with size when considered over a wide range of sizes (McGurk 1996, 1999), we would expect that the survival of the wild (smaller) smolts to potentially be lower than what we measured here.

The survival estimates presented here may also be biased as a result of two confounding factors. First, total survival estimates reported for 2005 and 2007 are biased high as a result of overestimating survival in the segment from the river mouth to NSOG, due to the confounding factor of small numbers of fish swimming south after ocean entry in those years. However, as noted earlier, this bias is expected to be minor as only two fish were detected migrating south through Juan de Fuca in 2005 and only six fish were detected in 2007 (Table 6.3). Second, survival is actually a joint estimate of the probability of migration and survival. Residualization (non-migration) in freshwater (either Cultus Lake or the streams and rivers leading to the Fraser R mouth) is confounded with mortality during the downstream migration, so our reported survival estimates are biased low to some degree. However, the surveys carried out in 2005 and 2007 suggested a relatively low minimum residualization rate of between 5-6% of all tagged fish.

6.4.2 Migration highways

The POST lines (particularly those between the mainland and Vancouver Island) provide a unique means to identify whether salmon have preferred migration routes or "highways". Limited evidence suggests that specific "marine highways" may be as common under the ocean (e.g., Atlantic cod off Newfoundland; Rose 1993) as they are observed to be on land for mammals and birds. Our results for Cultus Lake sockeye salmon confirm the importance of the Johnstone Strait migration pathway proposed for migrating juvenile Fraser River sockeye salmon by Groot and Cooke (1987). These authors found that smolts predominantly move north in a directed migration with a preference for staying to the east side of the Strait of Georgia and Johnson Strait. Our results further extend the persistence of this migratory preference to Queen Charlotte Strait, some 500 km from the release site. As in our study, Groot and Cooke (1987) also found that Fraser River sockeye salmon enter Howe Sound. The ecological reason for these migration routes in some years is unclear, as are the reasons for the inter-annual variation in saltwater distribution we have documented with the array.

Cultus Lake sockeye salmon displayed relatively rapid, directed movement once they commenced their downstream migration with little evidence of milling. Earlier work on sockeye salmon calculated average freshwater migration speeds of between 5.1 and 7.8 km per day in lakes but up to 40 km per day in the Columbia River (Burgner 1991). Our results indicated travel rates of between 15-25 km per day for Cultus Lake sockeye. Obviously river flow is an important influence on travel rate, although the results show that sustained travel rates of 10-30 km per day were also achieved in the marine inshore environment. Thus continued rapid migration occurred without the influence of river flow. The faster downstream migration observed in 2005 and 2007 is likely related to release time, as river flow generally increases later in the season, exposing the 2005 and 2007 cohorts to greater stream flows.

The mean swimming speeds of Cultus sockeye salmon smolts of 0.5-1.8 body lengths per second in both freshwater and marine environments is comparable to results from acoustic tracking studies on other salmonids. Freshwater and marine swimming speeds of steelhead trout in southern British Columbia waters were found to be between 0.5-2.0 body lengths per second (Welch et al. 2004; Melnychuk et al. 2007). In western Atlantic waters, Thorstad et al. (2007) recorded swimming speeds of 0.53 and 0.56 for wild and hatchery Atlantic post-smolts respectively (but only 0.06 body lengths per second for brown trout post-smolts) in a Norwegian fjord.

6.4.3 The POST Array

Our work represents the first direct estimates of survival and movement rates of sockeye salmon (*Oncorhynchus nerka*) smolts during the freshwater and early marine phases of the migration period, and demonstrates the utility of large-scale telemetry arrays for monitoring smolt migrations over repeated years. Acoustic technology, properly implemented, provides an essentially seamless monitoring system covering both freshwater and marine environments. It is thus possible to study salmon smolt migrations along the full length of their migration along the continental shelf as they move out of their natal stream. The POST array provides a level of resolution not previously available in marine studies, and allows us to specify the speed, directionality, migration routes, and survival of tagged smolts with substantial precision even when using modest numbers of tagged smolts. Pinpointing areas of potentially elevated levels of mortality is of particular relevance to endangered stocks of salmon, as this can help direct research towards the most relevant parts of the life history.

The results from this study demonstrate that it is technically feasible to measure survival in both large river and coastal marine environments. Further miniaturization of the tags now allows smolts in the 100mm range to be tagged, but at a substantially increased cost for operating an array of equivalent detection efficiency and thus statistical precision. However, a key point is that technical advances will thus likely allow future array designs to be extended to smaller fish and potentially resolve some of the limitations associated with only tagging larger smolts.

In summary, our study provides useful new data on Cultus Lake sockeye salmon smolt migration and mortality during an important life history period when the transition occurs from freshwater to marine life. The development of baseline data for salmon stocks can assist with managing them under climate change, not just by monitoring changes in survival but by also allowing the formal testing of experimental hypotheses about the factors controlling salmon abundance. The POST array concept also provides a useful demonstration of the potential of continental-scale acoustic arrays for simultaneously monitoring a wide range of marine species for conservation and management. Such a concept is now being developed worldwide in the global initiative of the Ocean Tracking Network which is establishing acoustic lines and arrays at strategic locations around the world (O'Dor et al. 2007). Developments like those reported here will help to incorporate biological observations into broader global ocean observing systems.

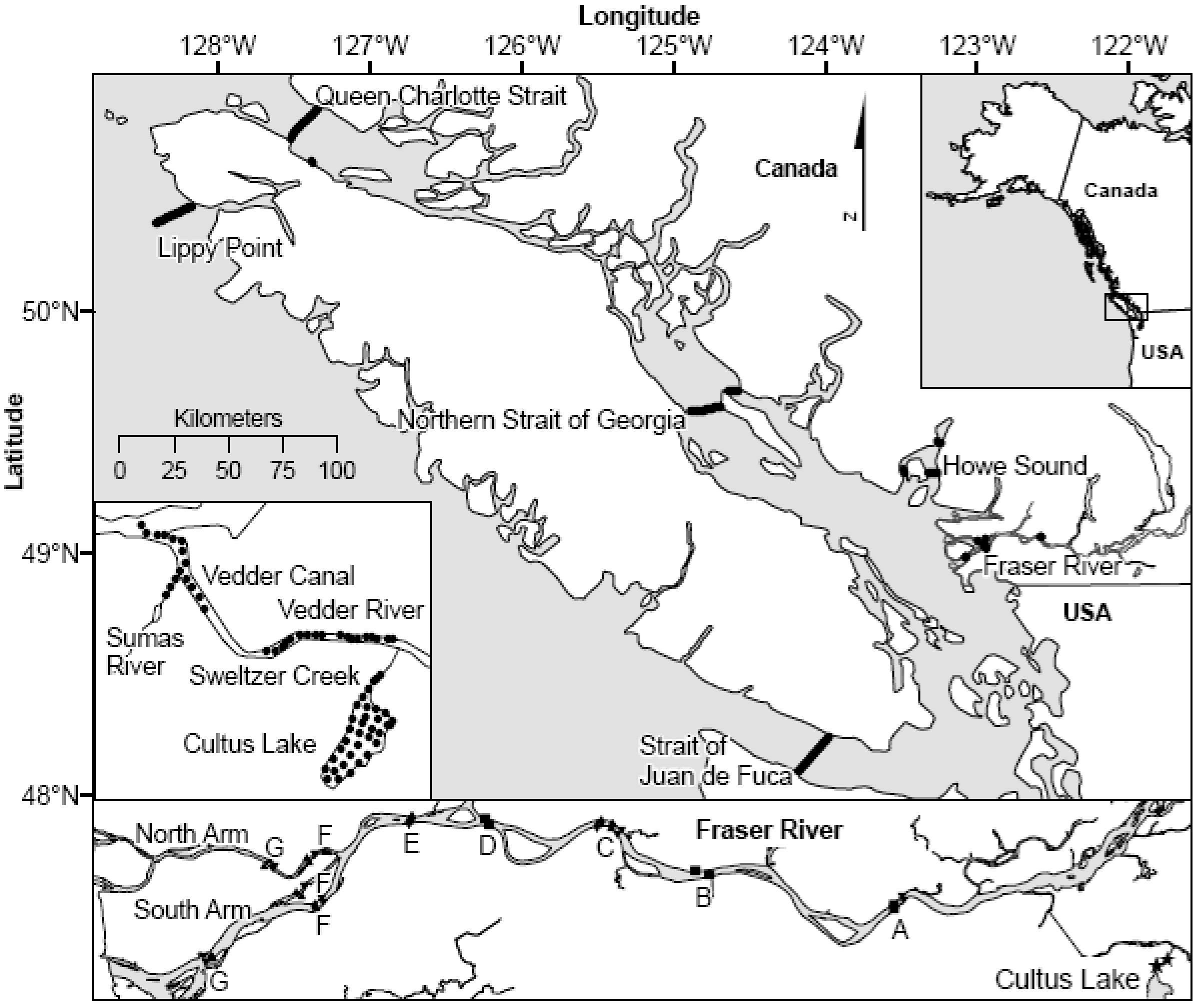

Figure 6.1. The southern British Columbia components of the POST array. The black lines indicate POST sub-arrays, which are formed of a linearly arranged sequence of independent receivers. Inserts provide details of the POST lines within Howe Sound and Cultus Lake and its outlets, along with mobile sampling locations in those areas (dots). The bottom panel shows the array deployment within the Fraser River over the four years of the study. Sub-array locations in the Fraser River differed between years and are identified by symbols and letters. Squares (A,B,D) = 2004, diamonds (C,E) = 2005, triangles (C,F,G) = 2006, inverted triangles (A,C,F,G) = 2007.

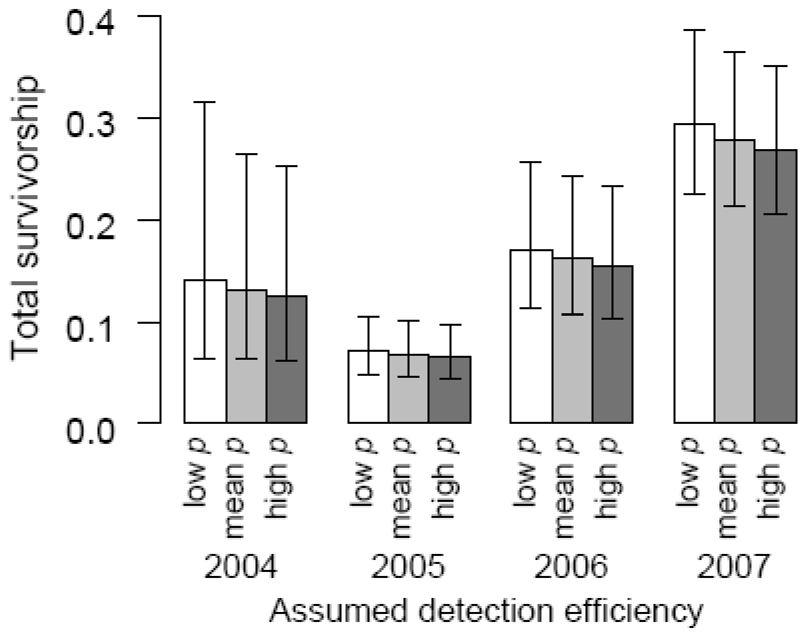

Figure 6.2. Survivorship estimates from release to exit from the Strait of Georgia system for different assumed detection probabilities on the final QCS and JDF lines. The mean, lower 95%, and upper 95% confidence limits of NSOG detection probabilities, *p*, are assumed for QCS detection probabilities. Error bars show 95% confidence limits on resulting survivorship estimates.

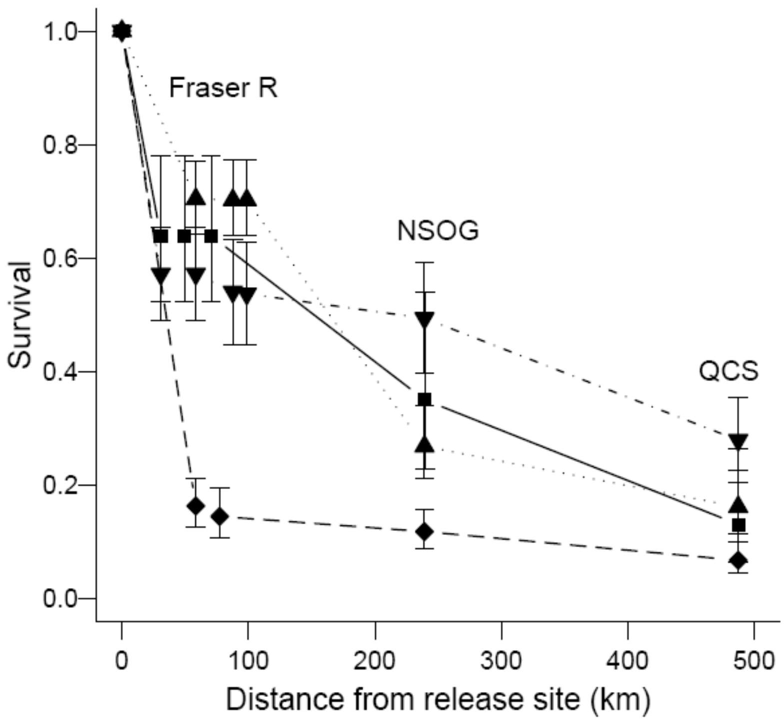

Figure 6.3. Survivorship relative to cumulative distance migrated for acoustically tagged Cultus Lake sockeye. Vertical bars represent 95% confidence intervals. (2004: ■; 2005: ◆; 2006: ▲, 2007: ▼).

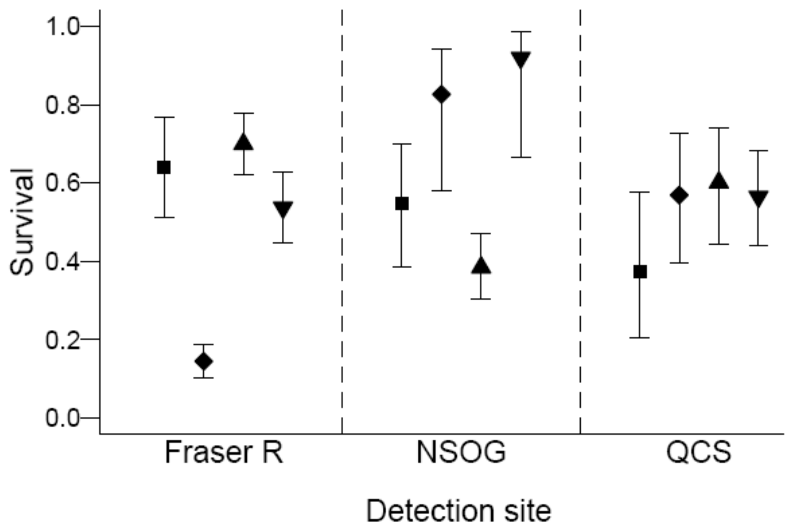

Figure 6.4. Segment-specific survival estimates for acoustically tagged Cultus Lake sockeye salmon from release to the lower Fraser River, lower Fraser River to NSOG, and NSOG to QCS, 2004-07. Vertical bars represent 95% confidence intervals. (2004: ■; 2005: ◆; 2006: ▲, 2007: ▼).

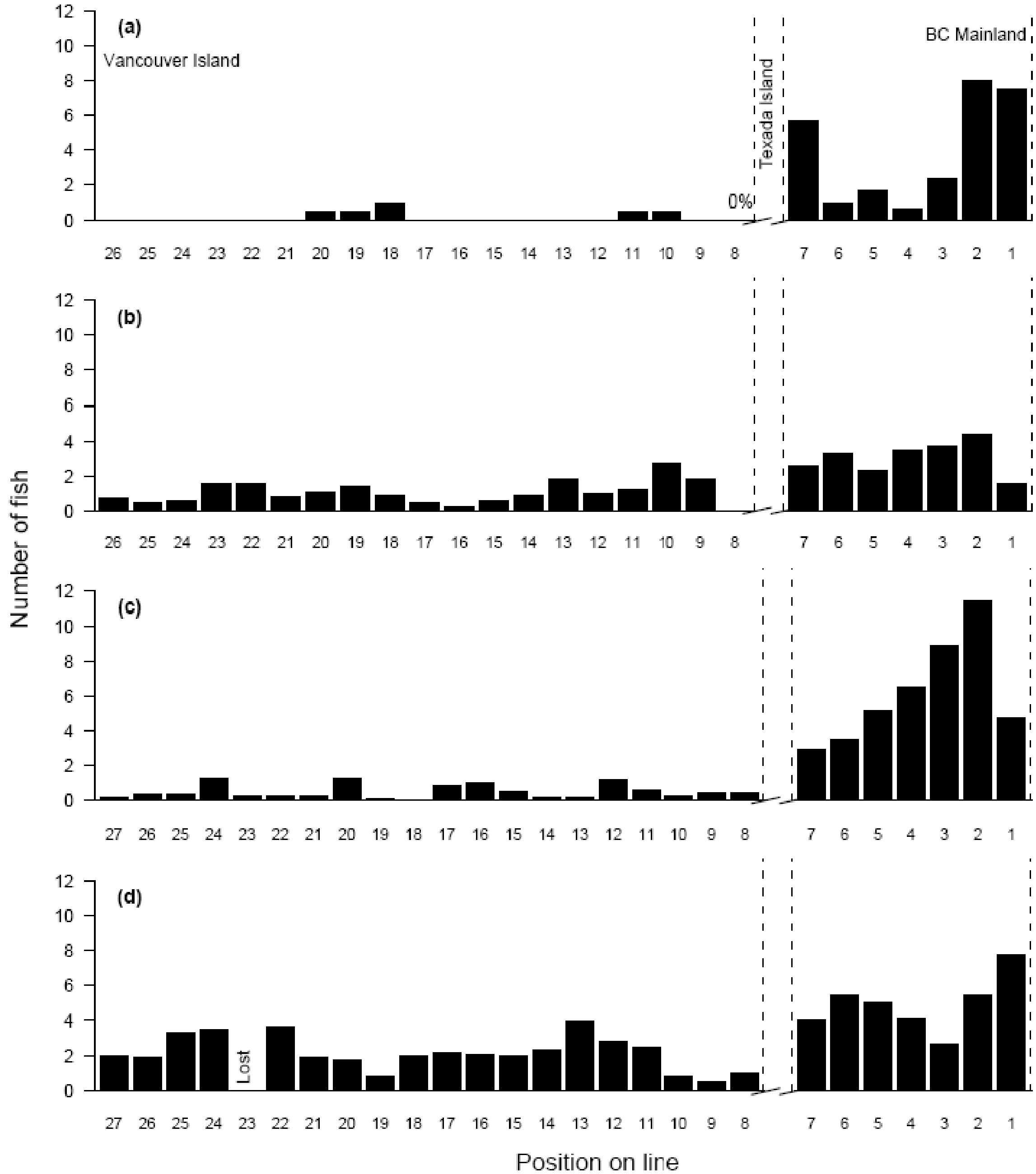

Figure 6.5. Distribution of migrating acoustically tagged Cultus Lake sockeye salmon on the Northern Strait of Georgia lines in 2004 (a), 2005 (b), 2006 (c), and 2007 (d). Each numbered bar represents a receiver in the line. If a fish was heard on multiple receivers, that individual's detection was allocated equally across all receivers on which it was detected. The 0% above receiver 8 in 2004 indicates that this receiver was not operational during the time that the fish were crossing the line. Receiver 23 in 2007 was not recovered.

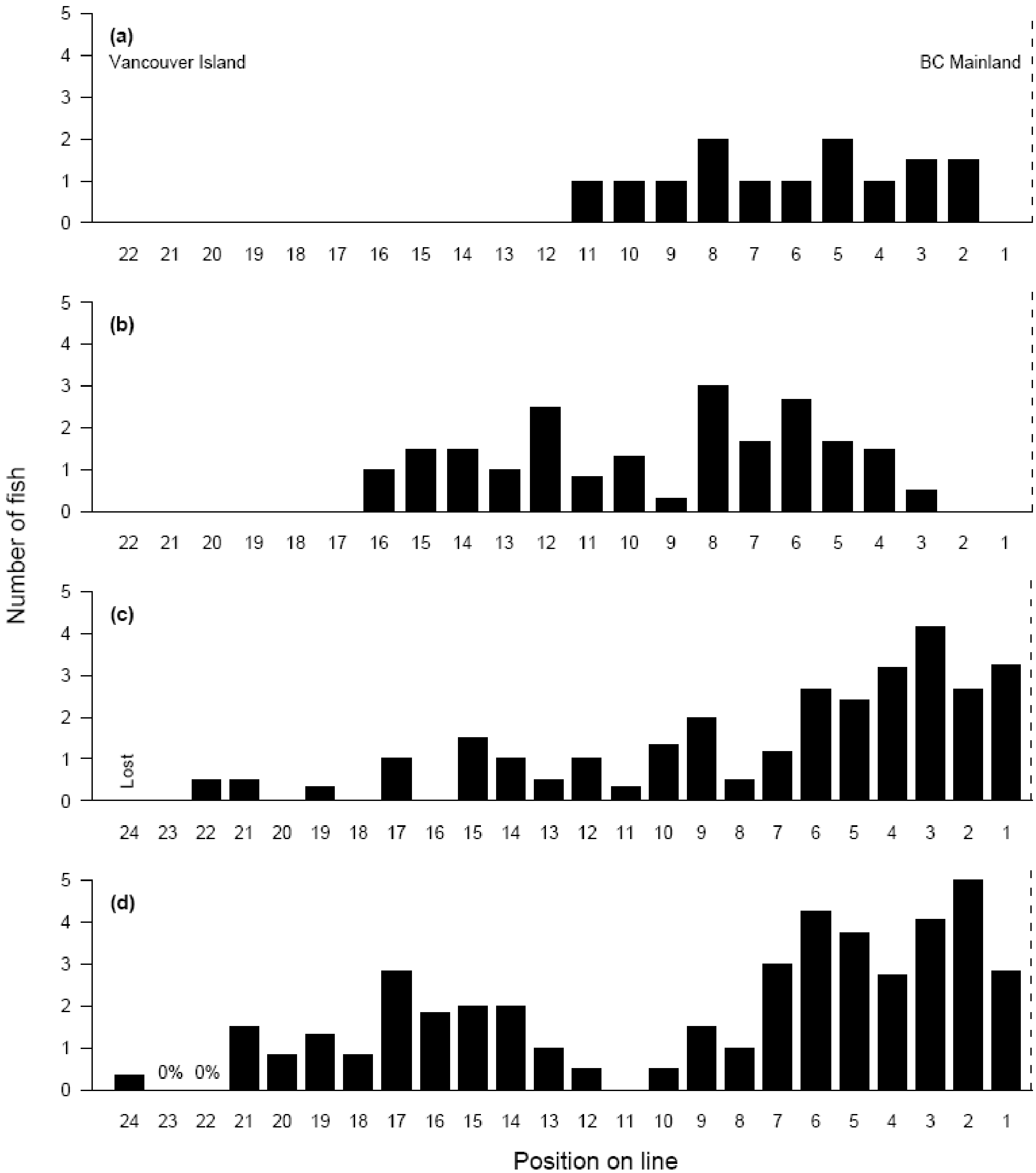

Figure 6.6. Distribution of migrating acoustically tagged Cultus Lake sockeye salmon on the Queen Charlotte Strait line in 2004 (a), 2005 (b), 2006 (c), and 2007 (d). Each numbered bar represents a receiver in the line. If a fish was detected on multiple receivers that detection was allocated across all receivers on which it was detected. The 0% above receivers 22 and 23 in 2007 indicates that these receivers were not operational during the time that the fish were crossing the line. Receiver 24 in 2006 was not recovered.

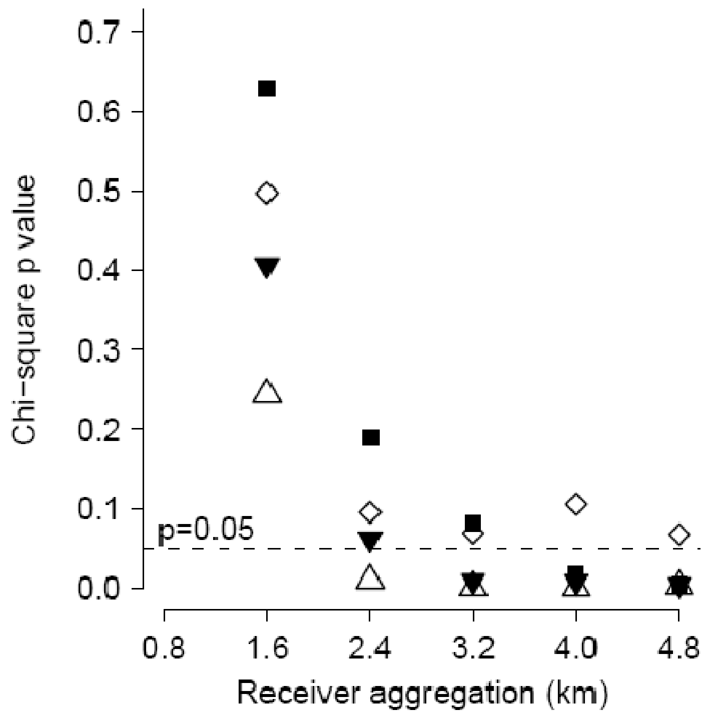

Figure 6.7. Significance of a series of χ^2 goodness of fit tests obtained by grouping fish detected on neighbouring receivers. For spatial aggregations >3 km (i.e., aggregating the data from four or more adjacent receivers) statistical support for significant spatial pattern on the QCS sub-array is evident. (2004: ■; 2005: ◆; 2006: ▲, 2007: ▼).

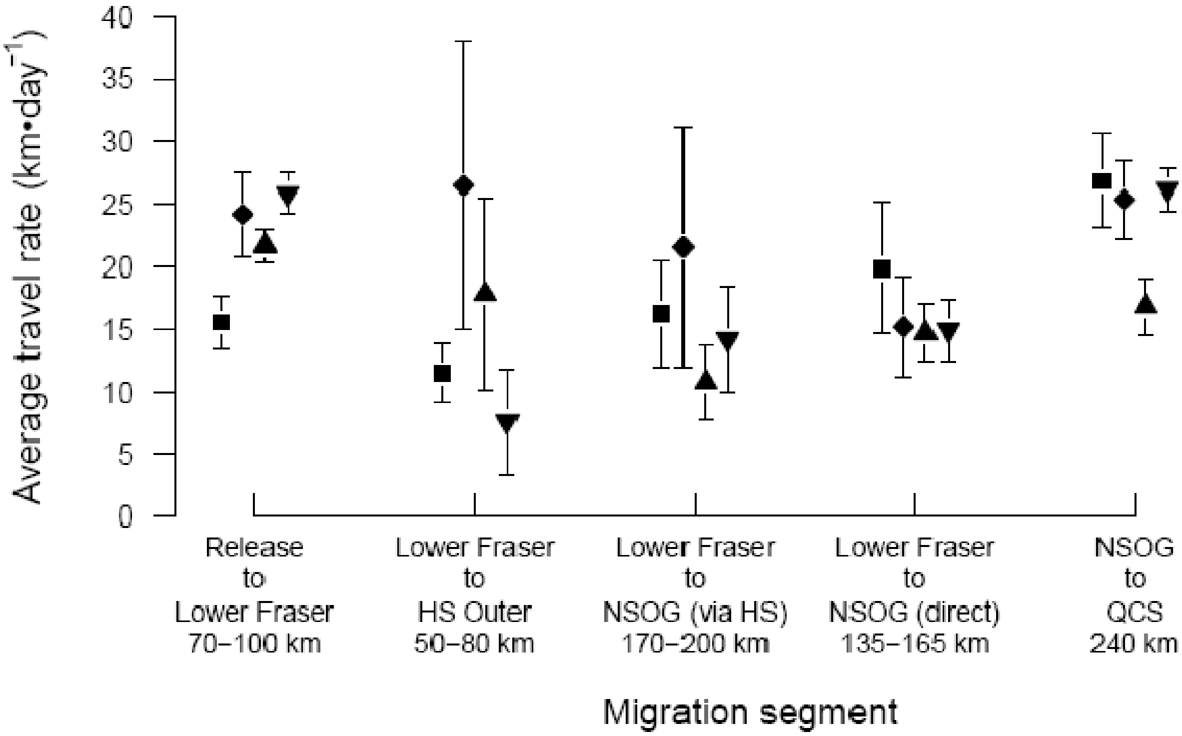

Figure 6.8**.** Average travel rates for different sections of the migration route. Vertical bars represent 95% confidence intervals. (2004: ■; 2005: ◆; 2006: ▲, 2007: ▼).

Table 6.1. Summary of Cultus Lake sockeye salmon smolts tagged and released [1].

Year	Tag Type2	Release Date (UTC)	Number	Fork Length (mm)	
				Average	SD
2004	V9-6L	04/May/2004 03:30	100	178	13
2005	V9-1L	09/Jun/2005 03:00	92	172	5
	V9-2L	09/Jun/2005 03:00	188	188	8
	V9-6L	09/Jun/2005 03:00	96	159	5
2006	V9-1L	21/Apr/2006 01:00	200	178	9
2007	V9-1L	16/May/2007 22:00	200	189	8

[1]Detailed data is available in the POST database (POST 2008).
[2]Tag dimensions: V9-6L tags are 21 mm x 9 mm diameter and weigh 2.9 g in air;, V9-1L tags are 24 x 9 mm diameter and weigh 3.6 g in air; and V9-2L tags are 29 mm x 9 mm diameter and weigh 4.7 g in air.

Table 6.2. Model selection results for recaptures-only survival probability estimates[1].

Model	Number of parameters	QAICc	ΔQAICc	Akaike weight
$\phi_{(time*year+body)}p_{(time*year)}$[2]	43	2284.5	0.0	0.52
$\phi_{(time*year)}p_{(time*year)}$	42	2284.6	0.1	0.48
$\phi_{(TravTime+habitat*year+body)}p_{(time*year)}$[2,3]	28	2309.1	24.6	0.00
$\phi_{(TravTime+habitat*year)}p_{(time*year)}$	29	2309.3	24.8	0.00
$\phi_{(distance+habitat*year+body)}p_{(time*year)}$	28	2394.2	109.8	0.00
$\phi_{(distance+habitat*year)}p_{(time*year)}$	29	2394.2	109.8	0.00
$\phi_{(TravTime+year)}p_{(time*year)}$	24	2441.7	157.2	0.00
$\phi_{(distance+year)}p_{(time*year)}$	24	2465.1	180.6	0.00

1 AIC values are adjusted for small sample sizes and extra-binomial variation with $\hat{c}$ =1.3325.
2 "time" in models refers to segment- or line- specific probabilities, whereas TravTime is a group covariate and refers to average travel time of the population in a particular segment of the migration.
3 "habitat" in models means that the intercept between survival and either distance or travel time was allowed to differ in river and ocean segments. Models with an interaction term added so the slope was also allowed to differ (TravTime*habitat and distance*habitat) were also tested, but these reduced AIC by less than 2, so the incorporation of the extra parameter was not supported.

Table 6.3. Migratory behaviour categories for Cultus Lake sockeye salmon in 2004-2007. The first number in each column is the number of fish detected. The number in parentheses indicates the percentage of fish detected in relation to all fish released that year. Milling is defined as either being detected for >24 h on a line or (on Fraser River lines) being detected downstream, upstream, and then downstream again.

Migration Behavior	2004	2005	2006	2007
North (direct)	21(21.0)	37 (9.8)	40 (20)	69 (34.5)
North through HSD	9 (9.0)	6 (1.6)	13 (6.5)	8 (4.0)
South	0	2 (0.5)	0	6 (3.0)
Milling on NSOG	0	5 (1.3)	5 (2.5)	5 (2.5)
Milling on QCS				1 (0.5)
Milling on JDF		1 (0.27)		1 (0.5)
Milling on Fraser	0	0	10 (5.0)*	1 (0.5)
Residualization in Cultus Lake	Not surveyed	17 (4.5)	Not surveyed	12 (6.0)

* Five of these 10 fish were detected downstream, upstream then downstream again. Three of these five were subsequently heard on ocean lines and two were not; we suspect these two tags may have been in seals. The remaining five fish were heard on a Fraser River line for >24 h (3 fish) or moved between sub-arrays within stations F or G (Fig. 1), thereby requiring upstream travel (2 fish).

Table 6.4. Residualization and initial downstream migration surveys of Cultus Lake and the rivers that connect it to the Fraser River. Sweltzer Creek was not surveyed in 2005 and the Fraser River was not surveyed in 2007 (see methods).

Detection Year	Tag Year	Cultus Lake	Sweltzer Creek	Vedder River	Lower Vedder Canal	Lower Sumas River	Fraser River
Mobile surveys							
2005	2005	13	NA	0	0	2	0
2007	2005	6	0	0	0	0	NA
	2007	NA	NA	NA	NA	NA	NA
Number of 2005 tags heard in both years							
	NA	5	NA	0	0	0	NA
Additional tags heard in DFO survey (not heard in either mobile survey)							
2007	2005	7	NA	NA	NA	NA	NA
	2007	12	NA	NA	NA	NA	NA

NA – Not applicable.

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7 General Conclusions

Early marine survival data are essential for assessing the population dynamics of threatened salmonids and for evaluating recovery strategies. This thesis presents in-river and early marine survival estimates for seaward migrating hatchery salmon from the Columbia and Fraser rivers, obtained by implanting transmitters into the smolts and tracking their movements with a large scale acoustic telemetry array.

7.1 Transmitters had little effect on migrating salmon smolts

For survival estimates to be representative of the population under study, tag effects must be minimal. I conducted captive tag effects studies to quantify tag-induced mortality, growth, and tag loss of salmon smolts implanted with 9 mm or 7 mm acoustic tags. In general, tag effects were minimal for smolts implanted with 7 mm transmitters, but smolts tagged with 9 mm transmitters showed effects over the longer term. For both transmitter types, short term (<30 d) survival and tag retention was high and did not differ from the control group. Medium term (30-90 d) survival and tag retention was high for smolts implanted with a 7 mm tag, but smolts implanted with a 9mm tag began to show signs of tag effects. In particular, the Yakima population of spring Chinook salmon used in the study began to lose transmitters at a higher rate towards the end of the study; it is unclear whether this was attributable to the ca. 4°C temperature difference between the two holding sites or to innate differences in the Yakima River stock. Yakima fish exhibited noticeably thinner, softer skin during tagging and when fish were inspected six weeks later, it was noted that sutures were tearing through the thin skin allowing the transmitter to potentially exit from the wound. Growth rates following surgery were depressed for smolts tagged with both transmitter types compared to the control group, which was likely due to the cumulative effect of surgery and the tag. There was evidence that growth rates returned to that of the control group during the second month of the study.

Similar results have been obtained from other acoustic tag effects studies involving Pacific salmon. Chittenden et al. (2009) implanted coho salmon smolts >125 mm FL with the same 7 mm tags used in Chapter 2 of this thesis and found 100% survival and retention of tags for the duration of the study (300 days). Welch et al. (2007) found that steelhead trout >130 mm FL tagged with a 1.4 g dummy acoustic tag retained their tags for 39 days before the first tag was extruded and that survival of this group was 90% after 29 weeks; tag retention and survival of 140 mm FL steelhead trout was higher. The effect of tags on growth rate was similar for fall Chinook salmon; an initial period of impaired growth followed by growth at the same rate as control fish was observed in smolts ranging from 114-159 mm FL and implanted with 1.0 g radio transmitters (Adams et al. 1998).

To determine how tag loss or tag-induced mortality might affect survival estimates of fish migrating in the river, I did a simple calculation to correct estimated survival for combined tag loss and mortality observed in captivity. Since short term tag loss and mortality was minimal, correction had little or no impact on survival estimates of smolts migrating from the Columbia River to the Lippy Point detection site (NW Vancouver Island), located some 1,500 km from the release site. A field study comparing survival of salmon smolts tagged with passive integrated transponder (PIT) tags or 1.5 g acoustic tags migrating through a short (35 km) reach of the upper Columbia River concluded that survival was not significantly different for yearling Chinook salmon smolts (Steig et al. 2005), which is consistent with short term captive results and "corrected' field-based survival estimates reported in this thesis (i.e., acoustic tags did not affect short term survival when compared to PIT tags). Short term field studies are useful for assessing comparative survival, however, mark-detection methods in the field can not differentiate between tag loss or tag induced mortality, and may require PIT tags sample sizes up to two orders of magnitude greater than acoustic tags.

Although captive studies do not simulate the natural environment, they apparently provide a reasonable assessment of tag effects when those effects are not too large. Further, in-river survival estimates presented in this thesis (for Columbia River salmon) are consistent with in-river survival estimates reported in the literature based on less intrusive marking methods (CWT and PIT tags), except in 2007 (as a result the data were not interpreted for the year).

7.2 Marine survival co-varied with predicted ocean conditions

For both species studied there was an improvement in marine survival that corresponded to predicted survival conditions based on ocean indicators. Early marine survival (Willapa Bay to Lippy Point) of in-river migrating Columbia River spring Chinook salmon was 3-5 times higher in 2008 when compared to early marine survival in 2006. The U.S. National Oceanographic and Atmospheric Administration (NOAA) forecasts general survival conditions for Chinook and coho salmon entering the ocean (good, intermediate, or poor) each year. In 2006, ocean conditions were predicted to be poor to intermediate for salmon survival, and in 2008 ocean indicators improved to intermediate but mostly good

Cultus Lake sockeye salmon were studied from 2004-7. Early marine survival through Johnstone Strait (from the Northern Strait of Georgia to Queen Charlotte Strait) was consistently high in 2005-7, ranging from 57-60%. This was 1.5-1.6 times higher than was observed in 2004. The Canadian Department of Fisheries and Ocean (DFO) uses the same methodology as NOAA for predicting Fraser River sockeye salmon survival. In 2004 and 2005 ocean conditions were poor, but there was a marked improvement in 2006 and 2007. These predictions are consistent with survival estimates, except for 2005 when ocean conditions were predicted to be poor but survival of Cultus Lake sockeye salmon was high. (In 2005, more than 80% of smolts died in the Fraser River, possibly due to late release, therefore the ocean survival estimate is based on few fish.)

7.3 Delayed mortality hypotheses challenged with early marine survival data

Two important hypotheses regarding delayed mortality of Columbia River spring Chinook salmon were tested in this thesis (Chapters 3, 4 and 5). Hydrosystem- induced delayed mortality was hypothesized to occur because survival from seaward migration until adult return is substantially lower for Snake River spring Chinook salmon relative to mainstem Columbia River populations, and smolts from the Snake River migrate through four additional dams. Estimates of early marine survival for a Snake River population and a mainstem Columbia River population of spring Chinook salmon demonstrated that the Snake River population did not have lower survival below the hydrosystem and well into the ocean, indicating that some other factor besides delayed mortality is likely responsible for differences between these stocks in overall marine survival rate.

Transportation-induced differential delayed mortality was hypothesized to occur because transported Snake River spring Chinook salmon have not consistently returned (2-3 years later) in higher numbers than their in-river counterparts despite being transported around the dams. Survival from below the final dam (Bonneville Dam) to Willapa Bay (estuary and plume) in 2006 and 2008 demonstrated an initial survival benefit for in-river smolts. This differential mortality may be attributed to stress from the transportation process; however, the estimated mortality immediately after release from the transportation barge was equivalent to the immediate post-release mortality for the in-river smolts after release from the hatchery. Therefore, it would be interesting to determine if stress-induced mortality after release from a hatchery is similar to stress-induced mortality after release from a barge, or whether the elevated mortality is simply to be expected as a result of releasing naïve captive animals into the wild, irrespective of the release location. Early marine survival from Willapa Bay to Lippy Point was significantly higher for transported smolts in 2006 and similar to in-river smolts in 2008. Thus, a delayed effect was not observed during the ~27 day, 485 km journey.

7.4 Early marine survival data promote hypothesis testing

Marine survival is generally estimated by the proportion of adults that return to natal rivers to spawn (e.g.,Buchanan et al. 2007) or from tag returns from fisherman (e.g., Kallio-Nyberg et al. 2009) or collected by research vessels (e.g., Farley et al. 2007); however a direct estimate of early marine survival was not available for testing hypotheses regarding juvenile survival. The availability of a tool for estimating early marine survival opens the doors to testing previously intractable hypotheses regarding juvenile survival in the ocean. In the Columbia River basin, salmon survival and hydro power are paramount. The ongoing litigation over the Federal Columbia Power System Biological Opinion is partly due to lack of knowledge on the longer term effects of the hydropower system on juvenile salmon survival. A number of post-Bonneville survival questions can be answered about how to maximize salmon survival, such as which spill regimes at the dams result in the highest in-river and early marine survival? When is the best time to transport smolts, i.e., should transportation match the time of ocean arrival of in-river smolts? Does differential mortality occur in transported smolts as a result of small size at ocean entry? Should smolts only be transported when ocean condition are deemed “good”?

Other general questions regarding early marine survival and behaviour of salmonids can also be addressed with the POST technology: do hatchery smolts have the same early marine survival as wild smolts? Are their distributions across the continental shelf and their migration rates similar? Do they migrate to the same places and have access to the same food sources? How similar is survival for the same species salmon migrating from different rivers? Is there a longitudinal gradient in early marine survival of juvenile salmon originating from different rivers? Does habitat restoration translate into higher early marine survival?

Several studies have alluded to the need for early marine survival estimates to address hypotheses regarding declining or fluctuating salmon populations. In addition to concerns over Columbia River salmon survival (e.g., Scheuerell and Williams 2005), survival of sockeye salmon in the Fraser River has become a major concern in recent years (Cooke et al. 2004). The disastrous decline in returning late run sockeye salmon witnessed in 2009 is particularly alarming given the crash and lack of rebuilding of BC’s Rivers Inlet sockeye salmon population despite a moratorium on fishing since 1996 (McKinnell et al. 2001; Walters et al. 1993). Although many hypotheses regarding the demise of Rivers Inlet sockeye salmon have been explored, poor marine survival has been implicated as one of the main causes (McKinnell et al. 2001). Early marine survival data for Fraser River sockeye salmon may aid in determining factors causing the decline.

7.5 Tag size and other study limitations

There are several limitations to the studies presented in this thesis, most of which are related to tag size. While the size of acoustic tags has decreased significantly over the last decade, it was still necessary to tag only the larger individuals. Columbia River salmon smolts were tagged with 9 mm tags in 2006 which meant that smolts had to be larger than 140 mm FL. In 2008 the tag was smaller (7 mm), and thus the lower limit was 130 mm FL. The fork length of spring Chinook smolts typically ranges between 100-160 mm FL, therefore we were limited to tagging the upper end of the size distribution, particularly in 2006.

To assure that there were ample smolts of the appropriate size it was necessary to transfer smolts from Dworshak hatchery to Kooskia hatchery where the water is warmer and smolt growth rate is higher. Therefore, a consequence of transferring smolts to the hatchery with warmer water was that smolts were released ~60 km upstream of Dworshak hatchery. Also, smolts were held until they had reached a taggable size, and thus they were not released with the other hatchery fish. Another consequence of tag size was that release timing was several weeks later than the typical release date.

The situation was similar for Cultus Lake sockeye salmon. Tagged smolts ranged from 159-189 mm FL which was significantly larger than a typical hatchery reared sockeye salmon smolt. Tagged sockeye salmon smolts were however released in the same location and at the same time as the other hatchery smolts, with the exception of 2005 when smolts were released ~1 month later and 500 m downstream of the typical release site.

For each species studied there was one year of data that was essentially inconclusive due to unusually high post-release mortality. This elevated mortality was a consequence of tagging logistics at all hatcheries during the year when high post-release mortality occurred. In 2005, an unfortunate power outage killed nearly all of the tagged Cultus Lake sockeye salmon smolts prior to release (and those that survived were almost certainly oxygen deprived). Fortunately, other fish were available for tagging; however the late release of this group was associated with an 85% loss to the Fraser River mouth (but subsequently similar ocean survival); it is not possible from the available data to determine whether it was the anomalously late release that caused the mortality, but this is certainly a credible possibility. In 2007, at both Prosser hatchery and Kooskia hatchery, smolts were transferred several times into different tanks prior to and during tagging, due to lack of tank availability and/or size grading (size sorting into release groups and tag study groups required >6 tanks). Size grading also required that the fish be sedated, therefore some fish were lightly anesthetised several times prior to surgery. Likely as a result of this added handling and sedation, immediate post-release mortality (i.e., before reaching any of the downstream detection arrays) for both groups was >70% in 2007.

7.6 Future research

Acoustic tags have decreased in size since the completion of the field work portion of this thesis. As outlined above, transmitter size creates limitations. With a smaller transmitter, future research will focus on tagging the complete size distribution of spring Chinook salmon from the Columbia River, as well as tagging additional hatchery populations (both upstream and downstream) and wild fish to further investigate early marine survival and delayed effects of in-river migration through hydropower dams or from transportation. The basic approach can also be extended to fall (or subyearling) spring Chinook salmon which are also the subject of much debate in the Columbia River basin. Fall Chinook salmon migrate at a smaller size, and may utilize the estuary before migrating to sea (Groot and Margolis 1991); therefore they present more of a challenge for estimating survival. However, with smaller tag size comes lower detection efficiencies for the array, raising interesting questions concerning the appropriate balance between economic cost and scientific performance for future generations of telemetry arrays.

Cultus Lake sockeye salmon recovery efforts are underway; however no continuing effort is being made to estimate juvenile survival once smolts migrate from the lake. The removal of predators and invasive aquatic plants will likely aid in improving freshwater survival. By monitoring the seaward migration and early marine survival of smolts through the Georgia basin, the effectiveness of freshwater recovery efforts, such as predator control in the lake (Tovey et al. 2007) can be separated from effects of changes in early ocean survival. Further, the recent decline in returning late run Fraser River sockeye salmon may have serious consequences for the future of Cultus Lake sockeye, and continuous monitoring of juvenile and adult fish in the ocean should be a priority.

Over the past two decades it has become clear that large scale climate regimes have a significant impact on salmon survival and productivity (e.g., Beamish et al. 1997; Beamish et al. 1999; Bisbal and Mcconnaha 1998; Botsford 1997; Mueter et al. 2002; Welch et al. 1998). Changes in ocean conditions are monitored seasonally; however, in the future, oceanographic data will likely be collected contemporaneously with fish migration data by sensors installed on individual acoustic receivers nodes deployed on the continental shelf. By deploying a suite of sensors it may be possible to identify the oceanographic conditions experienced by a species, population, release group, or even an individual fish as it migrates northward.

7.7 Applications of early marine survival data

Probably the most important application of early marine survival data is to determine where and when mortality occurs, and to incorporate this information into recovery, fishery and ecosystem management plans to ensure long-term sustainability. Forecasting adult returns could be greatly enhanced by early marine survival data, particularly if most of the overall marine mortality occurs within the first month after ocean entry. NOAA and DFO monitor numerous ocean indicators to predict general survival conditions for juvenile salmon. Direct estimates of survival measured in this thesis corroborate their predictions and therefore marine survival data can also be used to ground truth or verify prediction models. Lastly, marine survival data may help resolve disagreements over causes of mortality of Columbia River spring Chinook salmon (Kareiva et al. 2000), not only by comparing survival estimates after ocean entry, but also by incorporating these data into the population dynamics models that have previously assumed there to be a common year effect regarding ocean mortality.

7.8 References

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Appendix A. Travel Time Tables

Table A.1. Segment specific travel time of Dworshak and Yakima spring Chinook salmon smolts (mean days (st. dev.)). Dworshak fish were released at Kooskia Hatchery (870 km from Columbia River mouth); Yakima fish were released at the Chandler Juvenile Monitoring Facility (615 km from Columbia River mouth). NA- not applicable. Parentheses below detection sites indicate segment distance (km). (a) calculated from only one individual; *applicable to Dworshak smolts; ‡ applicable to Yakima smolts.

2006		Snake River	Lower Columbia River			Pacific Ocean		
Release Date	Population	Release-Lake Bryan (190)	Lake Bryan* /Release‡-Lake Wallula (179*/113‡)	Lake Wallula-Lake Celilo (162)	Lake Celilo-McGowan's Channel (116)	McGowan's Channel-Willapa Bay (264)	Willapa Bay-Lippy Point (485)	Lippy Point-Grave's Harbor (1105)
1-May	Dworshak	8.0 (4.0)	6.9 (2)	3.4 (1.3)	1.4 (0.3)	5.3 (3.1)	no data	no data
8-May	Dworshak	4.9 (1.7)	5.9 (1.5)	2.8 (0.5)	1.5 (0.5)	4.8 (3.2)	29.6 (3.9)	38.4 [(a)]
	Pooled Mean	6.4 (3.4)	6.4 (1.8)	3.2 (1.1)	1.4 (0.4)	5.1 (3.1)	29.6 (3.9)	38.4 [(a)]
30-May	Yakima	NA	1.4 (1.0)	3.4 (1.3)	1.4 (0.2)	6.0 (1.7)	32.1 (1.6)	no data
6-Jun	Yakima	NA	1.6 (3.5)	2.4 (0.7)	1.2 (0.2)	4.6 (7.1)	no data	no data
	Pooled Mean	NA	1.5 (2.6)	2.9 (1.1)	1.3 (0.2)	5.0 (6.3)	32.1 (1.6)	no data

Table A.1 cont. Segment specific travel time of Dworshak and Yakima spring Chinook salmon smolts (mean days (st. dev.)).

2007		Snake River	Lower Columbia River				Pacific Ocean		
Release Date	Population	Release-Lake Bryan (190)	Lake Bryan* /Release‡-Lake Wallula (179*/113‡)	Lake Wallula-Lake Celilo (162)	Lake Celilo-McGowan's Channel (116)	McGowan's Channel-Astoria Bridge (201)	Astoria Bridge-Willapa Bay (63)	Willapa Bay-Lippy Point (485)	Lippy Point-Grave's Harbor (1105)
1-May	Dworshak	9.8 (5.1)	8.9 (3.2)	3.6 (1.1)	1.6 (0.3)	2.4 (0.3)	16.2 (12.2)	no data	no data
14-May	Dworshak	7.6 (3.6)	10.3 (3.8)	4.0 (1.9)	1.6 (0.2)	2.6 (0.4)	12.3 (7.0)	no data	no data
	Pooled Mean	8.6 (4.4)	9.6 (3.6)	3.8 (1.6)	1.6 (0.2)	2.5 (0.4)	14.3 (9.5)	no data	no data
28-May	Yakima	NA	1.3 (0.2)	4.3 (2.0)	1.7 (1.0)	2.5 (0.3)	3.4 (1.3)	no data	no data
3-Jun	Yakima	NA	1.5 (0.8)	4.9 (1.7)	1.6 (0.3)	2.7 (0.7)	8.3 (6.0)	no data	no data
	Pooled Mean	NA	1.4 (0.5)	4.5 (1.9)	1.7 (0.9)	2.5 (0.4)	4.8 (3.9)	no data	no data

2008		Snake River	Lower Columbia River				Pacific Ocean		
Release Date	Population	Release-Lake Bryan (190)	Lake Bryan* /Release‡-Lake Wallula (179*/113‡)	Lake Wallula-Lake Celilo (162)	Lake Celilo-McGowan's Channel (116)	McGowan's Channel-Astoria Bridge (201)	Astoria Bridge-Willapa Bay (63)	Willapa Bay-Lippy Point (485)	Lippy Point-Grave's Harbor (1105)
25-Apr	Dworshak	12.4 (6.7)	10.2 (4.7)	3.2 (0.9)	1.7 (0.2)	2.5 (0.4)	8.7 (6.1)	31.6 (5.0)	no data
2-May	Dworshak	11.5 (6.4)	8.4 (3.4)	2.8 (0.8)	1.6 (0.2)	2.7 (0.5)	6.5 (3.8)	21.7 (0.3)	no data
	Pooled Mean	11.9 (6.5)	9.3 (4.2)	3.0 (0.9)	1.7 (0.2)	2.6 (0.4)	8.0 (5.5)	28.3 (6.4)	no data
15-May	Yakima	NA	1.5 (0.3)	3.6 (1.1)	3.6 (2.1)	2.5 (0.3)	10.1 (10.8)	29.5 (6.1)	no data
21-May	Yakima	NA	1.5 (0.7)	2.7 (1.5)	1.8 (0.2)	2.4 (0.2)	12.4 (15.6)	42.9 (12.0)	no data
	Pooled Mean	NA	1.5 (0.6)	3.0 (1.4)	2.2 (1.1)	2.5 (0.2)	11.3 (13.3)	34.9 (10.8)	no data

Table A.2. Cumulative travel time of Dworshak and Yakima spring Chinook salmon smolts to detection sites (mean days (st. dev.)). Dworshak fish were released at Kooskia Hatchery (870 km from Columbia River mouth); Yakima fish were released at the Chandler Juvenile Monitoring Facility (615 km from Columbia River mouth). NA- not applicable. Parentheses below detection sites indicated cumulative distance (km) from Dworshak and Yakima release sites, respectively. (a) Only one ID code detected.

2006		Snake River	Lower Columbia River				Pacific Ocean		
Release Date	Population	Lake Bryan (190/NA)	Lake Wallula (369/113)	Lake Celilo (531/275)	McGowan's Channel (647/391)		Willapa Bay (911/655)	Lippy Point (1395/1140)	Grave's Harbor (2501/2245)
1-May	Dworshak	8.0 (4.0)	15.5 (3.8)	18.2 (3.6)	19.6 (4.4)		26.2 (4.8)	57.9 [(a)]	94.5 [(a)]
8-May	Dworshak	4.9 (1.6)	11.0 (2.3)	13.5 (2.3)	14.1 (3.0)		19.0 (4.2)	52.9 (1.8)	90.2 [(a)]
	Pooled Mean	6.4 (3.4)	13.1 (3.8)	16.0 (3.8)	17.1 (4.7)		22.4 (5.8)	54.2 (2.9)	92.3 (3.0)
30-May	Yakima	NA	1.4 (1.0)	5.0 (1.9)	6.0 (1.1)		12.6 (2.6)	42.8 (2.9)	no data
6-Jun	Yakima	NA	1.6 (3.5)	3.9 (2.1)	4.8 (0.8)		9.4 (6.6)	no data	no data
	Pooled Mean	NA	1.5 (2.6)	4.5 (2.1)	5.3 (1.1)		10.1 (6.0)	42.8 (2.9)	no data

2007		Snake River	Lower Columbia River				Pacific Ocean		
Release Date	Population	Lake Bryan (190/NA)	Lake Wallula (369/113)	Lake Celilo (531/275)	McGowan's Channel (647/391)	Astoria Bridge (848/592)	Willapa Bay (911/655)	Lippy Point (1395/1140)	Grave's Harbor (2501/2245)
1-May	Dworshak	9.8 (5.1)	22.0 (5.5)	22.1 (5.5)	25.5 (6.6)	38.1 (9.4)	38.1 (9.4)	no data	no data
14-May	Dworshak	7.6 (3.6)	22.8 (5.1)	22.3 (5.9)	24.4 (6.0)	34.3 (10.4)	34.3 (10.4)	no data	no data
	Pooled Mean	8.6 (4.4)	22.4 (5.2)	22.2 (5.6)	24.9 (6.2)	36.2 (9.6)	36.2 (9.6)	no data	no data
28-May	Yakima	NA	5.7 (2.0)	7.6 (2.5)	10.2 (2.8)	13.1 (2.7)	13.1 (2.7)	no data	no data
3-Jun	Yakima	NA	6.3 (1.9)	8.2 (2.1)	10.6 (2.7)	20.1 (4.8)	20.1 (4.8)	no data	no data
	Pooled Mean	NA	5.9 (2.0)	7.7 (2.4)	10.3 (2.8)	15.0 (4.6)	15.0 (4.6)	no data	no data

Table A.2 cont. Cumulative travel time of Dworshak and Yakima spring Chinook salmon smolts to detection sites (mean days (st. dev.)).

2008		Snake River		Lower Columbia River				Pacific Ocean	
Release Date	Population	Lake Bryan (190/NA)	Lake Wallula (369/113)	Lake Celilo (531/275)	McGowan's Channel (647/391)	Astoria Bridge (848/592)	Willapa Bay (911/655)	Lippy Point (1395/1140)	Grave's Harbor (2501/2245)
25-Apr	Dworshak	12.4 (6.7)	23.7 (6.7)	26.9 (6.7)	25.2 (4.5)	31.8 (5.9)	39.4 (6.8)	66.0 (9.2)	93.9 [(a)]
2-May	Dworshak	11.5 (6.4)	20.2 (6.7)	23.0 (7.6)	20.8 (8.6)	26.1 (5.6)	32.3 (5.6)	54.7 (0.3)	no data
	Pooled Mean	11.9 (6.5)	21.9 (6.9)	25.2 (7.3)	22.8 (7.1)	29.3 (6.4)	36.7 (7.2)	63.5 (9.4)	93.9 [(a)]
15-May	Yakima	NA	1.5 (0.3)	5.3 (1.1)	7.2 (2.3)	9.6 (2.0)	18.2 (10.2)	48.6 (7.1)	no data
21-May	Yakima	NA	1.5 (0.7)	4.3 (1.8)	5.7 (0.9)	8.4 (1.7)	21.0 (16.5)	65.5 (24.9)	no data
	Pooled Mean	NA	1.5 (0.6)	4.6 (1.7)	6.4 (1.8)	9.0 (1.9)	19.6 (13.7)	56.4 (19)	no data

Appendix B. Migration Rate Tables

Table B.1. Segment specific rate of movement of Dworshak and Yakima spring Chinook salmon smolts (mean km/day (st. dev)). Dworshak fish were released at Kooskia Hatchery (870 km from Columbia River mouth); Yakima fish were released at the Chandler Juvenile Monitoring Facility (615 km from Columbia River mouth). NA- not applicable. Parentheses below detection sites indicate segment distance (km). (a) calculated from only one individual; * applicable to Dworshak smolts; ‡ applicable to Yakima smolts.

2006		Snake River	Lower Columbia River			Pacific Ocean		
Release Date	Population	Release-Lake Bryan (190)	Lake Bryan* /Release‡- Lake Wallula (179*/113‡)	Lake Wallula- Lake Celilo (162)	Lake Celilo- McGowan's Channel (116)	McGowan's Channel- Willapa Bay (264)	Willapa Bay-Lippy Point (485)	Lippy Point- Grave's Harbor (1105)
1-May	Dworshak	31.8 (18.4)	28.4 (9.3)	52.0 (13.5)	84.0 (13.0)	62.3 (24.6)	no data	no data
8-May	Dworshak	43.6 (14.9)	32.4 (8.6)	58.9 (10.4)	82.6 (14.5)	67.1 (23.2)	16.5 (2.2)	28.8 [(a)]
	Pooled Mean	37.8 (17.7)	30.5 (9.1)	55.2 (12.6)	83.4 (13.6)	64.7 (23.8)	16.5 (2.2)	28.8 [(a)]
30-May	Yakima	NA	91.8 (17.7)	53.1 (16.2)	85.8 (9.5)	48.2 (15.4)	15.1 (0.8)	no data
6-Jun	Yakima	NA	97.8 (19.9)	72.1 (15.6)	99.2 (11.4)	76.4 (17.4)	no data	no data
	Pooled Mean	NA	95.0 (19.1)	62.9 (18.5)	93.7 (12.5)	69.8 (20.7)	15.1 (0.8)	no data

Table B.1 cont. Segment specific rate of movement of Dworshak and Yakima spring Chinook salmon smolts (mean km/day (st. dev)).

2007		Snake River	Lower Columbia River				Pacific Ocean		
Release Date	Population	Release-Lake Bryan (190)	Lake Bryan* /Release‡-Lake Wallula (179*/113‡)	Lake Wallula-Lake Celilo (162)	Lake Celilo-McGowan's Channel (116)	McGowan's Channel-Astoria Bridge (201)	Astoria Bridge-Willapa Bay (63)	Willapa Bay-Lippy Point (485)	Lippy Point-Grave's Harbor (1105)
1-May	Dworshak	23.8 (9.7)	22.6 (8.2)	49.0 (14.7)	75.7 (12.6)	84.5 (10.4)	6.6 (5.4)	no data	no data
14-May	Dworshak	28.9 (10.2)	20.1 (7.9)	45.8 (12.5)	75.4 (6.7)	77.8 (11.2)	6.4 (3.2)	no data	no data
	Pooled Mean	26.6 (10.3)	21.2 (8.1)	47.2 (13.3)	75.5 (9.4)	80.8 (11.1)	6.5 (4.1)	no data	no data
28-May	Yakima	NA	88.4 (11.0)	42.6 (13.7)	76.6 (15.8)	82.1 (8.6)	23.8 (16.6)	no data	no data
3-Jun	Yakima	NA	84.6 (17.8)	37.3 (15.0)	76.7 (12.8)	79.0 (14.4)	22.3 (32.5)	no data	no data
	Pooled Mean	NA	87.0 (14.0)	41.3 (14.0)	76.6 (14.9)	81.3 (10.4)	23.4 (21.3)	no data	no data

2008		Snake River	Lower Columbia River				Pacific Ocean		
Release Date	Population	Release-Lake Bryan (190)	Lake Bryan* /Release‡-Lake Wallula (179*/113‡)	Lake Wallula-Lake Celilo (162)	Lake Celilo-McGowan's Channel (116)	McGowan's Channel-Astoria Bridge (201)	Astoria Bridge-Willapa Bay (63)	Willapa Bay-Lippy Point (485)	Lippy Point-Grave's Harbor (1105)
25-Apr	Dworshak	19.3 (8.4)	21.8 (10.8)	55.0 (15.3)	68.6 (7.8)	83.9 (12.2)	10.7 (6.9)	15.6 (2.1)	no data
2-May	Dworshak	21.4 (11.1)	25.7 (12.3)	61.3 (14.3)	72.9 (7.7)	77.0 (12.4)	12.6 (6.7)	22.3 (0.3)	no data
	Pooled Mean	20.4 (9.9)	23.7 (11.7)	57.6 (15.1)	70.0 (7.6)	80.7 (12.4)	11.4 (6.8)	17.8 (3.8)	no data
15-May	Yakima	NA	76.1 (9.4)	48.0 (10.5)	39.2 (23)	80.2 (8.9)	14.5 (17.6)	17.0 (3.7)	no data
21-May	Yakima	NA	85.5 (21.7)	66.6 (14.6)	65.6 (7.6)	82.8 (6.3)	8.1 (3.6)	12.2 (4.3)	no data
	Pooled Mean	NA	81.2 (17.8)	60.0 (16.0)	59.8 (15.7)	81.8 (7.3)	11.2 (12.8)	15.1 (4.5)	no data

Table B.2. Cumulative migration rate of Dworshak and Yakima spring Chinook salmon smolts to detection sites (mean km/day (st. dev.)). Dworshak fish were released at Kooskia Hatchery (870 km from Columbia River mouth); Cle Elum fish were released at the Chandler Juvenile Monitoring Facility (615 km from Columbia River mouth). NA- not applicable. Parentheses below detection sites indicated cumulative distance (km) from Dworshak and Yakima release sites, respectively. (a) Only one ID code detected.

2006		Snake River	Lower Columbia River			Pacific Ocean		
Release Date	Population	Lake Bryan (190/NA)	Lake Wallula (369/113)	Lake Celilo (531/275)	McGowan's Channel (647/391)	Willapa Bay (911/655)	Lippy Point (1395/1140)	Grave's Harbor (2501/2245)
1-May	Dworshak	31.8 (18.4)	25.7 (8.4)	30.6 (7.3)	35.7 (14)	35.6 (4.8)	24.1 [a]	26.5 [a]
8-May	Dworshak	43.6 (14.8)	35.2 (7.9)	40.6 (7.5)	48.7 (15.3)	49.7 (8.1)	26.4 (0.9)	27.7 [a]
	Pooled Mean	37.8 (17.6)	30.7 (9.4)	35.2 (8.9)	41.6 (16)	42.9 (9.7)	25.8 (1.3)	27.1 (0.9)
30-May	Yakima	NA	91.8 (17.7)	59.9 (16.3)	66.8 (10.9)	53.7 (8.7)	26.7 (1.8)	no data
6-Jun	Yakima	NA	97.8 (19.9)	76.9 (15.5)	82.8 (11.6)	77.6 (14.3)	no data	no data
	Pooled Mean	NA	95.0 (19.1)	68.7 (18)	76.5 (13.7)	72 (16.7)	26.7 (1.8)	no data

2007		Snake River	Lower Columbia River				Pacific Ocean		
Release Date	Population	Lake Bryan (190/NA)	Lake Wallula (369/113)	Lake Celilo (531/275)	McGowan's Channel (647/391)	Astoria Bridge (848/592)	Willapa Bay (911/655)	Lippy Point (1395/1140)	Grave's Harbor (2501/2245)
1-May	Dworshak	23.8 (9.7)	21.1 (7.6)	25.8 (7.6)	31.2 (8.7)	35.3 (9.1)	25.1 (6.1)	no data	no data
14-May	Dworshak	28.9 (10.2)	22.0 (6.4)	24.6 (6.1)	31.2 (9.1)	36.7 (8.9)	28.6 (8.7)	no data	no data
	Pooled Mean	26.6 (10.3)	21.6 (6.9)	25.1 (6.7)	31.2 (8.7)	36.0 (8.8)	26.9 (7.3)	no data	no data
28-May	Yakima	NA	88.4 (11.0)	51.9 (12.7)	55.8 (13.2)	61.4 (12.8)	51.5 (7.9)	no data	no data
3-Jun	Yakima	NA	84.6 (17.8)	47.3 (14.8)	50.9 (13.9)	58.6 (13.4)	34.1 (8.4)	no data	no data
	Pooled Mean	NA	87.0 (14.0)	50.7 (13.3)	54.5 (13.4)	60.7 (12.8)	46.7 (11.2)	no data	no data

Table B.2 cont. Cumulative migration rate of Dworshak and Yakima spring Chinook salmon smolts to detection sites (mean km/day (st. dev.)).

2008		Snake River	Lower Columbia River				Pacific Ocean		
Release Date	Population	Lake Bryan (190/NA)	Lake Wallula (369/113)	Lake Celilo (531/275)	McGowan's Channel (647/391)	Astoria Bridge (848/592)	Willapa Bay (911/655)	Lippy Point (1395/1140)	Grave's Harbor (2501/2245)
25-Apr	Dworshak	19.3 (8.4)	17.0 (5.3)	20.9 (5.4)	26.4 (4.8)	27.5 (4.8)	23.7 (3.9)	21.4 (2.5)	26.6 [(a)]
2-May	Dworshak	21.4 (11.1)	20.6 (8.5)	26.0 (10.6)	36.6 (15.7)	34.2 (8.5)	29.0 (5.1)	25.5 (0.1)	no data
	Pooled Mean	20.4 (9.9)	18.8 (7.3)	23.1 (8.3)	31.8 (12.7)	30.4 (7.4)	25.7 (5.0)	22.3 (2.8)	26.6 [(a)]
15-May	Yakima	NA	76.1 (9.4)	54.1 (8.8)	58.3 (15.7)	63.5 (10.1)	42.6 (15.9)	23.9 (3.3)	no data
21-May	Yakima	NA	85.5 (21.7)	70.5 (15.6)	70.1 (8.9)	73.2 (12.6)	39.5 (12.2)	19.3 (6.5)	no data
	Pooled Mean	NA	81.2 (17.8)	64.8 (15.7)	64.8 (13.4)	68.5 (12.4)	41.0 (14.0)	21.8 (5.3)	no data

Appendix C. Distribution of Mortality Rates

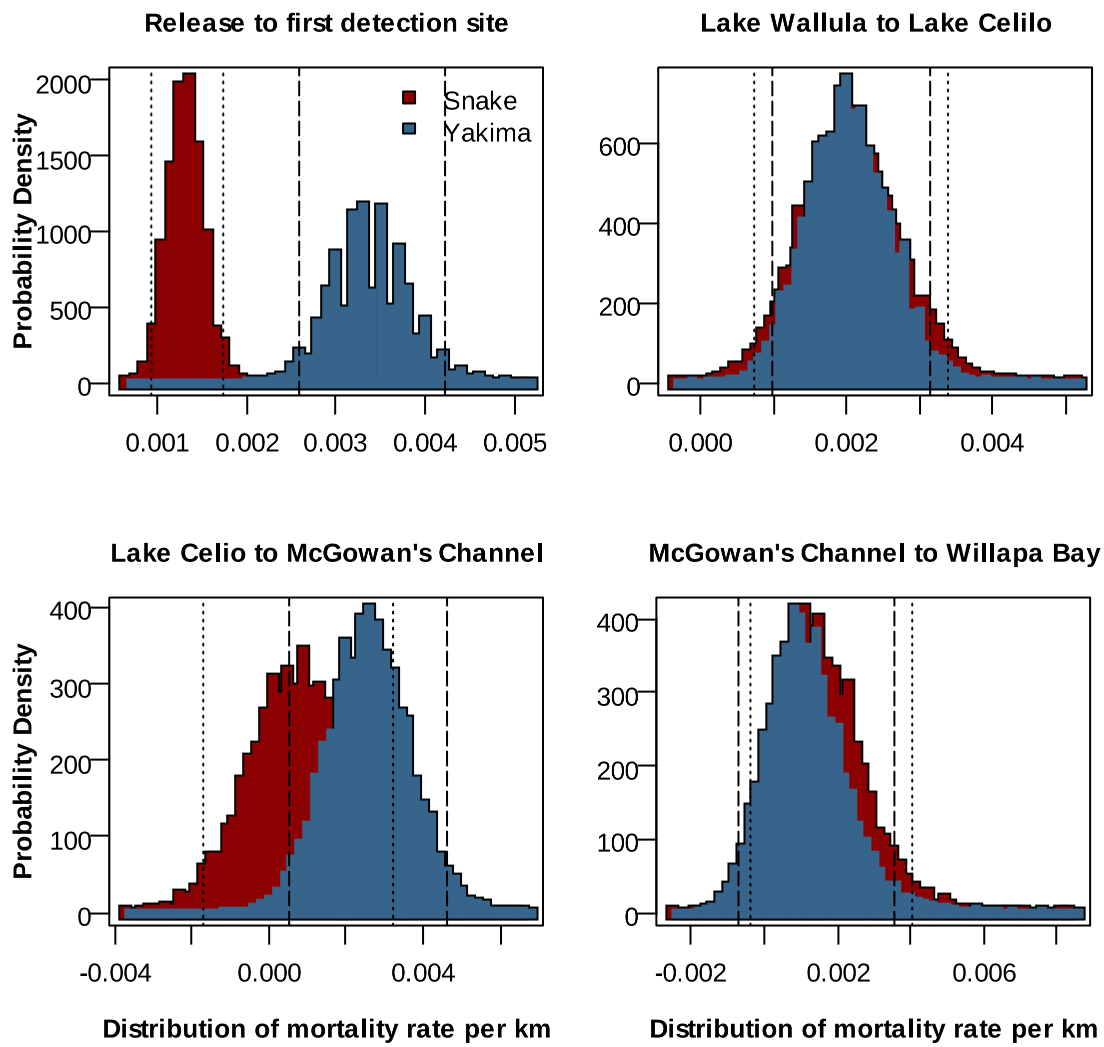


Figure C.1. Bootstrapped distribution of mortality rates per km of travel of seaward migrating Dworshak and Yakima spring Chinook salmon smolts in 2006 (higher positive values represent greater mortality). Dashed lines and dotted lines represent the 95% confidence interval for Dworshak and Yakima populations, respectively. Mortality rate per km was significantly greater for Yakima smolts from release to the first detection site. The first detection site for Dworshak smolts was Lake Bryan, and Lake Wallula for Yakima smolts.

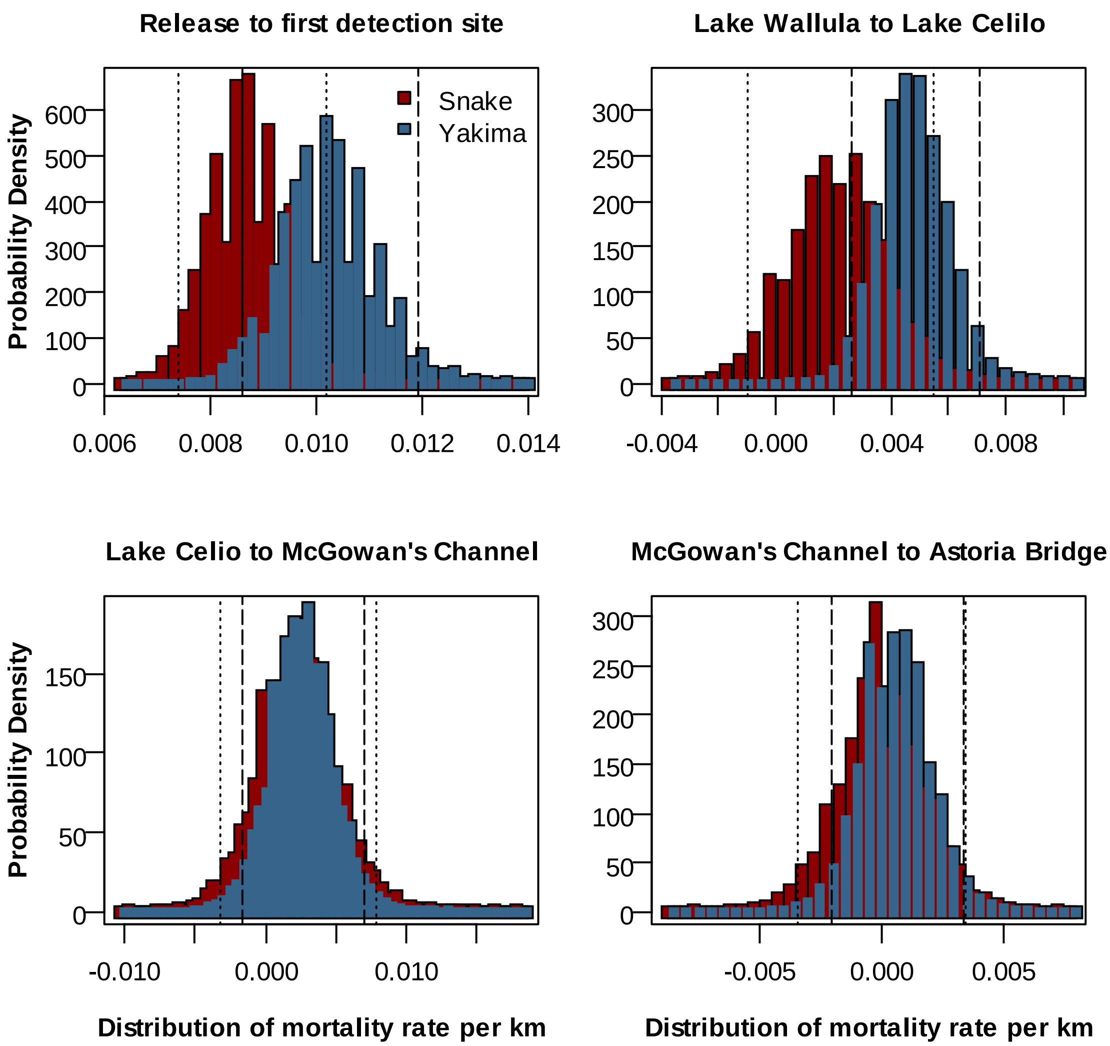
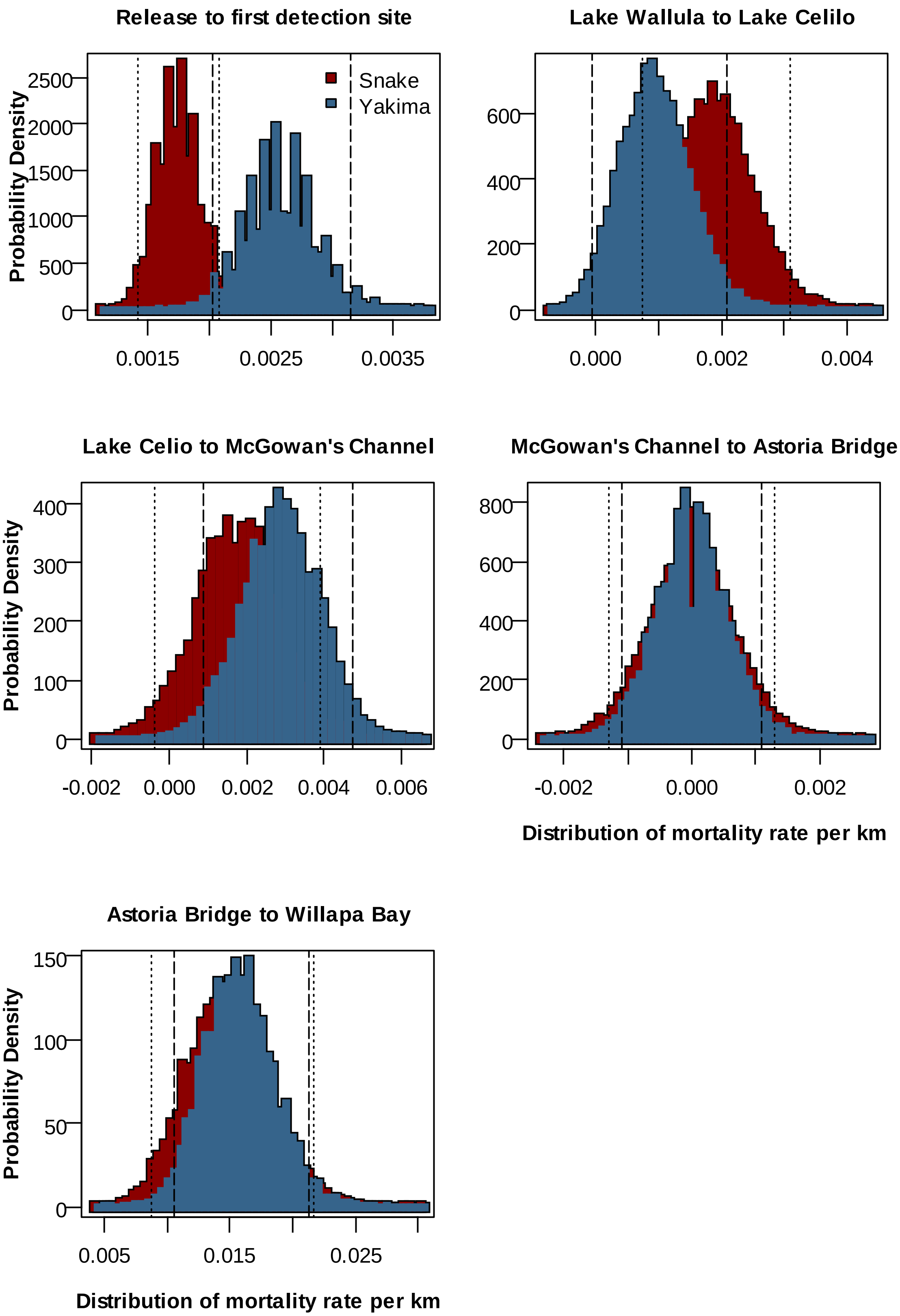


Figure C.2. Bootstrapped distribution of mortality rates per km of travel of seaward migrating Dworshak and Yakima spring Chinook salmon smolts in 2007 (higher positive values represent greater mortality). Dashed lines and dotted lines represent the 95% confidence interval for Dworshak and Yakima populations, respectively. The first detection site for Dworshak smolts was Lake Bryan, and Lake Wallula for Yakima smolts.

Figure C.3. Bootstrapped distribution of mortality rates per km of travel of seaward migrating Dworshak and Yakima spring Chinook salmon smolts in 2008 (higher positive values represent greater mortality). Dashed lines and dotted lines represent the 95% confidence interval for Dworshak and Yakima populations, respectively. Mortality rate per km was significantly greater for Yakima smolts from release to the first detection site. The first detection site for Dworshak smolts was Lake Bryan, and Lake Wallula for Yakima smolts.


Release to first detection site
Snake
Yakima
Probability Density
0
500
1000
1500
2000
2500
0.0015
0.0025
0.0035
Lake Wallula to Lake Celilo
0
200
400
600
0.000
0.002
0.004
Lake Celio to McGowan's Channel
Probability Density
0
100
200
300
400
-0.002
0.000
0.002
0.004
0.006
McGowan's Channel to Astoria Bridge
0
200
400
600
800
-0.002
0.000
0.002
Distribution of mortality rate per km
Astoria Bridge to Willapa Bay
Probability Density
0
50
100
150
0.005
0.015
0.025
Distribution of mortality rate per km

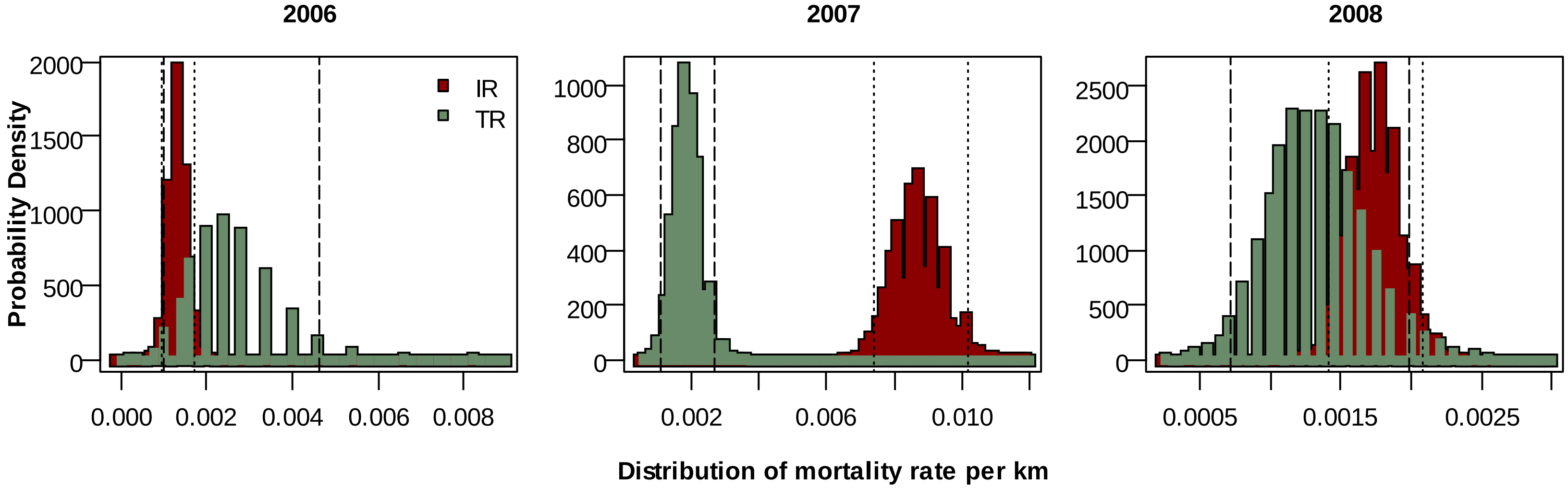


Figure C.4. Bootstrapped distribution of post-release mortality rates per km of travel of seaward migrating juvenile Dworshak spring Chinook salmon migrating in-river (IR) or transported (TR) in 2006-8 (higher positive values represent greater mortality). Mortality rate for in-river smolts was estimated from release at Kooskia hatchery to the first detection site in Lake Bryan (below Lower Granite Dam). Mortality rate for transported smolts was estimated from release in McGowan's Channel (below Bonneville Dam) to Willapa Bay in 2006 and to the Astoria Bridge in 2007 and 2008. Dashed lines and dotted lines represent the 95% confidence interval for in-river and transported groups, respectively. In 2006 and 2008 post-release mortality rates were not significantly different for IR and TR smolts. In 2007, post-release mortality was unusually high for IR smolts.

Appendix D. Additional Peer-reviewed Thesis Related Publications

D.1 Published papers

Welch, D.W., Rechisky, E.L., Melnychuk, M.C., Porter, A.D., Walters, C.J., Clements, S., Clemens, B.J., McKinley, R.S., and Schreck, C. 2008. Survival of migrating salmon smolts in large rivers with and without dams. PLoS Biol. **6**: 2101-2108.

Greene, C.H., B.A. Block, D. Welch, G. Jackson, G.L. Lawson, E.L. Rechisky. 2009. Advances in conservation oceanography: New tagging and tracking technologies and their potential for transforming the science underlying fisheries management. Oceanography. Vol. 22, no. 1, pp 210-223.

Lindley, S. T., M. L. Moser, D. L. Erickson, M. Belchik, D. W. Welch, E. L. Rechisky, J. T. Kelly, J. Heublein, A. P. Klimley. 2008. Marine migration of North American green sturgeon. Transactions of the American Fisheries Society. Vol. 137, no. 1, pp. 182-194.

D.2 Papers in review

Welch, D.W., Jackson, G.D., Melnychuk, M.C., Rechisky, E., Porter, A., Neaga, L., and O'Dor, R. Applications of the Pacific Ocean Shelf Tracking System (POST): A permanent continental-scale acoustic tracking array for marine management, conservation and ocean observing.

D.3 Non-peer-reviewed book chapters submitted

Payne, J., Andrews, K., Chittenden, C., Crossin, G., Goetz, F., Hinch, S., Levin, P., Lindley, S., Melnychuk, M., Nelson, T., Rechisky, E., and Welch, D. Tracking fish movements on the northeast Pacific shelf. Ch. 14 in: Marine Life: Diversity, Distribution and Abundance. Wiley-Blackwell, Census of Marine Life Special Publication.

Appendix E. Animal Care Certification

DFO Pacific Region Animal Care Committee

ANIMAL USE PROTOCOL REVIEW

STUDY TITLE: Comparative surgical trials of prototype 6 & 7 mm acoustic tags for salmon smolts with existing 9 mm acoustic tag
D. Welch – 05-004

REVIEW DATE: March 17, 2005

THIS APPROVAL EXPIRES: March 31, 2006

DFO is subject to inspection of any and all research animal care details by the Canadian Council on Animal Care. The questions on the Protocol Application are those asked by CCAC inspectors. DFO has made it a departmental commitment to abide by the CCAC's standards. Regional Animal Care Committees and the Protocol review process are the principal means of carrying out this commitment.

The review report following is NOT an assessment of a study's scientific worth. Information which may be requested as to the benefits of a study is used only to determine if a use of animals in research, which may be objectionable to some persons, is sufficiently compensated by benefits to animals and society as a whole.

Please be reminded:

1. Your application is not approved until signed by the ACC Chairperson.

2. Science Branch proposals involving the holding of animals for experimentation and testing cannot be approved in the main workplan review process without a valid signed protocol.

3. Use extra pages if insufficient space on the application.

RESULT

ACCEPTED

✓ HK 05.03.17

Your Animal Use Protocol (AUP) has been accepted.
Please keep this signed original to refer to.
You will need it if you carry this work into another year. The CCAC requires details from foregoing AUP's when you reapply, which must be done annually. Also, some journals will not accept manuscripts without an approved AUP.

CONDITIONAL ACCEPTANCE: our committee gave approval to the animal use set out in your application, <u>conditional</u> upon providing information on

NOT ACCEPTED: our committee was unable to determine if your study would meet CCAC standards. We are asking for further information on

---

ACC members:
Gordon Bell (250)754-6114
Jennifer Liu (604)666-4427 loc 250
Henrik Kreiberg (250)756-7019 (Chair)
Carlo Biagi (604)666-4805
Hans Galesloot (250)745-3321
Dave Lane (250)740-6372

Date: 23 March, 2006

Dr. David Welch
Kintama Research

Dear Dr. Welch,

Your protocol application, ***POST – Pacific Ocean Shelf Tracking Project,*** has been **approved** by the Animal Care Committee and assigned the protocol number **2006-08 R**.

This protocol will be valid for one year, from **2006-04-01** to **2007-03-31**. It may then be renewed, with minor revisions as applicable, via submission of a Request to Renew-Amend an Approved Project form, in each of the second and third years. At the end of the third year, a full protocol application must be submitted once again.

Yours truly,

Dr. David Drakeford, Chair
Animal Care Committee
Malaspina University-College
Local: 6360   *Email:* drakefordd@mala.bc.ca

For information contact:
Patricia Stuart
ACC Administrative Assistant
Local: 6361   *Email:* stuartp@mala.bc.ca

Melinda Jacobs

From: Patricia Stuart [stuartp@MALA.BC.CA]
Sent: 10 Apr 2007 09:28
To: David Welch
Cc: Melinda Jacobs
Subject: Welch Renewal Revisions Approved 2007.doc

Date: 10 April, 2007

Dr. David Welch
Kintama Research

Dear Dr. Welch,

Your protocol renewal application, ***2006-08 R,*** has been approved by the Animal Care Committee and assigned the protocol number **2006-08 R-1**.

This protocol will be valid for one year, from **2007-04-01** to **2008-03-31**. It may then be renewed, with minor revisions as applicable, via submission of a Request to Renew-Amend an Approved Project form, in each of the second and third years. At the end of the third year, a full protocol application must be submitted once again.

Yours truly,

David Drakeford, Ph.D.
Chair, Animal Care Committee
Dean, Science and Technology
Local: 6360 *Email:* drakeford@mala.bc.ca

Date: April 1, 2008

Dr. David Welch

Dear Dr. Welch,

Congratulations! Your request for renewal of protocol application, ***2006-08R-1,*** has been **approved** by the Animal Care Committee and assigned the protocol number ***2006-08R-2***.

This protocol will be valid for one year, from ***APRIL 1, 2008*** to ***MARCH 31, 2009***. This protocol will be at the end of its third and final year to renew as of March 31, 2009 therefore; a new protocol application must be submitted.

Yours truly,

Dr. Andy Spencer, Vice-Chair
Animal Care Committee
Email: spencera@mala.ca

For information contact:
Rae-Anne Savard
Administrative Assistant, ACC
Phone: (250) 740-6361 *Email:* savard@mala.ca

June 11, 2009

Dr. David Welch
Kintama Research

Dear Dr. Welch,

Your protocol application, ***Kintama Research - POST,*** has been **approved** by the VIU Animal Care Committee and assigned the protocol number **2009-11 R**.

This protocol will be valid for one year, from **June 11, 2009** to **June 10, 2010**. It may then be renewed, with minor revisions as applicable, via submission of a Request to Renew-Amend an Approved Project form, in each of the second and third years. At the end of the third year, a full protocol application must be submitted once again.

Yours truly,

Dr. Andy Spencer, Chair
Animal Care Committee
Vancouver Island University
Local: 6517 *Email:* andy.spencer@viu.ca

For information contact:
Rae-Anne Savard
ACC Administrative Assistant
Local: 6361 *Email:* rae-anne.savard@viu.ca

Date: 07 December, 2009

Dr. David Welch
Kintama Research

Dear David,

Your protocol renewal application, ***Kintama Research - POST Tagging,*** has been **approved** by the Animal Care Committee and assigned the protocol number **2009-11 R-1**.

This protocol will be valid for one year, from **2010-01-01** to **2010-12-31**. It may then be renewed once again, with minor revisions as applicable, via submission of a Request to Renew-Amend an Approved Project form. At the end of the third year, a full protocol application must be submitted once again.

Yours truly,

Dr. Andy Spencer, Chair
Animal Care Committee
Vancouver Island University
Local: 6517 *Email:* andy.spencer@viu.ca

For information contact:
Rae-Anne Savard
ACC Administrative Assistant
Local: 6361 *Email:* rae-anne.savard@viu.ca