

**Science for community fisheries – population
assessment and climate impact monitoring for
Heiltsuk-led salmon stewardship**

by

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Abstract

Small scale fisheries support the livelihoods of more than 20 million people and provide food security for millions more around the world, yet science has been slow to embrace the challenge of managing these fisheries. Salmon are foundational for the ecosystems and economies of coastal British Columbia, supporting food, social and ceremonial (FSC) fisheries for 196 First Nations. Despite their cultural and ecological importance, and their vulnerability to ongoing anthropogenic change, we lack the data necessary for management and conservation of wild salmon in much of BC, particularly the remote north and central coast (NCC). Juvenile sockeye rear in lakes for one or two years, so population sizes are often limited by the size and productivity of rearing lakes. Using limnological data collected by Fisheries and Oceans Canada, we built a landscape model of sockeye lake productivity and predicted population capacity for 157 lakes on the NCC. We used these predictions of capacity as priors in a hierarchical-Bayesian stock-recruit model, to estimate productivity, capacity, and conservation benchmarks for 70 sockeye populations. Sockeye are particularly vulnerable to changes in climate, with elevated rates of pre-spawn mortality among migrating adult sockeye at high temperature. Working with the Heiltsuk First Nation, QCs Projects Society, and the Hakai Institute, we established a community-based population monitoring program using a traditional-style salmon weir to capture and tag fish for mark-recapture and telemetry-based estimates of annual population size and temperature-mediated mortality among migrating adult sockeye in the Koeeye River. We found rapid declines in survival to spawning when temperatures exceeded 15 °C. Furthermore, river entry measured by the number of fish tagged each day, ceased when the river level dropped below 0.4 m. When water levels are low, migrating sockeye may experience prolonged delays in marine waters, increasing vulnerability to fisheries and predators. Climate impacts on coastal sockeye may therefore be driven by the dual effects of warming temperature and low-water delays. This work will support the development of a Heiltsuk sockeye management plan, establishing management goals and conservation strategies across a territory spanning 15,000 km² and more than 20 sockeye populations on the NCC.

Keywords: Salmon; Community-based Management; Traditional Management Systems; Stock assessment; *Oncorhynchus nerka*; Wild Salmon Policy

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Chapter 1. Introduction

Ecosystem structure, species distributions and population dynamics are shaped by physical and biological processes spanning multiple spatial and temporal scales (Levin 1992; Rogers and Schindler 2011). These hierarchical drivers of ecosystem dynamics create challenges for understanding and managing ecosystems and conserving species (Poiani et al. 2000 Ruckleshaus et al. 2008), particularly among migratory animals (Lascelles et al. 2014). In an era of rapid anthropogenic change and limited resources for natural resource stewardship, scientific research and ecosystem monitoring that illuminate ecological drivers across scales are essential for conservation and management. Despite the accelerating pace of global biodiversity loss, accurate or recent data is lacking for many species of cultural or ecological importance (Ricard et al. 2012). In the absence of this data we lack essential information to inform decision making, hindering conservation and management of ecosystems, and undermining social-ecological systems supporting livelihoods and food security for billions of people around the globe (e.g. Costello et al. 2012). In light of these challenges, there is a critical need for investments in monitoring to support management, planning and adaptation (Schindler and Hilborn 2015). There is also a need for the development and application of theory and tools to take advantage of patchy or disparate data on ecosystems and species and support conservation. Therefore, research that leverages knowledge of the common constraints and drivers of ecosystem dynamics and species demography can provide a path towards rigorous scientific understanding for conservation and resource management (Myers and Mertz 1998; Soranno et al. 2010; Kindsvater et al. 2018)

Salmon in the Pacific Northwest of North America are an iconic and foundational component of coastal ecosystems and cultures. With freshwater spawning and rearing, and multi-year oceanic migrations spanning thousands of miles, salmon populations integrate environmental drivers across multiple hierarchical scales (Pyper et al. 2005; Rogers and Schindler 2011). In British Columbia, Canada, five species of anadromous Pacific Salmon from hundreds of populations (Holtby and Ciruna 2007) support subsistence fisheries for at least 196 First Nations (Chan et al. 2011) and contribute more than \$1 billion annually to provincial GDP (BC Wild Salmon Advisory Council 2018). In recent years, many populations of wild salmon have experienced declines in

productivity (e.g. Peterman and Dorner 2012). These declines in abundance and productivity have led to fisheries closures with severe negative consequences for salmon-dependent communities (Walters et al. 2019; Connors et al. *in review*). Despite the importance of salmon for the prosperity and food security of coastal communities and widespread concern over population declines, reduced government investment in monitoring and assessment have undermined management and conservation for many stocks, particularly in remote areas of coastal BC (Price et al. 2008). Thus, there is a critical need for scientific research that draws upon existing datasets to provide understanding of the status and drivers of salmon populations, as well as on the ground research that builds new capacity for salmon stewardship through novel community partnerships.

Indigenous people manage and hold ancestral rights to more than 40% of earth's ecologically intact landscapes (Garnett et al. 2018), and First Nations in Canada play a large and growing role in the management of lands and natural resources (Ban et al. 2018). Prior to colonization, traditional management systems guided by generations of local knowledge supported vibrant salmon fishing economies and resilient social-ecological systems for millennia (Haggan et al. 2006; Campbell and Butler 2010). The arrival of European colonists to Western North America in the 19th century displaced Indigenous management systems, and fundamentally reshaped First Nations people's rights and modes of access to salmon (Newell 1993, Harris 2001). However, in a landmark ruling in the case of *R. v. Sparrow* (1990) Canada's Supreme Court recognized the unextinguished ancestral rights of Indigenous people to fish for salmon. This decision and others that followed (e.g. Gladstone, Delgamuuk, and Tsilhqot'in) have affirmed the legal authority of First Nations as co-managers of lands and natural resources, including fisheries.

The Heiltsuk Nation on British Columbia's central coast, hold ancestral title to more than 15,000 square kilometers, encompassing hundreds of watersheds and locally adapted salmon populations. Salmon have supported the Heiltsuk people since time before memory, and remain a vital for Heiltsuk livelihoods, food security, and cultural wellbeing (Jones 2000, Brown and Brown 2009). Sockeye salmon are among the most important traditional foods consumed by First Nations people in coastal British Columbia (Marushka et al. 2019). Nonetheless, decades of declining federal budgets for wild salmon management and the remote nature of watersheds within Heiltsuk territory have

led to a lack of basic population monitoring among sockeye salmon populations that support Food, Social and Ceremonial (FSC) fisheries. Beginning in 2012 we launched a collaborative research initiative with the Heiltsuk Integrated Resource Management Department (HIRMD), Qqs Projects Society, and the Hakai Institute, to improve annual population monitoring and evaluate current factors limiting the survival of sockeye salmon in the watersheds of the north and central coast (NCC).

There is increasing recognition that many First Nations management systems promoted adaptive management through the generation and transmission of knowledge related to culturally important resources (Berkes et al. 2000). Salmon weirs and fish traps were a ubiquitous part of pre-colonial fisheries management and have been documented by archaeologists and cultural historians from California to Alaska (Swezy and Heizer 1977; Moss and Erlandson 1998; White 2011). These methods which operated in the river or at the river mouth offer several advantages over current salmon harvesting methods, since they avoid the conservation risks associated with mixed-stock fisheries (e.g. Walters et al. 2008). Furthermore, by operating a weir or trap traditional managers could qualitatively evaluate salmon abundance in-season and set harvest rates accordingly. Despite the proven success of these traditional salmon management systems, they were banned by the colonial government in the late 19th century. By 2012 when our project began, there was no living memory of weir building among the Heiltsuk Nation. We therefore set out to revive the practice of weir building as a tool for population monitoring and salmon harvesting. By coupling this time-tested traditional management system with scientific mark-recapture and radio frequency identification (RFID) telemetry, we produced annual estimates of sockeye abundance and survival during spawning migrations and built long-term capacity for Heiltsuk cultural stewardship of salmon through training and education.

There are at least 120 populations of lake-rearing sockeye on the NCC, including more than 20 in Heiltsuk traditional territory. Given limited capacity and budgets for local monitoring, we set out to compile and analyze the existing data on these populations, to evaluate their potential carrying capacity and provide preliminary estimates of conservation status. Since sockeye population sizes are often limited by lake size and productivity (Juday 1932; Shortreed et al. 2001), we compiled data on the physical and biological conditions in lake rearing environments. For lakes lacking limnological assessment, we developed a model to predict lake productivity based on a suite of

landscape and lake level variables. We then linked these estimates of lake productivity with timeseries of spawner abundance and recruitment for 70 sockeye populations in a hierarchical-Bayesian model, using estimates of lake capacity derived from limnological models as prior information on carrying capacity in a stock-recruit framework. By leveraging these two data sources we estimated stock-recruit parameters, conservation benchmarks, and stock status for each of these 70 populations, with varying degrees of uncertainty. In almost all cases, the inclusion of limnologically-based lake capacity priors improved model fits, highlighting the value of combining inference from multiple data sources for populations in data-limited landscapes.

Together, the chapters of this thesis constitute the scientific foundation for the development of a Heiltsuk sockeye management plan, supporting local management of salmon fisheries. As communities grapple with rapid environmental change, robust population monitoring, and data-driven management are essential components of sustainable and resilient fisheries. By co-creating research with both HIRMD and DFO we have contributed significant new understanding of sockeye salmon populations on the NCC, information needed for co-management of salmon populations under the Wild Salmon Policy.

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Chapter 2. Ancient fish weir technology for modern stewardship: lessons from community-based salmon monitoring

William I. Atlas, William G. Housty, Audrey Béliveau, Bryant DeRoy, Grant Callegari, Mike Reid, and Jonathan W. Moore

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2.1. Abstract

The UN Declaration on the Rights of Indigenous Peoples states that indigenous people have a fundamental right to contribute to the management of the resources that support their livelihoods. Salmon are vital to the economy and culture of First Nations in coastal British Columbia, Canada. In this region, traditional systems of management including weirs – fences built across rivers to selectively harvest salmon – supported sustainable fisheries for millennia. In the late-19th century traditional fishing practices were banned as colonial governments consolidated control over salmon. In collaboration with the Heiltsuk First Nation we revived the practice of weir building in the Koeye River. Over the first four years of the project we tagged 1,226 sockeye, and counted 8,036 fish during fall stream walks. We used a mark-recapture model which accounted for both pre-spawn mortality due to variation in temperature, and tag loss, to produce the first mark-resight estimates of sockeye abundance in the watershed (4,600 – 15,000 escapement). High river temperatures are associated with increased en route mortality in migrating adult sockeye. We estimated pre-spawn mortality ranged from 8 – 72% across the four years of study, highlighting the degree to which climate conditions may dictate future viability in sockeye salmon populations. These results demonstrate the power of fusing traditional knowledge and management systems with contemporary scientific approaches in developing local monitoring.

2.2. Introduction

Globally, more than 20 million people - nearly 50% of all fishers - work in small-scale fisheries (Teh and Sumaila 2011), and these fisheries play a key role in poverty alleviation and food security (FAO 2005). Despite their importance for the well-being of coastal communities, science has been slow in developing management and monitoring strategies catered to these smaller-scale fisheries, focusing instead on large, economically valuable fisheries which dominate global catch (Andrew et al. 2007). Most fisheries management is data intensive, depending on centralized data collection and management, which are costly and ill-suited for small-scale or subsistence fisheries (Berkes 2003). In the absence of evaluation and management, many small-scale fisheries around the globe are depressed due to overfishing, limiting their ability to provide benefits to fisheries dependent communities (Costello et al. 2012). There is a critical need for the development of management approaches which recognize the interdisciplinary complexity of managing small-scale fisheries, building capacity for locally responsive management that does not hinge on centralized management authority and stock-assessment expertise (Berkes 2003, Andrew et al. 2007).

Traditional ecological knowledge and resilient systems of local management have been essential to the survival of aboriginal societies (Johannes 1978, Troster 2002, Groesbeck et al. 2014), however local management ethics and practices have been undermined by colonial governments and the influence of globalization (Johannes 1978, Harris 2001). Further, the loss of traditional management systems and fishing practices can lead to social-ecological traps, whereby ecosystems and social institutions undergo lasting shifts towards conditions that provide fewer sustainable benefits to communities (Cinner 2011). In recent times, there has been increasing focus on the benefits of local management and conservation; strengthening local management and monitoring capacity are essential prerequisites to management at the local level (Berkes 2003, Garcia and Lescuyer 2008). While scientists and conservation policy makers increasingly recognize the importance of engaging local communities in monitoring initiatives (Adams et al. 2014), efforts at local monitoring and management have met with mixed success (Garcia and Lescuyer 2008). This is particularly true when programs are prescriptive in nature and do not adequately involve community members in development and planning (Adams et al. 2014). Thus, successful local monitoring should

be developed in close partnership with community members, be rooted in existing traditions of management, include a strong education and outreach component, and work to build capacity for ongoing monitoring and implementation.

In British Columbia, Canada, First Nations people have harvested salmon for millennia and fisheries remain a backbone of local economies and culture. Prior to the colonial period, indigenous communities developed highly successful management based on traditional laws and practices (Harris 2001, Trospen 2002). In much of British Columbia, these systems of management persisted into the 19th century until colonial governments passed laws to prohibit First Nations fisheries and consolidate control of salmon resources (Newell 1993, Harris 2001). In recent years, there has been growing legal and societal recognition of the rights and title of First Nations over the lands within their traditional territories. In 1990, a unanimous decision by the Supreme Court of Canada in the case of *Regina v. Sparrow* ruled that Section 35(1) of the constitution act guaranteed the right of aboriginals to fish, and a series of legal decisions have subsequently strengthened aboriginal title and rights. On a global scale, the UN Declaration on the Rights of Indigenous Peoples (2007) affirms the rights of indigenous peoples to co-manage their natural resources. While co-management remains a work in progress (e.g. Natcher and Davis 2007), First Nations are working to build management capacity and conduct stewardship that reflects the needs and interests of their communities. There is therefore a critical need for research and monitoring that builds capacity and supports management that fosters long-term sustainability of food, social and ceremonial (FSC) fisheries.

Fish weirs were used for thousands of years among First Nations in the Pacific Northwest, as a means of selectively harvesting returning salmon (Moss and Erlandson 1998). Stone fish traps were also commonly used as recently as the 1950's and remain partially intact in many locations throughout the Central Coast of British Columbia (White 2011). Both technologies provided a foundation for adaptive management, as fishers could evaluate the strength of salmon returns and adjust harvest accordingly (Harris 2001). However, the use of fish weirs and traps was discouraged and ultimately banned during the late 19th century, as the colonial government sought to promote and develop the commercial fishing sector (Newell 1993, Harris 2001). Weirs are still routinely used for population monitoring and management, allowing biologists to count or tag fish as a means of abundance estimation. However, these monitoring efforts typically occur in

isolation from the socio-cultural context in which they evolved. Despite their historic importance and potential as contemporary fishing and management tools, traditional weirs are rarely used in First Nations fisheries or their management.

In 2013 we launched a collaborative initiative to revive traditional-style weir building at the Koeye River, on the Central Coast of British Columbia. The project is a collaboration between the Heiltsuk Nation, NGOs and academics, providing a means of enumerating returning sockeye salmon (*Oncorhynchus nerka*). It also has a strong community engagement and educational focus. The goals of the project were to: (1) revitalize weir building within the Heiltsuk community of Bella Bella, (2) build long-term capacity for the stewardship of salmon resources within Heiltsuk Nation through training, education and community outreach, and (3) develop a simple Bayesian mark-recapture method to produce estimates of population abundance that can inform local management. Here we present our methods and findings from four years of operating a traditional-style weir, providing information on the techniques, materials and best practices associated with weir construction and operation. We hope these experiences and insights can inform community-led salmon stewardship around the region, and inspire other culturally relevant monitoring initiatives which empower local communities in managing natural resources.

2.3. Methods

Weir construction – techniques and considerations

Weir design was based on images and archaeological evidence from traditional salmon weirs (Figure 2.1) (e.g. Prince 2005, Stewart 2008). Built from a combination of locally harvested materials and modern building supplies, the basic design involves the construction of tripods which support a series of fence panels spanning the river, forming a barrier to the upstream movement of salmon. Fish are then forced to swim into an aluminum trap box, fitted with one-way trigger trap fingers from Neptune Marine Products. Traditional weirs were built from a variety of materials, including cedar, alder and willow (Harris 2001). The Koeye River weir was built entirely from cedar because of its rot resistance, availability in the area, and the ease with which it splits (video S1). In total the construction of the weir and associated tagging equipment cost approximately \$8,500 CAD. This simple design draws on the simplicity of ancient weir designs, using

cost effective, locally sourced materials as well as affordable and widely available materials, making it attractive for communities seeking to monitor or harvest wild salmon.

Weir operation

The weir is installed each year on June 1st and operates until late-July. Fish are anesthetized with MS-222 (0.1 g/L), and tagged with colored t-bar anchor tags from FLOY tag & MFG (Figure 2.2). Tags are inserted behind the dorsal fin on both sides, allowing resighting and estimates of tag loss. Fish are then passed upstream of the weir to continue migrating to Koeye Lake, where they hold until spawning begins in mid-September. Unique tag colors are used for each week, creating color groups that can be identified visually during counts. Spawning fish are counted during regular fall visits to the tributaries of Koeye Lake. Live sockeye are counted and all tagged and untagged fish are recorded for mark-resight estimates.

Mark-resight model

Sockeye abundance is estimated from peak fall counts of live fish in the tributaries of Koeye Lake, using a Bayesian adaptation of the pooled-Petersen estimator (Chapman 1951) that incorporates tag loss and the effect of daily variation in river temperature on pre-spawn mortality of tagged fish. Daily mean and maximum temperature values were monitored at a station in the lower Koeye River using Hobo Pendant temperature loggers from Onset Computer. Annual temperature summary data (Table 1) reflect the weighted annual mean of daily peak temperatures during the sockeye migration, weighted by the number of fish tagged on a given day. We assume (1) that all live fish in the tributaries of Koeye Lake have an equal probability of being counted, (2) a closed population and (3) that all fish have the same probability of losing a tag and the loss of each tag is independent. These assumptions are likely robust in our study system where fish migrate quickly through the lower river, then hold and mix in the lake for several months prior to spawning.

R_i is the number of fish tagged at the weir on day i . The number of fish tagged on day i surviving to the spawning ground (n_i^t) is modeled using:

$$n_i^t | R_i, \theta_i \sim \text{Binomial}(R_i, \phi_i),$$

where ϕ_i is the individual probability for tagged fish to survive to the spawning grounds. Temperatures in the lower Koeye River regularly exceed 20°C during June and July, and the link between warm temperatures and pre-spawn mortality for sockeye salmon is well-established (e.g. Crozier et al. 2011). Lacking information on the survival of individual fish tagged within the Koeye River, we modeled the effect of temperature on pre-spawn mortality based on other sockeye salmon populations (Crozier et al. 2011), using the logistic function:

$$\phi_i|a, b, T_{50} = \frac{a}{1 + e^{-b(Tmax_i - T_{50})}}$$

where $Tmax_i$ is the maximum temperature on day i ; a , b and T_{50} are parameters that are given normally distributed prior distributions with mean and variance values obtained from Crozier et al. 2011 (Figure 2.3). For a , the maximum rate of en route survival, the mean was set to 0.9 with a standard deviation of 0.015. For b , the rate at which survival declines with temperature, the mean was set to -1.78 with a standard deviation of 0.38. Finally, for T_{50} , the temperature at which 50% of fish die before spawning was set at 19.25 °C with a standard deviation of 0.09.

To account for potential tag loss, we tagged each fish twice - once on each side of the dorsal muscle - and modeled the total number of tagged fish surviving to the spawning grounds as $N^t = \sum_{i=1}^K n_i^t$, with an unknown number of them making it with two tags, one tag or no tags. We denote those quantities by $N^{t,2}$, $N^{t,1}$, and $N^{t,0}$ respectively, and modeled their distribution as:

$$(N^{t,0}, N^{t,1}, N^{t,2}) \sim \text{Multinomial}(N^t; (\theta^2, \theta, 1 - \theta^2 - \theta)'),$$

where θ is the probability of losing one tag, and the loss of each tag is independent. We used a vague uniform(0,1) prior distribution on θ .

The count of tagged fish with two tags, $Y^{t,2}$, and the count of tagged fish with one tag, $Y^{t,1}$, are modeled using binomial distributions:

$$Y^{t,2}|N^{t,2}, p \sim \text{Binomial}(N^{t,2}, p);$$

$$Y^{t,1}|N^{t,1}, p \sim \text{Binomial}(N^{t,1}, p),$$

where p represents the individual probability of a fish being detected during the fall counts. A vague uniform(0,1) prior distribution is used on the parameter p .

The count of untagged fish, Y^u , is modeled using a binomial distribution based on the unknown total number of untagged fish surviving to the spawning grounds, N^u , as well as the unknown number of tagged fish that lost both of their tags, $N^{t,0}$:

$$Y^u | E, N^u, N^{t,0}, p \sim \text{Binomial}(N^u + N^{t,0}, p).$$

We express the quantity N^u as $N^u = E - N^t$, where E is the unknown total spawner escapement, for which we use a vague normally distributed prior distribution, truncated above 0 and rounded to the nearest integer, with a mean of 5,000 and a standard deviation of 50,000. For all mark-recapture parameters the use of vague priors limits the degree to which prior information influences model estimates.

Our Bayesian analysis was implemented using R and JAGS software. Three chains were run for 100,000 iterations with a burn-in period of 5,000 iterations. Convergence of the algorithm was assessed using traceplots. Parameter estimates were taken as the mean of the marginal posterior distributions and 95% quantile-based credible intervals.

2.4. Progress and Perspectives

Over the four years of the study, we tagged between 193 and 562 sockeye per year, enabling annual mark-resight estimates of population abundances (Table 2.1). However, high flows and tides occasionally provided windows for unimpeded passage. In 2015 we adopted the practice of opening the weir on a regular basis, minimizing unnatural delays and reducing the risk of pre-spawn mortality from warm water temperatures and handling. Prior to opening the weir, we conducted seine sets in the pool downstream, leading to increased capture rates and tagging success. In 2016 we again opened the weir regularly, the weir was damaged on July 3rd by a bankfull flow event, bringing the season to an early end. However, prior to the end of the 2016 weir season we tagged 193 adult sockeye.

Fall counts in the two tributaries of Koeys Lake during late-September and early-October yielded a mean of 2,678 sockeye, with an average proportion of tagged fish

resighted of 22% across the four years of study. Estimates of spawner escapement varied across years, with a low of 4,671 (CI 3,756 – 5,793) in 2015, and a high of 15,275 (CI 11,460 – 20,528) in 2016. Estimated temperature-mediated pre-spawn mortality varied considerably across years owing to a high degree of variability in June and July water temperatures. In 2015, the warmest year during the study period, the predicted rate of pre-spawn mortality for tagged sockeye was 72% (CI 67 – 77%). Contrasting with this high mortality was 2016, when temperatures remained cool throughout the migration season and estimated mortality was only 8% (CI 3 – 14%) (Table 2.1). High water and anomalously high densities of spawning pink salmon in the fall of 2014 made it impossible to count and resight tagged sockeye in the tributaries of Koeye Lake. Consequently, run size for that year is unknown.

Working with the Heiltsuk Nation and QQs Projects Society – a community driven NGO – the project has built capacity in the Heiltsuk community of Bella Bella, employing and training 10 technicians over the first four years of the project. The learning and professional development of these individuals over four years provides a foundation for the ongoing success of Heiltsuk-led resource stewardship efforts, and many who have moved on to other employment remain in natural resource management jobs. The weir has also supported educational outreach. We work closely with the Bella Bella community school, and have hosted 12 field trips bringing close to 200 students to the weir, to learn about Heiltsuk cultural practices related to harvesting and stewardship of salmon. Campers at QQs' Koeye summer camp also make regular visits to the weir.

2.5. Conclusions

The Koeye River weir has revitalized the practice of weir building in the Heiltsuk community of Bella Bella. The well-being of First Nations communities is inextricably linked to the land and resources which have sustained them for millennia. By building capacity for the stewardship of Food Social and Ceremonial (FSC) sockeye fisheries, and creating an opportunity for education and outreach, the weir is contributing to ongoing cultural and social revival among the Heiltsuk. By fusing a traditional management system with contemporary quantitative approaches to population monitoring, the weir and associated fall counts have produced rigorous estimates of sockeye salmon abundance. The model accounts for annual variability in temperature mediated survival and tag loss, and expands count data collected during the fall

spawning period to an estimate of sockeye escapement. The resulting estimates of population size range from 4,600 – 15,000 across the four-year period of study, with up to 70% pre-spawn mortality for tagged fish in the warmest year. Historical data on water temperature is lacking, however the summer of 2015 was among the hottest and driest on record for the BC Coast (Anslow 2016), suggesting warm water temperatures and elevated risk of pre-spawn mortality may become more regular occurrences under future climate conditions. These data provide a foundation for understanding the status of salmon in the Koeve River system, and the potential for climate driven changes in the survival and productivity of sockeye salmon. Overall, sockeye salmon in the Koeve River appear to be stable and remain capable of supporting sustainable FSC fisheries. Ongoing tagging and enumeration will provide greater insight into the effects of climate on survival, and facilitate estimates of population productivity and carrying capacity, allowing the Heiltsuk to set escapement targets that limit the risk of overfishing under current and future climate conditions.

Fishing remains a vital part of the economy and culture of British Columbia's coastal First Nations. However, centralized and data-intensive scientific approaches to fisheries management will be insufficient for the management of small-scale fisheries if programs fail to build local capacity through employment and training, and are not rooted in local knowledge and values (Berkes 2003). The fusion of traditional and local knowledge with scientifically rigorous monitoring and management provides a promising avenue towards sustainable fisheries. Efforts to promote and develop community-driven management and traditional approaches to resource stewardship have shown promise in increasing abundance of economically important species (Groesbeck et al. 2014, Frid et al. 2016), and can bolster the sustainability of fisheries (Aswani and Hamilton 2004, Defeo et al. 2014). Hybrid management systems which integrate local knowledge with science may also be effective tools for helping communities avoid or escape social-ecological traps (Aswani et al. 2007). Salmon weirs have been used for at least 5,000 years as an effective means of selective harvest and management (Moss and Erlandson 1998). Our findings highlight the utility and feasibility of using traditional-style salmon weirs for some monitoring applications, particularly in smaller rivers with relatively stable hydrographs. These approaches may be particularly valuable in instances where cultural and educational objectives of local communities overlap with the goal of enumerating adult salmon.

Academics and government scientists are increasingly forging meaningful partnerships with indigenous communities, and the reciprocal exchange of knowledge and ideas should be at the foundation of these collaborations (Adams et al. 2014). First Nations across Canada are asserting their rights as stewards of their traditional territories, and given the well documented erosion of government monitoring and legal frameworks for habitat protection (Price et al. 2008, Hutchings and Post 2013), these communities will play a major role in shaping the future of lands and natural resources. While this shift in power back towards long-marginalized indigenous communities marks a major milestone in Canada's journey towards a more equitable relationship with First Nations, there is a critical need for scientific collaborations with local communities, supporting resource management and informed decision making. We hope that the Koeye River weir can provide a template for other communities seeking to understand and manage salmon populations, and serve as a powerful example of the creative approaches to resource monitoring and stewardship which can arise from collaborations between First Nations communities and academic scientists.

2.6. Acknowledgements

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2.8. Tables

Table 2.1. Number of fish tagged at the weir for all years of the study, average annual temperature weighted by the daily number of fish tagged, with estimates of the number surviving to spawn, the total spawning ground counts and number of fish resighted, as well as the resulting spawner estimate. For estimated survival and abundance, we report mean estimates and 95% credible intervals from the Bayesian mark-recapture model.

Year	Tagged	Temp. (C°)	Survival est.	Count / recap	Spawner est.
2013	233	17.5	158 (CI 146 - 170)	2149 / 71	4,685 (CI 3,877 - 5,690)
2014	242	16.3	195 (CI 183 - 208)	NA	NA
2015	562	20.3	158 (CI 131 - 186)	2769 / 91	4,671 (CI 3,756 - 5,793)
2016	193	15.4	177 (CI 166 - 187)	3118 / 36	15,275 (CI 11,460 - 20,528)

2.9. Figures

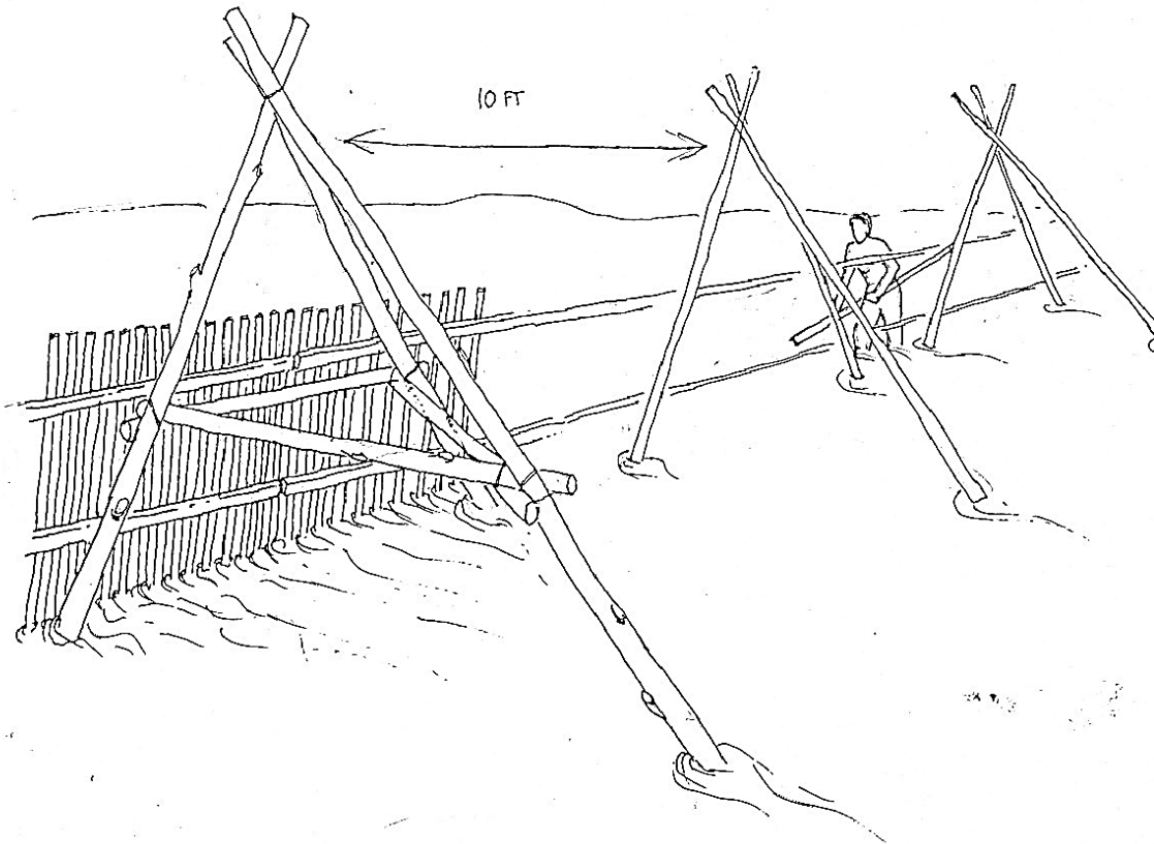


Figure 2.1 Original drawings of the design for the Koeve River weir. Sketches were based on historical images of fish weirs from around the Pacific Northwest.

Note: Courtesy of G. Callegari.



Figure 2.2 (a) Heiltsuk weir technician Richard Wilson-Hall releases a tagged sockeye. (b) The Koeye River weir pictured during June of 2015. The weir is built entirely from locally sourced materials and readily available construction supplies.
Courtesy of B. DeRoy.

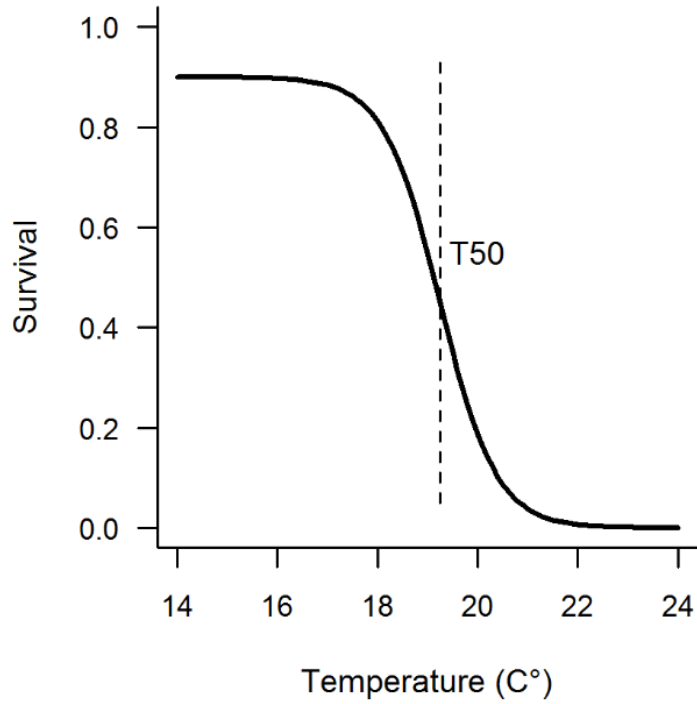


Figure 2.3 The logistic survival function relating maximum daily river temperature to survival of migrating adult sockeye salmon. The dashed line indicates the T50 value – temperature at which 50% of migrating adults die prior to spawning – and was set to 19.25 C° based on Crozier et al. 2011.

Chapter 3. Thermal sensitivity and low-flow-mediated migratory delays drive climate risk for a coastal sockeye salmon (*Oncorhynchus nerka*) population.

William I. Atlas, Karl Seitz, Ben Millard-Martin, William G. Housty, Dani Ramos, Mike Reid, and Jonathan W. Moore

3.1. Abstract

Anthropogenic climate change is subjecting aquatic species to temperature and hydrologic conditions unprecedented in their evolutionary history. Predicting and managing for species persistence under climate change requires understanding the effects of temperature on individual survival and population viability. Climate warming is having well documented effects on the survival and productivity of anadromous Pacific salmon (*Oncorhynchus* spp.) and may threaten some populations with extinction if evolution in phenology or thermal tolerance cannot keep pace. By tagging individuals and tracking their fate from river entry to spawning, we estimated the effects of temperature and river flow on survival and migration behavior in a population of sockeye salmon (*Oncorhynchus nerka*) in the Koeye River, on the central coast of British Columbia. Survival declined rapidly when temperature surpassed 15 °C, with 50% estimated mortality among tagged individuals at 17.4 °C. River level (gauge height) did not have a discernable effect on survival during spawning migrations, however river entry among adult sockeye ceased when river flows dropped. Our results suggest that temperature-mediated mortality and migration delays resulting from low water may act synergistically to depress survival among adult sockeye salmon returning to coastal watersheds, with increasing risk to populations as climate warming drives elevated summer air temperatures and prolonged drought.

3.2. Introduction

Variation in climate is a key determinant of species distributions (Parmesan and Yohe 2003, Perry et al. 2005), population productivity (Gjerdrum et al. 2003), age structure (Carlson and Quinn 2007), and rates of individual growth and survival (Ludwig et al. 2006, Martins et al. 2012). Migratory animals link climate variability spanning vast distances, traversing seasonal gradients across diverse habitats to link feeding areas with productive breeding grounds. Given their reliance on these varied and distant habitats, and the energetic demands of migration (Dingle 1996), migratory species may be especially vulnerable to climate change (Robinson et al. 2009). Timing of migration, breeding, and other critical life-history events has evolved to match climate conditions that maximize the survival and fitness of individuals (Cushing 1990, Bradshaw and Holzapfel 2008). Given the paramount role of climate in survival among migratory species and the rapid ongoing progression of anthropogenic climate change (IPCC 2013), understanding environmental drivers of migration and survival is foundational for conservation and management of these species.

In the coastal ecosystems of the Pacific Northwest of North America, anthropogenic warming is predicted to increase air temperatures and reduce precipitation during the summer and early fall months, altering water temperatures and flow during the freshwater phase of Pacific salmon (*Oncorhynchus* sp.) spawning migrations (Murdock et al. 2011, Isaak et al. 2018). Climate warming has the potential to undermine the long-term viability of cold-water fish populations such as salmon (Isaak et al. 2010). In well-studied systems such as the Fraser River, research has documented increased en route mortality of salmon during their annual spawning migration in response to climatic warming (Martins et al. 2011). Water temperature and hydrology play a key role in the phenology of summer and fall spawning migrations (Beechie et al. 2006, Lisi et al. 2013), and changes in river temperature and flow may have profound effects on behavior and survival of anadromous salmon during these migrations (Crossin et al. 2008). Populations are adapted to the prevailing temperature and flow conditions within their natal watersheds (Hodgson and Quinn 2002, Eliason et al. 2011). However, climate change has already increased water temperatures in many systems, pushing species to the limits of their thermal tolerances, and driving shifts in migratory phenology (Kovach et al. 2013). Thus, there is a critical need to evaluate the behavioral and

demographic consequences of increasing water temperatures for populations of salmon, and to incorporate this understanding of climate impacts into the management of fisheries.

Migratory salmon in smaller coastal watersheds may be particularly vulnerable to climate change. While mortality during spawning migrations has been well documented in populations of sockeye in the Fraser and Columbia Rivers (Quinn and Adams 1996, Crossin et al. 2008, Crozier et al. 2011, Martins et al. 2011), the extent and impact of temperature mediated pre-spawn mortality in these smaller watersheds, such as those on the BC coast, is virtually unknown. In the low-elevation coastal watersheds of Washington, British Columbia and Alaska, small to medium sized lakes support hundreds of populations of sockeye salmon. In British Columbia alone, these coastal watersheds support at least 120 unique stocks, more than half of the 214 lake-type sockeye populations in the province (Holtby and Ciruna 2007). These lakes often share common features such as rain-dominated hydrology and unproductive humic-stained waters (Stockner and McIsaac 1996). In coastal watersheds, sockeye typically migrate during late-spring and early-summer, thereby avoiding late-summer water temperatures which can exceed 20°C (Hodgson and Quinn 2002, Katinić et al. 2015); temperatures known to induce physiological stress and mortality among sockeye in the Fraser and Columbia Rivers (Crossin et al. 2008, Crozier et al. 2011, Eliason et al. 2011). With small to medium catchment sizes (e.g. < 300 km²), minimal snow-melt, and darkly colored water resulting from humic staining, coastal watersheds are likely to absorb solar energy readily, making them sensitive to warming air temperatures (Lisi et al. 2015, Chezik et al. 2017). Smaller watersheds have more variable hydrology (Moore et al. 2015), and during summer drought periods many coastal systems experience low-flow conditions that limit movements by adult salmon (Quinn et al. 2015). Importantly, these coastal sockeye stocks support subsistence fisheries that are vital to the culture, economy and food security of many remote and Indigenous communities. Despite their importance for the evolutionary legacy of their species, and the socio-cultural value of these populations, few data exist on the migratory behavior and thermal sensitivity of sockeye in coastal river systems.

To address major gaps in current understanding of sockeye abundance and survival, we built a traditional-style wooden weir near the top of tidal influence in the Koeeye River, which we have operated since 2013 to tag adult sockeye for subsequent

mark-resight estimates of population size (Atlas et al. 2017). Beginning in 2016, we installed a network of radio frequency identification (RFID) antennas to track migration and climate driven pre-spawn mortality among fish tagged at the weir. Over the ensuing three years, we tracked the movement and survival of sockeye salmon across the Koeye watershed, from river entry to spawning in tributaries of Koeye Lake. Using these data, we asked three questions: (1) How long does it take tagged sockeye to reach Koeye Lake? (2) What is the relationship between temperature, river level, and mortality prior to spawning ground entry? (3) Does sockeye river entry cease during periods of summer low water, causing migratory delays? By reconstructing detection histories for individual sockeye and modeling apparent survival in relation to the temperature and flow conditions encountered during their spawning migrations, we reveal new understanding of climate vulnerability for sockeye salmon in coastal watersheds. Estimates of temperature-mediated pre-spawn mortality will support forecasting of future climate impacts on sockeye populations in coastal ecosystems, underpinning adaptive management under climate change.

3.3. Methods

Tagging and tracking

Since 2013, we have used a traditional-style cedar fish weir to capture and tag sockeye in the lower Koeye River, shortly after their freshwater entry (Atlas et al. 2017). Most years, the weir is installed in early June and operated until the end of July. Fish are captured in the trap box of the weir and in weekly seining events in the pool downstream, anesthetized with MS-222, tagged with visually identifiable FLOY anchor tags (FLOY tag, Seattle WA) on both sides of the posterior dorsal muscle, and evaluated for visual indications of recent injuries including wounds, net scarring and major scale loss. Following weekly pool seining a panel is removed from the weir to minimize migration delays imposed by the fence. These tagged fish are subsequently resighted during repeated fall stream counts to make estimates of spawner abundance.

Beginning in 2016, we installed a permanent network of solar and fuel-cell powered RFID antennas across the longitudinal extent of the Koeye watershed. Initially, antennas were installed at three locations: the top of tidal influence about 300 meters upstream of the weir, the lake outlet, and the lower end of the Upper Koeye River where

~85% of sockeye spawning typically occurs. In 2017, we added a seasonally deployed antenna site in a tributary of Koeye Lake which enters on the lake's south shore – referred to hereafter as Left Tributary – and supports a few hundred spawners annually. RFID antennas in the Koeye River below the lake are installed in spring, prior to the onset of sockeye spawning migrations. Antennas above the lake are installed in late-August or early-September, prior to spawning ground entry for sockeye. RFID network configuration and operation schedules in the tributaries of Koeye Lake varied somewhat between years. For example, the antenna in the Left Tributary of Koeye Lake was not installed until 2017, and in that year a bear damaged the Upper Koeye site shutting down the antenna for 8 days in mid-September. All antenna sites are operated until late-October when spawning and river entry is complete for sockeye.

Sockeye captured at the weir are tagged with Passive Integrated Transponder (PIT) tags (23 or 32mm) implanted in the dorsal muscle in addition to the FLOY tags. Using this network of four RFID antenna locations, we tracked the migration and survival of PIT tagged adult sockeye throughout their freshwater spawning migrations. Across the three years of study, we PIT tagged total of 1,162 adult sockeye at the Koeye River weir (Table 3.1), redetecting 681 on the spawning grounds. Daily mean temperatures and river levels on the day of tagging were estimated using a Hobo U20 water level logger (Onset Corporation, Bourne MA) deployed in the lower Koeye River about 500m above the weir. Injuries on tagged fish were recorded during handling, and net and predator injuries were considered the same when analyzing their effects on survival.

Study system

The Koeye River drains a watershed of 185 km² on the mainland coast of British Columbia, in the ancestral territory of the Heiltsuk First Nation. The hydrology of the watershed is transitional rain-snow dominant, with peak flows typically occurring during late-fall and winter, and a small pulse of snowmelt driven discharge during late-spring. The watershed has two medium-sized lakes, Lower (450 ha) and Upper Koeye Lake (227 ha), which are lightly stained and mildly acidic (pH ~ 6.7). Lower Koeye Lake is located 6.2 km from tidewater at 53 m elevation and supports all sockeye salmon spawning and rearing, as they are not believed to ascend the canyon downstream of Upper Koeye Lake. Sockeye return to Koeye from June through September, with most fish entering freshwater between mid-June and mid-July. Spawning occurs during

September and October in two tributaries of the lake, and lakeshore spawning is undocumented and not believed to occur. Since the 1950s spawning sockeye abundance in Koeye has ranged from a few thousand to 18,000, however prior to 2013 population estimates were infrequent and unreliable.

Data analysis

We estimated the effects of water temperature, river level, injury, and tag size on the apparent survival of adult sockeye salmon from the weir to their spawning areas above Koeye Lake. To understand associations between environmental conditions and sockeye survival we compared coefficient estimates and statistical support for a series of Bayesian logistic regression models. These models were pared down from a full model which included the interaction between river level and mean daily water temperature, their main effects, and the effects of individual injuries and tag size on the probability of being detected on the spawning grounds. Continuous environmental covariates were centered and standardized by subtracting the mean and dividing by two standard deviations to facilitate comparisons of effect sizes across covariates (Gelman 2008). We accounted for the non-independence of fish tagged on the same day by fitting a cohort-level random intercept term and evaluated support for including a year specific variance term, since RFID network configuration and operation schedules varied slightly between years.

(Equation 1)

$$\text{logit}(p_i) = \alpha_j + \beta_{\gamma_1 \dots \gamma_n} \gamma_{1_j} \dots \gamma_{n_j} \dots + \beta_{Inj} Inj_i + \beta_T Tag_i + \epsilon_{year}$$

Our model estimated the probability of survival for individual sockeye tagged in the three-year study (p_i). The model included a random intercept (α) for each cohort (j), continuous environmental covariates γ_n with the estimated coefficient β_{γ_n} , the effect of injury (β_{Inj}), the categorical effect of tag size (β_T), and a year specific variance term (ϵ_{year}) (Equation 1). Priors for α were drawn from a hyper-distribution with a normally distributed mean of zero and a variance term τ , which was one over the standard deviation squared. Standard deviations for τ were drawn from a uniform distribution bounded between 0 and 2. For β , we used uninformative normally distributed priors with a mean of zero and a standard deviation of 10. Models were then run for 20,000

iterations in JAGS using the statistical program R, with three parallel chains, a burn in period of 10,000 iterations, and a thinning rate of three. Model convergence was evaluated visually using trace plots.

We compared models of apparent survival to spawning using an information theoretic approach, computing widely applicable information criterion (WAIC) scores for each model using the R-package 'loo' (Vehtari et al 2018). We then evaluated evidence for effects of environmental conditions, injury, and tag size on the probability of redetection in spawning areas above Koeye Lake by comparing median coefficient estimates and credible intervals. For the suite of models receiving a high degree of support, we further estimated model predictive performance using an area under the curve approach (AUC) implemented in the R-package 'ROCR' (Sing et al. 2015) and tested the prediction accuracy at a 0.5 probability cutoff.

To estimate the migration rate and survival of sockeye from the weir to Koeye Lake, we used detections at the lake outlet antenna site as indication of successful migration to over-summer holding areas in the lake. Survival estimates accounted for detection efficiency by estimating survival as part of a Bayesian multinomial probability statement, where N^t is the number of fish tagged at the weir in a given year. This multinomial probability accounted for all possible detection histories (e.g. $N^{1,1}$ for fish detected at outlet and spawning area) to estimate the probability of surviving to the lake outlet (φ_o), surviving to spawning (φ_s) and being detected while passing over lake outlet and spawning ground antennas (ρ_d). All antennas spanned the full width of the wetted channel and had roughly equivalent detection ranges (~80-90 cm) during regular in-season testing, so detection efficiency was assumed to be equal across sites. For 2018, when RFID antennas operated in both spawning tributaries across the entire spawning season, we interpreted estimates of apparent survival from tagging to spawning.

(Equation 2)

$$(N^{1,1}, N^{1,0}, N^{0,1}, N^{0,0}) \sim \text{Multinomial}(N^t; (\theta^{1,1}, \theta^{1,0}, \theta^{0,1}, \theta^{0,0}))$$

$$\theta^{1,1} = \varphi_o * \varphi_s * \rho_d^2$$

$$\theta^{1,0} = \varphi_o * \rho_d * \varphi_s * (1 - \rho_d) + \varphi_o * \rho_d * (1 - \varphi_s)$$

$$\theta^{0,1} = (1 - \rho_d) * \varphi_o * \rho_d * \varphi_s$$

$$\theta^{0,0} = (1 - \varphi_o) + (1 - \rho_d) * \varphi_o * (1 - \varphi_s) + (1 - \rho_d) * \varphi_o * (1 - \rho_d) * \varphi_s$$

3.4. Results

Sockeye spawning migrations began in early-June with a peak in late-June and early-July (Figure 3.1). Fish tagged at the weir migrated quickly to Koeye Lake taking an average of 3.5 days to reach the lake outlet antenna across the three years (Figure 3.2). Estimated survival during summer-time migrations to Koeye Lake was 94.5% (CI 85.1 to 99.7%) in 2016, 89.8% (CI 87.1 to 92.2%) in 2017, and 83.7% (CI 79.6 to 87.4%) in 2018. Detection efficiency at the lake outlet site was lowest in the first year of the study (55.4%; CI 48.9 to 62.7%), however modifications to antennas and power systems designed to reduce electrical interference yielded dramatic improvements in detection efficiency in the latter two years of the study (mean = 96.9%). In 2018 when antennas in both spawning tributaries ran continuously, an additional 19.5% (CI 14.2% to 24.9%) mortality was estimated to have occurred during over-summer lake holding. Combined estimates of survival from tagging at the weir to Koeye Lake, and from lake entry to spawning ground entry yielded an estimate of 67.4% (CI 61.9 to 72.9%) apparent survival to spawning in 2018.

Bayesian logistic models of apparent survival to spawning, based on detection at RFID antennas in tributaries of Koeye Lake, revealed evidence for negative effects of both increasing river temperature and injury on the probability of survival. Across models receiving a high degree of support, temperature, sex, and injury were consistently the most important variables predicting en route mortality among tagged sockeye. The mean standardized coefficient estimate for temperature was negative and did not overlap zero -0.48 (CI -0.94 to -0.05). Female sockeye had consistently lower probability of survival to spawning -0.32 (CI -0.57 to -0.07), with a median reduction in survival of 13% at mean temperatures. There was also strong support for a negative effect of injury on survival probability, with a mean coefficient estimate of -0.75 (CI -1.27 to -0.25), and a 23% lower probability of survival among injured fish at the mean temperature. Among the 1,162 individuals handled in the study, 75 had recent injuries from predators or gill nets. The model receiving the greatest support from WAIC included only river temperature and injury, with both variables appearing in all models that fell within 2-delta units of the top

model. The effects of river level on sockeye survival was less clear. Across all models, coefficient estimates for river level overlapped zero, however river level was included in two of the three top models. Further, there was no evidence for differences in detection probability with tag size, and in all cases models without tag size and year specific variance received higher support (Table 3.2, Figure 3.3). Comparisons of predictive performance revealed similar AUC values across models receiving the highest level of support, with predictive accuracy ranging from of 63.9% to 64.0% with a 0.5 probability cut off for predicted survival (Table S3.1).

Temperature had a negative effect on apparent survival, with a steep decline in the probability of detection on the spawning grounds for fish tagged when water temperatures exceeded 15°C. For example, increasing water temperature from 10 to 15 °C produced a predicted 30% decline in survival probability (Figure 3.4). While increasing waters temperature from 15°C to 18.8°C – the maximum temperature observed for a tagging cohort – was associated with a collapse in median predicted survival from 70% to 9%. The estimated T50 for Koeye River sockeye – the temperature at which 50% of tagged individuals were not subsequently detected on the spawning grounds – had a mean of 16.5°C (95% CI: 15.8 – 16.9°C). Across the 1,162 fish in our study, mean temperature at tagging was 15.7 °C with our top model yielding a median prediction of 56% apparent survival at this temperature. Daily mean temperature exceeded 15.7 °C for 39 of 71 tagging cohorts, and mean daily temperature in the lower Koeye River exceeded the estimated T50 (16.5°C) on 29% of all days in June and July.

Counter to our prediction that sockeye would experience lower survival when river levels dropped, model estimates trended towards lower survival at higher water, but were ultimately inconclusive (Figure 3.3). Peak capture numbers occurred at intermediate flows, likely a reflection of higher capture efficiency at the weir during moderate and low flow, rather than reduced river entry by sockeye at higher water levels. However, river entry as indexed by daily tagging numbers showed a sharp decline when the gauge height (m) dropped below 0.4 meters (Figure 3.5). The cessation of river entry meant that very few fish encountered the most inhospitable river conditions. For example, across the three-year study only 261 sockeye entered the river when temperatures exceeded the 16.5 °C, and < 25% of the total 1,162 were tagged at temperatures above the estimated T50.

3.5. Discussion

We found strong evidence for a rapid increase in mortality among migrating sockeye when temperatures surpassed 15 °C, with 50% of tagged fish predicted to die prior to spawning when temperatures reach 16.5 °C. The overall thermal sensitivity of sockeye salmon in Koeye River therefore appears comparable to that of sockeye populations occupying interior watersheds at similar latitude in the Fraser Basin (Martins et al. 2011), despite the shorter duration of exposure to unfavorable conditions during their summer migrations. Furthermore, we found higher risk of en route mortality among female sockeye, with females having a 7% lower apparent survival across all tagging temperatures. These findings match previous research revealing greater temperature sensitivity among female salmon (Martins et al. 2012). Importantly, handling and tagging are likely associated with elevated mortality risk, particularly when water temperatures are warm (Kieffer 2000, English et al. 2005), and the observed relationship between survival rate and temperature in our study was most comparable to fish that were handled shortly after freshwater entry by Martins et al. (2011). Thus, rates of temperature-mediated en route mortality among unhandled fish in the Koeye River are likely lower than we report here. Imperfect detection of surviving sockeye on the spawning grounds likely increases uncertainty in estimated temperature effects but is unlikely to bias overall temperature and survival trends, since detection probability during spawning ground entry is unrelated to the temperature experienced during summer migration.

Half of the mortality among migrating sockeye during 2018 occurred between tagging and the lake outlet, suggesting that both immediate survival through lower river migrations and delayed mortality related to physiological stress and condition can contribute to reduced spawning success. In general, sockeye transited the lower river to Koeye Lake rapidly, with an average migration time of 3.5 days across the three years. Early migration comes at an energetic cost, since fish forgo foraging opportunity in marine environments and fast in freshwater during pre-spawn holding (Quinn et al. 2015, Katinić et al. 2016). On average, sockeye in Koeye entered spawning tributaries 84.5 days after tagging at the weir (range = 42 – 123 days). Despite these forgone growth opportunities, early migration and prolonged lake holding is characteristic of many coastal sockeye populations (Katinić et al. 2015) and may increase reproductive success

by allowing sockeye to behaviorally thermoregulate by moving across temperature gradients in lake hypolimnions (Newell and Quinn 2005). Early arriving fish with prolonged lake holding can more readily regulate their thermal exposure, contributing to longer spawning ground residence and lower egg retention, indicative of higher reproductive output (Minke-Martin et al. 2018).

Injuries from fishing nets or predators can have lasting negative consequences for the physiological status, infection risk, and survival of migrating adult salmon (Teffer et al. 2018, Bass et al. 2018, Cook et al. 2019), and we found that sockeye with injuries from predators or recent gillnet scarring experienced much lower survival to spawning. Overall, injured fish had a 36% lower probability of being redetected on the spawning grounds. We found no clear statistical support for an effect of river level on survival to spawning, and a slightly negative mean coefficient estimate for the effects of this parameter. We had predicted higher mortality at lower river levels, as migrating salmon can be vulnerable to predation or become stranded in low and warming pools when water levels drop (Carlson and Quinn 2007). The surprising absence of this pattern may be partly explained by the relatively rapid migrations sockeye make to Koeeye Lake, which likely reduce the risk of predation or acute temperature-driven mortality. In addition, the near cessation of river entry during periods of low flow meant that we tagged very few fish at the lowest river levels.

The fact that river entry by migrating adult sockeye appears to stop during low water has important implications for how we understand and forecast climate impacts in populations of coastal sockeye. Climate models predict warmer and drier summers in the coastal Pacific Northwest (Murdock et al. 2011). Increased en route mortality associated with warming in large river systems is already having significant negative effects on rates of individual survival and population viability in some sockeye salmon stocks (Patterson et al 2007). However, if sockeye in Koeeye and other coastal river systems delay freshwater entry because of low water and remain in coastal marine waters longer, increased vulnerability to predation and fisheries may act as proximate drivers of pre-spawn mortality and reduced population viability. During the summer of 2018, the Central Coast region experienced a prolonged drought, with less than 6 mm of rainfall between July 8th and August 24th (Hakai Insitute – unpubl.). Drought conditions overlapped with the latter half of the sockeye spawning migration, and in late-August we observed large numbers of sockeye displaying spawning colors while holding in

saltwater at the mouth of the nearby Namu River, almost a month before spawning typically begins.

As climate warms and summer droughts intensify, the interactive effects of increased temperature stress and migratory delays in saltwater could reduce individual survival among coastal sockeye arriving at their natal river mouths at historically optimal times. Steep declines in the probability of individual survival when river temperatures exceed 15 °C indicates that coastal sockeye have relatively low thermal tolerance, despite the regularity of low, warm water conditions which often surpass this threshold during mid-summer. The cessation of migration during the lowest water conditions suggests that behavioral mechanisms may drive migratory delays, allowing fish to avoid the most stressful river conditions. However, waiting for summer rains to increase river level and reduce water temperatures may increase the risk of predation, capture in fisheries, or injury during prolonged marine holding, reducing the overall likelihood of survival (Morita 2019). In addition, the impacts of climate-induced delays in migrations could be exacerbated by increasing marine mammal populations (Olesiuk 2010, Chasco et al. 2017, Nelson et al. 2019). The dual impacts of temperature and prolonged saltwater holding are likely to have consequences for population productivity and sustainable harvest rates, as well as the long-term viability of hundreds of sockeye populations across the coastal watersheds of Washington, British Columbia, and Alaska. Thus, management strategies that account for migration conditions by reducing fishing pressure during prolonged periods of low-warm water may be necessary to mitigate the effects of migration delays resulting from changing climate conditions. Similar climate-linked management models have been developed for the Fraser River, with reductions in harvest rates when temperatures reach levels predicted to elevate the risk of en route mortality among adult sockeye (Hague and Patterson 2007).

Adaptive shifts in migration timing are likely to be an important process in maintaining viable populations of coastal sockeye given projected climate warming (Hague et al. 2010, Reed et al. 2011). However, the ability of species to adapt to a changing climate depends on both the heritability of traits associated with phenology, the diversity of phenotypes within a population, and the plasticity of migration timing and thermal tolerance (Hoffman and Sgró 2011). Migration timing is highly heritable (Carlson and Seamons 2008), and species phenology may be more capable of rapid contemporary evolution than thermal tolerance (Bradshaw and Holzapfel 2008).

Sockeye grow slowly during their last summer of marine life, thus the fitness tradeoffs between early migration reducing mortality risk and additional marine growth associated with later migration likely favor earlier migration (Katinić et al. 2016). Within coastal sockeye populations there is precedent for earlier migration than is currently observed in Koeeye (Hodgson and Quinn 2002). For example, most populations of sockeye in Haida Gwaii have long been known to migrate earlier (Katinić et al. 2015), and some populations in smaller, low-elevation watersheds within Heiltsuk traditional territory begin their freshwater migrations as early as late-April (W. Housty pers comm). Given this precedent for the evolution of earlier-run timing, and ongoing examples of adaptive shifts in sockeye migration timing (e.g. Quinn and Adams 1996), climate warming and the loss of late-spring snowmelt may drive populations of sockeye in Koeeye and other transitional rain-snow watersheds towards earlier migrations. Alternatively, some sockeye populations in the Lower Fraser with short migrations have traditionally delayed freshwater entry until September when river temperatures cool (Hinch et al. 2012). Thus, climate-driven adaptation in run timing may act to push sockeye migrations later, particularly if summer droughts preclude river entry during the latter half of the run.

Species conservation and management should seek to maintain diverse phenotypes by minimizing artificial selection imposed by harvest or other human activities (Allendorf and Hard 2009). Maintaining phenotypic diversity and population size underpins the potential for adaptation to drive evolutionary rescue in populations threatened by changes in climate, promoting the persistence and recovery of species in the face of ongoing anthropogenic climate change (Rice and Emery 2003, Carlson et al. 2014). Thus, quantifying climate impacts and risks during animal migrations is a critical element of management and conservation efforts seeking to promote adaptation and resilience under climate change.

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3.8. Tables

Table 3.1. Dates of weir operation, number of sockeye, and the mean temperature at tagging for all sockeye PIT tagged across the three year study.

Year	Dates of operation	Total tagged	Mean temp.
2016	June 8 th - July 2 nd	193	14.42 °C
2017	June 10 th - August 1 st	587	15.88 °C
2018	June 15 th - July 26 th	382	16.15 °C

Table 3.2. Bayesian logistic models of adult sockeye survival probability, ranked by widely applicable information criterion (WAIC) score. α_j represent cohort specific intercept, β s represent coefficient estimate for the effect of a given parameter on the logit probability of survival in the model.

Num	Model	WAIC	SE
1	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Sex}}\gamma_{4i} + \beta_{\text{Inj}}\gamma_{3i}$	1531.4	18.5
2	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Sex}}\gamma_{4i} + \beta_{\text{Inj}}\gamma_{3i} + \epsilon_{\text{year}}$	1534.1	18.6
3	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} : \beta_{\text{Flow}}\gamma_{2j} + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Sex}}\gamma_{4i} + \beta_{\text{Inj}}\gamma_{3i} + \beta_{\text{Flow}}\gamma_{2j}$	1534.2	18.9
4	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Sex}}\gamma_{4i} + \beta_{\text{Inj}}\gamma_{3i} + \beta_{\text{Tag}}\gamma_{5i}$	1534.3	18.7
5	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Flow}}\gamma_{2j} + \beta_{\text{Sex}}\gamma_{4i} + \beta_{\text{Inj}}\gamma_{3i}$	1534.7	18.6
6	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} : \beta_{\text{Flow}}\gamma_{2j} + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Sex}}\gamma_{4i} + \beta_{\text{Inj}}\gamma_{3i} + \beta_{\text{Flow}}\gamma_{2j} + \beta_{\text{Tag}}\gamma_{5j}$	1535.2	19.0
7	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Inj}}\gamma_{3i}$	1538.3	17.6
8	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Sex}}\gamma_{4i}$	1538.8	17.7
9	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} : \beta_{\text{Flow}}\gamma_{2j} + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Inj}}\gamma_{3i} + \beta_{\text{Flow}}\gamma_{2j}$	1539.0	18.1
10	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Inj}}\gamma_{3i} + \beta_{\text{Tag}}\gamma_{5i}$	1539.5	17.8
11	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Inj}}\gamma_{3i} + \beta_{\text{Flow}}\gamma_{2j}$	1539.5	17.7
12	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} : \beta_{\text{Flow}}\gamma_{2j} + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Flow}}\gamma_{2j} + \beta_{\text{Inj}}\gamma_{3i} + \beta_{\text{Tag}}\gamma_{5i}$	1540.0	18.1
13	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Inj}}\gamma_{3i} + \beta_{\text{Tag}}\gamma_{5i} + \epsilon_{\text{year}}$	1540.3	17.9
14	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Flow}}\gamma_{2j} + \beta_{\text{Inj}}\gamma_{3i} + \beta_{\text{Tag}}\gamma_{5i}$	1540.7	17.8
15	$\text{logit}(p_i) = \alpha_j + \beta_{\text{Temp}}\gamma_{1j} : \beta_{\text{Flow}}\gamma_{2j} + \beta_{\text{Temp}}\gamma_{1j} + \beta_{\text{Flow}}\gamma_{2j} + \beta_{\text{Inj}}\gamma_{3i} + \beta_{\text{Tag}}\gamma_{5i} + \epsilon_{\text{year}}$	1540.8	18.3

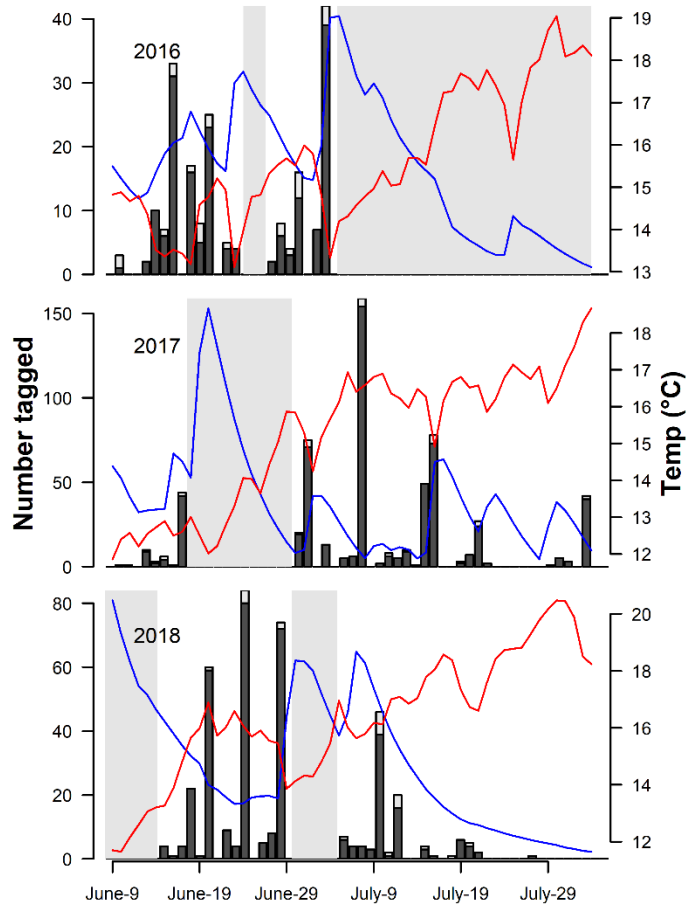


Figure 3.1 Daily tag numbers of injured (light grey) and uninjured (dark grey) fish, mean daily river temperature (red line), and river level (blue line) across the three seasons of study. Gray shading indicates periods when the weir was not operating.

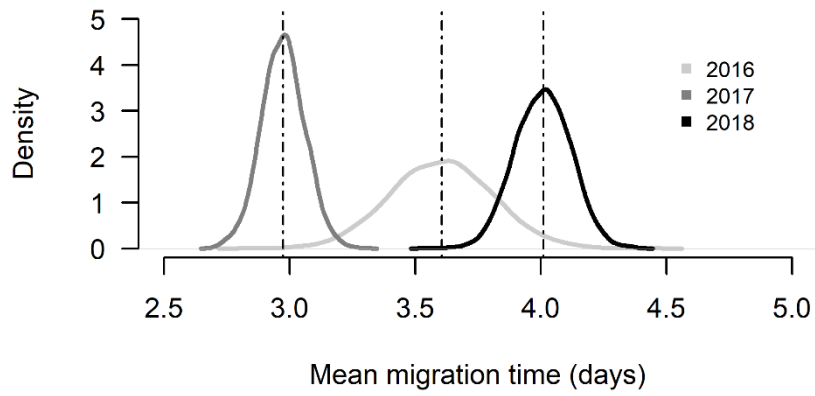


Figure 3.2 Density distributions of the estimated mean migration time to Koeye Lake for sockeye tagged at the weir. Vertical dashed lines are median estimates for each of the three years.

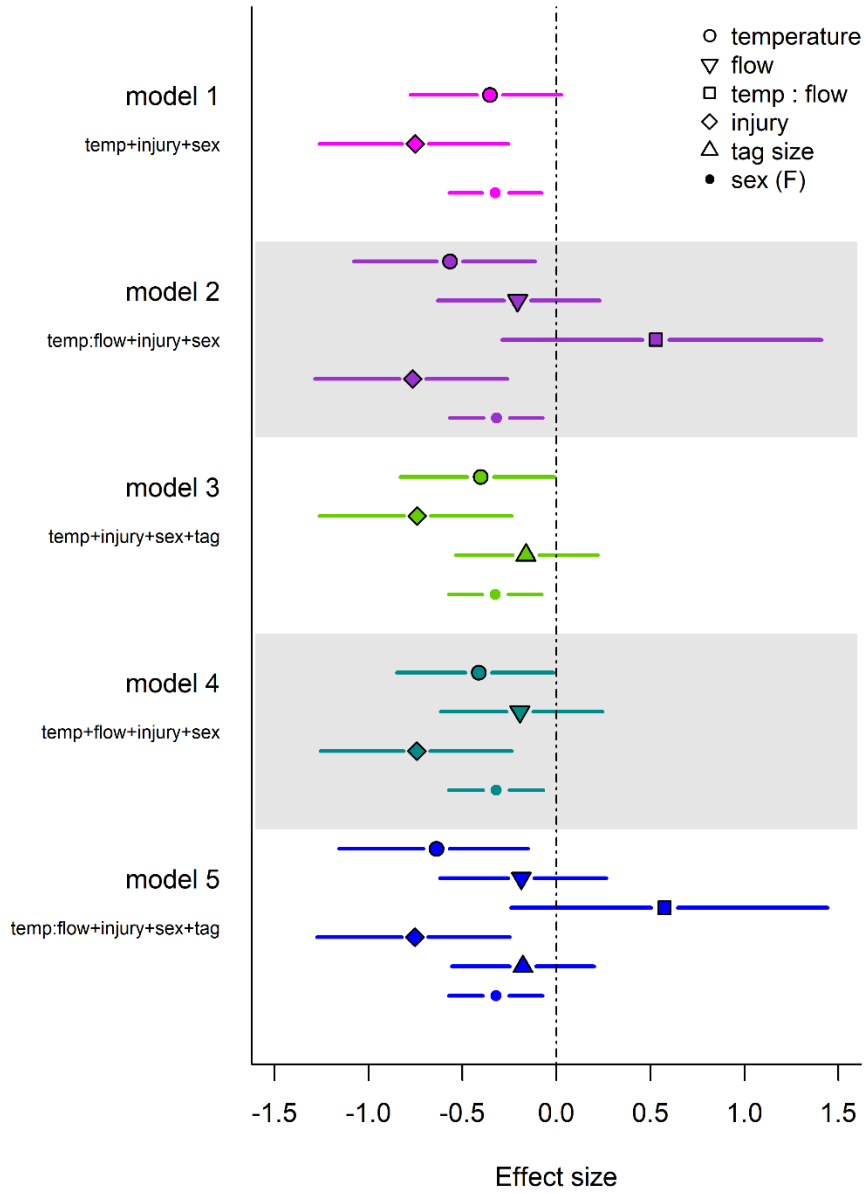


Figure 3.3 Median and 95% credible intervals for standardized coefficient estimates across the five models receiving the greatest support from WAIC. Model structure is written along the y-axis.

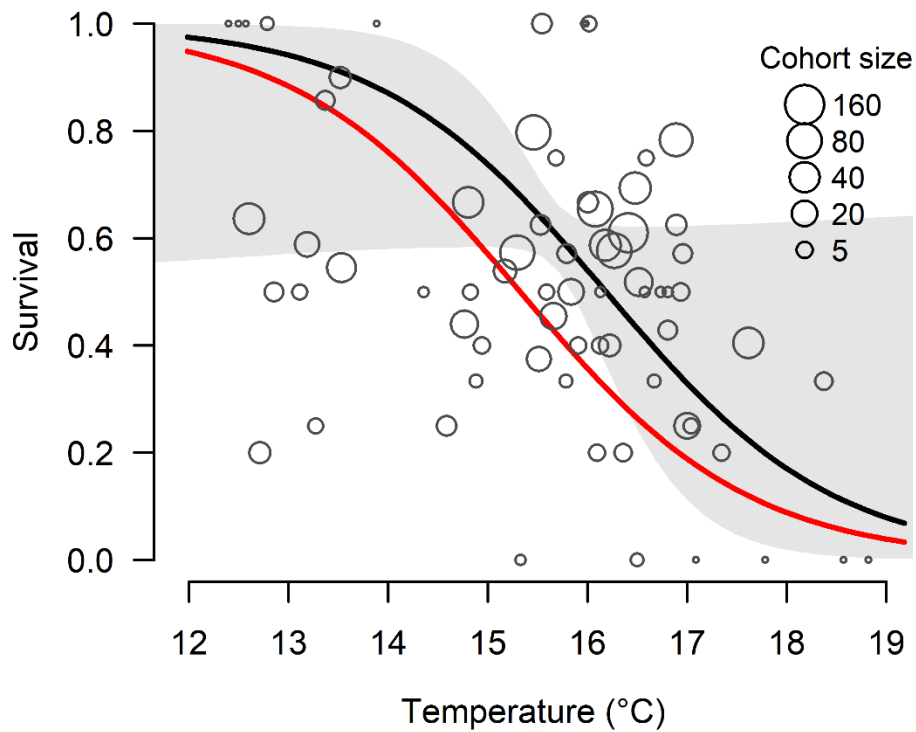


Figure 3.4 Median estimate and 95% credible intervals (gray shading) for the relationship between temperature and survival from the model relating survival probability to temperature and injury (model 1). Black line and predicted fit reflects expected survival for a fish without injury, red line represents median predicted survival for fish with gillnet or predator injury. Circles represent apparent survival to spawning for each cohort of tagged sockeye, with circle size scaled to the number of fish in each cohort.

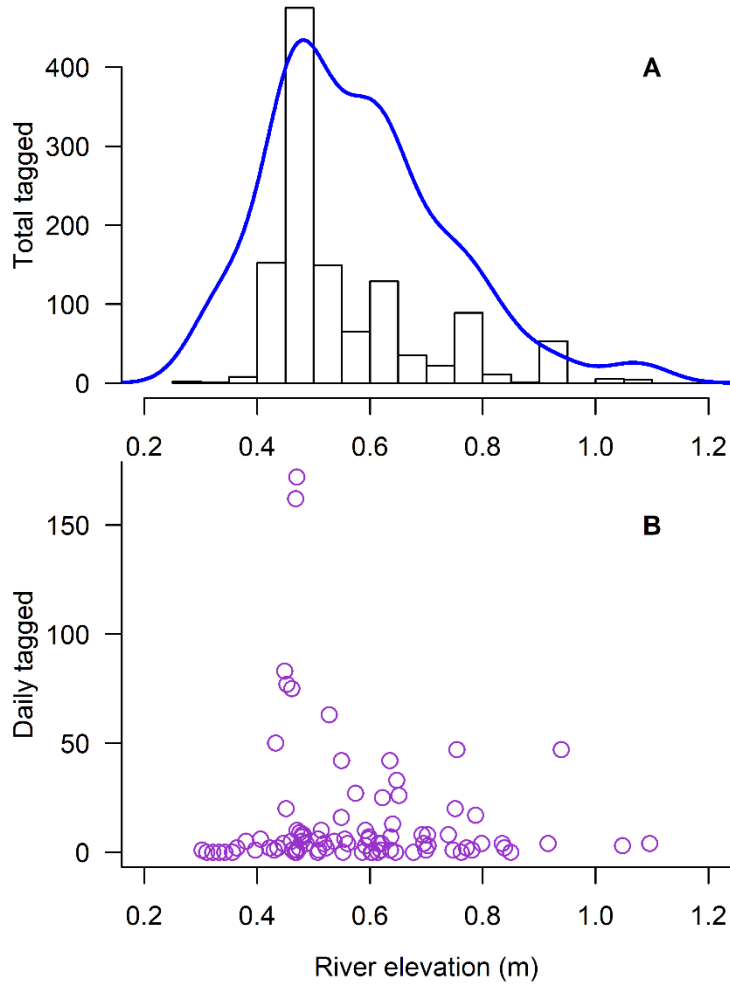


Figure 3.5 (A) Histogram of the number of sockeye tagged across the observed range of river levels, with the blue line depicting the density distribution of river levels on days when the weir was operational. (B) The number of fish tagged on each day of weir operation plotted against daily river level.

3.9. Supplemental Materials

Table S3.1 Model predictive performances metrics, area under the curve and prediction success rate at a 0.5 prediction threshold, evaluated for top models not including tag size effects.

Model	AUC	Prediction rate
$\alpha_j + \beta_{Temp}\gamma_{1j} + \beta_{Inj}\gamma_{3i} + \beta_{Sex}\gamma_{4i}$	0.674	0.6403
$\alpha_j + \beta_{Temp}\gamma_{1j} + \beta_{Flow}\gamma_{2j} + \beta_{Temp}\gamma_{1j} + \beta_{Sex}\gamma_{4i} + \beta_{Inj}\gamma_{3i} + \beta_{Flow}\gamma_{2j}$	0.673	0.6394
$\alpha_j + \beta_{Temp}\gamma_{1j} + \beta_{Flow}\gamma_{2j} + \beta_{Inj}\gamma_{3i} + \beta_{Sex}\gamma_{4i}$	0.672	0.6386

Chapter 4. Landscape and biophysical controls of lake capacity to inform evaluation of sockeye salmon populations (*Oncorhynchus nerka*) in data-limited regions.

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4.1. Abstract

Landscape models are increasingly used to classify and predict the structure and productivity of data-limited aquatic ecosystems. One such suite of ecosystems is on the remote North and Central Coast (NCC) of British Columbia, where sockeye salmon (*Oncorhynchus nerka*) rear in more than 150 lakes. Given their remoteness, and limited resources for assessment, limnological and population monitoring in many of these lakes has been periodic, or has not occurred, limiting understanding of the status of populations and their habitats. Lake photosynthetic rate (PR) estimates are the foundation for models of sockeye salmon nursery lake productive capacity. Using data from 61 lakes across the NCC, we compared a suite of landscape and lake variables in an information theoretic framework producing a set of models relating these characteristics to lake PR. A categorical variable related to lake biogeochemistry – whether a lake is humic stained, clear, or glacially turbid – was the most important variable predicting lake PR and was included in all models. Lake surface area relative to upstream catchment size and lake perimeter to surface area ratio were also important, with smaller upstream catchments yielding higher production, and high shoreline complexity correlated with lower productivity as measured by limnetic PR. The model receiving the highest support explained more than 50% of the variation in lake PR, allowing predictions of PR in 96 other lakes currently lacking limnological assessments. These landscape-scale models therefore represent a valuable starting point for evaluating lake-specific carrying capacities for data-poor sockeye salmon populations under Canada’s Wild Salmon Policy.

4.2. Introduction

A key emerging challenge for ecologists is to quantify the productivity and capacity of ecosystems for the management and conservation of species in data-limited regions. In light of this challenge, landscape-scale models have been proposed as a tool to leverage information on regional and local habitat conditions for prediction and prioritization of conservation and management over broad spatial scales (Soranno et al. 2010, Schwenk and Donovan 2011). Adjacent or closely located habitats often share similar geomorphic and habitat conditions and may therefore exhibit similar patterns of community productivity and structure (Legendre 1993, Lichstein et al. 2002). Regional similarities in geomorphology and habitat characteristics, coupled with shared regional climate conditions can drive spatial synchrony in population dynamics, in a process known as the Moran effect (Moran 1953, Sutcliffe et al. 1996). These shared regional environmental conditions create potential for models that incorporate the effects of landscape, geomorphic, and climate conditions, drawing on high quality information from a few systems to build broader regional understanding of ecosystem conditions (Legendre and Fortin 1989, Turner et al. 2001). In recent years there has been a dramatic increase in the use of geospatial data paired with data on species distribution or abundance to evaluate habitat suitability and use. For example, spatial models of mountain caribou habitat that account for both land cover and geomorphology have shown promise for prioritizing conservation and land use planning (Johnson et al. 2004). Indeed, models which examine species distribution data in relation to landscape level variation in geomorphology and habitat structure are used to predict the distribution and abundance of a wide variety of at-risk species, ranging from fish to fishers (Carroll et al. 1999, Pess et al. 2002).

In lake ecosystems, productivity and community structure are driven by a complex suite of physical and chemical processes, and biological interactions such as predation and competition (Horne and Goldman 1983, Carpenter and Kitchell 1988). Hydrology and geomorphology of lake catchments play a key role in governing water chemistry and nutrient availability, flushing rates, temperature and euphotic depth (Kratz et al. 1997, Kamenik et al. 2001). Through these diverse pathways, landscapes contribute to the regulation of primary productivity and the abundance of species at higher trophic levels within lakes (Hershey et al. 1999, Quinlan et al. 2003). Limnologists

and fisheries biologists have long sought to understand linkages between lake ecosystem parameters and fisheries yields (e.g. Northcote and Larkin 1956, Jones and Hoyer 1982, Hanson and Leggett 1982). Early efforts examined the relationship between fisheries productivity and simple metrics such as total dissolved solids and depth (Northcote and Larkin 1956, Ryder 1965). More recently researchers have measured the rate of primary production within the limnetic food web of lakes and found that photosynthetic rates (PR) are highly correlated with fish biomass (McConnell et al. 1977, Downing et al. 1990, Hume et al. 1996, Shortreed et al. 2000). While predictive models of lake productivity necessarily simplify ecosystem dynamics, the similarities among lakes and regions provide the opportunity to make generalizable predictions about ecosystem conditions across broad spatial scales. Landscape models of ecosystem productivity are therefore attractive for managers seeking to inform management of fisheries with limited resources.

Sockeye salmon typically depend upon lake habitats for juvenile rearing. They span a pan-North Pacific range, and are of major cultural, economic and ecological significance. Thus, models linking lake productivity to landscape and lake conditions could improve conservation and management prospects for many data-limited populations of sockeye salmon (*Oncorhynchus nerka*). Sockeye salmon typically spend a year or two rearing in lakes prior to emigrating to the Pacific Ocean. Due to the tight coupling of juvenile sockeye salmon with the pelagic food webs of their natal rearing lakes, their populations are often limited by lake productivity and size (Juday et al. 1932, Shortreed et al. 2001). In recent decades, researchers and managers in Alaska and British Columbia have developed rearing capacity models for sockeye salmon nursery lakes (Koenings and Burkett 1987, Hume et al. 1996, Shortreed et al. 2000). In British Columbia, managers have used data on lake photosynthetic rates (PR) to predict juvenile rearing capacity for sockeye lakes (Hume et al. 1996; Shortreed et al. 2000). Model outputs have been used to understand conservation status, inform harvest rates, and estimate stock-specific recovery potential. While these approaches are particularly relevant in populations where stock-recruit data are scarce (e.g. Cox-Rogers 2010), informative priors based on lake rearing capacity are often used in stock assessment to improve model fits and reduce uncertainty in estimates of biological or management benchmarks (Grant et al. 2011).

On the Pacific coast of Alaska and British Columbia, lakes with the same biogeographic regions often share similar water chemistry, hydrology and climate, resulting in broad, regionally-defined patterns of lake productivity. For the purposes of management and prediction, lakes in the area are commonly classified as either stained, clear, or glacially turbid (Edmundson and Mazumder 2001, Shortreed et al. 2007). Most coastal lakes are stained, resulting from high concentrations of dissolved organic material (DOM), while glacial influences are more common in mountainous, interior watersheds. With the exception of glacially turbid lakes, interior lakes in our study area tend to have clear water, with neutral or slightly basic pH, and higher rates of primary productivity (Stockner and MacIsaac 1996). Lakes within these groups exhibit variation in nutrient availability, primary productivity and food web structure, and whether a lake is stained, glacial or clear is related to similarities in the physical, chemical and biological conditions influencing primary, secondary, and fish production. For example, humic stained lakes tend to be unproductive and ultra-oligotrophic, with mildly acidic waters, and strong seasonal stratification (Jackson and Hecky 1980, Stockner and MacIsaac 1996; Shortreed et al. 2001). Glacial lakes, by contrast, tend to be more turbid and colder, with productivity strongly limited by light availability (Lloyd et al. 1987, Stockner et al. 1993; Shortreed et al. 2001). Therefore, previous researchers have used these three categories of water clarity – clear, glacial, and stained – when seeking to characterize patterns of sockeye lake productivity (Edmundson and Carlson 1998, Shortreed et al. 2007).

Linking landscape conditions to lake productive capacity would be particularly useful in remote regions where population monitoring, and routine collection of full growing season PR data is challenging. On the North and Central coast (NCC) of British Columbia, sockeye salmon support important subsistence and commercial fisheries, and many populations have shown declining productivity and abundance in recent decades (Peterman and Dorner 2012). There are at least 157 lake systems supporting populations of sockeye (Holtby and Ciruna 2007), and each is considered sufficiently genetically or demographically distinct to justify protection and management as a conservation unit (CU). From low elevation NCC coastal lakes to the mountainous watersheds in the interior, such as those of the Skeena and Nass Rivers, these sockeye populations represent the diverse evolutionary and ecological legacy of their species (Wood et al. 1994). Given their remote nature and the limited resources for fish and fish

habitat monitoring, many stocks lack basic assessment information. To understand the physical, chemical, and biological factors limiting freshwater productivity of sockeye salmon in Canada, Fisheries and Oceans Canada's (DFO) Lakes Research Program conducts limnological surveys of sockeye salmon nursery lakes to estimate lake foodweb productivity and structure, producing habitat-based estimates of optimal adult and juvenile production through application of the PR Model (Hume et al. 1996, Shortreed et al. 2000, Cox-Rogers et al. 2010). For this purpose, growing-season (i.e. May to October) limnological assessments have occurred for 61 lakes across the NCC (e.g. Shortreed et al. 2000, Shortreed et al. 2007). In the NCC, these physical, chemical, and biological conditions have not been integrated into landscape-scale predictive models to provide broader insights into regional patterns of PR and sockeye production. Therefore, there is interest in developing a regional-scale predictive model which links easily-derived landscape metrics to PR, providing model predictions of sockeye population capacity for the 96 lakes where data is currently lacking.

Our goal was to predict PR across the NCC region by understanding the linkages between biophysical and geomorphic conditions related to productivity at the lake and landscape level. We used principal component analysis (PCA) to examine regional-scale patterns of lake productivity and the landscape characteristics that underpin regional variation in limnological conditions and lake rearing capacity. Using models linking landscape and hydrological conditions in 61 lakes to their observed PR, we developed a quantitative framework for broadly predicting PR across 96 previously unsampled sockeye lakes. These estimates can inform future detailed assessment, management planning, and evaluation of stock status, particularly when habitat-based productive capacity estimates are used as benchmarks for population assessment in data-limited sockeye populations (Cox-Rogers et al. 2010). More broadly, this work highlights opportunities to apply landscape approaches to inform the management and conservation of data-limited and culturally-important systems.

4.3. Methods

Limnological data and PR estimates

Estimates of individual lake PR were obtained from a series of DFO reports estimating annual primary productivity and juvenile rearing capacity for each of the 61

lakes (Table S4.1). PR estimates were derived using *in situ* light and dark bottle incubations, spanning the euphotic zone of each lake, from which the autotrophic uptake of ^{14}C isotopes was measured (Shortreed et al. 2000). These measurements are integrated with concurrent euphotic depth data and morphometry to yield photosynthetic rate estimates ($\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). In most instances, lakes were monitored monthly throughout the growing season (e.g. May-October), and growing season averages were used. However, in more remote lakes only a single late-summer sampling occurred, and seasonal mean PR estimates were estimated from the equation for NCC lakes ($\text{PR}_{\text{seasonal mean}} = 0.7479(\text{PR}_{\text{fall}})$; $r^2=0.60$, $P < 0.05$, $n = 113$) (Cox-Rogers et al. 2004). For lakes with multiple years of data, we took the average of available seasonal mean PR estimates.

In the sockeye salmon PR rearing capacity model developed by Hume et al. (1996), estimates of mean growing season production are converted to total lake-wide growing season production by multiplying mean daily PR by lake surface area of the focal lake and growing season length. Total growing season production is related to sockeye juvenile rearing capacity because juvenile production is limited by the productivity of lake foodwebs (Hume et al. 1996, Shortreed et al. 2000). Given the scarcity of robust timeseries of sockeye spawner abundance, these PR model estimates of lake capacity have been used as stock-specific benchmarks for evaluation of stock status in data-limited sockeye populations in the Skeena watershed (Cox-Rogers et al. 2010).

Landscape variables

Previous investigations of sockeye salmon nursery lake productivity have revealed major biological and physical differences related to lake water clarity (i.e., stained, glacial, clear) (Edmundson and Carlson 1998, Edmundson and Mazumder 2001, Shortreed et al. 2007). Preliminary data exploration revealed strong gradients in lake productivity associated with these water clarity groups, and we included lake water clarity as a categorical, independent variable in all models. For the 96 unsampled lakes where water clarity was unsurveyed, we assigned a water clarity based on the values assigned to surrounding lakes and confirmed lake color using Google Earth™ imagery.

We selected a suite of 11 landscape and lake variables, derived using ArcMap 10.3 Geographic Information Systems (GIS) software, to be used as potential predictor

variables for lake productivity. These variables were chosen based on specific hypothesized relationships between landscape and productivity of freshwater ecosystems (Table 4.1). These variables included lake specific variables and watershed level variables. More specifically, the lake variables were: latitude, categorical water clarity (stained, clear, glacial), distance to coast (m), and the ratio of lake perimeter to surface area (perimeter-to-area ratio). Lake specific information was obtained from the British Columbia Freshwater Atlas, with the distance to coast (m) variable being measured as a straight line from the lake outlet to the nearest coastline.

Watershed variables, defined as the watershed area upstream from the outlet of each respective sockeye-bearing lake (n=157) included, watershed elevation (mean and max), mean watershed slope, the proportion of upstream watershed occupied by lakes and bogs (upstream lake), the proportion of upstream watershed occupied by the focal lake (lake-to-watershed proportion), % glacial cover, % forested, annual precipitation and mean growing season temperatures. Watershed area, elevation and slope were derived using a 20 m digital elevation model (DEM). Glacier area was obtained from the Randolph Glacier Inventory (RGI Consortium 2017), vegetation data (tree cover specifically) was obtained from the Vegetation Resources Inventory with data inputs ranging from 1990-2018, and percent cover data were calculated using respective watershed area. We obtained historical climate data using the ClimateBC tool (Wang et al. 2016), whereby we estimated annual precipitation and mean growing season temperatures evenly across each watershed based on the climate normal period (1975-present) overlapping the period when PR data was collected. For the purpose of air temperature data, growing season was defined as May through August. Because of low topographical relief we were not able to obtain separate watershed characteristics for the lower and middle Mikado lakes, and therefore combined the two lakes into a single data point for our analysis.

Four variables, the proportion of watershed area occupied by the sockeye-rearing lake (referred to hereafter as 'lake-to-watershed proportion' ~ lake area/watershed area), the proportion of upstream watershed area occupied by lakes and bogs (referred as 'upstream lake' ~ upstream lake area/watershed area), and the landcover variables (proportion glacier cover and proportion tree covered) were transformed using logit transformations commonly applied to proportion data. Another derived variable (termed 'perimeter-to-area ratio') intended to capture the littoral

influence of a given lake was the ratio of perimeter (m) to surface area (m²) for a given lake, and was natural-log transformed.

Principal Components Analysis

We used Principal Components Analysis (PCA) to evaluate the association between all 11 lake and landscape variables and the degree of geomorphic differentiation between lakes of different clarity groups (stained, glacial, clear) for all 157 sockeye rearing lakes across the NCC. The degree of differentiation was interpreted visually, but also using PCA loadings (Table S4.2).

Model selection and lake predictions

PCA and preliminary data exploration both revealed a high degree of correlation among some landscape variables. To reduce the number of candidate variables and eliminate problems associated with collinearity, we performed stepwise variable reduction by estimating generalized variance inflation factors (VIF) for each continuous landscape variable among the candidate set and sequentially eliminated those with VIF scores greater than 10 (Craney et al. 2002). This procedure was repeated until only variables with VIF less than 10 remained among the candidate set. This eliminated mean watershed elevation, max watershed elevation, and distance from coast from our candidate variable set.

We then compared a suite of multivariate linear mixed-effects models relating the remaining landscape variables (1. latitude, 2. water clarity category, 3. upstream lake, 4. perimeter-to-area ratio, 5. watershed slope, 6. lake-to-watershed proportion, 7. tree cover, 8. glacier cover) to lake PR for the 61 lakes with available PR data, and evaluated the support for each combination of landscape variables in explaining PR across the NCC using Akaike's Information Criterion for small sample sizes (AICc) (Burnham and Anderson 2002). All models included a random effect of watershed identity to account for the fact that multiple lakes were nested within some watersheds (e.g., Kispiox, Atnarko). Lake PR was natural-log transformed to meet the assumptions of normality associated with linear modeling. We limited the number of interactions considered to a single potential interaction between our categorical variable water clarity and latitude. Given differences in light penetration, heat retention, and nutrient availability, we

hypothesized that changes in temperature and growing season length could manifest differently across water clarity categories. Further, data visualization suggested differences in the slope of the relationship between latitude and productivity across the lake clarity types (Figure 4.3b). We evaluated all additive combinations of variables, as well as the interaction between water clarity and latitude, using the dredge function in R (R-package MuMIn version 1.42.1; Bartoń 2018). Because AICc identified several models with a high degree of support, we estimated model-averaged coefficients for all models within 4 delta units of the top model ($n = 19$). The sensitivity of model predictions to the delta AICc threshold chosen was evaluated and deemed to be minimal (Figure S4.1). To further evaluate fit for models selected using AICc, we computed conditional R-squared values using piecewiseSEM in R (R-package piecewiseSEM version 2.0.2; Lefcheck 2018). All models contained watershed as a random variable, and conditional R-squared values facilitated evaluation of differences in model fit given differing fixed effects.

Predictions of lake PR in the 96 previously unsampled lakes were generated using the predict function in R (R-core development team). We generated AICc weighted predictions using model-averaged coefficients, as described above. These coefficients reflect the effect of each parameter on lake PR across the full suite of models, therefore parameters included in all of the top models exerted greater influence on predicted lake PR than those appearing in fewer models. Given that only 10 of the 96 unsampled lakes fell in watersheds included in our dataset of 61 lakes, we excluded the random effect of watershed from the predictive model.

4.4. Results

Variation in lake conditions and PR

Geomorphology, hydrology, and climate vary widely among sockeye lakes in the NCC. Lake elevations ranged from a minimum of 5 m above sea level (asl) in Bonilla, Curtis and Moore Lakes, to 1448 m asl for Johanson Lake in the Sustut watershed, a tributary of the Skeena River. Accordingly, annual rainfall and temperature varied dramatically between low elevation coastal and mountainous interior watersheds. Mean annual precipitation in coastal watersheds was 3,879 mm, compared to 974 mm in interior watersheds. Growing season temperatures also reflected strong climatic

gradients, with interior watersheds experiencing a mean air temperature of 9.21 °C from May through August, and coastal watersheds having a mean air temperature of 11.65 °C during that same period.

Stained lakes tended to be concentrated along the coast in the NCC, while clear water lakes were found primarily in the interior. Glacial lakes were more evenly distributed but concentrated in watersheds with higher elevations (Figure 4.1). These clarity categories were associated with significant differences in limnological conditions and productivity. Euphotic depth, alkalinity, and pH were highest in clear lakes. Stained lakes had the most acidic water (mean pH = 6.02), compared to less acidic glacial lakes (6.59), and neutral clear lakes (6.95) ($p < 0.0001$). These physical differences were associated with differences in chlorophyll concentrations among lake clarity groups, with clear lakes having significantly higher concentrations of chlorophyll ($p = 0.0046$) (Figure 4.2).

Variation in lake biophysical conditions and regional variations in landscape, climate, and lake clarity were associated with significant differences in mean lake photosynthetic rate ($p < 0.001$). Clear water lakes had the highest PR ($124.87 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), while both glacial ($39.22 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), and stained lakes ($63.87 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) had significantly lower mean PR (Figure 4.3).

Principal Components Analysis

PCA revealed strong differentiation by water clarity category, with the landscape characteristics for watersheds having stained water diverging strongly from those with either clear or glacial water (Figure 4.4). The first two principal components explained 49.4%, and 18.1% of the total variance in landscape conditions respectively. While several variables loaded relatively strongly on PC1, watershed elevation (mean and max) had the strongest negative loadings, while mean growing season temperature and annual precipitation had the strongest positive loadings. PC2 was dominated by strongly positive loadings of watershed slope and annual precipitation, with slightly weaker negative loadings on distance from coast, upstream lake area, tree area, and perimeter-to-area ratio (Table S4.2).

In general, PCA results indicated clustering among lake water clarity types. Stained lakes clustered tightly, and were associated with landscape characteristics such as high annual precipitation (loading J) and growing season temperatures (K), and low elevation lakes and watersheds (D). Glacial and clear water lakes exhibited less clustering, indicating a greater degree of variation in geomorphic and climate conditions among these two categories, with significant overlap between the two. However, in general glacial lakes tended to be found in catchments with the highest watershed elevations (D), glacialized area (H), watershed slopes (F), and coolest growing season temperatures (K) (Figure 4.4).

Landscape v. PR relationships

AICc supported a range of possible model structures, with 19 different models falling within 4 delta units of the top model. These models all included water clarity, and the top model included only the main effects of water clarity, latitude and their interaction. The random effect of watershed was included in all models. Among the landscape and lake level variables considered, lake-to-watershed ratio (9 models), and perimeter ratio (8 models) appeared in the highest number of models receiving support. Mean watershed slope, % glacial cover, and annual precipitation did not appear in any of the top models suggesting that they explain very little additional variation in the lake PR data. Notably, a model including only the main effect of water clarity received the fifth highest level of support (weight = 0.062). Clear water lakes were the most productive, with model-weighted coefficients reflecting lower productivity for the stained lake category (-4.788, SE 8.857) (Table 4.3). Lake-to-watershed proportion had a positive coefficient estimate (0.0366, SE 0.154), indicating higher productivity in lakes which comprise a greater proportion of their watershed area. Higher values for perimeter-to-area ratio (-0.147, SE 0.187) had a negative effect on lake PR, such that lakes with longer shorelines relative to their surface area were less productive. The model also included a negative interaction between glacial lakes and latitude, with lower PR values among glacial systems as latitude increased (-0.246, SE 0.298) (Figure 4.3). Contrasting the negative trend in PR among glacial lakes as latitude increased, there was a slight trend towards higher productivity in both clear and stained lakes as latitude increased (Table 4.3, Figure 4.3). Among the other landscape variables explored, % tree cover (6 models), upstream lake area (4 models), and mean growing season temperature (3

models), appeared in several of our top models (Table 4.2). Estimated coefficient values for % tree cover (-0.061; SE 0.123) and upstream lake area (-0.0373; SE 0.105) were both negative, while growing season temperature had a slight positive effect on estimated PR (0.18; SE 0.059). All were highly uncertain.

Predicted lake PR

Model averaged predictions of lake PR ranged from 10.14 to 139.50 ($\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), and on average clear lakes were more than twice as productive as stained lakes and almost ten times as productive as glacial lakes. Given the distribution of lake clarity across the NCC – with a high proportion of stained lakes in low elevation coastal watersheds – predicted lake PR showed spatially coherent patterns of productivity across the region. Among the stained lakes, the highest predicted PR values were in the north in Haida Gwaii and in watersheds around the lower Skeena River, while the lowest predicted PR values were in the more southerly, low elevation watersheds in the Hecate Lowlands. Lakes with the highest predicted PR included Kimsquit (139.50; SE 1.85), Hodder (107.6; SE 1.35), and Damshilgwit (105.48; SE 1.32), all clear water lakes. Kimsquit is a highly mountainous drainage in a coastal fjord and has virtually no drainage area above the lake, while Hodder and Damshilgwit are both interior watersheds. (Map – Figure 4.5, Predictions – Table S4.3). Among the lakes with the lowest predicted PR, Lower & Upper Kluatantan (10.14 & 10.74; SE 1.80), Oweege (11.88; SE 1.75) were all glacial lakes.

4.5. Discussion

Our findings revealed strong, regionally-coherent patterns of sockeye lake productivity across the NCC. Consistent with previous studies, variation in lake biophysical conditions and PR were closely associated with water clarity, reflecting variable light penetration, euphotic volumes and possibly relative nutrient bioavailability (Hume et al. 1996; Shortreed et al. 2000; Shortreed et al. 2007), and was further informed in our study by landscape variables at lake and watershed scales. PCA analysis of 11 candidate variables related to geomorphic and climatic conditions within the watersheds of 157 sockeye rearing lakes revealed clustering by water clarity, suggesting that strong physical and climatic gradients underpin differences in water

clarity and lake productivity. Given this strong, regionally-coherent variation in lake productivity, and the degree to which variation in lake PR was effectively explained by a suite of landscape variables, we generated predictions for 96 sockeye lakes where empirical estimates of lake PR have not yet been made.

Categories of water clarity (clear, glacial, stained) have long been known as an important correlate of lake productivity (Stockner and McIsaac 1996, Edmundson and Mazumder 2001, Shortreed et al. 2007). Clarity may influence lake productivity through several pathways, including physical limitation via reduced light penetration in humic stained and glacial lakes (Lloyd et al. 1987, Xenopoulos et al. 2003), dampening or amplifying seasonal stratification with effects on lake mixing and nutrient limitation (Stockner and Shortreed 1989, Fee et al. 1996), and mediating the bioavailability of phosphorus and other limiting nutrients (Jackson and Hecky 1980, Edmundson and Carlson 1998, Maranger and Pullin 2002). In the NCC region the distribution of lake clarity types is non-random, with stained lakes concentrated in coastal watersheds with high winter rainfall and peak discharge and occurring between January and March. Clear lakes typically occupy interior watersheds with snowmelt-dominated hydrology and peak discharge during late spring (Stockner and Shortreed 1985, Stockner and Shortreed 1989). Lacking seasonal ice cover, coastal lakes are typically monomictic, while interior lakes with continental climates and winter ice cover tend to exhibit dimictic stratification (Stockner 1987, Stockner and Shortreed 1989). Most coastal and interior lakes are oligotrophic, but stained coastal lakes are particularly unproductive. High winter discharge delivers nutrients to coastal lakes during a period when lakes are well mixed and light availability is low, yielding low rates of biological production and limited nutrient retention within lake food webs. Interior lakes by contrast receive peak water and nutrient inputs during the late-spring and early-summer when lakes are beginning to stratify, producing higher rates of nutrient uptake and retention, and higher primary production (Stockner and Shortreed 1985). Glacial lakes are distributed across the longitudinal extent of the NCC. Given their typically mountainous drainages and the contribution of glacial meltwater to their hydrology, glacial lakes typically receive high inputs of water and suspended sediment during spring and summer runoff season, driving physical limitation of biological productivity stemming from high turbidity and shallow euphotic depth (Lloyd et al. 1987, Stockner and MacIsaac 1996, Edmundson and Carlson 1998).

Our results revealed evidence for an interaction between water clarity and latitude, with a negative trend in glacial lake PR moving north across our study systems, but none for clear or stained lakes. If turbidity and its effects on light availability are key limiting factors in glacial systems, then primary productivity in more northerly watersheds with larger inputs of glacial meltwater and sediment may be limited to a greater degree by light availability. Furthermore, a higher proportion of phosphorus in glacial lakes is nonbiologically available, and the bioavailability of phosphorus may decline in the presence of higher glacial turbidity (Edmundson and Carlson 1998). Over broad geographic scales latitude is a good predictor of primary productivity in lakes (Håkonsen and Boulion 2001), however with the exception of glacial lakes, relationships between latitude and PR in other clarity categories were weak and opposite of the predicted direction.

While lake water clarity and latitude explained a large proportion of the variance in lake PR, the geomorphic and climatic attributes of lakes and their watersheds also played an important role in explaining lake productivity. For example, the estimated effect of lake-to-watershed ratio suggests higher productivity in lakes which occupy a larger proportion of their watershed, and the negative effect of perimeter-to-area ratio indicated lower productivity in lakes with more complex shorelines. Lakes which occupy a large proportion of their watershed area have lower flushing rates and thus retain water and nutrients longer, permitting autotrophic attenuation (Kratz et al. 1997). The estimates of PR used for lakes in the NCC reflect rates of limnetic primary production, and do not account for littoral production (Cox-Rogers et al. 2004). Lakes with complex shorelines have more shallow-water littoral habitat supporting benthic algae and macrophytes to comprise a larger proportion of lake-wide primary production and nutrient uptake (Jeppesen et al. 1998, Vadeboncouer et al. 2002). In highly oligotrophic systems such as those found in coastal British Columbia, increased primary production and nutrient uptake in the littoral zone may further reduce rates of limnetic production measured by lake PR, particularly given low rates of coupling between littoral and limnetic zones (France 1995). This source of production is not captured in pelagic-focused modeling (e.g. PR Model, Hume et al. 1996, Shortreed et al. 2000), however its contribution to energy flows supporting juvenile sockeye salmon is largely unquantified. Freshwater lake-rearing sockeye salmon feed primarily on limnetic zooplankton, but in some instances consume littoral aquatic and terrestrial invertebrates (Narver et al. 1970,

Hume et al. 1996). PR model estimates of lake rearing capacity for sockeye salmon do not currently account for littoral production. Capacity estimates in systems with complex shorelines and large areas of shallow water habitat may therefore underestimate juvenile rearing capacity for sockeye (Cox-Rogers et al. 2004).

While predictions of lake PR serve as meaningful approximations of lake productivity and its influence on secondary production for planktivores, lake PR may be more representative of total lake-wide production in some systems than others. Microbial pathways often contribute substantially to production in lake ecosystems (Porter et al. 1988, Weisse 2005), particularly in highly stained lakes where high rates of microbial production can produce net heterotrophy (Jansson et al. 2000, Ask et al. 2009). Food web structure and community composition often differentiate strongly between stained and clear lakes in the coastal British Columbia and Alaska (Stockner 1987, Stockner and Shortreed 1989, Koenings et al. 1990). With strong nutrient limitation and low rates of autotrophic production, stained lakes typically have high concentrations of picoplankton, and a greater dependence on microbial pathways for basal production (Stockner 1987, Stockner and Shortreed 1989). Given their small size, the high abundance of picoplankton and bacteria in stained lake food webs adds additional trophic levels between primary production and planktivorous fish (Stockner and Shortreed 1989). Unproductive stained and glacial lakes often lack *Daphnia* and other large-bodied cladocerans, with limnetic grazer communities dominated by rotifers and other smaller-bodied zooplankton (Stockner and Shortreed 1989, Koenings et al. 1990). These small zooplankton may serve as an energy sink if they are too small to be consumed by planktivorous fish (O'Neill and Hyatt 1987, Stockner and Shortreed 1989). These differences in food web structure ultimately reduce the amount of energy available to higher trophic levels in the limnetic foodwebs of stained lakes. Heterotrophic energy flows therefore represent an important and currently unquantified contributor to lake energy budgets, and may constitute a majority of lake-wide production in some instances (Nürnberg and Shaw 1999). We urge the development of trophic models of juvenile rearing capacity that account for the diversity of trophic pathways supporting food webs in coastal lakes, particularly since changes in nutrient availability (Weisse and MacIsaac 2000) and DOM inputs (Jansson et al. 2000) can act to modulate the importance of microbial pathways in lake food webs.

Regardless, estimating lake PR and the composition of lake autotrophs is an essential part of quantifying lake productivity and its effects on juvenile sockeye rearing capacity, making ongoing limnological assessment a vital component of managing lake-dependent sockeye populations. Lake PR and total food web productivity can exhibit both directional and stochastic change (Fee 1980) in response to climate and hydrologically mediated variability in the delivery of nutrients and organic material (e.g. Jansson et al. 2000), and changes in the biogenic delivery of nutrients via spawning salmon (Stockner and MacIsaac 1996, Schindler et al. 2005, Chen et al. 2011). Climate change may therefore drive changes in nutrient dynamics and lake productivity in unexpected ways (Adrian et al. 2009) as the hydrology of many systems transitions from snowmelt to rain-dominated (Klos et al. 2014), and ongoing declines in the survival of salmon in the ocean reduce the delivery of salmon derived nutrients to coastal watersheds (Larkin and Slaney 1997). In light of the dynamic nature of sockeye rearing lakes, continued monitoring of lake food web productivity and structure will provide necessary insight into the physical and biological conditions that drive the freshwater population dynamics of sockeye.

Canada's Wild Salmon Policy (WSP) was established in 2005 with the goal of protecting wild salmon for the benefit of Canadians in perpetuity. Among the goals of the WSP is the establishment of conservation benchmarks for management and recovery. On the remote NCC of British Columbia access to many sockeye rearing lakes is difficult, posing significant challenges for population and lake monitoring. As a result, almost 70% of sockeye salmon populations in the region are currently lacking sufficient timeseries of spawner abundance to evaluate stock status (Pacific Salmon Foundation 2018). To better understand the productivity and juvenile rearing capacity of data-limited sockeye lakes, DFO has conducted rotational limnological sampling in many sockeye rearing lakes across the NCC (e.g. Shortreed et al. 1998, Shortreed et al. 2007) since the 1970s. These monitoring efforts have provided key insights into ecosystem conditions in sockeye rearing lakes, as well as estimates of sockeye carrying capacity that have been used as benchmarks for evaluating current conservation status. However, to date sampling has occurred in fewer than 65 of the 157 sockeye rearing lakes on the NCC. Through our landscape modeling, we generated predictions of photosynthetic rates for the 96 previously unsampled lakes known to support rearing sockeye.

Landscape ecology perspectives and approaches are increasingly being applied to aquatic systems, with researchers and conservation practitioners seeking to understand the influence of spatial patterns, landscape context, and linkages between adjacent habitat patches for aquatic ecosystem structure and function (Wiens 2002). Landscape-scale models have been proposed for classification and management of aquatic ecosystems in regions where monitoring and managing individual lakes or stream ecosystems may be infeasible (Soranno et al. 2010). These approaches are tailored to the needs of resource managers attempting to inform management across broad spatial scales in data-limited landscapes. Given the remote nature of NCC lakes and the cost and logistical challenges associated with monitoring, generating predictive models of ecosystem productivity or function can provide foundational insight for conservation and management. Model outputs will therefore provide interim estimates of lake juvenile rearing capacity, which can be improved through future sampling of lake trophic structure and productivity.

Our results demonstrate the close links between lake and landscape attributes and lake primary productivity, yielding predictions of lake PR for remote watersheds across the NCC which have previously been unsampled. Given previous research linking lake PR to sockeye juvenile rearing capacity (Hume et al. 1996), our findings and the resulting predictions of lake PR will provide a valuable starting point for evaluating the productive potential of sockeye rearing lakes across the NCC. However, these predictions should not be viewed as a substitute for robust limnological and population monitoring, which are essential for precautionary management of fisheries and detection of environmental changes. Efforts are currently underway to assess the status of data-poor sockeye populations in British Columbia and understanding the links between lake and landscape characteristics and lake PR will serve as an important stepping stone towards evaluating conservation status and developing data-driven management approaches for sockeye populations with limited data.

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4.7. References

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4.8. Tables

Table 4.1 Predicted relationship between 11 candidate variables and lake photosynthetic rate.

Landscape feature	Hypothesis
Latitude	Latitude influences temperature and growing season length, and is correlated with lake productivity (Håkanson and Boulion 2001)
Water clarity category (clear, glacial, stained)	Humic stained, glacially turbid, and clear water lakes exhibit distinct physical and biological conditions. These differences in nutrients, light, pH, seasonal temperature stratification, and trophic structure act to control primary productivity contributing to regional variation in lake productivity (Lloyd et al. 1987, Stockner and McIsaac 1996, Jansson et al. 2000).
Distance from coast	Climatic and biogeographic variation from coastal to interior watersheds creates gradients in precipitation, temperature, land cover, hydrology, nutrient and sediment delivery. Accordingly, productivity varies moving inland from low coastal watersheds to mountainous and interior plateau lakes (Shortreed et al. 2007).
Mean watershed elevation	Elevation mediates temperature and growing season length, snowpack and hydrology (Isaac and Hubert 2001, Lisi et al. 2015). These physical factors underpin rates of biological productivity including lake PR.
Maximum watershed elevation	Maximum elevation captures the degree to which snowpack contributes to discharge during the growing season, stabilizing temperature, and controlling the timing of water and nutrient delivery (Lisi et al. 2015).
Upstream lake (Upstream lake area/Drainage Area)	The amount of upstream lake area can influence water chemistry, temperature and nutrient availability with potential implications for primary and secondary production (Quinlan et al. 2003, Sadro et al. 2012)
Perimeter-to-area ratio	Lake morphometry is related to primary production (e.g. Oglesby 1977). High lake perimeter ratio indicates greater extent of littoral habitat, increasing coupling between littoral and terrestrial habitat with lake nutrient dynamics and food webs (Vadeboncouer et al. 2002).
Watershed slope	Watershed slope is related to peak discharge and flushing rates, control nutrient delivery and export (Kamenik et al. 2001). Low watershed slopes may be associated with increased temperature accumulation (Lisi et al. 2015) and high delivery of dissolved organic carbon (Rasmussen et al. 1989).
Lake-to-watershed proportion (Lake Area/Drainage Area)	Lakes with larger upstream watersheds receive higher contributions of water and organic matter from upstream catchment (Rasmussen et al. 1989). Large upstream drainages relative to lake area influences pathways of water delivery and flushing rates, nutrient delivery and retention (Kratz et al. 1997).
Watershed % tree cover	Tree cover is related to temperature (Isaac and Hubert 2001), weathering and nutrient delivery (Kamenik et al. 2001) in lotic ecosystems, influencing rates of primary production.
Watershed % glacier	Glaciers linked to variation in timing and intensity of discharge, temperature, as well as sediment and nutrient delivery. Glacial turbidity may also limit euphotic depth and hinder primary productivity (Lloyd et al. 1987)

Table 4.2 AICc model selection for linear models of lake PR. Includes all models within 4 delta units of the top model and their respective weight. Colour indicates the categorical water-clarity variable. Interactions are denoted with colons, and all variables included in interactions are also included as main effects. All models also included a random effect of watershed to account for multiple lakes within some watersheds.

Rank	Model	logLik	AICc	Δ	ω	R ²
1	~ colour : latitude	-58.116	135	0	0.146	0.487
2	~ colour : latitude + perimeter ratio	-57.263	136.1	1.05	0.086	0.519
3	~ colour + perimeter ratio	-61.316	136.2	1.19	0.081	0.389
4	~ colour : latitude + lake watershed ratio	-57.417	136.4	1.36	0.074	0.506
5	~ colour	-62.809	136.7	1.71	0.062	0.339
6	~ colour + perimeter ratio + tree area	-60.361	136.8	1.83	0.058	0.432
7	~ colour + perimeter ratio + tree area + lake watershed ratio	-59.055	136.9	1.88	0.057	0.465
8	~ colour + perimeter ratio + lake watershed ratio	-60.484	137.1	2.08	0.051	0.414
9	~ colour + perimeter ratio + tree area + lake watershed ratio + upstream lake	-57.915	137.4	2.36	0.045	0.495
10	~ colour : latitude + perimeter ratio + lake watershed ratio	-56.539	137.5	2.48	0.042	0.538
11	~ colour + growing temp	-61.982	137.5	2.52	0.041	0.388
12	~ colour + lake watershed ratio	-62.015	137.6	2.58	0.04	0.363
13	~ colour : latitude + lake watershed ratio + upstream lake	-56.596	137.6	2.59	0.04	0.527
14	~ colour : latitude + upstream lake	-58.187	137.9	2.9	0.034	0.495
15	~ colour + perimeter ratio + growing temp	-60.927	138	2.97	0.033	0.426
16	~ colour : latitude + growing temp	-58.238	138	3.01	0.032	0.506
17	~ colour + tree area	-62.41	138.4	3.37	0.027	0.368
18	~ colour + tree area + upstream lake + lake watershed ratio	-59.847	138.5	3.46	0.026	0.429
19	~ colour + tree area + lake watershed ratio	-61.236	138.6	3.58	0.024	0.400

Table 4.3 Model averaged coefficient estimates for the effect of landscape and climate variables on the natural log of lake PR from AICc model selection. The number of models each variable appears in is reported in the right column.

Variable	Coefficient	SE	No. models
Intercept	3.78	5.17	--
Water clarity (Stained)	-4.788	8.857	19
Water clarity (Glacial)	11.862	16.436	19
Lake-to-watershed ratio	0.206	0.322	9
Perimeter ratio	-0.147	0.187	8
Stained : latitude	0.075	0.165	7
Glacial : latitude	-0.246	0.298	7
Latitude (°N)	0.004	0.090	7
Tree area proportion	-0.06	0.123	6
Upstream lake	-0.0373	0.105	4
Mean growing season temperature (°C)	0.018	0.059	3
Watershed slope	0.000	NA	NA
Glacier area proportion	0.000	NA	NA

4.9. Figures

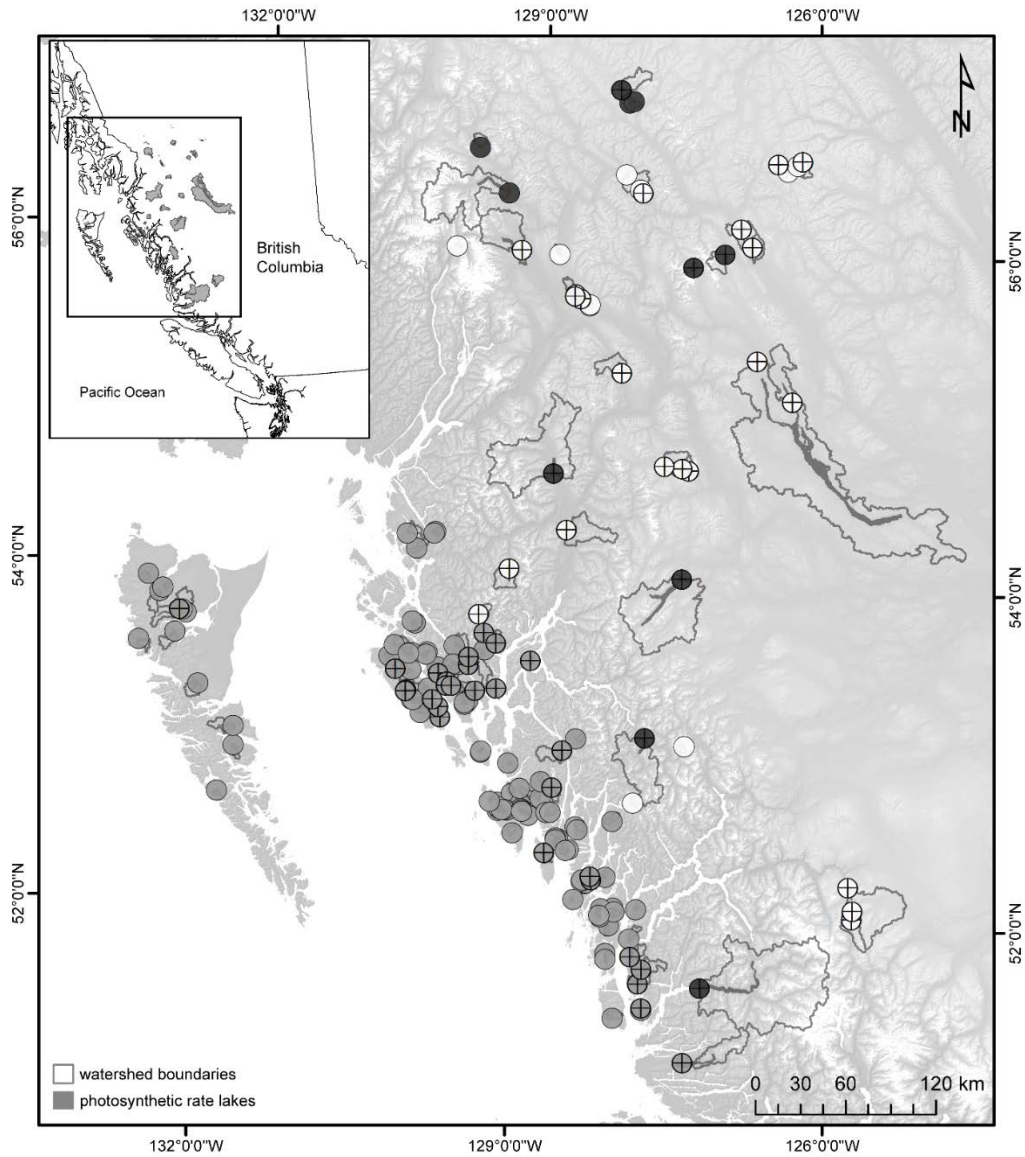


Figure 4.1. Map of focal watersheds across the NCC region of British Columbia. Shades indicate water clarity category – stained (light grey), clear (white), glacial (dark grey) – with cross hatched points representing watersheds with photosynthetic rate data, and solid points representing previously unsampled lakes (n = 157).

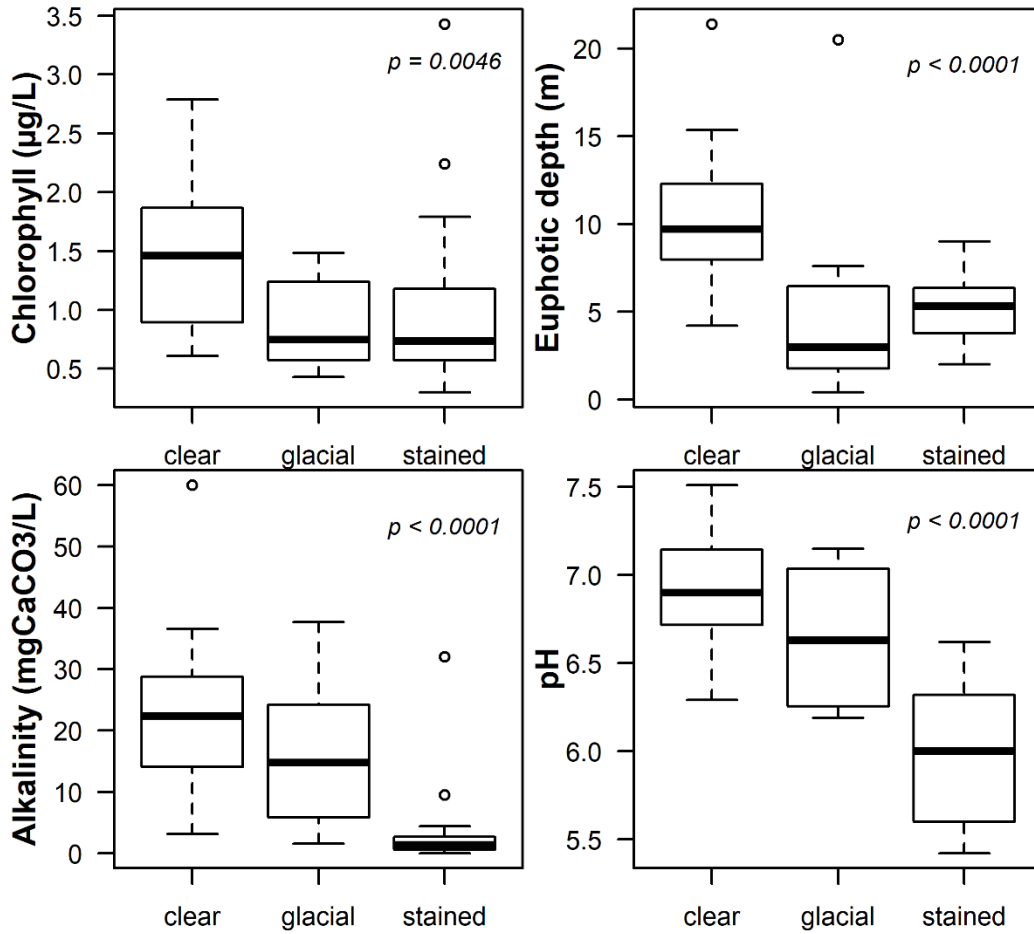


Figure 4.2. Differences among water clarity categories for four measures of lake biophysical conditions. P-values indicate model-wide significance of lake clarity category for each response variable.

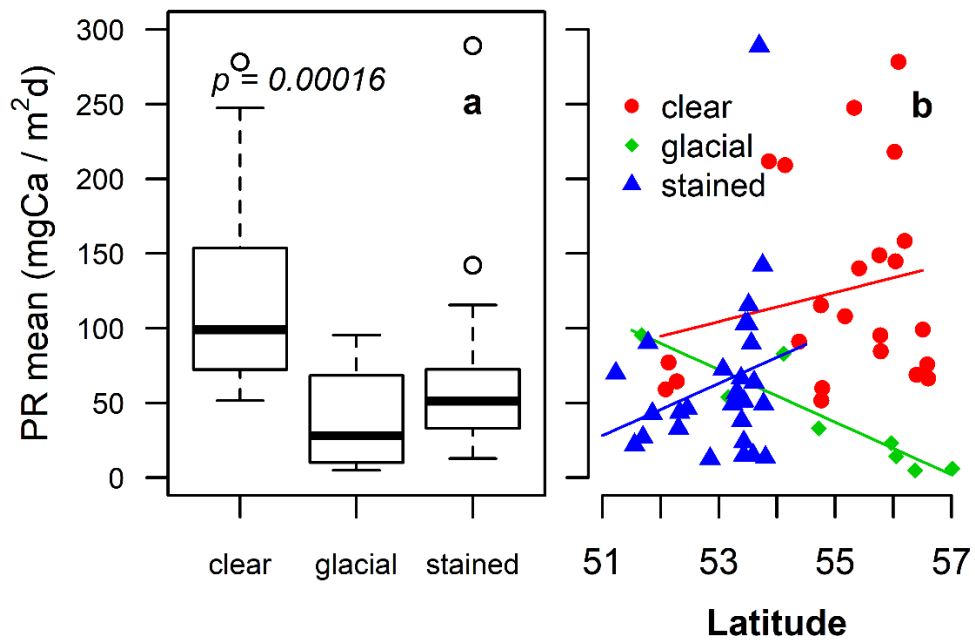


Figure 4.3. (a) Daily mean photosynthetic rate (PR), p-value indicates statistical significance of differences in PR across lake clarity categories, and (b) the interaction between clarity and latitude for mean PR, lines indicate directional trend in interaction between latitude and PR (n = 61)

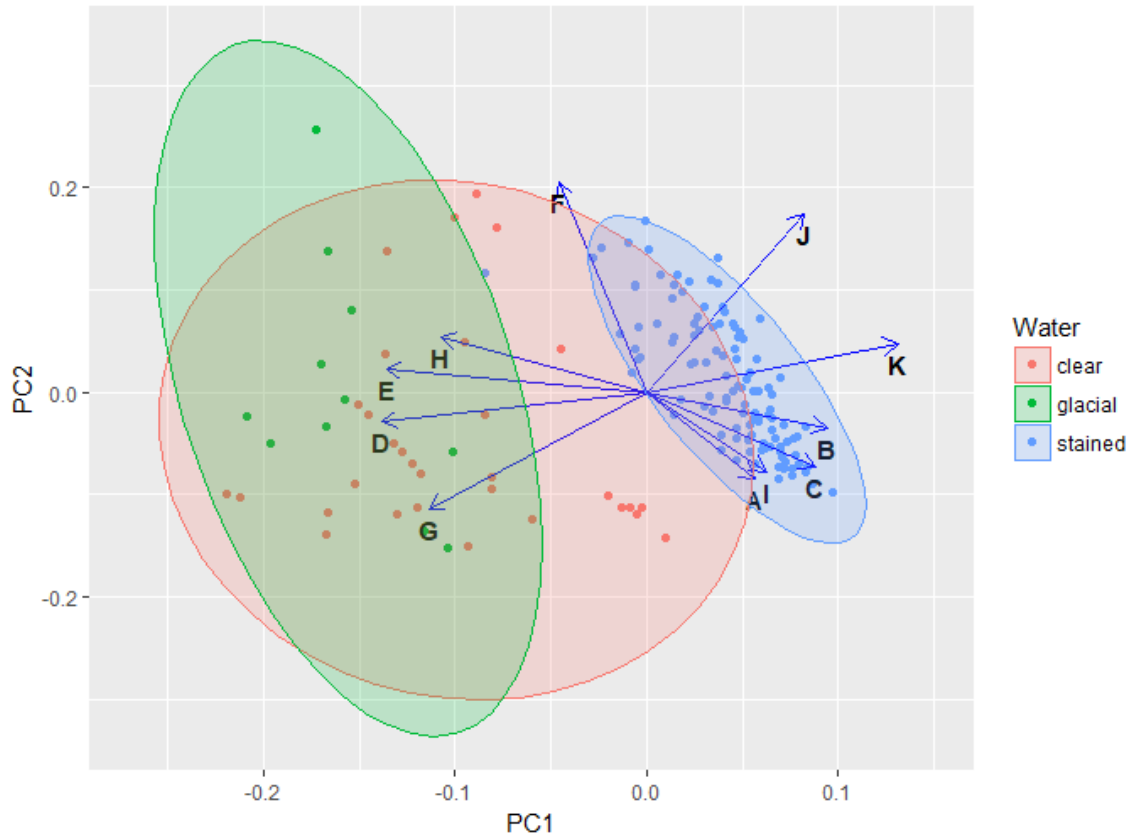


Figure 4.4. PCA biplot depicting first two principal components of geomorphic and climate conditions for 157 sockeye bearing lakes in the NCC. Letters represent loadings for landscape variables: (A) upstream lake area, (B) proportion of watershed occupied by focal lake, (C) perimeter-to-area ratio, (D) mean watershed elevation, (E) max watershed elevation, (F) watershed slope, (G) distance from coast, (H) glacial coverage, (I) tree coverage, (J) annual precipitation, and (K) mean growing season temperature. Hypothesized linkages between landscape variables and lake photosynthetic rate are presented in Table 4.1

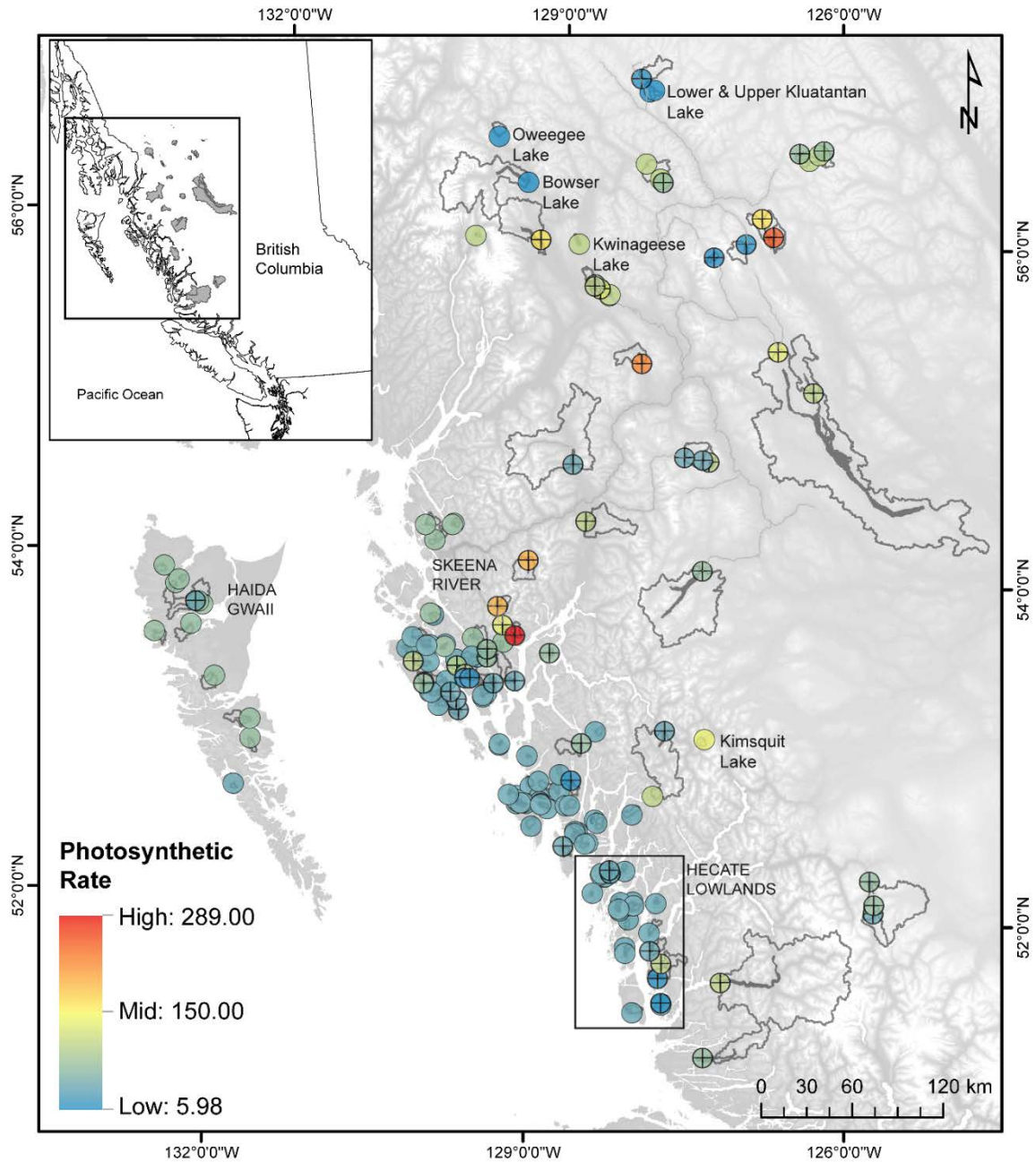


Figure 4.5. Map of measured (cross hatched) predicted (solid) mean daily photosynthetic rate (PR) for 157 lakes on British Columbia's NCC. PR data is summarized in Table S4.1 and mean predictions and uncertainty for PR in unsampled lakes are presented in Table S4.3

4.10. Supplemental Materials

Table S 4.1 Data and references for empirical estimates of lake photosynthetic rate. Area is reported in hectares, and PR is in mgCm⁻²d⁻¹

Lake	Watershed	Years	Freq.	Area	PR mean	S _{MAX} _PR	Study
Alastair	Gitnadoix	1978	multiple	686	209.00	49,064	1
Aldrich	Zymoetz	2001	single	64	115.19	2,523	7
Azuklotz	Bear	2003	single	219 46,10	278.26	20,854 2,208,62	7
Babine	Babine	1994-1995	multiple	0	140.00	3	2
Banks East	Banks	2004	single	204	38.15	2,663	4
Banks West	Banks	2004	single	160	66.57	3,645	4
Bear	Bear	1978, 2003	multiple	1,975	158.40	107,057	1, 4
Bloomfield	Bloomfield	2006	single	147	12.80	644	3
Bonilla	Bonilla	1979	multiple	220	115.64	8,706	2, 5
Bowser	Upper Nass	2008	single	3,409	6.60	5,610	8
Canooka	Canooka	2004	single	345	72.56	8,566	4
Club	Kispiox	2002	single	39	84.52	1,128	4
Curtis Inlet	Curtis	1979	multiple	300	103.00	10,574	2
Damdochax	Damdochax	2008	single	148	99.00	4,862	8
Deer	Deer	2004	single	323	49.37	5,457	4
Dennis	Zymoetz	2001	single	90	51.61	1,590	7
Devon	Devon	1979	multiple	174	103.00	6,133	2
Ecstall	Ecstall	2005	single	102	142.20	4,964	6
End Hill	End Hill	2008	single	219	15.00	545	8
Elbow	Atnarko	1999	single	150	59.09	3,033	4
Elizabeth	Elizabeth	2006	single	643	27.00	5,941	3
Evelyn	Evelyn	2001	single	59	63.58	1,284	4
Fred Wright	Kwinageese	1978	multiple	397	152.50	20,195	2, 8
Hartley Bay	Gabion	2005	single	93	51.39	1,635	6
Hoy	Hoy	2006	single	122	22.00	918	3
Ian	Ian	2005	single	1,878	49.40	31,748	6
Johanson	Sustut	1994	multiple	140	66.35	3,179	1
Johnston	Johnston	2005	single	186	211.70	13,475	6
Keecha	Keecha	2004	single	332	56.85	6,459	4
Kenzuwash	Kenzuwash	2008	single	66	7.20	170	8
Kilpatrick	Scoular	2008	single	43	3.10	40	8
Kitkiata	Kitkiata	2005	single	270	289.00	26,703	6
Kitlope	Kitlope	1978	multiple	1,170	54.00	21,621	2
Kitsumkalum	Kitsumkalum	1994	multiple	1,969	33.00	22,236	1
Kitwancool	Kitwancool	1995, 2003	multiple	777	247.50	65,810	1, 4
Kluayaz Lake	Kluayaz	2004	single	138	5.98	283	4

Lake	Watershed	Years	Freq.	Area	PR mean	S _{MAX} _PR	Study
Koeye	Koeye	2006	single	450	90.30	13,906	3
Kooryet	Kooryet	2004	single	509	55.35	9,641	4
Kwinageese	Kwinageese	2008	single	266	218.00	19,074	8
Lakelse	Lakelse	1994, 2003	multiple	1,460	91.00	45,466	1, 4
Lonesome	Atnarko	1999	single	410	64.33	9,026	4
Long	Long	1980	multiple	2,100	70.00	50,305	2
Lowe	Lowe	1978	multiple	390	89.93	12,002	2, 5
Mcdonell	Zymoetz	2001 1978,	single	223	59.84	4,567	4
Meziadin	Meziadin	1979, 2008	multiple	3,321	144.67	175,032	2, 8
Mikado Lower	Mikado	2001	single	148	14.96	758	4
Mikado Upper	Mikado	2001	single	119	23.94	975	4
Moore	Moore	2001	single	280	51.00	4,887	4
Morice	Morice	1980, 2001	multiple	9,754	83.00	277,047	2, 4
Morrison	Morrison	1995	multiple	1,460	108.00	53,960	1
Motase	Motase	2003	single	1,403	14.21	6,823	4
Namu	Namu	2006	single	317	42.90	4,654	3
Owekino	Owekino	1978, 2001	multiple	9,450	95.50	308,836	2, 4
Price	Price	2006	single	93	46.10	1,467	3
Rainbow	Atnarko	1999	single	170	77.04	4,482	4
Scoular	Scoular	2008	single	54	13.60	245	8
Sicintine	Sicintine	2004	single	72	23.19	571	4
Simpson	Lowe	1982	multiple	890	64.00	19,492	2
Slamgeesh	Slamgeesh	2001	single	41	68.82	966	4
Stephens	Kispiox	2002	single	187	148.85	9,526	4
Sustut	Sustut	1994	multiple	250	75.69	6,476	1, 5
Swan	Kispiox	1978, 2002	multiple	1,738	95.12	56,574	1, 4
Tankeeah Lower	Tankeeah	2006	single	151	33.00	1,705	3
Tankeeah Upper	Tankeeah	2006	single	129	43.70	1,929	3

Citations: (1) Shortreed et al. 1998, (2) Shortreed et al. 2001, (3) Shortreed and Hume 2007, (4) Shortreed et al. 2007, (5) Shortreed et al. 2000, (6) Hume and Shortreed 2006, (7) Cox-Rogers et al. 2004, (8) Shortreed and Hume 2009

Table S 4.2 Variable loadings and proportion of variance explained for each principal component

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
SD	2.33	1.41	1.02	0.90	0.81	0.66	0.57	0.37	0.32	0.24	0.12
Prop. variance	0.49	0.18	0.09	0.07	0.06	0.04	0.03	0.01	0.01	0.01	0.00
upstream_lake	0.17	-0.25	0.64	-0.21	-0.59	0.06	0.28	0.01	-0.05	-0.15	0.00
lake_watershed	0.28	-0.10	0.34	0.58	-0.03	-0.31	-0.59	0.11	-0.01	0.00	0.04
perim_ratio	0.26	-0.22	-0.06	-0.72	0.11	-0.02	-0.52	0.26	0.00	0.05	0.10
wat_elev_mean	-0.41	-0.09	0.01	-0.06	-0.17	-0.13	-0.17	0.19	-0.03	0.19	-0.82
wat_elev_max	-0.41	0.07	0.05	0.07	-0.23	0.02	0.01	0.50	-0.08	0.53	0.48
slope	-0.14	0.61	-0.10	-0.11	-0.31	-0.28	-0.13	0.25	0.01	-0.57	0.07
dist_coast	-0.34	-0.34	-0.08	-0.06	-0.12	-0.37	-0.05	-0.26	0.70	-0.07	0.20
glacier_logit	-0.32	0.16	0.31	0.02	0.07	0.72	-0.38	-0.12	0.26	-0.16	0.02
tree_logit	0.19	-0.23	-0.60	0.21	-0.59	0.35	-0.17	-0.01	-0.01	-0.05	0.00
annual_precip	0.25	0.52	0.05	-0.16	-0.28	-0.08	-0.14	-0.47	0.16	0.54	-0.06
growing_temp	0.39	0.14	0.00	0.09	0.09	0.14	0.25	0.52	0.64	0.08	-0.20

Table S 4.3 Predicted lake photosynthetic rate for 96 NCC lakes lacking assessment

Lake	Watershed	Clarity	Latitude	Longitude	PR _{mean}	SE
Ain	Ian	stained	53.756	-132.437	52.20	1.226
Asitka	Sustut	clear	56.544	-126.367	95.16	1.352
Awun	Awun	stained	53.636	-132.533	59.67	1.294
Backlund	Quall	stained	53.653	-129.407	60.27	1.384
Bolton	Bolton	stained	53.409	-129.951	39.85	1.385
Borrowman	Borrowman	stained	52.751	-129.209	47.88	1.306
Busey	Busey	stained	52.785	-128.789	47.92	1.162
Chic Chic	Calvert	stained	51.489	-128.014	38.82	1.329
Clements	Clements	clear	56.048	-129.904	100.67	1.399
Dallain	Dallain	stained	52.680	-128.899	42.15	1.253
Damshilgwit	Slamgeesh	clear	56.423	-127.959	105.48	1.320
Dome	Dome	stained	53.147	-128.456	48.57	1.174
Douglas Creek	Douglas Ck	stained	52.986	-129.121	38.54	1.377
East Kwakwa	Kwakwa	stained	52.548	-128.598	39.16	1.308
Eden	Marian Eden	stained	53.868	-132.722	63.99	1.407
Elsie	Hoy Elsie	stained	51.541	-127.740	42.15	1.296
Evinrude	Evinrude	stained	52.807	-129.074	44.52	1.283
Fairfax	Fairfax	stained	52.714	-131.980	46.46	1.189
Footsore	Kispiox	clear	55.726	-128.465	104.24	1.357
Freeda Brodie	Freeda Brodie	stained	53.670	-129.713	56.18	1.201
Hauyat	Hauyat	stained	52.039	-128.078	49.36	1.242
Hodder	Kispiox	clear	55.732	-128.461	107.60	1.349
Jalun	Jalun	stained	53.964	-132.855	54.54	1.343
Kainet	Kainet	clear	52.773	-127.872	104.52	1.395
Kdelmashan	Kdelmashan	stained	52.573	-129.050	35.59	1.428
Kent	Kent	stained	52.746	-128.981	44.62	1.208
Kenzuwash	Kenzuwash	stained	53.261	-130.019	45.775	1.208
Keswar	Keswar	stained	53.656	-130.317	43.89	1.321
Kildit	Kildit	stained	51.874	-128.102	43.07	1.260
Kilpatrick	Kilpatrick	stained	53.792	-130.119	43.19	1.403
Kimsquit	Kimsquit	clear	53.116	-127.376	139.50	1.852
Kisameet	Kisameet	stained	51.964	-127.873	48.23	1.248
Leverson	Splitmountain	stained	54.341	-129.964	57.96	1.293
Lower Cartwright	Cartwright	stained	53.044	-129.398	51.13	1.240
Lower Hevenor	Hevenor	stained	53.623	-129.983	49.60	1.232
Lower Kadjusdis	Kadjusdis	stained	52.144	-128.037	43.86	1.254
Lower Kluatantan	Kluatantan	glacial	56.940	-128.102	10.14	1.809
Lower Lewis	Lewis	stained	53.338	-130.113	41.75	1.337
Lower Limestone	Limestone	stained	52.706	-129.112	39.90	1.304

Lake	Watershed	Clarity	Latitude	Longitude	PR _{mean}	SE
Lower Monckton Inlet	Monckton Inlet	stained	53.323	-129.582	43.27	1.296
Lower Powels	Powels	stained	52.702	-128.723	40.06	1.291
Lower Ryan	Ryan	stained	53.615	-130.138	46.45	1.244
Lower Salter	Salter	stained	53.558	-129.661	43.32	1.316
Lower Ship Point	Ship Point	stained	52.090	-128.163	36.65	1.403
Lower Sockeye Creek	Sockeye Creek	stained	52.485	-128.492	37.85	1.337
Lower Talamoosa	Talamoosa	stained	52.718	-128.975	44.00	1.253
Marian	Marian Eden	stained	53.891	-132.695	61.76	1.253
Mary Cove	Mary Cove	stained	52.623	-128.433	41.57	1.262
Mathers	Mathers	stained	52.993	-131.852	58.86	1.704
McLoughlin	McLoughlin	stained	52.139	-128.155	42.92	1.291
Mercer	Mercer	stained	53.572	-132.890	49.69	1.270
Middle Cartwright	Cartwright	stained	53.050	-129.395	53.62	1.214
Middle Kwakwa	Kwakwa	stained	52.549	-128.622	42.78	1.232
Middle Limestone	Limestone	stained	52.710	-129.140	40.63	1.281
Middle Talamoosa	Talamoosa	stained	52.709	-128.966	47.12	1.199
Middle Treneman	Treneman	stained	52.703	-129.203	38.83	1.396
North Kwakwa	Kwakwa	stained	52.551	-128.622	41.62	1.253
North Treneman	Treneman	stained	52.713	-129.192	45.54	1.219
Oweegee	Upper Nass	glacial	56.640	-129.710	11.88	1.753
Pine	Pine	stained	52.661	-128.071	47.36	1.184
Port John	Hooknose	stained	52.140	-127.816	50.17	1.252
Prudhomme	Prudhomme	stained	54.238	-130.148	52.86	1.269
Roderick	Roderick	stained	52.605	-128.411	59.10	1.287
Shawaltan	Shawaltan	stained	54.324	-130.254	56.71	1.289
Sheneeza	Sheneeza	stained	53.539	-129.870	46.80	1.218
Skidegate	Skidegate	stained	53.107	-131.868	56.22	1.213
Skundale	Ian	stained	53.771	-132.479	56.91	1.234
South Kwakwa	Kwakwa	stained	52.541	-128.621	43.80	1.216
Spawning	Sustut	clear	56.579	-126.263	92.68	1.429
Spencer	Spencer	stained	53.514	-130.137	43.40	1.298
Splitmountain	Splitmountain	stained	54.333	-129.979	49.38	1.326
Stannard	Stannard	stained	52.726	-129.208	42.02	1.279
Tuno East Lower	Tuno	stained	52.287	-128.319	43.48	1.267
Tuno East Middle	Tuno	stained	52.291	-128.309	38.83	1.357
Tuno West Lower	Tuno	stained	52.300	-128.355	36.69	1.462
Tuno West Upper	Tuno	stained	52.308	-128.349	44.30	1.239
Tuwartz	Tuwartz	stained	53.347	-129.550	53.63	1.172
Tyler	Tyler	stained	52.884	-128.790	40.33	1.297
Upper Hevenor	Hevenor	stained	53.610	-129.990	53.35	1.307
Upper Kadjusdis	Kadjusdis	stained	52.123	-128.027	43.55	1.260
Upper Klutantan	Klutantan	glacial	56.948	-128.055	10.74	1.792

Lake	Watershed	Clarity	Latitude	Longitude	PR _{mean}	SE
Upper Lewis	Lewis	stained	53.335	-130.096	44.79	1.258
Upper Limestone	Limestone	stained	52.708	-129.163	39.95	1.320
Upper Monckton Inlet	Monckton Inlet	stained	53.333	-129.582	45.39	1.250
Upper Powels	Powels	stained	52.704	-128.682	41.16	1.262
Upper Ryan	Ryan	stained	53.610	-130.168	44.27	1.304
Upper Salter	Salter	stained	53.561	-129.714	44.36	1.306
Upper Ship Point	Ship Point	stained	52.101	-128.172	43.91	1.236
Upper Sockeye Creek	Sockeye Creek	stained	52.479	-128.520	37.35	1.390
Upper Talamoosa	Talamoosa	stained	52.702	-128.964	44.14	1.251
Wale	Wale	stained	52.838	-128.996	42.54	1.302
Watt	Watt	stained	51.840	-128.099	44.53	1.274
West	West	stained	52.753	-129.285	44.45	1.248
Yaaklele	Yaaklele	stained	52.189	-128.429	44.70	1.315
Yakoun	Yakoun	stained	53.341	-132.255	59.09	1.263
Yeo	Yeo	stained	52.326	-128.124	49.82	1.328

Chapter 5. Estimating conservation targets for data-limited sockeye salmon (*Oncorhynchus nerka*) populations: integrating prior information on habitat quantity and productivity

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5.1. Abstract

Management of data-limited populations is a key challenge for the sustainability of global fisheries. For example, sockeye salmon (*Oncorhynchus nerka*) spawn and rear in many remote coastal watersheds of British Columbia (BC), Canada, making population assessment a challenge. Estimating conservation and management targets for these populations is particularly relevant given their importance to First Nations and commercial fisheries. Most sockeye have obligate lake-rearing as juveniles, and total abundance is typically limited by production in rearing lakes. Although methods have been developed to estimate population capacity based on nursery lake photosynthetic rate (PR) and lake area or volume, they have not been rigorously evaluated or widely applied. We tested the value of combining these lake-based capacity estimates with traditional stock-recruit based approaches to population assessment using a hierarchical-Bayesian Ricker model of stock-recruit dynamics for 70 populations across coastal BC. Models revealed regional variation in sockeye population productivity (Ricker α), with coastal stocks exhibiting lower mean productivity than interior. Using moderately informative PR estimates of capacity as priors also improved model certainty, with a more than five-fold reduction in credible interval width for estimates of spawner abundance at carrying capacity (S_{MAX}). Thus, we found that habitat-based capacity estimates can dramatically reduce scientific uncertainty in model estimates of the management targets that underpin sustainable sockeye fisheries.

5.2. Introduction

Assessing population status and estimating conservation or management targets for data-limited fish populations is a major challenge to the sustainability of fisheries globally. In the absence of information to support management, many small unassessed fisheries around the world are depressed due to overfishing (Costello et al. 2012). This overfishing has resulted in the loss of billions of tonnes in potential fisheries yields per year (Ding et al. 2017), creating economic hardship and undermining food security in coastal communities (Golden et al. 2016). Given this challenge, a variety of approaches have been proposed for setting management targets without lengthy timeseries of population abundance and thus limited data. These range from management that relies the principles of precautionary management or local knowledge rather than stock-assessment data (Johannes 1998), to quantitative approaches such as meta-analysis that combine information from multiple sources to reduce uncertainty associated with short timeseries of abundance within a single population (Myers and Mertz 1998, Punt et al. 2011).

Meta-analytic approaches allow researchers to combine insights from multiple populations and are a valuable tool for understanding and managing populations with limited data (Myers and Mertz 1998). These analyses rely on the assumption that population parameters are drawn from a shared underlying distribution. Under this assumption, feasible population parameters – for example the maximum annual reproductive rate (α) in a Ricker stock-recruit model (Ricker 1954) – are more readily estimated for data-poor populations, as the model can borrow information from populations with more robust time series (Gelman 2006, Thorson and Minto 2015). Similarly, researchers now routinely pool information across populations using hierarchical-Bayesian methods which assume that some population parameters are drawn from common hyper-distributions (Punt and Hilborn 1997). These approaches have been used by many researchers to examine stock-recruit relationships (e.g. Liermann and Hilborn 1997, Michielsens and McAllister 2004) and understand the impacts of climate on recruitment across multiple populations (Mueter et al. 2002, Malick et al. 2016).

Another potential approach to inform management in data-limited fisheries involves predicting targets based on habitat information, when habitat limits production

(e.g. Sundblad et al. 2014). For fish populations where density-dependent population regulation occurs in well-delineated habitats, such as the use of freshwater habitat by juvenile salmon, habitat quantity and food web productivity can impose constraints on the carrying capacity of fish populations. For example, the amount and gradient of available stream-rearing habitat has been used to predict coho production (Bradford et al. 1997, Bocking and Peacock 2004), and accessible watershed area has been used to inform estimation of population parameters in data-limited Chinook populations (Parken et al. 2006, Liermann et al. 2011). While stock-recruit modeling is data intensive, often requiring decades-long time series, these habitat-based models offer the advantage of only requiring information on the amount or quality of available habitat that could be estimated remotely using geospatial analysis, or with as little as a single year of field sampling. By coupling data from populations with intensive population monitoring and the known habitat constraints for the species of interest, researchers can model the underlying relationship between habitat conditions and population parameters estimated from stock-recruit timeseries (e.g. Hume et al. 1996, Parken et al. 2006). This relationship can then be extended to estimate management targets such as carrying capacity or maximum sustainable yield (MSY) for fish populations. These habitat-based estimates of capacity can be merged with stock-recruit analyses in a Bayesian framework, either through their inclusion in the model as a covariate modifying the strength of density dependence (e.g. Liermann et al. 2010), or as a population-specific prior on the spawner abundance at the produces maximum recruitment (e.g. Korman et al. 2013).

Sockeye salmon are a semelparous and anadromous species of Pacific Salmon, and are a primary target of commercial, recreational, and First Nations subsistence fisheries in coastal British Columbia and Alaska. Sockeye salmon generally have an obligate juvenile lake-rearing phase of one or two years prior to their seaward migration, during which time they feed on zooplankton and invertebrates (Groot and Margolis 1991). Given this dependence on rearing habitat in lakes, lake size and food-web productivity can control the carrying capacity of sockeye populations (Juday et al. 1932, Hyatt and Stockner 1985, Shortreed et al. 2001). In recent decades, researchers and managers in Alaska and British Columbia have developed different rearing-capacity models for sockeye bearing lakes, predicated upon these physical and ecological constraints. Among these models is the euphotic volume model which relates sockeye

rearing capacity to the amount of volume in a lake's euphotic zone, as surrogates for lake productivity (Koenings and Burkett 1987). However, models which measure lake productivity directly generally produce more reliable predictions of fish production (Downing 1990), and Hume et al. (1996) developed a model that related lake photosynthetic rate (PR) to sockeye production. The PR model scales-up monthly estimates of photosynthetic rates to total annual growing season carbon production, using lake area and a defined growing season length. Hume et al. (1996) used data from several populations with juvenile population enumeration (i.e. fall fry or smolt) and lake PR monitoring to model the empirical relationship between smolt output and total autotrophic production. This relationship between annual PR and smolt output has subsequently been used to predict carrying capacity for approximately 60 lakes in coastal British Columbia (e.g. Shortreed et al. 1998, Shortreed et al. 2001, Shortreed et al. 2007). To date, these data have not been fully integrated with existing timeseries of spawner abundance to estimate sustainable harvest rates or evaluate conservation status of sockeye populations, an important step towards providing management advice particularly in populations where stock-recruit data are scarce (e.g. Cox-Rogers 2010).

While sockeye salmon are relatively well-studied in many parts of their range, time series of spawner abundance and recruitment are often sparse in more remote regions and for smaller populations, creating challenges for setting management and conservation targets. On the north and central coast (NCC) of BC there are more than 120 genetically and demographically distinct populations of lake-type sockeye salmon, designated as Conservation Units (CU) under Canada's Wild Salmon Policy (WSP). However, the implementation of management and conservation policy for these populations, such as the WSP, is currently hindered by data-limitations for many populations. The WSP was originally adopted in 2005 by Fisheries and Oceans Canada (DFO), with the goal of safeguarding the genetic and ecological diversity of wild Pacific Salmon for the benefit of Canadians in perpetuity (DFO 2005). Among the actions called for in the WSP is the establishment of conservation benchmarks for evaluating population status and implementing management and recovery efforts. Conservation benchmarks rely solely on biological information and differ from management targets which consider socio-economic factors (Holt and Irvine 2013). Most watersheds in the NCC region are remote, and only accessible by boat or air, making population monitoring logistically challenging and costly. Further, many of these populations are

small, with average run sizes of less than 10,000 fish, and monitoring efforts have historically been focused on the largest and most commercially important populations. Understanding the status and capacity of remote coastal sockeye salmon populations is particularly important to coastal First Nations. These communities are increasingly taking leadership of resource monitoring and management within their traditional territories, and managing food, social and ceremonial sockeye fisheries for sustainable economic and cultural benefits is a primary goal (e.g. Atlas et al. 2017). Thus, using methods that integrate multiple sources of information on populations and their habitats is a critical step towards informing management of data-limited sockeye salmon populations.

Here we integrate habitat-based and Bayesian meta-analytic approaches to inform conservation and management for 70 populations of sockeye salmon in coastal BC. Specifically, we developed a hierarchical-Bayesian Ricker model of spawner-recruit dynamics for sockeye salmon, integrating information on lake productivity and size through the inclusion of habitat-based estimates of carrying capacity as prior information, and asked the following questions: (1) How does the inclusion of a habitat-based prior affect estimates of population productivity and capacity and (2) how do current sockeye population abundances in the NCC compare to conservation benchmarks derived using habitat-based priors?

5.3. Methods

Overview

We estimated the following parameters for each of the 70 sockeye populations: 1) population abundance over the last 15 years, 2) spawning abundance at carrying capacity (S_{MAX}), and 3) spawning abundance at maximum sustainable yield (S_{MSY}). These parameters can inform conservation targets and conservation status. For each of 70 sockeye populations, we fit stock-recruitment models to timeseries of spawner abundance, catch, and average brood year age composition (English et al. 2016). These stock-recruitment models incorporated habitat-based priors drawn from more than 20 years of limnological assessments conducted by DFO's Lakes Research Program in the sockeye-bearing lakes of the NCC (e.g. Shortreed et al. 1998, Shortreed et al. 2001, Shortreed et al. 2007). These data were then combined in a series of models to evaluate the degree to which information on the productivity of rearing habitats was a suitable

source of prior information on population carrying capacity, and how the inclusion of these priors affected estimates of carrying capacity (S_{MAX}) and spawner abundance at maximum sustainable yield (S_{MSY}).

Photosynthetic rate model

We used published estimates of lake carrying capacity (S_{MAX_PR}) derived from the photosynthetic rate (PR) model first developed by Hume et al. (1996) and refined by Shortreed et al. (2000) (Table S5.1). Hourly and daily photosynthetic rates were estimated *in situ* using light and dark bottle incubations within the euphotic zone, which measure autotrophic uptake of inoculated ^{14}C isotopes in relation to incident light levels (see Shortreed et al. 1998 for detailed methods). These hourly estimates of PR were typically made multiples times over a growing season. They were then temporally expanded to daily rates and seasonal mean photosynthetic rates based upon growing season length (May 1st - October 31st) and lake surface area, to estimate total annual growing season carbon production (Shortreed et al. 2000).

The PR model assumes that sockeye populations are limited by lake productivity and area, and previous research in BC has suggested that in most cases this assumption is valid (Shortreed et al. 2001). Drawing on the work of Koenings and Burkett (1987), Hume et al. (1996) used the correlation between empirically-derived estimates of spawner abundance at carrying capacity (S_{MAX}) and total annual primary production (PR_{TOTAL}), to estimate S_{MAX} for lakes using only PR data (S_{MAX_PR}). This effort yielded a relationship between lake productivity and sockeye population capacity which has subsequently been used to estimate carrying capacity in lakes across the NCC (Shortreed et al. 1998, Shortreed et al. 2001, Shortreed et al. 2007). The model assumes a fixed relationship between lake productivity and maximum smolt output, thus PR_{TOTAL} (tons·C·year⁻¹) can be multiplied by the constant 187 (spawners· tons·C⁻¹) to yield an estimate of the number of adult spawners required to maximize smolt production (Shortreed et al. 2000).

$$S_{MAX_PR} = 187 \times PR_{TOTAL}$$

In most applications, PR measurements are made throughout the growing season, accounting for seasonality in primary production (see Shortreed et al. 2001 for summary). However, across the numerous remote NCC lakes access is difficult and assessment costs are high. Thus, single estimates of PR made in late-August or early-September have been successfully related to seasonal mean PR values yielding a correction factor of 0.748, which can be applied to produce estimates of seasonal mean PR (Cox-Rogers et al. 2004). When estimates of annual primary production (PR_{TOTAL}) were available for multiple years, we used the average of these estimates as our prior. In other cases, multiple lakes support rearing sockeye within a single population (e.g. Elbow, Lonesome, and Rainbow Lakes for Atnarko sockeye), and priors reflected the sum of productivity of all lakes known to support sockeye rearing. For more information on data sources and methods see the supplemental materials (Table S5.1).

While field measurements of PR were only available for 40 of 70 populations in our study, recent parallel modeling efforts have led to the creation of a landscape-scale predictive model for lake PR across the NCC (Atlas et al. *in review*). We previously examined a series of potential landscape and geographic variables as predictors of S_{MAX_PR} and found there were strong regional trends and that sockeye lake productivity was well predicted by whether the lake is clear, humic stained or glacially turbid. We therefore used predicted S_{MAX_PR} values from this landscape model as priors for S_{MAX} in populations where rearing lakes were unsampled.

Escapement and catch data

We used abundance and harvest data from 70 populations on the NCC collected since the 1950s by DFO. In cases where harvest data was not available for a specific population, we used the average harvest rate for other populations in the same DFO statistical area to reconstruct catch. These data represent the best available information on harvest rates over time, however several key assumptions were made in reconstructing sockeye catch which may not apply for all populations uniformly (English et al. 2016), thus harvest data should be interpreted with caution. Harvest rates ranged from more than 70% in the early part of the timeseries for some populations to less than 10% in more recent years. Using available age data (English et al. 2016) as well as model estimates of age composition (see below), we constructed brood tables assigning recruits to previous parent cohorts to estimate the relationship between population size

and recruitment. We examined each population timeseries individually, identifying and removing years which produced unreasonably high estimates of per capita recruitment (more than 20 adult recruits per spawner). These outliers were likely because of poor data quality or extrapolated estimates of harvest that inflated per capita recruitment. We also dropped data points of fewer than 100 spawners, as population sizes that small are rare and are likely a reflection of poor data quality. This process resulted in the elimination of 73 data points out of a possible 1,850 spawner-recruit pairs. Data richness varied widely across the 70 populations of interest, with the number of stock-recruit pairs ranging from 4 to 57.

Age structure

The quality and availability of age data was highly variable across populations. In some large and commercially-important populations (Atnarko, Babine, Long, Meziadin, and Owekino) estimates of annual age data are available. For Babine, age-composition data is available throughout the timeseries. For Atnarko, age data is available in 33 years from 1976 to 2016 and in years missing age data we assumed age composition was equal to the long-term average. In the remaining three populations, annual age data was available only since 1989, so estimated recruitment to cohorts after 1986 reflects annual age variation, while earlier estimates of recruitment reflect mean age composition. In many other populations ($n = 19$), age estimates are limited to a few years, and we used average brood-year age composition values reported in English et al. (2016), data from Todd and Dickinson (1970) for Bowser Lake, and brood-year age composition reconstructed from scale and otoliths collected since 2012 during annual monitoring in Koeye, Namu, Port John, and Kadjusdis (W.Atlas unpublished data). We then modelled the available multinomial age proportion data against environmental correlates using Dirichlet regression (R-package *DirichletReg* version 0.6-3; Maier 2015), using model outputs to predict age structure for the remaining 45 populations without age data. Maximum watershed elevation was found to be the best predictor of age composition, and age structure was predicted for watersheds lacking data from this relationship (Figure S5.1, Table S5.2). This novel approach to predicting population age composition across the landscape facilitated the creation of brood tables for stock-recruit analysis, however these estimates of population age structure are uncertain.

Accordingly, estimates of S_{MAX} and S_{MSY} are more uncertain in populations lacking age data.

Stock-recruit modeling

We modeled density-dependent population dynamics for each timeseries of spawner abundance (S) and recruitment (R) using a Ricker model (Ricker 1954), where α controls the per-capita productivity (slope) at the origin, and β dictates the strength of density-dependence at different population sizes. For each population α was assumed to be lognormally distributed with a mean of 1, and a standard deviation of 1. This equation is widely used in part because it can be adapted to a linear relationship by taking the natural-log value of the number of recruits per spawner at a given population size. Spawner abundance at carrying capacity (S_{MAX}) is then estimated as the reciprocal of β

$$\ln(R/S) = \ln(\alpha_i) - \beta_i S$$

$$\alpha_i \sim \text{lognormal}(1, 1)$$

$$S_{MAX\ i} = 1/\beta_i$$

Models were then run for 100,000 iterations in JAGS using the statistical program R, with three parallel chains, and a burn in period of 50,000 iterations. Model convergence was evaluated visually using trace plots.

Validation of PR model as S_{MAX} prior

Given the variability in the availability and quality of data across the NCC, populations were differentiated into two groups: (1) those with relatively high-quality stock-recruit and age data, and (2) those with lower quality stock-recruit timeseries and poor or missing age data where stock-recruit modeling may produce biased or highly uncertain estimates of population parameters in the absence of informative priors. We compared estimates of spawner abundance at carrying capacity derived from the PR model (S_{MAX_PR}) (Equation 1), and those estimated from the Ricker stock-recruit model (S_{MAX}) (Equation 2), for populations with more than 25 stock-recruit pairs and where there was available information on population age structure (group one). The productivity parameter (α) in this Ricker model was fit independently for each the 12 populations.

This model included a log-normal prior for S_{MAX} with a mean ($mu.E$) that was the long-term mean escapement for each population and a variance estimated as half of the standard deviation of each population time series squared.

$$S_{MAX\ i} \sim \text{lognormal}(mu.E_i, tau.E_i)$$

$$tau.E_i = (SD(E_i)/2)^2$$

We then fit a linear regression with the intercept constrained through the origin, to compare estimates of spawner abundance at carrying capacity values from the stock-recruit and PR model. We considered a slope that did not statistically differ from 1 as support for using estimates of S_{MAX_PR} as a prior for Ricker S_{MAX} in subsequent stock-recruit modeling.

Alternative modeling approaches

To evaluate the effects of estimating productivity (α) hierarchically and using S_{MAX_PR} as a prior, we estimated Ricker stock-recruit parameters for each population (i) using three models.

(1) Productivity values were estimated independently for each of the 70 populations, with a uniform prior for $S_{MAX\ i}$ ranging from 0 to 10 times the maximum observed escapement in a population ($MaxE_i$) (Equation 2).

$$S_{MAX\ i} \sim \text{dunif}(0, 10 \times MaxE_i)$$

(2) Productivity values were estimated hierarchically with values of α drawn from a common hyper-distribution with a mean of $mu.a$ and a variance of $tau.a$, and a uniform prior on $S_{MAX\ i}$. We used uninformative uniform priors for $mu.a$ and $tau.a$.

$$\alpha_i \sim \text{logN}(mu.a, tau.a)$$

$$mu.a \sim \text{uniform}(0,3)$$

$$tau.a \sim \sigma^{-2}$$

$$\sigma \sim \text{uniform}(0, 25)$$

(3) Alpha values estimated hierarchically as in model 2, with a semi-informative log-normal prior for S_{MAX_i} , with a mean of S_{MAX_PR} (Table S5.1) and a standard deviation of 0.9. This prior distribution providing a moderately informative prior with values typically spanning a range of approximately 0.1 to 10 times the long-term mean population size and the highest probability density at $S_{MAX_PR_i}$.

$$S_{MAX_i} \sim \text{lognormal}(S_{MAX_PR_i}, 0.9)$$

The sockeye bearing watersheds NCC span broad hydrological and climatological gradients, from low elevation coastal bog-forest through deep mountainous fjords, and into the interior plateau. Given the potential differences in environmental conditions influencing sockeye productivity across these regions, we evaluated whether there was support for including three regional priors on $mu.\alpha$, by fitting models 2 and 3 with region-specific hyper-distributions (coastal, fjord, interior). We then compared the density distributions of the regional $mu.\alpha$ estimates to evaluate the degree of statistical support for regional differences in productivity. All models were fit using minimally informative log-normal priors on productivity (α) and $mu.\alpha$.

For all models we estimated population size at maximum sustained yield (S_{MSY}) using Scheuerell's method, where W is the solution to Lambert's function, implemented in the R-package `gsl` (Scheuerell 2016).

$$S_{msy} = \frac{1 - W(e^{1-\alpha})}{\beta}$$

Evaluation of model performance

To evaluate the benefit of including habitat-based priors on S_{MAX} we standardized model estimates of S_{MAX} by the mean timeseries abundance for each population and compared the width of credible intervals (CI) between models with (Model 4) and without PR priors (Model 2). For the purpose of this analysis we removed five populations – Bear, Kitwanga, Morice, Motase, and Swan – which are not thought to be limited by lake rearing habitat (Shortreed et al. 2001, Cox-Rogers 2010).

Assessment of population status

To facilitate comparisons across populations spanning several orders of magnitude in average abundance, median estimates of spawner abundance at carrying capacity (S_{MAX}) as well as lower and upper 95% credible intervals were standardized by mean escapement across the timeseries. We then compared mean escapement (S) since 2000 to modeled estimates of S_{MAX} and S_{MSY} to assesses the relative population status of each population. Abundance relative to S_{MSY} has previously been proposed as a benchmark for delineating populations that are considered healthy and those at risk of population declines. Therefore, populations where $S/S_{MSY} > 1$ are above conservation targets, populations where $S/S_{MSY} < 1$ are currently below conservation targets. Populations with fewer than 3 estimates of escapement since 2000 were dropped from the analysis, leaving a total of 54 populations where status could be assessed.

5.4. Results

Our initial analysis of 12 data-rich systems supported the use of S_{MAX_PR} as prior information for stock-recruit derived estimates of S_{MAX} . The linear relationship between Ricker estimates of S_{MAX} and S_{MAX_PR} had an estimated slope of 1.05 (95% CI 0.99 – 1.11) (Figure 5.1). Thus, there was agreement between estimates of sockeye carrying capacity based on habitat and limnology, and estimates based on relatively high quality timeseries of abundance and age structure. We therefore used both empirical and predicted PR-based estimates of capacity (S_{MAX_PR}) as priors on S_{MAX} for all 70 populations.

Across all regions, modeling population productivity (α) hierarchically resulted in more constrained estimates of productivity, particularly in data-poor populations (Figure 5.2). Hierarchical estimates of productivity (α) were shifted towards the mean of the hyper-distribution, resulting in a reduction in the range of values falling within the 95% credible intervals for α for all but four populations. On average, 95% CIs of α for the single population model (Model 1) spanned 2.8 R/S, while hierarchical estimation of α reduced the mean 95% CI to 2.23 R/S (Model 2). Across the 70 populations we analyzed, mean productivity in the single population and regional-hierarchical model were 3.12 and 2.97 (R/S) respectively (Table S5.4). Estimated α values in populations with the lowest and highest productivities experienced the greatest shrinkage when

analyzed hierarchically, with the lowest median α value increasing from 1.4 to 1.65 and the highest median α declining from 8.86 to 5.5 between our single population (Model 1) and hierarchical models (Model 2). There was statistical support for modeling productivity (α) hierarchically by region. Different regions had different productivities—specifically, hierarchical mean productivity ($\mu.\alpha$) of low elevation coastal sockeye was substantially lower (2.6 R/S; 95% CI 2.29 – 2.96) than interior sockeye (3.84 R/S; 95% CI 3.17 – 4.66). Hierarchical mean productivity for coastal fjord populations was intermediate between low coastal and interior regions ($\mu.\alpha = 3.1$ R/S; 95% CI 2.44 – 3.95). Given this statistical evidence we used this regional-hierarchical productivity model as the base model for comparing the performance of uniform and lake PR-based priors.

The inclusion of lake-based priors for S_{MAX} tended to reduce uncertainty in estimated population parameters. In many populations, model fits for the hierarchical-Ricker model with uninformative priors produced highly uncertain estimates of S_{MAX} and S_{MSY} (Model 2). In the absence of prior information on lake productivity, only 14 populations had 95% credible intervals that spanned less than two times their mean escapement, and the median credible interval for S_{MAX} spanned a range of abundances that were 9.68 times the mean escapement. In some populations, parameter estimates were extremely uncertain with credible intervals for S_{MAX} in 20 populations were greater than 20 times their mean escapement, with a maximum of more than 47 times mean escapement (Figure 5.3, Table S5.4). Informative priors were particularly valuable in populations with high uncertainty in Ricker model fits (Figure 5.4). For 63 of the 65 populations (excluding aforementioned populations not limited by lake productivity), including informative priors (Model 3) resulted in greater certainty in estimates of S_{MAX} , with a median 95% CI spanning 1.78 times the mean escapement (Figure 5.3, Table S5.4). The number of populations for which the range of S_{MAX} estimates fell within two times mean escapement increased to 35 of 65 (from 14 when uninformative priors were used).

There was not always agreement between values of S_{MAX_PR} and S_{MAX} estimated from stock-recruit models, and cases where capacity estimates diverged between the two may highlight systems where lake productivity is not the primary factor limiting sockeye production. In population models that included lake-PR priors (model 3), credible intervals for estimates of S_{MAX} overlapped mean values for PR-based capacity

priors in fewer than half of populations, suggesting that capacity not always well predicted by freshwater habitat productivity and size (Figure 5.4). The inclusion of lake-based priors led to lower median values of S_{MAX} in 55 populations, and roughly equivalent (within 10%) estimates of S_{MAX} for 10 populations, when compared to the median estimates when uniform priors were used (model 2). Thus, while lake-based priors helped reduce uncertainty in estimated stock-recruit parameters, they frequently yielded lower capacity estimates (S_{MAX}) for sockeye populations on the NCC.

Population status

While the lack of recent escapement data made assessment impossible for many systems (16 of 70 populations), we evaluated population status relative to S_{MSY} and S_{MAX} for the remaining 54 systems with three or more years data in the 15 years preceding the analysis. About half of sockeye populations on the NCC have experienced recent spawner abundances above those predicted to maximize fisheries yield (S_{MSY}). For models (2) with uniform and (3) lake-based priors, recent sockeye escapement averaged 1.19 and 1.05 median estimates of S_{MSY} and 0.60 and 0.49 of S_{MAX} respectively. Given differences in estimates of S_{MSY} between the models for, the two models produced slightly different assessments of status among some populations. The uniform prior model estimated that 25 of 54 populations had recent mean escapements above median estimates of S_{MSY} . When lake-based priors for S_{MAX} were used, 30 populations were above median S_{MSY} . However, given uncertainty in estimates of S_{MSY} , recent escapement estimates for all but six populations fell within the 95% credible interval of S_{MSY} when lake-PR priors were used. Seven populations fell below this same threshold in the uniform prior model. Because estimates of S_{MSY} varied slightly between models, the populations deemed to be below S_{MSY} differed between them (Figure 5.5). However, there was consensus between models that sockeye populations in Swan, Mary Cove, Kitkiata, Fred Wright, Kadjudis, Kwakwa, Damdochax, Owikeno, Kitwancool, Kitlope, Atnarko, Long, Port John, Namu, Curtis Inlet, Bloomfield, Yakoun, and Morice had a greater than 50% probability of being below S_{MSY} , suggesting that these populations are depressed relative to both their habitat potential, and previously observed abundances.

5.5. Discussion

Here we developed and applied stock recruitment models that incorporate habitat information to assess the conservation status of data deficient sockeye salmon populations. We used a hierarchical-Bayesian Ricker model that combines spawner-recruit dynamics and lake habitat information to estimate population productivity (α), spawner abundance at carrying capacity (S_{MAX}), and the escapement levels that would maximize fisheries yield (S_{MSY}) for 70 populations of sockeye across the North and Central Coast (NCC) of British Columbia. Comparing estimates of S_{MAX} derived from stock-recruit methods with lake productivity-based capacity estimates (S_{MAX_PR}) from 12 populations with relatively good spawner abundance and age data indicated that the two sources of information are comparable, supporting the use of lake-based photosynthetic rate (PR) model estimates as a prior for S_{MAX} in stock-recruit models. For many of these populations, our analyses represent the first effort to estimate stock-recruit parameters necessary for conservation and management planning. While survival and abundance of sockeye have declined for some populations on the NCC in recent years (Peterman and Dorner 2012, Connors et al. 2016), we found that 30 of the 54 populations with recent escapement data are likely to be at or above spawner abundances that maximize yield (S_{MSY}). S_{MSY} has been proposed as a benchmark, below which populations are at an elevated level of conservation concern warranting management intervention. These results demonstrate the promise of combining stock-recruit based population assessments with habitat information to reduce uncertainty in stock-recruit model estimates of population parameters that underpin management.

Our population model built on a large body of research showing the value of meta-analytic or hierarchical approaches for estimating stock-recruit parameters in data-limited systems (e.g. Punt and Hilborn 1997, Myers and Mertz 1998). The integration of stock-recruit analysis with habitat-based models to inform estimates of carrying capacity is another promising avenue for evaluating population status and setting conservation targets in data-limited populations (e.g. Parken 2006). This approach is particularly relevant for Pacific salmon species with freshwater rearing, where density-dependent population regulation occurs during the freshwater phase of the life cycle. Previous studies have taken different quantitative approaches to integrating information on habitat quantity and productivity into population assessments. Liermann et al. (2011) set habitat

area as a covariate with capacity. We opted instead to use habitat-based estimates of capacity as prior information for S_{MAX} . The latter approach offers the advantage of allowing investigators to modify the degree to which priors influence parameter estimation by making priors either weakly or strongly informative (Punt and Hilborn 1997), and we used lake-based estimates of spawners at capacity (S_{MAX_PR}) as an informative prior. Given the dearth of stock-assessment for many NCC sockeye populations, there is an opportunity to link existing data on spawner and recruit abundance, and habitat-derived estimates of lake capacity to generate management targets for data-poor populations across the region.

Overall, models that shared information across populations and integrated lake-based estimates of carrying capacity reduced uncertainty in estimates of demographic parameters for our 70 populations of sockeye salmon. In recent decades, hierarchical models assuming a common distribution for productivity (α) have become commonplace in fisheries stock-assessment (Thorson and Minto 2015), as populations of the same species often face the same fundamental constraints on their productivity (Myers and Mertz 1998). In our analysis, hierarchical models produced more biologically-conservative estimates of productivity at low abundance, than single population models, as well as a greater degree of certainty in estimates of productivity. At the population level, shrinkage in estimates of the productivity parameter between the population-specific and regional-hierarchical models were most pronounced in populations with limited data, or where the assumption of population-specific productivity produced extreme estimates of α . Reduced uncertainty, and shrinkage towards the hierarchical mean ($\mu.\alpha$) are significant from a conservation and management standpoint because productivity has a direct influence on sustainable harvest rates, and the expected rate of population recovery from short-term downturns in adult abundance. Shrinkage in productivity (α) values towards the hierarchical mean shifted estimates of spawner abundance at MSY (S_{MSY}), resulting in more biologically-conservative estimates of sustainable harvest rates in populations with high productivity but less biologically-conservative estimates of sustainable harvest rates for populations with low productivity.

Inclusion of prior information on lake productivity or size also served to reduce uncertainty in estimates of spawner abundance at carrying capacity (S_{MAX}) in almost all cases. Given the scarcity of data for some populations and high temporal variability in per-capita recruitment inherent in adult-to-adult spawner-recruit data, estimates of S_{MAX}

for many populations were highly uncertain in the absence of prior information. In these cases, the use of a uniform prior likely led to even greater uncertainty with higher estimates of S_{MAX} (Thorson and Cope 2017). Given the fundamental constraint of lake size and productivity for most lake-rearing sockeye populations (Groot and Margolis 1991, Shortreed et al. 2001), inclusion of this information through the specification of priors is a logical way to narrow the range of possible values for S_{MAX} in a population. We found a greater degree of certainty in estimates of population parameters through the integration of hierarchical approaches with lake-based priors with Ricker population models. However, S_{MAX_PR} was often lower than stock-recruit based estimates of carrying capacity and model estimates of S_{MAX} tended to be lower when lake-PR priors were used, leading to lower estimates of S_{MSY} . Management targets estimated with lake-PR priors should therefore be implemented with precaution, particularly when S_{MAX_PR} falls well below stock-recruit based estimates of capacity. Perhaps these populations use additional habitats for rearing (e.g., estuary or river) or estimates of lake productivity could have changed through time. Alternatively, systems where S_{MAX_PR} is well above S_{MAX} may have population capacity set by spawning habitat, not lake rearing habitat. Despite this call for caution, our estimates of S_{MAX} and S_{MSY} were consistent with previous escapement targets derived from a variety of stock-recruit and habitat-based approaches in well studied populations like Meziadin Lake (Bocking et al. 2002), suggesting that these approaches can add to and strengthen the scientific basis of management, reducing uncertainty in data-limited salmon fisheries.

Despite the recent trend of reduced productivity for sockeye in British Columbia (Peterman and Dorner 2012), about half (30 of 54 with escapement data) of sockeye populations with at least three years of escapement data since 2000 were above spawner abundance at maximum sustained yield (S_{MSY}) (mean = 1.19 times). While declining productivity has resulted in elevated conservation concern, harvest rates have been curtailed dramatically in most areas of the NCC over the last 25 years (English et al. 2016, Walters et al. 2019), allowing many populations to maintain abundance above estimated S_{MSY} . Other populations (16 of 70 evaluated) lacked recent escapement data required to evaluate conservation status, highlighting some of the challenges associated with evaluating population status in remote regions of coastal BC. Twenty four of the 70 populations evaluated had recent escapement levels below their median estimate of S_{MSY} . Among the populations assessed by both models to be below S_{MSY} , both Owikeno

and Atnarko were historically important for commercial and food, social and ceremonial fisheries, and the collapse of these populations has led to severe reductions in fisheries openings with impacts on salmon dependent communities along the central coast. Both populations have been the focus research and recovery planning (McKinnell et al. 2001, Connors et al. 2016). While these efforts have failed to identify a single causal factor driving declining abundance and productivity, researchers have consistently identified reduced survival from smolt to adult as the most likely life stage limiting productivity (McKinnell et al. 2001, Peterman et al. 2010). Given these lines of evidence, and the coherent regional declines in productivity identified in other studies (e.g. Peterman and Dorner 2012), the most likely causes of declining productivity and abundance for sockeye on the north and central coast are large-scale processes affecting growth and survival of sockeye in the North Pacific. In particular, regional climate-driven shifts in oceanographic conditions (Mantua et al. 1997, Mueter et al. 2002), and increased competition between sockeye and other salmon species (Ruggerone and Connors 2015) are likely contributing factors.

Our work confirms the utility of limnological studies from sockeye rearing lakes to inform conservation and management targets. PR-based estimates of capacity can typically be made with data from one or a few years (Hume et al. 1996), whereas producing reliable estimates of capacity with stock-recruit modeling requires decades of continuous monitoring of abundance. However, managers should interpret PR model outputs, whether independently or as priors in stock-recruit modeling carefully, particularly if PR model estimates of capacity fall well above or below stock-recruit estimates of capacity. In such cases differences between PR model and stock-recruit models may provide important clues about the factors limiting population size and productivity. Since PR models capture only autotrophic energy pathways they may underestimate lake productivity supporting sockeye, particularly in lakes where microbial pathways comprise a high proportion of total production (Stockner and Shortreed 1989, Atlas et al. *in review*). In other cases zooplanktivorous competitors such as three-spine stickleback (*Gasterosteus aculeatus*) may limit food availability for sockeye and reduce system-specific carrying capacity relative to the overall primary productivity of a given lake (O'Neill and Hyatt 1987, Shortreed et al. 2001). Efforts have been made by some investigators to account for competitor biomass in PR-based capacity estimates (Cox-Rogers et al. 2004), however given the broad geographic scope of our study, and the

lack of data on fish community composition for many of the lakes, we did not incorporate competitor biomass. This omission likely inflated PR-based estimates of capacity for lakes with large populations of competitors such as Alastair.

In its most basic form the PR model yields estimates of the total mass of carbon produced by photosynthesis and translates that primary production into an estimate of smolt biomass. The model assumes a mean smolt mass at carrying capacity of 4.5g (Hume et al. 1996, Shortreed et al. 2000). While this assumption is probably robust on average (e.g. Koeys Lake - Atlas unpublished data), mean smolt weight is variable across lakes. However, because smolt size data is not available for most lake systems on the BC coast, we used 4.5g as the mean smolt mass for all populations. Finally, the model assumes that all sockeye juveniles are lake rearing, and that density-dependent population regulation occurs in lakes. While lake rearing is certainly the dominant juvenile life-history for sockeye on the BC coast, ocean-type and stream-rearing life histories have also been documented in the several areas of the NCC (e.g. Beveridge et al. 2015, Connors et al. 2016) and undocumented life-history diversity likely exists in many other populations in this study. If stream- or ocean-rearing sockeye are included in spawner enumeration, their contribution to the population will inflate S_{MAX} relative to the productivity capacity of the rearing lake (S_{MAX_PR}). In other cases, population growth may be limited by the amount of available spawning habitat, rather than the productivity of the rearing lake (e.g. Bear Lake) (Shortreed et al. 1998). In these instances, the PR model will fail to capture the habitat processes that limit population growth, leading to inflated estimates of S_{MAX} when PR-based capacity values are integrated with stock-recruit models as prior information. Regardless of these important biological considerations, our study highlights the utility of the PR model in representing the productive capacity of sockeye salmon nursery lakes, with strong coalescence in predicted carrying capacity from traditional stock-recruit and PR model approaches across a diversity of coastal sockeye stocks. This finding confirms the value of limnological information such as PR-based capacity estimates as a source of prior information for sockeye population assessment.

The integration of hierarchical-Bayesian stock-recruit models with prior information on lake-productivity is a promising avenue towards better informed management of sockeye in the NCC. However, understanding the limitations and potential biases associated with the dataset and modeling approaches are important if

model outputs are to be used to guide management. For instance, because enumeration methods are not uniform between study systems and can change through time, and observation error in escapement estimates likely varies across populations. While salmon populations tend to show regional coherence in population trends (Pyper et al. 2005), the absence of recent population monitoring data may produce inaccurate assessments of regional populations status if reductions in monitoring efforts have been biased towards underperforming populations (Price et al. 2008). Population productivity and carrying capacity can vary through time (Walters 1987), creating the possibility of autocorrelation among recruitment residuals and population size that can introduce negative bias in estimates spawner abundance at carrying capacity ($1/\beta$) and positive bias in productivity (α). This bias will be greatest for unproductive populations with temporal autocorrelation in stochastic natural mortality (Korman et al. 1995, Myers and Barrowman 1995). Ideally, stock-recruit models would be fit with temporal autocorrelation in residuals or with time-variant productivity to account for temporal trends in recruitment variation (e.g. Liermann et al. 2010). However, given the frequency of missing data for many populations in our study we opted to treat productivity as time invariant. Finally, for most populations – with the exception of Babine, Atnarko, Owikeno, Long, and Meziadin – only average age structure was available, and we assumed that age structure was fixed across brood years. Zabel and Levin (2002) have cautioned against the use of fixed age structure in stock-recruit models, as it will tend to smooth recruitment variability, resulting in biased estimates of S_{MAX} (low) and productivity (α)(high).

The model we developed can serve as a roadmap for future efforts to estimate conservation and management goals for data-limited fish stocks. While the demographic parameter estimates we present are preliminary, the modeling approach provides a foundation for conservation and fisheries management under the Wild Salmon Policy (DFO 2005). Our results suggest that despite reductions in productivity and abundance in recent decades, most sockeye populations on the NCC with intact habitats and moderate harvest rates are at or above MSY and presumably of low immediate conservation concern. Given these findings it is likely that these populations can support sustainable directed fisheries under precautionary management approaches.

Our analysis demonstrates the utility of merging hierarchical stock-recruit analysis with information derived from habitat-based models. Hierarchical models are a powerful tool for estimating stock-recruit parameters in populations with variable data quality or quantity, and the inclusion of habitat-based priors on carrying capacity provides a logical and biologically grounded means of defining priors for S_{MAX} . Combining insights from habitat-based models of population capacity with stock-recruit analyses in a Bayesian framework can reduce uncertainty associated with estimates of population parameters and management targets resulting from highly stochastic adult-to-adult recruitment data. These modeling approaches have been applied to chinook (e.g. Parken et al. 2006) and could be further adapted to inform conservation and management of data limited coho salmon populations. While we advise caution in setting management targets for fisheries with limited data, habitat-based models are a useful starting point for evaluating stock status and setting precautionary harvest goals even with limited stock-recruit data. Together these approaches provide key tools for managers of fisheries in developing economies or remote landscapes where a lack of population data currently hinders scientific decision making.

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5.7. References

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5.8. Figures

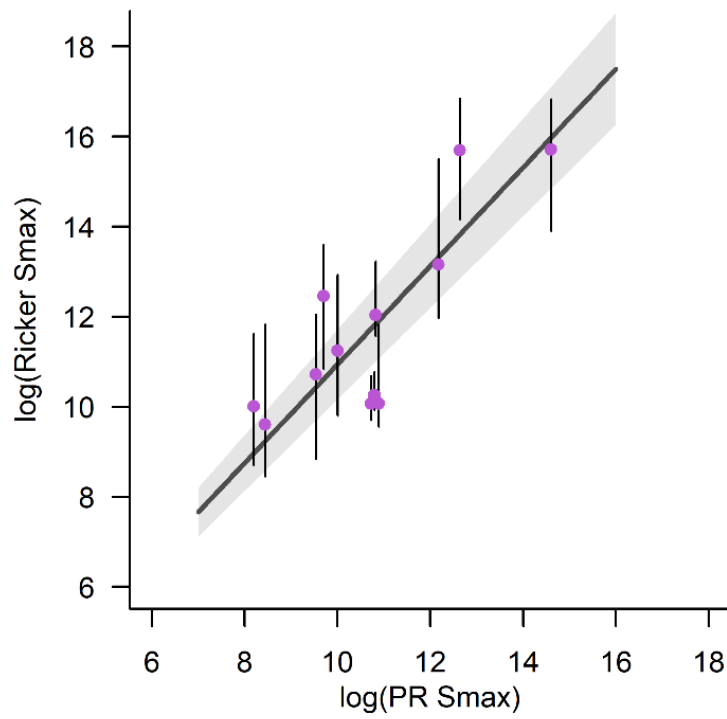


Figure 5.1. Comparison of stock-recruit derived estimates of spawning abundance at capacity to $S_{\text{MAX_PR}}$ for 12 data-rich lakes

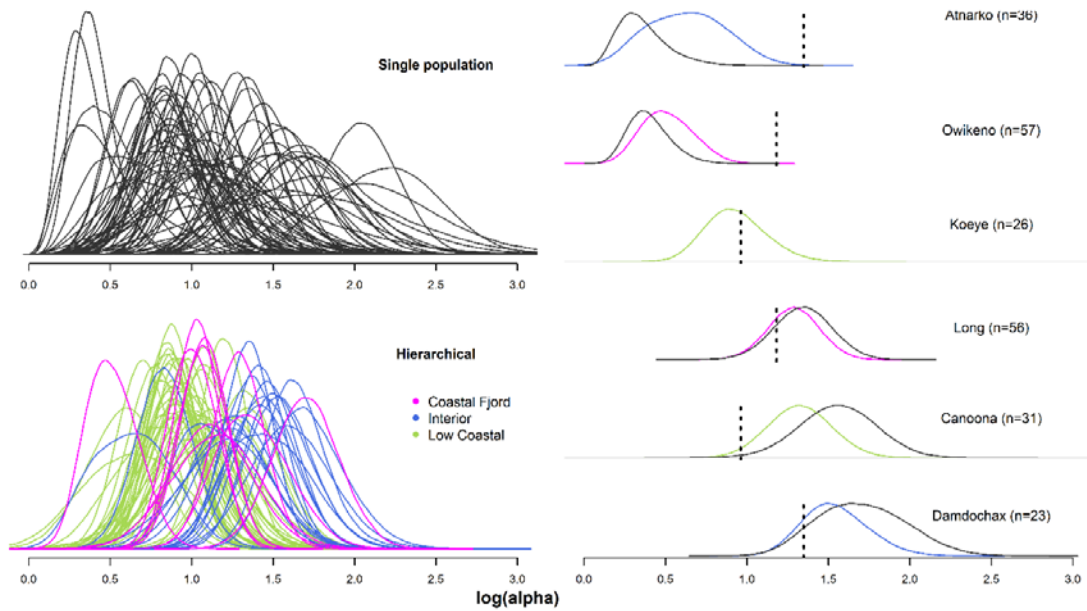


Figure 5.2. Estimated values for the natural log of alpha (population productivity) for all 70 populations with estimates from the independent (non-hierarchical) population model shown in black and estimates from the regional-hierarchical model shown in pink (Coastal Fjord), green (Low Coastal), and blue (Interior). Individual population plots show shrinkage resulting from hierarchical estimation of alpha, with the vertical dashed line representing the hierarchical mean alpha for a given region.

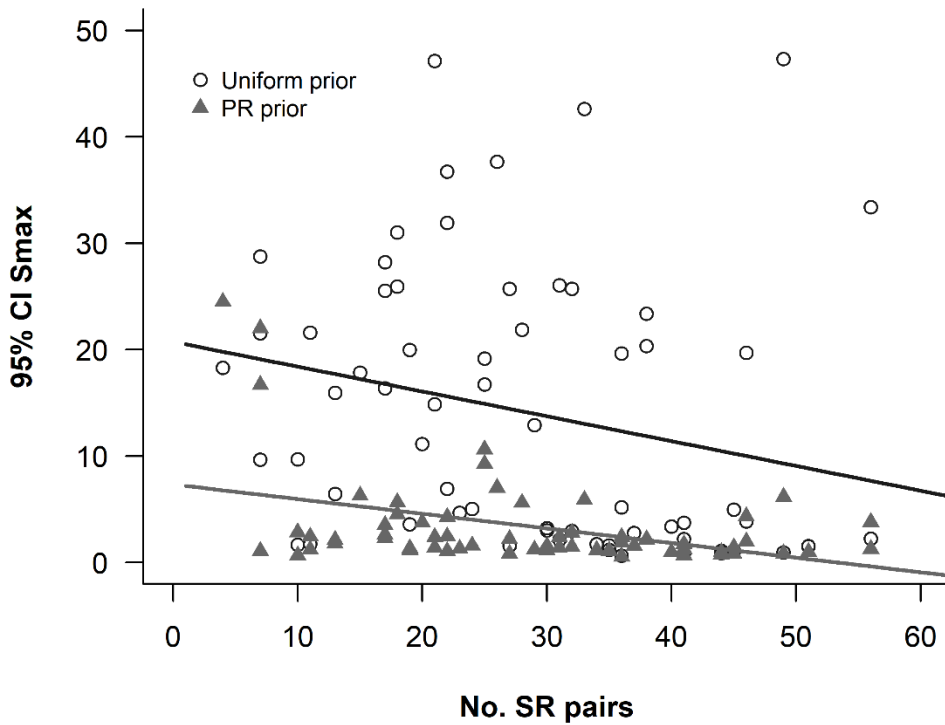


Figure 5.3. Relationship between width of 95% credible interval for S_{MAX} and the number of stock recruit pairs used in modeling, for models with uninformative uniform priors (open circles), and lake PR based priors (solid triangles).

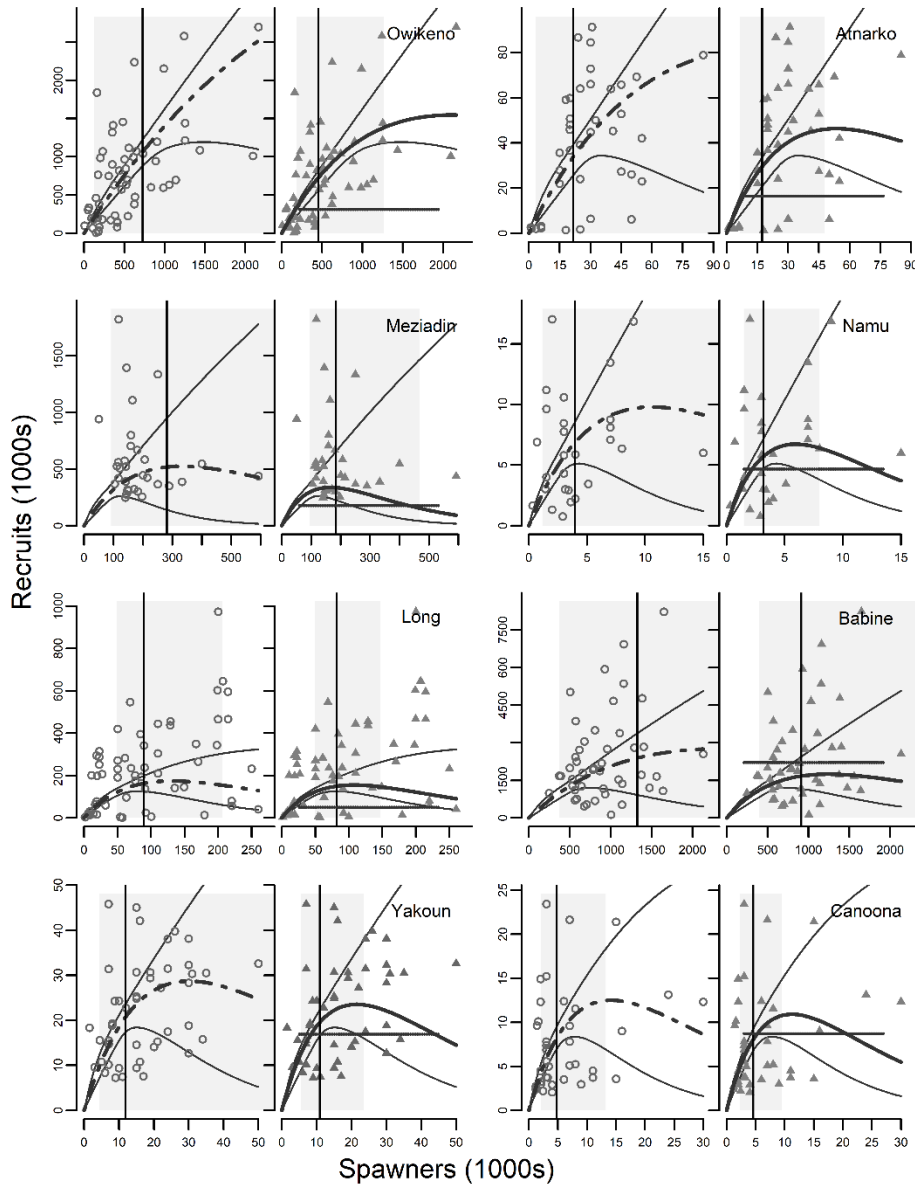


Figure 5.4. Stock recruit relationships with uniform (circles and dashed lines) and lake PR-based priors (triangles and solid lines) on S_{MAX} for eight of the 70 populations on the NCC with spawner escapement data. Gray rectangles and vertical lines are 95% credible interval and median S_{MSY} . Horizontal dashed lines indicate PR priors on spawner abundance at carrying capacity (S_{MAX_PR}).

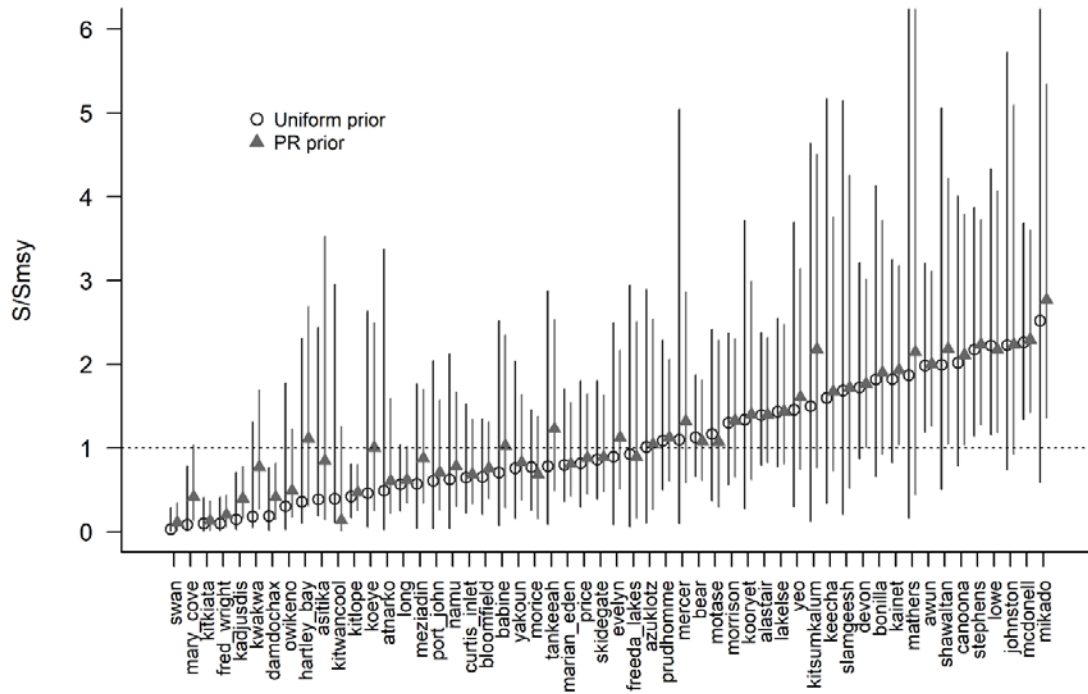


Figure 5.5. Relationship between recent escapements (S) and estimated spawner abundance at MSY (S_{MSY}) for 52 populations with recent escapement data. Vertical lines represent 95% credible intervals for estimated stock status. The dashed line is indicative of a population size equal to MSY .

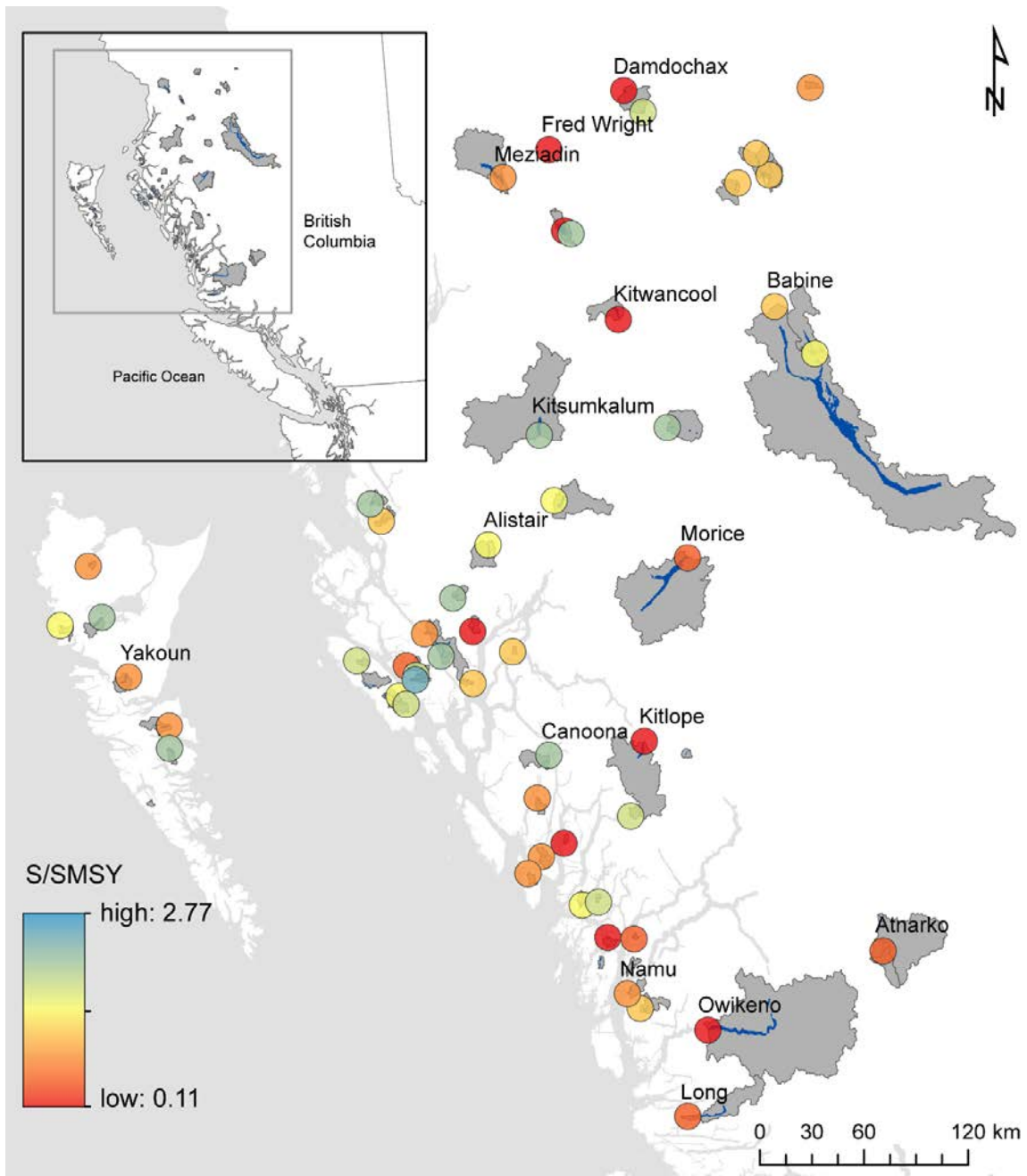


Figure 5.6. Estimated status (S/S_{MSY}) for the 54 populations of sockeye on the NCC with recent escapement data.

5.9. Supplemental Materials

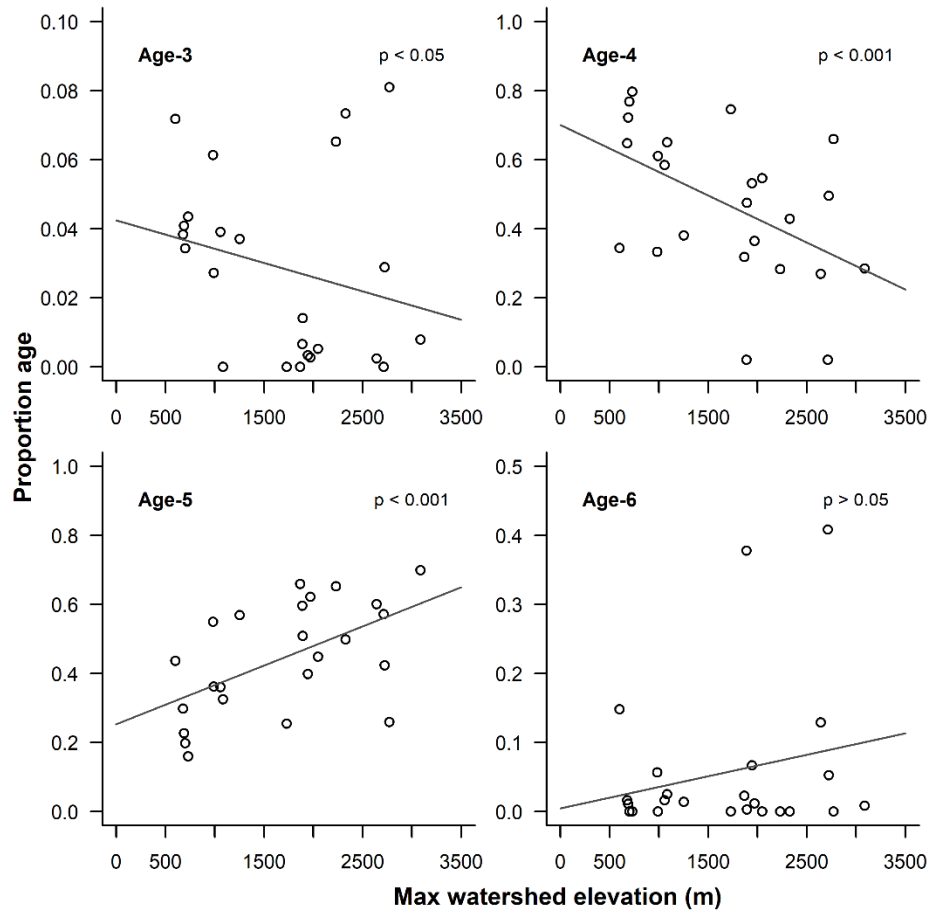


Figure S5. 1 Relationship between mean population age composition and maximum watershed elevation (m), with p-values from multinomial regression fits reported in the top right corner of each panel.

Table S5.1 Age data and estimated age composition for sockeye salmon populations in the NCC

Lake	Lat.	Long.	Mean elev	Max elev	Data	3	4	5	6
Alastair	54.14	-129.19	857	1890	yes	0.007	0.020	0.596	0.378
Babine	55.41	-126.68	1002	2328	yes	0.073	0.429	0.498	0.000
Bear	56.20	-126.87	1255	2232	yes	0.065	0.283	0.652	0.000
Atnarko	52.28	-125.75	1520	2772	yes	0.081	0.660	0.259	0.000
Bowser	56.38	-129.37	1296	2726	yes	0.029	0.496	0.423	0.052
Damdochax	56.51	-128.12	1124	1866	yes	0.000	0.319	0.658	0.023
Kadjusdis	52.14	-128.04	88	602	yes	0.072	0.345	0.436	0.148
Kitwancool	55.33	-128.10	855	1946	yes	0.003	0.532	0.398	0.067
Koeye	51.78	-127.75	443	1253	yes	0.037	0.380	0.569	0.014
Kwakwa	52.55	-128.62	173	729	yes	0.044	0.797	0.159	0.000
Lakelse	54.39	-128.63	670	2050	yes	0.005	0.546	0.449	0.000
Long	51.23	-127.33	808	1970	yes	0.003	0.364	0.622	0.011
Mary Cove	52.62	-128.43	200	677	yes	0.038	0.648	0.298	0.016
Mathers	52.99	-131.85	385	990	yes	0.027	0.611	0.362	0.000
Meziadin	56.04	-129.21	856	2642	yes	0.002	0.269	0.600	0.129
Morice	54.11	-127.43	1254	2715	yes	0.000	0.020	0.571	0.408
Morrison	55.17	-126.31	956	1894	yes	0.014	0.475	0.508	0.003
Namu	51.86	-127.86	314	1057	yes	0.039	0.585	0.360	0.016
Owikeno	51.68	-127.18	1212	3087	yes	0.008	0.285	0.699	0.008
Port John	52.14	-127.82	272	985	yes	0.061	0.333	0.549	0.057
Skidegate	53.11	-131.87	195	700	yes	0.034	0.769	0.197	0.000
Slamgeesh	56.40	-127.93	884	1731	yes	0.000	0.746	0.254	0.000
Tankeeah	52.31	-128.26	124	689	yes	0.041	0.722	0.226	0.011
Yakoun	53.34	-132.26	363	1085	yes	0.000	0.650	0.325	0.025
Asitika	56.54	-126.37	1496	2137	predicted	0.067	0.351	0.505	0.077
Awun	53.64	-132.53	267	808	predicted	0.063	0.565	0.326	0.046
Azuklotz	56.09	-126.75	1275	1969	predicted	0.068	0.377	0.483	0.073
Banks	53.38	-130.18	167	657	predicted	0.062	0.589	0.306	0.043
Bloomfield	52.85	-128.68	297	933	predicted	0.064	0.545	0.342	0.049
Bonilla	53.51	-130.29	170	620	predicted	0.062	0.595	0.301	0.042
Borrowman	52.75	-129.21	102	261	predicted	0.058	0.650	0.257	0.035
Canoona	53.07	-128.59	351	1096	predicted	0.065	0.518	0.364	0.052
Curtis Inlet	53.50	-129.86	248	859	predicted	0.064	0.557	0.332	0.047
Devon	53.45	-129.77	255	748	predicted	0.063	0.575	0.318	0.045
End Hill	53.59	-130.36	104	461	predicted	0.060	0.620	0.281	0.039
Evelyn	53.60	-128.94	312	1011	predicted	0.065	0.532	0.353	0.050
Fairfax	52.71	-131.98	401	953	predicted	0.064	0.542	0.345	0.049
Freeda									
Brodie	53.67	-129.71	538	1343	predicted	0.067	0.478	0.398	0.058

Lake	Lat.	Long.	Mean elev	Max elev	Data	3	4	5	6
Hartley Bay	53.43	-129.27	203	737	predicted	0.063	0.577	0.316	0.044
Hauyat	52.04	-128.08	80	339	predicted	0.059	0.638	0.266	0.037
Johanson	56.60	-126.21	1727	2354	predicted	0.067	0.319	0.532	0.082
Johnston	53.86	-129.48	739	1920	predicted	0.068	0.385	0.476	0.072
Kainet	52.77	-127.87	733	1642	predicted	0.067	0.429	0.439	0.065
Kdelmashan	52.57	-129.05	68	327	predicted	0.059	0.640	0.265	0.036
Keecha	53.30	-129.84	132	476	predicted	0.060	0.617	0.283	0.039
Keswar	53.66	-130.32	112	352	predicted	0.059	0.636	0.268	0.037
Kimsquit	53.12	-127.38	993	1921	predicted	0.068	0.384	0.476	0.072
Kisameet	51.96	-127.87	239	848	predicted	0.064	0.559	0.331	0.047
Kitkiata	53.69	-129.29	482	1263	predicted	0.066	0.491	0.387	0.056
Kitlope	53.16	-127.77	893	2145	predicted	0.067	0.350	0.506	0.077
Kitsumkalum	54.72	-128.78	1014	2221	predicted	0.067	0.338	0.515	0.079
Kooryet	53.34	-129.90	115	433	predicted	0.060	0.624	0.278	0.038
Lowe	53.56	-129.56	298	1154	predicted	0.066	0.509	0.372	0.054
Marian Eden	53.89	-132.69	177	686	predicted	0.062	0.585	0.310	0.043
McDonell	54.78	-127.64	1201	2568	predicted	0.066	0.289	0.558	0.087
McLoughlin	52.14	-128.16	88	227	predicted	0.058	0.655	0.253	0.034
Mercer	53.57	-132.89	299	860	predicted	0.064	0.557	0.332	0.047
Mikado	53.43	-129.77	266	687	predicted	0.062	0.585	0.310	0.043
Motase	56.05	-127.04	1537	2324	predicted	0.067	0.323	0.528	0.081
Price	52.46	-128.73	59	200	predicted	0.058	0.659	0.250	0.034
Prudhomme	54.24	-130.15	315	1012	predicted	0.065	0.532	0.353	0.050
Shawaltan	54.32	-130.25	357	1021	predicted	0.065	0.531	0.354	0.051
Sheneeza	53.54	-129.87	372	872	predicted	0.064	0.555	0.334	0.047
Stephens	55.76	-128.56	657	1097	predicted	0.065	0.518	0.364	0.052
Sustut	56.59	-126.47	1548	2163	predicted	0.067	0.347	0.508	0.078
Swan	55.78	-128.62	681	1097	predicted	0.065	0.518	0.364	0.052
Tuno East	52.29	-128.32	40	81	predicted	0.056	0.676	0.236	0.032
Tuno West	52.30	-128.36	31	64	predicted	0.056	0.678	0.234	0.032
Yeo	52.33	-128.12	211	706	predicted	0.062	0.582	0.312	0.044

Table S5.2 Estimated sockye spawner abundance at carrying capacity (S_{MAX}).

Population	Model 1		Model 2		Model 3	
	S_{MAX}	S_{MAX} CIs	S_{MAX}	S_{MAX} CIs	S_{MAX}	S_{MAX} CIs
Alastair	27,938	21,068	27,602	21,145	26,963	20,878
		41,675				39,948
Atnarko	234,805	53,609	74,702	34,481	45,779	29,663
		807,340				711,057
Azuklotz	9,357	3,645	6,493	3,652	6,074	3,624
		70,712				49,432
Babine	5,055,852	1,095,597	2,740,382	1,077,994	1,665,057	955,413
		20,172,338				19,009,249
Banks	10,176	6,407	10,548	7,096	8,985	6,495
		28,686				22,080
Bear	5,927	4,468	5,942	4,552	6,195	4,696
		8,877				8,590
Bloomfield	3,763	2,431	3,940	2,536	3,148	2,265
		9,812				10,262
Bonilla	12,701	8,285	12,405	8,345	10,907	7,785
		31,381				26,409
Canooka	4,272	2,955	5,239	3,479	4,763	3,334
		8,177				11,055
Curtis Inlet	24,646	15,995	23,851	16,023	20,480	14,745
		58,822				52,628
Devon	9,285	6,714	9,711	7,122	8,841	6,739
		15,169				15,420
Evelyn	5,329	2,805	5,364	2,940	3,727	2,529
		50,197				43,720
Fred Wright	14,580	7,763	41,704	11,934	18,835	10,285
		171,746				232,598
Hartley Bay	8,876	1,755	10,766	2,282	2,874	1,555
		28,691				28,815
Johanson	4,585	528	3,899	608	1,769	567
		11,596				11,526
Johnston	6,303	3,851	6,188	4,083	5,903	4,027
		24,182				14,065
Keecha	8,554	4,852	8,262	5,187	6,841	4,726
		60,848				27,751
Kitkiata	10,049	4,073	14,738	5,349	9,860	4,983
		87,696				90,665
Kitlope	111,942	73,915	108,682	73,555	92,828	67,624
		267,342				226,070

Population	S _{MAX}	S _{MAX} Cls	S _{MAX}	S _{MAX} Cls	S _{MAX}	S _{MAX} Cls
Kitsumkalum	47,331	17,744	40,770	17,479	25,812	15,625
		393,629		376,632		62,422
Kitwancool	9,009	1,922	16,639	2,768	49,058	6,494
		48,397		49,374		332,962
Koeye	27,848	6,776	29,111	7,488	11,308	6,229
		168,195		167,674		36,104
Koorjet	11,943	7,251	11,463	7,357	9,840	6,843
		70,410		40,381		17,350
Lakelse	22,912	16,804	22,513	16,870	22,040	16,730
		35,956		34,082		32,312
Long	158,289	108,221	168,601	115,426	147,147	107,423
		311,568		330,452		229,617
Lowe	20,074	14,986	19,700	14,911	19,342	14,759
		30,651		29,371		28,055
McDonell	3,437	2,583	3,563	2,732	3,420	2,666
		5,187		5,146		4,755
Meziadin	314,765	155,352	482,793	205,786	283,008	176,257
		4,643,300		5,100,444		623,430
Mikado	5,681	3,400	6,234	3,943	4,882	3,479
		28,182		19,971		8,022
Morice	22,606	14,442	22,507	14,673	25,846	15,830
		65,187		58,378		96,272
Morrison	21,741	14,535	22,263	15,190	21,411	14,995
		45,981		44,305		37,609
Motase	715	450	746	484	814	510
		2,687		1,961		2,470
Namu	9,913	4,650	9,758	5,016	6,674	4,361
		122,404		111,785		13,499
Owikeno	5,667,941	1,464,134	3,094,675	1,155,832	1,451,276	926,853
		20,456,400		19,586,955		3,015,524
Price	5,384	3,557	5,359	3,597	4,528	3,281
		12,314		11,667		7,165
Slamgeesh	947	347	580	344	543	340
		8,393		3,564		1,404
Stephens	7,925	5,549	8,305	6,049	7,787	5,847
		14,200		13,316		11,610
Sustut	12,810	1,575	11,981	1,796	3,964	1,555
		38,452		38,350		22,796
Swan	436,015	86,551	342,311	59,811	86,207	40,179
		787,852		781,116		315,147

Population	S _{MAX}	S _{MAX} Cls	S _{MAX}	S _{MAX} Cls	S _{MAX}	S _{MAX} Cls
Tankeeah	15,190	5,948	16,345	6,780	8,529	5,473
		107,080		105,093		17,386
Asitika	3,641	428	4,499	941	1,971	602
		7,584		7,636		9,571
Awun	8,165	6,322	8,548	6,619	8,163	6,444
		11,534		12,073		11,123
Borrowman	10,386	2,527	10,542	2,742	2,951	1,935
		74,638		74,347		5,535
Bowser	101,156	19,845	213,564	44,075	42,130	23,145
		412,289		422,917		104,788
Damdochax	11,086	4,642	19,304	5,852	8,076	4,799
		129,745		138,072		20,211
End Hill	12,172	6,336	10,183	5,857	7,034	4,936
		100,424		80,072		11,930
Fairfax	3,022	1,763	3,392	2,047	2,506	1,764
		31,280		17,686		4,176
Freeda	1,104	544	1,162	626	1,186	653
		15,353		13,352		5,137
Hauyat	14,623	3,355	12,747	3,156	4,861	2,307
		29,156		29,004		18,713
Kadjusdis	14,163	4,715	22,248	6,025	6,757	4,250
		91,320		93,967		13,848
Kainet	1,900	1,383	2,470	1,683	2,273	1,627
		3,110		4,768		3,731
Kdelmashan	2,108	1,323	2,832	1,632	2,038	1,412
		8,871		33,388		3,512
Keswar	1,307	750	1,567	1,015	1,321	928
		4,165		4,268		2,241
Kimsquit	28,523	15,080	48,933	19,385	25,336	16,157
		359,603		483,629		51,853
Kisameet	3,019	1,844	4,473	2,541	3,362	2,256
		14,751		38,090		6,301
Kwakwa	55,857	10,194	54,551	10,413	10,771	6,369
		144,585		144,450		24,928
Marian Eden	26,099	18,286	25,334	18,193	23,012	17,191
		46,604		42,562		34,517
Mary Cove	19,563	3,410	18,296	3,229	2,848	1,632
		38,936		38,838		6,864
Mathers	4,155	1,114	2,775	1,160	1,778	1,024
		18,502		17,715		5,858

Population	S _{MAX}	S _{MAX} Cls	S _{MAX}	S _{MAX} Cls	S _{MAX}	S _{MAX} Cls
McLoughlin	526	356	710	451	584	411
		1,061		1,955		979
Mercer	18,537	7,725	14,811	7,930	9,392	6,462
		136,823		113,656		16,486
Port John	1,056	602	1,601	840	1,193	759
		10,170		17,476		2,610
Prudhomme	10,998	7,643	10,664	7,624	9,433	7,096
		20,194		18,116		13,992
Shawaltan	5,622	3,424	5,974	3,784	4,865	3,409
		22,555		18,177		8,221
Sheneeza	2,599	1,035	2,338	1,082	1,401	909
		26,269		24,971		2,845
Skidegate	37,257	25,771	36,343	25,933	32,085	24,114
		69,532		62,527		47,948
Tuno East	25,520	3,426	24,066	3,808	3,399	2,029
		58,156		58,042		7,612
Tuno West	22,680	3,139	23,417	3,955	3,663	2,183
		57,894		57,939		8,247
Yakoun	28,648	17,022	28,668	18,012	23,437	16,345
		162,983		103,013		40,830
Yeo	2,015	1,249	2,366	1,464	1,927	1,330
		7,814		8,859		3,398

Table S5.3 Estimated productivity (α) for 70 sockeye populations on the NCC.

Population	Model 1		Model 2		Model 3	
	α	α CIs	α	α CIs	α	α CIs
Alastair	2.89	2.09	2.94	2.20	3.02	2.27
		4.00		3.93		4.01
Atnarko	1.40	1.13	1.87	1.20	2.36	1.61
		2.06		3.01		3.44
Azuklotz	2.71	1.57	3.39	2.01	3.63	2.27
		5.78		5.49		5.72
Babine	2.69	1.96	3.14	2.16	3.83	2.61
		5.17		5.16		5.77
Banks	2.78	1.49	2.67	1.68	3.15	2.08
		5.16		4.17		4.79
Bear	3.94	2.55	3.93	2.75	3.94	2.75
		6.09		5.63		5.61
Bloomfield	3.06	2.16	2.94	2.17	3.29	2.49
		4.29		3.96		4.35
Bonilla	2.35	1.61	2.41	1.73	2.64	1.94
		3.40		3.31		3.58
Canoona	4.75	2.92	3.76	2.56	4.11	2.88
		7.53		5.58		5.96
Curtis Inlet	2.28	1.57	2.36	1.67	2.62	1.91
		3.34		3.27		3.58
Devon	3.10	2.10	2.93	2.11	3.22	2.35
		4.58		4.09		4.43
Evelyn	2.60	1.71	2.59	1.80	3.08	2.26
		3.96		3.70		4.21
Fred Wright	8.86	4.58	5.51	3.76	6.65	4.49
		16.77		9.09		10.34
Hartley Bay	2.79	1.96	2.69	2.00	3.48	2.46
		4.96		3.98		5.13
Johanson	2.97	1.66	3.42	2.15	3.84	2.39
		7.22		5.69		6.34
Johnston	2.95	1.48	3.05	1.83	3.24	2.02
		6.21		5.01		5.22
Keecha	2.38	1.33	2.47	1.51	2.93	1.91
		4.57		3.90		4.48
Kitkiata	3.19	1.85	2.77	1.89	3.21	2.16
		6.54		4.56		5.00
Kitlope	2.73	2.02	2.80	2.14	3.00	2.33
		3.65		3.65		3.86

Population	α	α CIs	α	α CIs	α	α CIs
Kitsumkalum	2.63	1.97	2.73	2.06	3.03	2.34
		3.69		3.70		3.96
Kitwancool	5.60	3.27	4.67	3.18	4.60	3.20
		11.31		7.28		6.66
Koeye	2.51	1.73	2.51	1.81	3.05	2.17
		4.22		3.77		4.36
Kooryet	2.30	1.44	2.39	1.59	2.70	1.88
		3.68		3.49		3.85
Lakelse	2.84	2.03	2.91	2.15	2.99	2.22
		4.01		3.94		4.01
Long	3.83	2.67	3.62	2.63	3.94	2.96
		5.43		4.95		5.29
Lowe	2.26	1.63	2.33	1.73	2.43	1.81
		3.14		3.12		3.24
McDonell	4.58	2.92	4.32	3.00	4.58	3.21
		7.17		6.26		6.54
Meziadin	5.40	2.81	4.30	2.82	5.52	3.73
		10.63		7.25		8.45
Mikado	3.04	1.58	2.79	1.71	3.44	2.32
		5.59		4.36		5.15
Morice	3.83	2.71	3.84	2.84	3.74	2.75
		5.32		5.15		5.02
Morrison	4.19	2.81	4.10	2.92	4.25	3.09
		6.17		5.70		5.86
Motase	4.39	2.37	4.14	2.68	4.14	2.68
		7.80		6.36		6.31
Namu	2.48	1.52	2.51	1.64	3.07	2.13
		4.35		3.85		4.45
Owikeno	1.47	1.20	1.65	1.25	1.98	1.51
		1.99		2.31		2.62
Price	2.50	1.73	2.51	1.81	2.80	2.07
		3.61		3.45		3.79
Slamgeesh	2.31	1.30	3.37	1.84	3.65	2.15
		6.12		5.76		6.06
Stephens	4.50	2.64	4.23	2.82	4.56	3.10
		7.60		6.34		6.73
Sustut	3.32	1.82	3.60	2.28	4.13	2.60
		7.39		5.86		6.67
Swan	1.92	1.40	2.30	1.65	2.68	1.88
		2.73		3.28		3.85

Population	α	α CIs	α	α CIs	α	α CIs
Tankeeah	2.62	1.73	2.57	1.80	3.35	2.37
		4.63		3.97		4.80
Asitika	7.95	3.56	4.97	3.07	5.56	3.43
		20.82		8.43		9.40
Awun	3.56	2.58	3.31	2.49	3.50	2.65
		4.91		4.43		4.63
Borrowman	2.48	1.66	2.49	1.76	3.36	2.39
		4.18		3.73		4.79
Bowser	6.55	3.98	5.11	3.62	7.04	4.65
		16.86		7.79		11.45
Damdochax	5.45	3.34	4.61	3.23	5.67	3.97
		9.58		7.16		8.32
End Hill	1.57	1.15	1.79	1.14	2.23	1.52
		2.46		2.70		3.21
Fairfax	3.18	1.62	2.85	1.77	3.58	2.41
		5.98		4.49		5.41
Freeda	3.28	1.61	3.16	1.86	3.25	2.03
		7.15		5.34		5.27
Hauyat	1.90	1.39	2.04	1.49	2.42	1.71
		2.86		2.92		3.53
Kadjusdis	3.30	2.23	2.98	2.20	4.02	2.90
		5.68		4.47		5.72
Kainet	7.66	4.86	5.48	3.67	5.86	4.06
		11.93		8.23		8.57
Kdelmashan	4.62	2.45	3.44	2.16	4.27	2.90
		8.19		5.45		6.43
Keswar	3.56	1.39	2.71	1.48	3.36	2.00
		11.82		4.80		5.79
Kimsquit	5.13	2.87	3.91	2.62	4.91	3.38
		9.07		6.32		7.34
Kisameet	5.52	2.01	3.13	1.82	3.96	2.44
		14.65		5.53		6.72
Kwakwa	2.38	1.80	2.42	1.86	2.97	2.24
		3.32		3.24		3.98
Marian Eden	2.23	1.57	2.32	1.68	2.52	1.85
		3.19		3.16		3.41
Mary Cove	2.05	1.45	2.18	1.57	2.88	2.00
		3.07		3.08		4.16
Mathers	1.57	1.13	1.92	1.07	2.53	1.41
		4.15		3.59		4.42

Population	α	α CIs	α	α CIs	α	α CIs
McLoughlin	5.31	3.06	3.80	2.45	4.46	3.06
		9.07		5.91		6.67
Mercer	1.93	1.25	2.19	1.35	2.95	1.97
		3.72		3.51		4.44
Port John	4.56	1.85	3.02	1.78	3.76	2.37
		10.80		5.26		6.14
Prudhomme	2.28	1.62	2.35	1.72	2.60	1.94
		3.23		3.20		3.48
Shawaltan	2.91	1.70	2.77	1.81	3.23	2.27
		4.81		4.12		4.67
Sheneeza	2.25	1.41	2.38	1.55	2.99	2.03
		4.11		3.71		4.42
Skidegate	2.34	1.64	2.40	1.75	2.65	1.97
		3.33		3.27		3.56
Tuno East	2.18	1.49	2.29	1.61	3.42	2.28
		3.82		3.46		5.28
Tuno West	2.39	1.50	2.44	1.64	3.60	2.33
		4.88		3.81		5.78
Yakoun	2.58	1.56	2.58	1.70	2.98	2.11
		4.12		3.77		4.22
Yeo	3.60	1.92	3.05	1.94	3.60	2.43
		6.43		4.75		5.40

Table S5. 4 Estimated spawner abundance at maximum sustained yield (S_{MSY}).

Population	Model 1		Model 2		Model 3	
	S_{MSY}	S_{MSY} CIs	S_{MSY}	S_{MSY} CIs	S_{MSY}	S_{MSY} CIs
Alastair	12,706	7,012	12,718	7,452	12,682	7,631
		23,407		22,230		21,360
Atnarko	37,419	3,279	21,529	3,131	17,381	6,630
		264,654		333,734		47,772
Azuklotz	4,034	777	3,309	1,160	3,225	1,321
		46,934		32,181		12,611
Babine	2,168,015	335,149	1,324,707	372,147	912,896	399,016
		12,808,391		12,060,487		3,256,743
Banks	4,489	1,220	4,497	1,710	4,352	2,148
		18,206		12,671		8,864
Bear	3,303	1,831	3,305	1,988	3,449	2,054
		6,010		5,644		6,021
Bloomfield	1,785	841	1,813	880	1,570	906
		5,715		5,735		2,978
Bonilla	4,808	1,858	4,811	2,118	4,603	2,354
		16,002		13,232		9,500
Canoona	2,613	1,355	2,841	1,430	2,715	1,514
		5,934		7,239		5,518
Curtis Inlet	9,043	3,377	9,067	3,850	8,602	4,381
		29,688		26,157		17,413
Devon	4,448	2,246	4,468	2,392	4,352	2,549
		9,127		8,768		7,609
Evelyn	2,217	701	2,226	799	1,776	920
		28,048		23,478		3,914
Fred Wright	11,065	4,671	27,177	6,471	13,145	6,125
		147,561		177,654		46,040
Hartley Bay	3,927	540	4,620	717	1,489	616
		17,896		16,128		5,290
Johanson	2,130	125	1,997	209	971	218
		8,308		7,606		8,055
Johnston	2,915	721	2,927	1,141	2,919	1,281
		16,483		8,810		7,055
Keecha	3,278	667	3,285	1,016	3,141	1,399
		36,571		15,369		7,207
Kitkiata	4,910	1,155	6,472	1,558	4,846	1,722
		60,845		54,410		28,889
Kitlope	48,616	23,565	48,247	25,115	43,394	25,332
		142,601		120,599		80,322

Population	SMSY	SMSY Cls	SMSY	SMSY Cls	SMSY	SMSY Cls
Kitsumkalum	19,888	5,468	17,713	5,729	12,177	5,893
		211,357		202,525		34,858
Kitwancool	5,909	956	10,098	1,350	29,577	3,182
		38,846		35,469		232,504
Koeye	11,228	1,716	11,735	2,046	5,357	2,162
		97,159		91,038		21,213
Koorjet	4,419	1,252	4,422	1,595	4,236	1,981
		37,703		20,958		9,545
Lakelse	10,291	5,389	10,298	5,794	10,279	5,964
		20,223		18,983		18,181
Long	86,785	46,144	89,425	48,553	81,950	49,692
		201,879		205,862		147,155
Lowe	7,289	3,443	7,384	3,792	7,562	4,039
		14,823		14,133		13,858
McDonell	2,068	1,183	2,084	1,278	2,056	1,310
		3,709		3,517		3,301
Meziadin	203,550	69,023	281,724	91,727	184,549	95,168
		3,678,676		3,658,800		467,275
Mikado	2,683	727	2,756	984	2,508	1,299
		18,473		11,735		5,086
Morice	12,392	6,244	12,366	6,576	13,982	6,923
		41,900		37,002		60,348
Morrison	12,509	6,464	12,663	6,967	12,421	7,174
		31,277		29,269		25,092
Motase	421	172	427	207	465	218
		1,970		1,348		1,693
Namu	3,961	922	3,940	1,163	3,175	1,484
		71,786		61,444		8,006
Owikeno	1,038,337	127,709	726,139	124,918	452,478	180,409
		6,394,057		7,299,543		1,263,517
Price	2,161	905	2,166	983	2,008	1,077
		6,518		6,011		3,905
Slamgeesh	353	44	294	97	289	117
		5,690		2,362		949
Stephens	4,725	2,342	4,801	2,696	4,674	2,803
		10,333		9,144		8,133
Sustut	6,438	435	6,334	660	2,265	649
		27,749		25,589		15,928
Swan	129,819	13,878	126,648	13,991	36,858	11,630
		342,645		388,810		173,184

Population	SMSY	SMSY Cls	SMSY	SMSY Cls	SMSY	SMSY Cls
Tankeeah	6,381	1,511	6,740	1,841	4,306	2,090
		64,772		58,781		10,689
Asitika	2,683	225	2,808	447	1,288	309
		6,703		5,720		7,371
Awun	4,286	2,618	4,283	2,648	4,242	2,732
		7,166		7,144		6,728
Borrowman	4,137	600	4,224	716	1,494	744
		42,917		40,164		3,401
Bowser	70,249	11,121	134,903	23,380	29,944	14,028
		354,499		309,886		84,318
Damdochax	7,192	2,340	11,652	2,888	5,325	2,685
		100,386		98,661		15,086
End Hill	2,573	447	2,749	380	2,517	983
		39,710		34,473		5,862
Fairfax	1,475	401	1,527	542	1,321	686
		21,030		10,536		2,702
Freeda	550	122	564	178	587	209
		10,968		8,591		3,288
Hauyat	4,293	529	4,105	598	1,897	575
		13,134		13,298		9,769
Kadjusdis	7,082	1,691	10,353	2,127	3,804	1,936
		60,217		55,848		9,156
Kainet	1,386	854	1,606	900	1,517	922
		2,523		3,549		2,807
Kdelmashan	1,273	522	1,455	564	1,184	644
		6,594		21,663		2,423
Keswar	686	119	676	190	669	292
		3,373		2,623		1,489
Kimsquit	18,050	6,812	27,124	8,142	15,736	8,218
		274,547		331,639		37,344
Kisameet	1,969	585	2,156	700	1,879	888
		12,414		24,856		4,413
Kwakwa	21,455	2,755	21,247	2,960	5,004	2,294
		72,620		71,323		13,954
Marian Eden	9,363	3,894	9,450	4,422	9,318	4,878
		22,800		20,666		17,628
Mary Cove	6,360	602	6,393	681	1,290	515
		18,516		18,526		3,938
Mathers	881	69	828	37	723	167
		10,599		9,355		3,463

Population	S _{MSY}	S _{MSY} Cls	S _{MSY}	S _{MSY} Cls	S _{MSY}	S _{MSY} Cls
McLoughlin	338	169	387	178	347	195
		810		1,309		684
Mercer	5,550	835	5,212	1,136	4,341	2,001
		73,790		59,194		9,768
Port John	634	170	753	224	647	290
		8,085		11,175		1,772
Prudhomme	4,036	1,721	4,044	1,927	3,924	2,141
		9,959		8,871		7,240
Shawaltan	2,573	848	2,626	1,036	2,401	1,243
		13,881		10,371		4,990
Sheneeza	942	171	895	223	654	292
		14,962		13,445		1,682
Skidegate	14,040	5,979	14,053	6,713	13,597	7,445
		35,006		31,087		25,167
Tuno East	8,924	651	8,863	855	1,740	744
		31,855		29,935		4,875
Tuno West	8,739	605	9,190	916	1,937	820
		35,867		31,681		5,474
Yakoun	11,868	3,586	11,881	4,442	10,909	5,504
		93,030		55,958		23,584
Yeo	1,064	373	1,121	443	1,019	520
		5,391		5,422		2,198

Chapter 6. Conclusions

Salmon pose unique challenges for management and conservation, requiring understanding and coordination from local-scale monitoring of population dynamics and stressors, to Pacific basin-wide coordination for multinational management agreements. The diverse research presented in the preceding chapters reflects this multi-faceted complexity; downscaled to focus on the management and conservation issues facing sockeye salmon populations that support Food, Social and Ceremonial fisheries for the Heiltsuk Nation. From the creation of a community-run population monitoring program to monitor abundance and survival of sockeye salmon across their life cycle, to regional models of sockeye habitat productivity and population dynamics, the contents of my thesis chapters are deliberately cross-disciplinary and nested within the hierarchy of salmon population ecology and management. Despite the disparate themes and intellectual foundations for my thesis, the need to build broad understanding across multiple life stages and watersheds demanded this approach, and over the coming years this work will constitute the scientific basis of a Heiltsuk management plan for sockeye. By revealing new understanding of climate risks in coastal watersheds, stock-status and population dynamics across the North and Central Coast, and regional patterns of food web productivity in sockeye rearing lakes, my thesis illuminates the linkages between climate, habitats and conservation risks to inform fisheries management under climate change.

From high elevation interior plateaus of the Nass and Skeena watersheds to boggy rain-dominated systems in the low elevation landscapes of the Hecate Lowlands and Haida Gwaii, there are at least 120 locally adapted populations of lake-rearing sockeye on the North and Central Coast (NCC) (Holtby and Ciruna 2007). No feature of the landscape plays a greater role in shaping these populations than the lakes where they rear as juveniles. The hydrology, water chemistry, and food webs of these lakes defines the productive capacity watersheds to support sockeye (Shortreed et al. 2001), and controls the delivery of water and thermal energy downriver to riverine migration corridors. Across the landscape of the NCC, lakes exhibit strong regional patterns in water chemistry, particularly nutrient availability and the concentration of dissolved organic carbon (DOC) (Stockner and Shortreed 1985). Interior lakes with clear water are typically more nutrient rich and have deeper euphotic zones, yielding higher rates of

primary productivity which propagates through food webs to support rearing sockeye. Coastal lakes with humic-stained waters resulting from high concentrations of DOC are ultra-oligotrophic, with a greater relative contribution of microbial processing to lake energy budgets (Stockner and Shortreed 1989). However, these heterotrophic pathways transfer energy inefficiently to higher trophic levels, resulting in lower productivity for higher-level consumers like sockeye (Stockner 1987). Lake water clarity also plays a key role in filtering climate variability. Humic-stained waters resulting from high DOC inputs absorb solar energy efficiently and warm rapidly during the summer months, with intense stratification and low light penetration (Read and Rose 2013). These shallow euphotic zones support a narrow band of primary production near the lake surface with limited mixing between surface waters and cooler waters at depth. During extended periods of stratification, primary production is limited by low nutrient availability in the euphotic zone, and temperature sensitive sockeye may be excluded from lake surface waters (Koenings and Burkett 1987). Thus, physical and biological gradients in lake conditions play a key role in structuring the productivity and life history of sockeye populations.

In the low elevation watersheds of the BC coast, sockeye may face intense physiological stress and predation risk during their summer migrations. Yet the effects of temperature and river flow on sockeye migration success were previously unquantified among coastal sockeye. During mid-summer the lower Koeeye River routinely exceeds 20 °C, and in nearby Kadjudis, a lower-elevation watershed with dark humic-stained water and several large lakes, we have recorded summer temperatures in excess of 25 °C. Any sustained exposure to these temperatures is deadly for sockeye (Martins et al. 2012). Despite the naturally warm temperatures occurring in coastal watersheds, my second chapter revealed relatively low thermal tolerance among sockeye salmon in the Koeeye River. This is likely because sockeye in coastal watersheds have historically migrated in late-spring or early-summer before the rivers warm and drop to summer baseflows (Hodgson and Quinn 2002; Katinić et al. 2015). With accelerating climate change, sockeye in coastal rivers will need to migrate even earlier if they hope to avoid increased stress and mortality risk from warming river temperatures.

In addition to warming rivers, my second chapter suggested that migratory delays resulting from summer droughts may contribute to climate risk for sockeye salmon. Prolonged holding in marine waters may increase their vulnerability to fisheries or marine predators such as seals or sealions. The relative importance of migration delays

and thermal stress in mediating climate risk for adult sockeye likely depends on watershed size and location. For example, sockeye spawning in some interior watersheds in the Fraser Basin make migrations in excess of 1,000 km (Crossin et al. 2004), but river entry is never physically limited by low water. Thus, during warm years the energetic costs and physiological stress of migrating at high temperatures produce high rates of pre-spawn mortality (Rand et al. 2006). By contrast, fish in small coastal watersheds delay migrations when river temperatures are highest, since low flows impede river entry. In these cases, prolonged delays in marine waters increase their vulnerability to exploitation in fisheries, predation, and physiological stress from unplanned energetic demands. Many coastal watersheds fall into this latter category, and migratory delays are likely to play an outsized role in driving population responses to climate change. Future research into climate impacts should examine the effects of low-flow mediated migration delays as a driver of climate risk.

Given the low productivity of coastal lakes as rearing environments, and the vulnerability of sockeye in these systems to heat and drought, it is perhaps unsurprising that stock-recruit modeling in my final chapter revealed evidence of lower mean productivity (Ricker α) among coastal sockeye stocks. The productivity of a population dictates sustainable harvest rates (Ricker 1975), and as a result of their lower productivity most coastal sockeye populations can support lower rates of harvest. Differences in sustainable harvest rates across populations can pose major challenges to the sustainability of mixed-stock fisheries (Walters et al. 2008), and even modest incidental harvest may pose a threat to the recovery of collapsed populations such as Atnarko River sockeye (Connors et al. *in review*). Interestingly, the median estimates of α for collapsed Atnarko and Owikeno sockeye stocks were among the lowest of all the populations we evaluated (2.36 and 1.98 R/S respectively). Despite their associated risks, mixed-stock marine fisheries dominate commercial and sport harvest of salmon in British Columbia. However, in many cases a lack of data on the stock composition of fish captured in marine fisheries limits our ability to estimate population-specific harvest rates accurately. For example, Fisheries and Oceans Canada (DFO) has previously based estimates of sockeye catch composition in Area 8 on only 94 samples collected in 2003 (Connors et al. *in review*). In other cases, the erosion of budgets for routine population monitoring hinders our capacity to track changes in population size and status (Price et al. 2008). In the absence of rigorous monitoring data on escapement and harvest,

managers have reduced harvest rates in commercial fisheries to avoid impacts on at-risk or data-poor stocks (Walters et al. 2019), creating economic and cultural hardship for salmon-dependent communities.

Given the conservation risks associated with current marine fisheries and the declining viability of the commercial fishing industry, there is a need for innovation and transformation in wild salmon fisheries if they are to continue to support livelihoods for coastal communities in British Columbia (BC Wild Salmon Options Paper 2018). The revival of traditional terminal fisheries systems formerly banned under the Fisheries Act is a promising avenue towards increased opportunity and sustainability in wild salmon fisheries. The expertise we gained from building a traditional-style weir for population monitoring in Koeye is directly relevant to this task, and in 2019 we are working with the Heiltsuk Nation to build a similar weir in the Kunsot River, near Bella Bella, to create a linked subsistence harvest and population monitoring program. We have also been in contact with the Haida Fisheries about traditional-style weir building for population monitoring and hosted a delegation from the Yekoochee Nation with an interest in building a weir for subsistence harvest of sockeye. Traditional management of salmon supported resilient social-ecological systems for millennia prior to colonization (Haggan et al. 2006; Campbell and Butler 2010), recognizing and revitalizing these Indigenous systems of adaptive management should be a priority as we seek to revitalize wild salmon fisheries.

First Nations communities will play a major role in shaping the future of wild salmon in Canada. Despite the displacement of Indigenous management by colonization, these Nations never relinquished their sovereignty or ancestral rights to harvesting salmon (Harris 2001). Command and control management of natural resources has created a siloed, bureaucratic and failing system that has repeatedly produced ecological collapse, with catastrophic impacts on human and ecological communities (Holling and Meffe 1996). Management systems that engage resource users and empower local communities can increase resilience of ecological systems and promote social-equity in natural resource management (Castilla and Fernandez 1998; Moller et al. 2004; Frid et al. 2016). Traditionally, salmon management and harvesting were coupled through localized fisheries and culturally-enforced management practices (Swezey and Heizer 1977). Knowledge keepers and chiefs who held hereditary rights to weir or fish trap sites would harvest fish and regulate access to ensure the viability of the

resource for future prosperity (Johnsen 2009). Since the 1990s there have been calls for the transformation of salmon fisheries in Canada, and for increased local authority in management (Greer 1993). While these changes have been slow to come, there is a critical need for collaboration with Indigenous communities towards the co-creation of research that can increase capacity for salmon stewardship, supporting sustainable livelihoods and food security. Salmon and the communities they sustain will face unprecedented challenges in the 21st century, but both are inherently resilient, having persisted in the face massive cultural disruption and natural disturbances. It is my hope that the collaborative work in my thesis will propel further emphasis on and investment in community-driven ecological research and empower the Heiltsuk Nation as they work to maintain the cultural and economic vitality that flows from their connection to salmon.

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