PREDATION BY PACIFIC GREAT BLUE HERONS ON JUVENILE SALMON

by

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B.Sc., St. Francis Xavier University, 2016

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

MASTER OF SCIENCE
in
THE FACULTY GRADUATE AND POSTDOCTORAL STUDIES
(Resources, Environment, and Sustainability)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)

May 2020

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Predation by Pacific great blue herons on juvenile salmon

submitted by Zachary Thomas Sherker in partial fulfillment of the requirements for

the degree of Master of Science

in Resources, Environment, and Sustainability

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Abstract

An array of foragers prey on salmon in rivers and estuaries while salmon smolts out-migrate from their natal streams—and may account, in part, for the poor returns of adult salmon to the Salish Sea. However, the Pacific great blue heron (*Ardea herodias fannini*) has not been identified as a predator of smolts despite being regularly seen near salmon streams. I investigated the role that herons may be playing in the depredation of salmon by scanning fecal remains under heron nests for Passive Integrated Transponder (PIT) tags that had been implanted in wild and hatchery-reared salmon smolts from 2008-2018. These nests were located in three heron rookeries that were within 35 km of the mouth of the Cowichan, Big Qualicum, and Capilano Rivers. Using a mobile PIT antenna, I recovered 1,199 smolt tags, representing a minimum annual predation rate of 0.3–1.3% of all smolts in the three rivers. Correcting for tags consumed by herons and defecated outside of the rookery raised the estimated proportion of smolts to 0.7–3.2% of the outmigrating fish, but predation rates as high as 6% were documented during a low river-flow year in the Cowichan River. The distribution and timing of tag depositions under the heron nests indicated that most great blue herons prey on salmon smolts and that consumption occurs in late spring during the chick-rearing phase of the breeding season. Energetic analyses suggest that smolt consumption provides a substantial proportion of the heron chick diet during a time of peak energy demand. Predation on smolts occurred primarily in the lower rivers and upper estuaries. Smaller salmon smolts were significantly more susceptible to heron predation in all systems, and predation rates were comparable between wild and hatchery-reared smolts. Recovering so many tags from smolts at heron rookeries was unexpected and indicates that great blue herons are a new predator of wild and hatchery-reared juvenile salmon. Locations of heron rookeries relative to salmon bearing rivers are likely good predictors of heron impacts on local salmon runs, and a potential means to assess coast-wide effects of great blue herons on salmon recovery.

Lay Summary

I identified a previously unknown predator of juvenile Pacific salmon — the Pacific great blue heron — based on scanning under the nests of herons for small electronic tags that have been previously implanted in the young fish from three British Columbia river systems. I found that smaller juvenile fish were preyed on more heavily by herons than larger individuals. The timing and distribution of tag deposition under the nests at the heron colonies further suggests that consumption of the young fish occurred during the chick-rearing phase of the heron breeding season, and that most herons took part in the documented predation. The size of heron breeding colonies and their relative distance to salmon bearing rivers may be a good predictor of the coast-wide impact of heron predation on survival of juvenile salmon.

Preface

I was the principal designer of the research presented in this thesis, with support and suggestions my supervisor, Dr. Andrew Trites, and collaborators from the British Columbia Conservation Foundation (BCCF) and Cowichan Tribes. All salmon tagging in the Cowichan and Big Qualicum Rivers was conducted by members of BCCF. Tagging in the Capilano River was completed by MetroVancouver. I performed all data collection with help from members of BCCF, Cowichan Tribes, and local volunteer Chaise Costain. I conducted and designed all data analyses and wrote all section of this thesis with guidance from Dr. Trites. All parts of this research were reviewed and approved by the UBC Animal Ethics Committee under Animal Care Permit #A17-0091.

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Acknowledgements

This research was conducted in collaboration with members of the British Columbia Conservation Foundation (BCCF) and Cowichan Tribes. This project and thesis were greatly improved by the guidance and suggestions provided by my supervisor Dr. Andrew Trites. I extend many thanks to my committee members, Dr. Rob Butler and Dr. Carl Walters, for providing expert advice and invaluable suggestions that helped shape this thesis. I would also like to thank Chaise Costain for his many hours volunteered assisting me in the field and discussing ideas for this project.

I am greatly indebted to Pamela Rosenbaum for all her hard work keeping me on track to finish my degree in a timely manner and helping to secure funding for me to survive in Vancouver throughout that time, as well as for often providing highly insightful reality checks. Many members of the Marine Mammal Research Unit and the Institute for the Oceans and Fisheries at UBC provided friendship and support that carried me through this degree, including Rhea Storlund, Aaron Purdy, Sarah Fortune, Selina Agbayani, Brianna Cairns, Rob Marshall, Kate Colson, Johanna Fee, Beth Volpov, Ron Togunov, Katie Florko, Lian Kwong, Sarah Dier-McComb, Ravi Maharaj, and Juliano Palacios Abrantes.

This research was funded by the Pacific Salmon Foundation through a Mitacs Accelerate grant. I would like to thank all the members of BCCF and Cowichan Tribes that assisted in data collection and provided support and guidance throughout this project, as well as MetroVancouver for running all salmon tagging operations in the Capilano River and allowing me access to their data. In particular, I thank Kevin Pellet, Jamieson Atkinson, Jeramy Damborg, and Tim Kulchyski for their many collaborative efforts.

Finally, I would like to thank my family and friends who accentuated my joys and damped my defeats over the last two years. My parents, Carolyn Finkle and Averell Sherker, for always insisting I should save the world, and my siblings, Sam, Jake and Alana, for making time for a chat when our time zones were misaligned. My Granny, Roz Sherker, stole many muffins from her assisted living home to ensure that I had enough food in my belly to fuel my work. Baby Avery has been a great source of love and motivation since the moment I met him.

Dedication

For my family.

Chapter 1: General Introduction

Pacific salmon (*Oncorhynchus* spp.) are an integral part of the ecology, culture, and economy of British Columbia. In recent decades, the population sizes of some salmon runs in B.C. have been decimated, in part, by reduced freshets during spawning runs (Najafi et al. 2017; Sergeant et al. 2017), a loss of rearing habitat to river damming (Katz et al. 2013), late-stage marine predation (Seitz et al. 2019) and overfishing (Slaney et al. 1996; Coronado and Hilborn 1998; Gresh et al. 2000; Finney et al. 2000; Scott and Gill 2008; Labelle 2009; Price et al. 2017). Attempts to increase adult returns by reducing commercial and recreational salmon fisheries, augmenting wild populations with hatchery-reared smolts, and restoring freshwater habitats have failed to reverse recent trends (Barnett-Johnson et al. 2008; Labelle 2009; Walters et al. 2019). Something else, potentially outside of human control, may be inhibiting the revival of these populations. Poor survival to adulthood has been documented in many salmon populations, but determining where along the salmon life history mortality is occurring has been elusive.

Survival during outmigration of young salmon (smolts) from natal streams to the ocean may be limiting the recovery of Pacific salmon populations (Holtby et al. 1990; Welch et al. 2008; Melnychuk et al. 2014). It is commonly postulated that most of the mortality experienced during outmigration occurs in the months following entry into the marine environment (Welch et al. 2000; Melnychuk et al. 2007; Goetz et al. 2015). However, recent research using radio telemetry to investigate smolt migration rates and survival out of natal streams has found high mortality prior to ocean entry (Buchanan et al. 2013; Melnychuk et al. 2014; Michel et al. 2015; Clark et al. 2016; Michel 2019), with predation suspected to be the main source of death (Healey 1991; Thorstad et al. 2012).

Streams with juvenile fish attract an array of opportunistic foragers, such as the North American river otter (*Lontra canadensis*), the American mink (*Neovison vison*), and the Pacific harbour seal (*Phoca vitulina richardsi*) (Melquist and Hornocker 1983; Heggenes and Borgstrøm 1988; Greenstreet et al. 1993; Ben-David et al. 1997). Juvenile salmon can make up a large portion of the diets of mink and river otters when the fish are available (Melquist and Hornocker 1983; Heggenes and Borgstrøm 1988; Ben-David et al. 1997). The young fish are also preyed upon by some harbour seals at river mouths during seaward migrations (Greenstreet et al. 1993; Chasco et al. 2017; Thomas et al. 2017). In addition to stock depletion inflicted by these mammalian piscivores, avian predators are also known to affect smolt survival.

Avian piscivores that nest on the shores of rivers and estuaries are particularly effective predators of salmon smolts during seaward migrations (Mace 1983; Wood 1986; Ruggerone 1986; Wood 1987; Kennedy and Greer 1988; Feltham 1990, 1995a, 1995b; Collis et al. 2001; Ryan et al. 2001; Collis et al. 2002; Glabek et al. 2003; Roby et al. 2003; Ryan et al. 2003; Antolos et al. 2005; Hostetter et al. 2012; Evans et al. 2012; Sebring et al. 2013; Hostetter et al. 2015). Common mergansers congregate in the lower river following hatchery releases and switch to an almost exclusively salmonid diet during smolt migration (Wood 1986, 1987; Feltham 1990). They are known to consume a substantial proportion of smolts, with the highest predation rates occurring early in the migration run (Wood 1987; Feltham 1990, 1995a, 1995b). Merganser aggregates are further thought to impact smolt survival beyond direct consumption, by causing fish to reduce feeding activities and increase evasive movements (Dionne and Dodson 2002). However, mergansers are not the only avian piscivores to exploit salmon populations during smolt migrations.

A series of extensive smolt-tagging studies conducted on the Columbia River identified Caspian terns (*Hydroprogne caspia*), double-crested cormorants (*Phalacrocorax auritus*), and, to a lesser degree, various gull species as substantial sources of mortality for salmon smolts during passage through the lower river and upper estuary (Ruggerone 1986; Collis et al. 2001; Ryan et al. 2001; Collis et al. 2002; Roby et al. 2003; Ryan et al. 2003; Antolos et al. 2005; Hostetter et al. 2012; Evans et al. 2012; Sebring et al. 2013; Hostetter et al. 2015; Evans et al. 2016; Phillips et al. 2017). These Columbia River studies found that predation rates were highest during the estuary portion of the smolt migration, though in-river predation can be substantial in years of low river flow (Collis et al. 2002; Antolos et al. 2005). Estuary predation was likely greater in the upper, rather than lower, estuary, because of increased availability of alternative prey items, particularly marine forage fish, near the mouth of the estuary (Collis et al. 2002). With technological improvements, researchers have been better equipped to measure the effects of avian predators on juvenile salmonids and even identify previously unknown predators. However, it is unknown what impact another avian piscivore may have on smolt survival —the Pacific great blue heron (*Ardea herodias fannini*).

The Pacific great blue heron is a non-migratory bird that feeds primarily on small fish in rivers and estuaries along the coast of Washington, British Columbia and Alaska (COSEWIC 2008). In Canada, Pacific great blue herons are listed as a Species of Special Concern under the Canadian Species at Risk Act (SARA). Numbers of herons have been relatively stable, though overall productivity in British Columbia has declined since the 1970s (COSEWIC 2008). The main threats to Pacific great blue heron numbers have been predation by bald eagles (*Haliaeetus leucocephalus*), human disturbance, and the loss of nesting habitat (COSEWIC 2008). In 2008, there were an estimated 4,000-5,000 Pacific great blue herons in British Columbia, most of whom nested in the Strait of Georgia (COSEWIC 2008). Understanding the great blue heron diet and the role that juvenile salmon may play during the breeding season will help determine if food limitation is influencing recent declines in productivity.

Most great blue herons are highly social birds that nest in close quarters near food sources during the breeding season (COSEWIC 2008). Heron foraging is constrained by the timing and duration of low tides, which means that heronries tend to be located close to easily accessible intertidal areas (COSEWIC 2008). Herons nest and forage extensively in areas used by migrating juvenile salmon, and may therefore contribute to the high levels of mortality incurred by smolts in the lower-river and estuary (Jepsen et al. 1998; Koed et al. 2002; Thorstad et al. 2012).

Quantifying rates of fish predation by herons cannot be done by identifying prey remains in fecal samples because fish bones are fully broken down in heron digestive tracts (Cook 1978). As a result, predation studies have been limited to direct observations during foraging events (Glahn et al. 1999; Hodgens et al. 2004). These studies suggest that juvenile salmon are within the preferred prey size range of herons (Glahn et al. 1999; Hodgens et al. 2004). However, juvenile salmon have seldom been identified in dietary analyses. Exceptions include observations of one colony of great blue herons consuming stocked rainbow trout (Hodgens et al. 2004), and reports of grey herons (*Ardea cinerea*) preying on Atlantic salmon smolts in another system (Koed et al. 2002). Pacific great blue herons may be a significant source of mortality for juvenile salmon in British Columbia, though few dietary studies have been conducted in salmon bearing streams and estuaries.

Great blue herons are drawn to local fish abundances, and are commonly seen feeding along rivers and the edges of estuaries—the same areas used by juvenile salmon entering the ocean.

Herons can have a strong influence on local fish communities, both through direct consumption and fish displacement (Huang et al. 2015). However, the extent to which they prey on juvenile salmon is unknown, nor is the impact that herons may be inflicting on salmon populations known. One means of addressing these shortcomings is to estimate smolt consumption rates from implanted fish tags recovered under the nests at local bird colonies.

My study set out to estimate rates of heron predation on wild and hatchery-reared populations of Chinook and coho salmon from the Cowichan River, Big Qualicum River, and Capilano River through Passive Integrated Transponder (PIT) tag deployment and subsequent scanning at surrounding heronries. Tag recoveries were corrected using published off-colony PIT-tag deposition rates for avian smolt predators to determine the relative impact of heron predation on smolt survival during outmigration. Daily heronry scans conducted throughout the smolt outmigration revealed the timing of heron predation relative to their breeding season. Smolt releases in both the river and estuary sites uncovered where smolts were most vulnerable to heron predation. Predation estimates and published heron energetic requirements were employed to calculate the proportion of the heron diet fulfilled by salmon smolt consumption. My research also investigated the relationship between smolt size and susceptibility to heron predation in the Cowichan and Capilano Rivers, and annual predation rates revealed the effect of river flow during outmigration on smolt consumption. Overall, this project is the first to assess Pacific great blue herons as a predator of salmon smolts in the wild, and to quantify predation rates by herons during salmon smolt outmigration from natal rivers.

Chapter 2: Pacific great blue herons are a new predator of Pacific salmon smolts

2.1 Introduction

Many salmon (*Oncorhynchus spp.*) populations in the Pacific Northwest have declined in recent decades (Slaney et al. 1996; Coronado and Hilborn 1998; Gustafson et al. 2007; Scott and Gill 2008; Labelle 2009; Irvine and Akenhead 2013). Their declines may be due to high numbers of young salmon (smolts) dying during outmigration from natal streams (Holtby et al. 1990; Michel 2019; Henderson et al. 2019). Salmon tracking studies suggest that >50% of mortality occurs prior to ocean entry (Buchanan et al. 2013; Michel et al. 2015; Clark et al. 2016; Michel 2019; Henderson et al. 2019)—with predation suspected as being the main source of death (Heggenes and Borgstrøm 1988; Healey 1991; Cavallo et al. 2013).

Salmon smolts attract an array of predators during freshwater outmigration. These include common mergansers (*Mergus merganser*), North American river otters (*Lontra canadensis*), American minks (*Neovison vison*), Caspian terns (*Hydroprogne caspia*), double-crested cormorants (*Phalacrocorax auritus*) and Pacific harbour seals (*Phoca vitulina richardsi*) (Melquist and Hornocker 1983; Wood 1986; Heggenes and Borgstrøm 1988; Greenstreet et al. 1993; Ben-David et al. 1997; Collis et al. 2001; Ryan et al. 2001; Collis et al. 2002; Roby et al. 2002, 2003; Ryan et al. 2003; Antolos et al. 2005; Schreck et al. 2006; Hostetter et al. 2012; Evans et al. 2012). The avian piscivores on this list are known to cause significant mortality of outmigrating salmon smolts (Wood 1986; Collis et al. 2001, 2002; Roby et al. 2002, 2003; Antolos et al. 2005; Schreck et al. 2006; Hostetter et al. 2012; Evans et al. 2012). However, the impacts of another avian piscivore known to feed along the riverbanks and estuaries of smolt-bearing rivers is unknown—the Pacific great blue heron (*Ardea herodias fannini*).

The Pacific great blue heron is a non-migratory bird that nests along the coast of Washington, British Columbia, and Alaska (COSEWIC 2008). These birds feed primarily on small fish in freshwater streams and estuarine marshes during their breeding season (March-June) when energy demand to support reproduction is the highest (Butler 1993, 1997; Hodgens et al. 2004). Observational studies suggest that herons consume fish ranging from 10-30 cm in length (Glahn et al. 1999; Hodgens et al. 2004), though small fish (<15 cm), such as salmon smolts, may be underrepresented in these studies (Cook 1978). One study found juvenile rainbow trout made up as much as 67% of the daily energy requirements of one breeding population of great blue herons (Hodgens et al. 2004), while another study found a significant number of radio tags from juvenile Atlantic salmon under the nests of grey herons (*Ardea cinerea*) (Koed et al. 2002). It is conceivable that salmon smolts are nutritionally important for Pacific great blue herons in British Columbia, but difficulty in quantifying heron diets has precluded herons from being considered as predators of salmon smolts.

My study aimed to assess the extent to which Pacific great blue herons prey on salmon smolts based on recovering Passive Integrated Transponder (PIT) tags from the remains of fish defecated at local heron rookeries. PIT tags were implanted in both wild and hatchery-reared salmon smolts prior to outmigration from select rivers in British Columbia. I used the recovered tags to calculate a minimum predation estimate and determine the proportion of the heron diet comprised of salmon smolts during the breeding season. Finally, I investigated the influence of smolt size and river flow during outmigration on the susceptibility of smolts to heron predation. The size of heron rookeries and their proximity to salmon-bearing rivers may be a good predictor of the coast-wide impact of heron predation on salmon populations, as well as the importance of smolt consumption in the breeding heron diet. Identifying major sources of mortality and the factors that influence survival is a crucial step in developing an effective recovery plan to mitigate the decline of Pacific salmon populations.

2.2 Methods and materials

2.2.1 Study sites

My study focused on the Cowichan River, the Big Qualicum River, and the Capilano River (Fig. 1). The Cowichan River flows 47 km east from Lake Cowichan to Cowichan Bay in the Salish Sea at the southeast end of Vancouver Island, British Columbia. The Cowichan is home to a key indicator stock of Chinook salmon used by the Fisheries and Oceans Canada (DFO) to monitor the health and recovery of salmon populations in the Salish Sea. The Big Qualicum River is situated on the east coast of Vancouver Island running 11 km northeast from Horne Lake to the Strait of Georgia—while the Capilano River flows 6 km south from Capilano Lake into Burrard Inlet on the mainland of B.C. Extensive hatchery programs operate on all three of these river systems.

2.2.2 Local heron rookeries

There were ~4,000-5,000 great blue herons nesting in B.C. in 2008 (COSEWIC 2008). Of these, about 29-38% are distributed among my four study sites (5-7% Cowichan Bay, 1-2% Qualicum Estuary, 5-6% English Bay, and 18-23% Fraser Estuary).

The Cowichan Bay heronry is the closest nesting site to the Cowichan River and Bay (located within 1 km of the river mouth). It was established in 2004 and has been steadily increasing in the numbers of active nests since that time (Jenna Cragg, pers. comm.). Since 2017, there have been ~100 active nests (Jenna Cragg, pers. comm.). The next closest rookeries to the Cowichan River are at Maple Bay (10 km north of Cowichan River, 7 active nests) and Chemainus (20 km north of Cowichan River, ~30 active nests).

Local heron rookeries surrounding the Qualicum Estuary include the Deep Bay rookery (10 km north of Big Qualicum River, 20 nests) and the Little Qualicum Estuary rookery (10 km south of Big Qualicum River, 10 nests).

English Bay is the primary feeding area for birds nesting in the Stanley Park heronry. This heronry has ~90 nests and is ~1 km from the Capilano River. Herons started to nest here in 1921 and have relocated several times to different locations within the park since then, settling at its current location in 2001. Another local rookery within feeding range of English Bay is the Deer Lake Park heronry (15 km southeast of the Capilano River, 30 nests). It has grown considerably since forming in 2005. Capilano River salmon likely transit through English Bay to the Fraser River Estuary during their seaward migration, taking them within close proximity of the Tsawwassen heronry (35 km south of Capilano River, ~350-450 nests). The Tsawwassen heronry is the largest heron rookery in B.C.

2.2.3 PIT-tag releases

From 2014 to 2018, ~5,000 PIT tags were inserted annually into wild and hatchery-reared Chinook salmon smolts released into the Cowichan River to determine survival rates (PSF 2016). Tags were inserted directly into the stomach cavity of the fish using a PIT tag applicator that created a small incision (<1 mm) in the abdomen, through which the tag entered the fish (PSF 2016). All tagging was conducted by members of the B.C. Conservation Foundation and employees at the Cowichan Fish Hatchery.

Hatchery-reared smolts were tagged at the Cowichan Fish Hatchery in early May of each year, and were allowed to recover from the effects of tagging in holding tanks for a minimum of 14 days prior to being released into the river. Half of the PIT-tagged hatchery fish were released with ~600,000 untagged hatchery smolts in each year. This major release of tagged fish took place ~25 km upstream of Cowichan Bay. The remaining PIT-tagged hatchery smolts were released in smaller groups at 5 sites along the Cowichan River (100-500 smolts per group; sites ranging from 5-40 km upstream of Cowichan Bay) to evaluate the effect of release site on smolt survival. All releases took place on May 22nd of each year.

Wild Chinook smolts were opportunistically caught and PIT-tagged along the Cowichan River using a single beach seine from May until the end of the smolts' freshwater residency in late June in all years except 2017. Wild smolt tagging occurred over 7-14 days in the field and resulted in ~10,000 smolts being captured and tagged over the course of my study. Following smolt entry into the ocean (late May-July), beach and purse seining was used in Cowichan Bay to deploy ~5,000 additional PIT-tags annually in wild and hatchery-reared fish (PSF 2016). Hatchery smolts captured in the estuary were identified by adipose fin clips given prior to release.

In 2015, 40,000 hatchery-reared coho smolts were PIT-tagged and released with ~380,000 untagged smolts from the Big Qualicum Fish Hatchery, located 1 km upstream of the Strait of Georgia (PSF 2016). In the Capilano River, an average of 4,000 PIT tags were deployed annually from 2008-2018 in hatchery-reared coho smolts from the Capilano Fish Hatchery (Braun et al.

2016). These tagged fish were released with ~600,000 untagged hatchery smolts downstream of the Cleveland Dam on the Capilano River (Braun et al. 2016).

2.2.4 Smolt downstream movement and survival

Prior to releasing tagged smolts in the Cowichan River, PIT-tag receivers were placed 5 and 7 km upstream of Cowichan Bay to track smolt movements and monitor survival. PIT-tag receivers had a read range of ~1 meter when flow conditions were ideal. The detection efficiencies of these in-stream arrays fluctuated with river conditions throughout smolt runs, making survival data for the relatively few migrating smolts recovered at the heron rookery insubstantial for the purposes of my study.

2.2.5 Scanning heron rookeries

Forest floors in Heron rookeries were scanned using a custom designed mobile PIT antenna comprised of a Biomark IS1001 reader board and 3 conduit, 12-gauge cable-wire looped at the end of a 4-foot pole housed in PCV tubing. The array was powered by a 24-volt, 7 Ah lead acid battery and equipped with a beeper to notify the operators when a tag was detected. The battery and reader board were carried in a 150 L backpack. Two people systematically scanned each rookery by dividing the rookery into sections based on natural borders (e.g. standing or fallen trees) and scanning along transects within sections. Areas that appeared to have high tag density were scanned multiple times along different transects to minimize the effect of PIT-tag signal collisions on the array’s detection efficiency. A similar methodology for PIT-tag recovery in nesting sites has successfully been used to assess avian predation on salmon smolts in the Columbia River (Collis et al. 2001; Ryan et al. 2001; Roby et al. 2002; Ryan et al. 2003; Antolos et al. 2005; Hostetter et al. 2012; Sebring et al. 2013; Hostetter et al. 2015; Evans et al. 2016).

2.2.6 Predation rates

Annual minimum predation rates for each river system equaled the number of PIT-tags recovered in local heron rookeries divided by the total number of tags deployed. The tags recovered under the nests reflect the minimum proportion of tagged smolts that great blue herons consumed. However, this is a conservative rate of predation because it does not account for tags that herons consumed and defecated away from their rookeries.

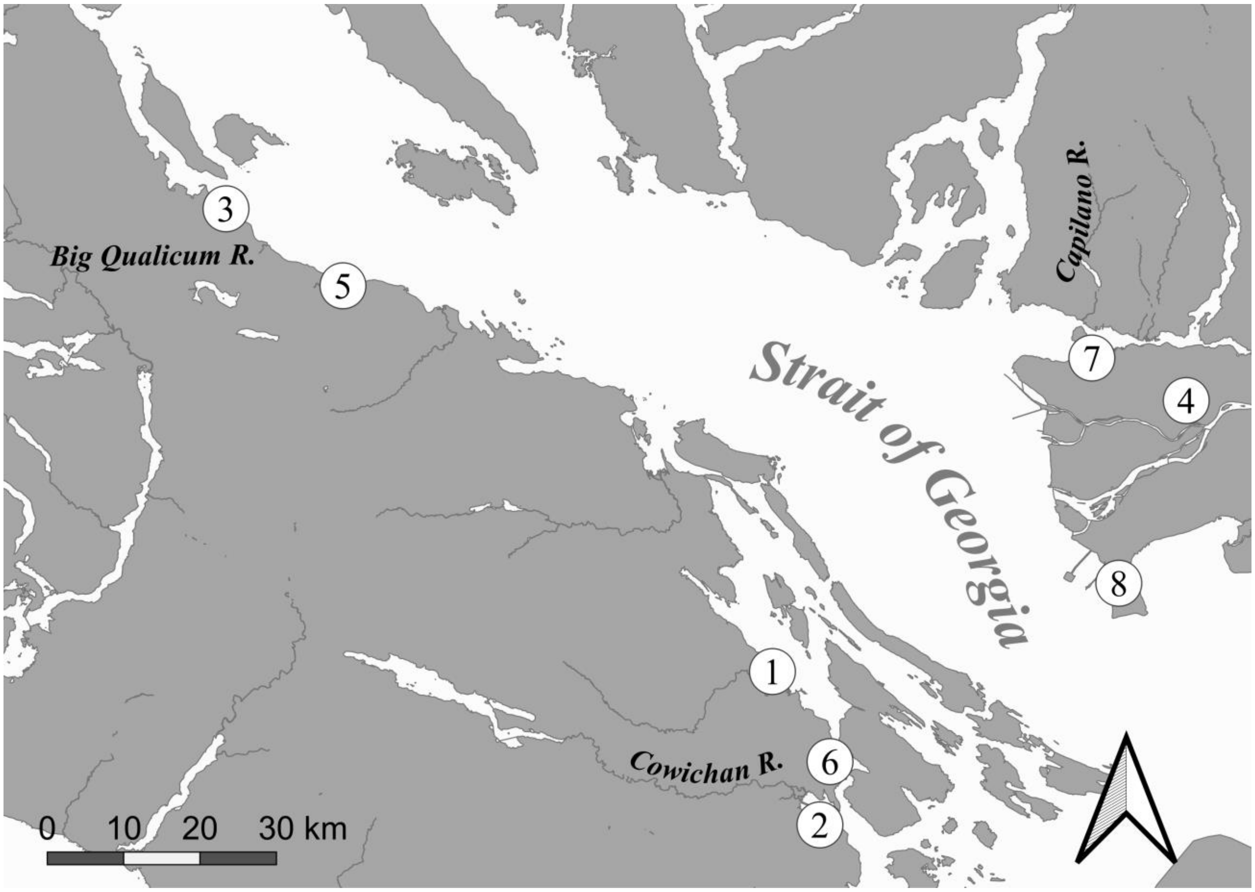

Figure 1. Map of the study system showing the Cowichan, Capilano, and Big Qualicum Rivers—and the neighboring heron rookeries (1. Chemainus, 2. Cowichan Bay, 3. Deep Bay, 4. Deer Lake Park, 5. Little Qualicum Estuary, 6. Maple Bay, 7. Stanley Park, 8. Tsawwassen).

Unfortunately, there are no heron data to estimate the proportion of tags defecated outside of rookeries. I therefore used data from a cormorant study that fed known numbers of tagged fish to a colony of birds, and counted the numbers of tags deposited at the rookery (Hostetter et al. 2015). This study yielded a probability distribution (mean and standard deviation) for the likelihood of recovering tags at a cormorant rookery. In the absence of a similar study for great blue herons, I assumed that the probability of recovering a tag at a heron rookery was similar to the probability of recovering a tag at a cormorant rookery.

I used a Monte Carlo simulation procedure to randomly select deposition rates from the probability distribution of recovering a fish tag at a cormorant rookery (n = 6 trials). I also randomly selected the proportion of salmon tags recovered under heron rookeries from the probability distribution of tags I recovered from each site and all years (*n* = 5 y hatchery-reared Cowichan Chinook; *n* = 4 y wild Cowichan Chinook; and *n* = 11 y hatchery-reared Capilano coho). Each simulation selected one value for each site from the heron tag recovery distributions and one from the cormorant tag recovery distribution to estimate the corrected annual predation rate as follows:

$$P_c = \frac{\mathrm{T}_{herons}}{T_{cormorants}}$$

where P_c is the corrected annual predation rate by herons, T_{herons} is the proportion of salmon tags recovered at a given heron rookery, and $T_{cormorant}$ is the proportion of tags consumed by cormorants that were deposited in cormorant colonies.

I ran the simulation with 10,000 trials for each site and tagged population to produce mean-corrected annual rates of predation (with standard deviations) inflicted on salmon smolts by herons for each heron rookery and cohort of fish (i.e., hatchery or wild).

I logit transformed the parameters that describe the probability distributions prior to running the Monte Carlo simulations to assure that no negative values could be randomly selected in the trials. Logit transformations are commonly used when working with proportional values to avoid misinterpreting datasets ranging from 0 to 1. I back-transformed the Monte Carlo-selected values prior to applying them in the corrected predation rate formula.

I ran simulations for the hatchery-reared Cowichan Chinook (*n* = 5 y of annual tag recovery rates), wild Cowichan Chinook (*n* = 4 y of annual tag recovery rates), and hatchery-reared Capilano coho (*n* = 11 y of annual tag recovery rates). I also directly applied the mean and standard deviations from the on-colony cormorant tag deposition trials to the Big Qualicum annual rookery tag-recovery rate to calculate corrected predation estimates for this site. Big Qualicum data were not corrected using Monte Carlo simulations because there was only one year of annual tag recovery data available for this river system.

2.2.7 Heron observations

I opportunistically observed great blue herons from the Cowichan Bay rookery during low tide foraging events in May and June of 2018. Observational counts were conducted from the southwestern shore of Cowichan Bay near the confluence zone of the south arm of the Cowichan

River. A total of 7 low tide events were included in these observations, and total counts were averaged to estimate a mean flock size with a 90% confidence interval.

2.2.8 River flow and annual predation

Average flow during smolt outmigration in the Cowichan was calculated using hourly hydrometric measurements taken by a Government of Canada water station located approximately 7 km upstream of Cowichan Bay (station code 08HA011). Similar data was provided by Metro Vancouver that consisted of hourly flow measurements taken downstream of the Cleveland Dam, where hatchery smolts were released in all years of our study. The influence of flow on heron smolt predation was assessed using correlations between average flow during outmigration and annual tag recoveries in local heron rookeries.

2.2.9 Smolt size and predation

Fork lengths were collected for both wild and hatchery-reared smolts tagged in the Cowichan and Capilano Rivers just prior to release into the freshwater environment. I used these values to evaluate the influence of smolt size on susceptibility to heron predation. The fork lengths of river-released smolts detected under the nests at local heron rookeries and those whose tags were not detected were compared using a general logistic regression model, with the independent variable of fork length upon release tested against rookery detection as a binomial response variable. Smolts from the 2016 Cowichan River release were excluded from this analysis due to high levels of predation resulting from low-flow conditions in that year, which rendered all smolts increasingly vulnerable to heron predation regardless of size.

2.2.10 Timing of predation

Daily rookery scans were conducted under the nests at the Cowichan Bay heron colony during smolt migration in 2018 to determine at what point in the heron breeding season predation occurred. A total of 18 full scans of the heronry were completed from May 22-June 22, 2018, covering the entire Cowichan Chinook hatchery release and the bulk of the outmigration run of both hatchery and wild Chinook smolts. Two scans were subsequently completed every two weeks thereafter to document any further predation of late migrants, with the final scan taking place on July 23, 2018. A discovery curve was constructed from the cumulative detections of 2018 smolt tags from each scan of the Cowichan Bay heronry.

2.2.11 Tag distribution within rookeries

Sectioned scans were conducted in the heronries with the highest rates of tag recoveries (Cowichan Bay and Stanley Park) to explore tag distributions relative to nest positioning. This allowed us to deduce whether most herons were taking part in the smolt predation or if there were just a few smolt specialists. Heronry sections contained 15-30 nests and were separated by flagging tape to assure there was no overlap between sections during scanning. The total number of tags detected in each section was divided by the number of nests present to obtain the average number of tags per nest in each section of the heronry. The resulting tags per nest ratios were then compared using ANOVA, with individual sections serving as the independent variable and tags/nest ratios as the response.

2.2.12 Heron dietary analysis

Daily heronry scans throughout smolt outmigration in the Cowichan indicated that predation occurred during chick rearing, when chicks had emerged from eggs and remained in the nests to be fed by both parents. Published heron adult and chick energetic requirements from this period were used to determine what proportion of the diet was made up of hatchery salmon smolts. Whole nest energetic requirements were calculated for 2 adult herons and 2 chicks, which is the average number of chicks per active nesting attempt in North America (reviewed by Butler 1997b).

Hatchery and wild Cowichan Chinook energy densities (kJ/g wet weight) and weights were obtained from in-river and estuary sampling of Chinook smolts conducted by DFO throughout late-May and June in all years that our study was conducted. For Capilano River hatchery-reared coho smolts, published energy densities (kJ/g wet weight) were applied to the average wet weight collected from smolts tagged in our study and released in the Capilano from 2008-2018.

Estimates of overall annual hatchery smolt consumption were derived from the total number of smolts released into the rivers in each year multiplied by the proportion of smolt tags recovered at local heron rookeries. This total consumption was then multiplied by the average wet weight of in-river smolts to obtain a total weight of consumed smolts. This weight was used, in conjunction with the energy density of Cowichan Chinook, to determine overall energy input of hatchery Chinook to the heron diet in each year. Dividing this number by the total dietary requirements of herons and chicks in major rookeries during the smolt run produced the proportion of heron diets comprised of hatchery-reared smolts.

2.3 Results

2.3.1 Heron predation on outmigrating salmon smolts

I detected 1,199 PIT tags in heron rookeries near the three river systems where salmon smolt tagging had been conducted, suggesting that herons are a new predator of outmigrating salmon smolts. These detections included 458 tags from the Cowichan River, 136 tags from the Big Qualicum River, and 605 tags from the Capilano River (Appendix A). These detections represent tag recoveries of 1.24% (SD = 1.14%) for hatchery Chinook smolts released in the Cowichan River from 2014-2018, 1.15% (SD = 0.34%) for wild Chinook smolts released in the Cowichan River from 2014-2018, 0.34% for coho hatchery smolts released into the Big Qualicum River in 2015, and 1.3% (SD = 0.62%) for coho hatchery smolts released in the Capilano River from 2008-2018 (Fig. 1).

As herons do not defecate exclusively in the heronry, and not all defecated tags are detectable due to damage or deposition in inaccessible areas within the heronry (e.g. tree branches, nests), these tag recoveries represent a minimum predation estimate, and actual predation rates may be considerably higher. Correcting for tags that had been consumed, but not recovered, yielded predation estimates of 3.24% (SD = 1.14%) for hatchery Cowichan River Chinook, 2.17% (SD = 0.34%) for wild Cowichan River Chinook, 0.67% for hatchery Big Qualicum coho, and 2.90% (SD = 0.62%) for hatchery Capilano coho.

2.3.2 River vs. estuary predation

From 2014-2018, an equal number of PIT-tags were implanted in Chinook salmon smolts tagged and released in the Cowichan River and during their estuary residency. However, 90% of the tags recovered in the Cowichan Bay heronry were from river-tagged fish (Fig.2). This finding indicates that herons in the Cowichan fed on smolts primarily in the freshwater segment of their migration, upon entry into the estuary, or during early bay residency when smolts inhabit the shallow nearshore habitat.

2.3.3 Heron observations

Most herons observed in the southwestern reach of Cowichan Bay from May-June during the 2018 smolt migration were seen wading along the tide line of estuary near the outlet of the

South arm of the Cowichan River. An average of 55 herons (90% CI = 16-94) were observed actively foraging during the low tide events monitored at this time.

2.3.4 River flow and annual predation rates

Average river flow in the Cowichan during outmigration was negatively correlated with annual heron predation rates throughout all tag release years (R = -0.67, p = 0.23), and a majority of the tags detected in local heronries (52.4%) were from fish released in 2016, a critically low flow year (Fig. 2). Average river flow during outmigration in 2016 (4.31 m/s^2) was comparable to that of 2015 (6.23 m/s^2), a year with only moderate levels of heron predation (0.66% of tags recovered at rookery; Fig. 1). The point of entry of smolts into the estuary was not assessed during the years our study was conducted in the Cowichan River system. Average flow during outmigration was not correlated with annual heron predation rates in the Capilano River (R = -0.02, p = 0.95).

2.3.5 Smolt size

Smaller salmon smolts were more susceptible to Pacific great blue heron predation in our study (Fig. 3; Appendix B). Tags recovered at heronries were from fish with significantly smaller fork lengths than those of undetected smolts tagged and released in the river for hatchery-reared Chinook smolts from the Cowichan River in all years except a critically low flow year in 2016 (p = 0.016; Recovered smolt FL = 74.0 mm, SD= 8.8 mm; Tagged smolt FL = 76.8 mm, SD = 9.2mm) and hatchery-reared Coho smolts from the Capilano River (p < 0.0001; Recovered smolt FL = 90.4 mm, SD = 12.3 mm, Tagged smolt FL = 94.4 mm, SD = 14.4 mm). Heronry-detected smolts were also smaller than river released smolts for wild Chinook tagged in the Cowichan River, though the difference in fork lengths was not significant (p = 0.174; Recovered smolt FL = 65.7 mm, SD = 7.8 mm, Tagged smolt FL = 66.6 mm, SD = 7.1 mm). Smolts fork lengths were not measured for hatchery-reared Coho tagged and released in the Big Qualicum River.

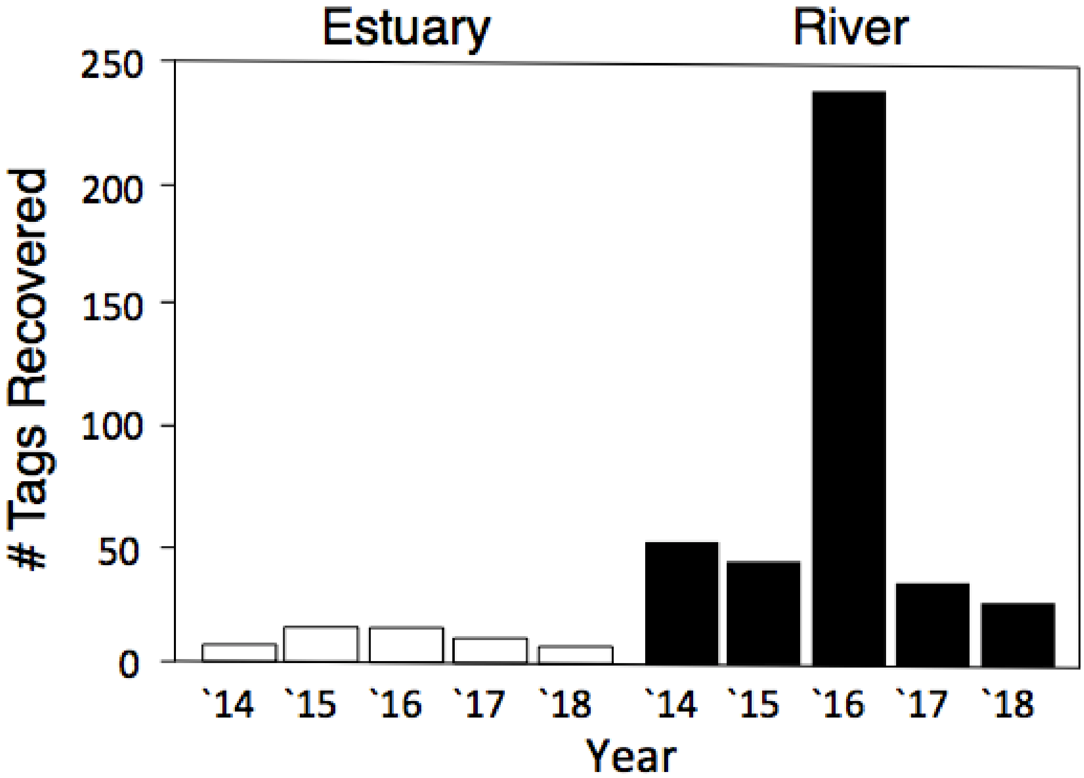

Figure 2. Annual number of tags recovered in the Cowichan Bay heron rookery from estuary- and river-released Chinook smolts from the Cowichan River, 2014-2018. Approximately 5,000 tagged fish were released in both the estuary and the river each year.

2.3.6 Timing of predation

PIT-tags from Chinook smolts released in late May 2018 were detected within 48 hours at the Cowichan Bay heronry. Most of the 2018 tags (>80%) were deposited in the heronry within the first month following smolt release, and 100% of the 2018 tags were detected by July 8, 47 days after hatchery tag releases (Fig. 4). Tag deposition averaged approximately one new tag per day throughout the freshwater portion of smolt migration in the Cowichan in 2018, a year of relatively low heron predation.

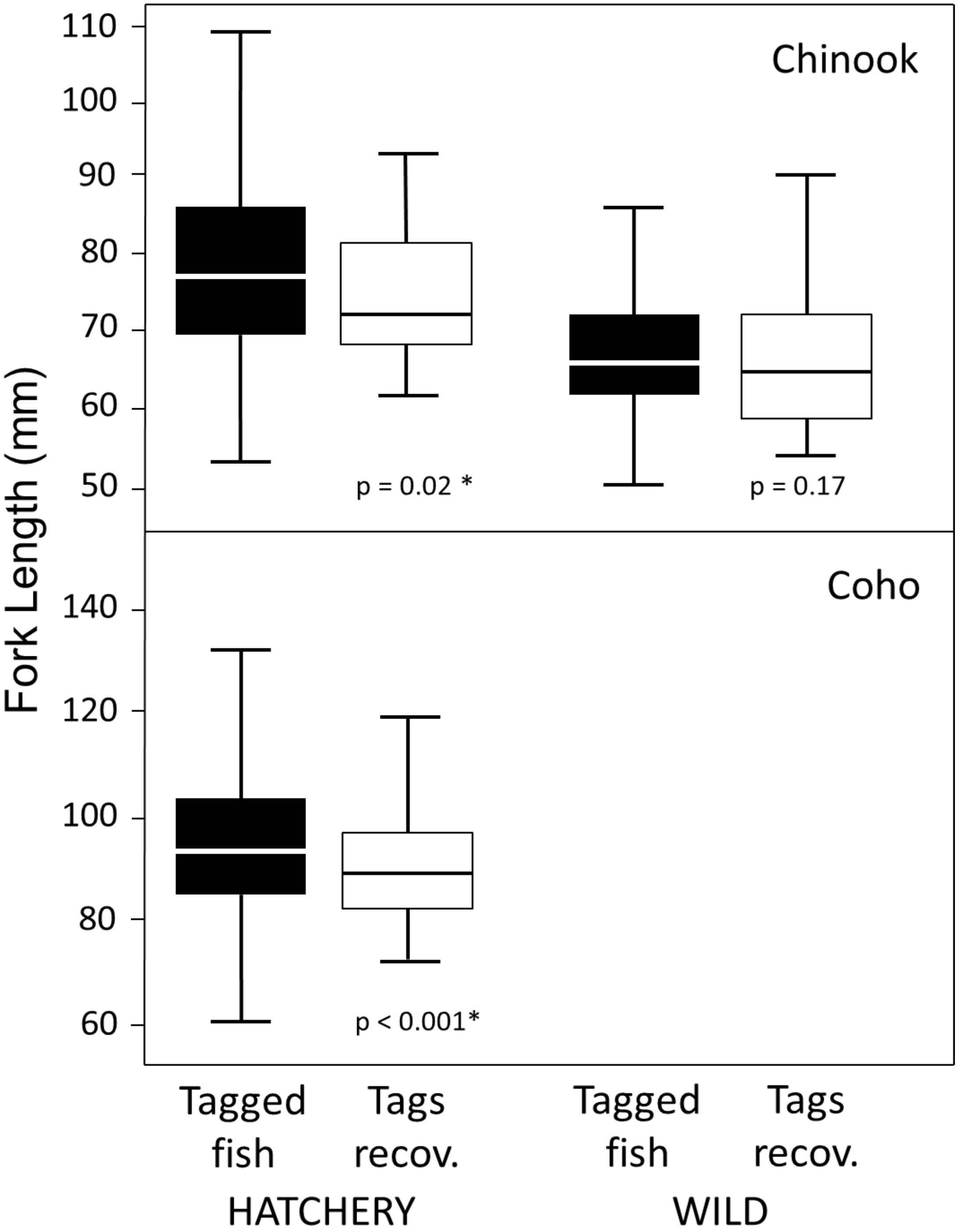

Figure 3. Fork length distributions of wild and hatchery-reared PIT-tagged salmon smolts (black) compared to those of fish detected in local heron rookeries (white) from Chinook released in the Cowichan River (2014-2018) and Coho released in the Capilano River (2008-2018). Heron predation was significantly higher on smaller hatchery smolts in both river systems (as indicated by p-values).

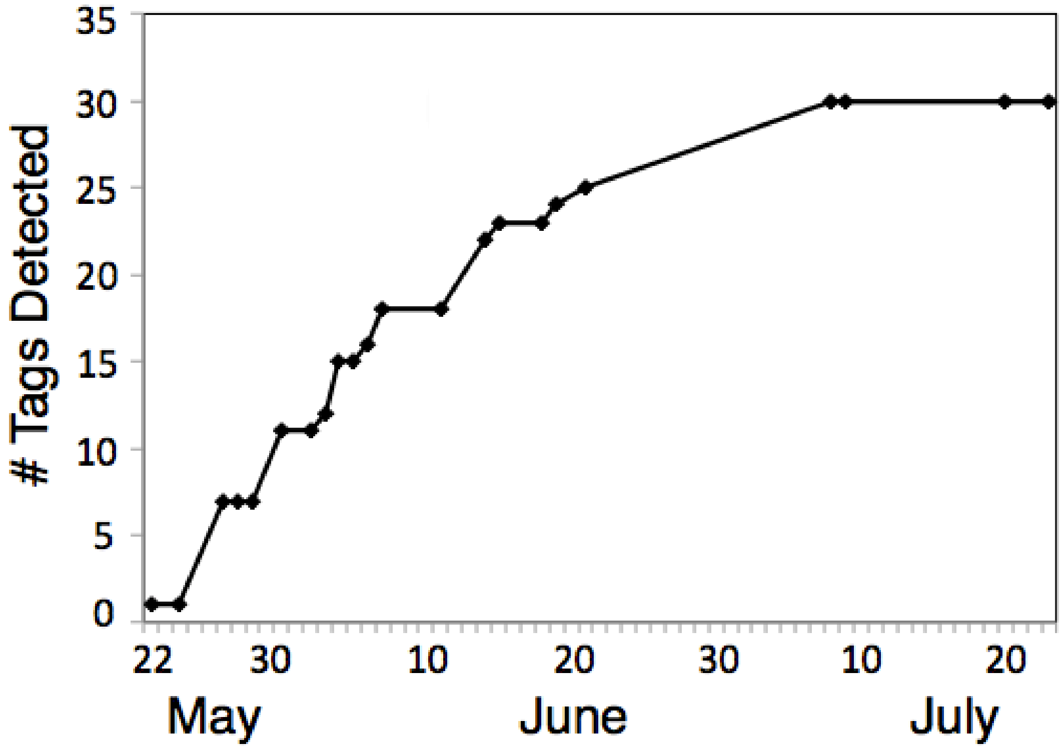

Figure 4. Discovery curve showing cumulative number of PIT-tags from Chinook smolts released in the Cowichan River in 2018 detected per scan at the Cowichan Bay heron rookery during outmigration (May 22 - July 23, 2018). Cowichan hatchery release occurred on May 22.

2.3.7 Tag distribution in rookeries

Sectioned scans of the rookeries at Stanley Park and Cowichan Bay indicated that PIT-tags were evenly distributed under the heron nests. Tags were detected in all rookery sections scanned in our study, with an average of 3.7 tags per nest (SD = 0.8 tags) at the Cowichan Bay rookery and 6 tags per nest (SD = 2.3 tags) at the Stanley Park rookery near the Capilano River. A sectioned scan was not conducted at the Deep Bay heron rookery, where most of the PIT-tags from Big Qualicum River smolts (93%) were detected.

2.3.8 Predation as a factor of rookery distance

Full PIT-tag scans conducted at heron rookeries within 35 km of the study rivers revealed that most herons feeding on smolts were from relatively large rookeries (30-100 nests) within 15 km of the lower river. In the Cowichan River, 436 of the 438 salmon smolt tags detected in heron rookeries occurred under the nests at the Cowichan Bay heron rookery (100 active nests, <1 km from the mouth of the Cowichan River), while one tag was detected at the Maple Bay heron rookery (7 nests, 10 km from river mouth) and two tags were detected at the Chemainus heron rookery (30 nests, 25 km from river mouth) (Fig. 1). For the Capilano River, 605 tags were detected at the Stanley Park heron rookery (100 nests, 5 km from the mouth of the Capilano River) and 3 tags were detected at both the Deer Lake Park heron rookery (15 nests, 15 km from river mouth) and the Tsawwassen heron rookery (300 nests, 30 km from river mouth) (Fig. 1). A total of 126 tags from the Big Qualicum release in 2015 were detected at the Deep Bay heron rookery (30 nests, 10 km north of the Big Qualicum River) and 8 tags were detected at the Little Qualicum Estuary heron rookery (10 nests, 10 km south of the Big Qualicum River) (Fig. 1).

2.3.9 Heron energetics

Using the documented energy requirements of adult herons (1,860 kJ/day) and heron chicks during peak energy demand (2,027 kJ/day) (Bennett et al. 1995), the total energy demand of breeding herons is 7,774 kJ/day per nest and 4,054 kJ/day per set of chicks. The average energy densities of hatchery smolts caught exiting the Cowichan River in our study years averaged 57.1 kJ per fish, and the published average energy density of coho smolts (5.7 kJ/g: Trudel et al. 2005) and wet weight of fish tagged in our study resulted in energy density estimates of 61.2 kJ per fish.

Annual estimates of hatchery smolt predation rates at major heron rookeries along the Cowichan, Capilano, and Big Qualicum Rivers corrected for off-colony tag deposition indicated that an average of 5.6% (4.1%-8.4%; 95% CI) of chick energy requirements could be provided by hatchery smolt predation alone. This represents annual consumption rates of 116 hatchery smolts per nest (85-175 smolts, 95% CI) over all years and rookeries.

Throughout our study, hatchery-reared Chinook smolts from the Cowichan River accounted for 7.5% (5.5%-11.3%, 95% CI) of the annual dietary requirements of heron chicks nesting in the Cowichan Bay rookery in the month following tag releases. Hatchery-reared coho smolts supplied 5.0% (3.6%-7.4%) of the annual energy requirements of heron chicks rearing in the Stanley Park heron rookery and 4.3% (3.1%-6.4%) for chicks nesting in the Deep Bay rookery.

2.4 Discussion

Many PIT tags were recovered under the nests of great blue herons from the remains of wild and hatchery-reared juvenile salmon. My results show that the blue heron is a prevalent predator of tagged salmon smolts that has not been previously recognized. The recovered tags provide information about the rates of predation, size classes of fish targeted, the influence of water flow on predation rates, and the locations where herons are effective at catching smolts. This information helps to place herons among the list of other suspected predators of salmon smolts. It also reveals where and why smolts are vulnerable to heron predation, and provides a means to assess the contribution smolts make to the growth and development of heron chicks. Ultimately, the information gained from the tagged fish fills in a previously unknown piece of the salmon life history, and shows one more way in which salmon contribute to sustaining life of marine and freshwater predators.

2.4.1 Heron smolt predation

Pacific great blue heron preyed on outmigrating salmon smolts in all river systems and years that tagging was conducted. Approximately 1% of the PIT-tags released in wild and hatchery-reared Chinook and coho salmon smolts were subsequently recovered under the nests at Pacific great blue heron rookeries. However, these tag recovery rates represent minimum predation estimates since not all heron-consumed tags are deposited within the rookery, nor are all rookery-deposited tags detectable (e.g. tags deposited in nest or branches, broken tags). For example, only 51% (95% CI = 34-70%) of the tags consumed by double-crested cormorants were subsequently detected in their rookery (Hostetter et al. 2012). Since double-crested cormorants and Pacific great blue herons exhibit similar nest attendance during the breeding season (Vennesland and Butler 2011; Dorr et al. 2014), it is plausible to assume that this detection probability is applicable to tags consumed by Pacific Great Blue herons.

When corrected for undetected tags consumed by herons during our study, estimated annual predation rates were about 1-3%, though predation was as high as 6% in a particularly low river-flow year in the Cowichan. The lowest annual predation rate occurred in the Big Qualicum River, where the hatchery is located very close to the estuary. Low predation in this system may also have been due to a high number of tags being synchronously released within a large hatchery smolt population (PSF 2016), resulting in a “predator swamping” effect that limited heron predation (Fury et al. 2016). Sectioned scans in the two largest rookeries further revealed an even distribution of deposited tags under all nests, suggesting that most herons take part in the documented smolt predation, as opposed to a few smolt-consuming specialists. Over 99% of the tags I detected under heron nests were in the nearest rookery, alluding to a potential partitioning of foraging habitats between heron colonies. It has been noted that a 5% reduction in early life mortality could reverse the declining trends of some Pacific salmon populations (Kareiva et al. 2000). As such, predation by herons could be ecologically significant, potentially impacting the recovery of some salmon populations.

Historically, great blue herons have not been considered a predator of juvenile salmonids, though breeding herons are known to forage extensively in the freshwater and estuarine habitats used by salmonid smolts during their seaward migration (Butler 1997). Juvenile salmonids have not been reported as part of great blue heron diets in rivers and estuaries (Owen 1955; Quinney 1982; Butler 1993, 1997; Adams and Mitchell 1995; COSEWIC 2008)—although some herons take juvenile fish at salmonid-rearing facilities (Glahn et al. 1999; Hodgens et al. 2004). More recently, however, great blue herons nesting along the Columbia River were found to have consumed salmon smolts (based on recovered smolt PIT-tags in heronries; Myrvold and Kennedy 2018)—similar to my findings. Thus, juvenile salmon consumption by Pacific great blue herons may be a relatively new phenomenon that reflects herons keying in on increasingly large hatchery releases in British Columbia (pers. comm. Rob Butler).

While juvenile salmon appear to have become a recent part of the great blue heron diet in rivers and estuaries, grey herons are known to consume juvenile salmonids in the Baltic Sea, and juvenile masu salmon in Japan. In the Baltic Sea, juvenile salmonids made up ~ 40% of the biomass of prey taken by one population of breeding grey herons, despite representing <7% of the available fish community (Jakubas and Manikowska 2011). Another field experiment in Japan investigating riparian predation on juvenile salmonids stocked in an experimental stream found that grey herons were the most effective salmonid predator documented (Miyamoto et al. 2018).

2.4.2 How herons rank among other smolt predators

Predation by great blue herons, along with smolt consumption from other known predators, might explain some of the high mortality associated with this stage of the salmon life history (Buchanan et al. 2013; Melnychuk et al. 2014; Michel et al. 2015; Clark et al. 2016; Michel 2019).

In the Cowichan River, as many as 50% of juvenile salmon die throughout the downstream migration, with variability between years (pers. comm. Kevin Pellett). In-stream detections imply that tagged fish were removed from the system by land-based predators. However, mobile PIT-tag scans that I conducted at river otter latrines, mink dens, mergansers roosts, and along raccoon trails in the Cowichan system during my study failed to detect even a single juvenile salmon tag. Instead I found ~500 tags in the nearby blue heron nesting site. While the heron predation I documented accounts for only a small part of the overall mortality incurred by juvenile salmon, its occurrence near the end of the freshwater migration may impose a heavy toll on the fish that make it past the preceding freshwater gauntlet.

It is not possible to know the full impact that great blue herons have on smolt survival because unknown numbers of tags were excreted outside of heronries was not estimated. However, it is possible to gage the potential impact that a heron population could theoretically have on salmon if they acquired all their dietary needs from juvenile salmon alone during freshwater outmigration. Using the Cowichan system as an example, herons from the nearby heronry would have to consume as many as ~410,000 juvenile salmon during outmigration to meet all adult and chick energy demands through smolt consumption alone. To put this into perspective, this represents more than 100% of the hatchery smolts that entered the Cowichan Bay in any given year of our study (pers. comm. Kevin Pellett). The similarity in rates of predation between wild and hatchery juvenile salmon further means that herons could have a substantial impact on both wild and hatchery-reared salmon populations.

Avian predation on salmon smolts is being increasingly well documented with technological improvements. In the Columbia River, large-scale telemetry studies have investigated salmon smolt survival during outmigration, and subsequent tag recoveries at local bird colonies have identified avian predators as a major source of mortality for salmonid populations (Ruggerone 1986; Collis et al. 2001; Ryan et al. 2001; Collis et al. 2002; Glabek et al. 2003; Roby et al. 2003; Ryan et al. 2003; Antolos et al. 2005; Hostetter et al. 2012; Evans et al. 2012; Sebring et al. 2013; Evans et al. 2016). Steelhead smolts were the salmon species most heavily preyed on by Caspian terns, double-crested cormorants, and gulls in the Columbia River system, with coho and Chinook being removed at rates comparable to those documented in my study (Ryan et al. 2001, 2003; Antolos et al. 2005; Evans et al. 2012). PIT-tag detections at Caspian tern and double-crested cormorant colonies in the Columbia River estuary produced minimum predation estimates of 11.5% for steelhead, 4.6% for coho, and 2.6% for Chinook smolts that entered the estuary (Ryan et al. 2003), and approximately 3% of the salmonid tags released in the Columbia River from a previous study turned up in avian breeding colonies (Ryan et al. 2001). Caspian terns have a particularly large impact on salmon smolt survival in the Columbia River, consuming as many as 15% of estuary-rearing smolts from vulnerable populations (Roby et al. 2003). Caspian tern predation has also been recorded during in-river migration, though predation rates are considerably lower than those observed in the estuary (Antolos et al. 2005). Aside from avian piscivores, there are a host of other predators that forage opportunistically on cohorts of outmigrating salmon smolts.

Seals are known to prey heavily on salmon smolts during their estuary residence prior to continuing out to the open ocean. Scanning efforts at seal haul-outs in Cowichan Bay yielded 18 PIT-tags from Chinook smolts tagged in my study, though potentially poor tag retention at tidally inundated haul-outs and unknown seal defecation rates in other areas away from the haul-outs render this an inadequate method for quantifying seal predation rates. Other studies have found that Pacific harbour seals congregate in river mouths during smolt outmigration and consume significant numbers of juvenile salmon in the estuary (Greenstreet et al. 1993; Thomas et al. 2017), and the number of seals present during estuary residence was negatively correlated to Chinook production in most of the river systems assessed in one study conducted in the Pacific Northwest (Nelson et al. 2019). The large numbers of harbour seal populations in this area is estimated to adversely affect the survival of salmon smolts (Chasco et al. 2017). While seals consume smolts in estuaries, avian predators may be intercepting smolts earlier in the migration run.

Unlike other avian predators that prey on salmon smolts higher in the river system (e.g. mergansers, kingfishers) or lower in the estuarine system (e.g. double-crested cormorants, Caspian terns, common murres, various gull species) (Wood 1987; Feltham 1990, 1995b, 1995a; Wilson et al. 2003; Penaluna et al. 2016; Collis et al. 2002; Antolos et al. 2005; Phillips et al. 2017; Wells et al. 2017), great blue herons primarily consumed juvenile salmon in the lower river or early upon estuary residency prior to the young fish migrating away from the nearshore habitat into the deeper waters of the bay. And unlike these other birds that plunge or dive in pursuit of smolts in the deeper waters of the mid-river and upper estuary, great blue herons are restricted to wading and feeding in shallow waters along the lower river and estuary. There is thus considerable partitioning among the avian predators in terms of where and how they catch salmon smolts.

Efforts to put PIT-tags into salmon smolts in the Cowichan River were divided equally between the river migration and estuary residency phase of the smolt run. However, 90% of the tags recovered in the Cowichan Bay heron rookery were from river-tagged fish. Heron predation likely occurred in the lower river or upper estuary, based on heron observations during smolt outmigration. Daily rookery scans conducted throughout the smolt run in 2018 indicated that tags were still being deposited after smolts exited the river, suggesting that heron predation also occurred early in estuary residency when smolts inhabited the shallow nearshore environment. PIT-tagging efforts focused on smolts during their estuary residence in Cowichan Bay were conducted by purse seine in deeper waters near the center of the bay. These estuary-tagged smolts had likely moved away from the nearshore environment, potentially explaining the small number of bay-released tags subsequently detected in heron rookeries. A number of abiotic conditions associated with the lower river and nearshore estuary designate these areas ideal smolt foraging habitat for herons.

The lower river and upper estuary are shallower and slower moving than upstream and downstream environments, providing prime feeding habitat for Pacific great blue herons, whose foraging success is depth-limited (Power 1987; Ntiamoa-Baidu et al. 2008). Wading birds that prey on fish are more successful when foraging in shallow water (Hodgens et al. 2004; Gawlik and Crozier 2007) and herons exhibit higher capture rates when fishing in shallow habitats compared to deep pools in the freshwater environment (Power 1987; Harvey and Stewart 1991). Reduced water flow in tidally influenced portions of the lower river may also reduce smolt migration rates and increase exposure to predation (Anderson et al. 2005; Buchanan et al. 2013), while salinity shock upon entry into the bay can render smolts increasingly susceptible to heron predation. Annual variability in abiotic conditions may also play a role in the intensity of heron smolt consumption.

2.4.3 Factors influencing predation rates

Tags have the potential to influence the survival, swimming, and buoyancy of tagged fish. However, tags under 8-10% of the fish weight should have minimal to no effects on survival and swimming (Brown et al. 2006; Collins et al. 2013; Clark et al. 2016; Furey et al. 2016). This implies that the tags used in my study (0.1 g, <1% of smolt weight) did not influence downstream survival and migration. In terms of buoyancy, Atlantic salmon smolts tagged with 5.6 g PIT tags have been found to recover neutral buoyancy within 6 hours if they can gulp air at the surface and expand their swim bladders to counteract the weight of the tags (Fried et al. 1976). All hatchery smolts used in our study should therefore have recovered neutral buoyancy by the time they began downstream migration because they were held for a minimum of 14 days with access to air before being released. Similarly, wild smolts would have had days to weeks to recover after being tagged before encountering herons downstream. Thus, I believe that the PIT tags did not significantly influence susceptibility to being preyed upon—but recognize that it cannot be completely ruled out as contributing factor.

Another factor that may influence rates of predation by herons on salmon smolts is water depth and flow rate. In 2016, water flow rates were critically low in the Cowichan River and predation levels were the highest recorded. River flows were so low in 2016 that the primary migration corridor for outmigrating salmon smolts through the north arm of the Cowichan River dried up, potentially stranding a large number of juvenile salmon. Combining data from other years showed that river flow was negatively correlated with annual predation rates in the Cowichan River. River flow has also been identified in other river systems as the most important environmental factor influencing the downstream survival of outmigrating salmon smolts (Smith et al. 2003; Gauld et al. 2013; Zeug et al. 2014; Michel et al. 2015; Michel 2019; Henderson et al. 2019; Antolos et al. 2005; Hostetter et al. 2012). Flow rates correlate positively with migration speed and survival.

Herons likely have increased access to foraging habitat under low flow conditions (Master et al. 2005; Gawlik and Crozier 2007). Low flow means slower smolt migration rates (Cavallo et al. 2013; Boavida et al. 2017) and increased exposure to heron predation (Høgåsen 1998; Cavallo et al. 2013) due to reduced volumetric space to evade predation (Buchanan et al. 2013), higher smolt densities increasing heron predation success (Draulans 1987), and limited access to cover (Power 1987; Harvey and Stewart 1991; Reinhardt and Healey 1997; Sommer et al. 2001; Hakala and Hartman 2004; Penaluna et al. 2016). Shallow waters with low flow may also translate into higher foraging success for visual predators due to reduced turbidity and higher water clarity (Gregory and Levings 1998; Antolos et al. 2005; Hostetter et al. 2012; Ferrari et al. 2014). Salmon smolts may also experience greater salinity shock when entering the bay if the low flow results in less mixing of fresh and salt waters in the confluence zone.

Unlike the Cowichan River, water flow did not influence predation rates in the Capilano River. Flow may have a lesser impact on heron predation in this system because herons nesting in the Stanley Park rookery, where nearly all recovered Capilano-released tags were detected, do not congregate primarily at the mouth of the river, as is in the case for herons at the Cowichan Bay rookery. Rather, herons from this rookery forage for fish along the tide lines of the comparably larger estuary system of the Burrard Inlet and English Bay near Stanley Park, Spanish Banks, and along the West Vancouver waterfront (Rob Butler, pers. comm.). The spread of these heron foraging efforts suggest that Stanley Park herons are consuming smolts in the nearshore environment of the estuary, after the fish have exited the Capilano River. All tagged smolts released in the Big Qualicum River were released in one week in 2015, so no river flow data was analyzed for this system. The physical characteristics of salmon smolts released in this study may have also predisposed some individuals to heron predation.

I found that smaller smolts tagged and released in the river were more susceptible to heron predation than larger smolts. This was true for all hatchery smolts released in all years in the Capilano River save a low flow year in the Cowichan River, and was nearly significant for wild smolts in the Cowichan River. The observed trend in the low flow year on the Cowichan was likely due to heightened susceptibility to predation for all smolts, regardless of size, in years of low flow conditions, which is consistent with findings that size-selective mortality in juvenile salmonids weakens with reduced flows (Good et al. 2001). Lab studies indicate that smaller fish are disproportionately preyed upon by predators in the aquatic environment (Mesa et al. 1994). Field studies investigating avian predation on salmon smolts also support this theory (Hostetter et al. 2012; Tucker et al. 2016). Tucker et al. (2016) found that 85.5% of juvenile salmonids preyed on by rhinoceros auklets (*Cerorhinca monocerata*) in the coastal marine environment were undersized. Smaller juvenile salmonids were also preyed upon more heavily by belted kingfishers in a riverine environment (Penaluna et al. 2016), though this is may reflect a size refuge for larger conspecifics from the gape-limited predator (Salyer and Lagler 1949).

Other studies have suggested that piscivorous birds target larger smolt species because they are more visible than smaller ones (Britton and Moser 1982; Eriksson 1985; Magnhagen 1988;

Trexler et al. 1994) or intermediate-sized smolts within a population for capture efficiency (Hostetter et al. 2012; Osterback et al. 2014). Caspian terns, for example, have a disproportionately higher predation impact on larger species of salmon smolts (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005; Evans et al. 2012), while Caspian terns and double-crested cormorants selectively prey on intermediate-sized individuals within a the larger species population of smolts (Hostetter et al. 2012; Osterback et al. 2014).

It seems unlikely that herons selectively chose small smolts over larger individuals based on visual size-based cues given there was relatively little difference in the size of smolts released in each year of my study. A more likely explanation is that smaller smolts were more susceptible to predation due to their reduced ability to evade predators (Taylor and McPhail 1985; Mesa et al. 1994; Healey and Reinhardt 1995), slower migration speeds (Giorgi et al. 1997), and riskier behavior (Grant and Noakes 1987; Reinhardt and Healey 1997; Reinhardt 1999; Naman et al. 2019). Smaller smolts are also found in shallower habitats that are more effectively foraged by herons, and can be excluded from predator refuge habitat by larger smolts (Jenkins 1969; Reinhardt and Healey 1997; Reinhardt 1999; Vehanen et al. 1999; Heggenes 1990; Harvey and Stewart 1991; Bremset and Berg 1997; Bardonnet and Baglinière 2000). Relative tag-burden, as previously discussed, may also have contributed to smaller smolts being more susceptible to heron predation (Brown et al. 2006; Collins et al. 2013).

Herons may have selected shallower foraging habitats during chick emergence to target smaller fish that were appropriately sized for their brood (Moser 2008). This is consistent with the tendency for great blue herons to feed their young small prey items early in the hatchling phase, providing their chicks with increasingly larger items as they grow to match the gape-limitations of chicks and avoid choking hazards (Quinney 1982).

2.4.4 What smolts mean for herons

Daily scans conducted at the Cowichan Bay heron rookery throughout the smolt migration in 2018 indicated that predation occurred primarily in the month following tag releases (May 22-June 23), with an average of 1 new tag deposited a day under the nests. This window of time overlaps with the period of peak energy demand from recently hatched chicks (Bennett et al. 1995). Since great blue herons are known to feed their chicks relatively small prey items during this time

(Quinney 1982), and the smolts tagged in our study were considerably smaller than other prey fish commonly targeted by adult herons (Glahn et al. 1999; Hodgens et al. 2004), it is likely that adult herons targeted the smolts to feed their chicks during the critical stage of chick growth and development. Smolt predation by adult herons in my study systems may have provided a sizeable portion of the energy requirements of rearing chicks in the nearest rookeries.

Energetic analyses of herons nesting in the largest rookeries on the Cowichan, Capilano, and Big Qualicum Rivers suggest that hatchery salmon smolts could provide 5.4% (3.9%-8.1%) of the daily energy requirements of heron chicks in the month following hatchery releases. Due to a lack of information regarding the size of wild smolt populations in my study systems, I was unable to include the impact of wild smolt consumption in these energetics analyses. However, historic evidence suggests there were considerably more wild smolts of 2-3 million in my study rivers during the 1960s and 1970s, compared to the current hatchery releases of 400,000-600,000 (DFO 1962; Lister et al. 1971). Given that I observed similar predation rates on wild and hatchery-reared smolts from the Cowichan River, it is possible that wild salmon smolt consumption provides a substantially larger share of the energy demands of heron chicks in local rookeries than that documented for hatchery smolts. Nonetheless, the hatchery-reared Cowichan Chinook consumption in my study could have provided 4.3% (3.1%-6.4%) of the total energy demands of both adult and juvenile herons in the Cowichan Bay rookery, while hatchery-reared coho smolts likely accounted for 2.4% (1.7%-3.5%) of the requirements of adults and chicks in the Stanley Park rookery and 2.2% (1.6%-3.3%) for herons in the Deep Bay rookery.

2.4.5 Conclusion

My study is the first to quantify heron predation rates on salmon smolts during their seaward migration from natal rivers. I recovered 0.93% (SD = 0.79%) of the 108,842 PIT-tags released in the wild and hatchery-reared smolt populations of three major salmon-bearing rivers in British Columbia from 2008-2018, representing predation rates of approximately 1-3% annually. Daily rookery scans conducted during the smolt migration in 2018 indicated that predation occurred primarily in the month following releases of hatchery fish in the Cowichan River, overlapping with early chick-rearing in local heron populations. Smolt consumption comprised about 5-10% of the daily energy requirements of juvenile herons during this time, indicating that smolts may supplement heron diets at a time of peak energy demand and food limitation (Bennett et al. 1995).

Nearly all heron predation in the Cowichan River occurred on river-tagged smolts, rather than estuary-tagged, suggesting that herons extract smolts primarily in the nearshore environment prior to bay entry or during early residence in the upper estuary. Predation was highest during years of low river flow, which may be indicative of future trends in smolt predation as reduced freshets result in lower flows during outmigration (Najafi et al. 2017). Predation was also higher on smaller smolts than on larger conspecifics.

Since smaller smolts show poorer survival to adulthood (Parker 1971; West and Larkin 1987; Henderson and Cass 1991; Beamish et al. 2004), heron predation may benefit the overall health of salmon populations by reducing competition for limited resources in the early marine stage. Future research could compare the heron diet composition to the composition of nearby fish communities to determine if herons target salmon smolts during outmigration. Efforts to document off-colony tag deposition rates for Pacific great blue herons would also improve smolt predation estimates, because off-colony deposition rates are highly species-specific due to variable nest attendance and foraging behaviors (Osterback et al. 2013; Hostetter et al. 2015).

Chapter 3: Conclusion

The goal of my study was to identify freshwater and estuarine predators of juvenile salmon during their outmigration from natal streams and quantify the effects of predation on the survival of juvenile salmon to sea. I achieved this by detecting PIT-tags implanted in wild and hatchery-reared juvenile salmon of the Cowichan, Capilano, and Big Qualicum Rivers in the stomachs and scat of potential predators through the deployment of stationary arrays and a mobile PIT antenna. I was able to recover 1-3% of the PIT-tags released annually in juvenile salmon in B.C. under the nests at local Pacific great blue heron breeding rookeries. This is only the second study to document Pacific great blue heron predation on both wild and hatchery-reared salmon smolts in the natural environment (Myrvold and Kennedy 2018), and the first to quantify predation rates.

3.1 Summary of findings

Annual rookery PIT-tag recoveries were corrected to account for tags consumed by herons and either deposited off-site from the rookery or rendered undetectable for other reasons (e.g. deposited in nests or branches, broken tags, buried tags). Correction factors from a similar study conducted on the Columbia River, in which double-crested cormorants were voluntarily fed a known number of PIT-tagged salmon smolts and local rookeries were subsequently scanned for deposited tags (Hostetter et al. 2012), were applied using Monte Carlo simulations. These simulations produced annual predation estimates of 1-3% for all rivers included in my study. These predation rates are comparable to those published for other species of avian predators known to feed on salmon smolts during their freshwater outmigration (Ryan et al. 2001, 2003; Antolos et al. 2005; Evans et al. 2012). However, herons may be extracting juvenile salmon along a different segment of the outmigration than these previously identified avian smolt predators.

Pacific great blue herons from the Cowichan Bay rookery were observed foraging primarily along the mouth of the Cowichan River during smolt outmigration. Additionally, over 90% of the PIT-tags recovered in the Cowichan Bay heron rookery were from river-tagged fish, as opposed to estuary-tagged fish, despite similar tagging efforts being conducted in these two migration corridors. These findings suggest that herons primarily consume juvenile salmon in the lower river or early upon estuary residency prior to fish migrating away from the nearshore habitat into the deeper waters of the bay. This differs from other avian predators, which are known to prey on salmon smolts higher in the river system (e.g. mergansers, kingfishers) or lower in the estuarine system (e.g. double-crested cormorants, Caspian terns, common murres, various gull species) (Wood 1987; Feltham 1990, 1995b, 1995a; Wilson et al. 2003; Penaluna et al. 2016; Collis et al. 2002; Antolos et al. 2005; Phillips et al. 2017; Wells et al. 2017). Heron predation within this section of the smolt migration was influenced by river flow during outmigration.

We found that the highest levels of smolt predation in the Cowichan River occurred during a critically low flow year in 2016. The majority of all tags detected in the Cowichan Bay heron rookery from 2014-2018 were from the 2016 out-migrating class. River flow during outmigration is the abiotic factor most heavily influencing smolt survival (Smith et al. 2003; Gauld et al. 2013; Zeug et al. 2014; Michel et al. 2015; Michel 2019; Henderson et al. 2019). Low river flow is similarly suspected of causing steep increases in Caspian tern smolt predation in the Columbia River (Antolos et al. 2005; Hostetter et al. 2012). Smolt size was also found to impact susceptibility to heron predation in my study.

I found that smaller juvenile salmon were preyed on by herons at significantly higher rates than larger conspecifics. This is consistent with the conclusions of others that smaller fish are typically preyed on more heavily in aquatic systems (Mesa et al. 1994), and is further supported by other field studies investigating avian predation on salmon smolts (Hostetter et al. 2012; Tucker et al. 2016). This finding may account, in part, for the poor survival to adulthood in smaller salmon smolts (Hendersen & Cass 1991). Given that the size of salmon smolts preyed on in my study were generally smaller than other piscine prey items consumed by herons (Glahn et al. 1999; Hodgens et al. 2004), herons may be foraging in shallower habitats to target smaller fish during smolt outmigration and provide appropriately sized food for their gape-limited chicks (Quinney 1982; Moser 2008).

Daily scans conducted at the Cowichan Bay heron rookery throughout the 2018 smolt outmigration indicated that predation coincided with chick emergence and early chick rearing (Bennett et al. 1995). This represents the time of peak energy demand by heron chicks (Bennett et al. 1995). Sectioned rookery scans determined that tags in the two major rookeries in my study (Cowichan Bay and Stanley Park) were evenly distributed under the nests, suggesting that most herons partook in smolt predation. Using published energetic requirements of breeding herons and rearing chicks, energetic content of hatchery smolts, and annual rookery nest counts, I determined that 4-11% of the heron chick energy requirements in the Cowichan Bay, Stanley Park, and Deep Cove rookery could be provided by hatchery smolt predation during outmigration. These relatively small fish could be a particularly important food source for chicks during this period of high energy demand and gape-limitation.

3.2 Strengths and weaknesses

One of the strengths of my research lies in the technology used. One of the best qualities of PIT-tags is that they remain dormant until being charged by a magnetic array, allowing the tags to last for years in the wild before being detected. As a result, smolt tags were recovered from all years that tagging was conducted on my three study systems, dating back as far as 2008. This allowed me to compare predation rates among different years and identify herons as a consistent predator of juvenile salmon during seaward migrations. Furthermore, because the tags can be scanned multiple times, I was able to compute detection efficiency by comparing tag recoveries between subsequent scans. Although my mobile antenna produced high detection efficiencies (>95%) and allowed for rookeries to be scanned with minimal disturbances to the environment (simply walking around under the trees), one limitation was that rookeries had to be scanned on a very small scale. This took considerable time to conduct a single scan and allowed for high variability in the areas covered by different scanner operators. Furthermore, due to tag signal collisions, tag “hot spots” had to be scanned multiple times along different angled transects to maximize the detection efficiency for tags deposited in that section.

One other shortcoming of my research was my inability to obtain a Pacific great blue heron-specific off-colony tag deposition rate. As a result, I had to settle for using data collected from a rookery PIT-tag recovery study run on the Columbia River using double-crested cormorants. This was not ideal seeing as these off-colony tag deposition rates may be highly species-specific due to variable breeding behaviors among nesting bird species (Osterback et al. 2013; Hostetter et al. 2015).

Although Pacific great blue herons and double-crested cormorant exhibit similar nest attendance during the breeding season (Vennesland and Butler 2011; Dorr et al. 2014), the correction factor estimates I applied are an imperfect indicator of the proportion of consumed tags that were subsequently detectably deposited in a heron rookery. However, they seem reasonable in the absence of any other information. The cormorant rookery used in the Columbia River study was a colony inhabiting a man-made island named East Sand Island in the Columbia River estuary that was built from the deposition of refuse material created during dredging operations. As a result, there are no trees for the cormorants to nest in and nests were constructed directly on the bare substrate. This means that nearly all tags deposited in the cormorant rookery were detectable by ground-based scanning operations, as opposed to my study, where heron nests were situated up to 30 m in the trees. This is problematic since deposited tags in the heron rookery were likely caught up in the nests or branches on their way towards the ground. I had some evidence that this was the case since tags from previous release years would appear in my scans after a major wind event, suggesting that they were shaken loose from the trees. Additionally, all downed nests discovered in the rookeries were associated with at least one PIT-tag. Tags caught in the heron nests are likely a common occurrence, especially considering a sizable amount of the direct smolt consumption may be carried out by the chicks. This likely means that our correction factors underestimated the overall predation rates in my study systems.

One strength of my study is that the fork lengths of hatchery smolts were taken just a few days before the fish were released, and were likely highly representative of the sizes of smolts upon heron predation due to the rapid migration through the freshwater system. One disadvantage is that wild smolts took considerably longer to transit through the freshwater system, suggesting that fish sizes may have changed between the time of measurement and heron predation. Further, larger wild smolts transit through the system more rapidly, and there may have been less disparity in smolt sizes at the heron foraging grounds than suggested by the documented fork lengths. This may have resulted in the relatively weak relationship between wild smolt fork lengths and their susceptibility to heron predation compared to that of hatchery smolts in my study.

3.3 Future research

Future research investigating Pacific great blue heron predation on outmigrating juvenile salmon through PIT-tag deployment paired with scanning at local rookeries would benefit from generating heron-specific off-colony tag deposition rates to serve as accurate correction factors for rookery-recovered salmon tags. This has been done with other avian smolt predators by allowing birds to voluntarily feed on a known number of tagged juvenile salmon, and scanning local colonies to determine the proportion that are subsequently recovered. This would best be done by setting up juvenile fish pens that are accessible to herons near their foraging grounds. These fish pens could then be stocked with PIT-tagged juvenile salmon, which are captured and scanned each evening to document the number of smolts taken in a given day. Motion-triggered trail cameras should be set up around the fish pen to document predation events and ensure that only herons are feeding on the entrapped juvenile salmon.

Furthermore, stationary PIT-tag detectors could be set up in the trees at the bayside entrance of heron rookeries to detect smolts tags in the digestive tract of predatory herons. Motion-triggered trail cameras could also be installed to determine whether herons are leaving the rookery or coming back. In addition, the direction in which the herons enter the rookery from could be recorded. Similarly, it would be interesting to use motion-triggered trail cameras at the entrance of rookeries and bird-banding to document rookery attendance, the lengths and timing of foraging bouts, and flock size throughout the breeding season, and compare these attributes before, during, and after the juvenile salmon outmigration.

In my study, I was unable to disentangle if herons were specifically targeting juvenile salmon during their foraging bouts or just capturing them opportunistically. It would be interesting to assess the diet of foraging herons during smolt outmigration and compare this to beach seine captures conducted around the same time in the same location to determine if salmon are overrepresented in heron captures compared to their proportional representation in the beach seine catches. Additionally, these beach seining efforts could be used to compare the relative presence of wild and hatchery-reared smolts in the nearshore environment during outmigration. This would allow researchers to estimate the total number of wild smolts present in the system, based on known numbers of hatchery smolts present at this stage of the migration determined from the size of the release group and freshwater survival from telemetry studies. This information regarding the size of the wild population could then be used to estimate a total heron consumption rate for wild juvenile salmon, based on tag recoveries, which may be used in energetic analyses to assess the proportion of the breeding heron diet that is comprised of wild smolts.

In 2017, I assisted the British Columbia Conservation Foundation (BCCF) in identifying avian and mammalian juvenile salmon predators using stationary antennas and motion-triggered trail cameras to detect salmon tags in the digestive tract of predators during freshwater residency and outmigration. We conferred with local fur trappers and First Nations biologists to identify mammal hotspots and set up arrays at the mouths of river otter latrines, mink dens, along raccoon trails, and near merganser haul-outs. This resulted in identifying over 200 instances where potential predators were in the detection field of a PIT-tag antenna. However, this did not produce any detections. These stationary antenna efforts were deployed during the 2017 smolt outmigration, which was a year of considerably high river flows. It may be that there was not a high level of predation from freshwater predators in this year, resulting in the relatively high observed freshwater survival from in-stream arrays. I would recommend that future research revisit this project design in a year of suspected high predation, as it could provide a good indication of other smolt predators active in the freshwater system during seaward migrations.

3.4 Conclusions

My research has identified a previously unknown predator of juvenile salmon, accounting for a portion of the high mortality associated with seaward migrations. Although the thought of predation often carries negative connotations, I found that this predation took place primarily on smaller juvenile salmon. Research has found that these smolts often exhibit poorer survival to adulthood than larger conspecifics (Parker 1971; West and Larkin 1987; Henderson and Cass 1991; Beamish et al. 2004). Taking this into consideration, heron predation may benefit salmon populations by weaning out smolts that were unlikely to survive to adulthood and reducing competition for limited food sources in the early marine stage of the salmon life history. I was also able to elucidate the impact of river flow during outmigration on annual heron predation rates, indicating that the highest levels of predation occur in years of critically low flow. Herons may play a role in the poor survival of salmon smolts in low flow conditions that has been documented in other research (Smith et al. 2003; Gauld et al. 2013; Zeug et al. 2014; Michel et al. 2015; Michel 2019; Henderson et al. 2019). This research may inform efforts to mitigate poor smolt survival to sea through coordinated flow releases by dam operators to ensure adequate river conditions for seaward migrations.

These findings shed light on the wide range of predators that juvenile salmon encounter throughout their migration from natal streams, and the factors that influence their ability to survive to the sea. On the other side of this interaction, my research also found that juvenile salmon consumption is likely an important food source for herons and their chicks during a time of peak energy demand. In our yearning to understand the plight of the salmon, it is important to appreciate the main role of these iconic species, separate from all economic benefits associated with healthy populations, is to serve as a source of energy and nutrients bridging land to sea, benefitting a host of important species along the way.

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Appendices

Appendix A Summary data of PIT-tagged fish and rookery-recovered tags

Table 1. River released hatchery-reared Chinook salmon smolts PIT-tagged in the Cowichan River from 2014-2018 and the number and percentage of tags subsequently recovered in the Cowichan Bay heron rookery.

Year	River released tags	Recovered tags	Percent recovered
2014	1887	33	1.75%
2015	5037	32	0.64%
2016	5093	157	3.08%
2017	5304	36	0.69%
2018	4676	14	0.30%

Table 2. River released wild Chinook salmon smolts PIT-tagged in the Cowichan River from 2014-2018 and the number and percentage of tags subsequently recovered in the Cowichan Bay heron rookery. No wild smolts were tagged in 2017.

Year	River released tags	Recovered tags	Percent recovered
2014	2128	18	0.85%
2015	1954	13	0.67%
2016	5708	83	1.45%
2018	563	5	0.89%

Table 3. River released hatchery-reared coho salmon smolts PIT-tagged in the Capilano River from 2008-2018 and the number and percentage of tags recovered in the Stanley Park heron rookery.

Year	River released tags	Recovered tags	Percent recovered
2008	6495	125	1.93%
2009	12603	235	1.87%
2010	11750	169	1.44%
2011	2752	6	0.22%
2012	728	3	0.41%
2013	2539	10	0.39%
2014	1619	7	0.43%
2015	2299	18	0.78%
2016	2781	11	0.40%
2017	1216	11	0.91%
2018	1710	10	0.59%

Table 4. River released hatchery-reared coho PIT-tagged in the Big Qualicum River in 2015 and number and percentage of tags recovered in the Deep Cove heron rookery.

Year	River released tags	Recovered tags	Percent recovered
2015	40,000	136	0.34%

Appendix B Fork length and susceptibility to heron predation

B.1 Sub-Appendix - Annual boxplots

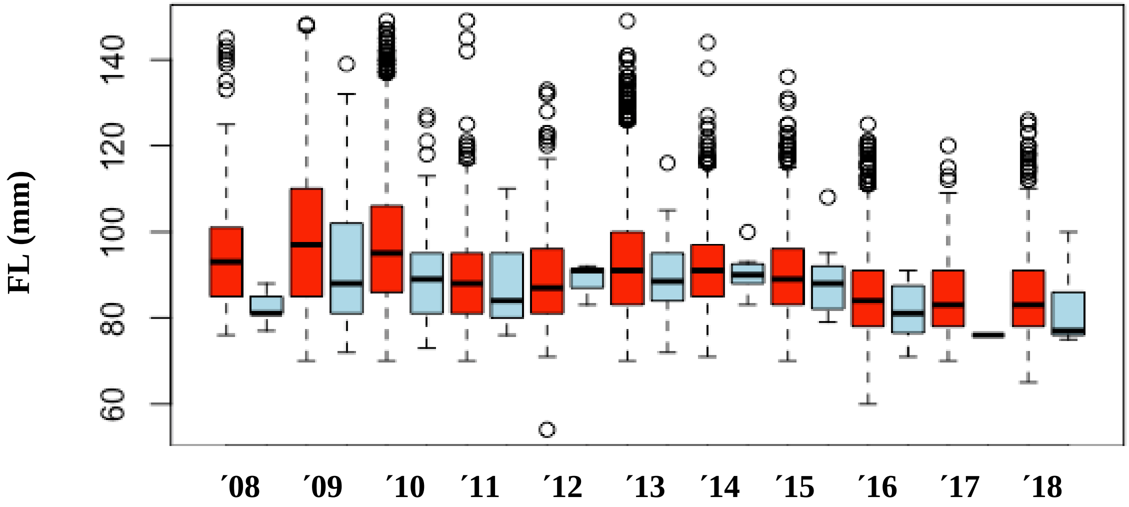

Figure 5. Boxplot comparing fork lengths (FL) of river released (red) and rookery detected (blue) hatchery-reared coho salmon smolts PIT-tagged in the Capilano River from 2008-2018.

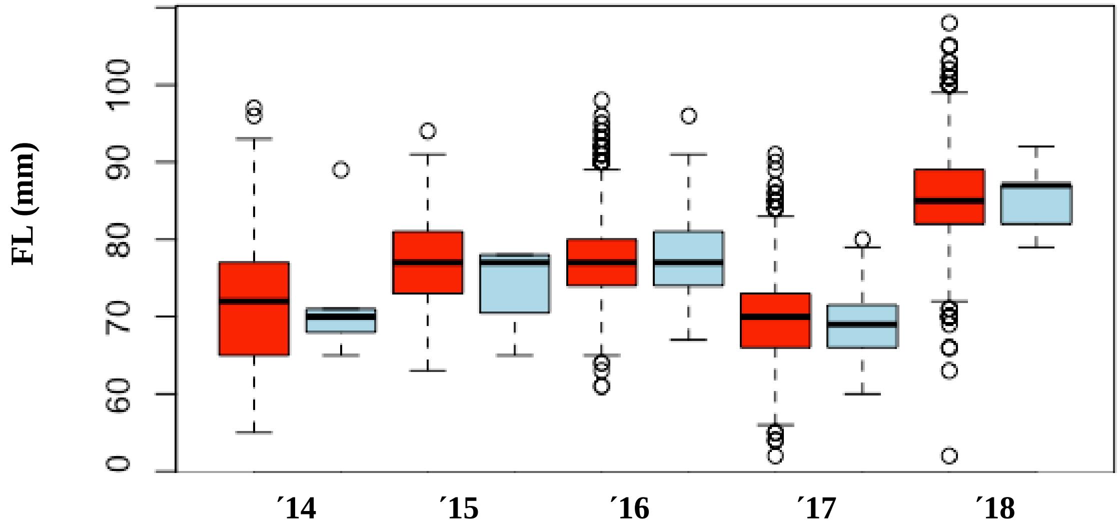

Figure 6. Boxplot comparing annual fork lengths (FL) of river released (red) and rookery detected (blue) hatchery-reared Chinook salmon smolts PIT-tagged in the Cowichan River from 2014-2018.

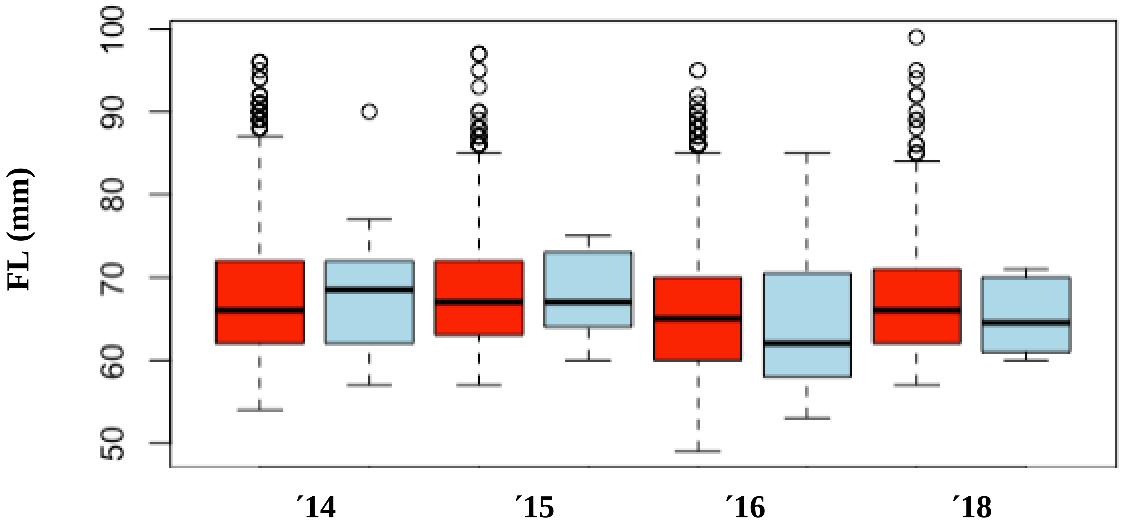

Figure 7. Boxplot comparing annual fork lengths (FL) of river released (red) and rookery detected (blue) wild Chinook salmon smolts PIT-tagged in the Cowichan River from 2014-2018, excluding 2017 when no wild smolt tagging was conducted.

B.2 Sub-Appendix – Trend lines

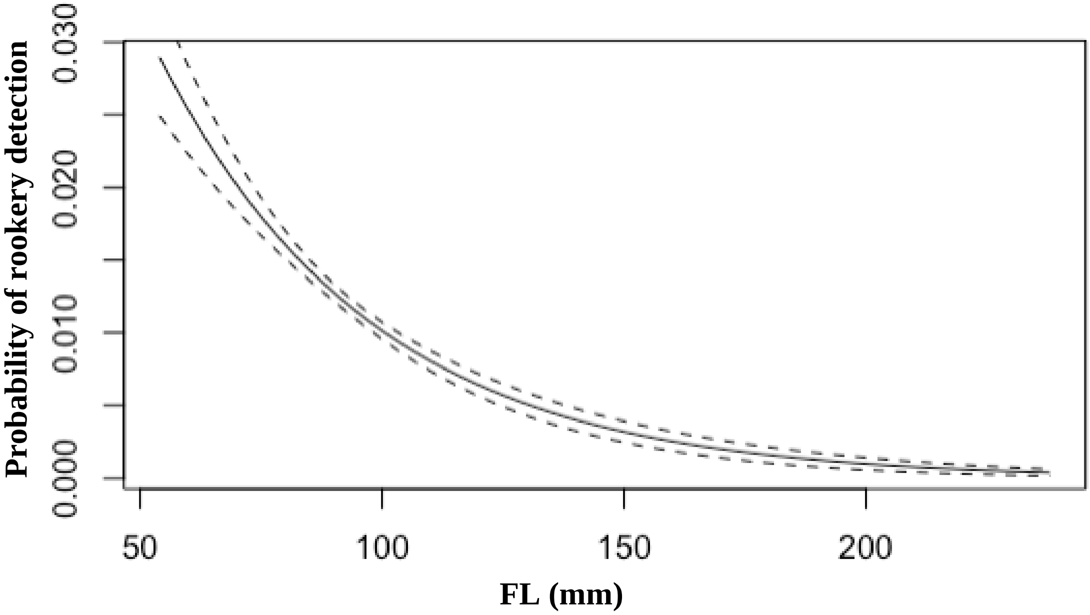

Figure 8. Trend line showing the relationship between smolt fork length (FL) and probability of being detected in the heron rookery for hatchery-reared coho smolts PIT-tagged and released in the Capilano River from 2008-2018. Dashed lines represent the 90% Confidence Interval.

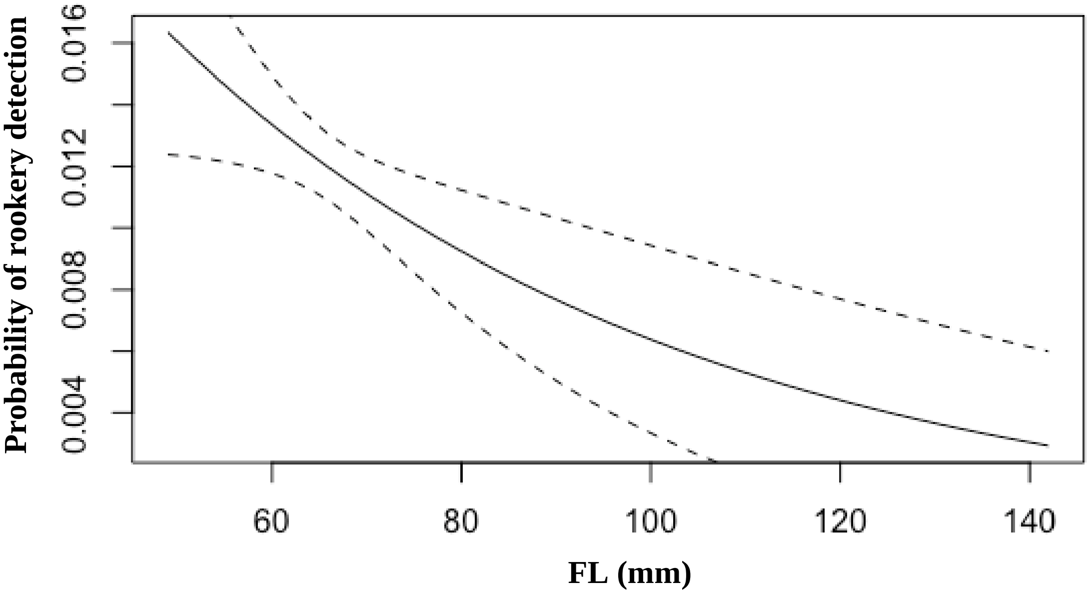

Figure 9. Trend line showing the relationship between smolt fork length (FL) and probability of being detected in the heron rookery for hatchery-reared Chinook salmon PIT-tagged and released in the Cowichan River from 2014-2018. Dashed lines represent the 90% Confidence Interval.

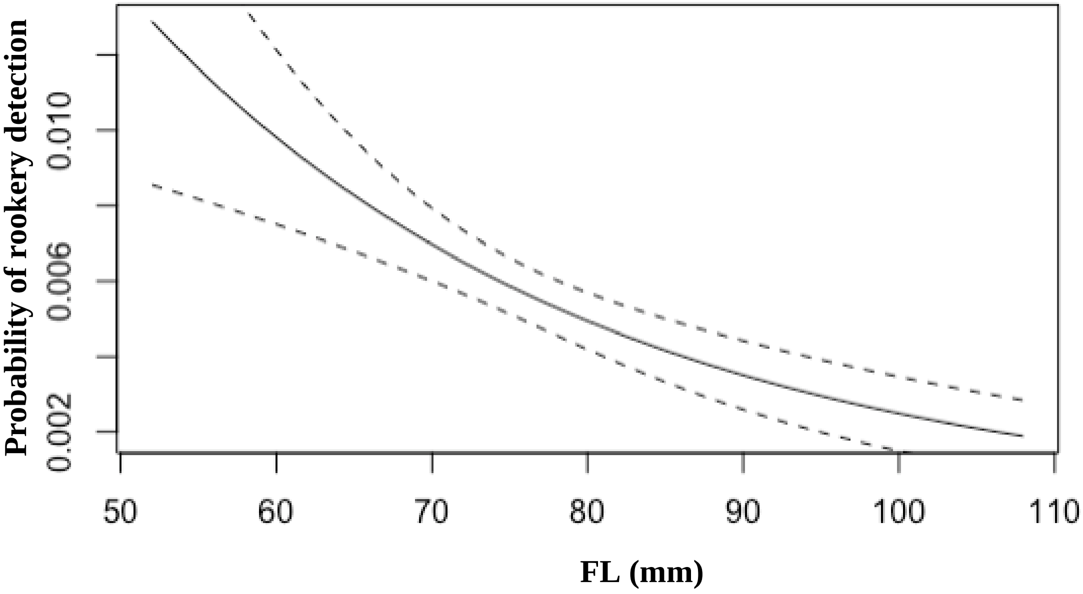

Figure 10. Trend line showing the relationship between smolt fork length (FL) and probability of being detected in the heron rookery for wild Chinook salmon PIT-tagged and released in the Cowichan River from 2014-2018. Dashed lines represent the 90% Confidence Interval.