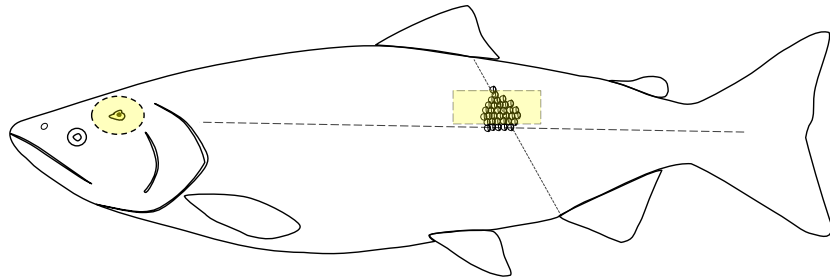


## Final Report

### Scale Analysis of Puget Sound chum salmon (*Oncorhynchus keta*)



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## Executive Summary

An improved understanding of the mechanisms that influence productivity and abundance of Puget Sound (PS) chum salmon is critical for accurately determining the number of harvestable fish and for identifying years of conservation concern. Recent research has found environmental factors such as the Pacific Decadal Oscillation and the abundance of potential competitors (Pink Salmon) during the first few years of marine life to be related to trends in age-at-maturity and productivity of PS chum salmon. Relatively little, however, is known about how marine growth varies in relation to environmental factors and population productivity. In this study we evaluate yearly marine growth increments of three spatially distinct stocks of PS chum salmon (*Oncorhynchus keta*) over 16 brood years (1997-2012). We found growth increments of all three stocks to be significantly positively correlated with one another across all ocean growth years. GAMM modeling provides evidence of density dependent effects occurring during the first ocean year as abundance of local competitors (PS pink and chum salmon) increases, while indicating that third year ocean growth is more closely related to large scale climate indicators including the North Pacific Gyre Oscillation and the Aleutian Low-Beaufort Sea Anticyclone. Surprisingly, models indicated that second year ocean growth was strongly positively correlated with copepod species richness (CSR) in the Northern California Current, suggesting CSR may be an indicator of larger ecological processes occurring in the North Pacific and has the potential to be a useful tool for predicting chum salmon growth. Lastly, in contrast with numerous past Pacific Salmon studies, we identified only second-year ocean growth as a significant predictor of cohort survival (recruits-per-spawner), suggesting that for PS chum salmon this is a critical growth period. As relationships between large-scale ocean indicators and growth and productivity of Pacific Salmon continue to shift, understanding how these relationships are

changing and identifying new indicators that may become useful forecasting tools is increasingly important.

## Introduction

Chum salmon are the second most abundant *Oncorhynchus* species in the North Pacific, and their collective abundance and biomass has increased since the 1970s, in part due to increases in hatchery production (Ishida et al. 1993, Irvine and Fukuwaka 2011, Ruggerone and Irvine 2018). However, at the southern extent of their range, productivity and abundance of natural populations in Puget Sound (PS) have largely declined since the 1980s (Litz et al. in review, Malick and Cox 2016). Variation in productivity of chum salmon populations in PS has been linked to large scale indices of sea surface temperature (Pacific Decadal Oscillation, PDO), primary productivity (North Pacific Gyre Oscillation, NPGO), and the abundance of pink salmon, a potential competitor (Litz et al. in review, Yasumiishi et al. 2016). It stands to reason that growth of PS chum salmon may also be linked to these large-scale ocean indicators, and to variation in population productivity, as has been observed in other PS salmon species (Beauchamp and Duffy 2011, Duffy and Beauchamp 2011). Improving our understanding of the mechanisms driving patterns of growth throughout estuarine, coastal, and offshore ocean residence, and the relationship between ocean growth and population productivity is paramount for accurately determining the number of harvestable fish and for identifying years of conservation concern.

Chum salmon (*O. keta*) spend little or no time rearing in freshwater environments, initiating their seaward migration almost immediately upon emerging from the gravel and becoming free swimming (Urawa et al. 2018). Rapid growth during this early marine period is thought to be paramount to Pacific Salmon cohort survival (Cross et al. 2009, Tomaro et al. 2012, Miller et al. 2013), and may be limited by local conditions such as sea surface temperature (SST), prey density, and abundance of conspecifics (Healey 1982, Fukuwaka and Suzuki 2000,



Saito et al. 2009). Growth in subsequent years, on the other hand, may be limited by large scale ocean conditions in the North Pacific, where chum salmon spend their second through final ocean growth years before initiating their spawning migration. Throughout their life cycle, spatial and diet overlap exists between chum populations as well as other species of Pacific Salmon (*Oncorhynchus* spp.), and there exists the potential for intra- and inter-species competition (Ruggerone and Nielsen 2004, Ruggerone and Nielsen 2009).

Studying the growth of individual fish in the ocean poses a significant challenge due to the immense spatial area over which those individuals may rear. However, the relationship that exists between salmonid fork length and scale radius provides a powerful tool that can allow us to retrospectively evaluate growth during the ocean life stage (Dahl 1911, Gilbert 1913, Fisher and Pearcy 1990, Fukuwaka and Kaeriyama 1997, Fukuwaka 1998). Numerous studies have evaluated ocean growth of chum salmon across their range in the Pacific, linking growth to SST (Kaeriyama et al. 2007, Seo et al. 2011, Agler et al. 2013), NPGO (Debertin et al. 2017), metrics of the Aleutian Low (Agler et al. 2013), zooplankton biomass (Seo et al. 2006), and abundance of potential intra- and inter-specific competitors (Ishida et al. 1993, Kaeriyama 1998, Walker et al. 1998). However, very little is known about the ocean growth of PS chum salmon (Yasumiishi et al. 2016).

We examined relationships between marine growth and environmental and biological indices to assess processes that may be driving variation in PS chum salmon productivity. Our first objective was to identify environmental and biological factors related to variation in marine growth of PS chum salmon. We expected first-year growth to be correlated with local sea surface temperature and abundance of potential competitors, while in subsequent ocean years we expected growth to be more closely related to large scale climate indices such as PDO and

NPGO. Our second objective was to describe the relationship between ocean growth and population productivity. We hypothesized that first-year ocean growth would be positively correlated with productivity (recruits-per-spawner), but did not expect there to be a consistent relationship between productivity and growth in subsequent ocean years.

## Methods

### *Study Area and Scale Selection*

This study focused on three spatially distinct stocks of PS Fall run chum salmon: Skagit River (North PS) Stock, South PS stock, and Hood Canal stock (Figure 1). Scales from chum salmon gill net fisheries associated with these stocks were obtained from the Washington Department of Fish and Wildlife (WDFW) archives spanning 16 brood years (1997-2012). For each brood year (BY) of each stock we selected scales of 15 males and 15 females from the three dominant age classes – 3<sub>1</sub>, 4<sub>1</sub>, and 5<sub>1</sub> (Gilbert-Rich notation, Gilbert and Rich 1927).

### *Scale Imaging, Measuring, and Preliminary Analysis*

Once selected, we imaged acetate impression of scales using a Leica DM 1000 compound microscope at 25X magnification with a mounted Leica DC 30 camera. We used Image-Pro 7.0 to measure each scale in microns ( $\mu\text{m}$ ) along the longest growth axis as described in Walker et al. (1998) (Figure 2). Measurements were taken from the scale focus to the end of the first annulus, between any subsequent annuli, and from the last annulus to the scale edge.

We defined ocean growth years as the period from April through the following March, as this corresponds temporally with annual scale growth increments (Bilton and Ludwig 1966). To be included in the analysis for a particular ocean growth year a fish must have fully completed that year of ocean growth. For example, an age 4<sub>1</sub> fish would be included in the analysis for ocean

growth years 1 (OA1), 2 (OA2), and 3 (OA3), but not 4, because at the time of capture it had not fully completed its fourth-year of ocean growth (see Figure 2).

To test for differences in yearly growth increments between age classes, sexes, and populations we used analysis of variance (ANOVA) of raw growth increments (in  $\mu\text{m}$ ). We performed two-way ANOVAs of yearly growth increments vs. age and population.

#### *GAMM Modeling (OA1, OA2, OA3, and Productivity)*

To evaluate inter-annual age specific growth patterns and their underlying ecological correlates, we used generalized additive mixed models (GAMMs) with an information theoretic and full subsets approach (Fisher et al. 2018, Wood 2006). GAMMs allow for flexible functional dependence of the response variable on the covariates with non-integer varying degrees of freedom by the addition of a smoothed function (Guisan et al. 2002), thus they are particularly useful for tracking the inherent nonlinearity of ecological processes (Fisher et al. 2018). The general form of the model is described as:  $Y_i \sim \beta_0 + f_1(x_i\beta_1) + f_2(x_i\beta_2) + \dots + f_n(x_i\beta_n) + \epsilon_i$ , where the functions  $f_i$  are the non-parametric smoothing terms. To account for correlation in the data we included random effects.

We produced independent candidate GAMM sets for each ocean age year – OA1, OA2, and OA3. Each ocean age specific model set evaluated and compared models with continuous environmental effects: SST, PDO, NPGO, and ALBSA (Aleutian Low – Beaufort Sea Anticyclone) and biological effects: copepod species richness (CSR), 4B (PS + strait of Juan de Fuca) pink salmon abundance, and 4B chum salmon abundance (Table 1). We also tested for regional variability in growth by including stock as a fixed factor effect: Hood Canal, South PS, and North PS. Additionally, we independently evaluated age specific growth effects on

productivity by using productivity (recruits-per-spawner) as a response variable and yearly standardized scale growth increments as candidate predictors.

All GAMMs were fit with the random effect ‘brood year’ to allow each BY of individuals to have their own growth trajectory slope (i.e., accounts for even/odd year growth trajectories). To equate scales for variable comparison, all explanatory variables were standardized, and the response variable ‘growth’ was converted into a z-score. Additionally, all GAMMs were fitted using restricted maximum likelihood (REML) in the mgcv package in R (Wood and Wood 2015). Finally, the outputs of all best models were assessed using the function gam.check (Wood 2017), which plots residuals and presents diagnostic measures related to model fit and the appropriateness of the smoothing parameter.

Model selection was based on Akaike’s Information Criterion, corrected for small sample size (AICc). To overcome issues with collinearity among explanatory variables, we used a full subsets approach to construct the GAMMs (Fisher et al. 2018) which was developed for ecological applications and has great utility for evaluating the influence of correlated environmental factors on the ecology of biota (Bond et al. 2018, McLean et al. 2016). We used the R package FSSgam (Fisher et al. 2018) to generate the best fitting model(s) for each ocean age year. Within each ocean age year set, we considered models with  $\Delta AICc < 3$  supported. To minimize overfitting given our large set of potential covariates, we limited the maximum number of explanatory variables to 5 (with all combinations tested) and restricted the complexity of the smooth for each parameter within a given model to 3 (i.e., degrees of freedom). These parameters were set to prevent overfitting and create conservative, ecologically interpretable models (Wood 2006, Fisher et al. 2018).

All statistical analyses and graphs were generated using R version 3.6.1 (R Development Core Team 2018), and statistical significance was established at  $\alpha < 0.05$ . In R, we used functions FSSGAM 1.11 (Fisher et al. 2018), mgcv (Wood and Wood 2015), visreg (Breheny and Burchett 2013) and gamm4 (Wood and Scheipl 2014).

## Results

We imaged and measured scales from 3,906 individual PS chum salmon. We were unable to reach the full target sample size for some BYs due primarily to limitation of scale availability in the 5<sub>1</sub> and 3<sub>1</sub> age classes (Table 2).

### *Scale Growth in relation to Age, Sex, and Population*

Annual scale growth increments differed by population and return age for OA1, OA2, and OA3 respectively (Table 3). For OA1, growth increments of South PS (SPS) and Hood Canal (HC) fish were on average greater than those of North PS (NPS) fish (SPS OA1 growth increments averaged  $4.1\% \pm 0.4\%$  SD greater than NPS, HC OA1 growth increments averaged  $3.5\% \pm 0.4\%$  greater than NPS). For OA3, growth increments of NPS fish were on average greater than those of SPS and HC fish (NPS OA3 growth increments averaged  $11.6\% \pm 1.2\%$  greater than SPS and  $8.3\% \pm 0.2\%$  greater than HC, Figure 3a). In general, fish that returned to spawn at younger ages experienced greater growth than those that returned at older ages for each respective growth year (i.e., OA1 average growth of age 3<sub>1</sub> fish > 4<sub>1</sub> fish > 5<sub>1</sub> fish, Figure 3b). Growth increments of all three populations were significantly positively correlated with one another in OA1, OA2, and OA3, although correlations were stronger in OA2 and OA3 than OA1 (Figure 4).

### *GAMM Modeling*

GAMM modeling indicated OA1 growth was best predicted by a model fit with CSR (by stock), 4B chum abundance, and 4B pink abundance (by stock) (Figure 5). CSR demonstrated a negative relationship with growth to a turning point after which the relationship became positive. The growth-4B chum abundance relationship was positive at low chum abundances but became strongly negative as chum abundance increased. The growth-4B pink abundance relationship differed by stock but showed a negative trend overall.

GAMM modeling indicated OA2 growth was best predicted by a model fit with CSR, 4B chum abundance (by stock), and 4B pink abundance (by stock) (Figure 5). CSR had a strong positive relationship with predicted growth. 4B chum abundance demonstrated a positive relationship with predicted growth overall, but the strength of the positive relationship differed by population. 4B pink abundance demonstrated a negative quadratic relationship with predicted growth until a turning point where the relationship became strongly positive.

GAMM modeling indicated OA3 growth was best predicted by a model fit with ALBSA (by stock) and NPGO (Figure 5). ALBSA demonstrated a negative linear relationship with growth, and NPGO demonstrated a negative relationship with growth to a turning point after which the relationship became positive.

GAMMs that evaluated growth effects on productivity (recruits-per-spawner) across ocean years indicated that only OA2 growth was significantly correlated with productivity, such that increased growth during OA2 lead to increased productivity (Figure 6). However, once growth reached a certain threshold the relationship became negligible.

## Discussion

In this study we sought to identify factors driving patterns of ocean growth in PS chum salmon and to understand the relationship between ocean growth and population productivity (cohort survival). A more comprehensive understanding of these relationships has the potential to enhance management of PS chum salmon commercial, tribal, and recreational fisheries by improving accuracy of pre-season forecasting estimates to allow for earlier and more reliable identification of years with poor survival and low run sizes. This is of particular importance as relationships between climate indicators and salmon populations continue to change with Pacific climate regime shifts, causing previously documented patterns and their resulting assumptions to become less reliable (Wolkovich 2014, Litzow et al. 2019, Malick 2020, Litzow et al. 2020a, Litzow et al. 2020b).

### *OAI*

The abundance of 4B chum and pink salmon both emerged as significant predictors of growth in OA1. Our top model indicates a negative relationship between PS chum abundance and predicted growth at above average chum abundances, and a negative relationship with growth at low to medium pink abundances (Figure 5). Both of these relationships suggest that density dependent effects are occurring.

Because pink salmon have a fixed 2-year life cycle, direct competition between pink and chum salmon in OA1 only exists for odd BY cohorts. Pink salmon are thought to be superior competitors to chum and other Pacific Salmon species (Ruggerone and Nielsen 2004), and studies have documented declines in chum growth and feeding rates in relation to presence of pink salmon (e.g., Sano 1963, Ivankov and Andreyev 1971, Yasumiishi et al. 2016). Regional

differences between stocks supports this idea that high abundances of pink salmon have a negative impact on PS chum growth. NPS chum salmon had significantly less OA1 growth than SPS or HC populations (Figure 3a), and over the time series we examined, the North PS produced by far the most pink salmon of the three regions. In six of the eight odd BYs we evaluated, the North PS region accounted for >50% of all 4b (PS and Strait of Juan de Fuca) pink salmon production. We posit that juvenile pinks may outcompete juvenile chum salmon, severely depleting or altering available estuary prey resources, leading to less OA1 growth in the NPS population.

## OA2

Our top OA2 model included the same three covariates as the top OA1 model (4B pink abundance, 4B chum abundance, and CSR), but the relationships between growth and 4B pink and chum abundances don't suggest the same density dependent effects we observed in OA1. In fact, as pink and chum abundances move from medium to high values, PS chum growth increases. We cannot be certain as to why the growth-abundance relationships are positive from medium to high competitor abundances, but it could be related to highly favorable ocean conditions that benefit both species, and more abundant prey resources in the ocean compared with the estuary and coastal environment.

By their second ocean year, PS chum are located somewhere in the Gulf of Alaska or the Bering Sea. Despite being representative of shelf waters in the Northern California Current (Peterson 2009, Lamb 2011), the strongest predictor of OA2 growth was CSR. We recognize that CSR is likely not representative of foraging conditions in the North Pacific, however, CSR was significantly correlated with every other environmental variable we considered in our models



(Pearson correlation coefficients: PDO = 0.59, NPGO = -0.69, SST = 0.64, ALBSA = -0.62).

This suggests it represents relevant ecosystem processes occurring in regions of the North Pacific where subadult PS chum salmon are foraging.

Another unexpected result connected to OA2 growth was our top ranked productivity model. For decades, the literature has largely agreed that cohorts exhibiting rapid early marine growth often experience increased survival compared with cohorts made up of slower growing individuals (Cross et al. 2009, Tomaro et al. 2012, Miller et al. 2013). Consequently, the early marine period or first year at sea is often described as a “critical growth period” for Pacific Salmon and is thought to strongly influence population productivity. Our findings suggest that for PS chum salmon, growth during the second ocean year (OA2) is most critical for survival, however, once fish reach a certain growth threshold, the benefits of any additional growth appear to be negligible. Given this result, and our finding that CSR is strongly positively connected to OA2 growth, we recommend future work focus on the relationship between CSR and PS chum salmon productivity to determine if CSR could be a useful forecasting tool.

### OA3

ALBSA and NPGO emerged as top predictors of OA3 growth which is consistent with our hypothesis that large-scale Pacific climate indices will drive third year growth. The strong negative relationship between predicted growth and ALBSA suggests chum experience better growth in years of late spring ice out and strong Aleutian Lows. We are less certain as to the nature of the growth-NPGO relationship which is negative from low to medium NPGO values but then reverses to positive from medium to high values. The only other chum salmon study to date comparing growth to NPGO evaluated British Columbia chum salmon scales collected from

1970-2010 (Debertin et al. 2017). Despite their data spanning multiple Pacific Ocean regime shifts (1976/77 and 1988/89), Debertin et al. (2017) found positive growth-NPGO relationships across all ocean age years. Relationships between fish populations and large basin scale indicators shift over decadal or multi-decadal time scales, and it is important to recognize that our findings only represent a relatively short snapshot in time.

### *Conclusions*

Here we provide evidence that variation in growth during the first and second years at sea is related to abundance of conspecifics, PS pink salmon, and ocean conditions in the Northern California Current. PS pink salmon abundance has been shown to play a role in shaping both age structure and run size of PS chum populations (Litz et al. in review), and here we demonstrate that inter- and intra-specific density dependent effects occur during the first growth year as chum salmon rear in the PS estuary and make their way out to sea. We identified copepod species richness in the Northern California Current as a strong predictor of second year growth, and a potentially useful indicator of large-scale processes occurring in the North Pacific Ocean. The second ocean year emerged as the most important growth period for chum cohort survival, however, the nature of the relationships between drivers of second year growth and cohort survival warrants further investigation. As relationships between basin-scale ocean indicators and growth and productivity of Pacific Salmon continue to shift, understanding how these relationships are changing and identifying new indicators that may become useful forecasting tools is increasingly important.

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Table 1. Summary of modeling components.

Variable	Description	Variable Type	Time Frame	Location
Annual scale growth increment	Year specific standardized scale growth estimates of individual PS chum salmon.	biological (individual specific)	approx. April - March	N/A
Recruits-per-spawner	A measure of brood year stock productivity (survival) calculated using adult chum return year abundances and their age structures.	biological (stock specific)	Brood year specific	N/A
4b chum abundance	Abundance of returning adult chum salmon originating from a particular brood year.	biological (Brood Year Specific)	Brood year specific	PS + Strait of Juan de Fuca stocks
4b pink abundance	Abundance of returning adult pink salmon originating from a particular brood year (catch + escapement) applied to the chum growth year with which they had spatiotemporal overlap.	biological (growth year specific)	Returning adult run size lagged backwards 1 year	PS + Strait of Juan de Fuca stocks
Copepod species richness	Represent zooplankton community structure in the Northern California Current and indicates source water location. High richness occurs when community is dominated by lipid poor southern species. Low richness occurs when community is dominated by lipid rich species from subarctic region.	biological	May - Sept of growth year	Off coast of Newport, OR
Stock (origin effect)	Indicates which of the three study stocks an individual belongs to.	biological (3-level factor)	NA	"North PS", "South PS", or "Hood Canal"
Sea surface temperature		environmental	April - March of growth year	Strait of Juan de Fuca
PDO	The Pacific Decadal Oscillation is a large-scale basin indicator of the North Pacific associated with sea surface temperature and sea level pressure anomalies (Mantua et al. 1997).	environmental	April - March of growth year	N/A
NPGO	The North Pacific Gyre Oscillation is a large-scale basin indicator associated with salinity, nutrients, and chlorophyll-a in the North Pacific Ocean (Di Lorenzo et al. 2008).	environmental	April - March of growth year	N/A
ALBSA	The ALBSA captures variability in the Aleutian Low and the Beaufort Sea Anticyclone, two atmospheric phenomena that drive numerous environmental processes in the North Pacific and are associated with timing of arctic snow and sea ice melt (Cox et al. 2019).	environmental	Dec - March preceding growth year	N/A

Scale analysis of Puget Sound chum salmon (*Oncorhynchus keta*).

Table 2. Scale sample sizes by return age and population. PS = Puget Sound.

Age	<u>North PS</u>		<u>South PS</u>		<u>Hood Canal</u>	
	Male	Female	Male	Female	Male	Female
3 <sub>1</sub>	224	207	240	226	206	194
4 <sub>1</sub>	240	240	240	240	225	225
5 <sub>1</sub>	229	214	229	186	208	133

Table 3. F statistics and p values of ocean year specific two-way ANOVAs of age and population vs. growth. Bold indicates significance at the alpha = 0.05 level.

Growth Year	<u>Age</u>		<u>Population</u>	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
OA1	111.088	<b>&lt; 0.001</b>	53.725	<b>&lt; 0.001</b>
OA2	385.629	<b>&lt; 0.001</b>	13.464	<b>&lt; 0.001</b>
OA3	575.725	<b>&lt; 0.001</b>	65.683	<b>&lt; 0.001</b>

Figure 1. Map of Puget Sound and WA coastal rivers that contain chum salmon runs (black lines) and natal watersheds of chum salmon populations evaluated in this study. Scale samples were collected from individuals captured via gill net in marine catch and/or terminal areas associated with populations of interest (Map: D. Gombert, WDFW).

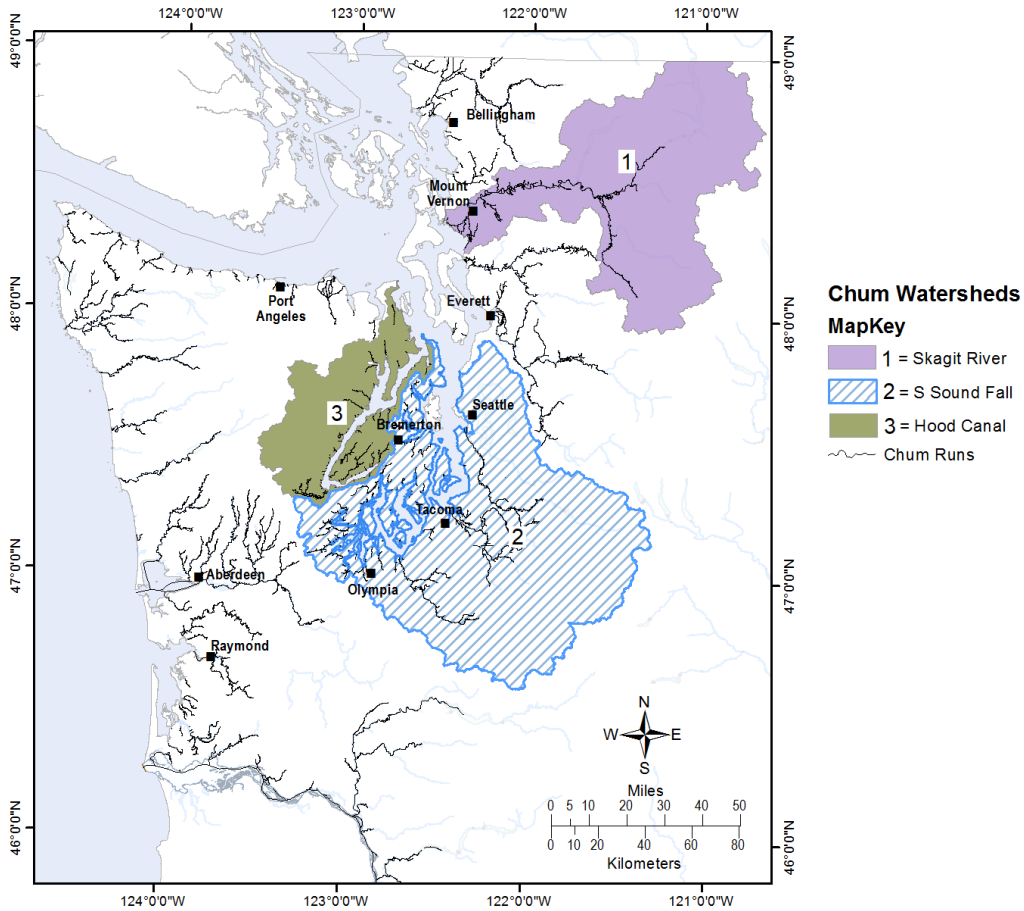


Figure 2. Scale image from an age 4, Puget Sound fall run chum salmon used in this study. We measured distance between the scale focus and the first ocean annulus, between any subsequent annuli, and from the last annulus to the scale edge along the longest axis.

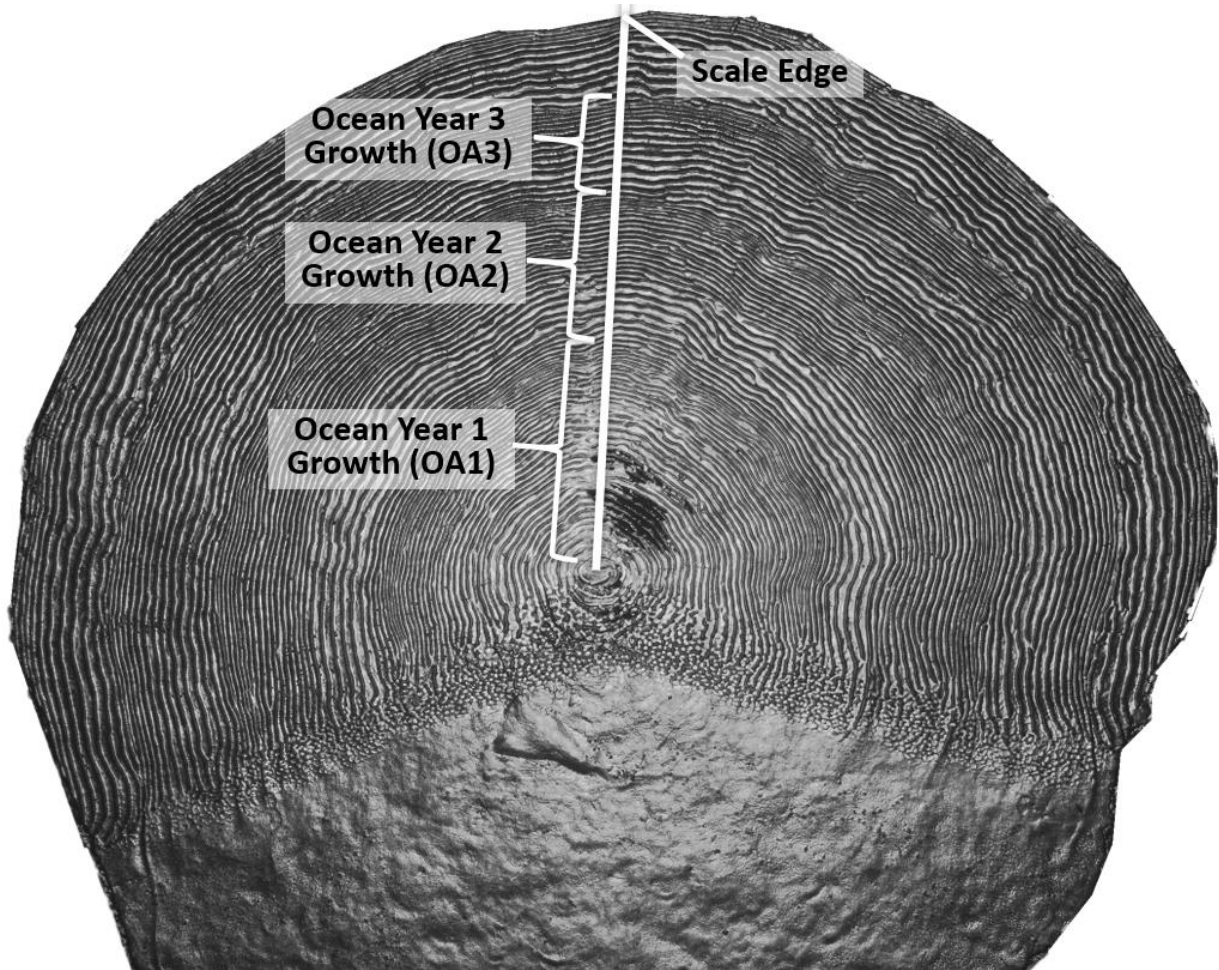


Figure 3. Scale growth increments by ocean growth year and a) population and b) return age.

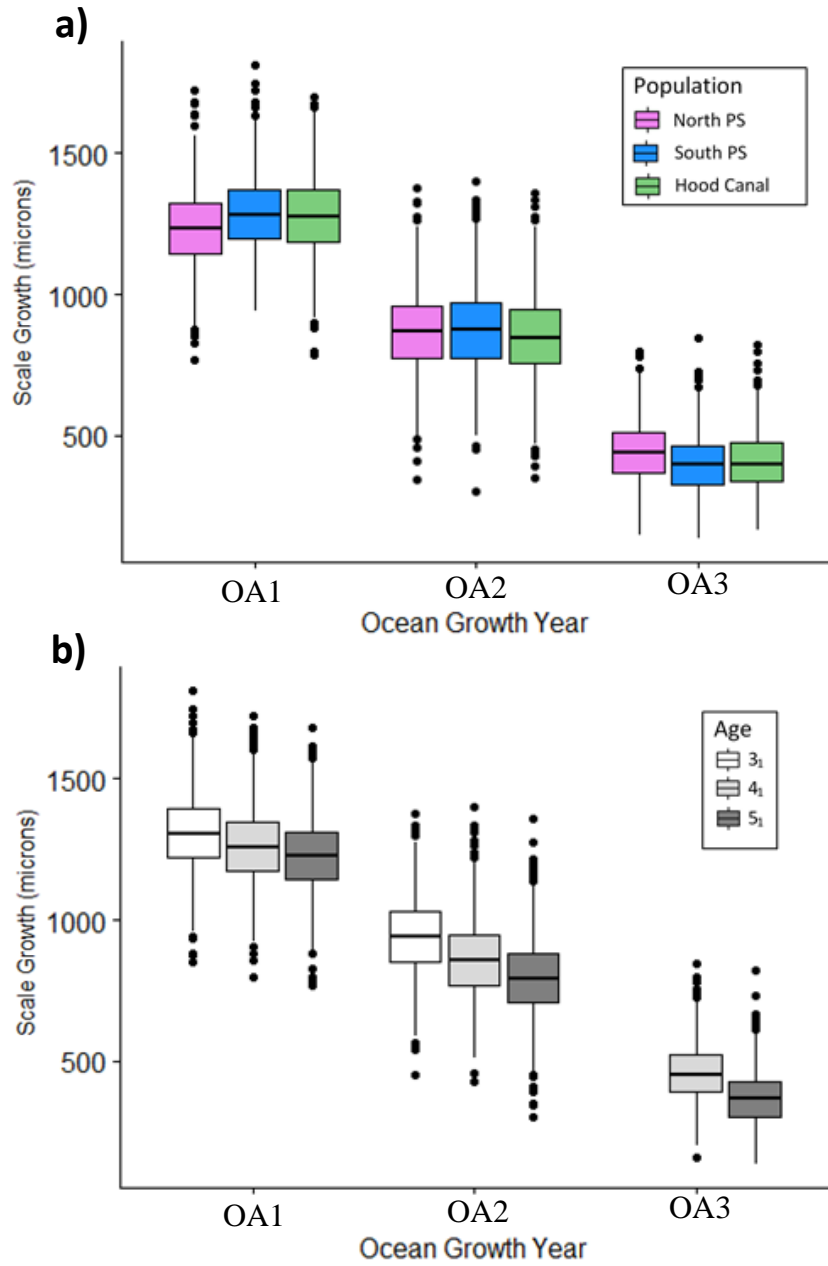


Figure 4. Calendar year versus Chum salmon standardized scale growth of a) ocean growth year 1 (OA1),  
 b) ocean growth year 2 (OA2), and 3) ocean growth year 3 (OA3) + trendlines.

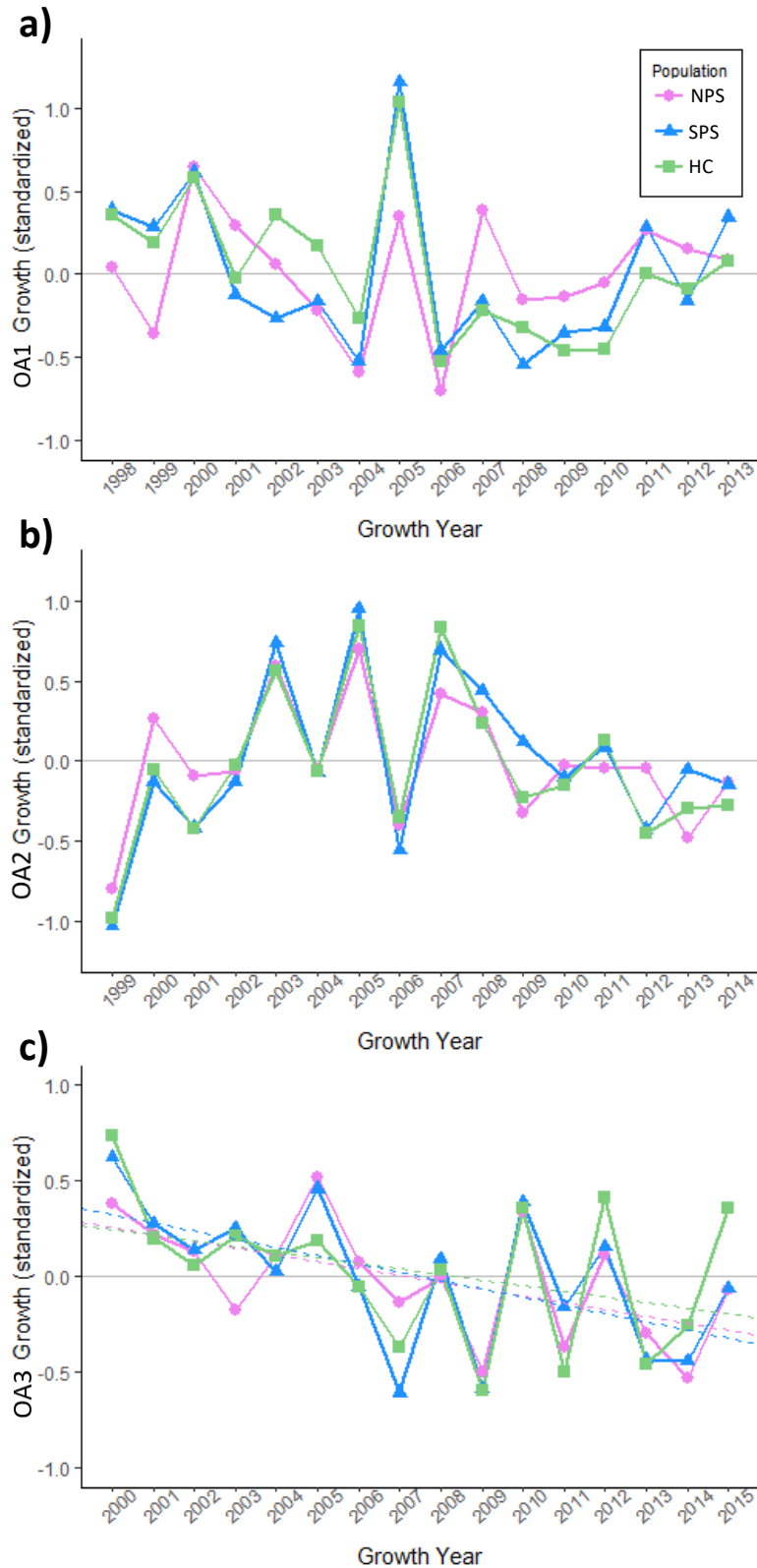


Figure 5. Top fitted GAMMs predicting growth by ocean age year for chum salmon across three different populations: Hood Canal (HC), North Puget Sound (NPS), and South Puget Sound (SPS). (BY = brood year, ALBSA = *Aleutian Low – Beaufort Sea Anticyclone*, NPGO = *North Pacific Gyre Oscillation*).

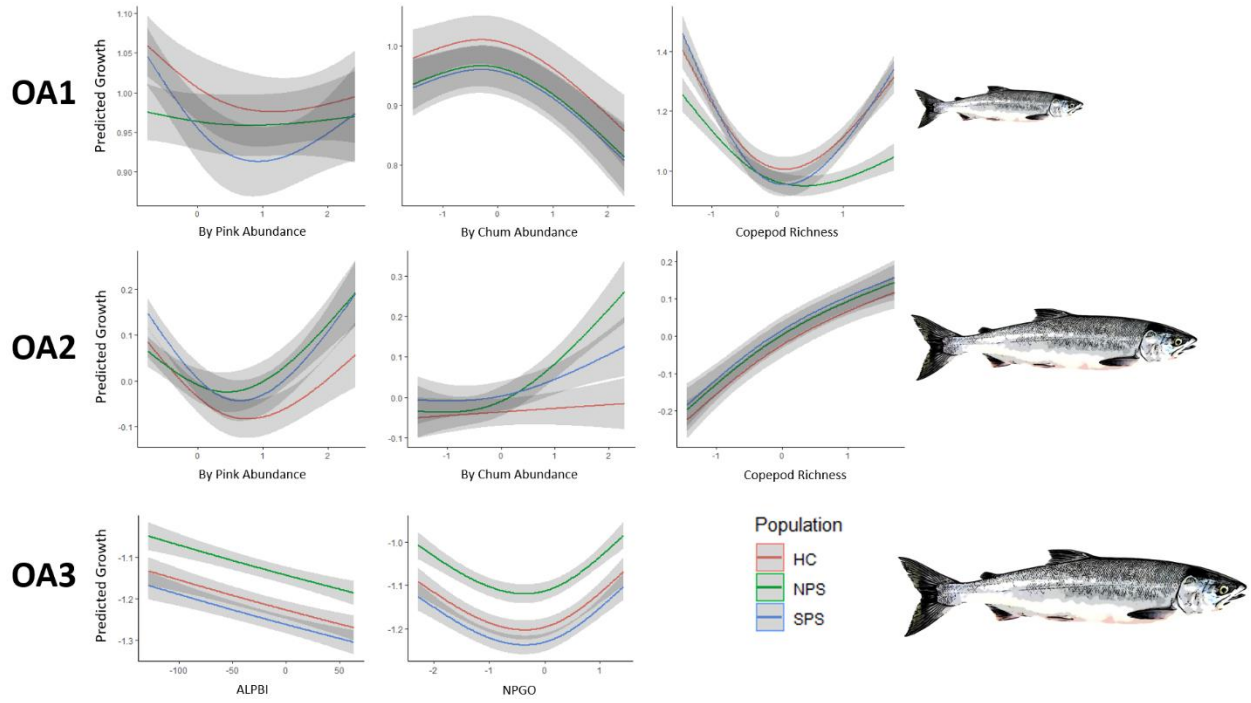


Figure 6. Mean predicted recruits-per-spawner (R/S, standardized) vs. ocean age 2 growth (standardized) for chum salmon across three different populations in Washington State

