**The Effects of Climatic Variables on Sockeye Salmon Size and Growth:**

**Literature Review and Proposed Study**

**Introduction**

There is mounting evidence that scale-dependent climate patterns, and the resultant oceanic conditions for prey, significantly impact the marine growth and survival of salmon populations in the Pacific Ocean. Climatic impacts on salmon are often complex and difficult to capture, as they are in part due to indirect changes to prey populations (Schindler *et al.* 2005) as well as competition with other salmon species (Ruggerone and Connors 2015). Accordingly, we aim to investigate predictors of salmon growth by analyzing the condition factor (Futon’s K) of fish as an indicator of relative nourishment, whereby changes in condition over time can represent reduced nutritional availability. The data we will analyze to address this question were gathered by two fisheries biologists, C.H. Gilbert and W.A. Clemens, between 1914 and 1946 in two river systems in Northern British Columbia (BC): the Nass Watershed and Rivers Inlet. Adult Sockeye Salmon, returning to their natal habitat to spawn, were caught weekly at the mouth of the river using gillnets. Length (mm) and weight (g) were recorded and used to calculate Fulton’s K condition factor. By analyzing this data, we aim to infer how historical Sockeye Salmon populations have responded to changes at multiple spatial scales and projected impacts on ocean conditions. We aim to test the relative importance of climatic and density dependent variables using generalized additive mixed models (GAMMs; Hastie and Tibshirani 1990). This modeling technique is used to account for temporal autocorrelation and the nonlinear responses expected when describing phenomena such as ecosystem change (Smith *et al.* 2009). The predictor variables we will be investigating are Sea Surface Temperature (SST), the Pacific Decadal Oscillation Index (PDO), the Aleutian Low Pressure Index (ALPI) and density dependence, calculated from catch data. These indices were chosen based on their documented effect on Pacific Salmon populations (Wells *et al.* 2006) as well as the availability of long term datasets spanning the same time period as our data. As these indices have all been shown to affect the growth and survival of Sockeye Salmon, I will here review their effects as have been documented in the literature for over 30 years. I will conclude by discussing our hypotheses based on the available literature.

**Climatic Variables – Sea Surface Temperature (SST)**

Some of the earliest research investigating climatic effects on Pacific Salmon species tested for the relationship between temperature and growth (Ricker 1982). The negative correlation he observed was attributed to one of two possible mechanisms: the maximum physiologically tolerable temperature or the indirect effect of increased food supply in cooler British Columbian waters. This trend of greater zooplankton abundance during cool years was found to differ regionally, with the Gulf of Alaska typically experiencing reduced biomass of zooplankton during a time of bounty in the south (Brodeur et al. 1996). This trend in abundance appeared to be mirrored in juvenile Sockeye numbers, that were similarly affected by temperature and associated prey availability (Farley et al. 2007). Along the Eastern Bering Continental shelf, fish were found to be significantly larger and in better condition during warmer years. However, it would appear that northern and southern populations of Sockeye respond differently to temperature due to differences in productivity during warm or cool periods (Hare *et al.* 1999).

Sea surface temperature has been modeled as a predictor of Sockeye Salmon growth in Alaska. Using a spatially specific bioenergetics model, Farley and Trudel (2009) predicted the growth rate potential of juvenile Sockeye Salmon under variable sea surface temperature (SST) in the Eastern Bering Sea. The model incorporated the distribution of fish, prey and the physical conditions of the environment in the study area to determine the importance of bottom-up controls on the fish. The result was an observed increase in growth potential in years with high SST coupled with an increase in available prey. Further investigation into this area revealed that the energy density of prey (a function of temperature, quantity and quality) was strongly correlated to marine survival (Farley *et al.* 2011) suggesting that bottom-up controls on available prey were linking growth, and overwinter survival in the Eastern Bering Sea. Thus SST has been shown to act as a bottom-up control of Sockeye Salmon growth by altering the oceanic conditions experienced by juvenile Sockeye Salmon.

**Climatic Variables – Pacific Decadal Oscillation (PDO) and Environmental Regimes**

Environmental variables act on numerous different scales. Previous research on the effect of climate on Sockeye growth has focused on levels of organization ranging from single stocks to whole species ranges. In a general context, Pyper *et al.* (1999) found that body length was positively correlated among 31 stocks throughout BC and Alaska, however stronger covariation existed between stocks within regions. This suggested that large-scale environmental variables affect the period of critical growth similarly throughout stocks, but fine-scale differences create regional patterns. Peterman *et al.* (1998) however, demonstrated seemingly contrasting results observing no evidence of covariation in Sockeye survival from spawners to recruits between southern BC and Alaska stocks. Based on this evidence, the authors suggest that the environmental processes that govern marine survival are largely different than those that affect body size and age-at-maturity.

Typically, large-scale climatic forcing is analyzed in the form of various indices to capture characteristic changes in an ecosystem (Wells *et al.* 2006). In Pacific Salmon research, the Pacific Decadal Oscillation (PDO) is one such index that corresponds well with population dynamics. Mantua *et al.* (1997) first identified this index when characterizing an inter-decadal trend in ocean-atmosphere climate dynamics. PDO describes sea surface temperature (SST) anomalies in the North Pacific that create decades long regimes of warm or cool conditions with positive and negative index values respectively. The utility of using PDO values as opposed to SST is that they capture a trend occurring on a larger scale and can be used to define a specific environmental regime. Mantua *et al.* (1997) also observed that the annual catch of Sockeye Salmon in Alaska tended to be positively correlated with the index. Further investigation into regional trends revealed that Sockeye Salmon abundance varied with PDO in opposite directions in the Gulf of Alaska (GOA) and Pacific Northwest (BC, Washington, Oregon and California) regions (Hare *et al.* 1999). Thus during warm PDO regimes like those observed between 1977 and the late 1990s, conditions seem to be favourable for Alaskan salmon whereas Pacific Northwest stocks suffer.

As PDO is ultimately dependent on SST, the mechanisms that explain the degree and direction to which Sockeye Salmon vary with PDO center around food availability. As mentioned above, Sockeye Salmon abundance along with zooplankton biomass trends are negatively correlated in the GOA and Pacific Northwest (Brodeur *et al.* 1996). Thus during warmer periods (positive PDO) characteristic of high Sockeye productivity in the Gulf of Alaska, we observe an increase in zooplankton abundance. This trend is opposite in Pacific Northwest locations, i.e. warm periods are coupled with reduced zooplankton biomass and worse returns in general. This correspondence was confirmed by Beamish *et al.* (2004b) during what was termed as a regime shift from warm to cold conditions in 1998. They found a significant improvement in juvenile Pacific Salmon production from the Strait of Georgia in southern BC. Juvenile Salmon consumed more prey and a greater quantity of preferred items when compared to previous years. Thus, Beamish *et al.* (2004b) extended the mechanism for increased growth to include prey quality. Stocks that returned as adults after feeding in this favourable environment showed higher than expected marine survival, lending support to the hypothesis proposed by others that overall marine survival is dependent on conditions encountered in the early marine, coastal phase of life (Francis and Hare 1994). This latitudinal variability appears to be present on a finer scale as well. Ferriss *et al*. (2014) observed regional and inter-annual trends in juvenile Sockeye Salmon growth within coastal BC stocks by measuring the blood concentration of insulin-like growth factor 1 (IGF1). IGF1 is a protein integral to endocrine growth in vertebrates and is used to infer instantaneous growth rate in juvenile salmon (Beckman *et al*. 2004). Individuals sampled in northern locations near Haida Gwaii contained greater concentrations of IGF1 than their southern counterparts indicating a higher growth rate potential in northern latitudes. The authors attribute this difference in growth rate to high-quality food availability brought into the northern system by the Alaskan Current.

Climate variability can also affect Sockeye Salmon growth within fine scale regions such as rearing watersheds (Griffiths *et al.* 2014). In this study, the authors found that within a watershed, populations of Sockeye that inhabit lakes with varying morphometric characteristics responded differently to changes in temperature. This, along with evidence from other Alaskan populations (Rogers and Schindler 2011; Kovach *et al.* 2014) suggests that within-watershed bio-complexity can create stock-specific responses to changing climate. This response was observed to carry over into the marine environment, where retrospective stable isotope analysis showed river-specific increases in variability of isotopic characteristics (inferring feeding behaviour) during times of higher ocean productivity (positive PDO regime; Johnson and Schindler 2012). Thus increased stock diversity within a given watershed may promote long-term population survival by increasing production and stability over the long term (Greene *et al.* 2010). This increase in stability arising from population diversity within a species or region is termed the “portfolio effect” (Schindler *et al.* 2010) due to its analogy with asset diversity positively affecting financial portfolios. This portfolio effect may help to explain variability in the growth and survival of Sockeye Salmon from watersheds differing in habitat complexity.

Recent research has been investigating the relative contribution of large-scale climate indices as predictors of body size and abundance. Jeffrey *et al.* (2016) modeled changes in the size of commercially caught adult salmonids in Canada between 1951 and 2012 with climatic indices such as PDO to determine how the body size of Canadian Pacific Salmon has changed over the sixty-year period. While long-term directional patterns were observed for other species, they found relatively little change in the mean body size of Sockeye Salmon over time. However, using GAMMs the authors were able to produce a model indicating that these indices could be used to predict body size of returning Sockeye. Their top model showed a positive effect on body size for PDO as well as the Northern Pacific Gyre Oscillation index (NPGO) at high values of either. The NPGO index represents the strength of wind-driven upwelling and horizontal advection corresponding to increased primary productivity in the system (Di Lorenzo *et al*. 2008). Other indices such as Multivariate ENSO (El Niño – Southern Oscillation) Index (MEI), a predictor measuring the intensity of ENSO events, were useful predictors of body mass representing a negative correlation with high index values. Unfortunately, NPGO and MEI indices are not included in our proposed research, as data for our study period does not exist.

**Climatic Variables – Aleutian Low Pressure Index (ALPI)**

Another climatic index periodically used to predict differences in salmon production is the Aleutian Low Pressure Index (ALPI). This index represents the strength of the Aleutian low-pressure system which influences wind stress and mixed-layer depth (Beamish and Bouillon 1993) . Positive values for this index represent a strong Aleutian low-pressure system, which will in turn typically produce a stronger Alaskan Gyre. Increased strength of this current has been suggested to stimulate coastal production by upwelling nutrients to promote phytoplankton and subsequent zooplankton production (Brodeur *et al.* 1996).

Beamish and Bouillon (1993) evaluated commercial catch data from four countries that harvest salmon in the North Pacific between 1925 to 1989 to compare production trends to large-scale climate indices. Of these, they found that ALPI corresponded to trends in catch as well as copepod production in the North Pacific. This correlation was observed between species and nations, which suggested that common climate stressors were affecting all salmon. Regionally, intense Aleutian Lows (high values of APLI) corresponded to higher marine survival for Fraser River Sockeye Salmon signaling a change in climate (Beamish *et al.* 1997). Beamish *et al.* (2004a) showed that these and other stocks vary with climate indices in an approximately decadal manor. They describe this as a regime shift when a ‘persistent trend in an index of climate and the ocean environment’ occurs. The production of Sockeye Salmon from the Fraser River appeared to vary with this change in climate regime. In their 2004 study, Beamish *et al.* (2004a) identified this regime as a composite of pressure indices like ALPI and PDO. By partitioning the data by regime, they were able to produce improved predictions of spawning stock biomass and recruitment for Fraser River stocks. It is important to note however that trends in ALPI do not confer increased production for all stocks. For example, Ishida *et al.* (2002) found no significant correlation between ALPI and catch-per-unit effort (CPUE) on body size in the Bering Sea, north of 55oN between 1972 and 2000.

**Biotic Variables – Density Dependence**

Density-dependent interactions such as competition with other salmon species influence the growth and survival of Sockeye Salmon (Ruggerone and Connors 2015). In general, the body size of Sockeye populations was observed to be inversely related to aggregate salmon abundance (Eggers and Irvine 2007). Within the salmonids, which are competing for similar resources in the marine environment, Pink Salmon appear to most significantly affect the survival (Ruggerone *et al.* 2003) and growth (Bugaev *et al.* 2001) of other salmon species. The mechanism explaining the disproportionate effect of Pink Salmon on Sockeye populations have been investigated by Ruggerone and Nielsen (2004). They found that Pink Salmon affected other salmonids through the exploitation of prey resources and attributed their success to high abundances, high consumption rates/growth as well as an earlier seaward migration. Thus Pink Salmon appear to be a competitive dominant in those years in which they are abundant. Large-scale studies confirmed this effect observing patterns of decreased productivity and length-at-age following the alternating-year life-history pattern of Pink Salmon (Ruggerone and Connors 2015).

Density dependent effects on growth may occur between species other than pink salmon as well. For instance, intraspecific competition with other Sockeye Salmon stocks has been observed (McKinnell 1995). In this study, McKinnell reports a negative density-dependent effect on mean length of BC Sockeye Salmon when the abundance of Bristol Bay Sockeye is high. Interestingly, this density-dependent effect varied depending on the life-history pattern of the fish, namely the amount of time that the fish spent at sea. As Sockeye Salmon can spend anywhere from one to four years in the ocean, this is likely explained by cyclical variations in the abundance of Alaskan populations creating food limitation in years when total salmon abundance is high. Thus, it seems as though having a diversity of life-history patterns within a stock may buffer density-dependent effects. This may in turn increase the long-term stability of the population through a ‘portfolio-effect’ like process with a diversity of life-history types (Schindler *et al.* 2010). Interestingly, the overall abundance of some salmon species has been shown to correlate positively with Sockeye Salmon. Jeffrey *et al.* (2016) for instance, found that an increase in Asian chum salmon biomass predicted an increased in Sockeye size. This trend was suggested to be due to improved overall ocean conditions for salmon in years with increased Chum biomass, increasing the ‘ocean carrying capacity for salmon’. As Chum Salmon are present in lesser abundance than Pink Salmon, which significantly depress Sockeye Salmon growth, this remains a possibility.

Although density dependent growth has been shown to significantly affect Sockeye Salmon populations, these trends are not independent of climatic variables. During years of increased productivity for Sockeye Salmon, one would likely expect increased productivity in competing salmonids as well. Pyper and Peterman (1999) examined the relationship between adult body size of BC and Alaskan Sockeye Salmon, total abundance and ocean temperature (SST). They found that total salmon abundance (a proxy for density dependence effects) and SST accounted for 71% of the observed variability in body length between 1967-1997 suggesting that when favourable SST and high overall abundance were observed together, they amplified competition creating an overall negative effect on adult body size. The authors also suggest that this increased competition may offset any benefits gained through greater food availability, resulting in a pattern of decreased body size over time. Ruggerone *et al*. (2007) also observed these effects following the climatic shift in 1977 towards a warm regime on salmon populations. They showed that Sockeye Salmon experienced greater marine growth during their first two years at sea after this climate shift. This led to higher rates of survival and abundance, which created density dependent limitations on growth during the later stages of life. Further research determined that density-dependent growth occurs at all life stages for Sockeye Salmon suggesting that even a regime shift towards cooler temperatures in BC may result in an observed effect of competition with Alaskan stocks (Martinson *et al.* 2008).

**Conclusions and Description of Proposed Research**

Over the past 40 years, much of salmon research has focused on the mechanisms that drive oceanographic change that lead to variability in growth and survival. Sockeye Salmon appear to respond to a suite of biotic and abiotic variables to varying degrees based on the scale of the factor being investigated. The underlying mechanisms appear to be bottom-up controls in temperature and nutrient availability, which affect the primary and secondary production during each life-history stage. These bottom-up processes drive the abundance of all salmon species in the marine environment and contribute to direct biophysical as well as indirect, density-dependent limitations on growth.

Because bottom-up controls of salmon productivity are variable on an annual basis, we aim to use climatic indices at various scales to predict the size of returning Sockeye Salmon. We will perform GAMMs to estimate the direction and magnitude of marine climatic as well as biotic factors as predictors for condition-at-age of returning Sockeye. PDO values, obtained from the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) as well as ALPI values, obtained from Fisheries and Oceans Canada will be used as estimates of large-scale climate patterns driving changes in condition-at-age. SST will be parameterized on a broad scale, as the mean temperature in surface waters of the feeding grounds for adult Sockeye in the Gulf of Alaska as well as on a narrow scale, which will include the mean temperature of the coastal feeding region reaching out to the edge of the continental shelf. By using these parameters, we hope to infer the relative effect of regional and broad scale climatic variability on returning Sockeye condition-at-age. An autoregressive moving average (ARMA) structure will be used to account for temporal autocorrelation and correlated climatic factors such as SST and PDO will not be included in the same models. To account for biotic variables, the total catch of Pink Salmon in the Gulf of Alaska will be included in each model we run. Our model outputs will be ranked using Akaike's information criterion (AIC) to determine the best-fit model.

Understanding how and to what degree climatic and biotic variables have affected these two BC stocks is important for their future management. Along with answering questions of scale for when these variables are most important, we will examine possible differences in how these two river systems may have been differentially affected. This is an especially interesting question, as the Nass Watershed remains a healthy stock that is fished annually, whereas the Rivers Inlet fishery has collapsed and has been closed since 1996 (McKinnell *et al.* 2001). We hope that by analyzing the relative contribution of these variables to condition-at-age in each watershed, we can infer possible causes that lead to this collapse. If trends in these two systems vary in a similar manner, we may infer that they are experiencing similar conditions in the marine environment. Differences between the two patterns may show that these stocks are experiencing different feeding environments during their marine life-history phase. With a deeper understanding of the factors that affect Sockeye Salmon growth and survival, we can hope to better manage these stocks in a future where warming trends and changing ocean conditions are of particular concern to their long-term stability and health.

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