Potential Mechanisms of Population Change in Southwest Alaskan Sockeye Salmon

Grace Henry

A thesis

submitted in partial fulfillment of the

requirements for the degree of

Master of Science

University of Washington

2025

Committee:

Daniel Schindler

Gordon Holtgrieve

Megan Feddern

Program Authorized to Offer Degree:

School of Aquatic and Fishery Sciences

University of Washington

Abstract

Potential Mechanisms of Population Change in Southwest Alaskan Sockeye Salmon

Grace Henry

Chair of the Supervisory Committee:

Daniel Schindler

School of Aquatic and Fishery Sciences

Bristol Bay, Alaska, is home to the world's largest commercial sockeye salmon (*Oncorhynchus nerka*) fishery. This fishery not only produces more than half of all sockeye salmon globally, but also supports cultural and economic livelihoods across North America. Over the last century, there have been substantial changes in this fishery due to shifts in climate, biological composition of the ocean, and management practices and sockeye populations fluctuated drastically in response. The freshwater and marine life stages of Pacific salmon are deeply interconnected and although historically the freshwater life stage has been much more thoroughly researched, substantial knowledge gaps exist in both of sectors. In order to thoroughly understand how the dynamics of this valuable resource have shifted through time, it is necessary to fill in the knowledge gaps in both the marine and freshwater systems impacting sockeye salmon population responses. I explore two potential mechanisms of sockeye salmon production through time; marine trophic shifts and density dependence on the spawning grounds. In chapter 1 I use a novel compound specific isotope analysis (CSIA) approach to reconstruct 60 years of trophic position and nitrogen assimilation in the North Pacific Ocean and relate observed changes to regionally relevant environmental shifts. I find that periods of high productivity are associated with truncated food chain lengths and enrichment of the nitrogen isotope baseline of the ecosystem. Although I do not directly assess how food chain length relates to salmon production in the region, I identify this as an area that

requires future exploration. In chapter 2 I build a population model to explore how density dependence on the spawning ground impacts recruitment and apply this model to a case study of two small creeks in Southwest Alaska. This model suggests a relationship between environmentally optimal spawn timing in a system and stock-recruit relationships, however when applied to our empirical data, this relationship does not hold up, indicating the need for further investigation.

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

ACKNOWLEDGEMENTS

I would like to thank my advisors, Daniel Schindler and Gordon Holtgrieve, and my committee member Megan Feddern for the extraordinary amount of support and mentorship that they provided over the course of this thesis. Daniel, thank you for welcoming me into your lab and supporting me in becoming a better writer, presenter, thinker and field scientist. Gordon, thank you for supporting me in pursuing grad school and giving me the opportunity to take ownership of my research while always being available for support when necessary. Megan, thank you for the many hours spent helping me decode GC chromatographs and your wisdom with the process of what it takes to be a successful grad student and the career advice that has come with that. I am endlessly grateful for the support that I received from this committee over the last three years and I strive to move forward into my scientific career with the same patience and generosity that was extended to me.

My degree was supported by several funding sources including the SAFS Fellowship and the Future Rivers Program. I am thankful to both these funding sources for giving me the opportunity to pursue a graduate education and it has greatly supported my development as both a scientist and a person. I also greatly appreciated the opportunity to be a teaching assistant in Watershed Ecology, Aquatic Ecological Research in Alaska and Introduction to Limnology and deeply value the connections I made with both students and faculty through these positions.

To my parents, Diane and David Henry, thank you for being my home and giving me a space where I can always go when I need a good meal or someone to listen. Thank you for always encouraging me to challenge myself while also reminding me that its ok to take breaks and slow down. I truly couldn't ask for more supportive, gentle and understanding parents and I will be eternally grateful to both of you for all the love, support and reassurance you have given me.

To all my friends and the entire SAFS graduate student community, thank you for the unwavering support through both joyous and challenging times. From providing an outlet to talk through complex ideas, troubleshoot buggy code, write side by side, plan for the future, develop our perspectives on what science is and how to move into the career world as the best scientists possible, I truly would not be here without the support I received from all of you. The sense of community that I felt throughout this entire degree will stick with me in all future endeavors and I hope to bring that mentality of community support into all my future work places. I am especially grateful to my lab mates Ben Makhlouf, Emma Christman, Cirque Gammelin, Jonny Singleton, Nick Chambers, Kelly Neal, Angela Dillon, Sabikunnahar Shorna, Liz Elmstrom, and Jenny Stern for providing endlessly helpful feedback on presentations, project directions, and general grad school advice.

Chapter 1

Six Decades of Shifting Trophic Ecology in the North Pacific: Sockeye, Scales and Stable Isotopes

Daniel E. Schindler

Megan Feddern

Gordon W. Holtgrieve

1.1 INTRODUCTION

Understanding the ecological mechanisms underlying large-scale population shifts to commercially exploited species is a critical step in planning for an uncertain future. Watersheds in Bristol Bay, Alaska (Figure 1.1), support the world's largest commercial sockeye salmon (*Oncorhynchus nerka*) fishery that produces more than half of all sockeye salmon globally (Ruggerone et al., 2010) and supports livelihoods across North America. The marine life stages of Pacific salmon are historically understudied, giving rise to the early belief that growth and survivorship is determined primarily by freshwater life history, despite 99% of somatic growth occurring after outmigration into marine environments (Welch & Parsons, 1993). There is now a widespread recognition that changes to the marine environment are associated with significantly altered population dynamics in a wide variety of species including sockeye salmon (Hare and Mantua, 2000); however, there are critical gaps in identifying the mechanisms through which marine environmental change impacts sockeye salmon feeding ecology, life history, and ultimately fisheries.

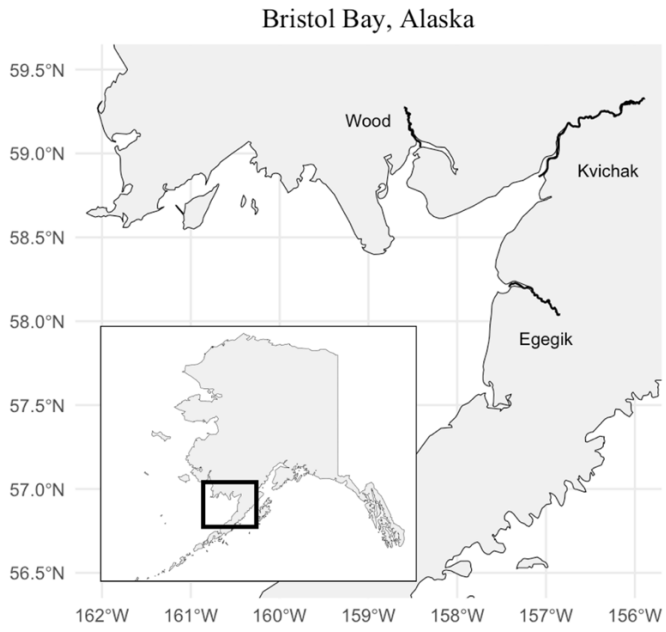

Figure 1.1: Map of Bristol Bay Alaska. Samples used in this study originated from the Wood, Kvichak and Egegik river systems.

The Pacific Decadal Oscillation (PDO) (Figure 1.2) is a key descriptor of North Pacific climate variability, primarily characterized by sea surface temperatures, that shifts on interdecadal scales (Mantua & Hare, 2002). In 1977, there was a shift to the warm phase of the PDO that caused widespread ecological shifts and led to a near doubling in production of sockeye salmon returning to Bristol Bay (Mantua et al., 1997), though responses varied in magnitude among rivers of this region (Hilborn et al., 2003). A second shift back towards a cool phase of the PDO was identified in 1989, after which environmental conditions across the North Pacific Ocean once again changed but did not return to the conditions of the pre-1977 ocean (Hare & Mantua, 2000). Coinciding with this 1989 shift was a decline in the relative importance of PDO in predicting salmon abundance, while simultaneously emerged a new climate regime, coined the North Pacific Gyre Oscillation (Di Lorenzo et al., 2008), as the dominant predictor of salmon production in the region (Litzow et al., 2018). While salmon response to climate forcing in the North Pacific Ocean are now thoroughly documented, the biological mechanisms that link physical forcings to variability in salmon ecology and abundance remain poorly understood.

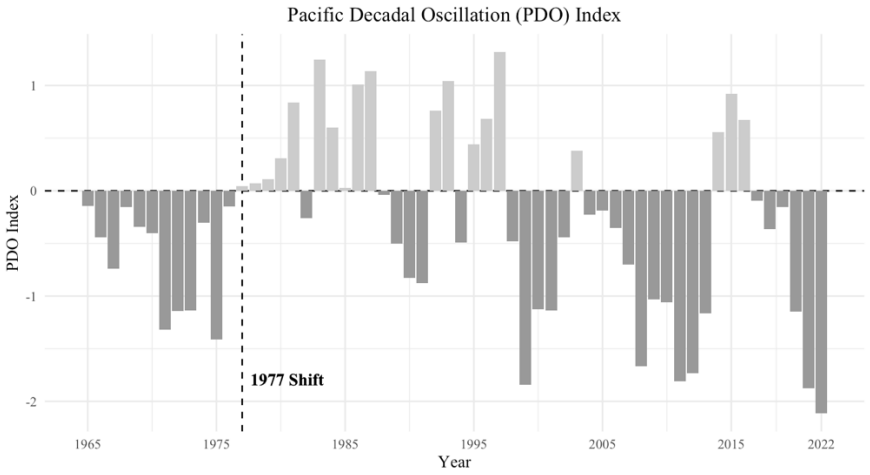

Figure 1.2: PDO index through time. All values <0 represent periods of anomalously low PDO (cool phase) while all values >0 represent periods of anomalously high PDO (warm phase).

Both the biological composition and physical environmental forcings of the North Pacific Ocean experienced significant change in response to shifting climate regimes. Following the 1977 PDO shift to warm phase, the community composition of the Gulf of Alaska shifted from one dominated by crustaceans and forage fish to one dominated by groundfish (Anderson & Piatt, 1999). In this same time period, there was also a significant increase in zooplankton biomass in the Gulf of Alaska (Brodeur & Ware, 1992), where Bristol Bay sockeye salmon achieve nearly all of their marine growth. While the abundance of both pink salmon and chum salmon have increased substantially over the last 60-years (Cline et al., 2019a; Connors et al., 2024) there has been a subsequent decrease in marine growth rates of sockeye salmon (Ohlberger et al., 2023), further complicating understanding of how climate regime and food webs have translated into impacts on commercially important fisheries. Despite this evidence of plausible shifting food webs, there is limited information about trophic position changes during the marine life stage of sockeye salmon using long-term datasets.

Stable isotope ratios of nitrogen ($^{15}N/^{14}N$) in archived biogenic material provide a means for characterizing the trophic history of a species (DeNiro & Epstein, 1981; B. J. Peterson & Fry, 1987). Although previous studies have investigated the connection between trophic ecology of Bristol Bay sockeye and oceanic conditions using bulk stable isotope analysis (BSIA) all have found little to no

evidence of trophic variability (Johnson & Schindler, 2009; Satterfield & Finney, 2002). Despite these negative results, the fundamental connection between marine condition and trophic response remains unclear partly due to the simplifying assumption of a constant $\delta^{15}N$ of primary producers at the base of the food web (referred to as the $\delta^{15}N$ baseline) through time and space (Feddern et al., 2024; Post, 2002). The $\delta^{15}N$ baseline is determined by the concentration of nitrate in surface waters, the source of nitrate to the marine system and the community composition of primary producers (Zhu et al., 2021). Inorganic nitrogen concentration and source $\delta^{15}N$ are controlled by a number of processes including, but not limited, to nitrification, denitrification, upwelling, and terrestrial runoff that can vary by as much as -6‰ to +10‰ across space and time (Sigman & Casciotti, 2018). Most previous isotope-based studies using archived tissues typically do not have additional information on concurrent shifts in the $\delta^{15}N$ baseline and are therefore forced to assume stability through time, which is a highly unlikely scenario (Post, 2002).

Compound specific isotope analysis of amino acids (CSIA-AA) is an emerging method to address some of the limitations of traditional bulk stable isotope analysis (McClelland & Montoya, 2002). This method significantly improves upon trophic position estimations that use bulk isotope analysis alone by adding a measurement of the ecosystem $\delta^{15}N$ baseline. While estimation errors originating from assumptions about the ecosystem baseline propagate up the food web using bulk isotopes, CSIA estimation error is both consistently lower, and does not magnify as trophic level increases (Feddern et al., 2024). CSIA-AA analyzes the isotope composition of individual amino acids, taking advantage of the unique metabolic pathways of each amino acid that lead to unique isotopic fractionation with trophic transfers. Amino acids are commonly categorized into either trophic (e.g., glutamic acid) or source (e.g., phenylalanine) amino acids (Popp et al., 2007). Trophic amino acids are strongly enriched in ^{15}N during each trophic transfer whereas source amino acids show minimal difference in $^{15}N/^{14}N$ across trophic levels and reflect the $\delta^{15}N$ of the primary producers in a given ecosystem at the time of nutrient assimilation into primary producers (McClelland & Montoya, 2002). This amino acid method therefore allows for a more robust measurement of trophic position shifts through time by accounting for a dynamic baseline that was incorporated at

approximately the same temporal scale as the trophic amino acid (Downs et al., 2014), thereby providing a new lens through which to observe the correlation between basal food web changes, trophic position and environmental change.

As opportunistic feeders (LeBrasseur, 1966), sockeye salmon (*Oncorhynchus nerka*) are an excellent study organism for understanding the link between climate and trophic ecology. As omnivores and opportunistic feeders, sockeye diet shifts between zooplankton, squid, small fish and other micronekton dependent on marine feeding location and prey availability (Davis et al., 2009). These shifts can lead to measurable variations in assimilated $^{15}N/^{14}N$ in sockeye tissues. Archival tissues are a powerful resource for identifying mechanistic links between climate, competition, and the trophic dynamics through time which is fundamental in understanding how environmental conditions impact commercially important species (Feddern et al., 2023). Since 1964, the Alaskan Department of Fish and Game (ADF&G) has collected and archived sockeye salmon scales from each of the seven major river systems in Bristol Bay. Scales are a useful archival tissue because they are metabolically inert, capturing a lifetime of growth in a single scale, where core tissue is laid down during periods of freshwater growth and outer layers correspond with the marine life stages (Hutchinson & Trueman, 2006). To understand further how marine environmental change has impacted salmon life histories and food webs, we generated a representative, time series dataset of amino acid $\delta^{15}N$ to calculate shifts in trophic position of Bristol Bay sockeye salmon during periods of significant marine change. With this data set, which ranges from 1965-2022, we aimed to quantify changes in trophic position, as well as shifts to assimilated $\delta^{15}N$ at the base of the food web. We hypothesized that (1) the baseline $^{15}N/^{14}N$ will respond to large-scale climate regimes reflecting changes in N availability and source, and (2) trophic positions will shift in respond to changes in N incorporation into primary producers.

1.2 METHODS

Approximately thirty individual sockeye salmon scales were selected per year, per river system from the years 1965-2022. Three river systems were chosen; Wood, Egegik and Kvichak, based on the unique patterns of sockeye salmon abundance exhibited in each system during the study period (Hilborn et al., 2003). To account for isotopic differences between age classes (Johnson & Schindler, 2013) only scales of fish spending two years in the ocean prior to return, the dominant age class in Bristol Bay (Cline et al., 2019b), were included in our final analysis. The center of individual scales, corresponding to the juvenile freshwater phase, were removed so that each scale could be assumed to be dominated by material accumulated during marine life stages only. The thirty sampled scales per river system per year were pooled and samples were run as composites.

Sample processing followed the protocol of Feddern et al. (2021), using amino acid pivaloyl chloride-acetyl acid derivatization paired with GC-IR-MS to analyze the $^{15}N/^{14}N$ of five individual amino acids from a total of 86 samples. Only two amino acids were used in trophic position estimations; glutamic acid (trophic) and phenylalanine (source). Samples were processed in the University of Washington Facility for Compound-Specific Isotope Analysis of Environmental Samples using a Thermo Scientific Trace GC + GC IsoLink coupled to a Delta V irMS. Each composite sample was analyzed in triplicate alongside a mixed AA standard of known isotopic composition. Post-processing included internal and external standard correction, within run drift correction, and mass correction. All values are expressed in the standard delta notation relative to atmospheric nitrogen (1).

$$Equation\ 1\text{: } \delta^{15}\mathrm{N}(‰ \text{ vs. air}) = \left(\frac{(^{15}\mathrm{N}/^{14}\mathrm{N})_{\mathrm{Sample}}}{(^{15}\mathrm{N}/^{14}\mathrm{N})_{\mathrm{Air}}} - 1\right) * 1000$$

CSIA-AA inherently has higher among-sample variance (i.e., observation error) compared to BSIA. This error adds to the process-based variance arising from ecological variation among individuals in a population over time.

Multivariate Auto-Regressive State-Space (MARSS) models can be used to analyze time series data with significant observation and process-based error. MARSS models consist of two parts, a state process ($\mathbf{x}_t$) representing the true "hidden" ecosystem state that is observed through measurements characterized by an observation process ($\mathbf{y}_t$) (2b). These models estimate an ecosystem state and collected data are treated as an observation of this state (Tolimieri et al., 2017). In this case, the hidden ecosystem states estimated by the model was the phenylalanine and glutamic acid $^{15}N/^{14}N$ through time, which was observed through measured data. The MARSS model is specified by the following equations:

$$Equation\ 2a\text{: } \mathbf{x}_t = \mathbf{B}\mathbf{x}_{t-1}, \text{where } \mathbf{w}_t \sim \text{MVN}(0, \mathbf{Q})$$

$$Equation\ 2b\text{: } \mathbf{y}_t = \mathbf{Z}\mathbf{x}_t + \mathbf{v}_t, \text{where } \mathbf{v}_t \sim \text{MVN}(0, \mathbf{R})$$

where 2a represents the process equation to model the hidden true state (phenylalanine and glutamic acid), and 2b represents the observation equation, to relate the isotope data ($\mathbf{y}_t$) to the estimated ecosystem state ($\mathbf{x}_t$). The matrices **Q** and **R** represent the variance-covariance matrices for process and non-process errors respectively, and were structured to be diagonal and equal (Holmes et al., 2024). To separate the introduced noise from the true state through time in both the phenylalanine and glutamic acid data sets, two models were fit per amino acid, the first of which assumes all observations are pulled from one population (called the "bay-wide" model) and the second of which assumes that salmon populations from individual rivers exhibit unique foraging behaviors (called the "river-specific" model). Model fitting was done using the MARSS package (Holmes et al. 2024) in which the $\mathbf{Z}_t$ matrix varied between model types either as a 18x1 matrix in the bay wide model or a 18x3 matrix in the river-specific model.

Trophic position was calculated as follows:

$$Equation\ 3\text{: } \mathrm{TP_{Glu/Phe}} = (\delta^{15}\mathrm{N_{Glu}} - \delta^{15}\mathrm{N_{Phe}} - \beta)/\mathrm{TDF} + 1$$

where $\delta^{15}N_{Glu}$ is the modeled state of glutamic acid annually and $\delta^{15}N_{Phe}$ is the modeled state of phenylalanine annually (Lerner et al., 2021), each of which was estimated independently as described

above. TDF represents the trophic discrimination factor of glutamic acid and phenylalanine, or the amount that glutamic acid is enriched as compared to phenylalanine with each trophic transfer. We used a TDF value of 7.6 based from controlled feeding studies on Chinook salmon conducted by Lerner et al (2021). β represents the difference between the $\delta^{15}N_{Glu}$ and $\delta^{15}N_{Phe}$ in primary producers (Nielsen et al., 2015) and a value of 3.4 was used, as recommended by Chikaraishi et al. (2009).

1.3 RESULTS

The bay-wide model (Figure 1.3) revealed that phenylalanine (source AA) $\delta^{15}N$ increased by 1.6‰ from 1965 to 1985, stabilized at approximately 5.0‰ during the middle of the time series, and began declining back to pre-1980 values in the mid-2000s. In contrast, glutamic acid (trophic AA) $\delta^{15}N$ ranged from 22.6‰ to 25.1‰ and fluctuated throughout the time series without an observable relationship with climate conditions. The mean trophic position (TP) across the full time series, calculated from these modeled amino acid states, was 3.3. TP anomaly plots (Figure 3c) highlight three key time periods: 1965–1976 (period 1), 1977–2007 (period 2), and 2008–2022 (period 3). Relative to the long-term mean TP of 3.3, period 2 (1977–2007) exhibited a sustained decline in TP, with a weighted mean of 3.16, which was approximately **7** standard errors below the long-term mean. In contrast, period 1 (1965–1976) and period 3 (2008–2022) showed elevated TP values of 3.38 and 3.34, respectively, which was 6.7 and 4.7 SEs above the long-term mean. This pattern suggests a mid-time series drop in trophic position followed by a partial recovery in recent decades.

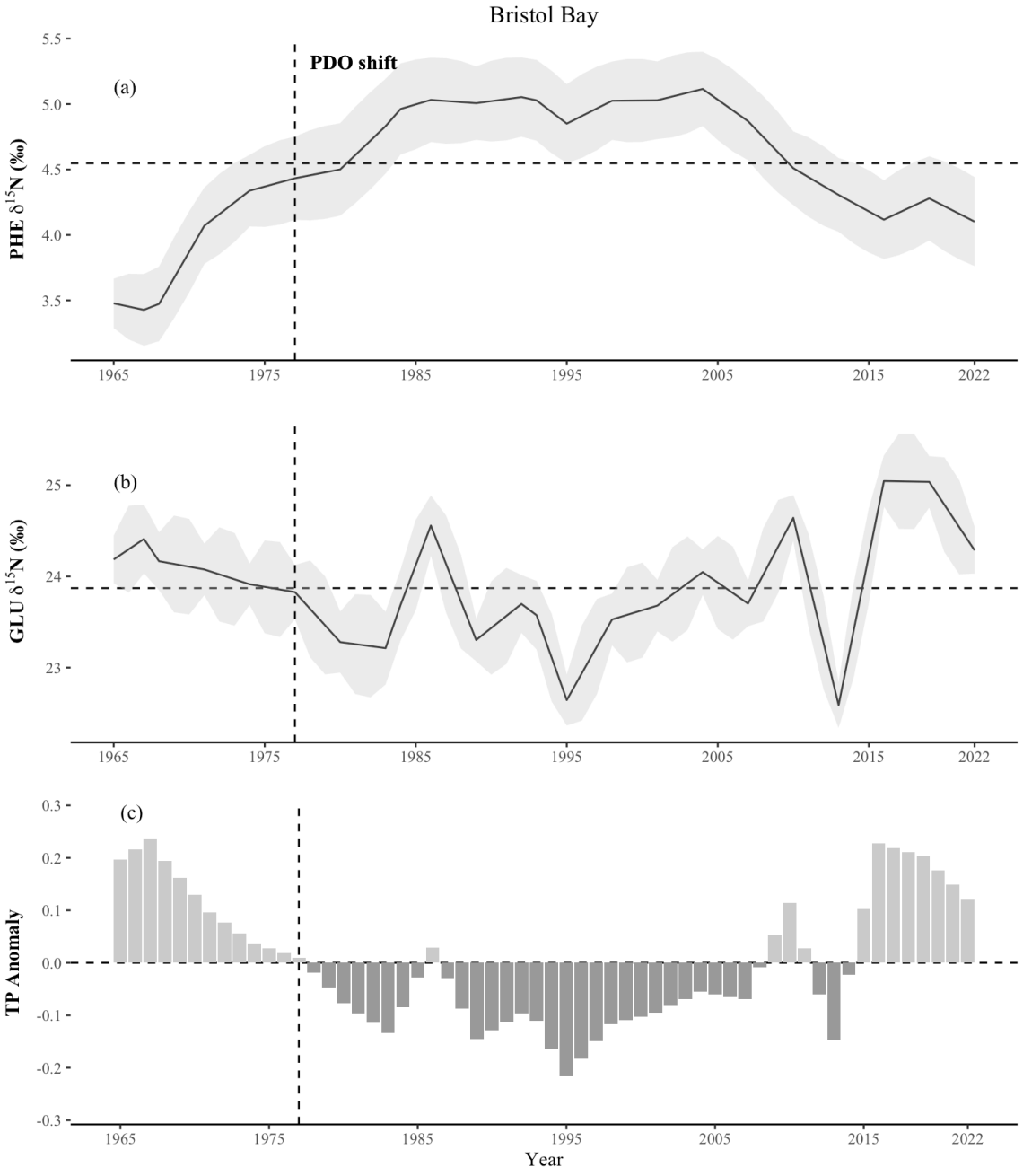

Figure 1.3: Bay wide model outputs. A) Modeled phenylalanine (baseline) hidden state over the time period. Light grey area represents one standard error above and below the modeled state. B) Glutamic acid hidden state through time. Light grey area represents one standard error above and below the modeled state. C) Trophic position anomaly calculated using above equation and inputting two modeled baselines.

We compared the aggregate Bristol Bay response to river-specific changes to determine whether foraging patterns of different sockeye salmon populations responded uniquely to changing ocean conditions. Using

AIC model selection, the river-specific model, in which individual river systems were allowed to vary independently, outperformed the bay wide model in both the glutamic acid and phenylalanine models (Table 1). In the phenylalanine river-specific model (Figure 1.4 a-c) of sockeye salmon in the Kvichak and Egegik rivers followed similar patterns through time, which map closely onto the bay wide model, with generally increasing trends at the beginning of the time series and decreases at the end of the time series. The $\delta^{15}N$ - PHE of sockeye salmon – which reflects the $\delta^{15}N$ of nitrogen at the base of the marine food web – from the Wood River varied significantly year to year but showed no systematic trend over the time series. Glutamic acid trends (Figure 1.4 d-f) of sockeye through time in the Kvichak and Egegik rivers showed no systematic trend through time, while the Wood shows a U-shaped trend through time with decreases at the beginning of the time series and increases at the end. The mean trophic positions of sockeye in the Wood, Kvichak and Egegik rivers were 3.3, 3.2 and 3.3 respectively. Similar to trophic position estimates from the bay wide model, in all three river systems, TP at the beginnings and ends of the time series was higher than the mean, however there was more variation in the intervening years. The key change points in trophic position are relatively consistent, with the first shift to lower TP occurring in the late 1970s and subsequent shift to higher TP occurring in the mid-2000s.

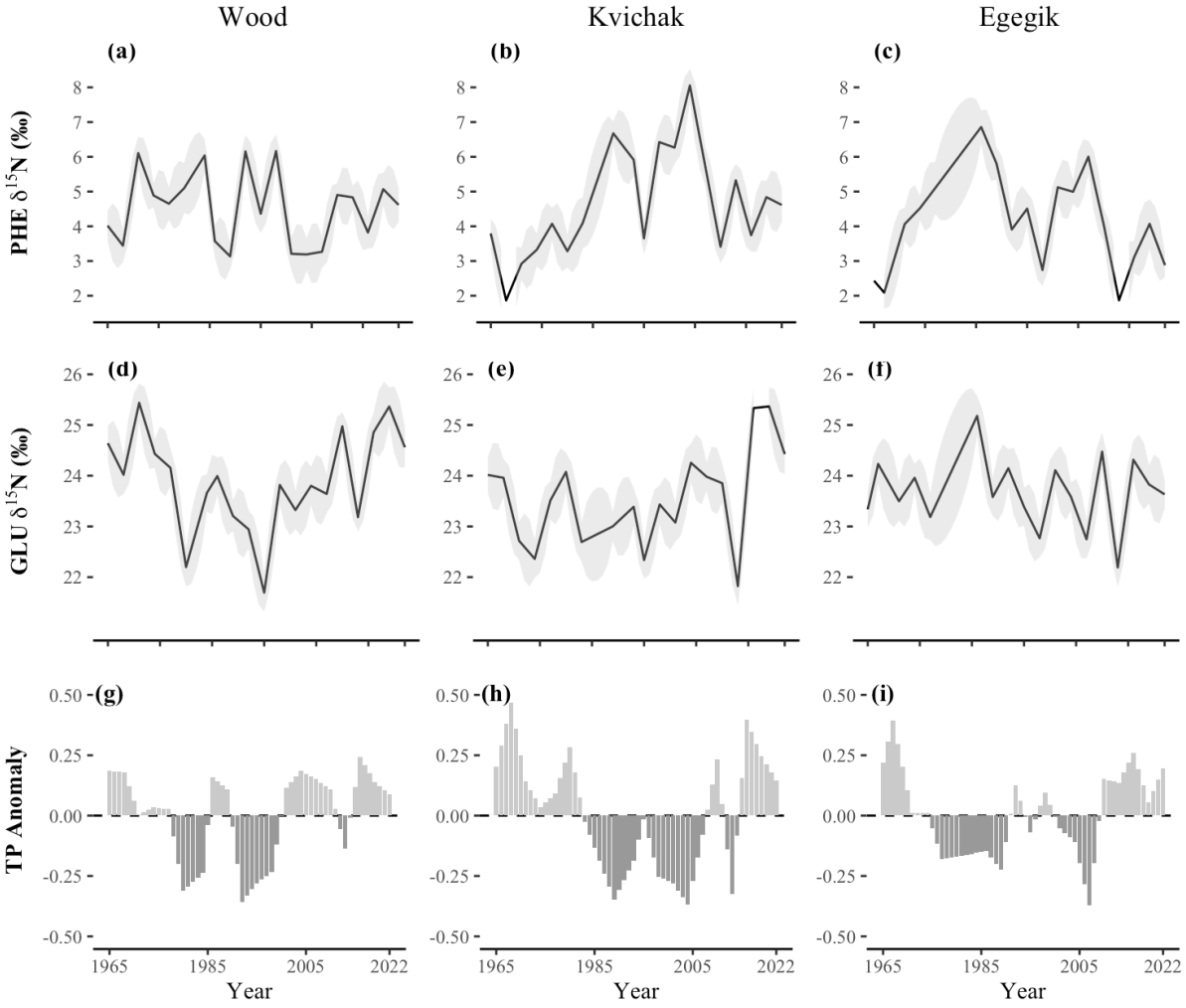

Figure 1.4: River-specific model outputs for phenylalanine through time, glutamic acid and trophic position anomaly through time. Light grey shaded area in panels a-f represent one standard error above and below the modeled trends. Wood river (first column) is classified as a west-side river system, while Egegik and Kvichak are both considered east-side systems.

1.4 DISCUSSION

We analyzed the $\delta^{15}N$ of two amino acids in scales of sockeye salmon from Bristol Bay between 1965 and 2022, a time period over which there were drastic changes in climate forcing on the North Pacific Ocean to which fishery production responded substantially. The trophic position of sockeye salmon returning to Bristol Bay has varied through time with years in which $\delta^{15}N_{PHE}$ was enriched corresponding with truncated food chains and lower sockeye trophic position. We assume $\delta^{15}N_{PHE}$ to reflect available nitrate concentration, nitrogen source to the ecosystem and community composition of primary producers at the

base of the food web (McClelland & Montoya, 2002; Michener & Lajtha, 2007; Sherwood et al., 2011, 2014; Zhu et al., 2021) at the time of incorporation into the food web by primary producers. Additionally, we show that isotopic baselines in this ecosystem have varied through time with changes in climate forcing in the North Pacific.

1.4.2 BAY-WIDE TROPHIC RESPONSE THROUGH TIME

In 1977, coinciding with the shift to the warm phase of the PDO, we observed a bay-wide shift to anomalously low trophic position in sockeye salmon among all major river systems that persisted until the mid-2000s (Figure 3). Pacific salmon are trophic generalists with prey selection reflecting the available community composition (Naydenko et al., 2007) and diet preference based on salmon size and life stage (Zavolokin et al., 2007). The observed decrease in trophic position we document between 1977 and 2007 suggests that zooplankton became a more dominant component of sockeye diet, supported by literature accounts of significantly increased zooplankton biomass in the Gulf of Alaska following the mid-1970s climate phase shift (Brodeur & Ware, 1992). Shifts in feeding location could also explain the relationship between climate phase and trophic position. In warm phase PDO years, out-migrating salmon spend a larger proportion of their marine life history in highly productive, inshore habitats with higher abundance of zooplankton (Springer & van Vliet, 2014), potentially explaining the lower-than-average lifetime trophic position in warm phase years.

In the mid-2000s, bay-wide trophic position showed a shift back to higher values and a subsequent shift back to low phenylalanine $\delta^{15}N$ that persisted through 2022. This shift to higher-than-average trophic position in the mid-2000s suggests the emergence of a new climate pattern, ocean circulation regime or ecological forcing that impacted productivity into modern day. Growing evidence indicates that regional primary production has been declining along a similar timeline, beginning in 2003 and persisting through 2020 (Frey et al., 2022), supporting the hypothesis that regional primary production is inversely related to trophic position (Lerner et al., 2022). Unlike the shift to low trophic position in the late 1970s, the shift to

higher trophic position in the mid-2000s does not closely align with a notable climate phase shift in the PDO, suggesting other significant environmental shifts. In the late 1980s there was a decoupling of the relationship between PDO phase and sockeye salmon production in Bristol Bay in which this correlation declined to near zero (Malick, 2020). Along this same timeline NPGO emerged as the leading predictor of salmon production (Litzow et al., 2018) and was thought to better explains fluctuations in chlorophyll-a, nutrient and phytoplankton concentrations (Di Lorenzo et al., 2008), thus potentially enacting more influence over sockeye trophic position and $\delta^{15}N_{PHE}$ in this time period than PDO phase. This shift in NPGO coupled with the declining regional primary productivity suggests that near the end of our time series, these factors played a larger role in shaping trophic position patterns in the region than PDO.

1.4.3 BAY-WIDE BASELINE RESPONSE THROUGH TIME

Corresponding with the period of anomalously low sockeye trophic positions, we estimated anomalously high $\delta^{15}N_{PHE}$, suggesting that in response to climate phase shifts, either the $\delta^{15}N$ of source nitrogen, the concentration of nitrate or the biological composition of primary producers in the Gulf of Alaska shifted. Enrichment in $\delta^{15}N$ of plankton has been associated with decreases in nitrate concentration and increased phytoplankton productivity (Zhu et al., 2021) due to preferential uptake of ^{14}N by phytoplankton which enriches the residual pool of nitrate in non-nitrogen limited ecosystems like the Gulf of Alaska (Sigman et al., 1999). This suggests that in highly productive warm phase years, phytoplankton become more highly enriched in ^{15}N, which becomes a signal transferred through the food web to out measurements of $\delta^{15}N_{PHE}$ in sockeye. This is further supported by literature showing a strong negative correlation between primary production and food chain length, in which highly productive years led to shorter food chain lengths and therefore lower trophic positions (Lerner et al., 2022).

Enriched $\delta^{15}N_{PHE}$ during productive, warm phase years could also be explained by regional shifts in the source of nitrogen to the Gulf of Alaska. The Gulf of Alaska is a primarily downwelling driven, iron limited, productive system in which the majority of nutrients to support high primary productivity are

supplied from freshwater runoff (Stabeno et al., 2004). During warm phase years, runoff generally increases to the Gulf of Alaska (Stabeno et al., 2004), potentially leading to changes in baseline enrichment depending on the $\delta^{15}N$ of source nitrogen. Alternatively, denitrification, which exclusively takes place in anoxic environments, such as the deep ocean, discriminates against ^{15}N which results in a highly enriched residual nitrogen pool (Michener & Lajtha, 2007) that when upwelled, may enrich $\delta^{15}N_{PHE}$. Reports have shown that years of strong upwelling decrease overall trophic positions by increasing primary productivity (Brodeur & Ware, 1992). Beginning in late 1976, an intensification of the Aleutian Low increased offshore wind stress and upwelling, increasing nutrient supply to this region (Beamish, 1993). This shift could feasibly be reflected in sockeye $^{15}N/^{14}N$ if these areas overlapped with primary feeding habitat. Changes to nitrogen source and concentration of nitrate are therefore both viable hypotheses to explain the enrichment of $\delta^{15}N_{PHE}$ that corresponded with the warm and highly productive phase of our time series.

1.4.4 RIVER-SPECIFIC RESPONSE THROUGH TIME

The river-specific model suggests variance in trophic response and baseline $\delta^{15}N$ among river systems. Salmon stocks are locally adapted to their rivers of origin (Quinn, 2018) and this biocomplexity is widely understood to stabilize fishery production and decrease year to year variation in bay-wide production (Hilborn et al., 2003; Schindler et al., 2010). Studies looking at bulk isotope values among river systems in Bristol Bay found significant variation in $\delta^{15}N$ through time suggesting different marine foraging strategies or foraging locations between populations (Johnson & Schindler, 2012). Notably, this same study hypothesized differences in foraging strategies between the east-side and west-side rivers of Bristol Bay; with Egegik and Kvichak characterized as east-side and the Wood characterized as west-side. Despite similar key change points in our estimations of trophic position across rivers, (higher than average trophic position early in the time series, lower than average following 1977 and a return to higher than average in the mid-2000s) the $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Glu}$ exhibit distinctly different patterns between Kvichak and Egegik rivers and the Wood River. In the Wood River there is a distinct lack of trend in the

$\delta^{15}N_{Phe}$ through time, while both Egegik and Kvichak show a bell-shaped curve similar to that in the bay-wide model. This suggests that Wood River salmon stocks are exploiting distinct foraging locations compared to their east-side counterparts during their marine growth, therefore assimilating a unique $\delta^{15}N$ signature. While data we present suggests river-specific foraging patterns in Bristol Bay sockeye, these responses are superimposed on a broader pattern that is expressed at the scale of Bristol Bay sockeye.

Table 1.2: AIC and delta AIC model outputs. The bay-wide model considers all three river systems as coming from the same population, whereas the river-specific model recognizes all rivers as individual populations and allows for variability among rivers. PHE model uses raw phenylalanine data while GLU model uses raw glutamic acid data.

Model	AIC	ΔAIC
PHE – bay wide	726.8	73.3
PHE – river specific	653.5	0
GLU – bay wide	612.7	10.6
GLU – river specific	602.1	0

1.4.5 CONFOUNDING FACTORS

Although the sum of scientific work to date tends to support the hypothesis of primary production being the link between climate phase and trophic position, overall abundance of Pacific salmon and theories of marine competition may confound results late in the time series. From 2005-2024 pink salmon abundance reached a record high, making up 70% of all Pacific salmon (Ruggerone et al., 2023). Sockeye, chum, and pink salmon exhibit significant diet overlap (Graham et al., 2021; Johnson & Schindler, 2009) leading to growing concern about the impact competition has on sockeye growth and survivorship (Ruggerone et al., 2003; Welch & Parsons, 1993). Evidence suggests that pink salmon have exerted top-down forces significant enough to reduce the overall abundance of large copepods in spring and summer months (Ruggerone et al., 2023) and this has been associated with declining marine growth rates of Bristol Bay sockeye salmon (Ohlberger et al., 2023). In the Gulf of Alaska, sockeye and pink salmon compete for zooplankton and higher trophic position species of micronekton such as squid and small fish (Graham et al., 2021), suggesting that if high pink salmon abundance were to modify zooplankton availability, subsequent shifts to micronekton by sockeye may be observable as an increase in overall trophic position.

Our analysis uncovered a return to anomalously high trophic position beginning in 2009 with only a short-term return to low trophic position for three years from 2012-2014, and a continually increasing trophic position from 2014 up through the end of our time series in 2022. This suggests that in years of high pink abundance and low copepod abundance, sockeye trophic position could be a result of either climate induced food web change, competition induced change or a combination of the two. To disentangle the relationship between competition, climate and trophic ecology research with a higher temporal resolution (i.e., sampling annually or during marine life stages) would be necessary.

Mechanisms driving sockeye feeding ecology, trophic position and production through time are complex and multi-faceted. Measurements of shifting nutrient baselines and trophic position through time provide only one lens through which to observe changing population dynamics and food webs in the North Pacific. We demonstrated that North Pacific food webs have shifted throughout six decades of significant oceanic change, however disentangling the specific ecological mechanisms remains challenging due to the complexities of how food webs respond to changes in bottom-up forcing. Linking oceanic change with mechanisms driving salmon ecology and ultimately production in the Bristol Bay fishery will be a crucial next step in developing reasonable scenarios for how future environmental change will impact populations, production and ultimately, long-term fishery outcomes.

Chapter 2

Density Dependence and Habitat Saturation of Sockeye Salmon in Southwest Alaskan Streams

Daniel E. Schindler

Timothy Cline

Samuel May

Lorenz Hauser

Kerry Naish

Ray Hilborn

2.1 INTRODUCTION

Classic understanding of how density-dependence affects recruitment suggests that at high densities, populations experience compensatory mortality due to competition among individuals for limited resources (Ricker, 1954). The Ricker model of stock-recruitment relationships reflects this idea by producing 'overcompensation', where recruitment declines at very high spawning densities rather than simply leveling off, or 'saturating'. Evidence of overcompensation in fish populations is relatively strong for salmonids, presumably because they spawn in confined habitat areas that can result in particularly strong competition for suitable spawning habitat (Foss-Grant et al., 2016; Semenchenko, 1988). In years of high salmon density, high quality habitat can become quickly saturated leading to superimposition of early redds by later-spawning individuals, in which individuals construct redds on top of those constructed earlier in the spawning season (Essington et al., 2000; Fukushima et al., 1998; Heard, 1978; McNeil, 1964). This process of redd superimposition can physically disturb or dislodge previously buried eggs and contributes to density-dependent mortality on the spawning grounds (McNeil, 1964; Moore et al., 2008).

Despite these observations, the specific mechanisms by which redd superimposition might drive overcompensation rather than simply saturating the stock-recruit curve remains unclear. Here, we use a

simple model of spawning ground competition to demonstrate that redd superimposition alone should favor late spawners but does not, by itself, generate overcompensation. However, by including evolutionary constraints on optimal spawn timing, which are environmentally determined, the model shows that strong selection on spawn timing, coupled with superimposition can produce overcompensation in stock-recruit relationships.

Variation in local spawn timing and regional run timing is beneficial because it decreases the chance of variation in temperature eliminating entire brood years, thus dispersing the risk to the population in aggregate (Schindler et al., 2013, 2015). The timing of salmon runs are based on local environmental conditions to optimize reproductive success (Beacham & Murray, 1990; Koch & Narum, 2021) and stream entry is generally centered around an environmentally optimal spawning date that is associated with the water temperatures of a spawning site (Lisi et al., 2014). Using a genetic pedigree constructed from genetic samples of spawning salmon in Alaska (May et al., 2025, *in prep*), we compare spawning population size with reproductive success throughout the season to determine if reproductive success is higher late in the season in years of particularly large run sizes. We expect superimposition during years of high salmon density to decrease the reproductive success of the earliest spawning individuals and to redistribute the recruitment later in the season. If we observe no bias in reproductive success late in the season in high density years this may suggest that the habitat that has not yet hit its saturation threshold, or survivorship and redd defense by early spawning salmon plays a more significant role than superimposition. If there is a local selection for spawn timing, then we expect to see overcompensation in recruitment from high density spawning events.

We apply this model framework to empirical data from two small streams in southwest Alaska, A and C creeks, that support small populations of sockeye salmon (*Oncorhynchus nerka*). Using a multi-year genetic pedigree (May et al., 2025, *in prep*) we tracked all individuals spawning in these streams from 2004-2012 and related their seasonal spawn timing to their reproductive success (measured as recruitment

in the next generation of spawners per spawning female). This study design allowed us to identify when in each season produced the most recruits, and whether this temporal distribution of successful spawners was dependent on the spawning population size. From this, we were able to determine if redd superimposition is a driving mechanism of density dependent morality in these systems.

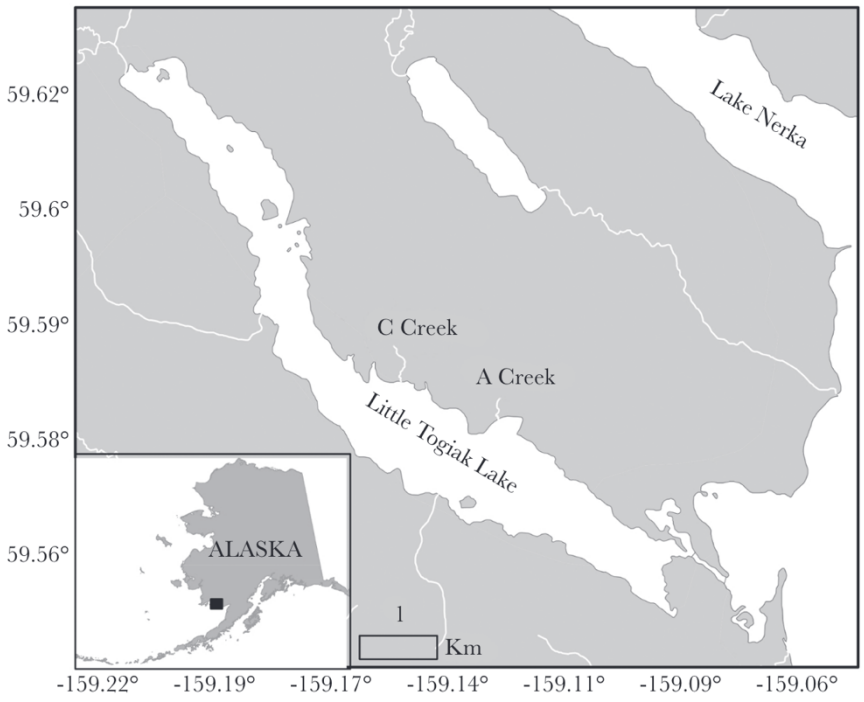

Figure 2.1: Map showing geographic location of A and C creeks in the Wood River system of Bristol Bay (D. A. Peterson et al., 2016).

2.2 METHODS

2.2.1 SITE DESCRIPTION AND SAMPLE COLLECTION

A and C creeks are located in the Wood River system of Bristol Bay in southwestern Alaska (Figure 1), approximately 1.5 km apart (D. A. Peterson et al., 2016). Both systems are shallow, averaging 10cm deep throughout, groundwater fed and relatively short, each having less than 500 meters of stream length. C Creek is wider than A Creek, averaging 2.1 m as compared to 1.4 m wide (Pess, 2009). Temperature, flow regime and gravel size are similar between the two streams, but C Creek has more undercut banks, woody debris and habitat complexity (Pess, 2009). During our study period, approximately 100-600 sockeye

salmon returned to these streams per year to spawn, although much larger, record-breaking runs were observed in 2021 and 2022. Sockeye populations from each stream are genetically distinct (Lin et al., 2008) although there is some level of dispersal mediated by local environmental conditions (May et al., 2025, *in prep*; Peterson et al., 2016). Because of their small size, and relatively large spawning population sizes, and empirical evidence of mortality caused by redd superimposition (Moore et al., 2008) A and C creeks are excellent systems within which to study the effect of habitat saturation on recruitment.

Sampling of the spawning sockeye salmon population was conducted from 2004-2012. The full length of spawning habitat in both A and C creeks (350 m and 460 m respectively) was surveyed daily from late July through early September. All sockeye salmon were captured, measured, individually labeled with a 2.5-cm disc tag and fin clips were taken for genetic analysis. If any untagged dead fish were found, fin clips, length and depth measurements were taken. Although complete population sampling is not possible, previous studies conducted in these stream suggest that greater than 90% of spawning individuals in these systems were captured and sampled throughout the time period (Hauser et al., 2011; D. A. Peterson et al., 2014).

2.2.2 GENETIC PEDIGREE AND DATA

Reproductive success was defined as the number of offspring produced per individual female fish that survive long enough to be sampled after returning to its stream of natal origin. Genetic analysis of samples from all fish from 2004-2012 were used to determine the number of recruits produced by every female spawner in the two systems. (May et al., 2025, *in prep*).

Our data consists of the unique identifier, stream entry date, and reproductive success of all females in the streams from 2004-2012. In both A and C creeks, most individuals initiate spawning activity on the first day they are observed in the stream, while the majority of fish deaths are caused by bear foraging occurring within 4 – 7 days of stream entry (Carlson et al., 2007). Further, it is clear that most individuals

initiate spawning activity on the first day they are observed in the stream. We therefore assume that the first day on which a fish was observed in a stream (entry date) was a valid approximation of their seasonal spawning date. We include only female fish in the analysis in an attempt to not double count recruits and because females dig redds, meaning that density of females is what would mostly dictate superimposition and habitat saturation. Recruitment, however, included both females and males in the subsequent generations.

2.2.3 POPULATION MODEL

We developed a simple population model to simulate how optimal spawn timing paired with habitat saturation affects the shape of a stock-recruit curve. This model considers mean spawning date, standard deviation of the mean spawning date, the variation in fitness associated with spawn date, and habitat capacity. The fitness curve (Figure 2) describes the relationship between spawning date and fitness and is assumed to be Gaussian, centered on an optimal spawning date as determined by local environmental conditions and water temperature (Lisi et al., 2014). Fitness is defined as the total reproductive success on a given day divided by the total number of female fish that entered the stream to spawn on the same day. We hypothesize that cumulative entry into a stream over the course of a season is inversely related to the number of competitors that an individual fish will interact with. Fish that enter the stream on the first day of the season will potentially compete with all subsequent fish for spawning habitat, while fish that enter the stream on the last day will have very few fish to compete with, given the assumption that fish die soon after entering the stream. The number of spawners that any individual competes with (Figure 3) is therefore directly related to the number of fish that enter a stream in a given year and its own spawn timing. We calculate viable spawners (Figure 3) per day as a function of the number of competitors on a given day and the number of individuals needed to saturate the capacity of the spawning habitat. The model assumes that later spawning fish displace those that have spawned earlier in the season, if the total number of fish in the stream exceeds the capacity of the stream. For example, if that habitat capacity is 300, then the model assumes that the last 300 fish spawning in the stream are viable, and any fish that

spawn earlier than these 300 had their redds destroyed, thus producing no recruits. Relative recruitment per day is calculated by multiplying the relative fitness on a given day and the number of viable spawners on that day. Total recruitment from a single spawning year is then calculated by summing relative recruitment across the season. Recruitment was calculated over a range of escapement levels, using the same model parameters, which allowed for the generation of a stock-recruit curve to represent each model scenario. We implement this simple model with a range of parameter combinations to explore how habitat saturation interacts with the variation in the fitness timing curve to determine the strength of density dependence in the population.

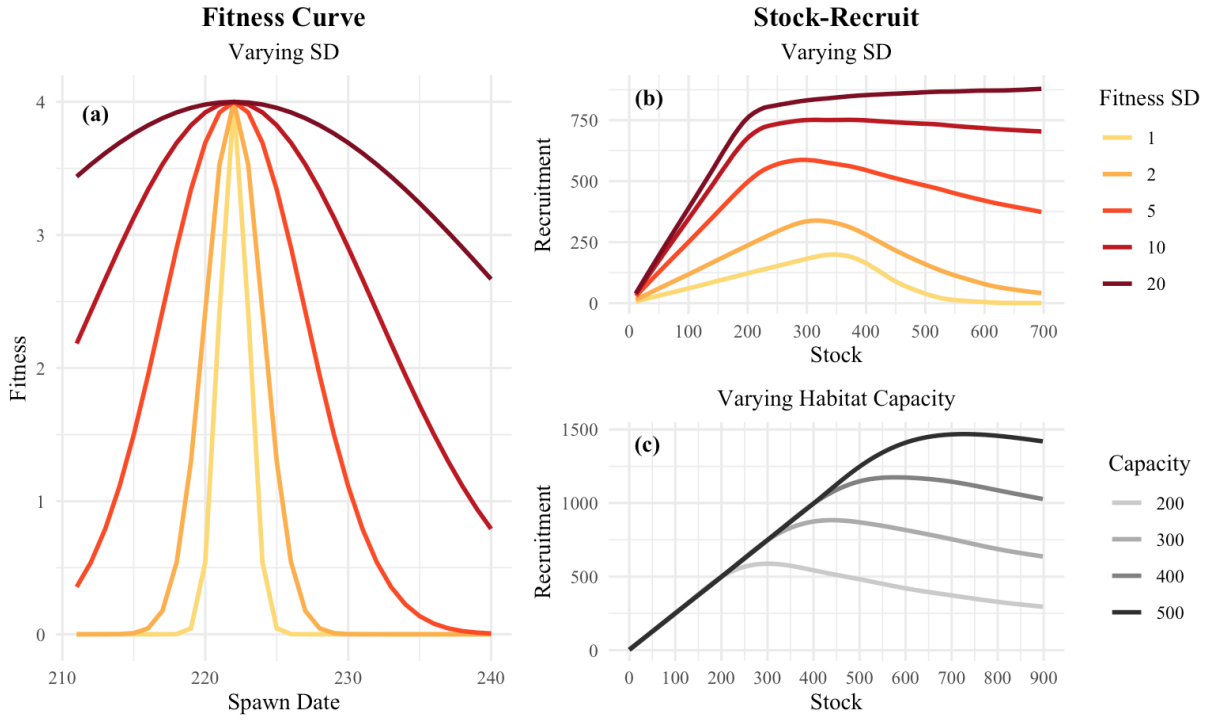

Figure 2.2: Hypothetical fitness curves and stock-recruit relationships produced at different habitat saturation thresholds and standard deviations on the fitness curve. Panel A is a fitness function of spawn date across different standard deviation thresholds, fitness is defined in this case as the number of recruits produced per spawner. Panel B shows how stock-recruit relationships vary when changing only the standard deviation of the fitness curve. Panel C shows the effect of varying only habitat capacity on stock-recruit relationships, at the set standard deviation of 5.

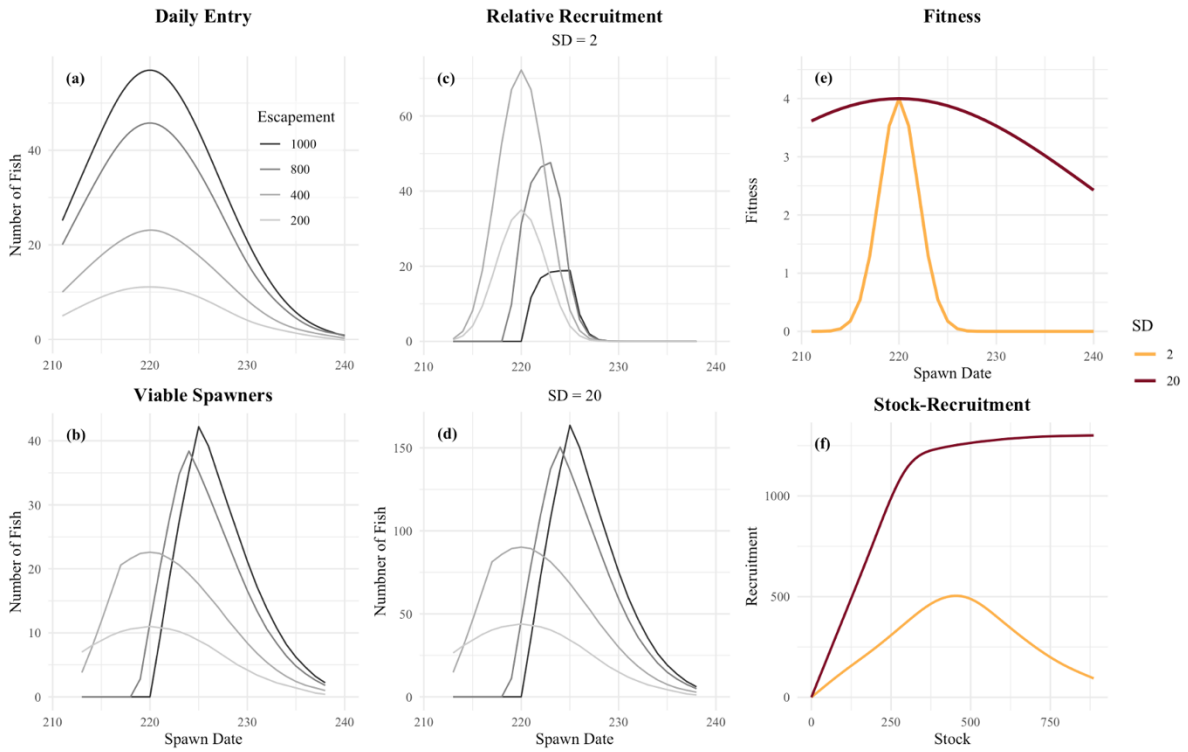

Figure 2.3: Two simulated examples of population responses to two different standard deviations on the fitness curve. Both simulations assume a habitat saturation threshold of 300. A) Daily entry curves showing individual fish entry throughout the spawning season at four levels of escapement (200, 400, 800, 1000). B) Viable spawners, assuming that only the last 300 fish to enter the stream have reproductive success. C and D) Relative recruitment at two different fitness curve standard deviations. When the fitness curve has a low standard deviation (c), late spawning fish have no reproductive success, leading to less recruitment. F) Stock-recruit curves produced from the two simulated standard deviations on the fitness curve. A fitness curve with a high standard deviation produces saturation of the stock-recruit relationship, whereas a fitness curve with a low standard deviation produces over compensation.

2.2.4 DATA ANALYSIS

We compared this model with our reproductive success data throughout the spawning season in A and C creeks to better understand how these dynamics play in real populations and test the hypothesis that, due to superimposition, habitat saturation favors late spawning individuals in high abundance situations. We generate fitness curves in both A and C creeks by first determining the total number of recruits produced on each day of the spawning season, and then dividing this by the total number of fish that entered on that same day. To compare across years, we standardize fitness among years by dividing daily fitness by the maximum daily fitness within that year, meaning that the day per year in which fitness peaked will be equal to one. A Gaussian curve was then fit to the data from each stream using non-linear least squares regression (NLS). The model followed the form:

$$Y = \mathrm{a} * \left(-\frac{(X - \mathrm{b})^2}{2\mathrm{c}^2} \right)$$

Where Y is the relative fitness, X is the entry date, *a* is the peak fitness value, *b* is the mean entry date, and *c* is the standard deviation of the distribution. To calculate the stock recruit curve in each stream we first calculated the stock as the total number of fish per year and then the total number of recruits and plotted each year.

We estimated the best-fitting Ricker curve on the stock-recruit plot by minimizing the negative log-likelihood, following the formula:

$$R = aSe^{-bS}$$

Where R is recruitment, S is the number of spawners (stock), *a* represents productivity at low stock size, and *b* describes the strength of density dependence. Model parameters were estimated using the optim() function in R, using the "L-BFGS-B" method.

As an alternative to the Ricker model, we also estimated a fit to the stock-recruit data using a Shepherd model (Shepherd, 1982) in which:

$$R = \frac{a * S}{1 + \left(\frac{S}{K}\right)^c}$$

Where R and S are again recruitment and stock, respectively, *a* is productivity at low stock and K is carrying capacity. This model differs from the traditional Ricker model with the addition of the *c* parameter, which controls the strength of density dependence. A large *c* ($c > 1$) implies overcompensation in the stock-recruit curve. The Shepherd model allows for more variability in the shape of the stock-recruit curve to account for more potential types of density-dependent relationships (Foss-Grant et al., 2016).

We calculated and plotted potential competitor plots where x is the day of the year that a fish enters the stream and y is the number of fish that will enter after that day (e.g., the possible number of fish that could superimpose a previously established redd) in each year. On each entry day, we calculate relative fitness as the total number of recruits produced by fish from that entry day divided by the number of fish that entered on that day scaled to the total number of fish per year. We do this for both A and C creeks.

2.3 RESULTS

2.3.1 SIMULATED POPULATION MODEL RESULTS

Our population model shows that the shape of the stock-recruit curve is sensitive to the variance of the fitness curve as a function of spawning date. A fitness curve with a large standard deviation, where there is no benefit to spawning at any particular day of the spawning season, (i.e., no clear date on which fitness peaks during the season), produces a simple saturating relationship between recruitment and the parental spawning escapement (i.e. no overcompensation; Figure 2). A fitness curve with a small standard deviation, meaning that there is a day of the season with significantly increased fitness, leads to a stock-recruit curve that bends over at high densities, demonstrating strong overcompensation. The sensitivity of the shape of the stock-recruit function to the standard deviation of the fitness function is controlled by the habitat capacity, such that higher capacity leads to a larger spawning population needed to generate overcompensation in the stock-recruit function.

2.3.2 EMPIRICAL EVIDENCE FOR FITNESS BENEFITS OF SPAWN TIMING

Across the years of our study the number of fish returning to each stream varied from 63-639 in A creek (39 - 435 females) and 102 - 511 in C creek (49 – 336 females). The ratio of females: males ranges from 1.43 – 2.61 in A Creek and 0.92 – 1.43 in C Creek. The vast majority of fish in this system produce zero recruits; on average only 30% of female fish in A creek and 37% of female fish in C creek produced at least 1 recruit.

The Gaussian model of fitness as a function of spawning date had similar peak dates in the two streams (A Creek had a peak date of August 7th, and C Creek peaked on August 8th; Figure 2.4). However, the standard deviation of the fitness curve was better defined for C Creek (std dev = 9.0) as compared to A Creek (std dev= 16.9).

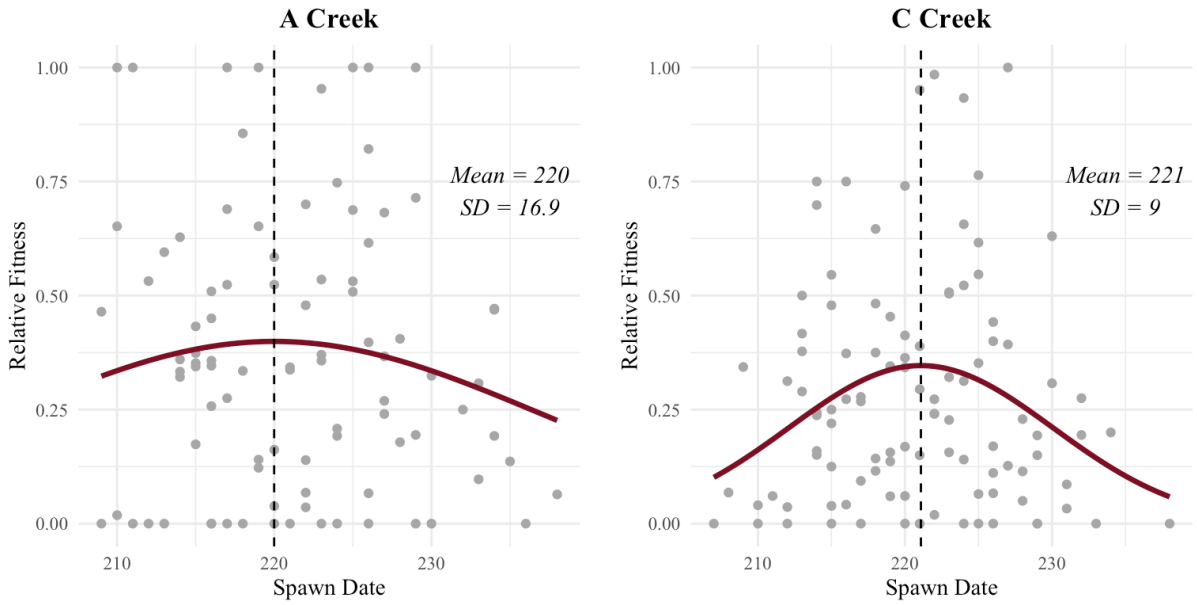

Figure 2.4: Gaussian model fits to fitness data from A and C creeks. Fitness was calculated as total recruits produced on a given spawning date divided by the total number of fish entering on that same date. Fitness was then standardized among years by dividing fitness on each entry day by the maximum fitness within each year. A Creek had an estimated mean of 220 (August 7th) and estimated standard deviation of 16.9 whereas C Creek had an estimated mean of 221 (August 8th) and estimated standard deviation of 9. Days in which the number of spawning fish present was less than four were filtered out prior to model fitting to remove points that would be particularly influential.

The stock-recruit relationships for A and C Creek (Figure 2.5) follow similar patterns and showed little evidence of any overcompensation (i.e., the relationships were nearly linear). C Creek supports more recruitment than A Creek, with a maximum recruitment of 834 as compared to a maximum recruitment of 689 in A creek. Our Ricker model fit found parameter values in A creek of $a = 0.73$, $b = 0.0$ and sigma = 0.97 and values in C creek of $a = 1.31$, $b = 0.0$ and sigma = 0.97. The b values of 0.0 indicate that there is no evidence of density dependence from this Ricker fit. Our Shepherd model found a c value of 0.01 in A Creek and $c = 0.03$ in C Creek. Because these values are so small this suggests that there is no overcompensation, or bend in these stock-recruit curves, the same conclusion as is reached using a Ricker model.

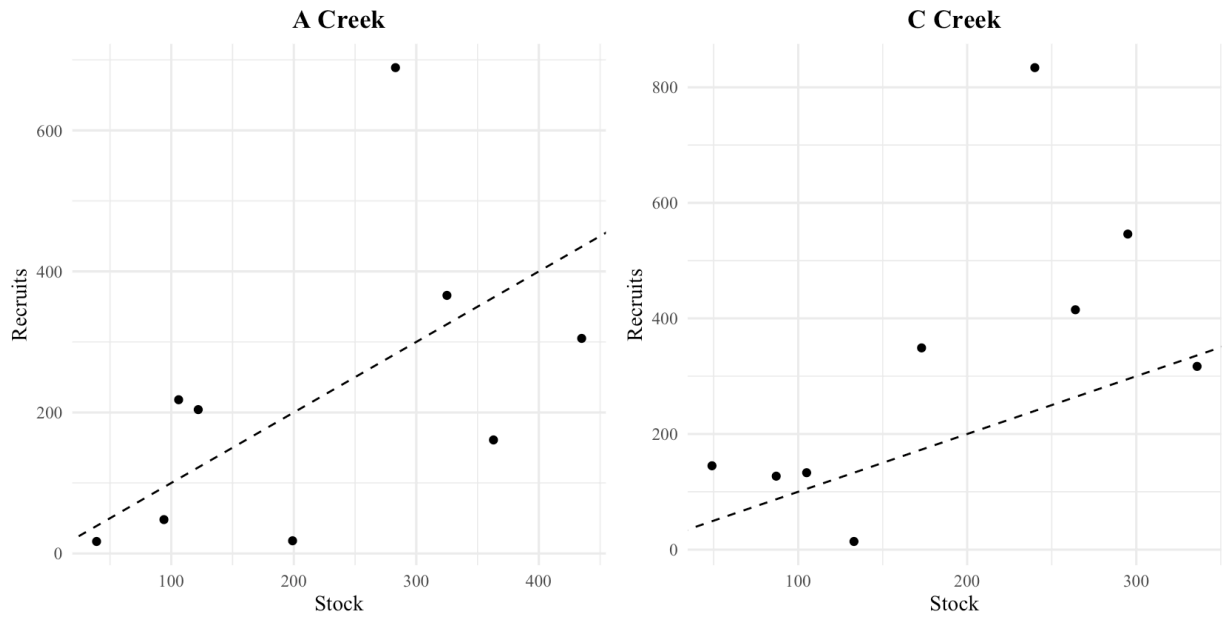

Figure 2.5: Stock-recruit relationship in A and C creeks across years. Stock is represented by the total number of spawning females in the population per year (not total return) and recruitment represents all total offspring produced, both male and female. Dashed line shows 1:1 relationship.

Plotting the number of competitors in each stream over the course of the spawning season (Figure 2.6) highlights the vastly different spawning population sizes across years. However, this plot also shows that the seasonal timing of relative recruitment within each year did not have an obvious pattern with the size of the spawning population. Some years have fairly constant relative fitness throughout the spawning season whereas others have a few key days of high fitness while the rest are low. Our expectation that the relative fitness of late spawning individuals would be higher than early spawning individuals when the spawning population is large was not supported by the data. In fact, in years with the largest spawning populations, the highest levels of recruits per spawner were often observed from fish that spawned early in the season (Figure 2.6).

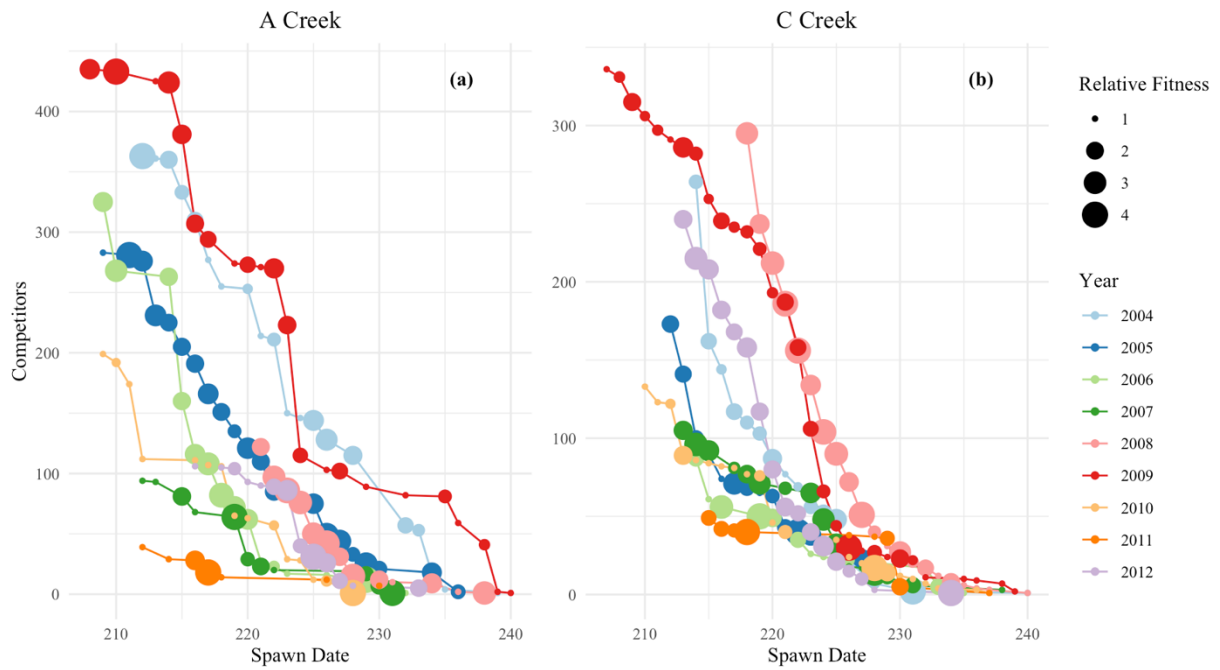

Figure 2.6: Number of competitors in A and C creeks for every fish entry day. Symbol size represents the relative fitness (recruits per female spawner) on each spawning day within each year.

2.4 DISCUSSION

We present a population model that demonstrates a biologically plausible mechanism for producing overcompensation in the stock-recruit relationship for species that compete for space in spawning habitat. This model assumes that there is a temporal distribution of spawn timing among individuals in a population, and that there is evolutionary selection for an optimal spawn timing, that is quantified by a fitness function with a stable mean and variance. The model demonstrates that if spawning habitat is a limiting resource, that the shape of the fitness function can determine the strength of overcompensation in the population. When the standard deviation of the fitness curve is small (i.e., there is a clear environmentally mediated optimal spawn date) we see overcompensation at high spawner densities, whereas if the fitness curve is relatively flat, we see saturation of the spawn-recruit curve but no overcompensation. Overcompensation in the stock-recruit relationship occurs because late spawning, poorly adapted individuals excavate the redds of earlier spawning, better adapted individuals. A sharp fitness curve with a large population size means that in the optimal fitness window essentially none of the

present fish will be viable spawners, because all will experience superimposition from later entering individuals, leading to negligible reproductive success from the optimal window, and reduced reproductive success from outside the optimal window. In contrast, when the fitness curve is flat (i.e., relative fitness varies little throughout the spawning season) there are viable spawners late in the season that still have a high predicted fitness, therefore they produce recruits.

When comparing the hypotheses produced by this model against data from A and C creeks, we found little evidence that late spawning individuals produce higher recruitment as a result of superimposition during high abundance years. We estimated fitness curve parameters for both streams and found somewhat different patterns between the two, leading us to expect differences in the stock-recruit relationships between these two similar systems. The A Creek fitness curve had a standard deviation of 16.9, producing a relatively flat curve, suggesting there is no obvious optimal spawning date to maximize fitness in this system. The C Creek fitness curve had a standard deviation of 9, suggesting a stronger optimal spawn date. These differences in standard deviation did not result in differences to the stock-recruit relationships between these two systems which were both remarkably linear, suggesting that the habitat had not reached saturating capacity.

Of note is the fact that in this analysis only nine years of data were included. Although samples have been collected annually since the end of our time series, the pedigree does not extend beyond the 2012 brood year at this time. In 2021 and 2022 Bristol Bay, and particularly the Wood River system, experienced record-breaking returns of sockeye salmon. If this data set is expanded and added to the stock-recruit plot, it is possible that either overcompensation or saturation of the curve would appear at very high spawning populations. From our model, we would expect more pronounced overcompensation in C Creek and more of a saturating relationship in A Creek (Figure 2.7). At low stocks or with high habitat capacities, our model shows that all stock-recruit curves appear to be linear. Based on the observations of run size we have, spawner densities have not yet achieved the levels necessary to saturate the habitat. We generated

estimated stock-recruit curves for A and C creeks based on the estimated standard deviations (Figure 2.7). These predict no over compensation in A Creek and slight overcompensation in C Creek, but only at high-capacity thresholds. The empirical data suggest that the fitness function is sufficiently broad that it is not likely to produce overcompensation in the stock-recruit relationship.

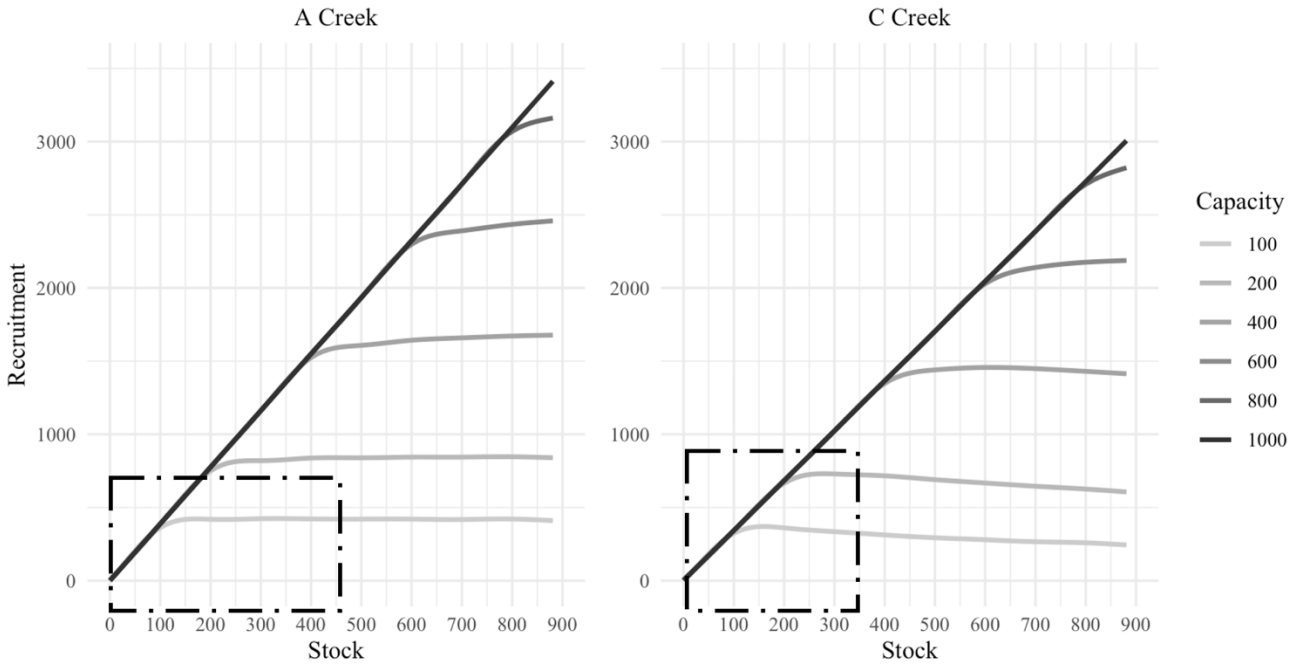

Figure 2.7: Expected stock-recruit curves in A and C creeks using fitness curve standard deviations fit from the data (16.9 in A Creek and 9 in C Creek). Tested at different habitat capacities. Dashed boxes represent the observed stock and recruit ranges in both A and C creeks.

Contradictory to what we expected and our model results, our plot of competitors through time and relative recruitment (Figure 2.6) showed recruitment was almost always distributed evenly throughout the spawning season, and even showed that early spawners sometimes produced more recruits than their late spawning counterparts in big years. This is a surprising result given that it is well-known and studied that there is superimposition occurring in these systems (Moore et al., 2008; Van Den Berghe & Gross, 1989). We make the assumption that fish spawn on, or very closely following their date of stream entry and then die soon after, leaving their redds vulnerable to superimposition. This assumption is potentially problematic in interpreting our data and comparing with the model outputs. Generally, individuals that enter earlier in the season survive longer than late entering fish, meaning that they defend their redds for

longer time periods, decreasing the chance of superimposition (Figure 2.8). Our model does not have a built-in mechanism to control the lifespan of fish, and instead assumes that all later entering fish have the potential of superimposing. Fish lifespan would impact the number of competitors each individual faces and thus also impact the number of viable spawners, potentially changing the stock-recruit relationship.

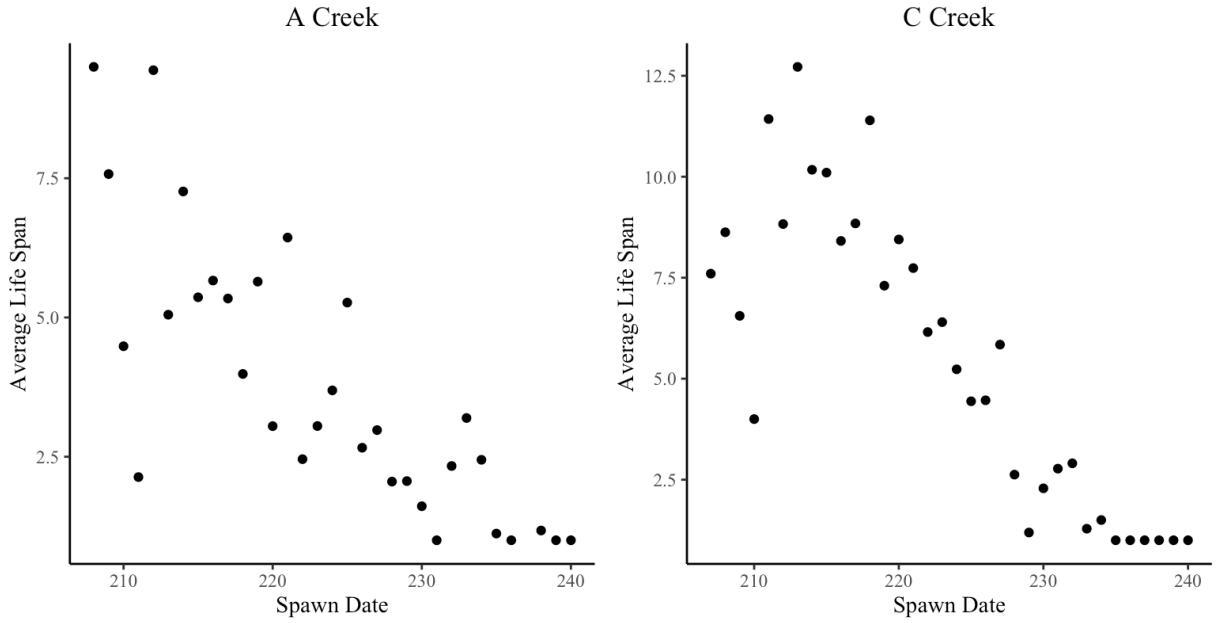

Figure 2.8: Average life span of fish throughout the spawning season. Data was averaged between years to produce one average life span per spawn date across all fish that spawned on that given date.

We assume that recruitment is a product of only processes that occur on the spawning grounds. In reality, this is a vast simplification of extremely complex systems. Mortality of potential recruits can and does occur at every life stage beyond just egg survival, including annual exploitation prior to returning to the spawning grounds by the fishery and known density dependent relationships at other life stages such as competition among juveniles. Although this is a known limitation of our data set, we assume that exploitation rate to be fairly constant through time, and therefore would not impact the shape of the stock-recruit curve between years. A more accurate way to assess the impact of redd superimposition as a density dependent process may be to sample alevin upon emergence from the gravel to determine which spawners produced the most recruits, however this is not a realistic sampling plan given the limitations that sampling season imposes. Recruitment is impacted by many drivers beyond processes on the

spawning ground, and because our sampling system accounts only for total recruitment, not recruitment specific to different life stages, this is a limitation and challenge that is difficult if not impossible using the data available to us for this study.

Our model provides a parsimonious framework for understanding how spawn timing and recruitment are governed by density-dependent processes, particularly redd superimposition. While we found clear theoretical support for density dependent morality when there is a clear optimum in the fitness curve, data from A and C creeks did not fully support this relationship, likely due to limitations in data availability, and model assumptions. These discrepancies highlight the complexity of real-world systems and emphasize the necessity of better understanding systems so that we may move forward with the most accurate assumptions possible. Nonetheless, our findings suggest that once more years of data are added to the time series, especially recent years with exceptionally high escapements, overcompensation in the stock-recruit curves may still emerge but only if the fitness function is more defined than it currently is given the data in hand. A and C creeks are small and relatively pristine habitats whose populations are heavily managed by the Wood River fishery managers. Other systems outside of Alaska that may experience less management and more year-to-year variation in the number of fish returning, including years of extreme high returns, may be more equipped to observe some of the dynamics we predicted at the onset of this study. If our hypothesis is supported in other systems, these results would further suggest the benefits of active fishery management to avoid over compensation due to density dependent processes. Ultimately, this work highlights the importance of both models and observation of natural systems to disentangle the drivers of density dependent mortality in salmon populations and offers a new perspective in better understanding the role that spawn timing plays in recruitment.

REFERENCES

Anderson, P. J., & Piatt, J. F. (1999). Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series*, *189*, 117–123. https://doi.org/10.3354/meps189117

Beacham, T. D., & Murray, C. B. (1990). Temperature, Egg Size, and Development of Embryos and Alevins of Five Species of Pacific Salmon: A Comparative Analysis. *Transactions of the American Fisheries Society*, *119*(6), 927–945. https://doi.org/10.1577/1548-8659(1990)119<0927:TESADO>2.3.CO;2

Beamish, R. J. (1993). Climate and Exceptional Fish Production off the West Coast of North America. *Canadian Journal of Fisheries and Aquatic Sciences*, *50*(10), 2270–2291. https://doi.org/10.1139/f93-252

Brodeur, R. D., & Ware, D. M. (1992). Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. *Fisheries Oceanography*, *1*(1), 32–38. https://doi.org/10.1111/j.1365-2419.1992.tb00023.x

Carlson, S. M., Hilborn, R., Hendry, A. P., & Quinn, T. P. (2007). Predation by Bears Drives Senescence in Natural Populations of Salmon. *PLoS ONE*, *2*(12), e1286. https://doi.org/10.1371/journal.pone.0001286

Chikaraishi, Y., Ogawa, N. O., Kashiyama, Y., Takano, Y., Suga, H., Tomitani, A., Miyashita, H., Kitazato, H., & Ohkouchi, N. (2009). Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnology and Oceanography: Methods*, *7*(11), 740–750. https://doi.org/10.4319/lom.2009.7.740

Cline, T. J., Ohlberger, J., & Schindler, D. E. (2019a). Effects of warming climate and competition in the ocean for life-histories of Pacific salmon. *Nature Ecology & Evolution*, *3*(6), 935–942. https://doi.org/10.1038/s41559-019-0901-7

Cline, T. J., Ohlberger, J., & Schindler, D. E. (2019b). Effects of warming climate and competition in the ocean for life-histories of Pacific salmon. *Nature Ecology & Evolution*, *3*(6), 935–942. https://doi.org/10.1038/s41559-019-0901-7

Connors, B., Ruggerone, G. T., & Irvine, J. R. (2024). Adapting management of Pacific salmon to a warming and more crowded ocean. *ICES Journal of Marine Science*, fsae135. https://doi.org/10.1093/icesjms/fsae135

Davis, N., Volkov, A., Efimkin, A., & Kuznetsova, N. (2009). Review of BASIS Salmon Food Habits Studies. *North Pacific Anadromous Fish Commission*, *Bulletin No. 5*, 197–208.

DeNiro, M. J., & Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, *45*(3), 341–351. https://doi.org/10.1016/0016-7037(81)90244-1

Di Lorenzo, E., Schneider, N., Cobb, K. M., Franks, P. J. S., Chhak, K., Miller, A. J., McWilliams, J. C., Bograd, S. J., Arango, H., Curchitser, E., Powell, T. M., & Rivière, P.

(2008). North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters*, *35*(8). https://doi.org/10.1029/2007GL032838

Downs, E. E., Popp, B. N., & Holl, C. M. (2014). Nitrogen isotope fractionation and amino acid turnover rates in the Pacific white shrimp Litopenaeus vannamei. *Marine Ecology Progress Series*, *516*, 239–250. https://doi.org/10.3354/meps11030

Essington, T. E., Quinn, T. P., & Ewert, V. E. (2000). Intra- and inter-specific competition and the reproductive success of sympatric Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(1), 205–213. https://doi.org/10.1139/f99-198

Feddern, M. L., Holtgrieve, G. W., & Ward, E. J. (2021). Stable isotope signatures in historic harbor seal bone link food web-assimilated carbon and nitrogen resources to a century of environmental change. *Global Change Biology*, *27*(11), 2328–2342. https://doi.org/10.1111/gcb.15551

Feddern, M. L., Holtgrieve, G. W., & Ward, E. J. (2023). Delayed trophic response of a marine predator to ocean condition and prey availability during the past century. *Ecology*, *104*(1), e3865. https://doi.org/10.1002/ecy.3865

Feddern, M. L., Nielsen, J. M., Essington, T. E., & Holtgrieve, G. W. (2024). The influence of dynamic resources and stable isotope incorporation rates on aquatic consumer trophic position estimation. *Limnology and Oceanography: Methods*, *22*(3), 119–134. https://doi.org/10.1002/lom3.10595

Foss-Grant, A. P., Zipkin, E. F., Thorson, J. T., Jensen, O. P., & Fagan, W. F. (2016). Hierarchical analysis of taxonomic variation in intraspecific competition across fish species. *Ecology*, *97*(7), 1724–1734. https://doi.org/10.1890/15-0733.1

Frey, K. E., Kinney, J. C., Stock, L. V., & Osinski, R. (2022). Observations of Declining Primary Productivity in the Western Bering Strait. *Oceanography*, *35*(3/4), 140–143.

Fukushima, M., Quinn, T. J., & Smoker, W. W. (1998). Estimation of eggs lost from superimposed pink salmon (Oncorhynchus gorbuscha) redds. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(3), 618–625. https://doi.org/10.1139/f97-260

Graham, C., Pakhomov, E. A., & Hunt, B. P. V. (2021). Meta-Analysis of Salmon Trophic Ecology Reveals Spatial and Interspecies Dynamics Across the North Pacific Ocean. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.618884

Hare, S. R., & Mantua, N. J. (2000). Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, *47*(2), 103–145. https://doi.org/10.1016/S0079-6611(00)00033-1

Hauser, L., Baird, M., Hilborn, R., Seeb, L. W., & Seeb, J. E. (2011). An empirical comparison of SNPs and microsatellites for parentage and kinship assignment in a wild sockeye salmon (Oncorhynchus nerka) population. *Molecular Ecology Resources*, *11*(s1), 150–161. https://doi.org/10.1111/j.1755-0998.2010.02961.x

Heard, W. R. (1978). Probable case of streambed overseeding—1967 pink salmon, Onchorhynchus gorbuscha, spawners and survival of their progeny in Sashin Creek, southeastern Alaska. *Fisheries Bulletin*, *76*, 569–582.

Hilborn, R., Quinn, T. P., Schindler, D. E., & Rogers, D. E. (2003). Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences*, *100*(11), 6564–6568. https://doi.org/10.1073/pnas.1037274100

Holmes, E. E., Ward, E. J., & Scheuerell, M. (2024). Analysis of multivariate time-series using the MARSS package. *NOAA Fisheries, Northwest Fisheries Science Center*, *version 3.11.24*. https://doi.org/DOI: https://doi.org/10.5281/zenodo.5781847

Hutchinson, J. J., & Trueman, C. N. (2006). Stable isotope analyses of collagen in fish scales: Limitations set by scale architecture. *Journal of Fish Biology*, *69*(6), 1874–1880. https://doi.org/10.1111/j.1095-8649.2006.01234.x

Johnson, S. P., & Schindler, D. E. (2009). Trophic ecology of Pacific salmon (Oncorhynchus spp.) in the ocean: A synthesis of stable isotope research. *Ecological Research*, *24*(4), 855–863. https://doi.org/10.1007/s11284-008-0559-0

Johnson, S. P., & Schindler, D. E. (2012). Four decades of foraging history: Stock-specific variation in the carbon and nitrogen stable isotope signatures of Alaskan sockeye salmon. *Marine Ecology Progress Series*, *460*, 155–167. https://doi.org/10.3354/meps09772

Johnson, S. P., & Schindler, D. E. (2013). Marine trophic diversity in an anadromous fish is linked to its life-history variation in fresh water. *Biology Letters*, *9*(1), 20120824. https://doi.org/10.1098/rsbl.2012.0824

Koch, I. J., & Narum, S. R. (2021). An evaluation of the potential factors affecting lifetime reproductive success in salmonids. *Evolutionary Applications*, *14*(8), 1929–1957. https://doi.org/10.1111/eva.13263

LeBrasseur, R. J. (1966). Stomach Contents of Salmon and Steelhead Trout in the Northeastern Pacific Ocean. *Journal of the Fisheries Research Board of Canada*, *23*(1), 85–100. https://doi.org/10.1139/f66-007

Lerner, J. E., Forster, I., & Hunt, B. P. V. (2021). Experimentally derived trophic enrichment and discrimination factors for Chinook salmon,. *Rapid Communications in Mass Spectrometry*, *35*(13), e9092. https://doi.org/10.1002/rcm.9092

Lerner, J. E., Marchese, C., & Hunt, B. P. V. (2022). Stable isotopes reveal that bottom-up omnivory drives food chain length and trophic position in eutrophic coastal ecosystems. *ICES Journal of Marine Science*, *79*(8), 2311–2323. https://doi.org/10.1093/icesjms/fsac171

Lin, J., Quinn, T. P., Hilborn, R., & Hauser, L. (2008). Fine-scale differentiation between sockeye salmon ecotypes and the effect of phenotype on straying. *Heredity*, *101*(4), 341–350. https://doi.org/10.1038/hdy.2008.59

Lisi, P. J., Schindler, D. E., Pess, G., & Olden, J. (2014). *Watershed Controls on Stream Thermal Regimes: Effects on Salmon Spawn Timing and Species Interactions*. University of Washington.

Litzow, M., Ciannelli, L., Puerta, P., Wettstein, J., Rykaczewski, R., & Opiekun, M. (2018). *Non-stationary climate–salmon relationships in the Gulf of Alaska*. *285*. https://doi.org/10.1098/rspb.2018.1855

Malick, M. J. (2020). Time-varying relationships between ocean conditions and sockeye salmon productivity. *Fisheries Oceanography*, *29*(3), 265–275. https://doi.org/10.1111/fog.12469

Mantua, N. J., & Hare, S. R. (2002). The Pacific Decadal Oscillation. *Journal of Oceanography*, *58*(1), 35–44. https://doi.org/10.1023/A:1015820616384

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production. *Bulletin of the*

American Meteorological Society, *78*(6). https://doi.org/10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2

May, S., Paez, D., Hilborn, R., Schindler, D. E., Westley, P. A. H., Hard, J., Hauser, L., & Naish, K. (2025). Local adaptation and ecological variation influence natal dispersal in a wild salmon metapopulation. *Proc. B*.

McClelland, J. W., & Montoya, J. P. (2002). Trophic Relationships and the Nitrogen Isotopic Composition of Amino Acids in Plankton. *Ecology*, *83*(8), 2173–2180. https://doi.org/10.1890/0012-9658(2002)083[2173:TRATNI]2.0.CO;2

McNeil, W. J. (1964). Redd Superimposition and Egg Capacity of Pink Salmon Spawning Beds. *Journal of the Fisheries Research Board of Canada*, *21*(6), 1385–1396. https://doi.org/10.1139/f64-119

Michener, J., & Lajtha, K. (2007). *Stable Isotopes in Ecology and Environmental Science* (1st ed.). John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470691854

Moore, J. W., Schindler, D. E., & Ruff, C. P. (2008). Habitat Saturation Drives Thresholds in Stream Subsidies. *Ecology*, *89*(2), 306–312. https://doi.org/10.1890/07-1269.1

Naydenko, S. V., Efimkin, A., & Lazhentsev, A. E. (2007). Regional diversity of juvenile pink salmon diet in autum in the Bering, Okhtsk, and Japan seas. *North Pacific Anadromous Fish Commission*, *Bull. 4*, 117–126.

Nielsen, J. M., Popp, B. N., & Winder, M. (2015). Meta-analysis of amino acid stable nitrogen isotope ratios for estimating trophic position in marine organisms. *Oecologia*, *178*(3), 631–642. https://doi.org/10.1007/s00442-015-3305-7

Ohlberger, J., Cline, T., Schindler, D. E., & Lewis, B. (2023). *Declines in body size of sockeye salmon associated with increased competition in the ocean*. *290*. https://doi.org/10.1098/rspb.2022.2248

Pess, G. (2009). *Patterns and processes of salmon colonization*.

Peterson, B. J., & Fry, B. (1987). Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology and Systematics*, *18*, 293–320.

Peterson, D. A., Hilborn, R., & Hauser, L. (2014). Local adaptation limits lifetime reproductive success of dispersers in a wild salmon metapopulation. *Nature Communications*, *5*(1), 3696. https://doi.org/10.1038/ncomms4696

Peterson, D. A., Hilborn, R., & Hauser, L. (2016). Exploratory behavior of dispersers within a metapopulation of sockeye salmon. *Behavioral Ecology*, *27*(1), 126–133. https://doi.org/10.1093/beheco/arv129

Popp, B., Graham, B., Olson, R., Hannides, C., Lott, M., Lopez-Ibarra, G., Galvan-Magana, F., & Fry, B. (2007). *Insight into the Trophic Ecology of Yellowfin Tuna, Thunnus albacares, from Compound-Specific Nitrogen Isotope Analysis of Proteinaceous Amino Acids*. *1*. https://app.paperpile.com/view/?id=a4a9c1d5-3e11-0cb9-ab82-e35ead31379e

Post, D. M. (2002). Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology*, *83*(3), 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Quinn, T. P. (2018). *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington Press.

Ricker, W. E. (1954). Effects of Compensatory Mortality upon Population Abundance. *The Journal of Wildlife Management*, *18*(1), 45–51.

Ruggerone, G. T., Peterman, R. M., Dorner, B., & Myers, K. W. (2010). Magnitude and Trends in Abundance of Hatchery and Wild Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean. *Marine and Coastal Fisheries*, *2*(1), 306–328. https://doi.org/10.1577/C09-054.1

Ruggerone, G. T., Springer, A. M., Vliet, G. B. van, Connors, B., Irvine, J. R., Shaul, L. D., Sloat, M. R., & Atlas, W. I. (2023). From diatoms to killer whales: Impacts of pink salmon on North Pacific ecosystems. *Marine Ecology Progress Series*, *719*, 1–40. https://doi.org/10.3354/meps14402

Ruggerone, G. T., Zimmermann, M., Myers, K. W., Nielsen, J. L., & Rogers, D. E. (2003). Competition between Asian pink salmon (Oncorhynchus gorbuscha) and Alaskan sockeye salmon (O. nerka) in the North Pacific Ocean. *Fisheries Oceanography*, *12*(3), 209–219. https://doi.org/10.1046/j.1365-2419.2003.00239.x

Satterfield, F. R., & Finney, B. P. (2002). Stable isotope analysis of Pacific salmon: Insight into trophic status and oceanographic conditions over the last 30 years. *Progress in Oceanography*, *53*(2), 231–246. https://doi.org/10.1016/S0079-6611(02)00032-0

Schindler, D. E., Armstrong, J. B., Bentley, K. T., Jankowski, K., Lisi, P. J., & Payne, L. X. (2013). Riding the crimson tide: Mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters*, *9*(3), 20130048. https://doi.org/10.1098/rsbl.2013.0048

Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, *13*(5), 257–263. https://doi.org/10.1890/140275

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, *465*(7298), 609–612. https://doi.org/10.1038/nature09060

Semenchenko, N. N. (1988). Mechanisms of innate population control in sockeye salmon, Oncorhynchus nerka. *Journal of Ichthyology*, *28*(3), 149–157.

Shepherd, J. G. (1982). A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *Journal Du Conseil*, *40*(1), 67–75. https://doi.org/10.1093/icesjms/40.1.67

Sherwood, O. A., Guilderson, T. P., Batista, F. C., Schiff, J. T., & McCarthy, M. D. (2014). Increasing subtropical North Pacific Ocean nitrogen fixation since the Little Ice Age. *Nature*, *505*(7481), 78–81. https://doi.org/10.1038/nature12784

Sherwood, O. A., Lehmann, M. F., Schubert, C. J., Scott, D. B., & McCarthy, M. D. (2011). Nutrient regime shift in the western North Atlantic indicated by compound-specific δ15N of deep-sea gorgonian corals. *Proceedings of the National Academy of Sciences*, *108*(3), 1011–1015. https://doi.org/10.1073/pnas.1004904108

Sigman, D. M., Altabet, M. A., McCorkle, D. C., Francois, R., & Fischer, G. (1999). The δ15N of nitrate in the southern ocean: Consumption of nitrate in surface waters. *Global Biogeochemical Cycles*, *13*(4), 1149–1166. https://doi.org/10.1029/1999GB900038

Sigman, D. M., & Casciotti, K. L. (2018). Nitrogen isotopes in the ocean. *Encyclopedia of Ocean Sciences*, *3rd Edn*, 40–54.

Springer, A. M., & van Vliet, G. B. (2014). Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea.

Proceedings of the National Academy of Sciences, *111*(18), E1880–E1888. https://doi.org/10.1073/pnas.1319089111

Stabeno, P. J., Bond, N. A., Hermann, A. J., Kachel, N. B., Mordy, C. W., & Overland, J. E. (2004). Meteorology and oceanography of the Northern Gulf of Alaska. *Continental Shelf Research*, *24*(7), 859–897. https://doi.org/10.1016/j.csr.2004.02.007

Tolimieri, N., Holmes, E. E., Williams, G. D., Pacunski, R., & Lowry, D. (2017). Population assessment using multivariate time-series analysis: A case study of rockfishes in Puget Sound. *Ecology and Evolution*, *7*(8), 2846–2860. https://doi.org/10.1002/ece3.2901

Van Den Berghe, E. P., & Gross, M. R. (1989). Natural Selection Resulting from Female Breeding Competition in a Pacific Salmon (coho: Oncorhynchus Kisutch). *Evolution*, *43*(1), 125–140. https://doi.org/10.1111/j.1558-5646.1989.tb04212.x

Welch, D. W., & Parsons, T. R. (1993). δ13C-δ15N values as indicators of trophic position and competitive overlap for Pacific salmon (Oncorhynchus spp.). *Fisheries Oceanography*, *2*(1), 11–23. https://doi.org/10.1111/j.1365-2419.1993.tb00008.x

Zavolokin, A., Efimkin, A., Slabinskiy, A. M., & Kosenok, N. S. (2007). Food supply and trophic relationships of Pacific salmon (Oncorhynchus spp.) and Atka mackerel (Pleurogrammus monopterygius) in the west- ern Bering Sea in fall 2002–2004. *North Pacific Anadromous Fish Commission*, *Bull. 4*, 127–131.

Zhu, J., Chen, M., Hu, W., Zheng, M., & Qiu, Y. (2021). Biogeochemical cycling of nutrient in the western Bering Sea as revealed by nitrogen isotopic composition of nitrate and suspended particles. *Deep Sea Research Part I: Oceanographic Research Papers*, *174*, 103551. https://doi.org/10.1016/j.dsr.2021.103551