The Utility of Juvenile Sablefish Otoliths in Reconstructing Life History and Growth in the Gulf of Alaska

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Abstract

Sablefish are commercially important, and their populations have undergone significant fluctuations over time. Juvenile growth may be a strong indicator of sablefish recruitment potential. Previous projects have reconstructed juvenile sablefish life history using otoliths; therefore, otolith analyses may be useful in predicting recruitment success. To evaluate this utility, comparisons of otolith and otolith increment measurements across structures and with fish size and growth were made. Specifically, daily age estimates from paired lapillar and sagittal otolith samples were compared to determine agreement between structures, otolith dimensions were compared to body length to support the correlation between daily increment width and somatic growth, and paired otolith samples recovered from a previous temperature and feeding ration study were used to investigate otolith increment width with known growth rates. The evidence reported herein suggests both lapillar and sagittal otoliths produce reliable age

estimates, and growth planes between structures are highly correlated with somatic growth. Daily otolith increment width mirrored the results of the somatic growth study in both structures. Generally, the lapillus had fewer complications resulting in a better fit to growth and treatment data, primarily due to the lack of accessory growth centers.

Introduction

The abundance of sablefish (*Anoplopoma fimbria*) in the Gulf of Alaska (GOA) has declined substantially since 1988, with only a few strong year classes supporting the fishery (Hanselman et al., 2019). Understanding the factors driving year-class success and recruitment can reduce uncertainty in stock assessment models. The recruitment of Alaska sablefish is believed to be decoupled from spawning stock biomass and driven by environmental variability (Hanselman et al., 2019). Previous research has suggested a relationship between large-scale oceanographic indices and sablefish recruitment in the California Current and off the coast of Vancouver Island, British Columbia (Coffin and Mueter, 2016; King et al., 2000; Schirripa and Colbert, 2006; Shotwell et al., 2014; Sigler et al., 2001; Sogard, 2011); however, the relationship between juvenile sablefish growth/life history, environmental drivers, and recruitment success in Alaska has not been investigated.

Juvenile growth tends to have a positive and predictive relationship with recruitment in many fishes (Metcalfe and Monaghan, 2003), including sablefish in the California Current ecosystem (Sogard, 2011). Juvenile sablefish growth rates observed under laboratory conditions were among the fastest recorded for any juvenile marine fish (Sogard, 2011). This accelerated growth likely comes at a physiological cost, making juvenile sablefish more vulnerable to environmental fluctuations. Measuring and comparing juvenile sablefish growth between environmental conditions and in the context of recruitment in the GOA could help identify potential drivers for

survival and reduce uncertainty within stock assessment results. The generally accepted "bigger is better" approach to understanding growth rates and survival in marine fishes lends support to the strategy of maximizing growth. While the physiological cost of rapid growth may render fishes more susceptible to environmental conditions, the tradeoff is a reduced period spent within a smaller, more vulnerable size class (Houde, 1987).

Variation in fish growth is reflected in the microstructure of otoliths. Analysis of visible banding patterns within the otolith structure are used to estimate growth rates, daily age, migration patterns, and stock structure (Campana, 2005; Panfili et al., 2002). Larval and juvenile otolith size and growth has been shown to be highly correlated to somatic growth or fish length in other temperate species (Fey, 2006; Moksness and Wespestad, 1989; Otterlei et al., 2002; Wright et al., 1990) as well as other fast-growing species (Megalofonou, 2006). For example, lapillus growth was highly correlated with standard length in larval and early juvenile Atlantic cod, and otolith growth was linked to temperature effects, providing context for environmental variation (Otterlei et al., 2002). Previous studies on juvenile sablefish have successfully developed growth indices using otolith microstructure analysis (Beamish and McFarlane, 1983; Boehlert and Yoklavich, 1985; Courtney and Severin, 2007; King et al., 2000; Sigler et al., 2001; Sogard, 2011). These studies have shown clear temperature effects on growth in laboratory-reared fish and correlations between Pacific Decadal Oscillation indices, sea surface height, and Ekman transport in juvenile sablefish caught in the California Current. Juvenile sablefish have demonstrated a dome-shaped relationship between temperature and growth (Krieger et al., 2019), similar to many other species (Hofmann and Fischer, 2003; Takasuka and Aoki, 2006; Xing et al., 2021). If juvenile otolith increment width is predictive of somatic growth, then you would expect to see a similar relationship.

68 The microstructure of otoliths consists of concentric layers of relatively protein rich, opaque (D-
69 zone) and calcium carbonate-rich, translucent (L-zone) material, which form interpretable
70 bipartite increments representing sub-daily to annual growth periods (Campana, 2001; Panfili et
71 al., 2002). However, for otolith microstructure to be informative, it must be entrained to cyclical
72 environmental events or endogenous circadian rhythms that continue, even in the absence of
73 somatic growth (Geffen, 1987). Otolith growth corresponds to environmental stimuli such as diel
74 light/dark cycles (daily increments), seasonal growth patterns (temperature and food
75 availability), and inter-annual patterns which are reflected in the degree of opacity and amount of
76 material accreted to the otolith (Høie et al., 2008). Areas of discontinuity in fish otoliths (check
77 marks) typically denote stress, or large thermal changes, such as those used for thermal marking
78 in hatcheries (Volk et al., 1999). The incidence of sub-daily increments tends to increase during
79 periods of rapid growth, complicating the interpretation of daily increment patterns (Stevenson
80 and Campana, 1993). These increments can typically be differentiated as they tend to be less
81 well defined and break up a more normal pattern observed within daily increments (Stevenson
82 and Campana, 1993). Studying these interpretable patterns and their relationship to internal and
83 external stimuli can give insights into the conditions experienced during the life of an individual
84 and the impacts of varying environmental conditions on fish health.

85 Otolith microstructure can be used to examine recruitment dynamics of sablefish (Beamish and
86 McFarlane, 1983; Boehlert and Yoklavich, 1985; Courtney and Severin, 2007; King et al., 2000;
87 Sigler et al., 2001; Sogard, 2011), but a clear understanding of the relationship between otolith
88 and somatic growth is needed. To accurately estimate daily age, otoliths need to have an
89 identifiable hatch mark and the daily formation of increments needs to be validated. The hatch
90 mark (Deary et al., 2019) and daily increments of sablefish have been validated for the sagittal

otolith (Courtney and Severin, 2007). Issues with processing and measuring sablefish sagittal otoliths include the presence of accessory growth centers (e.g., accessory primordia as defined in Panfili et al., 2002) and the convex shape of the otolith (Courtney & Severin, 2007). Lapillar otoliths have also been used to investigate individual responses to stimuli (Sogard, 2011). The lapillus may not form accessory growth centers, but the method has not been validated for daily age. Given the potential utility of both structures and the resulting data, a comparison and evaluation of structures and growth is warranted.

The objectives for this study were as follows:

1. Compare daily age estimates from the lapillus and sagitta to provide a corroboration for daily increment periodicity for lapillar otoliths using a validated structure.

2. Compare otolith dimensions to fish length to investigate the relationship between otolith growth and somatic growth.

3. Compare mean daily increment width with temperature and feeding ration treatments to investigate their effect on daily increment formation.

4. Examine the relationship between mean daily somatic growth and mean daily otolith increment width (sagittal and lapillar) from specimens subjected to temperature and ration treatments.

Methods

Both lapillar and sagittal otoliths were collected from juvenile sablefish sampled in multiple locations in the eastern Gulf of Alaska (EGOA) during 2014, 2016, and 2017 (Table 1). July and August samples were collected during the National Marine Fisheries Service (NMFS) EGOA

Eastern Gulf of Alaska Ecosystem Assessment Survey (Strasburger et al., 2018). October otoliths (sagitta only) were collected in Saint John Baptist Bay in Southeast Alaska (Callahan et al., 2021). Additional juvenile otoliths were sampled from a controlled temperature and feeding ration growth study conducted at Auke Bay Laboratory /Alaska Fishery Science Center (Krieger et al., 2019). A detailed description of the experimental design is available within Krieger et al., 2019 and 2020. Briefly, juvenile sablefish were randomly assigned to one of four temperature treatments combined with one of three ration treatments, resulting in twelve treatment levels. Temperature treatment levels were 6.5, 12.7, 16.8, and 19.5°C and feeding rations were C_{25}, C_{50}, C_{max}. Feeding rations were based on fish weight and consumption data collected during a 2017 feeding trial experiment (Krieger et al., 2019). C_{max} was feeding to satiation, C_{50} was feeding at one half of C_{max}, and C_{25} was feeding at one quarter of C_{max}. Fish were held on a natural photo period cycle. Due to the small sample size of recoverable otoliths available at the onset of this study, we rely on results from Krieger et al., 2019 and 2020 in finding no tank effect with a larger sample size. Juveniles from this growth study were originally sampled during the 2017 EGOA survey (Strasburger et al., 2018). Treatment levels, and individual mean daily growth (mm/day FL) from Krieger et al., 2019, were used with permission for further analyses.

Sagittal and lapillar otoliths were mounted to petrographic slides using Crystalbond™ 509 thermal plastic cement and whole otolith images (Figure 1) were taken using a LeicaMZ6 stereoscopic microscope with a Leica DFC450 camera at 1.25-4.0× magnification with reflected lighting. Images were taken using Image-Pro Premiere® 9.3 software. After the whole otolith was imaged, the distal and proximal surface of the otoliths were polished using Buehler 1200 grit (P2400) micro-cut silicon carbide grinding paper and 0.3-micron FibrMet abrasive discs. After

the distal surface of the otolith was ground, the slide was heated on a hot plate and the otolith was flipped and remounted on its distal side. The proximal side of the otolith was then ground until the nucleus and daily growth increments were visible.

After daily growth increments and the nucleus were visible, images were taken of otoliths using a Leica DMLS compound microscope, DFC450C camera at 6.3×, 12.3×, 25.2×, and 63× magnification with both air and oil immersion objectives and single- or double-polarization. Image-Pro Premier® and Image-Pro® were used to measure the whole otolith and daily growth increments. For whole otoliths, linear measurements were collected along anterior-posterior (length), dorsal-ventral (height), and nucleus to common feature transects to investigate otolith/fish size relationships and to corroborate daily increment count and measurement results (Figure 2). For daily growth increment counts and measurements, the primordium were identified, the hatch mark was marked as the beginning of the first daily increment, and a transect was drawn from the primordia to the edge of the otolith. Daily increments were defined as a pair of continuous, consecutive light/dark bands, where the darkest part (typically the middle of the dark zone) was labeled as the start/stop of an increment. Transects were drawn where the most consecutive increments were visible. Daily increment measurements from otoliths collected from fish included in the temperature/feeding ration growth study were restricted to the last 30 days of the study to ensure increments were the result of each treatment. Temperature and ration treatments were not sampled evenly due to mortality events during the growth trial (Table 1).

Daily increment counts from the lapillus and sagitta were compared (Figure 3) to investigate lapillar otolith utility for daily age estimation. A linear regression comparing sagittal and lapillar daily increments was calculated as:

157 $$SDA_i = \beta_0 + \beta_1 \cdot LPA_i + \varepsilon_i \,,$$

158 where SDA_i was the sagittal daily age estimate, LPA_i was the lapillar daily age estimate, β_0 was
159 the intercept, β_1 is the slope, and ε_i was the error. McNemar, Evans-Hoenig, and Bowker bias
160 tests were completed, as suggested by (McBride, 2015). Daily age estimation methods were
161 considered comparable if the linear model and bias tests did not suggest significant bias between
162 ages.

163 Linear models were also used to compare linear otolith measurements to fish length (Figure 4).
164 Based on initial fish length to otolith size comparisons and to target the axis where daily
165 increments were counted and measured, the lapillus diameter and sagitta height were used for
166 modeling. The significance of linear relationships between otolith and fish size were used to test
167 whether otolith growth could be used as a proxy for fish growth:

168 $$FL_i = \beta_0 + \beta_1 \cdot D_i + \varepsilon_i \,,$$

169 where FL_i was the individual fish fork-length (mm), D_i was either lapillus diameter or sagitta
170 height (μm), β_0s were the estimated intercepts for each respective model, and β_1s were the
171 estimated slope coefficients for each respective model, and ε_i was the error.

172 Separate quadratic models for lapillus and sagittal otoliths were used to evaluate the effects of
173 temperature and feeding ration on mean daily increment width over the study period:

174 $$Inc_{iTR} = \beta_1 \cdot Temp + \beta_2 \cdot Temp^2 + \varepsilon_{iTR}$$

175 where Inc_{iTR} is the average increment width (μm) at temperature T and ration R for specimen i,
176 $Temp$ is the temperature treatment (°C), and ε_{iTR} was the individual specimen treatment error
177 (Figure 5).

178 Lastly, we tested for differences in the slope of the relationship between mean observed growth
179 rates from Krieger et al., (2019) and mean increment widths from each structure, temperature
180 and feeding ration group using fitted linear models (Figures 6 & 7), and an anova. If the
181 interaction term between mean increment width and either treatment group (temperature or
182 ration) was significant, the slope was deemed to be significantly different for that respective
183 structure (sagitta or lapillus). All statistical analyses were completed using RStudio (Ogle, 2016;
184 R Core Team, 2019), all R code and original/reproduced data used to produce the preceding
185 models, tests, and referenced figures are available at the public url:

186 https://github.com/Strasburger/Sablefish-Otolith-Utility

187 **Results**

188 Ages were between 105 and 160 days from hatch and daily age counts were similar between
189 lapillar and sagittal otoliths (mean difference between paired ages was -0.23 days ± 3.39 SD;
190 Figure 3). A linear model suggested no significant difference between paired structure age
191 estimates ($p = 0.00$, $df = 20$). Bias tests support the linear model results and were not significant
192 (McNemar: $p = 0.80$; Evans-Hoenig: $p = 0.87$; Bowker: $p = 0.45$). These findings support the use
193 of either otolith for daily age estimation (Figure 3). Further, there were strong linear trends
194 between fish length and lapillar and sagittal otolith measurements (lapillus: $p < 0.01$; sagitta: $p <$
195 0.01; Figure 4), suggesting that otolith growth could be used as a proxy for somatic growth.

196 Quadratic models of both lapillar and sagittal otolith daily increment width and
197 temperature/feeding treatments were significant (lapillus: $p < 0.01$; sagitta: $p < 0.01$). Both
198 models suggested that peak daily increment width occurred at approximately 13°C and at the
199 maximum feed ration (C_{max}; Figure 5); however, the lapillus model explained a greater

200 proportion of the variance (adjusted $r^2 = 0.90$ vs. 0.60 for the sagitta model). Both the quadratic
201 coefficients and the interaction terms (temperature and ration) were significant ($p < 0.01$).
202 Though sample sizes were not uniform across treatments due to fish survival in extreme
203 treatments (Table 1), dome-shaped relationship between temperature and otolith increment width
204 mirrors the growth trends in the previous study (Krieger et al., 2019).

205 The linear relationships between mean daily increment width and mean daily growth (lapillus: p
206 < 0.01; sagitta: $p < 0.01$) provide further support that somatic growth and otolith growth are
207 coupled in juvenile sablefish (Figures 6 & 7). The slope of this relationship remained similar
208 across feeding rations for both otolith structures, but varied at the extreme temperature
209 treatments, suggesting that the temperature effect is stronger than the ration effect across the
210 range of treatments tested. The interaction term between average increment width and
211 temperature was significant for the lapillus only ($p < 0.03$), there were no significant interactions
212 between increment width and ration for either otolith structure. This suggests that there may be a
213 temperature threshold after which the relationship between somatic and otolith growth changes.

214 **Discussion**

215 The findings presented here support the utility of both the lapillar and sagittal otolith to assess
216 growth in juvenile sablefish. Daily age estimates from the lapillus and sagitta were highly
217 correlated, suggesting that both otoliths record daily age in juvenile sablefish, given previous
218 validation on sagittal otoliths (Courtney and Severin, 2007; Deary et al., 2019). Further, the
219 strong linear relationship between otolith dimensions and somatic length, and the effects of
220 temperature and feed ration on otolith growth support past and future use of lapillar and sagittal
221 otoliths for modeling juvenile sablefish growth in changing environments.

222 The quadratic relationship between temperature and otolith increment width within feeding
223 ration treatments agrees with the growth response published in Krieger et al. (2019) using the
224 same specimens. However, interpretation of otolith model results should be done with care. The
225 otolith-somatic growth relationship may decouple at temperature extremes, suggested by the
226 changes in slope detected across temperature treatment between mean somatic growth and mean
227 otolith increment width (Figure 6). This concern may be marginal due to the extreme
228 temperature treatment (19.5°C), which is not likely to occur in the GOA. Further, the
229 relationship between temperature and increment width was relatively stable across temperatures
230 commonly experienced by wild juvenile sablefish (Strasburger et al., 2018).

231 Although either structure may be used to reliably estimate daily age in juvenile sablefish, some
232 thought should be exercised in the selection of which otolith to examine. The sagitta is larger,
233 more easily identified, and more manageable initially; however, they have numerous accessory
234 growth centers (Courtney & Severin, 2007). These growth centers are the most common
235 distortion in the shape of early otoliths in marine fish, which are usually associated with the end
236 of the transformation from larvae to juveniles (Panfili et al., 2002). In addition, the crenulations
237 along the dorsal margin can distort increment widths and make following a consistent
238 counting/measurement transect difficult. These factors introduce the possibility of losing
239 information using a sagittal plane preparation and may produce lower quality preparations and
240 imprecise counts and measurements. Conversely, the lapillus is more difficult to excise and
241 manipulate prior to mounting to a slide; however, accessory growth centers were not an issue,
242 the growth and margins were more uniform, and increment width measurement axes were more
243 consistent. Both otoliths exhibited sub-daily increments. Caution should be exercised in the
244 preparation and imaging of juvenile sablefish otoliths. These increments can be differentiated

with experience, and future work should evaluate criteria for defining daily increments to assess the accuracy of data.

The overarching objective of this study was to understand the relationship between otolith and somatic growth in juvenile sablefish. Results indicated that otolith microstructure can be used to examine connections between juvenile sablefish growth, changing temperature and prey field conditions, and potential subsequent recruitment success. Evidence from previous studies suggests that growth of juvenile sablefish has the potential to be predictive of year class success. The results presented here support these previous studies and further inform the relationship between somatic growth, otolith growth, and temperature and prey field conditions needed to produce growth models from the daily increments of juvenile sablefish otoliths.

Growth in juvenile sablefish correlates with local temperatures and large-scale climate variability (Sogard and Olla, 1998). Juvenile sablefish growth in the California Current system was correlated to the monthly Pacific Decadal Oscillation (PDO) index, sea surface height, and Ekman transport (Sogard, 2011). A persistent Aleutian low, above average southwesterly winds, and warmer coastal sea surface temperature in the Northeast Pacific were correlated to an increased average year-class survival and decadal patterns in the relative success of sablefish off Vancouver Island, British Columbia (King et al., 2000). Laboratory-reared juvenile sablefish (30 – 50 mm total length) exhibited a rapid rise in daily growth rates between 6 and 14° C, a gradual rise between 14 and 22° C, and a precipitous drop at 24° C (Sogard and Olla, 2001). Similar results were observed in a laboratory study using larger (220 – 290 mm total length) juveniles (Krieger et al., 2019). Conversion efficiency of food ration into somatic tissue in juvenile sablefish increases with temperature under both low and high daily ration, albeit at different rates (Sogard and Olla, 2001). This indicates that temperature has a benefit to juvenile sablefish

growth, even in the presence of sub-optimal prey conditions (Sogard & Olla, 2001), as observed in this study. Results described here and by Krieger et al. (2019) suggest an optimal temperature window for juvenile sablefish growth in the Gulf of Alaska.

Juvenile length was selected for this analysis because otolith growth is likely to be related to structural growth (i.e length) in fishes. While in some cases, energy density (commonly linked to the likelihood of overwinter survival) may be predicted with weight, particularly percent dry weight, length is more appropriate for juvenile fishes that store energy as proteins (Bavčević et al., 2020; Krieger et al., 2020; Sogard and Spencer, 2004). Sablefish do not begin to accumulate lipids until approximately age-3 (AFSC, unpublished data). In addition, juvenile sablefish weight predictably and reliably increases as a cubic function of length, a relationship that holds well beyond their first year (Harvey et al., 2000). Describing the relationship between juvenile somatic growth in terms of length and otolith growth, in effect, also describes the relationship between fish somatic growth in terms of weight and otolith growth. However, structural growth (length) is the metric most often associated with predator avoidance and the ability to capture larger and more efficient prey (Sogard, 1997). Finally, many of the archived and continuously collected samples available for juvenile sablefish were collected at sea or in remote field sites where the accurate measurement of weight is often a challenge. Length can be quickly and accurately assessed while samples are fresh, while any preservation method is likely to affect water weight of the sample (Baltasar et al., 2021).

Recent conditions in the Gulf of Alaska (the persistent oceanic heatwave known as “the Blob”, persistent El Niño) had observable effects on the temperature experienced by juvenile sablefish and prey availability in their first summer. Sea surface temperatures have persistently had maximums around 15-16° C from 2014 to 2017 (Litzow et al., 2020; Strasburger et al., 2018).

These maximum temperatures coincide with observed maximum growth rates within laboratory settings (Krieger et al., 2019; Sogard, 2011). Further, prey abundance has shifted recently in the Gulf of Alaska, and zooplankton communities have been predominantly gelatinous species and small copepods (Batten et al., 2022; Pinchuk et al., 2021;Strasburger et al., 2018). Copepods and copepod nauplii are important prey for early sablefish larvae (Grover & Olla, 1990; Grover & Olla, 1987). If potential higher growth rates due to increased temperatures are sustainable within the context of shifting prey fields, and juvenile sablefish benefit from the increased size at age, measuring Alaska juvenile sablefish growth rates and tracking these across cohorts could be an important metric for estimating subsequent recruitment. Further, understanding the factors driving year-class success and recruitment would reduce uncertainty in stock assessment models.

This work supports the use of otolith microstructure to examine linkages between wild juvenile sablefish growth to environmental and ecological conditions experienced during their first year. Given the relationship between otolith dimensions and fish length, otolith increment width and temperature/feeding ration, and the relationship between observed somatic growth and daily increment width, it is reasonable to reconstruct daily growth histories for juvenile sablefish from the Gulf of Alaska, and to relate those growth histories to covariates such as temperature and prey availability.

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Figures:

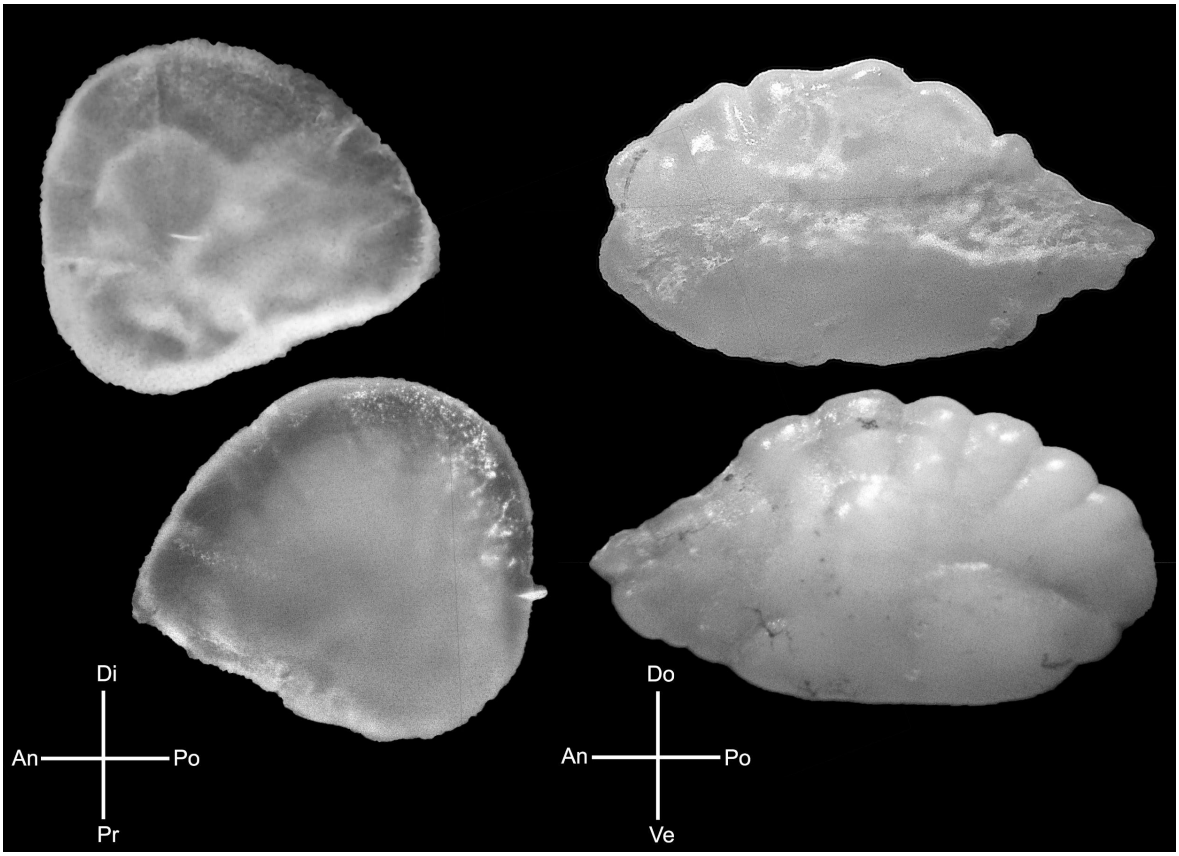


Figure 1. Lapillar (left) and sagittal (right) otoliths from a juvenile sablefish. The top row shows the dorsal lapillar and proximal sagittal otolith surface, and the bottom row shows the ventral lapillar and distal sagittal otolith surface. Keys refer to distal (Di), proximal (Pr), dorsal (Do), ventral (Ve), anterior (An), and posterior (Po). Due to the large variation in otolith size a scale bar was not included. Lapillar diameter ranged from 300 – 900 µm, sagittal height ranged from 450 – 2600 µm.

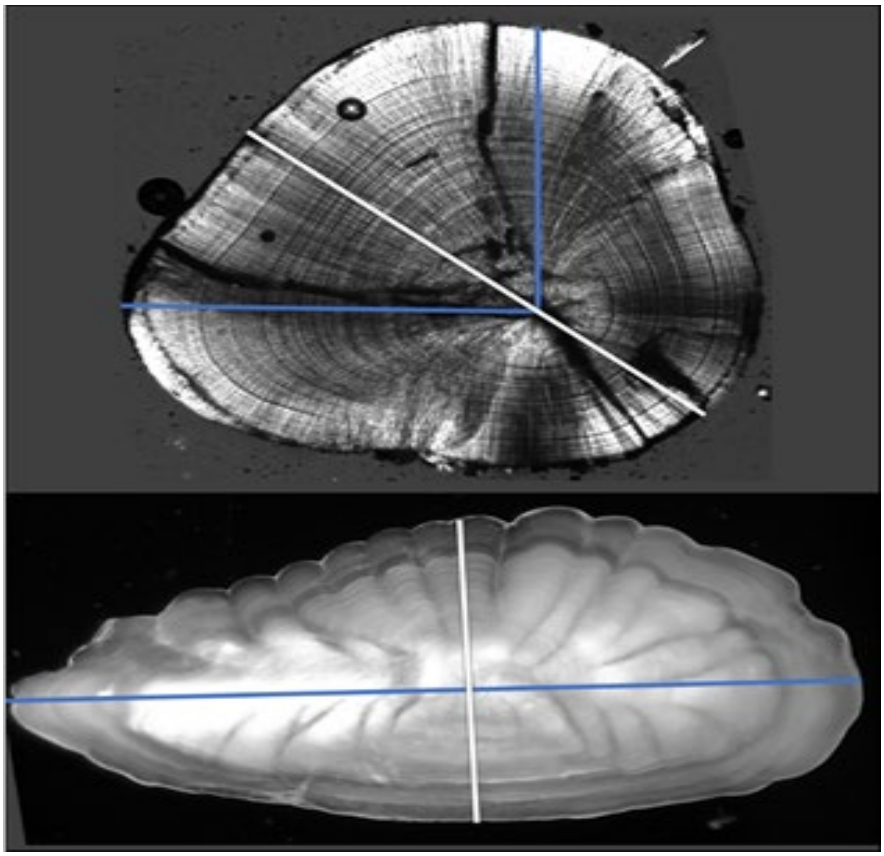


Figure 2. Juvenile sablefish lapillar (top) and sagittal (bottom) otoliths. White lines indicate lapillus diameter and sagitta height used in final otolith-fish size models, blue lines indicate other transects considered. Due to the large variation in otolith size a scale bar was not included. Lapillar diameter ranged from 300 – 900 μm, sagittal height ranged from 450 – 2600 μm.

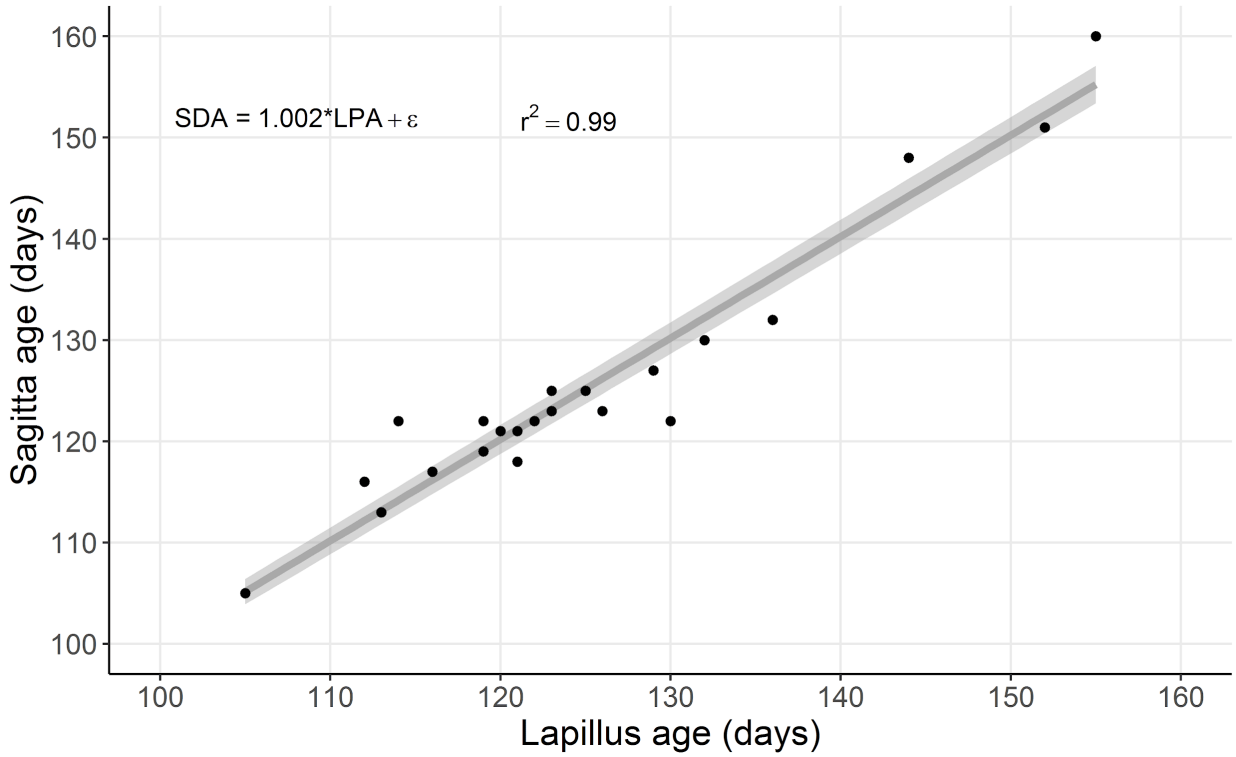


Figure 3. Paired daily ages estimated using lapillar and sagittal otoliths of juvenile sablefish sampled during August of 2014 and 2016.

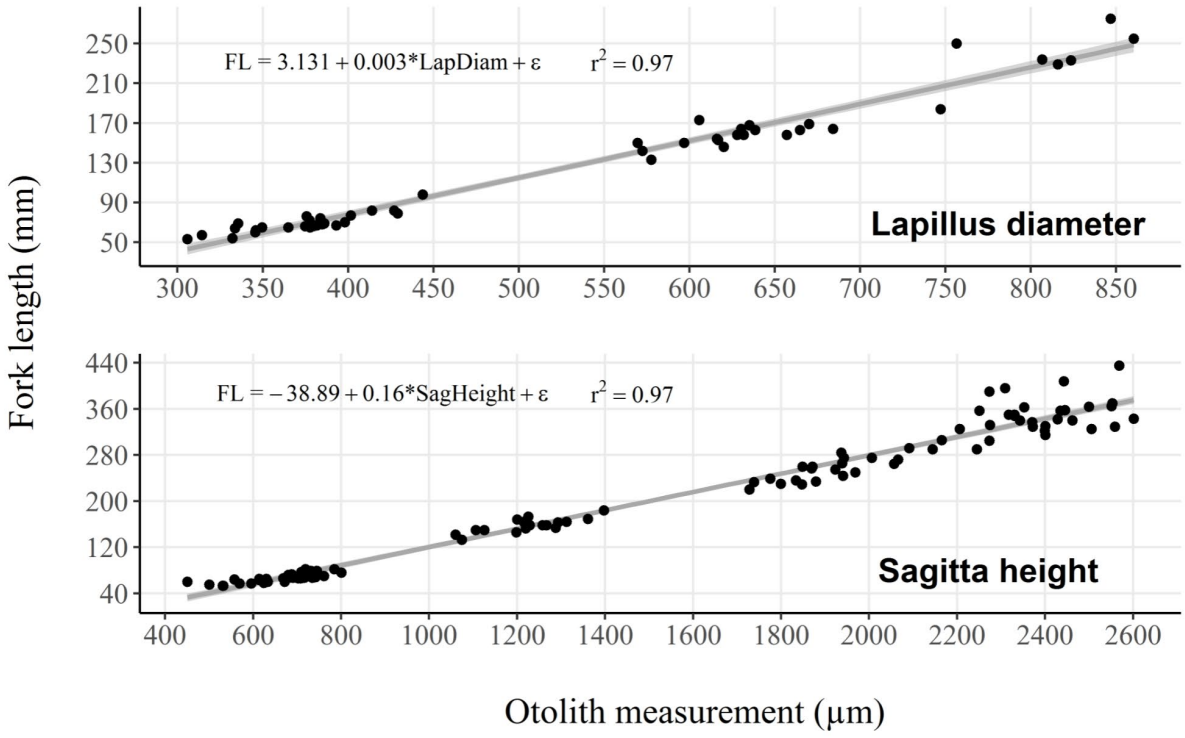


Figure 4. Linear models of lapillar otolith diameter and sagittal otolith height against juvenile sablefish fork length of age-zero fish sampled from July through October of 2017.

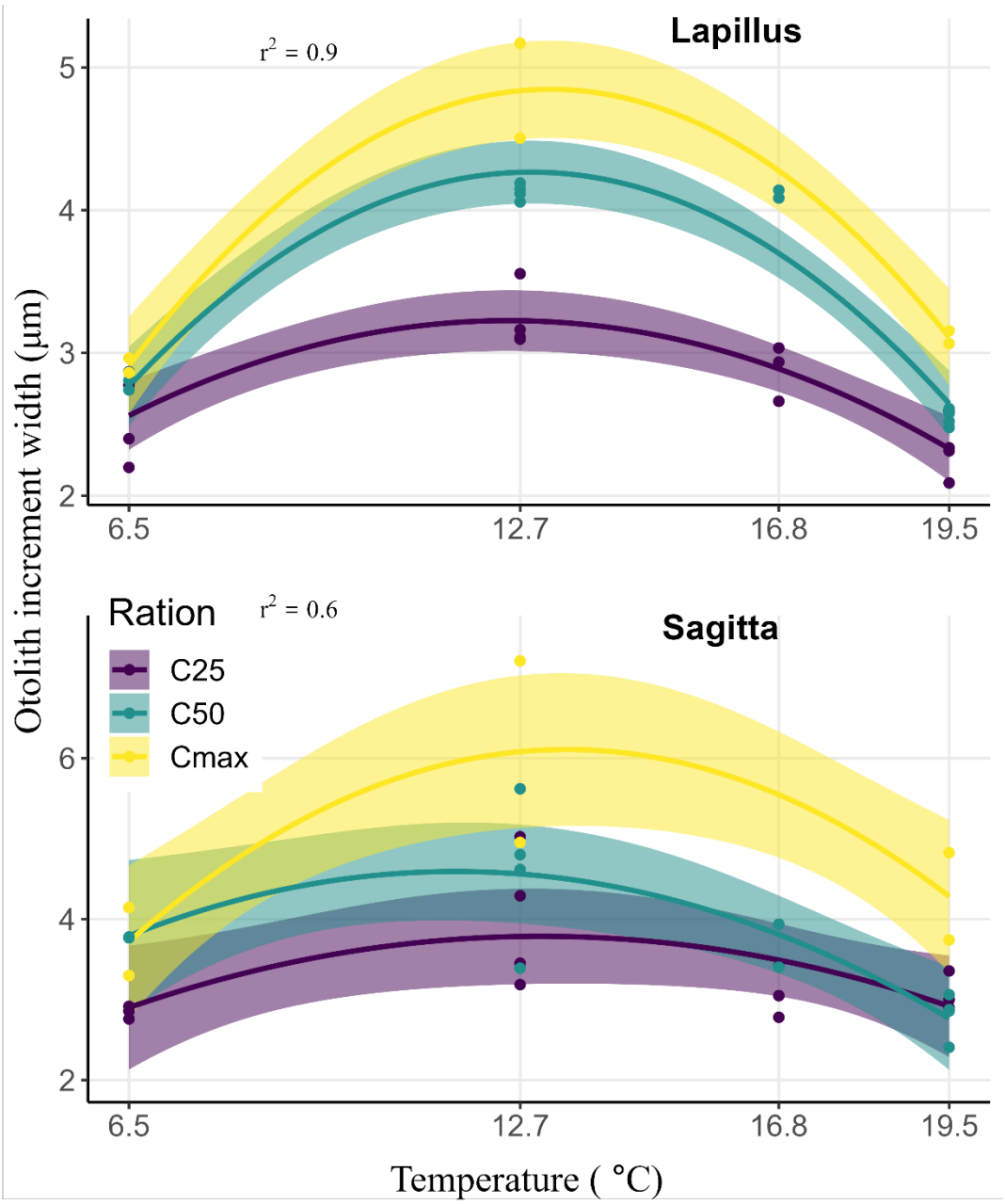


Figure 5. Average daily increment widths of lapillus and sagitta collected from juvenile sablefish reared in varying temperature and feed-ration trials. Lines and intervals represent fitted quadratic equations and 95% confidence intervals. Increments were only measured during the last 30 days of the trial.

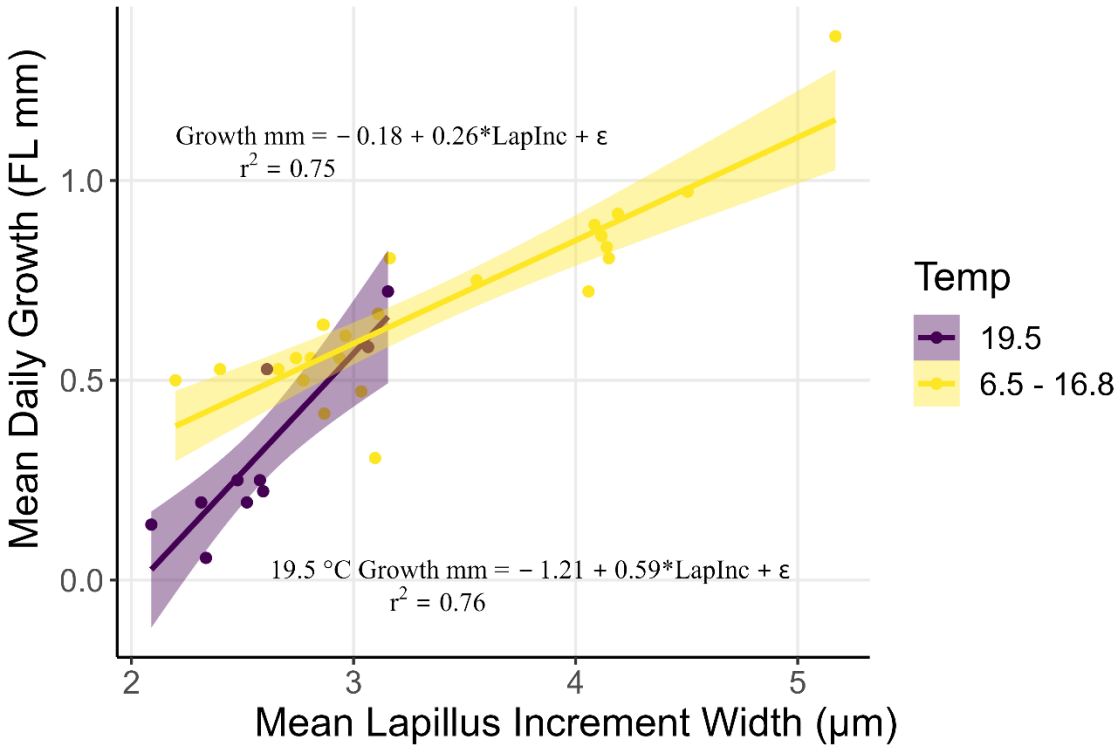


Figure 6. Observed mean daily juvenile sablefish fork length (FL) growth vs. mean daily lapillus increment width across temperature treatments. A significantly different slope (more steep) was only observed at 19.5 °C and only within the lapillus.

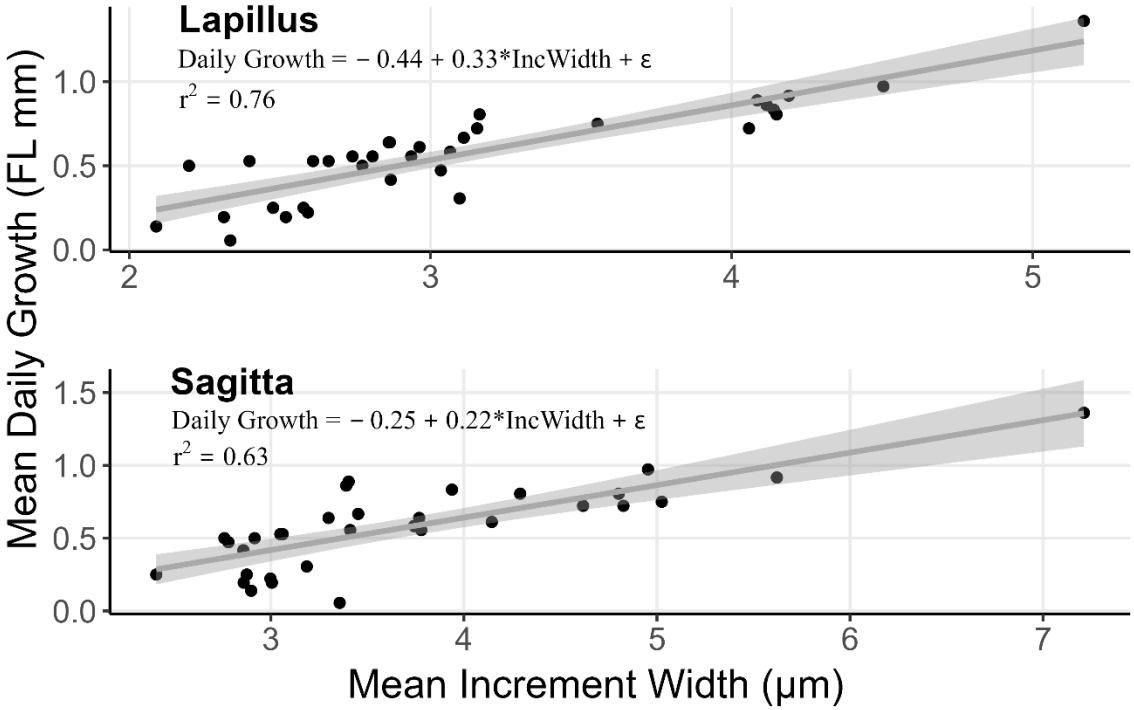
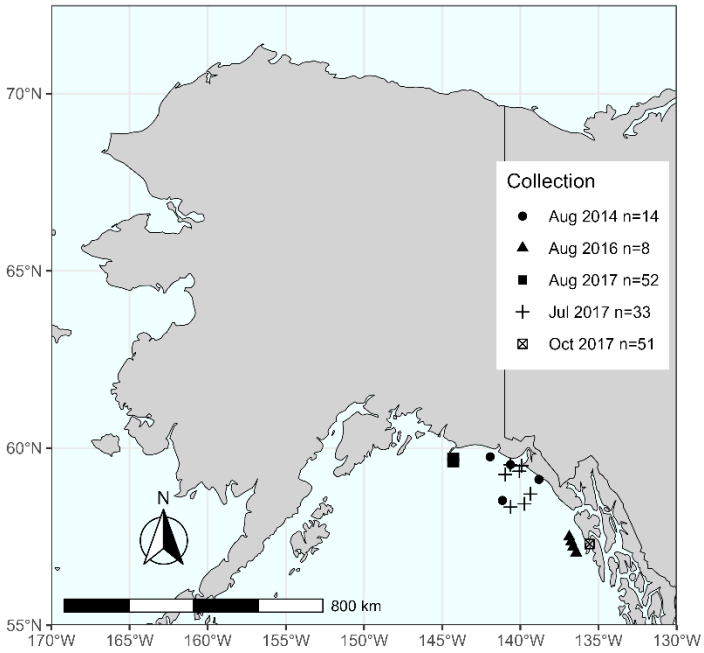


Figure 7. Observed mean daily juvenile sablefish fork length (FL) growth vs. mean daily increment width for both structures.



Supplemental Figure 1. Collection map by month and year demonstrating the location of capture and number of individuals used for this study.