Environmental and spatial drivers of quillback rockfish (*Sebastes maliger*) growth in the northeast Pacific Ocean from California to Alaska

By

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ABSTRACT

Environmental and spatial drivers of quillback rockfish (*Sebastes maliger*) growth in the northeast Pacific Ocean from California to Alaska

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Quillback rockfish (*Sebastes maliger*) are a nearshore fishery species found across the Northeast Pacific Ocean, but recent stock assessments have identified a research gap for biological growth parameters, particularly for the southern end of their range. Age-length data compiled from California to Alaska (n=34,396) was used to generate extended von Bertalanffy models with spatial, biological, and environmental covariates, specifically region, sex, depth, and an upwelling index. The objectives of this study were to explore how 1) spatial and 2) environmental covariates affect model parameters L_∞, *k*, and t_0. Four total models were developed: one model included spatial covariates of region, depth, and sex from California to southeastern Alaska; and three models included an environmental covariate of upwelling (the Biologically Effective Upwelling Transport Index, BEUTI) and sex, with one model for each coastal region that had BEUTI data available (California, Oregon, and Washington). L_∞, *k*, and t0 estimates for all four models had varying significant relationships with covariates. Notably, among regions, L_∞ estimates were larger in the southern regions (California to Washington) than the northern regions (British Columbia to southeast Alaska) and smallest for Washington Puget Sound, and *k* estimates tended to increase from northern to southern regions.

Environmental impacts of BEUTI on growth parameter values were significant for models in the CA and OR regions, but not the WA region. In CA, the effect of BEUTI on all three model parameters was greater in magnitude to OR, however the relationship with L_∞ was negative in CA and positive in OR. Sex was significant for nearly all parameters in most models, but effect sizes were generally small, suggesting there is not a large biological effect of sex on growth parameters. This study shows that spatial and environmental conditions play an important role in quillback rockfish growth and can contribute to improved stock assessments for the species.

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INTRODUCTION

The rockfish genus (*Sebastes spp*.) is a highly diverse group of fishes with cultural, commercial, and recreational value in the Northeast Pacific Ocean. From 2019-2023, commercial landings of rockfish in United States waters generated over $32 million dollars (NOAA Fisheries 2025). The sustenance rockfish provide to coastal communities contribute to their cultural and economic significance (Anderson 2009). In California specifically, rockfish have supported the recreational fishery in the face of statewide closures on salmon due to stock depletion and inland habitat loss. Historically salmon had been the most profitable fishery; however, rockfish are a reliable and almost year-round alternative for the marine recreational fishery (NOAA Fisheries 2025).

Quillback rockfish (*Sebastes maliger*, henceforth referred to as quillback) are a member of the *Sebastes* genus and found from central California to Alaskan Kodiak Islands in rocky habitat, from shallow kelp forests to depths of 274 meters (m) (Love et al. 2002). They are part of the nearshore complex, which includes other rockfish species, lingcod (*Ophidon elongatus*), Cabezon (*Scorpaenichthys marmoratus*), and greenlings (*Hexagrammos* sp.), commonly caught in depths of < 37 m (California Department of Fish and Wildlife 2002). Like other rockfish, quillback are long-lived, with the oldest recorded age at 95 years, and late-maturing, reaching sexual maturity between 5 and 12 years old (Hannah and Blume 2001, Yamanaka and Lacko 2001, Love et al. 2002). Relative to many other rockfish, quillback have a later season of parturition, or release of live young, in April-July (Wylie Echeverria, 1987). Pelagic larval quillback rely on specific favorable conditions for recruitment, such as appropriate winds and currents to transport them to shallow kelp beds that act as nursery habitat (Laidig et al. 2007; Wilson et al 2008; Ottmann et al. 2018; Schroeder et al 2019). During this time, known as the critical growth period, young quillback experience the most dramatic growth, and successful recruitment depends on ideal conditions in the ecosystem. Adults (>200 mm) are typically found in deeper waters, preferring high relief rocky reefs (Matthews 1990), and exhibit high site fidelity, not typically migrating from their home ranges of 10-4000m^2 (Tolimieri et al. 2009; Hannah and Rankin 2011). In productivity-susceptibility analyses, quillback repeatedly scored higher on a vulnerability index than other rockfish, indicating that they are biologically more sensitive to overfishing (Patrick et al. 2010, Jara et al. 2022).

Stock assessments for quillback have occurred on varying spatial and species-complex scales across political boundaries. Quillback from the continental United States are currently assessed as an individual species on a state-level through the Pacific Fishery Management Council (PFMC). Assessments from this area have varied over time due in part to limited data; for example, quillback were assessed in 2010 as a data-poor stock from California to Washington using a Depletion-Based Stock Reduction Analysis, which estimated a 52% chance that quillback were experiencing overfishing (Dick and McCall 2010). In the province of British Columbia, the Department of Fisheries and Oceanography Canada (DFO) separates quillback stocks as ‘Inside’ and ‘Outside’ populations, or quillback found within the Salish Sea or the Strait of Georgia (Inside) and elsewhere along the coastline (Huynh et al. 2025). In Alaska, quillback are part of a demersal shelf rockfish complex that includes other species such as Yelloweye rockfish (*Sebastes ruberrimus*), China rockfish (*Sebastes nebulosus*) and Copper rockfish (*Sebastes caurinus*). They are all assessed together for the coastal waters of the Gulf of Alaska region through the North Pacific Fishery Management Council (NPFMC). For inland waters of Southeastern Alaska, quillback are assessed and managed entirely by the Alaska Department of Fish and Game (AFDG) as part of the demersal shelf rockfish complex, dominated by Yelloweye rockfish (Ehresmann et al. 2024).

In 2020, the PFMC organized quillback assessments using state boundaries from California to Washington, and recent stock assessments for California-specific quillback directly led to contentious management decisions for the nearshore rockfish fishery. The 2021 California quillback assessment (Langseth et al. 2021) used a Productivity-Susceptibility analysis that was mainly catch-based, using fishery-dependent data from California Department of Fish and Wildlife (CDFW) surveys to determine quillback were falling below the minimum stock size threshold in California. This triggered a shift in management that culminated in the emergency closure of the nearshore fishery (within 50 fathoms or 91 m) for the Northern Groundfish Management Zone in August of 2023 (California Department of Fish and Wildlife 2023).

The 2021 California quillback assessment was considered data-moderate and may not have reflected the true state of the local fishery (Jara et al. 2022). The northern coast of California (Mendocino, Humboldt, and Del Norte counties) is considered an understudied region (Dick and MacCall 2011). Although this area has less fishing pressure than other regions due to remoteness, lower human population, and intense weather that keep boats off the water during certain times of the year, there are still abundant and culturally significant local fisheries that rely on good management for healthy marine resources (Abrams 2014, Mulligan et al. 2017). An identified primary uncertainty in the 2021 assessment was the lack of California-specific biological and growth parameters, which had been extrapolated from studies in states north of California. These included fecundity models from Oregon (Hannah and Blume 2011) and von Bertalanffy growth parameters from Washington and British Columbia, Canada (Yamanaka and Lacko 2001; Palsson et al. 2009; West et al. 2014). The most recent published growth metric (age-at-maturity) calculated for California-specific fish was evaluated from only 53 samples (Wyllie Echeverria 1987). A sensitivity analysis was performed within the 2021 stock assessment to address this statistical uncertainty in biological parameters using additionally collected data from the California Collaborative Fisheries Research Program (CCFRP) and Cal Poly Humboldt, but growth information was nevertheless identified as a major research gap. The 2025 assessment on California quillback addressed these gaps by utilizing the assistance of local charters throughout 2023 and 2024 in efforts to collect additional California-specific data. With biological parameters now calculated for California quillback specifically, the assessment has estimated quillback slightly above the minimum stock size threshold (NOAA Fisheries 2025; Langseth et al. 2025). As a result, the northern California nearshore fishery was restored to normal seasonal and spatial limitations in September 2025, but quillback remain a prohibited-take species.

Growth patterns and biological parameters used in quillback stock assessments may differ according to where assessments occur. The relationship between growth and location is often complex. Latitudinal gradients for growth rates, body size, and reproduction in marine fish generally follow the Temperature-Size Rule, where fish in cooler temperatures (i.e. higher latitudes) grow larger with slower growth rates (Atkinson 1994). Ocean temperature is a common environmental factor considered when modeling biological responses, as colder temperatures are correlated with a slower metabolism and growth (Lindmark et al. 2022). Another general pattern, known as Bergmann's rule, is a general positive correlation between size and distance from the equator (Blackburn et al. 1999). Environmental factors, adaptations, and trophic ecology all contribute to growth patterns. Extreme oceanographic events that influence temperature can influence the growth of fish, affecting them indirectly via bottom-up nutrient limitations (von Biela et al. 2015). Examples of such events in the Northeast Pacific Ocean include the North Pacific heatwave ("the Blob") in 2014-2016, strong El Niño or La Niña years (El Niño-Southern Oscillation or ENSO), or warm and cool regimes of the Pacific Decadal Oscillation (Black et al. 2011, von Biela et al. 2019).

Wind-driven, coastal upwelling is a seasonal oceanographic event that occurs in certain regions when spring northernly winds push warmer surface water offshore, displacing it with colder benthic water. In the Northeast Pacific Ocean, the California Current System (stretching from northern Washington to the Baja Peninsula, Mexico) is an upwelling-driven system, whereas the Alaska Current System (from British Columbia to the Gulf of Alaska) is a downwelling-driven system. In upwelling systems, the cold benthic water that rises into coastal zones carries bottom nutrients with it, not only providing a transport mechanism for early life history stages but also supporting adult and juvenile growth through bottom-up trophic forcing (Ainley et al. 1993, Black et al. 2011, von Biela et al 2015, McClure et al 2023). In a study by Black et al. 2008, adult Yelloweye rockfish growth was correlated with oceanographic conditions based on a dendrochronology analysis of otolith increments. This study found spatially-distinct growth patterns for Yelloweye rockfish; in California, colder ocean temperatures (correlated with upwelling) favored growth whereas in northern British Columbia, warmer ocean temperatures were correlated with increased growth (Black et al. in 2008).

Quillback growth is typically modeled as a non-linear age-length relationship, with the von Bertalanffy growth equation being the most common model (von Bertalanffy 1938). Age and growth studies on quillback across their range contribute to more accurate predictions in stock assessments. An age-growth analysis from California-specific fish is lacking in the literature (Langseth et al. 2021). Von Bertalanffy models can be extended to include spatial, environmental, or biological covariates which may influence growth and better describe the differences in patterns between groups (Kimura 2008). Quillback growth metrics (e.g. von Bertalanffy model parameters and age-at-maturity estimates) have been reported to differ based on latitude when comparing populations in British Columbia, Canada, and California (Love et al. 2002). In the Salish Sea, quillback from four distinct locations yielded four different von Bertalanffy growth curves, suggesting that even spatially close groups can display different growth patterns (West et al. 2014). Extending the von Bertalanffy model using other variables such as region, year class, sex, etc. may further describe differences among multiple groups spatially and biologically.

Quillback populations will benefit from an in-depth analysis of their growth patterns. California-specific fish likely exhibit unique von Bertalanffy model parameters distinct from their northern counterparts, the influence of which was shown to contribute to stock assessment outcomes (Langseth et al. 2025). The goals of this study were to examine patterns of quillback growth across the species range and examine how oceanographic conditions affect growth parameters, particularly for the understudied north coast of California. Extended von Bertalanffy models were used to (1) examine the influence of spatial covariates on the growth parameters, and (2) examine the influence of environmental covariates on growth parameters. I hypothesized that quillback growth parameters would differ significantly across the species range, denoted by regions, and that upwelling would have significant effects on parameters as well. This research provides insight into quillback growth patterns and contributes to an improved understanding of environmental drivers and biological relationships of quillback growth across the species range.

METHODS

Data Collection

Quillback age and length data were compiled from multiple state and federal-level management agencies and independent research groups across the Northeast Pacific coastline (Figure 1, Table 1). Data were obtained from various projects, including both fishery dependent and independent surveys. The gears used were predominantly hook and line, longline, or trawl gear, but for some projects the specific gears were unknown (See Appendix A for supplementary table on all projects [Table A 1].)

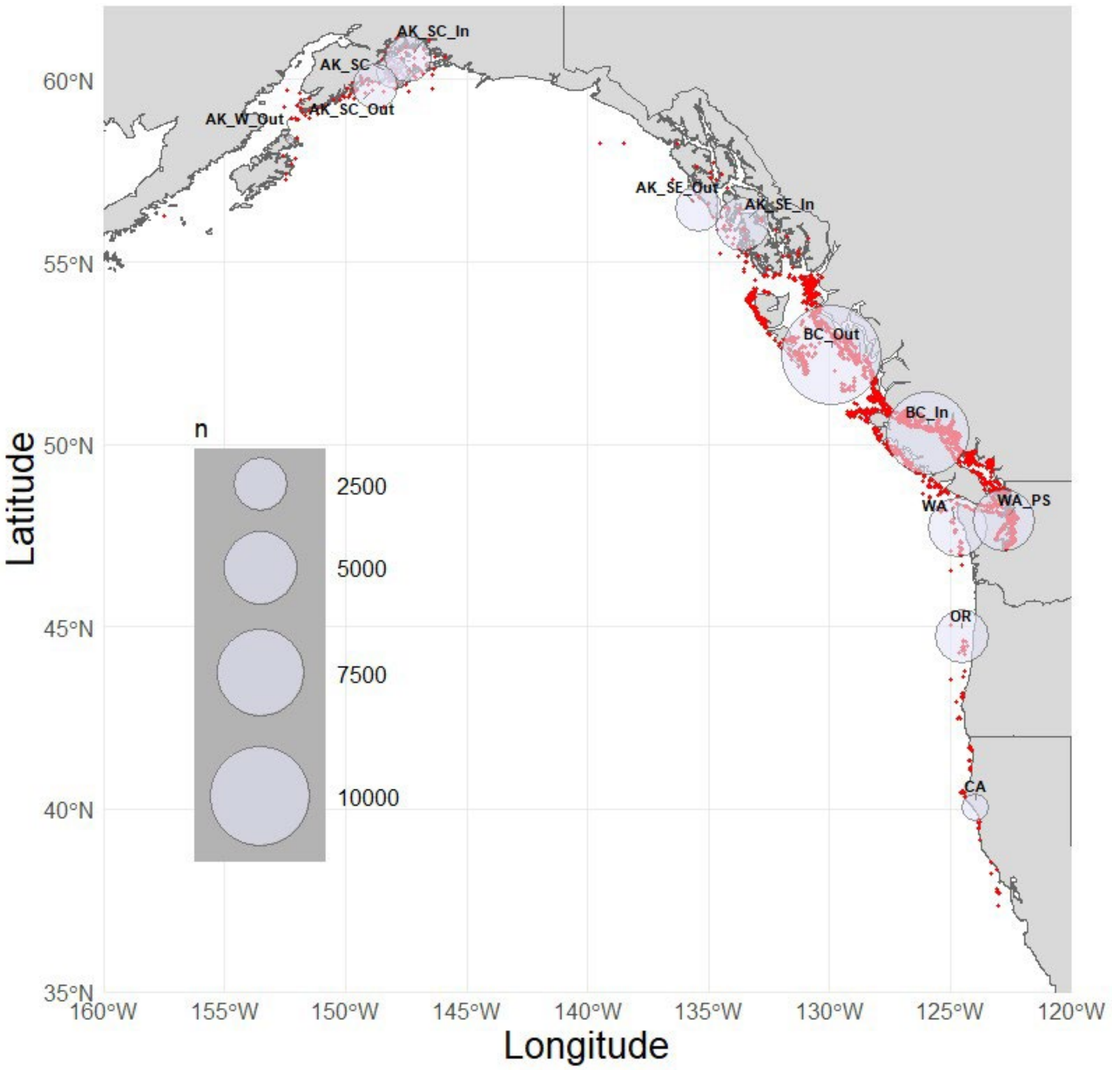


Figure 1- Map of quillback rockfish locations in the dataset across the Northeast Pacific Ocean. Fish with available latitude and longitudes are shown as red points and density bubbles show the relative amounts of data coming from each region. Coastlines and U.S. state boundaries were obtained from the rnaturalearth (Massicotte and South, 2025) and tigris (Walker, 2025) R packages.

Table 1. Data sources and projects that contributed quillback data for the complete dataset used in this study. Project codes refer to sampling sources (see Appendix A).

Data Source	N	Projects
Alaska Department of Fish and Game (ADFG)	8250	ADFG_Com, ADFG_Com_jig, ADFG_Com_LL, ADFG_Sport, IPHC
British Columbia Department of Fisheries and Oceans Canada (DFO)	16703	BC_HBLL, DFO_jig, DFO_HStrawl, DFO_LCDtrawl, DFO_QCStrawl, IPHC
Washington Department of Fisheries and Wildlife (WDFW)	6266	WDFW_Com, WDFW_PSTrawl, WDFW_Research, WDFW_Sport, West, IPHC
Oregon Department of Fish and Wildlife (ODFW)	2540	ODFW_Com, ODFW_Sport, HannahBlume, IPHC
California Department of Fish and Wildlife (CDFW)	161	CRFS, RBG, 2019Comm, IPHC
Northwest Fisheries Science Center, NOAA Fisheries (NWFSC)	196	WCGBTS
California Collaborative Fisheries Research Program (CCFRP)	169	CCFRP
Cal Poly Humboldt	116	Abrams collection

Data sharers were requested to provide the following information on any quillback samples: age (years), length, sex, location of sample (e.g., latitude and longitude or statistical fishing area), date of capture, capture depth, and ager information (see Appendix B for data request flyer). Lengths were provided as either fork or total length, but no length conversion from total to fork length was implemented, as quillback do not have forked caudal fins. Precision of measurements varied by data source, but all lengths were converted to millimeters (mm). Length was also constrained to measurements below 610 mm (the recorded maximum size; Love et al. 2002), to exclude four large outliers (648, 640, 636, and 630 mm) that were assumed to be data entry mistakes.

Ages were estimated by experienced readers from the different agencies. Examining otoliths is considered the most accurate way to determine the age of many fishes, especially for long-lived species (Maceina et al. 2007). Quillback otoliths are typically read using the break-and-burn method. All agencies followed break-and-burn standard protocols when estimating ages (Chilton and Beamish 1982, Committee of Age Reading Experts 2006, Matta and Kimura 2012, Neil 2019, Anderson et al. 2019, NOAA Fisheries 2023). Ages from quillback otoliths have been validated by bomb radiocarbon studies with an age estimation coefficient of variation of 2.6% (Kerr et al. 2005). Ageing precision from the break and burn technique was calculated for British Columbia quillback using multiple readers and generally followed a one-to-one agreement (Anderson et al. 2019). All estimated ages were treated as final for the purposes of this study.

Not all fish had every piece of information provided, and some data were extrapolated from existing information. If latitude and longitude were unavailable, latitude was approximated to the nearest decimal degree using information on the statistical fishing area or port complex where the fish was landed. If depth of sampling location was not provided, depth was estimated based on average depth of the sampling area or starting and end trawl depths, if available, and converted to meters. Much of the data received from fishery dependent sources needed to have latitude and longitude estimated and depths were not available. Some fish were assigned an "Unknown" sex in original datasets. Most of the unknown sexed fish were young, smaller fish, and it was assumed that there were negligible sex-based differences in size at age for these. Fish with an unknown sex were randomly assigned Male or Female (M or F) and maintained the same sex assignments for all further analysis.

Fish were organized into discrete regions using the exact or approximate location of capture. Specifically, regions were based on 1) the state or province of capture, 2) subregions within the state if appropriate (e.g., Southeastern Alaska vs. South-Central Alaska), and 3) a designation between "inside" vs. "outside" waters, if appropriate (Figure 1). "Inside" waters include the Strait of Georgia, Salish Sea or various sounds, bays, and inlets in Alaska that are differentiated from "outside" coastal waters. This distinction was based on advice from British Columbia DFO collaborators who manage their fishery this way and have documented differences in biological parameters (D. Haggarty, pers. comm., 2023). Quillback from Puget Sound, Washington were assigned their own region (WA_PS) due to documented differences from the surrounding Salish Sea (West et al. 2014).

Environmental data on temperature and upwelling were collected from publicly available online sources. Three upwelling indices that characterize the Northeastern Pacific Ocean were considered for this study: the Bakun index (Bakun 1973), the Coastal Upwelling Transport Index (CUTI) and the Biologically Effective Upwelling Transport Index (BEUTI) (Jacox et al. 2018). Both the Bakun index and CUTI represent a vertical transport calculation based on atmospheric sea level pressure fields, or in other words, modeling vertical velocity; BEUTI represents vertical nitrate flux, which can be more relevant to biological responses in the ecosystem. BEUTI index units are μmol $m^{-1}s^{-1}$, which is a nitrate measurement multiplied by CUTI index ($m^{-1}s^{-1}$). However, since it is an index, units are not referenced further. The Bakun Upwelling index was sourced from https://oceanview.pfeg.noaa.gov/products/upwelling/dnld and the BEUTI and CUTI indices were downloaded from https://mjacox.com/upwelling-indices/. All upwelling indices were calculated by NOAA’s Southwest Fisheries Science Center (SWFSC) and were available as monthly averages. BEUTI and CUTI were available from 1988-2025 at 1° Latitude resolution from 31-47°N, and the Bakun index was available from 1946-2024 at 3° resolution from 21-60°N, specifically from 15 stations along the Northwest Pacific Ocean coastline. Model-derived sea water potential temperature at sea floor (referred to as bottom temperature, or btemp) was obtained from the GLORYS12V1 product from the European Union Copernicus Marine Service Information database (https://doi.org/10.48670/moi-00021). Bottom temperatures were available from 1993-

2021 in 1/12° (~8 km^2) grid cells and extracted within the spatial bounds that quillback are found (36-61°N and 158-122°W).

Environmental covariates were calculated from the three upwelling indices and btemp for the first 5 years of a quillback's life. This was done because quillback are a long-lived fish, and a lifetime average of an environmental variable would remove too much variability in the covariate and render it statistically meaningless. Environmental conditions in early life stages are known to have a strong impact on survival and growth rate (Crane, 2014). The first 5 years of life also captures a period of faster growth for this species based on preliminary assessments of available age-length data, so each environmental variable was averaged across this timespan, based on each fish's back-calculated birth year (assuming all fish were born on January 1). Notation for these covariates have a '5yr' subscript after the environmental variable (e.g. $\text{BEUTI}_{5\text{yr}}$).

Statistical Analysis

The von Bertalanffy model predicts size at age using a non-linear function that has three distinct parameters to describe the shape of the curve (L_∞, k, and t_0), and is defined as:

$$l_i = L_\infty\left(1 - e^{-k(t_i - t_0)}\right) + e_i$$

where l_i is the length of the i^{th} individual and t_i represents the age of fish i. L_∞ is the asymptotic maximum length, k is a growth constant, and t_0 is the hypothetical age at which a fish has a length of zero, or the y-intercept of the curve. The residual error (e_i) is assumed to be independent, identically distributed, and additive following a normal distribution, ~$N(0, \sigma^2)$.

To extend the von Bertalanffy model, model parameters can be written as functions of covariates (Kimura 2008). For this study, all covariates were written as linear functions to describe model parameters. For example, L_∞ could be written as a function of depth using the equation:

$$L_\infty = \beta_{0L} + \beta_{1L} * \text{depth}$$

In doing so, the L_∞ parameter is a function of the depth of capture and the slope of the line (β_{1L}) describes the relationship between the L_∞ parameter and covariate. β_{0L} acts as the base L_∞ value when depth = 0. Covariates could be either categorical (e.g., region) or quantitative (e.g., depth). For categorical covariates, parameter estimates for a given level are interpreted as deviations from the intercept or base (β_0) level. Effects of covariates were also re-expressed as a level-specific value with 95% confidence intervals, calculated as 1.96 * the standard error (SE), which was reported in model output for each parameter. Models were fit by minimizing the sum of square residuals using the nls() function in R, assuming an additive error structure. Once fit, model residuals were assessed graphically for assumption violations (i.e. heteroscedasticity or non-normality of residuals).

Two versions of extended von Bertalanffy models were considered to address the two objectives of 1) examining spatial growth differences and 2) exploring environmental influences on growth. Spatial and environmental variables were considered separately because of data limitations from certain covariates, preventing the development of a single, comprehensive model. Variables that were considered as covariates for the spatial model included sex, region, and depth; and for environmental model, sex and the 5-year average values of monthly BEUTI, CUTI, and Bakun indices and bottom temperature were considered. (Table 2). No interactions among covariates were included. Fitted models were used to generate predictions while holding numerical covariates at mean or median values. The only variables with no missing values were region and sex. This “full” version of a von Bertalanffy model was explored in Appendix C.

Table 2 – List of variables in the quillback dataset used or considered in the spatial and environmental growth models.

Variable	Description	Variable Type
Age	Fish age (yrs) at capture based on otoliths	Independent Variable, X
Length	Fork length in millimeters of the fish at capture.	Dependent Variable, Y
Sex	A categorical variable labeling a fish as either male (M) or female (F).	Biological
Depth	The reported depth (in meters) of the capture location. Missing depths were estimated from trawl start and end depths (average) or the average depth of a sampling area.	Spatial
Region	A categorical spatial variable describing a fish's capture location based on the state/province and if it was in coastal or inland waters (12 levels: AK_W_Out, AK_SC, AK_SC_In, AK_SC_Out, AK_SE_In, AK_SE_Out, BC_In, BC_Out, WA, WA_PS, OR, and CA).	Spatial
$\mathbf{BEUTI_{5yr}}$	The average BEUTI index for the first 5 years of a fish's life from the closest 1° latitude	Environmental
$\mathbf{CUTI_{5yr}}$	The average CUTI index for the first 5 years of a fish's life from the closest 1° latitude	Environmental
$\mathbf{Bakun_{5yr}}$	The average Bakun index for the first 5 years of a fish's life from the closest 3° latitude	Environmental
$\mathbf{btmp_{5yr}}$	The average GLORYS12V1 model-derived sea water potential temperature at sea floor in °C for the first 5 years of a fish's life from the closest 8 km^2	Environmental

Spatial Model

Covariates for the spatial model were selected by using the spatial and biological variables from the dataset: region, sex, and depth. Preliminary investigations explored other versions of spatial covariate types, such as state, a North-South Division designation, or categorical depth strata as alternates, but these were found to not describe the data as well. To assess collinearity between covariates, figures and pairwise plots were used. Data limitations for each covariate were explored using plots and histograms. It was determined that there was not an even spread of young fish across regions, and therefore region was removed as a covariate for the t_0 parameter, which requires young fish to make accurate predictions.

Environmental Model

Environmental model covariates were considered among the environmental and biological variables in the dataset, including the BEUTI_{5yr}, CUTI_{5yr}, Bakun_{5yr}, btemp_{5yr}, and sex (Table 2). Spatial and temporal data limitations among the environmental variables were calculated and compared, and collinearity and correlations among covariates were assessed graphically. It was determined that upwelling indices had distinct ranges of values with little overlap between regions. This was addressed by generating separate models for each region present in the available data, with the exception of WA_PS. WA_PS was not considered in the environmental modeling due to prior knowledge about the unique system which may influence upwelling impacts and growth characteristics of quillback in the Salish Sea (West et al 2014, Wray et al., 2024).

RESULTS

The age-length data available and assembled into a “master” dataset included 12 regions, 24 unique projects, and 34,392 records of QBK collected from 1977 to 2024, with birth years ranging from 1909-2020. Ages ranged from 0 to 95 years old (average: 23 yrs) and lengths from 78 to 593 mm (average: 360 mm). There were approximately 886 observations of unknown sex, which made up approximately 2.6% of the data but 25% of the fish less than 200 mm. The sex ratio of all samples was approximately even, with males representing 50.96% of the data. Data among regions was unevenly spread, with BC_Out having the most data (n=10,096) and AK_W_Out the least (n=56) (Figure 2).

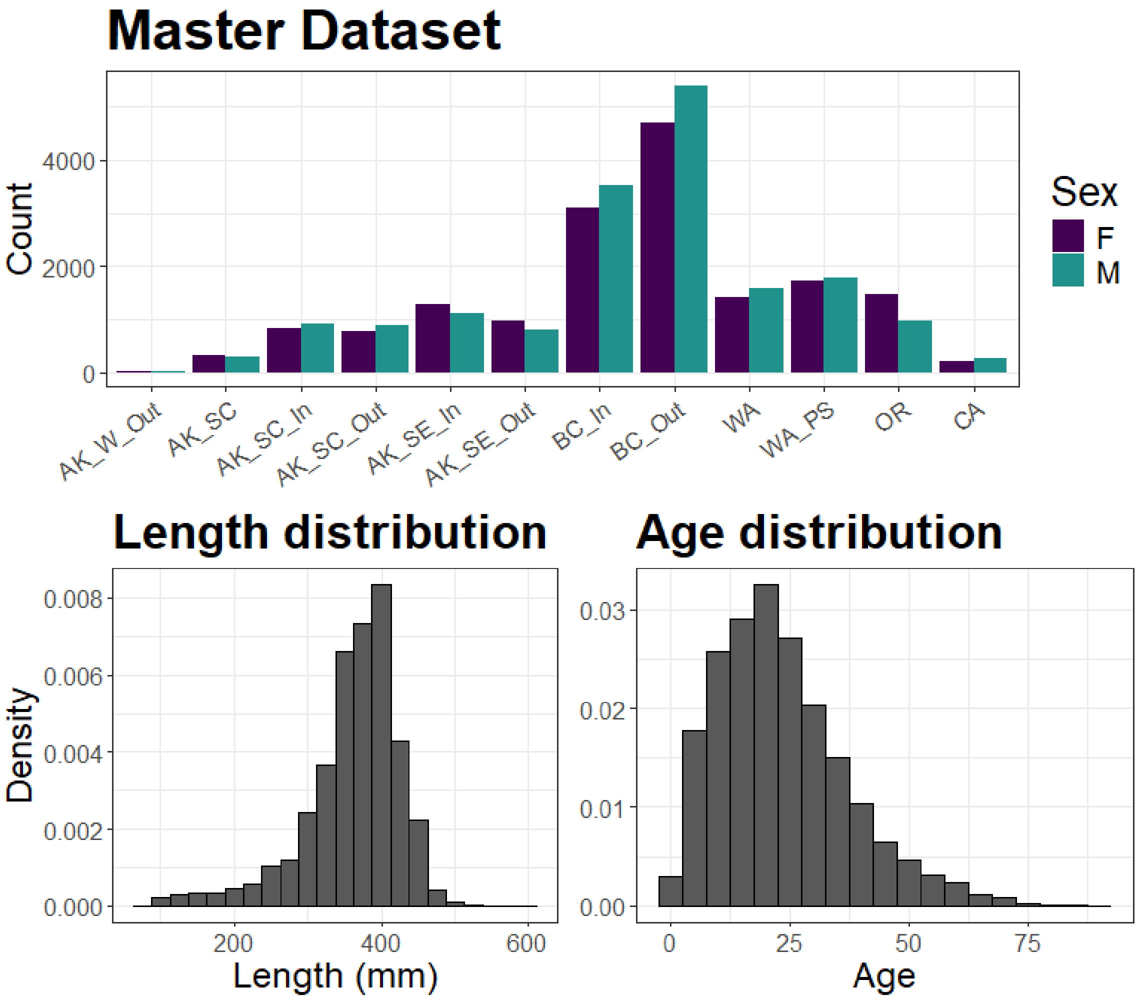


Figure 2 - Counts of quillback rockfish available in the dataset by region and sex (top), along with length and age histograms (bottom).

Sample sizes and available data for each of the extended models differed due to missing covariate values (Table 3; Figure 3). Due to limited availability of depth information, the dataset used for the spatial von Bertalanffy model was reduced to 21,798 fish, removing 4 levels of region (AK_SC, AK_SC_In, AK_SC_Out, and AK_W_Out), and substantially reducing data from the OR and WA regions. Length and age for this spatial dataset ranged from 78 to 593 mm and 0 to 92 years, with averages of 353 mm and 25 years (Figure 4). Similarly, the environmental models were limited by the availability of the environmental covariates (Table 4). The spatial and temporal limitations of btemp_{5yr} were great enough that it was excluded as a covariate (1.3% of fish in the dataset had this information). Among upwelling indices, spatial limitations were greatest for BEUTI_{5yr} and CUTI_{5yr}, which were only available from 31-47°N (excluding regions north of WA), and restricted to 11.5% of the dataset. Bakun_{5yr} allowed for 95% of the master dataset to be used, however the majority of data included had negative values.

Table 3 - Descriptive statistics of region-specific data used for each of the fitted von Bertalanffy models. Environmental models were fitted to each region separately (CA, OR, and WA).

	Master dataset			**Spatial Dataset**			**Environmental Datasets**		
Region	N	Length range (mm)	Age range (years)	N	Length range (mm)	Age range (years)	N	Length range (mm)	Age range (years)
AK_W_Out	56	330-490	9-71						
AK_SC	622	210-561	8-74						
AK_SC_In	1732	220-543	3-80						
AK_SC_Out	1660	240-590	5-75						
AK_SE_In	2391	136-490	3-89	2044	250-490	8-89			
AK_SE_Out	1789	280-495	9-92	1739	280-495	9-92			
BC_In	6607	90-493	1-80	4163	90-493	1-80			
BC_Out	10096	120-593	2-84	10096	120-593	2-84			
WA	3020	150-560	2-73	356	150-500	2-45	**1303**	150-540	2-31
WA_PS	3501	78-500	0-73	2879	78-490	0-60			
OR	2437	110-591	1-63	137	110-500	1-46	**2233**	110-523	1-32
CA	481	115-500	1-57	384	115-481	1-21	**449**	115-481	1-33
Total:	**34392**	78-593	0-92	**21798**	78-593	0-92			

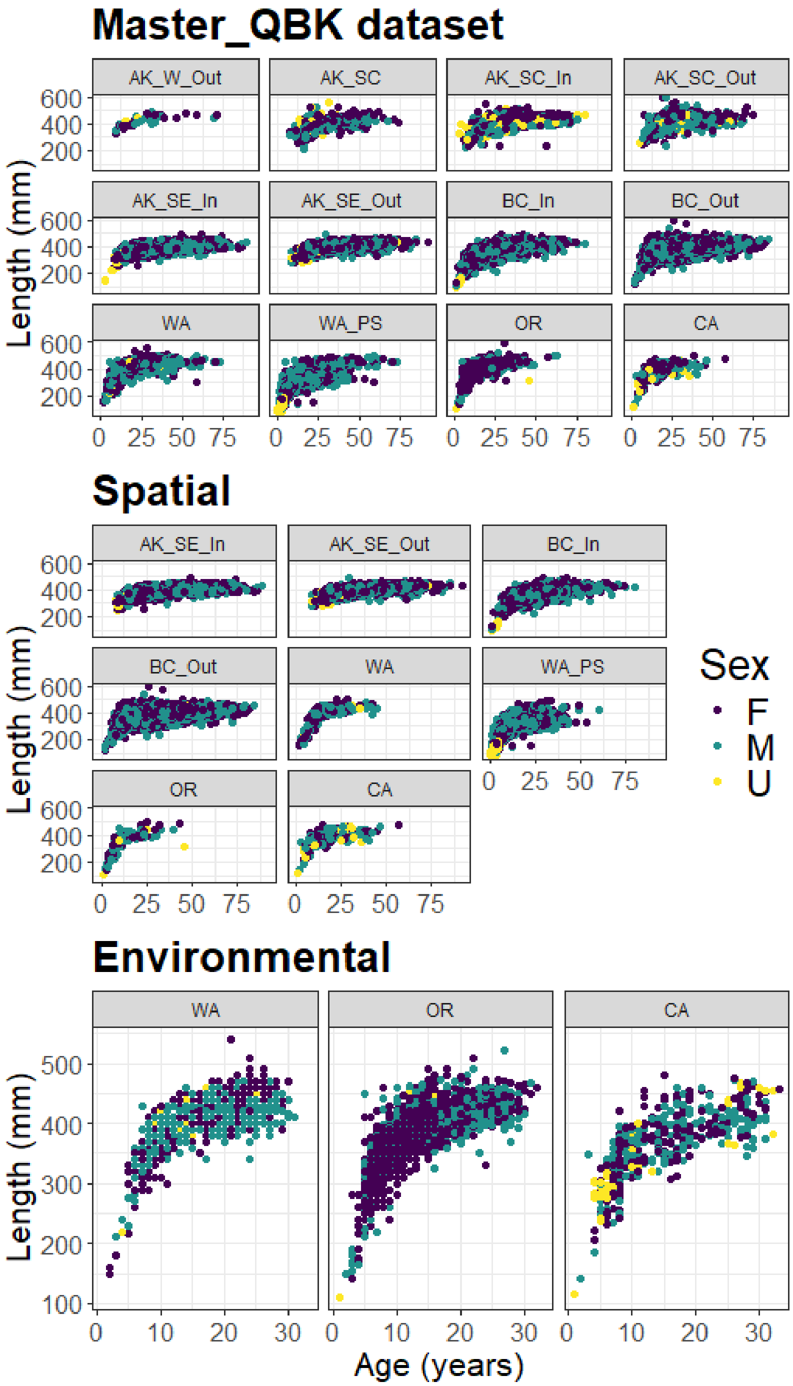
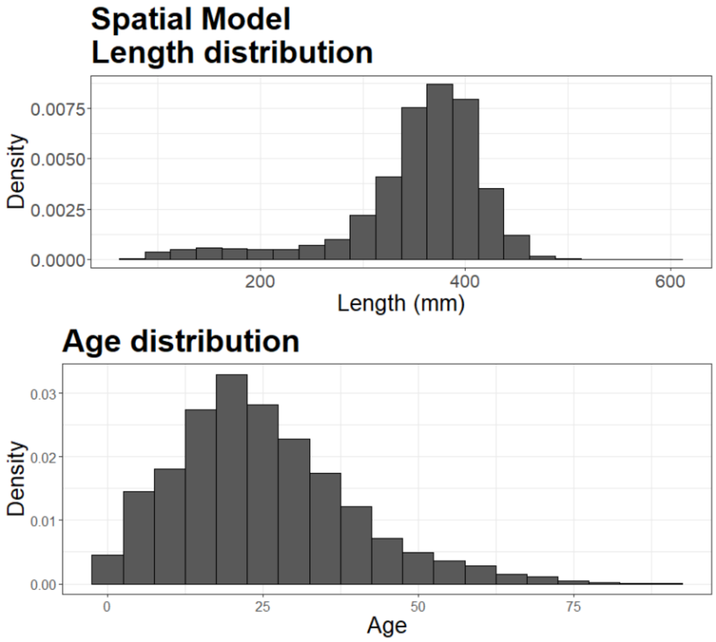


Figure 3 - Quillback age-length data within the full (top), spatial (middle), and environmental (bottom) models, by region and sex (F=female, M=male, U=unknown).


Spatial Model Length distribution

Age distribution

Figure 4 - Histograms of the spatial model's dataset for quillback rockfish length (top) and age (bottom). Binwidth for lengths is 25 mm and 4 years for ages.

Table 4 - Quillback data availability (n) for each environmental covariate when formatted for extended von Bertalanffy modeling.

Env. Model Covariate Combination	**n**	**% of data included**	**Timespan**	**Latitude range**
BEUTI$_{5yr}$/CUTI$_{5yr}$	5,337	15.5%	1988-2020	36.75-50°
btemp$_{5yr}$	4,380	12.7%	1993-2016	37.37-60.9°
Bakun$_{5yr}$	32,572	95%	1946-2019	36.75-61.14°
BEUTI$_{5yr}$ /CUTI$_{5yr}$ & btemp$_{5yr}$	444	1.3%	1993-2016	37.37-50°
Bakun$_{5yr}$ & btemp$_{5yr}$	4,380	12.7%	1993-2016	37.37-60.9°

Inter-covariate correlations influenced model structure for spatial and environmental models. No strong correlations among region, sex, or depth were detected on plots or with pairwise comparisons for the spatial model. Depth was generally similar across regions (typically ranging from 25-150 m) except for CA, which tended to be shallower from 10-75 m (Figure 5). $\text{BEUTI}_{5\text{yr}}$, $\text{CUTI}_{5\text{yr}}$, and $\text{Bakun}_{5\text{yr}}$ were found to be collinear with strong correlations using pairwise plots ($r>=0.85$; Figure A 1). The $\text{BEUTI}_{5\text{yr}}$ covariate was chosen over other indices because the BEUTI index represents the biological response to upwelling and has higher spatial resolution than the Bakun index (every 1° vs. every 3° of latitude), even though the $\text{Bakun}_{5\text{yr}}$ covariate would have allowed for a larger dataset (Table 4). $\text{BEUTI}_{5\text{yr}}$ values were only available for CA, OR, and WA, and there was strong collinearity by region. CA had the highest $\text{BEUTI}_{5\text{yr}}$ average of 7, with OR at 1.05, and WA with -1.38 (Figure 6). Median $\text{BEUTI}_{5\text{yr}}$ values were 6.584, 0.116, and -1.435 for CA, OR, and WA respectively. Due to the strong collinearity and minimal overlap of $\text{BEUTI}_{5\text{yr}}$ values, three individual models were built for CA, OR, and WA. The resulting environmental models had sample sizes of 449 fish for CA, 2,233 fish for OR, and 1,303 fish for WA (Table 3). Length and age distributions for the CA, OR, and WA environmental models were similar with average lengths of 357, 375, and 410 mm and average ages of 14, 12, and 18, respectively (Figure 7).

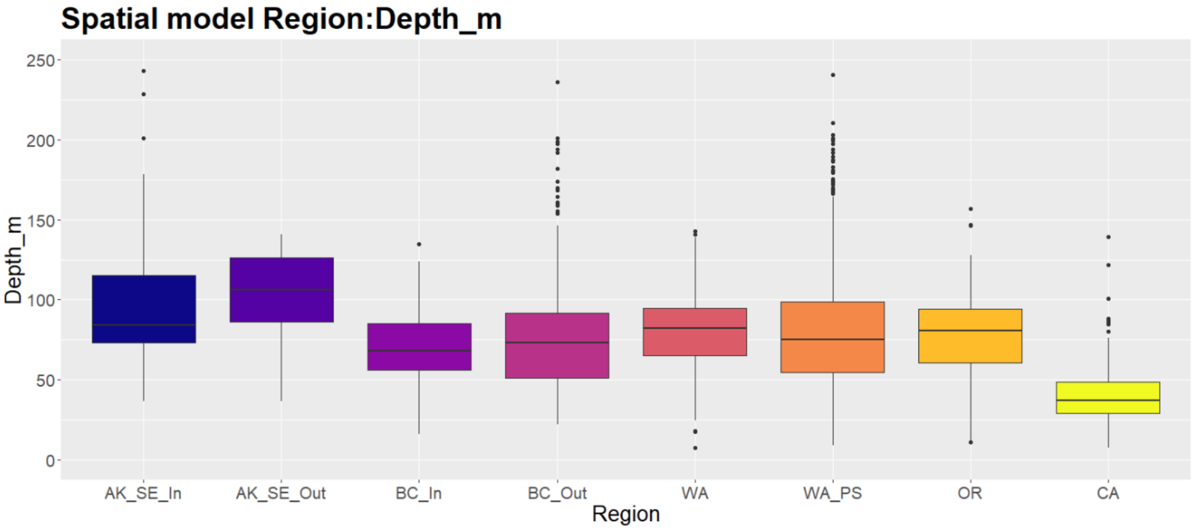


Figure 6 - Boxplot of depth (m) by region for quillback rockfish used in the spatial von Bertalanffy model. One depth outlier from WA is excluded in this figure (398m).

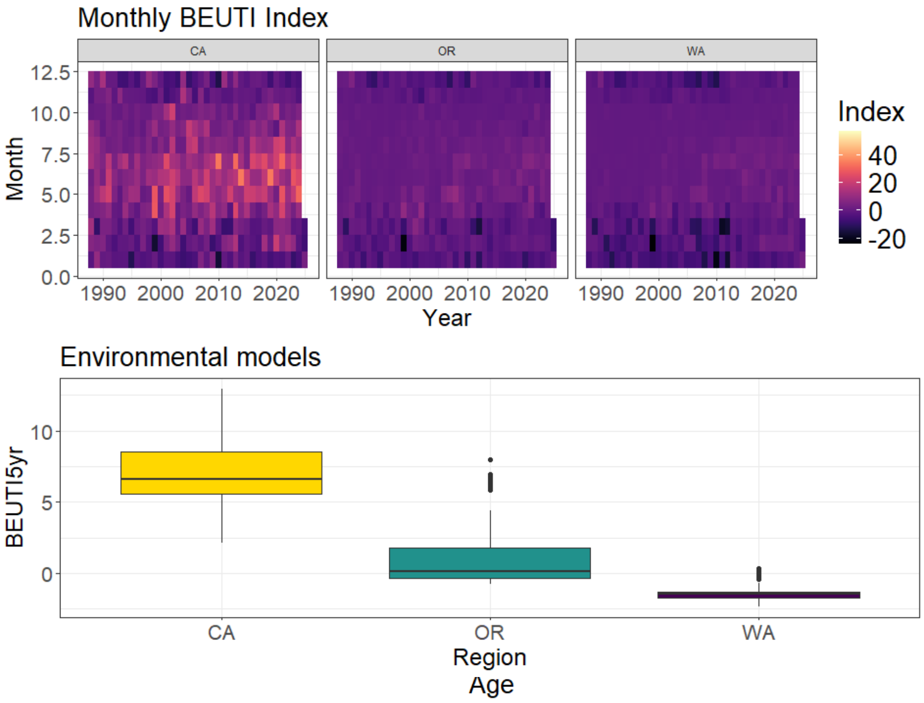


Figure 5 - Plots depicting raw monthly BEUTI index values (top) across years (1988-2024) for the three regions (CA, OR, and WA) with available data. The spread of BEUTI$_{5yr}$ values (bottom) from each regional dataset at also plotted. The BEUTI$_{5yr}$ covariate value represents the average annual BEUTI values for the first 5 years of each fish's life.

Figure 7 - Histograms depicting the distribution of quillback rockfish lengths and ages used in the three region-specific environmental growth models. Length (top row) is represented in bins of 25 mm while age (bottom row) is in bins of 5 years.

Spatial Model

The spatial von Bertalanffy model covariates of sex, region, and depth all had significant effects on the von Bertalanffy parameters (Table 5, Figure 8). The intercepts or base values of the categorial covariates (region and sex) represented female fish from AK_SE_In. Males were found to have significant differences from females in all three model parameters. All regions had significant parameter differences from AK_SE_In, except the L_∞ parameter of BC_Out and the k parameter of OR. Depth of capture had a positive effect on L_∞ and a negative relationship with k and t_0. The spatial model was visually displayed as predicted growth curves for each region and sex, standardizing depth to the median value of 77 m (Figure 9). Assumptions of normality, homogeneity of residuals, and additive error structure were found to be satisfactory, and graphs did not indicate major violations of those assumptions (Figure A2).

Table 5 – Coefficient parameter estimates from the spatial von Bertalanffy growth model with standard error (SE) and p-values. Estimated values are interpreted as deviations from the base value (β_0). All parameters denoted with ‘$_L$’ represent L_∞ estimates, ‘$_k$’ represents *k*, and *t* represents t_0. Bold p-values denote significance at the 0.05 level.

Coefficient	**Parameter**	**Estimate**	**SE**	***t* value**	***P* value**
Base intercept (AK_SE_In, Female)	β_{0L}	378.282	1.523	248.384	**<0.001**
	β_{0k}	0.134	0.00280	47.642	**<0.001**
	β_{0t}	-0.695	0.112	-6.196	**<0.001**
Sex: Male	β_{1L}	-8.917	0.694	-12.857	**<0.001**
	β_{1k}	0.0114	0.00166	6.883	**<0.001**
	β_{1t}	0.191	0.0867	2.200	**0.028**
Region: AK_SE_Out	β_{2L}	9.250	1.642	5.633	**<0.001**
	β_{2k}	-0.0172	0.0022	-7.73	**<0.001**
Region: BC_In	β_{3L}	-12.352	1.347	-9.172	**<0.001**
	β_{3k}	0.0237	0.00245	9.672	**<0.001**
Region: BC_Out	β_{4L}	-1.0117	1.153	-0.878	0.380
	β_{4k}	0.0147	0.00201	7.320	**<0.001**
Region: CA	β_{5L}	24.671	2.976	8.291	**<0.001**
	β_{5k}	0.0466	0.00486	9.585	**<0.001**
Region: OR	β_{6L}	50.634	6.941	7.294	**<0.001**
	β_{6k}	0.00835	0.00531	1.573	0.116
Region: WA	β_{7L}	55.703	3.692	15.0868	**<0.001**
	β_{7k}	0.0145	0.00374	3.900	**<0.001**
Region: WA_PS	β_{8L}	-27.163	2.329	-11.662	**<0.001**
	β_{8k}	0.0113	0.00268	4.207	**<0.001**
Depth (of capture)	β_{9L}	0.271	0.0117	23.122	**<0.001**
	β_{9k}	-0.000256	0.0000181	-14.184	**<0.001**
	β_{9t}	-0.0137	0.00131	-10.429	**<0.001**

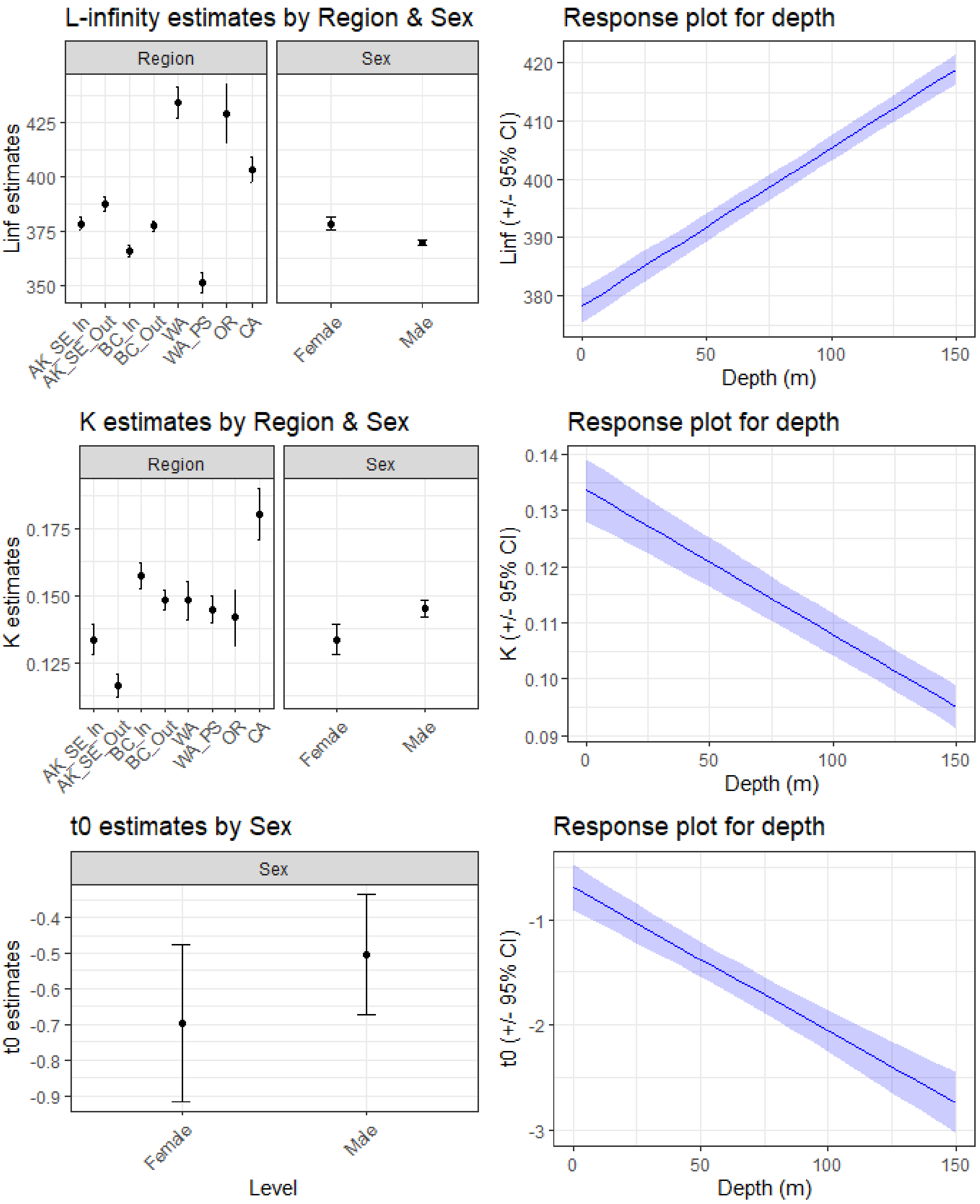


Figure 8 - Parameter estimates for the spatial von Bertalanffy model, showing the relationship between the covariates and each of the three parameters of the model (L_∞, k, and t_0). Categorical covariates of region and sex are shown on the left, with estimates between males and females displayed as points with 95% confidence bars and values reflecting a depth of 0 m. Linear depth relationships are on the right, shown as a line with 95% confidence bands depicting the slope across a 0-150m depth range for Females in the AK_SE_Out region.

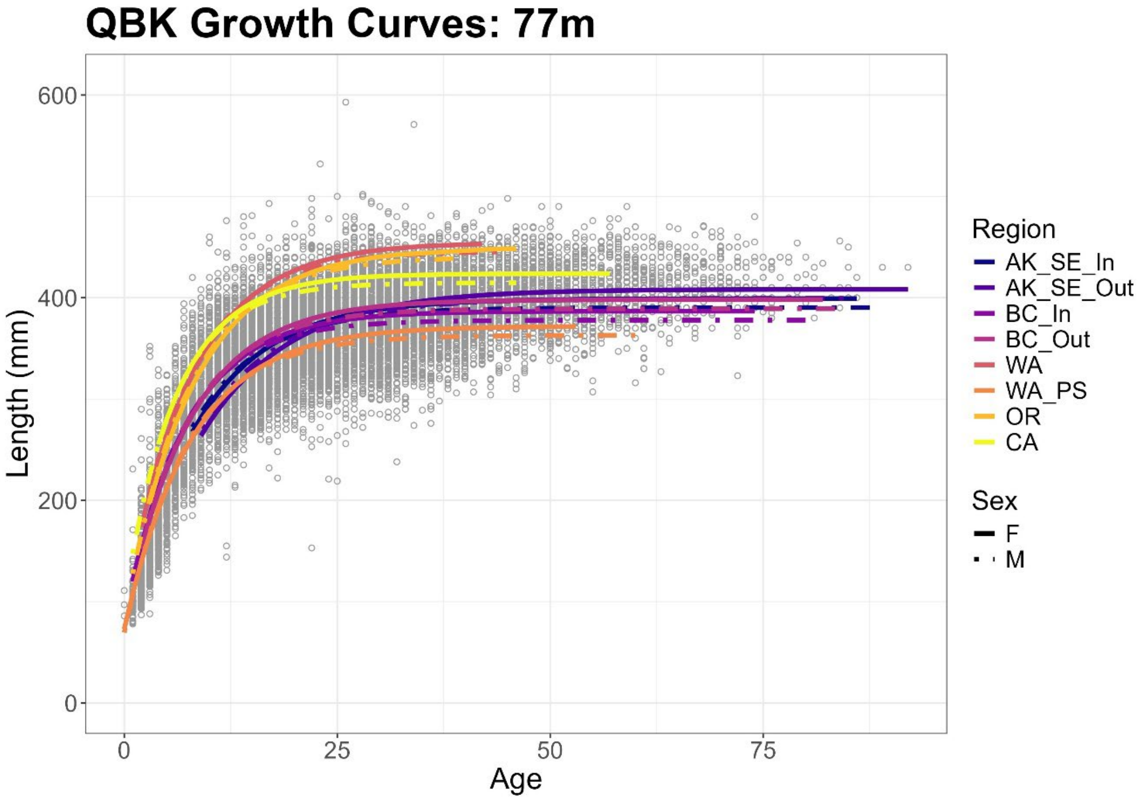


Figure 9 - Predicted curves for the von Bertalanffy spatial model by region and sex. Levels of region are shown as colors. Solid lines represent female predictions and dashed lines represent males. All predictions displayed were standardized at the overall median depth of 77 m.

L_∞ was significantly different between males and females, with males 8.9 mm smaller than females (p<0.0001). The regions of WA and OR had overlapping confidence intervals, as did AK_SE_In and BC_Out, but AK_SE_Out, BC_In, WA_PS, and CA had non-overlapping confidence intervals for their L_∞ estimates from all other regions. The relationship between L_∞ and depth had a positive slope of 0.271, suggesting a 40 mm increase (+10.7%) in L_∞ as depth changes from 0 to 150 m.

Sex also had a significant effect on *k*, with males having a higher *k* by 0.0114 yr^{-1} (p<0.0001). Regional estimates of *k* were similar with overlapping confidence intervals for half the regions: BC_Out, WA, WA_PS, and OR. Estimates of *k* for AK_SE_Out and CA were completely distinct from all other regions, with CA having the highest value (0.180 yr^{-1}) and AK_SE_Out having the lowest (0.116 yr^{-1}). *k* decreased by a slope of -0.000257 with every meter increase in depth. In other words, from 0 to 150 m, k decreases by approximately 27.5% (for females from 0.134 yr^{-1} to 0.095 yr^{-1} and males 0.145 yr^{-1} to 0.106 yr^{-1}).

The t_0 parameter was significantly different between males and females (-0.695 yrs for females and -0.505 yrs for males, p=0.0278), however 95% confidence intervals overlapped between sexes (Figure 8). t_0 had a significant negative relationship with depth, declining by 2 yrs as depth increased from 0 to 150 m.

Environmental Model

The effects of sex and $BEUTI_{5yr}$ on model parameters for the three environmental models varied. Female was the base value for the categorical sex covariate. Sex was significant to all three model parameters in the OR and WA models but not for any parameters in the CA model (Table 6). For the CA and OR models, $BEUTI_{5yr}$ was found to have significant relationships with all three model parameters. For both CA and OR models, $BEUTI_{5yr}$ had a positive relationship with *k* and t_0, but for L_∞, the OR model had a negative relationship while the CA model had a positive relationship (Figure 10). In the WA model, $BEUTI_{5yr}$ had no significant influence on any model parameters. The three environmental models were displayed as growth curves by standardizing each at their median $BEUTI_{5yr}$ value (Figure 11). Assumptions of normality, homogeneity of residuals, and additive error structure were found to be satisfactory for each model (Figure A 3).

Table 6 – Coefficient parameter estimates for the environmental von Bertalanffy growth models from CA, OR, and WA with standard error (SE) and p-values. Estimates values are interpreted as deviations from the base value (β_0). All parameters denoted with '$_L$' represent L_∞ estimates, '$_k$' represents *k*, and *t* represents t_0. Bold p-values denote significance at the 0.05 level.

Model	**Coefficient**	**Parameter**	**Estimate**	**SE**	**t value**	***P* value**
CA	Base intercept (Female)	β_{0L}	449.682	11.889	37.824	**<0.001**
		β_{0k}	0.070	0.016	4.370	**<0.001**
		β_{0t}	-3.861	0.888	-4.348	**<0.001**
	Sex: Male	β_{1L}	-9.826	6.595	-1.490	0.137
		β_{1k}	0.004	0.012	0.333	0.739
		β_{1t}	-0.375	0.502	-0.748	0.455
	$BEUTI_{5yr}$	β_{2L}	-4.160	1.380	-3.014	**0.003**
		β_{2k}	0.013	0.003	4.972	**<0.001**
		β_{2t}	0.329	0.071	4.664	**<0.001**
OR	Base (Female)	β_{0L}	436.691	2.749	158.869	**<0.001**
		β_{0k}	0.154	0.007	23.284	**<0.001**
		β_{0t}	-1.786	0.295	-6.061	**<0.001**
	Sex: Male	β_{1L}	-18.408	3.331	-5.527	**<0.001**
		β_{1k}	0.073	0.011	6.436	**<0.001**
		β_{1t}	1.579	0.356	4.438	**<0.001**
	$BEUTI_{5yr}$	β_{2L}	2.374	0.638	3.722	**<0.001**
		β_{2k}	0.006	0.002	3.301	**0.001**
		β_{2t}	0.192	0.044	4.357	**<0.001**
WA	Base (Female)	β_{0L}	437.305	4.257	102.720	**<0.001**
		β_{0k}	0.163	0.013	13.001	**<0.001**
		β_{0t}	-1.224	0.469	-2.611	**0.009**
	Sex: Male	β_{1L}	-16.895	2.632	-6.420	**<0.001**
		β_{1k}	0.057	0.015	3.728	**<0.001**
		β_{1t}	1.116	0.558	2.000	**0.046**
	$BEUTI_{5yr}$	β_{2L}	-3.999	2.254	-1.774	0.076
		β_{2k}	0.002	0.008	0.248	0.804
		β_{2t}	0.448	0.362	1.237	0.216

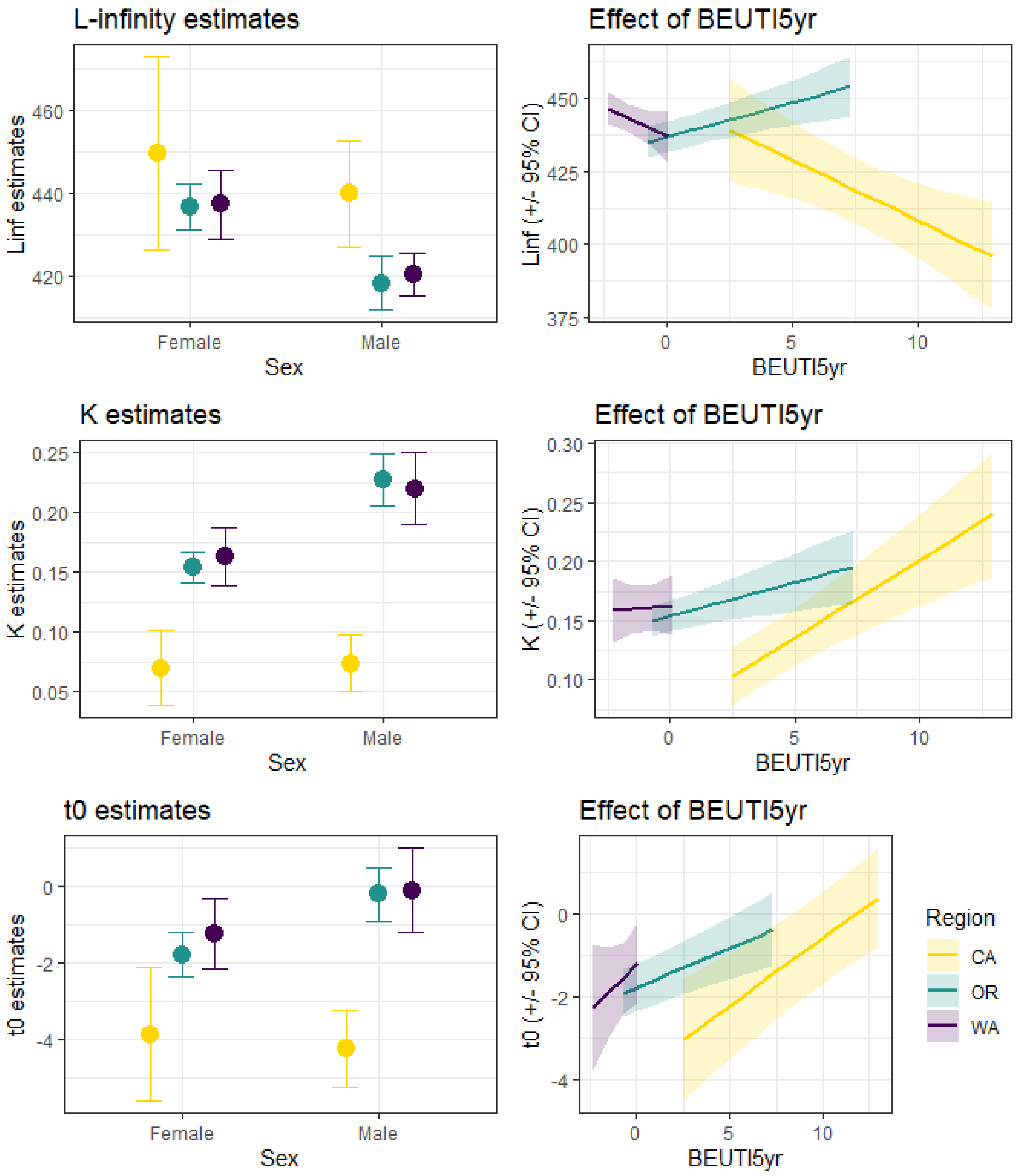


Figure 10 - Parameter estimates for the environmental models from CA, OR, and WA, showing the relationship between the covariates and model parameters (L_∞, *k*, and t_0). Sex is shown on the left as points for males and females at a $BEUTI_{5yr}$ value of 0 with 95% confidence bars. The linear relationships between the $BEUTI_{5yr}$ covariate and model parameters are on the right, standardized for females, with 95% error bands around the lines. Lines for each model are only shown for the range of $BEUTI_{5yr}$ values observed in the region.

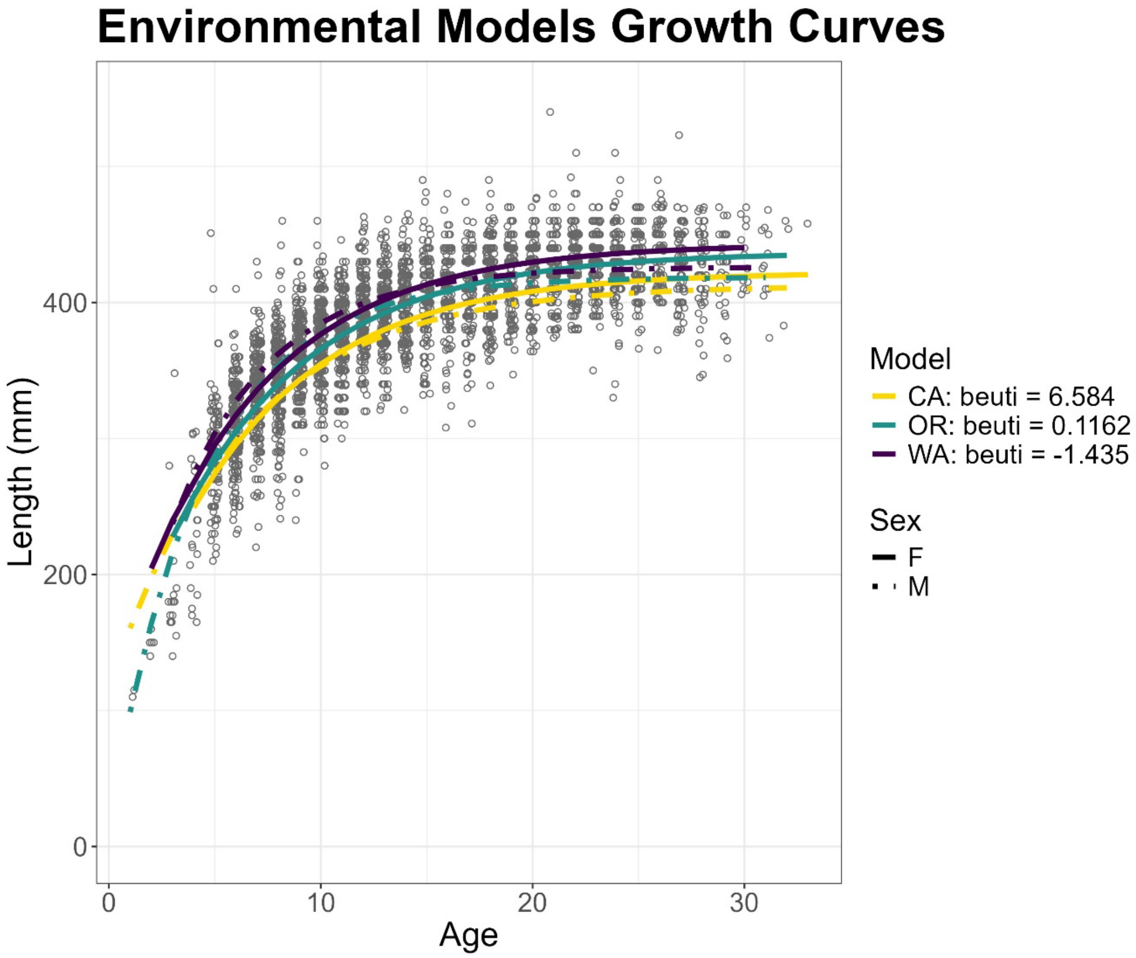


Figure 11 - Predicted von Bertalanffy growth curves for the three region-specific environmental models. Each region's model is shown as a different color. Females are solid lines while Males are dashed. Points are the available data within all the three datasets. Model predictions were made holding BEUTI$_{5yr}$ values at the median for each dataset (see values in legend).

The three environmental models representing the regions of CA, OR, and WA varied in their estimated effects of sexes and BEUTI5$_{yr}$. Among the three models, 95% confidence intervals of L_∞ and t_0 overlapped for all females (Figure 10). For males, all three parameter estimates from the OR and WA models overlapped between models. For OR and WA models, females and males were within each other's 95% confidence intervals for the t_0 parameter, while L_∞ and *k* male and female estimates were separate from each other's 95% confidence intervals. BEUTI_{5yr} had effects of higher magnitude in CA models than in OR models. (Table 6).

DISCUSSION

The extended von Bertalanffy models utilizing spatial and environmental covariates for quillback growth patterns indicate that region, sex, depth, and $BEUTI_{5yr}$ have significant effects on L_∞, *k*, and t_0. Region was found to be a major factor explaining growth patterns, specifically for L_∞ and *k* parameters. Significant differences were estimated even between spatially close regions, such as CA and OR, and patterns did not necessarily reflect expected latitudinal or temperature-related gradients. $BEUTI_{5yr}$ was a significant driver for these southernmost regions of CA and OR, but not WA. Sex also was also a significant covariate for parameters in the models, but effect sizes tended to be smaller and likely negligible biologically. By quantifying how quillback growth differs across region, sex, and environmental conditions, this study describes the population across their range, points to potential mechanisms for the differences, and informs future assessments and management.

Region

The spatial model, utilizing region as a covariate for L_∞ and *k*, most strikingly showed three groupings (Figure 9). The southern regional grouping, made up of CA, OR, and WA, had 4.5 cm or 12% greater L_∞ than the northern regions. There was also a trend in L_∞ values between the inside and outside regions of the same state, with AK_SE_In and BC_In showing lower estimates (by ~1 cm) than their AK_SE_Out and BC_Out counterparts. This supports the claim from data collaborators that growth metrics are distinct for quillback populations found in protected inshore waters vs open coastal waters. Furthermore, non-overlapping confidence intervals for L_∞ estimates between spatially close regions (such as OR and CA) indicate notable growth pattern separation based on location. Notably for the *k* parameter, the CA and AK_SE_Out regions were outside of any other region's 95% confidence intervals and on either end of the spectrum (Figure 8). This means quillback at the southernmost end of their geographical range (CA), grew the fastest with the highest *k*, while those at the northern end of the range (AK_SE_Out), grew the slowest.

Latitude is a recognized predictor in many species' growth patterns, as it relates to large-scale temperature patterns. The Temperature-Size Rule describes the general pattern of slower growth rates and larger sizes obtained for ectotherms in colder environments, but there are often exceptions to this (Atkinson 1994; Arendt 2011). The regional pattern described here for quillback having larger asymptotic sizes in the south, where sea surface temperatures tend to be warmer (Yin et al. 2024), does not match the Temperature-Size Rule, whereas the gradient of *k* (from the highest estimate in CA to the lowest in AK_SE_Out) does. Other rockfish growth studies in the Northeast Pacific Ocean observed regional differences in model parameters that also did not follow straightforward latitudinal gradients. For Greenstriped rockfish (*Sebastes elongatus*), which have a range similar to quillback, a study occurring from the U.S.-Mexico border to the U.S.-Canada border found that the highest *k* was present in a geographically-defined region between Cape Mendocino, CA and Pt. Conception, CA, rather than following a clean north to south latitudinal pattern (Keller et al. 2012). Likewise, a study on Splitnose rockfish (*Sebastes diploproa*) found no latitudinal trend between estimated growth rates (*k*) in five biogeographic regions across the same study area, with the lowest k occurring in the southernmost region between the U.S.-Mexico border and Pt. Conception, CA, where low productivity is characteristic of the region (Gertseva et al. 2010).

The regional outlier in the model groupings was WA_PS. This region is better thought of as the Salish Sea entirely, not just limited to Puget Sound. Quillback within the Salish Sea are found to have distinct growth phenotypes, where the farther inland the population is, the smaller the asymptotic length, from 47 cm in the Strait of Juan de Fuca (oceanic conditions) to 32 cm inside Puget Sound proper (West et al. 2014). This corresponds to a comparatively low WA_PS L_∞ value observed in the spatial model, at approximately 35 cm. The geography of Puget Sound and the Salish Sea is unique – it is a large-scale fjord protected from the coastal ocean with depths reaching over 600 m in some areas and it is subjected to freshwater influence, complex tidal currents, and much urban development on the coastline. There have been many theories on why there is such a differentiation of quillback from Puget Sound, including environmental pollutants, overfishing, limited ideal habitat, high temperatures, and low salinity (West et al. 2014).

Another potential explanation for the growth pattern differences detected among regions could be genetically based. In Washington state, genetic studies on quillback determined that coastal quillback are genetically distinct from inland Puget Sound quillback (Seeb 1998). Within Puget Sound, low frequencies of hybridization with Copper and Brown rockfish are present (Wray et al. 2024). Although evidence of hybridization did not seem to affect the population structure in Puget Sound, the study also found that the two populations of quillback studied had little interbreeding. Quillback are known to remain in one location as adults with little to no migration (Tolimieri et al. 2009) and therefore may exhibit behavioral genetic isolation, even with the possibility of larval dispersion as a method of genetic mixing. Quillback adapted to upwelling systems may be genetically differentiated due to this behavioral isolation, but this has not been explicitly explored. A comparative genetic study on quillback along the Pacific coastline could address if populations are genetically distinct and at what resolution these populations may exist.

Regional patterns in L_∞ and k estimates likely relate to the environmental differences between the North and South. The Northeast Pacific Ocean north of WA is a coastal downwelling system, where productivity is associated with downwelling and warmer ocean temperatures (Black et al. 2008). CA, OR, and WA is a coastal upwelling system, driven by the northernly California Current. Productivity in these southern regions is associated with colder ocean temperatures and it is notably high during the upwelling season, with cascading effects through the trophic systems and growth, evidenced in otolith increment chronologies in multiple species of marine fish such as Yelloweye rockfish, Splitnose rockfish and Chinook salmon (*Oncorhynchus tshawytscha*) (Black et al. 2005, Black et al 2008, Black et al 2011).

Environmental Model: $BEUTI_{5yr}$

$BEUTI_{5yr}$ was a significant covariate to all model parameters in the CA and OR models, but not in the WA model for any parameters (Table 6). Regional differences in the BEUTI index could account for these results. The raw scale of the BEUTI index across the 3 regions fell on a gradient, where WA experiences more negative values on average and CA experiences the highest values (more intense upwelling and primary productivity) (Figure 6). For the CA and OR models, all three parameter relationships with $BEUTI_{5yr}$ were greater in magnitude in CA than for OR. Notably, the relationship with *k* for the CA model was 2.3x the slope of the OR model and there were opposite relationships for L_∞ between CA and OR, with OR having a positive slope (2.37) and CA a negative (-4.16) (Figure 10). The extremely high values of upwelling California experiences may be influencing this relationship. High upwelling, which is associated with turbulent seas, may cause conditions to reach a point where the environment becomes unsuitable for young developing quillback. Although Laidig et al. 2007 found no correlation between the abundance of juvenile rockfish in northern California and offshore Ekman transport (advection from coastal upwelling), Caselle et al. 2010 made the connection that upwelling facilitates rates of replenishment, or delivery of juveniles to nearshore adult populations. If intense upwelling is moving fish out of nursery habitat before they're ready, this could relate to the negative relationship of $BEUTI_{5yr}$ with asymptotic size in the CA model due to this increased environmental stress.

The significance of BEUTI_{5yr} for both CA and OR highlights the importance of early growth on future growth trajectories. The significance of BEUTI_{5yr} to not only the t_0 parameter (which could theoretically be associated with larval size) but also the k and L_∞ parameters suggests that environmental conditions at the beginning of a fish's life might be influencing growth patterns for the entirety of the fish's life. In other words, upwelling during the first 5 years of a fish's life could be impacting the overall growth trajectory that fish experience throughout their life as described by k and L_∞. Upwelling strength has been linked to successful rockfish recruitment (Caselle et al. 2010; Markel and Shurin 2020) and increased individual growth for larvae (Wheeler et al. 2017). While the effects of upwelling disproportionately affect larval growth and survival, it can also influence adult growth through bottom-up mechanisms, as increased primary production and larval abundances provide more food for secondary consumers (Ainley et al. 1993; von Biela et al. 2015).

Net primary productivity is likely the mechanism driving the biological influences of upwelling indices, and it is reflected in the BEUTI index calculation as the nitrate metric. While BEUTI is an index that specifically reflects the biological response to upwelling in relation to this (Jacox et al. 2018), systems outside of the California Current System also have environmental conditions that result in increased net primary productivity. Net primary productivity surges are associated with high upwelling in the California Current, but they are also associated with high downwelling in systems farther north (Brodeur et al. 1996). Off Vancouver Island, Canada, high quillback recruitment was associated with prolonged downwelling, and adult yelloweye rockfish growth was positively correlated with warm ocean temperatures and downwelling (Black et al. 2011; Markel and Shurin, 2020). Future work could explore using net primary productivity as a covariate instead of an upwelling index potentially allowing for a wider spatial range and more data incorporated, but for the purposes of this study, we focused on an upwelling index that captured both the physical oceanography and productivity in the system, albeit at a limited spatial range.

Depth

In the spatial model, depth had a significant positive linear relationship with L_∞ and a significant negative linear relationship with *k* and t_0, but life history could play a role in these effects. Quillback are typically found in the nearshore environment, with larger individuals at deeper depths (Love et al. 2002). This is reflected in the higher L_∞ values estimated with increasing depth. Quillback larvae and juveniles settle in shallower nursery kelp habitat and adults migrate to offshore benthic zones with rocky structure (Matthews 1990; Markel et al. 2017). This might be influencing the positive relationship of L_∞ with capture depth, instead of an inherently greater asymptotic body size or different growth for quillback found in deeper waters. However, the difference in the L_∞ estimate between a quillback captured at 50m vs 100m (17-80th percentile for observed depths) was only approximately 1.4 cm, suggesting that depth does not have a large effect on L_∞, biologically. The negative relationship of growth rate (*k*) and t_0 with depth makes sense considering the life history patterns of quillback, with younger and growing individuals typically found in shallower depths.

Depth is correlated with temperature and therefore relates to the Temperature-Size Rule. Deeper depths correspond to lower temperatures and have been associated with slower growth rates, and vice versa (Thresher et al. 2007; Lindmark et al. 2022). Greenstriped rockfish were found to have significant relationships in their von Bertalanffy growth parameters with depth strata (deep vs. shallow) between Cape Mendocino, CA and northern Washington state, with deep fish having greater L_∞ estimates and males having higher *k* in the shallow strata (Keller at al. 2012). This reflects the pattern seen with quillback and corresponds to the expectations for the Temperature-Size Rule, with greater asymptotic sizes at lower temperatures (i.e. greater depths). However, this is not always the pattern. For Pacific ocean perch (*Sebastes alutus*), an extended von Bertalanffy model utilizing log-transformed capture depth as a covariate also reported significant relationships with L_∞ and *k* parameters, but the relationship with asymptotic size was negative while the growth rate was positive (Kimura 2008). The effects of depth and temperature on growth parameters may also be influenced by things other than direct physiological factors, such as spawning migrations to deeper waters, higher mortality in warmer waters, or trophic advantages of being large in deeper waters (Gertseva et al. 2010; Gertseva et al. 2017).

Sex

Results from both spatial and environmental models had sex as a significant influence on parameters. Typically, males had a lower L_∞ and a higher *k* than females, except for the CA environmental model in which sex was not significant for any parameters. The greatest sex difference in L_∞ estimates among models presented here was between the environmental OR and WA models, where males had an L_∞ of ~2 cm less than females (approximately a 4.2% reduction), but these models had smaller data sets and thus higher uncertainty; for the spatial model with substantially more data, the differences between males and females was less than 1 cm. Despite statistically significant sex effects in the growth models, the minor differences between males and females suggest that quillback sexes can still be grouped together in models, as has been done in previous assessments (Langseth et al. 2021, Langseth et al. 2025).

This pattern of higher k estimates and lower L_∞ for males is reflected in other rockfish with apparent sexual dimorphism. Greenstriped rockfish von Bertalanffy growth parameters follow this sex-specific trend, but in higher magnitudes (female L_∞ was generally higher than males by 5 cm or more (approximately 18.9% of male L_∞), and female k was lower by ~0.05 yr^{-1} relative to males (Keller et al. 2012). Canary rockfish (*Sebastes pinniger*) also have significant variation in growth parameters between sexes (Keller et al. 2018). Based on body size alone, many other rockfish species have males that are considerably smaller than females on average (Lenarz and Echeverria 1991; Haldorson and Love 1991). This size difference is likely due to reproductive requirements in females, and growth rate differences between sexes likely reflect the trade-off of metabolic demands for somatic and reproductive growth (Wourms 1991; Helser et al. 2007).

Data and Model Limitations

Many factors needed to be considered during the data processing and compilation phase, as well as their implications on model results. With the large amount of data the spatial model incorporates (n=21,798), parameter differences among groupings of sex or region were found to be statistically significant, even if the values themselves may not be as biologically meaningful. For example, in all models, t_0 was significantly associated with sex, depth, and region but had overlapping confidence intervals between males and females in all models (except the environmental OR model) (Figure 8, Figure 10). T_0 could be considered as a fixed parameter rather than varying with covariates, as has been done with other von Bertalanffy modeling, as fish at Age-0 are not expected to vary between sexes or regions (Keller et al. 2012; TenBrink and Helser 2021; Langseth et al. 2025).

A common challenge with von Bertalanffy models is having sufficient smaller and younger fish to anchor growth curves. Across regions in the dataset, smaller fish were typically scarce, notably for regions in Alaska, necessitating the removal of region as a covariate to t_0 (Figure 3). A potential cause of this may have been sampling selectivity within regions; Alaska projects were mostly fishery dependent surveys which didn’t select for small fish.

The sampling methods used by the various projects differed across the dataset (Table A 1) with implications for size selectivity. However, residuals for the spatial model did not have strong associates with project, which can be considered a proxy for potential gear effects (Figure A 4). Future modeling could consider including project as a random effect, but this was not expected to have a substantial effect on the conclusions.

Age distributions among regions in the spatial model were distinct between northern and southern regions (Figure A 5). The northern regions (BC_In northwards) include fish that had estimated ages greater than 50 years old, whereas fish over 50 years were rare for the southern regions (WA southward). This might reflect a true state of the population, where fish from southern regions just don't live as long, matching the findings of Munch and Salinas 2009, who use the metabolic theory of ecology to claim that lifespan generally increases with latitude in relation to colder temperatures in many species of fish. However, the regional differences in ages could also be influenced by effects of historical overfishing, which tends to remove larger individuals from the population, changing the population dynamics and size structure (Fisher et al. 2010, Langseth et al. 2021). For example, a study completed for 16 species of Pacific rockfish from Point Sur, CA to Washington determined that changes in mean length over time were related to fishing pressure, which varied by region (Harvey et al. 2006). The relative influence of such age differences (and their causes) on the von Bertalanffy models fit in the study remains unknown but could be explored in future work.

The traditional von Bertalanffy equation is a common growth model that has been used with many other rockfish species and within assessments (Kimura 2008; Keller et al. 2012; West et al. 2014; Langseth et al. 2025), but there are inherent correlations among its parameters, namely a strong negative correlation between L_∞ and k estimates (Ruttenberg et al. 2011; Ogle 2013). Alternate model parameterizations, such as the

Schnute or Francis parameterizations (Schnute 1981; Francis 1988), could be explored in future work to avoid the issue of correlated parameters. Other growth models, such as negative exponential models or Gompertz models (Panik 2013) could also be considered; however, we focused on the traditional equation to have these results be easily relatable to stock assessment biological parameters.

The availability of suitable environmental data was arguably the most limiting constraint for growth modeling in this study. Temperature, a common variable when investigating environmental influences, was considered for the environmental model. We chose to focus on bottom temperature as opposed to surface temperature because quillback are a benthic species. However, the $\text{btemp}_{5\text{yr}}$ estimates we were able to generate limited the available dataset too greatly to be considered as a covariate along with an upwelling index. The BEUTI index also limited the dataset spatially to the California Current System regions of CA, OR, and WA, which was then further limited by the distinct, nonoverlapping values each region experiences in $\text{BEUTI}_{5\text{yr}}$ (Figure 6). Utilizing the $\text{Bakun}_{5\text{yr}}$ covariate to increase the available data for environmental models was considered as an alternative, but it was determined that the Bakun index's spatial scale was too coarse (3° latitude resolution) and overwhelmingly represented negative values within the dataset. Future research could explore the Bakun index and other environmental covariates (e.g. net primary productivity, sea surface temperature), but spatial and temporal limitations to environmental time series will continue to be a challenge given the breadth of the quillback dataset, with fish born as early as 1909.

Data scarcity has been identified as a primary area of uncertainty for the California quillback stock assessments, particularly with respect to age and growth parameters, and it remains an important data need to inform future assessments (Langseth et al. 2025). While this study contributed greatly to and compiled the available quillback age-length data across their entire range, limitations within regions are still apparent. More detailed data would be beneficial for more comprehensive studies on growth patterns and quillback assessments, especially in areas that are considered understudied such as the north coast of California. Stock assessments, particularly in California and Oregon, would benefit from increased region-specific data collection to further refine how variables like sex, depth, or other environmental conditions influence growth patterns.

Research Implications

This study has management implications for quillback rockfish on a coastwide scale. Previously, quillback have been assessed as stocks not distinguished by state boundaries, reflecting unique environmental conditions, or including sex-specific considerations. Notably, quillback from California had growth parameters extrapolated from aged quillback from Washington and British Columbia in the 2021 stock assessment. The von Bertalanffy models described here suggest that the L_∞ and k growth parameters for quillback are region-specific and should be considered when determining age-growth relationships. Furthermore, assessing “inside” vs “outside” stocks separately is biologically supported in this study through the significant differences in L_∞ estimates.

Assessments and management for these areas should continue to distinguish between those separate stocks.

The environmental models indicate that the magnitude, significance, and effect of upwelling on growth patterns differ by region. Areas of coastal Washington, Oregon, and California are currently assessed on a state-by-state basis, which may be easier political and management boundaries for stock assessments, but they may not be the best reflection of the environment. Regions in the California Current System may be better described with biogeographical regions that reflect environmental boundaries instead of state boundaries. Biogeographical regions, which are constructed using geographic barriers or breakpoints (capes, points, benthic geography), reflect environmental zones that differ in conditions such as upwelling intensities. While management cannot ignore political boundary divisions or established fishing zones, assessments may be able to utilize the differing growth patterns within biogeographically arranged stocks and determine more accurate estimates.

While upwelling was the major environmental driver explored in this study, the effects of downwelling have been found to influence growth in similar ways. Due to the limitations of the BEUTI index, this study did not explore quillback growth patterns in downwelling systems. Understanding the explicit differences between upwelling and downwelling systems as it relates to adult growth and specific environmental conditions could be explored with otolith increment analysis, as was done with Yelloweye rockfish and Splitnose rockfish (Black et al 2011, Black et al 2005).

An otolith increment analysis for quillback from Cape Mendocino, CA and Southeastern Alaska was initially part of this study but was incomplete due to a deficiency of useable otoliths and lack of correlation between increment time series (Appendix D). Future work may be able to build off this and determine finer environmental influences on growth patterns for quillback. This has implications on how we predict their vulnerability, resilience to overfishing, and overall stock status.

CONCLUSIONS

The large amount of data compiled in this dataset is extremely valuable to comparisons for growth between quillback across their range. von Bertalanffy models extended with covariates of sex, region, depth, and $\text{BEUTI}_{5\text{yr}}$ show that patterns of growth among groups and environmental conditions can be significantly different. Some of these differences are small and may be biologically inconsequential, but a wider implication is that quillback have unique growth patterns because of the specific environmental conditions characterizing the regions, and patterns don’t follow a clean latitudinal gradient. This is likely explained by differences in coastal upwelling strength, at least in the California Current System, as shown with the greater positive relationship between the $\text{BEUTI}_{5\text{yr}}$ covariate and k for CA compared to the spatially close and otherwise geographically similar OR region. Future studies investigating quillback growth patterns throughout their range should consider environmental variables that have been shown to affect growth patterns. Variables beyond the limitations of this study, such as net primary productivity and temperature, and the implications of using biogeographic regions instead of political boundaries could provide further understanding of what affects quillback rockfish growth patterns across their range.

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APPENDICES

Appendix A: Supplementary Figures and Tables

Table A 1 - List of Projects present in the Master Dataset with information on number of quillback fish sampled (N), gear and data type associated with capture.

Project	Description	N	Fishery Independent/Dependent	Gear type
ADFG_Com	Alaska Department of Fish and Game Commercial sampling	3	Fishery Dependent	Unknown
ADFG_Com_jig	Alaska Department of Fish and Game Commercial sampling: hook and line (jig) fishery	69	Fishery Dependent	Hook and Line
ADFG_Com_LL	Alaska Department of Fish and Game Commercial sampling: longline (LL) fishery	4030	Fishery Dependent	Longline
ADFG_Sport	Alaska Department of Fish and Game Sport fishery sampling	4070	Fishery Dependent	Hook and Line
BC_HBLL	British Columbia Department of Fisheries and Oceans Canada Hard Bottom Longline Survey (HBLL)	12221	Fishery Independent	Longline
DFO_jig	Department of Fisheries and Oceans Canada jig surveys	2428	Fishery Independent	Hook and Line
DFO_HStrawl	Department of Fisheries and Oceans Canada Hecate Straight Synoptic Bottom trawl surveys	515	Fishery Independent	Trawl
DFO_LCDtrawl	Department of Fisheries and Oceans Canada Strait of Georgia Lingcod Young-of-Year bottom trawl surveys	36	Fishery Independent	Trawl
DFO_QCStrawl	Department of Fisheries and Oceans Canada Queen Charlotte Sound Synoptic Bottom trawl surveys	300	Fishery Independent	Trawl
WDFW_Com	Washington Department of Fish and Wildlife Commercial sampling	47	Fishery Dependent	Trawl

Project	Description	N	Fishery Independent/Dependent	Gear type
WDFW_PSTrawl	Washington Department of Fish and Wildlife Puget Sound Bottom Trawl survey	1668	Fishery Independent	Trawl
WDFW_Research	Washington Department of Fish and Wildlife various research surveys, including Marine Fish Science Longline Surveys and Rod and Reel surveys	212	Fishery Independent/Unknown	Trawl, Hook and Line, Longline survey, Unknown
WDFW_Sport	Washington Department of Fish and Wildlife Sportfishing surveys and Marine Fish Science Barge surveys	2368	Fishery Dependent/Unknown	Hook and Line, Barge, Unknown
West	Data collected by West et al. 2014 for publication from various sources	1924	Fishery Independent & Dependent	Otter trawl, bottom trawl, Hook and Line, spearfishing
ODFW_Com	Oregon Department of Fish and Wildlife Commercial sampling and special projects	505	Fishery Dependent	Unknown
ODFW_Sport	Oregon Department of Fish and Wildlife Recreational sampling and special projects	1522	Fishery Dependent	Hook and Line
HannahBlume	Oregon Department of Fish and Wildlife Recreational sampling for Hannah and Blume, 2011 report of female QBK maturity	513	Fishery Dependent	Hook and Line
IPHC	International Pacific Halibut Commission surveys	1324	Fishery Independent	Longline, setline
CRFS	California Recreational Fishery Survey	95	Fishery Dependent	Hook and Line
RBG	California Department of Fish and Wildlife Rockfish Biological Groundfish sampling project	55	Fishery Dependent	Hook and Line
2019Comm	California Department of Fish and Wildlife Commercial collections in 2019	6	Fishery Dependent	Unknown
WCGBTS	Northwest Fisheries Science Center West Coast Groundfish Bottom Trawl Survey	196	Fishery Independent	Trawl
CCFRP	California Collaborative Fisheries Research Program	169	Fishery Independent	Hook and Line

Project	**Description**	**N**	**Fishery Independent/Dependent**	**Gear type**
Abrams	Collaborative Fisheries Research project through Cal Poly Humboldt in conjunction with graduate projects of J. Abrams and D. Barrett	116	Fishery Independent	Hook and Line

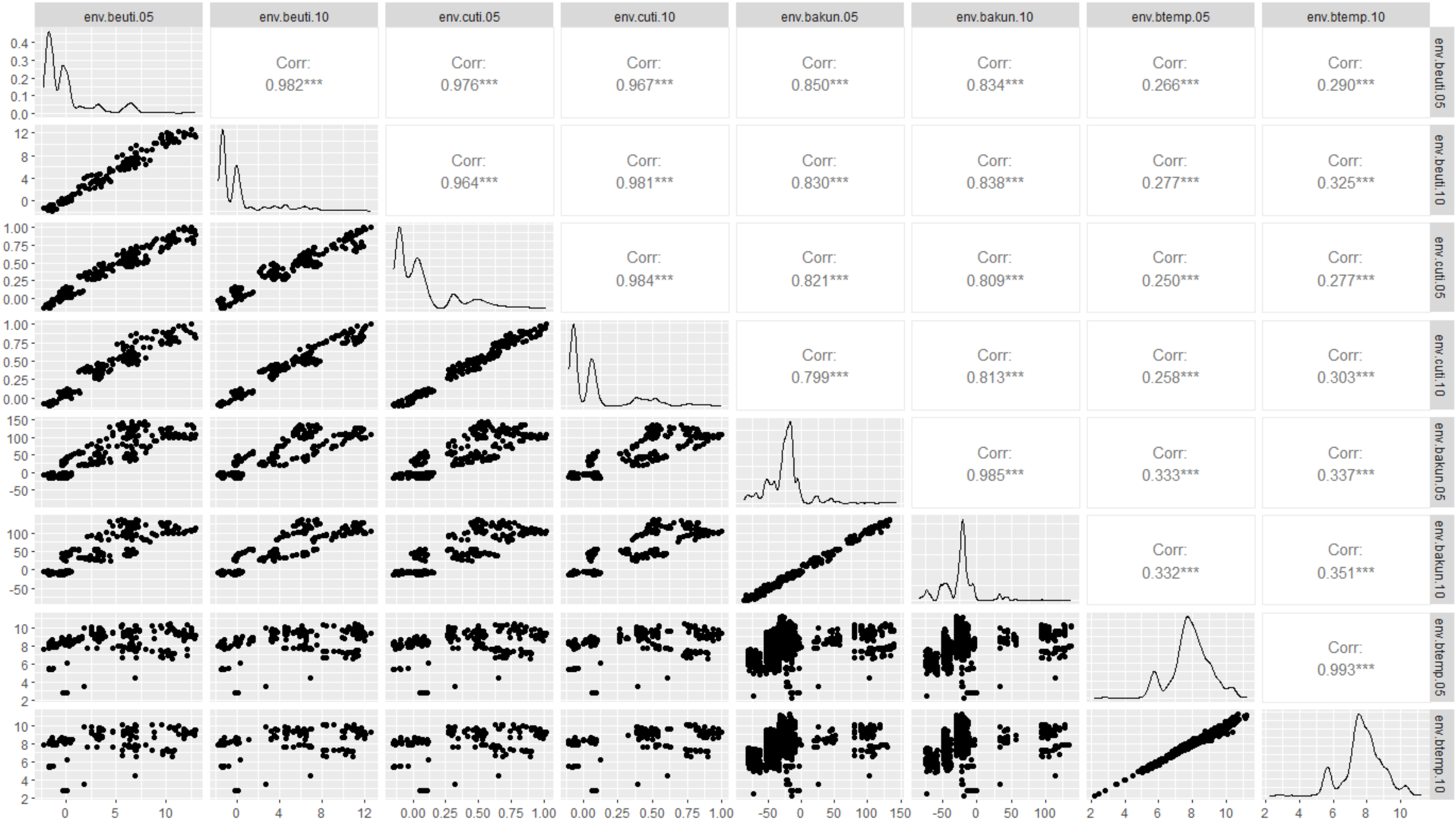

Figure A 1 – Correlation plots for the environmental covariates considered.Env.beuti.05 refers to BEUTI$_{5yr}$, with this notation following for the env.cuti.05, env.bakun.05, and env.btemp.05 as well. All other covariates ending in .10 were environmental variables calculated for the first 10 years of a fish’s life.

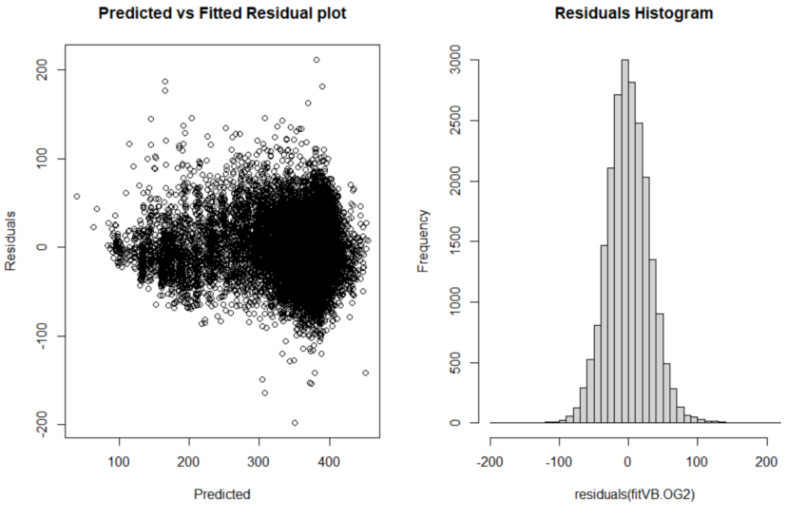

Figure A 2 - Residuals vs Predicted value plot and histogram to assess assumptions of normality and homogeneity of variance for spatial model with an additive error structure.

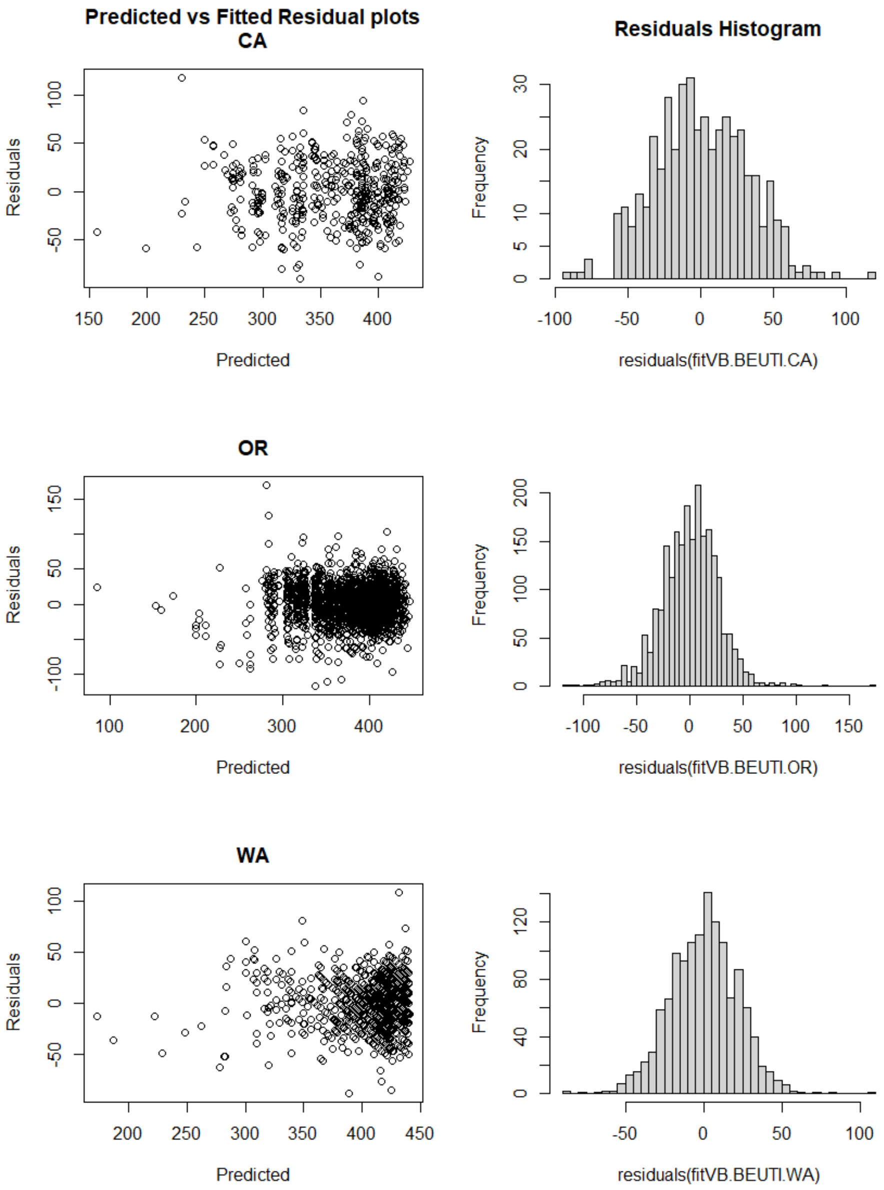

Figure A 3 - Residual plots for all three environmental von Bertalanffy models (for CA, OR, and WA), checking homogeneity of variance and residual normality.

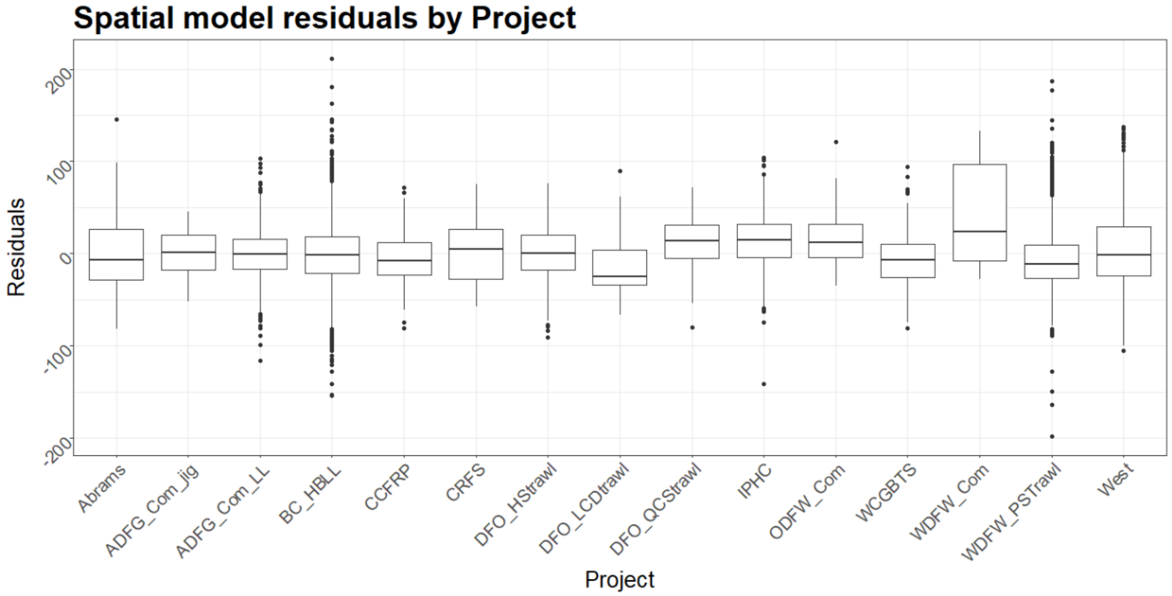

Figure A 4 – Model residuals shown against Projects included in the spatial model’s dataset (n = 15).

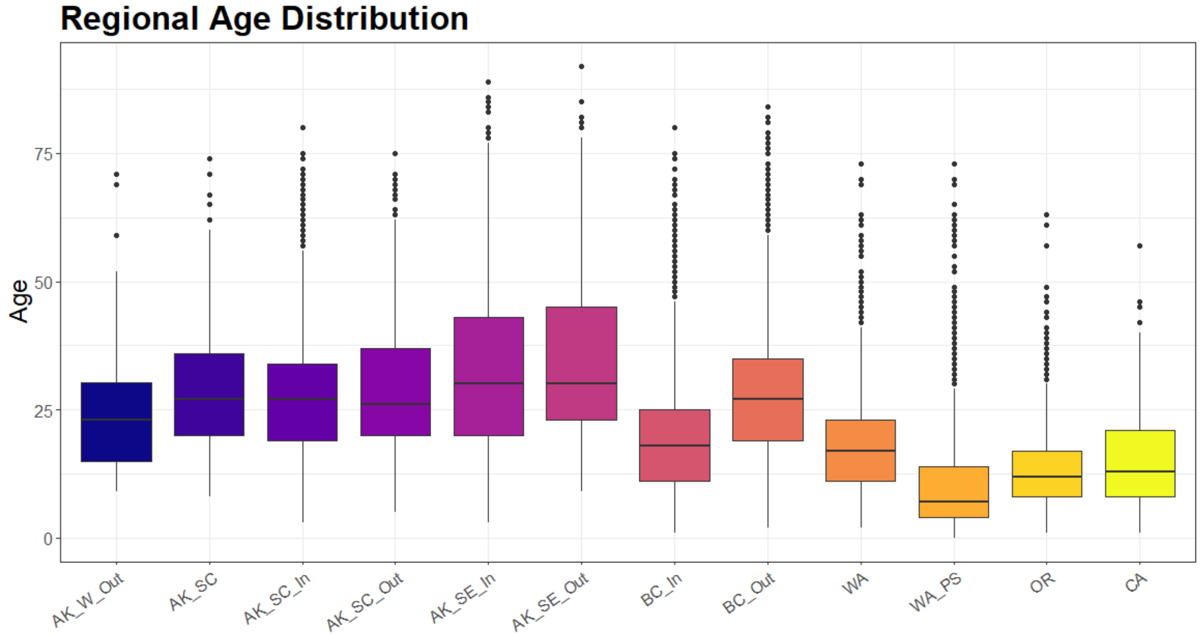

Figure A 5 – Quillback rockfish age distributions by region within the dataset.

Appendix B: Quillback Data Request Flyer

S. maliger Ageing Study Request for Otoliths

Master's thesis by Claire Stuart[1,2]: **Environmental and spatial drivers of growth patterns in Quillback Rockfish (*Sebastes maliger*) in Northern California and the Northeast Pacific Ocean**

Study Objectives:

- *Use growth models with environmental covariates (latitude, depth, temperature) to analyze quillback rockfish growth patterns across the Northeastern Pacific Ocean.*
- *Use thin-sectioned otoliths to conduct an increment analysis and identify years of conspicuous growth in connection with environmental effects via the method of cross-dating (following a study done on yelloweye rockfish by Black et al. 2008).*
- *Design a model of how climatic and oceanographic factors influence quillback growth by region, based on otolith chronologies developed from cross-dating.*

Request 1: Quillback rockfish age and length data with the following associated fields as available (capture date, capture location and depth, sex). These individuals will be already aged, but do not have to be all from the same location or time frame.

Request 2: Quillback otoliths that I can thin-section or existing images of thin-sections, preferably from fish >400mm (and older than 20 yrs). Additional information needed are length, capture date, and capture location. It's preferable to have been collected from 1983-2022.

Collection Location (Agency)	**Request 1:** Available age-at-length data	**Request 2:** Otoliths to thin-section or existing thin-sectioned images
California (CCFRP, Cal Poly Humboldt, CDFW, WCGBTS)	No limit	Abrams collection, CCFRP
Oregon (ODFW, WCGBTS)	No limit	50-75
Washington (WDFW, WCGBTS)	No limit	50-75
British Columbia (DFO)	No limit	50-75
SE Alaska (AFSC, ADFG)	No limit	50-75
SW Alaska (AFSC, ADFG)	No limit	50-75

Please contact Claire Stuart (claire.stuart@humboldt.edu) with questions and available data. Images and the thin-sections of otoliths can be made available to contributors post-analysis.

Appendix C: Von Bertalanffy model fit to full dataset

The master dataset contains 34,392 quillback spread across 12 regions and 24 projects. The same process of assigning unknown sexed fish (n=886) was implemented to this dataset. Depth or environmental covariates were not considered in this model, but otherwise the same model structure was implemented, with linear relationships between covariates of region and sex to model parameters of L_∞ and *k*, and t_0. Region was not included as a covariate for t_0, as some regions did not have enough young fish to accurately estimate region-specific t_0 parameters. Corresponding figures and tables for model results and parameter plots are below (Table C 1, Figure C 1, Figure C 2).

Table C 1 - Parameter estimates from the full dataset von Bertalanffy growth model with standard error (SE) and p-values. Estimated values are interpreted as deviations from the base value (β_0). All parameters denoted with '$_L$' represent L_∞ estimates, '$_k$' represents *k*, and *t* represents t_0.

Type	**Parameter**	**Estimate**	**SE**	***t* value**	***P* value**
Base (AK_SC, Female)	β_{0L}	428.309	2.289	187.132	**<0.0001**
	β_{0k}	0.099	0.003	32.456	**<0.0001**
	β_{0t}	-2.161	0.083	-26.027	**<0.0001**
Sex: Male	β_{1L}	-11.359	0.646	-17.585	**<0.0001**
	β_{1k}	0.015	0.002	9.802	**<0.0001**
	β_{1t}	0.377	0.095	3.995	**<0.0001**
Region: AK_SC_In	β_{2L}	-3.840	2.64	-1.471	0.141
	β_{2k}	0.010	0.004	2.836	**0.005**
Region: AK_SC_Out	β_{3L}	4.289	2.597	1.652	0.099
	β_{3k}	0.015	.004	3.977	**<0.0001**
Region: AK_W_Out	β_{4L}	29.183	7.806	3.739	**0.0001**
	β_{4k}	0.013	0.009	1.329	0.184
Region: AK_SE_In	β_{5L}	-25.703	2.467	-10.419	**<0.0001**
	β_{5k}	0.010	0.003	2.876	**0.004**
Region: AK_SE_Out	β_{6L}	-13.907	2.601	-5.347	**<0.0001**
	β_{6k}	-0.008	0.003	-2.458	**0.014**
Region: BC_In	β_{7L}	-36.907	2.403	-15.187	**<0.0001**
	β_{7k}	0.013	0.003	4.201	**<0.0001**
Region: BC_Out	β_{8L}	-28.558	2.318	-12.318	**<0.0001**
	β_{8k}	0.022	0.003	6.980	**<0.0001**
Region: CA	β_{9L}	-6.149	3.524	-1.745	0.081
	β_{9k}	0.050	0.005	10.461	**<0.0001**
Region: OR	β_{10L}	16.161	2.713	5.956	**<0.0001**
	β_{10k}	0.0485	0.004	13.658	**<0.0001**
Region: WA	β_{11L}	18.847	2.516	7.490	**<0.0001**
	β_{11k}	0.036	0.003	10.742	**<0.0001**
	β_{12L}	-20.654	2.900	-7.122	**<0.0001**

Type	**Parameter**	**Estimate**	**SE**	***t* value**	***P* value**
Region: WA_PS	β_{12k}	0.004	0.003	1.342	0.180

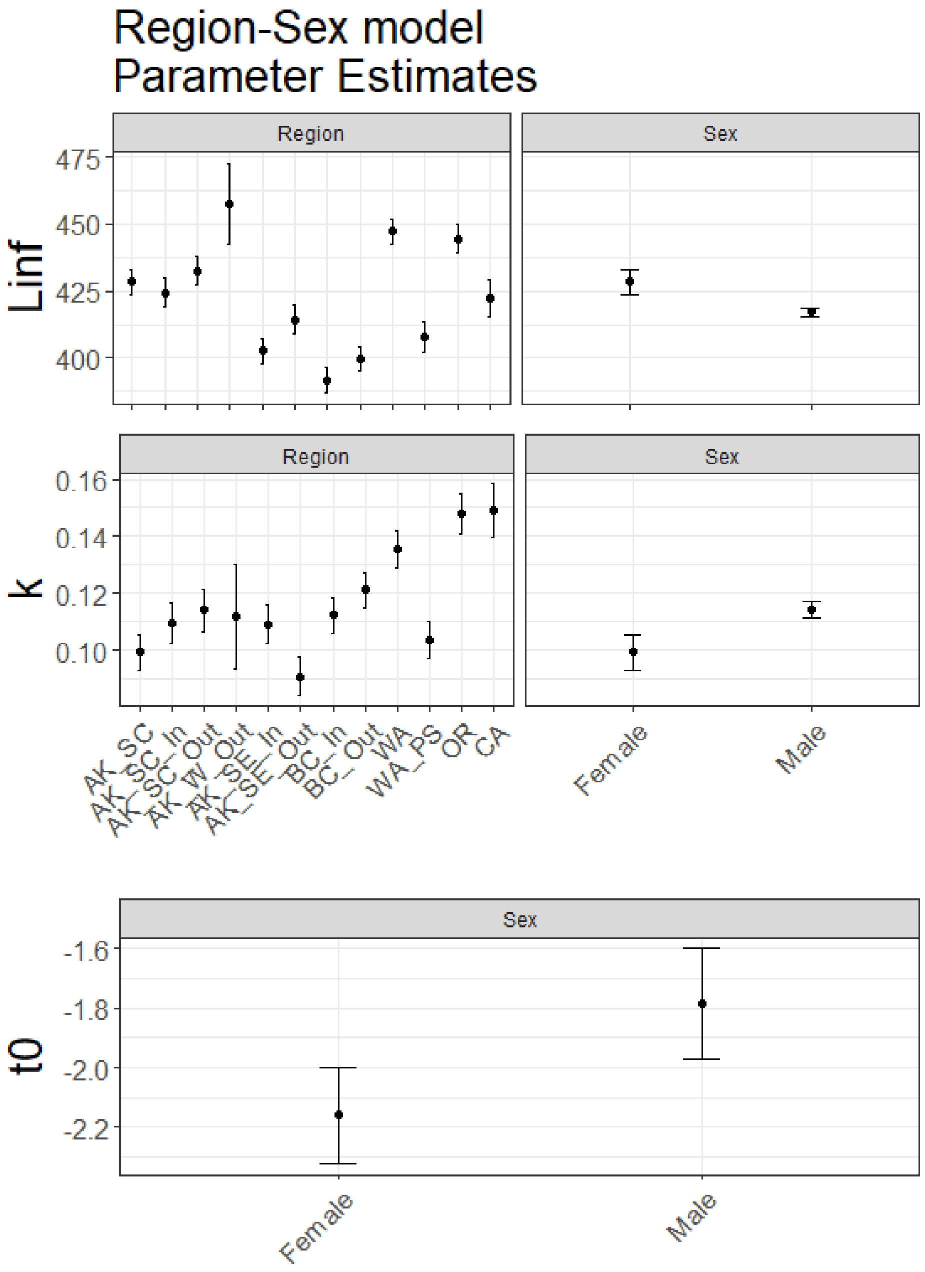

Figure C 1 - Parameter estimates for the full dataset von Bertalanffy model, showing the relationship between the two covariates (region and sex) and each of the three parameters of the model (L∞, *k*, and t_0). Estimates are displayed as points with 95% confidence bars. The region of AK_SC and females were the base model values.

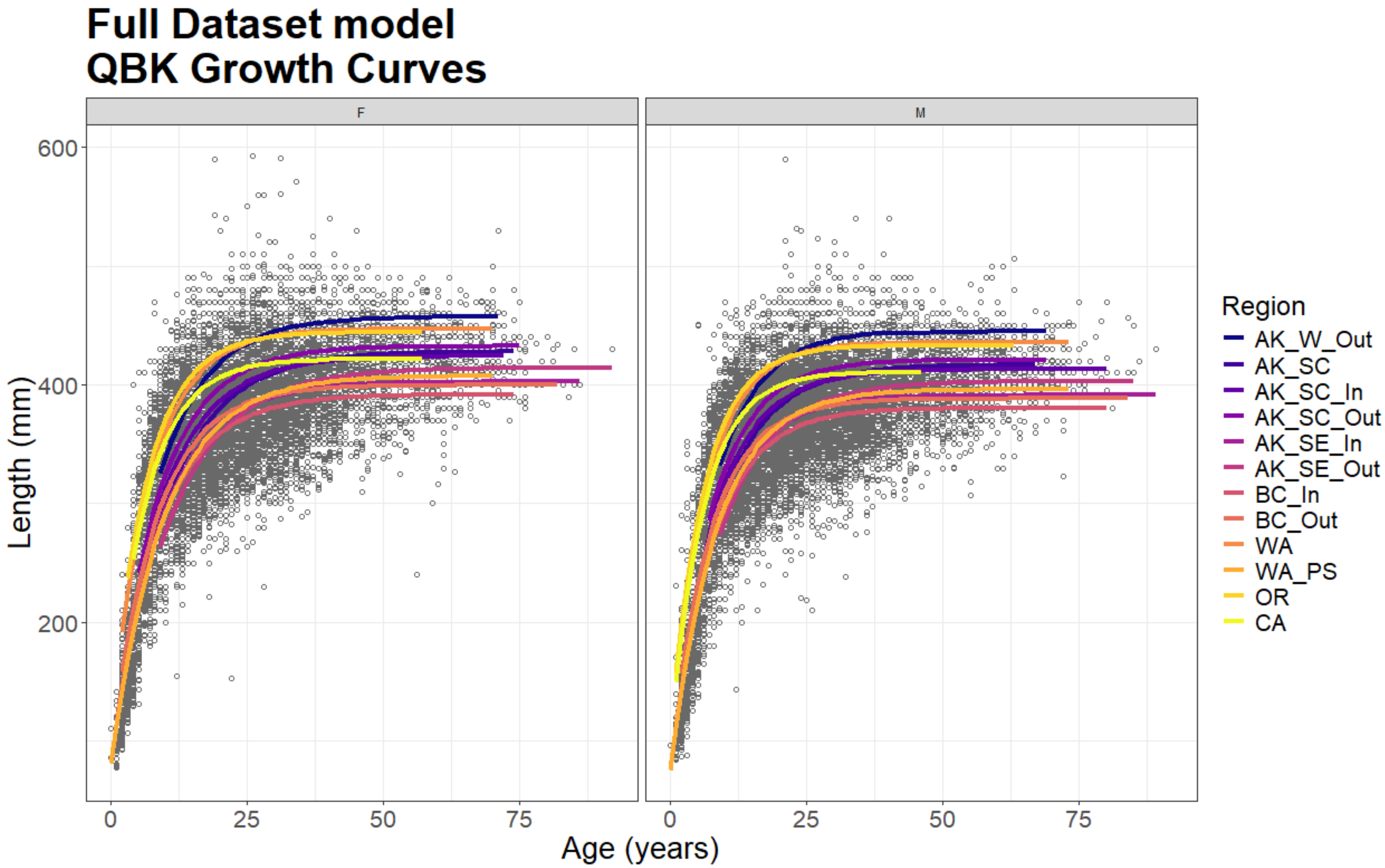

Figure C 2 - von Bertalanffy model predicted curves for the model utilizing the full dataset, including covariates of region and sex. Levels of region are shown as multiple curves while sex is faceted.

Assumptions for the von Bertalanffy model are normality and homogeneity of variance. The model has an additive error structure and meets assumptions (Figure C 3). Project did not have a substantial relationship with model residuals, with most region-specific residuals centered around 0 (Figure C 4). However, some exceptions occurred in part due to smaller sample sizes.

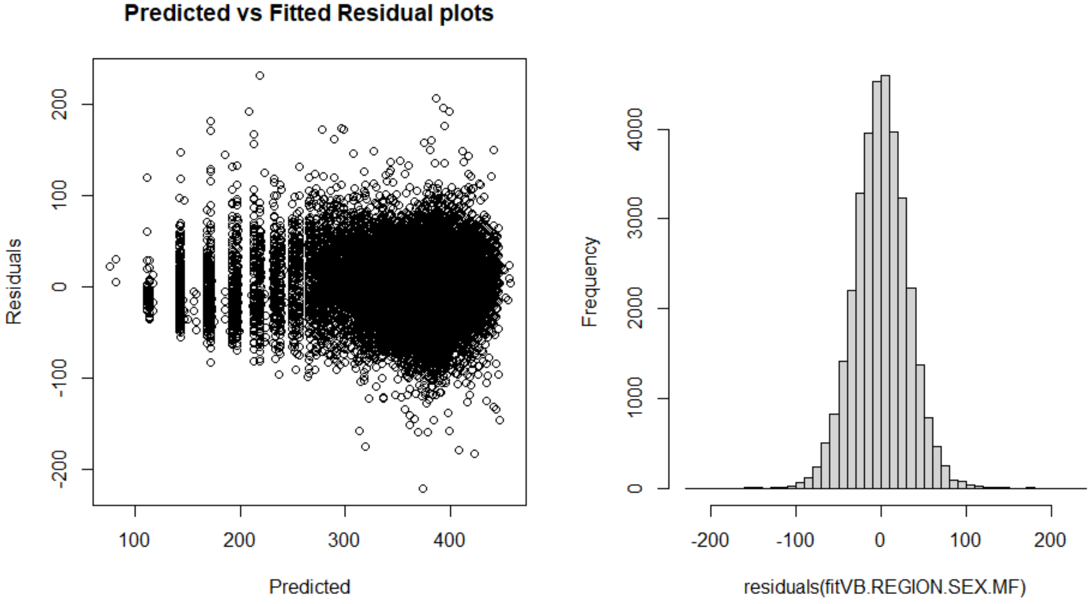

Figure C 3 - Residuals vs Predicted value plot (right) and histogram (left) to assess assumptions of normality and homogeneity of variance for full model with an additive error structure.

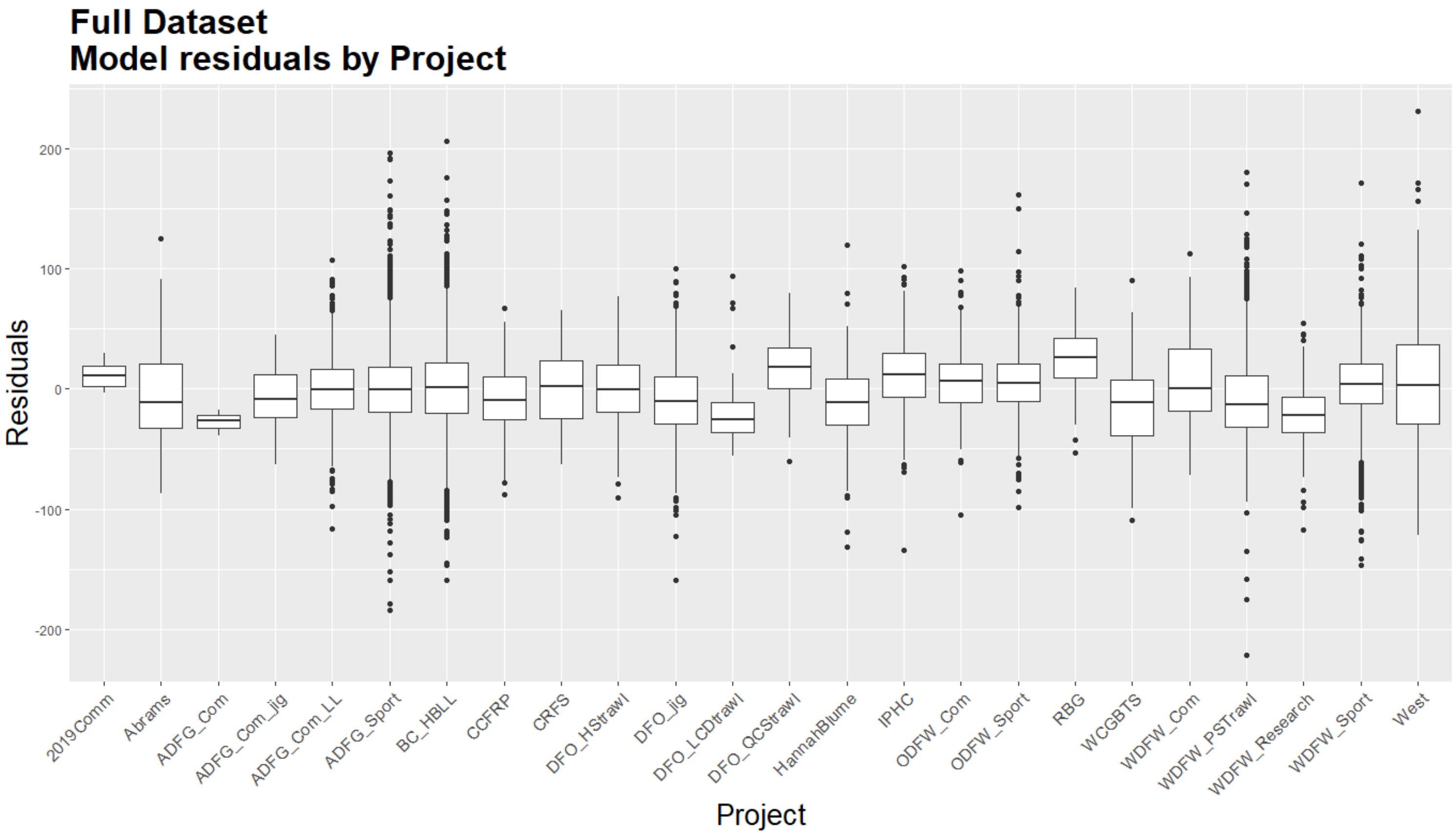

Figure C 4 - Projects included in the full von Bertalanffy model's dataset (n = 24) shown against model residuals.

Results for the full dataset had some differences from the spatial model, and there are some interesting patterns and data considerations to note. WA_PS no longer looks so stand-alone, it now more closely aligns with regions of AK_SE_Inside, AK_SE_Outside, BC_In, and BC_Out in both L_∞ and *k* estimates. CA now more closely aligns with AK_SC regions (AK_SC, AK_SC_In, AK_SC_Out) with L_∞ estimates and OR and WA are still together with the highest L_∞ estimates. AK_W_Out L_∞ is also closer with the OR and WA estimates but there was higher uncertainty for AK_W_Out due to the low sample size (n=61). Males and females remain significantly distinct for L_∞ and *k* parameters, and now t_0 estimates are much lower than the spatial model (t_0 = -2.161 yrs for females vs t_0 = -0.695 for the spatial model). *k* estimates for OR, CA, and WA are now grouped together and outside the confidence intervals of the other regions, whereas in the spatial model, only CA had a significantly high *k* estimate relative to the other regions. *k* estimates follow a North-South trajectory of northern regions having the lower estimates while CA maintains the highest estimate, overlapping in 95% confidence intervals with OR and WA.

Appendix D: Otolith Increment Analysis

One of the original objectives of this thesis was to conduct cross-dating and increment analysis on quillback rockfish otolith annuli to identify years of conspicuous growth in connection with climatic events. This analysis was meant to correlate oceanographic conditions such as sea level anomalies and upwelling/downwelling indices to significant years of growth, reflected in otolith annuli width patterns. This has been completed before for other rockfish in the Northeast Pacific Ocean using the principles of dendrochronology, notably with two populations of the long-lived yelloweye rockfish (*Sebastes rubberimus*), which were found to express increased growth according to region-specific climatic drivers (Black et al. 2011). This type of study has the potential to work for quillback rockfish, as another long-lived species that have high site fidelity as adults, and this could elucidate how environmental influences directly impact adult growth. This work and analysis was attempted for Quillback rockfish following the methods of Black et al. (2011) using fish collected off of Cape Mendocino, California, but correlations between otolith width indices were not robust enough to continue with this analysis. This appendix is intended to document the work done and provide a starting point for future otolith increment studies.

Cross-dating is a technique that creates a quantitative increment pattern for multiple individuals in order to validate ages. This is based in dendrochronology, the study of tree rings over time. Climatic patterns are on of the drivers behind the variation that occurs in tree rings and otoliths (Stokes and Smiley 1996; Black et al. 2005). Years of greater or lesser growth can be attributed to certain historic climatic conditions.

Otoliths from individuals who experienced the same oceanographic conditions can be cross-referenced and their ages statistically verified based on the patterns in the otolith increments. In order to cross-date, you need a collection of multiple long-lived individuals from the same area (assumed to have experienced the same conditions over a similar time period). Quantitative otolith increment measurements for each fish can be detrended (removing the influence of age on increment widths) and if correlations among otolith increment series from different fish are apparent, a single otolith increment series can be produced. Once standardized to vary around a central value of 1.0, these are called chronologies. Chronologies can then be used to describe the overall fish growth patterns and can also be related back to certain oceanographic events or conditions with further models.

Methodology

Otoliths and associated fish data were obtained from the entities that were willing to share the physical structures. These included the Alaska Department of Fish and Game (ADFG) and California Collaborative Fisheries Research Program (CCFRP), as well as collections from previous rockfish research at Cal Poly Humboldt. All otoliths received were from previously-aged fish and are part of the dataset used for this thesis. Ages had been determined using the break and burn method on at least one otolith, in which an otolith is snapped in half and the broken edge is passed through a flame to help highlight annuli (Committee of Age Reading Experts 2006) (Figure D 1). Each annulus is counted as a year, and each fish is assumed to have been born on January 1. Quillback have been validated to deposit one annulus per year, with each dark annuli (slow growth season) paired with an opaque (fast growth season) increment (Kerr et al. 2005).

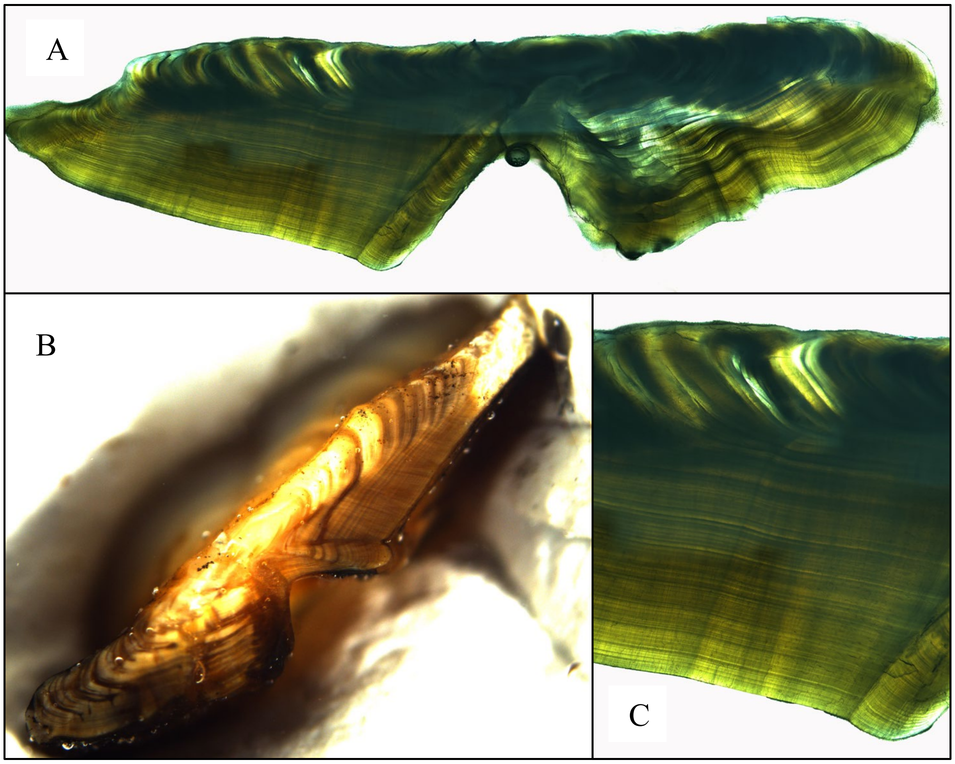

Figure D 1 - Otoliths imaged under magnification that show annuli as they are counted to estimate age of a fish. 1a shows a thin-section of a quillback rockfish estimated to be 55 years old, under 10x magnification. 1b shows another otolith prepared in the break and burn method for reading. This fish was estimated to be 17 years old. 1c is a closer look at a common reading axis of the same otolith shown in 1a along the anterior ventral section, to better see how the individual annuli are laid in long-lived quillback rockfish.

Otoliths that could be included in this analysis were limited by the condition of the received otoliths (i.e., if both otoliths had been used in the break and burn method to age, they could not be used) and by age of the fish and location of capture. Only quillback otoliths that were estimated to be ≥20 years old were considered for use, because a longer adult growth zone is necessary for cross-dating and building chronologies. Furthermore, quillback had to have been captured in the same general spatial area, to meet the assumption that the fish had experienced similar oceanographic conditions over its lifetime. A minimum of 40 otoliths from a single spatial grouping had to meet the age and quality criteria to be considered. Two groups were derived from available otoliths: one sourced from Cape Mendocino, California and another from Southeastern Alaska around Suemez Island.

Thin sectioning of whole otoliths was completed to have a level viewing pane, which allowed for increment measurements. Otoliths to be thin sectioned were embedded within epoxy and then a slice was cut from the approximate center using a Buehler Isomet^{TM} low speed saw and two diamond wafer blades spaced approximately 0.5 mm apart. The otolith was held in place with a double saddle chuck while being cut (Figure D 2). The resulting thin section was fixed to a glass slide using Crystal-Bond^{TM} adhesive resin and if needed, polished with aluminum oxide solution over a felt surface.

Figure D 2 - Thin-sectioning set up for otoliths mounted within epoxy blocks.

Otoliths were read and imaged from the thin-sections, using Image Pro 11 software and a Teledyne Lumenera Infinity 8 high performance digital scope camera on an Olympus BX40 microscope with 10x magnification. Images were captured using the camera, which had been spatially calibrated with a stage micrometer for calculating increments, and Image Pro's Live Tiling tool. Once determined to be acceptable for increment analysis, a line profile along the anterior ventral side of otolith was created. Annuli were manually marked along the line profile using the Image Pro software to measure growth increment between annuli. Generally, the innermost 5 years of growth and outermost marginal growth year were excluded from the increment analysis. Age was also estimated at this step, to ensure it was within +/- 3 years of the previous age estimate. Time of year when the fish was sacrificed was important in interpreting otolith margins and assigning years to the annuli year assignments in each sample. If discrepancies between the previously estimated age and thin-sectioned age were found, the available broken and burnt halves were viewed under a dissection scope as necessary, using mineral oil for enhanced clarity. The goal was to obtain a minimum of 20 acceptable otolith increment series to proceed with a chronology.

Visual cross-dating was performed across individuals from the same group using signature years apparent in the images. Years were assigned to each marked annuli on the line profile, starting from the edge and moving in, according to what year and time of year the fish was captured. Signature years (i.e. years with distinctly wide or narrow annuli) were noted on each individual and compared visually across other otoliths for similar signatures and for matching up years if there was temporal cross over. The best otolith thin section from each spatial grouping was chosen to act as the "baseline" profile and compared to other thin sections' line profile dark/bright patterns, as well apparent large and small increments. I used tools like Microsoft PowerPoint to help with visualization.

Statistical cross-dating was conducted within the R package 'dplR' (Bunn 2008; Bunn 2010). Once otoliths increments were extracted from the line profile as a spreadsheet, they were formatted in a time series data format (.rwl file) within dplR. Increment time series were assessed for inter-correlation using dplR and shiny package extension tool xDateR, found at https://github.com/OpenDendro/xDateR. Spaghetti plots were produced for all increment time series to show the raw increment data for multiple individuals and the temporal spread. Correlation between increment time series was assessed using the ‘Correlations between Series’ tab in xDateR. This tool generates a figure that shows correlations (we chose Kendall Rank Correlation due to low sample size) between the individual series and a generated master chronology, which by default are built with the "leave-one-out-principle" (means the chronology is built using all the other series **except** the one you're looking at). The tool allows for different temporal bin widths or segment lengths, detrending options on increment time series, and adjusting the p-critical value that determines what is considered a significant correlation. Periods of low correlation (p.crit < 0.1) between increment time series were rechecked in the individual’s line profiles and with the otolith images themselves to revisit the visual cross-dating process and determine if a change to one or more increment series resolved the correlation issue.

Detrending was explored within xDateR functions and on individual increment series as a way to isolate the high frequency variation that corresponds to environmental events. Splines were considered as the detrending equation, as well as the “pre-whiten” and Hanning filter ‘(n=)’ functions in xDateR. At least 20 increment time series with satisfactory correlations were required to move forward.

Theoretically, once all increment time series were found to have satisfactory correlation, a master chronology or otolith time-series would be estimated from them using a biweight robust mean method. The master chronology values for annual growth would then be used as the dependent variable in a multivariate regression model including oceanographic variables to draw connections between environmental influences and adult growth.

Preliminary Results

An adequate sample size for thin sectioning was found for n=43 quillback otoliths from Cape Mendocino, California, collected by the Humboldt CCFRP, and n=92 otoliths from Southeastern Alaska around Suemez Island, collected from International Pacific Halibut Commission surveys and commercial longline sampling, loaned by the ADFG Age Determination Lab. A portion of these samples were thin sectioned and assessed (n=40 for CA, n=30 for AK), with approximately 20 otoliths from Cape Mendocino and 10 otoliths from Alaska cross-dated.

Visual cross-dating for each spatial grouping had some suspected signature years. For the Cape Mendocino group, 2015 and 2016 were noted as years we might expect a signature as those years were a heatwave off the coast of California, however no single signature year was consistent across individuals. For the Alaska group, 1997, 1991, 1985, 1978, and 1971 showed a visual signature across multiple fish (5 or more) that had line profiles completed.

Statistical cross dating was attempted in xDateR; however, correlations were not satisfactory at this stage to continue with a master chronology. Spaghetti plots generated for the Cape Mendocino grouping (Figure D 3) and the Suemez Island group (Figure D 4) did not show similar increment patterns between individuals. Correlation plots were similarly non-significant for both groupings, although Alaska had slightly more correlations between some time periods and individuals (Figure D 5, Figure D 6). Ideally, plots would show only blue and green segments, indicating correlation is sufficient across otolith increment time series.

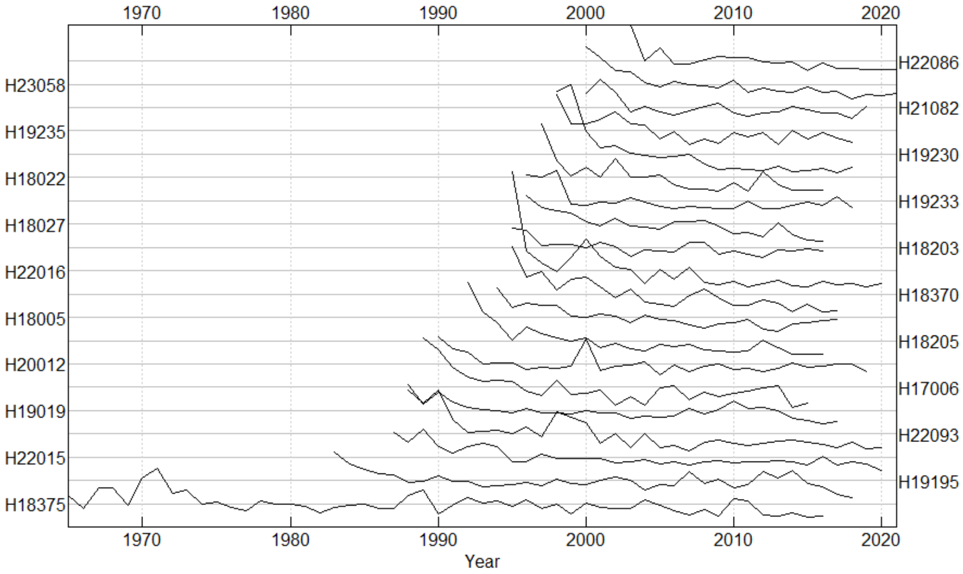

Figure D 3 – Spaghetti plot of the 20 Cape Mendocino otolith increment series. Variance in lines correspond to raw increment widths.

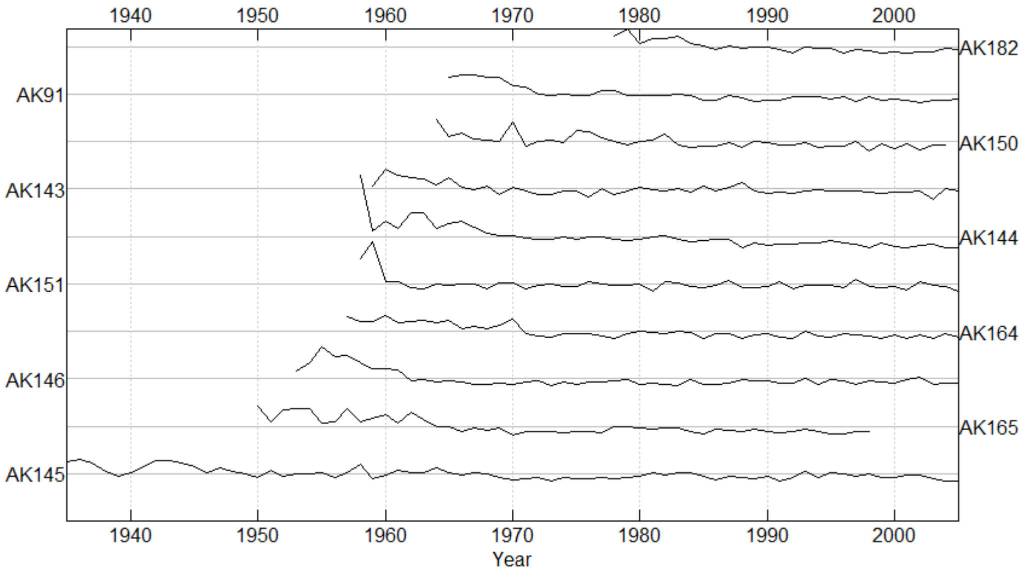

Figure D 4 - Spaghetti plot of the 10 Alaska otolith increment series. Variance in lines correspond to raw increment widths.

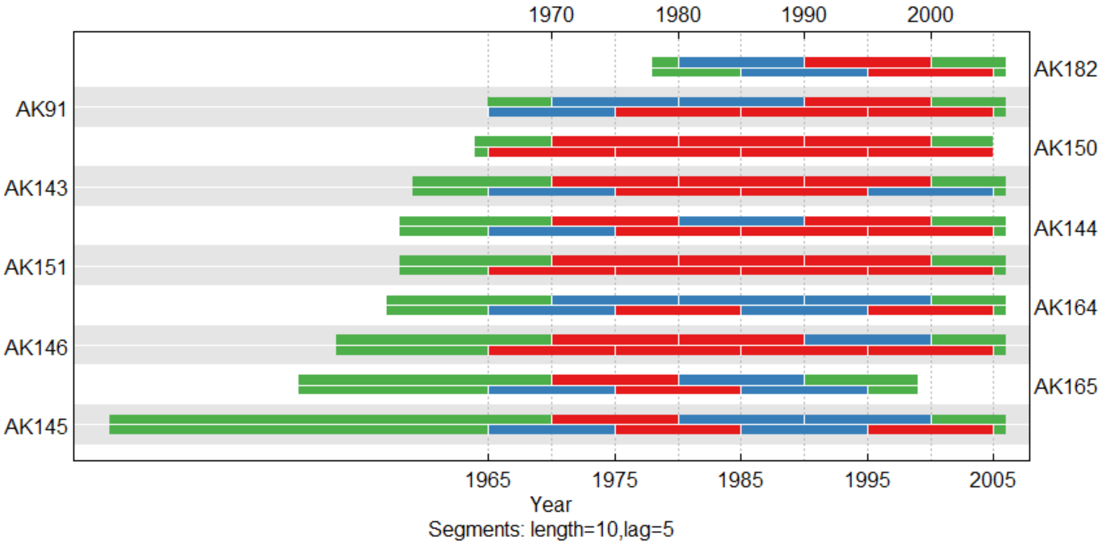

Figure D 5 - Correlation plots depicting 10 Alaska otolith increment time series in 10-year bins with an overlap of 5 years calculated between series. Correlation coefficients followed Kendall Rank correlation, with blue depicting anything <0.1 p-critical value, and red as non-significant. Green depicts sections of the increment series that are not included in the full chronology and therefore not included in the statistical cross-dating.

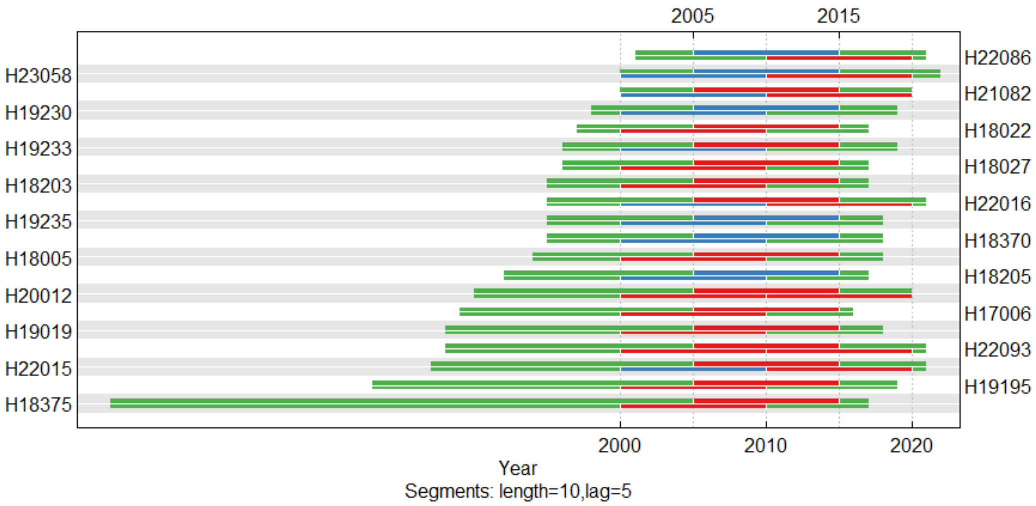

Figure D 6 - Correlation plots depicting 20 California otolith increment time series in 10-year bins with an overlap of 5 years calculated between series. Correlation coefficients followed Kendall Rank correlation, with blue depicting anything <0.1 p-critical value, and red as non-significant. Green depicts sections of the increment series that are not included in the full chronology and therefore not included in the statistical cross-dating.

Discussion

The discordant nature of the otolith time series halted this analysis for quillback rockfish. We did not attempt to further cross-date or detrend from either spatial group to increase correlations between increment series, however that could be a future option with the groundwork already laid out. The Alaska group was noted to have older and cleaner otoliths, which hold more promise for this kind of analysis. The Cape Mendocino group otoliths are best described as “messy”, even though those chosen for the analysis had clear increments and were readable for the purposes of aging. Furthermore, otoliths from the California group were younger than the Alaska group, with an average age of 27 and one older individual with a clear increment line profile acting as the "base". Cape Mendocino is known to have erratic oceanographic conditions, which may have influenced the inconsistent otolith increment patterns we see in this analysis. Many factors go into adult growth besides oceanographic conditions, such as food availability, community effects, and sex-specific differences involved in reproductive energy allotments. Future attempts with this study for quillback should focus on having enough old-growth samples from a specific area as well as expert knowledge of otolith reading and interpretations to make the cross-dating stage smoother.

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