# MIGRATORY BEHAVIOUR AND SURVIVAL OF WILD AND HATCHERY COHO SALMON USING ACOUSTIC TELEMETRY 

by<br>CEDAR MARGET CHITTENDEN<br>B.Sc., Simon Fraser University, 2002

# A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF 

DOCTOR OF PHILOSOPHY
in

THE FACULTY OF GRADUATE STUDIES
(Animal Science)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)

October 2008
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#### Abstract

Climate is emerging as a primary determinant of marine survival and migratory behaviour for Pacific salmon. For example, a regime shift in the mid-1990s was correlated to a major change in the migratory behaviour of coho salmon (Oncorhynchus kisutch) in the Strait of Georgia, BC. The details of this new behaviour pattern remain relatively unknown. Furthermore, many coho stocks have been declining during the past three decades. Mitigative strategies -such as hatchery programs- have done little to reverse the trend, and little is known about how hatchery fish are affecting wild populations. The objective of this dissertation was to identify key mortality areas and provide the first look at the migratory behaviour of juvenile wild and hatchery coho in southwestern British Columbia using new telemetry technologies. As coho pre-smolts are relatively small compared with other salmonid species that are typically studied using acoustic telemetry, the identification of the appropriate sizes of fish and tags to use was critical. The first study tested the effects of surgically implanting the three smallest sizes of acoustic tags available on the growth, survival, performance and condition of coho pre-smolts. The first of three field studies to follow investigated the early migratory behaviour and survival of an endangered coho population. The second field study examined differences in physiology, survival and migratory behaviour between wild and hatcheryreared coho smolts. Finally, the third study analysed the altered marine migratory behaviour of juvenile coho in the Strait of Georgia. This dissertation provides the first evidence of high freshwater mortality rates in the endangered coho population, which has implications for the management and conservation of this and other at-risk stocks. I found differences in migratory behaviour and physiology between wild and hatchery-reared coho, suggesting that mitigative strategies need further evaluation. Finally, the timing of the anomalous coho migration out of the Strait of Georgia confirmed that population changes in the strait are a consequence of ecosystem-related impacts. These findings demonstrate how new technologies could be used to fill major information gaps and improve the management and conservation of Pacific salmon.


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## ACKNOWLEDGEMENTS

My first thank-you must go to Mike, for returning from the wilds of Alberta with me so I could follow my dreams, and introducing me to my supervisor, Scott McKinley. Scott, thank-you for giving me wings. The past four years have changed my life. Thank-you forever; I can never say it enough.

Thanks to my supervisory committee, Marina von Keyserlingk and Patricia Schulte. I really appreciate all the time and support you gave me. You are both so kind and generous to students; your advice and questions helped me grow in so many ways.

To everyone at the Centre for Aquaculture and Environmental Research, Kevin, Fiona, Nancy, Malin, William, Lisa, Kris, Shannon, Hidehiro and Susie: thanks for all the help, the laughs, and the trips to Subway, Cypress and beyond. Thanks to Bob Devlin for the many office chats, the advice, support and inspiration. Carlo Biagi (C-Lo), you are a kindred spirit -running in rainstorms, farming in fish tanks, swimming with seals; I hope the adventures continue for a long time to come. Thank-you for your unwavering loyalty and strength, you were a rock for me when I was trying to overcome, and always so happy for me when I did! Thanks for everything you've done for me. You know I'll never forget.

To Srinivas Sura, Brett Zuehlke, and Allison McKnight, thank-you for your long hours, hard work and friendship. You were there for me through thick and thin (wild animal encounters, tedious lab trials, endless hours animating, crazy boat rides) and helped pull off the impossible! I wouldn't be here now if it weren't for you three.

A heartfelt thanks to everyone at the Spius Creek Hatchery, the Quinsam Hatchery, the Seymour Hatchery, the Chehalis Hatchery and the Weaver Creek Spawning Channel. Your assistance to me and support of research demonstrates the immense strength of your characters. I was humbled by your generosity and kindness. I hope that the fruit of our efforts will help to provide more funding for hatchery improvements and staff. You all worked so hard and showed that you want to make a difference.

Thanks to John Duncan and the A'Tlegay Fisheries Society (I'll never forget our 'wild' river runs), Steve Payne and the Campbell River Coast Guard (for the BBQs, long chats and my first ever motorbike ride) and Bob and Linda Latham (my CR parents) for making Campbell River a home away from home. That truly was a summer to remember. My first field season in charge and no major disasters just a ton of great memories- thanks to all of you for your help and warmth.

To DJ, thank-you for the time we shared, laughing in Alba, London, Galway, Barca, France, BC, OR, and WA. You will be one of the greats, so keep that beat! Nights spent talking about philosophy, history, culture, music, science, art, and adventure in the belly of Noreena the sailboat with JY were magical. Joël, votre esprit et joie de vie sont contagieux. Merci mille fois pour être grand inspirateur dans ma jeunesse, et pour votre amitier aujourd'hui. To my neighbour Jorge (the PP), thanks for hooking me up with the sweet pad, thanks for the Lions games, dinners under the stars, and for always being there whenever I needed a cup of salt.

Thanks to the hard-working crews of the Frosti, Haida Girl and Georgia Girl for welcoming me on board and sharing your sea life with me. To Fisherman Dan, wherever you are, thanks for being you. David Welch, Melinda Jacobs, Jonathan Thar, and everyone else with the POST project, you made it all happen amidst many challenges. Thanks for everything you've taught me, for the opportunities you've given me and for being so available to answer my questions. Your hard work and energy are changing things.

Skål Norge! Amund, Anette, Audun, Bengt, Elina, Finn, Gunn, Ingebrigt, Jan, Rolf, Ronny, Rune, Trond, and everyone else I met doing fieldwork in Norway -tusen takk! Knowing you has meant so much to me. Til en fremtid av arbeid sammen!

Jay Senetchko, thanks for letting a poor student paint for free at your studio. Being able to paint again has been cathartic. Thursday all-nighters at the studio with Chad and all the other creative souls will go down in history. I was so thankful to be a part of that.

Gideon Leonardo, I recognised you from the moment we met. Conversations about sunglass slippers, love, life and art freed me. Being in time with you reminds me of a grain of sand in the juiciest oyster, as a wise surfer once said. Thank-you for always being somewhere beyond the dance.

To the ladies of the SSC (and pseudos), the Cocompton Beavs, Angie, Melissa, Christine, Núria, Maria, you are my sisters from other misters; your lifelong friendships are sacred to me. Thank-you for being so understanding when I had to turn down yet another event because I needed to be in the field or to write a paper. You've been so giving and loving to me, even when I did not have the money or time to be much of a friend back. I can not wait for the next Cinco de Mayo, SSC party and outdoor adventure!

Kris, you flew into my life, blowing me away daily with your energy, devotion, and unwavering support. Your fire fills me with light; thank-you for always being there for me in every way (YTTA).

Mom (Eel), Dad, Minda, Mike, Kasey, Nanny, Poppa, Granny, Grampa, and the rest of the family near and far (the Lathams, Lowes, Landys, Catherwoods, Hansens, Chittendens), thank-you for your unconditional love, for encouraging me to do my best, and for supporting me every step of the way. I am the luckiest girl on Earth.

Thanks to the First Nations of the Pacific Northwest.
"The modern community economy is at risk because of a few short decades of short-sighted polices and practices. Our economic needs can and must be brought into balance with the capacity of the land to function and provide" (Council of the Haida Nation, 2005).

Finally, thanks to all of the animals involved in these studies. Salmon are truly amazing creatures; the more I learn about them, the more in awe I become.

To Earth -may the future be more like the past.

## CO-AUTHORSHIP STATEMENT

## Chapter 2

I was responsible for writing the manuscript.
Richard Beamish and Scott McKinley contributed to the presentation of the manuscript.

## Chapter 3

I was responsible for the experimental design, data collection, statistical analyses, and writing the manuscript.
Kevin Butterworth and Fiona Cubitt contributed to the choice of statistical tests and to the interpretation and presentation of the manuscript. Melinda Jacobs, Adrian Ladouceur, David Welch and Scott McKinley contributed to the experimental design, data collection and presentation of the manuscript.

## Chapter 4

I was responsible for the experimental design, data collection, part of the statistical analyses, and writing the manuscript.
Michael Melnychuk and David Welch contributed to the experimental design, data collection, the statistical analyses and to the interpretation of the manuscript. Scott McKinley contributed to the presentation of the manuscript.

## Chapter 5

I was responsible for the experimental design, data collection, statistical analyses, and writing the manuscript.
Srinivas Sura, Kevin Butterworth, Fiona Cubitt, Núria Plantalech Manel-la, Shannon Balfry, Finn Økland and Scott McKinley contributed to the experimental design, data collection, and to the interpretation and presentation of the manuscript.

## Chapter 6

I was responsible for the experimental design, data collection, all statistical analyses, and writing the manuscript.
Richard Beamish, Chrys Neville, Ruston Sweeting and Scott McKinley contributed to the experimental design, data collection, and to the interpretation and presentation of the manuscript.

## CHAPTER 1: General Introduction

### 1.1 Introduction

Several studies in the northwest Pacific Ocean have documented the consequences of rising sea surface temperatures on ocean productivity (e.g. Beamish and Bouillon, 1993; Klyashtorin, 1998; McGowan et al., 1998). Changes in ocean productivity have also been correlated to changes in the marine survival and the geographic occurrence of some Pacific salmon (Oncorhynchus spp.) populations (Bardach and Santerre, 1981; Beamish, 1993; Beamish et al., 1997; Mantua et al., 1997; Johnson, 1998; Williams, 1998; Beamish et al., 1999a; 1999b; 2000; Cole, 2000; Hare and Mantua, 2000; McFarlane et al., 2000; Welch et al., 2000; Hobday and Boehlert, 2001; Mote et al., 2003; Beamish et al., 2004; 2008). However, the effects of climate on salmon stocks are not universal in all regions. Northern populations have increased while southern populations declined during regime shifts (Coronado and Hilborn, 1998; Bradford, 1999; Hare et al., 1999; Welch et al., 2000; Hobday and Boehlert, 2001). In southern areas, some stocks are endangered (Bradford and Irvine, 2000) and others have been rendered extinct (Nehlsen et al., 1991; Allendorf et al., 1997).

Climate effects on salmon are also complex temporally. Short-term El Niño/La Niña Southern Oscillation (ENSO) events (Rasmussen and Wallace, 1983; Philander, 1983; 1990), decadal regimes (e.g. the Pacific Decadal Oscillation; Mantua et al., 1997), and long-term climate trends (IPCC, 2007) interact in ways that can only be speculated on at this point. Even without these climatic complexities, information on the marine behaviour of salmon populations is lacking and there is a high degree of variation between stocks (French et al., 1976; Groot and Margolis, 1991; Waples et al., 2001). Furthermore, existing knowledge of the marine survival and position of salmon in the Pacific Ocean is typically derived from mark-recapture studies (Hankin et al., 2005). As a result, details about the migratory behaviour of different life stages of salmon and associated marine survival estimates in real time are not known.

Internationally, scientists have expressed a need for marine ecosystem assessments -particularly in the face of climate change (Beamish and Mahnken, 1999; DFO, 2000; Commission of the European Communities, 2002; NOAA, 2002). Collaborative research efforts employing electronic devices to study climatic effects on the migratory behaviour and survival of hatchery and wild salmon stocks could fill
significant information gaps and improve fishery management and conservation decisions. These modern tools enable researchers to answer specific questions about environmental, physiological, and genetic effects on individual salmon survival and behaviour, which had not been possible previously. The use of sensory acoustic transmitters, for example, can help to show how a salmon of known origin, health and size reacts physically to its environmental conditions in real time. Correlating changes in oceanographic conditions to the movement and survival of Pacific salmon in their ecosystems is key to the future conservation and management of these species.

### 1.2 History of Pacific Salmon Research and Management

The first humans arrived in North America from Northeast Asia at least 11,000 years ago (calibrated date; Haynes, 1992; Hoffecker et al., 1993; Roosevelt et al., 1996; Diamond, 1999). North America's Pacific coastline was populated soon after, and had many established chiefdoms when Europeans first arrived in 1774 (Hoffecker et al., 1993). The Pacific salmon species were of great importance to these coastal First Nations, whose world view states "Hishukishtswalk," meaning 'everything is one’ (Dumont, 1993; Cajete, 1999; Atleo, 2004; Turner, 2005). Salmon were viewed not only as food for survival, but also as a cherished part of the interconnected natural world and traditions dictated that one only take what was needed (Chittenden, 1882; Lichatowich, 1999).

As introduced diseases, including smallpox, decimated native human populations on the northwest coast —from approximately 180,000 people at first contact to 35,000 one century later (Diamond, 1999)— European settlement increased. The available resources in the newly inhabited land were seen to be limitless (Chittenden, 1884). Human consumption of Pacific salmon was correlated to declining salmon populations in the late 1800s (Beamish et al., 2003). In response to these declining stocks, the Fisheries Act was adopted in British Columbia, Canada, in 1877 (Harris, 2001). Despite the laudable aims of this Act, some stocks are now endangered (Bradford and Irvine, 2000). Suggested reasons for these declines including over-fishing, lower marine survival rates, freshwater habitat alteration, and climate regime shifts- are not well understood; more focused research is needed (Beamish et al., 2000; Bradford and Irvine, 2000; Sweeting et al., 2003; Cooke et al., 2004).

Pacific salmon are highly diverse in terms of their migratory behaviour and physiology (Groot and Margolis, 1991; Mueter et al., 2002). Initial Pacific salmon research focused on freshwater population dynamics because it was believed that there was unused ocean carrying capacity and that climate effects were either random or not believed to be a factor (Beamish et al., 2003). The numerous variables in marine research were daunting, and the ocean was seen as too vast to be noticeably impacted by anthropogenic factors. Finding ways to predict adult returns was the primary goal of fisheries management, and overall survival was assumed to be determined in freshwater (Ricker, 1954). Studies examined factors affecting the freshwater survival of pre-smolts and returning adults, including predators, competition, diseases and parasites, as well as water quality and habitat alterations due to agriculture, road density, logging, and climate change (Hargreaves and LeBrasseur, 1985; Bradford and Irvine, 2000; Beamish et al., 2003; Lawson et al., 2004). For example, there is ongoing monitoring of returning Fraser River sockeye ( $O$. nerka) to test the hypothesis that as river temperatures increase yearly, disease and parasite levels are rising, and return migration timing and reproductive success are being affected (Cooke et al., 2004; Crossin et al., 2008). While freshwater research has been the main focus during the last century, significant knowledge gaps remain in salmonid marine biology (Pearcy and Masuda, 1982; Perry et al., 1998; Brodeur et al., 2000; Weitkamp and Neely, 2002; Beamish et al., 2003).

In 1955 when Canada, Japan and the US formed the International North Pacific Fisheries Commission and declared marine research on salmon a high priority, there was a dearth of scientific information in this area (Parker, 1965). Tracking salmon migratory behaviour in the marine phase of their lifecycle has been challenging, due in large part to our inability to accurately and reliably track freeswimming fish. Prior to the 1960 's, salmon migratory behaviour was studied from discrete samples collected at sea primarily with surface gillnets. Following this period, there was a shift to the use of long lines, purse seines and trawlers. Rope trawls allowed for the rapid sampling of large volumes of water in most weather conditions and depths (Beamish et al., 2004). This approach was used when the offshore distribution patterns of juvenile salmon was first investigated in BC (Welch et al., 1998).

The tracking of individual fish began in the 1960's when researchers started clipping and tagging adult and juvenile salmon at sea. The use of mechanical tags, or "spaghetti tags", in these initial studies provided some information about harvest patterns, and revealed the complexities of Pacific salmonid
migratory behaviour. Simple mark and recapture methods, however, could not provide sufficient survival and behaviour data due to the limitations of the technology and the sheer number of individual stocks (Beamish et al., 2003).

In the 1970's, coded-wire tags (CWTs) were introduced, enabling researchers to tag large numbers of young salmon, with each stock given a unique identifier (Hankin et al., 2005). While this technology has been useful, it again requires the recapture of tagged fish, which limits the type of data that can be gained. The complex interactions between an individual fish and its environment are all but impossible to study using mark and recapture technologies. Furthermore, the recovery of CWTs has become more difficult. Firstly, with the introduced mass-marking of all hatchery fish by removal of the adipose fin in 1997, clipped fins no longer identified CWT fish, creating challenges in identifying which fish had tags. Secondly, declining salmon populations caused a reduction in catch; thus, estimates of fishing mortality became more unreliable as reduced harvest rates meant less data were collected (Hankin et al., 2005). Thirdly, the unknown percentage of non-landed mortalities from by-catch, as well as changing catch methods and effort levels, added uncertainty to survival estimates. Unreported fishing catches, missed wild escapements and reduced freshwater sampling rates all contributed to further bias in CWT-based estimates (Hankin et al., 2005). Further details on the history of salmon fishing and research in Canada, the United States, Japan and Russia can be found in reviews by Augerot (2001) and Morita et al. (2006).

With more accurate, stock-specific data, managers could eliminate some of the bias existing in survival prediction calculations. For example, Hankin et al. (2005) reported that natural marine mortality rates are assumed to be known and constant in chinook salmon ( $O$. tshawytscha) cohort analyses, and other forecast models assume that catchability and stock densities are uniform. Furthermore, very few wild stocks are tagged, thus CWT estimates of abundance represent primarily hatchery fish. This is problematic, as differences have been found in the migratory behaviour and survival of wild and hatchery fish of the same stock (Hill et al., 2006; Araki et al., 2007a; 2007b; Chittenden et al., 2008). Filling in knowledge gaps and gaining a more detailed understanding of the behaviour and survival of each wild stock would improve the predictive ability of fishery managers.

### 1.3 Mitigative Strategies

With the uncertainty that lies ahead for salmon populations, well-developed mitigative strategies based upon the best technology may be necessary. Fisheries and Oceans Canada created the Salmon Enhancement Program in 1971 to mitigate declining salmon populations in the Strait of Georgia, BC (Cross et al., 1991). However, there has been little evidence to show that hatchery releases are increasing the abundances of wild stocks (Sweeting et al., 2003). While increasingly large numbers of hatchery-reared coho salmon were being released into the Strait of Georgia every year, the marine survival of many stocks continued to decline (Beamish et al., 2008).

Understanding the effects of hatchery-reared fish on wild populations is crucial for effective fisheries management, though these effects are relatively unknown (Sweeting et al., 2003). In 2001, 70\% of the coho salmon caught in the Strait of Georgia were found to be hatchery-reared (Sweeting et al., 2003). Concern arose that hatchery fish were supplanting the wild fish and hypotheses were developed to explain why hatchery-reared fish seemed to be surviving better (Sweeting et al., 2003). However, by 2006 and despite higher releases of hatchery fish from rivers in the area, the percentage of hatchery fish caught in the Strait of Georgia had dropped significantly (Beamish et al., 2008). Many factors could have influenced this dramatic difference in survival rate between hatchery and wild populations. The genetic, physiological and behavioural advantages of wild stocks are emerging as primary suspects (Araki et al., 2007a; 2007b; Chittenden et al., 2008). Climate change may also be affecting hatchery-reared fish differently than wild fish (Beamish et al., 1999b). For example, recent work suggests that as temperatures increase and wild fish leave the rivers earlier, they may be able to consume much of the marine food resources and reach a critical size before the later-migrating hatchery fish (Beamish et al., 2008).

### 1.4 New Techniques

New developments in marine telemetry methods provide tools that could help scientists better understand the effects of climate on Pacific salmon marine survival and migratory behaviour, and fill other major knowledge gaps in marine ecosystem dynamics. Passive Induced Transponder (PIT) tags and Radio Frequency Identification (RFID) tags have been used for decades to track individual fish in freshwater, but they lose their effectiveness in marine environments. Acoustic tags -electronic devices that each send out a
unique code- were developed more recently to track the marine movements of fish (e.g. Johnstone et al., 1995; Voegeli et al., 1998; Thorstad et al., 2004; Finstad et al., 2005). As the tagged fish passes near a hydrophone receiver, the transmitted code is detected and recorded by the receiver along with the date and time of the detection. Receivers moored on the bottom of the ocean contain built-in modems, enabling researchers to download them from a boat on the surface. Acoustic telemetry has been used in the Pacific to study stocks of coho (O. kisutch; Ogura et al., 1992; Miller and Sadro, 2003), chinook (Candy et al., 1996), chum (O. keta; Yano et al., 1997), sockeye (Cooke et al., 2005; Crossin et al., 2007), and steelhead trout (O. mykiss; Welch et al., 2004; Melnychuk et al., 2007). However, very few studies have correlated environmental data with migratory data in Pacific salmon using acoustic telemetry (Walker et al., 2000; Cooke et al., 2004; Crossin et al., 2008).

As marine telemetry projects are often expensive and time consuming, it is highly beneficial to have large teams of people working co-operatively. The Pacific Ocean Shelf Tracking project (POST) is an international collaboration that has deployed arrays of hydrophone receivers on the ocean floor off the west coast of North America to facilitate the tracking of salmon and other migratory species (Welch et al., 2003). Researchers are beginning to see the value of these large-scale projects and their potential benefits (Melnychuk, 2007; Cooke et al., 2008). For a more comprehensive description of new technologies and research on Pacific salmon relating to climate, see Chapter 2.

### 1.5 Objectives

This introduction has identified key information gaps in Pacific salmon research -namely stockspecific salmonid marine survival, migratory behaviour and ecosystem dynamics, especially as they relate to environmental changes. Coho salmon were chosen as a study species for this dissertation, as the number of endangered coho salmon stocks is increasing in the southern part of their range (Nehlsen et al., 1991; Allendorf et al., 1997; Bradford and Irvine, 2000). Furthermore, during the 1990s in the Strait of Georgia, BC , coho populations underwent a complete change in migratory behaviour and a decline in marine survival, which was correlated to a climate shift at the time (Beamish et al., 1999a; Irvine, 2004). Some believed that the population declines were due to overfishing; however when the coho fishery was closed in

1998, the marine survival of coho did not improve (Bradford and Irvine, 2000). Little is known about the causes or details of the changes in coho marine survival and migratory behaviour.

Tracking coho salmon smolts with acoustic telemetry has been challenging due to their small body size. There has only been a single telemetry study published on the early marine (estuarine) survival of coho (Moser et al., 1991), and no work to date has addressed the influences of climate on the detailed behaviour and survival of an individual coho stock. Smaller tags are continually being developed, and there are acoustic tags available now that are 6 cm in diameter (VEMCO Ltd., Halifax, NS). However, minimum body size to tag size ratios are not known for coho.

The overall objective of this dissertation is to provide a unique insight into the early marine migratory survival and behaviour of juvenile wild and hatchery coho in southern BC , using newly available technologies. Chapter 2 is a critical review of the literature with an outline of how advanced technologies can be used to fill the major information gaps that exist in Pacific salmon ecology. Tag effects are investigated in chapter 3 with a two-year laboratory study to determine the appropriate tag to body size ratios for coho salmon. The survival and migratory behaviour of Canada's most endangered coho stock were observed over a three-year period and are discussed in Chapter 4. One possible cause of poor survival rates in wild coho is the continual introduction of hatchery fish into the Strait of Georgia ecosystem. Chapter 5 examines differences between a population of wild and hatchery-reared coho salmon in terms of physiology, survival and migratory behaviour. Finally, in Chapter 6, the altered migratory behaviour and survival of juvenile Strait of Georgia coho salmon are studied in the field using acoustic telemetry.

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## CHAPTER 2: A Critical Review of Pacific Salmon Marine Research Relating to Climate ${ }^{1}$

### 2.1 Introduction

Pacific salmon have existed in the North Pacific Ocean for over five million years (Neave, 1958; Shedlock et al., 1992; McPhail, 1997). Natural climatic changes have caused fluctuations in salmon abundance over several thousand years (Finney et al., 2000). Their impressive adaptive ability (Hendry et al., 2000) has been one of the major factors enabling salmonid survival to this day. However, recent changes in climate are occurring at an unprecedented rate (Emanuel, 2005; Jouzel et al., 2007). Scientists have declared that the major trends in climate observed in the past fifty years have been caused by human activity, and warn that if present emission levels continue global climate systems could be damaged for thousands of years (IPCC, 2007).

Fishery scientists face the challenging task of distinguishing between the influences of 6-18 month weather patterns (e.g. El Niño), 20-30 year regimes (e.g. the Pacific Decadal Oscillation), and longer-term climate change on salmon populations (Rasmussen and Wallace, 1983; Philander, 1983; 1990; Kerr, 1995; Mantua et al., 1997). The Pacific Decadal Oscillation, a large-scale climate pattern in the North Pacific, has had direct impacts on salmon populations (Mantua et al., 1997; Beamish et al., 1999a; Hare and Mantua, 2000). Regime shifts have been correlated to significant changes in the migratory patterns, abundance and marine survival rates of Pacific salmon (Beamish et al., 1997a; Welch et al., 2000; Hobday and Boehlert, 2001; Beamish et al., 2004). These correlations may also change during El Niño years and similarly, over time, long-term climate change may counteract decadal regime effects and alter the marine environment in unforeseen ways (IPCC, 2007).

The need for marine ecosystem assessments of anadromous salmon has been demonstrated globally (Beamish and Mahnken, 1999; DFO, 2000; Commission of the European Communities, 2002; NOAA, 2002). Ecosystem-based fisheries management that incorporates biotic and abiotic data from an ecosystem rather than from solely a target species is essential to the creation of sustainable fisheries, particularly with the changing marine environment (Beamish and Mahnken, 1999). Even without taking into account the complexities of climatic effects, the task of understanding ecosystem effects on Pacific

[^0]salmonid migratory behaviour is a challenge, largely due to the high degree of variability that exists between species, stocks and brood years (French et al., 1976; Groot and Margolis, 1991; Waples et al., 2001). The use of new technologies combined with environmental monitoring systems, will improve our limited understanding of how climatic changes affect the marine survival and migratory behaviour of Pacific salmon. This critical review assesses the current understanding of climate effects on Pacific salmon and where knowledge gaps could best be addressed through the employment of electronic devices and other advancing technologies.

### 2.2 The Pacific Climate

Scientists and economists have stated that reversing climate change should be a global priority (Tolimieri and Levin, 2004; IPCC, 2007; Stern, 2007). The long-term economic benefits of preserving natural resources are being examined as changes in the environment become more noticeable (Mote et al., 2003; Stern, 2007). Recent changes in global climate patterns have been attributed to the build-up of greenhouse gases in the atmosphere (Kerr, 1995). Emissions of carbon dioxide, methane and nitrous oxide have increased during the last century as the human population has grown exponentially (Lashof and Ahuja, 1990). Ice cores in Antarctica provide evidence that atmospheric carbon dioxide levels are higher now than they have been in the past 800,000 years and are increasing at a rate never before recorded (Petit et al., 1999; Jouzel et al., 2007). Greenhouse gases trap energy from the sun and as a result, cause Earth's surface temperature to rise. The warmest year on record (average surface air temperature) in the U.S. was 2006 (NOAA Public Affairs, 2007), and if current trends continue, the average surface air temperature of the northern hemisphere is estimated to rise more than $3{ }^{\circ} \mathrm{C}$ by 2050 (Mann et al., 1999). Elevated carbon dioxide levels in the atmosphere could also raise the acidity of the oceans, which may have major effects on the marine ecosystem (Caldeira and Wickett, 2003).

Earth's increasing surface temperature has resulted in disturbing changes in global wind patterns and the cryosphere (the frozen areas of Earth's surface). Ice breakup in the spring is happening earlier than it did fifty years ago, the area and thickness of ice sheets are decreasing, and precipitation patterns are changing (Magnuson et al., 2000; Livingstone, 2001; Robertson et al., 2001). The cryosphere is an integral part of the global ecosystem, controlling the water supply to many areas and influencing ocean currents
(Magnuson, 2002). A rise in sea levels due to the thermal expansion of the oceans and the increased melting of ice has altered coastal habitat (Morris et al., 2002). The disappearance of the polar ice cap and other important ice sheets will transform the marine environment in ways that can only be speculated upon (Alley, 2002). Increases in global surface temperatures have also been correlated to increases in zonal wind strength (Kalnay et al., 1996), which are a major driver of oceanic currents (Munk, 1950; McGowan et al., 1998; Walther et al., 2002). Wind patterns are becoming more extreme (IPCC, 2007) and the number of category four and five hurricanes has doubled during the past 30 years (Emanuel, 2005).

Oceanic currents are the circulation system for the entire marine ecosystem (McPhaden and Zhang, 2002). Cold, nutrient-rich waters from the deep are drawn up to the surface, allowing for the growth of phytoplankton, which form the base of the ocean food chain (Pickett and Schwing, 2006). Phytoplankton are extremely sensitive to temperature, nutrient concentrations and sunlight levels, making them good indicators of climate pattern changes and environmental conditions (Roemmich and McGowan, 1995). If the currents change, the depth and concentration of nutrient layers change and oceanic productivity is affected (McGowan et al., 1998). These effects are manifested in Pacific salmon size, abundance, marine survival and migratory behaviour (Bardach and Santerre, 1981; Beamish, 1993; Johnson, 1998; Williams, 1998; Beamish et al., 1999a; 199b; 2000; Cole, 2000; McFarlane et al., 2000; Hobday and Boehlert, 2001; Mote et al., 2003; Beamish et al., 2008).

Correlations between population size and climatic indices have been recorded in many species, including Pacific salmon (Beamish and Bouillon, 1993). From the subtropic to the arctic zones of the Atlantic and Pacific Oceans, the productivity of the main commercial fish stocks was closely related to the atmospheric circulation index (ACI a measure of the dominant direction of air mass transport) and the earth rotation velocity index (ERVI a measure of Earth's rotational velocity, which affects the length of day; Klyashtorin, 1998). The Aleutian low pressure index (ALPI), a measure of the area of the North Pacific Ocean covered by the Aleutian low pressure system less than 100.5 kPa , was significantly correlated to the catch of Pacific salmon (Beamish and Bouillon, 1993). The catch of sockeye, pink (O. gorbuscha) and chum salmon in Alaska was significantly correlated to temperature at the time and location of the return migration, as well as environmental conditions during the smolt run (Downtown and Miller, 1998). A study
sampling Alaskan sockeye salmon along the eastern Bering Sea shelf found that the diet, condition, and distribution varied with ocean temperature (Farley et al., 2007).

Not all salmon stocks appear to be affected equally during climate shifts however. When salmon populations off Oregon and Washington approached all-time lows in 1972, abundances in Alaska increased significantly - possibly due to differences in marine survival rates or altered migratory behaviour patterns (Coronado and Hilborn, 1998; Bradford, 1999; Hare et al., 1999; Welch et al., 2000; Hobday and Boehlert, 2001). Ocean productivity is the main determining factor of overall marine survival for salmon and northern waters are increasing in productivity while the biomass in southern waters declines (Nickelson, 1986; Fisher and Pearcy, 1988; Beamish and Bouillon, 1993; Hare and Francis, 1995; Mantua et al., 1997; Beamish et al., 2000). The early marine survival rate of salmon is influenced by individual body size (Holtby et al., 1990; Beamish et al., 1997b). The number of juveniles to reach a critical size by a particular time has been associated with brood year survival and abundance (Beamish and Mahnken, 2001; Ruggerone et al., 2007). If prey availability is low, juvenile salmon may not reach their critical body size before winter and would suffer high mortality as a result.

Shifting currents and higher water temperatures may be affecting the ability of Pacific salmon stocks to return to natal streams to spawn (Richter and Kolmes, 2008). Researchers in Canada, Japan, Russia and the United States have found correlations between changes in climate and the migratory behaviour of Pacific salmon populations (Welch et al., 1998; Beamish et al., 1999b). Trans-Pacific surveys conducted by the Japanese and Canadian governments during the 1990s, combined with historical data since the 1950s, found that there were strong sea-surface temperature (SST) limits for sockeye salmon that significantly affected their migratory behaviour and could limit the species to the Bering Sea in fifty years (Welch et al., 1998). Sockeye salmon in the Columbia River, WA (Figure 2.1) have been migrating upriver more than a week earlier on average than they did fifty years ago (Quinn et al., 1997). In the Strait of Georgia and the Juan de Fuca Strait (Figure 2.1), the average annual SSTs have increased by one degree over the last century (Environment Canada, 2008; Figure 2.2) and adult Fraser River sockeye have been returning to rivers on the west coast of Vancouver Island to spawn (McKinnell et al., 1999). Migratory routes of coho salmon in the Strait of Georgia have been altered since 1995, when virtually all of the resident juvenile coho salmon left the Strait during late fall (Beamish et al., 1999b). Furthermore, the final
ocean weight of Fraser River sockeye decreased with an increasing SST, potentially affecting their reproductive success (Hinch et al., 1995; Pyper and Peterman, 1999). Temperature barriers exist not only due to lethal temperature limits, but also to tight energy budgets faced by salmon during the winter months (Richter and Kolmes, 2008). When prey availability is low, salmon need to keep their basal metabolism at a minimum, since metabolism increases exponentially with temperature (Brett et al., 1969). Thus, the migratory behaviour, feeding behaviour and trophic dynamics of Pacific salmon can be affected when the fish are faced with climate-induced changes in water temperature and prey resources (Kaeriyama et al. 2004).

Other effects of climate, such as an earlier onset of spring, can further affect salmon stocks (Beamish et al., 1999a). The mean daily discharge of the Fraser River, BC in April has been increasing (Environment Canada, 2008; Figure 2.3), which is indicative of an advancing spring freshet, and an earlier marine productivity bloom (Beamish et al., 2001). This trend towards an earlier productivity bloom favours smolts that migrate out earlier in the spring (Beamish et al., 1999a; Beamish and Mahnken, 2001). Therefore, earlier migrating species such as pink and chum salmon may have an advantage over later migrating coho and chinook salmon (Beamish et al., 2000). Additionally, as wild smolts migrate downstream earlier, hatchery fish generally have a static release time, which may be contributing to their reduced marine survival (Beamish et al., 2008).

Changes in climate can be grouped into short-term patterns, decadal regimes and long-term trends. The El Niño/La Niña Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) resemble each other spatially but differ temporally. More extreme in tropical areas, ENSO patterns generally occur every 2-7 years and last for 6-18 months (Philander, 1983; Rasmussen and Wallace, 1983; Philander, 1990). The PDO has occurred in 20-30 year regimes during the $20^{\text {th }}$ century, and is more noticeable in the North Pacific (Mantua et al., 1997). Cooler PDO periods lasted from 1890-1924 and 1947-1976, whereas warmer regimes occurred from 1925-1946 and 1977 onward (Beamish et al., 2004). A cold regime may be beginning in 2008, however long-term warming trends could affect the regime cycle. Long-term alterations of the global climate systems due to climate change are potentially irreversible (IPCC, 2007). Interactions between short-term climate patterns, decadal regimes and long-term climate change trends are complex. If
the consumption rate of Pacific salmon is to continue at present levels, improvements in the precision of fisheries data and climate prediction capabilities are essential (Bardach and Santerre, 1981; Cole, 2000).

### 2.3 Electronic Devices as Tools to Study Climatic Effects

The great diversity of Pacific salmon has been attributed to the changing topography, climate and glaciations of the west coast of North America during the past five million years (Montgomery, 2005). Each Pacific salmon species has unique migration strategies related to the timing of life stages, rates and routes of travel, habitat use and responses to environmental factors such as flow rates, temperature, and salinity (Groot and Margolis, 1991; Mueter et al., 2002). For example, pink salmon have a two-year lifecycle, migrating to the ocean quickly and returning after 18 months to spawn and die (Heard, 1991); whereas, sockeye salmon spend the first few years of their life in freshwater before traveling great distances in the ocean and returning up to four years later (Burgner, 1991). Though some pink and coho salmon spend their entire marine life in coastal waters, juvenile steelhead trout prefer offshore areas (Pearcy and Masuda, 1982; Argue et al., 1983; Hartt and Dell, 1986; Fisher and Pearcy, 1988). Within each species there are thousands of spawning populations and variation exists among stocks co-inhabiting the same river system (Groot and Margolis, 1991). For example, in the Fraser River watershed, the timing of sockeye salmon out-migration tends to depend on the lake system in which the stock originates (Burgner, 1991).

Whereas the freshwater stage has been the primary focus of salmon research, scientific information about estuarine and early marine survival for Pacific salmon stocks remains lacking (Pearcy and Masuda, 1982; Perry et al., 1998; Brodeur et al., 2000; Weitkamp and Neely, 2002; Beamish et al., 2003). Marine research has typically made use of catch data from fishing vessels to estimate population sizes and migration patterns (Beamish et al., 2003). Coded-wire tags (CWTs) enabled researchers to tag large numbers of young salmon, with each stock given a unique identifier. CWTs and other mechanical tags have provided a vast amount of stock migratory data; however, the technology requires the re-capture of tagged animals. Little detailed and accurate information can be gained about the fish's habitat use, swimming speed, small-scale movements, exact timing of migration, or residence times. Thus, the influences of a rapidly changing environment on fish movement, survival, and growth are limited to
speculation with mechanical tags. For a thorough review of the CWT program and biases in catch data models, see Hankin et al. (2005).

The further development of modern stock identification methods, such as microsatellite DNAbased genetic stock identification (GSI) technology and single nucleotide polymorphisms (SNPs), could allow any fish caught in the ocean to be traced back to a specific stock and brood year (Nielsen et al., 1997; Bravington and Ward, 2004; Liu et al., 2004). While these methods could provide a wealth of distribution data for individual stocks in time, they still require the capture of fish in the ocean and do not allow for the monitoring of a live fish in its environment. The lack of information regarding the spatial and temporal migratory patterns and survival of individual stocks and how they react to changing environmental conditions is the primary reason that fisheries models provide unreliable estimates of predicted returns, and as a result are limited in their usefulness to management plans and conservation strategies. Furthermore, as some salmon stocks become more threatened, catch data is in some cases non-existent. The removal of large numbers of endangered fish from the sea for research is controversial. The primary knowledge gaps in Pacific salmon biology as it relates to climate include stock-specific marine survival and marine migratory behaviour, and ecosystem dynamics. New methods using electronic devices can help fill these and other knowledge gaps that exist in fisheries research.

### 2.3.1 Marine Survival

Advances in the field of hydro-acoustic telemetry during the last thirty years allow for marine survival data to be obtained independent of fish harvest. Fish as small as 11 cm can be tagged without adverse effects on their growth or survival (Chittenden et al., 2008a), which makes field studies of Pacific salmon species with smaller smolts possible (Chittenden et al., 2008b). For reviews of early acoustic telemetry work see Ireland and Kanwisher (1978), Mitson (1978), and Stasko and Pincock (1977). Later studies are summarised in Baras (1991), Arnold and Dewar (2001), and Jepsen et al. (2002). Coded acoustic transmitters have also been developed that contain an Electromyograph (EMG) to record heart rate, feeding activity, breathing activity, swimming speed, acceleration and movement patterns of individual fish as they pass through different environments (e.g. Armstrong et al., 1989; Whitney et al., 2007). For a comprehensive review on the applications of EMG tags, see Cooke et al. (2004a).

Additionally, archival and coded tags that monitor temperature, depth, oxygen, pH and light levels experienced by the fish are available (e.g. from VEMCO Ltd., Halifax, NS, or Thelma AS, Trondheim, Norway).

As discussed in the previous section entitled The Pacific Climate, environmental changes have been correlated to catch and return rates of Pacific salmon stocks. However, this type of data provides little detail in terms of high marine mortality areas, exact causes of mortalities, or how individual fish respond to environmental changes. Acoustic telemetry has been used to study the early marine survival of steelhead trout (Welch et al., 2004; Melnychuk et al., 2007) and sockeye salmon (Cooke et al., 2005a) using listening lines of hydrophone receivers moored on the ocean floor (Welch et al., 2003). These studies are good examples of how acoustic telemetry could be employed to fill the knowledge gaps in stock-specific marine survival rates; however they do not incorporate climate data. Only one published report could be found regarding climate effects on the marine survival of Pacific salmon using acoustic telemetry. Crossin et al. (2008) examined the relationship between exposure to high temperature during spawning migration and the survival, behaviour and physiology of adult sockeye salmon. They found that fish exposed to higher temperatures during their homing migration had significantly lower survival to the spawning site and higher infection levels of Parvicapsula minibicornis.

Much can be done to improve the quality and quantity of data concerning climate effects on the marine survival rates of Pacific salmon. EMG tags monitoring heart beat, feeding rate, depth or swimming speed can indicate metabolic rates, or whether a fish has died (Cooke et al., 2004a) if detected by a manual tracking device or autonomous underwater vehicle / glider (AUV; Webb Research Company, Falmouth, MA). Satellite tags (recording depth and temperature for example) attached externally to migrating species, can be programmed to pop-off and transmit when the fish has remained at one depth for an extended period of time (e.g. from Microwave Telemetry Inc., Columbia, MD). This technology is being used by researchers studying the marine survival and migratory behaviours of European eels (Anguilla anguilla) on their journey across the Atlantic (Aarestrup et al., unpublished data), and by the Tagging of Pacific Predators (TOPP) project to monitor many other species, including sharks and turtles (Weng et al., 2005; Shillinger et al., 2008). Telemetry data can be analysed in conjunction with environmental data (e.g. water temperature, pH , salinity, current, dissolved oxygen, pollutants) recorded by archival tags or sensors
located in the area of the detected fish to find correlations. For example, assessments of high mortality areas with possible links to long-term climate change are being conducted on the endangered Thompson River coho salmon with acoustic telemetry (see Chapter 4).

The long-term monitoring of every Pacific salmon stock, including yearly baseline health assessments, would be ideal. However, there are many limitations to this type of work; namely the cost and time involved in telemetry studies. Transmitters and receivers are fairly expensive; perhaps with time the cost of this equipment will decrease, but as with most new technologies not yet widely used, considerable funding is required for an acoustic telemetry study. Archival tags also require the tagged fish to be recaptured to obtain the data. Furthermore, deploying receiver equipment, manual tracking and analysing the data are time consuming and require expertise. Permanent listening arrays, gliders and databases that automatically edit and animate telemetry data may help cut down on time costs, however. There is also the possibility of tag effects on the fish. While tag effect studies have been done on Atlantic salmon Salmo salar (Greenstreet and Morgan, 1989; Moore et al., 1990; Lacroix et al., 2004), chinook salmon (Anglea et al., 2004), coho salmon (Moser et al., 1990; Chittenden et al., 2008a), sockeye salmon (Steig et al., 2005), and steelhead trout (Brown et al., 1999; Welch et al., 2007), every stock is unique and it is advisable to do a tag effect trial with each project. The smolts of pink and chum salmon are too small to implant with the available sizes of acoustic transmitters. Therefore, these species would need to be caught at sea (e.g. with a purse seine) once they have grown to a more adequate size, for studies of early marine survival. Finally, causal relationships are difficult to determine in these types of open field experiments. Laboratory studies investigating individual and multiple environmental stressors on the physiology and health of the tagged stocks would complement field work.

### 2.3.2 Marine Migratory Behaviour

Coded acoustic transmitters and archival tags have been developed that can be used to study the marine migratory behaviours of individual fish over several years (Moore and Potter, 1994; Johnstone et al., 1995; Voegeli et al., 1998; Thorstad et al., 2004; Finstad et al., 2005). In addition to the marine survival studies previously mentioned, these technologies have been used to track the marine migratory behaviour
of coho (Moser et al., 1991; Ogura et al., 1992; Miller and Sadro, 2003; Chittenden et al., 2008b) sockeye (Crossin et al., 2007), chinook (Candy et al., 1996) and chum salmon (Yano et al., 1997).

Purely descriptive studies that do not touch on mechanistic reasons for behaviours, or employ an experimental approach to telemetry field work do little to further our understanding of environmental effects on salmonid behaviour. Cooke et al. (2008) outline how acoustic telemetry should unify research across disciplines, combining laboratory and field work. Some studies combined environmental and marine migratory data (Walker et al., 2000; Crossin et al., 2008). Temperature and light levels experienced by pink, coho and chum salmon, and steelhead trout in the North Pacific were analysed by Walker et al. (2000), who found that the offshore distribution of salmon may be more linked to prey distribution than SST. Teo et al. (2004) used light level and sea surface temperature data recorded by electronic tags to validate geolocation estimates. There is also ongoing monitoring of returning Fraser River sockeye salmon adults to test the hypothesis that as river temperatures increase yearly, disease and parasite levels are rising, and the timing of the return migration and the reproductive success of this species are being affected (Cooke et al., 2004b; Crossin et al., 2008).

With the number and variability of Pacific salmon stocks in existence, the gap in stock-specific marine migratory behaviour research -especially as it relates to climate- is significant. The generalised home ranges of the Pacific salmonids have been known for many years (Groot and Margolis, 1991). However as the marine climate changes, the migratory behaviours of some populations are changing (e.g. McKinnell et al., 1999; Beamish et al., 2008). Ongoing work by Chittenden et al. (see Chapter 6), in collaboration with the POST project, is investigating climate-induced changes in the migratory behaviour of coho and chinook salmon in the Strait of Georgia, BC (Figure 2.1). This project required the use of acoustic tags to answer specific questions about migratory timing and marine mortality rates, possible size effects on migratory behaviour and survival, and differences between early and late summer groups. Without the use of electronic devices, the hypotheses of this study would not have been possible to test.

Manual tracking, while time-consuming, can provide a continuous stream of information about the migratory behaviour of an individual fish within its environment. For example, the migratory behaviour of manually-tracked Atlantic salmon post-smolts tagged with acoustic depth sensing transmitters was enhanced with information about light intensity (Davidsen et al., 2008) and temperature (Plantalech Manel-
la, unpublished data) recorded from the boat. A relevant but non-salmonid study in South Africa examined environmental factors (turbidity, salinity, temperature and tidal phase) that may influence the movement of Spotted grunters (Pomadasys commersonnii) in an estuary (Childs et al., 2008). Using coded EMG transmitters (e.g. monitoring feeding, swimming, or heart rates) and environmental sensing transmitters (e.g. depth, temperature, salinity) in manual tracking studies expands the possibilities of analysing the physical responses of fish to environmental cues. Mooring arrays of fixed hydrophone receivers with attached environmental monitoring devices to track tagged fish, while not as data-rich as manual tracking, is likely to be less time consuming and provide larger and more reprentative sample of fish populations. Moored listening stations can relay telemetry and environmental data to satellites, which in turn can send the real-time data directly to the offices of fishery managers. Thus, as temperatures and current patterns change in areas of prime Pacific salmon habitat, fishery managers can observe how tagged fish are reacting and adjust their management decisions accordingly. This would be especially effective for restricting fishing when the adults of an endangered salmon stock are migrating through an area. The topic of combining telemetry with other new technologies will be further discussed in Ecosystem Dynamics.

As mentioned previously, it would be ideal to have an international program in place to tag and monitor sample sets of every Pacific salmon stock, and analyse marine migratory data in conjunction with environmental data. An on-going, long-term program would allow stocks to be monitored during years with and without major climatic changes such as regime shifts or El Niño and La Niña events. This would greatly improve our understanding of how such events -and long-term climate change- affect salmon distributions and survival at sea, which would be an expensive endeavour. However, the alternative may be more costly in the long run.

### 2.3.3 Ecosystem Dynamics

Salmon have a great deal of phenotypic plasticity, meaning that they are able to adapt physically to their environment (Hendry et al., 2000). New molecular and genomic techniques are revolutionising marine microbiology by enabling the study of marine ecosystems from the microbe up in efforts to understand the complex interactions between organisms within their changing environment (Doney et al.,
2004). This new interdisciplinary science will be integrating information gained from marine fishery research and can assist in the furthering of Pacific salmon biology within the marine ecosystem.

Developments in electronic devices used in marine research also have the potential to greatly improve the present understanding of Pacific salmonid marine ecosystem dynamics. Telemetry was used in the study of an Oregonian estuary that found harbour seals (Phoca vitulina) to be predating heavily on returning adult salmon (Wright et al., 2007). Acoustic technologies were also used to monitor fish aggregations in Marine Protected Areas (e.g. O’Dor et al., 2001; Cooke et al., 2005b; Meyer et al., 2007), at aquaculture sites (e.g. Begout Anras and Lagardere, 2004; Cubitt et al., 2005; Conti et al., 2006), and around Fish Aggregating Devices (e.g. Ohta et al., 2001; Dagorn et al., 2007). Most of these studies did not examine environmental influences on behaviour.

The ecosystem effects of the annual release of billions of hatchery-reared salmon into the Pacific Ocean by the US, Canada, Russia and Japan are relatively unknown (Beamish et al., 1997b); however differences in performance, survival, behaviour and physical condition between wild and hatchery-reared salmon have been found (Fleming and Gross, 1993; Shrimpton et al., 1994; Berejikian et al., 1996; Nielsen et al., 1997; Weber and Fausch, 2003; Hill et al., 2006; Araki et al., 2007; Chittenden et al., 2008b). If hatchery programs continue to exist as attempted mitigative strategies, it is crucial that their ecological effects are understood and that best practices strategies are created. In addition to using electronic devices, the possibility of using otoliths and scales to distinguish between salmon of wild or hatchery origin would allow any fish captured in the ocean to be a source of data and could further the study of hatchery fish in the Pacific ecosystem (Hartt and Dell, 1986; Schwartzberg and Fryer, 1993; Zhang and Beamish, 2000).

When advanced technologies are combined, the benefits are great. Sonar and light detection and ranging (lidar) technologies allow for the study of salmon aggregation behaviours in the ocean (Gauldie et al., 1996; Misund, 1997; Tollefsen and Zedel, 2003; Churnside and Wilson, 2004). Monitoring stations could be positioned on the bottom of the ocean scanning upward, or on the surface scanning downward, at important migratory passageways, to observe groups of fish passing by (O'Dor and Gallardo, 2005). Environmental sensors could be attached to the stations to monitor climatic conditions in the area (e.g. including marine productivity levels). These observatory nodes could also be fixed to ocean platforms or to the bottom of slow moving vessels. Combining acoustic telemetry with these other imaging technologies
would effectively enable researchers to study individual fish of known stock, size and physical condition within aggregations, as well as their inter- and intra-specific behaviours.

Sea floor sensor arrays allow the observation of oceanic conditions and ecosystem productivity in real-time. Examples of large-scale sea floor arrays include the American National Science Foundation's Ocean Observatories Initiative (OOI), Japan's Dense Ocean floor Networking system for Earthquakes and Tsunamis (DONET), and the European Multidsiciplinary Seafloor Observatories research infrastructure (EMSO). Data from these underwater monitoring systems as well as other governmental environmental recording stations could be used by fishery researchers in conjunction with marine survival and migratory data from acoustic technologies.

International telemetry projects aimed at studying marine ecosystems have governments and scientists working in collaboration. The TOPP and POST projects, as parts of the Census of Marine Life (COML), have pushed the boundaries of marine science in the Pacific (Welch et al., 2003; Shillinger, 2008). Marine animals from squid to salmon smolts have been tracked across the Pacific with satellite tags and acoustic arrays, including some mammals that have collected vast amounts of environmental data along their journeys (Weng et al., 2005). These projects allow for the study of inter-and intra-specific interactions, with newer technologies being developed all the time -such as the "chat" tag that allows tagged animals passing by each other to "chat" with each other and record the interaction so that it can be passed on to a receiver at a later time (VEMCO Ltd.) Receivers attached to floats, marine mammals or gliders can record data from any other tagged animal in their vicinity, as well as environmental data, before relaying the information to satellites from the surface. Dalhousie University's Ocean Tracking Network (OTN) is developing a global infrastructure with the goal of collecting data on marine animals in relation to the changing ocean environment. While progressive and necessary to deal with existing knowledge gaps, these initiatives have limitations -including the challenge of dealing with the vast amounts of data produced, and gaining enough buy-in from researchers, governments and funders to support the infrastructure required for long-term studies.

### 2.4 Conclusion

Salmon have adapted to changes in climate over millions of years, however scientists are only beginning to understand how climate affects salmon productivity in the Pacific. The majority of Pacific salmon research has focused on freshwater survival (Beamish et al., 2003). However, recent observations in the decline of marine survival rates of many stocks and the increasing rate of changes in global climate add urgency to the need for information about their ocean phase (Beamish et al., 2008). There is limited understanding of how free-ranging fish respond to environmental stimuli, which presents a serious challenge to fishery managers trying to accurately predict how salmonid populations will be affected by climate change. A coordinated international research effort should be undertaken to develop a baseline understanding of the marine survival and migratory behaviour of individual Pacific salmon stocks, especially in the face of imminent environmental changes. The consequences of short- and long-term climate trends on ecosystem dynamics should also be investigated. Using advanced electronic technologies to compare the effects of marine environmental conditions on individual salmon populations would improve the predictive ability of fishery managers.


Figure 2.1 The Columbia and Fraser Rivers, the Strait of Georgia and the Juan de Fuca Strait, off the west coast of North America.


Figure 2.2 Mean annual sea surface temperature (SST) in the Strait of Georgia from 1922 to 2007. Data from the Race Rocks Lighthouse ( $48.18{ }^{\circ} \mathrm{N}, 123.32{ }^{\circ} \mathrm{W}$ ) in the Strait of Juan de Fuca is shown in circles; data from the Entrance Island Lighthouse ( $49.13{ }^{\circ} \mathrm{N}, 123.48^{\circ} \mathrm{W}$ ) in the Strait of Georgia is shown in triangles (Environment Canada, 2008).


Figure 2.3 The April mean daily discharge of the Fraser River at Hope, BC from 1912 to 2006 (Environment Canada, 2008).

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## CHAPTER 3: Maximum Tag to Body Size Ratios for an Endangered Coho Salmon Stock Based on Physiology and Performance ${ }^{2}$

### 3.1 Introduction

As with many fish populations world-wide, some Pacific salmon stocks have declined substantially over the last three decades. The largest tributary to the Fraser River, British Columbia's Thompson River contains a severely depleted population of coho salmon (Bradford and Irvine, 2000). The Thompson River coho, currently the most endangered salmon stock in Canada, is derived from the extinct Upper Columbia coho run and is genetically distinct from all other coho populations in BC (Small et al., 1998; Shaklee et al., 1999; Beacham et al., 2001). Investigations into the poor status of this stock have suggested that declining ocean productivity, freshwater habitat alteration, and over-fishing are likely causes (Bradford and Irvine, 2000), although a complete fishing closure in 1998 did not improve the situation. In an effort to pinpoint areas of high mortality for this stock, researchers with the POST project (Welch et al., 2003) have used biotelemetry to track the riverine and early marine migratory behaviour of free-ranging Thompson River coho salmon since 2004. This research involves surgically implanting acoustic tags into the body cavity of coho pre-smolts and subsequently tracking them in the freshwater and marine environments. Critical to this type of study is the understanding of what effects the tags and surgery may have on the survival, condition, growth and swimming performance of the animals being monitored.

To date there are no published studies that examine tag effects on coho salmon pre-smolts. Acoustic transmitters small enough to be implanted in coho salmon pre-smolts have only been developed recently, offering a new and unique opportunity to study the early migratory behaviour and survival of this animal. Guidelines for tag to transmitter ratios have been discussed for salmonid species with larger smolts, including Atlantic salmon (Greenstreet and Morgan, 1989; Moore et al., 1990; Lacroix et al., 2004), chinook salmon (Adams et al., 1998a; 1998b; Jepsen et al., 2001; Anglea et al., 2004), cutthroat trout Salmo clarki (Zale et al., 2005) and rainbow trout/steelhead (Lucas, 1989; Brown et al., 1999; Welch et al., 2007). The maximum tag to body weight ratios discussed in these studies range from 2-12\%, demonstrating

[^1]the high variability in sensitivity and physiology among salmon species (Jepsen et al., 2004). Therefore, the effects of acoustic tags on coho salmon cannot be inferred from studies on other species. Given the small size of the animals being tracked, it is critical that the effects of transmitters on the physiology and performance of the individuals are known. In British Columbia alone, field studies using acoustic telemetry to track coho salmon migration have been carried out in the Thompson, Nimpkish, Stamp, Keogh, Campbell and Cheakamus Rivers (Welch et al., 2004; Melnychuk et al., 2007; Chittenden et al., 2008). The results from this tag effects study are thus important to ongoing coho salmon field work and the Pacificwide coho conservation effort.

The tracking of salmon pre-smolt migratory behaviours using acoustic telemetry has been limited by tag size. Increasingly smaller transmitters have allowed for the study of smaller fish; however, the limits of tag size to body size are not clear. Jepsen et al. (2002) stated that "few studies have systematically investigated the effects of different tag to body weight ratios". The objective of our research was to determine the minimum size at which coho salmon pre-smolts could be implanted with three sizes of acoustic tag and suffer no effects. To meet this objective, morphological, behavioural and physiological parameters were measured. A significant difference in any of these parameters between tagged and sham or control fish would suggest that the acoustic tags were having an effect on behaviour and/or survival of tagged fish in the field.

### 3.2 Methods

Hatchery-reared Thompson River (Coldwater Creek) coho salmon pre-smolts from the Spius Creek Hatchery near Merritt, BC, were sedated with 0.1 ppm Aquacalm (Syndel Laboratories, Vancouver, Canada) and transported with supplemental oxygen to the DFO/UBC Centre for Aquaculture and Environmental Research in West Vancouver during the springs of 2005 and 2006. The fish were placed in an outdoor 244 cm -diameter fiberglass tank, supplied with aerated fresh water from Cypress Creek and fed to satiation daily for the duration of the study.

### 3.2.1 Treatment Groups

The experiments were conducted during 2005 and 2006. In mid-April 2005 (one week after transport), 224 fish were divided into seven size classes ranging from 9.5 cm to 13.0 cm fork length (Table 3.1a). Within each size class, the fish were randomly assigned to one of four treatment groups -control (PIT tag only), sham (surgery without transmitter), 6 mm tag (surgery with transmitter: $6 \times 19 \mathrm{~mm}, 0.9 \mathrm{~g}$ in air, 0.5 g in water $)$ and $7 \mathrm{~mm} \operatorname{tag}(7 \mathrm{x} 19 \mathrm{~mm}, 1.5 \mathrm{~g}$ in air, 0.8 g in water). An additional group of fish $(\mathrm{N}=$ 120) were reared separately for another 100 days, until they were large enough ( $12-14 \mathrm{~cm}$ ) to be implanted with 9 mm tags $(9 \times 21 \mathrm{~mm}, 3.0 \mathrm{~g}$ in air, 2.0 g in water). During this second set of surgeries, in July 2005, the fish were divided into four size groups and randomly assigned to three treatment groups (control, sham, and 9 mm tag). Following surgery these fish were placed into the same tank as the first group. All of the experimental fish were held in the same tank to minimise tank effects. To identify the control fish, it was necessary to mark them with PIT tags. The duration of this study ( 300 days) reflected the $9-10$ month lifespan of acoustic tags being used by many researchers throughout the world.

During 2006, control and 9 mm tag treatments were repeated with 200 fish to add larger size classes (up to 16.5 cm , Table 3.1b) because all of the size groups tested with 9 mm tags in 2005 had low survival and tag retention. The same surgical procedures and rearing methods were used, however no sham group was required as the sham and control fish had already demonstrated similar growth rates during the first year of study.

### 3.2.2 Surgical Procedure

Prior to surgery, the fish were sedated with 0.1 ppm Aquacalm and anesthetised in 60 ppm buffered MS222 (Syndel Laboratories, Vancouver, Canada). They were weighed, measured and placed on the surgery table ventral side up. The gills were gently irrigated with a maintenance dose ( 30 ppm ) of MS222, and a wet paper towel was placed over the head of the fish to reduce visual stimuli. Supplemental air and Vidalife (Syndel Laboratories, Vancouver, Canada) were included in all water baths. Oxygen levels and water temperatures were maintained to emulate source water ( $12.2 \pm 0.3 \mathrm{ppm}$ and $6.7 \pm 0.8^{\circ} \mathrm{C}$ during the April 2005 surgical period, $9.5 \pm 0.8 \mathrm{ppm}$ and $15.5 \pm 0.6{ }^{\circ} \mathrm{C}$ during the July 2005 surgical period, and $10.2 \pm 0.8 \mathrm{ppm}$ and $15.5 \pm 0.8^{\circ} \mathrm{C}$ during 2006.

PIT tags were inserted through a 2 mm incision along the midline of the fish, anterior to the pelvic girdle. For the tag treatment groups, a dummy acoustic tag containing a PIT tag was placed into the body cavity through a 10 mm incision in the same location. The incision was closed with two simple interrupted sutures (absorbable Ethicon Monocryl Y513 reverse cutting 4-0, 1.5 metric, 45 cm, PS-2 $19 \mathrm{~mm}, 3 / 8$ circle needle). Sham fish underwent the same procedure as tagged fish, however, only a PIT tag was inserted into the body cavity. The VEMCO dummy tags were created to mimic the three smallest acoustic transmitters available, using the same coating and weight distribution as regular VEMCO acoustic tags. The surgical tools were disinfected between surgeries with Ovadine (Dynamic Aqua Supply, Canada) and rinsed twice with distilled water. All of the fish were placed in a recovery bath following surgery until normal swimming behaviour was resumed, whereupon they were returned to the communal tank.

### 3.2.3 Sampling

A total of fourteen measurements of weight, fork length and healing stage were taken for the first surgery group (at $0,13,27,41,55,69,83,95,119,136,168,213,254$, and 300 days post-surgery). Similar measurements were taken for the second surgery group on day $0,22,39,71,116,157$, and 203 postsurgery. The fish were anesthetised in 60 ppm buffered MS222 prior to sampling, and were allowed to recover before being returned to their tank. Tag weights were subtracted from fish weights prior to analysis. The stage of healing was categorised as 'poor' (having no evidence of healing, possibly with gaps between stitches or tag protruding), 'fair' (healing had started with a thin film visible over the incision), 'good' (incision mostly fused, no inflammation, some stitches may remain), or 'complete' (incision completely fused, no stitches remaining). The tank was monitored twice daily for expelled tags and mortalities. The percentage of tags available for detection was calculated as: $100 \% *$ ((\#tags implanted - \#mortalities of tagged fish - \#tags expelled) / (\#tags implanted)). During 2005, all of the fish were necropsied following termination of the experiment, 300 days after the first surgery. Photographs were taken of each healing stage and tag position within the body. During 2006, all pre-smolts were euthanised after 90 days, weighed and measured.

### 3.2.4 Swimming Performance

From 24 to 48 hours after the April 2005 surgeries, the swimming performance of 40 fish from the growth and survival study was measured using procedures similar to Lacroix et al. (2004). Five fish from each treatment group ('control', 'sham', ' 6 mm tag' and ' 7 mm tag ') with fork lengths of $10.5-11 \mathrm{~cm}$ and five from each treatment group with fork lengths of $11.5-12 \mathrm{~cm}$ were swum in a 4 L Blazka-style swim tube (Smit et al., 1971) for a total of ten fish per treatment. The average weight was $15.08 \pm 2.24 \mathrm{~g}$ (standard deviation); the average length was $11.25 \pm 0.52 \mathrm{~cm}$. Each smolt was collected from the rearing tank with a dip net, placed in a bucket and transferred into the half-filled swim tube chamber. The chamber was then sealed and filled with water. Each pre-smolt was given 20 minutes to acclimate at $0.1 \mathrm{~m} \cdot \mathrm{~s}^{-1}$, whereupon the speed was increased by $0.2 \mathrm{~m} \cdot \mathrm{~s}^{-1}$. The velocity was then increased by $0.1 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ every 10 minutes. The trial ended when the fish rested on the back screen for 2 sec . No shocks or prodding were used so as to reduce stress to the fish. The fish were returned to the rearing tank following their swim trial.

During July 2005 ( 9 mm tag), an additional 72 fish were prepared for the second set of swimming performance trials. Twenty-four fish were surgically implanted with 9 mm tags; 24 fish were given sham surgeries and 24 were controls. All pre-smolts had initial fork lengths of 13.5 to 14.5 cm . The average fork length post-swim was $14.18 \pm 0.55 \mathrm{~cm}$. The average mass of the pre-smolts post-swim was $29.79 \pm 5.01 \mathrm{~g}$. The fish were divided up equally by treatment group and raised indoors in four tanks. Six extra control fish were placed in each tank for later blood analysis ('Control (2005, NS)', Table 3.2). Ten of the 9 mm tagged pre-smolts expelled their tags during the 92 days leaving a total of 14 dummy tagged fish to be swum. Thus, to keep the three treatment groups even, a total of 42 pre-smolts were swum in the 40 L Blazka-style swim tube using the same methods as previously mentioned. The larger size of the fish tagged with 9 mm tags required a longer swim trial, necessitating a different experimental schedule from the 6 mm and 7 mm tag groups. Three fish from the same tank (one from each treatment) were swum per day in random order for a total of 14 swim days, up to 90 days post-surgery (on day $1,2,3,4,5,7,25,27,28,31,33,34,40$ and 90). Critical swimming speeds (Ucrits) were calculated using the following formula: $U_{\text {crit }}=\mathbf{V}_{\mathrm{f}}+\left(\frac{T}{t} * \delta \mathbf{V}\right)$

Where $\mathrm{V}_{\mathrm{f}}$ is the highest velocity maintained for the prescribed time period, $\delta \mathrm{V}$ is the velocity increment, T is the amount of time the fish swam at fatigue speed and $t$ is the prescribed time period (Brett, 1964). Following each swim trial, the fish were euthanised in 120 ppm MS222, weighed and measured. Blood samples and necropsies were performed on each individual to compare post-exhaustive state relative to the different treatment types. In addition to the swim trial fish, one control (a fish that did not swim) was sampled at the end of each trial day. Blood from untreated fish was sampled during July 2005 and May 2006 to give a baseline for comparison ('2005 initial', '2006 initial', Table 3.2). All experimental procedures were approved by the Canadian Council of Animal Care (Appendix A).

### 3.2.5 Blood Analyses

Whole blood samples were taken from the caudal vessel of anesthetised fish with a sterile heparinised syringe for erythrocyte counts and analysis of hematocrit (Klontz, 1994). A $5 \mu \mathrm{~L}$ capillary tube was filled with fresh blood and placed into $995 \mu \mathrm{~L}$ Hendrick's solution for erythrocyte counts. The remaining blood was centrifuged at $13,000 \mathrm{rpm}$ for 5 minutes. Plasma was collected and stored at $-80^{\circ} \mathrm{C}$ until it was analysed for levels of sodium, potassium, chloride, calcium, glucose and lactate using a Stat Profile Plus 9 blood gas machine (Nova Biomedical Corporation, MA). Cortisol was measured using a cortisol Elisa kit from Immuno Biological Laboratories America, Inc. (Minneapolis, MN). Condition factors were calculated as mass * fork length ${ }^{-3} * 100$ (Goede and Barton, 1990). Erythrocyte counts were determined manually with a microscope and hemacytometer.

### 3.2.6 Statistical Analyses

The size data were found to be normally distributed (normal scores > 0.2 using KolmogorovSmirnov) with equal variance ( $\mathrm{F}_{76 ; 3410}=31.927-54.67, \mathrm{p}<0.0001$ ). General Linear Models (GLM) were developed for each initial size group (Tables 3.1, 3.2) with days since surgery and treatment as fixed factors, and weight, fork length and healing as dependent variables. GLMs were also created for swimming performance data and blood data. Multivariate analyses and Scheffe's post-hoc method were used to analyse differences between treatments, as N values varied between treatments and sample days. Percent
data (hematocrits) were arcsine transformed prior to statistical analysis. In all cases, significance was established at $\mathrm{p}<0.05$.

### 3.3 Results

For each tag type, we examined growth, healing rates, survival, tag retention, swimming performance and physical condition for up to 300 days post-surgery. All control and sham groups had $88 \%$ survival or higher until the termination of the study.

### 3.3.1 Growth

For the smallest tag ( 6 mm diameter), there was a significant difference in body size (weight and length) among the three treatments in the $9.5-10 \mathrm{~cm}$ group until 140 days post-surgery. Similarly, in the $10-$ 10.5 cm and $10.5-11 \mathrm{~cm}$ groups, there was a significant difference between the tagged and control/sham fish in body size until 140 days post-surgery; however there was no observable difference between the sham and control groups (Figure 3.1a). For the three previously mentioned size groups, there was no size difference among treatment groups after 140 days post-surgery. The $10.5-11 \mathrm{~cm}$ group tagged with 7 mm diameter transmitters had significant differences between the control/sham groups and the tagged group in length (data not shown) but not weight (Figure 3.2a). There was no significant size difference among treatments above an initial fork length of 11 cm for fish implanted with either the 6 or 7 mm tag (Figures $3.1 b, 3.2 b)$.

Survival and tag retention were low in the 9 mm tag treatment group when the initial fork length was $<13 \mathrm{~cm}$, which left too few fish to compare size statistically. The size groups were therefore pooled into 1 cm size groups to get large enough numbers for a statistical analysis. There was no significant difference in size between tagged and control/sham fish above an initial fork length of 14 cm .

### 3.3.2 Healing Rates

The controls in all size groups of the first set of surgeries had a 'good' healing status 2.5 months post-surgery, and were all completely healed 3 months post-surgery. The sham groups showed greater variance in healing time; $90 \%$ of individuals reached a 'good' status between 2.5 and 3 months, and a
'complete' status between 3 and 5 months. Eighty percent of fish tagged with 6 mm and 7 mm tags had a 'good' status by three months and were completely healed at seven months post-surgery. Healing improved slightly as initial size at surgery increased.

For the second group of surgeries (larger fish, 9 mm tag), the control fish reached a 'good' healing status by the first sampling 22 days post-surgery, and were completely healed by day 71 . The sham fish had a 'good' healing status between day 39 and 116, however they never reached 'complete'. In the largest size group (13-14 cm) tagged with large tags in the first year's study a few survivors had a 'good' status at day 116. During the second year, the majority of pre-smolts of initial fork length 14-16.5 cm tagged with large tags were completely healed by 90 days post-surgery. Necropsies of the experimental fish showed that some tags were adhering to the body cavity wall, fat tissue or organs. Some tags were surrounded by tissue and expelled through the incision site.

### 3.3.3 Survival and Tag Retention

We observed $100 \%$ survival and tag retention in all size groups of fish tagged with 6 mm tags up to 50 days post-surgery. There were two mortalities in the smallest size group 75 and 78 days post-surgery, and some tag loss in three of the size groups (Table 3.3a). Above initial fork lengths of 10 cm , survival was $100 \%$ and tag retention was over $88 \%$ until the termination of the experiment, 300 days post-surgery. For the 7 mm tag group there was $100 \%$ survival in four out of five of the tagged groups, however there was some tag loss in pre-smolts up to an initial fork length of 12.5 cm (Table 3.3b). All control fish and over $90 \%$ of the sham fish survived until the end of the study.

The 9 mm tag was too large to fit in the body cavity of the smallest size group (12-13 cm ) and as a result, many fish had to be euthanised during surgery. Of those that did survive, the majority expelled their tags very quickly and few lived until the end of the experiment (Table 3.3c). Above initial fork lengths of 14 cm , there was $100 \%$ survival to day 50 post-surgery; however tag retention began to fall after three weeks. By three months, there were only $42 \%$ of the tags remaining in fish up to 16 cm . Above 16 cm there was 55\% tag retention (Table 3.2c).

### 3.3.4 Swimming Performance

There were no significant differences in Ucrit or variance between treatment groups in either $\mathrm{m} \cdot \mathrm{s}^{-1}$ or $\mathrm{bl} \cdot \mathrm{s}^{-1}$ (Table 3.4). Pre-smolts that were included in the swim trials had no difference in survival, tag retention, healing or growth when compared with pre-smolts that were not included in the swim trials. There was no difference in swimming performance between rearing tanks.

### 3.3.5 Blood Analyses

Plasma levels of calcium were lower in sham groups than in control and tag groups (Table 3.2). No other significant differences were found in blood analyses between swum groups. Initial levels of plasma sodium, potassium, chloride, glucose and cortisol were all significantly lower than levels observed in swum fish.

### 3.4 Discussion

Acoustic telemetry has proven to be a very useful method to track the early marine migratory behaviour and survival of fish species, including salmon pre-smolts (Welch et al., 2003). With the development of 6 mm and 7 mm diameter acoustic tags, the pre-smolts of smaller salmonids such as coho, are now able to be tracked. We conducted this study to determine the maximum tag to body size ratios at which coho pre-smolts would suffer no adverse effects on survival, growth, physiology and swimming performance.

Further investigations could be made into the tags' effects on the buoyancy, startle response, disease resistance, and foraging ability of coho salmon pre-smolts. Laboratory environments can not replicate conditions that the tagged fish might encounter in the wild. Therefore, while we are able to find tag to body size ratios at which the survival, growth, swimming performance and physiology of coho presmolts was not significantly affected in an artificial environment, there may be affected behaviours in the field, such as foraging or predator avoidance ability.

Surgically implanted tags that were up to $8 \%$ of the fish's mass and up to $17 \%$ of their fork length had no significant effect on the survival, growth, swimming performance, or physical condition of Thompson River coho salmon pre-smolts. Swimming performance trials conducted on 5-10 g rainbow trout
implanted with acoustic tags demonstrated no observable effect from tags that were $6-12 \%$ of the fish's weight (Brown et al., 1999), which contradicted Winter's controversial ' $2 \%$ rule' (1983). Predator avoidance and swimming performance in juvenile chinook were not significantly affected by implanted tags that were $6.7 \%$ of the fish's body mass (Anglea et al., 2004). Adams et al. (1998b) found that radio tags implanted in chinook up to 12 cm lowered their critical swimming speeds; a lower 2.2-5.6\% tag to body mass ratio was recommended. Cutthroat trout implanted with tags that were $4 \%$ of their body weight had only slight decreases in growth and performance (Zale et al., 2005). Thompson River coho salmon presmolts had no difference in swimming performance 24 to 48 hours post-surgery for fish $10.5-12 \mathrm{~cm}$ long implanted with $6 \times 19 \mathrm{~mm}$ ( $6 \%$ by weight, $17 \%$ by length) and $7 \times 19 \mathrm{~mm}$ tags ( $10 \%$ by weight, $17 \%$ by length). The Ucrit values we measured (Table 3.4) were similar to those observed for coho smolts (3.5-5.5 $\mathrm{bl} \cdot \mathrm{s}^{-1}$ ) by Glova and McInerney (1977). Coho salmon pre-smolts with fork lengths of $13.5-14.5 \mathrm{~cm}$ implanted with $9 \times 21 \mathrm{~mm}$ tags had similar Ucrits to sham and control fish (the tags were $10 \%$ of their weight in air and $7 \%$ of their fork length).

The condition factors of the Coldwater River coho salmon pre-smolts were $>1.0 \mathrm{~g} \cdot \mathrm{~cm}^{-3}$ on average, which resembled other hatchery-reared coho populations but was likely greater than their wildreared counterparts (Chittenden et al., 2008). Plasma levels of sodium and chloride were much higher than normal in all groups (Wedemeyer et al., 1990), suggesting a possible bias due to measurement or storage time. Potassium was high for swum fish only (Wedemeyer et al., 1990). Plasma concentrations of sodium, chloride and potassium ions have been found to increase with exercise and stress levels in fresh water, which could explain differences found between swum and non-swum fish (Graham et al., 1982). Erythrocyte counts, hematocrits, mean cell volumes, calcium, glucose, lactate and cortisol levels were within normal ranges for coho pre-smolts (Wedemeyer et al., 1990).

Previous work examining the effects of tag insertion into salmonids has shown substantial variation between species in terms of growth, survival and tag retention. In their research on Atlantic salmon, Lacroix et al. (2004) compared the effects of three lengths of 8 mm diameter tags. They recommended using fish with a tag to fork length ratio of $16 \%$ or less, and a tag to fish mass ratio of $8 \%$ or less. With the tags they used, this corresponds to fish that were $14-15 \mathrm{~cm}$ long or $35-45 \mathrm{~g}$. This study, carried out on coho salmon pre-smolts between 9.5 and 16.5 cm long, found no differences in growth
between tag, control and sham groups above fork lengths of 11 cm for 6 mm and 7 mm -diameter surgically implanted acoustic tags and above 14 cm for 9 mm -diameter tags. All coho salmon pre-smolts implanted with 6 mm tags had excellent survival and tag retention above fork lengths of 10 cm ; the same results were found in pre-smolts over 12.5 cm for the 7 mm tag. Rainbow trout/steelhead were found to have reduced growth to day 21 for 11.4-15.9 cm fish (Lucas, 1989) and less than $15 \%$ tag loss to day 84 in fish over 14 cm tagged with $8 \times 24 \mathrm{~mm}$ acoustic tags (Welch et al., 2007). The coho salmon pre-smolts implanted with $9 \times 21 \mathrm{~mm}$ tags had excellent survival above initial fork lengths of 14 cm ; however tag retention in presmolts up to 16.5 cm dropped from $81-91 \%$ after one month to $42-55 \%$ after three months. These results are of major importance to long-term field studies that estimate survival of coho salmon pre-smolts implanted with 9 mm transmitters. For shorter-term telemetry studies, smaller fish could be tagged to cover more of the population curve, as long-term survival, growth and tag retention may not be as important. However, the swimming ability and behaviour of the smaller fish could be more affected than that of the larger fish.

This study examined the effects of three sizes of implanted acoustic tags on the long-term growth, healing, survival, tag retention, swimming performance and physical condition of endangered Thompson River coho salmon pre-smolts. We recommend that coho be greater than $11 \mathrm{~cm}(17 \%$ tag to fork length ratio) or 15 g ( $7 \%$ tag to body mass ratio) for implantation with a $6 \times 19 \mathrm{~mm}$ tag ( 0.9 g in air, 0.5 g in water $)$. Although 11 cm fish tagged with a $7 \times 19 \mathrm{~mm}$ tag ( 1.5 g in air, 0.8 g in water) grew at similar rates to control groups, when survival and tag retention are taken into consideration, a minimum of 12.5 cm is more appropriate ( $15 \% \mathrm{tag}$ to fork length ratio or $7 \%$ tag to body mass ratio). If a $9 \mathrm{x} 21 \mathrm{~mm} \operatorname{tag}$ ( 3.0 g in air, 2.0 g in water) is being used, pre-smolts over 14 cm ( $15 \%$ tag to fork length ratio), or 35 g ( $8 \%$ tag to body mass ratio) are recommended, however tag retention levels dropped significantly after one month.

Table 3.1 Number of fish ( N ) in each initial fork length group by treatment for a) the 6 and 7 mm tag groups, and b) the 9 mm tag group.

| a) | $9.5-10 \mathrm{~cm}$ | $10-10.5 \mathrm{~cm}$ | $10.5-11 \mathrm{~cm}$ | $11-11.5 \mathrm{~cm}$ | $11.5-12 \mathrm{~cm}$ | $12-12.5 \mathrm{~cm}$ | $12.5-13 \mathrm{~cm}$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Control | 9 | 10 | 10 | 10 | 10 | - | - |
| Sham | 8 | 10 | 10 | 10 | 10 | 11 | 9 |
| 6 mm | 7 | 9 | 10 | 8 | 10 | 9 | 9 |
| 7 mm | - | - | 9 | 9 | 9 | 8 | 10 |

b)

|  | $12-13 \mathrm{~cm}$ | $13-14 \mathrm{~cm}$ | $14-15 \mathrm{~cm}$ | $15-16 \mathrm{~cm}$ | $16-16.5 \mathrm{~cm}$ |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Control | 16 | 18 | 24 | 20 | 8 |
| Sham | 15 | 18 | - | - | - |
| 9 mm | 27 | 26 | 21 | 24 | 11 |

Table 3.2 Physiological measurements of coho salmon pre-smolt surgical treatment groups. Pre-smolts sampled after the completion of a swim trial were labeled with an ' $S$ '; those that did not swim were labeled 'NS'.

| Dependent Variable | Treatment Group | N | Mean | Standard Error |
| :---: | :---: | :---: | :---: | :---: |
| Weight (g) | 2005 initial (NS) | 12 | 24.2667 | 1.7588 |
|  | Control (2005, S) | 11 | 34.2364 | 1.5900 |
|  | Sham (2005, S) | 12 | 28.2333 | 1.8130 |
|  | $9 \mathrm{~mm} \operatorname{tag}(2005, \mathrm{~S})$ | 13 | 28.8923 | 2.5640 |
|  | Control (2005, NS) | 10 | 26.9200 | 0.0320 |
|  | 2006 initial (NS) | 30 | 16.7367 | 0.5292 |
| Fork Length (cm) | 2005 initial (NS) | 12 | 13.1917 | 0.3880 |
|  | Control (2005, S) | 11 | 14.6273 | 0.2300 |
|  | Sham (2005, S) | 12 | 14.0250 | 0.2200 |
|  | $9 \mathrm{~mm} \operatorname{tag}(2005, \mathrm{~S})$ | 13 | 14.1462 | 0.2120 |
|  | Control (2005, NS) | 10 | 13.7400 | 0.2420 |
|  | 2006 initial (NS) | 30 | 11.6400 | 0.1230 |
| Condition Factor ( $\mathrm{g} / \mathrm{cm}^{3}$ ) | 2005 initial (NS) | 12 | 1.0493 | 0.0485 |
|  | Control ( $2005, \mathrm{~S}$ ) | 11 | 1.0865 | 0.0330 |
|  | Sham (2005, S) | 12 | 1.0161 | 0.0470 |
|  | $9 \mathrm{~mm} \mathrm{tag}(2005, \mathrm{~S})$ | 13 | 1.0207 | 0.2470 |
|  | Control (2005, NS) | 10 | 1.0010 | 0.2370 |
|  | 2006 initial (NS) | 30 | 1.0507 | 0.0116 |
| Erythrocytes (\#/mL) | 2005 initial (NS) | 12 | $1.3883 \mathrm{e}^{6}$ | $5.5882 \mathrm{e}^{4}$ |
|  | Control (2005, S) | 11 | $1.2932 \mathrm{e}^{6}$ | $7.6495 \mathrm{e}^{4}$ |
|  | Sham (2005, S) | 12 | $1.3658 \mathrm{e}^{6}$ | $7.3238 \mathrm{e}^{4}$ |
|  | $9 \mathrm{~mm} \operatorname{tag}(2005, \mathrm{~S})$ | 13 | $1.1508 \mathrm{e}^{6}$ | $7.0365 \mathrm{e}^{4}$ |
|  | Control (2005, NS) | 10 | $1.2720 \mathrm{e}^{6}$ | $8.0228 \mathrm{e}^{4}$ |
| Hematocrit | 2005 initial (NS) | 12 | 0.5477 | 0.0519 |
|  | Control ( $2005, \mathrm{~S}$ ) | 11 | 0.4258 | 0.0360 |
|  | Sham (2005, S) | 12 | 0.4451 | 0.0350 |
|  | $9 \mathrm{~mm} \operatorname{tag}(2005, \mathrm{~S})$ | 13 | 0.3880 | 0.0330 |
|  | Control (2005, NS) | 10 | 0.3937 | 0.0380 |
|  | 2006 initial (NS) | 24 | 0.4675 | 0.0137 |
| Mean Cell Volume ( $\mathrm{nm}^{3}$ ) | 2005 initial (NS) | 11 | $3.3247 \mathrm{e}^{-4}$ | 0.0000 |
|  | Control (2005, S) | 14 | $3.2084 \mathrm{e}^{-4}$ | 0.0000 |
|  | Sham (2005, S) | 13 | $4.1697 \mathrm{e}^{-4}$ | 0.0000 |
|  | $9 \mathrm{~mm} \mathrm{tag}(2005, \mathrm{~S})$ | 13 | $3.1432 \mathrm{e}^{-4}$ | 0.0000 |
|  | Control (2005, NS) | 12 | $3.7125 \mathrm{e}^{-4}$ | 0.0000 |
| Sodium, plasma (mmol/L) | 2005 initial (NS) | 10 | 207.9600 | 2.7237 |
|  | Control (2005, S) | 11 | 241.6727 | 10.7290 |
|  | Sham (2005, S) | 12 | 236.4000 | 10.2720 |
|  | $9 \mathrm{~mm} \operatorname{tag}(2005, \mathrm{~S})$ | 13 | 239.9077 | 9.8690 |
|  | Control (2005, NS) | 10 | 233.8800 | 11.2530 |
| Potassium, plasma (mmol/L) | 2005 initial (NS) | 10 | 4.0880 | 0.4378 |
|  | Control (2005, S) | 11 | 8.3091 | 1.0330 |


| Dependent Variable | Treatment Group | N | Mean | Standard Error |
| :---: | :---: | :---: | :---: | :---: |
|  | Sham ( 2005 , S) | 12 | 11.6667 | 0.9890 |
|  | $9 \mathrm{~mm} \operatorname{tag}(2005, \mathrm{~S})$ | 13 | 7.1354 | 0.9500 |
|  | Control (2005, NS) | 10 | 9.9640 | 1.0840 |
|  | 2006 initial (NS) | 26 | 5.7651 | 0.5544 |
| Chloride, plasma | 2005 initial (NS) | 10 | 176.9200 | 3.0264 |
| ( $\mathrm{mmol} / \mathrm{L}$ ) | Control ( 2005 , S) | 11 | 171.6727 | 4.6260 |
|  | Sham (2005, S) | 12 | 170.5667 | 4.4290 |
|  | $9 \mathrm{~mm} \mathrm{tag}(2005, \mathrm{~S})$ | 13 | 175.3231 | 4.2560 |
|  | Control (2005, NS) | 10 | 174.4800 | 4.8520 |
|  | 2006 initial (NS) | 26 | 146.7532 | 3.9209 |
| Calcium, plasma | 2005 initial (NS) | 10 | 1.8280 | 0.0253 |
| ( $\mathrm{mmol} / \mathrm{L}$ ) | Control ( 2005 , S) | 11 | 1.6218 | 0.0390 |
|  | Sham (2005, S) | 12 | 1.4300 | 0.0370 |
|  | $9 \mathrm{~mm} \mathrm{tag}(2005, \mathrm{~S})$ | 13 | 1.6431 | 0.0350 |
|  | Control (2005, NS) | 10 | 1.5120 | 0.0400 |
|  | 2006 initial (NS) | 26 | 1.1873 | 0.0331 |
| Glucose, plasma | 2005 initial (NS) | 10 | 6.0000 | 0.5750 |
| ( $\mathrm{mmol} / \mathrm{L}$ ) | Control ( 2005 , S) | 11 | 8.1455 | 0.5700 |
|  | Sham (2005, S) | 12 | 8.3333 | 0.5460 |
|  | $9 \mathrm{~mm} \mathrm{tag}(2005, \mathrm{~S})$ | 13 | 8.1231 | 0.5240 |
|  | Control (2005, NS) | 10 | 7.3600 | 0.5980 |
|  | 2006 initial (NS) | 26 | 6.0780 | 0.3231 |
| Lactate, plasma | 2005 initial (NS) | 10 | 6.6000 | 0.4511 |
| (mmol/L) | Control ( $2005, \mathrm{~S}$ ) | 11 | 6.9455 | 0.7290 |
|  | Sham ( 2005 , S) | 12 | 5.9333 | 0.6980 |
|  | $9 \mathrm{~mm} \mathrm{tag}(2005, \mathrm{~S})$ | 13 | 7.8154 | 0.6710 |
|  | Control (2005, NS) | 10 | 4.7600 | 0.7650 |
|  | 2006 initial (NS) | 25 | 7.6220 | 0.5171 |
| Cortisol, plasma | 2005 initial (NS) | 5 | 35.8605 | 13.7980 |
| ( $\mathrm{mmol} / \mathrm{L}$ ) | Control (2005, S) | 11 | 94.5211 | 32.4660 |
|  | Sham (2005, S) | 12 | 70.2966 | 31.0840 |
|  | $9 \mathrm{~mm} \mathrm{tag}(2005, \mathrm{~S})$ | 13 | 84.3371 | 29.8640 |
|  | Control (2005, NS) | 10 | 92.7771 | 34.0510 |

Table 3.3 Percent survival and tags available for detection over time in the a) 6 mm tag group, b) 7 mm tag group and c) 9 mm tag group.


Table 3.4 Critical swimming speeds of control, sham and tag groups.

|  | Treatment Group | N | Mean | Standard Error |
| :---: | :---: | :---: | :---: | :---: |
|  | Control (6, 7 mm ) | 10 | 0.3531 | 0.0260 |
|  | Sham (6, 7 mm ) | 10 | 0.4436 | 0.0260 |
| $\stackrel{T}{\square}$ | 6 mm tag | 10 | 0.3705 | 0.0260 |
| E | 7 mm tag | 10 | 0.3470 | 0.0260 |
| ${ }^{\text {E }}$ | Control (9 mm) | 13 | 0.9963 | 0.0630 |
| E | Sham (9 mm) | 13 | 1.0548 | 0.0600 |
| $\bigcirc$ | 9 mm tag | 13 | 1.0908 | 0.0600 |
|  | Control (6, 7 mm ) | 10 | 3.1558 | 0.2340 |
|  | Sham (6, 7 mm ) | 10 | 3.9390 | 0.2340 |
| T | 6 mm tag | 10 | 3.3076 | 0.2340 |
| $\dot{0}$ | 7 mm tag | 10 | 3.0718 | 0.2340 |
| e | Control (9 mm) | 13 | 6.8218 | 0.4310 |
| O | Sham (9 mm) | 13 | 7.5346 | 0.4140 |
| $\bigcirc$ | 9 mm tag | 13 | 7.7811 | 0.4140 |



Figure 3.1 Weight over time for the 6 mm tag group of initial fork length a) $10.5-11 \mathrm{~cm}$, and b) $11-11.5$ cm . The control group is defined by a dashed line, the sham group a dotted line and the tagged group a solid line. Standard error bars are included for all three. In the $10.5-11 \mathrm{~cm}$ group, note the significant difference between tagged and control/sham weight up to 140 d post-surgery. There were no significant differences between treatment groups for fish with initial fork lengths over 11 cm .


Figure 3.2 Weight over time for the 7 mm tag group of initial fork length a) $10.5-11 \mathrm{~cm}$, and b) $11-11.5$ cm . The control group is defined by a dashed line, the sham group a dotted line and the tagged group a solid line. Standard error bars are included for all three. There were no significant differences in weight among treatment groups in either group.

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## CHAPTER 4: Evidence for Poor Freshwater Survival of Endangered Thompson River Coho Salmon Smolts During the Fraser River Out-Migration ${ }^{3}$

### 4.1 Introduction

Genetically distinct from coho salmon populations in the lower Fraser River and the rest of British Columbia, Thompson River coho salmon (Thompson coho) are closely related to the extinct upper Columbia River coho stocks (Small et al., 1998; Shaklee et al., 1999; Beacham et al., 2001). Returns of wild Thompson coho were relatively stable during the 1970s, and increased during the 1980s (COSEWIC, 2000). However, between 1988 and 2000, the Thompson River coho salmon population declined by $90 \%$, making it one of Canada's most endangered salmon stocks (Irvine and Bradford, 2000; COSEWIC, 2002). An urgent request for investigations into the cause of the Thompson coho's demise was made shortly thereafter by the Government of Canada (Routledge and Wilson, 1999).

Over-fishing, changes in ocean climate and freshwater habitat alteration are believed to be the primary causes of the Thompson coho decline (Bradford and Irvine, 2000). An unprecedented moratorium on the coho fishery was implemented in 1998; however the Thompson coho population was not affected (Bradford and Irvine, 2000). Thus over-fishing alone was not preventing the recovery of the stock.

Climate fluctuations were found to coincide with changes in coho marine survival (Pearcy, 1992; Coronado and Hilborn, 1998; Koslow et al., 2002). When a regime shift occurred in 1989-1990, ocean productivity decreased in southern BC and smolt-to-adult marine survival of both coho (Beamish et al., 1999; Noakes et al., 2000) and steelhead trout (Ward, 2000; Welch et al., 2000) plummeted. While the southern populations dwindled, northern populations of coho and steelhead had record-high abundances (Hare et al., 1999; Welch et al., 2000; Hobday and Boehlert, 2001). In addition to altering salmonid marine survival rates, ocean conditions have been correlated to changes in the migratory pattern of Strait of Georgia coho populations (Beamish et al., 1999) and other salmon species (Cooke et al., 2004; Young et al., 2006; Crossin et al., 2007; Crossin et al., 2008). As the Strait of Georgia was traditionally a juvenile rearing ground for Thompson coho, climatic changes taking place in the Strait may affect their marine

[^2]survival and migratory behaviour. Freshwater productivity and habitat quality are also affected by changes in climate (Beamish, 2002). The freshwater survival of coho salmon in Oregon and Washington correlated strongly to annual air temperatures and second winter flows (Lawson et al., 2004). Fluctuations in Thompson coho abundances were correlated to agriculture land use, road density and stream habitat quality (Bradford and Irvine, 2000). Routledge and Wilson (1999) highlighted local concerns about freshwater habitat quality in the Thompson watershed, expressing the need for young coho riverine survival data that could provide evidence linking weak stocks to freshwater habitat concerns.

To investigate freshwater and early marine survival rates as well as the migratory behaviour of Thompson coho smolts, hatchery-reared fish were tagged during three consecutive years (2004-2006) and monitored using the POST array (Welch et al., 2003). The objective of this study was to identify areas of high mortality for this stock, with the goal of providing a focus for conservation efforts. A two-year tag effects study was carried out concurrently to evaluate the post-surgical growth, survival, tag retention, health and swimming ability of acoustically tagged smolts (Chittenden et al., 2008a).

### 4.2 Methods

### 4.2.1 Study Area

Near the end of the last ice age approximately 15,000 years ago, the Fraser River canyon was blocked by ice, forcing the upper Fraser and Thompson Rivers to drain southward into the Columbia River. This provided the opportunity for many species, including coho salmon, to colonise the Thompson River from the Columbia River refugium (McPhail and Lindsey, 1986). The Fraser canyon continues to act as a velocity barrier to many fish species and stocks, dividing the Upper and Lower Fraser River into distinct habitat zones. Thompson coho can be divided into three subregions: the North Thompson, the South Thompson and the Lower Thompson / Nicola. The stocks used in this study were part of the Lower Thompson / Nicola group.

The $1,370 \mathrm{~km}$ long Fraser River (Figure 4.1) is the largest river in British Columbia, with a watershed of $233,100 \mathrm{~km}^{2}$, and an average yearly flow rate of $3,540 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$. The Thompson River, at 489 km long, is the largest tributary of the Fraser River, with a watershed of $55,400 \mathrm{~km}^{2}$. Water quality and flow rate monitoring of the Thompson River began in 1911 at the Spences Bridge station, 40 km upstream
from Thompson River mouth at Lytton. Average annual flow rates during 2004, 2005, 2006 were 672, 784 and $656 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$ respectively, which fall near the 1912-2006 annual average of $765 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$ (Environment Canada, 2008). Peak flow rates were $1820 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$ on 4 June 2004, $2230 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$ on 19 May 2005, and 2630 $\mathrm{m}^{3} \cdot \mathrm{~s}^{-1}$ on 27 May, 2006. Low flow rates were $171 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$ on 4 March 2004, $250 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$ on 17 June 2005, and $193 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$ on 28 October 2006 (Environment Canada, 2008). The timing of the spring freshet in the Fraser River has been advancing during the past century (Beamish et al. 1999), and a similar trend has been observed in the Thompson River (Figure 4.2).

The Thompson River water quality is described as well-buffered and soft, with pH and oxygen levels "within normal ranges for aquatic life" (Environment Canada, 2001). However, levels of nonfilterable residue, turbidity, total aluminum, iron and phosphorus often exceed recommended levels for fish during high flow periods (Environment Canada, 2008). There was an increasing trend from 1973-1997 in dissolved chloride and copper (Environment Canada, 2001). Non-filterable residue and turbidity level increases have been attributed to increased agriculture, forestry and residential development (Environment Canada, 2001). The mean summer temperatures of the Fraser River system have also been increasing over the last century; in the next 100 years, the potential for salmon to be exposed to temperatures higher than $20^{\circ} \mathrm{C}$ is predicted to increase by a factor of ten (Morrison et al., 2002).

Most Thompson coho salmon spend their first year in freshwater and the following two years in the ocean, before returning to their natal streams to spawn (Bradford and Irvine, 2000). Hatchery production was initiated in the Thompson watershed in the early 1980s to test enhancement strategies for coho (Pitre and Cross, 1993; Perry, 1995). Smolt production began at the Spius Creek Hatchery in 1984 to rebuild depressed stocks. Assessments of returns for both wild and hatchery stocks were carried out regularly thereafter. The coho broodstock is collected from the wild population each year.

### 4.2 2 Surgical Protocols and Smolt Releases

Coho smolts from two different tributaries -Spius Creek $(2004,2005)$ and the Coldwater River (2006) - were tagged at the Spius Creek Hatchery using previously established protocols (Welch et al., 2004, 2007). During 2004, forty Spius Creek coho smolts from the 2002 brood were implanted with V7-2L acoustic transmitters [12 fish; $7 \times 18.5 \mathrm{~mm}$, mass in air 1.4 g , mass in water 0.7 g , frequency $69 \mathrm{kHz}, 30-90 \mathrm{~s}$
random delay, VEMCO Ltd., Halifax, Nova Scotia Canada], and V9-6L acoustic transmitters [28 fish; 9x20 mm , mass in air 3.3 g , mass in water 2.0 g , frequency $69 \mathrm{kHz}, 30-90 \mathrm{~s}$, VEMCO Ltd., Halifax, Nova Scotia Canada]. The surgeries were carried out 30 May 2004. The average fork length (and standard deviation) of the fish tagged with 7 mm tags was $128.1 \pm 1.0 \mathrm{~mm}$ (range $127.0-129.0 \mathrm{~mm}$ ), and for those with 9 mm tags, $132.0 \pm 2.3 \mathrm{~mm}(130.0-141.0 \mathrm{~mm})$. This represents average tag length to body length ratios of $5 \%$ and $7 \%$ respectively. The river temperature was $11.5 \pm 0.6^{\circ} \mathrm{C}$ during the surgeries. The release date of 88,300 hatchery coho smolts occurred 19-22 May 2004; the tagged fish were released 31 May 2004 at 1400 PDT in Spius Creek (Figure 4.1).

During 2005, fifty Spius Creek coho smolts from the 2003 brood were implanted with V7-2L tags. The river temperature averaged $9.0 \pm 0.7^{\circ} \mathrm{C}$ on the day of the surgeries, 17 May 2005. The smolts had an average fork length of $128.0 \pm 3.9 \mathrm{~mm}(124.0-139.0 \mathrm{~mm})$ representing an average tag length to body length ratio of $5 \%$ and were released 19 May 2005 at 1115 PDT in Spius Creek to coincide with the hatchery release of 58,450 coho smolts.

The 2004 brood of the Coldwater River stock was tagged in 2006 from 25-26 May. One hundred smolts were implanted with V7-2L transmitters and released 29 May 2006, at 1300 PDT. The average fork length of the tagged smolts was $130.1 \pm 3.3 \mathrm{~mm}(125.0-141.0 \mathrm{~mm})$ representing an average tag length to body length ratio of $5 \%$. The river temperature during the surgeries was $8.2 \pm 0.9^{\circ} \mathrm{C}$. Hatchery releases were as follows: 43,000 smolts were released 9 May 2006, 20,000 were released 26 May 2006 and 6,460 were released 29 May 2006 in the Coldwater River (Figure 4.1) at the time of the release of the tagged smolts.

Tag effect studies carried out concurrently at the UBC/DFO Centre for Aquaculture and Environmental Research in West Vancouver, BC with 500 Thompson coho smolts during 2005 and 2006 demonstrated that the implantation of V7-2L tags did not impact fish health or swimming ability at the body sizes used in the field study when compared with control groups (Chittenden et al., 2008a). Physiological assessments, swimming performance and growth were all similar to control values (Chittenden et al., 2008a). We comment further on these results later, when we compare the observed survival of free-ranging coho smolts with the results from the surgical trials.

### 4.2.3 Acoustic Receiver Array

The total distance from the release site to the mouth of the Fraser River is approximately 385 km from the 2004-2005 release sites and 420 km from the 2006 release site. Distances from release sites to the last detection station in the Fraser River were 346, 353, and 410 km for 2004-2006, respectively. Acoustic receivers [models VR2 and VR3, VEMCO Ltd., Halifax, Nova Scotia Canada] were located both in the Fraser River and in the ocean to form the POST array (Figure 4.1) to track the smolts' downstream migration. During 2004, there were six receivers in the Fraser River arranged in three lines of paired units from April to August, then five receivers from August to November. Four receivers (two lines of paired units) were deployed in the Fraser River in April of 2005 and recovered in December. Eighteen receivers were deployed in the Fraser River from April to December of 2006. These were arranged in three main lines, where the lower two lines contained two or three sublines each to cover multiple channels of the braided lower river (Figure 4.1).

In ocean waters, acoustic receivers were located in lines across the northern Strait of Georgia, the Queen Charlotte Strait, the Juan de Fuca Strait, and Howe Sound. Also, in 2006, receivers were moored in Burrard Inlet and the southern Strait of Georgia. During 2005 and 2006, three receivers operated by the Vancouver Aquarium were located at Point Atkinson.

### 4.2.4 Data Analysis

We compiled a database of detections from acoustic receivers consisting of the time and location where an individual tag was detected. First, we identified a list of suspect detections likely to be false positives due to tag collisions or other noise sources. Detections of fish were excluded as false if they were detected only once on a line within 60 minutes, had one or more 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 temporal sequence of detections from the release date along the migration path. After eliminating the suspect detections, we used these filtered data to estimate survival and detection probabilities as well as the travel times of tagged smolts during the downstream migration. Travel times in each segment were measured as the difference between successive lines in the cumulative travel
times from release until the first detection of a tag on a line. Median travel times were calculated as the linearly interpolated time at which $50 \%$ of the survivors reached a detection point.

### 4.2.5 Survival Probability Estimation

We used variations of the fully time-varying Cormack-Jolly-Seber (CJS) mark-recapture model for live recaptures to estimate survival probabilities $(\phi)$ in each segment of the downstream migration. This model simultaneously estimates detection probabilities $(p)$ at each line of receivers in the Fraser River and adjusts survival estimates accordingly. We determined the detection history of individual fish at each receiver (i.e. "re-capture") line. Fraser River salmon smolts migrated past 2-3 detection lines in the Fraser River (depending on year). There were multiple receiver lines or units in the ocean where they could be detected (with some variation among years), but typical migration routes after ocean entry could not be established because few fish were detected on ocean receivers. As a result, we lumped all ocean receiver detections into the final digit of a fish's detection history sequence, and limited our inferences of survival to the downstream freshwater migration phase and not to the early ocean migration (i.e. we disregard any estimates of the confounded parameters $\phi$ in the final ocean "segment" and $p$ at the final ocean "line").

Detections of Thompson coho were relatively few on river or ocean lines, when compared to detection data for Thompson spring chinook and steelhead, and Cultus Lake sockeye. Therefore, we used information from smolts of other Fraser River stocks tagged as part of the POST project to better estimate $p$ on river lines. We constructed similar detection histories for steelhead and chinook smolts released in the Thompson watershed or sockeye smolts released from Cultus Lake. We assume that the same tag type (and therefore acoustic power) passing over a river receiver line around the same time have the same probability of being detected regardless of the species or stock from which the tagged smolts originated. We used the detection history sequences of individual fish with various mark-recapture models implemented with Program MARK (White and Burnham, 1999) through RMark (Laake and Rexstad, 2007) to estimate $\phi$ in river segments as well as $p$ on river lines in each year for each stock.

To determine whether survival or detection probabilities were best described as functions of factors such as tag size, river flow, release date, or average travel time, we tested several candidate models. We combined all three years in a detection history dataset and assigned 'year', 'species' and 'stock' as
group covariates on survival probability estimates. Combining years allowed us to constrain the relative difference in $p$ between V7 tags and V9 tags to be consistent (in logit-space) across receiver lines and years (i.e., tag size was an additive covariate). It also allowed us to maintain a consistent relationship (slope) between either $\phi$ or $p$ and river flow across lines and years (while permitting intercepts to differ).

We considered six candidate models for $p$ and four candidate models for $\phi$ (Table 4.1). First, we compared sub-models for $p$ by assuming a common sub-model for $\phi$ where parameter estimates for each segment ('seg', or 'time' in usual nomenclature) and group (year, species, stock) varied freely ( $\phi_{(\text {seg.group })}$ ). One sub-model for $p$ had freely-varying parameters for each detection line (i.e., replacing 'time') and group (along with $\phi$, this is the classic CJS model). All other sub-models also maintained independence between different lines and years $\left(p_{\text {(lineyear...) }}\right)$. One of these assumed no difference in detection probability between V7 and V9 tags while the others assumed an additive difference that was consistent among years ( $p_{(\ldots+\operatorname{tag}}$ size...); Table 4.1). Three of these sub-models took into account the mean date of arrival of a population on a receiver line and assumed that $p$ at each line was a function of Julian date or water level at that particular mean arrival date, thereby allowing for variation in $p$ among populations through use of these covariates. Water level (which is correlated with river flow) was measured at either the Mission (near the first receiver line in 2004; Figure 4.1) or Port Mann (near the second receiver line in 2005) gauge stations (Environment Canada, 2008). One of these sub-models involved the Julian date of arrival at a line as a covariate ( $p_{(\ldots+\text { Julian }}$ day) $)$, another involved the water level at Mission $\left(p_{(\ldots+f l o w ~ M i s s i o n)}\right)$, and a third involved the water level at Port Mann at the mean arrival time at a line $\left(p_{(\ldots+f l o w ~ P o r t ~ M a n n)}\right)$. After using model selection methods to identify the best sub-model(s) for $p$, we held fixed this sub-model for $p$ in order to compare sub-models of $\phi$ (Table 4.1). This two-step process of first comparing hypotheses of $p$ sub-models before comparing hypotheses of $\phi$ sub-models has been used in several other studies (e.g. Zabel and Achord, 2004). To reduce the effect of incorporating other species and stocks into the same dataset on $\phi$ estimates of Thompson coho, we maintained independence between groups and segments in all four sub-models, $\phi_{\text {(segment•group...). }}$. One of these sub-models contained no extra covariates so represented complete independence in $\phi$ estimates between groups in each segment of the migration. The other three sub-models involved group covariates that were used to explain some of the among-stock variation in survival probabilities in terms of variables specific to each stock; these could reveal potential correlates of survival that would not be possible by considering

Thompson coho alone. One sub-model involved the Julian release date as a covariate on all river segments of the migration. The second sub-model involved the average travel time of the population within each segment. The third sub-model involved the water level at the Mission gauge at the start time of each segment of each population (the time of fish release for the first segment and the mean time of arrival at a receiver line for the second or third segments).

We estimated a variance inflation factor $(\hat{c})$ to compensate for extra-binomial variation in estimated probabilities (Burnham et al., 1987). We estimated $\hat{c}$ assuming the general CJS model, $\phi_{(\text {seg.year }}$ $p_{\text {(line•year) }}$, using two methods through Program MARK: the deviance ratio bootstrapping method $(\hat{c}=$ 1.600) and median- $\hat{c}$ method ( $\hat{c}=1.281+0.037$ s.e.) We used the larger value from the bootstrapping routine to be more conservative about the precision of estimated parameters, as these $\hat{c}$ values were used to expand standard errors of real parameter estimates and values in the variance-covariance matrix. Estimated $\hat{c}$ was also used for model comparison, with computed $\mathrm{QAIC}_{\mathrm{c}}$ values corrected for both extra-binomial variation and small sample sizes.

After the best sub-model for $p$ was identified and sub-models for $\phi$ were compared, we computed model-averaged parameter estimates for $\phi$ in each segment for each population and year. We calculated survivorship estimates from release until the last in-river detection line in each year as the product of segment-specific $\phi$ estimates. We used the Delta method to calculate the variance of this product.

### 4.3 Results

### 4.3.1 Model Selection

Of the six detection probability sub-models evaluated across all years, the strongest support by far was found in the sub-model that involved line- and year-specific estimates with an additive term for tag size and an additive term for river level at the Mission gauge during the mean time of arrival of populations on receiver lines (Table 4.1). The difference in $\Delta$ QAICc values between this and the next-best sub-model was fairly large $(\approx 8)$, suggesting little support for this model and essentially no support for any remaining models ( $\triangle$ QAICc > 16) compared with the best sub-model. Detection probability across receiver lines and
years therefore varied strongly with both tag size (or acoustic output) and river level (or flow), with lower $p$ estimates associated with the smaller V7 tags and higher water levels (greater flow).

Assuming this best sub-model for $p$, the strongest support among the four survival probability models was found in the sub-model that involved Julian release date as a covariate, as measured by $\Delta$ QAICc values and Akaike weights (Table 4.1; a proportional measure of support for each model within the model set). The model "beta" coefficient for this parameter was significantly less than zero ( -0.036 ; $95 \%$ confidence limits: -0.062 to -0.010 ). Across all river segments and years, populations with later release dates therefore tended to have lower downstream survival rates. A moderate level of support ( $\triangle$ QAICc values of 2.3-4.4) was still seen in the other three sub-models, however. The classic CJS submodel without group covariates had $21 \%$ support. The sub-model with a covariate of water level at Mission at the mean start time of each segment for each population as well as the sub-model with a mean travel time covariate for each population in each segment each had > $7 \%$ support within this set of sub-models.

### 4.3.2 Detection Probability Estimates

Survival estimates depend on simultaneously estimated detection probabilities at receiver stations. Estimated detection probabilities of Thompson coho on individual receiver lines in the Fraser River $\left(p_{\mathrm{i}}\right)$ ranged widely from 10-85\% across receiver lines and years (average of $43 \%$ ). In 2004, V9 tags had higher associated $p_{i}$ estimates than V7 tags as a result of the additive tag size covariate used across populations. Detection probabilities tended to be lower in 2005 and 2006 due to changed location of receivers and/or different river conditions at the time of crossing receiver lines. Taking the product of (1-p $p_{\mathrm{i}}$ ) for all Fraser River lines $i$ in each year results in the probability of a smolt crossing all Fraser lines without being detected (Melnychuk et al., 2007). This product ranged widely from 8, 67, and $59 \%$ for V7 tags in 20042006, respectively, and was $2 \%$ for V9 tags in 2004. Estimated survival rates account for such imperfect detection probabilities.

### 4.3.3 Survival Probability Estimates

We model-averaged the survival estimates from the four models listed in Table 4.1 to admit our uncertainty as to which model(s) best fit the observed detection history sequences. As a result of differing

Akaike weights, the model-averaged results depend mostly on the model $\phi_{\text {(seg•group }+ \text { Julian release day) }} p_{\text {(line•yeartag }}$ size+flow Mission) (Table 4.1), but were also influenced by the other three in proportion to these weighting terms. Thompson coho survival rates (and those of other Fraser River populations) are therefore best explained by taking account of the variation among populations and years in Julian day of fish release, and constraining estimated $\phi$ parameters to be a function of these dates.

For two consecutive years, the freshwater survival estimates for Thompson coho smolts reaching the mouth of the Fraser River were extremely low (Figure 4.3). Of the 40 fish tagged with V7 (12 individuals) and V9 (28 individuals) tags in 2004, only two tags (one V7 and one V9) were detected in the lower Fraser River. None were recorded in the ocean by the POST array. Survival estimates from release to the lowest receiver line in Fraser River were $<0.01 \% \pm 0.01 \%$ s.e. for the V7 group, and $5.6 \% \pm 9.0 \%$ for the V9 group. Survival estimates from release to the first and second Fraser River lines were both $14.2 \% \pm$ $21.4 \%$ s.e. for the V7 group and both $5.6 \% \pm 9.0 \%$ for the V9 group, implying that most mortality was estimated to have occurred before the first detection station (with an additional component of mortality between the second and third stations for the V7 group). The two smolts detected in the lower Fraser River were detected 14 days and 18 days post-release (Table 4.2).

During 2005, 50 smolts were tagged with V7 tags, four of which were detected at the Fraser mouth sub-array 8-23 days post-release ( $\mathrm{T}_{\text {median }}=12$ days; Table 4.2 ). Two smolts passed through the Fraser array undetected and were subsequently detected at Point Atkinson 16 and 23 days post-release. An additional smolt was recorded in the ocean at the northern Strait of Georgia line one month after release, without having been detected previously in the Fraser (Table 4.3). Survival to the mouth of the Fraser River was estimated to be $7.0 \% \pm 6.2 \%$ s.e. (Figure 4.3). Survival estimates from release to the first and second Fraser River lines were $45.6 \% \pm 31.4 \%$ s.e. and $7.0 \% \pm 31.4 \%$ s.e. respectively, implying that considerable mortality occurred in both the first and second segments of the migration.

During 2006, 16 of the 100 tagged smolts were detected in the lower Fraser 7-19 days post-release $\left(\mathrm{T}_{\text {median }}=10\right.$ days $)$, yielding a survival estimate of $50.9 \% \pm 18.6 \%$ s.e. from release to each of the three Fraser River lines, implying that in-river mortality only occurred before the first station. Of these 16 , three were subsequently recorded in the ocean -one in Burrard Inlet 24 days post-release (in June), and two on the northern Strait of Georgia line 37 and 48 days post-release (in July, Table 4.3). An additional eight fish
were detected in the ocean and not the river. During the summer, one smolt was detected in Howe Sound, one in the southern Strait of Georgia, two at Point Atkinson, and four in the northern Strait of Georgia (Table 4.3).

### 4.4 Discussion

Fishing pressure and marine productivity affect the smolt-to-adult survival of many salmon stocks (Beamish et al., 1997; Coronado and Hilborn, 1998; Beamish et al., 1999; 2000; Welch et al., 2000). However, evidence from this study suggests that the poor overall survival rate of Thompson coho (at least from 2004-2005) may be influenced strongly by mortality during the freshwater outmigration phase of their lifecycle.

Although concern was expressed that coho smolts leaving the Thompson watershed likely had very low freshwater survival, no data existed to support this hypothesis (Routledge and Wilson, 1999). During the time of this study (2004-2006), return abundances continued to decrease and were consistently lower than predicted based on spawner abundances in the brood year (DFO, 2006). During 2006, the total escapement of Thompson coho was 11,300 , which is at the lower threshold for maintaining demographic and genetic needs in the Management Unit and represents a $1.5 \%$ smolt-to-adult survival rate (DFO, 2006). Our results from tracking out-migrating Thompson coho smolts implanted with acoustic tags has provided the first strong evidence of low survival during the downstream migration for this endangered species.

The overall marine survival of coho salmon in southern BC has declined significantly during the past three decades (Coronado and Hilborn, 1998; Bradford and Irvine, 2000). Since the 1970s, coho salmon production off the west coast of North America has varied with latitude; northern populations generally thrived while declines were observed in the south (Coronado and Hilborn, 1998; Hare et al., 1999; Hobday and Boehlert, 2001). Four Canadian salmon populations became endangered after 1989, including the Thompson coho, likely due to a regime shift at the time (Irvine, 2004). During the mid-1990s the Strait of Georgia coho fishery collapsed due to a decline in marine survival and a complete migratory behaviour change to residence on the shelf off the west coast of Vancouver Island instead of residence in the Strait of Georgia (Beamish et al., 1999). This important body of water, which once supported large commercial and
recreational coho fisheries (valued at CDN $\$ 218.5$ million by Gislason et al., 1996), has had an increasing surface temperature and other oceanographic changes due to climate trends (Beamish et al., 2004).

The Thompson coho, one of the primary Strait of Georgia stocks, historically spent the marine part of their life cycle almost entirely within the Strait of Georgia (Irvine et al., 1999a). From 2004-2006, Thompson coho made up an average of $27 \%$ of the juvenile summer coded-wire tagged coho catch during DFO research trawl surveys (R. Sweeting, pers. comm.) However, since 1995 nearly all the coho have left the Strait by the February following their first ocean summer (Beamish et al., 2008). The cause of this behavioural change is not known, but as with most recent changes in salmon survival and behaviour, the leading hypothesis attributes it to shifting ocean productivity (Beamish et al., 2004).

Climate change has also affected freshwater salmon production similarly to marine production (Lawson et al., 2004). The effects of regime shifts on the freshwater habitat of coho salmon should be a primary concern for the conservation of this species, as its most physiologically stressful life stages occur in freshwater: the outmigration of smoltifying young and the upriver return of spawning adults. Quantitative evidence for the effects of climate change on the freshwater production of coho salmon smolts is lacking, however (Bradford, 1999). Recent climate trends in the North Pacific have been correlated to higher temperatures and earlier spring flows in the Fraser River system (Beamish et al., 2000), which seems to be advancing the outmigration timing of wild coho smolts (Beamish et al., 2008). In the Thompson River system, an increasing average April flow rate (Figure 4.2) -indicating an earlier spring freshet- may be affecting the early freshwater survival and behaviour of wild and hatchery Thompson coho smolts in various ways. If wild fish migrate out earlier and hatchery releases remain static, hatchery smolts may be at a disadvantage (Beamish et al., 2008). At the final freshwater stage in the salmon lifecycle, climate may continue to be a major influence on behaviour and physiology. The return migration of Thompson River (late-run) adult sockeye has been occurring several weeks earlier than normal (Cooke et al., 2004; Young et al., 2006). An investigation of coho spawning habitat in the Thompson system found that approximately one third of the spawning beds used in 1988 were devoid of spawners a decade later, in 1997 (Irvine and Bradford, 2000). Irvine et al. (1999b) also observed declines in the body size, fecundity, and proportion of females in the Thompson coho spawning populations since 1995.

While climatic effects on freshwater systems are only beginning to be understood, the influence of direct anthropogenic habitat degradation has been studied extensively (Labelle et al., 1997; Simpson et al., 1997). Bradford and Irvine (2000) found that the decline in Thompson coho smolt production was not due to density-dependent mortality, but more likely a basin-wide deterioration in physical habitat quality due to land use practices. The Thompson River valley has been altered by silviculture and agriculture over the past fifty years (Harding et al., 1994; Bradford and Irvine, 2000). Timber clear-cutting, animal feedlots, dairy farms and free-ranging livestock are common (Burt and Wallis, 1997). Loss of riparian vegetation has contributed to bank destabilization and siltation, and small tributaries and wetlands have been isolated or destroyed in many cases (Bradford and Irvine, 2000). As wild coho spend their first year in the river environment, they are especially sensitive to flow levels, temperature extremes, siltation, predation, and disease (Groot and Margolis, 1991). Optimal survival conditions for coho smolts were found to be in rivers with relatively cooler temperatures, deep pools, structurally complex habitats, intermediate second winter flows, and high second spring flows (Lawson et al., 2004). Rood and Hamilton (1995) found that during the summer months in this semi-arid valley, large amounts of water are being withdrawn from the Thompson River for irrigation purposes, lowering flows and increasing mean summer temperatures. Decreased water quality during high flow periods is also a major concern in the Thompson watershed (Environment Canada, 2008). Salmon exposed to higher temperatures have been found to have lower reproductive success and higher prevalence of parasites (Crossin et al., 2008).

The relatively long freshwater migratory distance traveled by Thompson coho smolts through highly developed areas may be part of the reason for their high freshwater mortality rate when compared with other coho populations in British Columbia. Thompson coho smolts must travel $>350 \mathrm{~km}$ to reach the ocean, with about one quarter of this distance in the Thompson River and the rest in the Fraser River mainstem. The Fraser River watershed drains approximately one quarter of the land area of British Columbia, including runoff from agriculture, sewage and effluent from mines and pulp mills. The lower Fraser River valley is inhabited by over two million people, which has had a detrimental effect on the river, its estuary and tributaries. Although it seems that the majority of the smolt mortality is occurring in the Upper Fraser / Thompson Rivers, there was a noticeable estimated mortality between the upper and mid Fraser lines in 2005. Aside from ecological and health reasons, the economic value of maintaining good
quality freshwater habitat in the Thompson system was estimated to be CDN \$1,322-7,010 per km salmon stream per year (Knowler et al., 2003).

In two out of three years, the freshwater survival estimates of Thompson steelhead and spring chinook measured during the downstream migration using the POST array were generally higher than they were for coho using the same model assumptions (Figure 4.3). Coho may not be faring as well as other salmon species in the Thompson because of physiological differences influencing health, foraging ability and predator avoidance. Some of the Thompson coho may also remain in fresh water for an extra year and not migrate out to sea until the following spring. Coho are the last salmon species to be released from hatcheries in the Thompson. This means that they are entering the river at higher flow rates and temperatures. Food availability may be lower and predators may be more numerous.

Concurrent tag effects studies determined that smolts with an initial fork length $\geq 10.5 \mathrm{~cm}$ had $100 \%$ survival over a 300 day period in freshwater when tagged with V7-2L transmitters, and smolts $>12.5$ cm (the minimum size used in this study) had $100 \%$ tag retention over this same period (Chittenden et al., 2008a). Smolts with $\geq 14 \mathrm{~cm}$ fork length implanted with V9-6L transmitters had $100 \%$ survival up to 50 days post-surgery. The same smolts had $80 \%$ tag retention up to one month post-surgery and $50 \%$ tag retention at day 50. At the body sizes of smolts tagged in the field study, the 9 mm diameter tag group had $92 \%$ survival up to day 30 . The 7 mm tag group had perfect survival and tag retention to day 200 (Chittenden et al., 2008a). Therefore, it is unlikely that the tags or surgical procedure had an effect on the survival of the fish in this study.

Hatchery programs in BC may be producing fish that vary physically and genetically from wild fish (Taylor, 1986; Swain et al., 1991; Chittenden et al., 2008b). Hatchery-reared coho in the Strait of Georgia have been found to have different survival rates than their wild-reared counterparts (Sweeting et al., 2003; Beamish et al., 2008). Concerns have been raised about the possibility that releasing hatchery fish may negatively affect the ability of wild populations to adapt to climate change (Hill et al., 1991; Riddell and Swain, 1991; Berejikian et al., 1996; Nickelson, 2003; Hinder et al., 2006; Araki et al., 2007a; 2007b). There is a need to investigate the environmental and genetic effects of artificial rearing methods on smolt phenotype to improve hatchery methods and conserve endangered stocks such as the Thompson coho (Perry, 1995; Pitre and Cross, 1993; Brown and Day, 2002). While the Thompson coho populations were
declining, hatcheries released increasingly greater numbers of smolts into the system, which was not found to improve the situation (Bradford and Irvine, 2000).

In this study, only hatchery smolts were tagged, therefore the applicability of our results to the wild population is not known. Hatchery-reared smolts may be more susceptible to poor habitat quality in the Thompson and Fraser Rivers, and less adapted to surviving in the wild environment. Therefore, our estimates may be lower than actual survival rates for wild Thompson coho. Alternatively, the larger hatchery smolts may have been better able to deal with the stresses of the freshwater migration, and may have had higher survival rates than wild smolts. The frequency of freshwater residualisation could also differ among wild and hatchery-reared smolts. This rate is unknown for both groups as we were not able to assess it in our study. With the development of smaller acoustic tags, it may become possible in the future to compare wild and hatchery survival rates in this system.

There may also be survival differences between the Lower Thompson / Nicola populations used in this study, and the North Thompson and South Thompson groups. Two Lower Thompson stocks were used in this study: coho from Spius Creek in 2004 and 2005, and coho from the Coldwater River in 2006. The Coldwater coho released in 2006 had significantly higher freshwater and early marine survival then did the Spius coho released in 2004 and 2005. Although rearing was at the same hatchery facility, genetic or disease differences between the stocks may be responsible for survival differences between the two. A health assessment (Goede and Barton, 1990; Adams et al., 1993) should be conducted on wild and hatchery populations in the Thompson watershed to determine whether any physiological or health differences may be influencing stock survival. The Coldwater coho were also given 1-3 extra days of recovery from surgery prior to release, and the release site was also different in 2006. These differences should be examined further.

The endangered status of the Thompson River coho was thought to be caused by over-fishing, low marine survival rates and freshwater habitat alteration. This is the first study of the freshwater survival of migrating Thompson River coho smolts. Our results for three consecutive years using acoustic telemetry provide evidence for poor survival to the mouth of the Fraser River during 2004 and 2005, and demonstrate a need for further research.

Table 4.1 Model selection results for recaptures-only survival $(\varphi)$ and detection probability $(p)$ estimates. ${ }^{1}$

Model \begin{tabular}{c}
Number of <br>
parameters

$\quad$ QAICc $\Delta$ QAICc 

Akaike <br>
weight
\end{tabular}

Detection probability sub-models ${ }^{2}$

| $\varphi_{\text {(seg•group) }} p_{\text {(line•year +tag size+ flow Mission) }}{ }^{4}$ | 94 | 2384.8 | 0.00 | 0.98 |
| :---: | :---: | :---: | :---: | :---: |
| $\varphi_{\text {(seg•group) }} p_{\text {(line•yeartag size }+ \text { flow Port Mann) }}{ }^{4}$ | 94 | 2392.8 | 7.96 | 0.02 |
| $\varphi_{\text {(seg.group) }} p_{\text {(line•year+tag size }+ \text { Julian day) }}{ }^{4}$ | 94 | 2400.9 | 16.11 | 0.00 |
| $\varphi_{\text {(seg.group) }} p_{\text {(line•group) }}$ | 160 | 2454.8 | 69.98 | 0.00 |
| $\varphi_{\text {(seg.group) }} p_{\text {(line•year }+ \text { tag size) }}$ | 93 | 2464.1 | 79.30 | 0.00 |
| $\varphi_{\text {(segrgroup) }} p_{\text {(line•year) }}$ | 92 | 2496.7 | 111.90 | 0.00 |

Survival probability sub-models ${ }^{3}$

| $\varphi_{(\text {seg.group }+J u l i a n ~ r e l e a s e ~ d a y) ~}$ |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- |
| $p_{(\ldots)}$ | 95 | 2382.6 | 0.00 | 0.65 |
| $\varphi_{(\text {seg.group) }} p_{(\ldots)}$ | 94 | 2384.8 | 2.28 | 0.21 |
| $\varphi_{(\text {seg.group+flow Mission) }} p_{(\ldots .)}^{5}$ | 95 | 2387.0 | 4.45 | 0.07 |
| $\varphi_{(\text {seg.group+TravelTime) })} p_{(\ldots)}$ | 95 | 2387.0 | 4.45 | 0.07 |

[^3]Table 4.2 The number of fish ( N ) detected at riverine and marine POST listening stations by year and tag type, including their mean fork lengths (FL) and median travel times ( $\mathrm{T}_{\text {median }}$ ) to the lower Fraser lines.

| Stock | Year | Tag Type | N | Mean FL (mm) | $\mathrm{T}_{\text {median }}$ (Range) |
| :--- | :--- | :--- | :--- | :--- | :--- |
| Spius | 2004 | V9-6L | $1 / 28$ | 141 | $14(14)$ |
| Spius | 2004 | V7-2L | $1 / 12$ | 127 | $18(18)$ |
| Spius | 2005 | V7-2L | $7 / 50$ | 127 | $12(8-23)$ |
| Coldwater | 2006 | V7-2L | $24 / 100$ | 124 | $10(7-19)$ |

Table 4.3 Post-release detection locations, time to detection and fork lengths (FL) of acoutiscally tagged Thompson River coho salmon smolts (NSOG is the northern Strait of Georgia, SSOG is the southern Strait of Georgia).

| Year | Tag Type | FL (mm) | Location (Days Post-Release) |
| :--- | :--- | :--- | :--- |
| 2004 | V9-6L | 141 | Fraser R. (14) |
| 2004 | V7-2L | 127 | Fraser R. (18) |
| 2005 | V7-2L | 125 | Fraser R. (8) |
| 2005 | V7-2L | 123 | Fraser R. (12) |
| 2005 | V7-2L | 128 | Fraser R. (12) |
| 2005 | V7-2L | 120 | Pt. Atkinson (16) |
| 2005 | V7-2L | 139 | Fraser R. (23) |
| 2005 | V7-2L | 125 | Pt. Atkinson (23) |
| 2005 | V7-2L | 130 | NSOG (34-41) |
| 2006 | V7-2L | 129 | Fraser R. (7) |
| 2006 | V7-2L | 131 | Fraser R. (8) |
| 2006 | V7-2L | 132 | Fraser R. (9) |
| 2006 | V7-2L | 132 | Fraser R. (9), NSOG (47) |
| 2006 | V7-2L | 130 | Fraser R. (9) |
| 2006 | V7-2L | 134 | Fraser R. (9) |
| 2006 | V7-2L | 127 | Fraser R. (9) |
| 2006 | V7-2L | 128 | Fraser R. (9) |
| 2006 | V7-2L | 129 | Fraser R. (10) |
| 2006 | V7-2L | 132 | Fraser R. (10), Pt. Atkinson (13), NSOG (38) |
| 2006 | V7-2L | 133 | Fraser R. (11) |
| 2006 | V7-2L | 132 | Fraser R. (11), Burrard Inlet (24) |
| 2006 | V7-2L | 126 | Fraser R. (15) |
| 2006 | V7-2L | 125 | Fraser R. (16) |
| 2006 | V7-2L | 130 | Fraser R. (16) |
| 2006 | V7-2L | 126 | Pt. Atkinson (17-21) |
| 2006 | V7-2L | 130 | Fraser R. (19) |
| 2006 | V7-2L | 127 | Pt. Atkinson (19) |
| 2006 | V7-2L | 129 | Howe Sound (25) |
| 2006 | V7-2L | 132 | NSOG (36) |
| 2006 | V7-2L | 131 | NSOG (37) |
| 2006 | V7-2L | 125 | NSOG (58) |
| 2006 | V7-2L | 129 | SSOG (67-121) |
| 2006 | V7-2L | 130 | NSOG (102) |
|  |  |  |  |



Figure 4.1 Geographic location of part of the POST acoustic array and smolt release sites. The edge of the continental shelf ( 200 m depth contour) is shown, as well as acoustic listening lines located in the Fraser River, Strait of Juan de Fuca (JDF), the northern Strait of Georgia (NSOG), and the Queen Charlotte Strait (QCS). Thompson River coho salmon smolts were released at 1) Spius Creek and 2) the Coldwater River.


Figure 4.2 Average April daily flow of the Thompson River from 1912-2006, as recorded at Spences Bridge (Environment Canada, 2008). Increasing average April flows are indicative of an earlier spring freshet.


Figure 4.3 Mark-recapture survival estimates and error bars for Thompson River steelhead trout, chinook and coho salmon smolts during the downstream migration from 2004-2006 by tag type, as determined by the POST array. Chinook and steelhead data are unpublished POST estimates (M. Melnychuk, personal communication). Survival was estimated to near the Fraser River mouth using V7 or V9 acoustic tags. Standard error bars are shown. The smolts were of wild (W), hatchery (H) and unknown (U) origin, from the Coldwater River (CR), the Deadman River (DR), the Nicola River (NR) and Spius Creek (SC) stocks. The same model assumptions were used for chinook and steelhead as for coho (as described in the text). N values were (from left to right) 53, 50, 50, 19, 100, 99 for chinook, 31, 50, 57, 25, 26, 50, 38 for steelhead, and $12,28,50$ and 100 for coho.

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# CHAPTER 5: Riverine, Estuarine and Marine Migratory Behaviour and Physiology of Wild and Hatchery-Reared Coho Salmon Smolts Descending the Campbell River, BC ${ }^{4}$ 

### 5.1 Introduction

During the 1990s, many coho salmon populations in British Columbia displayed their lowest return rates on record (DFO, 2006). The mean return rates of wild coho indicator stocks decreased from $10.2 \%$ (brood years 1983-1992) to $4.4 \%$ (brood years 1993-2001). Mean hatchery indicator return rates also decreased over similar periods from $6.6 \%$ to $2.5 \%$ (DFO, 2006). Reasons for these declines are believed to be related to their marine migratory behaviour and survival, however there is a scarcity of data in this area (Pearcy, 1992; Brodeur et al., 2000; Beamish et al., 2003), particularly with respect to the less abundant coho (Sandercock, 1991). Coho salmon have region-specific distribution patterns and diverse life histories (Weitkamp and Neely, 2002). As a result, it is difficult to generalise about the marine migration patterns of coho salmon populations in BC.

Fisheries and Oceans Canada created a coho salmon hatchery program in 1971 to enhance coho salmon populations in the Strait of Georgia, BC (Cross et al., 1991), and by 2001, $70 \%$ of the coho salmon caught in the Strait of Georgia were found to be hatchery-reared (Sweeting et al., 2003). Wild salmon however, have generally been reported to be more adapted than their hatchery-reared counterparts to the natural environment. An important difference between wild and hatchery-reared coho has been the superior ability of wild fish to adapt to saltwater (Shrimpton et al., 1994). The Quinsam River, on Vancouver Island (Figure 5.1) has populations of both wild and hatchery coho. Like many areas in BC, there is a lack of information about the migratory behaviour and survival of Quinsam River coho. Previous studies have shown that both hatchery-reared and wild smolts are using the Campbell River estuary to adapt to the salt water environment and grow larger before entering the ocean (Levings et al., 1987). However, detailed studies of the freshwater and estuarine migratory behaviours of these fish, including the timing and duration of habitat use of individual salmon smolts, are lacking.

[^4]With the continual development of smaller acoustic tags, coded acoustic telemetry is successfully being used to track the movements of salmon pre-smolts in the field (Moore and Potter, 1994; Johnstone et al., 1995; Voegeli et al., 1998; Thorstad et al., 2004; Finstad et al., 2005). This technology can provide valuable information about individual fish and their interactions with the environment, enabling us to track the movements of each stock and species. Linking migratory behaviours to key physiological measures of readiness will provide insight into the survival rates of salmon stocks. To better understand coho salmon marine survival, a field study was conducted to examine the riverine, estuarine, and marine migratory behaviour (speeds, direction and timing) of wild and hatchery-reared coho salmon smolts using coded acoustic telemetry. If wild and hatchery-reared smolts differ in terms of migration speed, timing and physical condition, then they may have different marine and freshwater survival rates. Releases were conducted during daylight and after dark to determine whether the time of day at release has an affect on migration behaviour and survival. The physical condition and hematological properties of both wild and hatchery-reared coho salmon smolts were also assessed prior to their outward migration to estimate their physical fitness and readiness to enter the marine environment.

### 5.2 Methods

### 5.2.1 Study Area

The Quinsam River Salmon Hatchery is a major federal enhancement facility, producing coho salmon, chinook salmon, pink salmon, steelhead and cutthroat trout. The Quinsam River is a tributary of the Campbell River, which drains an area of $1,460 \mathrm{~km}^{2}$ on Vancouver Island (Figure 5.1). Mean flow rates from 21 May to 6 July 2006 for the Quinsam were $9 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$ with a primary water level of 1.1 m (government of Canada hydrological data). The mean temperature of the Quinsam during the surgeries was $14.4{ }^{\circ} \mathrm{C}$.

The Quinsam River Salmon Hatchery releases approximately 800,000 coho smolts each spring from the hatchery, however the adult returns in 2005 and 2006 were below 5,000 individuals. From the hatchery, the smolts travel 4 km down the Quinsam River, then 4 km down the Campbell River to reach the estuary. Since the late 1940s, a hydroelectric dam upstream in the Campbell River has been controlling flow rates. From 1 May to 30 June, the target flow rate was between 100 and $126 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$. The tides ranged from 0.4 to 4.3 m during the same time period. The Campbell River estuary begins at the head of tide, 2.5
km from Tyee Spit at the river mouth (Figure 5.1). It is approximately 300 m across, with a sand and gravel bottom. Marsh bench habitat has been constructed along the intertidal margins of the estuary, some subtidal areas in the upper estuary have been planted with eel grass, and many floating docks provide cover for fish. There is heavy boat and plane traffic in the estuary, with numerous predatory birds and mammals.

The Campbell River empties into Discovery Passage, a roughly 2 km -wide stretch of ocean up to 350 m deep in the middle. Twelve kilometres north of the river mouth in Discovery Passage, is Seymour Narrows -a dangerous stretch of water where tidal currents can near 16 knots. To reach the northern tip of Vancouver Island, a smolt would have to travel 230 km through Discovery Passage, Seymour Narrows and Johnstone Strait from Campbell River. Ten kilometres south of the river mouth, Discovery Passage opens into the Strait of Georgia, which extends roughly 300 km to the southern tip of Vancouver Island and the Strait of Juan de Fuca (Figure 5.1).

### 5.2.2 Acoustic Materials

Quinsam Hatchery coho salmon smolts were implanted with V9-6L-R46K transmitters [VEMCO Ltd., Halifax, Nova Scotia Canada, $9 \times 20 \mathrm{~mm}$, mass in air 3.3 g , mass in water 2.0 g , frequency 69 kHz , 20$60 \mathrm{~s}]$. Wild coho salmon smolts were surgically implanted with V7-2L-R64K transmitters [7x18.5 mm, mass in air 1.4 g , mass in water 0.7 g , frequency $69 \mathrm{kHz}, 60-180 \mathrm{~s}$. Acoustic receivers [VEMCO Ltd, Halifax, Nova Scotia Canada, model VR2] were stationed along potential migratory routes to monitor the smolts' behaviour. The detection ranges of the acoustic receivers were determined in the Quinsam River, the Campbell River estuary and in the ocean, 1 km north and 1 km south of the river mouth. During range testing, four receivers were suspended at $1 \mathrm{~m}, 3 \mathrm{~m}, 5 \mathrm{~m}$ and 8 m from the surface. Two of the V9-6L-R46K transmitters were attached to a string, one at 2 m and one at 4 m below surface to simulate approximate smolt depth range. Two V7-2L-R64K transmitters were also attached to the same string at the same depths. The receivers were held stationary and the transmitters were suspended from a boat for five minutes at set distances away. The receivers were downloaded afterwards to determine their detection efficiency at the ranges tested. The detection ranges of VR2 receivers were found to be $5-15 \mathrm{~m}(\mathrm{~V} 7-2 \mathrm{~L})$ and $10-20 \mathrm{~m}$ (V96L) in the Quinsam River, 100-150 m (V7-2L) and 150-200 m (V9-6L) in the estuary, and 200-300 m (V7-

2L) and 300-400 m (V9-6L) in the ocean. Detection ranges fluctuated with changes in water current, salinity, depth and substrate.

Following range testing, receivers [VEMCO Ltd, Halifax, Nova Scotia Canada, model VR2] were deployed at various locations along the potential coho migratory route (Figure 5.1). One VR2 was fastened to concrete anchors in the middle of the Quinsam River under the highway bridge, to record smolts just before they entered the Campbell River. Two receivers were located in the Campbell River estuary to ensure complete coverage of its entire width. The VR2 nearer the western bank was attached to a piling 1 m below the surface at low tide, whereas the eastern bank VR2 was fastened to a floatplane dock 1 m below the surface and held vertical with an anchor. The estuary receivers were suspended in $1.5-4 \mathrm{~m}$ of water (tide dependent).

Local knowledge assisted in site selection for the marine receivers. Areas that were known for being smolt habitat were preferred. In the ocean, six receivers were placed both north (1 km) and south (1 $\mathrm{km}, 4 \mathrm{~km}$ ) of the river mouth, on the east and west sides of Discovery Passage. They were suspended from floating structures (e.g. docks, buoys) 2 m below the surface, with the hydrophone pointing upwards and the attachment line held vertical by a 22.7 kg cannonball 1 m below the receiver. Due to high boat traffic and strong currents, it was not logistically possible to place any in the middle of Discovery Passage, and receivers only covered half of the width of the passage. Marine detections therefore, could be used to determine initial swimming speeds and directions, but not survival, as not all of the fish were being detected. In the ocean, the depths where receivers were placed ranged from 4-100 m , and their distances from shore ranged from $50-150 \mathrm{~m}$. During week seven of the study, six receivers were re-located up to 50 km north of the Campbell River mouth along both sides of Discovery Passage to detect any fish traveling north. The receivers were suspended from floating structures located 10 km NE (just south of Seymour Narrows), 15 km NW (north of Seymour Narrows), 25 km NW, $30 \mathrm{~km} \mathrm{NE}, 40 \mathrm{~km}$ NW and 40 km NE of the estuary (Figure 5.1). The receivers at 1 km NE and 4 km SE remained in place until all eight were removed 23 August, 2006 (94/95 days post release). The POST project listening lines were also located 50 km south and 230 km north of Campbell River (Figure 5.1).

### 5.2.3 Tagging Procedures

Hatchery-reared $(\mathrm{n}=40)$ and wild $(\mathrm{n}=40)$ coho salmon smolts were surgically implanted with coded acoustic transmitters on 21 and 22 May 2006 from the Quinsam River Hatchery in Campbell River, BC. Hatchery-reared smolts had a mean fork length of 14.2 cm , range $14.0-15.4 \mathrm{~cm}$, and a mean mass of 29.3 g , range $25.4-35.5 \mathrm{~g}$. Wild smolts (mean fork length 13.5 cm , range $12.5-16.0 \mathrm{~cm}$, mean mass 23.0 g , range $16.7-36.0 \mathrm{~g}$,) were caught in a trap during their downstream migration in the Quinsam River and were tagged between 24 and 48 hours post-capture. All of the fish caught in the downstream traps had spent at least six months in the Quinsam River system prior to capture. As the wild smolts were significantly smaller than the hatchery-reared smolts, the use of smaller transmitters was necessary. The hatchery coho salmon had been reared at the hatchery since the fall of 2004 and were scheduled to be released 24 May, 2006. This was the third of three releases of coho salmon from the Quinsam Hatchery, timed to coincide with the wild smolt out-migration.

The fish were anesthetised in 70 ppm buffered tricane methane sulphonate (MS222, Syndell Laboratories, Canada) and placed on the V-shaped surgery table ventral side up with gentle irrigation of 30 ppm MS222 over the gills. The tags were inserted into the body cavity via a midline incision, anterior to the pelvic girdle. The incisions were closed using two interrupted sutures. Surgical tools were sterilised and rinsed between surgeries with Ovadine (Dynamic Aqua Supply, Canada) and distilled water. The fish recovered in outdoor holding tanks for 24 to 36 hours post-implantation before being released. The surgeries were performed on twenty wild and twenty hatchery-reared smolts each day.

The smolts were released in four groups of twenty over two days, with each release including ten wild and ten hatchery-reared individuals. Each release day had two releases -one during daylight and one after dark. The releases were carried out 24 h after surgery from an in-river holding pen. The smolts were placed in the holding pen an hour prior to release and the pen gate was opened at the specified release time. The fish were left to enter the river freely. Manual tracking was conducted in the river from the release site to the estuary 16 days post-release to search for any remaining transmitters.

A separate laboratory trial was carried out to monitor smolt survival and tag retention for three months following surgery. Fourteen wild smolts of the same population and size group used in the field study, were implanted with mock V7-2L tags. Fourteen hatchery-reared smolts were implanted with mock

V9-1L tags. An additional ten fish from each group were implanted with PIT tags. The mock V9-1L tags were 4 mm longer than the V9-6L tags used in the field experiment. The smolts were placed into a communal outdoor tank, provided with aerated groundwater and fed daily to satiation for three months. Tag drops and mortalities were recorded twice daily. Out of the fourteen hatchery-reared smolts implanted with mock V9-1L tags, eight expelled their tags near the end of the three month trial. None of the wild smolts expelled their tags, however four died near the end of the trial. All the control fish survived, as did all of the hatchery-reared smolts.

### 5.2.4 Physiological Sampling

Thirty wild and thirty hatchery-reared fish, taken from the same populations as the field study fish, were euthanised in 120 ppm buffered MS222 to provide a health baseline and compare their stage of smoltification. Masses and lengths were measured and condition factors were calculated (Goede and Barton, 1990). Blood was sampled from the caudal vessels with a sterile syringe rinsed with lithium heparin. Whole blood was collected for hematocrit measurements (Klontz, 1994). The remaining blood was centrifuged at $13,000 \mathrm{rpm}$ for five minutes. Plasma was collected, stored on dry ice, then in a $-80^{\circ} \mathrm{C}$ freezer until analysis. Levels of plasma sodium, potassium, calcium, chloride, glucose and lactate were measured using a Stat Profile Plus 9 blood gas machine (Nova Biomedical Corporation, MA). Gill samples were frozen on dry ice and stored in a $-80^{\circ} \mathrm{C}$ freezer until $\mathrm{Na}+\mathrm{K}+$-ATPase activity assays were conducted (McCormick, 1993; Shrock et al., 1994).

### 5.2.5 Analyses

The time taken by an individual smolt to get from point $A$ to point $B$ was calculated by subtracting the time of first detection at the arrival receiver by the last detection time at the departure receiver. Minimum time in the estuary was inferred as the time from the first to last detection by an estuary receiver. This included the time taken by some smolts to enter the ocean briefly before returning to the estuary. If the smolts were detected once only, they were given a minimum estuary residence time of one hour, which is an estimate of the time taken for a smolt to pass through the estuary. The marine speeds were estimated by dividing the distance between two ocean receivers by the time taken to get from receiver A to B. As the
smolts did not likely swim directly from receiver A to B, these are minimum travel speeds. Outlier values exceeding $3.0 \mathrm{bl} \cdot \mathrm{s}^{-1}$ were not included in the calculations as they were in part due to strong ocean currents at the time of travel. All means were quoted at a $95 \%$ confidence interval, and significance was noted at $\mathrm{p}<$ 0.05. Migration data were compared using a one-sided ANOVA and two-sided Mann-Whitney U-test (Mendenhall, 1971). Physiological measures were compared using a one-sided ANOVA, Levene's Test for Equality of Variance and the Independent Samples T-test for Equality of Means (Sokal and Rohlf, 1995). Percent data (hematocrit) were arcsine transformed prior to statistical analysis.

### 5.3 Results

Of the 40 tagged wild coho salmon smolts, 39 ( $98 \%$ ) were detected in the estuary. While $85 \%$ of the 40 hatchery-reared smolts traveled past the first receiver 4 km from release, only $80 \%$ survived to the estuary. During their downstream migration in the Quinsam River, eighteen wild and thirteen hatcheryreared smolts were recorded by the first receiver. Wild smolts took significantly less time (mean 12.16 h ) to reach the first receiver than the hatchery-reared smolts (mean $32.34 \mathrm{~h}, \mathrm{p}<0.01, \mathrm{Z}=2.70$, Figure 5.2 a ). No difference in time taken to reach the first receiver was found between wild or hatchery-reared coho smolts released during daylight hours and those released after dark. Of the eighteen wild smolts detected by the first receiver, fifteen ( $83 \%$ ) were recorded traveling after dark. All of the hatchery smolts ( $100 \%$ ) were detected by the first receiver after dark. Hatchery-reared fish tended to spend more time near the receiver, which was situated under a bridge at the confluence of the Quinsam and Campbell Rivers. Two of the hatchery smolts spent 13 h at the receiver together before continuing downstream. Four other hatchery smolts spent one to six hours at the same location. Only two of the eighteen wild smolts waited near the receiver; their length of stay was thirty to fifty minutes.

The wild coho salmon smolts took less time to arrive at the Campbell River estuary than the hatchery-reared smolts ( $\mathrm{p}<0.01, \mathrm{Z}=3.60$, Figure 5.2 b ). Whereas hatchery-reared smolts took an average of 92.67 h to reach the estuary from release, wild smolts took only 35.56 h . No differences in survival or time taken to reach the estuary were found between the smolts released during daylight hours and those released after dark. No significant difference was found between wild and hatchery-reared smolts in terms of time taken to travel the 4 km from the first receiver to the estuary (mean 11.37 h for wild, 16.90 h for
hatchery, p $<0.25$, Figure 5.2 c ). No fish were detected in the Quinsam and Campbell Rivers when they were tracked manually with a receiver on 6 June 2006 ( $15 / 16$ days after the last release). Six ( $15 \%$ ) of the hatchery smolts and one ( $2.5 \%$ ) of the wild smolts were never detected; these fish were either removed from the river by avian or land-based predators, or they stayed in very shallow water near the banks and could not be picked up by the mobile or fixed receivers.

Wild smolts spent less time on average ( 179.16 h ) in the estuary than hatchery-reared smolts (274.05 h, p < 0.16, Figure 5.2 d ). No significant differences in time spent in the estuary were found between the smolts released during daylight hours and those released after dark. The majority of the wild smolts were detected in the estuary by 26 May 2006 (4/5 days post release); for hatchery-reared fish, this occurred five days later, on 1 June 2006 (Figure 5.3). On 7 June 2006 (16/17 days post-release), the receiver was placed in five areas of the estuary for five minutes each. Seven fish were detected in four of the locations. The last known location of 22 (55\%) wild and 19 ( $47.5 \%$ ) hatchery-reared smolts was in the estuary.

The coho salmon smolts traveled both north (twelve wild, six hatchery-reared) and south (five wild, seven hatchery-reared) in Discovery Passage from the river mouth, along both the eastern and western shorelines. Whereas the hatchery smolts did not favour either direction, the majority of the wild coho salmon smolts went north (Table 5.1). Two of these ventured south into Strait of Georgia before returning to Discovery Passage. One wild smolt was detected 250 km north of Campbell River at the north end of Vancouver Island (Table 5.1). Twelve wild fish were detected in the ocean between 23 May (two days post-release) and 30 May 2006 (nine days post-release). No hatchery-reared fish was detected in the ocean until 30 May 2006. Six marine bays north of the Campbell River mouth were checked for five minutes each on 6 June 2006 ( 15 days after the last release). These were at 4 km (on both the east and west side), 14 km (east side only), 16 km (east and west side) and 20 km north (west side only). Only one fish was detected, 4 km north of the estuary on the east side of the Passage. The estimated average minimum marine speeds after removing outliers over $3.0 \mathrm{bl} \cdot \mathrm{s}^{-1}$ were $0.67 \pm 0.85 \mathrm{bl} \cdot \mathrm{s}^{-1}(\mathrm{n}=13)$, and $0.31 \pm 0.08 \mathrm{bl} \cdot \mathrm{s}^{-1}(\mathrm{n}=3)$ for wild and hatchery-reared coho salmon smolts respectively, which was not significantly different. The wild and hatchery smolts that were last detected in the ocean were not significantly different in terms of body size from their original populations.

The wild smolts were smaller than hatchery-reared smolts in terms of mass, fork length and condition factor, and had more variability in all three (Table 5.2). Furthermore, the wild smolts had higher plasma levels of sodium, potassium and chloride ions, and less lactate. The wild and hatchery-reared smolts had similar hematocrits, calcium and glucose levels (Table 5.2). The gill $\mathrm{Na}+\mathrm{K}+$-ATPase activity for the wild smolts was significantly higher than that of the hatchery-reared smolts (Table 5.2, Figure 5.4).

### 5.4 Discussion

Coho salmon are known to reside in surface waters and have highly regionalised migration patterns (Weitkamp and Neely, 2002). Coded-wire tagged coho smolts from the Quinsam Hatchery were caught both north and south of Campbell River during 2006 (R. Sweeting, pers. comm.) However, prior to this study the early migratory movements of wild and hatchery coho smolts were relatively unknown for the Campbell River. The importance of the Campbell River estuary to coho salmon out-migration was also a topic of interest, as its restoration has been a community priority for the past twenty years.

The differences found in the migratory behaviour of wild and hatchery-reared smolts may be due to the local experience of the wild fish, to physical advantages they may have, or both. A study of wild and hatchery-reared steelhead smolts found that the hatchery-reared fish had lower gill $\mathrm{Na}+\mathrm{K}+$-ATPase activity (Hill et al., 2006), making them less adapted to entering the marine environment. Hatchery-reared coho salmon smolts have also been found to have significantly lower salt water tolerance than wild smolts (Shrimpton et al., 1994). As the wild smolts descending the Quinsam River had higher gill $\mathrm{Na}+\mathrm{K}+$-ATPase activity, they were likely more physiologically ready to enter seawater than the hatchery-reared smolts. Plasma sodium, potassium and chloride levels of the Quinsam River wild coho salmon smolts were also significantly higher than levels in hatchery-reared smolts, and were higher than estimated normal ranges (Wedemeyer et al., 1990). These blood electrolytes have been found to rise with high exercise levels in fresh water (Graham et al., 1982), which may reflect the higher physical activity of the wild smolts in their downstream migration prior to capture. The wild smolts were likely exercising more than the hatcheryreared smolts, which may have increased their swimming abilities. The lower condition factor of the wild smolts is further evidence that they may have had less body fat content and a higher level of physical fitness than hatchery smolts. Plasma lactate concentrations were significantly lower in wild fish, which is a
sign of elevated stress levels in fish commonly associated with smoltification (Pankhurst and Dedualj, 1994). The higher variability of wild smolts over hatchery-reared smolts in terms of mass, length, condition factor and various plasma electrolytes, supports findings from Taylor (1986). Hematocrit values were within normal range for healthy coho salmon (Wedemeyer et al., 1990). Physiological assessments therefore demonstrate that wild coho smolts, while smaller than hatchery-reared smolts, were perhaps more physiologically fit and ready to enter the marine environment. Further studies could evaluate the influence of the wild smolts' local experience on the differences found in the migratory behaviour and survival of wild and hatchery-reared smolts.

If hatchery-reared smolts are slower and less physically adapted to their environment than their wild counterparts, they may suffer higher mortality rates, especially in predator-rich areas like the estuary. Some studies have found hatchery-reared Atlantic smolts to be less aggressive (Metcalfe et al., 2003) and have higher mortality rates in marine environments than wild smolts (Jonsson et al., 2003), whereas other research found no difference between the two (Lacroix and McCurdy, 1996; Voegeli et al., 1998; Thorstad et al., 2006). Wild coho salmon smolts released in the Quinsam River had higher survival rates to the estuary than the hatchery-reared smolts, arriving in significantly less time, and entering the ocean earlier. Rhodes and Quinn (1998) suggest that wild smolts may be out-competed by more dominant and agonistic hatchery-reared coho salmon. However, the reason for the higher speeds of wild Quinsam coho salmon smolts was more likely to be due to their physiological advantage over the hatchery-reared smolts.

Campbell River's newly rehabilitated estuary was found to be of great importance, particularly for the hatchery-reared smolts. Wild smolts spent a week on average, and hatchery-reared fish nearly two weeks in the estuary before heading out into the ocean. Beach seining conducted in the estuary by the Campbell River Department of Fisheries and Oceans during the same period that the tagged fish were detected, also found large populations of coho salmon smolts and an abundant food supply for them (S. Anderson, pers.comm.)

Receivers placed north and south of Campbell River along both sides of Discovery Passage (Figure 5.1) detected out-migrating coho salmon smolts traveling in both directions and along both shorelines. A greater number of wild smolts were last detected north of the Campbell River estuary, whereas the hatchery smolts were roughly divided evenly between north and south (Table 5.1). This
northward migration of coho smolts out of the Campbell River may help to explain the relatively lower recapture rates of Quinsam coho in the Strait of Georgia (Beamish, 1999). Some of the monitored fish traveled back and forth across Discovery Passage, without having one direct migration pathway out of Campbell River. Results from this study suggest that there is more than one migration route for this stock. Accurate marine survival measurements were not possible due to incomplete receiver coverage, however more wild than hatchery-reared individuals were detected in all three environments (river, estuary and ocean). This is likely a reflection of the greater fitness of the wild smolts in the freshwater environment, as well as their physical readiness to enter the ocean (Olla et al., 1998). Wild smolts were calculated to have twice the average marine swim speed of hatchery-reared smolts. Swim speeds were based on the shortest possible route between two points, so could have been underestimations of the actual speeds. Currents were constantly fluctuating and changing direction within Discovery Passage, which would have also affected actual swim speeds. Therefore, some of the extremely elevated swim speeds noted may have been due to predation, or simply to ocean currents. Large populations of harbour seals (Phoca vitulina) in Discovery Passage could be a major contributor to high early marine mortality rates of salmon smolts leaving the river. There is also a possibility that these marine mammals may favour the larger, fattier hatchery-reared smolts over the wild smolts, which would further increase the post-release mortality rates of hatcheryreared smolts.

The V9-1L dummy tags used in the tag effects trial were 4 mm longer than the actual tags used in the field work (V9-6L), which may have increased trial expulsion rates. Wild Atlantic salmon have been found to be more affected by the tagging procedure than hatchery-reared fish (Peake et al., 1997). The wild coho salmon smolts in the tag effects trial may have had elevated stress levels due to their unfamiliarity with the hatchery environment, feed, and handling. They could have also been stressed from being held back from entering salt water during smoltification.

This first study on Campbell River coho salmon using coded acoustic telemetry found significant differences in the physiology and migratory behaviour of wild and hatchery-reared coho salmon. The differences found could be useful in future hatchery management and planning, if post-release survival of hatchery fish is a concern. The time of day at release did not affect the survival and migratory behaviour of coho salmon smolts, and both hatchery and wild smolts preferred to travel downstream after dark. The

Campbell River estuary was found to be important to coho salmon smolts, with both wild and hatcheryreared smolts using it as their primary habitat for over one week on average before entering the ocean. In the marine environment, the fish traveled north and south from the river mouth on both sides of Discovery Passage. Long-term studies correlating marine survival data with the early marine behaviour and physiology of wild and hatchery-reared coho salmon are crucial to the effective management of coho salmon populations.

Table 5.1 Marine behaviour of smolts by day post-release (pr) and distance from estuary (dfe).

| Final Dir. | North |  |  |  | South |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Wt (g) | FL (cm) | $\begin{aligned} & \text { Days } \\ & \text { (pr) } \end{aligned}$ | Location (dfe) | Wt (g) | FL (cm) | $\begin{aligned} & \begin{array}{l} \text { Days } \\ \text { (pr) } \end{array} \\ & \hline \end{aligned}$ | Location (dfe) |
| Wild | 20.5 | 13.0 | 15 | 1 km NW | 22.8 | 13.3 | 2, 3 | 1 km SW |
|  | 23.5 | 13.5 | 9 | 1 km NW | 18.5 | 12.8 | 1,2 | 1 km SW |
|  | 21.2 | 13.1 | 7 | 1 km NW | 22.0 | 13.1 | 4-10 | 1 km SW |
|  | 23.2 | 13.2 | 6 | 1 km SW | 20.3 | 12.8 | 13-17 | 4 km SE |
|  |  |  | 7 | 1 km NW |  |  | 41 | 4 km SW |
|  | 21.4 | 13.5 | 3 | 1 km NW | 18.5 | 12.5 | 12-14 | 4 km SE |
|  | 32.8 | 15.2 | 1-4 | 1 km NW |  |  |  |  |
|  | 28.0 | 14.5 | 5-9 | 1 km NE |  |  |  |  |
|  | 18 | 12.5 | 3 | 4 km SE |  |  |  |  |
|  |  |  | 4 | 1 km NE |  |  |  |  |
|  | 16.7 | 12.5 | 10-26 | $\begin{aligned} & 4 \mathrm{~km} \text { SW- } \\ & 1 \mathrm{~km} \mathrm{NE} \end{aligned}$ |  |  |  |  |
|  | 22.5 | 13.3 | 28,29 | 50 km S |  |  |  |  |
|  |  |  | 39 | 1 km NW |  |  |  |  |
|  |  |  | 50 | 3 km NE |  |  |  |  |
|  | 21.3 | 13.0 | 13 | 1 km SW |  |  |  |  |
|  |  |  | 55 | 33 km NW |  |  |  |  |
|  | 31.5 | 15.2 | $22-43$ | $\begin{aligned} & 50 \mathrm{~km} \mathrm{~S} \\ & 230 \mathrm{~km} \mathrm{~N} \end{aligned}$ |  |  |  |  |
| Hatchery | 29 | 14.4 | 16 | 1 km NW | 32.0 | 14.4 | 10 | 1 km NW |
|  |  |  |  |  |  |  | 11 | 1 km SW |
|  | 28.3 | 14.0 | 11, 12 | 1 km NW | 27.5 | 14.3 | 10 | 1 km NW |
|  |  |  |  |  |  |  | 11,12 | 1 km SW |
|  | 28.8 | 14.0 | 9 | 1 km NW | 35.5 | 15.1 | 22 | 4 km SW |
|  | 28.3 | 14.0 | $\begin{aligned} & 16 \\ & 17 \end{aligned}$ | 1 km SW | 34.2 | 14.7 | 16 | 4 km SW |
|  |  |  |  | 1 km NE |  |  |  |  |
|  | 27.2 | 14.0 | 16 | 5 km NE | 29.0 | 14.0 | 16 | 4 km SW |
|  |  |  |  |  |  |  | 17, 18 | 1 km NE |
|  |  |  |  |  |  |  | 20-22 | 4 km SW |
|  | 28.5 | 14.0 | 30,31 | 12 km NE | 25.7 | 14.0 | 13 | 1 km SW |
|  |  |  |  |  |  |  | 21-24 | 50 km S |
|  |  |  |  |  | 25.4 | 14.0 | 22 | 1 km NW |
|  |  |  |  |  |  |  | 41-55 | 50 km S |

Table 5.2 Physiological characteristics of wild (W) and hatchery-reared (H) coho salmon smolts (significant differences are denoted by a '*').

|  |  | $n$ | Mean | SD | F | df | $p$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Gill $\mathrm{Na}+\mathrm{K}+$-ATPase activity ( $\mu \mathrm{M}$ ADP/mg protein $/ \mathrm{h}$ ) | W | 19 | 9.39* | 4.32 | 15.83 | 38 | < 0.01 |
|  | H | 20 | 5.13* | 2.02 |  |  |  |
| Sodium, plasma | W | 16 | 180.72* | 49.24 | 10.76 | 16.14 | < 0.01 |
| ( $\mathrm{mmol} / \mathrm{L}$ ) | H | 21 | 139.30* | 10.97 |  |  |  |
| Potassium, plasma ( $\mathrm{mmol} / \mathrm{L}$ ) | W | 16 | 6.60* | 2.29 | 0.019 | 35.00 | 0.02 |
|  | H | 21 | 4.55* | 2.73 |  |  |  |
| Chloride, plasma (mmol/L) | W | 16 | 145.35* | 32.08 | 9.48 | 18.41 | 0.01 |
|  | H | 21 | 122.12* | 12.37 |  |  |  |
| Calcium, plasma (mmol/L) | W | 16 | 0.98 | 0.23 | 3.32 | 35.00 | 0.48 |
|  | H | 21 | 0.94 | 0.15 |  |  |  |
| Glucose, plasma (mmol/L) | W | 10 | 8.08 | 3.80 | 1.04 | 23.00 | 0.96 |
|  | H | 15 | 7.99 | 5.39 |  |  |  |
| Lactate, plasma, (mmol/L) | W | 16 | 2.78* | 0.99 | 12.95 | 27.02 | < 0.01 |
|  | H | 21 | 8.22* | 2.61 |  |  |  |
| Hematocrit | W | 18 | 0.44 | 0.09 | 0.58 | 38.00 | 0.06 |
|  | H | 22 | 0.49 | 0.06 |  |  |  |
| Condition | W | 19 | 0.95* | 7.08 e-2 | 5.39 | 25.80 | <0.01 |
| Factor (g/cm ${ }^{3}$ ) | H | 24 | 1.00* | 7.61 e-3 | 5.39 | 25.80 | < 0.01 |
| Mass (g) | W | 59 | 20.14* | 6.27 | 11.15 | 92.29 | < 0.01 |
|  | H | 64 | 27.77* | 3.69 |  |  |  |
| Fork length (cm) | W | 59 | 12.78* | 1.39 | 21.55 | 75.66 | < 0.01 |
|  | H | 64 | 13.97* | 0.57 |  |  |  |



Figure 5.1 The study area, including the Quinsam and Campbell Rivers, the Campbell River estuary and Discovery Passage. The release site and the head of tide line (T) for the Campbell River estuary are shown, as well as all receiver (VR2) locations and distances from the Campbell River mouth. POST listening lines are shown in grey on the Vancouver Island map.


Figure 5.2 Time spent in hours by hatchery-reared (H) and wild (W) coho smolts (a) from release (R) to the first receiver $(\mathrm{Q})$, located 4 km downstream at the confluence of the Quinsam and Campbell Rivers, (b) from R to the estuary ( E ), (c) from Q to E and (d) within the estuary (from the first to last estuary detection) including ANOVA diamonds (means $\pm 95 \% \mathrm{CI}$; diamond width represents samples size). Significant differences noted in $a$ and $b$.


Figure 5.3 Relative number of smolt detections over time in the Campbell River (circle), estuary (square), and ocean (triangle) environments for a) wild and b) hatchery-reared coho.


Figure 5.4 Gill Na+K+-ATPase activity for hatchery and wild smolts at time of release, including ANOVA diamonds showing a significant difference (means $\pm 95 \% \mathrm{CI}$; diamond width represents samples size).

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## CHAPTER 6: The Use of Acoustic Tags to Determine the Timing and Location of the Juvenile Coho Salmon Migration Out of the Strait of Georgia ${ }^{5}$

### 6.1 Introduction

The Strait of Georgia, British Columbia (Figure 6.1) historically supported a strong recreational and commercial fishery for coho salmon (Beamish et al., 1999). Prior to the early 1990s, coho salmon were fished from early spring through to the fall when they returned to the rivers to spawn. However, the marine survival of coho salmon declined from about $10 \%$ in the mid-1980s to about $2 \%$ in the mid-1990s (Beamish et al., 2000; Beamish et al., 2004). This decline has continued, with an average marine survival for coho salmon of $1.4 \%$ between 1996 and 2004 (Beamish et al., 2008). Coho salmon within the Strait of Georgia exhibited major migratory changes in recent years. Beginning about the mid-1990s, young coho salmon left the Strait of Georgia and did not return during the normal fishing times in the next year (Beamish et al., 1999). This change in behaviour along with some regulatory changes essentially ended the once lucrative recreational fishery.

Studies have been conducted that linked changes in marine survival of salmon with fluctuations in climate and ocean conditions (Beamish et al., 2000; Hare and Mantua, 2000). These changes were related to the larger-scale regime shifts as well as specific factors driving changes in the local ecosystem. Beamish et al. (2008) conducted a long-term study on the behaviour and survival of juvenile coho salmon in the Strait of Georgia between 1997 and 2006. They used modified midwater trawls to examine the growth and distribution of the juveniles. The changes in the population dynamics that they reported depended on the juvenile coho salmon remaining in the Strait of Georgia through September. This determination was based on the estimated abundance of juveniles caught in the Strait of Georgia in September, coded wire tag (CWT) recoveries within the Strait and the lack of CWTs from Strait of Georgia hatcheries recovered in surveys in regions outside of the Strait (Beamish et al., 2008). It was important to be certain that coho salmon remained in the Strait of Georgia past September because if juvenile coho salmon were rearing for extended periods in the Strait of Georgia it would be the conditions within this area that were critical for

[^5]their marine survival. For example, using the abundance estimates from the trawl surveys, and the assumption that the majority of the coho salmon were rearing in the Strait of Georgia, they estimated that on average, only $10 \%$ of coho smolts entering the Strait in the spring survive to mid September and only $13 \%$ of these subsequently returned as adults. This poor early marine survival compares with low estimated freshwater survival rates of $0 \%-51 \%$ (Chapter 4) and higher estimates of $75 \%$ to $98 \%$ (Chittenden et al., 2008a; Kintama Research Corporation, 2006). Thus, the early marine portion of the coho lifecycle is of critical importance to overall population abundances of returning adults. The objective of this study was to use acoustic tags to obtain the specific dates that coho salmon leave the Strait of Georgia as well as the direction of this out-migration.

### 6.2 Methods

### 6.2.1 Catch and Release

Juvenile coho salmon were caught in the Strait of Georgia during July and September 2006 using a 150 m purse seine with a small mesh bunt $(6 \mathrm{~mm})$. The fish were removed from the seine with a small mesh ( 8 mm ) dip net. To minimise scale loss and handling stress on the fish during sorting, surgery and release, Vidalife and MS222 (Syndel Laboratories, Vancouver, Canada) were used during handling. For identification the fish were partially sedated in a seawater bath containing 20 ppm MS222. Once identified the salmon were transferred to a tank with circulating sea water.

For tagging, coho salmon were anaesthetised in 60 ppm MS222. They were surgically implanted with VEMCO V7 (7 x 19 mm ) and V9 ( $9 \times 21 \mathrm{~mm}$ ) acoustic transmitters using methods described in Chittenden et al. (2008a). In this study V7 and V9 transmitters were implanted in coho salmon with a minimum fork length of 12 cm and 17 cm respectively, as previous tag effect trials had shown no change in survival, growth, swimming performance or physiology for coho salmon this size (Chittenden et al., 2008b).

The presence (mostly wild fish) or absence (all hatchery fish) of adipose fins on the coho salmon was recorded for all fish tagged, however, there was no attempt to tag a specific number of any one rearing type. Following surgery, each fish was allowed to recover in a circulating sea water tank until normal swimming behaviour was resumed. They were then released in the region they had been collected. Tags
were estimated to be active for approximately 200 (V7) to 400 (V9) days. In this study we assumed that all tags were active until February 2007.

### 6.2.2 Receiver Arrays

The Pacific Ocean Shelf Tracking project has established a number of receiver arrays in the vicinity of the Strait of Georgia (Figure 6.1). These arrays are maintained by POST and provide detection information to researchers using acoustic tag technology in their research. The POST arrays were designed to have as close to $100 \%$ detection efficiency as possible. Data from range testing indicated that efficiency averaged 83\% (Kintama Research Corporation, 2006). There are three major arrays in this region. These major arrays completely transect the waterways providing information on the movement of fish in and out of the Strait of Georgia. In this study we call these major arrays, lines. The Juan de Fuca Strait line transects the Juan de Fuca Strait 340 km to the southwest of our release site (Figure 6.1). Fish detected at this line left the Strait of Georgia to the south and west. The Queen Charlotte Strait line is located in Queen Charlotte Strait, 280 km from the release site at the northern tip of Vancouver Island (Figure 6.1). It marked the northern exit point for this study. The third listening line in the northern Strait of Georgia at Texada Island (Figure 6.1) was located north of our tagging site. In addition there were receiver arrays located in Discovery Passage, in the southern Strait of Georgia, and at the Vancouver Aquarium and Marine Science Center/Fraser River (Figure 6.1). These additional receivers did not completely transect any waterway. However, they did provide information and added verification on general directional movements of some of the tagged coho salmon during the study. Detection of fish at these additional arrays along with the northern Strait of Georgia line are all reported as Strait of Georgia. POST receiver arrays on the west coast of Vancouver Island, Washington and Oregon were used to obtain information on fish movement outside the Strait of Georgia. The Cascade Head line off of Oregon was 750 km from the release site and the Willapa Bay line off the Washington coast was 560 km from the release site (Figure 6.1). The Lippy Point line is off the west coast of Vancouver Island and was 780 km from the release site (Figure 6.1). These lines extend from the shoreline to the continental shelf.

### 6.2.3 Analyses

Differences in migratory behaviour due to body size were examined by dividing coho salmon from each tagging period into four length groups (average - average +1 SD , average - average -1 SD , average average $+>1 \mathrm{SD}$, average - average $->1 \mathrm{SD}$ ). Analysis of movement was based on the last major line that detected the fish and was divided into three groups: Strait of Georgia (SOG), Juan de Fuca Strait (JDF) and Queen Charlotte Strait (QCS). Fish that were never detected were included in the Strait of Georgia totals. Directional differences between length groups were compared using the Chi-square test. Significance was established at $\mathrm{p}<0.05$.

### 6.3 Results

### 6.3.1 Early and Late Summer Releases

From 17-19 July, 94 coho salmon were tagged and 79 were tagged from 11-13 September. The mean fork length of the fish tagged in July and September was $190 \mathrm{~mm}(\mathrm{SD}=26 \mathrm{~mm})$ and $253 \mathrm{~mm}(\mathrm{SD}=$ 25 mm ) respectively. The number of tagged fish detected at least once was 66 for the July group and 65 for the September group. There were 4 coho salmon detected at the Queen Charlotte Strait line that were tagged in July (Table 6.1) and detected between 25 July and 11 September 2006. One fish was detected over 50 times. There were 14 coho salmon detected at the Juan de Fuca Strait line that were tagged in July (Figures 6.2, 6.3). These detections occurred mostly from October to December 2006 (Figure 6.2). Five fish were detected here more than 20 times. None of the 79 fish tagged in September were detected at the Queen Charlotte Strait line (Figure 6.3). Forty-one of the coho salmon from the September tagging were detected between October 2006 and April 2007 at the Juan de Fuca line (Table 6.2). The largest number of individual detections (26) occurred here in November. Fish that were tagged in July had an earlier mean date of travel out of Juan de Fuca Strait (9 November 2006) compared to the fish tagged in September (2 December 2006) and spent less time near the Juan de Fuca Strait line ( $6 \pm 12$ days compared to $36 \pm 44$ days).

There were 48 fish from the July tagging and 24 fish from the September tagging (a total of 72 fish) that were detected but did not leave the Strait of Georgia. There were 28 fish from the July tagging and 14 fish from the September tagging that were never detected. If all of these detected and not detected
fish remained in the Strait of Georgia, then 114 or $66 \%$ of the tagged coho salmon probably did not leave the Strait of Georgia (Tables 6.1, 6.2). Of the 72 fish that were detected in the Strait of Georgia but not outside of the strait, 65 fish were detected before January 2007. Of the seven fish that were detected later in 2007, two were last recorded in January 2007, one in February 2007, two in March 2007 and two in April 2007.

### 6.3.2 Detections in Relation to Length

Six of the 94 coho salmon tagged in July were missing the adipose fin indicating that they were from a hatchery. In September, 18 of the 79 coho salmon tagged were missing their adipose fin indicating they also were hatchery fish. Therefore, there were 88 and 61 tagged coho salmon that did not have the adipose fin removed in July and September respectively. The average length of the fish with an adipose fin in July was 190 mm . These fish were smaller than the 6 hatchery chinook salmon (average 201 mm ), however the difference was not significant ( t -test, $\mathrm{p}>0.05$ ). In September, the average length of fish with an adipose fin ( 251 mm ) was significantly smaller than fish with the adipose fin removed ( $263 \mathrm{~mm}, \mathrm{t}$-test, p < 0.05). Because the size of the fish with a clipped adipose fin was larger and the number of these individuals was small, only coho salmon with an adipose fin were used to examine relationships between length and movement out of the strait.

There was no relationship between the percentage of fish in the four size groups (Table 6.3) and the percentages that were detected leaving the strait (chi square $\mathrm{p}>0.05$ ). All fish from the July tagging, detected at the Juan de Fuca Strait line were from the two mid-sized length groups. The largest percentage of coho salmon that were tagged in September and detected at the Juan de Fuca line was also from the midsize group. None of the fish in the smallest size group in July were detected outside of the Strait of Georgia. There was no significant difference ( t -test, $\mathrm{p}>0.05$ ) in the mean fork length of all the fish tagged in either July (192 mm) or September ( 248 mm ) and the fish that were eventually detected leaving the strait (Juan de Fuca Strait and Queen Charlotte Strait lines, 196 mm and 249 mm respectively, t-test, p > 0.05). Fish tagged in July that were not detected were significantly smaller ( 180 mm ) than those that were detected leaving the Strait of Georgia (189 mm, t-test, $\mathrm{p}<0.05$ ). This relationship was not significant for fish tagged in September. Of the 10 largest July release fish, 5 (45.5\%) were detected on receivers in Discovery

Passage or on the Queen Charlotte Strait line, whereas none of the smallest 55 fish were detected on northern receivers. The four fish detected from the July tagging at the Queen Charlotte Strait line were from the two largest size groups.

### 6.3.3 Local Movements

Of the July releases, 15 fish (10\%) were detected by the eight scattered receivers in Discovery Passage during late summer (Figure 3). Of these fish, four were detected three to six days later at the Queen Charlotte Strait line. The distance between the Discovery Passage receivers and the Queen Charlotte Strait line was approximately 180 km , indicating a minimum speed of 36 km per day. Six of the fish that traveled north during the summer were detected back in the Strait of Georgia during the fall, two of which were later observed in the Juan de Fuca Strait during October and November.

One of the tagged coho that was detected in the Juan de Fuca Strait 29 July 2006 returned to the southern Strait of Georgia the next day to a receiver at the Vancouver Aquarium and Marine Science Centre. It then returned to the Juan de Fuca Strait line 22 August 2006 and was detected there nearly every day until its final detection 1 October 2006. Another fish was detected in August and September moving between the southern Strait of Georgia array and the Juan de Fuca Strait line, remaining at the Juan de Fuca Strait line from 7 September to 23 October 2006, after which it was not detected again.

Fish that were detected in the Strait of Georgia, Juan de Fuca Strait and Queen Charlotte Strait were recorded for an average period of $33 \pm 48$ days, $28 \pm 40$ days, and $16 \pm 19$ days, respectively. The average time of residence near the northern Strait of Georgia detection area was 20 August to 30 September 2006 for the July releases $(\mathrm{n}=49)$, and 18 September to 11 October 2006 for the September releases $(\mathrm{n}=$ 39). The average time of residence near the Juan de Fuca Strait detection area was 6 November to 12 November 2006 for the July releases $(\mathrm{n}=16)$, and 14 November to 19 December 2006 for the September releases $(\mathrm{n}=41)$.

### 6.3.4 Long-Range Movements

Seven of the fish that left the Strait of Georgia through Juan de Fuca Strait (three from the July release group and four from the September release group) were detected on the outer coast; one was at

Lippy Point 23 days after the last detection on the Juan de Fuca Strait line (26 December 2006), and five were at Willapa Bay, in Washington State near the Columbia River, between 24 and 103 days (21 January to 15 April 2007) after departing the Juan de Fuca Strait (Figure 6.1). The fish detected at Lippy Point took 23 days to travel approximately 360 km , or 15.7 km per day. One of the fish detected at Willapa Bay ( 22 to 25 January 2007) was recorded 33 days later back at the Juan de Fuca line (27 and 28 February 2007). The average time taken to travel the 220 km between the Juan de Fuca Strait line and the Willapa Bay line was $57 \pm 28$ days, or 3.9 km per day $(\mathrm{n}=6)$. One of the unclipped coho released in July was detected at the Cascade Head line off of Oregon (Figure 6.1) from 31 January to 1 February 2007; however it was neither detected at the Juan de Fuca Strait line nor at the Queen Charlotte Strait line.

### 6.4 Discussion

Most coho salmon that left the Strait of Georgia migrated out through Juan de Fuca Strait from October to December. The percentage of fish detected at the Juan de Fuca Strait or Queen Charlotte Strait lines from the July tagging was smaller than from the September tagging probably indicating a higher mortality of these fish. Beamish et al. (2008) showed that the mortality of juvenile coho salmon from the time of entry into the Strait of Georgia to mid-September 2006 was approximately $90 \%$. We could not determine the reason that about $30 \%$ of all fish tagged in July were not detected, but it is probable that these fish died. The few fish from the July tagging that were detected at the Queen Charlotte Strait line, moved there shortly after they were tagged (within 17 days). Either they were migrating north when captured, or the tagging stimulated the migration. It is not possible to determine which possibility is correct, however, the behaviour is anomalous in relation to the general pattern of migration.

Beginning in early October, most tagged coho salmon began to be detected at the Juan de Fuca Strait line indicating a movement through Juan de Fuca Strait. The reasons for the earlier arrival of the fish tagged in July could be a result of the different behaviour of stocks, but this is only speculation.

Only 4\% of the fish that were last detected in the Strait of Georgia were recorded after December, indicating that most of the tagged juvenile coho salmon left the Strait of Georgia before winter, or died. This observation is consistent with the results of trawl studies (Beamish et al., 2008), that showed very few juvenile coho salmon in the Strait of Georgia after the winter of their first ocean year. If there was no
tagging mortality, or minimal tagging mortality, and detections were approximately $100 \%$ (Kintama Research Corporation, 2006), then the natural mortality of all tagged coho salmon in the Strait of Georgia was $66 \%$ prior to their first ocean winter. Much of this mortality occurred between July and September, as only $19 \%$ of the fish tagged in July survived to leave the strait, compared to $52 \%$ of the fish tagged in September that left the strait.

In general, we did not observe a significant relationship between the size of coho salmon that were tagged and a movement out of the strait. We observed that the smallest fish tagged in July were not observed leaving the Strait of Georgia and presumably died. The few fish from the July tagging detected at the Queen Charlotte Strait line were in the largest size groups but the sample size (4) was too small to determine if this was significant. We also found that the undetected fish from the July tagging were significantly smaller than detected fish leaving the strait. There is a possibility that the smallest tagged fish had the highest mortality within the strait but the number of fish tagged may have been too small to detect size related survival trends. Beamish et al. (2008) reported that there was no relationship between average size of juvenile coho salmon in the Strait of Georgia in September and average marine survival. This is similar to our observation of no apparent relationship between average size in September and average marine survival.

The detections of fish at the POST arrays along the Washington and Oregon coastline is consistent with previous reports that indicate that about $10 \%$ of Strait of Georgia hatchery coho salmon were recovered in fisheries in this region (Weitkamp et al., 1995). One fish that was detected at the Cascade Head line near the Columbia River (Figure 6.1) was not previously detected crossing the Juan de Fuca Strait line or the Queen Charlotte Strait line. This could be either an error in detection at the Cascade Head line or a missing detection at the other two lines. Although there exists a low probability of tag detection errors, the data were checked. The frequent detections of some individuals at listening lines could indicate that the receivers may attract prey and thus attract coho salmon in a similar fashion to aggregating tuna at fish aggregating devices (Marsac and Cayré, 1998).

Our observations that juvenile coho salmon remained in the Strait of Georgia late into the year and then left through Juan de Fuca Strait just prior to winter identifies a migratory pattern of coho that differs from those in Puget Sound (Beamish et al., 2008). Coho salmon in Puget Sound virtually all leave in

August and migrate out through the Juan de Fuca Strait. The reasons for the different timing of migration are not known, but may relate to their marine growth rates (Beamish and Mahnken, 2001). The simultaneous movement of most coho salmon late in the year in the Strait of Georgia and in August in Puget Sound may be an indication of a common mechanism that regulates their migration. It is probable that the mechanism relates to their physiological condition and is associated with climate impacts on the dynamics of each ecosystem. Understanding why the migration timing is different may help identify the factors that regulate migration. Thus, it would be important to repeat our study with larger samples of hatchery coho salmon and with coho salmon tagged in Puget Sound in July as well as in the Strait of Georgia.

Prior to the mid-1990s there was a higher percentage of coho caught outside of the Strait of Georgia in years of high Fraser River flow but there was never a period when virtually all juvenile coho salmon left the Strait of Georgia and did not return until late in the next year (Beamish et al., 1999). It was proposed in Beamish et al. (1999) that coho salmon were migrating south and out of the Strait of Georgia in the fall, but it was not until this study, using acoustic tags, that we could verify the percentage of the population that took this route and that the movement occurred very late in the year. This information is vitally important to our efforts to understand why the marine survival of these coho salmon is declining (Beamish et al., 2008) because it confirms that processes within the Strait of Georgia are causing the variations in early marine survival rather than the juvenile abundance changes being a consequence of movement out of the study area.

The reasons for the change in behaviour in the mid-1990s were thought to be related to climate and ocean effects (Beamish et al., 1999). However, the mechanisms remain to be discovered. It is possible that there have been stock composition changes resulting in the population of coho salmon in the Strait of Georgia consisting of a larger percentage of stocks that had a tendency to migrate out of the Strait of Georgia late in their first marine year. An acoustic tagging study combined with DNA stock identification would be an excellent study to determine if there are stock specific differences in movement.

Table 6.1 The percentage of coho salmon tagged in July 2006 and detected in the Strait of Georgia (SOG), or at the Juan de Fuca (JDF) or Queen Charlotte Strait (QCS) lines. Detections are recorded as the last observed detection each month. Individuals that were never detected (29.8\%) were included in the SOG group.

| Month | SOG | QCS | JDF |
| :--- | :---: | :---: | :---: |
| July | $95.7 \%$ | $2.1 \%$ | $2.1 \%$ |
| August | $92.5 \%$ | $4.3 \%$ | $3.2 \%$ |
| September | $92.5 \%$ | $4.3 \%$ | $3.2 \%$ |
| October | $90.4 \%$ | $4.3 \%$ | $5.3 \%$ |
| November | $84.0 \%$ | $4.3 \%$ | $11.7 \%$ |
| December | $79.8 \%$ | $4.3 \%$ | $14.9 \%$ |
| January + | $79.8 \%$ | $4.3 \%$ | $14.9 \%$ |

Table 6.2 The percentage of coho salmon tagged in September 2006 detected in the Strait of Georgia (SOG), or at the Juan de Fuca (JDF) line. Detections are recorded as the last observed detection each month. Individuals that were never detected (17.7\%) were included in the SOG group. None of the fish tagged in September were detected at the Queen Charlotte Strait line.

| Month | SOG | JDF |
| :--- | :---: | :---: |
| September | $100.0 \%$ | $0.0 \%$ |
| October | $86.1 \%$ | $13.9 \%$ |
| November | $63.3 \%$ | $36.7 \%$ |
| December | $49.4 \%$ | $50.6 \%$ |
| January + | $48.1 \%$ | $51.9 \%$ |

Table 6.3 The number (n) of coho salmon detected at the Straight of Georgia arrays (SOG), Juan de Fuca line (JDF) and Queen Charlotte Strait line (QCS). The number of coho salmon not detected (ND) are also indicated. The detections are divided into length groups by the number of SD above and below the mean FL for the a) July ( 189 mm ) and b) September ( 250 mm ) tagging groups. Fish that were known to be of hatchery origin were omitted.
a) July

| Length Group | FL $(\mathrm{mm})$ | n | ND | SOG | JDF | QCS |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| $<1$ SD | $120-162$ | 15 | 8 | 7 | 0 | 0 |
| Mean - 1 SD | $162-189$ | 24 | 5 | 10 | 9 | 0 |
| Mean + 1 SD | $189-216$ | 35 | 6 | 24 | 4 | 1 |
| $>1$ SD | $216-241$ | 14 | 5 | 6 | 0 | 3 |
| Total | 88 | 24 | 47 | 13 | 4 |  |

b) September

| Length Group | FL (mm) | n | ND | SOG | JDF |
| :--- | :---: | :---: | :---: | :---: | :---: |
| < 1 SD | $212-227$ | 4 | 1 | 2 | 1 |
| Mean - 1 SD | $227-248$ | 26 | 3 | 5 | 18 |
| Mean + 1 SD | $248-269$ | 25 | 6 | 8 | 11 |
| $>1$ SD | $269-293$ | 6 | 0 | 3 | 3 |
| Total | 61 | 10 | 18 | 33 |  |



Figure 6.1 The study area and three major POST array lines (Queen Charlotte Strait, Strait of Georgia, and Juan de Fuca Strait). The location of other arrays in the Strait of Georgia and the arrays on the west coast are also identified. The catch and release area in the Strait of Georgia is denoted by a star.


Figure 6.2 The number of coho salmon from the July release group detected by month in the Strait of Georgia (SOG) and outside the SOG in the Queen Charlotte Strait (QCS) and Juan de Fuca Strait (JDF) during 2006 and 2007.


Figure 6.3 The number of coho salmon from the September release group detected by month in the Strait of Georgia (SOG) and outside the SOG in the Queen Charlotte Strait (QCS) and Juan de Fuca Strait (JDF) during 2006 and 2007.

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## CHAPTER 7: General Discussion

The objective of my dissertation was to identify key mortality areas and analyse the migratory behaviour of juvenile wild and hatchery coho in detail using acoustic telemetry. The use of acoustic telemetry in fish biology necessitates an understanding of the tag's effects on the animal. Therefore, the objective of my first study was to determine the appropriate sizes of tags to use on coho pre-smolts. The objective of my second study was to identify areas of high mortality and observe the migratory behaviour of the smolts of an endangered coho population. The third study of this dissertation aimed to compare the behaviour, physiology and survival of outmigrating wild and hatchery-reared coho smolts. Finally, the objective of the fourth study was to investigate the altered marine migratory behaviour of juvenile coho in the Strait of Georgia.

### 7.1 Research Findings

The first comprehensive study of acoustic tag effects on coho pre-smolts found that the maximum tag size to body size ratios ranged from $15-17 \%$ by fork length and $7-8 \%$ by mass for the three tag sizes (11 cm fork length for a $6 \times 19 \mathrm{~mm}$ tag, 12.5 cm for a $7 \times 19 \mathrm{~mm}$ tag, and 14 cm for a $9 \times 21 \mathrm{~mm}$ tag). It is unlikely that acoustic transmitters implanted in coho salmon pre-smolts following these size guidelines would have significant effects on smolt growth, survival or performance in the field. The only other study found that tested the effects of acoustic tags on coho smolts used $9 \times 33 \mathrm{~mm}$ tags that weighed 4.6 g in air $(2.5 \mathrm{~g}$ in water), which was longer and heavier than the largest ( $9 \times 21 \mathrm{~mm}$ ) tags used in my field work (Moser et al., 1991). Moser et al. (1991) also inserted the transmitters through the animals' mouths into their stomachs, instead of surgically implanting them into the body cavity as I did. Therefore, the findings of Moser et al. (1991) were not able to be used as a tag effects baseline for field work in this dissertation.

Previous work on Atlantic salmon, rainbow trout and chinook salmon found no observable effect on swimming performance from tags that were $6-12 \%$ of the fish's weight (Brown et al., 1999; Anglea et al., 2004; Lacroix et al., 2004), which was comparable to the 6 -10\% weight ratio I found with Thompson River coho salmon. However, the results from my coho tag effects study contradicted other leading
hypotheses such as Winter's controversial ' $2 \%$ rule' for maximum tag to body weight ratio (1983), Adams et al.'s (1998) recommendation of 2.2-5.6\%, and Zale et al.'s result of $4 \%$ with cutthroat trout (2005).

Endangered coho smolts from the Thompson River were acoustically tagged during three consecutive years and their movements and survival were estimated using the POST array. The freshwater survival of endangered Thompson coho smolts during 2004-2006 was $0-6 \%, 7 \%$, and $51 \%$, with median times of arrival on the lower Fraser River sub-array of 16,12 and 10 days, respectively. Subsequent detections on the marine components of the POST array were $0 \%, 10 \%$ and $11 \%$ during 2004-2006. The estimated freshwater survival rates of out-migrating Thompson River coho salmon smolts were extremely low, and may be the reason for the poor conservation status of this stock. This was the first evidence of high freshwater mortality rates for this endangered population.

While the laboratory experiments provide support for the assumption that implanted tags do not have a significant effect on the behaviour and survival of migrating fish in the field, some uncertainty remains, as they are not able to fully replicate field conditions. Therefore, there may be untested stressors that affect implanted fish more than untreated fish in the wild. Stock differences between the coho tested in the laboratory trials and those tagged in the field are another potential source of bias that needs addressing in future work. The low freshwater survival rates noted in the Thompson River field trials were both from the Spius Creek stock. When the Coldwater River stock was monitored in 2006, freshwater survival rates were higher. The tag effects trials were conducted with the Coldwater River stock, therefore it is possible that the difference in field results was due to the tag having an effect on one stock more than the other. However, many other factors could have caused the differences between the survival rates of the two stocks -including differences in physiology, behaviour, release site and year.

Differences in physiology, travel time and migratory behaviour were found between wild and hatchery-reared coho smolts from the Quinsam River. Detection ranges of the acoustic receivers were tested in the river, estuary and ocean in a variety of flow conditions and tide levels. Wild smolts were smaller by mass, fork length and condition factor than hatchery-reared smolts, and exhibited higher levels of sodium, potassium and chloride in their blood plasma than hatchery-reared smolts. The gill $\mathrm{Na}+\mathrm{K}+-$ ATPase activity was also higher in the wild coho smolts at the time of release. Ninety-eight percent of wild and eighty percent of hatchery-reared fish survived to the estuary, eight kilometers downstream of the
release site. No difference was found in migratory speed, timing or survival between smolts released during daylight and those released after dark. However, wild smolts spent less time in the river and estuary, and as a result entered the ocean earlier than hatchery-reared smolts. Average marine swimming speeds for wild smolts doubled those of their hatchery-reared counterparts. While hatchery smolts dispersed in both a northward and southward direction upon entering the marine environment, the majority of wild smolts traveled north from the Campbell River estuary. The wild coho salmon smolts were more physiologically fit and ready to enter seawater than the hatchery-reared smolts, and as a result had higher early survival rates and swim speeds.

Finally, the study of the anomalous coho migration out of the Strait of Georgia in 2006 found that $19 \%$ of the fish tagged in July, and $52 \%$ of the fish tagged in September left the Strait of Georgia. Most of these tagged coho salmon left the Strait of Georgia in October and November through Juan de Fuca Strait and not by a northward migration through Queen Charlotte Strait. A small number of coho salmon that moved out of the Strait of Georgia migrated south to areas off the coast of the states of Washington and Oregon. The documentation of a movement out of the Strait of Georgia late in the year was important as it confirmed that the population changes of juvenile coho salmon that have been reported in the strait in the spring and summer are a consequence of ecosystem-related impacts within the Strait of Georgia.

### 7.1.1 Freshwater and Marine Survival

Fishing pressure and marine productivity are thought to be the main factors influencing the smolt-to-adult survival rates of most salmon stocks (Beamish et al., 1997a; Coronado and Hilborn, 1998; Beamish et al., 1999; 2000; Welch et al., 2000). However, results from acoustic telemetry trials on Thompson River coho from 2004-2005 demonstrated that freshwater mortality may be the primary cause of low returns for some stocks. Routledge and Wilson (1999) expressed concern that this may be the case in the Thompson River, but until the results from our work no data existed to support this hypothesis. Quinsam River coho smolts had much higher freshwater survival rates than were estimated in the Thompson River, although the distance from release to the estuary was over 350 km in the case of the Thompson River coho and 8 km for the Quinsam River coho. The survival of other salmon species from the Thompson watershed was also
generally higher than that of the coho, which may be indicative of physiological or behavioural or timing differences between the species influencing freshwater survival.

Coho from the Quinsam and Thompson Rivers traditionally entered the Strait of Georgia as smolts and spent their lives in inside waters before returning to their natal rivers to spawn (Beamish et al., 1999). Currently, juvenile coho in the Strait of Georgia are hypothesised to leave the strait or die at some point during their first marine year, due to a regime shift that changed their migratory behaviour beginning in the mid 1990s (Beamish et al., 1999). Trawl studies carried out during early spring caught Strait of Georgia coho on the outer coast, but very few within the strait (Beamish et al., 2008). Results from the acoustic telemetry field trials described in Chapter 6 confirmed this hypothesis, providing survival estimates and a timeframe for the migration. Differences in survival and behaviour between size classes were also found. Smaller fish were less likely to migrate out of the strait and presumably died, but there was no apparent relationship between average coho marine survival and the average size of juvenile coho salmon during September in the Strait of Georgia, which supports earlier findings by Beamish et al. (2008).

In summary, survival rates were determined for Thompson and Quinsam River coho smolts as well as for juveniles in the Strait of Georgia. Stock differences in freshwater survival were found between coho from the Thompson ( $0-7 \%$ ) and Quinsam Rivers ( $80 \%$ for hatchery, $98 \%$ for wild). Coho in the Strait of Georgia had an $80 \%$ mortality rate between July and December. Therefore, in the case of the Thompson coho, high freshwater and marine mortality rates both contribute to their endangered status. Acoustic telemetry has proven to be a useful tool to study survival rates of fish in the ocean, by providing real-time data about the locations of free-swimming fish along their migratory route. Weaknesses of the technology include the cost and time requirement. Survival calculations using progression across a series of hydrophone arrays also have some error, as there is a possibility that some migrating fish are not detected by the receivers and others may residualise between receiver lines.

### 7.1.2 Migratory Behaviour

Estuaries are thought to be important rearing areas for migrating coho smolts, however there is limited data on the duration and timing of coho estuarine residence (Miller and Sadro, 2003). The ability to protect and rehabilitate damaged estuary environments may depend on the availability of evidence showing
that these sensitive areas are crucial for salmon. The Campbell River estuary was found to be important for wild and especially hatchery-reared coho salmon smolts. The data also supports the hypothesis that restoration work done on the Campbell River estuary has improved salmon habitat. Due to the massive size of the Fraser River estuary, it was not logistically possible to monitor estuarine residence and habitat use of the Thompson River coho. However, due to the low freshwater survival rates of these coho smolts, I would encourage coho habitat restoration work and research to be done in the Thompson as well.

Coho salmon are known to have highly regionalised migration patterns, meaning that every coho stock exhibits different migratory behaviours (Weitkamp and Neely, 2002). Prior to the Campbell River acoustic study, the early marine migratory behaviour of Quinsam River coho smolts was unknown. For the first time, this telemetry data showed that coho travel both north and south from the Campbell River estuary, and that there may be behavioural differences between the wild and hatchery fish in terms of direction as well as timing. These results were consistent with data from the Strait of Georgia work that showed a small northward movement of coho from the strait into Discovery Passage in August and back south into the strait during fall. The marine behaviour of the Thompson River coho smolts may have also followed these trends, although there were too few marine detections to generalise.

Beamish et al. (1999) proposed that coho salmon were leaving the Strait of Georgia during fall. The acoustic telemetry study determined the direction, timing and percentage of the population that exhibited this behaviour. These details are vital to the identification of reasons for declining coho marine survival rates, as they demonstrate that juvenile abundance changes during the summer and fall are caused by processes within the Strait of Georgia and not movement out of the study area. Detections of coho on the outer coast of Washington and Oregon were consistent with previous reports stating that Strait of Georgia hatchery-reared coho salmon were recovered in that region (Weitkamp et al., 1995). The migratory behaviour of Strait of Georgia coho was different from the behaviour of coho from Puget Sound (Beamish et al., 2008). Puget Sound coho salmon migrate out through the Juan de Fuca Strait during August. The differences in migratory behaviour between these two geographically proximate groups of coho salmon are thought to be due to differing early marine growth rates (Beamish and Mahnken, 2001). There may be a common mechanism regulating the outmigration of Strait of Georgia and Puget Sound coho, but this has yet to be confirmed.

### 7.1.3 Ecosystem Dynamics

Mitigative strategies such as hatchery programs aim to increase salmon catches, however little consideration has been made about the ecosystem effects of releasing billions of domestic fish into the wild every year (Beamish et al., 1997b; Sweeting et al., 2003). Metcalfe et al. (2003) reported that hatcheryreared Atlantic salmon smolts were less aggressive than wild smolts. Hatchery Atlantic salmon smolts also had lower marine survival than wild smolts (Jonsson et al., 2003). In their review of wild and hatchery salmon in Russia, Zaporozhets and Zaporozhets (2004) found differences in migratory timing, survival, feeding and competition. Other studies reported little difference between wild and hatchery Atlantic salmon smolts (Lacroix and McCurdy, 1996; Voegeli et al., 1998; Thorstad et al., 2006). The acoustic study of wild and hatchery coho salmon movement out of the Quinsam River found wild smolts to have higher survival rates, faster migratory speeds and less time spent in the estuary than the hatchery-reared smolts. More wild fish were detected in the marine environment as well. These differences may have been due to competition (Rhodes and Quinn, 1998); however results from the Quinsam study suggest that the reason is more likely to be physiological. These differences are a cause for concern, as they demonstrate that the billions of hatchery-reared fish being released into the Pacific Ocean every year may be negatively affecting wild salmon populations.

In the Thompson River and laboratory tag effects studies, only hatchery fish were used, as wild Thompson coho smolts are too small to tag with the available sizes of acoustic tags. Therefore, the low freshwater survival rates of Thompson River coho may be only applicable to hatchery smolts. The frequency of residualisation in freshwater may differ between wild and hatchery coho in the Thompson as well, which would add further bias to the results. As the tag effects trials were conducted on hatchery fish, the recommendations may only be applicable to hatchery-reared fish. Peake et al. (1997) reported that wild salmon were more affected by the tagging procedure, and data from tag effect trials at the Quinsam Hatchery were consistent with these results. Wild smolts may be more stressed by handling and being kept the unfamiliar hatchery environment. The number of hatchery coho tagged in the Strait of Georgia was too small to be able to detect any behavioural or survival differences from wild coho.

### 7.2 Applications and Future Directions

The tag effects trial results can serve as a guideline for minimum body sizes and approximate tag retention rates in the field (by both fish and tag size) for future acoustic telemetry studies of coho smolt survival and behaviour. Ideally, every field study should carry out a complimentary tag effects trial, as every salmon stock and every surgeon are different. However, this may add a substantial time cost to the project. Further research on the effects of tag implantation on the startle response, buoyancy, foraging ability and disease resistance of coho pre-smolts would also be important work. Differences found between tag effects on wild and hatchery fish in the Quinsam River should also be investigated further.

### 7.2.1 Freshwater and Marine Survival

In the Thompson River watershed, silviculture, agriculture, livestock rearing, and development are degrading salmon habitat (Harding et al., 1994; Rood and Hamilton, 1995; Burt and Wallis, 1997). The freshwater survival of wild coho may be influenced by siltation, flow levels, temperature extremes, competition, disease and predation (Groot and Margolis, 1991). Bradford and Irvine (2000) studied the relative influences of agricultural land use, road density, stream habitat quality and the proportion of land recently logged on Thompson coho survival. This type of work is important and could be expanded to look at climate effects.

While changes in climate have affected freshwater salmon production (Lawson et al., 2004), quantitative evidence for the influence of climate on coho smolt production is lacking (Bradford, 1999). The outmigration phase of salmon smolts and upstream migration of returning adults are physiologically demanding periods in the salmon's lifecycle. Therefore, the understanding of climate effects on freshwater systems, and the consequences of these effects on salmon survival should be a priority for salmon conservation efforts. For example, the advancing spring freshet may be selecting for stocks that migrate out to sea earlier than those migrating out later (Beamish et al., 2008). Ongoing work at the Seymour and Quinsam Hatcheries are examining release time effects on survival and could provide further insight into this hypothesis (Beamish et al., unpublished data; Appendix B). Water temperature increases may also be affecting the survival rates and migratory behaviour of Pacific salmon. Work by Crossin et al. (2008) found that exposing sockeye salmon to higher temperatures during their return migration decreased their survival
to the spawning site and increased infection rates. Future telemetry work could pinpoint exactly where on the downstream migration the highest mortalities occur by placing receiver lines more frequently along the migratory path. Temperature and flow rates could be monitored during the migration as well as other environmental factors such as water quality. EMG tags, coded sensory tags and archival tags would be useful tools to observe environmental influences on the freshwater survival of the migrating salmon.

Acquiring information about the health and physical condition of each Pacific salmon stock could provide insight into stock differences in survival. Temporal changes in stock health and survival could also be compared with environmental information. Evaluating environmental effects on fish of varying heath levels is the next step. Electronic devices could assist in the study of diseased versus immune fish in a nonlaboratory environment.

In the Strait of Georgia, the early marine survival of coho salmon was found to be low. The same factors causing the low survival may somehow be triggering the fish to leave the strait during the winter of their first year. While it is known that ecosystem dynamics are likely causing the coho to leave, the mechanisms need to be better understood. Other strait species should be monitored using acoustic telemetry to look at similarities and differences in the patterns found. Appendix C outlines an example of ongoing work that is trying to understand the reasons for extremely low marine survival of chinook salmon in the Strait of Georgia.

The long-term monitoring of every Pacific salmon stock would be ideal; however considerable funding would be required. The smolts of pink and chum salmon are too small to implant with the available sizes of acoustic transmitters, therefore the juveniles would need to be caught at sea as was done for the Strait of Georgia coho work. Permanent listening arrays and databases operated by large collaborations such as POST may help cut down on time and equipment costs. Survival estimates for species that do not migrate very far would be more difficult to measure using acoustic telemetry. For these species, enhanced array systems, gliders or manual tracking would be required, possibly combined with EMG tags to monitor muscle activity of the fish.

### 7.2.2 Migratory Behaviour

Salmon migratory behaviour is changing and it is vitally important that managers understand how and why so that future decisions can be based on accurate information. The role of climate on the migratory behaviour of salmon could be better understood by combining electronic tracking devices with enhanced environmental monitoring. This type of research is being carried out with Atlantic salmon smolts in Norway (e.g. Davidsen et al., 2008) and should be done in the Pacific. Climate is changing the timing of the freshwater migratory behaviour of coho in various ways (Beamish et al., 2008). Earlier outmigrating wild fish may reach the estuary to coincide with earlier productivity blooms than hatchery fish released at the same time each year (Beamish et al., 2008). Support for this hypothesis was found in the Campbell River study, where wild coho smolts entered the ocean earlier than hatchery-reared smolts. Returning adults are migrating upriver earlier as well (Cooke et al., 2004; Young et al., 2006; Crossin et al., 2008). Very little data is available to record these trends; ongoing monitoring of wild stocks is needed immediately. Coho fishery managers in BC use a long-term data set from a wild stock in Black Creek on Vancouver Island to generalise wild trends across the province (Hankin et al., 2005). Stock variability is considerable however, so using this solo dataset to predict wild coho behaviour across the province adds a high degree of uncertainty to fishery models. Long-term, international monitoring programs combining telemetry and environmental data are needed. In this way, the effects of short-term and long-term climatic trends on the migratory behaviour of each salmon stock could be investigated, and management decisions could incorporate current information on stock distribution. These programs would be especially valuable for endangered and at-risk stocks.

The Fraser River watershed supports many major salmon runs, including populations that are now endangered (Bradford and Irvine, 2000). The identification of important habitat areas for salmon, and further details on migration timing in relation to environmental cues would assist freshwater habitat conservation efforts. The Fraser River estuary is changing with climate and very little information exists about how changes in the estuary are affecting salmon migration (Beamish et al., 1997a; Rand et al., 2006). A good example of a study using coded transmitters and environmental sensors to look at climate effects on fish movements in an estuary was carried out in South Africa by Childs et al. (2008). This study used manual tracking, which provides a lot of data on an individual fish over a short period of time. This method
is time consuming however, and difficult to monitor many fish simultaneously. In the Fraser estuary, a network of moored receivers could be installed with environmental sensors attached to track ingoing and outgoing fish. However, these would likely need to be removed and re-installed every year due to the siltation and movement of sand in the estuary.

The Strait of Georgia and Puget Sound are geographically close; however the salmon populations in these areas exhibit vastly different migratory behaviour. Puget Sound coho exit the Juan de Fuca Strait in August whereas Strait of Georgia coho leave during the winter. The reasons for these differences remain a mystery. Understanding the mechanisms for these mass migrations is a priority for the conservation and management of these coho populations.

### 7.2.3 Ecosystem Dynamics

The results from the Strait of Georgia coho study are important to coho management as they confirm that ecosystem processes within the strait are the cause of variations in early marine mortality. The mechanisms of the change in migratory behaviour remain to be understood. Coho stock composition changes may have resulted in there being a larger percentage of stocks in the strait that have a tendency to leave during their first marine year. Combining further acoustic tagging studies with DNA stock identification would identify any stock-specific migratory behaviour differences within the Strait of Georgia ecosystem. Competition, predation, food availability and environmental cues such as temperature could also be influencing coho to leave the strait. Further research is required to determine the relative influences of each of these potential causes on salmon behaviour and survival in the strait. Improvements to climate prediction capabilities and the role of climate on the strait ecosystem are also needed.

During field trials in the Quinsam and Campbell Rivers in 2006, differences in the physiological characteristics and migratory behaviour were noted between hatchery-reared and wild coho smolts (Chittenden et al., 2008). The causes and effects of these differences are unclear, which brings up a question that has needed answering for over thirty years: what roles do genetic and rearing environment effects play in creating these observed phenotypic differences between wild and hatchery-reared salmonids?

The genetic changes in wild populations caused by hatchery fish are of grave concern to fisheries biologists (Hilborn, 1992; Meffe, 1992; Araki et al., 2008). Traditional-type hatcheries produce fish that tend to have less genetic variation than wild salmon, which poses a threat to the genetic integrity of wild stocks (Hindar et al., 1991; Crozier, 1998; Policansky and Magnuson, 1998; Wang et al., 2001; Waples et al., 2001). Biodiversity provides the variation that is crucial to the long-term survival of a population. Larger smolts released by hatcheries may have better success in the short term, but this practice could be reducing the fitness of subsequent generations of wild fish. Recent studies have found that genetic effects from hatchery-rearing have decreased the fitness of steelhead trout (Araki et al., 2007a; 2007b). In order to understand how Oncorhynchus species will be influenced by changes in climate, and how genetic changes brought about by enhancement programs will affect their behaviour and survival, research needs to determine to what degree the characteristics of hatchery-reared fish are due to their genetic makeup, or conversely, to their rearing environment.

Salmon have a great deal of phenotypic plasticity, meaning they have a strong ability to physically adapt to their environment. For example, salmonids have been shown to evolve reproductive isolation in fewer than thirteen generations (Hendry et al., 2000). This quality makes them particularly sensitive to environmental change. Berejikian et al. (1996) compared agonistic behaviours between the newly-emerged fry from a wild population and a hatchery population of steelhead. Riddell and Swain (1991) conducted a similar study on coho salmon. Atlantic salmon smolts reared in the hatchery developed genetic differences between smolting and non-smolting $1+$ parr, whereas the wild smolts retained their original genetic composition and did not smolt until a year later (Crozier, 1998). Another study on Atlantic salmon conducted territorial contests on wild smolts reared in the wild, and both wild and hatchery smolts reared in a hatchery (Metcalfe et al., 2003). There appears to be no published work comparing the strength of genetic versus environmental influences on the phenotypic expression, migratory behaviour and marine survival of salmon. An example of ongoing research on the progeny of wild and hatchery fish reared in both wild and hatchery environments to compare their physiology, migratory behaviour, and post-release survival is found in Appendix D.

For enhancement to be used as a mitigative strategy, smolt health and quality is of utmost importance. Variation found between same-stock populations of wild and hatchery fish is a cause for
concern. Significant differences have been observed between wild and hatchery populations in terms of survival, morphology, physiology and habitat preference, as well as in foraging, social, migratory and reproductive behaviours. For example, wild salmon were more agonistic (Berejikian et al., 1996; Metcalfe et al., 2003), better adapted to the natural environment (Shrimpton et al., 1994; Hill et al., 2006) and showed improved survival rates in rivers, estuaries and coastal ocean areas than their hatchery-reared counterparts (Greene, 1952; Miller, 1952; Reimers, 1963; Fleming and Gross, 1993; Coronado and Hilborn, 1998; Jonsson et al., 2003; Zaporozhets and Zaporozhets, 2004; Araki et al., 2007a; 2007b). Wild coho salmon smolts descending the Quinsam River were smaller on average than the hatchery-reared smolts being released at the same time. However, they had higher hypo-osmoregulatory ability, travelled to the estuary in less time and spent less time in the estuary, entering the ocean earlier (Chittenden et al., 2008). The results of these and many other studies, suggest that there exists great variation in the quality of the billions of cultured fish that are being released into the wild every year. Behavioural deficiencies due to artificial rearing environments are thought to be the primary cause of these failures (Nickelson, 2003). Hatchery techniques and strategies that act to improve the genetic diversity and physical condition of wild populations need to be developed and tested in the wild.

Conservation aquaculture as a mitigative strategy, aims to return fish stocks to their original genetic, physiological and behavioural characteristics (Berejikian et al., 1999; Flagg and Nash, 1999; Brown and Day, 2002). Scientists at the Oregon Hatchery Research Center are conducting research on conservation aquaculture to better understand differences between wild and hatchery fish and to improve hatchery practices, so that hatchery fish will ultimately assist in the conservation of wild fish populations (e.g. Araki et al., 2008; Berejikian et al., 2008). Examples of hatcheries that are using conservation aquaculture methods to naturalise the behaviour of their smolts include the Nez-Pearce Hatchery, the Dungeness Hatchery, and the Lower Elwha Tribal Hatchery in Washington State. These hatcheries have created enriched rearing environments, including matrices for egg and alevin development, natural substrates, in-stream structures and cover. Water temperature and quality is maintained to resemble the local conditions, flow rates are higher to promote exercise, and food is introduced below the surface of the water using belt feeders. Studies have found that hatchery fish raised in semi-natural conditions had improved health, quality and genetic diversity (Mundie et al., 1990; Banks, 1994; Maynard et al., 1996).

Hatchery fish raised in semi-natural conditions had body colouring more closely resembling that of wild fish, and $50 \%$ higher survival rates than traditionally-reared smolts to a weir 2.2 km downstream (Maynard et al., 1998a). Fish reared in natural environments also demonstrated better physical condition and had less disease (Mundie et al., 1990; Banks, 1994). Reduced rearing densities further improve smolt growth, condition, gill $\mathrm{Na}^{+} / \mathrm{K}^{+}$-ATPase activity levels, and survival (Banks, 1992). High densities raise agonistic behaviour in smolts, which could increase the likelihood that they will suffer higher predation rates postrelease (Berejikian et al., 1996).

In addition to raising hatchery fish in a natural setting for improved colouring and physical health, conditioning the smolts in various ways can improve their swimming, foraging and predator-avoidance abilities. The swimming ability and growth rate of Atlantic salmon and brook trout improved with swim training (Besner and Smith, 1983; Leon, 1986). Logically, post-release survival also improved in smolts that were exercised (Burrows, 1969; Cresswell and Williams, 1983; Leon, 1986). Predator avoidance training increased the in-stream survival of test subjects up to $26 \%$ over un-conditioned fish (Thompson, 1966; Maynard et al., 1998b). The artificial diet of hatchery fish may be decreasing their ability to recognise and find suitable food once in the wild (Mason et al., 1967; Johnson, 1978; Sosiak, 1978). Releases of hatchery brook trout and Atlantic salmon that had been hand-fed pellets were more surfaceoriented and more likely to approach moving objects than were wild fish (Mason et al., 1967; Sosiak, 1978). When the diet of hatchery chinook salmon was supplemented with live feed, their foraging ability improved two-fold (Maynard et al., 1996), and naturally-fed tiger muskellunge had higher post-release survival than those fed only pellets (Johnson, 1978).

Release strategies are also important to post-release survival. Acclimating smolts prior to release with in-river holding pens improved survival (Finstad et al., 2003). Volitional releases allow smolts to migrate out when they are physically ready. This type of release maintains out-migration diversity and allows smolts to travel at night when the risk of predation is lower (Flagg and Nash, 1999). The timing of the development and outmigration of wild smolts should be monitored for each stock so that hatchery rearing can be synchronised with wild smolt development and release. Predictions of ocean climate and carrying capacity during the release year should also be considered so that an appropriate number of smolts
are produced and released. This would ensure a more efficient use of resources and reduce hatchery competition with wild fish during less productive years.

Marine aquaculture sites are numerous on the west coast of North America, especially in BC's Broughton Archipelago. Hydrophone receivers were attached to three net pens in Discovery Passage during the Quinsam River coho study to detect migrating wild coho. While this study was not designed to examine the attractiveness of aquaculture sites to wild salmon, many smolts were detected by these receivers for extended periods of time. If wild fish are more likely to travel in the direction of a fish farm, they may be at a higher risk for diseases and parasites. Further laboratory and field work could investigate potential chemical attractants produced by aquaculture sites, and whether these sites are affecting the migratory behaviour and survival of wild salmon in the ocean.

Escape events from aquaculture sites are another potential threat to ecosystem dynamics in the Pacific. There is a lack of research on this topic, however. The most common species raised in BC fish farms is the Atlantic salmon (BC Ministry of Agriculture and Lands, 2008). As this species is not native, field research simulating escapes would be more appropriately done in the Atlantic Ocean. Appendix E summarises a project using telemetry to study the dispersal behaviour of escaped farm fish in northern Norway. With more studies like these, potential ecosystem effects can be better understood, and recapture strategies can be developed for escape events in the Pacific.

The development of large-scale collaborative projects that unite scientists, government and industry researchers of different disciplines is crucial to the understanding and conservation of Pacific ecosystems. International networks of sea floor sensor arrays combined with acoustic telemetry listening lines and sonar monitoring stations could provide a wealth of detailed real-time data about individual fish within aggregations, their inter- and intra-specific behaviours relative to oceanic conditions and ecosystem productivity. With the improved ability to accurately predict the ocean climate conditions, productivity levels that will be encountered by individual salmon stocks, and how these stocks are likely to react to the predicted conditions, better fishery models can be designed that will enable managers to make more informed decisions.

### 7.3 Summary

The global climate is changing at an increasing rate, which is altering the marine survival and migratory behaviour of Pacific salmon. The abundance of coho salmon has declined in the southern half of its range and stock migratory patterns have changed, yet little is known about the mechanisms of these phenomena. This lack of knowledge is a serious problem for fishery managers. My dissertation identified key mortality locations and provided a first look at early migratory behaviour patterns of wild and hatchery-reared coho salmon in southern BC using acoustic telemetry. Appropriate size limits were first determined for coho smolts implanted with acoustic transmitters, which provides guidelines for future coho telemetry work. The first evidence of high freshwater mortality rates for the most endangered coho stock in Canada was also observed, raising questions about the health and management of BC's freshwater ecosystems. Differences were noted between young wild and hatchery-reared coho, suggesting that Canadian mitigative strategies need to be evaluated and improved. Finally, a detailed examination of the altered coho migratory patterns and early marine survival in the Strait of Georgia discovered that population changes in the strait are due to ecosystem-related impacts. Further research into the dynamics of climate change, and how they affect the Pacific environment and salmon stocks, is strongly recommended. International collaborations using advanced technologies and a multi-disciplinary experimental approach would be most efficient at producing the amount of data required to suitably study, manage and conserve Pacific salmon stocks.

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## APPENDIX A: Animal Care Certificate



## THE UNIVERSITY OF BRITISH COLUMBIA

## ANIMAL CARE CERTIFICATE

Application Number: A06-0153

Investigator or Course Director: Scott McKinley

Department: Land and Food Systems

Animals:

Salmon Coho (Oncorhynchus kisutch) 190
Start Date: May 1, 2006 Approval Date: March 2, 2007

Funding Sources:

Funding Agency: Natural Science Engineering Research Council
Funding Title: Determining early ocean survival and migration patterns of Pacific salmonids using a large-scale tracking array

Unfunded title: Early migration study for Campbell River wild and hatchery coho smolts

The Animal Care Committee has examined and approved the use of animals for the above experimental project.

This certificate is valid for one year from the above start or approval date (whichever is later) provided there is no change in the experimental procedures. Annual review is required by the CCAC and some granting agencies.

A copy of this certificate must be displayed in your animal facility.

Office of Research Services and Administration
102, 6190 Agronomy Road, Vancouver, BC V6T 1Z3
Phone: 604-827-5111 Fax: 604-822-5093

# APPENDIX B: Abstract of a Study of the Riverine and Marine Migratory Behaviour and Physiology of Early and Late Release Coho and Steelhead Smolts in the Seymour River, BC 

C. M. Chittenden ${ }^{1}$, S. K. Balfry ${ }^{1}$, D. W. Welch ${ }^{2}$, and R. S. McKinley ${ }^{1}$<br>${ }^{1}$ The University of British Columbia / Department of Fisheries and Oceans Centre for Aquaculture and Environmental Research, 4160 Marine Drive, West Vancouver BC, V7V 1N6, Canada<br>${ }^{2}$ Kintama Research Corp., 1850 Northfield Rd, Nanaimo, BC, Canada V9S 3B3

As global changes in climate are affecting the timing of spring productivity blooms, selection pressures on the outmigration timing of salmon smolts are being altered. Species and stocks of salmon leaving natal streams earlier may be favoured over later-migrating fish. This study examined the effects of release time, physiology and health on the migratory behaviour and survival of wild and hatchery-reared coho and steelhead salmon in the Seymour River. Fifty hatchery steelhead smolts were tagged with acoustic transmitters in 2006 and released at night and during daytime. Sixty steelhead and sixty coho were tagged in 2007 and released in three groups. Physiological sampling was carried out on 30 fish from each group in 2007, in addition to 30 wild coho from the river. Both the coho and steelhead smolts took an average of three days to reach the river mouth. The early release groups spent longer in the estuary than the later release groups and were less physically adapted for entry into marine waters. Smolts that spent less time in the estuary exhibited higher marine survival. Freshwater survival was $50 \%$ for coho and $72 \%$ for steelhead, whereas only $8 \%$ of the coho and $56 \%$ of the steelhead were detected outside the estuary.

# APPENDIX C: Overview of a Study of the Early Survival and Migratory Behaviour of Juvenile Chinook Salmon in the Strait of Georgia 

C. M. Chittenden ${ }^{1}$, C. M. Neville ${ }^{2}$, R. J. Beamish ${ }^{2}$, and R. S. McKinley ${ }^{1}$<br>${ }^{1}$ The University of British Columbia / Fisheries and Oceans Canada Centre for Aquaculture and Environmental Research, 4160 Marine Drive, West Vancouver BC, V7V 1N6, Canada<br>${ }^{2}$ Fisheries and Oceans Canada Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo BC, V9T 6N7, Canada

The marine survival of chinook salmon originating from the Strait of Georgia region has declined to less than $1 \%$ over the past decade. Although in the 1970s it was assumed that the number of chinook salmon available to the sport and commercial fisheries could be increased by adding more juvenile salmon to the Strait of Georgia, this assumption is now known to be invalid. The marine environment is not constant, and environmental changes impact the productivity of chinook salmon in the strait. In addition, there are changes in the distribution and growth of the juvenile chinook salmon. Understanding the processes that result in reduced chinook production in the Strait of Georgia is important to the effective management of the species. Surveys have shown that there is $85 \%$ mortality up to mid July and $94 \%$ mortality up to mid-September for juvenile chinook in the strait. There is also a declining trend of juvenile stream type and an increasing trend of ocean type chinook in the catches. The smaller ocean type tends to remain within the British Columbia area and the larger stream type migrates north into the US zone. Juvenile stream-type chinook salmon enter the Strait of Georgia earlier in the year and are larger than the ocean type. In recent years surveys have shown a dramatic decline in abundance of stream-type chinook salmon between the July and September surveys. There are two explanations for the recent change in catches. The stream type either left the strait between the two sampling periods or they died. There are limited CWT data from offshore areas and the lack of tag recoveries from Strait of Georgia chinook salmon in this region would suggest that the chinook salmon are dying within the strait. If this interpretation is correct, the consequences are highly relevant to the salmon treaty negotiations as well as to future management.

In September 2007, we tagged 100 juvenile chinook salmon, but all were ocean type as there were no larger, stream-type chinook salmon in the September survey catches in the Strait of Georgia. To explain the failure to catch stream type fish, the declining percentage of stream type fish, and the very poor early marine survivals and the timing of the movement of juvenile chinook out of the Strait of Georgia, 50 stream-type and 50 ocean-type chinook were tagged in the Strait of Georgia during June, July and September 2008. In addition, 50 chinook salmon from the Gulf Islands and 50 net-held Cowichan chinook salmon were tagged during June and July 2008, respectively. Cowichan River and Puntledge River chinook salmon stocks are important because they are key to understanding what is affecting marine survival. The CWT tagged juvenile chinook from the Puntledge River are common in survey catches. Conversely, CWTs from chinook from the Cowichan River are rare. We propose that it is the early marine survival that results in these extreme differences.

Otoliths from previous surveys will also be processed to confirm the life history types in our surveys and process adipose or operculum punch samples for DNA analysis to identify the stocks of stream-type chinook salmon. Information from the otolith analysis combined with length frequency analysis will be used to determine the abundance of juvenile stream-type chinook salmon in July 2007.

The acoustic tagging study will compliment a major international study of the mechanisms affecting the production of chinook salmon in the Strait of Georgia and Puget Sound. The results of the acoustic tagging study will assist in making effective use of hatchery production with emphasis on restoring the production of Cowichan River chinook. The combined studies will provide the first major assessment of the population ecology of juvenile chinook salmon in the Strait of Georgia in over 25 years. The expected results should identify how Canada and the United States can cooperate through the Pacific Salmon Treaty to protect southern chinook salmon stocks and sustain fishing opportunities for both countries.

# APPENDIX D: Overview of a Study of the Genetic Versus Environmental Effects on the Phenotypic Characteristics and Fitness of Wild and Hatchery Salmon 

C. M. Chittenden ${ }^{1}$, R. H. Devlin ${ }^{1}$, A. H. Rikardsen ${ }^{2,3}$, J. G. Davidsen ${ }^{2}$, A. G. Davidsen ${ }^{2}$, H. Kondo ${ }^{1}$, and R. S. McKinley ${ }^{1}$<br>${ }^{1}$ The University of British Columbia / Department of Fisheries and Oceans Centre for Aquaculture and Environmental Research, 4160 Marine Drive, West Vancouver BC, V7V 1N6, Canada<br>${ }^{2}$ Norwegian College of Fishery Science, University of Troms $\varnothing$, NO-9037 Troms $\varnothing$, Norway<br>${ }^{3}$ Norwegian Institute for Nature Research, Polar Environmental Centre, NO-9296 Tromsø, Norway<br>${ }^{4}$ Institute of Marine Research, 5817 Bergen, Norway

Millions of dollars are being spent annually on hatchery programs in Canada. To ensure the efficient use of funds, hatcheries need to maximise their benefit-to-cost ratio by improving the quality and fitness of the hatchery smolts they produce. Furthermore, the effects of the annual release of millions of traditionally-reared hatchery smolts on the genetic makeup and phenotypic characteristics of wild populations have scarcely been assessed at this time, leaving a great deal of uncertainty. Although it is too late to be able to study purely wild populations for many river systems, attempts should be made to learn as much as possible about the impact, if any, we are having before any more time passes.

The objectives of this study were a) to determine the relative roles that genetics vs. environment play in the phenotypic expression of coho young, b) to evaluate differences in survival, growth, physiology, health, swimming performance and predator avoidance between smolts reared in the wild and those reared in the hatchery, and c) to evaluate differences in post-release survival and migratory behaviour between smolts reared in the wild and those reared in the hatchery. Returning adults from the 2003 brood year were crossed to create pure hatchery strains, pure wild strains and hybrids. The returning wild adults were defined as those individuals that had survived for at least one generation in the natural environment. To test for genetic effects, environmental effects, and the genotype by environment interaction effects on these smolts, half of the progeny from each cross were reared in a traditional hatchery environment, and the other half were left to grow naturally in a contained natural side channel of the Chehalis River, BC. The following spring, after one year in freshwater, the coho pre-smolts were re-captured for genetic identification and assignment to groups (e.g. pure hatchery, pure wild, and reciprocal crosses of wild by hatchery).

Comparisons of survival and phenotypic expression were made between the replicates, the natural and hatchery rearing environments, and the genetic groups. The characteristics used to compare phenotypic expression included growth rate in length, weight and condition factor, colouring, fin quality, health, gill $\mathrm{Na}+\mathrm{K}+$-ATPase activity levels, microarray gene expression profiles, hematocrit, red and white blood cell counts, plasma ions, predator avoidance ability, swimming performance, migratory behaviour -including speed, timing and habitat use- and post-release survival. The migratory behaviour and post-release survival studies will be carried out with the use of acoustic telemetry, in collaboration with the Pacific Ocean Shelf Tracking project. The outcome of this work has the potential to improve hatchery techniques and smolt quality, increase the post-release survival of hatchery fish, to aid in the conservation of wild stocks, improve the economic value of hatchery programs, as well as to provide an effective mitigative strategy for climate change.

# APPENDIX E: Abstract of a Study of the Dispersal Behaviour and Recapture Rates of Escaped Adult Farmed Atlantic Salmon in Northern Norway 

C. M. Chittenden ${ }^{1}$, A. H. Rikardsen ${ }^{2,3}$, O. Skilbrei ${ }^{4}$, J. G. Davidsen ${ }^{2}$, E. Halttunen ${ }^{2}$, R. S. McKinley ${ }^{1}$
${ }^{1}$ The University of British Columbia / Department of Fisheries and Oceans Centre for Aquaculture and Environmental Research, 4160 Marine Drive, West Vancouver BC, V7V 1N6, Canada
${ }^{2}$ Norwegian College of Fishery Science, University of Troms $\emptyset, ~ N O-9037$ Troms $\emptyset$, Norway
${ }^{3}$ Norwegian Institute for Nature Research, Polar Environmental Centre, NO-9296 Troms $\varnothing$, Norway
${ }^{4}$ Institute of Marine Research, 5817 Bergen, Norway
Escaped farm fish are a potential threat to wild fish populations around the world, however studies examining the individual behaviour of escaped farm fish are lacking. In the first study on the dispersal behavior of escaped salmon in northern Norway, thirty-nine full-grown Atlantic salmon were implanted with acoustic tags and released in Altafjord, one of Norway's designated National Salmon Fjords. The fish were released from two aquaculture sites at high and low tide. The fish were tracked using mobile and fixed receivers. Depth sensors on the tags and external markers provided additional information regarding the migratory behaviour of the released fish. Seventy-seven percent of the fish were recaptured. Most of these ( $90 \%$ ) were caught by fishermen in the ocean, whereas $10 \%$ were found migrating up the Alta River, presumably to spawn. Swimming depth data shows that the majority of escapees dove down below 20 m within an hour post-release. Recapture strategies are being developed based on our results, however further studies are required to investigate the migratory behaviour of escapees from different year classes, at different times of year, and in other fjord systems.


[^0]:    ${ }^{1}$ A version of this chapter has been submitted for publication. Chittenden, C. M., R. J. Beamish, and R. S. McKinley. A critical review of Pacific salmon marine research relating to climate. ICES J. Mar. Sci.

[^1]:    ${ }^{2}$ A version of this chapter has been published. Chittenden, C. M., K. G. Butterworth, K. F. Cubitt, M. C. Jacobs, A. Ladouceur, D. W. Welch, and R. S. McKinley. 2008. The physiology, performance, and maximum tag to body size ratios of an endangered coho salmon ( $O$. kisutch) stock. Environ. Biol. Fishes. DOI: 10.1007/s10641-008-9396-9

[^2]:    ${ }^{3}$ A version of this chapter has been submitted for publication. Chittenden, C. M., M. C. Melnychuk, D. W. Welch, and R. S. McKinley. Evidence for poor survival of endangered Thompson River coho salmon smolts during the Fraser River out-migration. Can. J. Fish. Aquat. Sci.

[^3]:    ${ }^{1}$ QAIC $_{c}$ values are adjusted for small sample sizes and extra-binomial variation with $\hat{c}=1.60$.
    ${ }^{2}$ Sub-models for $p$ are compared while the fully time- ("seg") and group-varying CJS sub-model for $\varphi$ is held constant, $\varphi_{\text {(seg•group) }}$. Groups consist of separate combinations of species, stock, and year.
    ${ }^{3}$ Sub-models for $\varphi$ are compared while the sub-model for $p$ is held constant at the best model from the above model set, $p_{\text {(line•year+tag size+flow Mission) }}$.
    ${ }^{4}$ Flow covariate terms specify that $p$ estimates on receiver lines are dependent upon the river water level measured at either Mission or Port Mann guage stations (Environment Canada data) or upon Julian day. See text.
    ${ }^{5}$ The flow covariate term specifies that $\varphi$ estimates in river segments are dependent upon the river water level measured at the Mission guage station at the start of each segment. See text.

[^4]:    ${ }^{4}$ A version of this chapter has been published. Chittenden, C. M., S. Sura, K. G. Butterworth, K. F. Cubitt, N. Plantalech Manel-la, S. Balfry, F. Økland, and R. S. McKinley. 2008. Riverine, estuarine and marine migratory behaviour and physiology of wild and hatchery-reared coho salmon Oncorhynchus kisutch (Walbaum) smolts descending the Campbell River, BC, Canada. J. Fish Biol. 72: 614-628.

[^5]:    ${ }^{5}$ A version of this chapter has been submitted for publication. Chittenden, C. M., R. J. Beamish, C. M. Neville, R. M. Sweeting, and R. S. McKinley. 2008. The use of acoustic tags to determine the timing and location of the juvenile coho salmon migration out of the Strait of Georgia, Canada. Trans. Am. Fish. Soc.

