Nearshore habitat use, estuarine residency, and conservation priorities for Pacific Salmon in the Fraser River, British Columbia

by

Lia Chalifour
B.Sc., University of Victoria, 2011

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We acknowledge with respect the lək̓ʷəŋən peoples on whose traditional territory the University stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

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## Abstract

Cumulative effects from multiple anthropogenic stressors over the past three centuries have severely impacted estuarine and coastal habitats, with cascading effects on the species that rely upon them. Pacific salmon (*Oncorhynchus sp.*) are migratory species that use estuaries as juveniles and as adults and deliver critical nutrients to coastal ecosystems as they move between fresh and marine waters. Many once abundant salmon populations have been extirpated or are in severe decline relative to historic levels, yet the strength of the relationship between habitat loss and population productivity has been challenged. In this dissertation, I applied field studies, otolith analyses, and conservation decision science tools to investigate the relative importance of estuarine habitat to salmon populations, with the aim of advancing effective management solutions for these species and their habitats.

First, I conducted a two-year field survey of fish communities in the Fraser River estuary, British Columbia, Canada comparing the species richness and relative catch amongst three distinct habitats. I found that this impacted estuary still supported a rich community of migratory marine and anadromous fishes, as well as resident estuarine fish species. Each habitat supported some unique fish assemblages, with eelgrass supporting the highest catch and diversity of fishes overall but brackish marsh supporting the highest and most consistent catch of salmonids. Next, I used otolith analyses to quantify the residency and growth of juvenile Chinook salmon in the estuary. I found that for one of the only two remaining Chinook salmon stocks abundant enough to still support limited harvest in the Fraser River, the estuary provides vital rearing habitat, with juveniles residing in the estuary for an average of 6 weeks, during which time they had mean daily growth rates of 0.57 mm fork length, approximating growth in healthier estuarine systems. The use of these habitats by juvenile Chinook salmon had not been quantified previously, so

these findings directly inform management of this population, which was recently designated as Threatened by the Committee on the Status of Endangered Wildlife in Canada. Finally, I applied Priority Threat Management, a conservation decision science framework, to predict the future status of Pacific salmon in the lower Fraser River and identify the most cost-effective conservation solutions out of a suite of alternative management strategies. On our current trajectory none of these populations were predicted to be assessed as 'green' or healthy status at the end of 25 years. In contrast, implementation of broad scale habitat restoration, protection, and watershed management could considerably improve the viability of the lower Fraser to support these salmon, such that many (14/19) of these populations would have a >50% likelihood of being assessed as healthy.

Together, this research provides novel evidence of active and selective use of estuarine habitats by juvenile salmon, reliance on estuarine habitat for early marine growth by juvenile Chinook salmon, and a direct link between habitat health and population status for lower Fraser River salmon populations.

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## Acknowledgments

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## Dedication

*To my grandpa, George Chalifour, who grew up on a farm in Debden, Saskatchewan through the Great Depression, recorded the coldest day in Canadian history in Snagg, Yukon, is now powering through the COVID-19 pandemic, and understands the values of social justice and climate action. I'm sorry that my doing this Ph.D. didn't amount to getting you a good deal on salmon; thank you for being proud of me anyway.*

# Chapter 1 - Introduction

Habitat loss is a primary driver of biodiversity decline (WWF, 2020). Despite ambitious international conservation targets to halt biodiversity loss under the United Nations Convention on Biological Diversity (Secretariat of the Convention on Biological Diversity, 2010), biodiversity continues to decline globally as human expansion drives the loss of important habitat (Li *et al.*, 2022). While projecting large scale habitat loss into the future paints a clear picture of the potential impacts to species, incremental habitat loss can be difficult to curtail due to ambiguity of the impacts from each minor loss (Murray *et al.*, 2018). However, the combined changes to the environment from anthropogenic impacts (including land use change, pollution, natural resource exploitation, and climate change) and natural processes that accumulate over space and time - together known as ‘cumulative effects’- can have significant effects on species (Blakley, 2021). Stronger evidence of the impacts of habitat loss on species and improvements to regulatory processes to prevent these losses are warranted (Warkentin *et al.*, 2019; zu Ermgassen *et al.*, 2019; Andrade and Turra, 2021). At the same time, there are clear thresholds after which delaying action to conduct further research significantly reduces the ability to achieve species recovery (Martin, Nally, *et al.*, 2012; Camaclang *et al.*, 2022). Conservation decision science can be applied in situations where data is scarce and systems are complex to identify optimal management interventions to prevent biodiversity decline (Hemming *et al.*, 2022). Coastal ecosystems are well suited for the application of these tools, given that they often support important biodiversity and ecosystem services, host dense human settlements, and are subject to complex governance frameworks (Barbier *et al.*, 2011; Neumann *et al.*, 2015; Kehoe *et al.*, 2020).

Estuaries and coastal areas support population densities nearly three times higher than the global average (Small and Nicholls, 2003) and have been sites of intensifying habitat loss and degradation over the last 300$^{+}$ years, with severe consequences to species diversity, productivity, and ecosystem services (Lotze *et al.*, 2006). Estuaries are naturally dynamic zones at the interface of land and sea, with fluctuating water levels from both freshwater inputs and marine tidal influences (Chapman and Brinkhurst, 1981). While these low lying and trade-accessible habitats provide numerous ecosystem services (Barbier *et al.*, 2011), including fertile soils and flat lands for agriculture and human settlement, their dynamic nature is counteracted with alterations that have negative environmental impacts, such as shoreline armoring, dredging, infilling, and dikes to maintain these settlements (Munsch *et al.*, 2017; Conger and Chang, 2019). Population growth and further densification are increasing the strain on remaining habitat as infrastructure demands and pollution inputs rise (Dafforn *et al.*, 2012; Mahoney and Bishop, 2017). As cumulative impacts begin to be felt, flood control structures are combining with sea level rise to produce "coastal squeeze", a shrinking available footprint for remaining habitat to survive rising water levels (Torio and Chmura, 2013). Cumulative impacts to estuarine habitat have been demonstrated to have population level effects on migratory Pacific salmon (*Oncorhynchus spp.*) (Hodgson, Wilson and Moore, 2020). To prevent ongoing incremental losses of fish habitat, stronger evidence linking the importance of habitat to fish survival and productivity is needed (Warkentin *et al.*, 2019).

Estuaries are nutrient-rich environments that provide important habitat for fishes (Barbier *et al.*, 2011), however, a detailed understanding of how fish use nearshore habitats and to what extent the loss and degradation of habitat impacts the productivity of these species has been lacking (Whitfield, 2017). This is exemplified by anadromous species such as Pacific salmon, which pass through estuaries and nearshore coastal habitats both as juveniles emigrating to the open ocean and as returning adults. A seminal review on estuarine habitat use by juvenile salmon (Weitkamp *et al.*, 2014) highlighted that significant knowledge gaps remain, including how degradation of estuarine habitat impacts salmon populations. Two key lines of evidence to demonstrate estuarine habitat use and importance to fish, including Pacific salmon, are active feeding and growth within that habitat, and evidence that changes to that habitat correspond to changes in population productivity (Beck *et al.*, 2001). Juvenile salmon spend variable amounts of time in estuarine habitats, with some passing through in as little as a few days and others residing in the estuary for weeks to months (Weitkamp *et al.*, 2014). Regardless of species or life history strategy, however, juvenile salmon appear to actively feed in estuaries (Weitkamp *et al.*, 2014; Arbeider *et al.*, 2019). Recent research has demonstrated a positive relationship between estuarine habitat connectivity and productivity and juvenile salmon foraging success and growth, emphasizing the importance of estuarine habitat quality for salmon (Davis *et al.*, 2018). Estuaries with severe habitat loss may intensify density-dependent foraging competition for juvenile salmon, and have been linked to declines in foraging success (David *et al.*, 2016). For Pacific salmon, early marine growth has been identified as a critical period for survival through the first ocean year (Beamish and Mahnken, 2001; Quinn, 2018). Several studies have now demonstrated that improvement to growth during the first months of ocean emigration corresponds to improved survival at the population level (Pearsall *et al.*, 2021). Therefore, measurements of selective habitat use and rapid growth within estuarine habitats during this period may be used as evidence to support the importance of nearshore habitat to Pacific salmon.

While understanding threats to species is important, identifying the optimal management actions in which to invest limited funds for species recovery is difficult and the solutions are not intuitive, particularly in cases involving multiple species and competing objectives (McCarthy, Thompson and Garnett, 2008). The challenges facing Pacific salmon are precisely the complex scenarios for which the application of conservation decision science frameworks, such as Priority Threat Management (PTM), are appropriate to elucidate the primary objective and most cost-effective management strategies to optimize species recovery for a given region (Carwardine *et al.*, 2019; Hemming *et al.*, 2022). Priority Threat Management facilitates rapid and effective conservation action by prioritizing alternative strategies based on their benefits to the target species, their feasibility of technical success as well as social uptake, and their projected real-world costs (Carwardine *et al.*, 2019). This process includes decision makers, stakeholders, and titleholders throughout the process and provides a conservation prospectus for a region based on the best available data, which maximizes the number of species or populations that can be conserved for a given budget, facilitating uptake and implementation of the results (Carwardine *et al.*, 2019). This framework has been widely adopted in Australia and successfully applied across large spatial scales to manage species at risk (Carwardine *et al.*, 2012; Chadés *et al.*, 2015; Ponce Reyes *et al.*, 2016) and invasive species (Firn, Maggini, *et al.*, 2015; Firn, Martin, *et al.*, 2015; Rees *et al.*, 2020). More recently, PTM has been applied in Antarctica, Indonesia, and Canada (Carwardine *et al.*, 2019), including endangered species management in Saskatchewan's grasslands (Martin *et al.*, 2018) and the St. John River watershed (Camaclang *et al.*, 2021). In 2016, the first Priority Threat Management project for the Fraser River estuary was initiated (Kehoe *et al.*, 2020), which determined that 102 species are at risk of extinction, but timely management investments can prevent their loss. This was followed by a salmon-focused application of PTM on the Central Coast of British Columbia, which found that 25% of the salmon populations assessed were unlikely to be thriving in 20 years and highlighted preventing habitat loss as the most cost-effective solution, followed by habitat restoration and protection (Walsh *et al.*, 2020). The intensity of cumulative impacts, complexity of governance structures, and natural variety of salmon lifecycles make salmon conservation planning in the lower Fraser River and estuary particularly challenging, and thus a prime example for the application of PTM.

## 1.1 Study System

The 230,400 km$^2$ 'Mighty Fraser' River basin has an undammed mainstem and drains approximately ¼ of British Columbia, passing through silty mountain trenches, dryland forests and rainforests, agricultural zones, mining and logging operations, and large urban centres before draining into the Salish Sea (Fig. 1.1; Birtwell *et al.*, 1988). The lower Fraser River and estuary were long inhabited by Indigenous peoples prior to European contact in the late 1700s, and today more than 70 Nations and Tribes continue to live and rely on its natural resources, including Pacific salmon (https://native-land.ca/maps/territories/puget-sound-salish/). The Fraser has a rare, expansive delta forming the largest estuary in British Columbia, which was prioritized for settlement by Europeans and continues to act as a hub for urban, agricultural, and industrial development and transport for Canada (Birtwell *et al.*, 1988; Groulx *et al.*, 2004), with a current population of more than 3 million people in the lower mainland that is projected to increase to >4 million by 2040 (Province of British Columbia, 2019). This intense human footprint has profoundly altered the landscape, such that approximately 85% of the floodplain and 64% of the naturally accessible stream habitat in the lower Fraser River is now lost to Pacific salmon, with much of the remaining habitat severely degraded by land use change (Finn *et al.*, 2021). The fastest growing suburb in the lower Fraser, the City of Surrey, experienced a period of exceptionally rapid growth between 1991 and 2011 with a 91% increase in population and corresponding 82% increase in population density (Statistics Canada, 1998, 2012). This growth was coupled with extensive development and land use change, which continues to this day (City of Surrey, 2022). These cumulative effects are tied to decreases in fish community diversity across the Fraser basin, with low elevation habitats in the lower Fraser region particularly affected (Iacarella, 2022).

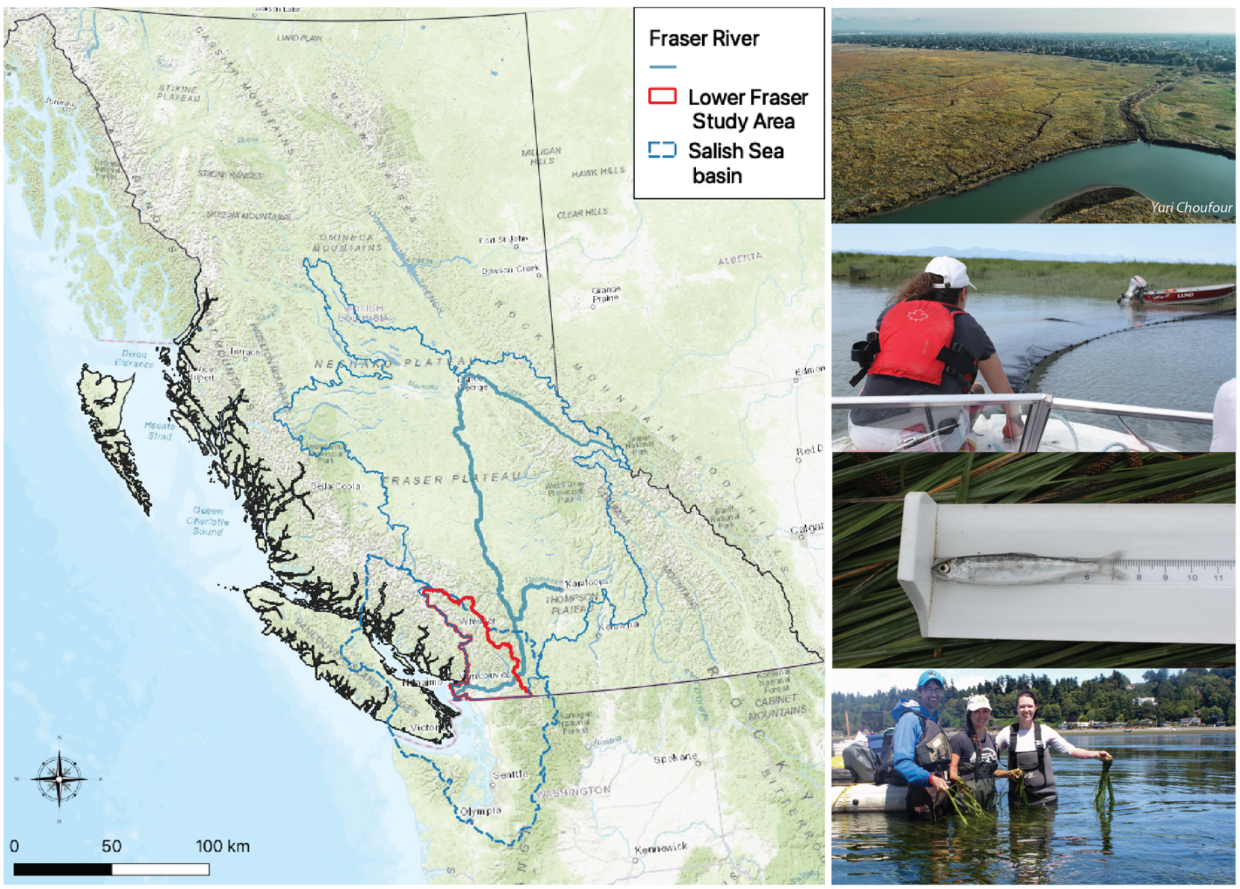


**Figure 1.1** Overview of study area showing a map of British Columbia with the Fraser River (thick blue line) and basin, the Salish Sea drainage basin (dashed blue line), and the lower Fraser study region (red line) along with photos of the estuary. Photos from top right: Fraser River estuary by Yuri Choufour; Lia beach seining in Fraser marsh site; juvenile Chinook salmon retained for analysis; Geoffrey Osgood, Lia, and Jessie Lund in Fraser eelgrass site.

Over the last three decades climate impacts have begun to be recorded in the Fraser basin, with changes in precipitation and temperatures leading to lower and earlier spring freshets, longer and more intense summer droughts, increasing river temperatures, and flash flood events (Groulx *et al.*, 2004; Chezik, Anderson and Moore, 2017). Between 1999-2015, climate change facilitated a massive outbreak of mountain pine beetle (*Dendroctonus ponderosae*) that impacted approximately half of BCs harvestable lodgepole pine (*Pinus contorta*), in turn contributing to increased wildfires and decreased carbon storage due to tree death and subsequent extensive salvage logging measures (Meyer *et al.*, 2018). In 2021, British Columbia faced two states of emergency related to severe weather events within the Fraser River basin, including wildfires in the summer followed by flooding in the fall (Ministry of Public Safety and Solicitor General, 2021a, 2021b). These extreme climate-water events impact the entire river ecosystem, including the anadromous Pacific salmon that rely on the Fraser for multiple stages of their lifecycle: eggs, alevin, fry, parr, smolt, and spawning adult stages.

The Fraser is home to all five species of eastern Pacific salmon: sockeye (*Oncorhynchus nerka*), pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), and Chinook (*O. tshawytscha*) salmon in addition to the anadromous salmonids: steelhead trout (*O. mykiss*), coastal cutthroat trout (*O. clarkii clarkii*), brown trout (*Salvelinus confluentus*), and Dolly Varden (*Salvelinus malma lordi*). Salmon exhibit considerable diversity in life history characteristics (i.e., Size and age at maturity, optimal spawning habitat, optimal rearing habitat, time spent in freshwater, time spent in marine waters, migration patterns, etc.) both within and across species (Quinn, 2018), making generalizations about threats or conservation solutions difficult. Weitkamp et al.'s (2014) review of salmon habitat use in estuaries focused on two river systems that are heavily dammed: the Columbia River estuary in the Pacific Ocean and Penobscot River estuary in the Atlantic

Ocean. The salmon populations in these highly altered systems are of majority hatchery origin, which generally rely less on estuarine habitat than their wild counterparts (Weitkamp *et al.*, 2014). From 2014-2018 an international effort to study observed declines in marine survival of Chinook salmon, coho salmon and anadromous steelhead trout in the Salish Sea, dubbed the Salish Sea Marine Survival Project, included targeted research on nearshore habitat use by juvenile salmonids (Pearsall *et al.*, 2021). At the beginning of my graduate program in 2016, many of these studies were again focused on juveniles of hatchery origin, which are easier to tag and track, and none included the Fraser River estuary - Canada's most productive salmon river and the largest single freshwater source to the Salish Sea. Further to the lack of empirical studies on habitat use by wild salmon, there continued to be debates among researchers and conservation practitioners about the primary threats to salmon recovery. Prior to this study, the last in-depth research on salmon habitat use in the Fraser River estuary was conducted by the Westwater Research Institute in the late 1970s and early 1980s. Specific knowledge gaps that were identified for the Fraser River estuary in these reports include validation of population-specific habitat use and residency timing within the estuary, and prediction of the effects of estuarine habitat loss and degradation on salmon productivity (Levy and Northcote, 1979; Levy, Northcote and Birch, 1979). In the decades that have passed since this research was conducted, additional questions include: what is the status of remaining salmon habitat, and should habitat restoration be a management priority for salmon recovery in the Fraser? While answering these questions for all 54 genetically and geographically distinct conservation units (CUs) of salmon in the Fraser River calls for a long-term research program, my dissertation addresses these questions for multiple populations in the lower Fraser River.

## 1.2 Dissertation Focus

The lack of detailed evidence for specific habitat use by fishes, including migratory Pacific salmon, in combination with lenient environmental assessment processes has allowed for ongoing deterioration of these habitats in favour of coastal development (Wheeler, Angermeier and Rosenberger, 2005; Malick, Rutherford and Cox, 2017; Warkentin *et al.*, 2019). Today, as salmon face cumulative threats including fishing, predation, disease, and climate change, the historic and ongoing loss and degradation of habitat is a clear focal point for management intervention (Munsch *et al.*, 2022). The Fraser River estuary exemplifies these issues, as many of the salmon populations passing through this system are experiencing record low returns (DFO, 2020a) and despite active management of the estuary, their habitat continues to be threatened by industrial and urban expansion. These concerns inspired this dissertation, which assesses the differential use of estuarine habitats by multiple fish species including juvenile salmon, as well as the predicted effects of alternative management actions on population productivity for Pacific salmon in the lower Fraser River and estuary. In doing so, this research aims to inform salmon conservation efforts by elucidating the importance of estuarine habitat for salmon population resilience, particularly for juvenile salmon in the Fraser River estuary (Figure 1.2).

| Problem | Theory | Chapter | Conservation Application |
|---|---|---|---|
| Pacific salmon populations are declining across much of British Columbia, yet salmon recovery is hindered by an inability for managers to prevent ongoing habitat loss. Therefore, better evidence is needed to support the link between salmon and their habitats to facilitate improved habitat management for salmon | Estuarine habitat connectivity is important for a functioning seascape because each habitat is used differentially by fishes | 2 | Project partners for Chapters 2 and 3 - Raincoast Conservation Foundation - implemented three breaches to the Steveston Jetty to improve connectivity to Sturgeon Banks for juvenile salmon passage in the Fraser River estuary |
| | Estuarine habitat provides a nursery role for juvenile salmon, facilitating early growth and a transition between freshwater and marine environments | 2,3 | Research supported submissions under the Canadian Environmental Assessment Act regarding the potential impacts of the Roberts Bank Terminal 2 port expansion on the Fraser estuary |
| | Habitat protection and restoration will improve Pacific salmon population trajectories | 3,4 | PTM results presenting a combined habitat strategy as a cost-effective solution for salmon conservation in the lower Fraser River will be shared with study participants and management agencies as well as the public to provide a detailed prospectus for conservation action to support salmon recovery |
| | Habitat protection, restoration, and holistic management can improve salmon resilience to cumulative impacts | 4 | |

**Figure 1.2** Outline of the problem, key theories, and conservation applications related to each chapter of this dissertation.

The first two chapters of this dissertation focus on juvenile habitat use in the Fraser River estuary. In Chapter 2, I assess nearshore fish community assemblages and their habitat use in the Fraser River estuary, including juvenile Chinook and chum salmon (the salmon species with the highest catch throughout the emigration season), other migratory species such as surf smelt (*Hypomesus pretiosus*), and resident species such as shiner surfperch (*Cymatogaster aggregata*). This systematic habitat comparison study elucidates the temporal and biogenic influences that shape these communities, including the level of connectivity between fish assemblages in three distinct habitats and the patterns of habitat use by species as determined by the relative catch across habitats, seasons, and two years of sampling. Eelgrass supported the highest catch, particularly during summer months, and the highest species richness of all habitats. However, sand flat and marsh each supported unique species assemblages, with juvenile salmon most consistently found in the brackish marsh. This is notable, as recent studies in smaller estuaries had emphasized the importance of eelgrass for juvenile salmon (Semmens, 2008; Kennedy, Juanes and El-sabaawi, 2018; Rubin, Hayes and Grossman, 2018; Sharpe *et al.*, 2019), which I found to be less used by salmon in the Fraser. This assessment led me to investigate in Chapter 3 the specific use of estuarine habitat by subyearling migrant ("ocean-type") juvenile Chinook salmon from the Harrison River, which appeared to be the most consistently abundant Chinook salmon population in the estuary. Building on the efforts by the Westwater Research Institute (Levy, Northcote and Birch, 1979; Levy and Northcote, 1982), I validate the estuarine entry timing, long-term residency, and early marine growth of juvenile Harrison Chinook salmon using otolith analysis. This detailed assessment provides evidence of sustained habitat use by this population and suggests reliance on the brackish marsh specific to this life-history strategy, with implications at the population-level.

Given the cumulative impacts on the lower Fraser River and estuary, I then turned in Chapter 4 to investigate the optimal management strategies that could be taken to benefit salmon populations in this region. The ability to identify a set of management strategies that can benefit the most salmon populations for the least cost to society is a powerful tool, which I sought to apply to the heavily impacted region of the lower Fraser River and estuary. Specifically, in Chapter 4, I apply the Priority Threat Management framework to elicit expert predictions of the benefits of a suite of management alternatives to 19 conservation units (CUs) of salmon in the lower Fraser over 25 years. These predicted benefit estimates were then combined with the feasibility of success and the real-world costs of implementation to identify the optimal strategies to improve the status of the most CUs for the least cost. Of 14 alternative strategies a combined habitat strategy, which included estuarine, freshwater, and riparian habitat restoration, protection, and improved watershed management, was predicted to have the most significant influence on the future trajectories of these populations aside from implementing every management strategy available. While the strength of the predicted outcome varied by species and population, the combined habitat management strategy consistently improved the outlook of future status for all CUs.

Overall, this dissertation provides new empirical evidence that the habitats in the lower Fraser River and estuary are actively used by, and connected to the productivity of, the salmon populations assessed. This research strengthens the link between habitat and salmon population status and is now being applied to improve salmon habitat protection and to facilitate salmon recovery in the Fraser River and estuary.

## 1.3 Positionality

I was born and raised in what is now known as Victoria, British Columbia in the territories of the lək̓ʷəŋən peoples, including the Songhees, Xwsepsum (Esquimalt), and WSÁNEĆ peoples. I have experienced a settler's version of the meaning of lək̓ʷəŋən, which means "the place where the herring fish are smoked", as I accompanied my father and brother several times to fish for Pacific herring off the Craigflower bridge and proceeded to my grandpa's house to pickle them. I was taught from an early age to observe the world around me, to value nature, to work hard, and to use my voice. During my graduate degree I have been learning to identify the unearned privileges that I carry as a multi-generation European settler in what is now known as Canada and the inherent impacts my lived experiences have on my approach to the world, including my research. While Western science practices were new to me as a first-generation academic, my cultural status as a cisgender white female in a Western country has disproportionately supported my success relative to those who identify as 'other', particularly for racialized and Indigenous persons (Henry *et al.*, 2017). During my PhD journey I have come to understand that my cultural upbringing glossed over the direct and indirect violence against Indigenous peoples and their territories that my ancestors have participated in, that we as Canadians continue to participate in, and that I have directly benefitted from. During my research I have had the extreme privilege of working with Coast Salish, Stó:lō, and St'át'imc Indigenous collaborators, and this research would not have been possible without their generous acceptance and deep contributions of knowledge. I acknowledge that I am still learning how to be an effective ally to racialized and Indigenous peoples and that I may never fully appreciate the connections between Indigenous peoples and their territories, in which I live and work. To dismantle systemic racism both within and beyond the spheres of academia, it is vital that I and all others in academia acknowledge the role that we and our institutions play in perpetuating this discrimination by subjecting Black, Indigenous, and other researchers of colour to an unwelcoming academic culture (Barber *et al.*, 2020). I endeavour to provide better support and be a stronger ally for my colleagues, collaborators, mentees, and community moving forward.

# Chapter 2 - Habitat use by juvenile salmon, other migratory fish, and resident fish species underscores the importance of estuarine habitat mosaics

Adapted from the Author Accepted Manuscript (AAM) version of: Lia Chalifour[1*], David C. Scott[2], Misty MacDuffee[2], Josephine C. Iacarella[3], Tara G. Martin[4], Julia K. Baum[1]. (2019) *Marine Ecology Progress Series* 625: 145-162, https://doi.org/10.3354/meps13064

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## 2.1 Abstract

Interfacing with land and sea, estuaries support a mosaic of habitats that underpin the production of many coastal fisheries. These ecosystems are threatened by multiple stressors, including habitat loss and climate change, but the relative importance of estuarine habitat types for different fish species remains poorly understood since direct habitat comparisons are rare. This knowledge gap is exemplified in temperate estuaries by salmon: ecologically and commercially important species that use estuaries during their migrations to and from the ocean. Here, we tested for species-specific habitat use by sampling fishes in three interconnected estuarine habitats (brackish marsh, eelgrass, sand flat), across seasons and temperature regimes. We quantified fish species richness, community distinctness and catches (of Chinook and chum salmon, other migratory fishes, and resident fishes), in the Pacific Northwest's heavily urbanized Fraser River estuary, the terminus of what was once the world's most productive salmon basin. Overall, eelgrass habitat supported the greatest fish species richness (n = 37) and catches (37,402 fish), exceeding that of either the marsh (19 species, 7,154 fish) or sand flat (22 species, 6,697 fish). However, the majority of salmon were caught in the marsh (61%). These differences, coupled with our finding that at least one unique fish species inhabited each habitat (eelgrass = 15, marsh = 8, sand flat = 1), demonstrate species-specific habitat use and underscore the importance of connected seascapes for biodiversity conservation.

## 2.2 Introduction

Estuaries provide vital ecosystem services including nutrient cycling and fish production (Barbier *et al.*, 2011; McDevitt-Irwin, Iacarella and Baum, 2016; Mahoney and Bishop, 2017), but coastal development threatens these ecosystems globally, through habitat degradation and shoreline modification, alteration of hydrology, nutrient and waste runoff, and noise pollution (Lotze *et al.*, 2006; Mahoney and Bishop, 2017). These important ecosystems encompass a mosaic of interconnected habitat patches, including seagrass, marsh, and sand flats, which together form a "seascape" and may each support a different composition and biomass of fish species (Boström *et al.*, 2011). Seagrass meadows are highly productive, offering invertebrate food resources (Kennedy, Juanes and El-sabaawi, 2018; Unsworth, Nordlund and Cullen-Unsworth, 2018) and providing structural shelter that appears to be particularly important for small or juvenile fishes (Jackson *et al.*, 2001). Estuarine marsh vegetation also provides shelter when inundated, and increases food availability in the surrounding water column relative to unvegetated habitats, making it another important nursery habitat for resident fishes and migratory species, including Pacific salmon (Levings, Conlin and Raymond, 1991; Baltz, Rakocinski and Fleeger, 1993). For some fishes, particularly in subadult and adult phases, unvegetated habitats such as sand and mud flats have proven equally or more important (Hindell and Jenkins, 2004). Use of these habitats varies by species, but understanding their relative importance is challenging given habitat spatial variability and patchiness, and as such direct comparisons between multiple vegetated habitats are rare (McDevitt-Irwin, Iacarella and Baum, 2016; Whitfield, 2017). Although a recent meta-analysis found that half of studies (n=25/51) did compare seagrass fish communities to fish in other structured habitats, very few of these comparisons (n=6) were for temperate estuaries, and of these only two directly compared seagrass and marsh habitat in the same system (McDevitt-Irwin et al. 2016). Importantly, we found no studies comparing the use of seagrass and marsh habitat by salmonids, which is a critical gap in our understanding and management of imperiled salmon stocks.

The temporal dynamism of estuaries, which arises from seasonal shifts in temperature and hydrology, species-specific life-cycle patterns, and other factors (Jackson *et al.*, 2001), adds to the complexity of determining the relative importance of estuarine habitat types. Many migratory fish and bird species, for example, use estuarine habitats seasonally for reproduction and feeding (Baltz, Rakocinski and Fleeger, 1993; Bond *et al.*, 2008). Seasonal variation in water temperature and flow in temperate marine systems stimulates plankton blooms and vegetation growth, providing increased food availability to fishes during summer (Chandler, King and Boldt, 2017). This temporal variation can result in under- or over-estimation of the importance of each habitat type for fish communities if repeat surveys that span across seasons are not conducted. Sampling over a range of conditions and seasons may be necessary to accurately quantify fish habitat use in these dynamic systems, which is critical for accurate impact assessment of development proposals and for informing management (Cohen, 2012c; Shaffer *et al.*, 2017).

Of the commercially important fish species inhabiting temperate estuarine ecosystems, salmon arguably have the broadest ecological, economic and cultural footprint, but many populations are threatened (Northcote and Atagi, 1997; Cohen, 2012c). In British Columbia, overall abundance and commercial catch of the five major Pacific salmon species have declined precipitously over the last several decades (BC Wild Salmon Advisory Council, 2019), and despite interest and effort, several depressed populations have failed to recover for reasons that remain unclear (Beamish *et al.*, 1995; Zimmerman *et al.*, 2015). In particular, Chinook salmon (*Oncorhynchus tshawytscha*) in British Columbia's Salish Sea have not recovered despite tighter catch restrictions and increased hatchery production (Ruff *et al.*, 2017). A critical bottleneck for salmon survival is believed to occur shortly after emigration from rivers, when different species spend varying amounts of time in estuarine habitats, before moving out to the ocean (Zimmerman *et al.*, 2015). One hypothesis for survival during this period is that mortality is size-dependent, with smaller fish unable to outpace their predators in growth and less likely to survive their first winter before reaching size refugia (Beamish and Mahnken, 2001). The productivity and relative shelter offered by the habitats experienced during this period are therefore believed to be highly important for survival (Rubin, Hayes and Grossman, 2018).

All Pacific salmon species feed in estuaries and many will reside for days to months during their downstream migrations (Weitkamp *et al.*, 2014; Moore *et al.*, 2016). Of these, subyearling (migrating to sea within the first year after hatching) Chinook and chum (*O. keta*) salmon spend the greatest length of time in estuaries (Levings *et al.*, 1989; Volk *et al.*, 2010; Carr-Harris, Gottesfeld and Moore, 2015), but the extent to which they rely on estuaries for survival, and which estuarine habitats they use most during this critical period remains poorly understood (Weitkamp *et al.*, 2014). For example, although two recent studies provided evidence that juvenile Chinook and chum salmon use eelgrass habitat during their emigration, because neither study considered other estuarine habitats, such as marsh, it is unclear if juveniles of these species require eelgrass specifically or simply some vegetated habitat (Kennedy, Juanes and El-sabaawi, 2018; Rubin, Hayes and Grossman, 2018). Understanding these distinctions is critical, especially in urban estuaries, where localized impacts may mean different habitat types are being lost at different rates, and conservation efforts need to prioritize habitat recovery. This challenge is exemplified by the heavily urbanized Fraser River estuary. The Fraser was once the world's most productive salmon basin, and still produces more salmon than any other river in British Columbia (Northcote and Atagi, 1997), while also being the site of one of Canada's largest cities (Vancouver) and most active port (Fig. 2.1). Historical use of the Fraser estuary by Chinook, chum, and pink salmon (*O. gorbuscha*) has been documented (Levy, Northcote and Birch, 1979; Greer *et al.*, 1980). Today, much of the estuarine habitat in the Fraser has been lost or degraded, with uncertain implications for salmon.

Our objective here was to advance understanding of the relative importance of temperate estuarine habitat types for resident and migratory fish populations, including juvenile salmon. To achieve this, we tested for species-specific habitat use by sampling fishes in three interconnected estuarine habitats (brackish marsh, eelgrass, sand flat), across seasons (spring, summer, fall), and over two years with distinct temperature regimes (an El Niño year (2016) and more typical year

(2017)). We examined the influence of habitat type, as well as season and temperature regime, on estuarine fish species richness, community distinctness, and catch of four distinct fish species groups: Chinook salmon, chum salmon, other migratory fishes (other salmonids and forage fish), and resident fishes (e.g. shiner surfperch (*Cymatogaster aggregata*), three-spined stickleback (*Gasterosteus aculeatus*), and others) (Nightingale and Simenstad, 2001). In doing so, we tested three hypotheses:

*(1)* estuarine fish preferentially inhabit eelgrass meadows, such that fish species richness and catch will be highest within this habitat;

*(2)* within each habitat, salmon and migratory fish species richness and catch will peak in summer (May - August), owing to migration patterns and to seasonal increases in food availability and vegetation growth (marsh and eelgrass);

*(3)* resident species richness will be consistent across seasons, but relative abundance will peak in summer as these species take advantage of optimal conditions for reproduction (i.e., seasonal increases in food availability and vegetation growth).

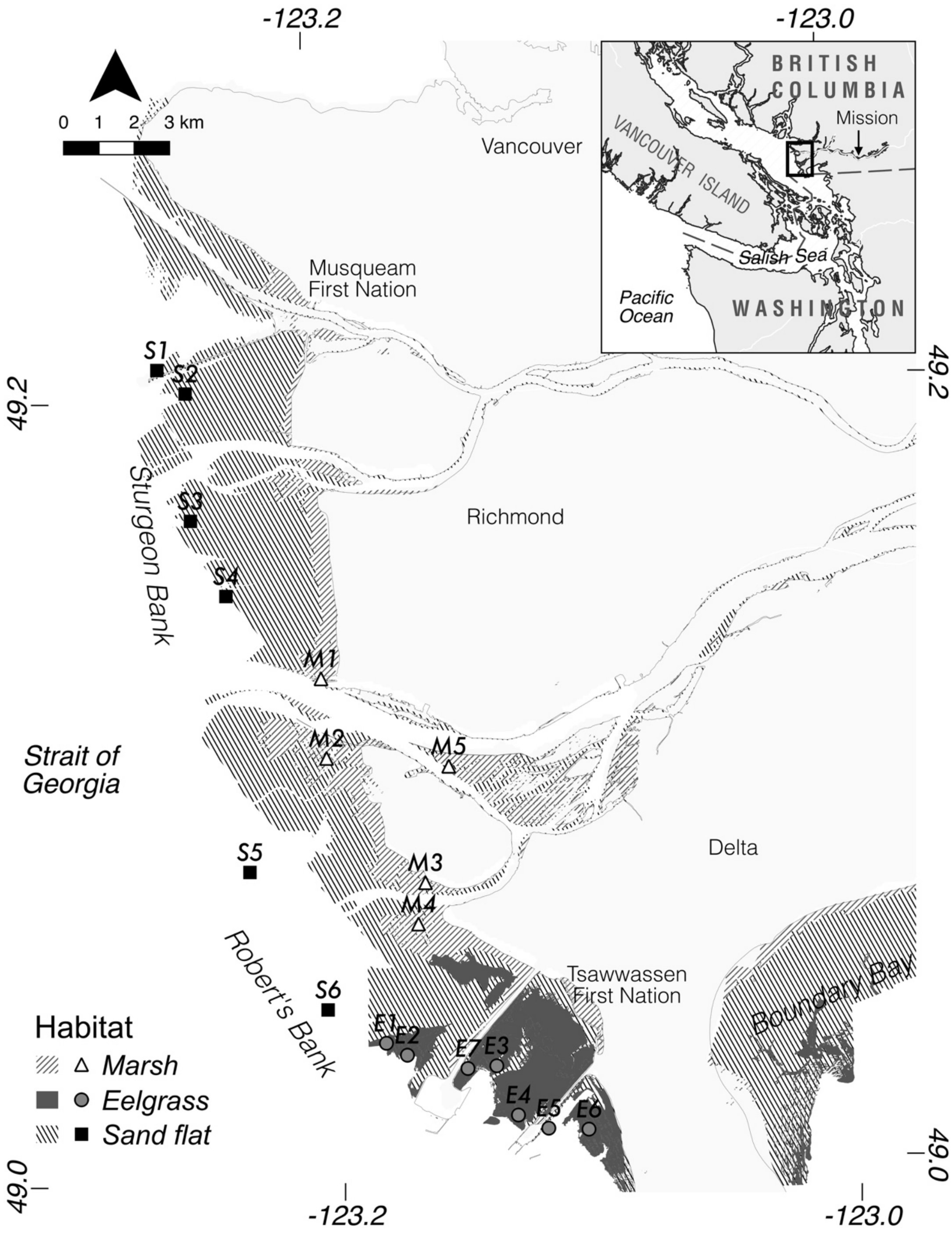


**Figure 2.1** Sites sampled in 2016 and 2017 within the Fraser River estuary, British Columbia, Canada: five marsh sites (white triangles; M1-M5), six sand flat sites (black squares; S1-S6), and six eelgrass sites (grey circles; E1-E6). All sites were sampled each year, with the exception of E6, which was replaced by E7 in 2017. Habitat polygons are approximations from the 2002/3 FREMP

Habitat Inventory of the Lower Fraser River Estuary, and boundaries may vary. Sand flat habitat extends seaward beyond the shown polygons to a drop-off between five and six km from shore.

## 2.3 Materials and Methods

### *2.3.1 Study system*

The Fraser River estuary extends from the tidal wedge at Mission, BC to a steep drop-off into the Strait of Georgia, where the river enters the Salish Sea (Fig. 2.1). Between the mouth of the river and this drop-off are the tidal flats known as Sturgeon Bank and Robert's Bank, which are characterized by shallow slopes and moderate salinity (Levy, Northcote and Birch, 1979). The Fraser River is the largest contributor of freshwater into the surrounding marine environment, providing terrestrial nutrients to fish communities, influencing the migration pathways of emigrating salmon, and dictating the nutrient cycling processes of the surrounding Salish Sea (Barraclough and Phillips, 1978; Riche, Johannessen and Macdonald, 2014). The lower reaches of the estuary provide important habitat for freshwater, estuarine, and marine fish communities, comprising over 50 fish species (Greer *et al.*, 1980; Conlin *et al.*, 1982); the main (southern) river mouth hosts small islets and channels that represent some of the last intact brackish marsh habitat in the estuary. More than 70% of the estuary has been permanently converted or altered by industrial, agricultural, and urban development, resulting in decreased connectivity between habitat patches (Waldichuk, 1985; Sutherland, Elner and O'Neill, 2013). The majority of the remaining marsh habitat is near the mouth of the South (main) arm of the river, and the eelgrass is limited to Robert's Bank, which is segregated by two large causeways (Fig. 2.1).

*2.3.2 Fish sampling*

We quantified fish communities in three distinct estuarine habitat types: brackish marsh (dominant species *Carex lyngbyei*), eelgrass (*Zostera marina*) meadows, and sand flats (unvegetated), by sampling at seventeen sites spanning Sturgeon and Robert's Bank and around the Fraser River mouth (Fig. 2.1). We surveyed each site approximately every two weeks between March and July in both 2016 and 2017, to capture seasonal shifts in fish distribution and abundance. Two additional sampling rounds (i.e., sampling all sites) were conducted in the fall (September and October) of 2016, and one round of marsh sites only was conducted in August 2017.

Our survey design followed previous surveys in the estuary (Greer *et al.*, 1980; Levings, 1985; Archipelago Marine Research Ltd., 2014b, 2014a), with sites a minimum of 500 m apart. Sites were selected non-randomly, to be relatively evenly distributed across the estuary, within habitat types. We attempted to ensure that all habitats were equally accessible to fish and under similar environmental conditions at the time of sampling, by selecting sites that were relatively consistent in depth (2.0 - 4.3 m during sampling), and by surveying at high tide (minimum 2.9 m above Chart Datum at Tsawwassen tidal station #7590), and during daylight hours (minimum one hour from sunrise or sunset). A few of the marsh channels experienced delayed tidal shifts, resulting in a small number of sampling events at depths less than two meters. However, for small fish such as salmonids, which may remain in marsh channels at depths less than 0.5 m (Hering *et al.*, 2010), we do not believe that this made a significant difference in detectability.

Each sampling event at a site consisted of three non-overlapping, round-haul seine sets; after each set, we identified all fish to species. Set success was assigned a rating (1: poor (i.e., highly deviant time to completion, snag, likely release of fish during haul in), 2: fair, 3: good, 4:

perfect (i.e., consistent pace throughout set, ideal round-haul shape, tight management of cod-end and retrieval of sampled fish to buckets). All sets ranked 1 were excluded from the analyses, and the set was repeated to achieve three non-overlapping sets ranked 2 or higher per sampling event. We used a custom purse seine (40m long x 4m wide bunt [4mm mesh] and 3m wide cod end [6mm mesh]) to survey outer (eelgrass and sand flat) sites, and a beach seine (20 m long x 3 m wide, 1.5 x 1.5 m bag [3mm mesh]) to survey the inner (marsh) sites. Past surveys in the Fraser estuary typically employed beach or purse seines (e.g. Greer et al. 1980, Levings 1985, Archipelago 2014a), and habitat constraints necessitated the use of both gear types to adequately sample all three habitat types. In the marsh channels we used a small beach seine, the most commonly used method historically in this area and ideal as the channels are quite narrow and relatively shallow. In contrast, for safety on the flats (eelgrass and sand flat sites), which can experience rapid tidal shifts and have unconsolidated mud that personnel can sink into (Sutherland, Elner and O'Neill, 2013), and to sample at high tide, we designed the small purse seine that could be easily deployed without disembarking the vessel. Both seines reached the bottom substrate during sampling and successfully caught motile pelagic and epibenthic fishes. The difference in size between the purse and beach seine resulted in approximately half the area swept for each marsh sampling event relative to the eelgrass and sand flat sampling events. Seine set haul times were approximately twice as long and more variable for the beach seine (87.8 seconds +/- 78.4 SD) when compared to the purse seine (55.4 seconds +/- 29.7 SD), reflecting faster seine setting and retrieval with the larger vessel, which also employed an automated pulley to cinch the purse line. We did not conduct efficiency tests for the gear, but it is likely that the catch efficiency was lowest in the marsh habitat for these reasons (Franco *et al.*, 2012).

*2.3.3 Abiotic variables*

At each site, we measured a suite of water quality and habitat characteristics that can influence fish communities. Water quality parameters, including temperature, salinity, pH, and dissolved oxygen, were measured at each site 0.5 m from the water surface once per sampling round (i.e., approximately every two weeks) each year using a Hanna Instruments 9829 Multiparameter Meter. Turbidity was measured in the same way but only in 2016. In some cases, one or more water quality values could not be recorded at a site. We estimated these missing values (7 % total; n = 72 / 624 measurements in 2016; 18 / 647 in 2017) from cubic spline interpolations of the existing field data, separating measured values by habitat type and ordering by Julian day (na.spline, "zoo" package in R; Zeileis & Grothendieck 2005). We assessed the effect of year, habitat, and month on each continuous abiotic environmental variable using general linear mixed models with site as a random effect (lmer, “lme4” package in R, Bates et al. 2015).

We also quantified the following habitat characteristics at each marsh site: marsh tidal channel width, because this directly influences water levels and dictates the accessibility of the channel to fish (Levy, Northcote and Birch, 1979); and vegetation elevation (i.e. the height from the channel bottom to the nearest marsh vegetation, as a measure of the relative extent of submerged / overhanging vegetation, which can affect water quality by providing shade, facilitating nutrient cycling and reducing turbidity by stabilizing sediments; Seliskar & Gallagher 1983). Vegetation has also been linked to increased food availability to fish via increased invertebrate abundance in the water column (Seliskar and Gallagher, 1983; Levings, Conlin and Raymond, 1991). Although we measured several other habitat characteristics (e.g., eelgrass shoot density, leaf area index, marsh channel bank slope and elevation), we did not include these in our final catch models because of collinearity with other abiotic variables (Fig. 2A1).

*2.3.4 Species richness*

We compared fish species richness across habitats and seasons using sample-based rarefaction curves (999 bootstrapped replications) as implemented for incidence-based data ("iNEXT" in R, Hsieh et al. 2016). We estimated rarified species richness to account for the effects of bias associated with unequal sampling effort (i.e., number of sampling events among habitats, or among the seasons within each habitat compared) and fish abundance per seine haul. We performed sample-based rarefaction rather than individual-based rarefaction because the independent sample is at the level of the sample unit (seine) rather than at the level of the individual fish. Rarefying the data allowed us to accurately compare richness across habitats, despite differences in sample size (Chao *et al.*, 2014). We defined seasons as spring (sampling events in March - April), summer (May - August), and fall (September - October). Year did not have a strong effect on richness in preliminary analyses, so we pooled sampling events across years.

*2.3.5 Community composition*

We visualized community distinctness across habitats using an Euler diagram ("eulerr" in R, Larsson 2018) and non-metric multidimensional scaling ('NMDS', "vegan" in R, Oksanen et al. 2018). The Euler diagram shows area-proportional relationships between the number of species captured in each habitat over all seasons and all years. We used presence-absence data for each species and habitat, and calculated the number of intersections, unions and disjoints, representing the number of species in common or unique to each habitat type. The NMDS ordination plot depicts variation in fish communities by site. The ordination uses Bray-Curtis dissimilarity index and the data were submitted to Wisconsin double standardization, which standardizes species first by their count maxima and then by their sample totals, improving the quality of the ordination (Oksanen, 2015).

*2.3.6 Catch*

To determine which factors contributed to observed catch patterns, we modeled the catch of each of four species groups (Table 2.1) in the estuary, with separate models for beach-seined sites (marsh) and purse-seined sites (eelgrass and sand flat) (8 total models), because of inherent differences in the catch efficiency of these two gear types (Franco *et al.*, 2012). We classified species other than Chinook and chum salmon as either residents or migratory, following Nightingale and Simenstad's (2001) categories, but simplifying by aggregating their resident and seasonal resident species into a single 'resident' group. For the marsh habitat data, we implemented generalized linear models (GLMs) with a negative binomial error structure to account for large counts at the tail of the distribution (glm.nb, "MASS" package in R, Venables & Ripley 2002), and included the fixed effects of year, Julian day, temperature, salinity, pH, dissolved oxygen, mean turbidity, channel width, and vegetation elevation. Based on an apparent non-linear seasonal effect on abundance, which was strongly evident for some fish species groups, Julian day was modeled as a quadratic term (Julian day + Julian day squared) in the full models. We did not include 'site' as a random effect because there were only five marsh sites (which is at the lower threshold of capacity for mixed-effects models to provide accurate estimates of among-population variance (Harrison *et al.*, 2018)); nor did we include site as a fixed-effect in the models because it was highly collinear with the site-level habitat variables. For the eelgrass/sand flat models, we implemented generalized linear mixed-effects models (GLMMs) with a negative binomial error structure and site as a random-effect, to account for repeat measures within 13 sites (glmer, “lme4” package in R, Bates et al. 2015). We included the fixed effects of year, Julian day (as a quadratic term, as above), temperature, salinity, pH, dissolved oxygen, mean turbidity, and habitat type (eelgrass and sand flat only). All continuous variables were standardized and centered on the mean prior to analysis (“robustHD” package in R; Alfons 2016). A summary of covariates included in the eight global catch models is provided in the electronic supplement (Table 2S3).

For each fish group and gear type, we examined the collinearity of the variables using variance inflation factors (VIF) in the context of model stability (O’Brien, 2007). Several variables had very high collinearity within the data sets (Fig. 2A1), and these were removed one by one, following a hypothesis-based approach and VIF scores, from each full model until the model converged and collinearity was sufficiently addressed. VIF for all variables retained in our reduced global models were below 3.50, with the exception of the marsh Chinook model (6.18, Julian day). We then performed model selection on these eight reduced global models for each fish group and data type. Model selection was carried out using Akaike’s information criterion for small sample sizes (AICc) following an examination of all possible subsets of explanatory variables (dredge, “MuMIn” package in R, Bartoń 2018). In complex biological systems, model averaging can provide more robust conclusions by incorporating the uncertainty inherent in the model using the model’s Akaike weight (Harrison *et al.*, 2018). Due to the low weights of our top models, we averaged all models with an AICc score within 4 of the top-ranked model to ensure the best estimates of the top coefficients (Harrison *et al.*, 2018). Including models with a delta AIC up to 4-7 in the model set can help to minimize Kullback-Leibler information loss and incorporate plausible hypotheses for estimating the response variable, particularly when model weights are low (Burnham, Anderson and Huyvaert, 2011; Harrison *et al.*, 2018). In our case, delta 4 included the majority of the expected model variability while also reducing the model set to a reasonable number for multimodel inference, given our sample sizes (Burnham, Anderson and Huyvaert, 2011). We report pseudo r-squared values for each model following the methods detailed in Nakagawa & Schielzeth (2013), using the "MuMIn" package in R. All statistical analyses were computed using R version 3.4.1 (R Core Team, 2019).

**Table 2.1** Fish species caught in marsh, eelgrass, and sand flat habitats in the Fraser River estuary in 2016 and 2017. Species[1] are listed alphabetically by common name within each of four species groups: Chinook salmon (Chin.), chum salmon (Chum), resident (R), and migratory (Mig.) (i.e., all migratory species other than Chinook and chum salmon). Species that were only found in a single habitat (M = marsh; E = eelgrass; SF = sand flat) are noted under Unique Habitat. Species that were caught in only one of the two years are noted under Year. * indicates invasive species.

| **Common name** | **Latin name** | **Species Group** | **Unique Habitat** | **Year** |
|---|---|---|---|---|
| Chinook salmon | *Oncorhynchus tshawytscha* | Chin. | | |
| Chum salmon | *Oncorhynchus keta* | Chum | | |
| Arrow goby | *Clevelandia ios* | R | | |
| Bay pipefish | *Syngnathus leptorhyncus* | R | | |
| Big skate | *Raja binoculata* | R | E | 2016 |
| Buffalo sculpin | *Enophrys bison* | R | E | 2017 |
| Crescent gunnel | *Pholis laeta* | R | | |
| English sole | *Parophrys vetulus* | R | | |
| Kelp greenling | *Hexagrammos decagrammus* | R | | 2017 |
| Kelp perch | *Brachyistius frenatus* | R | E | 2016 |
| Kelp poacher | *Agonomalus mozinoi* | R | E | 2017 |
| Largescale sucker | *Catostomus macrocheilus* | R | M | |
| Pacific herring | *Clupea pallasii* | R | | |
| Pacific sanddab | *Citharichthys sordidus* | R | E | 2017 |
| Pacific tomcod | *Microgadus proximus* | R | E | 2016 |
| Peamouth chub | *Mylocheilus caurinus* | R | M | |
| Penpoint gunnel | *Apodichthys flavidus* | R | E | |
| Northern pikeminnow | *Ptychocheilus oregonensis* | R | M | |
| Pile perch | *Rhacochilus vacca* | R | E | |
| Plainfin midshipman | *Porichthys notatus* | R | E | |
| Prickly sculpin | *Cottus asper* | R | M | |
| Pumpkinseed* | *Lepomis gibbosus* | R | M | |
| Redside shiner | *Richardsonius balteatus* | R | M | 2017 |
| River lamprey | *Lampetra ayresi* | R | | |
| Saddleback gunnel | *Pholis ornata* | R | E | |
| Sand sole | *Psettichthys melanostictus* | R | | 2016 |
| Shiner surfperch | *Cymatogaster aggregata* | R | | |
| Snake prickleback | *Lumpenus sagitta* | R | | |
| Speckled sanddab | *Citharichthys stigmaeus* | R | | |
| Staghorn sculpin | *Leptocottus armatus* | R | | |
| Starry flounder | *Platichthys stellatus* | R | | |

| Common name | Latin name | Species Group | Unique Habitat | Year |
|---|---|---|---|---|
| Three-spined stickleback | *Gasterosteus aculeatus* | R | | |
| Tidepool sculpin | *Oligocottus maculosus* | R | | |
| Tubesnout | *Aulorhynchus flavidus* | R | E | |
| Walleye pollock | *Gadus chalcogrammus* | R | E | 2016 |
| White crappie* | *Pomoxis annularis* | R | M | 2016 |
| Whitespotted greenling | *Hexagrammos stelleri* | R | E | 2016 |
| Coho salmon | *Oncorhynchus kisutch* | Mig. | M | 2016 |
| Longfin smelt | *Spirinchus thaleichthys* | Mig. | SF | 2016 |
| Northern anchovy | *Engraulis mordax* | Mig. | | |
| Pacific sand lance | *Ammodytes hexapterus* | Mig. | | |
| Pink salmon | *Oncorhynchus gorbuscha* | Mig. | | 2016 |
| Sockeye salmon | *Oncorhynchus nerka* | Mig. | | |
| Steelhead | *Oncorhynchus mykiss* | Mig. | E | 2017 |
| Surf smelt | *Hypomesus pretiosus* | Mig. | | |
| Tiger rockfish | *Sebastes nigrocinctus* | Mig. | E | 2017 |

[1] Eight types of juvenile fishes were identified to genus or family only, and classified as resident (6: unidentified flatfish, unidentified gadid, unidentified gunnel, unidentified greenling, unidentified sanddab, unidentified sculpin) or migratory (2: unidentified salmonid; unidentified smelt). Because these juveniles were assumed to represent one of the previously identified species they were not included in the richness totals. Additionally, two larval taxa that could not be classed as resident or migratory were excluded from analyses.

## 2.4 Results

### *2.4.1 Species richness*

We identified 46 fish species (39 in 2016, 36 in 2017), of which 35 were classified as resident and 11 were classified as migratory species (including Chinook and chum salmon) (Table 2.1). Resident fishes included two introduced species that are invasive in coastal British Columbia (pumpkinseed (*Lepomis gibbosus*), white crappie (*Pomoxis annularis*); Table 2.1). Of the three sampled estuarine habitats, eelgrass had significantly higher fish species richness (37) than either the marsh (19) or sand flats (22), which were similar to each other (rarefied comparison, Fig. 2.2a). An influx of fish species in the summer resulted in significantly greater richness in summer than the fall in eelgrass, with a similar (though not significant) trend in sand flat (Fig. 2.2c,d). No other significant trends between seasons were detected (Fig. 2.2).

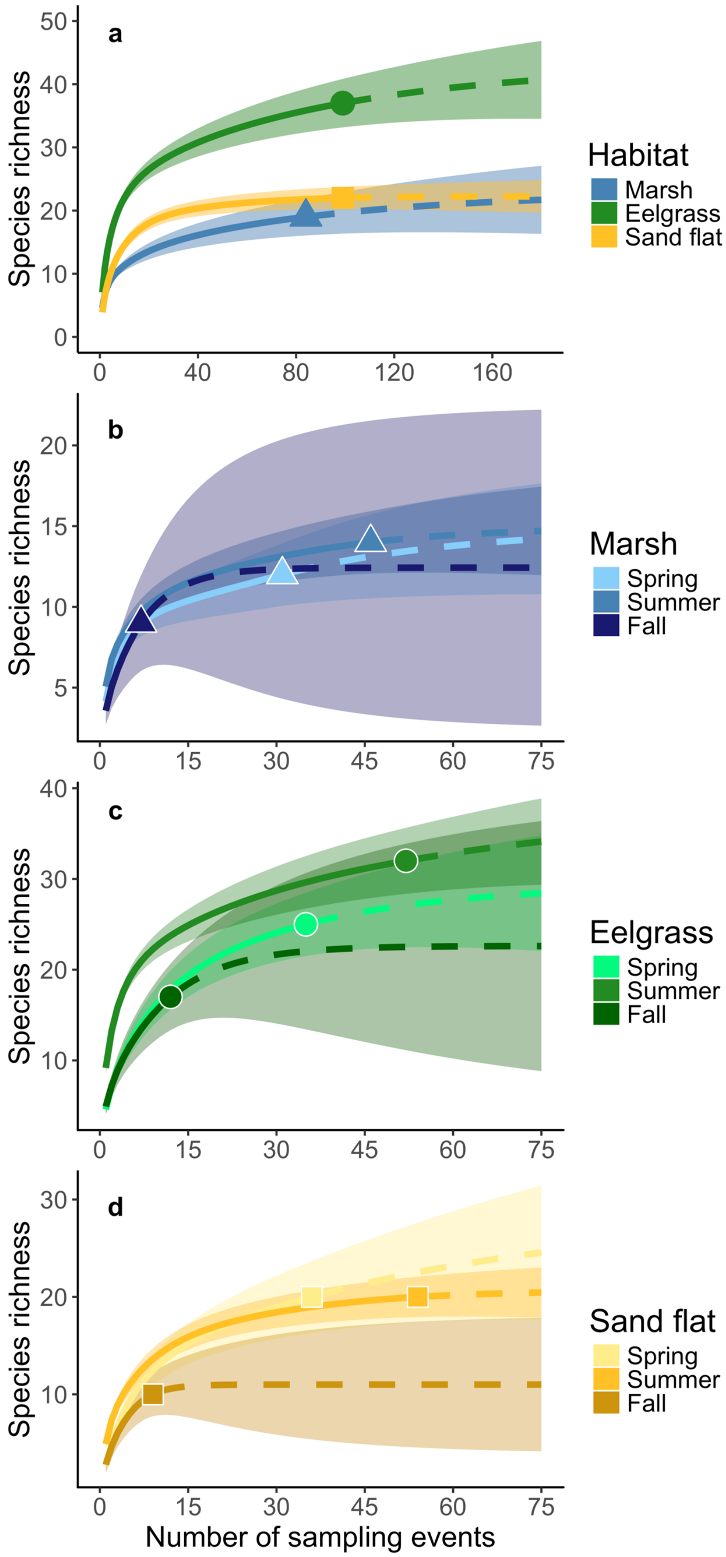


**Figure 2.2** Rarefied species richness curves for marsh (blue triangles), eelgrass (green circles), and sand flat (yellow squares) habitats, combining data across seasons and years (a); and species richness curves by season for marsh (b), eelgrass (c), and sand flat (d) habitats. Symbols reflect observed species richness, solid lines represent interpolated values, and dashed lines represent extrapolated values. Shading represents 95 % confidence intervals.

*2.4.2 Catch and community composition*

Overall, in 288 sampling events over two years (Table 2S1), we caught 51,143 fish, the majority of which were in eelgrass (37,385 fish; mean = 378 ± 546 fish / sampling event, where one sampling event is three seine sets taken per site per day) followed by marsh (7,126; mean = 85 ± 131 fish / sampling event) and sand flat (6,632; mean = 63 ± 135 fish / sampling event). The three habitats differed considerably in their most abundant species (Fig. 2.3), and each habitat supported distinct species that were not found in the other sampled habitats (Fig. 2.4, Fig. 2S1). Resident fishes comprised the majority of all those caught (46,141; 90 % of total), and of these, two species accounted for the vast majority: shiner surfperch (49 % of all fish caught) and three-spined stickleback (26 % of all fish) (Fig. 2.3). In total, we caught 1,193 Chinook and 1,088 chum salmon (Fig. 2.3). The remaining fish were other migratory species (2,347 individuals) and 374 unclassified fish (Fig. 2.3).

Marsh habitat supported the highest and most consistent salmonid catches in the estuary (1,514 salmonids total, mean = 18 ± 37 fish / sampling event, 6 species, 61 % of overall salmonid catch) (Fig. 2.3a). Marsh sites had more freshwater-tolerant resident fishes, 8 of which were only found in this habitat type, including peamouth chub (*Mylocheilus caurinus*) and Northern pikeminnow (*Ptychocheilus oregonensis*) (Fig. 2.4). The marsh was also the source of a high catch of juvenile flatfish in 2017 (1,366 unidentified flatfish total, Fig. 2.3a). Invasive fishes were only caught in marsh habitat, and in low abundance (1 fish each year, Table 2.1).

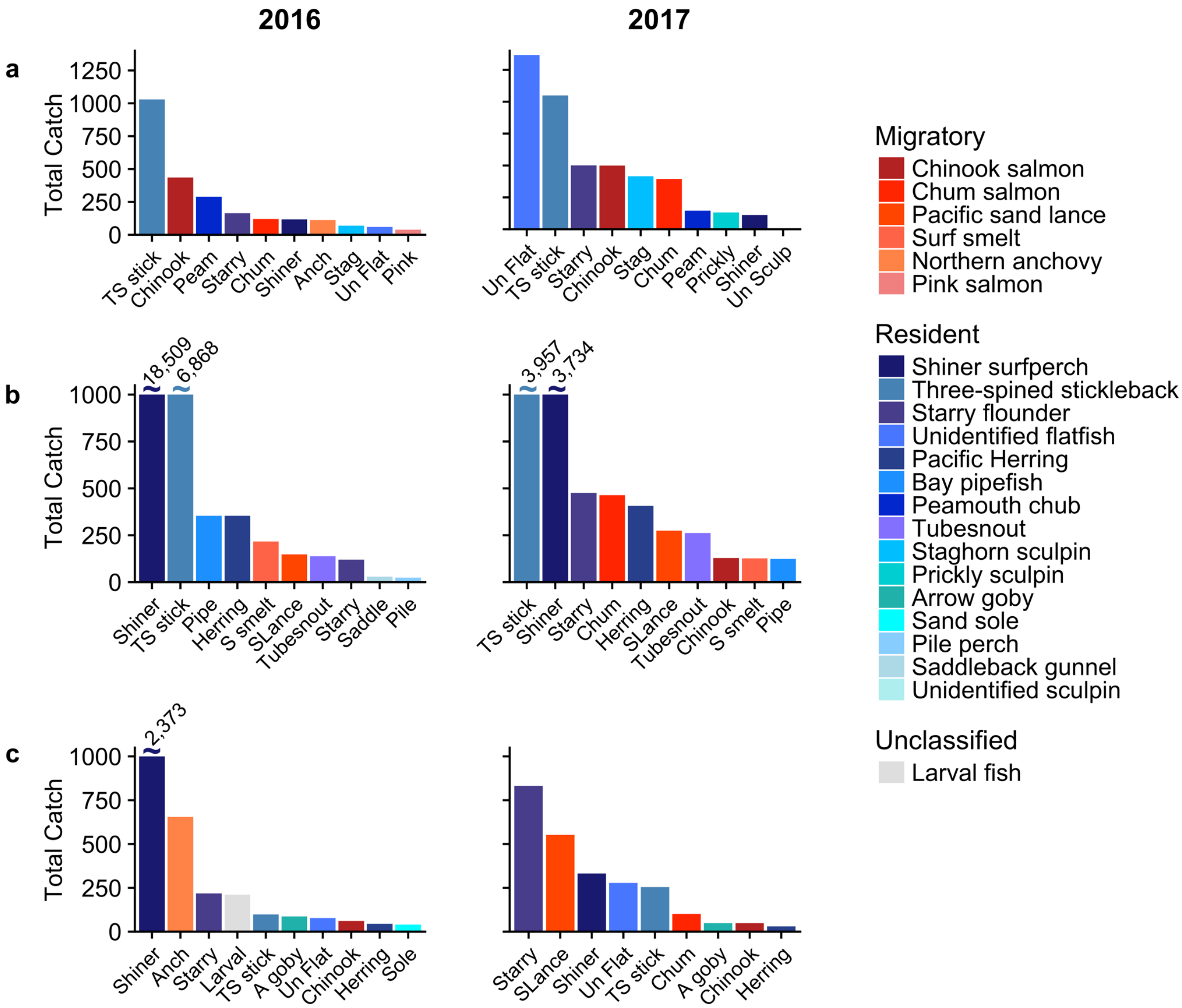


**Figure 2.3** Top ten fish species caught in 2016 (left 3 panels) and 2017 (right 3 panels) by habitat: a) marsh channel, b) eelgrass meadow, and c) sand flat sites in the Fraser River estuary. Migratory species, including Chinook and chum salmon, are shown on a red scale, resident fishes on a blue scale. Numbers above bars for shiner surfperch and three-spined stickleback indicate total catch when catch scale was exceeded.

Eelgrass habitat supported a high catch of shiner surfperch and three-spined stickleback, particularly in 2016, and was also the primary habitat for Pacific herring (*Clupea pallasii*), surf smelt (*Hypomesus pretiosus*), and bay pipefish (*Syngnathus leptorhyncus*) (Fig. 2.3b). Over one third of species caught in the study were only found in eelgrass habitat (Table 2.1; Fig. 2.4). Eelgrass-specific species were commonly demersal fishes with high site fidelity (e.g., penpoint gunnel (*Apodichthys flavidus*), buffalo sculpin (*Enophrys bison*), plainfin midshipman (*Porichthys notatus*)) or deep dwellers that were found in the shallows as juveniles (e.g., big skate (*Raja binoculata*), walleye pollock (*Gadus chalcogrammus*)).

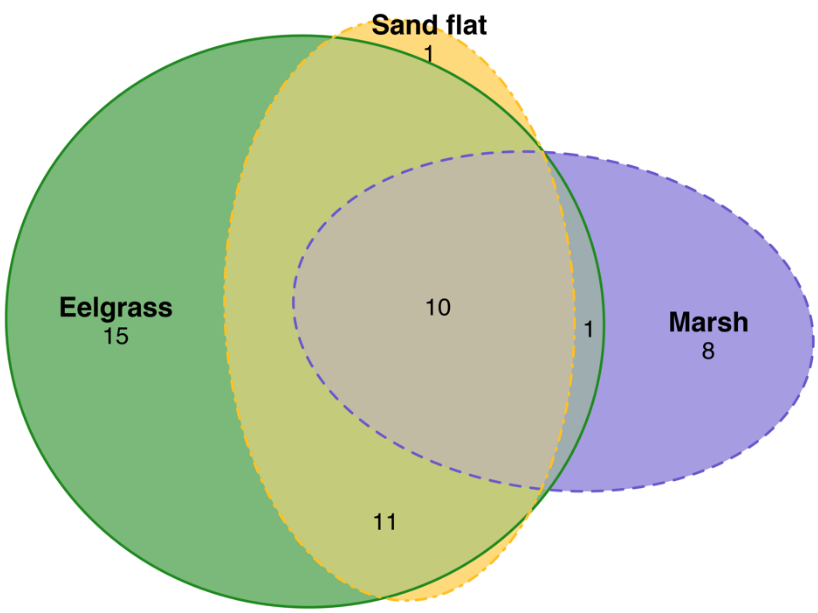


**Figure 2.4** Euler diagram showing area-proportional representation of fish community composition among habitats in the Fraser River estuary in 2016 and 2017. There are 8 unique and 11 shared species in marsh (blue ellipse, dashed outline), 15 unique and 22 shared species in eelgrass (green ellipse, solid line), and 1 unique and 21 shared species in sand flat (yellow ellipse, dash-dot line) habitat. Numbers within each segment represent the number of species either shared between habitats (unions) or distinct within each habitat (disjoints).

Sand flat habitat included a variety of migratory species, such as Northern anchovy (*Engraulis mordax*) in 2016 and Pacific sand lance (*Ammodytes hexapterus*) in 2017, but resident fishes such as arrow goby (*Clevelandia ios*), snake prickleback (*Lumpenus sagitta*), and flatfish spp. were also abundant (Fig. 2.3c). Sand flat sites had the highest incidents of empty nets. The only species that was uniquely found in sand flat was a single longfin smelt (*Spirinchus thaleichthys*) (Fig. 2.4).

We observed substantial differences in environmental conditions, fish catches, and community composition between years, potentially due to the El Niño in 2016. Surface temperature was greater in 2016 (14.82 ± 1.81 ºC, mean ± 1 SD) than 2017 (13.87 ± 2.53 ºC, Fig. 2.5), with a significant effect of year ($p < 0.001$, Table 2S2). These differences were larger for marsh and sand flat habitats (Fig. 2.5), which are more strongly influenced by the Fraser River outflow than the eelgrass sites (Fig. 2.1). Dissolved oxygen was also higher in 2016 (10.47 ± 0.96 vs. 10.42 ± 1.43 mg $L^{-1}$, $p < 0.001$, Table 2S2), except during the month of May (10.46 ± 0.74 vs. 11.06 ± 0.78 mg $L^{-1}$). Both salinity and pH were significantly higher in 2016, with elevated salinity reflecting low river flows particularly during the freshet months (Table 2S2, Fig. 2.5). Nearly two thirds of the total fish catch occurred in the El Niño year (2016; 33, 435 fish), despite having only 53 % of the total sampling effort (Table 2S1), and fish community composition differed considerably between years (Fig. 2.3). This difference in total catch between years was primarily a result of a more than 400 % higher catch of shiner surfperch in 2016 (20,999 (mean = 136 ± 373 fish / sampling event) in 2016 vs. 4,177 (mean = 31 ± 133 fish / sampling event) in 2017) (Fig. 2.3). Three-spined stickleback were also 34 % more abundant during the El Niño year (7,995 vs. 5,260). A notable difference in estuarine fish species composition was the large schools of Northern anchovy of various life stages we caught in 2016, particularly in the sand flat, which shifted to greater abundances of starry flounder and Pacific sand lance in 2017 (Fig. 2.3c).

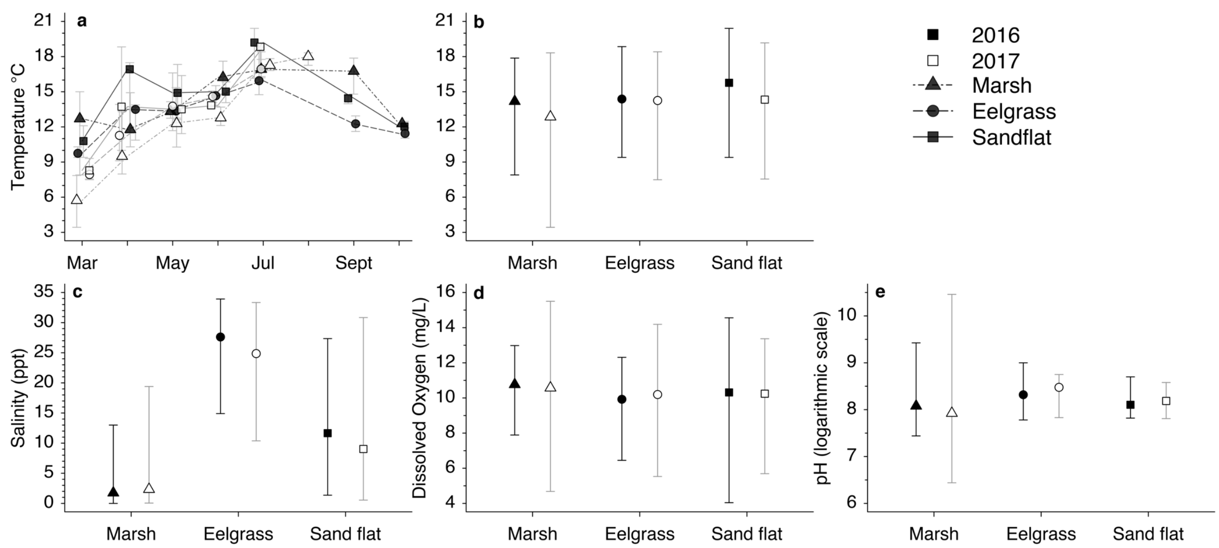


**Figure 2.5** Mean surface temperature (a:b), salinity (c), dissolved oxygen (d), and pH (e) over time for marsh (triangles), eelgrass (circles), and sand flat (squares) in 2016 (black) and 2017 (white) in the Fraser River estuary. Error bars show minimum and maximum measured values. Values were averaged across all sites for each sampling month (a) and year (b:e) in each habitat.

*2.4.3 Chinook salmon catch*

The majority of Chinook salmon occurred in the marsh habitat in both years (78 %). Within the marsh, Chinook catch was best explained by year, Julian day, water temperature, pH, and marsh channel width (pseudo $R^2$ = 51 %, *df* = 7, *w* = 0.21, Table 2S4). Chinook catch was slightly higher in the marsh in 2017 (500 (mean = 13 ± 21 fish / sampling event)) than 2016 (435 (mean = 10 ± 25 fish / sampling event)) when water temperatures were higher, earlier in the season, and in wider marsh channels (Fig. 2.6a, Fig. 2A2). Although Chinook catch was also greater in 2017 than 2016 in eelgrass habitat, neither water temperature nor pH were important predictors of abundance in the eelgrass and sandflat model. Instead, dissolved oxygen had a positive effect on Chinook catch, and more were caught in eelgrass than on the sand flats (conditional $R^2$ = 50 %, *df* = 6, *w* = 0.27, Fig. 2.6e, Table 2S5).

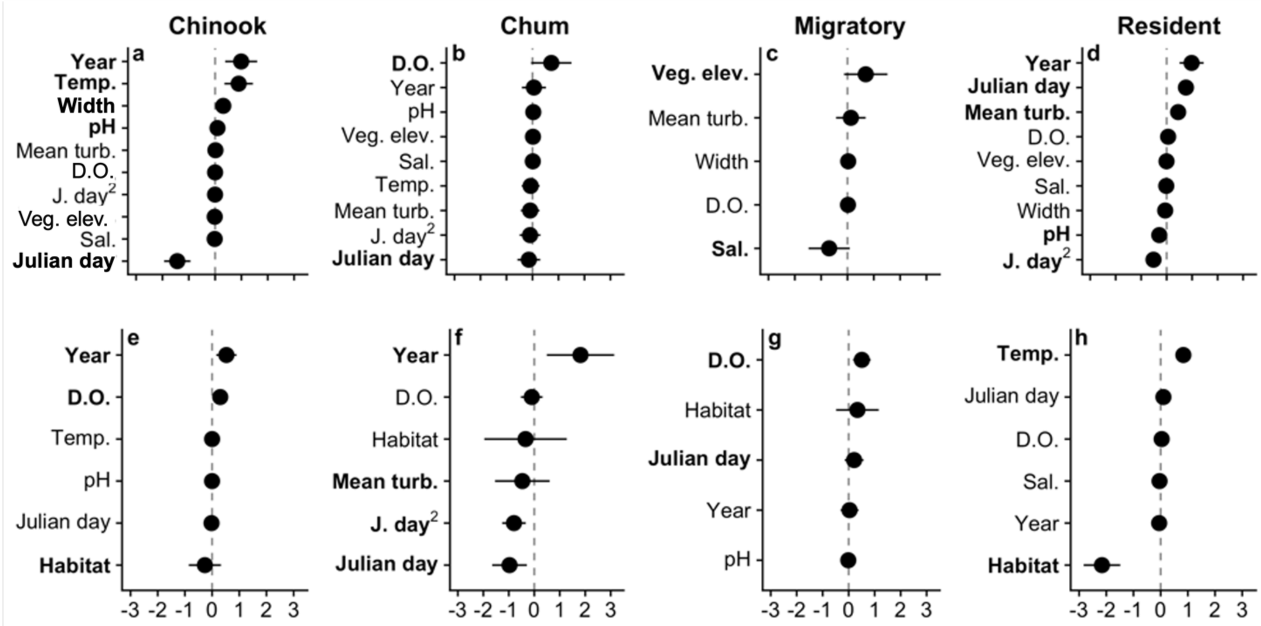


**Figure 2.6** Multimodel-averaged model coefficients for marsh (a-d) and eelgrass / sand flat (e-h) catch models for each species group (Chinook = a,e; Chum = b,f; Other migratory = c,g; Resident = d,h). Data included sampling from 2016 and 2017 in the Fraser River estuary. Temp. = Temperature, D.O. = Dissolved oxygen, J. day$^2$ = Julian day squared, Sal. = Salinity, Width = marsh channel width, Mean turb. = mean turbidity in 2016, Veg. elev. = vegetation elevation. Within each panel, coefficients are ordered from most to least positive effects; coefficients with relative variable importance (cumulative Akaike weight) > 0.5 are bolded on each y-axis. Error bars represent 95 % confidence intervals.

*2.4.4 Chum salmon catch*

Chum salmon were caught in far greater numbers in 2017 than 2016 (total 959 (mean = 7 ± 25 fish / sampling event) vs. 129 (mean = 1 ± 4 fish / sampling event) fish, respectively), and were distributed across habitats differently between years. In 2016, almost all (93 %) chum were caught in marsh sites, whereas less than half (41 %) were caught there in 2017. In 2017, almost half (48 %) of chum salmon were caught in large schools in the eelgrass habitat. Within the marsh habitat, however, year was not identified as a significant explanatory variable for chum ($R^2$ = 33 %, *df* = 4, *w* = 0.08, Table 2S4, Fig. 2.6b); instead, chum were most abundant when dissolved oxygen levels were high, which occurred earlier in the season. In the eelgrass and sand flat model, year and turbidity were significant, reflecting the high chum catch in 2017 in eelgrass sites with low turbidity relative to the sand flats ($R^2$ = 95 %, *df* = 7, *w* = 0.35, Fig. 2.6f, Table 2S5). Within these habitats, more chum were caught early in the season, with a quadratic relationship for day of year, due to an increase in catch in April-May followed by a sharp decline (Fig. 2.6f).

*2.4.5 Other migratory fish catch*

Migratory fishes consisted of other salmonid species, including sockeye salmon (*O. nerka*, 147 over both years), as well as forage fishes, such as surf and longfin smelts (368 combined), and Pacific sand lance (990). Some species were only seen in 2016, including pink salmon (43), which display an alternating year life history pattern (Beamish *et al.*, 1994), and anchovy (788), which respond to changing temperature and current regimes in the Salish Sea (Duguid *et al.*, 2019). In the marsh, vegetation elevation was the most significant parameter for these species, indicating greater catch within the marsh for sites with steeper or taller banks ($R^2$ = 54 %, *df* = 7, *w* = 0.38, Fig. 2.6c, Table 2S4). Migratory fishes were also caught in higher numbers when marsh sites had lower salinity. Migratory fishes in the eelgrass and sand flat habitats were more abundant later in the season and when dissolved oxygen was high, with slightly higher abundance in sand flat habitat ($R^2$ = 91 %, *df* = 5, *w* = 0.20, Fig. 2.6g, Table 2S5).

*2.4.6 Resident fish catch*

Within the marsh habitat, resident fish catch peaked bimodally in May and July (Fig. 2A2), which was represented by significant Julian day and Julian day squared parameter estimates (Fig. 2.6d). In the marsh, resident fish catch was higher in 2017, in more turbid sites, and at lower pH levels, indicating the effect of a stronger freshet in 2017 and higher river input to the marsh ($R^2$ = 54 %, *df* = 7, *w* = 0.22, Fig. 2.6d, Table 2S4). In the eelgrass/sand flat, resident fish catch peaked in July (Fig. 2A2). Resident fishes were far more abundant in eelgrass compared to sand flat (35, 779 vs. 4, 868 total catch), and were strongly positively affected by water temperature, reflecting the high catches of shiner surfperch and three-spined stickleback during the El Niño conditions of 2016 ($R^2$ = 100 %, *df* = 5, *w* = 0.16, Fig. 2.6h, Table 2S5). Year was not significant despite the considerably higher catches of these two species in 2016.

## 2.5 Discussion

Our study found unique roles of different habitat types and multiple environmental influences on total biodiversity and catch of fishes in an urbanized estuary. The spatiotemporal variation among habitat types within this continuous seascape supports the theory that connectivity of nearshore habitats is integral to the maintenance of diverse and productive nearshore ecosystems (Bishop *et al.*, 2017). As predicted, eelgrass provided the largest contribution and had the greatest seasonal variation in both estuarine fish species richness and abundance. Though marsh supported the fewest species, this habitat had more unique species than sand flat and notably was the most used habitat for juveniles of five species of commercially important salmon. Although this study did not attempt to elucidate true population abundances in the estuary, by comparing catches across habitat types we were able to estimate the relative abundances of fishes across temporal and spatial scales within this system. Comparing these vegetated habitats yielded important results that would have been missed had we assessed only a single vegetated habitat, as in the majority of estuarine studies (McDevitt-Irwin, Iacarella and Baum, 2016). Habitat use is still seldom incorporated into fisheries stock assessments, an oversight that may be leading to over- or under-exploitation of stocks (Brown *et al.*, 2019). Our results underscore the importance of understanding fish use of multiple nearshore habitats and conserving or restoring a mix of critical habitats for maintenance of these populations. Finally, we show that a warmer water regime coincided with novel migratory species, increases in select hardy species (i.e. tolerant to high temperature, low oxygen, varying salinity, and/or high nutrient input conditions (Wiebe, 1968; Healey, 1997; Moran *et al.*, 2010; Taugbøl *et al.*, 2014; Christensen *et al.*, 2018)), and declines in abundance of the majority of resident species.

This study employed two seine nets, which are highly efficient methods to capture small resident coastal fishes and migrant marine fishes, but which inherently vary in efficiency between habitat types and species (Franco *et al.*, 2012). On the scale of the Fraser River estuary, sampling at high tide when fish have the largest potential area across which to scatter, in turbid waters where schools cannot be visually targeted, is inherently limiting. However, previous seining at low tide on the outer flats of Roberts and Sturgeon Banks yielded similar species composition and catch to our study, but with higher catches of schooling fishes, including Chinook salmon (i.e., 1,253 Chinook salmon in 158 seines) (Greer *et al.*, 1980). Interestingly, this past survey found that Pacific Herring comprised the highest catch overall in the seine surveys, with shiner surfperch the fourth-highest after staghorn sculpin and starry flounder (Greer *et al.*, 1980). Due to the potential differences in gear efficiency between our net and theirs, and between high and low tide sampling, it is uncertain whether these differences in catch composition reflect changes in the fish community or are artifacts of the sampling methodology. Gear efficiency is difficult to quantify, but we assume that the presence of vegetation (eelgrass and marsh) decreased catch efficiency. The mesh size was very close between nets and targeted demersal and motile juvenile fishes successfully. The marsh net was approximately half the size of the purse seine, and a preliminary assessment of the area swept by each net using our GPS tracks supported that overall, the purse seine sampled roughly double the area of the beach seine for each set. Based on this, we assume the beach seine had decreased catch efficiency relative to the purse seine (eelgrass and sand flat). While the differences in gear type prevent a direct quantitative comparison of catches between the two vegetated habitats, such a dramatic difference in catch (73% of all fish in eelgrass, and 61% of all salmonids in marsh) suggests that there is a true difference between habitats and is noteworthy given that these habitats presumably had lower catch efficiency.

*2.5.1 Species richness and composition within habitats*

Our study supports a growing body of evidence that eelgrass meadows provide integral habitat for migratory and resident fish species (Unsworth, Nordlund and Cullen-Unsworth, 2018). The higher species richness in eelgrass than in marsh or sand flat habitat is potentially due to its greater productivity and provision of shelter. Eelgrass meadows support complex food webs, linking nutrients from primary productivity to higher trophic levels (Duffy *et al.*, 2015). The diet of juvenile chum salmon, for instance, may be predominantly comprised of eelgrass-associated zooplankton and benthic invertebrates (Kennedy, Juanes and El-sabaawi, 2018).

Aquatic vegetation can also provide shelter from predators for juvenile fishes (Magnhagen, 1988; Semmens, 2008), and spawning habitat (e.g. Pacific herring) (Fox, Paquet and Reimchen, 2018). Species richness and abundance have previously been shown to fluctuate in synchrony with eelgrass shoot density and blade length (Xu *et al.*, 2015), and indeed we found fish species richness in eelgrass to be significantly greater during summer months, when the vegetation had reached maximum growth, and lowest in fall months as the vegetation died back.

Each habitat reflected unique species communities, likely based on a combination of selectivity, life history traits, and abiotic tolerances. Increasingly, the connectivity between habitats has been emphasized as a foundation for functioning estuarine ecosystems (Boström *et al.*, 2011; Whitfield, 2017). It is imperative, then, that we understand the integrated use of connected estuarine habitats and their combined role in supporting nearshore fish communities. The combination of habitat types available and the connectivity and structure of the estuary may greatly influence the use of habitats across systems (Litvin *et al.*, 2018; Schrandt *et al.*, 2018). For salmon, which were caught in surprisingly low numbers in the eelgrass, the use of eelgrass vs. marsh may depend more on the estuary conditions that are present than the vegetation itself.

Vegetated habitats are influenced by water conditions: brackish marsh plants typically grow in turbid, low salinity (0.5 - 15 ppt) waters (Balke, 2017), whereas eelgrass thrives in clear, saline (10 - 30 ppt) water (Precision Identification, 2002). In the Fraser estuary, coal port and ferry terminal causeways block the flow of river water to Robert's Bank, resulting in clearer, more saline water, and leading to the expansion of the eelgrass meadows (Sutherland, Elner and O'Neill, 2013). These causeways also significantly lengthen the distance from the river mouth to the densest eelgrass habitat for emigrating salmon (Fig. 2.1). Meanwhile, the severe reduction and ongoing recession of brackish marsh owing to human activities and development in the

Fraser River estuary is especially concerning for salmon in this system (Balke, 2017). Restoration of tidal inundation to these habitats would increase connectivity and likely increase the use of these habitats by subyearling salmon migrants (Weitkamp *et al.*, 2014).

For juvenile salmon, precise habitat use appears to vary between estuaries, depending on local conditions (Sibert and Kask, 1978; Levings, McAllister and Chang, 1986), interspecific competition (Fraser, Starr and Fedorenko, 1982; Levings and Kotyk, 1983), and hatchery-wild intraspecific competition (Taylor, 1990; Korman, Bravender and Levings, 1997). In this system, marsh appears to be the most used habitat by emigrating salmon. Despite using a smaller net for marsh sampling, we consistently caught salmon in substantially higher numbers in marsh sites than eelgrass or sand flat sites throughout the emigration period. Importantly, we caught a very low proportion of the estimated total juvenile salmon migrating through the estuary during the emigration period, which would be on the order of tens of millions of fish. Many juvenile salmon pass relatively quickly through estuarine habitats (Weitkamp *et al.*, 2014) and sampling on the high tide when the full extent of the estuary would be accessible to fast moving salmon almost certainly contributed to our low catch rates. Brackish marsh is the first estuarine habitat encountered by emigrating salmon, as it is situated around the mouth of the river and the shoreline (Fig. 2.1). The repeated capture of juvenile salmon in the marsh signals the active use of these areas as the channels largely dewater at low tide. Recent sampling in the brackish marsh channels of the Fraser River estuary using fyke nets has yielded much higher catch (i.e., on the order of 500 - 1000 fish per sampling event during peak salmon emigration; David Scott, unpublished data), which supports our conclusion that this habitat is actively used by juvenile salmon, though catch of fast-moving species and life history types including sockeye salmon and Chinook yearling migrants remain low. Chinook salmon in the Fraser consist of both larger yearling migrants (growing in fresh water for the first year), and very small subyearling migrants, the latter of which include fish that may enter the estuary as newly emerged fry. Chum and subyearling Chinook salmon rear in the estuary for extended periods (Levy and Northcote, 1982), and the marsh offers less osmotically stressful and more sheltered habitat than the outer flats (Taylor, 1990; Gregory and Levings, 1998). Chum are adapted to osmotic changes at an earlier life stage (Björnsson, Stefansson and McCormick, 2011) and were found to use eelgrass habitat more extensively than Chinook in this study. Fraser River chum salmon populations had particularly high escapement in 2016 (Fisheries and Oceans Canada 2018, *Day 1 Post-season Presentation Fraser Chinook, Coho and Chum Salmon **amended Dec. 12, 2018*, retrieved from www.frafs.ca/Forum_Documents), resulting in much higher densities of juveniles migrating through the estuary in 2017. During years of high abundance, juvenile salmon may leave fresh water habitats early due to density-dependent effects (Freshwater *et al.*, 2017), which could explain the large schools of chum salmon we captured in eelgrass in 2017.

Differences in species composition between habitats diminished during peaks in abundance. For example, shiner surfperch were most abundant in eelgrass habitat, but were also caught in high numbers in marsh and sand flat habitats during their peak abundance in July. The sand flats physically connect the two vegetated habitats in the Fraser River estuary, which was reflected in the greatest species overlap between this habitat with the other two. The single unique fish found in the sand flats (longfin smelt) has previously been found in the eelgrass (Archipelago Marine Research Ltd., 2014b) and marsh (Levy, Northcote and Birch, 1979) in the Fraser, and likely would have been caught across all habitats in this study had it been more abundant. However, sand flat supported high abundances of arrow goby and flatfish in the estuary. The overarching compositional differences between habitats is consistent with results from a tropical estuarine system (Bloomfield and Gillanders, 2005) and with a recent meta-analysis (McDevitt-Irwin, Iacarella and Baum, 2016), with seagrass supporting the most species, and other vegetated habitats ranking higher than unvegetated sand, suggesting a broad pattern for similar coastal habitats. Spatiotemporal variation in community composition among habitats further highlights the importance of maintaining an intact seascape to allow migration and movement of fishes across seasons and changing life history needs (Duffy, 2006).

*2.5.2 Seasonal shifts in catch*

As predicted, we found temporal variation in the peak catch of different migratory fish species that was indicative of their unique life history strategies. Juvenile salmon peaked in spring as they entered the estuary and in the following months migrated out to the ocean (Fig. 2A2). Conversely, other migratory fishes had multiple peaks in catch and were virtually absent from the marsh during summer (Fig. 2A2), a pattern which was driven by Northern anchovy and Pacific sand lance. Anchovy are continuous spawners, and indeed we observed adults in the estuary followed by high catches of juveniles. This pattern occurred multiple times, with hundreds of anchovy caught in April, July, and September in 2016, interspersed by near zero catch outside of those times. Similarly, sand lance were virtually absent from the estuary until April, then were numerous until July, when they disappeared again. Resident fishes, however, had a consistent presence in the estuary and experienced much higher peaks in catch during warmer months (Fig. 2A2d,h), as predicted. Specifically, we noted increases in catch of adult resident fishes in the spring, followed by large numbers of juveniles in the summer, indicating reproduction during peak productivity in the estuary. Seasonal variation in productivity is common in temperate systems, with changes in flow, light, and temperature regimes leading to plankton blooms, vegetation growth, and subsequent increases in food availability for fishes during summer months (El-Sabaawi *et al.*, 2012; Chandler, King and Boldt, 2017). Smaller scale effects of localized temperature, salinity, pH, and dissolved oxygen may have a greater impact on resident species, which remain in the nearshore environment, as opposed to migratory species, which pass through over periods of days to weeks. Temperature can impact metabolic rates and affect food web interactions and fish growth (Attrill and Power, 2004; O'Connor, Gilbert and Brown, 2011), or cause physiological stress near the thermal limit of a fish (Teffer *et al.*, 2018); salinity and pH are physiologically limiting to fish and influence species composition in many systems (Martino and Able, 2003); dissolved oxygen is important for fish respiration and can be detrimental to fish at low levels (Schein *et al.*, 2011; Scott *et al.*, 2016). These environmental conditions vary by habitat and by season, both of which were found to have strong effects on resident species abundances. Temperature and year in particular played an important role in resident fish abundance, highlighting the effects of the 2016 El Niño.

### *2.5.3 El Niño effects*

The climate change-amplified 2016 El Niño consistently broke global records for highest sea surface temperatures, with a persistent warm water 'blob' remaining in North Pacific coastal waters, and the U.S. National Oceanic Atmospheric Administration recorded 2016 as the warmest year in their 137-year time series (Chandler, King and Boldt, 2017). These effects were apparent in our study, with increased water temperatures, a decreased freshet leading to higher and more stable salinity, increased pH, and increased dissolved oxygen content relative to 2017. Changes in sea surface temperature and hydrologic regimes lead to shifts in the migratory patterns of many fish species (Kortsch *et al.*, 2015), including Northern anchovy, which are currently at the northern extent of their range in British Columbia (Duguid *et al.*, 2019). During the 2016 El Niño, we caught a high number of anchovy at a variety of life stages, compared to a single adult anchovy in 2017, supporting the idea that El Niño effects cause range shifts in migratory species. This influx of biomass can potentially alter the food web by providing increased prey for piscivorous fishes and increased competition among planktivores (Duguid *et al.*, 2019). We also observed large increases of shiner surfperch and three-spined stickleback in 2016, hardy species that have been associated with anthropogenic disturbance (Iacarella *et al.*, 2018), and are known to have overlapping diets with juvenile Pacific salmon (Weitkamp *et al.*, 2014). This coincided with lower catches of several other species, particularly Pacific sand lance and flatfishes, which may be more sensitive to changes in temperature and hydrology. Earlier and weaker freshets may also lead to earlier spring blooms, potentially creating mismatches for fish food web interactions (Riche, Johannessen and Macdonald, 2014; Sato *et al.*, 2018). While interannual variation is expected in such a dynamic system, we encourage ongoing monitoring of the community composition in this system to detect potential climate impacts on the coastal food web.

### *2.5.4 Conclusions*

Estuarine fish communities exhibit complex spatiotemporal variation in habitat use, and multiple habitat types are required to conserve overall fish species richness and abundance. Focusing on a single habitat or species risks underestimating the value brought to the system by each component - in the case of the Fraser, focusing solely on eelgrass as the most productive habitat could lead to further declines in salmon populations with the loss of remaining marsh. This supports the premise that connected seascapes of different habitat types maintain greater biodiversity and productivity, and we suggest that estuaries be managed as such.

## 2.6 Acknowledgements

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# Chapter 3 - Chinook salmon exhibit long-term rearing and early marine growth in the Fraser River, B.C., a large urban estuary

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## 3.1 Abstract

Estuaries represent a transition zone for salmon migrating from freshwater to marine waters, yet their contribution to juvenile growth is poorly quantified. Here, we use genetic stock identification and otolith analyses to quantify estuarine habitat use by Chinook salmon (*Oncorhynchus tshawytscha*) – the Pacific salmon species considered most reliant on this habitat – in Canada's most productive salmon river, the Fraser. Two years of sampling revealed subyearling migrant ("ocean-type") Chinook from the Harrison River to be the estuary's dominant salmon population throughout the emigration period. These Chinook salmon were caught predominantly in the estuary's brackish marshes but shifted to more saline habitats as they grew. Otolith analyses indicated that these Chinook salmon have wide-ranging entry timing (from February to May), and longer estuarine residency (weeks to months, mean 41.8 days) than estimated by prior studies, but similar daily growth rates (mean 0.57 mm +/- 0.13 SD) across entry dates and residency periods, implying sufficient foraging opportunities throughout the emigration period and habitats. Together, these results suggest that estuarine habitat is more important for early marine growth of subyearling migrant Chinook salmon than previously recognized.

## 3.2 Introduction

Chinook salmon display high plasticity in their life history strategies, including the extent of rearing time in freshwater before downstream migration (Bourret, Caudill and Keefer, 2016; COSEWIC, 2018). Subyearling migrant ("ocean-type") Chinook salmon emigrate within their first year, sometimes shortly after hatching at sizes as small as 20 mm (Healey, 1991; Weitkamp *et al.*, 2014). These fish are smaller than their yearling migrant counterparts, which remain in freshwater for at least their first winter and may be more than 100 mm long before they migrate downriver. Conversely, subyearling migrants rely more heavily on estuarine and nearshore marine environments as they grow to smolt sizes (> 60 mm fork length on average) (Healey, 1991; Weitkamp *et al.*, 2014). Size-selective mortality influences Chinook salmon at multiple life stages, and there has been particular interest in how growth during emigration may influence survival (Beamish, Pearsall and Healey, 2003; Duffy and Beauchamp, 2011). The critical-size critical-period hypothesis proposes that juvenile salmon must reach a minimum size threshold to survive their first winter, and predicts that individuals that grow faster during the early marine phase, which begins in estuaries, will be better able to avoid predation and more resilient to periods of starvation if food becomes scarce (Beamish and Mahnken, 2001).

Estuaries provide a gradual transition for juvenile salmon from fresh to saline water conditions. This transition comes with metabolic costs and may cause physiological stress, but this stress generally decreases with increasing body size (Quinn, 2018). This may partially explain why subyearling migrant Chinook salmon spend more time in estuaries than do larger yearling migrants (Weitkamp *et al.*, 2014). Estuaries also provide an increase in food availability relative to freshwater habitat (Quinn, 2018), while still offering high energy density insect prey (Levings, Conlin and Raymond, 1991; Davis *et al.*, 2019).

The Fraser River estuary sits at the mouth of Canada's most productive salmon river, which supports 17 genetically- and ecologically-distinct Chinook salmon populations (Northcote and Atagi, 1997; COSEWIC, 2018). Most of these populations are now considered to be Endangered or Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Fisheries and Oceans Canada, 2019), and the estuary itself has been highly modified and continues to face multiple cumulative threats including urban, agricultural, and industrial developments (Schaefer, 2004; Kehoe *et al.*, 2020). Yet, few studies have examined the abundance or growth of juvenile salmon in the estuary, and none employed modern technologies such as genetic stock identification (GSI) or otolith analysis (i.e. Greer et al. 1980; Levy and Northcote 1982; Levings et al. 1991), such that its current importance for these populations is unknown. Studying the use of estuarine habitat by juvenile salmon can, however, be difficult, with low mark-recapture success rates and hazardous sampling conditions, particularly in large delta systems such as the Fraser River (Levings, Greer and Miller, 1983; Sutherland, Elner and O'Neill, 2013). Otolith analysis from fish captured post-migration can provide a detailed picture of the life history of individual fish, including quantitative measures of residency in different water bodies (Miller, Gray and Merz, 2010; Volk *et al.*, 2010).

Here, we present the first study to apply modern otolith and GSI technology to quantify estuarine emigration timing, residency, and growth of wild Chinook salmon in the Fraser River estuary. Our objectives were to determine whether (1) Chinook salmon display a wide range of entry timing and residency period, capitalizing on early estuarine entry to distribute density between freshwater and estuarine habitats, and (2) estuarine residency is positively correlated with growth and size at capture.

## 3.3 Methods

### *3.3.1 Study system*

The Harrison River, a tributary of the Fraser, once produced the highest proportion of fall subyearling migrant Chinook salmon in the Salish Sea (Fraser, Starr and Fedorenko, 1982; Murray and Rosenau, 1989). Declines in this population have led to its recent designation as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC)

(Fisheries and Oceans Canada, 2019). The juvenile emigration in 2016 followed the strongest return of Harrison Chinook salmon in the previous decade, presenting an important opportunity to study the natural rearing dynamics of this population. The Harrison River is a continuation from the glacier-fed Lillooet River, which feeds into Harrison Lake. Harrison River drains the lake for 18 km and is joined by the small Chehalis River just before it meets the Fraser. Here, pockets of freshwater riparian habitat may provide rearing habitat for juvenile salmon. From the Harrison River confluence the Fraser River extends another ~30 km to the tidal wedge near Mission, B.C., after which off-channel habitat loss has been extensive, with little remaining in the final 80 km of river until the Woodward Island marsh complex near the mouth (M5, Fig. 3.1). Extending from the mouth of the river are large tidal flats (Roberts and Sturgeon Banks), which were formed from thousands of years of fluvial deposits and are characterized by shallow slopes and low to moderate salinity (Balke, 2017). Much of the river has been channelized such that the majority of the flow exits via the Main (southern) arm and (a small proportion via) Canoe Pass (Dashtgard *et al.*, 2012), which together host small islets and channels that represent some of the last intact brackish marsh habitat in the estuary (Fig. 3.1). The majority of the Fraser delta has been permanently cut-off to salmon or altered by industrial, agricultural, and urban development (Waldichuk, 1985; Levings, Conlin and Raymond, 1991). While the exact boundaries of the Fraser estuary are subjective (e.g. influence of freshwater in the surface layer extends beyond the Strait of Georgia, however, man-made barriers along the northern and southern ends of the delta create local high salinity gradients by restricting the river flow), we define the estuary as the area spanning the maximum upstream saltwater intrusion (just after the splitting of the river into the North and Main arms ~30 km from the delta front; orange bar, Fig.

3.1) to the point of shelf drop-off into the Strait of Georgia at the seaward edge of Roberts and Sturgeon Banks (edge of habitat polygons, Fig. 3.1).

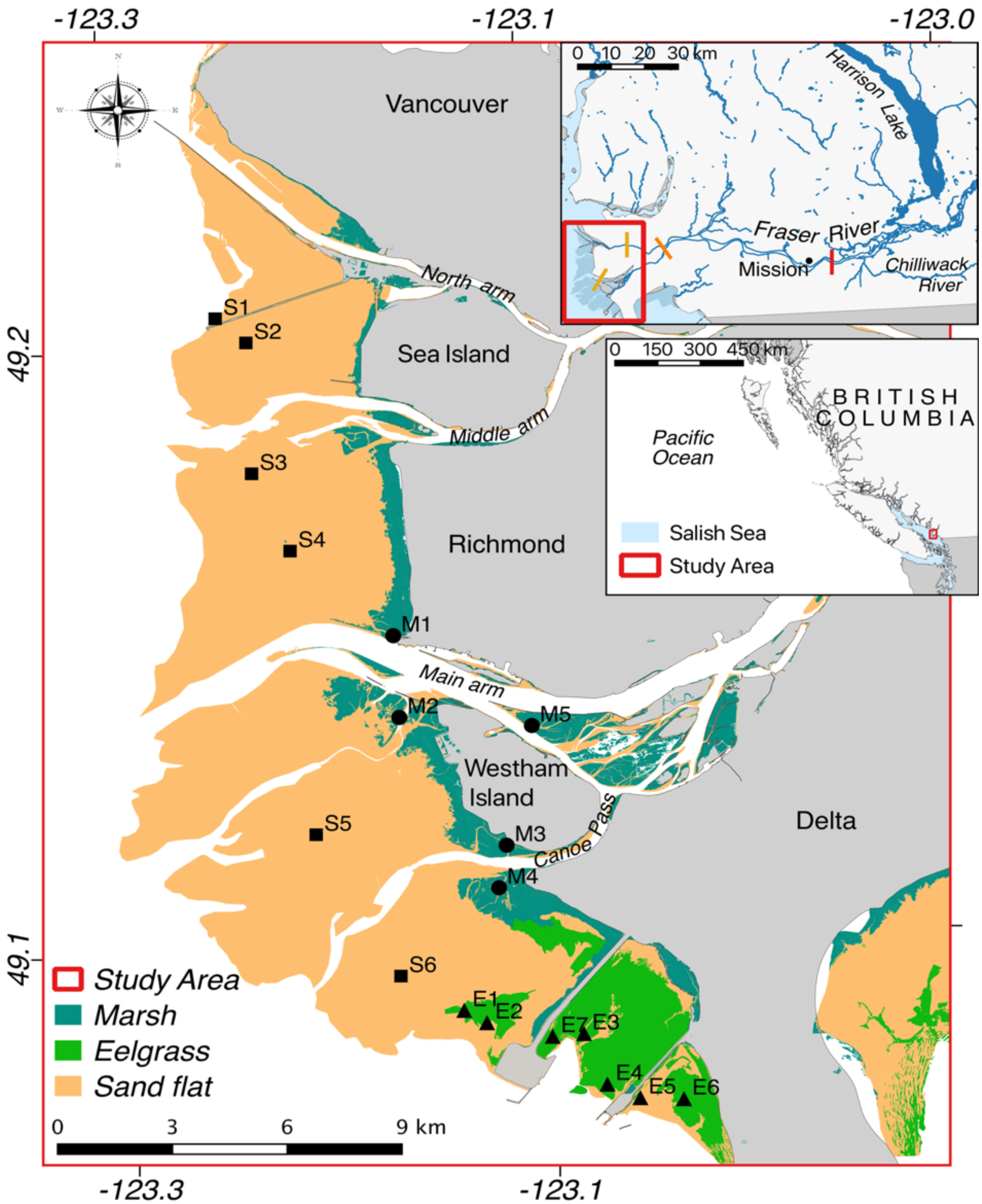


**Figure 3.1** Sampling locations within the marsh (M1-M5), sand flats (SF1-SF6), and eelgrass beds (E1-E6) of the Fraser River estuary, British Columbia, Canada. All sites were sampled each year, with the exception of E6, which was replaced by eelgrass site 7 (E7) in 2017. Gold lines in

top inset show the maximum upstream extent of saltwater intrusion during freshet (highest river flows). The dark orange line shows the maximum upstream extent of saltwater intrusion during base river flows (i.e., earliest point of estuarine entry) at ~30 km from the delta front. The red line marks the furthest upstream point of observable tides ~90 km from the delta front. Map data from the B.C. Data Catalogue's (https://catalogue.data.gov.bc.ca/dataset) Freshwater Atlas (freshwater) and Canadian Hydrographic Service (coastline), Natural Earth (British Columbia polygon), and Norman Maher (Salish Sea boundary). Habitat polygons adapted from the Habitat Inventory of the Lower Fraser River Estuary, 2002/3 (Fraser River Estuary Management Program). Saltwater intrusion points and tidal extent based on Dashtgard et al. (2012).

### *3.3.2 Fish sampling*

Sampling sites were selected based on historic surveys of the estuary and expanded to represent key habitat types available in the estuary - detailed description in Chalifour et al. 2019. We surveyed 17 estuarine sites approximately every two weeks at high tide from March 29 to July 15 in 2016, with an additional two sampling rounds (i.e., sampling all sites) between September 19 and October 12. In 2017, we repeated these surveys from March 05 to July 15, with two days of additional sampling August 21-22. Each sampling event at a site consisted of three non-overlapping, round-haul seine sets from a small vessel. We used a custom purse seine (40 m long x 4 m wide bunt [4 mm mesh] and 3 m wide bag [6 mm mesh]) to survey outer (eelgrass and sand flat) sites from a modified crab fishing vessel, and a beach seine (20 x 3 m with a 1.5 x 1.5 m bag [3 mm mesh]) to survey the inner (marsh) sites from a motorized dinghy.

In each set, we identified all juvenile salmonids to species and measured fork length and body depth prior to release. From these we obtained 293 and 543 fin clips in 2016 and 2017, respectively. Fin clips were stored on Whatman sheets for subsequent genetic stock identification

(GSI) via analysis of microsatellite variation (Beacham, Jonsen and Wallace, 2012). We also euthanized and retained the first 10 Chinook (maximum) collected per site, resulting in a total subsample of 254 juvenile Chinook salmon from 2016; no salmon were retained in 2017. All handling and sampling of fish was conducted following the guidelines set out by the Canadian Council of Animal Care and the approved animal use protocol 2016-010(1) with the University of Victoria. Retained fish were frozen at -20ºC for further analyses.

### *3.3.3 Otolith analyses*

Our sampling methodology did not efficiently capture faster moving populations of fish such as yearling migrant Chinook salmon populations (Chapter 2). Due to this limitation, we focused our otolith analysis on subyearling migrant Chinook salmon, which represented the majority of our catch throughout the emigration period. Based on our GSI results, we assessed the otoliths from a subsample of the retained 2016 Lower Fraser River (Harrison) Chinook salmon (final n=91) for variations in estuarine entry date, residency period, and back-calculated estimates of body growth. Sagittal otolith pairs from frozen juvenile Harrison Chinook salmon (initial n=153) were extracted and stored dry in plastic sample trays, with the left otolith preferentially analyzed unless lost or broken. We attempted to select otoliths from Harrison Chinook salmon that were caught throughout the season and represented all three estuarine habitat types, however, most of the retained fish were caught in May in marsh habitat and smaller otoliths were more subject to damage during analysis (Table 3.1). Otoliths were washed in distilled water and fixed sulcus-side up onto a glass slide using heated Crystalbond™ resin. To minimize external contamination and breaking, we wet-polished otoliths using distilled water and 30 μm and 3 μm aluminum oxide lapping film, finishing with 0.3 μm diamond lapping film from 3M. Otoliths were polished gradually on both sides by reheating the resin and flipping the otolith, until clear daily growth rings were visually apparent under a compound microscope at 20x magnification. Digital images were collected throughout the polishing process using a Lumix microscope-mounted camera. All otolith measurements were made using Fiji, a distribution of ImageJ (Schindelin *et al.*, 2012).

**Table 3.1** Summary of 2016 Harrison Chinook salmon otoliths analyzed by month and habitat of capture. For each month the number of otoliths extracted for polishing is shown with the final n analyzed via LA-ICPMS given in brackets.

| | April | May | June | July | Total |
|---|---|---|---|---|---|
| Marsh | 9 (3) | 60 (41) | 36 (23) | 0 | 105 (67) |
| Sand flat | 1 (0) | 26 (16) | 8 (2) | 0 | 35 (18) |
| Eelgrass | 0 | 7 (2) | 5 (3) | 1 (1) | 13 (6) |
| Total | 10 (3) | 93 (59) | 49 (28) | 1 (1) | 153 (91) |

After polishing, otoliths were fixed to petrographic slides and re-washed using distilled water for microchemical analysis using laser ablation with inductively coupled plasma mass spectrometry (LA-ICPMS). We used a New Wave UP-213 laser and Thermal X Series II ICPMS at the School of Earth and Ocean Sciences at the University of Victoria to measure otolith calcium ($^{43}Ca$), strontium ($^{86}Sr$), and barium ($^{138}Ba$) isotopes. The laser was set at a pulse rate of 10 Hz with a 30 µm spot size and firing rate of 5 $\mu m \cdot s^{-1}$. Strontium and barium to calcium ratios deposited in otoliths can be used to infer migratory patterns in fish, particularly from fresh to brackish or marine environments in juvenile salmon (Miller, 2011). To accurately capture these environmental transition zones for small otoliths, we ran a laser transect from the dorsal to ventral edge through the core across the widest point of the otolith (Sanborn and Telmer, 2003). We scanned 100 otoliths representing 98/153 fish (two pairs run). Of these fish, seven were excluded from final analyses due to either low detectability (likely due to over-polishing or glue interference with the LA-ICPMS) or difficulty in aligning the LA-ICPMS results with the visual growth measurements post-scan, leaving a final sample size of 91 fully measured otoliths (Table 1). At the beginning and end of each slide, and after every five otoliths, we ran three National Institute of Standards and Technology (NIST) glass standards to account for instrument drift (NIST615, 613, and 611). Ion data were calibrated by subtracting background count rates and correcting for the precision of measurements of the NIST glass standards. During the course of the study, the mean percent relative standard deviations for NIST 615 glass were $^{86}$Sr=1.1%, $^{138}$Ba=3.7%, for NIST 613 were $^{86}$Sr=1.0%, $^{138}$Ba=2.8%, and for NIST 611 were $^{86}$Sr=0.3%, $^{138}$Ba=2.1%, respectively. Ion concentrations were converted to molar ratios using calcium as an internal standard.

We identified the estimated estuarine entry point (i.e. below the maximum upstream saltwater intrusion, Fig. 3.1) as the first inflection of Sr:Ca concentration, where Ba:Ca were simultaneously increasing, indicating a brackish environment (Volk *et al.*, 2010; Miller, 2011). This was initially done visually, and then confirmed via a z-test on the running averages of 10 values in the region including the inflection to determine when the increase was significant (Volk *et al.*, 2010). Where growth lines were visible across the entire otolith, we further validated the dorsal inflection point against the ventral inflection point to ensure that they corresponded to the same visual growth line. Although line scans are less precise than point measures in deriving specific concentrations of isotopes, they consistently identify transition points between habitats by accurately capturing inflections in these concentrations (Sanborn and Telmer, 2003). In 44% of our samples the Sr:Ca concentrations and Ba:Ca concentrations at the otolith edge (reflecting the previous 2-14 days) were more aligned with a high barium, low salinity condition than with any of the high salinity conditions tested in Miller et al. (2011). However, based on the results of this study most of these fish had been in the estuary for three weeks or more, including six individuals caught in the outer estuary (in sand flat and eelgrass sites), reflecting the strong freshwater signature of the Fraser River estuary (Fig. 3S1).

The salinity of the Fraser River estuary ranges to 0 ‰ and declines over the emigration period with the onset of the spring freshet (La Croix *et al.*, 2015), which limits the extent of saltwater influence on the estuary (Dashtgard *et al.*, 2012) and may explain the post-estuarine entry ratios detected in our samples. Barium and strontium concentrations are naturally low in the Harrison River system (Voss *et al.*, 2014), so it may be possible that an increase in these isotopes would be seen after entry into the Fraser mainstem. Although they increase seasonally with the spring freshet, these ion concentrations are also at their lowest values at the mouth of the Fraser, relative to its headwaters (Cameron *et al.*, 1995; Voss *et al.*, 2014). Although our measured otolith concentrations of Sr:Ca were low, they were still comparable to the ranges of ratios observed in the Salmon River, a much smaller system with lower freshwater influence (Volk *et al.*, 2010). Given that the flow rates of the Fraser River are highest in the spring and peak freshet occurred in May in 2016, it is likely that saltwater intrusion was limited to the seaward edge of the brackish marsh (yellow bars, Fig. 3.1), resulting in a very weak marine isotopic signature in the estuary. We therefore assume that despite the relatively low Sr:Ca concentrations at the inflection point, the Sr:Ca inflection indicates entry into the estuary proper - below the maximum extent of saltwater intrusion during base river flows ~30 km from the delta front (orange bar, Fig. 3.1; i.e., likely maximum extent of marine isotopic signature), since the salinity measured at our marsh sites was often below 5‰ even at high tide (Hanna Instruments 9829 Multiparameter Meter; Table 3S1). Strontium accumulates over time in the otolith after entry into brackish waters, and tends to remain near its peak concentration, such that it does not return to pre-inflection levels despite fluctuations in salinity in estuarine environments (Volk *et al.*, 2010). The otoliths measured in this study demonstrated increasing Sr:Ca ratios at the otolith edge (post-inflection) as salmon migrated outward to habitats with increasing salinity and as salmon spent more time in the estuary (see results), aligning with Volk et al.'s findings.

One challenge with LA-ICPMS line scans is the lack of a standardized method for aligning the microchemistry results with post-ablation visual landmarks - such as otolith daily growth rings (Danek, Bell and Laroque, 2015). To address this, we used inflections in the calcium signatures to identify the otolith edges on the microchemistry scan and calculated the actual scan rate as the otolith scan time (using these edges) divided by the measured width of the otolith along the laser transect (Andrew Claiborne, Washington Department of Fisheries, Washington, personal communication, 2018). All otoliths were measured by the same trained reader, with each measurement taken three times and averaged (Fig. 3.2). A subsample of ten otoliths were re-evaluated three times in a blind precision study, with a final precision rate of over 90% for all averaged measurements (> 95% for most). When counting daily growth rings, we assumed that visual otolith increments approximated daily growth and counted a minimum of seven daily rings to account for natural variability (Chittaro et al. 2015). We avoided using the width of outermost increments in our growth measurements, as these may still have been forming at capture and are prone to damage during preparation (Campana, 2001). We calculated residency time as the total estuarine growth period divided by the average daily growth, to give an approximate number of days in the estuary prior to capture. This is considered to be a minimum residency time, as all fish were captured within the estuary and may have remained longer had they evaded capture. We obtained estuarine entry date by subtracting the residency period from the date of capture.

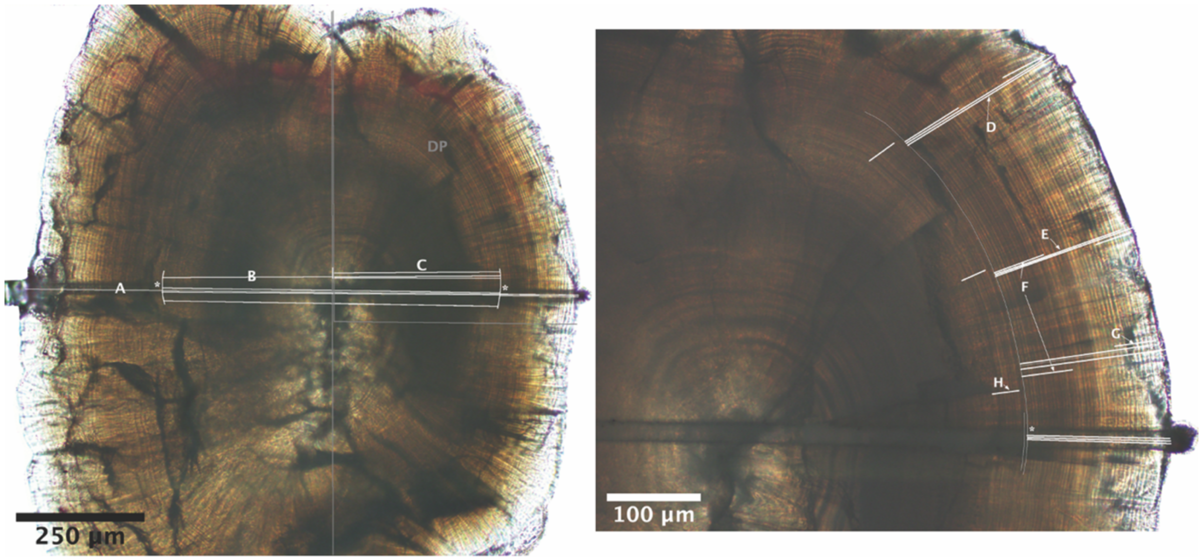


**Figure 3.2** Diagram of otolith measurements taken. Each measurement was taken three times and the mean result was used for subsequent analyses. A: Otolith width, B: Otolith width at estuarine entry, C: Otolith radius at estuarine entry, D: Total estuarine growth, E: Mean daily estuarine growth (measurement divided by count of daily increments), F: Early estuarine daily growth, G: Late estuarine daily growth, H: Freshwater daily growth. *: Estuarine entry inflection as identified by LA-ICPMS, DP: Dorso-posterior quadrant of the sagittal otolith.

*3.3.4 Growth statistics*

We back-calculated fork length at time of estuarine entry by testing a series of relationships between measured otolith radius and width (at entry and capture) and fork length (at capture), including linear regressions and a biological intercept model. While some studies have found a biological intercept model to best represent growth over time due to its ability to incorporate estimated size at hatching (Zabel et al. 2010), we did not see a strong discrepancy in the relationship at small sizes, the model did not fit our data as well as a linear model, and we could only measure size at hatching from a subset of our otoliths. We therefore determined that the best model for our data was a simple linear regression model using otolith width and following the Scale Proportion Hypothesis and the Body Proportion Hypothesis, taking the mean of the results from each hypothesis to minimize error (Fig. 3S2; Francis 1990). Based on these results, daily growth and total estuarine growth were converted into somatic growth using the calculated fork length at entry for each individual fish (e.g., mean daily growth of fish *i* = [fork length at capture of fish *i* - fork length at entry of fish *i*] / number of days in the estuary of fish *i*).

We assessed the relationship between growth and estimated entry date, and between growth and estuarine residency, using linear regression (function 'lm' in R :: stats). Similarly, we assessed the relationship between size at capture and catch date. We used ANOVA (function 'aov' in R :: stats) to test the differences in size between habitat types, and used a Tukey's honestly significantly different (HSD) post-hoc test to compare pairwise differences among groups (i.e. fork length of Harrison Chinook salmon captured in sand flat compared to marsh, fork length in eelgrass compared to marsh, and fork length in eelgrass compared to sand flat; function 'TukeyHSD' in R :: stats). The range of estuarine entry timing and estuarine residency period were summarized using frequency plots. When analyzing residency period, six outlier fish that were below 45 mm fork length were removed, as they were assumed to be too small to survive migration into the ocean, thus biasing the minimum residency period. All analyses and figures were completed using R version 3.6.2 (R Core Team, 2019), except for the site map (Fig. 1), which was created in QGIS version 3.6.3 (QGIS Development Team, 2019), and the otolith microscope images (Fig. 3.2), which were assembled in Adobe Photoshop 2020.

*3.3.5 Validation of wild vs hatchery fish*

The Harrison Chinook salmon population had an estimated wild spawner return of 91 906 in the Fall of 2015 (adjusted for hatchery influence (pNOS); NuSEDS database, DFO Pacific, Vancouver, B.C., unpublished data), which is the highest return since 2012. Based on estimated fecundity and egg to fry survival rates, this would have produced between 9.6-325 million fry in 2016 (Healey and Heard, 1984; Healey, 1991; Fisheries and Oceans Canada, 2019). This population has very low enhancement from hatcheries (~300 000 juvenile fish annually, all visually marked and released in June) within the spawning boundaries of the Harrison at the Chehalis River hatchery (Shaun Spenard, Chehalis River Hatchery, B.C., personal communication, 2020). However, genetically similar Harrison-origin fish are produced in large numbers at the Chilliwack River hatchery, located 35 km from the confluence of the Chilliwack/Vedder River with the Fraser mainstem above Mission (~ 1.5 million fry released annually, increased to 2.5 million in 2020; broodstock from the Chilliwack supplied to the Capilano hatchery beginning in 2013), and it is likely that straying between these two populations occurs. Microsatellite-based methods could not distinguish between natural-origin Harrison and hatchery-origin Chilliwack Chinook salmon in 2016, but this is now possible with the application of single nucleotide polymorphism (SNP) technology coupled with parentage-based tagging of hatchery fish (Beacham *et al.*, 2018) (SNP not used in this study).

In 2016 we caught sixteen Harrison Chinook salmon that were adipose fin-clipped (only two in 2017), indicating that they were hatchery produced and implanted with a coded-wire tag (CWT). In addition, we identified potential thermal marks in five of the 153 otoliths originally selected as 2016 Harrison fish and removed these from further otolith analyses. By comparing the size at release and the release date of the Chilliwack hatchery fish in 2016 (5.6 g, May 15-16, 1 004 219 smolts age 0+ with 194 702 marked by adipose fin-clip and CWT; Jeremy Mothus, Chilliwack Hatchery, B.C., personal communication, 2018) to the fork length (mean = 57.5 mm, range = 34.0-128.0 mm) and mass (mean = 2.64 g, range = 0.51-14.82 g) at capture and estimated fork length (mean = 37.7, range = 18.5-67.6 mm) and mass (mean = 0.76, range =

0.26-2.86 g) at entry of the Harrison Chinook salmon retained in the otolith analyses, we concluded a very low likelihood that any of the 91 analyzed fish were of hatchery origin.

In addition to the thermally-marked fry releases, the Chilliwack hatchery also supplies eggs and (in some years) thermally-marked fry to small community hatcheries in other Lower Fraser tributaries. In 2016, there were 120 000 unmarked eggs exported to the Alouette River hatchery and 70 000 to Chapman Creek. There were no additional thermally marked fry released to other locations in 2016 (Jeremy Mothus, Chilliwack Hatchery, B.C., personal communication, 2018). Thus, although it is possible that fish hatched from these eggs were included in our samples, it is unlikely given that the ratio of enhanced to wild fish was so low.

## 3.4 Results

Over two years of sampling, we caught 1 515 juvenile salmon in 288 sampling events, of which the majority (1 155) were Chinook (n=23 were determined as hatchery-origin and removed from following results). Based on 564 genetic samples over both years, 490 (87%) were identified as lower Fraser fall Chinook salmon from the Harrison or West Chilliwack tributaries (hereafter referred to as "Harrison").

### *3.4.1 Emigration timing*

Peak Chinook salmon catch per unit effort differed between the two sampling years (Fig. 3.3A). In 2016 the highest Chinook salmon catch was in April (CPUE=12, n=320), of which an estimated 94% were identified as Harrison (n=88/94 GSI samples; Fig. 3.3B), followed by an average of four Chinook salmon per sampling event in May (n=114), and only one in June (n=46, Fig. 3.3A). In 2017, sampling began three weeks earlier and Chinook salmon CPUE was four in March and April (n=119 and 146, respectively), with peak abundance in May (CPUE=8, n=255).

Harrison fish were the first Chinook salmon to arrive in the estuary in both years (Fig. 3.3B). These fish were caught on our earliest sampling days in March, having entered the estuary as early as February. Based on otolith back-calculated entry points, more than 80% (n=74/91) of Harrison Chinook salmon entered the estuary in March and April of 2016, with fish entering earlier residing for longer in the estuary prior to capture (Fig. 3.4). Compared to upriver Chinook salmon populations, Harrison Chinook were caught consistently in the estuary from March through July, after which all salmon catches rapidly declined to zero (Fig. 3.3B). In October 2016, a single Chinook salmon (210 mm fork length) was caught in the outer sand flats, and no other salmonids were seen in the fall.

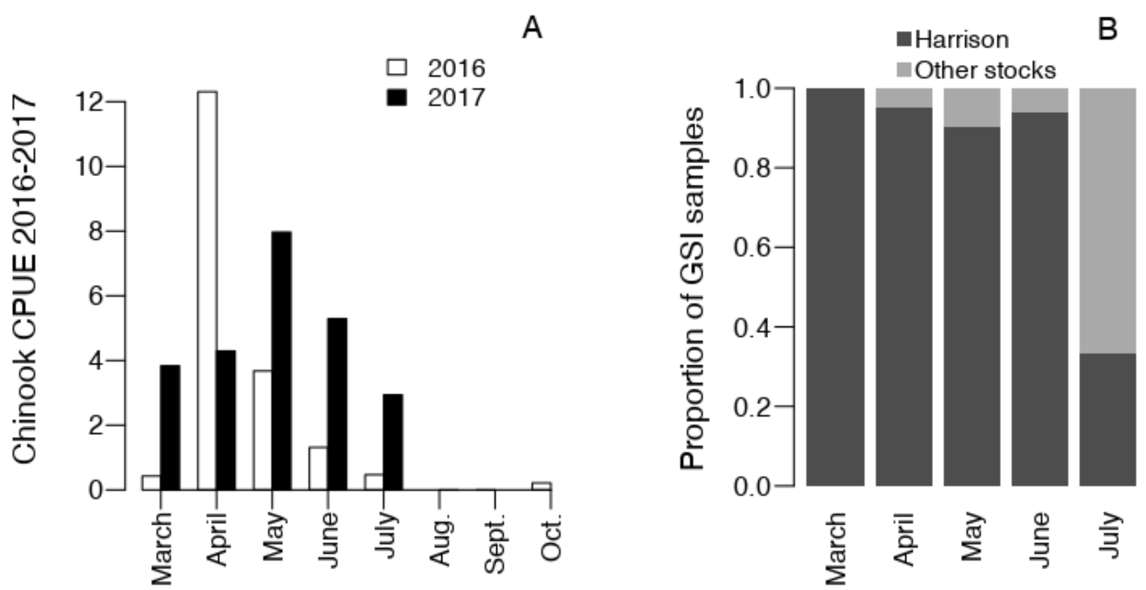


**Figure 3.3** Chinook salmon emigration patterns in the Fraser River estuary. A) Catch Per Unit Effort (CPUE; site*day sampling event) summarized by month for all Chinook salmon at 17 sites in the Fraser River estuary in 2016 (white bars) and 2017 (black bars). Effort was comparable

between years, with the exception of lower sampling effort in March in 2016 (n=14) vs 2017 (n=31), higher effort in June 2016 (n=35) vs 2017 (n=17), and no sampling in September or October in 2017. Note the single Chinook salmon in October 2016 has been inflated for visual purposes. B) Proportion of genetic stock identification (GSI) samples that were identified as lower Fraser fall Chinook (Harrison) or other stocks.

*3.4.2 Harrison Chinook Salmon Estuarine Residency*

Otolith analyses confirmed that Harrison Chinook salmon enter the estuary at different times throughout the emigration period, with most entering before May in 2016. Estuarine residency varied across the season among the captured fish (41.8 +/- 17.7 days (mean +/- SD); Fig. 3.4) and was negatively correlated to estuarine entry ($R^2 = 0.55$, $P = 6.1 \times 10^{-16}$; Fig. 4C), such that the earliest fish to enter the estuary resided the longest. The majority of fish appeared to reside in the estuary for 30-50 days (n = 41/91), with some captured after fewer than 20 days (n = 8/91, of which 4 were smaller than 45 mm indicating their minimal age and underestimation of the total residency calculation), and one fish 89 days after estuarine entry. Although there appeared to be a tendency for residency of fish caught in the sand flats to be lower than those caught in the marsh (Fig. 3.4C), the difference between the two was not statistically different. There also appeared to be two clusters of marsh fish (Fig. 3.4C), with one set of data points slightly higher than the other. This pattern was explained by catch date, with fish caught earlier (< Julian date 145; May 26, 2016) also entering the estuary earlier than those that were caught later (> Julian date 144). However, these two groups of marsh fish, based on their catch date, did not experience different total residency periods.

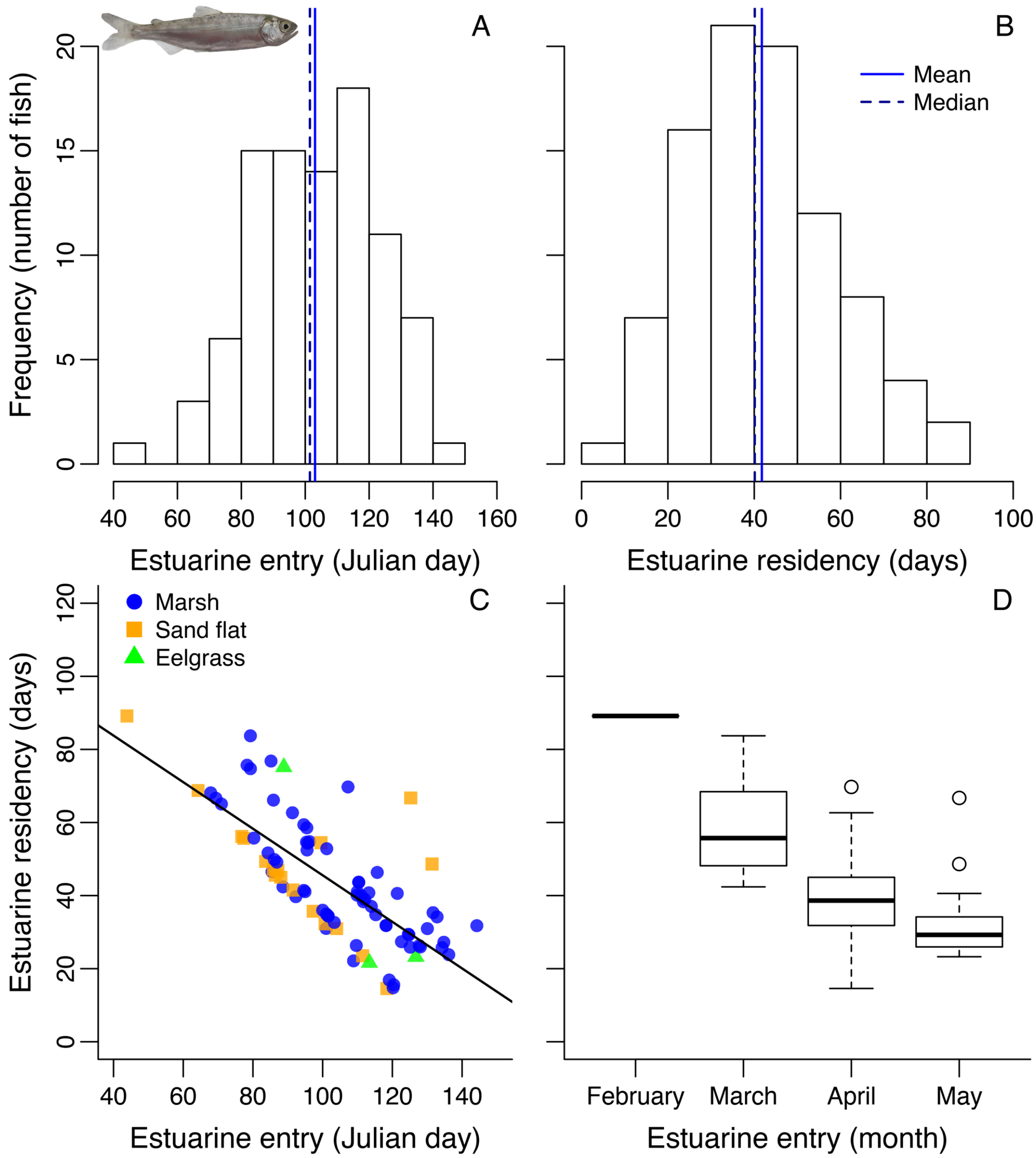


**Figure 3.4** Juvenile Harrison Chinook salmon estuarine entry timing and residency prior to capture, based on otolith-derived estimates. Panel A shows the range of entry timing and Panel B shows minimum residency. Panels C and D show the relationship between residency and entry timing. Entry day explained 54.7 % of the variation in residency period ($P = 6.1\text{x}10^{-16}$; C). Julian day 100 corresponds to April 9, 2016 (leap year).

*3.4.3 Estuarine Habitat Use*

Of the three estuarine habitats surveyed 78% of the salmon were caught in the brackish marsh, which is the first estuarine habitat encountered and the one with the lowest salinity (Table 3S1). This pattern was strong enough to suggest a true difference in abundance between habitats, despite the different gear types used in the marsh and outer habitats (Chalifour *et al.*, 2019). Concentrations of Sr:Ca at the otolith edge (i.e., the most recent bone deposition prior to capture) indicate that the marine signature increased both as Chinook salmon moved outward to more saline habitats and as they spent more days in the estuary, regardless of habitat (Fig. 3.5).

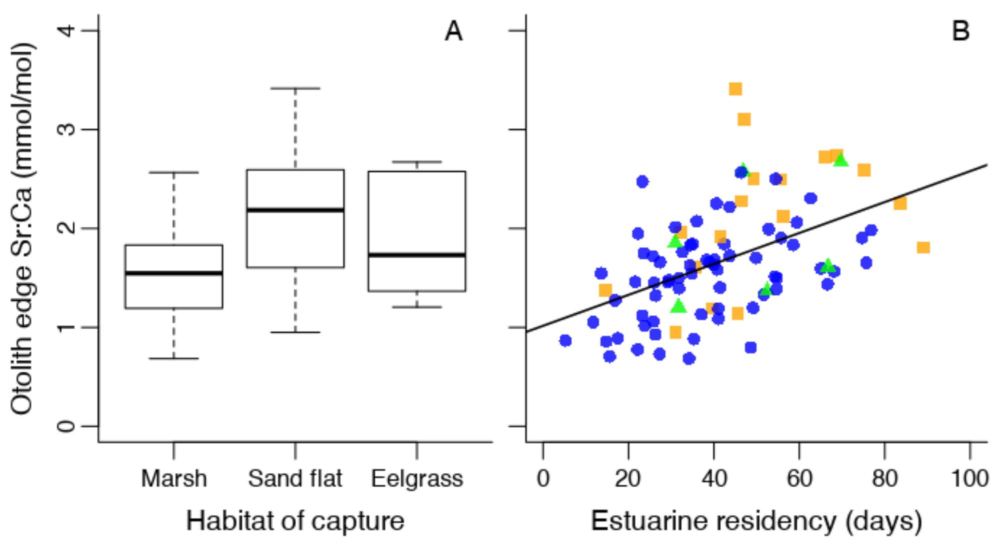


**Figure 3.5** Validation of estuarine signature in juvenile salmon otoliths. Harrison Chinook salmon caught in 2016 otolith edge Sr:Ca stable isotope concentrations increase with increasing salinity (A) and time in the estuary (B) in three habitat types: marsh (blue circles, n=67), sand flat (orange squares n=18), and eelgrass (green triangles n=6). Estuarine residency explained 24% of the variation in Sr:Ca across all habitats ($P$ = 1.5 x $10^{-07}$; B), showing the accumulation of strontium over time despite fluctuating salinity in the estuary.

Harrison Chinook salmon were predominantly caught in the marsh at small sizes, after which they migrated out to the flats into more saline environments, as indicated by the larger size composition of Harrison fish in eelgrass and sand flat (Fig. 3.6) and the increase in catch in these outer habitats later in the season (Fig. 6B; $R^2$ = 0.46, 0.38, and 0.15, $P$ = 2.2x10$^{-16}$, 6.1x10$^{-09}$, and 1.6x10$^{-04}$ for fork length vs. catch date in marsh, sand flat, and eelgrass sites, respectively). All size-habitat comparisons were statistically significant (ANOVA, $F_{2, 487}$ = 173, $P$< 2.2 x 10$^{-16}$).

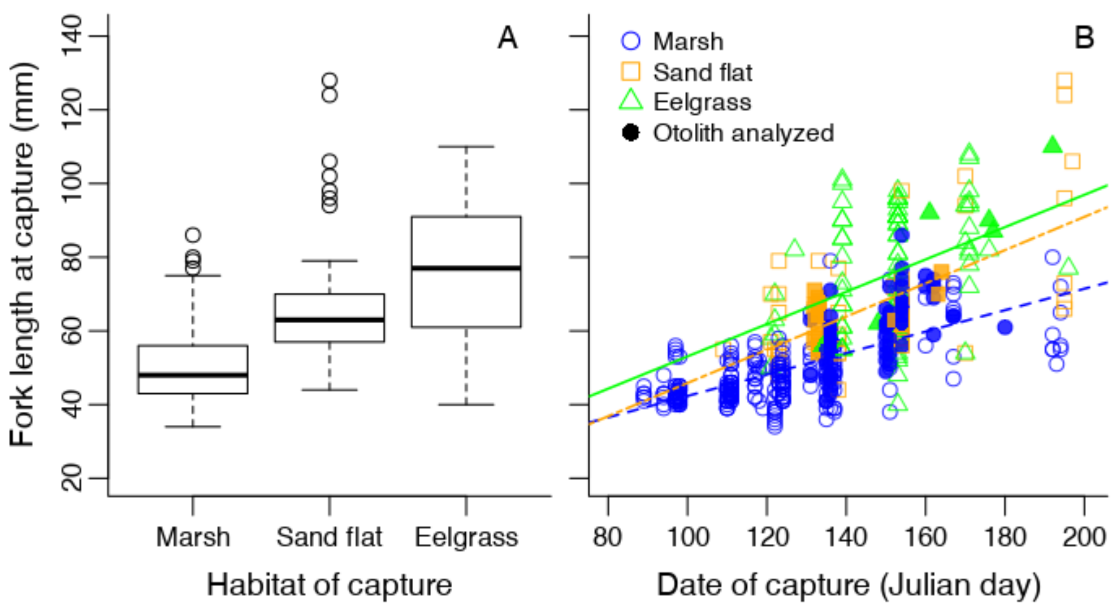


**Figure 3.6** Size of Harrison Chinook salmon at capture in relationship to habitat; panel A: boxplot showing 2016 and 2017 Harrison Chinook salmon catch by habitat; panel B: Harrison Chinook salmon size at capture in three habitat types: marsh (blue circles, n=328), sand flat (orange squares n=73), and eelgrass (green triangles n=89), with the linear regression between fork length and catch date depicted for each habitat. Solid symbols indicate fish with otoliths analyzed.

*3.4.4 Estuarine growth*

Harrison Chinook salmon exhibited an average daily growth rate of 0.57 +/- 0.13 mm (mean +/- SD) fork length in the estuary. We did not find a significant difference in daily growth rates among fish based on estuarine entry timing (Fig. 3S3A). Daily growth rate was not significantly related to estuarine residency time (Fig. 3S3B). Daily growth rate did increase over time and with greater fork length at capture (Fig 3.7A,B). However, when growth is converted to a proportion of fork length at capture, we found that smaller fish that were caught earlier also appear to grow faster (Fig. 3S4), indicating that this increase is allometric Davis et al. (2019). These interactions appear to be compensatory such that, overall, daily growth is similar among individuals regardless of entry or residency times. When comparing total estuarine growth, fish that entered the estuary smaller and resided longer experienced the greatest proportional increase in body size (Fig. 3.7C,D).

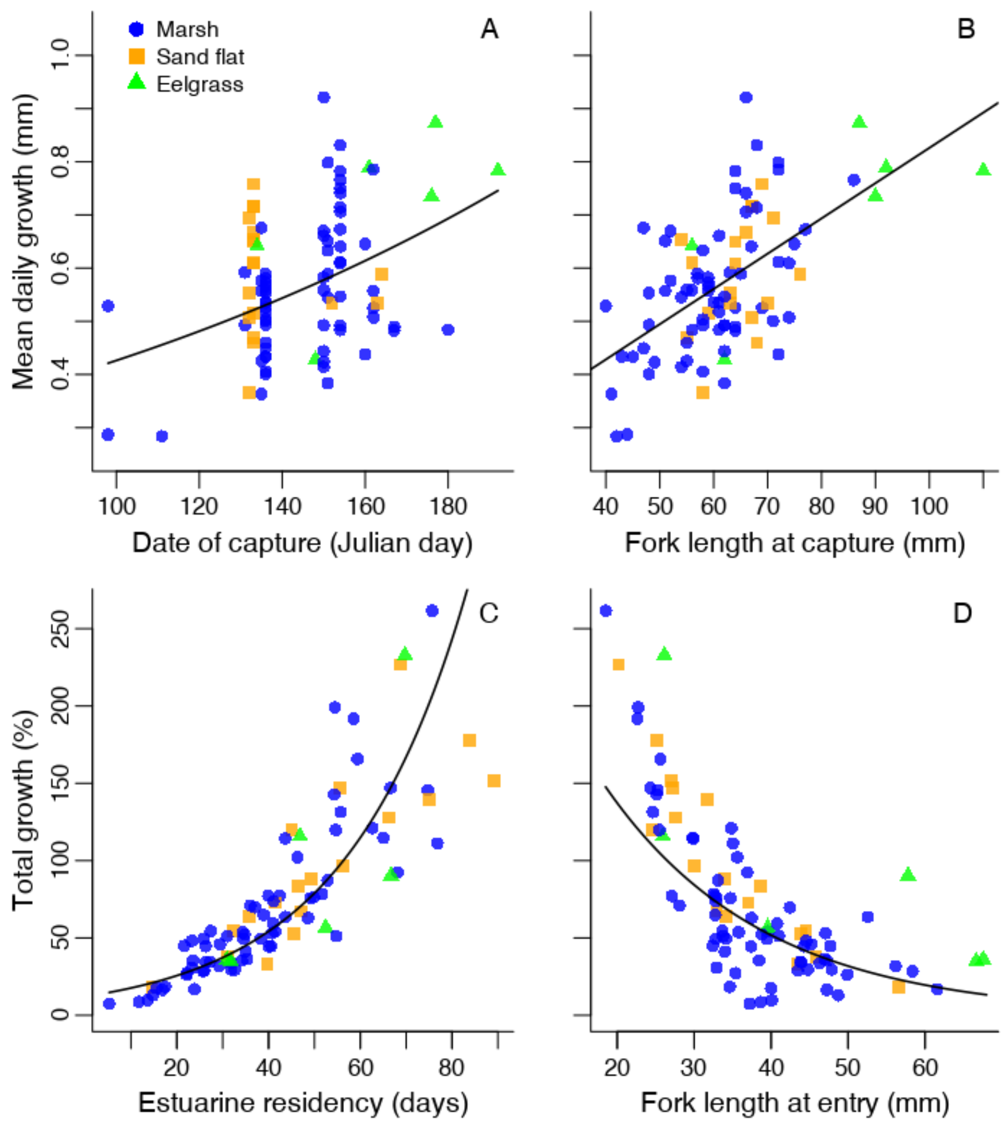


**Figure 3.7** Estuarine growth as a function of time and body size, categorized by habitat (marsh = blue circles (n=67), sand flat = orange squares (n=18), eelgrass = green triangles (n=6)). A) Average daily growth in fork length over time (exponential regression, $R^2$: 0.16, $P$: 8.3 x$10^{-05}$), B) Average daily growth in fork length as a function of body size (linear, $R^2$: 0.34, $P$: 1.1 x$10^{-09}$), C) Total estuarine growth (proportional to entry size) over residency period (exponential, $R^2$: 0.78, $P$: 2.2 x$10^{-16}$), and D) Total estuarine growth as a function of size at entry (exponential, $R^2$: 0.43, $P$: 1.1 x$10^{-12}$).

Within individual otoliths, growth during the freshwater period (2.60 +/- 0.51 $\mu m \cdot day^{-1}$, mean +/- SD) was lower than the early estuarine period (3.07 +/- 0.53 $\mu m \cdot day^{-1}$), which was in turn lower than the late estuarine period (4.00 +/- 0.64 $\mu m \cdot day^{-1}$; Fig. 3S4). However, this trend corresponds to differences between growth periods of less than 1mm$\cdot day^{-1}$ when converted to fork length, which are no longer statistically significant. Four individuals displayed mean daily growth rates during the late estuarine period (7-14 days prior to capture) that were more than 5% lower than the early estuarine period (7-14 days after entry), and one showed lower growth during the early estuarine period than the freshwater period (Table 3S2), which may indicate a period of starvation. However, only one of these fish had a corresponding low estimated somatic growth rate (0.4 $mm \cdot day^{-1}$).

## 3.5 Discussion

Using modern scientific techniques, we have confirmed the extent and variability in residency times and quantified estuarine daily growth for Harrison Chinook, one of the dominant populations of wild Chinook salmon in Canada's largest salmon-bearing river. We provide further support for the importance of estuarine habitat for early growth of subyearling migrant Chinook salmon, and report residency periods and growth rates that are comparable to populations throughout the Pacific Northwest.

Our research builds from early field studies that quantified juvenile salmonid habitat use in the Fraser River estuary in the late 1970s and early 1980s (e.g. Levy and Northcote 1979, 1982; Greer et al. 1980; Levings et al. 1983). The methodologies available at the time of those studies did not include modern genetic stock identification or LA-ICPMS otolith analysis, so the authors were limited in the inferences they could make, and there has been a lack of salmon research in the estuary since. Our mean otolith-based estimate of minimum residency of 41.8 days is more than 16x the mean (of three days) and 39% greater than the maximum recorded residency (of 30 days) from mark-recapture studies conducted by Levy and Northcote in 1978 in the Woodward Island marsh complex (M5, Fig. 3.1) of the Fraser estuary (Levy and Northcote, 1982). The authors' subsequent study, including channels overlapping with our site M3, yielded even lower recapture rates and shorter observed residency (Levy and Northcote, 1979). Recapture rates from juvenile salmon marking experiments on the outer flats of the Fraser estuary (Sturgeon and Roberts Banks, near sites S1, S2, S4, E7, E3, and E4) were even lower than in the tidal channels (Levings, Greer and Miller, 1983). Although Levy and Northcote's (1982) study primarily aimed to examine if various Pacific salmon had some residency in the estuary, such that most of their recapture efforts were made in the first week after release of marked fish, our longer-running study using otolith analysis demonstrates that mark-recapture approaches can vastly underestimate estuarine habitat use by Chinook salmon. While the authors speculated that the actual residency of Chinook salmon was on the order of weeks to months (Levy and Northcote, 1979), our study is the first to confirm their prediction quantitatively. In contrast to the findings of Levy and Northcote (1979, 1982), our results are similar to the more recent otolith study by Volk et al. (2010) for subyearling Chinook salmon in Oregon (mean minimum residency of 43.5 days, median 41.5), suggesting a potential pattern among early estuarine-rearing populations. We demonstrate the utility of otolith analysis in linking juvenile presence with estuarine use and recommend that these methods be used in place of mark-recapture studies in large systems where recapture rates are typically very low.

*3.5.1 Emigration timing and Residency*

We found that Harrison Chinook were among the first salmon to enter the Fraser River estuary in 2016 and 2017, similar to findings from Levy and Northcote (1979). However, peak emigration to the estuary in 2016 occurred about a month earlier than in 2017 and the historic records, which measured peak Chinook abundance in the second half of May (Levy and Northcote, 1979). We derived estuarine entry date from the otolith microchemistry as the fish grew, following Volk et al. (2010), who demonstrated that Sr:Ca concentrations increase asymptotically at salinities 0-5‰, and that despite variation in individual otoliths, the sudden increase in Sr:Ca is an accurate indicator of migration from fresh to brackish waters. These values align with the pattern of migration timing for juvenile Chinook salmon in the Fraser, which reach peak abundance at a rotary screw trap at Mission (~75 km from the river mouth, near the tidal limit) 1-3 weeks prior to the peak in the marshes at the mouth of the Main arm (Levy and Northcote, 1979). Historic records have demonstrated that the migration timing of Harrison Chinook fry coincides closely with catches downstream at Mission, suggesting rapid downstream movement (Fraser, Starr and Fedorenko, 1982). Given that little rearing habitat is available between Mission and the beginning of the estuary, and that salt-water influence is limited to the point where the river splits into the North and Main arms, we therefore believe that the otolith signatures that we recorded in fish captured in the Fraser River estuary reflect entry into brackish waters below the maximum extent of saltwater intrusion. While our otolith data are limited to 2016, we expect that aside from entry timing, the otolith results are likely representative of other years for two reasons. First, entry timing was seen to be a continuum, such that even though our peak catch occurred in March in 2016, Harrison Chinook entered the estuary between February and May. Second, Chinook achieved smolt sizes at similar times in both years (May-July), so we expect that the average minimum residency period would be similar to our 2016 results, if not slightly lower, in a given year. While the majority of our otolith samples were limited to fish captured in May, the nature of otoliths is such that they provide a permanent record of growth until the point of capture, which is why we were still able to record the spectrum of entry timing seen in our results. Combining the otolith data with our catch records lends further support to prolonged residency in the estuary from at least March (when our sampling efforts began).

*3.5.2 Growth and Implications for Survival*

The estuarine-rearing phase for Chinook salmon involves multiple trade-offs between habitat availability, predation, physiological stress from temperature and salinity, and food quality and quantity (Quinn, 2018; Davis *et al.*, 2019). Harrison Chinook salmon displayed similar daily growth rates regardless of entry date, indicating that the broad range of emigration timing to the estuary may still result in similar early marine growth. Growth rates were similar to the otolith-derived rates reported by Volk et al. (0.35-0.65 $mm \cdot day^{-1}$; 2010) and Campbell (mean 0.41 $mm \cdot day^{-1}$, range 0.11-0.67 $mm \cdot day^{-1}$; 2010), to marsh channel mark-recapture rates in the Columbia River estuary (mean 0.49 $mm \cdot day^{-1}$ for fish tagged at $\geq$55 mm fork length, 0.58 $mm \cdot day^{-1}$ for fish tagged at $\geq$60 mm; McNatt et al. 2016), and to population estimates based on stable isotope analyses in the Skeena River estuary (0.48 +/- 0.09 mm (mean +/- SE); Moore et al. 2016). Overall, we saw a benefit of early entry and long residency times for total proportional growth for subyearling migrant Chinook salmon.

Daily proportional growth rate decreased with increasing fork length (Fig. 3S4) - reflective of typical allometric patterns in juvenile Chinook salmon (Davis *et al.*, 2019). The importance of estuarine rearing in brackish marsh habitat may be higher for small individuals, which also tend to be wild fish. Davis et al. (2019) demonstrated increased growth rates of wild versus hatchery fish in tidal marshes, particularly for those below 100 mm fork length. There is also likely a shift in food quality and quantity as Chinook salmon make the ontogenetic migration outward from the marsh to sand flat and eelgrass habitats in the estuary. In the tidal marshes they likely access insects as well as some amphipods and copepods (Levings, Conlin and Raymond, 1991). In contrast, subyearling juvenile Chinook salmon in eelgrass and sand flats would be more restricted to crustaceans, which may be in high abundance but have lower energy density than terrestrial insects (Levings, 1985; Davis *et al.*, 2019). Further to this, the lingering marine heatwave effects in 2016 decreased the abundance of subarctic copepods in the Salish Sea, which were replaced by low energy-density southern copepods (Chandler, King and Boldt, 2017).

A few individuals in this study demonstrated periods of decreasing mean daily growth in otolith increments, which may represent declines in somatic growth due to starvation (Bradford and Geen, 1992). However, it is difficult to discern variation in otolith increment width due to environmental variations (e.g. fluctuating temperature) from actual starvation (Bradford and Geen, 1992; Walker and Sutton, 2016), and mean daily growth was still within one standard deviation of the population mean for all but a single small individual. Combined with the high projected density of Harrison fish in 2016, it is therefore reasonable to assume that some fish were not able to find sufficient ration to survive in the estuary, of which these few may be an example. Unfortunately, our sampling effort did not begin until late March 2016, so if a cohort of emigrating Harrison Chinook salmon entered in February and experienced poor growth, they were missed in our study. Overall, however, it appears that the fish that we caught throughout the season were able to achieve reasonable growth rates comparable to other studies.

While we did not find a statistically significant difference in growth rate between habitats, our otolith sample size for salmon caught in eelgrass was low (n=6), and a power analysis exploration suggested that a sample size of 21 to 53 per habitat type would have been required to conduct this comparison (k=3, significance level = 0.05, power = 0.8, f = 0.25 or 0.4, respectively). We did find that juvenile Chinook had a larger fork length at capture in the sand flats than the marsh and were largest in eelgrass. The growth trajectory based solely on fork length over time suggests that fish caught in eelgrass and sand flats were growing faster than those in the marsh. However, the otolith data had insufficient sample size to evaluate this. An alternative explanation for differences in mean fork length at capture between habitat types is the continued influx of small migrants and potential efflux of larger individuals to and from the marsh throughout the migration period. While growth rate was not comparable between habitats, there were strong patterns indicating an ontogenetic shift in habitat use over the migration period.

*3.5.3 Estuarine Habitat Use*

Small fry entering the Fraser estuary likely require a period of transition before being physiologically adapted to life in the ocean. We found that Chinook salmon below 54 mm fork length were exclusively caught in the low-salinity marsh, suggesting that fish below this size may not be optimized to transition to higher salinities. Morgan and Iwama (1991) conducted a growth trial on subyearling migrant Chinook salmon and found that even with gradual acclimation of 1-2‰·day$^{-1}$, fish less than 50 mm fork length reared in 28‰ salinity had a mortality rate of 24%, suggesting that this salinity level was stressful for Chinook salmon of this size. Similarly, Volk et al. (2010) found that all fish less than 45 mm that were caught in the Salmon River system spent at least 30 days in the estuary prior to migrating to the river mouth.

Alternatively, or in addition to physiological factors, smaller fish may prefer the higher turbidity of the marsh channels as a measure of protection against predators (Gregory and Levings, 1998). Previous studies in the Fraser estuary have suggested that Chinook salmon prefer the marsh to more open habitat or eelgrass, and found that Chinook salmon caught in Roberts bank eelgrass were larger and possibly near smolting (Greer *et al.*, 1980; Levings, Greer and Miller, 1983). Combined with the increase in residency time and total estuarine growth for smaller fish, this study supports the idea that the brackish marsh of the Fraser estuary represents a critical habitat for subyearling migrant Harrison Chinook salmon.

### *3.5.4 Historic Habitat Loss*

Historically, the Lower Fraser region including all tributaries South and West of Lytton, BC, supported 6 118-8 361 km of linear stream habitat and 659 km$^2$ of additional floodplain (Finn *et al.*, 2021). Today, approximately 64% of the accessible stream habitat and 85% of the floodplain in the Lower Fraser River has been lost due to human development (Finn *et al.*, 2021), particularly in the Fraser Valley (below the Harrison River confluence) and in the estuary where most of the river has been diked (Dashtgard *et al.*, 2012; Balke, 2017). The diking and filling of estuarine habitat has been particularly concentrated, with the areal extent of wetland habitat in the estuary reduced by over 70% since European settlement (Schaefer, 2004). While much of this loss occurred between the early 1800s to 1980 (Balke, 2017), an expansion of the Roberts Bank coal port in 1984 further altered more than 200 ha of estuarine habitat, which had documented impacts on juvenile Chinook salmon rearing habitat (Levings, 1985). Indeed, our catch rates of Chinook in this area (sites E3, E4, and E7) have consistently been lower than those reported by Levings (1985). Despite management efforts there have been continuous struggles to achieve ‘no net loss’ of salmon habitat in the estuary (Levings, Conlin and Raymond, 1991; Lievesley *et al.*, 2017). Ongoing small-scale projects including urban development and conversion of farmlands continue to degrade the remaining habitat, and several large-scale industrial developments are under current review, including a further expansion of the container terminal for the coal port and an expansion of the Vancouver International airport, which pose significant threats to the estuary. Restoration of historic wetlands may facilitate the expansion of estuarine habitat use, and diversify the range of life history strategies of existing fall ocean-type Chinook salmon populations (Bottom *et al.*, 2005; Volk *et al.*, 2010). Removal of barriers and restoration of marsh and estuarine habitats could further enhance the rearing capacity of the Fraser estuary for salmon and would be of particular benefit to the subyearling migrant Harrison Chinook population. Previous studies have suggested very high in-river mortality of early fry migrants (e.g. Healey 1982; Bottom et al. 2005), indicating that this may not be a winning life-history strategy in most years. However, this strategy may provide a buffer against increasingly variable marine conditions. Expanding the estuarine habitat available, and the quality of that habitat, is therefore likely to benefit wild Chinook salmon populations - both by bolstering diversity of emigration phenotypes (Bourret, Caudill and Keefer, 2016) and by increasing early marine survival (Magnusson and Hilborn, 2003).

Productivity of Harrison Chinook salmon has generally declined since the 1980s, with more severe declines observed over the last three generations. This has been broadly attributed to conditions encountered during the early marine stage (COSEWIC, 2018). This study suggests that the lack of estuarine habitat available for rearing may also be a contributor to that decline. Levy and Northcote (1982) documented high densities of juvenile salmonids in some of the last remaining brackish marsh channels in the Fraser River estuary and found that Chinook salmon had the highest density at a max of 0.18 fish$\cdot$m$^{-2}$. This is approaching the high-density scenario

(0.20-0.25 fish·$m^{-2}$) that led to significantly shorter residency times and decreased growth rates when food was scarce in the Nisqually delta (Davis *et al.*, 2018). If we assume that this approaches a minimum habitat requirement for each fish, and extrapolate to the entire population, Harrison Chinook fry in 2016 required a minimum of 1 620 $km^2$ to 59 400 $km^2$ of rearing habitat for maximum survival, which would be reduced by the staggered migration of fish across the emigration period. Given the clear reliance of this Chinook salmon population on estuarine habitat for early rearing, it is highly likely that the estuarine carrying capacity for Harrison River Chinook has been diminished. In addition to this decline in available habitat, there continues to be an increase in hatchery fish production, potentially exacerbating this loss by increasing density-dependent effects in the remaining habitat (David *et al.*, 2016).

The pattern of Chinook salmon catch between years suggests the potential for density-dependent effects to be occurring in this system. We caught fewer Chinook salmon in 2016 than 2017, despite the higher spawner returns in 2015. Examining the seasonal breakdown of this emigration it appears that an initial high volume of fry emigrated in the spring, as indicated by our higher catch of Chinook salmon in April in 2016 vs 2017. However, this was followed by a steep decline in May 2016 (the peak of the emigration in 2017) followed by consistently low catch throughout 2016 that resulted in the overall lower catch for that year. In 2016, the spring was anomalously dry and warm, likely due to El Niño and marine heatwave conditions, and the Fraser River freshet occurred more than a month early and was the lowest freshet on record (Chandler, King and Boldt, 2017). The high density of Chinook fry emigrating in 2016, a mild winter, and anomalously low flow conditions may have therefore increased early emigration to the estuary beyond the capacity of the remaining habitat, potentially resulting in large mortality for many of these fry. These patterns should be interpreted with caution, however, as our study was not designed to assess density or natural mortality in the estuary, and we only caught a single fish that entered the estuary in February 2016 due to our late sampling start date.

*3.5.5 Conclusions*

Given the dynamic nature of estuarine ecosystems and the regular movement of juvenile salmon throughout them, we recommend that otolith or isotope studies be used to estimate residency as opposed to mark-recapture methods, which may consistently underestimate the use of these habitats in large systems. We also suggest that sampling juvenile salmon throughout the emigration period is an important means of quantifying individual residency and growth across the population. Although catching fish before they are ready to leave the estuary may underestimate the total residency time and growth rate of the population, it also means some fish are caught that may not have survived to ocean entry - as indicated by the few individuals that showed evidence of starvation after estuarine entry. Based upon the strong brood year of Harrison Chinook salmon in 2015, and the overall similarity of daily growth rates for the majority of fish captured in this study, we propose that the remaining habitat in the Fraser estuary provides high-quality rearing opportunity, and that further protection and restoration of these habitats could boost productivity for this population. Important areas for future studies include directly linking early estuarine salmon growth to adult returns to elucidate the impacts of estuarine residency on survival.

## 3.6 Acknowledgements

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# Chapter 4 - Identifying a pathway toward recovery for depleted wild Pacific salmon populations in a large watershed under multiple stressors.

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Author contributions: Authors L.C., J.K.B., and T.G.M designed the study; L.C., A.C., R.J.R.F., V.H., and C.H. carried out data collection; L.C. and A.C. conducted data analysis; J.K.B., M.B., R.D., S.G.H., C.D.L., M.M., D.N., M.P., J.D.R., D.C.S., U.S, S.S., and J.S. participated as experts and contributed data. L.C. wrote the manuscript with input from all authors.

## 4.1 Abstract

1. Pacific salmon (*Oncorhynchus* spp.) support coastal and freshwater ecosystems, economies, and cultures, but many populations have declined. We used Priority Threat Management (PTM), a decision-support framework for prioritizing conservation investments, to identify management strategies that could support thriving populations of wild salmon over 25 years. We evaluated the potential benefits of 14 strategies spanning fisheries, habitat, pollution,

pathogens, hatcheries, and predation management dimensions on 19 conservation units (CUs) - genetically and ecologically distinct populations - of the five Pacific salmon species in the lower Fraser River, British Columbia, Canada.

2. The PTM assessment indicated that under the current trajectory of ‘business as usual’, zero CUs were predicted to have >50% chance of thriving in 25 years. Implementation of all management strategies at an annual investment between 45-110 million CAD was, however, predicted to achieve >50% chance of thriving for most CUs (n=16), with nearly half (7 CUs) having a >60% chance, indicating there is a pathway toward recovery for most populations if we invest now. In fact, substantial gains could be made by investing in five combined habitat strategies, costing 20M CAD annually. These habitat strategies were estimated to bring 14 of 19 salmon CUs above this 50% threshold.

3. Co-governance between First Nation and provincial and federal Canadian governments to manage salmon populations and harvest, and improved CU-level monitoring emerged from the expert elicitation as critical ‘enabling’ strategies. By improving the feasibility of different management options, co-governance brought an additional five CUs above the 60% threshold.

4. *Synthesis and applications.* Supporting wild salmon in the face of cumulative threats will require strategic investment in effective management strategies, as identified by this PTM assessment. With renewed commitments from provincial and federal Canadian governments to protect and restore salmon populations and their habitats, positive conservation outcomes may be within reach.

## 4.2 Introduction

As biodiversity loss outpaces conservation efforts globally, timely implementation of conservation action is a key challenge of our time (WWF, 2020). Three principal issues can lead to failed species recovery: insufficient funding for recovery actions (Buxton *et al.*, 2020), delays in action (Martin, Nally, *et al.*, 2012), and conflicts of interest between social-economic values and conservation (McCune *et al.*, 2013). Migratory fishes such as Pacific salmon (*Oncorhynchus* spp.) exemplify these issues. These species pass through multiple ecosystems and jurisdictions throughout their life cycle, and exhibit high natural variability in their productivity that can mask patterns of decline, making recovery challenging (Malick, Rutherford and Cox, 2017; Gayeski *et al.*, 2018). Wild Pacific salmon are foundational to the spiritual, cultural, subsistence, and economic practices of Indigenous peoples throughout the coastal region of the Northeast Pacific (Garibaldi and Turner, 2004). They support commercial and recreational salmon fisheries in the Northeast Pacific ocean averaging nearly five billion USD in valued output, three billion USD in Gross Domestic Product, and create over 39,000 Full Time Equivalent jobs annually to the United States and Canadian economies combined (Gislason *et al.*, 2017). Despite this, in recent decades the overall abundance and fisheries catch of Pacific salmon in British Columbia (BC) have declined (Argue *et al.*, 1983; Beamish *et al.*, 2004). Population diversity has also been declining (Slaney *et al.*, 1996; Price *et al.*, 2021). Conditions leading to the decline and repressed recovery of Pacific salmon are complex and interacting (Cohen, 2012a; Sobocinski, Greene and Schmidt, 2018) (Fig. 4.1), and in Canada management bodies charged with salmon governance, including recovery initiatives are also responsible for supporting harvest interests. This conflict has contributed to the slow reaction of management bodies to address these pressures (Cohen, 2012b).

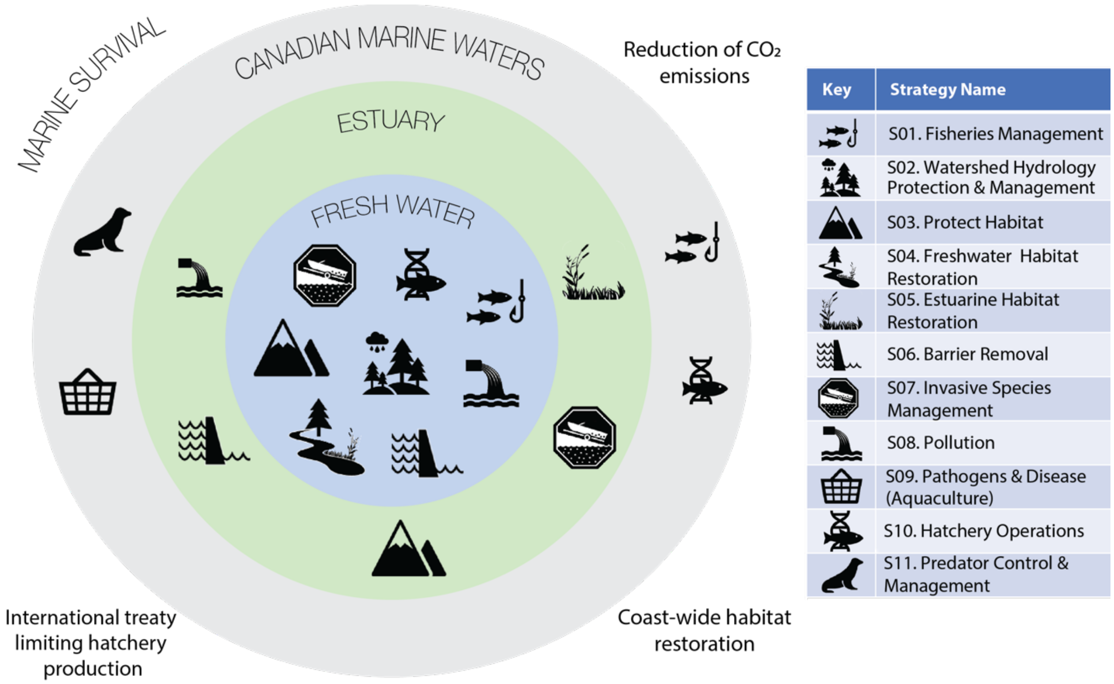


**Figure 4.1** Schematic of threats and management tools for Pacific salmon in the lower Fraser River region by habitat. The inner circle (blue) represents available strategies within the realm of freshwater habitat. The next circle (green) represents strategies within the estuary realm, followed by strategies within the nearshore marine realm (grey). Icons represent 11 management strategies identified in this project (Table 4.1) and are repeated where they apply across realms. Several strategies which influence marine survival were not included in this study due to their international scope, including global reduction of greenhouse gas emissions to reduce the impacts of climate change, international treaty negotiations to minimize hatchery-wild interactions, and large-scale habitat restoration spanning the North American Pacific coastline.

The Fraser River, BC, is one of the major systems in the Northeast Pacific where several salmon populations are now at historic lows (DFO, 2020a). The Fraser River supports the five Pacific salmon species found in Canadian and US waters and historically produced more salmon than any other river on the Pacific coast (Northcote and Atagi, 1997). The lower Fraser River is the bottleneck through which all Fraser salmon travel and is part of the traditional and unceded territories of more than 30 First Nations, who have relied on the Fraser and its network of tributaries for harvest, trade, and other cultural practices for millennia. Aside from salmon, the region supports the majority of BC's population and agricultural output, as well as Canada's most active port (Port of Vancouver), and a large international airport (Groulx *et al.*, 2004). As a result of agricultural, urban, and industrial development, 85% of the wetlands and floodplain have been lost to diking, draining, and ditching, 64% of the streams have been lost or are inaccessible because of dams, floodgates, and road culverts, and surrounding forests have been logged, culminating in the significant loss of salmon habitat (Birtwell *et al.*, 1988; Boyle *et al.*, 1997; Finn *et al.*, 2021). In response to the cumulative impacts to salmon and their habitats since colonization, there is increasing interest in developing new governance frameworks grounded in Indigenous stewardship practices and laws (Carlson *et al.*, 2001; Gayeski *et al.*, 2018; Atlas *et al.*, 2021). In particular, a framework that can support government mandates for wild salmon recovery by providing a rapid assessment of management strategies to guide strategic conservation investments is urgently needed.

Impacts to Pacific salmon can be addressed by identifying the actions that will lead to the greatest benefit to species for the least cost to society. Priority Threat Management (PTM) is a conservation decision-science framework that enables prioritization of cost-effective conservation actions for species recovery (Carwardine *et al.*, 2019). By structuring the problem and designing actions to meet clear objectives, it can facilitate discussion and engagement among diverse user groups under a shared goal (Carwardine *et al.*, 2019). The process also reveals the return on investment for conservation action, thus providing a decision aid for decision-makers, and facilitating more rapid uptake (Martin *et al.*, 2018). In this study, we apply the Priority Threat Management (PTM) framework to identify and evaluate a suite of management strategies intended to support wild salmon populations that spawn in the lower Fraser River region (Table 4.1). Our research integrates the expertise of Indigenous and local knowledge holders, fishers, fisheries scientists and managers, and conservation practitioners to identify the most cost-effective management alternatives to achieve recovery of wild Pacific salmon in the Fraser River. While this is not the first application of PTM to Pacific (Kehoe *et al.*, 2020; Walsh *et al.*, 2020), it demonstrates that PTM can be applied to complex systems involving migratory species affected by multiple stressors with complicated and evolving governance structures.

## 4.3 Methods

We identified management alternatives available to 19 Conservation Units - ecologically and genetically distinct groupings of salmon - (CUs) in the lower Fraser and assessed their benefit, cost and feasibility (Fig. 4.2; Carwardine *et al.*, 2019). PTM applies the steps of decision analysis, also called Structured Decision Making (PrOACT; Problem definition, Identifying Objectives, defining Alternatives, predicting Consequences, and evaluating Trade-offs) (Hammond, Keeney and Raiffa, 1999). We elaborate on each of these steps in the following sections. The process involved a three-day workshop at the University of British Columbia (November 13-15, 2019) and refined through follow-up conversations. Information required to inform each of the steps was collated prior to and after the workshop by the research team. We reached out to 104 knowledge holders with diverse perspectives and expertise in the ecology and management of salmon, of these 88 contributed to various aspects of knowledge gathering, 44 participants attended the workshop, and 55 contributed to estimates of consequences (benefits, costs, and feasibility) for each of the alternatives. The participants included First Nations, Canadian federal government, British Columbia provincial government, commercial fishing industry, recreational fishing industry, academic institutions, non-governmental organizations, and independent experts.

Participation and data collection protocols followed in this study were approved by the University of British Columbia and University of Victoria and Human Research Ethics Board (permit H19-00267).

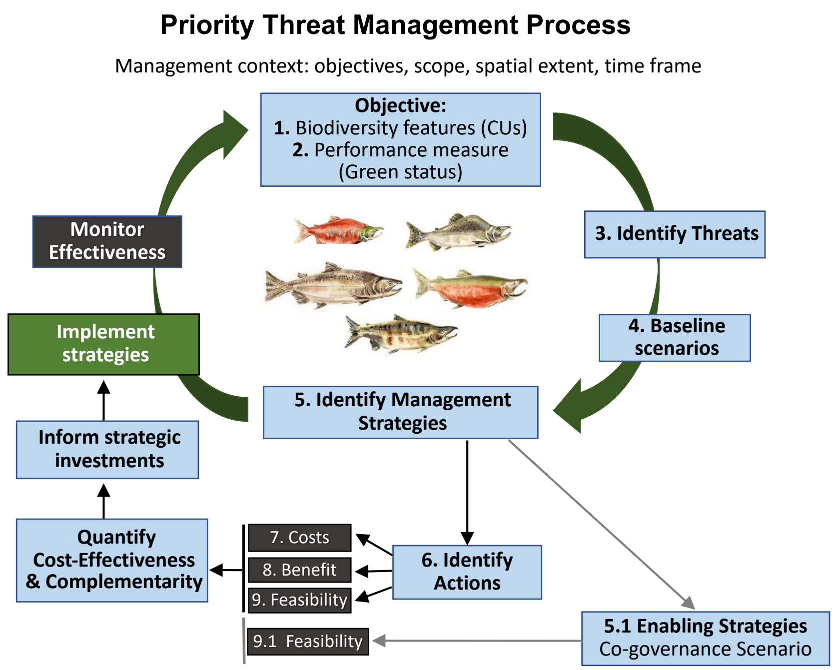


**Figure 4.2** Overview of the key inputs for Priority Threat Management adapted from Carwardine et al. (2019). For a given objective and project scope (i.e., maximize the number of lower Fraser River salmon CUs that will achieve green status at the end of 25 years), threats are identified and the performance measure for each biodiversity unit under baseline is assessed. Costs, benefits,

and feasibility are estimated for each strategy based on the component actions. In this study, a second feasibility estimate was elicited for a co-governance scenario. An assessment of the co-benefits of each strategy is an optional 10th input that was not completed in this study due to time constraints. The costs, benefits, and feasibility for each strategy are used to calculate the cost-effectiveness and complete the complementarity analysis, which provides the optimal management strategies to inform strategic investments for species recovery. Implementation should ideally follow an adaptive management process that monitors effectiveness according to the project objective. Illustrations of salmon species provided by the Pacific Salmon Foundation.

*4.3.1 Problem*

The initial problem formulation was developed in consultation with knowledge holders prior to the workshop, and subsequently refined during the workshop. The problem was to identify the most cost-effective portfolios of actions to recover wild salmon in the lower Fraser River region, which we defined as the Fraser River mainstem and tributary watersheds west of Hope, BC (Fig. 4.3). We included Boundary Bay CUs; although they use tributaries that are not part of the Fraser River basin, the identified actions will also impact salmon in this area. Together, these watersheds comprise the portion of the 230,400 $km^2$ Fraser River basin most heavily impacted by anthropogenic development (Birtwell *et al.*, 1988; Boyle *et al.*, 1997). The lower Fraser region supports 19 CUs (Table 4S2): six Chinook (*Oncorhynchus tshawytscha*), one chum (*O. keta*), three coho (*O. kisutch*), one pink (*O. gorbuscha*), and eight sockeye (*O. nerka*) comprising 35% of all Fraser basin salmon CUs (Holtby and Ciruna, 2007). The governance structures of this region are diverse and complex, and there is no single decision-maker responsible for achieving this objective. The timeframe of 25 years was chosen as it encompassed multiple generation times for each species, allows for results of implemented actions to be detected, can be divided into time periods that align with regional management plans, and was within the realm of experience and reasonable prediction by the expert participants.

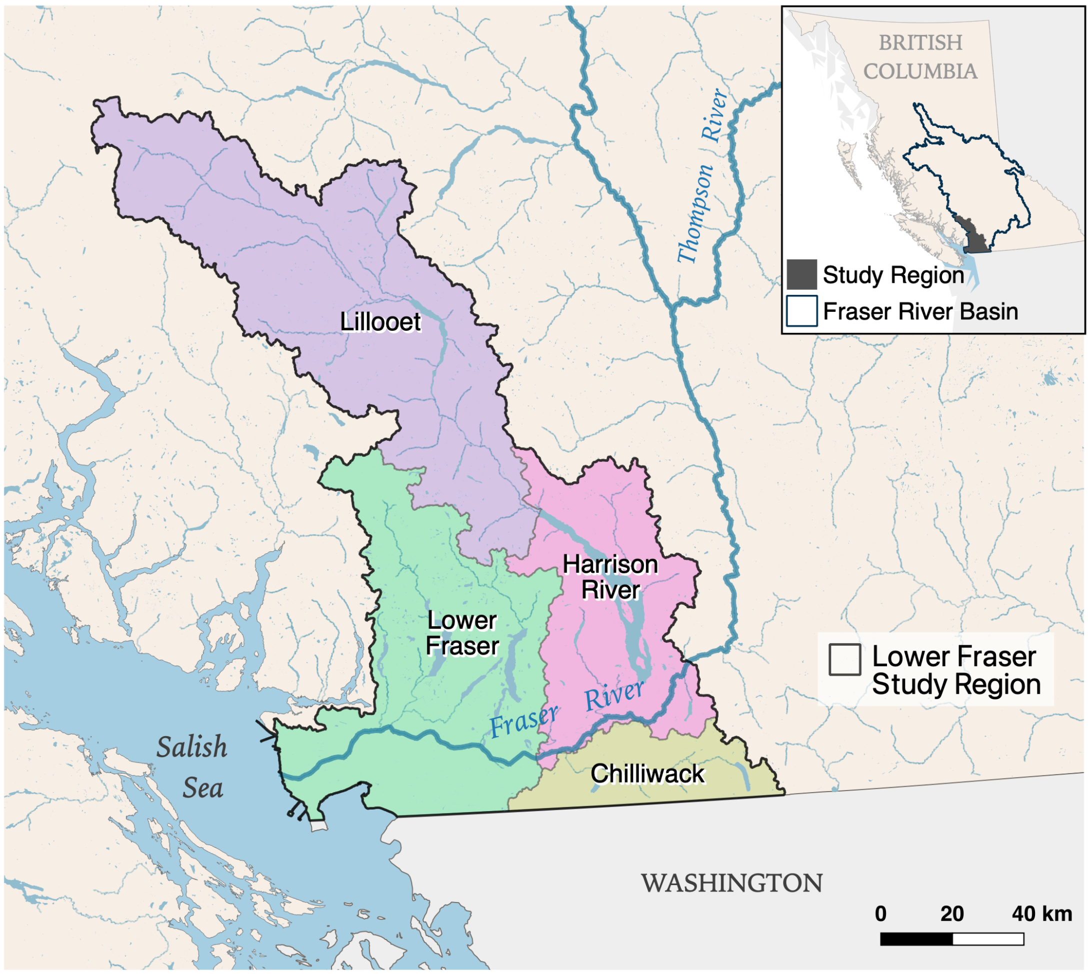


**Figure 4.3** Map of the lower Fraser study region, including the Lillooet, Harrison River, Lower Fraser, and Chilliwack River watershed groups in British Columbia, Canada. Inset map shows the boundary of the Fraser River basin, with the study area highlighted in dark grey. Data for watershed groupings obtained from the Freshwater Atlas (https://ww2.gov.bc.ca/gov/content/data/geographic-data-services/topographic-data/freshwater).

As part of the problem formulation, project leads (LC, CH, and TM) prepared a summary of key threats to wild salmon CUs based on status assessments from the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), the Canadian Science Advisory Secretariat (CSAS), and other appropriate federal, provincial, and local reports (SI). We also used biological status assessments and evaluations of freshwater habitat threats for each CU provided by the Pacific Salmon Foundation via the Pacific Salmon Explorer tool (Fig. 4S1; www.salmonexplorer.ca; Pacific Salmon Foundation 2020). We undertook a literature review to develop an initial set of actions that could be used to recover wild salmon in the lower Fraser. This list was circulated to workshop participants prior to the workshop, and subsequently refined during the workshop.

### *4.3.2 Objectives*

The primary objective of the PTM assessment was to “maximize the number of thriving lower Fraser salmon CUs”, over a 25-year timeframe. A ‘thriving’ CU was defined as one in a state of relatively high abundance that fulfills its ecological function and role and provides livelihood opportunities for present and future generations. We assumed a thriving CU would be the equivalent of being assessed in the ‘green status’ zone under Canada’s Wild Salmon Policy, where the need for conservation intervention is low and fishing is possible (Fig. 4S2; DFO, 2005). Project objectives also included “minimizing financial costs” (CAD) and “maximizing feasibility” (a proxy objective that takes the product of probability of social acceptance and probability of technical success).

### *4.3.3 Alternatives (Management Strategies)*

The PTM assessment explores potential portfolios of actions and identifies the best portfolio(s) that can achieve the objectives for increasing levels of investment and increasing levels of certainty in the recovery of salmon. Prior to and during the workshop participants identified a suite of 11 management strategies (portfolios of actions) that could abate threats to the salmon CUs in the lower Fraser region (Table 4.1; detailed in SI). Experts selected groups of strategies that if combined would likely have greater benefits than if implemented individually (combination strategies) (Chadés *et al.*, 2015). Two combination strategies were identified, the first, S12, combines fisheries management (S01), pathogens and disease (aquaculture) (S09), and hatchery operations (S10). The second, S13 combines all habitat strategies (S02, S03, S04, S05, S06), and a third combination strategy was assessed for all available management strategies combined (ALL). Two enabling strategies were also identified, which represent management strategies that have not been fully implemented to date, but which were considered to underpin the success of other strategies (detailed in SI). These were: improvements to salmon monitoring and assessment (ES1), and the formal establishment of co-governance structures between Indigenous and Crown governments (ES2). Enabling strategies were considered necessary to the future management of wild salmon in the region and were therefore not included in the prioritization. However, ES2 (co-governance) was predicted to impact the feasibility of implementing the strategies, and so feasibility was reassessed for each strategy under a scenario in which co-governance was implemented, and the complementarity analysis was run an additional time with these estimates (Table 4S5). Finally, to quantify the potential impacts from a suite of current major development proposals which were not included in the baseline (BSL), our analysis explored a second baseline scenario under which all these development projects are approved and completed (DEV BSL) (SI).

**Table 4.1** Overview of strategies considered in the prioritization for threat management of 19 Pacific salmon Conservation Units in the lower Fraser region. The complete list of actions and supporting details can be found in the SI. Benefits assessments assumed all actions were completed for each strategy. Strategies were assumed to be implemented within the 25-year project timeline, though estimated start and completion years varied.

| Strategy Name | Key | Abridged Summary of Actions |
|---|---|---|
| **Fisheries Management** | S01 | • Conduct assessments of salmon vulnerability to the impacts of climate change for all CUs and incorporate these into management procedures.<br>• Identify, develop, and enforce best practices that reduce bycatch and incidental mortality of non-target CUs to minimize collateral mortality in fisheries.<br>• Support the development of Tier 1 (Nation to Nation) and Tier 2 (First Nations to DFO) forums for exploring how food, social and ceremonial fisheries allocations can be distributed within First Nations communities. |
| **Watershed Hydrology Protection & Management** | S02 | • Develop and implement strategic watershed plans, including updated regulations, to maintain natural hydrological processes and patterns. |
| **Protect Habitat** | S03 | • Identify habitat requirements needed to support thriving salmon CUs and designate priority habitats for conservation/protection.<br>• Prevent the expansion of footprints of known habitat stressors into moderate- to high-quality habitat. |
| **Freshwater Habitat Restoration** | S04 | • Develop a central database of salmon restoration projects to highlight gaps and overlaps in the region.<br>• Identify and restore priority freshwater sites that support, or directly or indirectly impact, salmon and their spawning, rearing and migration habitats. |
| **Estuarine Habitat Restoration** | S05 | • Identify and restore priority estuarine sites. |
| **Barrier Removal** | S06 | • Upgrade flood control infrastructure at key access points to be salmon friendly.<br>• Upgrade and restore connectivity to culverts, sloughs, and estuarine jetties prioritized to benefit fish passage. |
| **Invasive Species Management** | S07 | • Implement applied research findings into ongoing surveillance and management of invasive species to reduce impacts to juvenile salmon and their habitats. |
| **Pollution** | S08 | • Implement planned wastewater treatment upgrades to Iona Island and Annacis Island facilities.<br>• Revise and implement legislation to incorporate total amount limits as well as timing restrictions to reduce pollutants. Implement targeted legislation to ban copper and other heavy metals in brake pads in British Columbia. |
| **Pathogens & Disease (Aquaculture)** | S09 | • Phase out open-net pen salmon aquaculture.<br>• Increase the frequency and scope of pathogen screening on fish farms and implement proactive sea louse treatment regimens to better control sea lice populations and pathogens in farmed finfish.<br>• Increase surveillance of wild salmon in both freshwater and marine environments to better understand harmful pathogen loads, and potential links of these to aquaculture and hatchery fish. |

| Strategy Name | Key | Abridged Summary of Actions |
|---|---|---|
| **Hatchery Operations** | S10 | • Develop a revised lower Fraser regional hatchery strategy in an adaptive management framework to manage hatchery-wild interactions in conjunction with CU-specific enhancement targets.<br>• Evaluate the fisheries interactions, biological and ecological risks to wild lower Fraser salmon from Fraser River and Salish Sea hatchery production.<br>• Develop robust evaluation criteria for the implementation of conservation enhancement of at-risk CUs in the lower Fraser River. |
| **Predator Control & Management** | S11 | • Conduct experimental fishery (or traditional First Nations harvest) of pinnipeds in an adaptive management framework to assess the impacts of pinniped predation on salmon populations. |
| **Fisheries & Aquaculture & Hatchery Reform Combined** | S12 | • All actions under S01, S09, and S10 implemented in concert. |
| **All Habitat Strategies Combined** | S13 | • All actions under S02, S03, S04, S05 and S06 implemented in concert. |
| **All Strategies Combined** | ALL | • All actions under all strategies implemented in concert. |

*4.3.4 Consequences*

We used structured expert elicitation to estimate benefits, feasibility, and costs for the proposed management strategies (Hemming et al 2018). Additional information for costs was gathered from published literature. Not all experts completed each stage of the elicitation process, however 34/55 initiated the feasibility and cost estimates and 26/55 completed the benefits estimates. The number of expert benefits estimates ranged from a minimum of 13 to a maximum of 22 for each CU response to each strategy (Table 4S1). An additional 33 experts provided validations of cost estimates and resources that were not otherwise accessible. All analyses of the estimates were conducted in R version 3.6.2.

*4.3.4.1 Benefits*

Experts used the background information provided including biological status, habitat pressures, trends in spawner abundance, harvest rates, and hatchery releases, as applicable (CU background example Fig. 4S1), as well as their own expertise to estimate the probability of each CU achieving green status at the end of 25 years (detailed elicitation methods in SI). They first estimated this under business as usual, including predicted pressures from ongoing human population growth, habitat loss, and climate impacts to establish a baseline trajectory for each CU. Then they estimated the probability of achieving green status under baseline conditions plus the implementation of each management strategy independently as well as the combination strategies. Finally, experts estimated the probability of achieving green status for the development baseline scenario under which all proposed development projects are completed (SI).

For each strategy, we calculated the expected benefit as the difference between the experts' best estimates of achieving green status with the strategy and the baseline, averaged across experts for each CU:

[1] $$B_{ij} = \frac{\sum_{k=1}^{K_{ij}}(p_{ijk} - p_{0jk})}{K_{ij}},$$

where $p_{ijk}$ is the probability of CU $j$ being assessed as green status under strategy $i$ as estimated by expert $k$, $p_{0jk}$ is the probability of CU $j$ being assessed as green status at baseline estimated by expert $k$, $K_{ij}$ is the number of experts who provided estimates for CU $j$ under strategy $i$, and $B_{ij}$ is the average benefit of strategy $i$ for CU $j$. Benefit estimates were then weighted by the feasibility of each strategy to give the expected performance for each CU and strategy. Complementary strategy benefits were reassessed for each CU by the experts assuming the component strategies were implemented in concert.

*4.3.4.2 Feasibility*

To ensure that only feasible actions were included in each strategy, for each action ($h$) identified within a strategy ($i$), experts provided an estimate of the probability that the action would have social-political support and be implemented, assuming funding was not a barrier ("uptake", $U_{hi}$) and the probability that, if implemented, the action would be technically successful ($S_{hi}$). The product of these two estimates created a feasibility score for each action:

$$F_{hi} = U_{hi} \times S_{hi}, \quad [2]$$

where $F_{hi}$ is the feasibility of action $h$ in strategy $i$. Feasibility estimates were then averaged across all actions for a given strategy. Combination strategy feasibility was calculated as the mean of all component strategy feasibilities. Experts then re-estimated the feasibility of each strategy with the establishment of an Indigenous-led co-governance framework (ES2, SI). The cost-effectiveness was then recalculated with the new feasibility estimates to quantify the potential effects of co-governance on salmon conservation.

*4.3.4.3 Costs*

Initial annual costs of implementing each action over the 25-year period were estimated by the experts by asking them to consider the materials, equipment, labour, overhead, or costs associated with planning, consultations, or monitoring. Working through these cost details encouraged experts to consider all elements of implementation for a given strategy and helped to refine actions where necessary. We conducted follow-up research to validate these data, then converted the annual costs of each action to present day values using a discount rate of 4%, in line with recommendations on social discounting rates in Canada (Boardman, Moore and Vining, 2010). These estimates were then summed to determine the total cost of implementing each management strategy over 25 years (Table 4S4). Combination strategy costs were calculated by summing the costs of each component strategy.

*4.3.5 Trade-offs*

We used multi-objective optimization to explore the best portfolio of management strategies that would maximize the conservation benefits of management across the populations of interest for incremental investment scenarios (Chadés *et al.*, 2015). This approach accounts for the complementarity of alternative management strategies by considering the number of CUs that achieve our objective of green status with a given probability. We defined the minimum conservation threshold as >50% chance of achieving green status and explored additional threshold values of >60% and >70% based on the range of performance estimates. We performed the complementarity analysis (Chadés *et al.*, 2015) for each threshold by solving the linear programming problem:

[3] $$\max \sum_{i=1}^{S} \sum_{j=1}^{CU} P_{ij} x_i, \text{ subject to } \min \sum_{i=1}^{S} C_i x_i,$$

where $P_{ij} = 1$ if CU $j$ exceeds the conservation threshold under strategy $i$, and $P_{ij} = 0$ otherwise; $C_i$ is the total cost of implementing strategy $i$; $x_i$ is a binary decision variable that indicates whether a strategy $i$ is selected (1) or not (0); $S$ is the total number of strategies and $CU$ is the total number of Conservation Units. The complementarity analysis assumes that the benefit of implementing two individual strategies, i.e., the number of CUs secured, is equivalent to the maximum of the two values (and not the sum). For each addition of funding, the strategy or combination of strategies that secured the maximum number of CUs above the conservation threshold was selected, such that the optimal strategy or set of strategies secures the most CUs per dollar invested (Table 4.2). This analysis was conducted using the 'consOpt' package in development (Nicolai Cryer, no date) and validated manually in Microsoft Excel.

*4.3.5.1 Uncertainty*

We examined the effect of uncertainty in the benefit, feasibility, and cost estimates on the resulting optimal strategies (detailed in the SI: Uncertainty, Table 4S3, Figs 4S3-4S7). To further examine the effect of uncertainty in benefit estimates, we performed the complementarity analysis using the most optimistic and pessimistic estimates, which represent the most extreme outcomes within the realm of possibility predicted by the experts in this study (Table 4S3, Fig. 4S3, Fig. 4S4). The high capital costs of two wastewater treatment facility upgrades, which have been under consideration for over a decade, led us to assess two scenarios for the pollution strategy (S08): one with the capital costs of these projects assumed by municipal budgets (Fig. 4S7), and one with them included in our assessment (primary results).

## 4.4 Results

Under 'business as usual' (i.e., baseline) all 19 salmon CUs in the lower Fraser study region were predicted to have less than 0.5 probability - or <50% chance - of achieving green status in 25 years (maximum 45%; BSL in Table 4.2). If all proposed development projects for the region were approved (development baseline scenario), these predictions declined further by 3-9% to a maximum of 39% chance (DEV BSL in Table 4.2). In contrast, implementing all identified management strategies would bring most salmon Conservation Units, 16 of 19 CUs, above a 50% chance of green status for an estimated cost between 45 and 110 million Canadian dollars per year (Table 4.2, Fig. 4.4). The combination of all habitat strategies (i.e., S02, S03, S04, S05, and S06) resulted in 14 of 19 CUs surpassing the 50% threshold (with three >60%) for an investment of 20M CAD per year (S13, Fig. 4.4). For a smaller budget of 2.5M CAD per year into improved fisheries management (S01) brought half of these salmon CUs (n=7) that were secured via S13 above the 50% threshold. Below 10M CAD annually several strategies had similar conservation outcomes at a higher cost, so were not identified as optimal strategies by the complementarity analysis (e.g., S10 hatchery operations, Table 4.2).

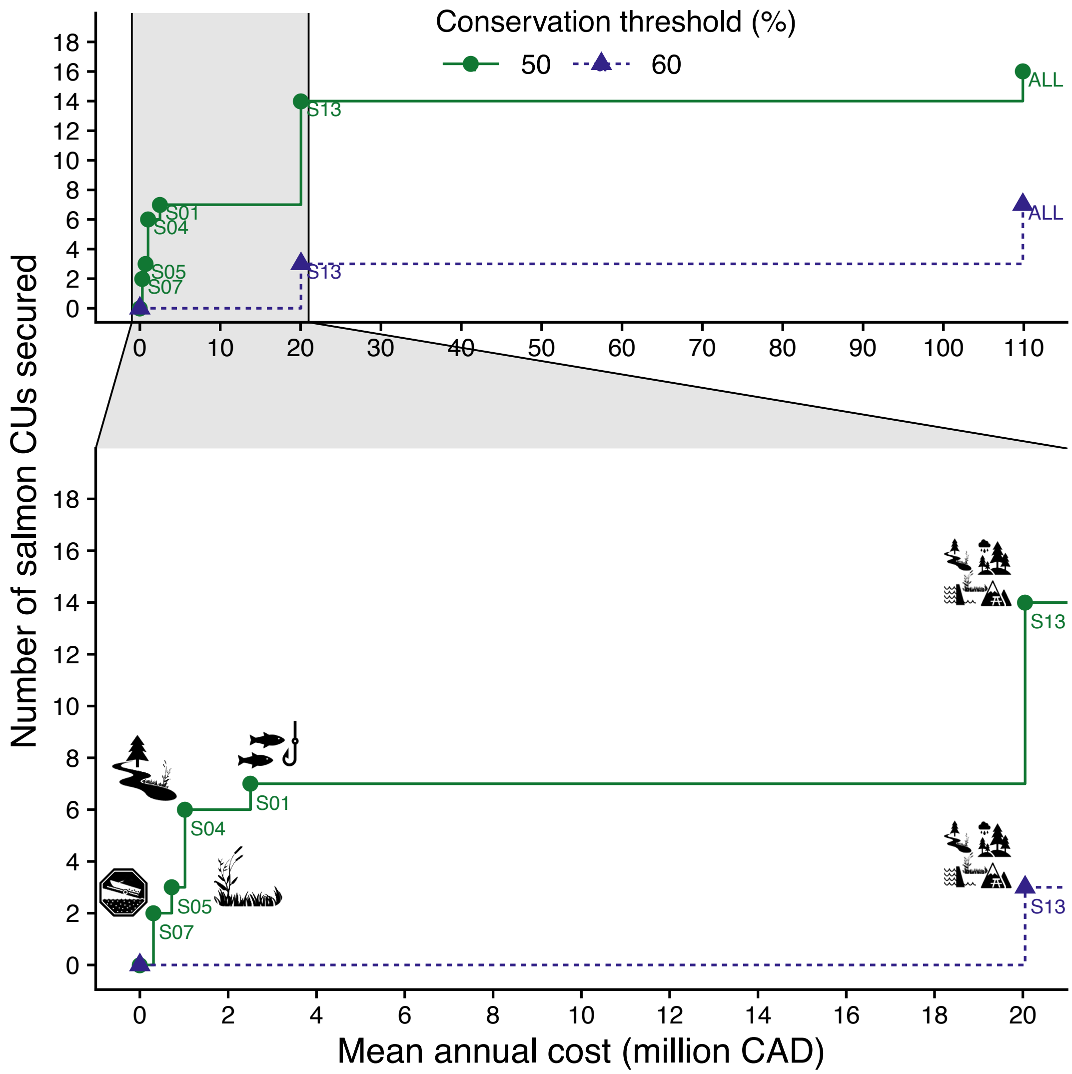


**Figure 4.4** The number of lower Fraser River salmon Conservation Units (CUs) that were predicted to achieve >50% (solid dark green line) or >60% (dashed dark blue line) chance of green status by implementing the optimal set of strategies for a given budget. Top: all optimal strategies. Bottom: optimal strategies between 0 - 20 million CAD magnified for clarity. ALL indicates all management strategies combined. Note that no CUs achieved a greater than 70% chance of being assessed as green status at the end of 25 years.

**Table 4.2** Conservation optimization showing the expected chance of each CU[2] achieving green status at the end of 25 years under each strategy (>49% blue (light), >50% green (dark), >60% magenta (medium)). Cut-off for threshold (and colour) applied prior to rounding. BSL: baseline; DEV BSL: development baseline scenario.

| Conservation Unit | BSL | DEV BSL | Strategy (sorted by annual cost, low to high) S07 *Inva* | S05 *Est* | S10 *Hatc* | S04 *Frsh* | S02 *Hydr* | S01 *Mgmt* | S11 *Pred* | S06 *Barr* | S03 *Prot* | S09 *Aqua* | S13 *Hab* | S12 *Mgt$^{+}$* | S08 *Poll* | ALL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Chinook** | | | | | | | | | | | | | | | | |
| Boundary Bay Fall 0.3 | 27 | 22 | 38 | 39 | 37 | 42 | 39 | 38 | 37 | 42 | 38 | 36 | 53 | 46 | 42 | 53 |
| Lower Fraser Fall 0.3 | 41 | 37 | 46 | 53 | 50 | 52 | 49 | 50 | 51 | 52 | 51 | 49 | 62 | 59 | 54 | 64 |
| Lower Fraser Spring 1.3 | 37 | 33 | 42 | 46 | 45 | 47 | 46 | 48 | 46 | 47 | 46 | 43 | 58 | 54 | 47 | 59 |
| Lower Fraser Summer 1.3 | 39 | 34 | 43 | 46 | 47 | 48 | 47 | 50 | 47 | 47 | 46 | 45 | 57 | 54 | 46 | 59 |
| Lower Fraser Upper Pitt Summer 1.3 | 28 | 24 | 32 | 35 | 37 | 39 | 37 | 37 | 38 | 36 | 36 | 34 | 49 | 44 | 36 | 51 |
| Maria Slough Summer 0.3 | 32 | 28 | 37 | 42 | 40 | 43 | 42 | 43 | 41 | 41 | 42 | 38 | 54 | 48 | 43 | 56 |
| **Chum** | | | | | | | | | | | | | | | | |
| Lower Fraser | 40 | 32 | 47 | 49 | 49 | 53 | 50 | 50 | 48 | 53 | 50 | 47 | 59 | 54 | 51 | 61 |
| **Coho** | | | | | | | | | | | | | | | | |
| Boundary Bay | 25 | 18 | 37 | 38 | 40 | 43 | 38 | 35 | 37 | 43 | 37 | 36 | 50 | 42 | 42 | 53 |
| Lower Fraser | 33 | 25 | 39 | 41 | 44 | 48 | 45 | 42 | 45 | 48 | 44 | 40 | 56 | 49 | 46 | 59 |
| Lillooet | 33 | 28 | 39 | 44 | 45 | 47 | 45 | 45 | 45 | 48 | 47 | 43 | 56 | 51 | 47 | 59 |
| **Pink** | | | | | | | | | | | | | | | | |
| Fraser River | 45 | 39 | 50 | 52 | 52 | 54 | 51 | 53 | 51 | 54 | 54 | 51 | 63 | 59 | 55 | 64 |
| **Sockeye** | | | | | | | | | | | | | | | | |
| Chilliwack Early Summer | 41 | 33 | 46 | 46 | 47 | 50 | 47 | 50 | 48 | 49 | 48 | 46 | 54 | 55 | 51 | 61 |
| Cultus Late | 14 | 11 | 20 | 17 | 19 | 22 | 18 | 23 | 19 | 19 | 20 | 17 | 25 | 25 | 24 | 30 |
| Harrison Down Late (Big Silver) | 42 | 33 | 46 | 46 | 48 | 51 | 48 | 51 | 50 | 49 | 50 | 48 | 56 | 54 | 50 | 61 |
| Harrison (River type) | 43 | 36 | 48 | 50 | 50 | 53 | 50 | 52 | 51 | 51 | 51 | 49 | 57 | 56 | 54 | 62 |
| Harrison Up Late (Weaver) | 26 | 23 | 31 | 32 | 34 | 36 | 34 | 38 | 34 | 36 | 35 | 33 | 43 | 42 | 36 | 48 |
| Lillooet/ Harrison Late (Birkenhead) | 31 | 26 | 36 | 38 | 40 | 41 | 37 | 41 | 41 | 41 | 39 | 38 | 45 | 46 | 41 | 51 |
| Pitt Early Summer | 45 | 37 | 50 | 54 | 54 | 53 | 52 | 53 | 55 | 53 | 52 | 54 | 61 | 58 | 56 | 64 |
| Widgeon (River type) | 23 | 17 | 28 | 29 | 28 | 29 | 27 | 31 | 28 | 29 | 29 | 28 | 35 | 35 | 32 | 40 |
| Feasibility | NA | NA | 0.71 | 0.70 | 0.67 | 0.69 | 0.68 | 0.70 | 0.70 | 0.73 | 0.64 | 0.57 | 0.69 | 0.64 | 0.81 | 0.69 |
| Annual Cost (million CAD) *(values with costs of facilities excluded)* | NA | NA | 0.31 | 0.72 | 0.76 | 1.02 | 2.08 | 2.51 | 3.62 | 6.19 | 10.0 | 18.5 | 20.1 | 21.7 | 64.2 *(0.14)* | 109.9 *(45.8)* |

[2] CU nomenclature uses unique geographic location and as needed, other distinguishing characteristics such as run timing, depending on the species. For Chinook salmon, which have the most detailed CU names, the format is 'geographic location - season of adult return - dominant age of returning adults' using the European age designation system (Koo, 1962), e.g., 'Lower Fraser - Fall - 0.3'.

Out of the 19 CUs assessed, Fraser River (odd year) pink salmon and Pitt early summer sockeye salmon most easily surpassed the 50% conservation threshold with the implementation of a given strategy (Table 4.2). Conversely, Lillooet/Harrison late sockeye salmon and Lower Fraser Upper Pitt summer 1.3 Chinook salmon only surpassed the threshold with all strategies implemented (ALL, Table 4.2). Coho salmon had the largest improvements from implementation of all strategies (28% increase from baseline in the likelihood of achieving green status for Boundary Bay and 26% increase for Lower Fraser and Lillooet CUs, Table 4.2).

When each strategy was assessed with an Indigenous-led co-governance framework in place (ES2), the predicted feasibility of successful implementation increased by an average of 14% per strategy (Table 4S5). This improved the expected performance of the strategies, so an additional CU (Harrison upstream late (Weaver) sockeye salmon) achieved >50% chance of green status and 12 CUs achieved >60% chance of green status with all strategies implemented, as compared to seven CUs >60% without co-governance (Fig. 4.5, Table 4S5).

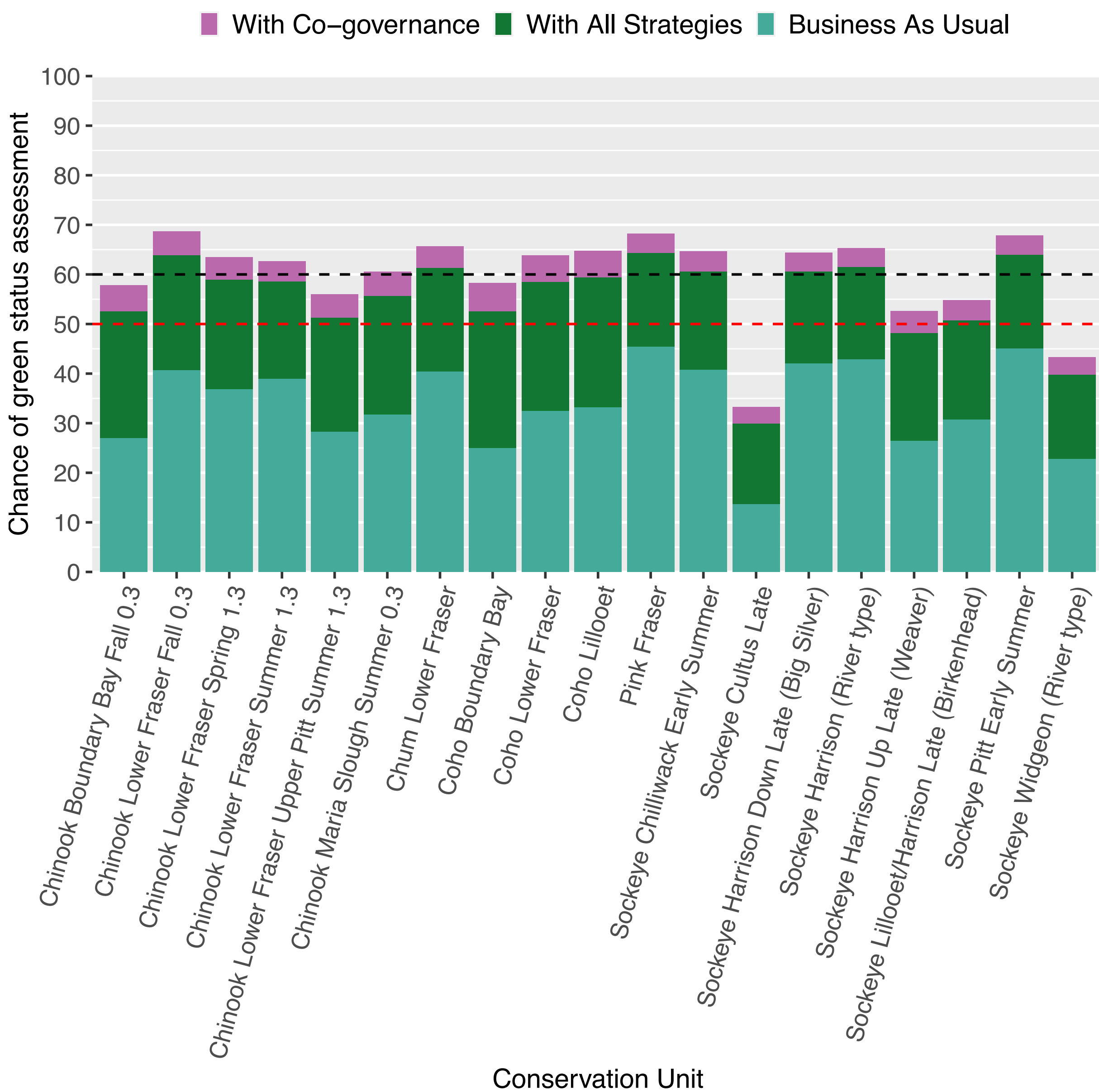


**Figure 4.5** Estimated chance of achieving green status for each of 19 Conservation Units under increasing levels of investment over 25 years. The conservation thresholds of 50% (red) and 60% (black) are highlighted with dashed lines. Business as Usual (turquoise, light) represents probabilities under no additional management; With All Strategies (green, dark): all management strategies implemented; With Co-governance (magenta, medium): implementation of Indigenous-led co-governance (detailed in SI) in addition to all management strategies.

Considering the most pessimistic and most optimistic benefit estimates in the complementarity analysis emphasized similar optimal strategies to the best estimates (Table 4S3). In the optimistic scenario an additional strategy was selected (hatchery operations, S10) and the number of CUs at each conservation threshold increased, such that a total of 18 CUs achieved >50% chance of green status with most >60% (six CUs between 60-70% and 11 CUs >70%) when all strategies were implemented (Fig 4S3). Conversely, under the most pessimistic scenario no salmon CUs achieved >50% chance of green status even with all management strategies implemented (Fig 4S4). The priority strategies identified by the complementarity analysis were unaffected by estimated changes to benefit, feasibility, and cost estimates, despite some sensitivity in cost-effectiveness scores (Fig 4S5, Fig 4S6). The results were affected by an alternative scenario in which we assumed that the costs of improving wastewater facilities (pollution control, S08) would be borne by municipalities (Table 4S4 values in parentheses; Fig 4S7); however, the top two strategies (combined habitat strategy S13 and ALL) remained the same.

## 4.5 Discussion

Our study provides support and a pathway forward for the comprehensive management of wild salmon ecosystems at a watershed scale, which has been increasingly called for (Gayeski *et al.*, 2018; Connors *et al.*, 2020; Atlas *et al.*, 2021). Despite two CUs currently doing well (Harrison River and Pitt early summer sockeye salmon CUs were assessed as green status (DFO) and not at risk (COSEWIC) in 2018; Table 4S2), none of the 19 CUs in this study were predicted to be in green status in 25 years if we continue the trajectory of ‘business as usual’. If a ‘development baseline’ scenario is realized, involving the approval and completion of several major development proposals in the lower Fraser, the likelihood of achieving green status further declines. Conversely, investment in a suite of management strategies at a cost of 45M annually (and up to 110M if wastewater treatment upgrades are included) improves the outlook for lower Fraser salmon, with >50% chance for 16 of 19 CUs to be assessed as green status in 25 years. Developing and implementing an Indigenous-led co-governance framework for wild salmon improved the likelihood of achieving green status for all CUs and brought one additional CU above the 50% threshold. Our results illustrate the plight of wild Pacific salmon in this region, the challenges posed by cross-realm ecosystem management (Camaclang *et al.*, 2021), and the limitations of regional management to fully abate the myriad threats to these CUs.

Of the regional strategies examined, investment in a combination of five habitat strategies consistently benefitted the most CUs. Fourteen CUs, including all three coho salmon CUs, had >50% chance of achieving green status with extensive habitat conservation costing an estimated 20M CAD annually. Recent estimates of habitat loss for salmon in the lower Fraser indicate that up to 85% of the floodplain and 64% of the stream habitat has been lost entirely or is no longer accessible (Groulx *et al.*, 2004; Finn *et al.*, 2021). While significant restoration efforts have been made in the lower Fraser, most of these projects have been on a scale insufficient to achieve desired outcomes (Levings, 2004).

To achieve the full potential of these combined habitat strategies would require a system-wide change in habitat management for the lower Fraser, including implementing stringent watershed hydrology management plans, protecting remaining salmon habitat via a combination of land acquisition and restriction of industrial footprints, and strategically restoring riparian areas, instream habitat, wetlands, and tidal marsh, including significant barrier removal. These strategies are each complex and some, such as watershed hydrology management plans, are emerging practices with few regional examples. However, numerous watershed governance projects have been initiated in BC and both funding sources and guidance documents to support these projects are increasing (Okanagan Basin Water Board, 2010; Hunter and Brandes, O., Moore, 2014; Polis Project on Ecological Governance, 2019; Tawaw Strategies, 2021). To avoid common pitfalls of failed restoration attempts practitioners must carefully consider the site-specific objectives, capacity, and current and future conditions (Beechie *et al.*, 2010, 2013; Roni *et al.*, 2011; Lievesley *et al.*, 2017). Estimates of the probability of the technical success of these restoration strategies ranged from 70 - 100%, however incorrect procedure can easily result in complete failure to achieve the biological objectives of restoration projects (Lievesley *et al.*, 2017). Improvements to connectivity are likely to have high efficacy and long term benefits for multiple species, but freshwater habitat restoration projects including riparian and instream enhancements are far more variable in their effectiveness and longevity and should be carefully considered in the regional context prior to implementation (Roni *et al.*, 2011; Beechie *et al.*, 2013). While other studies have estimated higher costs for aquatic habitat restoration (i.e., Walsh et al., 2020), identification of habitat restoration as a priority strategy was robust to uncertainty in costs according to the sensitivity analyses. In addition, this study benefitted from cost and feasibility data provided by local restoration practitioners, who successfully completed similar component projects, to inform the most likely scenario for this regional context. However, even if restoration costs were severely underestimated, applying the costs such as those estimated by Walsh et al. still results in the combined habitat strategy (S13) remaining a priority due to its high estimated benefits to 14 CUs.

The costs of implementing these strategies do not account for the co-benefits they provide, which could offset the up-front economic costs (i.e., Barbier et al., 2011; Rees, Carwardine, Reeson, & Firn, 2020). Watershed management and restoration in BC provided an estimated

4,200 jobs and contributed 432M CAD to the GDP in 2019, suggesting it can be an important contributor to the economy (Delphi Group, 2021). Additional co-benefits associated with regulating, provisioning, and cultural services are also likely to arise. For example, extensive habitat restoration and protection may alleviate some of the multiple threats faced by other Fraser River salmon (54 CUs), protecting existing diversity (Bottom *et al.*, 2005), and in turn increase resilience to press and pulse disturbances such as climate change and landslides (Hilborn *et al.*, 2003; Moore *et al.*, 2014; Schoen *et al.*, 2017). In addition, 102 species at risk identified within the Fraser River estuary (Kehoe *et al.*, 2020), including other aquatic species such as white sturgeon (*Acipenser transmontanus*), Nooksack dace (*Rhinichthys cataractae*) and Salish sucker (*Catostomus* sp. cf. *catostomus*), are likely to benefit from habitat conservation and restoration.

Three sockeye CUs are unlikely to achieve green status in 25 years, even if all strategies are implemented. One, Harrison River late (Weaver) sockeye, may achieve green status with the additional support of Indigenous-led co-governance. The Widgeon slough river type sockeye CU was determined unlikely to *ever* be assessed as green status under the Wild Salmon Policy due to its naturally small population size, which is limited by geographic constraints and therefore vulnerable to stochastic events (DFO, 2018). Cultus Lake late sockeye also have naturally low relative abundance (~20,000 spawning adults) and were consistently caught in fisheries targeting larger runs, leading to regular incidences of overharvest (DFO, 2020b). This CU has been monitored longer than any other sockeye salmon CU in BC and has had dedicated stewardship and federal funding since it was assessed as endangered in 2002 (DFO, 2020b). Yet in the present study it was predicted to be the least likely CU to achieve green status even with all strategies implemented under the most optimistic scenario. Some of the lower Fraser's most stable and productive salmon populations have recently declined, such as the Lower Fraser fall

0.3 Chinook CU, which was assessed as Threatened (COSEWIC, 2018). Timely investment in priority strategies to support these more productive CUs may buffer these populations against future stressors while providing some benefit to CUs that are unlikely to achieve green status.

One of the most pervasive threats to wild Pacific salmon survival across life stages is climate change (Hinch *et al.*, 2012; Hertz *et al.*, 2016; Grant, Macdonald and Winston, 2019), which was not directly addressed by the management strategies in this project. However, experts were asked to assume climate impacts would continue over the next 25 years when developing alternatives and assessing the potential benefits of implementing each strategy. This context helped to identify strategies to mitigate the expected effects of climate change, for example, intensive restoration of lost and degraded rearing and spawning habitat was predicted to provide substantial conservation benefit to Fraser River salmon populations. This strategy can facilitate enhanced capacity for salmon to withstand stochastic climate events and adapt to future change (Gayeski *et al.*, 2018; Atlas *et al.*, 2021; Munsch *et al.*, 2022).

PTM allows for the explicit and objective assessment of available strategies to determine optimal application of limited management resources for species recovery (Carwardine *et al.*, 2012; Martin *et al.*, 2018). This approach does not address the complex social and political ramifications of those strategies, apart from the requirement that all actions would be feasible to implement. Predator control (S11) had particularly divisive responses from experts with respect to feasibility, with some strong proponents and others voicing concerns that pinniped culls would be unethical and unlikely to achieve sufficient public support to be implemented in this region. However, the strategy was robust to changes in feasibility, which may alleviate concerns regarding the impact of the feasibility estimate on the priority ranking (SI). Ethics and uncertainty around unintended consequences of predator culls frequently divide scientists and resource managers (Yodzis, 2001), as occurred in this project. While predator control was not selected as an optimal strategy in this case, it did contribute to the overall success of the 'all strategies implemented' scenario, so we recommend that the ethical concerns and potential ecosystem consequences be reviewed prior to implementation of this strategy.

The efficacy of each strategy hinges on successful implementation, monitoring, and adaptation as needed (Carwardine *et al.*, 2019). While PTM does not produce a detailed implementation plan, the inclusion of local decision-makers and practitioners in the PTM process provides a realistic pathway forward for complex resource allocation problems, which can help to facilitate support and uptake. PTM uses the best available data to objectively assess the outcomes of available management alternatives. While uncertainty in the quantification of benefits, costs, and feasibility is expected, determining where to allocate management resources requires only the relative performance of the available strategies to support robust decisions. As additional data becomes available, such as explicit assessments of the pathways of effects of strategies on target species and populations, the PTM analysis can be easily repeated and, if warranted, implementation plans can be adapted. This approach has been applied to a diverse and complex set of conservation problems throughout Australia, Indonesia, Antarctica and Canada spanning multiple species, values, and a wide range of budgets (Carwardine *et al.*, 2019). In a world facing increasingly complex conservation problems requiring multiple trade-offs, we present this work as an example of the application of PTM to facilitate rapid and effective conservation decisions for migratory fishes.

### *4.5.1 Conclusions*

Our study highlights the urgent need for bold and sustained investment in strategic conservation strategies for wild salmon in the lower Fraser region, including improvements to monitoring and an Indigenous-led co-governance framework for managing salmon populations. PTM provides a framework to rapidly identify priority strategies for investment in species recovery compared to existing planning processes and may be useful to incorporate into wild salmon recovery planning. While the scope of our study was limited to actions within Canadian jurisdiction and focused within the lower Fraser region, additional strategies at an international scale are worth investigating, such as treaty negotiations to minimize hatchery-wild interactions. If the predicted benefits of these international strategies proved high, they could further improve the probability of Fraser salmon CUs achieving green status. Though the ability to recover lower Fraser River salmon remains uncertain, preventing further declines of wild salmon will almost certainly require a move away from 'business as usual' towards a restoration economy, with a shared vision among governing bodies.

## 4.6 Acknowledgements

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# Chapter 5 - Conclusion

Sustaining productive wild salmon populations into the future will require diverse and resilient portfolios of salmon and their habitats, which are able to collectively withstand and recover from pulse disturbances and adapt to press disturbances (Waples, Beechie and Pess, 2009; Griffiths *et al.*, 2014; Brennan *et al.*, 2019; Munsch *et al.*, 2022). Numerous salmon portfolios in the Northeast Pacific have been impacted by cumulative anthropogenic disturbances, resulting in reduced and more synchronous population productivity (Griffiths *et al.*, 2014; Dorner, Catalano and Peterman, 2018). While the Fraser River has been less impacted than some watersheds further south, its portfolio is considerably more vulnerable than relatively intact systems like Bristol Bay (Griffiths *et al.*, 2014). Salmon play a disproportionate role in maintaining the biodiversity of the Fraser basin's fish communities, but many of these populations are now at risk (Iacarella, 2022). Managing for resilient salmon populations likely requires a holistic approach, which includes anticipating and proactively managing fisheries for years of reduced productivity due to poor conditions, preventing overharvest of small populations, minimizing genetic diversity loss from hatchery production, and maintaining diverse and functioning habitats at a large landscape scale (Schoen *et al.*, 2017; Gayeski *et al.*, 2018; Munsch *et al.*, 2022). While careful restoration can improve salmon habitat availability and resilience to climate change (Waples, Beechie and Pess, 2009; Beechie *et al.*, 2013; Davis *et al.*, 2018), restoration of dynamic ecosystems is difficult and preserving intact habitat and watershed processes where possible is preferred (Bisson, Dunham and Reeves, 2009; Waples, Beechie and Pess, 2009; Roni *et al.*, 2011; Wohl, 2019). Underpinning a future management regime that prioritizes salmon resilience is the need to prevent further habitat loss and increase habitat capacity through restoration.

New proposals for development in Canada that may cause harm to fish habitat are currently evaluated individually via an Environmental Assessment process, which requires data on the potential impacts to species within the development footprint to determine whether to allow the project to proceed as planned or to require amendments or habitat mitigation if significant adverse effects are expected (Murray *et al.*, 2018). This process rarely prevents habitat loss for multiple reasons, including that in most cases, pre-existing habitat loss may positively influence project approval, that data for specific harms to or thresholds for species within a portion of a species' range are difficult to provide, and that these types of evaluations fail to effectively capture the cumulative effects of development within the overall ecosystem (Waldichuk, 1985; Lotze *et al.*, 2006; Murray *et al.*, 2018; Hodgson, Wilson and Moore, 2020). While Fisheries and Oceans Canada attempts to maintain a "no net loss" policy for fish habitat when considering development proposals, this has had limited success due to a lack of compliance and reporting by proponents, failure to consider the cumulative impacts of multiple developments across the region simultaneously, and lost habitat often being 'offset' with ecologically different habitat (Waldichuk, 1985; Harper and Quigley, 2005). In the Fraser River estuary these habitat 'offsets' often fail (Lievesley *et al.*, 2017). Habitat loss continues to undermine the resilience of salmon portfolios, particularly in the Fraser, but my research supports the importance of this habitat to salmon populations and suggests that habitat management should be made a priority in salmon recovery strategies.

In Chapter 2, I assessed the current fish community of the Fraser River estuary by systematically surveying three habitat types: brackish marsh, eelgrass, and sand flats. Despite the intense land use changes to this system, I found that the remaining habitats were highly productive. Using relative catch as a proxy for habitat use, I found distinct patterns of species-specific occupancy of these habitat types as well as indications of connectivity across the estuary, as predicted. Chapter 2 demonstrated that habitat mosaics and a connected seascape support greater biodiversity than any single habitat, which may contribute to ecosystem resilience. These findings are similar to studies of other temperate estuaries (Hosack *et al.*, 2006; Olson *et al.*, 2019) and to comparative habitat studies in tropical ecosystems (Whitfield, 2017), suggesting that seascape connectivity is important for fish diversity generally. Diversity of small fishes also provides alternate prey sources to predators of juvenile salmon, which can significantly reduce pressure on recovering salmon populations (Weitkamp *et al.*, 2014; Moore *et al.*, 2021). Conversely, competition with other species with overlapping dietary niches (i.e., shiner surfperch (*Cymatogaster aggregata*), three-spined stickleback (*Gasterosteus aculeatus*), Pacific herring (*Clupea pallasii*), starry flounder (*Platichthys stellatus*), and longfin smelt (*Spirinchus thaleichthys*) (Weitkamp *et al.* (2014), all of which were caught in our study) may cause interspecific resource competition and require additional productive habitat than what would support salmon alone. Habitat as well as the biophysical characteristics of the estuary informed species distribution in the Fraser, which was also found for salmon and forage fishes in the Skeena River estuary (Sharpe *et al.*, 2019), and which may be related to food availability or predator avoidance (Hosack *et al.*, 2006). In the Fraser River estuary, marsh habitat was thought to be of lower value to salmon than eelgrass meadows, due to the fact that it largely dewaters at low tide (Waldichuk, 1985). While I did find that eelgrass supported greater overall catch and species richness than the other two habitats assessed, brackish marsh supported the most juvenile salmon throughout the emigration period. This suggests that the previous emphasis on eelgrass alone does not capture the important habitats of the Fraser estuary for juvenile salmon.

The majority of the salmon that we caught during this study were juvenile Chinook salmon that were later determined to be resident in the estuary. While we know that millions of juvenile salmon pass through the estuary each year, our study caught a very small proportion of these fish, indicating that larger and faster migrating species (e.g., sockeye) were not adequately sampled by our methods. Larger salmon smolts are physiologically adapted to high salinity environments (Clark *et al.*, 2016; Quinn, 2018) and may use outer eelgrass habitats in the Fraser estuary more than the resident Chinook salmon. It is also possible that they use each of the habitats equally for a short duration, which could not be determined by my results. Age 1 and 2 year Chilko River sockeye smolts rapidly migrate through the lower reaches of the Fraser in less than 2 days, and while they slow by up to 50% and experience high survival in the estuary, their swift movement through these turbid waters would make catching them extremely challenging (Clark *et al.*, 2016; Stevenson *et al.*, 2019). While emigrating sockeye from the Fraser River are known to move rapidly north, there are a subset of juveniles that enter later and at smaller sizes that linger in nearshore environments (Freshwater *et al.*, 2016). These fish were either not lingering in the habitats we sampled in the estuary or were still moving rapidly enough that we missed them. Surveying on a falling tide can improve catch rates, and low tide refugia are an important component of estuarine habitat use for salmon (Levings, 1982). However, sampling at high tide while all estuarine habitat was accessible to the fish allowed me to demonstrate active use of these habitats. All salmon also face major barriers to accessing the densest eelgrass meadows in the Fraser River estuary due to large jetties and causeways that require fish to swim more than 8 km to a steep drop off into the Strait of Georgia before swimming back shoreward to access the eelgrass. Connectivity between habitats did not seem to be a primary consideration during past and recent environmental assessments of infrastructure expansion in the estuary

(Archipelago Marine Research Ltd., 2014a), likely because their movement had been previously impeded by developments prior to the implementation of environmental assessment requirements (Waldichuk, 1985). Anthropogenic structures have numerous impacts on coastal fish communities (Mahoney and Bishop, 2017; Munsch *et al.*, 2017) and the overlapping species composition we found demonstrates that the community assemblage of the Fraser River estuary is a continuum across habitats, which requires connectivity to be maintained.

Chapter 3 further elucidated the use of the estuary by Harrison Chinook salmon, providing clear evidence that this population is reliant on estuarine habitat for early marine growth. Harrison Chinook are subyearling migrants, meaning that they emigrate from the Harrison River to the ocean within their first year. Using otolith analysis, I demonstrated that, for many of these fish that journey occurs very soon after hatching, such that they enter the estuary in early spring at less than 40 mm fork length. This very small size at entry correlates to their movements in the estuary, with the smallest fish remaining in the estuary for longer time periods. Estuaries provide an opportunity for salmon to gradually transition between freshwater and marine conditions, which is a physiologically demanding process (Quinn, 2018). Later in the season we caught larger juveniles in the outer habitats, suggesting that this early growth in the brackish marsh may be a necessary first stop to allow for physiological adaptation to more saline environments. Our analysis also revealed daily growth rates in the estuary comparable to populations north of the Fraser in the Skeena River estuary (Moore *et al.*, 2016) and south of the Fraser in the Salmon River estuary in Oregon (Volk *et al.*, 2010). The smallest fish who entered earliest remained in the estuary the longest and experienced the greatest total proportional growth. Together these data demonstrate that this population is reliant on the estuary for this critical early growth period. This contributes to a growing body of evidence that all subyearling migrant Chinook salmon populations rely on estuarine habitat during early marine growth, and that other species may similarly depend on these habitats, though to a lesser extent (Volk *et al.*, 2010; Carr-Harris, Gottesfeld and Moore, 2015; McNatt, Bottom and Hinton, 2016; Moore *et al.*, 2016). While I found that daily growth rates appeared to be stable, the question remains whether competition for resources due to density dependent effects in this severely diminished habitat may be influencing population abundance. Similarly, contaminants in urban systems have been shown to have deleterious effects on juvenile salmon (Sandahl *et al.*, 2007; Tian *et al.*, 2021). Harrison Chinook salmon would be exposed to potential contaminants in the estuary for a longer duration than other salmonids and may experience decreased fitness as a result. Further research will be needed to determine how the health of the estuary affects the health of these juvenile salmon, but recent work in nearby Puget Sound has suggested that reductions in Chinook survival from passing through contaminated estuaries as juveniles may be as high as 45% (Meador, 2014). Juvenile Chinook salmon are also particularly vulnerable to climate impacts during the estuary rearing phase, which is exacerbated for subyearling migrant Chinook and estuaries with high habitat modification (Crozier *et al.*, 2019), emphasizing the need to improve the habitat resilience of the lower Fraser estuary. Subyearling migrant salmon populations are often small, but make important contributions to life history diversity in many river systems (Miller, Gray and Merz, 2010; Brennan *et al.*, 2019), which is critical for the maintenance of resilient wild salmon portfolios (Crozier *et al.*, 2019; Price *et al.*, 2021).

Disentangling the effects of habitat degradation or restoration from other influences on survival is difficult, especially for migratory species like Pacific salmon. In Chapter 4, I applied Priority Threat Management, a conservation decision-science framework, to predict the outcomes of a suite of management strategies on the population status of salmon in the lower

Fraser. Our results identified that habitat restoration and protection combined with effective watershed management was the most likely management strategy to facilitate recovery of 14/19 salmon conservation units (CUs) - genetically and ecologically distinct populations (Holtby and Ciruna, 2007), and that implementation of Indigenous-led co-governance with this strategy could support an additional CU. These findings imply a strong relationship between habitat condition and salmon survival. Compared to recent PTM projects aimed at securing diverse species groups across large swaths of Australia's wilderness in the Kimberley (Carwardine *et al.*, 2012), Pilbara (Chadés *et al.*, 2015), and Queensland Brigalow Belt (Reyes *et al.*, 2019), the conservation outlook for wild Pacific salmon in the lower Fraser is grim. These former studies achieved conservation thresholds of 70-90%, whereas none of the salmon CUs in this study had greater than 70% likelihood of achieving high abundance in 25 years except in the most optimistic scenario. These results may reflect the conservation challenges specific to salmon and to the Fraser River system, which has been heavily impacted by long-term human use. Widespread habitat degradation can reduce the overall resilience of salmon populations to climate impacts (Munsch *et al.*, 2022), and the recovery or maintenance of habitat must occur at a large scale to convey resilience to stressors for aggregate salmon production (Brennan *et al.*, 2019). Accordingly, the combined habitat strategy involves restoration across four watershed subbasins and each habitat realm in the study area: freshwater and estuarine, as well as removal of barriers to fish passage. Restoration work that occurs at a scale sufficient to influence natural processes such as this and that directly influences salmon survival via improvements to spawning habitat and flow regimes (freshwater restoration), rearing habitat (freshwater and estuarine restoration), increased spawning and rearing capacity and access to diverse habitats (barrier removal), as well as increased temperature refugia via riparian (freshwater) restoration can be highly effective in improving salmon productivity and resilience to climate change (Waples, Beechie and Pess, 2009; Roni *et al.*, 2011; Beechie *et al.*, 2013; Beechie and Timpane-padgham, 2021). In addition to these large-scale restoration efforts spread over 25 years, the habitat strategy includes modifications to watershed management that would have implications for agriculture and forestry industries, restricting water removal, nutrient loading, and any activities that threaten hydrological processes of each subbasin. Finally, the habitat strategy also includes protecting remaining areas of valuable habitat to prevent further losses. These management actions span all realms of salmon habitat outside of the open ocean, and therefore do not provide us with a quantitative understanding of the relative importance of habitat to salmon survival. However, the scale of this strategy, particularly when the effects of improved co-governance are included, emphasizes the value of holistic salmon management. In addition to habitat degradation in the Lower Fraser, these same populations have faced fluctuations in fishing pressure, increased exposure to pathogens and disease via coastal development and finfish aquaculture, competition from hatchery production both in the Fraser River watershed and in the ocean, and changes to the physical and biological environment due to climate change. However, for these populations, it is clear that experts believe holistic habitat management will significantly affect their overall productivity or capacity for recovery, which aligns with the ecosystem based management approach that has been called for in Pacific salmon management (Malick, Rutherford and Cox, 2017; Schoen *et al.*, 2017).

Over the last two decades, a widespread decline in marine survival for multiple species of salmon redirected much of the salmon research community’s attention away from freshwater processes (e.g., McFarlane, King and Beamish, 2000; Mueter, Peterman and Pyper, 2002; Malick *et al.*, 2017; Dorner, Catalano and Peterman, 2018). This decline was more extreme within the

Salish Sea than in outer coast populations, suggesting that environmental factors in the Salish Sea may be exacerbating the effects of the marine regime shift for salmon (Ruff *et al.*, 2017). This is echoed in the proportion of 'resident populations' of salmonids in the Salish Sea - i.e., fish that migrate into the Salish Sea and remain there for at least one year before returning to their natal streams, rather than migrating to outer Pacific waters. These resident salmonids have been declining since the 1990s, particularly the longest residing species: coho and Chinook salmon (Quinn and Losee, 2022). A recent study in the Koegh River on Vancouver Island demonstrated that for multiple salmonid species freshwater habitat degradation due to logging was detrimental to population productivity, and for steelhead salmon specifically, which have been highlighted as a particularly sensitive species to marine conditions (COSEWIC, 2020; Moore *et al.*, 2021), marine and freshwater regime changes influenced steelhead population productivity approximately equally (Wilson *et al.*, 2022). These realms are connected and interchangeably affect one another, such that both should be considered for effective management (Losee *et al.*, 2021). Furthermore, density-dependent compensatory changes in productivity during declining abundance fail after some threshold of cumulative impacts is reached, such that depressed salmon populations are held in a low productivity, low abundance state, which will make population recovery challenging (Wilson *et al.*, 2022). It is logical to assume that salmon are influenced by multiple habitats across their lifecycle, and that we should continue to focus on holistic recovery measures that can be taken in both marine and freshwater environments.

Freshwater habitat degradation may be more amenable to management interventions than marine survival dynamics, and may improve resilience to populations as they await the next marine regime change (Schoen, 2022). My findings from Chapter 4 suggest that implementing conservation actions in freshwater and estuarine habitat realms is not only reasonable but is the most cost-effective management approach for lower Fraser River salmon. Habitat alone will not sustain wild salmon populations as long as other cumulative effects remain, as evidenced by salmon declines in an otherwise intact watershed in northern British Columbia (Hill *et al.*, 2010). Habitat loss and degradation are only part of the myriad threats facing Pacific salmon populations (Slaney *et al.*, 1996). Their migratory nature and varied life history strategies make them a highly complex group of species to manage (Waples, Beechie and Pess, 2009; Malick, Rutherford and Cox, 2017). However, it is becoming clear that many salmon populations are being impacted by the cumulative threats that they face even in the absence of overfishing (Litzow, Mueter and Hobday, 2014; Ruff *et al.*, 2017; Sobocinski, Greene and Schmidt, 2018; Munsch *et al.*, 2022). Intact and functioning habitat is integral to salmon resilience and is a key component of the holistic management perspective that will be needed to sustain salmon into the future (Waples, Beechie and Pess, 2009; Brennan *et al.*, 2019; Munsch *et al.*, 2022). By this same token, habitat restoration must occur at a large enough scale to restore the fundamental watershed processes that provide enhanced resilience to salmon (Waples, Beechie and Pess, 2009; Brennan *et al.*, 2019). To be successful, restoration projects must also be well planned and executed, as well as monitored consistently, which can be a challenge if funding sources are not sustained over the long term (Bennett *et al.*, 2016). There is an imminent need for conservation intervention to support stable salmon populations into the future (Price *et al.*, 2017). By providing salmon and associated biological communities with healthy habitat mosaics for spawning, rearing, and early growth, we can offer them the best chance to survive, adapt, and withstand the cumulative threats that are less easily managed (Brennan *et al.*, 2019; Crozier *et al.*, 2019; Munsch *et al.*, 2022).

## 5.1 Limitations and Future Directions

The Fraser River has the largest estuary on the Canadian Pacific coastline, which makes it a volatile and difficult environment in which to conduct field studies. While our sites spanned three habitats and the breadth of the estuary, the size of this system makes it exceedingly difficult to capture the full extent of the biodynamic community within a single study. In addition, salmon are highly variable in their natural productivity, which can both mask and exacerbate declines and increases due to anthropogenic influences. Long-term research programs will be required to piece together the full picture of salmon patterns in the Fraser River estuary and allow for fluctuations to be identified as trajectories of change vs. artifacts of natural variation. Continued comparisons of habitat associations and conservation priorities for salmon populations within and outside of the Fraser are warranted: while some of my results align with findings across systems, others are inherent to the specific context of the Fraser system, and this is likely true across all estuary studies.

Salmon and their habitats have a complex jurisdiction in British Columbia, such that management strategies and even research may be subject to political influence. In my research I witnessed these influences in the form of resource allocation to research projects, and resistance to suggested management strategies for salmon recovery during preparation for Chapter 4. While I have employed the tools of decision science to minimize bias in this applied work, it is impossible to remove these influences entirely. Compared to other studies using expert elicitation to predict species outcomes for conservation planning (e.g., Martin *et al.*, 2018; Kehoe *et al.*, 2020; Walsh *et al.*, 2020), the expert panel for Chapter 4 was exceptionally large and diverse in terms of professional background, which improves the likelihood of overcoming these political biases in the final results (Hemming *et al.*, 2018). In each of my chapters, the scope of the work is narrower than the scope of cumulative effects that I have referenced in my conclusions. This has meant that in Chapter 4, for example, the suggested management strategies were limited to the jurisdictional ability of managers in the study region, which likely contributed to lower total benefits achieved by each CU under a given strategy. Importantly, PTM provides a comparative analysis of the predicted benefits, costs, and feasibility of management alternatives for species recovery. While the alternative strategies are given enough detail to estimate these parameters, the process does not provide a detailed implementation plan to execute the strategies, which is a necessary step to ensure the desired benefits are achieved. The outcome for each population is therefore dependent on the realized efficacy of strategy implementation.

Each of these chapters could be followed up with additional studies. Chapter 2 was the beginning of a longer (ongoing) field study, which will provide a more stable picture of juvenile salmon movements through the estuary over time and allow annual anomalies and long-term trends to be parsed apart. It would be useful for this approach to be mirrored across a range of estuaries of varying scales, exposure levels, and anthropogenic disturbance regimes to identify commonalities; as appears to be occurring for the Nisqually (Puget Sound, Washington), Cowichan (East Vancouver Island, BC), and Skeena (North coast, BC) estuaries to varying degrees. In the Fraser estuary this work is ongoing and being led by David Scott, Raincoast Conservation Foundation, and Dr. Scott Hinch, University of British Columbia. My findings from Chapter 3 may also be complimented by otolith analyses of the returning adults from the same cohort of Harrison Chinook salmon that I assessed. This will provide information on the estuarine use of actual survivors of the population, to better understand the benefits and costs of estuarine residency in the Fraser. Fyke net or ocean surveys will allow the estuarine residency for other populations in the Fraser to be assessed since otoliths retain data permanently. Similarly, examining otoliths for other populations of subyearling migrant Chinook salmon in different estuaries such as the Cowichan River would be useful to compare life history strategies, estuarine health, and other indicators of success.

Chapter 4 is a high-level overview of priority management strategies, which must be followed up by an implementation planning process to put theory to action. It would be useful to replicate this process for the middle and upper portions of the Fraser River to inform conservation decisions for the entire Fraser Basin. Similarly, the Priority Threat Management approach can be adapted to nearly any species or ecosystem scenario and would be well suited to other salmon watersheds to inform effective use of conservation funds. Finally, it would be incredibly useful to address cumulative effects management for salmon across jurisdictions. It may be that the legal tools to address many of the most pressing conservation issues for Pacific salmon in BC exist, but that we are not effectively applying them to prevent impacts. The loss of spawning salmon over time may have long-lasting impacts on the productivity of their natal rivers for other salmon populations and generations. Declining salmon productivity in an otherwise intact watershed has led to severely low nitrogen levels in the Kitlope, BC (Hill *et al.*, 2010). The natural enrichment of rivers from fluxes of spawning salmon positively influence recruitment productivity (Wilson *et al.*, 2022). These inputs may be increasingly important to salmon productivity for systems that have lost substantial portions of riparian habitat and other sources of natural enrichment (Roni *et al.*, 2011). Understanding and mitigating the cumulative effects of these losses is particularly important where both habitat extent and salmon populations have collectively declined for decades. Further research on cumulative effects in estuaries are warranted, including identifying ecological thresholds for salmon related to toxicology, habitat loss and connectivity, artificial structures, dredging, log storage, moorage, invasive species, and aquatic plant diversity or density. These thresholds may be vital to tracking estuarine condition with respect to climate change, including habitat changes and losses related to sea level rise, prolonged drought, and increased sediment loads due to intensified flood seasons.

## 5.2 Conclusions

A holistic approach to salmon conservation management is necessary to capture the broad scope of pressures on these migratory foundation species. Salmon conservation and management research has been largely divided into marine threats and freshwater threats despite our knowledge that both of these realms contribute to the success or decline of Pacific salmon (Sobocinski *et al.*, 2021; Wilson *et al.*, 2022). As our understanding of cumulative impacts and multiple stressors becomes clearer, it will be important to focus on the abatement of each threat, and to consider the likely outcomes of management strategies at the population and ecosystem levels. My research has demonstrated the importance of estuarine habitat to juvenile salmon and has highlighted the opportunity for significant habitat mitigation to improve the outlook for salmon in the lower Fraser River. In the face of escalating cumulative effects the timely implementation of conservation interventions is critical to sustainable salmon management, including freshwater and nearshore habitat restoration and protection, improved management of cumulative impacts in development permit processes, improved recognition of Indigenous governance authority over salmon systems, strengthened international cooperation and communication in setting fishing and hatchery release limits, and enhanced flexibility of management regimes that will allow for adaptation as we learn to 'expect the unexpected'(Malick, Rutherford and Cox, 2017; Schoen *et al.*, 2017; Atlas *et al.*, 2021; Blakley, 2021).

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# Appendices

## Appendix A: Supplemental Material for Chapter 2

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### Appendix included at the end of the published manuscript

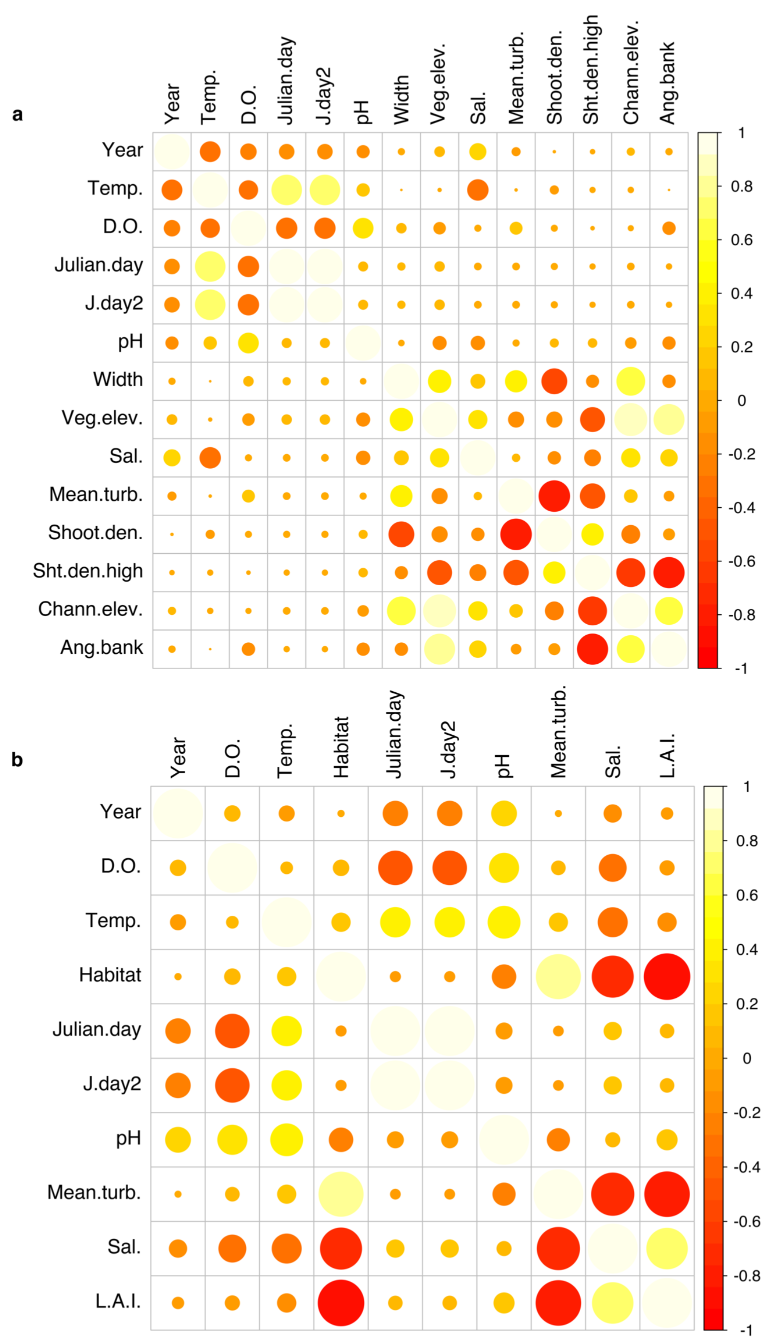


**Fig. 2A1.** Correlation plots for all variables considered in global marsh (a) and eelgrass / sand flat catch models (b) for the Fraser River estuary. Pale yellow indicates positive 1:1 correlation, red indicates negative 1:1 correlation, size indicates strength of correlation in either direction. Year = year of surveys (2016 and 2017); Temp. = surface water temperature; D.O. = dissolved oxygen; J. day = Julian day; J. day$^2$ = quadratic modifier of Julian day (Julian day squared); Width = marsh channel width; Veg. elev. = mean elevation of lowest marsh; Sal. = salinity; Mean turb. = mean turbidity measured over all sampling events in 2016; Shoot den. = mean density of lowest marsh vegetation; Sht. den. high = mean density of upper marsh vegetation; Channel elev. = elevation of channel bed relative to Chart Datum; Ang. bank = mean bank slope; Habitat = eelgrass or sand flat; L.A.I. = leaf area index of eelgrass. All variables were standardized and centered on the mean. Correlation scores varied slightly for each species group subset.

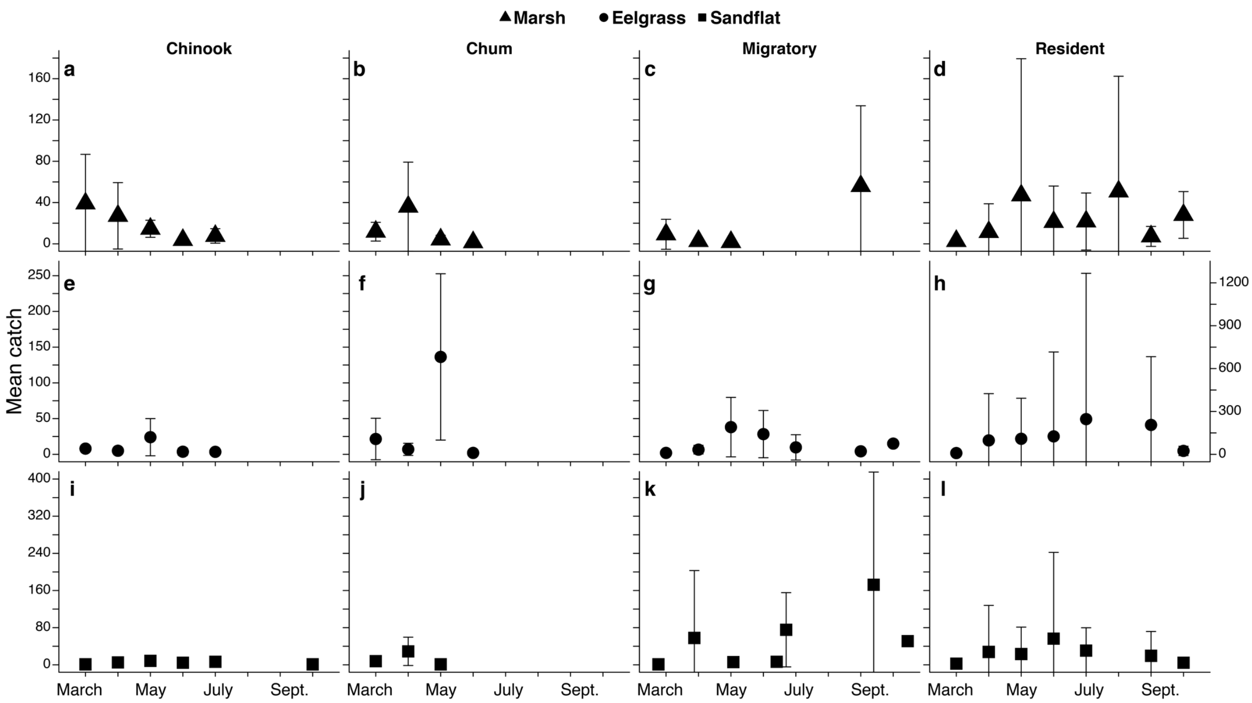


**Fig. 2A2.** Trends in catch over time in marsh (a:d), eelgrass (e:h), and sand flat (i:l) for Chinook salmon (a:i), chum salmon (b:j), other migratory fish (c:k), and resident fish (d:l). Mean catch is shown for each sampling month with standard deviation (error bars). Note the changing y-axis to match varying scales of abundance among groups, and the unique y-axis for eelgrass resident fish catch in panel h (right). Data includes both sampling years (2016 and 2017) in the Fraser River estuary.

**Supplemental Materials**

**Table 2S1.** Total sampling effort by habitat, season, and year. One sampling event represents one site visit with three non-overlapping seine hauls collected.

| | | **Marsh** | **Eelgrass** | **Sand Flat** | **Total** |
|---|---|---|---|---|---|
| 2016 | Spring | 12 | 12 | 16 | 40 (26 %) |
| | Summer | 25 | 28 | 30 | 83 (54%) |
| | Fall | 7 | 12 | 12 | 31 (20 %) |
| | | **44** | **52** | **58** | **154** |
| 2017 | Spring | 19 | 23 | 23 | 65 (49%) |
| | Summer | 21 | 24 | 24 | 69 (51%) |
| | Fall | 0 | 0 | 0 | 0 |
| | | **40** | **47** | **47** | **134** |
| | Grand totals | **84** | **99** | **105** | **288** |

**Table 2S2.** Summary of abiotic model results determining water quality parameter differences between years, habitats, and months. Site was included as a random effect in all models. Month estimates are relative to March, year estimates are relative to 2016, and habitat estimates are relative to marsh. N for each parameter = 51, 253. Number of sites with measurements = 18. * indicates significance level (p < 0.001 '***', 0.001 '**', 0.01 '*'). $R^2$ = conditional $R^2$, *Mar.* $R^2$ = marginal $R^2$.

| | Parameter | Estimate | (SE) | $R^2$ | *Mar.* $R^2$ |
|---|---|---|---|---|---|
| **Temperature C** | | | | | |
| | Year | -0.670*** | (0.013) | 0.738 | 0.579 |
| | Eelgrass | 0.638 | (0.529) | | |
| | Sand flat | 1.665** | (0.547) | | |
| | April | 2.619*** | (0.040) | | |
| | May | 3.456*** | (0.039) | | |
| | June | 4.352*** | (0.039) | | |
| | July | 6.428*** | (0.040) | | |
| | August | 8.608*** | (0.064) | | |
| | September | 2.504*** | (0.043) | | |
| | October | 0.869*** | (0.066) | | |
| **Dissolved oxygen (mg $L^{-1}$)** | | | | | |
| | Year | -0.493*** | (0.009) | 0.630 | 0.484 |
| | Eelgrass | -0.564 | (0.302) | | |
| | Sand flat | -0.203 | (0.313) | | |
| | April | 2.429*** | (0.028) | | |
| | May | 1.604*** | (0.028) | | |
| | June | -0.041 | (0.028) | | |
| | July | 0.651*** | (0.028) | | |
| | August | -1.087*** | (0.045) | | |
| | September | -0.129*** | (0.031) | | |
| | October | -2.057*** | (0.047) | | |
| **Salinity (PPT)** | | | | | |
| | Year | -1.919*** | (0.040) | 0.884 | 0.811 |
| | Eelgrass | 23.318*** | (1.633) | | |
| | Sand flat | 8.236*** | (1.689) | | |
| | April | -2.466*** | (0.121) | | |
| | May | -2.829*** | (0.118) | | |
| | June | -2.186*** | (0.119) | | |
| | July | -1.938*** | (0.119) | | |
| | August | 2.555*** | (0.194) | | |
| | September | 3.310*** | (0.131) | | |
| | October | 2.999*** | (0.198) | | |
| **pH** | | | | | |
| | Year | -0.008* | (0.003) | 0.580 | 0.466 |
| | Eelgrass | 0.255** | (0.080) | | |
| | Sand flat | 0.082 | (0.083) | | |
| | April | 0.557*** | (0.009) | | |
| | May | 0.259*** | (0.009) | | |
| | June | 0.127*** | (0.009) | | |
| | July | 0.574*** | (0.009) | | |
| | August | -0.476*** | (0.014) | | |
| | September | -0.113*** | (0.010) | | |
| | October | -0.083*** | (0.015) | | |

**Table 2S3.** Summary of covariates included in fish catch models for the Fraser River estuary (prior to standardization). Mean, median, and measured range across all sites are shown for each habitat. Julian day was modelled as a quadratic variable in models that had a strong non-linear relationship between abundance and time.

| | Marsh | | Eelgrass | | Sand flat | |
|---|---|---|---|---|---|---|
| **Variable** | **Mean** | **Median (Range)** | **Mean** | **Median (Range)** | **Mean** | **Median (Range)** |
| Year | 0.48 | 0 (0:1) | 0.45 | 0 (0:1) | 0.44 | 0 (0:1) |
| Julian day | 157 | 151 (64:282) | 163 | 153 (79:286) | 159 | 154 (79:285) |
| Temperature (°C) | 13.36 | 13.30 (3.43:18.32) | 13.64 | 13.85 (7.49:18.85) | 14.38 | 14.21 (7.55:20.41) |
| Dissolved oxygen (mg $L^{-1}$) | 10.46 | 10.74 (4.68:15.50) | 9.97 | 10.16 (5.53:14.19 | 10.28 | 10.36 (4.04:14.56) |
| pH | 8.06 | 7.91 (6.44:10.46) | 8.31 | 8.30 (7.78:9.00) | 8.19 | 8.14 (7.81:8.70) |
| Salinity (ppt) | 2.33 | 0.89 (0.00:19.4) | 25.56 | 27.36 (10.38:33.92) | 11.70 | 10.97(0.55:30.84) |
| Channel width (m) | 51.26 | 53.90 (18.80:170.07) | NA | NA | NA | NA |
| Vegetation elevation (m) | 1.25 | 1.25 (0.32:2.58) | NA | NA | NA | NA |
| Mean Turbidity (FNU) | 35.95 | 37.47 (29.87:41.52) | 4.43 | 3.47 (2.02:9.30) | 12.41 | 11.90 (8.97:17.81) |
| Habitat (categorical) | NA | NA | Eelgrass | NA | Sand flat | NA |

**Table 2S4.** Summary of top models (i.e., those with a **ΔAICc <4)** estimating the catch of the four species groups in marsh habitat (i.e., beach seine sites): Chinook salmon (a), Chum salmon (b), Other migratory fishes (c), and Resident fishes (d). Plus signs indicate the presence of variables within each model in the top model set. Variables with RVI scores greater than 0.5 are in bold.

| **Rank** | **Year** | **J. day** | **J. day$^2$** | **Temp** | **DO** | **pH** | **Sal** | **Turb** | **Width** | **Veg. elev.** | ***df*** | **AICc** | **ΔAICc** | ***w*** | ***$R^2$*** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **a) Chinook** | | | | | | | | | | | | | | | |
| 1 | + | + | | + | | + | | | + | | 7 | 434.82 | 0.00 | 0.21 | 0.51 |
| 2 | + | + | | + | | | | | + | | 6 | 435.31 | 0.48 | 0.16 | 0.48 |
| 3 | + | + | | + | | | | | + | + | 7 | 436.81 | 1.99 | 0.08 | 0.49 |
| 4 | + | + | | + | | + | + | | + | | 8 | 436.82 | 2.00 | 0.08 | 0.51 |
| 5 | + | + | | + | | + | | | + | + | 8 | 437.18 | 2.36 | 0.06 | 0.51 |
| 6 | + | + | | + | + | + | | | + | | 8 | 437.23 | 2.41 | 0.06 | 0.51 |
| 7 | + | + | | + | | | + | | + | | 7 | 437.39 | 2.56 | 0.06 | 0.49 |
| 8 | + | + | | + | | | | + | + | | 7 | 437.40 | 2.58 | 0.06 | 0.49 |
| 9 | + | + | | + | | + | | + | + | | 8 | 437.42 | 2.60 | 0.06 | 0.51 |
| 10 | + | + | + | + | | + | | | + | | 8 | 437.43 | 2.60 | 0.06 | 0.51 |
| 11 | + | + | | + | + | | | | + | | 7 | 437.56 | 2.74 | 0.05 | 0.48 |
| 12 | + | + | + | + | | | | | + | | 7 | 437.73 | 2.90 | 0.05 | 0.48 |
| 13 | + | + | | + | | | | + | | | 6 | 438.79 | 3.96 | 0.03 | 0.45 |
| RVI | **1.00** | **1.00** | 0.10 | **1.00** | 0.11 | **0.52** | 0.13 | 0.14 | **0.97** | 0.14 | | | | | |
| **b) Chum** | | | | | | | | | | | | | | | |
| 1 | | + | | | + | | | | | | 4 | 226.76 | 0.00 | 0.08 | 0.33 |
| 2 | | | | | + | | | | | | 3 | 226.91 | 0.15 | 0.07 | 0.27 |
| 3 | | | | + | + | | | | | | 4 | 227.53 | 0.77 | 0.05 | 0.32 |
| 4 | | + | | | + | | | + | | | 5 | 227.57 | 0.81 | 0.05 | 0.37 |
| 5 | | | | | + | | | + | | | 4 | 227.86 | 1.09 | 0.05 | 0.31 |
| 6 | + | + | | | + | | | | | | 5 | 228.49 | 1.73 | 0.03 | 0.36 |
| 7 | | | | | + | | | | | + | 4 | 228.78 | 2.02 | 0.03 | 0.29 |
| 8 | | | | | + | | + | | | | 4 | 228.91 | 2.15 | 0.03 | 0.29 |
| 9 | | + | | + | + | | | | | | 5 | 229.00 | 2.23 | 0.03 | 0.35 |
| 10 | + | | | | + | | | | | | 4 | 229.02 | 2.25 | 0.03 | 0.29 |
| 11 | | | + | | + | | | | | | 4 | 229.11 | 2.35 | 0.02 | 0.28 |
| 12 | | | + | | | | | | | | 3 | 229.12 | 2.35 | 0.02 | 0.23 |
| 13 | | | | + | + | | | + | | | 5 | 229.25 | 2.48 | 0.02 | 0.34 |
| 14 | | + | | | + | | | | | + | 5 | 229.25 | 2.48 | 0.02 | 0.34 |
| 15 | | | + | | | + | | | | | 4 | 229.26 | 2.50 | 0.02 | 0.28 |

| Rank | Year | J. day | J. day$^2$ | Temp | DO | pH | Sal | Turb | Width | Veg. elev. | *df* | AICc | ΔAICc | *w* | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **b) Chum continued** | | | | | | | | | | | | | | | |
| 16 | | | + | + | | | | | | | 4 | 229.28 | 2.52 | 0.02 | 0.28 |
| 17 | | + | + | | + | | | | | | 5 | 229.33 | 2.57 | 0.02 | 0.34 |
| 18 | | | | | + | + | | | | | 4 | 229.45 | 2.69 | 0.02 | 0.28 |
| 19 | | + | | | + | | + | | | | 5 | 229.48 | 2.72 | 0.02 | 0.34 |
| 20 | | | + | + | + | | | | | | 5 | 229.55 | 2.79 | 0.02 | 0.33 |
| 21 | | + | | | + | + | | | | | 5 | 229.58 | 2.81 | 0.02 | 0.33 |
| 22 | | | | | + | | | + | | + | 5 | 229.69 | 2.93 | 0.02 | 0.33 |
| 23 | | | | + | + | | | | | + | 5 | 229.74 | 2.98 | 0.02 | 0.33 |
| 24 | + | + | | | + | | | + | | | 6 | 229.75 | 2.99 | 0.02 | 0.39 |
| 25 | + | | + | | | | | | | | 4 | 229.77 | 3.00 | 0.02 | 0.27 |
| 26 | | | + | | | + | | + | | | 5 | 229.85 | 3.08 | 0.02 | 0.33 |
| 27 | | | + | + | | + | | | | | 5 | 229.92 | 3.15 | 0.02 | 0.33 |
| 28 | | | | | + | | + | + | | | 5 | 229.97 | 3.21 | 0.02 | 0.33 |
| 29 | | + | | | + | | | + | | + | 6 | 230.18 | 3.42 | 0.01 | 0.38 |
| 30 | | | | | + | + | | + | | | 5 | 230.20 | 3.43 | 0.01 | 0.32 |
| 31 | | + | | | + | + | | + | | | 6 | 230.23 | 3.47 | 0.01 | 0.38 |
| 32 | + | | | + | + | | | | | | 5 | 230.33 | 3.57 | 0.01 | 0.32 |
| 33 | + | | | | + | | | + | | | 5 | 230.35 | 3.59 | 0.01 | 0.32 |
| 34 | | | | + | + | + | | | | | 5 | 230.38 | 3.61 | 0.01 | 0.32 |
| 35 | | | | + | + | | + | | | | 5 | 230.39 | 3.62 | 0.01 | 0.32 |
| 36 | | + | | + | + | | | + | | | 6 | 230.41 | 3.64 | 0.01 | 0.38 |
| 37 | | | + | | + | | | + | | | 5 | 230.45 | 3.68 | 0.01 | 0.32 |
| 38 | | + | | | + | | + | + | | | 6 | 230.50 | 3.74 | 0.01 | 0.38 |
| 39 | + | + | + | | | | | | | | 5 | 230.57 | 3.81 | 0.01 | 0.31 |
| 40 | | + | + | | | + | | | | | 5 | 230.59 | 3.83 | 0.01 | 0.31 |
| 41 | | + | + | | + | | | + | | | 6 | 230.59 | 3.83 | 0.01 | 0.37 |
| 42 | | + | + | | | | | | | | 4 | 230.63 | 3.87 | 0.01 | 0.25 |
| RVI | 0.13 | 0.40 | 0.25 | 0.23 | **0.84** | 0.15 | 0.09 | 0.30 | NA | 0.10 | | | | | |
| **c) Other Migratory** | | | | | | | | | | | | | | | |
| 1 | | | | | | | + | | | + | 4 | 106.21 | 0.00 | 0.38 | 0.54 |
| 2 | | | | | | | + | + | | + | 5 | 107.68 | 1.47 | 0.18 | 0.61 |
| 3 | | | | | | | + | | | | 3 | 108.15 | 1.94 | 0.14 | 0.37 |
| 4 | | | | | | | | | | + | 3 | 109.19 | 2.98 | 0.09 | 0.33 |
| 5 | | | | | | | + | | + | + | 5 | 109.20 | 2.99 | 0.09 | 0.57 |
| 6 | | | | | + | | + | | | + | 5 | 109.59 | 3.37 | 0.07 | 0.56 |
| 7 | | | | | | | | + | | + | 4 | 110.04 | 3.82 | 0.06 | 0.42 |
| RVI | 0.16 | NA | NA | NA | 0.13 | NA | **0.76** | 0.20 | 0.07 | **0.88** | | | | | |

| **Rank** | **Year** | **J. day** | **J. day$^2$** | **Temp** | **DO** | **pH** | **Sal** | **Turb** | **Width** | **Veg. elev.** | ***df*** | **AICc** | **ΔAICc** | ***w*** | ***$R^2$*** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **d) Resident** | | | | | | | | | | | | | | | |
| 1 | + | + | + | | | + | | + | | | 7 | 746.75 | 0.00 | 0.22 | 0.54 |
| 2 | + | + | + | | + | + | | + | | | 8 | 747.74 | 0.99 | 0.14 | 0.55 |
| 3 | + | + | + | | | + | | + | + | | 8 | 747.77 | 1.02 | 0.13 | 0.55 |
| 4 | + | + | + | | + | + | | + | + | | 9 | 748.47 | 1.72 | 0.09 | 0.56 |
| 5 | + | + | + | | | + | + | + | | | 8 | 748.77 | 2.02 | 0.08 | 0.55 |
| 6 | + | + | + | | | + | | + | | + | 8 | 749.09 | 2.34 | 0.07 | 0.54 |
| 7 | + | + | + | | + | + | + | + | | | 9 | 749.80 | 3.05 | 0.05 | 0.55 |
| 8 | + | + | + | | + | + | | + | | + | 9 | 749.89 | 3.14 | 0.05 | 0.55 |
| 9 | + | + | + | | | + | + | + | + | | 9 | 749.97 | 3.22 | 0.04 | 0.55 |
| 10 | + | + | + | | | + | | + | + | + | 9 | 750.23 | 3.49 | 0.04 | 0.55 |
| 11 | + | + | + | | | | | + | | | 6 | 750.23 | 3.49 | 0.04 | 0.51 |
| 12 | + | + | + | | | | | + | + | | 7 | 750.32 | 3.58 | 0.04 | 0.52 |
| RVI | **1.00** | **1.00** | **1.00** | NA | 0.33 | **0.92** | 0.18 | **1.00** | **0.35** | 0.16 | | | | | |

Year = year of surveys (2016 and 2017); J. day = Julian day; J. day$^2$ = quadratic modifier of Julian day (Julian day squared); Temp = surface water temperature measured during each sampling event; DO = surface water dissolved oxygen measured during each sampling event; pH = surface water pH measured during each sampling event; Sal = surface water salinity measured during each sampling event; Turb = mean turbidity measured over all sampling events in 2016; Width = marsh channel width; Veg. elev. = mean elevation of lowest marsh vegetation relative to the base of the channel; *df* = degrees of freedom; $AIC_c$ = AIC corrected for small sample sizes; $\Delta AIC_c$ = difference from the lowest $AIC_c$ value; *w* = model weight; $R^2$ = pseudo $R^2$; RVI = relative variable importance.

**Table 2S5.** Top models (i.e., those with a ΔAICc <4) describing catch of four species groups in eelgrass/sand flat habitats (i.e., purse seine sites): Chinook salmon (a), Chum salmon (b), Other migratory fishes (c), and Resident fishes (d). Plus signs indicate the presence of variables within each model in the top model set. Variables with RVI scores greater than 0.5 that were included in the top model are in bold.

| **Rank** | **Hab** | **Year** | **J. day** | **J. day$^2$** | **Temp** | **DO** | **pH** | **Sal** | **Mean turb** | ***df*** | **AICc** | **Δ AICc** | ***w*** | ***R*$^2$** | ***Mar. R*$^2$** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **a) Chinook** | | | | | | | | | | | | | | | |
| 1 | + | + | | | | + | | | | 6 | 361.75 | 0.00 | 0.27 | 0.50 | 0.34 |
| 2 | | + | | | | + | | | | 5 | 362.31 | 0.56 | 0.20 | 0.50 | 0.25 |
| 3 | + | + | + | | | + | | | | 7 | 363.56 | 1.80 | 0.11 | 0.52 | 0.35 |
| 4 | | + | + | | | + | | | | 6 | 363.93 | 2.18 | 0.09 | 0.52 | 0.27 |
| 5 | + | + | | | | + | + | | | 7 | 364.04 | 2.29 | 0.08 | 0.51 | 0.34 |
| 6 | + | + | | | + | + | | | | 7 | 364.12 | 2.37 | 0.08 | 0.50 | 0.34 |
| 7 | | + | | | + | + | | | | 6 | 364.54 | 2.79 | 0.07 | 0.50 | 0.26 |
| 8 | | + | | | | + | + | | | 6 | 364.60 | 2.85 | 0.06 | 0.50 | 0.26 |
| 9 | + | + | + | | + | + | | | | 8 | 365.67 | 3.92 | 0.04 | 0.52 | 0.36 |
| RVI | **0.58** | **1.00** | 0.24 | NA | 0.19 | **1.00** | 0.2 | NA | NA | | | | | | |
| **b) Chum** | | | | | | | | | | | | | | | |
| 1 | | + | + | + | | | | | + | 7 | 220.62 | 0.00 | 0.35 | 0.95 | 0.44 |
| 2 | | + | + | + | | | | | | 6 | 222.22 | 1.60 | 0.16 | 0.96 | 0.33 |
| 3 | + | + | + | + | | | | | | 7 | 222.24 | 1.63 | 0.16 | 0.96 | 0.44 |
| 4 | | + | + | + | | + | | | + | 8 | 222.78 | 2.17 | 0.12 | 0.96 | 0.43 |
| 5 | | + | + | + | | + | | | | 7 | 223.03 | 2.42 | 0.11 | 0.96 | 0.32 |
| 6 | + | + | + | + | | | | | + | 8 | 224.33 | 3.72 | 0.06 | 0.95 | 0.45 |
| 7 | + | + | + | + | | + | | | | 8 | 224.53 | 3.92 | 0.05 | 0.96 | 0.41 |
| RVI | 0.26 | **1.00** | **1.00** | **1.00** | NA | 0.28 | NA | NA | **0.53** | | | | | | |
| **c) Other Migratory** | | | | | | | | | | | | | | | |
| 1 | | | + | | | + | | | | 5 | 720.21 | 0.00 | 0.20 | 0.91 | 0.55 |
| 2 | + | | + | | | + | | | | 6 | 720.26 | 0.06 | 0.20 | 0.90 | 0.69 |
| 3 | + | | | | | + | | | | 5 | 721.27 | 1.07 | 0.12 | 0.90 | 0.70 |
| 4 | | | + | | | + | + | | | 6 | 722.15 | 1.95 | 0.08 | 0.91 | 0.54 |
| 5 | + | + | + | | | + | | | | 7 | 722.23 | 2.02 | 0.07 | 0.90 | 0.73 |
| 6 | | + | + | | | + | | | | 6 | 722.27 | 2.06 | 0.07 | 0.91 | 0.57 |
| 7 | | | | | | + | | | | 4 | 722.58 | 2.37 | 0.06 | 0.91 | 0.43 |
| 8 | + | | + | | | + | + | | | 7 | 722.62 | 2.41 | 0.06 | 0.90 | 0.69 |

| Rank | Hab | Year | J. day | J. day$^2$ | Temp | DO | pH | Sal | Mean turb | *df* | AICc | Δ AICc | *w* | *R*$^2$ | *Mar. R*$^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **c) Other Migratory continued** | | | | | | | | | | | | | | | |
| 9 | + | | | | | + | + | | | 6 | 723.55 | 3.34 | 0.04 | 0.90 | 0.69 |
| 10 | + | + | | | | + | | | | 6 | 723.56 | 3.35 | 0.04 | 0.90 | 0.70 |
| 11 | | + | + | | | + | + | | | 7 | 723.97 | 3.77 | 0.03 | 0.91 | 0.58 |
| 12 | | | | | | + | + | | | 5 | 724.15 | 3.95 | 0.03 | 0.91 | 0.46 |
| RVI | **0.53** | 0.21 | **0.71** | NA | NA | **1.00** | 0.2 | NA | NA | | | | | | |
| **d) Resident** | | | | | | | | | | | | | | | |
| 1 | + | | | | + | | | | | 5 | 2116.58 | 0.00 | 0.16 | 1.00 | 0.91 |
| 2 | + | | + | | + | | | | | 6 | 2116.70 | 0.11 | 0.15 | 1.00 | 0.92 |
| 3 | + | | + | | + | + | | | | 7 | 2117.21 | 0.62 | 0.11 | 1.00 | 0.93 |
| 4 | + | | + | | + | | | + | | 7 | 2117.86 | 1.28 | 0.08 | 1.00 | 0.91 |
| 5 | + | + | | | + | | | | | 6 | 2117.95 | 1.36 | 0.08 | 1.00 | 0.91 |
| 6 | + | | | | + | | | + | | 6 | 2118.46 | 1.87 | 0.06 | 1.00 | 0.90 |
| 7 | + | | | | + | + | | | | 6 | 2118.53 | 1.94 | 0.06 | 1.00 | 0.91 |
| 8 | + | + | + | | + | | | | | 7 | 2118.54 | 1.96 | 0.06 | 1.00 | 0.92 |
| 9 | + | | + | | + | + | | + | | 8 | 2118.86 | 2.28 | 0.05 | 1.00 | 0.92 |
| 10 | + | + | + | | + | + | | | | 8 | 2119.05 | 2.46 | 0.05 | 1.00 | 0.93 |
| 11 | + | + | + | | + | | | + | | 8 | 2119.38 | 2.79 | 0.04 | 1.00 | 0.91 |
| 12 | + | + | | | + | | | + | | 7 | 2119.43 | 2.84 | 0.04 | 1.00 | 0.90 |
| 13 | + | + | | | + | + | | | | 7 | 2119.77 | 3.19 | 0.03 | 1.00 | 0.91 |
| 14 | + | + | + | | + | + | | + | | 9 | 2120.46 | 3.88 | 0.02 | 1.00 | 0.92 |
| 15 | + | | | | + | + | | + | | 7 | 2120.54 | 3.95 | 0.02 | 1.00 | 0.90 |
| RVI | **1.00** | 0.31 | **0.56** | NA | **1.00** | 0.34 | NA | 0.31 | NA | | | | | | |

Hab = habitat (effect of sand flat relative to eelgrass); Year = year of surveys (2016 and 2017); J. day = Julian day; J. day$^2$ = quadratic modifier of Julian day (Julian day squared); Temp = surface water temperature measured during each sampling event; DO = surface water dissolved oxygen measured during each sampling event; pH = surface water pH measured during each sampling event; Sal = surface water salinity measured during each sampling event; Mean turb = mean turbidity measured over all sampling events in 2016; *df* = degrees of freedom; $AIC_c$ = AIC corrected for small sample sizes; $\Delta AIC_c$ = difference from the lowest $AIC_c$ value; *w* = model weight; $R^2$ = conditional $R^2$ (proportion of variance explained by both fixed and random effects); *Mar.* $R^2$ = Marginal $R^2$ (proportion of variance explained by fixed effects only); RVI = relative variable importance.

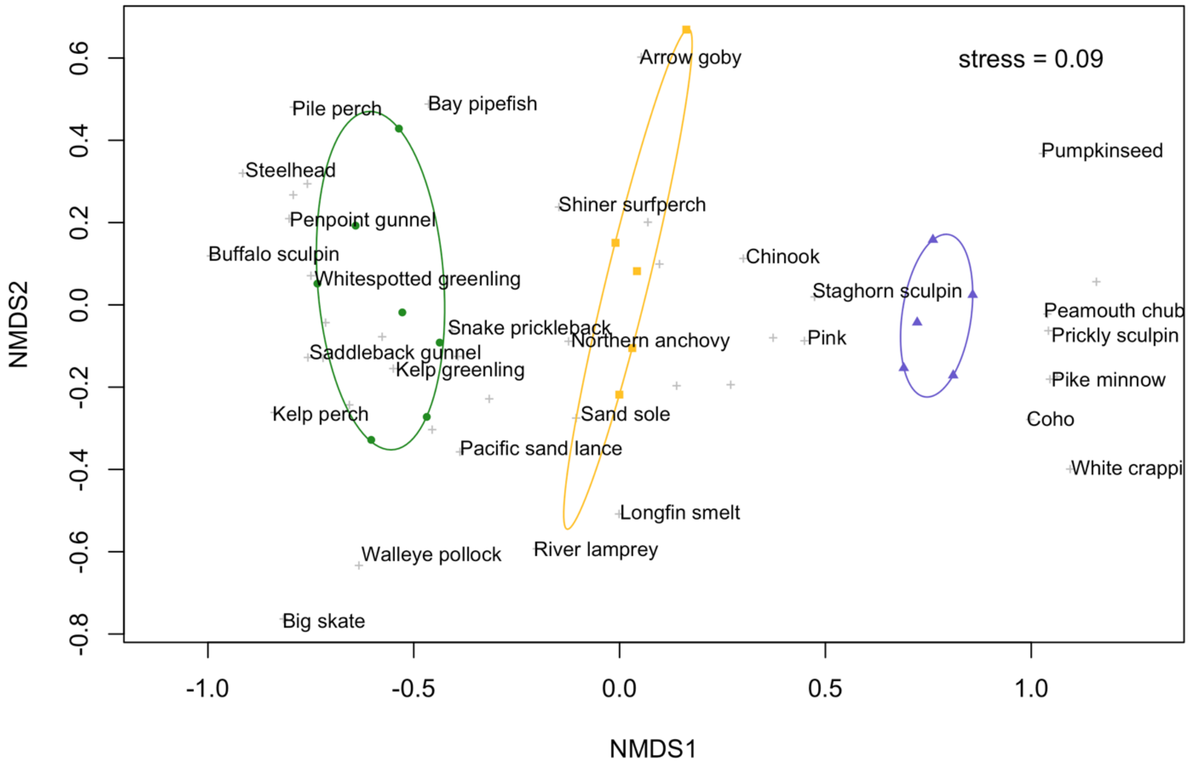


**Fig. 2S1.** Non-metric multidimensional scaling (NMDS) plot depicting Bray-Curtis deviation of fish communities by site. Species counts were summed across all sampling events for each site prior to analysis. Degree of clustering is shown for marsh (blue triangles), eelgrass (green circles), and sand flat (yellow squares) habitat categories. Select species (grey plus symbols) are identified by common name to highlight community examples.

# Appendix B: Supplemental Material for Chapter 3

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## Extended Methods and Results

*Otolith analyses*

Width and estuarine entry measurements were taken at 10x magnification or higher, and daily growth measurements were taken at 20x or 40x magnification in the dorso-posterior (DP) quadrant of the sagittal otolith, where growth increments are consistently the widest (Zhang et al. 1995[3], Fig. 3.1 in the main text). Daily growth measurements were averaged over at least 7 increments, in order to minimize variation due to natural fluctuations in environmental factors (Zhang, Beamish and Riddell, 1995). For each growth value, measurements were taken 3 times within the DP quadrant and averaged to reduce within-otolith variability.

We measured daily growth in the estuary in all otoliths, as well as early estuarine growth, late estuarine growth, and late freshwater growth (just prior to estuarine entry) in otoliths where 7 or more of these increments were clearly visible in the DP quadrant.

The estuarine entry inflection was identified on LA-ICPMS scans, and while our Sr:Ca and Ba:Ca values at entry (0.49-1.8 mmol:mol and 0.19-4.5 μmol:mol, respectively) were more aligned toward "freshwater" values than "estuarine" values indicated in a detailed study (Miller, 2011[4]), the inflection patterns were consistent among fish that had recently entered the estuary (within 14 days). Based on the number of daily increments post-inflection and the capture of some of these fish in high salinity estuarine environments (i.e., eelgrass sites), we believe these values to be representative of the Fraser River estuary microchemistry signature (Fig. 3S1). This aligns with the low salinity range measured at high tide throughout the emigration period in the marsh habitat of the Fraser estuary (Table 3S1).

[3] Zhang, Z., Beamish, R.J., and Riddell, B.E. 1995. Differences in otolith microstructure between hatchery-reared and wild Chinook salmon (Oncorhynchus tshawytscha). Can. J. Fish. Aquat. Sci. **52**(2): 344–352. doi:10.1139/f95-035.

[4] Miller, J.A. 2011. Effects of water temperature and barium concentration on otolith composition along a salinity gradient: Implications for migratory reconstructions. J. Exp. Mar. Bio. Ecol. **405**(1–2): 42–52. Elsevier B.V. doi:10.1016/j.jembe.2011.05.017.

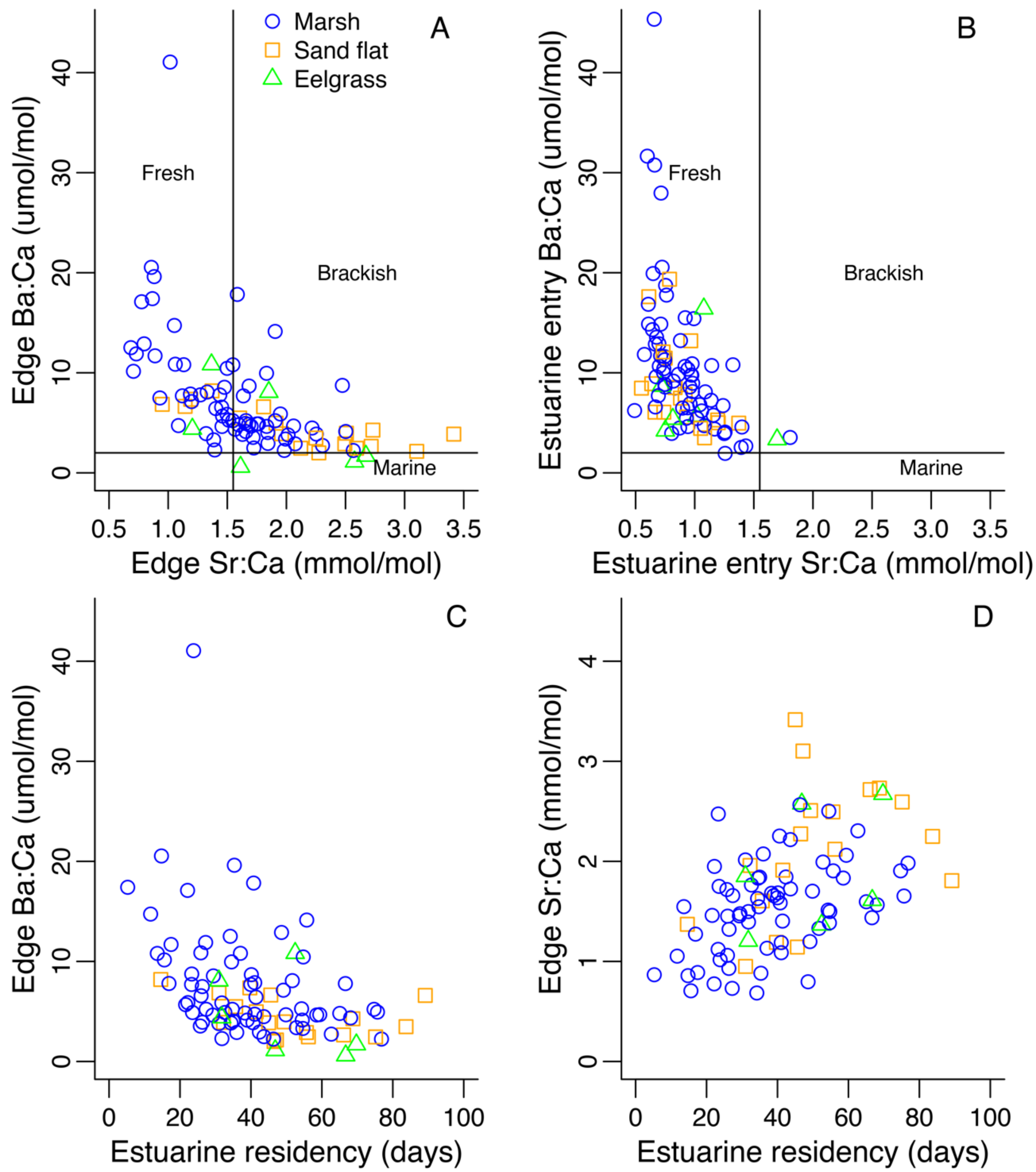


**Fig. 3S1.** Evaluation of otolith microchemistry in relation to estuarine residency and habitat. Lines demarking "Fresh" (>2 µmol/mol Ba:Ca and <1.55 mmol/mol Sr:Ca), "Brackish" (>2 µmol/mol Ba:Ca and >1.55 mmol/mol Sr:Ca), and "Marine" (<2 µmol/mol Ba:Ca and >1.55 mmol/mol Sr:Ca) elemental ratios are derived from Miller (2011). Shapes and colours indicate habitat at capture (Marsh = blue circles, Sand flat = orange squares, Eelgrass = green triangles).

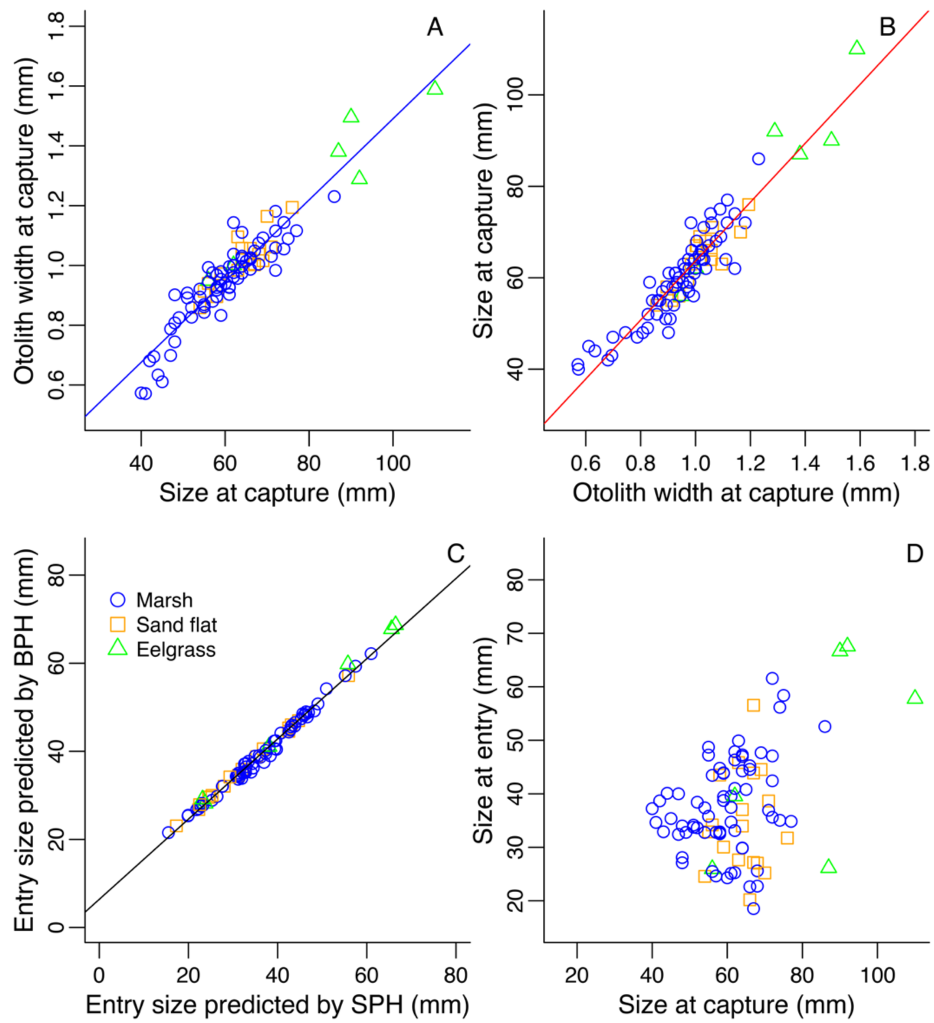


**Fig. 3S2.** Exploration of results of otolith back-calculation methods, following Francis (1990). Linear regressions of otolith width and fork length at capture were used to estimate A: otolith width at entry (from which fork length at entry was derived) following the Scale Proportional Hypothesis (blue line; $R^2$: 0.88, $P$: <2.2 x10$^{-16}$) and B: fork length at entry following the Body Proportional Hypothesis (red line; $R^2$: 0.88, $P$: <2.2 x10$^{-16}$). C: comparison of estimated fork length at entry calculated by each method ($R^2$: 0.99, $P$: <2.2 x10$^{-16}$). D: the mean of both methods was used to estimate the final fork length at entry, shown here in relation to fork length at capture. Habitat of capture shown for interest (marsh = blue circles (n=67), sand flat = orange squares (n=18), eelgrass = green triangles (n=6)).

**Table 3S1.** Environmental conditions measured at 17 sites representing three habitat types in the Fraser River estuary in 2016 and 2017.

| | Marsh | | Eelgrass | | Sand flat | |
|---|---|---|---|---|---|---|
| Variable | Mean | Median (Range) | Mean | Median (Range) | Mean | Median (Range) |
| Salinity (‰) | 2.33 | 0.89 (0.00:19.4) | 25.56 | 27.36 (10.38:33.92) | 11.70 | 10.97(0.55:30.84) |
| Temperature (°C) | 13.36 | 13.30 (3.43:18.32) | 13.64 | 13.85 (7.49:18.85) | 14.38 | 14.21 (7.55:20.41) |
| Dissolved oxygen (mg·L$^{-1}$) | 10.46 | 10.74 (4.68:15.50) | 9.97 | 10.16 (5.53:14.19) | 10.28 | 10.36 (4.04:14.56) |
| pH | 8.06 | 7.91 (6.44:10.46) | 8.31 | 8.30 (7.78:9.00) | 8.19 | 8.14 (7.81:8.70) |

*Estuarine Growth*

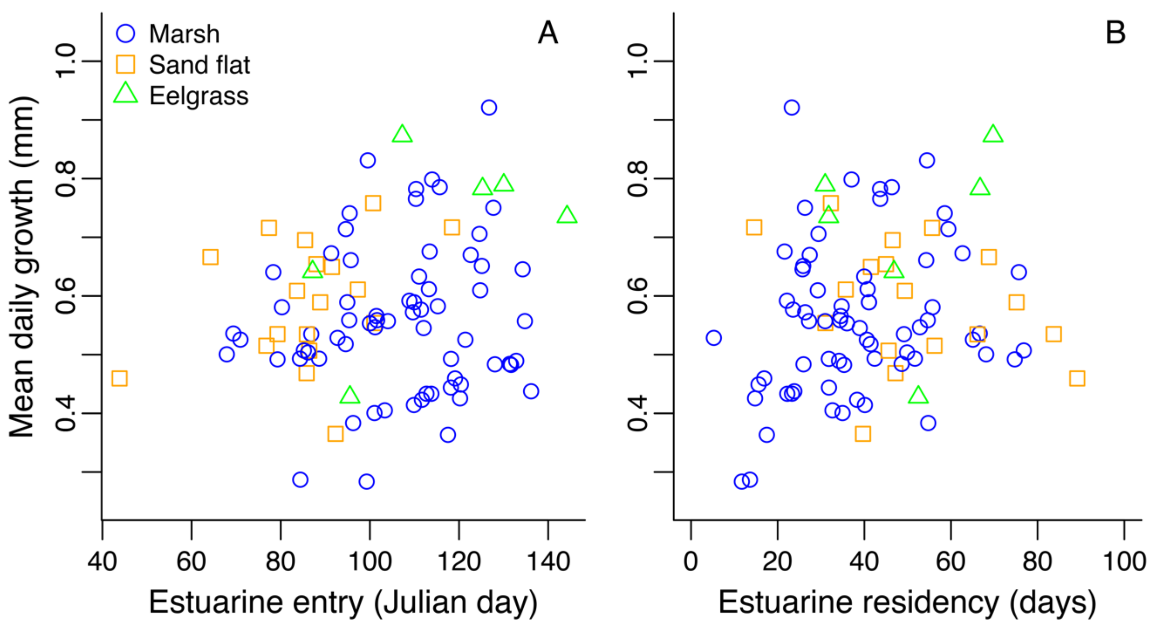


**Fig. 3S3.** Relationship between mean daily growth and estuarine entry timing (A) and estuarine residency (B). Neither of these patterns were significant ($p > 0.05$). Shapes and colours indicate habitat at capture (Marsh = blue circles, Sand flat = orange squares, Eelgrass = green triangles).

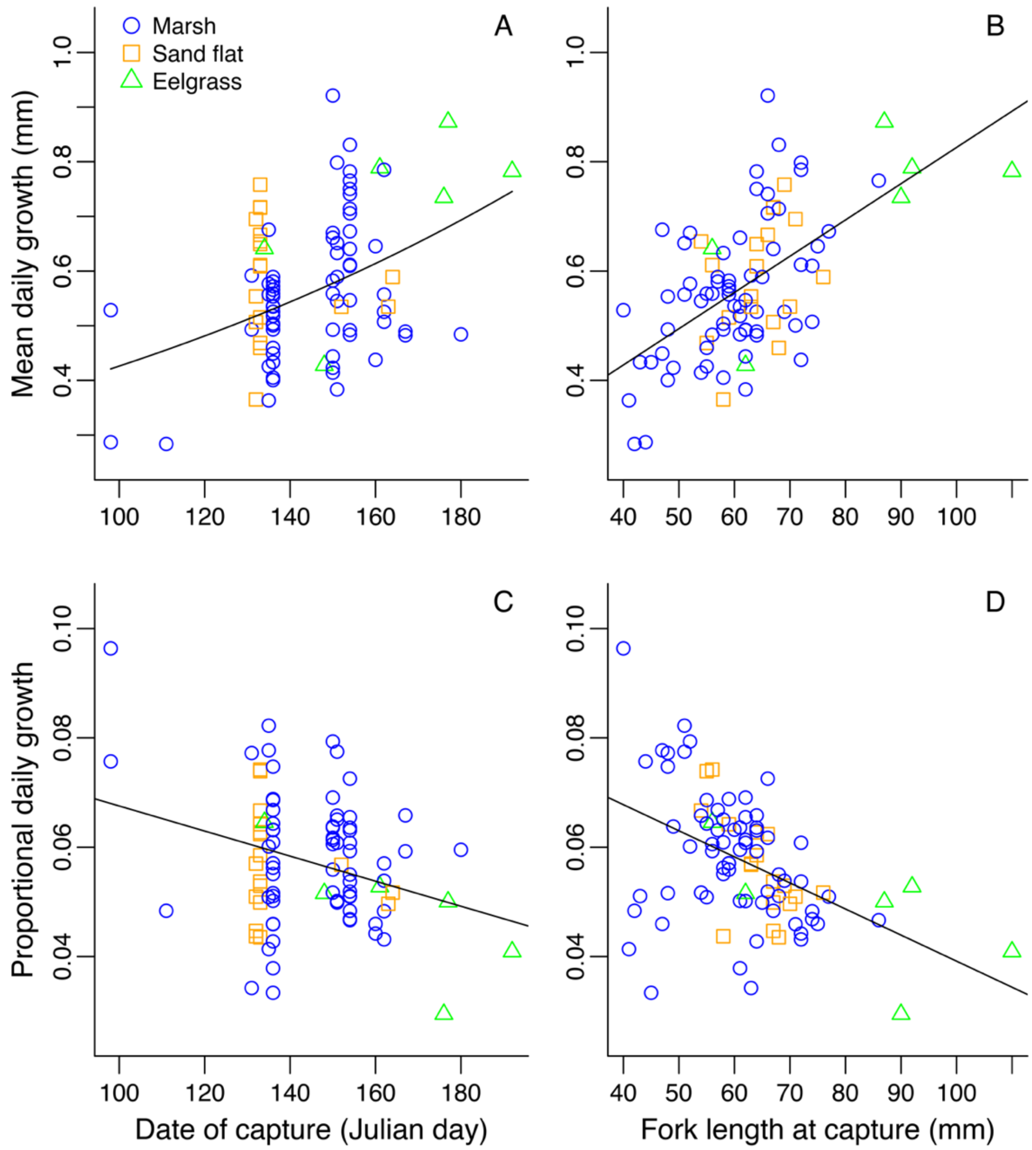


**Fig. 3S4.** Allometric patterns of growth by estuarine entry. A) Average daily growth in fork length over time ($R^2$: 0.15, $P$: 1.5 x$10^{-04}$), B) Average daily growth in fork length as a function of body size at capture ($R^2$: 0.34, $P$: 1.1 x$10^{-09}$), C) Average proportional daily growth (daily growth divided by fork length at capture) over time ($R^2$: 0.09, $P$: 3.8 x$10^{-03}$), and D) Average proportional daily growth in fork length as a function of body size at capture ($R^2$: 0.22, $P$: 2.8 x$10^{-06}$). Shapes and colours indicate habitat at capture (Marsh = blue circles, Sand flat = orange squares, Eelgrass = green triangles).

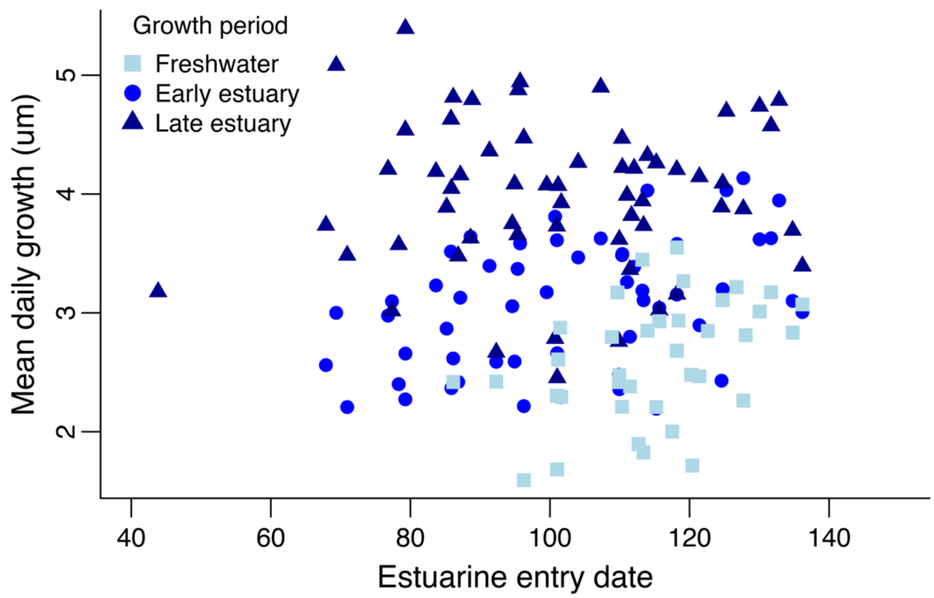


**Fig. 3S5.** Average daily width of otolith increments during the freshwater period prior to estuarine entry (light blue squares), just after estuarine entry (medium blue circles), and just prior to capture (dark blue triangles), shown by estuarine entry date. All measurements represent the mean width over 7-14 increments for each time period. Mean daily increment growth rates for each growth period are significantly different from one another (ANOVA, $F_{2, 148} = 76.93$, $P < 2.2 \times 10^{-16}$). However, following conversion to fork length these relationships are no longer significant.

**Table 3S2.** Individual juvenile Harrison Chinook that experienced a decline of >5% in mean daily growth over time (Early:Fresh or Late:Early). Note that three of the five fish were caught at the same marsh site (M2), possibly indicating site-specific influences on growth conditions. Despite a measured decline in otolith growth rate, all except for a single individual had mean daily somatic growth rates near or above the population mean of 0.57 +/- 0.13 mm (mean +/- SD).

| Site | Sr:Ca Entry ($mmol \cdot mol^{-1}$) | Sr:Ca Edge ($mmol \cdot mol^{-1}$) | Entry Day | Catch Day | Est. Res. (days) | Entry FL (mm) | Catch FL (mm) | Mean Daily GR FL ($mm \cdot day^{-1}$) | Mean Daily GR Oto. ($\mu m \cdot day^{-1}$) | Fresh GR ($\mu m \cdot day^{-1}$) | Early Est. GR ($\mu m \cdot day^{-1}$) | Late Est. GR ($\mu m \cdot day^{-1}$) | Early: Fresh | Late: Early |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SF3 | 0.74 | 1.96 | 100.7 | 133 | 32.3 | 44.5 | 69 | 0.76 | 3.65 | NA | 3.81 | 2.79 | NA | 0.73 |
| M4 | 1.25 | 1.50 | 118.2 | 150 | 31.8 | 46.3 | 62 | 0.49 | 4.28 | 3.55 | 3.58 | 3.16 | 1.01 | 0.88 |
| M2 | 0.99 | 1.84 | 101.0 | 136 | 35.0 | 34.0 | 48 | 0.40 | 2.48 | 1.68 | 2.66 | 2.45 | 1.58 | 0.92 |
| M2 | 0.69 | 0.93 | 127.7 | 154 | 26.3 | 44.3 | 64 | 0.75 | 4.07 | 2.26 | 4.13 | 3.88 | 1.83 | 0.94 |
| M2 | 0.61 | 1.58 | 113.2 | 154 | 40.8 | 47.1 | 72 | 0.61 | 3.87 | 3.45 | 3.19 | 3.94 | 0.92 | 1.24 |

# Appendix C: Supplemental Material for Chapter 4

## S1. Background and Expert Elicitation Details

At a three-day expert elicitation workshop, participants were asked to develop and agree upon a final suite of strategies and actions that would subsequently be evaluated using the Priority Threat Management (PTM) framework. To maximize the feasibility of successful implementation, strategies were limited to those that could be implemented within the scope of the study region. All strategies were required to have a direct measurable benefit to salmon CUs in the lower Fraser River. While in some cases data gaps were identified, research on its own does not convey a measurable benefit to species recovery. Therefore, research projects were embedded into strategies that included actions that can provide direct benefits to salmon. Actions currently being implemented and that have secure funding for at least the next 25 years or are a legislative requirement were included as baseline actions and considered to be 'business as usual'. For each management strategy it was assumed that all actions listed would be implemented within the 25-year time frame. For this reason, actions were required to be complementary to each other and to not negate other actions within the strategy. Each strategy addressed a key threat(s) to salmon populations in the lower Fraser River.

### Detailed Management Strategies

We defined three types of strategies:

1) Management strategies are comprised of multiple actions. The benefit of a strategy was assessed for each CU independently (S01-S11, Table 1 and detailed below);
2) Combination strategies are sets of individual strategies that have a greater expected impact (synergistic) when undertaken together (S12-S14, Table 1). The benefits of combination strategies were assessed for each CU independently;
3) Enabling strategies underpin the success of individual management strategies, yet on their own are difficult to quantify their direct benefit to salmon (i.e., monitoring and assessment, governance, detailed below). Enabling strategies were assumed to be necessary for the future management of wild salmon in this region, thus were not included in the prioritization.

**Strategy 1: Fisheries Management**

**Threat:** Overfishing leads to salmon population declines and/or reduced recovery potential.

**Goal:** Develop, implement, and enforce management procedures that are robust to climate change and avoid overfishing outcomes.

**Pathway(s) of effects:** Increase productivity via spawner returns

**Actions within strategy**

- Conduct assessments of salmon vulnerability to the impacts of climate change for all CUs.
    - E.g., following the Crozier et al. (NOAA) salmon vulnerability assessment;
    - Expert-based assessment that is completed for all 19 CUs over multiple (3) meetings;
    - Expert elicitation prior to meeting.
- Define biological benchmarks for all CUs.
    - Phase 1. develop the toolkit (methodological development) that can be used to define interim biological benchmarks for data deficient CUs;
    - Phase 2. collect data needed to evaluate spawner-based benchmarks - we are assuming that this is funded through the Enabling Strategy 1;
    - Phase 3. apply interim benchmark methodology for data limited CUs (initiated but augmentation is needed to expedite timelines);
    - Phase 4. apply spawner-based benchmarks based on new data collected from Phase 2 (funded through Enabling Strategy1).
- Define and implement limit reference points (habitat, biological) for all Management Units that take into account CU-level diversity.
    - Develop methodology, implement with monitoring and surveillance, re-evaluate procedure periodically.
- Augment ongoing work to determine management procedures (e.g., rebuilding objectives, harvest control rules, management measures) that are robust to climate change following DFO's precautionary approach.
    - This includes setting management objectives for the management units following the CU-level procedures described above, internal and external components (develop procedures internally and then consult); iterative, done by species.

  - Could complete in a year: 3 days meetings, harvest controls developed in year one, followed by consultations.
  - Update every 4-5 years.
  - Work towards establishing mark-selective fisheries, along with habitat/hatchery management practices, to further protect wild stocks.
- Identify, develop, and enforce best practices that reduce bycatch and incidental mortality of non-target CUs to minimize collateral mortality in fisheries.
  - Gather empirical data from marine fisheries to clarify CU-specific fishing-related incidental mortality (FRIM) rates.
  - Facilitate transition of all fishing sectors to best practices for reducing FRIM via demonstration projects (over 10 years).
    - E.g., provide trap nets and alternate selective gear types to reduce beach seine and gill net fishing in river.
    - E.g., demonstrate best practices for high-risk fisheries that reduce FRIM, such as using sorting conveyers and/or water sorting traps and reduced tow speeds for trawl fisheries; limiting non-retention fishing effort during periods of high water temperatures; etc.
    - E.g., transition high-risk FRIM fisheries such as unmanaged/unsustainable gillnet fishing via a combination of limiting locations, increasing 'hotpicking', or transitioning to alternate gear types, as appropriate, by the end of year 10.
- Facilitate, implement, and assess an incentive program to increase opportunities for targeted Food, social and ceremonial (FSC) fisheries using selective fishing gear.
  - Increase existing capacity of thirty monitors (employed by DFO) from one month FTE per year (existing baseline) to six months per year, employed for full 25 years to monitor 30 community-based projects.
  - Monitor catch, engage in ceremonies, facilitate community discussion. Organize fishing (distribution and set-up/take-down of traps). Reporting.
  - Estimate that projects will be implemented over 10 years; by year 10 non-selective fishing practices will be dramatically reduced.

- Support the development of Tier 1 (First Nation to First Nation) and Tier 2 (First Nations to DFO) forums for exploring how FSC allocations can be distributed within First Nations communities.
    - All communities together (Lower Fraser Fisheries Alliance and independent Nations).
    - Required for 5 years.
    - This is dependent on the Guardians program being in place (Governance Enabling Strategy 2).
- Increase surveillance and enforcement of fishing regulations to improve compliance with new and existing regulations across sectors.
    - Increase in DFO enforcement officer capacity by end of year 5.

**Strategy 2: Watershed Hydrology Protection and Water Management**

**Threat:** Changes to watershed hydrology, water quality and quantity, and timing of flow due to agriculture, forestry, mining, other anthropogenic development, and climate change - all development (not meant to be inclusive or exclusive). Collectively, these impacts reduce the viability of spawning and rearing habitat, affecting both adult and juvenile life stages of salmon.

**Goal:** Maintain and restore the physical processes affecting hydrologic integrity, minimum ecological flows, and water quality and quantity, incorporating future impacts of climate change, to improve spawning and rearing habitat.

**Pathway(s) of effects:** Increase productivity via improved survival at egg, alevin and fry stages and decreased pre-spawn mortality.

**Actions within strategy**

- Develop strategic watershed plans to maintain natural hydrological processes and patterns.
    - One each for the Fresh Water Areas (FWAs) corresponding to CUs in the regions: i.e., Lillooet, Harrison River, Chilliwack, Lower Fraser regions.
    - Plan should address:
        - Development of integrated stormwater management plans that minimize impacts to stream hydrographs/natural hydrology, or if plan is already in place, revise as needed;
        - Ensure flood management and mitigation strategies (policies and practices) incorporate salmon-friendly policies (nature-based solutions) that minimize impact on hydrology;
        - Recommendations for land-use practices (forestry, agriculture, mining) that would be in line with the goals of the plans (to maintain natural hydrological processes);
        - Expansion of research that identifies contaminants of concern for all salmon species entering the receiving environment in the lower Fraser;
        - Identify and implement enforcement consequences that would lead to changes in behaviour and full remediation after violations of the appropriate Acts;

        - Identify priority floodplains for reconnection to restore hydrological flow – identify issues and opportunities for reconnection;
        - Recommend the identification of minimum ecological flows as per Water Sustainability Act, and identify areas with flow issues (e.g., low flows) for action.
- Implement strategic plans, including monitoring and enforcement of the recommended practices identified above.
    - Includes an implementation fund for priority projects, a central management board with representatives from different agencies, and one representative from each First Nation group in the study area.
    - Includes hiring one watershed technician and one Indigenous guardian for each of the four FWAs, with two assigned to the Lower Fraser FWA, for a total of five technicians and five guardians.
- Fully implement the Water Sustainability Act to ensure minimum ecological flows are present in salmon-bearing waters.
    - Undertake hydrological modelling and biological surveys to determine what is the minimum ecological flow and produce a report for the province (or other regulatory authority).

**Strategy 3: Protect Salmon Habitat**

**Threat:** Loss and degradation of salmon habitat in the lower Fraser River reduces the available spawning and rearing habitat for salmon.

**Goal:** Protect areas of remaining intact habitat to maintain high quality spawning and rearing habitat.

**Pathway(s) of effects:** Increase productivity via improved rearing and spawning capacity.

**Actions within strategy**

- Identify what is not working in terms of protecting salmon habitat - why are we losing habitat in the first place (given the Fisheries Act and Water Sustainability Act)?
- Identify habitat requirements needed to support thriving salmon CUs and identify priority habitats for conservation/protection.
    - One post-doctoral researcher conducting a spatial optimization project
- Designate priority habitat as protected areas for salmon, such as Salmon Parks, under the Fisheries Act and Oceans Act.
    - Combination of designation of restricted use areas on Crown Lands and the purchase of private lands via a $250 M CAD endowment fund. Coordination among First Nations, DFO, land trusts and West Coast Environmental Law.
- Increase capacity within DFO and Provincial ministries to enforce habitat protection provisions of relevant legislation.
    - One additional FTE enforcement officer in each of the Fresh Water Areas (FWAs), with two in the Lower Fraser FWA. May be one FTE coordinator and part time representation from more than five personnel across governmental agencies, equating to 5 FTE. Ideally this would be complementary to the Indigenous guardian program; need to ensure that it captures enforcement of both habitat protection measures and water flow protection.
- Prevent the expansion of footprints of known habitat stressors into moderate- to high-quality habitat: e.g., log storage sites, contaminated waste sites, dredging.
    - Consultant to work with government and industry staff to identify current extent of footprints and determine new maximum extents incorporating biological data and stakeholder consultations. Assume monitoring & enforcement captured in action 4 above.

**Strategy 4: Restore Freshwater Salmon Habitat**

**Threat:** Loss and degradation of spawning and rearing habitat in the lower Fraser mainstem, tributary streams and lakes (loss of riparian vegetation, big logs, woody debris, erosion of stream banks) has reduced the available spawning and rearing habitat for salmon.

**Goal:** Restore lost and degraded freshwater habitat to improve functionality for salmon rearing and spawning.

**Pathway(s) of effects:** Increase productivity via improved rearing and spawning capacity.

**Actions within strategy**

- Develop a central database where all groups in the lower Fraser participating in salmon restoration projects can register their projects to highlight gaps and overlaps in the region.
- Identify and prioritize sites for restoration that support, or directly or indirectly impact, salmon and their spawning, rearing and migration habitats.
    - Analysis of limiting factors and regional needs for different CUs.
    - Collaboration and coordination with First Nations to determine priority sites.
- Restore priority riparian sites.
    - Restore ~460 $km^2$ by the end of year 25 (e.g., average site of 1 km of stream length with 10 m on either side of watercourse per year starting in year 3).
- Restore priority freshwater instream habitat.
    - Restore up to 345 $km^2$ by end of year 25 (20 sites per year starting in year 3, we characterized the average site as approximately 150m by 5m of streams this includes building riffles, meanders, holding pools).
- Restore and create wetlands.
    - Restore or create 10 $km^2$ by end of year thirteen (10 x 20 ha of wetlands every 2 years, for 10 years (i.e., 50 sites)). Limited by the realistic timeframe for wetland projects & available habitat.
- Monitor restoration projects as part of adaptive management.

**Strategy 5: Restore Estuarine Salmon Habitats**

**Threat:** Loss and degradation of rearing habitat in the Fraser River estuary (coastal development, shipping, industry, forestry practices, pollution, dredging, dumping)- all development (not meant to be inclusive or exclusive) has reduced the available rearing habitat for salmon.

**Goal:** Restore high quality rearing estuarine habitat for juvenile salmon.

**Pathway(s) of effects:** Increase productivity via improved rearing capacity and early marine growth.

**Actions within strategy**

- Identify and prioritize estuarine sites for restoration that support, or directly or indirectly impact, salmon and their rearing habitats.
- Restore priority lost/eroding marsh habitats in the estuary.
    - Restore 120 hectares (1.2 $km^2$) of eroding marsh habitats by the end of year 25 (~5 hectares per year, 10 ha project every 2 years).

**Strategy 6: Reduce Barriers to Fish Passage**

**Threat:** Non-natural barriers (e.g., culverts, flood infrastructure, dams) inhibit adult and juvenile migration and access to rearing and spawning habitat.

**Goal:** Remove and mitigate priority barriers to fish passage to improve habitat connectivity and increase access to available spawning and rearing habitat for salmon.

**Pathway(s) of effects:** Increase productivity via improved rearing and spawning capacity.

**Actions within strategy**

- Upgrade flood infrastructure at key access points to be salmon friendly and increase the capacity to operate and maintain current flood infrastructure in a more fish-friendly way.
    - Upgrade 48 flood infrastructure barriers by the end of year 25 (beginning in year 2, upgrade 2 sites per year).
    - Increase capacity for fish-friendly operations by 2 FTE per year for 10 years, scaling down to 1 FTE for remaining 15 years.
- Upgrade culverts prioritized to benefit fish passage.
    - Upgrade 576 culverts by the end of year 25 (beginning in year 2, ground-truth and upgrade 24 priority culverts per year).
- Restore connectivity to the upstream end of priority sloughs.
    - Complete approximately 6 projects (out of 8-12 candidate sloughs) throughout the lower Fraser by the end of year 25 (reopening 1 slough every 4 years due to high level of planning required).
- Restore connectivity within the estuary through the breaching of physical barriers such as dikes and jetties.
    - Restore connectivity at approximately 8 sites by the end of year 25 (one major project every 3 years).

**Strategy 7: Manage Invasive Species**

**Threat:** Invasive plant and animal species may cause structural (i.e., exclusion through habitat alteration), biogeochemical (i.e., disrupting nutrient pathways), and trophic (altering/disrupting food web relationships) impacts on salmon and their food web.

**Goal:** Reduce the negative impact of invasive species on salmon and their habitat.

**Pathway(s) of effects:** Indirectly increase productivity via improved rearing conditions, which may lead to improved survival due to better foraging opportunities and decreased predation.

**Actions within strategy**

- Research the extent and impact of invasive species (e.g., exotic *Typha*, yellow iris, *Spartina*, purple loosestrife, reed canary grass, zebra mussels, green crab, Canada geese) on critical riverine and estuarine habitats for juvenile salmon.
  - 2 PhD-level research projects to examine impacts on estuaries.
- Research the extent and impact of invasive predatory fish species (e.g., bass) on juvenile salmon.
  - 1 PhD-level research project to examine impact on juvenile salmon. Part 1: research extent of invasive fish species using eDNA metabarcoding. Part 2: diet study of subset of invasive fish to estimate rate of predation.
- Conduct invasive species management research experiments to identify the most cost-effective management strategies to protect critical habitat.
  - 2 PhD-level research projects to examine strategies in partnership with managers to allow for uptake of new management strategies in the long term.
- Implement research findings into ongoing management of invasive species to reduce impacts to juvenile salmon and their habitats.
  - Research projects are in partnership with existing organizations (e.g., Ducks Unlimited, Environment and Climate Change Canada, B.C. Ministry of Forests, Lands, Natural Resource Operations and Rural Development), but additional staff time will be required to implement the findings within existing invasive species management programs in the estuary.
- Develop surveillance programs (e.g., using eDNA) to enhance <u>early detection</u> and potential eradication or control of aquatic invasive species (e.g., Atlantic salmon, smallmouth bass).

  - Set up a dedicated eDNA facility for DFO on the West Coast that would be used for this program and others. Incorporate into the DFO Environmental Watch (EWatch) Program by expanding the team to include a geneticist and trained field staff and establishing new monitoring sites. Metabarcoding to be used for broad spatial scale, multi-species surveillance across the whole watershed, and qPCR testing to be used for more targeted purposes.
- Increase public awareness programs aimed at reducing the spread of potentially invasive species (e.g., largemouth and smallmouth bass, yellow perch).
  - Hire a coordinator and a team of two people to develop an updated communications strategy (e.g., including new website section that is maintained and up to date, commercials, bus stop poster and billboards, radio, tackle shops and outdoor recreation groups, etc.). Initiate a strong push in years 1 and 5 to broaden the reach of communications and maintain active campaign tools over 10 years.

**Strategy 8: Pollution Control**

**Threat:** Pollutants from urban, agricultural, and industrial sources can cause negative cumulative effects on salmon and degrade habitat.

**Goal:** Minimize pollutants in the environment to reduce negative impacts to salmon.

**Pathway(s) of effects:** Indirectly increase productivity via improved condition of emigrating juveniles and returning spawners, which may reduce premature mortality.

**Actions within strategy**

- Review the cumulative and individual risks to lower Fraser salmon CUs from exposure to legacy, current, and emerging chemicals of concern, including stormwater and agricultural runoff.
    - Expand on and complement existing programs to identify priority contaminants and sources in fresh water, aquatic sediments, air, and some salmonids (ECCC and DFO).
- Implement planned wastewater treatment upgrades to Iona Island and Annacis Island facilities.*
    - Annacis Island enhanced secondary treatment capacity and seismic stability upgrades were originally scheduled to begin in 2015 based on Metro Vancouver Regional District Liquid Waste Committee meeting minutes May 16, 2019, section 5.2.
    - Iona Island treatment plant was proposed to be upgraded from primary to tertiary treatment with the original start year in 2018 based on Iona Wastewater Treatment Plant project update report April 17, 2019.
- Revise and implement legislation to reduce pollutants (chemicals of concern, nutrient (e.g., manure spreading) and pesticide loading).
    - Include a total load limit (e.g., relating animal density to manure loading) in addition to existing seasonal limitations of pollutant use.
    - Adopt a provincial ban of residential cosmetic pesticides, following Quebec and Ontario.
- Implement a ban on copper and other heavy metals in brake pads in British Columbia.

* Note this action was assessed under two cost scenarios due to the high infrastructure costs that are likely to be borne by municipalities with support from federal and provincial grants.

**Strategy 9: Pathogens and Disease**

**Threat:** Transmission of pathogens (parasites, bacteria and viruses) to wild salmon, from finfish aquaculture (i.e., salmon farms) and hatcheries. High pathogen loads contribute to increased mortality of juveniles during emigration and/or increased pre-spawning mortality of adults during returns to spawn.

**Goal:** Minimize exposure of wild salmon to pathogens (parasites, bacteria and viruses) from finfish aquaculture and hatcheries.

**Pathway(s) of effects:** Indirectly increase productivity via improved condition of emigrating juveniles and returning spawners, which may reduce premature mortality.

**Actions within strategy**

- Phase out open-net pen salmon farms by restricting licenses and renewals to land-based and closed containment systems and providing incentives on associated capital costs.
    - Assessed over a 10-year period based on expert feedback on the likely time to roll out. Note that some financial incentive to defray capital costs was deemed necessary to support the feasibility of this action.
    - Acknowledge that companies will likely want to build their new facilities before shutting down their open-net pen facilities.
- Implement proactive sea louse treatment regimens and invest in alternate treatment methods to better control sea lice populations in farmed finfish.
- Increase the frequency and scope of pathogen screening on fish farms, with appropriate measures (e.g., antibiotic treatments, culling) to treat or remove diseased fish.
- Ensure that industry can only stock juvenile salmon that have been shown to be free of harmful pathogens (e.g., PRV virus).
- Increase surveillance of wild salmon in both freshwater and marine environments to better understand harmful pathogen loads, and potential links of these to aquaculture and hatchery fish.

**Strategy 10: Hatchery Operations**

**Threat:** Decreased fitness in wild salmon populations due to genetic homogenization; competition for resources including food availability and spawning habitat.

**Notes on Scope:** Hatchery operations include salmonid enhancement for conservation of diminished CUs (e.g., Cultus Late Sockeye) as well as production to boost fisheries opportunities across sectors, and production that directly supports research and stock assessment goals. These complex and interacting objectives of hatchery operations are each important, however for the scope of this project, which focuses on conservation strategies for wild salmon in the lower Fraser River, we have only assessed hatchery operations from the perspective of minimizing risk to wild salmon within this study region. We have attempted to only include actions that are feasible within the context of ongoing hatchery operations for these other objectives, however we have not directly included any actions that support or incorporate these other objectives. Hatchery management occurs at multiple scales, including small local enhancement projects, DFO Fisheries Management Areas, and international treaty agreements. While some CUs, particularly Fraser River sockeye salmon, would significantly benefit from reduced competition from hatchery fish in the North Pacific, we have avoided addressing hatchery actions at this international scale due to perceived low feasibility of success and the difficulty of aligning the timeline and scope of those efforts with that of this project.

This strategy focuses on the lower Fraser salmon CUs identified in this project, and on actions at the scale of this region. Where actions would likely be conducted at a larger scale (e.g., Action 3: Develop robust evaluation criteria for the implementation of conservation enhancement of at-risk CUs), we have assumed here that the costs born to this project would only include the subset of such work that directly pertains to the lower Fraser. We have also excluded any potential capacity costs required to support this work, however, should enhancement be deemed appropriate this may be a requirement, particularly for CUs outside of the study region.

**Goal:** Develop a strategy that minimizes the risk of hatchery operations to wild salmon while supporting appropriate hatchery production for conservation, human use, and other needs.

**Pathway(s) of effects:** Improve fitness and resilience of wild salmon populations to changes in environmental conditions. Indirectly increase productivity via potentially improved condition of juvenile salmon, reduced predation on juvenile salmon, and improved spawning success.

**Actions within strategy**

- Develop a revised lower Fraser regional hatchery management strategy in an adaptive management framework to manage hatchery-wild interactions in conjunction with CU-specific enhancement targets.
    - Review conservation priorities for CUs, focusing on lower Fraser CUs and assess potential wild-hatchery interaction risks for each CU given current & projected hatchery production within the lower Fraser, treaty obligations, and conservation strategies over the next 25 years (1 post docs, 1 enhancement specialist).
    - Coordinate with research studies on hatchery-wild interactions across scales, species, and CU-specific contexts (Action 2) and develop best practices to minimize the risk of negative impacts of hatchery production in the lower Fraser on wild salmon. Includes annual meetings with hatchery managers to facilitate adaptive management practices (0.3 x FTE x 25 years).
    - Implement measures to mitigate the genetic risks of hatchery production - thermally mark 100% of hatchery releases, and visually mark Chinook and coho salmon hatchery releases.
- Evaluate the fisheries interactions, biological and ecological risks to wild lower Fraser salmon from Fraser River and Salish Sea hatchery operations with a series of research projects. Note that this would likely occur at the Fraser Basin scale, however here we only cost the portion that pertains to lower Fraser CUs.
    - Review the state of knowledge on the fisheries and ecological risks to wild Fraser River CUs from regional hatchery production within the lower Fraser River.
    - Conduct CU-specific research on the potential risks of lower Fraser River hatchery operations on wild salmon, then identify and implement operational best practices to reduce these risks in an adaptive management framework (5 projects - e.g., locations could be at Chilliwack, Chehalis, Alouette, Inch Creek, Little Campbell).
    - Include research study (field work and analysis) to assess steelhead residuals risks to wild salmon CUs from the Chilliwack hatchery as 1 of 5 projects listed above.
    - Prioritize rebuilding strategy evaluation for lower Fraser River CUs within the context of findings from this research.

- Support a working group to foster partnerships with Puget Sound hatcheries to combine research efforts on hatchery-wild interactions.
  - Annual meeting & regular correspondence
- Develop robust evaluation criteria for the implementation of conservation enhancement of at-risk CUs in the lower Fraser River. Assume that this would occur at the Fraser Basin scale as this is more realistic to the priorities and functional operations for DFO's Salmonid Enhancement Program (SEP), however, only the portion of these costs that would be dedicated to the scope of the lower Fraser are included here.
  - One 0.5 FTE Research Scientist x 5 years for lower Fraser scope to contribute to:
  - Ongoing development of the guidelines for when, how hatcheries are appropriate for conservation of wild salmon.
  - Internal adaptive management DFO SEP & Science projects to conduct priority analysis and identify key priorities for Fraser SEP including: species production ratios, location production allocations
    - Evaluation framework to determine if hatchery supplementation is an appropriate measure for conservation of each CU [link this into biological assessment criteria for CUs in the context of climate change defined in Fisheries Management Strategy (S01)]

**Strategy 11: Predator Control and Management**

**Threat:** Predation from pinnipeds (seals and California sea lions), particularly on juvenile salmon, may be associated with an overall decrease in marine survival rates of some CUs in recent decades.

**Goal:** Reduce the impact of pinniped predation on salmon through population control.*

***Note:** this strategy has ethical considerations that should be addressed prior to implementation.

**Pathway(s) of effects:** Increase productivity via improved smolt survival.

**Actions within strategy**

- Conduct experimental fishery (or traditional First Nations harvest) of pinnipeds in an adaptive management framework to assess the impacts of pinniped predation on salmon populations.
    - Based on a draft proposal that would seek to reduce harbor seal populations by 50% and stabilize California and Stellar sea lion populations at their current levels in Southern BC.
    - Phase 1 (years 1-2) would use limited harvesting to demonstrate whether the fishery is technically feasible.
    - Phase 2 (years 3-5) would aggressively scale the fishery to reduce harbor seal populations by 50% (predicted to be MSY).
    - Phase 3 (years 6 - 25) would involve managing the fishery to sustain yields of pinnipeds near MSY for the foreseeable future, with ongoing DFO surveys conducted once every several years.
    - If the fishery was untenable, a similar experiment would be conducted by providing subsidies of $100/animal to First Nations to encourage harvest up to the above limits.

**Combination Strategies**

Benefits estimates were also completed for Combination Strategies, which are groups of strategies that have a greater expected impact when combined and implemented together than when implemented individually. The following strategies are considered complementary:

12. Strategies 1, 9 & 10 (fisheries, aquaculture + hatcheries)
13. Strategies 2-6 (all habitat related)
14. All strategies combined

**Enabling strategies**

Enabling strategies underpin the success of other strategies. For example, in order to make informed decisions, good monitoring data on the status of CUs is required. However, monitoring on its own does not lead to a measurable benefit to the conservation of salmon. For enabling strategies, we assumed the benefits and costs were shared equally across all strategies, and therefore did not include them in the prioritization analysis. The following strategies were identified as key components of existing mandates from government agencies (e.g., DFO under the Wild Salmon Policy and British Columbia and the federal Canadian government under the United Nations Declaration on the Rights of Indigenous Peoples (UNDRIP)) that have yet to be fulfilled. We highlight them here as important next steps for salmon recovery, independent of (but vital to) the strategies assessed in this study.

**ES1. Monitoring and Assessment**

In order to make informed harvest and conservation decisions, we require high quality monitoring data to assess the status of CUs.

**Actions within strategy**

- Review the current list of CUs and use the framework proposed by DFO (Wade et al. 2019) to determine whether changes should be made to CU delineations based on new genetic and life history data.
- Identify monitoring and surveillance gaps for CUs in the lower Fraser River region including:
    - o assessing whether the number of spawning streams being monitored in each CU is sufficient to quantify CU status and trends and is appropriate for the current

fisheries management system (i.e., does each CU have an appropriate number of indicator streams and monitoring effort to accurately estimate spawner abundance?).
    - identifying surveillance gaps for CUs that may be subject to high fishery-related incidental mortality (FRIM).

- Based on results from the above assessment, implement new monitoring and surveillance for CUs that would demonstrably benefit from additional monitoring.
    - increase the number of indicator streams regularly surveyed to improve estimates of successful spawners.
- Develop habitat monitoring protocols to coordinate habitat assessments as part of CU assessments.
- Strategically review and identify gaps in CU-level catch estimates through a variety of methods.
    - e.g., via wild coded wire tagging programs, thermal marking of otoliths of wild juvenile salmon, expanding ocean-based genetic stock-identification assessments, and increased assessments in partnership with Indigenous Guardian & community programs.
    - introduce fisher-independent monitoring program(s) to determine rates of discard and FRIM across fisheries, including estimates of multiple encounters. Prioritize effort to address fisheries impacting red/threatened/endangered CUs.
- Integrate updated estimates of recruits, successful spawners, and FRIM from these increased monitoring efforts into ongoing stock assessment efforts and address ongoing monitoring gaps using adaptive management in an iterative approach.
- Provide monitoring and assessment data to the public to improve understanding of the scientific basis for management decisions (e.g., via Pacific Salmon Explorer).

**ES2. Governance Solutions**

To date, governance developed by provincial and federal Crown agencies has fostered the Fraser River's utility as a transportation and trade corridor, with significant industrial, commercial, and urban development. Successful recovery of wild salmon will require coordinated efforts across multiple governments – First Nation, federal, provincial, and local, with a focus on decision making for achieving ecological outcomes. The legislative authority over salmon and their habitats rests with the Crown, which includes First Nation, federal, and provincial governments.

**Actions within strategy**

- Implementation of a Fraser River co-governance body to oversee the conservation and protection of salmon and their habitats, including water resources within the lower Fraser. This body would be jointly governed by First Nation, federal and provincial Governments and would liaise with municipalities and Tier 3 bodies. The purpose of this co-governance body would be to oversee and coordinate strategies to protect and restore salmon and their habitats in the lower Fraser Region.
- Objective of the co-governance body would be to secure long-term ecological resilience in the lower Fraser River and would include the following principles:
    - A commitment to sustainability that spans seven generations.
    - Honour aboriginal rights and title and the principles of the United Nations Declaration on the Rights of Indigenous Peoples (UNDRIP).
    - Clear enforcement mechanisms to ensure ecological resilience.
    - Sustainable funding for governance and ecosystem-based management.
    - Respect for the opinion, voices, experiences, and culture of others.
- Create a director-level position at DFO, Director of Wild Salmon Policy Implementation, whose focus would exclusively be wild salmon.
- Establish a formally recognized, federally and provincially supported, First Nations-led Guardian Watchmen program with guaranteed funding for a minimum of 25 years and legislate additional enforcement ability for Guardian Watchmen.
- This body would oversee the implementation of the Priority Threat Management assessment for salmon (for example) and would link with monitoring and assessment strategies to ensure feedback and adaptive management.

**Development Baseline Scenario**

In the lower Fraser region, there are currently several major industrial developments proposed, as well as ongoing residential development expansions (e.g., Boundary Bay Conservation Committee 2016, available at https://www.againstportexpansion.org/uploads/images/file_view/Fraser_River_Estuary_and_Mega_Projects_April_22_2016_A.pdf). These and other proposals known to experts at the workshop were discussed by the group to establish a common understanding of the active proposals within the study region. Due to the uncertainty of whether each development will proceed, we asked experts not to include these in their baseline estimates. To capture the potential impacts of these developments on lower Fraser River salmon, experts were instead asked to assess the likelihood of thriving for each CU under a development baseline scenario in which all proposed developments were completed within the 25-year study timeline (FUT BSL, Table 4.2).

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**S2. Data Collection and Methods**

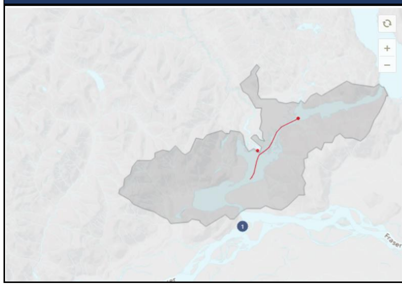
Experts used the background information provided for each CU including biological status, habitat pressures, trends in spawner abundance, harvest rates, and hatchery releases, as applicable (example Fig. 4S1), as well as their own expertise to estimate the probability of each CU achieving green status at the end of 25 years. We used a Delphi approach (Linstone and Turoff, 1975) and three-step question format to elicit expert judgement on a range of potential outcomes including their most pessimistic, most optimistic, and best-guess estimates for each CU-strategy combination. This format helps to minimize bias by encouraging experts to imagine all possible scenarios that may affect the outcome of each CU over the project timeline. We decided not to elicit confidence bounds for each estimate because the questions were about degrees of belief for a single event (i.e., the probability of salmon in being classified as green status in 25 years (rather than a frequency estimate)). Following the workshop, we collated all benefit estimates and provided anonymized summaries back to the experts, such that they could review their estimates relative to the group and revise them, if desired. This allows for reflection and can improve the reliability of expert estimates, while minimizing the effect of 'groupthink' (Martin, Burgman, *et al.*, 2012; Hemming *et al.*, 2018).

We used the final estimates to determine the benefit of implementing each strategy. One set of outlier benefit estimates was excluded due to a strong bias that appeared to indicate a lack of attention in completing the exercise. This was identified by a highly inconsistent response to strategies, whereby a single strategy received very optimistic benefit estimates and all others received very pessimistic estimates across all CUs, with differences up to 100%. No other estimates showed this pattern, even among experts who had voiced concerns about one or more strategies.

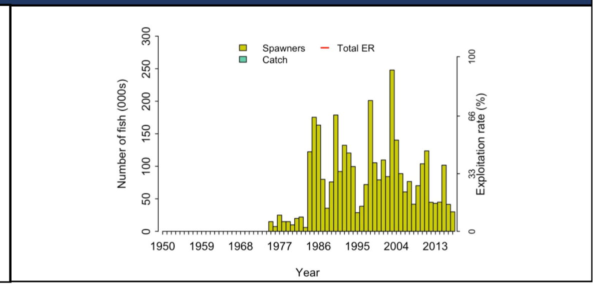
The relative cost-effectiveness of each management strategy was assessed by dividing the expected performance by the total present value cost of the strategy (Table 4S4).

**Species: Chinook** | **CU: Lower Fraser River_FA_0.3 (Harrison)** | **MU: Fraser Fall $4_1$**

**Spawning Locations** | **Biological Status** | **Catch, Run Size, and Exploitation Rate**

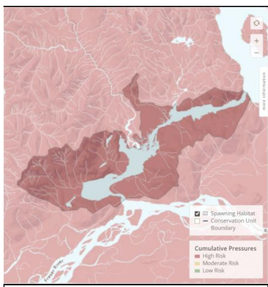


| DFO Integrated Status | COSEWIC Status |
|---|---|
| | NA |
| **Stock-recruitment** | **Historical Spawners** |
| | |




The biological status of the CU as estimated by four different assessment processes. DFO integrated status assessments are based on an examination of multiple metrics in combination with expert opinion (Grant & Pestal 2012). COSEWIC assessments evaluate the risk of extinction based on trends in abundance in addition to considering human and environmental threats to the CU (COSEWIC 2018). Stock-recruitment status compares the most recent estimate of spawner abundance to benchmarks based on the shape of the stock-recruitment relationship (using $S_{gen1}$ and 80% $S_{MSY}$ as the lower and upper benchmarks, respectively). Historical Spawners status compares the most recent estimate of spawner abundance to the 25th and 50th percentiles of historical spawner abundance (Connors et al. 2018).

**Habitat Status**



| Habitat Impact Categories | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Water Quality | | | | | | Human Development Footprint | | | | | | | | | | | |
| Wastewater Discharge | | | Water Licenses | | | Impervious Surfaces | | | Linear Development | | | Mining Development | | | Total Landcover Alteration | | |
| Green | Amber | Red | Green | Amber | Red | Green | Amber | Red | Green | Amber | Red | Green | Amber | Red | Green | Amber | Red |
| 0% | 0% | 100% | 0% | 0% | 100% | 50% | 50% | 0% | 0% | 100% | 0% | 50% | 0% | 50% | 50% | 50% | 0% |

| Hydrologic Processes | | | | | | Vegetation Quality | | | | | | Surface Erosion | | | Fish Passage | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Equivalent Clearcut Area | | | Forest Disturbance | | | Insect & Disease Defoliation | | | Riparian Disturbance | | | Road Development | | | Stream Crossing Density | | |
| Green | Amber | Red | Green | Amber | Red | Green | Amber | Red | Green | Amber | Red | Green | Amber | Red | Green | Amber | Red |
| 100% | 0% | 0% | 50% | 50% | 0% | 100% | 0% | 0% | 0% | 0% | 100% | 0% | 0% | 100% | 0% | 100% | 0% |

www.salmonexplorer.ca

Habitat pressure indicators are grouped into seven habitat "impact categories" representing key factors affecting general watershed conditions. Values indicate the percent of watersheds within each CU's spawning zone of influence that fall within a given risk category (low [green], moderate [amber] or high [red].

**Figure 4S1.** Example of a CU summary produced using data from the Pacific Salmon Explorer (https://salmonexplorer.ca/) tool and provided as part of the background information for experts to use during the Expert Elicitation workshop.

While we note that CU designation is a recent development and some delineations between CUs may shift over time as new information is obtained, we used the most recent categorization of Fraser River CUs as a measure of salmon population diversity in this region (Holtby and Ciruna, 2007). We also included an action within the monitoring and assessment enabling strategy (ES1) to review the current list of CUs and use the framework proposed by Fisheries and Oceans Canada (DFO; Wade et al., 2019) to determine whether CU delineations should be updated in this region based on new genetic and life history data. Just over half (10/19) of the existing CUs in the lower Fraser have not had recent biological assessments completed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) or by DFO under the Wild Salmon Policy (WSP; DFO, 2005). Only three of the nine CUs that have been assessed under WSP within the study region are in abundant or 'green' status, one of which (Lower Fraser

Fall Chinook) was recently assessed as Threatened by COSEWIC, due to population declines since the WSP assessment (Table 4S2). Experts were asked to include only wild salmon abundance in their CU predictions (i.e., salmon produced by hatchery enhancement were not included in abundance metrics), following the practices used by COSEWIC. Following the precautionary approach, experts agreed to assume that CUs classified as 'data deficient' should be considered red status under the Wild Salmon Policy (Fig. 4S2).

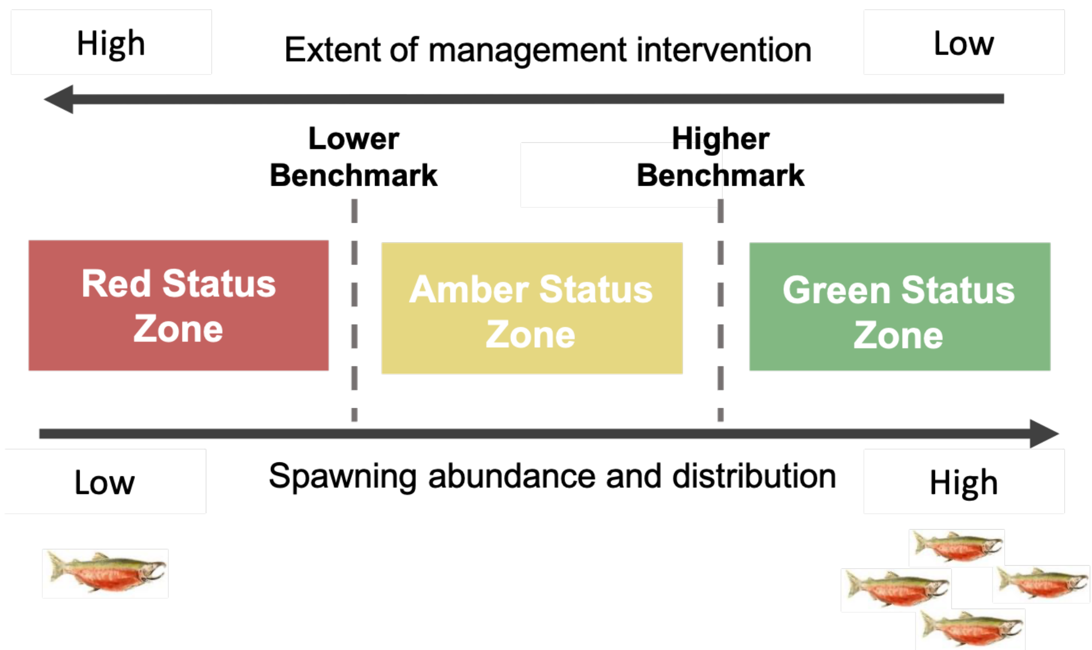



**Figure 4S2.** Wild Salmon Policy status ranks adapted from Canada's Policy for Conservation of Wild Pacific Salmon (DFO, 2005). Biological indicators and expert judgement are used to assign WSP Integrated Status to salmon Conservation Units as red ("… established at a level of abundance high enough to ensure there is a substantial buffer between it and any level of abundance that could lead to a CU being considered at risk of extinction by COSEWIC), amber ("while a CU in the Amber zone should be at low risk of loss, there will be a degree of lost production. Still, this situation may result when CUs share risk factors with other, more productive units"), or green ("identifies whether harvests are greater than the level expected to provide on an average annual basis, the maximum annual catch for a CU, given existing conditions…there would not be a high probability of losing the CU") (Grant and Pestal, 2013).

**Table 4S1.** Number of expert benefits estimates per Conservation Unit and Management Strategy. In total, 26 experts provided benefits estimates, however, not all experts completed estimates for all CUs or strategies. Minima and maxima for each strategy are highlighted in bold.

| Conservation Unit | Strategy | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **BSL** | **01** | **02** | **03** | **04** | **05** | **06** | **07** | **08** | **09** | **10** | **11** | **12** | **13** | **ALL** | **DEV** |
| ***Chinook*** | | | | | | | | | | | | | | | | |
| Boundary Bay Fall 0.3 | 18 | 18 | 17 | 17 | 17 | 17 | 15 | 16 | 17 | 18 | 16 | 17 | 17 | 16 | 17 | 15 |
| Lower Fraser Fall 0.3 | **23** | **23** | **22** | **22** | **22** | **22** | **20** | **21** | **22** | **21** | **20** | **22** | **21** | **19** | **20** | **17** |
| Lower Fraser Spring 1.3 | 22 | 22 | 20 | 20 | 20 | 20 | 18 | 19 | 20 | 19 | 18 | 20 | 19 | 17 | 18 | 16 |
| Lower Fraser Summer 1.3 | 20 | 20 | 19 | 19 | 19 | 19 | 17 | 18 | 19 | 18 | 17 | 19 | 18 | 16 | 17 | 15 |
| Lower Fraser Upper Pitt Summer 1.3 | 17 | 17 | 16 | 16 | 16 | 16 | 14 | 15 | 16 | 17 | 15 | 16 | 16 | 15 | 16 | 14 |
| Maria Slough Summer 0.3 | 20 | 20 | 18 | 18 | 18 | 18 | 16 | 17 | 18 | 17 | 16 | 18 | 17 | 15 | 16 | 14 |
| ***Chum*** | | | | | | | | | | | | | | | | |
| Lower Fraser | 22 | 22 | 21 | 21 | 21 | 21 | 19 | 20 | 21 | 20 | 19 | 21 | 20 | 18 | 19 | 16 |
| ***Coho*** | | | | | | | | | | | | | | | | |
| Boundary Bay | **16** | **16** | **14** | **15** | **15** | **14** | **13** | **14** | **14** | 14 | 13 | **14** | 14 | 14 | 14 | 12 |
| Lower Fraser | **16** | **16** | **14** | **15** | **15** | 15 | 14 | **14** | 15 | 14 | 14 | **14** | **13** | 13 | 13 | 12 |
| Lillooet | **16** | **16** | **14** | **15** | **15** | **14** | **13** | **14** | **14** | **13** | **12** | **14** | **13** | **12** | **12** | **10** |
| ***Pink*** | | | | | | | | | | | | | | | | |
| Fraser River | 21 | 21 | 20 | 20 | 20 | 20 | 18 | 19 | 20 | 19 | 18 | 20 | 18 | 16 | 17 | 14 |
| ***Sockeye*** | | | | | | | | | | | | | | | | |
| Chilliwack Early Summer | 19 | 19 | 17 | 17 | 17 | 17 | 15 | 16 | 17 | 16 | 16 | 18 | 16 | 15 | 15 | 13 |
| Cultus Late | 21 | 21 | 21 | 21 | 21 | 20 | 19 | 20 | 20 | 19 | 19 | 20 | 20 | 18 | 19 | 16 |
| Harrison Down Late (Big Silver) | 18 | 18 | 17 | 17 | 17 | 17 | 15 | 16 | 17 | 16 | 15 | 17 | 16 | 14 | 15 | 13 |
| Harrison (River type) | 19 | 19 | 17 | 17 | 17 | 17 | 15 | 16 | 17 | 16 | 16 | 18 | 16 | 15 | 15 | 13 |
| Harrison Up Late (Weaver) | 19 | 19 | 18 | 18 | 18 | 18 | 16 | 16 | 17 | 16 | 16 | 18 | 16 | 15 | 15 | 13 |
| Lillooet/ Harrison Late (Birkenhead) | 19 | 19 | 17 | 17 | 17 | 17 | 15 | 16 | 17 | 16 | 16 | 18 | 16 | 15 | 15 | 13 |
| Pitt Early Summer | 18 | 18 | 16 | 16 | 16 | 16 | 15 | 16 | 17 | 16 | 15 | 17 | 16 | 15 | 16 | 14 |
| Widgeon (River type) | 18 | 18 | 17 | 17 | 17 | 17 | 15 | 16 | 17 | 17 | 16 | 17 | 17 | 16 | 17 | 14 |

**Table 4S2.** Conservation status of 19 lower Fraser salmon Conservation Units as most recently assessed by the Department of Fisheries and Oceans Canada under the Wild Salmon Policy and by the Committee on the Status of Endangered Wildlife in Canada.

| Species | Conservation Unit | Main Spawning Population | DFO WSP Integrated Status | | Year (Report, Data) | COSEWIC Status | Year (Report, Data) |
|---|---|---|---|---|---|---|---|
| Chinook | Boundary Bay Fall 0.3 | Campbell, Nicomekl | TBD* | | 2016, 2012 | Threatened | 2020, 2015 |
| | Lower Fraser Fall 0.3 | Harrison | Green | | 2018, 2012 | Threatened | 2018, 2015 |
| | Lower Fraser Spring 1.3 | Birkenhead | TBD | | 2016, 2012 | Special Concern | 2018, 2015 |
| | Lower Fraser Summer 1.3 | Big Silver Creek | Data Deficient | | 2016, 2012 | Threatened | 2018, 2015 |
| | Lower Fraser Upper Pitt Summer 1.3 | Upper Pitt River | Data Deficient | | 2016, 2012 | Endangered | 2018, 2015 |
| | Maria Slough Summer 0.3 | Maria Slough | TBD | | 2016, 2012 | Endangered | 2020, 2015 |
| Chum | Lower Fraser | Harrison, Stave Rivers | NA** | | - | NA | - |
| Coho | Boundary Bay | Campbell, Nicomekl | NA | | - | NA | - |
| | Lower Fraser | Pitt, Salmon Rivers | NA | | - | NA | - |
| | Lillooet | Birkenhead | NA | | - | NA | - |
| Pink | Fraser River | Harrison (Fraser) | NA | | - | NA | - |
| Sockeye | Chilliwack Early Summer | Chilliwack | Amber | Green | 2018, 2015 | Not at Risk | 2018, 2015 |
| | Cultus Late | Cultus | Red | | 2018, 2015 | Endangered | 2018, 2015 |
| | Harrison Down Late | Big Silver Creek | Amber | Green | 2018, 2014 | Special Concern | 2018, 2015 |
| | Harrison (River type) | Harrison | Green | | 2018, 2014 | Not at Risk | 2018, 2015 |
| | Harrison Up Late | Weaver | Red | | 2018, 2014 | Endangered | 2018, 2015 |
| | Lillooet/ Harrison Late | Birkenhead | Amber | | 2018, 2014 | Special Concern | 2018, 2015 |
| | Pitt Early Summer | Pitt River | Green | | 2018, 2014 | Not at Risk | 2018, 2015 |
| | Widgeon (River type) | Widgeon Slough | Red | | 2018, 2014 | Threatened | 2018, 2015 |

*TBD = Status was classified as "to be determined" (CSAS 2016), in that an integrated status evaluation is incomplete due to unresolved methods and uncertainty associated with hatchery enhancement sites that are geographically proximate to wild sites. Unlike the data deficient CUs, an integrated status under WSP could be determined once methods are resolved around enhanced & wild sites. **NA = not assessed, whereas grey = assessed, but data deficient in that a status could not be determined based on the available information.

**S3. Uncertainty**

Estimating the benefit of implementing a management strategy for a given salmon CU is difficult and assumes an inherent level of uncertainty. To manage this uncertainty, we elicited lower (pessimistic), best (most likely), and upper (optimistic) estimates for each strategy and CU. This provided a range of probabilities for which to assess the lower and upper bounds, or least and most optimistic scenarios. In addition to this, we assessed the variability within expert estimates. All experts reviewed their estimates in relation to the range given by the group and were given an opportunity to modify their estimates (following the Delphi approach). Where experts appeared to be particularly optimistic or pessimistic relative to the group, a rationale for their estimates was requested.

We further assessed the outcome of the results if all outlier values were removed. Following Tukey's method of identifying outlier values as those above or below 1.5 times the interquartile range, we removed the outliers and recalculated all results. This method assessed all outliers at the CU x strategy x estimate type level (i.e., for each individual estimate across all experts). Following outlier removal, the results of the prioritization remained unchanged. Based on this and the potential for these outliers to represent true outcomes, we left these outlier values in the data for the final analysis.

Several CUs fell just below our 50% conservation threshold and were thus not considered in the count of CUs predicted to achieve green status. To explore the effect of their inclusion we performed the complementarity analysis with a threshold of 49%. While this did not affect the optimal strategies to invest in, it did change the number of CUs predicted to achieve green status with the implementation of a given strategy (e.g., eight CUs with the implementation of S01 instead of seven CUs, Table 4.2). To assess the variability in optimal management decisions given the uncertainty in benefits estimates, we completed the complementarity analysis using the best, most optimistic, and most pessimistic estimates from the experts. While eliciting this suite of estimates is primarily an exercise to increase the accuracy of the best-guess estimates from experts by encouraging them to imagine the range of possible outcomes over time, it is also a useful tool for examining whether conservation decisions are robust to changes in conditions over time. As an example, in the most optimistic scenario for Pacific salmon in the next 25 years, it is possible that current environmental projects are completed and have positive outcomes, global efforts to minimize the impacts of climate change are effective, and ocean conditions improve. Conversely, salmon could face increasingly poor marine conditions, increasing frequency of landslides, or cross some threshold of cumulative impacts that otherwise reduces productivity. These mental exercises allow experts to consider the reality of all unknown factors that could occur over the project timeline, and then assess their best estimate for what the true outcome is likely to be. The optimal strategies generally remained the same at these most extreme bounds of estimates, however, the number of CUs likely to surpass the 50% threshold varied considerably (Table 4S3).

**Table 4S3.** Strategies in order of optimization using best estimates, with the potential lower and upper bounds of CUs that achieve at least 50% chance of green status at the end of 25 years.

| | **Number of CUs with >50% chance of green status** | | |
|---|---|---|---|
| Strategy | Pessimistic | Best | Optimistic (*N* above baseline) |
| ALL | 0 | 16 | 18 (10) |
| S13 Combined Habitat | 0 | 14 | 17 (9) |
| S01 Fisheries management | 0 | 7 | 15 (7) |
| S04 Freshwater restoration | 0 | 6 | 17 (9) |
| S05 Estuarine restoration | 0 | 3 | 14 (6) |
| S07 Invasive species management | 0 | 2 | 12 (4) |
| S10 Hatchery operations | 0 | 2 | 16 (8) |
| Baseline | 0 | 0 | 8 |

Looking at the most optimistic scenario for the 19 CUs, there are eight that achieved a greater than 50% chance (0.5 probability) of being assessed as green status under business as usual (Baseline, Fig. 4S3). Freshwater restoration (S04) and hatchery operations (S10) were selected more often across conservation thresholds in this optimistic scenario, as they are relatively low cost and able to achieve greater conservation success with the optimistic estimates. In this scenario, freshwater restoration on its own was able to secure 17 CUs at >50% chance of achieving green status, highlighting that this habitat strategy has high impact for relatively low cost. If all habitat strategies were implemented (S13) the chance of achieving green status was elevated across CUs, with 10 surpassing 70%, 5 between 60-70%, and 2 between 50-60% thresholds. At a cost of up to 110M CAD per year implementing all available strategies, 18 CUs were conserved (11 at >70%, 6 at >60%, and 1 at > 50%) in the optimistic scenario.

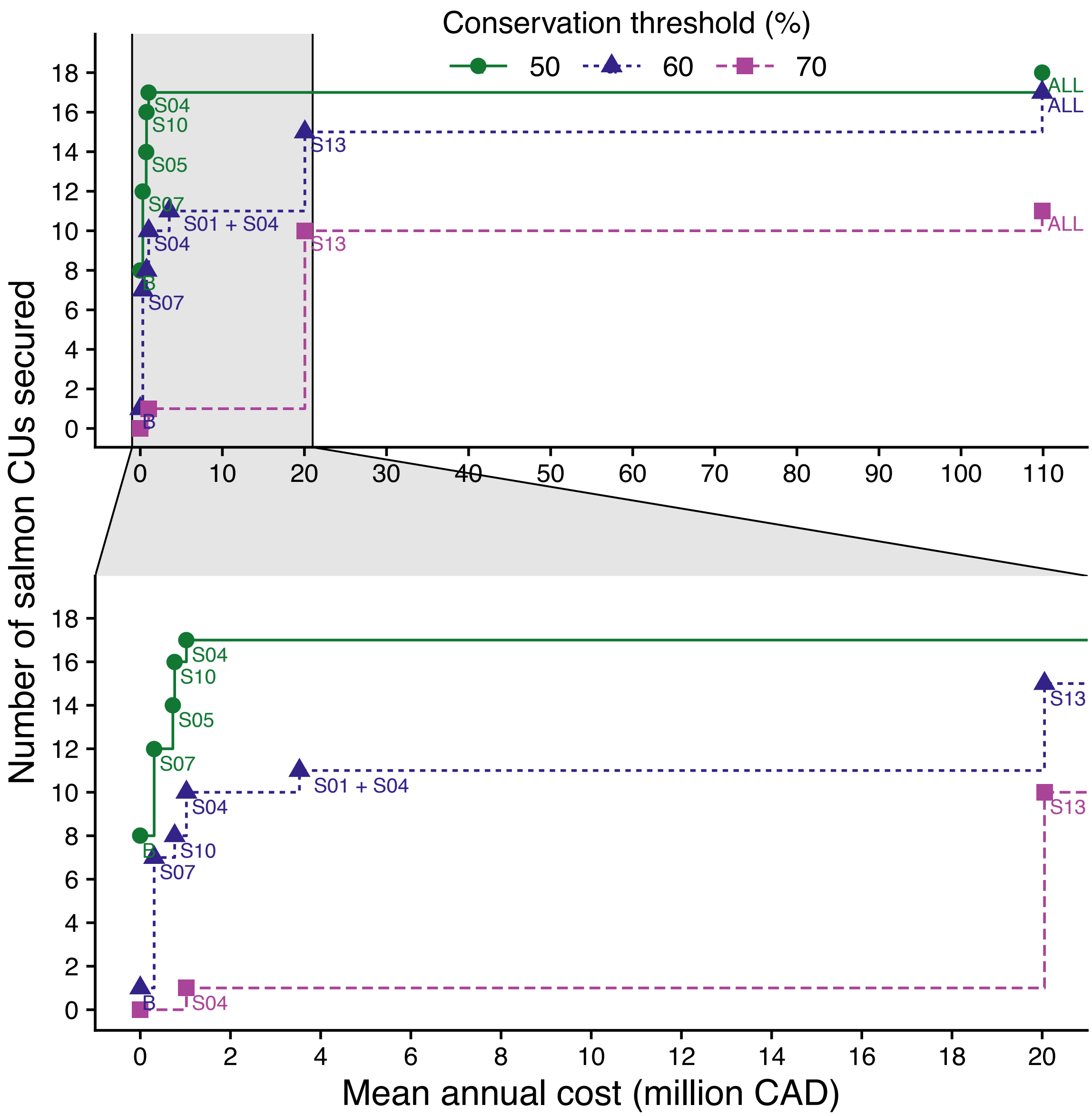



**Figure 4S3.** Optimistic scenario showing the number of lower Fraser River salmon CUs that were predicted to achieve >50% (dark green line), >60% (dark blue line), and >70% (dark pink squares) chance of green status at the end of 25 years by implementing the optimal set of complementary strategies for a given budget. Top: all optimal strategies. Bottom: optimal strategies costing up to 20M CAD annually magnified for clarity.

Unfortunately, no CUs achieved >50% chance of green status under the most pessimistic scenario (Fig. 4S4), highlighting the uncertain future of salmon in this system. Importantly, the implementation of all habitat strategies combined was still selected as the best conservation decision within this poor outlook. Despite no CUs achieving the >50% threshold, CUs still experienced benefits, which may result in improved or sustained status below the green status level (i.e., amber or red).

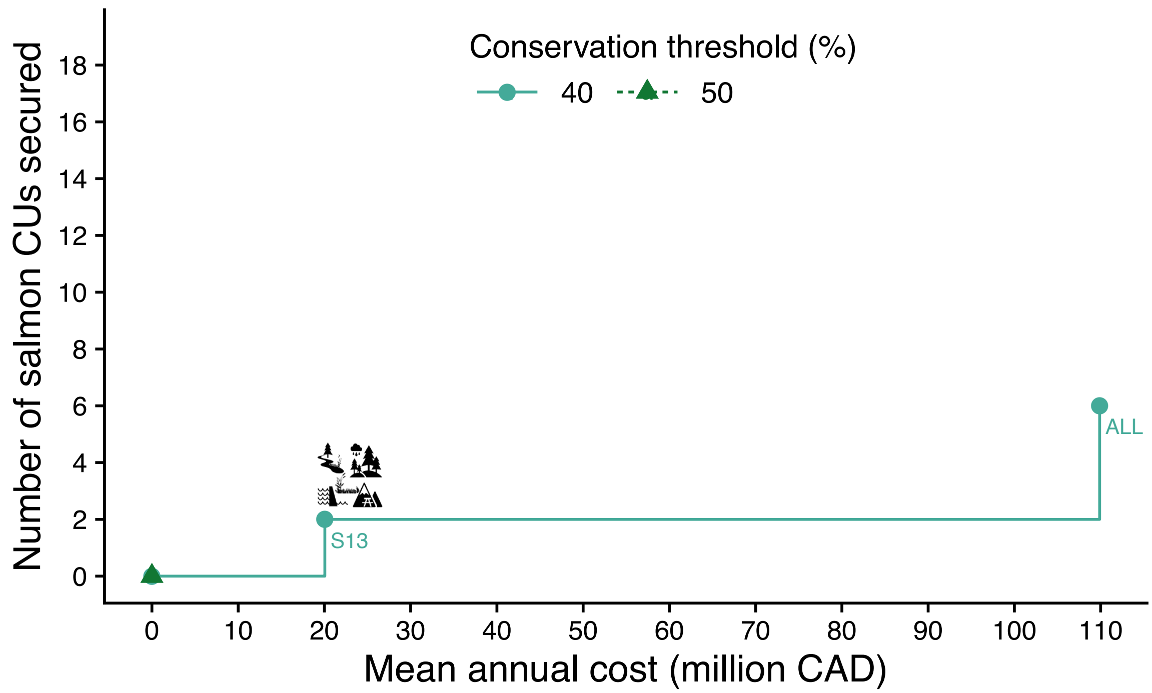



**Figure 4S4.** Pessimistic scenario showing the number of lower Fraser River salmon CUs predicted to achieve >40% chance of green status at the end of 25 years by implementing a given set of strategies. Note that the conservation threshold is reduced to 40% (turquoise line), and that no CUs achieved greater than 50% chance (dark green triangle).

In addition to assessing the widest range of outcomes of the complementarity analysis using the range of benefits estimates, we examined the effects of uncertainty in all estimates on the cost-effectiveness of each strategy. The results were reasonably robust to changes in costs, feasibility, and benefit estimates for each strategy. We tested the sensitivity of the cost-effectiveness ranking of each strategy across a sampled distribution bounded by +/- 30% change in costs (Fig. 4S5A, 4S6A), +/- 15% change in feasibility (Fig 4S5B, 4S6B), and across the range of lower, best, and upper benefit estimates given by the experts (Fig. 4S5C, 4S6C). We chose a 15% threshold for feasibility as this was slightly larger than the upper and lower quartiles of the range of estimates. For the benefit estimates we used the pessimistic, best, and optimistic estimates to bound the sampled distribution as they represent the full range of believable estimates identified by the experts.

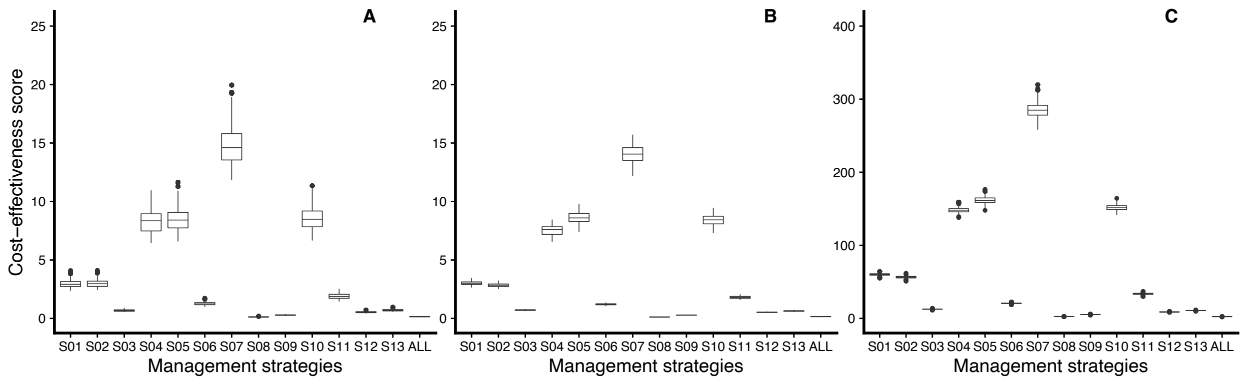



**Figure 4S5.** Sensitivity of cost-effectiveness scores for 14 strategies to fluctuations in A) cost by 30%, B) feasibility by 15%, and C) benefits from most pessimistic to most optimistic.

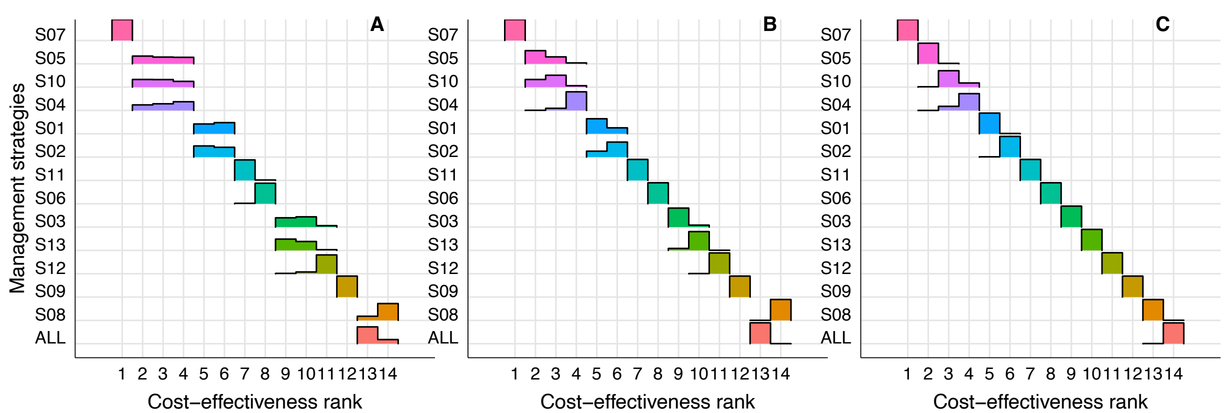



**Figure 4S6.** Sensitivity of cost-effectiveness ranks for 14 strategies to fluctuations in A) cost by 30%, B) feasibility by 15%, and C) benefits from most pessimistic to optimistic.

A few strategies showed sensitivity to changes in project costs, resulting in a spread of CE scores when repeatedly sampled (Fig. 4S5A). In particular, the CE scores of S04 and S05 (freshwater and estuarine habitat restoration, respectively) are close enough that when this uncertainty is considered, their CE ranks may switch (Fig. 4S6A). Implementing S04 brings twice as many CUs above the conservation threshold than S05 (6 vs. 3, respectively; Table 4.2) such that despite its higher cost, S04 is always selected in the complementarity analysis. Similarly, pairs S01 and S02 (fisheries management and hydrology protection) and S13 and S03 (all habitat strategies and protect habitat) may swap CE ranks with a change in project costs. However, these pairs are unlikely to result in different conservation decisions, based on the complementarity analysis (Table 4.2, Fig. 4.4). The CE scores for strategies 07 and 10 were highly variable in value, but not in relative value, such that this variation appears not to affect their CE rank.

The cost-effectiveness of each strategy was less impacted by fluctuations in feasibility estimates (Fig. 4S5B, 4S6B). We chose a sampled a variation of +/- 15% in order to capture changes within the realm of possibility (i.e., a maximum feasibility of slightly less than 100% and a minimum slightly less than 50%). Increasing this variation to 30% did not change the results, but simply exaggerated them. The same strategies that were sensitive to changes in cost were also sensitive to feasibility, but less so (Fig. 4S5B, 4S6B). Feasibility was largely similar across strategies (mean 69%, range 57-81%, Table 4S4).

Relative CE scores and ranks were least sensitive to changes in the benefit estimates for each strategy (Fig. 4S5C, 4S6C). While the scores did increase by more than an order of magnitude, they did so consistently across strategies such that the ranks remained unchanged. To assess the sensitivity of CE to changes in benefit estimates, we sampled a Monte Carlo distribution based on the pessimistic, best guess, and optimistic estimates given by the experts. While this does not equate to a confidence interval, it does reflect the space where experts believe the truth lies. In other words, sampling from this range produces estimates that are unlikely to surprise an expert. We also repeated the sensitivity analysis following the same methods as the costs above (sampling a range of +/- 30%) and found very similar results, with only strategies ALL and S08 showing any uncertainty in rank.

When only CE was assessed (i.e., ignoring complementarity of strategies and how many salmon CUs achieve the conservation threshold), the most cost-effective option was to implement invasive species management (S07, Table 4S4). However, this had the lowest expected benefit out of all available management strategies (expected benefit rank 14, Table 4S4), and would only bring two CUs above the 50% threshold (Table 4.2). This underscores the need to consider conservation thresholds and strategy complementarity when using CE (Chadés *et al.*, 2015).

While we ran the complementarity analysis for a select subset of scenarios (i.e., most pessimistic, best, and most optimistic benefits scenarios, two cost scenarios for pollution strategy S08), it would be ideal to derive a method to systematically perform this analysis for the full range of variation for each of the estimates, as we did for the cost-effectiveness scores and ranks. I imagine that this would entail coding a Monte-Carlo simulation into the analysis step for the ConsOpt package, which was beyond the capacity of myself and our team at the time of this study. While a change in estimated strategy costs of 30% may not affect the optimal strategy to invest in (i.e., the conservation decision), it would likely contribute to difficulties in obtaining or maintaining project funding and successful implementation. Similarly, while the likelihood of a CU achieving green status may only slightly fluctuate, the difference in realized outcome between a stable and productive salmon CU and one that remains in flux would have significant social and cultural ramifications. The PTM process is not currently set up to deal with these important caveats, though we recommend their consideration during project implementation and further emphasize the need for ongoing monitoring and adaptation over the project timeline. The results do support objectively informed decision making, which considers the full suite of available management alternatives, the best available estimates of benefits, costs, and feasibility, and the trade-offs between project objectives for these estimates.

**Table 4S4.** Cost-effectiveness data for management strategies collated for complementarity analysis. Benefit is the sum of benefit estimates for all CUs, averaged across experts, for each strategy. Total Cost is the Net Present Value for each strategy over 25 years. Feas. is strategy feasibility. CE is cost-effectiveness score (Benefit*Feasibility/Total Cost). CE rank: most (1) to least (14) cost-effective strategy. Expected Performance (EP) rank: highest (1) to lowest (14) performing strategy (Benefit*Feasibility). Cost rank: cheapest (1) to most costly (14) strategy.

| Strategy Name | Key | Benefit | Total Cost (million CAD, NPV) | Annual Cost (million CAD, NPV) | Feas. | CE | CE rank | EP rank | Cost rank |
|---|---|---|---|---|---|---|---|---|---|
| **Fisheries Management** | S01 | 266 | 62.7 | 2.5 | 0.70 | 2.97 | 6 *(7)* | 7 | 6 *(7)* |
| **Watershed Hydrology Protection & Management** | S02 | 228 | 51.9 | 2.1 | 0.68 | 3.00 | 5 *(6)* | 11 | 5 *(6)* |
| **Protect Habitat** | S03 | 267 | 250.9 | 10.0 | 0.64 | 0.68 | 10 *(11)* | 8 | 9 *(10)* |
| **Freshwater Habitat Restoration** | S04 | 297 | 25.6 | 1.0 | 0.69 | 8.05 | 4 *(5)* | 5 | 4 *(5)* |
| **Estuarine Habitat Restoration** | S05 | 219 | 18.1 | 0.72 | 0.70 | 8.42 | 2 *(3)* | 12 | 2 *(3)* |
| **Barrier Removal** | S06 | 264 | 154.9 | 6.2 | 0.73 | 1.25 | 8 *(9)* | 6 | 8 *(9)* |
| **Invasive Species Management** | S07 | 158 | 7.7 | 0.31 | 0.71 | 14.60 | 1 *(2)* | 14 | 1 *(2)* |
| **Pollution *(values with costs of facilities excluded)*** | S08 | 257 | 1,604.6 *(3.5)* | 64.2 *(0.14)* | 0.81 *(0.81)* | 0.13 *(58.77)* | 14 *(1)* | 4 *(4)* | 13 *(1)* |
| **Pathogens & Disease (Aquaculture)** | S09 | 228 | 461.3 | 18.5 | 0.57 | 0.28 | 12 *(14)* | 13 | 10 *(11)* |
| **Hatchery Operations** | S10 | 239 | 19.1 | 0.76 | 0.67 | 8.37 | 3 *(4)* | 10 | 3 *(4)* |
| **Predator Control & Management** | S11 | 238 | 90.6 | 3.6 | 0.70 | 1.84 | 7 *(8)* | 9 | 7 *(8)* |
| **Fisheries & Aquaculture & Hatchery Operations Combined** | S12 | 444 | 543.0 | 21.7 | 0.64 | 0.53 | 11 *(12)* | 3 | 12 *(13)* |
| **All Habitat Strategies Combined** | S13 | 509 | 501.3 | 20.1 | 0.69 | 0.70 | 9 *(10)* | 2 | 11 *(12)* |
| **All Strategies Combined *(values with costs of facilities excluded)*** | ALL | 591 | 2,747.1 *(1,146.1)* | 109.9 *(45.8)* | 0.69 *(0.69)* | 015 *(0.36)* | 13 *(13)* | 1 *(1)* | 14 *(14)* |

**Table 4S5.** Conservation optimization when ES2 Governance Solutions is implemented, showing the expected chance of each CU[1] achieving green status at the end of 25 years under each strategy (>49% light grey, >50% medium grey, >60% dark grey). Cut-off for threshold (and shading) applied prior to rounding. BSL: baseline; DEV BSL: development baseline scenario.

| Conservation Unit | BSL | DEV BSL | Strategy (sorted by annual cost, low to high) | | | | | | | | | | | | | ALL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | **S07** *Inva* | **S05** *Est* | **S10** *Hatc* | **S04** *Frsh* | **S02** *Hydr* | **S01** *Mgmt* | **S11** *Pred* | **S06** *Barr* | **S03** *Prot* | **S09** *Aqua* | **S13** *Hab* | **S12** *Mgt+* | **S08** *Poll* | |
| **Chinook** | | | | | | | | | | | | | | | | |
| Boundary Bay Fall 0.3 | 27 | 22 | 41 | 41 | 40 | 46 | 42 | 40 | 38 | 44 | 41 | 38 | 59 | 50 | 45 | 58 |
| Lower Fraser Fall 0.3 | 41 | 37 | 48 | 56 | 52 | 55 | 51 | 52 | 52 | 54 | 54 | 50 | 66 | 62 | 57 | 69 |
| Lower Fraser Spring 1.3 | 37 | 33 | 43 | 48 | 46 | 50 | 49 | 51 | 47 | 49 | 49 | 44 | 63 | 57 | 49 | 63 |
| Lower Fraser Summer 1.3 | 39 | 34 | 44 | 47 | 48 | 50 | 49 | 52 | 48 | 48 | 48 | 46 | 62 | 57 | 48 | 63 |
| Lower Fraser Upper Pitt Summer 1.3 | 28 | 24 | 32 | 37 | 38 | 42 | 39 | 39 | 39 | 38 | 37 | 35 | 54 | 47 | 38 | 56 |
| Maria Slough Summer 0.3 | 32 | 28 | 39 | 43 | 42 | 46 | 45 | 46 | 42 | 42 | 44 | 39 | 60 | 51 | 45 | 61 |
| **Chum** | | | | | | | | | | | | | | | | |
| Lower Fraser | 40 | 32 | 48 | 50 | 51 | 56 | 52 | 52 | 49 | 56 | 52 | 48 | 63 | 56 | 54 | 66 |
| **Coho** | | | | | | | | | | | | | | | | |
| Boundary Bay | 25 | 18 | 39 | 40 | 42 | 47 | 42 | 36 | 39 | 46 | 40 | 38 | 56 | 45 | 45 | 58 |
| Lower Fraser | 33 | 25 | 41 | 43 | 47 | 52 | 48 | 44 | 46 | 51 | 47 | 42 | 61 | 53 | 49 | 64 |
| Lillooet | 33 | 28 | 40 | 46 | 47 | 51 | 48 | 47 | 47 | 51 | 50 | 45 | 62 | 55 | 50 | 65 |
| **Pink** | | | | | | | | | | | | | | | | |
| Fraser River | 45 | 39 | 51 | 54 | 54 | 56 | 52 | 55 | 52 | 56 | 57 | 53 | 67 | 62 | 57 | 68 |
| **Sockeye** | | | | | | | | | | | | | | | | |
| Chilliwack Early Summer | 41 | 33 | 47 | 47 | 48 | 52 | 48 | 52 | 49 | 50 | 50 | 47 | 56 | 58 | 53 | 65 |
| Cultus Late | 14 | 11 | 21 | 18 | 20 | 24 | 20 | 25 | 20 | 20 | 21 | 18 | 28 | 27 | 26 | 33 |
| Harrison Down Late (Big Silver) | 42 | 33 | 47 | 47 | 49 | 53 | 50 | 53 | 51 | 51 | 52 | 49 | 59 | 56 | 51 | 64 |
| Harrison (River type) | 43 | 36 | 49 | 51 | 51 | 56 | 52 | 54 | 52 | 53 | 53 | 50 | 61 | 59 | 56 | 65 |
| Harrison Up Late (Weaver) | 26 | 23 | 32 | 33 | 35 | 39 | 36 | 41 | 35 | 38 | 37 | 35 | 47 | 45 | 38 | 53 |
| Lillooet/ Harrison Late (Birkenhead) | 31 | 26 | 37 | 39 | 41 | 43 | 38 | 42 | 42 | 43 | 41 | 39 | 49 | 49 | 43 | 55 |
| Pitt Early Summer | 45 | 37 | 52 | 55 | 55 | 55 | 53 | 54 | 56 | 54 | 54 | 56 | 65 | 61 | 59 | 68 |
| Widgeon (River type) | 23 | 17 | 29 | 30 | 29 | 31 | 28 | 32 | 29 | 30 | 30 | 29 | 38 | 37 | 34 | 43 |
| Feasibility | NA | NA | 0.88 | 0.82 | 0.84 | 0.87 | 0.86 | 0.83 | 0.79 | 0.87 | 0.80 | 0.69 | 0.84 | 0.79 | 0.97 | 0.84 |
| Annual Cost (million CAD) *(values with costs of facilities excluded)* | NA | NA | 0.31 | 0.72 | 0.76 | 1.02 | 2.08 | 2.51 | 3.62 | 6.19 | 10.0 | 18.5 | 20.1 | 21.7 | 64.2 *(0.14)* | 109.9 *(45.8)* |

[1]CU nomenclature uses unique geographic location and as needed, other distinguishing characteristics such as run timing, depending on the species. For Chinook salmon, which have the most detailed CU names, the format is 'geographic location - season of adult return - dominant age of returning adults' using the European age designation system (Koo, 1962), e.g., 'Lower Fraser - Fall - 0.3'.

**Wastewater Treatment Facility Upgrade Costs**

We analysed two cost scenarios for the pollution strategy. In the primary results, we included the full estimated costs (64M CAD per year) of completing proposed upgrades to the Annacis and Iona Island wastewater treatment facilities within the pollution strategy (S08). Cost was considered an important barrier to the implementation of these projects, which have been in various stages of planning for years. During the course of this study these projects have progressed: improvements to stability and secondary treatment capacity of the Annacis Island treatment plant are underway and the reconstruction and advancement to potential tertiary treatment of the Iona Island treatment plant is under public review with an anticipated completion date of 2030, with costs being managed by the municipality of Metro Vancouver (Metro Vancouver, 2021). Concerns remain that the goal of tertiary treatment at Iona may not be met by the current draft plans and these upgrades could be further delayed in this phase (Kwan, 2020).

We performed a second version of the optimization analysis with the capital costs of these upgrades removed, which significantly decreased the costs of both the pollution strategy (S08) and all strategies combined. Implementing all management strategies with these costs excluded still brought 16 of 19 lower Fraser CUs above a 50% chance of green status, but for a much lower cost of 45.4M CAD per year (Fig. 4S7, Table 4.2, Fig. 4.4). The next priority solution was identical to the primary results, with the combination of all habitat strategies (S13) bringing 14 of 19 CUs above the 50% threshold for an investment of 20M CAD per year (Fig. 4.4). After this point at lower budgets, the results diverged from those in the main text due to the high cost of the pollution strategy. Implementing freshwater restoration (S04) in combination with pollution control (S08) would bring 7 CUs above 50% chance of achieving green status for only 1.2M CAD annually, rendering fisheries management (S01) redundant (Fig. 4S7). This simplification of the results emphasizes the importance of pollution control for salmon CUs in the lower Fraser River, and the influence of these large infrastructure costs.

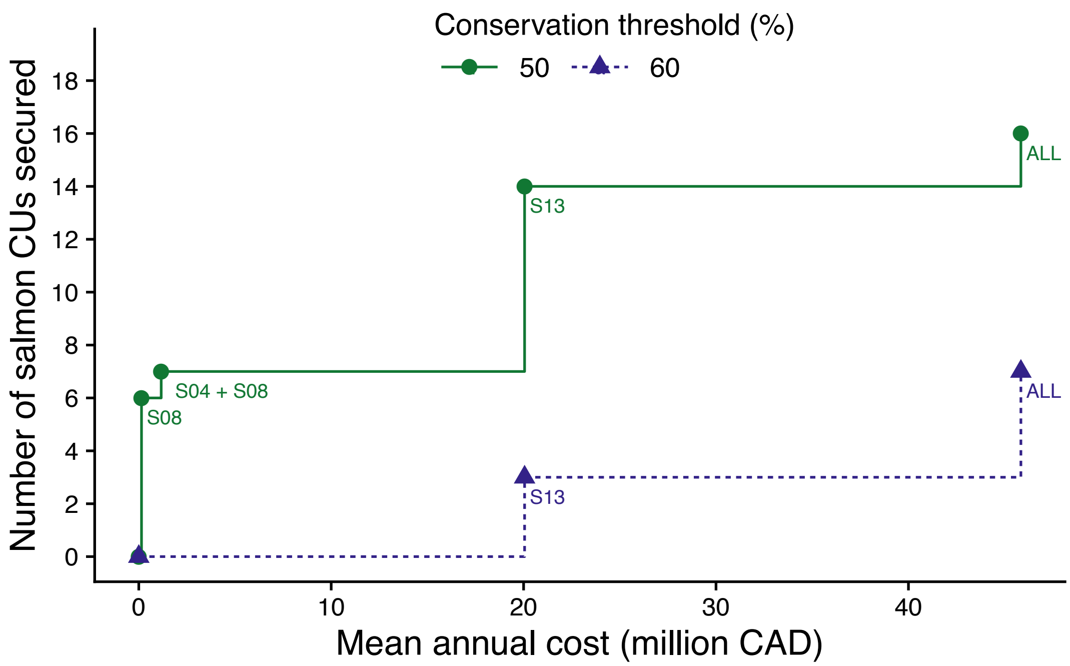



**Figure 4S7.** Wastewater treatment facility costs removed from analysis. The number of lower Fraser River salmon Conservation Units (CUs) that can achieve >50% (dark green line) or >60% (dark blue line) chance of green status by implementing the optimal set of complementary strategies for a given budget. Note that no CUs achieved >70% chance of green status.

When we exclude these facility costs from the analysis, pollution control becomes a priority strategy for wild salmon conservation in this region. Contaminants from wastewater and stormwater have been demonstrated to cause direct and indirect mortality of juvenile salmonids (Birtwell *et al.*, 1988; Sandahl *et al.*, 2007; Meador, 2014; Tian *et al.*, 2021), thus providing support for the high predicted benefit of the pollution control strategy for several salmon CUs in this study. New research in the lower Fraser has further elucidated the impacts of nutrient loading on coho salmon survival (Rosenfeld *et al.*, 2021). While this strategy captures several sources of pollution to the lower Fraser region, emerging contaminants are continuously being discovered (e.g., Tian et al., 2021), and further efforts will be needed to address these.

**Social Context for Implementation of the Study Results**

While a systematic change in current governance of salmon and their watersheds in the lower Fraser River is called for, inroads have been made and the political climate in this region supports further progress, such as implementation of the strategies identified in this study. The Wild Salmon Policy, developed in 2005 and with components of implementation underway, has an explicit goal to "restore and maintain healthy and diverse salmon populations and their habitats for the benefit and enjoyment of the people of Canada in perpetuity" (DFO, 2005), which inherently requires holistic management of these populations and their watersheds. Canada's Fisheries Act, which was once the strongest legislative tool to protect fish and fish habitat across the country, was stripped of much of its power in 2012 and has since been rebuilt in an attempt to return this power (https://www.dfo-mpo.gc.ca/pnw-ppe/policy-politique-eng.html), though implementation remains uncertain.

Both the Canadian federal government (https://www.canada.ca/en/services/environment/conservation/assessments/environmental-reviews/environmental-assessment-processes/cumulative-effects.html) and BC provincial government (https://www2.gov.bc.ca/gov/content/environment/natural-resource-stewardship/cumulative-effects-framework) are also currently embarking on the development of cumulative effects frameworks for environmental assessment processes. The provincial government has initiated a number of collaborative stewardship projects with groups of First Nations throughout the province, focusing on case-by-case design and implementation of co-governance frameworks for otherwise provincially regulated natural resources and their ecosystems (https://thestsa.ca/stsa-operations/csf/).

However, none of these existing projects or policies are currently effectively addressing the myriad threats for salmon throughout the province or the lower Fraser study region. While CU assessments under the Wild Salmon Policy have been initiated (and are perhaps most complete for the Fraser River watershed), recovery plans and actionable management strategies to achieve healthy and diverse salmon populations and their habitats remain undeveloped (Price *et al.*, 2017). We recommend the use of our findings, and similar structured decision-making processes, to expedite the implementation of these policies and provide actionable next steps in salmon recovery.

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