"Slim pickings?": Extreme large recruitment events may induce density-dependent reductions in growth for Alaska sablefish (*Anoplopoma fimbria*) with implications for stock assessment

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Abstract

Growth processes mediate survival and fecundity within fish populations, which are fundamental in regulating population dynamics. Therefore, accurate estimates of population scale and sustainable exploitation levels in contemporary fishery stock assessment models rely heavily on understanding and accurately characterizing growth processes. However, empirical studies that relate population-level changes in growth patterns to observable ecosystem and population conditions remain scarce. In particular, few studies directly consider the influence of intra-specific competition (i.e., cohort effects) on growth variability, and its associated implications for stock assessment estimates. Focusing on Alaska sablefish as a case study, we illustrate how multiple unprecedented large recruitment events since 2014 resulted in density-dependent declines in growth on the population-level scale, using a state–space growth model. Furthermore, we demonstrate how incorporating cohort-specific growth variability within the Alaska sablefish stock assessment model resulted in substantial differences in estimates of spawning biomass and recommended harvest levels. Overall, findings from this study underscore the significance of cohort effects on growth processes and their implications for stock assessment models and associated harvest recommendations.

Key words: density-dependence, time-varying growth, weight-at-age, length-at-age, stock assessment

1. Introduction

Growth of an individual is the result of both catabolic and anabolic processes, where catabolic processes pertain to basal maintenance, while anabolic processes promote increases in weight and size. Due to differences in vital rates, environmental conditions, and population dynamics, growth inherently varies among individuals within fish populations. These individual growth responses to localized conditions can therefore collectively result in variations in regional- and population-scale growth patterns. For instance, oceanographic features can impact system productivity and influence individual growth rates through spatial differences in prey composition and abundance, which can collectively manifest as regional differences in growth patterns (Kapur et al. 2020). Additionally, following the temperature-size rule, individuals residing in warmer aquatic environments are expected to exhibit accelerated growth rates as juveniles but reach smaller asymptotic sizes as adults (Atkinson 1994; Lindmark et al. 2022), which can similarly contribute to differences in regional- or population-level growth patterns. In addition to environmental factors, some studies have also shown that

both inter- and intra-specific competition can influence fish growth among individuals. These competitive interactions have the potential to result in annual growth variability on the population level (Lorenzen and Enberg 2002; Thorson and Minte-Vera 2016). Specifically, Lin and Ito (2024) demonstrated that increases in Japanese sardine (*Sardinops melanostictus*) biomass coincided with decreases in average weight across six species in the western North Pacific. Similarly, Denechaud et al. (2020) found that growth in Northeast Arctic cod (*Gadus morhua*) was negatively related to cod population size, which was attributed to increased competition for prey resources and cannibalism. Increased competition likely limits per capita food availability, leading to population-wide density-dependent declines in growth, often referred to as "cohort effects". Consequently, understanding the mechanistic drivers behind individual growth responses are crucial for generalizing patterns of growth variability to the population level and ascertaining realized population-level impacts.

Growth plays a critical role in regulating fish population dynamics, influencing survival (Lorenzen 2022; Lorenzen et al. 2022), reproductive dynamics (e.g., fecundity and skipped

spawning; Roff 1983; Rideout and Tomkiewicz 2011), and fishing mortality (e.g., size-based selection; Francis 2016). In fishery stock assessment models, which form the basis for scientifically informed fisheries management for harvested fish populations (Maunder and Piner 2015), population-level growth estimates are influential in determining removal estimates, population scale and status, and subsequent harvest recommendations. Typically, growth estimates are derived by fitting statistical models to age, length, and weight data to determine the average weight-at-age (WAA) and length-at-age (LAA) within the population. Estimates of WAA are then utilized to convert numbers-at-age into units of biomass, while LAA estimates facilitate the use of size-composition data via an age–length conversion matrix within stock assessment models. The use of size-composition data is critical for estimating recruitment into the population, particularly when direct aging data are sparse, which is common for many widely distributed large pelagic species (Francis 2016; Kolody et al. 2016; Lee et al. 2024).

Considering the importance of growth estimates in stock assessment models, an accurate characterization of population-level growth variability is necessary to provide robust estimates of key management quantities. Simulation studies consistently show that assuming constant growth in the presence of growth variability over time or among cohorts can introduce significant biases in estimates of spawning biomass, stock status, and biological reference points (Kuriyama et al. 2016; Stawitz et al. 2019; Correa et al. 2021). While empirical studies incorporating growth variability in stock assessment models are less common, Whitten et al. (2013) provided a notable example, illustrating that accounting for cohort-specific growth variability resulted in markedly different estimates of spawning biomass and recruitment for blue grenadier (*Macruronus novaezelandiae*) compared to a model assuming constant growth. However, assuming constant growth remains a common paradigm within contemporary fishery stock assessment models (Lorenzen 2016). Often, these simplified assumptions for estimating population-level growth stem from limited samples (e.g., of age, length, and (or) weight), a short time series, or unreliable aging methods (Kolody et al. 2016; Lorenzen 2016).

With an increased availability of age, length, and weight samples in recent decades, there has been a transition towards adopting more advanced approaches to characterizing population-level growth variability in stock assessments, facilitating a departure from the constant growth paradigm. Several approaches have been developed to incorporate growth variability within stock assessment models. For instance, conditional age-at-length approaches, which fit age–length data directly within the assessment, have been increasingly implemented to internally estimate time-varying growth processes (Whitten et al. 2013; He et al. 2016; Lee et al. 2019; Barbeaux et al. 2023). Additionally, empirical WAA approaches, which calculate the mean WAA from paired age and weight samples for each year external to a stock assessment model, have also been utilized (Kuriyama et al. 2016). Similarly, model-based methods that smooth across measurement errors from mean WAA values, while simultaneously accounting for age, year, and cohort effects, have gained increased attention in recent years to more adequately account for variation due to environmental and density-dependent growth responses (Ianelli et al. 2016; Cheng et al. 2023).

Despite the development of numerous methods for estimating growth variability, these approaches often do not provide a comprehensive mechanistic understanding of the factors influencing growth processes. Moreover, identifying environmental and population conditions that affect variability in population-level growth remains elusive for many marine fish species. In particular, while the mechanisms of cohort effects on growth are generally well established (Rose et al. 2001), there remain few examples illustrating the potential for successive large recruitment events to induce density-dependent growth responses among marine species at the population level. Moreover, as discussed by Lee et al. (2024), relatively few studies have investigated the impacts of variation in time- and cohort-specific growth processes within the context of fishery stock assessment models. Therefore, additional empirical studies that relate changes in growth patterns to observable ecosystem and population conditions are imperative to advancing our understanding of the numerous factors that contribute to growth variability and resultant population productivity. Ultimately, integrating empirical growth studies aimed at developing a more mechanistic understanding of growth variability with population models (e.g., stock assessment models) will help discern the impacts of growth variability on fisheries management advice and identify when it is necessary to incorporate time- or cohort-varying growth within stock assessment models.

Alaska sablefish (*Anoplopoma fimbria*), which are a long-lived and deep-dwelling species, represents a fitting case study to illustrate the potential for time- and cohort-specific growth variation, partly due to their highly spasmodic recruitment dynamics. Juvenile sablefish typically occupy nearshore regions before transitioning towards deeper waters of the continental shelf and slope (>300 m) as adults. Exceptionally large recruitment events in 2014, 2016, 2017, and 2019 resulted in an increased presence of young individuals in habitats typically favored by adults (i.e., deeper waters), as observed during annual fishery-independent surveys (Goethel et al. 2021, 2023). The influx of new recruits and shifts in habitat utilization have the potential to induce cohort effects in growth (i.e., density-dependent growth responses), through increased intra-specific competition both within and across a range of life-stages. Previous research has provided some evidence for the potential of time and cohort variation in growth for Alaska sablefish, but these investigations were limited to an interdecadal scale, pre-dating the high recruitment events observed in recent periods (Echave et al. 2012). Additionally, both laboratory and multiyear otolith increment studies have indicated that growth rates of juvenile sablefish generally increase with warmer temperatures, provided there is sufficient prey available (Sogard and Olla 2001). Furthermore, Sogard and Olla (1998) also demonstrated that juvenile sablefish exhibit sensitivity to cold temperatures. Despite these findings, how these effects impact population-level growth and the extent of annual and cohort growth variation in Alaska sablefish has yet to be fully characterized.

In this study, we first employ a state–space growth model that simultaneously accounts for age, year, and cohort effects (Cheng et al. 2023) to examine the presence of time- and cohort-specific variation in growth. Estimates of growth derived from these models are then utilized within a stock assessment framework to demonstrate the implications of alternative growth assumptions on key management quantities. We hypothesize that recent high recruitment events likely induced cohort effects on growth processes, impacting estimates of biomass and harvest recommendations derived from stock assessment models. The results of this study provide a basis for understanding the implications of time and cohort effects on growth for stock assessment models, and the potential need to consider annual growth variation in future assessments and management strategies for Alaska sablefish and for similar species that demonstrate spasmodic recruitment dynamics.

2. Methods

To investigate temporal and cohort-specific variations in weight and length for Alaska sablefish, we compared growth estimates (WAA and LAA) from a state–space growth model that incorporated age, year, and cohort effects (*Grwth_Vary*; Cheng et al. 2023) with estimates derived from a model assuming constant growth (*Grwth_Constant*). These growth models were fit to biological information collected by the Alaska Fisheries Science Center (AFSC) longline survey (Siwicke and Malecha 2024). We then evaluated the potential impacts of the two different growth variation assumptions on stock assessment outcomes by comparing two stock assessment model alternatives: one integrating growth estimates from the state–space growth model (*Assesmt_Vary*) and another maintaining the same growth assumptions as the 2023 status-quo stock assessment model (*Assesmt_SQ*; Goethel et al. 2023). Code associated with this study can be found at https://github .com/chengmatt/Sable_Growth (doi: 10.5281/zenodo.1390320 1).

2.1. Alaska sablefish biology and management

Alaska sablefish exhibit panmictic stock structure (Jasonowicz et al. 2017; Timm et al. 2024) and sexually dimorphic growth, with female asymptotic size ~15% larger than males (Echave et al. 2012). Recruitment dynamics for Alaska sablefish are spasmodic, with large recruitment events hypothesized to be attributed to prevailing environmental conditions that dictate the survival of juvenile sablefish (Shotwell et al. 2014; Gibson et al. 2019, 2023). In particular, historical large recruitment events have been associated with an intense Aleutian Low and a positive sign in the Pacific Decadal Oscillation (PDO), which promote positive sea-surface temperature anomalies (i.e., above average sea-surface temperatures) in the Northeast Pacific and are hypothesized to improve feeding conditions for Alaska sablefish through increases in prey (zooplankton) biomass (King et al. 2000, 2001; Shotwell et al. 2014). Likewise, recent large recruitment events in 2014, 2016, 2017, and 2019 coincided with and followed positive phases in the PDO and marine heatwaves (Di Lorenzo and Mantua 2016), which

were also suggested to improve feeding conditions due to reduced competition for prey (Goethel et al. 2020, 2023). Currently, sablefish in Alaskan federal waters are managed as a single unit-stock and fisheries management relies on an annual stock assessment. The stock assessment is primarily informed by data collected from the AFSC longline survey, and estimates biomass, stock status, and spawning potential ratio reference points (Clark 1991, 2002), along with associated projections of acceptable biological catch (ABC). Catch quotas are apportioned among five fishery management regions (Bering Sea, Aleutian Islands, Western Gulf of Alaska, Central Gulf of Alaska, and Eastern Gulf of Alaska) and two fishery fleets (fixed gear and trawl gear).

2.2. Development and evaluation of growth curves

Growth curves in this study were developed for each sex and growth process (WAA and LAA), utilizing biological data collected from the AFSC longline survey. The AFSC longline survey adheres to a systematic sampling design and is considered to be representative of population trends for Alaska sablefish (Sigler 2000). The survey is conducted annually across the Gulf of Alaska, with biennial sampling alternating between the eastern Bering Sea and Aleutian Islands (for further details, see Rutecki et al. 2016). Biological data utilized in this study span from 1996 to 2022, representing a period with sufficient data suitable for modeling (>1000 individuals aged annually). Although biological data prior to 1996 are available, they were excluded here given low sample sizes and differences in sampling protocols (Echave et al. 2012).

2.2.1. Weight-at-age

Time and cohort variation in WAA was estimated using a state–space growth model developed in Template Model Builder (TMB; Kristensen et al. 2016) that accounted for partial correlations within ages, years, and cohorts (Cheng et al. 2023). To ensure that estimates of WAA were representative of population densities and accounted for sampling variability between and within survey stations, as well as being adequately characterized during the ageing process, a bootstrap resampling process was undertaken, following the methods of Stewart and Hamel (2014) and Hulson and Williams (2024). Here, WAA samples from a given survey station were first weighted by the catch observed at that station. The bootstrap approach then resampled stations within a given year. Individuals were then resampled (i.e., ages, lengths, weights, and sexes) within a given station and ageing error was incorporated by resampling "tester" ages for a given "reader" age from an ageing-error matrix (Fig. S1). This bootstrap resampling process was repeated 2000 times.

Predicted values of WAA ($\widehat{W}_{a,t}$) were constrained to arise from a parametric von Bertalanffy LAA function:

$$(1) \quad \widehat{L}_a = \left[L_\infty - (L_\infty - L_0) e^{-ka} \right]$$

where $\widehat{L}_{a,t}$ represents the predicted LAA, L_∞ describes the asymptotic length, L_0 is the theoretical mean length at birth,

and k represents the Brody growth rate coefficient. Predicted values of LAA were then converted to WAA and were assumed to be lognormally distributed:

$$(2) \qquad \widehat{W}_{a,t} = \alpha \widehat{L}_a^{\beta} e^{\epsilon_{a,t}}$$
$$\log(W_{a,t}) \sim Normal\left(\log\left(\widehat{W}_{a,t}\right), \tau_{a,t}\right)$$

where α represents the average tissue density (weight per volume), β is an allometric scaling parameter, and $\epsilon_{a,t}$ denotes the latent random variables for ages, years, and cohorts (i.e., process error deviations; see eqs. 5 and 6 below). $W_{a,t}$ and $\tau_{a,t}$ represent the observed mean WAA and associated standard errors obtained from the bootstrap procedure, respectively. Note that in all WAA analyses, L_{∞} was fixed at 75 cm for females and 65 cm for males, given confounding with k and the exclusive use of weight data. β was fixed at 3.02 following a similar rationale (Quinn and Deriso 1999). Fixed values were obtained from Goethel et al. (2021) and estimates of WAA were generally insensitive to different prespecified values, which was also explored in Cheng et al. (2023).

2.2.2. Length-at-age

Annual variation in LAA was estimated using a similar model structure as described above, but with some differences. Specifically, the bootstrap resampling process was not utilized, and individual observations were fitted instead. Although fitting individual observations for LAA, rather than bootstrapping, does not account for the sampling design of the survey- or station-specific differences, this approach was taken to better characterize individual variability in lengths at a given age to reflect biological processes rather than a sampling processes due to the survey design. This was done to enable the derivation of a biologically meaningful (i.e., the survey design should not impact the probability of lengths being assigned to a given age) age–length conversion matrix for subsequent analyses (i.e., utilized as a stock assessment input).

Here, estimates of LAA followed eq. 1 and was allowed to vary across ages, time, and cohorts via the incorporation of a process error term, and assumed normally distributed observation error:

$$(3) \qquad \widehat{L}_{a,t} = \widehat{L}_a e^{\epsilon_{a,t}}$$
$$L_{a,t} \sim Normal\left(\widehat{L}_{a,t}, \xi_{a,t}\right)$$
$$\xi_{a,t} = CV * \widehat{L}_{a,t}$$

where $L_{a,t}$ and $\widehat{L}_{a,t}$ are observed and predicted LAA values, and CV is the estimated coefficient of variation. The annual variability in lengths for a given age ($\xi_{a,t}$) was a derived variable, governed by the estimated CV. To develop an annual age–length conversion matrix for subsequent analyses, a standard normal cumulative density function (Φ) was utilized:

$$(4) \qquad \eta_{l,a,t} = \begin{cases} \Phi\left(\dfrac{L'_{min} - \widehat{L}_{a,t}}{\xi_{a,t}}\right) & for\ l = 1 \\[2ex] \Phi\left(\dfrac{L'_{l+1} - \widehat{L}_{a,t}}{\xi_{a,t}}\right) - \Phi\left(\dfrac{L'_l - \widehat{L}_{a,t}}{\xi_{a,t}}\right) & for\ 1 < l < n_L \\[2ex] 1 - \Phi\left(\dfrac{L'_{max} - \widehat{L}_{a,t}}{\xi_{a,t}}\right) & for\ l = n_L \end{cases}$$

where l is a given length bin, L'_{min} is the upper limit of the smallest length bin, and L'_{max} is the lower limit of the largest length bin. L'_l represents the lower limit of length bin l and n_L denotes the total number of length bins utilized. The length bins utilized for this process were consistent with the 2023 status-quo sablefish assessment model, which ranged from 41 to 99 cm with a bin width of 2 cm (Goethel et al. 2023).

Following the methods of Cheng et al. (2023), nonparametric residuals deviating from an assumed parametric function were treated as latent random variables arising from a Gaussian Markov Random Field (GMRF) process:

$$(5) \qquad \epsilon \sim \mathbf{MVN}\left(\mathbf{0}, \mathbf{Q}^{-1}\right)$$

where ε is indexed by age α and year t and is a column vector that follows a multivariate normal distribution. The multivariate normal distribution arises from a mean vector of 0 s and the inverse of the precision matrix (i.e., the covariance matrix; $\mathbf{Q}^{-1}$), which was constructed as

$$(6) \qquad \mathbf{Q} = \left(\mathbf{I} - \mathbf{B^T}\right)\mathbf{\Omega}\left(\mathbf{I} - \mathbf{B}\right)$$

where $\mathbf{I}$ is an identity matrix and $\mathbf{\Omega}$ is a positive diagonal matrix that determines the variance of the GMRF process (i.e., $\mathrm{diag}(\mathbf{\Omega}) = \sigma^{-2}$). $\mathbf{B}$ is a square matrix representing the partial effect of ϵ on preceding ages and (or) years, governed by partial autocorrelation coefficients for ages, years, and cohorts. To demonstrate the formulation of $\mathbf{B}$, we provide a simplified example below with just 2 ages and 2 years. In this example, $\mathbf{B}$ is a 4 x 4 matrix, where both the rows and columns represent combinations of age and year. For instance, $B_{2,1}$ captures the correlation within the same year between age 1 in year 1, and age 2 in year 1, whereas $B_{4,1}$ constructs the correlation within the same cohort between age 1 in year 1, and age 2 in year 2:

$$(7) \qquad \mathbf{B} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ \rho_t & 0 & 0 & 0 \\ \rho_a & 0 & 0 & 0 \\ \rho_c & \rho_a & \rho_t & 0 \end{bmatrix}$$

Here, ρ_t, ρ_a, and ρ_c are parameters describing the partial autocorrelation among years within a given age, among ages within a given year, and years within a cohort, respectively.

2.2.3. Comparison of growth curves

Potential evidence of variation in growth was evaluated by comparing estimated values from models accommodating growth variation (i.e., *Grwth_Vary*; eqs. 1–3, and 5 and 6) with those assuming constant growth (*Grwth_Constant*). The latter models mirrored processes described in eqs. 1–3, and 5 and

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Can. J. Fish. Aquat. Sci. **82**: 1–13 (2025) | dx.doi.org/10.1139/cjfas-2024-0228

6 but excluded the estimation of $\epsilon_{a,t}$ and correlation coefficients. Support for modeling growth variation was identified by comparing standardized residual patterns, Akaike information criterion (AIC) values, and statistical significance between models with growth variation and those that assumed constant growth. Statistical significance at the $\alpha = 0.05$ level was inferred when 95% confidence intervals from models assuming growth variation did not overlap with those assuming constant growth, recognizing that this approach is approximate and generally leads to increased false negatives (Austin and Hux 2002).

To understand the potential impact of the unprecedented large recruitment events since 2014 on density-dependent growth responses, we compared estimated growth trajectories for the 2010–2016 cohorts among growth models, using the statistical significance criteria described above. Cohorts prior to 2010 were not evaluated because recruitment was comparatively low during these periods (Goethel et al. 2023). Additionally, we chose to only focus on the 2010–2016 cohorts as they were likely most susceptible to aforementioned recruitment events and due to considerations of time series length necessary to inform cohort-specific growth. Lastly, to further comprehend how growth responses were impacted by changes in population abundance, we conducted third-order polynomial regressions between weight and length estimates from model *Grwth_Vary* for each age and the AFSC longline survey relative population numbers (RPNs; Alaska-wide), which serves as a proxy for population abundance. These regressions assumed that that the predictor variable (RPNs) was known without error and that residual variances were homoscedastic, which we visually inspected. Although RPNs are observed with error, these regressions were primarily employed to understand and visualize the potential relationship of growth and population abundance, rather than for prediction purposes. Nonetheless, we expected to observe a descending relationship due to density-dependent growth responses at high population abundances.

2.3. Stock assessment application

Management implications of potential time and cohort variation in growth were assessed by incorporating estimates derived from growth models developed above into a modified version of the 2023 status-quo stock assessment model (Goethel et al. 2023). The assessment model is an integrated age- and sex-structured model, developed in AD Model Builder (ADMB; Fournier et al. 2012), and fits to catch data, abundance indices, and age- and length-composition data (Goethel et al. 2023). The minor modifications that were made to the 2023 status-quo stock assessment model included: (1) the incorporation sex-specific age-composition data, which improved estimation stability of sex-specific selectivity parameters, and (2) only utilizing length-composition data when age-composition data were absent for a given data source. Overall, discrepancies in key model outputs (terminal spawning biomass and recruitment) between the modified and status-quo assessments were minimal (~5%).

Two assessment model parameterizations were explored in this study, each with differing assumptions regarding time variation in WAA and LAA. In the first parameterization (*Assesmt_Vary*), growth variation in both WAA and LAA was incorporated by treating estimates from previously developed growth models as fixed inputs. Here, growth estimates were held constant prior to 1996, with annual updates for WAA and age–length transition matrices implemented thereafter. The second parameterization (*Assesmt_SQ*) maintained the same growth assumptions as the 2023 status-quo stock assessment model, which assumed constant WAA over time but estimated LAA (hence age–length transition matrices) in two periods: 1960–1995 and 1996–2023. The assumption of constant growth prior to 1996 for both assessment model parameterizations stemmed from limited biological sampling and variations in sampling protocols during those periods (Echave et al. 2012), as discussed earlier.

To ensure that the assessment models achieved a stable solution and adequately described the data, we verified that the Hessian matrix was positive definite, the maximum absolute gradient was less than 1.00E-04 (Carvalho et al. 2021), and inspected one-step ahead residuals (Trijoulet et al. 2023) for composition data and model fits to indices. We then evaluated the management implications of integrating potential variation in growth processes by comparing model estimates across key metrics commonly used for the basis of fisheries management. Specifically, we compared estimates of recommended harvest levels (ABCs), the estimated recruitment time series, and spawning biomass trajectories and projections. During these comparisons, emphasis was given to estimates from recent periods (e.g., 2014–terminal year). Recommended harvest levels were based on fishing at $_{40\%}$, which represents the fishing mortality rate that would result in 40% of unfished spawning biomass-per-recruit (Clark 1991) and a sloping harvest control rule (HCR). The sloping HCR adjusts harvest levels determined by $_{40\%}$ proportionally to population size (Deroba and Bence 2008; Goethel et al. 2023). Calculations for $_{40\%}$ assumed a 5-year average of the most recent WAA values. Projections of recommended harvest levels and spawning biomass assumed mean recruitment for future years, a fishing mortality rate of $_{40\%}$ adjusted by the sloping HCR, and similarly assumed a 5-year average of the most recent WAA values.

3. Results

Across the growth models evaluated (weight and length models for each sex), those that allowed for growth variation (*Grwth_Vary*) exhibited improved model fits when compared to constant growth models (*Grwth_Constant*). In particular, *Grwth_Vary* models were characterized by a lack of residual patterns (Fig. 1). By contrast, *Grwth_Constant* models exhibited notable residual patterns across years and within cohorts and were generally unable to adequately fit to the observed data. In addition to improved residual patterns, *Grwth_Vary* models were strongly favored by AIC, with differences in AIC values consistently exceeding 1000 units (Table 1).

Trends in WAA across the modeled time series generally exhibited two distinct periods of decline, with a general decreasing trend observed for some age groups (ages 9–13)

Fig. 1. Standardized residuals (black points) of weight-at-age (WAA; panels A and C) and length-at-age (LAA; panels B and D) across years (top row) and cohorts (bottom row). Column panels denote sexes and row panels represent the two growth model assumptions explored in this study. Central trends (colored lines) for these relationships are visualized using a loess smoother with a span of 0.75. Colored shading represents 95% confidence intervals.
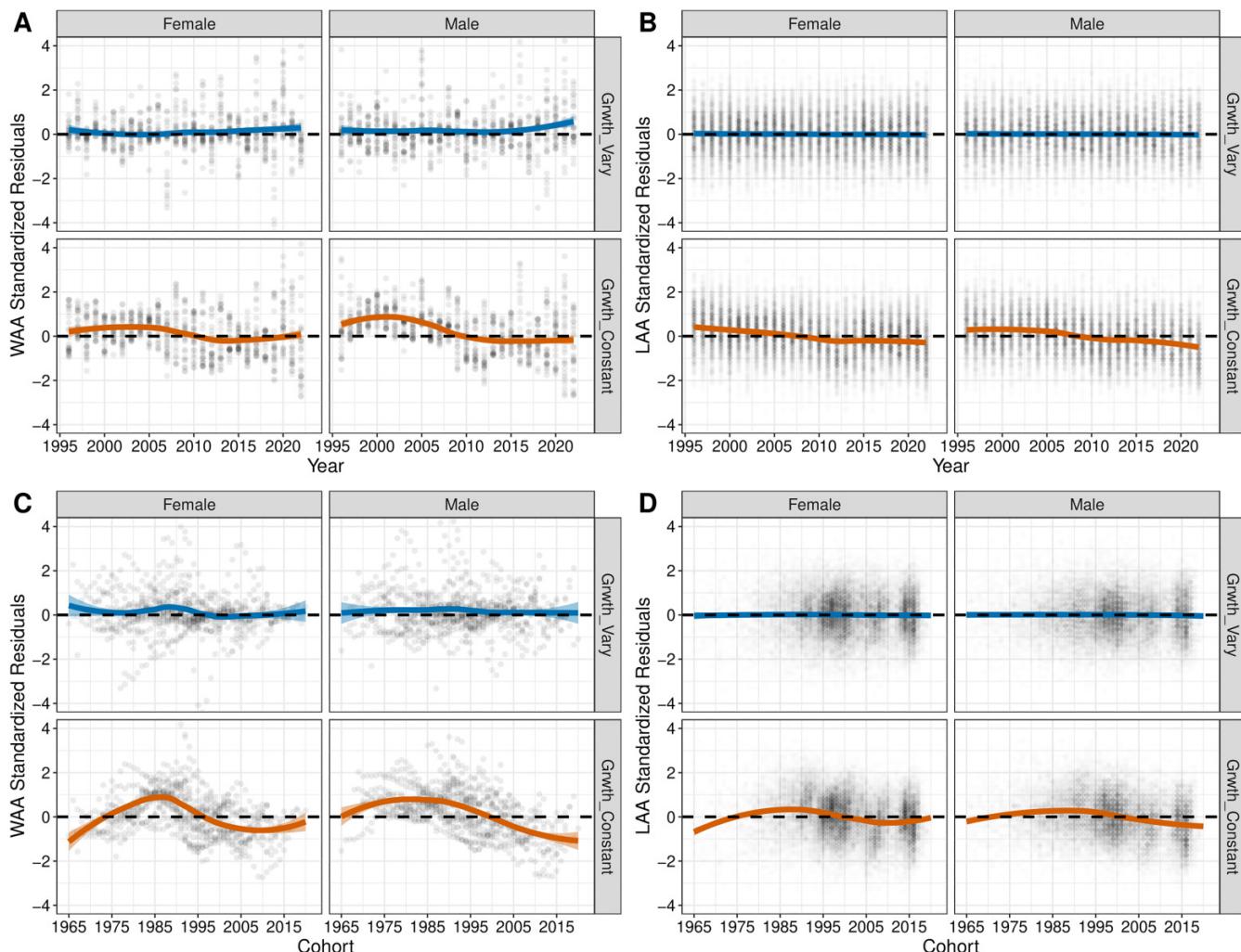

Table 1. Akaike information criterion (AIC) values for the two different growth model variants, applied individually to each sex and growth process (weight and length).
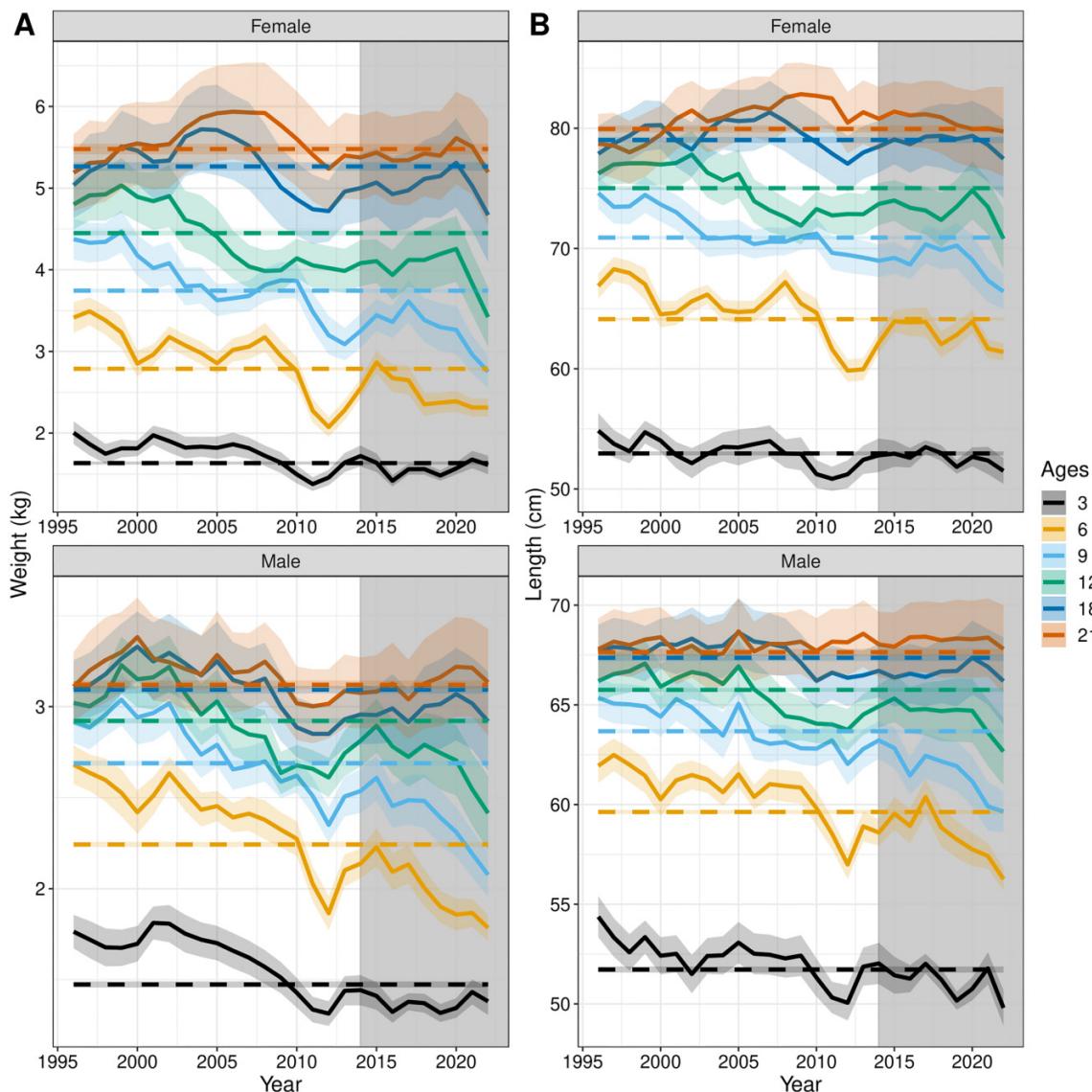
Model	Females (weight)	Males (weight)	Females (length)	Males (length)
Grwth_Vary	−1549.77	−2040.71	107 530.35	86 086.40
Grwth_SQ	408.09	−31.05	109 274.45	87 781.56

(Figs. 2A and S2). Nonetheless, significant declines in WAA were detected for young to intermediate-aged individuals (ages 2–19) from 2006 to 2011 and from 2015 to 2022. The former period generally coincides with a negative PDO sign (negative sea-surface temperature anomalies in the Northeast Pacific), while the latter period coincides with a positive PDO sign (positive sea-surface temperature anomalies in the Northeast Pacific) and the onset of multiple large sablefish recruitment events in Alaska. Conversely, older-aged individuals (ages 20–31) demonstrated less pronounced changes in WAA and exhibited higher uncertainty, likely due to relatively lower sample sizes. These trends remained

fairly consistent across sexes. Interestingly, predicted WAA for *Grwth_Vary* models occasionally decreased below the constant growth model for several preceding ages. For instance, the predicted WAA values for females at age 12 in the *Grwth_Vary* models were smaller than that for females at age 9 in a *Grwth_Constant* models during high recruitment periods (Fig. 2A).

Comparisons of cohort-specific WAA trajectories between *Grwth_Vary* and *Grwth_Constant* models indicated similar declines across sexes, with the 2010–2016 cohorts displaying depressed growth rates during periods following high recruitment events (Fig. 3A). Furthermore, polynomial regression

Fig. 2. Time series of estimated weights (panel A) and lengths (panel B) for both sexes. Solid lines are mean estimates from *Grwth_Vary* models across ages (colors), and dashed lines are mean estimates from *Grwth_Constant* models. Colored shading associated with lines denote 95% confidence intervals. The grey shaded region represents the onset of large recruitment events (2014, 2016, 2017, and 2019). Only a subset of ages is shown for visualization purposes.
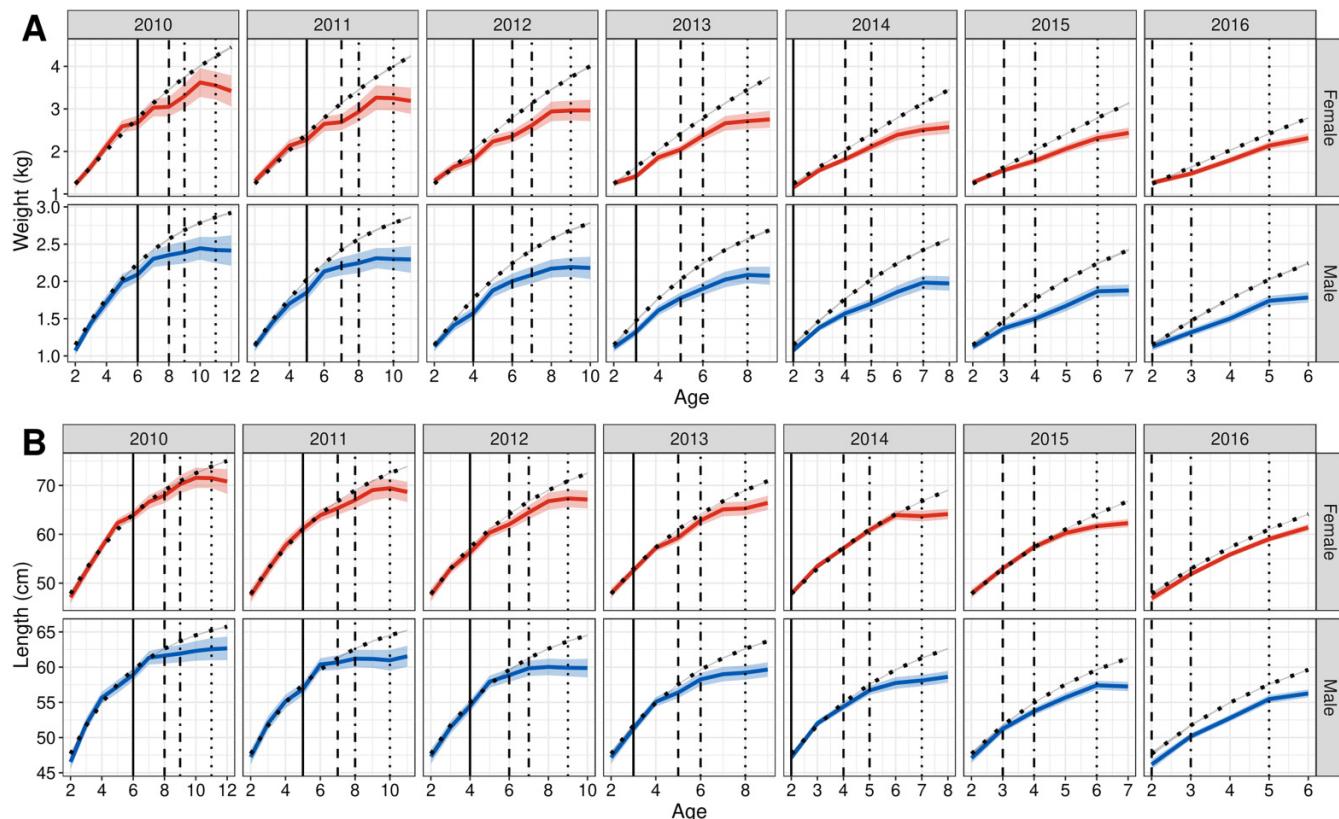

between survey RPNs (abundance proxy) and predicted WAA from *Grwth_Vary* revealed descending relationships. This relationship was evident for young to intermediate-aged individuals (ages 6–12) across sexes, with lower weights within a given age coinciding with higher survey RPNs (Fig. S4A). Although significant positive relationships were occasionally detected between weights for older individuals and survey RPNs, these relationships were more variable, likely attributed to the high uncertainty in estimated WAA for these individuals (Fig. S2), which were not accounted for in the polynomial regression.

In general, trends and patterns for LAA processes were comparable to those described for WAA. Similar declines in LAA were observed during the 2006–2011 and 2015–2022 periods (Figs. 2B and S3). Further, cohort-specific LAA trajectories for the 2010–2016 cohorts also displayed diminished

growth rates during periods following high recruitment events (Fig. 3B). Polynomial regressions similarly demonstrated descending relationships between LAA and survey RPNs for young to intermediate-aged individuals across sexes (Fig. S4B).

Integrating variation in growth processes into assessment model *Assesmt_Vary* resulted in consistent trends in spawning biomass with the *Assesmt_SQ* (Pearson's correlation coefficient = 0.99; Fig. 4A). However, differences in the scale of spawning biomass estimates were evident, with differences of up to 20% in the terminal year (2023; *Assesmt_Vary* spawning biomass: 118.17 kt, *Assesmt_SQ* spawning biomass: 148.03 kt; Fig. 4A). Additionally, large differences were also detected in spawning biomass projections. During the projection period (2024–2030), the average spawning biomass was 25% lower in *Assesmt_Vary* compared to *Assesmt_SQ* (Fig. 4A).

Fig. 3. Estimated weights (panel A) and lengths (panel B) for individual cohorts (2010–2016) across ages (column panels), for both sexes (row panels). Colored solid lines are mean estimates derived from *Grwth_Vary* models, while dotted lines are derived from *Grwth_Constant* models. Shading represents 95% confidence intervals. The solid, dashed, dot-dashed, and dotted vertical lines represent when a given cohort would have encountered the 2014, 2016, 2017, and 2019 high recruitment events, respectively.

Trends in the estimated recruitment time series were generally similar among assessment models (Pearson's correlation coefficient = 0.91), but large differences in annual recruitment were observed from 2016 to 2021 (Fig. 4B), which likely contributed to the differences observed in spawning biomass projections from 2024 to 2030. Despite these large differences, estimates of total recruitment during this period remained consistent among models. Specifically, a total of 300 million recruits and 308 million recruits were predicted for *Assesmt_Vary* and *Assesmt_SQ*, respectively. Lastly, estimates of ABC also demonstrated large differences, with assessment model *Assesmt_Vary* suggesting more conservative harvest levels in 2024 (31.24 t) relative to *Assesmt_SQ* (44.263 t) (Fig. 4C).
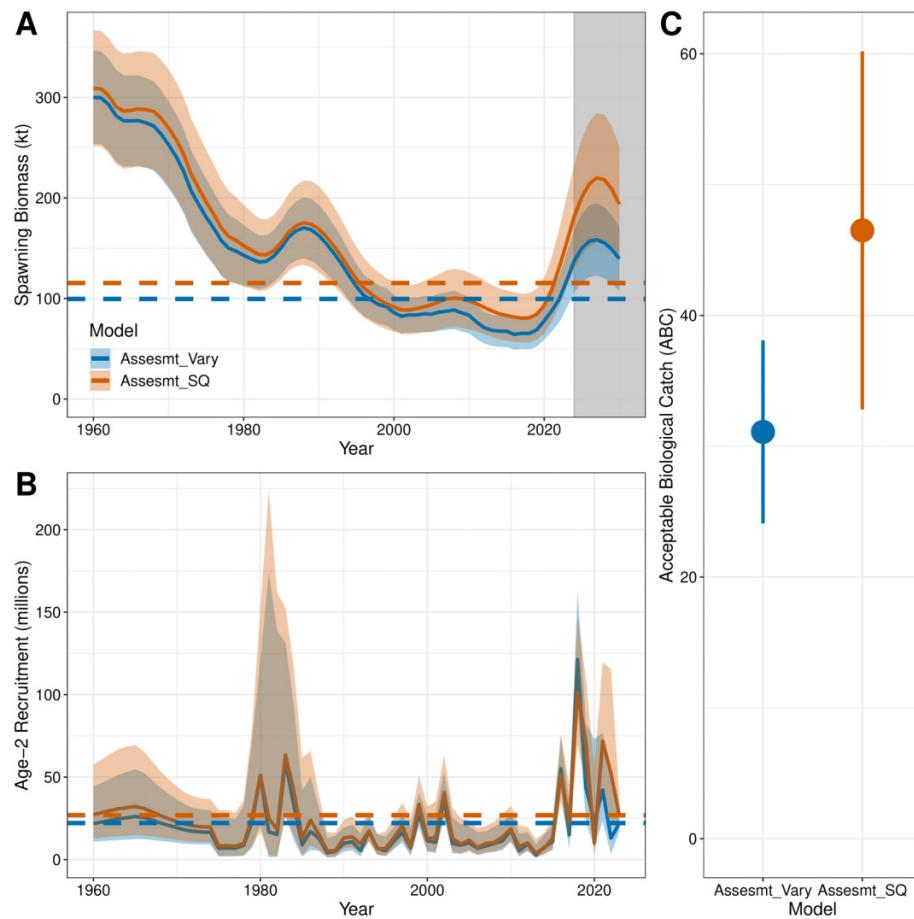
4. Discussion

The results of this study reveal variability in growth processes for Alaska sablefish, with recent successive large recruitment events likely contributing to density-dependent declines in growth. Pronounced reductions in growth rates were found to coincide with a large recruitment event in 2014, which was further compounded by subsequent recruitment events in 2016, 2017, and 2019, resulting in below average growth trajectories for recent cohorts. Potential evidence

of density-dependent declines in growth was suggested by descending relationships with surveyed population abundance for young to intermediate-aged individuals (up to age 12). However, these relationships were more variable for older individuals, likely attributed to sparse data available for informing their growth processes, minimal growth at old ages, and their long-lived life history. Consequently, we advise against overinterpreting growth trajectories for older-aged individuals.

In the case of Alaska sablefish, variability in growth processes likely represent complex interactions between ecosystem and population conditions. We speculate that declines in growth observed during 2006–2011, particularly for younger-aged individuals (~ages 1–4), were related to a negative PDO sign (negative sea-surface temperature anomalies), given their sensitivity to colder temperatures and reduced growth rates (Sogard and Olla 1998, 2001). Additionally, the reduced growth rates from 2006 to 2011 could have been compounded by increased interspecific interactions from several potential competitors that exhibited increasing population abundances during this time, including Pacific cod (*Gadus macrocephalus*), Pacific Ocean perch (*Sebastes alutus*), and arrowtooth flounder (*Atheresthes stomias*) (Hulson et al. 2017; Barbeaux et al. 2020; Shotwell et al. 2021; Goethel et al. 2023). However, additional analyses that are beyond the scope of

Fig. 4. Estimated spawning biomass trajectories (panel A), annual age-2 recruitment (panel B), and projected acceptable biological catch in 2024 (panel C) across stock assessment model alternatives (colors) explored. Grey shading in panel (A) represents spawning biomass projections (2024–2030) Dashed lines in panels (A) and (B) represent 40% of unfished spawning biomass and mean recruitment, respectively. Shading in panels (A) and (B) and point ranges in panel (C) represent 95% confidence intervals.

the current study are required to further support this claim. Nonetheless, considering the relatively low recruitment productivity of sablefish from 2006 to 2011 (Fig. 4), it is highly unlikely that these growth declines were the result of intra-specific competition inducing density-dependent declines in growth during this earlier period.

In contrast, we hypothesize that favorable ecosystem dynamics for sablefish through increased productivity and larval connectivity (Shotwell et al. 2014; Gibson et al. 2019) facilitated unprecedented large recruitment events in recent periods (2014–2022), likely intensifying intra-specific competition pressure, and inducing density-dependent declines in growth. While growth variation during 2014–2022 may partly be attributed to prevailing environmental conditions, we posit that density-dependent processes were also a contributing factor in regulating declines in growth for several reasons. Notably, periods of high recruitment events coincided with a positive PDO phase, warmer ocean conditions, and marine heatwaves (Di Lorenzo and Mantua 2016; Litzow et al. 2020), which are generally suggested to be beneficial for sablefish growth, provided sufficient prey availability (Sogard and Olla 2001). Furthermore, the temperature-size rule suggests that warmer conditions will typically accelerate growth

rates for younger individuals and reduce the asymptotic sizes of adults (Atkinson 1994; Lindmark et al. 2022). Therefore, the contrasting ecosystem and population conditions observed between the declines in 2006–2011 and those in 2014–2022 suggest the likely involvement of density-dependent factors in more recent periods.

Similar to previous studies, we found that accounting for variation in growth processes had large impacts on stock assessment estimates of population productivity (Whitten et al. 2013; Kuriyama et al. 2016). In particular, the inclusion of growth variation in age–length transition matrices altered the expected LAA distributions within the assessment model (Fig. S5) (as seen in Whitten et al. 2013), redistributing recruitment estimates across recent periods. However, levels of total recruitment remained fairly consistent among assessment models (Fig. 4). Additionally, reduced WAA in recent periods led to decreased levels of spawning biomass trajectories and projections, as well as recommended harvest levels. These decreases are likely multifaceted and are partly attributed to a redistribution of recruitment estimates and reduced WAA in recent periods. Moreover, the currently unbalanced age-structure, where the population consists of mostly young to intermediate-aged individuals resulting from periods of

high recruitment, likely compounded the effects on projected harvest levels. The impacts of growth variation on spawning biomass could potentially be less pronounced as recent cohorts begin to mature and reach asymptotic sizes. However, these generalizations are inhibited by complexities between reduced growth in recent periods, interactions with natural mortality rates (Lorenzen 2022; Lorenzen et al. 2022), and uncertainty regarding whether individuals will continue to experience reduced growth or exhibit smaller asymptotic sizes in the future.

Although the current study and assessment model assumes constant maturity due to macroscopic maturity observations being unreliable (Rodgveller 2018b), the impacts of reduced growth in recent periods may also have implications in regulating reproductive dynamics. In particular, studies have demonstrated that density-dependent processes have the potential to alter size-at-maturity, which may further impact estimates of spawning biomass (Cardinale and Modin 1999; Lorenzen 2008; Witthames and Marshall 2008; Rodgveller and Echave 2024). Moreover, the presence of skipped spawning, which appears to be a plastic trait that balances energy partitioned towards somatic growth and reproduction (Rideout and Tomkiewicz 2011), has previously been documented for sablefish (Rodgveller et al. 2016). Skipped spawning for Alaska sablefish is prevalent for individuals that are not fully mature (under 10 years old; Rodgveller 2018a), a group that is disproportionately represented in recent estimates of spawning biomass as discussed above. Considering the plasticity of skipped spawning, density-dependent processes stemming from large recruitment events could impede energy allocation towards reproductive processes and may lead to higher skipped spawning rates. The collective impact of reproductive dynamics and growth following such events may subsequently influence estimates of spawning biomass and resultant harvest recommendations. While previous studies that incorporated skipped spawning dynamics (based on limited histological maturity samples) in the Alaska sablefish stock assessment have demonstrated the potential for lower spawning biomass estimates (Rodgveller et al. 2016; Goethel et al. 2021), further research evaluating the cumulative effects of both growth and reproductive dynamics would be valuable. For species experiencing growth variation in response to large recruitment events, it may be of merit to explore alternative spawning output indicators (Minte-Vera et al. 2019) that reduce the reliance of recommended harvest levels on the dynamics of recent cohorts. For instance, computing spawning biomass by only considering fully mature individuals could alleviate the impacts of reduced WAA and the possibility of increased size-at-maturity and skipped spawning, which may facilitate more favorable management outcomes (e.g., increased catch stability). Currently, alternative spawning biomass metrics and associated HCRs are being explored via management strategy evaluation for Alaska sablefish, with the goal of developing strategies that consider the biological and socio-economic effects of spasmodic recruitment dynamics (https://ovec8hkin.github.io/SablefishMSE/).

Several aspects of this study were limited and could be elaborated upon in future work. Specifically, growth estimates for some cohorts were observed to decrease in subsequent years (i.e., fish appearing smaller as they aged), which may not be biologically plausible, and was likely attributed to the flexibility in the growth models used. While this issue is unlikely to have significantly impacted the conclusions of this work, future efforts could consider constraining these estimates through the use of penalties to prevent growth shrinkage. Furthermore, both WAA and LAA were estimated external to the assessment model and were treated as known inputs. This approach overlooks the potential impacts of survey selectivity (Taylor et al. 2005; Schueller et al. 2014) and underestimates the uncertainty in model estimates (Maunder and Punt 2013). Although using external estimates of growth is a common practice in contemporary stock assessments (Lee et al. 2024) and was necessitated by computational limitations (i.e., the assessment model was developed in ADMB, but growth analyses were developed in TMB for efficient estimation of random effects), future research efforts should seek to estimate growth within the assessment model using conditional age-at-length data following a state–space approach (e.g., Correa et al. 2023). Further, our study employed relatively simple methods to understand the influence of density-dependence on growth dynamics. In particular, simple polynomial regressions were utilized and limited to a single covariate (survey RPNs) to maintain focus and brevity in our results. However, it is likely that multiple interacting factors (e.g., environment, recruitment, and intra-specific competition) may have also influenced growth processes during these recent periods. Future investigations that directly integrate interactions among causal ecological mechanisms (e.g., through dynamic structural equation models; Thorson et al. 2024) into an assessment model framework could yield promising insights. Finally, growth analyses from this study may have been impeded by limited sample sizes and time series, especially given the longevity and spatial scale of a species like sablefish. Revisiting these analyses with an extended time series incorporating the additional large recruitment events observed recently could offer expanded insights and facilitate an improved understanding of linkages between the environment, recruitment, and growth.

Alaska sablefish represents a unique empirical case study highlighting the often-overlooked implications of large recruitment events on growth, which resulted in significant impacts on stock assessment estimates of spawning biomass, annual recruitment, and recommended harvest levels. Considering the sensitivity of stock assessments to growth assumptions (Stawitz et al. 2019; Correa et al. 2021), we encourage routine collection of growth data (weight, length, age) to support the characterization of variable growth processes when feasible, and additional consideration of these process within fishery stock assessment models. We further recommend continued research of cross-scale impacts of environmental and population conditions on growth processes. Ultimately, an improved understanding of ecosystem and resource interactions with growth processes will help facilitate the development of management strategies that promote more sustainable outcomes, advancing the transition towards ecosystem-based fisheries management.

Acknowledgements

Article information

History dates

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Data availability

All code and data utilized in this study can be found at https://github.com/chengmatt/Sable_Growth (doi: 10.5281/zenodo.13903201).

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Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2024-0228.

References

Atkinson, D. 1994. Temperature and organism size—a biological law for ectotherms? *In* Advances in ecological research. Elsevier. pp. 1–58. Available from https://linkinghub.elsevier.com/retrieve/pii/S0065250408602123 [accessed 16 April 2024].

Austin, P.C., and Hux, J.E. 2002. A brief note on overlapping confidence intervals. J. Vasc. Surg. **36**: 194–195. doi:10.1067/mva.2002.125015. PMID: 12096281.

Barbeaux, S., Ferriss, B., Palsson, W., Shotwell, K., Spies, I., Wang, M., and Zador, S. 2020. Assessment of the Pacific cod stock in the Gulf of Alaska. p. 181.

Barbeaux, S.J., Barnett, L., Hall, M., Hulson, P., Nielsen, J., Shotwell, S.K., et al. 2023. 2. Assessment of the Pacific cod stock in the Eastern Bering Sea.

Cardinale, M., and Modin, J. 1999. Changes in size-at-maturity of Baltic cod (*Gadus morhua*) during a period of large variations in stock size and environmental conditions. Fish. Res. **41**: 285–295. doi:10.1016/S0165-7836(99)00021-1.

Carvalho, F., Winker, H., Courtney, D., Kapur, M., Kell, L., Cardinale, M., et al. 2021. A cookbook for using model diagnostics in integrated stock assessments. Fish. Res. **240**: 105959. doi:10.1016/j.fishres.2021.105959.

Cheng, M.L.H., Thorson, J.T., Ianelli, J.N., and Cunningham, C.J. 2023. Unlocking the triad of age, year, and cohort effects for stock assessment: demonstration of a computationally efficient and reproducible framework using weight-at-age. Fish. Res. **266**. doi:10.1016/j.fishres.2023.106755.

Clark, W.G. 1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat.Sci. **48**: 734–750. doi:10.1139/f91-088.

Clark, W.G. 2002. $F_{35\%}$ revisited ten years later. North Am. J. Fish. Manage. **22**: 251–257. doi:10.1577/1548-8675(2002)022%3c0251:FRTYL%3e2.0.CO;2.

Correa, G.M., McGilliard, C.R., Ciannelli, L., and Fuentes, C. 2021. Spatial and temporal variability in somatic growth in fisheries stock assessment models: evaluating the consequences of misspecification. ICES J. Mar. Sci. **78**: 1900–1908. doi:10.1093/icesjms/fsab096.

Correa, G.M., Monnahan, C.C., Sullivan, J.Y., Thorson, J.T., and Punt, A.E. 2023. Modelling time-varying growth in state–space stock assessments. ICES J. Mar. Sci. fsad133.

Denechaud, C., Smoliński, S., Geffen, A.J., Godiksen, J.A., and Campana, S.E. 2020. A century of fish growth in relation to climate change, population dynamics and exploitation. Glob. Change Biol. **26**(10): 5661–5678. doi:10.1111/gcb.15298.

Deroba, J.J., and Bence, J.R. 2008. A review of harvest policies: understanding relative performance of control rules. Fish. Res. **94**: 210–223. doi:10.1016/j.fishres.2008.01.003.

Di Lorenzo, E., and Mantua, N. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nat. Clim. Change, **6**: 1042–1047. doi:10.1038/nclimate3082.

Echave, K.B., Hanselman, D.H., Adkison, M.D., and Sigler, M.F. 2012. Interdecadal change in growth of sablefish (*Anoplopoma fimbria*) in the northeast Pacific Ocean. Fish. Bull. **210**: 361–374.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N, et al. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Softw. **27**: 233–249. doi:10.1080/10556788.2011.597854.

Francis, R.I.C.C. 2016. Growth in age-structured stock assessment models. Fish. Res. **180**: 77–86. doi:10.1016/j.fishres.2015.02.018.

Gibson, G.A., Stockhausen, W.T., Coyle, K.O., Hinckley, S., Parada, C., Hermann, A.J., et al. 2019. An individual-based model for sablefish: exploring the connectivity between potential spawning and nursery grounds in the Gulf of Alaska. Deep Sea Res. Part II, **165**: 89–112. doi:10.1016/j.dsr2.2018.05.015.

Gibson, G.A., Stockhausen, W.T., Shotwell, K., Deary, A.L., Pirtle, J.L., Coyle, K.O., and Hermann, A.J. 2023. Can seamounts in the Gulf of Alaska be a spawning ground for sablefish settling in coastal nursery grounds? Fish. Res. **261**: 106625. doi:10.1016/j.fishres.2023.106625.

Goethel, D., Hanselman, D., Rodgveller, C., Echave, K.B., Williams, B., Shotwell, S.K., et al. 2021. 3. Assessment of the sablefish stock in Alaska. p. 347.

Goethel, D.R., Cheng, M.L.H., Echave, K.B., Marsh, C., Rodgveller, C.J., Shotwell, K., and Siwicke, K. 2023. 3. Assessment of the sablefish stock in Alaska. North Pacific Fishery Management Council, Anchorage, AK.

Goethel, D.R., Hanselman, D.H., Rodgveller, C.J., Fenske, K.H., Shotwell, S.K., Echave, K.B., et al. 2020. 3. Assessment of the sablefish stock in Alaska.

He, X., Field, J.C., Pearson, D.E., and Lefebvre, L.S. 2016. Age sample sizes and their effects on growth estimation and stock assessment outputs: three case studies from U.S. West Coast fisheries. Fish. Res. **180**: 92–102. doi:10.1016/j.fishres.2015.08.018.

Hulson, P.-J.F., and Williams, B.C. 2024. Inclusion of ageing error and growth variability using a bootstrap estimation of age composition and conditional age-at-length input sample size for fisheries stock assessment models. Fish. Res. **270**: 106894. doi:10.1016/j.fishres.2023.106894.

Hulson, P.J., Hanselman, D.H., Lunsford, C.R., and Fissel, B. 2017. 9. Assessment of the Pacific ocean perch stock in the Gulf of Alaska. p. 80.

Ianelli, J., Honkalehto, T., Barbeaux, S., Fissel, B., and Kotwicki, S. 2016. Assessment of the walleye pollock stock in the Eastern Bering Sea. Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Counci. p. 126.

Jasonowicz, A.J., Goetz, F.W., Goetz, G.W., and Nichols, K.M. 2017. Love the one you're with: genomic evidence of panmixia in the sablefish (*Anoplopoma fimbria*). Can. J. Fish. Aquat.Sci. **74**: 377–387. doi:10.1139/cjfas-2016-0012.

Kapur, M., Haltuch, M., Connors, B., Rogers, L., Berger, A., Koontz, E., et al. 2020. Oceanographic features delineate growth zonation in Northeast Pacific sablefish. Fish. Res. **222**: 105414. doi:10.1016/j.fishres.2019.105414.

King, J.R., McFarlane, G.A., and Beamish, J.R. 2001. Incorporating the dynamics of marine systems into the stock assessment and management of sablefish. Prog. Oceanogr. **49**: 619–639. doi:10.1016/S0079-6611(01)00044-1.

King, Mcfarlane, and Beamish. 2000. Decadal-scale patterns in the relative year class success of sablefish (*Anoplopoma fimbria*). Fish. Oceanogr. **9**: 62–70. doi:10.1046/j.1365-2419.2000.00122.x.

Kolody, D.S., Eveson, J.P., and Hillary, R.M. 2016. Modelling growth in tuna RFMO stock assessments: current approaches and challenges. Fish. Res. **180**: 177–193. doi:10.1016/j.fishres.2015.06.016.

Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., and Bell, B. 2016. TMB: automatic differentiation and Laplace approximation. J. Stat. Softw. **70**. doi:10.18637/jss.v070.i05. PMID: 29593450.

Kuriyama, P.T., Ono, K., Hurtado-Ferro, F., Hicks, A.C., Taylor, I.G., Licandeo, R.R., et al. 2016. An empirical weight-at-age approach reduces estimation bias compared to modeling parametric growth in integrated, statistical stock assessment models when growth is time varying. Fish. Res. **180**: 119–127. doi:10.1016/j.fishres.2015.09.007.

Lee, H., Maunder, M.N., and Piner, K.R. 2024. Good practices for estimating and using length-at-age in integrated stock assessments. Fish. Res. **270**: 106883. doi:10.1016/j.fishres.2023.106883.

Lee, H., Piner, K.R., Taylor, I.G., and Kitakado, T. 2019. On the use of conditional age at length data as a likelihood component in integrated population dynamics models. Fish. Res. **216**: 204–211. doi:10.1016/j.fishres.2019.04.007.

Lin, Z., and Ito, S. 2024. Fish weight reduction in response to intra- and interspecies competitionunder climate change. Fish Fish. **25**(3): 455–470. doi:10.1111/faf.12818.

Lindmark, M., Ohlberger, J., and Gårdmark, A. 2022. Optimum growth temperature declines with body size within fish species. Global Change Biol. **28**: 2259–2271. doi:10.1111/gcb.16067.

Litzow, M.A., Hunsicker, M.E., Ward, E.J., Anderson, S.C., Gao, J., Zador, S.G., Batten, S., et al. 2020. Evaluating ecosystem change as Gulf of Alaska temperature exceeds the limits of preindustrial variability. Prog. Oceanogr. **186**: 102393. doi:10.1016/j.pocean.2020.102393.

Lorenzen, K. 2008. FISH POPULATION REGULATION Beyond "Stock and recruitment": THE ROLE OF density- dependent growth in THE RECRUITED STOCK. Bull. Mar. Sci. **83**.

Lorenzen, K. 2016. Toward a new paradigm for growth modeling in fisheries stock assessments: embracing plasticity and its consequences. Fish. Res. **180**: 4–22. doi:10.1016/j.fishres.2016.01.006.

Lorenzen, K. 2022. Size- and age-dependent natural mortality in fish populations: biology, models, implications, and a generalized length-inverse mortality paradigm. Fish. Res. **255**: 106454. doi:10.1016/j.fishres.2022.106454.

Lorenzen, K., and Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proc. R. Soc. Lond. B Biol. Sci. **269**: 49–54. doi:10.1098/rspb.2001.1853.

Lorenzen, K., Camp, E.V., and Garlock, T.M. 2022. Natural mortality and body size in fish populations. Fish. Res. **252**: 106327. doi:10.1016/j.fishres.2022.106327.

Maunder, M.N., and Piner, K.R. 2015. Contemporary fisheries stock assessment: many issues still remain. ICES J. Mar. Sci. **72**: 7–18. doi:10.1093/icesjms/fsu015.

Maunder, M.N., and Punt, A.E. 2013. A review of integrated analysis in fisheries stock assessment. Fish. Res. **142**: 61–74. doi:10.1016/j.fishres.2012.07.025.

Minte-Vera, C.V., Maunder, M.N., Schaefer, K.M., and Aires-da-Silva, A.M. 2019. The influence of metrics for spawning output on stock assessment results and evaluation of reference points: an illustration with yellowfin tuna in the eastern Pacific Ocean. Fish. Res. **217**: 35–45. doi:10.1016/j.fishres.2018.09.022.

Quinn, T.J.I., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, Oxford.

Rideout, R.M., and Tomkiewicz, J. 2011. Skipped spawning in fishes: more common than you might think. Mar. Coastal Fish. **3**: 176–189. doi:10.1080/19425120.2011.556943.

Rodgveller, C.J. 2018a. Age-at-maturity and fecundity of female sablefish sampled in December of 2011 and 2015 in the Gulf of Alaska. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center. Available from https://repository.library.noaa.gov/view/noaa/17605 [accessed 25 January 2024].

Rodgveller, C.J. 2018b. A comparison of methods for classifying female sablefish maturity and skip spawning outside the spawning season. Mar. Coastal Fish. **10**: 563–576. doi:10.1002/mcf2.10053.

Rodgveller, C.J., and Echave, K.B. 2024. Trends in predicted age at maturity of sablefish from 22 years of surveys. Mar. Coastal Fish. **16**: e10295. doi:10.1002/mcf2.10295.

Rodgveller, C.J., Stark, J.W., Echave, K.B., and Hulson, P.-J.F. 2016. Age at maturity, skipped spawning, and fecundity of female sablefish (*Anoplopoma fimbria*) during the spawning season. Fish. Bull. **114**: 89–102. doi:10.7755/FB.114.1.8.

Roff, D.A. 1983. An allocation model of growth and reproduction in fish. Can. J. Fish. Aquat.Sci. **40**: 1395–1404. doi:10.1139/f83-161.

Rose, K.A., Cowan, J.H., Winemiller, K.O., Myers, R.A., and Hilborn, R. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis: compensation in fish populations. Fish Fish. **2**: 293–327. doi:10.1046/j.1467-2960.2001.00056.x.

Rutecki, T.L., Rodgveller, C.J., and Lunsford, C.R. 2016. National Marine Fisheries Service longline survey data report and survey history, 1990–2014. U.S. Dep. Commer., NOAA Tech. Memo., NMFS-AFSC: 329. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center.

Schueller, A.M., Williams, E.H., and Cheshire, R.T. 2014. A proposed, tested, and applied adjustment to account for bias in growth parameter estimates due to selectivity. Fish. Res. **158**: 26–39. doi:10.1016/j.fishres.2013.10.023.

Shotwell, S.K., Hanselman, D.H., and Belkin, I.M. 2014. Toward biophysical synergy: investigating advection along the Polar Front to identify factors influencing Alaska sablefish recruitment. Deep Sea Res. Part II, **107**: 40–53. doi:10.1016/j.dsr2.2012.08.024.

Shotwell, S.K., Spies, I., Ianelli, J.N., Aydin, K., Hanselman, D.H., Palsson, W., et al. 2021. 7. Assessment of the arrowtooth flounder stock in the Gulf of Alaska.

Sigler, M.F. 2000. Abundance estimation and capture of sablefish (*Anoplopoma fimbria*) by longline gear. Can. J. Fish. Aquat.Sci. **57**: 14. doi:10.1139/f00-066.

Siwicke, K., and Malecha, P. 2024. The 2023 Longline Survey of the Gulf of Alaska and Eastern Bering Sea on the FV Alaskan Leader: Cruise Report AL-23-01. U.S. Department of Commerce, NOAA Technical Memorandum, NMFS-AFSC-480: 39.

Sogard, S., and Olla, B. 2001. Growth and behavioral responses to elevated temperatures by juvenile sablefish *Anoplopoma fimbria* and the interactive role of food availability. Mar. Ecol. Progr. Ser. **217**: 121–134. doi:10.3354/meps217121.

Sogard, S.M., and Olla, B.L. 1998. Behavior of juvenile sablefish, *Anoplopoma fimbria* (Pallas), in a thermal gradient: balancing food and temperature requirements. J. Exp. Mar. Biol. Ecol. **222**: 43–58. doi:10.1016/S0022-0981(97)00137-8.

Stawitz, C.C., Haltuch, M.A., and Johnson, K.F. 2019. How does growth misspecification affect management advice derived from an integrated fisheries stock assessment model? Fish. Res. **213**: 12–21. doi:10.1016/j.fishres.2019.01.004.

Stewart, I.J., and Hamel, O.S. 2014. Bootstrapping of sample sizes for length- or age-composition data used in stock assessments. Can. J. Fish. Aquat.Sci. **71**: 581–588. doi:10.1139/cjfas-2013-0289.

Taylor, N.G., Walters, C.J., and Martell, S.J.D. 2005. A new likelihood for simultaneously estimating von Bertalanffy growth parameters, gear selectivity, and natural and fishing mortality. Can. J. Fish. Aquat.Sci. **62**: 215–223. doi:10.1139/f04-189.

Thorson, J.T., and Minte-Vera, C.V. 2016. Relative magnitude of cohort, age, and year effects on size at age of exploited marine fishes. Fish. Res. **180**: 45–53. doi:10.1016/j.fishres.2014.11.016.

Thorson, J.T., Andrews, A.G., Essington, T.E., and Large, S.I. 2024. Dynamic structural equation models synthesize ecosystem dynamics constrained by ecological mechanisms. Methods Ecol. Evol. **15**: 744–755. doi:10.1111/2041-210X.14289.

Timm, L.E., Larson, W.A., Jasonowicz, A.J., and Nichols, K.M. 2024. Whole genome resequencing of sablefish at the northern end of their range reveals genetic panmixia and large putative inversions. ICES J. Mar. Sci. fsae070.

Trijoulet, V., Albertsen, C.M., Kristensen, K., Legault, C.M., Miller, T.J., and Nielsen, A. 2023. Model validation for compositional data in stock assessment models: calculating residuals with correct properties. Fish. Res. **257**: 106487. doi:10.1016/j.fishres.2022.106487.

Whitten, A.R., Klaer, N.L., Tuck, G.N., and Day, R.W. 2013. Accounting for cohort-specific variable growth in fisheries stock assessments: a case study from south-eastern Australia. Fish. Res. **142**: 27–36. doi:10.1016/j.fishres.2012.06.021.

Witthames, P.R., and Marshall, C.T. 2008. The importance of reproductive dynamics in fish stock assessments. *In* Advances in fisheries science. 1st ed. *Edited by* A. Payne, J. Cotter and T. Potter. Wiley. pp. 306–324.

Can. J. Fish. Aquat. Sci. **82**: 1–13 (2025) | dx.doi.org/10.1139/cjfas-2024-0228

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