

1 **Density-dependent effects of eastern Kamchatka pink salmon (*Oncorhynchus gorbuscha*)**
2 **and Japanese chum salmon (*O. keta*) on age-specific growth of western Alaska chum**
3 **salmon**

4
5 **Running title:** Competition among pink and chum salmon populations

6
7 Tessa J. Frost^{1,4}, Ellen M. Yasumiishi², Beverly A. Agler³, Milo D. Adkison¹, and Megan V.
8 McPhee^{1,5}

9
10
11 ¹College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau, Alaska, USA

12
13 ²Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and
14 Atmospheric Administration, Juneau, Alaska, USA

15
16 ³Alaska Department of Fish and Game, Mark, Tag, and Age Lab, Juneau, Alaska, USA

17
18 **Acknowledgements:**

19 We thank B. Beckman (NOAA) and N. Davis for their input during development and realization
20 of this research, Dave Nicolls (NOAA) for preparing the Bering Sea scales for this project, and
21 John Baker, Megan Lovejoy, and Lorna Wilson (ADF&G) for reading and conducting quality
22 control analysis on Kuskokwim River scales. We also thank two anonymous reviewers for
23 comments that improved the manuscript. This study was funded by the Pollock Cooperative
24 Conservation Research Center, project number 14-02. The views expressed in this paper do not
25 necessarily reflect those of the funder.

26
27 **Conflict of Interest:** The authors do not have any conflicts of interest related to this work.

28
29 **Data Availability Statement:** Data are available from the authors upon reasonable request.
30 Some of the data are subject to privacy restrictions.

31
32

⁴ Present address: Southern Southeast Regional Aquaculture Association, Ketchikan, Alaska,
USA

⁵ Corresponding author; mvmcphee@alaska.edu

33 **ABSTRACT**

34 Hatcheries release > 4.5 billion juvenile Pacific salmon (*Oncorhynchus* spp.) into the North
35 Pacific Ocean annually, raising concerns about competition with wild salmon populations. We
36 used retrospective scale analysis to investigate how the growth of chum salmon (*O. keta*) from
37 western Alaska is affected by the abundance of chum salmon from Japanese hatcheries and wild
38 pink salmon (*O. gorbuscha*) from the Russian Far East. Over nearly five decades, the growth of
39 Kuskokwim River chum salmon was negatively correlated with the abundance of Japanese
40 hatchery chum salmon after accounting for the effects of sex and spring/summer sea surface
41 temperature in the Bering Sea. An effect of wild eastern Kamchatka pink salmon abundance on
42 the growth of Kuskokwim River salmon was detectable but modest compared to the intraspecific
43 competitive effect. A decrease in Japanese hatchery chum salmon releases in 2011-2013 was not
44 associated with increased growth of Bering Sea chum salmon. However, the abundance of wild
45 chum salmon from the Russian Far East increased during that time, possibly obscuring reduced
46 competition with hatchery chum salmon. Our results support previous evidence that chum
47 salmon are affected by intraspecific competition, and to a lesser extent interspecific competition,
48 in the North Pacific, underscoring that the effects of salmon hatchery production transcend
49 national boundaries.

50

51

52 **Keywords** (7): aquaculture; Bering Sea; competition; growth, hatcheries, North Pacific;
53 retrospective analysis

54

55 1 | INTRODUCTION

56

57 Abundance of Pacific salmon (*Oncorhynchus* spp.) has been increasing in North America
58 and Asia since the late 1970s, with record catches of pink salmon (*O. gorbuscha*) and chum
59 salmon (*O. keta*) beginning in the 1990s (Ruggerone & Irvine, 2018). Increases in salmon
60 abundance are attributed to favorable ocean growing conditions and increased hatchery output,
61 resulting in nearly twice as many salmon in the North Pacific Ocean during 1990-2005 compared
62 to 1952-1975. Despite favorable ocean conditions, decreases in growth rate and delayed maturity
63 have been observed throughout the chum salmon's range (Ishida, Kaeriyama, McKinnell, &
64 Nagasawa 1993; Ruggerone, Agler, & Nielsen 2011). Highly abundant Asian pink and chum
65 salmon in the Bering Sea may be driving density-dependent effects on salmon populations from
66 around the Pacific Rim (Cline, Ohlberger, & Schindler, 2019).

67 Chum salmon are widely distributed in the North Pacific Ocean regardless of stock of
68 origin (Seeb, Crane, Kondzela, et al. 2004; Myers, Klovach, Gritsenko, et al. 2007; Myers,
69 Walker, Davis, et al., 2009; Sato, Moriya, Azumaya, & Nagoya 2009). Chum salmon head to sea
70 soon after emergence and exhibit variable age at maturity, returning to spawn between two and
71 five years of age (Salo, 1991). Western Alaska chum salmon migrate between summer feeding
72 grounds in the Bering Sea and overwintering grounds in the Gulf of Alaska (Urawa, Sato, Crane,
73 Agler, et al. 2009). Japanese chum salmon exhibit a similar migration pattern, with the exception
74 of their first winter at sea which is spent in the western North Pacific Ocean (Urawa, 2004).
75 These migration patterns may lead to competition between Japanese chum salmon and western
76 Alaska chum salmon (after their first year at sea) when prey resources are limited (Ishida et al.,
77 1993).

78 Pink salmon are thought to be strong competitors due to their abundance (accounting for
79 ~ 60% of anadromous Pacific salmon; Heard, 1991; Ruggerone, Zimmerman, Myers, Nielsen, &
80 Rogers, 2003) and high prey consumption rates necessary to sustain rapid growth (Ruggerone &
81 Nielsen, 2005). Indirect evidence, based on correlative analysis and strong even/odd-year
82 abundance differences associated with the biennial life cycle of pink salmon, has been taken to
83 suggest that they can drive variation in zooplankton abundance and species composition (Batten,
84 Ruggerone, & Ortiz, 2018), depress the growth of sockeye salmon *O. nerka* (Ruggerone et al.,
85 2003; Ruggerone, Agler, Connors, et al., 2016; but see McKinnell & Reichardt, 2012), and
86 influence reproductive success in seabirds (Springer & van Vliet, 2014). Direct estimates of pink

87 salmon abundance have been linked to reduced growth of chum salmon (Agler, Ruggerone,
88 Wilson, & Mueter, 2013) and productivity of sockeye salmon (Ruggerone & Connors, 2015;
89 Ruggerone et al., 2016). Chum salmon, the second-most abundant species of Pacific salmon, also
90 appear to exert intraspecific competitive effects on growth within (Ishida et al., 1993) and among
91 (Agler et al., 2013; Ruggerone et al., 2011) populations. But with less inter-annual contrast in
92 abundance, the competitive effects of chum salmon are more difficult to detect and have received
93 less study compared to pink salmon.

94 Understanding the effects of competition on growth and life history of Pacific salmon is
95 an unresolved but consequential issue, particularly as hatcheries around the Pacific Rim continue
96 to release billions of juvenile salmon into the North Pacific every year (NPAFC, 2020). Here, we
97 focus on potential competitive effects on chum salmon stocks originating from western Alaska,
98 including the watersheds of Norton Sound and the Yukon and Kuskokwim Rivers. Unexpected
99 declines in Chinook (*O. tshawytscha*) and chum salmon populations in western Alaska between
100 1997-2002 prompted Alaska to declare a “fisheries disaster” (Krueger, Zimmerman, & Spaeder,
101 2009). Periodic reductions in harvests of salmon in western Alaska continue to have detrimental
102 economic and cultural consequences for rural Alaskan communities (Loring & Gerlach, 2010). It
103 is therefore important to understand how competition might affect regional chum salmon
104 populations.

105 We used retrospective analysis of scale growth to investigate the relationship between
106 growth of chum salmon, known to originate from the Kuskokwim River in western Alaska or to
107 rear in the Bering Sea, and the abundance of Asian pink and chum salmon, specifically two
108 major stocks: Japanese hatchery chum salmon, and pink salmon from eastern Kamchatka. The
109 correlation between scale radius and fish length allowed us to examine growth during defined
110 periods of ocean residence (Yasumiishi, Criddle, Helle, Hillgruber, & Mueter, 2016) and
111 therefore make specific predictions about the effects of competition on growth patterns. First, we
112 predicted that competition should manifest in reduced growth of Kuskokwim River chum salmon
113 from the second year of growth at sea onwards, but not during the first year of growth at sea
114 when these populations would have minimal overlap with Asian populations (Agler et al., 2013).
115 Second, we examined growth of chum salmon in the Bering Sea in relation to reduced abundance
116 of Japanese chum salmon associated with the Tōhoku earthquake and tsunami of 2011. This
117 disaster destroyed a number of hatcheries along the Pacific coast, reducing the numbers and

118 subsequent survival of hatchery chum salmon released that spring (Watanabe, Sasaki, Saito, &
119 Ogawa, 2015). Hatchery chum salmon releases were reduced in 2012 and 2013 as well (NPAFC,
120 2020). We hypothesized that this decrease in hatchery chum salmon production would result in
121 increased growth of chum salmon in the Bering Sea during years 2012-2016. In both cases, we
122 modeled competition effects while accounting for covariates expected to influence growth in
123 chum salmon: sex and age at maturity (Morita, Morita, Fukuwaka, & Matsuda, 2005) and sea-
124 surface temperatures (SST) in spring (Wechter, Beckman, Andrews, Beaudreau, & McPhee,
125 2017) and/or summer (Mueter, Peterman, & Pyper 2002).

126 The two-pronged approach we took provided additional insight into competition among
127 salmon in the North Pacific. First, by treating the first year of growth of Kuskokwim River chum
128 salmon as a ‘counterfactual’ (i.e., little to no competition with Asian pink and chum salmon), we
129 were better able to assess the possibility that spurious statistical associations between growth and
130 Asian pink and chum salmon abundance indices arose from coinciding time series, which can
131 confound inferences about causal effects of competition (e.g., Cunningham, Adkison, &
132 Westley, 2018). Second, the sharp decline in Japanese hatchery chum salmon beginning with the
133 2011 earthquake provided a way to test for density dependence in the Bering Sea against a
134 backdrop of limited contrast in hatchery releases of chum salmon over the previous three decades
135 (NPAFC, 2020), which has hampered efforts to understand the competitive effects of hatchery
136 chum salmon.

137

138

139 **2 | METHODS**

140

141 **2.1 | Study populations**

142

143 We analyzed two collections (‘Kuskokwim River’ and ‘Bering Sea’) of scales from chum
144 salmon that rear in the Bering Sea. The Kuskokwim River samples were collected by the Alaska
145 Department of Fish and Game (ADF&G) from mature chum salmon captured in commercial and
146 test fisheries, using set and drift gillnets with mesh sizes ≤ 15 cm (Bue, 2005), in district W-1
147 near Bethel, Alaska, in 1963 and 1968 – 2010 (Figure 1a). This dataset represented fish that
148 survived their ocean residence and provided stock-specific information on temporal trends in
149 growth. We targeted 25 samples for each sex and dominant age (4 or 5 years old) combination.

150 The Bering Sea dataset was composed of immature and maturing chum salmon caught
151 incidentally in the Bering Sea commercial trawl fishery for walleye pollock *Gadus*
152 *chalcogrammus*. Scales were collected by fishery observers deployed by the National Oceanic
153 and Atmospheric Administration (NOAA) on vessels and processing plants (Chilton, 2016). The
154 Bering Sea dataset included chum salmon captured within 52°N-60°N, 160°W-175°W (Figure
155 1a) from 16-31 July of each year, 2001-2016. This collection included chum salmon from an
156 uncharacterized mixture of populations (including hatchery origin) that were intercepted in the
157 Bering Sea prior to their homeward migration. Bering Sea sampling was opportunistic, with
158 sample sizes depending on the number of salmon intercepted in the pollock fishery.

159 160 **2.2 | Scale measurements**

161
162 Annual growth increments (Figure 1b) were measured from Kuskokwim chum salmon
163 scales ($n = 3,742$; Supporting Information Table S1) by ADF&G personnel following methods
164 described by Hagen, Oxman, & Agler (2001) and Agler et al. (2013). Briefly, images of salmon
165 scales were scanned from acetate impressions using an Indus 4601-11 Screen Scan microfiche
166 reader and measured using Image-Pro Premier 9.0 software with a customized application. Two
167 readers read a majority (91%) of the Kuskokwim scales, and their measurements were similar. A
168 randomly selected set of Kuskokwim scales ($n = 50$) was re-measured by an independent reader
169 to test for a reader effect using multiple analysis of variance (MANOVA) of growth
170 measurements and reader identity.

171 Annual growth increments were measured from Bering Sea chum salmon scales ($n =$
172 $1,845$; Supporting Information Table S2) as described by AFSC (2017). Acetate impressions
173 made of scales mounted on gum cards were scanned at 24x magnification using Z Scan 46-II
174 Image Scanner through NOAA's imaging lab and digitized using Image-Pro Plus 7.0 software
175 with a customized application. All Bering Sea scales were measured by a single reader.

176 We followed the same scale-quality criteria for both collections. A scale was only
177 measured if: 1) the scale came from the "preferred" zone of the fish (Hagen et al., 2001); 2) age,
178 sex, and length data could be matched to the scale; 3) the scale was not regenerated; 4) the annuli
179 were clearly visible and defined; and 5) the scale could be measured along its longest axis.
180 Individual fish lacking scales meeting these criteria were not included in the analysis. We
181 followed the growth-increment notation of Morita & Fukuwaka (2006) where g_i indicates growth

182 during the first year at sea, g_2 describes growth accrued during the second year at sea, and so on.
183 The width of each growth increment was measured as the distance between adjacent annuli
184 (Figure 1b).

185

186 **2.3 | Indices of eastern Kamchatka pink salmon and Japanese chum salmon abundance**

187

188 Analyses focused on interactions in the Bering Sea between western Alaska chum salmon
189 and the dominant stocks of pink and chum salmon during the study period: Japanese chum
190 salmon, assumed to be entirely of hatchery origin, and eastern Kamchatka pink salmon primarily
191 of wild origin (Urawa et al., 2004; Urawa et al., 2009; Myers et al., 2007; Irvine & Ruggerone,
192 2016). Abundance estimates (Figure 2a,b) were obtained from Irvine & Ruggerone (2016); see
193 also Ruggerone & Irvine (2018). Specifically, we used their estimates of the number of salmon
194 (including those harvested) returning to coastal waters for Japanese chum salmon and pink
195 salmon from the east coast of Kamchatka. These numbers corresponded to the ‘Japan’ column in
196 Table 9 and the ‘EKam’ column in Table 8, respectively, of Irvine & Ruggerone (2016).

197 Abundance indices were transformed by natural logarithm prior to analysis. Irvine & Ruggerone
198 (2016) also provided estimates of total biomass (immature and maturing) of salmon by species
199 and region; however, these estimates required additional, untested assumptions and were highly
200 correlated with returning adult abundance estimates for both Japanese chum salmon and pink
201 salmon from eastern Kamchatka ($r > 0.99$), so we used returning adult abundance estimates.

202

203 **2.4 | Environmental covariates**

204

205 To account for environmental influences on chum salmon growth represented by SST, we
206 developed a seasonal index for spring and summer SST in the Bering Sea (Figure 2c, d).

207 Temperature data were obtained from NOAA’s Earth System Research Laboratory’s Physical
208 Sciences Division website (available from <https://www.esrl.noaa.gov/psd/cgi->

209 [bin/data/timeseries/timeseries1.pl](https://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl)), based on National Centers for Environmental

210 Prediction/National Center for Atmospheric Research gridded reanalysis data (Kalnay et al.,

211 1996). Summer SST was averaged across July and August in the central Bering Sea (54.3°-

212 60.0°N, 170.6°-178.1°W; Figure 1a). This spans an area used by immature chum salmon during

213 their summer feeding months (Echave, Eagleton, Farley, & Orsi, 2012) and encompasses both

214 shelf and slope habitats. Spring SST was based on average SST during April and May at the M2
215 mooring buoy in the southeastern Bering Sea (56.87°N, 164.06°W; Figure 1a).

216 The timing of the spring phytoplankton bloom in the eastern Bering Sea is strongly
217 correlated with sea-ice extent (Sigler, Stabeno, Eisner, Napp, & Mueter, 2014). NOAA's ice
218 retreat index (IRI; available from www.beringclimate.noaa.gov/data/index.php) at the M2 buoy
219 did not span our entire study period, so we used the Spring SST index as a proxy for the date of
220 sea-ice retreat (justified by linear regression between IRI and mean April/May SST at M2, $R^2 =$
221 0.72 , $p < 0.001$; see also Wechter et al., 2017).

222
223

224 **2.5 | Statistical analyses**

225

226 Linear mixed-effects models were fit using the lme4 V1.1-12 package (Bates, Maechler,
227 Bolker, & Walker, 2015) in the statistical language R, v. 3.3.3 (R Core Team, 2017). Prior to
228 modeling, all variables were normalized (mean = 0, SD = 1) to facilitate comparison of model
229 coefficients. Each annual growth increment was normalized separately within each of the two
230 datasets (Kuskokwim River and Bering Sea). For objective 1 (growth of Kuskokwim River chum
231 salmon), we used the second-order Akaike information criterion (AICc) to compare full models
232 to models with all possible combinations of abundance indices and covariates, including null
233 models (random effects only). For objective 2, in which we tested for a signal of reduced
234 Japanese hatchery releases 2011-2013 on chum salmon growth in the Bering Sea, we used
235 likelihood-ratio tests to determine whether a model containing the reduction in releases fit the
236 data significantly better than the model without the reduction. Model comparison (for differing
237 fixed effects) was conducted on models fit with maximum likelihood; coefficients of selected
238 models were estimated with restricted maximum likelihood (Zuur, Ieno, Walker, Saveliev, &
239 Smith, 2009).

240 Preliminary analysis indicated that spring and summer SSTs were moderately correlated
241 in the Kuskokwim dataset (Pearson's $r = 0.53$) but more strongly correlated over the Bering Sea
242 dataset (Pearson's $r = 0.73$). Consequently, we included only spring SST in the models for
243 objective 2, as it showed considerable contrast over the study period (Figure 2) and might better
244 capture environmental variation affecting chum salmon growth (Wechter et al., 2017).

245 To determine if growth of western Alaska chum salmon varied with Asian pink and chum
246 salmon abundance (objective 1; Kuskokwim dataset), linear mixed-effects models were fit
247 separately for each growth increment $g_2 - g_4$ to examine the influence of predictor variables on
248 inter-annual variability in growth. The model (1) for each growth increment was:

$$249 \quad g_{iy} = \beta_1 Sex_i + \beta_2 Age_i + \beta_3 SprSST_y + \beta_4 SumSST_y + \beta_5 JpnChum_y + \beta_6 KamPink_y +$$
$$250 \quad \beta_7 (JpnChum * KamPink)_y + \alpha_y + \varepsilon_{iy} \quad (1)$$

251
252 where g_{iy} was the size of the growth increment of individual i during calendar year y of growth,
253 Sex_i was a factor (male vs. female), Age_i (factor: 4 vs. 5 years old) was age at maturity of
254 individual i ; $SprSST_y$ was spring SST during year y , $SumSST_y$ was summer SST during year y ,
255 $JpnChum_y$ was the abundance of Japanese chum salmon during year y , $KamPink_y$ was the
256 abundance of eastern Kamchatka pink salmon in year y , and the interaction between $JpnChum_y$
257 and $KamPink_y$ allowed for the competitive effect of one stock being dependent on the abundance
258 of the other stock. The random effect α_y accounted for correlated growth among individuals
259 growing during the same calendar year y , and ε_{iy} represented the residual variance. Age was not
260 included in the full model for g_4 (present only in age-5 fishes). The random intercepts α_y and the
261 residuals ε_{iy} were assumed to be independent and normally distributed with means of zero and
262 variances σ_a^2 and σ_ε^2 , respectively; these assumptions were checked with model diagnostic plots
263 (not shown). We repeated the same modeling approach using g_1 as a counterfactual response
264 variable, hypothesizing no effect of competition with Asian pink and chum salmon.
265

266 To determine if reduced Japanese hatchery chum salmon releases in 2011-2013 resulted
267 in increased growth of Bering Sea chum salmon (objective 2; Bering Sea dataset), linear mixed-
268 effects models were fit separately to each growth increment $g_2 - g_4$ to examine the influence of
269 reduced hatchery output while accounting for other sources of variation (sex, age, and spring
270 SST). Because the decrease in Japanese hatchery outputs occurred 2011-2013, the effect was
271 anticipated during growth years 2012-2016. The model (2) for each growth increment was:

$$272 \quad g_{iy} = \beta_1 Period_y + \beta_2 Sex_i + \beta_3 Age_i + \beta_4 SprSST_y + \alpha_y + \varepsilon_{iy} \quad (2)$$

273
274

275 where *Period_y* was a factor identifying years prior to versus during the period affected by
276 decreased hatchery chum salmon releases; *Age* represented age at capture (including immature
277 and maturing fish); and the other variables are as described for the previous model. *Age* was not
278 included in the full model for g_4 (present only in age-5 fishes). Likelihood-ratio tests were used
279 to determine whether addition of the reduced-release period significantly improved fit over a
280 model containing only sex, age, and spring SST; tests were evaluated at $\alpha = 0.05$. Model
281 assumptions, including no temporal autocorrelation, were checked with diagnostic plots (not
282 shown).

283

284 3 | RESULTS

285

286 Sample size varied by population, sex, age class, and growth increment (Supporting
287 Information, tables S1 and S2). Target sample size was generally achieved for Kuskokwim River
288 chum salmon except for the 1963 and 1969 brood years, which were represented by < 20
289 individuals each. No reader effect was found over the entire scale (MANOVA, $p = 0.97$) or for
290 single growth increments (ANOVA, $p > 0.5$ for all) for Kuskokwim River scales. Bering Sea
291 sample sizes ranged from 7 to 120 per sex, year, and growth increment, with g_4 tending to have
292 fewer samples than g_2 and g_3 . Average sizes of age-specific growth increments showed different
293 relationships over time, with only g_1 in the Kuskokwim River dataset showing an upward trend,
294 and g_4 in the Kuskokwim River dataset and g_3 in the Bering Sea dataset showing downward
295 trends (Supporting Information, figures S1 and S2).

296 In Kuskokwim River chum salmon, the top model for g_1 (no expected competition)
297 contained only a positive correlation with summer SST. Summer SST appeared in all of the best-
298 supported models for g_1 (those within two AICc units of the top model; Table 1). Three of the six
299 best-supported models included salmon abundance indices, but in all cases the coefficients were
300 positive and small (Figure 3). The null model for g_1 was >9 AICc units above that of the top
301 model (Supplementary Information, Table S3).

302 After the first year at sea, Kuskokwim River chum salmon growth decreased with
303 increasing abundance of Japanese chum salmon (Figure 4); additionally, faster growth was
304 associated with males and earlier-maturing individuals (Table 1). All of the best-supported
305 models for growth increments $g_2 - g_4$ included a negative correlation with Japanese chum salmon

306 abundance (Table 1). The coefficients for Japanese chum salmon abundance were consistently
307 more negative than those for Kamchatka pink salmon abundance, and null models were > 100
308 AICc units away from the top models (Supporting Information, Table S3). Coefficients for
309 Kamchatka pink salmon abundance and its interaction with Japanese chum salmon abundance
310 differed among the growth increments (Figure 3). For g_2 , the coefficient for Kamchatka pink
311 salmon abundance was slightly positive (included only in the fourth-ranked model), and no
312 interaction between Japanese chum salmon and Kamchatka pink salmon abundances appeared in
313 any of the best-supported models. In contrast, the coefficient for pink salmon abundance was
314 consistently negative for both g_3 and g_4 , and a positive interaction between the two salmon
315 abundance indices appeared in the three highest-ranking models for g_3 and in the fourth-ranked
316 model for g_4 .

317 Sea-surface temperature appeared in many of the best-supported models for increments
318 $g_2 - g_4$ in Kuskokwim River chum salmon, but differed among increments (Supplementary
319 Information, Table S3). For g_2 , the top model did not contain SST, but a negative correlation
320 with spring SST was included in the second-ranked model, a positive correlation with summer
321 SST was in the third-ranked model, and the fifth-ranked model contained both spring and
322 summer SST. Positive coefficients for spring SST appeared in the top models for both g_3 and g_4 ,
323 while summer SST (with positive coefficients) appeared only in the third-ranked model for g_3
324 and the sixth- and seventh-ranked models for g_4 .

325 Estimated parameters from the models for growth increments $g_2 - g_4$ in Bering Sea chum
326 salmon with and without accounting for decreased hatchery releases in 2011-2013 are shown in
327 Table 2. For g_2 and g_4 , the simpler model without the reduced-release period was preferred
328 (likelihood-ratio tests, $P > 0.5$). For g_3 , the model with the reduced-release period was preferred
329 ($P = 0.04$), but its coefficient was negative, opposite of the hypothesized effect. As in the
330 Kuskokwim dataset, faster growth was associated with males and younger fish. Growth during g_2
331 $- g_4$ was positively related to spring SST, but coefficients were < 0.20 (Table 2).

332

333 4 | DISCUSSION

334

335 Based on hypothesized competitive effects of wild Kamchatka populations of pink
336 salmon and chum salmon released by Japanese hatcheries, we expected reduced growth of

337 western Alaska chum salmon after their first year at sea during periods of high abundance of
338 these Asian salmon stocks. We found strong support that chum salmon returning to the
339 Kuskokwim River compete with Japanese chum salmon, as evidenced by the negative
340 correlation between the size of hatchery releases and marine growth ($g_2 - g_4$), and the absence of
341 such a correlation with g_1 , in chum salmon returning to the Kuskokwim River 1963-2010.
342 Despite the hypothesis that pink salmon are strong competitors with profound consequences on
343 marine food webs (Ruggerone & Nielsen, 2004; Springer et al., 2018), the effect of eastern
344 Kamchatka pink salmon on Kuskokwim River chum salmon growth was modest compared to the
345 effect of Japanese chum salmon. Agler et al. (2013) examined g_1 and g_3 in chum salmon
346 returning to the Yukon River, to the north of the Kuskokwim River, and to Bristol Bay to the
347 south. They similarly detected a greater competitive effect of Asian chum salmon than Asian
348 pink salmon on g_3 (and no effect on g_1). Our results suggest that these findings might be broadly
349 applicable to chum salmon populations from across western Alaska.

350 We detected no negative effect of eastern Kamchatka pink salmon abundance on growth
351 of Kuskokwim River chum salmon during their second year at sea, but we did find evidence for
352 competitive effects on later marine growth. This was particularly apparent in g_3 , for which three
353 of the four best-supported models included a positive interaction between eastern Kamchatka
354 pink salmon abundance and the magnitude of Japanese hatchery chum salmon releases. The
355 interaction indicated that Kuskokwim River chum salmon g_3 growth was particularly poor in
356 years when the combined abundance of these two stocks was particularly high. Chum salmon are
357 able to mitigate competition with pink salmon by feeding on gelatinous zooplankton not targeted
358 by other salmon (Tadokoro, Ishima, Davis, Ueyenagi, & Sugimoto, 1996). However, as chum
359 salmon grow they consume more fish (Karpenko, Volkov, & Koval, 2007), so perhaps by their
360 third year at sea Kuskokwim River chum salmon are less able to switch diets in order to avoid
361 competition with pink salmon, particularly in years when Japanese chum salmon is also
362 abundant. Chum salmon might adjust their oceanic distribution southward to avoid pink salmon
363 (Azumaya & Ishida, 2000), but perhaps during later growth years, homeward migration
364 pathways prevent Kuskokwim River chum salmon from doing so.

365 While Kuskokwim River chum salmon appear to compete with Japanese hatchery chum
366 salmon, a steady increase in hatchery production through the 1990s followed by little variation
367 has provided limited contrast for quantifying the extent of competition. We used a rapid decrease

368 in Japanese hatchery chum salmon production in 2011-2013 to contrast growth of chum salmon
369 intercepted in the Bering Sea during periods of normal (2001-2011) and low (2012-2016)
370 Japanese hatchery chum salmon releases. Contrary to our expectations and to our findings with
371 the Kuskokwim River dataset over a longer period, chum salmon in the Bering Sea did not
372 exhibit increased growth following the reduction in Japanese hatchery chum salmon production.
373 This contradiction could be resolved in several ways. First, the reduction in Japanese hatchery
374 chum salmon outputs may have been too small to cause a detectable effect on growth of chum
375 salmon in the Bering Sea. Second, our Bering Sea samples came from the Alaskan walleye
376 pollock trawl fishery. If these samples were size selective, changes in growth might have gone
377 undetected with this method of sampling. Finally, we observed a substantial increase in wild
378 chum salmon abundance over the study period for the Bering Sea dataset (2001-2016). Wild
379 Russian chum salmon increased by 264% from 2005-2015, reducing the proportion of hatchery
380 chum salmon from 62% in 2005 to 45% of total chum salmon abundance in 2015 (Ruggerone &
381 Irvine, 2018). Russian chum salmon follow an ocean migration pattern similar to that of Japanese
382 and western Alaska chum salmon (Urawa et al., 2009), and thus in the years that western Alaska
383 chum salmon were hypothesized to have experienced relief from competition with Japanese
384 hatchery chum salmon, they might have experienced increased competition with Russian chum
385 salmon. Future analyses of chum salmon growth should account for the abundance of Russian
386 chum salmon populations in addition to Japanese hatchery chum salmon.

387 The relationship between chum salmon growth and spring and summer SST in the Bering
388 Sea was smaller than expected. However, previous research has shown that the effects of SST on
389 chum salmon growth are variable. In southeast Alaska, Yasumiishi et al. (2016) observed a
390 positive relationship between g_2 growth and cooler summer/fall SST, but after accounting for
391 density-dependent effects (growth was more strongly correlated with population abundance),
392 growth was positively associated with SST. In contrast, Agler et al. (2013) observed a negative
393 relationship between western Alaska chum salmon growth and Gulf of Alaska SST. Analysis of
394 Kwiniuk River chum salmon in Norton Sound, western Alaska, detected no correlation between
395 $g_2 - g_4$ scale growth in four- and five-year old chum salmon and SST in the North Pacific Ocean
396 during winter, spring, or summer (Ruggerone & Agler, 2008). These contradictory findings
397 suggest that the relationship between salmon growth and SST is complex and may not be linear
398 across the range of variation experienced by chum salmon populations across years. Our

399 understanding might be limited by lack of information on population-specific ocean
400 distributions. Furthermore, the diving behavior of chum salmon (Azumaya & Nagasawa, 2009)
401 suggests that temperature measured at the ocean's surface may not be the best proxy for
402 environmental conditions affecting salmon growth and age/size trends (G. Brown, Department of
403 Fisheries and Oceans Canada, pers. comm.).

404 Both Kuskokwim River and Bering Sea chum salmon experienced decreases in growth
405 during a time of maximum releases of chum salmon by Japanese hatcheries. Similar size declines
406 have been observed in chum salmon populations throughout the Pacific Rim, including Russia,
407 Japan, Canada, and the United States (e.g., Ishida et al., 1993; Bigler, Welch, & Helle, 1996;
408 Zavolokin, Zavolokina, & Khokhlov, 2009; Ruggerone et al., 2011; Yasumiishi et al., 2016),
409 pointing to shared causes in the North Pacific. Density-dependent effects of Asian hatchery chum
410 salmon have been detected on both North American (Helle, Martinson, Eggers, & Gritsenko,
411 2007; Ruggerone et al., 2011; Agler et al., 2013) and Asian (Ishida et al., 1993; Zaporozhets &
412 Zaporozhets, 2004) chum salmon populations. In western Alaska, increased production of Asian
413 hatchery chum salmon was significantly related to reduced adult length at age, productivity, and
414 delayed age at maturity of Norton Sound chum salmon (Ruggerone et al., 2011). The reduced
415 growth of Kuskokwim chum salmon we observed during g_2 may contribute to increases in chum
416 salmon age at maturity, as slower growing salmon tend to mature at an older age (Morita et al.,
417 2005; Siegel, McPhee, & Adkison, 2017). Unfortunately, the abundance and age data collected
418 from chum salmon returning to the Kuskokwim River were of insufficient quality for estimating
419 age composition by brood year (H. Hamazaki, ADF&G, pers. comm.), so we were unable to
420 directly test this hypothesis.

421 Testing for density dependence in the open ocean is difficult, but our analyses provide
422 insight into the potentially adverse consequences of increasing hatchery salmon outputs into the
423 North Pacific ecosystem. Over the longer time series afforded by the Kuskokwim River chum
424 salmon scale collection, we found strong support for competitive effects of Japanese hatchery
425 chum salmon and to a lesser extent, competitive effects of wild pink salmon from eastern
426 Kamchatka. That we did not observe increased growth of Bering Sea chum salmon when the
427 production of Japanese hatchery chum salmon was reduced in 2011-2013 may be because
428 decreases in hatchery outputs were too small to detect a difference in growth, or because the
429 recent increase in wild Russian chum salmon abundance overwhelmed any reduction in Japanese

430 chum salmon abundance. Our study was limited to examining competition with two major Asian
431 stocks of salmon, Japanese hatchery chum salmon and eastern Kamchatka pink salmon, which
432 collectively have comprised up to 52% of Asian pink, chum, and sockeye salmon, and up to 46%
433 of these species in the Bering Sea (based on data in Ruggerone & Irvine, 2018). Western Alaska
434 chum salmon could also compete with other stocks in the Bering Sea, for example, wild pink and
435 sockeye salmon from western Alaska. Future work could incorporate the combined effects of
436 competition from multiple stocks, although including North American stocks would complicate
437 hypotheses about growth during the first year at sea. Despite the limited focus, our study adds to
438 the cumulative evidence indicating that Pacific salmon can experience density dependence in the
439 North Pacific and Bering Sea ecosystems, suggesting that hatchery production cannot continue to
440 increase without some detrimental consequences for wild salmon populations.

441

442 **Author Contributions:** TJJ led data compilation and analysis, interpretation, and drafting of
443 initial manuscript. MVM conceived the initial study design and contributed to analyses,
444 interpretation and writing of manuscript. EMY, BAA, and MDA assisted with analyses,
445 interpretation, and manuscript preparation.

446

447 REFERENCES

448

449 Alaska Fisheries Science Center (AFSC). (2017). *Observer Sampling Manual*. Fisheries
450 Monitoring and Analysis Division, North Pacific Groundfish Observer Program. AFSC, 7600
451 Sand Point Way N.E., Seattle, Washington, 98115. Available from
452 https://www.afsc.noaa.gov/fma/Manual_pages/MANUAL_pdfs/manual2017.pdf [accessed
453 16 February 2018].

454 Agler, B.A., Ruggerone, G.T., Wilson, L.I., & Mueter, F.J. (2013). Historical growth of Bristol
455 Bay and Yukon River, Alaska chum salmon (*Oncorhynchus keta*) in relation to climate and
456 inter- and intraspecific competition. *Deep Sea Research Part II*, 94, 165–177.
457 doi:10.1016/j.dsr2.2013.03.028

458 Azumaya, T. & Ishida, Y. (2000). Density interactions between pink salmon (*Oncorhynchus*
459 *gorbuscha*) and chum salmon (*O. keta*) and their possible effects on distribution and growth
460 in the North Pacific Ocean and Bering Sea. *North Pacific Anadromous Fish Commission*
461 *Bulletin*, 2, 165-174.

462 Azumaya, T., & Nagasawa, T. (2009). Reproduction of short-term vertical movements observed
463 using archival tags on chum salmon (*Oncorhynchus keta*) by a simple model. *North Pacific*
464 *Anadromous Fish Commission Bulletin*, 5, 61–69.

465 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models
466 using lme4. *Journal of Statistical Software*, 67, 1-48. [doi:10.18637/jss.v067.i01](https://doi.org/10.18637/jss.v067.i01)

467 Batten, S. D., Ruggerone, G. T., & Ortiz, I. (2018). Pink Salmon induce a trophic cascade in
468 plankton populations in the southern Bering Sea and around the Aleutian Islands. *Fisheries*
469 *Oceanography*, 27, 548-559.

470 Bigler, B.S., Welch, D.W., & Helle, J.H. (1996). A review of size trends among North Pacific
471 salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 455–
472 465.

473 Bue, D. G. (2005). *Data summary for the Kuskokwim River salmon test fishery at Bethel, 1984-*
474 *2003*. Alaska Department of Fish and Game, Fish. Data Series No. 05-14, Anchorage.
475 Available from <http://www.adfg.alaska.gov/FedAidPDFs/fds05-14.pdf> [accessed 30 January
476 2018].

477 Chilton, L. (2016). *On the front lines of sustainable fisheries*. Available from
478 www.st.nmfs.noaa.gov/observer-home/ [accessed 30 January 2018].

479 Cline, T. J., Ohlberger, J., & Schindler, D. E. (2019). Effects of warming climate and
480 competition in the ocean for life-histories of Pacific salmon. *Nature Ecology & Evolution*, 3,
481 935-042.

482 Cunningham, C. J., Westley, P. A. H., & Adkison, M. D. (2018). Signals of large scale climate
483 drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival
484 revealed with a Bayesian life history model. *Global Change Biology*, 24, 4399-4416.

485 Davis, N. D. (2003). *Feeding Ecology of Pacific Salmon (Oncorhynchus spp.) in the Central*
486 *North Pacific Ocean and Central Bering Sea, 1991-2000*. (Doctoral dissertation). Hokkaido
487 University, Hakodate, Hokkaido, Japan.

488 Debertain, A.J., Irvine, J.R., Holt, C.A., Oka, G., & Trudel, M. (2017). Marine growth patterns of
489 southern British Columbia chum salmon explained by interactions between density-
490 dependent competition and changing climate. *Canadian Journal of Fisheries and Aquatic*
491 *Sciences*, 74, 1077–1087. doi:10.1139/cjfas-2016-0265.

492 Echave, K., Eagleton, M., Farley, E., & Orsi, J. (2012). A refined description of essential fish
493 habitat for Pacific salmon within the U. S. Exclusive Economic Zone in Alaska. U. S.
494 Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-236.

495 Hagen, P., Oxman, D., & Agler, B. (2001). *Developing and deploying a high-resolution imaging*
496 *approach for scale analysis*. NPAFC Doc. 567.

497 Heard, W.R. (1991). Life history of pink salmon (*Oncorhynchus gorbuscha*). In C. Groot and L.
498 Margolis (Eds.), *Pacific Salmon Life Histories* (pp. 119-230). Vancouver: UBC Press.

499 Helle, J.H., Martinson, E.C., Eggers, D.M., & Gritsenko, O. (2007). Influence of salmon
500 abundance and ocean conditions on body size of Pacific salmon. *North Pacific Anadromous*
501 *Fish Commission Bulletin*, 4, 289–298.

502 Irvine, J.R., & Ruggerone, G.T. (2016). *Provisional estimates of numbers and biomass for*
503 *natural-origin and hatchery-origin pink, chum, and sockeye salmon in the North Pacific,*
504 *1952-2015*. NPAFC Doc. 1660. Fisheries and Oceans Canada, Pacific Biological Station and
505 Natural Resources Consultants, Inc. doi:10.13140/RG.2.1.5179.0960.

506 Ishida, Y., Ito, S., Kaeriyama, M., McKinnell, S., & Nagasawa, K. (1993). Recent changes in age
507 and size of chum salmon (*Oncorhynchus keta*) in the North Pacific Ocean and possible
508 causes. *Canadian Journal of Fisheries and Aquatic Sciences*, 50, 290–295. doi:10.1139/f93-
509 033.

510 Kaeriyama, M. (1998). Dynamics of chum salmon, *Oncorhynchus keta*, populations released
511 from Hokkaido, Japan. *North Pacific Anadromous Fish Commission Bulletin*, 1, 90-102.

512 Kaga, T., Sato, S., Azumaya, T., Davis, N.D., & Fukuwaka, M.A. (2013). Lipid content of chum
513 salmon *Oncorhynchus keta* affected by pink salmon *O. gorbuscha* abundance in the central
514 Bering Sea. *Marine Ecology Progress Series*, 478, 211-221. doi:10.3354/meps10179.

515 Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha,
516 S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J.,
517 Mo, K. C., Ropelewski, C., Wang, J., Leetmaa, A., Reynolds, R., Jenne, R., & Joseph, D.
518 (1996). The NCEP/NCAR 40-year reanalysis project. *Bulletin of the Meteorological Society*,
519 77, 437-471.

520 Karpenko, V. I., Volkov, A. F., & Koval, M. V. (2007). Diets of Pacific salmon in the Sea of
521 Okhotsk, Bering Sea, and Northwest Pacific Ocean. *North Pacific Anadromous Fish*
522 *Commission Bulletin*, 4, 105-116.

523 Krueger, C.C., Zimmerman, C.E., & Spaeder, J.J. (2009). Ecology and management of western
524 Alaska Pacific salmon: introduction to the proceedings. *American Fisheries Society*
525 *Symposium*, 70, 3-12.

526 Loring, P.A., & Gerlach, C. (2010). Food security and conservation of Yukon river salmon: Are
527 we asking too much of the Yukon river? *Sustainability*, 2, 2965–2987.
528 doi:10.3390/su2092965.

529 McKinnell, S., & Reichardt, M. (2012). Early marine growth of juvenile Fraser River sockeye
530 salmon (*Oncorhynchus nerka*) in relation to juvenile pink salmon (*Oncorhynchus gorbuscha*)
531 and sockeye salmon abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, 69,
532 1499-1512.

533 Morita, K., & Fukuwaka, M. (2006). Does size matter most? The effect of growth history on
534 probabilistic reaction norm for salmon maturation. *Evolution*, 60, 1516–1521.
535 doi:10.1111/j.0014-3820.2006.tb01230.x.

536 Morita, K., Morita, S.H., Fukuwaka, M., & Matsuda, H. (2005). Rule of age and size at maturity
537 of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus*
538 spp. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 2752–2759.

539 Mueter, F.J., Peterman, R.M., & Pyper, B.J. (2002). Opposite effects of ocean temperature on
540 survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern
541 areas. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 456–463.

542 Myers, K.W., Klovach, N. V., Gritsenko, O.F., Urawa, S., & Royer, T.C. (2007). Stock-specific
543 distributions of Asian and North American salmon in the open ocean, interannual changes,
544 and oceanographic conditions. *North Pacific Anadromous Fish Commission Bulletin*, 4, 159–
545 177.

546 Myers, K.W., Walker, R.V., Davis, N.D., Armstrong, J.L., and Kaeriyama, M. (2009). High seas
547 distribution, biology, and ecology of Arctic-Yukon-Kuskokwim salmon: direction
548 information from high seas tagging experiments, 1954-2006. *American Fisheries Society*
549 *Symposium*, 70, 201-239.

550 North Pacific Anadromous Fish Commission (NPAFC). (2020). *NPAFC Pacific salmon catch*
551 *and hatchery release data*. <https://npafc.org/statistics/> (accessed July 2020).

552 R Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation
553 for Statistical Computing, Vienna, Austria. Available from <https://www.r-project.org/>.

554 Ruggerone, G. T., & Agler, B. A. (2008). *Retrospective analyses of AYK chum and coho salmon*.
555 2008 Arctic Yukon Kuskokwim Sustainable Salmon Initiative Project Product. Natural
556 Resources Consultants, Inc, Seattle, WA and ADF&G Division of Commercial Fisheries,
557 Mark, Tag, and Age Lab, Juneau, AK. pp 1-57.

558 Ruggerone, G. T., Agler, B. A., Connors, B. M., Farley, E. V, Irvine, J. R., Wilson, L. I., &
559 Yasumiishi, E. M. (2016). Pink and sockeye salmon interactions at sea and their influence on
560 forecast error of Bristol Bay sockeye salmon. *North Pacific Anadromous Fish Commission*
561 *Bulletin*, 6, 349–361. <https://doi.org/10.23849/npafcb6/349.361>

562 Ruggerone, G.T., Agler, B.A., & Nielsen, J.L. (2011). Evidence for competition at sea between
563 Norton Sound chum salmon and Asian hatchery chum salmon. *Environmental Biology of*
564 *Fishes*, 94, 149–163.

565 Ruggerone, G. T., & Connors, B. M. (2015). Productivity and life history of sockeye salmon in
566 relation to competition with pink and sockeye salmon in the North Pacific Ocean. *Canadian*
567 *Journal of Fisheries and Aquatic Sciences*, 72, 818–833.
568 <https://doi.org/dx.doi.org/10.1139/cjfas-2014-0134>

569 Ruggerone, G. T., & Irvine, J. R. (2018). Numbers and biomass of natural- and hatchery-origin
570 Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean, 1925 – 2015.
571 *Marine and Coastal Fisheries*, 10, 152–168. <https://doi.org/10.1002/mcf2.10023>

572 Ruggerone, G.T., & Nielsen, J.L. (2004). Evidence for competitive dominance of pink salmon
573 (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. *Reviews in Fish*
574 *Biology and Fisheries*, 14, 371–390. doi:10.1007/s11160-004-6927-0.

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

579 Salo, E.O. (1991). Life history of chum salmon (*Oncorhynchus keta*). In C. Groot and L.
580 Margolis (Eds.), *Pacific Salmon Life Histories* (pp. 231-309). Vancouver: UBC Press.

581 Sato, S., Moriya, S., Azumaya, T., & Nagoya, H. (2009). Stock distribution patterns of chum
582 salmon in the Bering Sea and North Pacific Ocean during the summer and fall of 2002-2004.
583 *North Pacific Anadromous Fish Commission Bulletin*, 5, 29–37.

584 Seeb, L.W., Crane, P.A., Kondzela, C.M., Wilmot, R.L., Urawa, S., Varnavskaya, N. V., & Seeb,
585 J.E. (2004). Migration of Pacific Rim chum salmon on the high seas: insights from genetic
586 data. *Environmental Biology of Fishes*, *69*, 21–36.
587 doi:10.1023/B:EBFI.0000022900.82523.63.

588 Siegel, J.E., McPhee, M.V., & Adkison, M.D. (2017). Evidence that marine temperatures
589 influence growth and maturation of western Alaskan Chinook salmon *Oncorhynchus*
590 *tshawytscha*. *Marine and Coastal Fisheries*, *9*, 441–456.
591 doi:10.1080/19425120.2017.1353563.

592 Sigler, M.F., Stabeno, P.J., Eisner, L.B., Napp, J.M., & Mueter, F.J. (2014). Spring and fall
593 phytoplankton blooms in a productive subarctic ecosystem, the eastern Bering Sea, during
594 1995–2011. *Deep-Sea Research Part II*, *109*, 71–83. doi:10.1016/j.dsr2.2013.12.007.

595 Springer, A. M., & van Vliet, G. B. (2014). Climate change, pink salmon, and the nexus between
596 bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea. *Proceedings*
597 *of the National Academy of Sciences*, *111*, E1880–E1888.
598 <https://doi.org/10.1073/pnas.1319089111>

599 Springer, A. M., Van Vliet, G. B., Bool, N., Crowley, M., Fullagar, P., & Lea, M. (2018).
600 Transhemispheric ecosystem disservices of pink salmon in a Pacific Ocean macrosystem.
601 *Proceedings of the National Academy of Sciences*, *115*, E5048–E5045.
602 <https://doi.org/10.1073/pnas.1720577115>

603 Tadokoro, K., Ishida, Y., Davis, N. D., Ueyanagi, S., & Sugimoto, T. (1996). Change in chum
604 salmon (*Oncorhynchus keta*) stomach contents associated with fluctuation of pink salmon (*O.*
605 *gorbuscha*) abundance in the central subarctic and Bering Sea. *Fisheries Oceanography*, *5*,
606 89–99.

607 Urawa, S. (2004). Stock identification studies of high seas salmon in Japan: a review and future
608 plan. *North Pacific Anadromous Fish Commission Technical Report*, *5*, 9–10.

609 Urawa, S., Azumaya, T., Crane, P.A., & Seeb, L.W. (2004). *Origin and distribution of chum*
610 *salmon in the Bering Sea during the early fall of 2002: estimates by allozyme analysis*.
611 NPAFC Doc. 794.

612 Urawa, S., Sato, S., Crane, P.A., Agler, B., Josephson, R., & Azumaya, T. (2009). Stock-specific
613 ocean distribution and migration of chum salmon in the Bering Sea and North Pacific Ocean.
614 *North Pacific Anadromous Fish Commission Bulletin*, *5*, 131–146.

615 Walker, R., Myers, K., Davis, N. D., Aydin, K. Y., Friedland, K. D., Carlson, H. R., Boehlert, G.
616 W., Urawa, S., Ueno, Y., & Anma, G. (2000). Diurnal variation in thermal environment
617 experienced by salmonids in the North Pacific as indicated by data storage tags. *Fisheries*
618 *Oceanography*, *9*, 171–186. doi/10.1046/j.1365-2419.2000.00131.x/full

619 Watanabe, K., Sasaki, K., Saito, T., & Ogawa, G. (2015). Scenario analysis of the effects of the
620 Great East Japan Earthquake on the chum salmon population-enhancement system. *Fisheries*
621 *Science*, *81*, 803-814.

622 Wechter, M.E., Beckman, B.R., Andrews, A.G., Beaudreau, A.H., & McPhee, M. V. (2017).
623 Growth and condition of juvenile chum and pink salmon in the northeastern Bering Sea.
624 *Deep-Sea Research Part II*, *135*, 145–155. doi:10.1016/j.dsr2.2016.06.001.

625 Yasumiishi, E.M., Criddle, K.R., Hillgruber, N., Mueter, F.J., & Helle, J.H. (2015). Chum
626 salmon (*Oncorhynchus keta*) growth and temperature indices as indicators of the year-class
627 strength of age-1 walleye pollock (*Gadus chalcogrammus*) in the eastern Bering Sea.
628 *Fisheries Oceanography*, *24*, 242–256. doi:10.1111/fog.12108.

629 Yasumiishi, E.M., Criddle, K.R., Helle, J.H., Hillgruber, N., & Mueter, F.J. (2016). Effect of
630 population abundance and climate on the growth of 2 populations of chum salmon
631 (*Oncorhynchus keta*) in the eastern North Pacific Ocean. *Fisheries Bulletin*, *114*, 203–219.
632 doi:10.7755/fb.114.2.7.

633 Zaporozhets, O.M., & Zaporozhets, G.V. (2005). Interaction between hatchery and wild Pacific
634 salmon in the Far East of Russia: a review. *Reviews in Fish Biology and Fisheries*, *14*, 305–
635 319. doi:10.1007/s11160-005-3583-y.

636 Zavolokin, A.V, Zavolokina, E.A., & Khokhlov, Y.N. (2009). Changes in size and growth of
637 Anadyr chum salmon (*Oncorhynchus keta*) from 1962–2007. *North Pacific Anadromous*
638 *Fish Commission Bulletin*, *5*, 157–163.

639 Zavolokin, A.V., Kulik, V.V., & Khokhlov, Y.N. (2011). *Changes in size, age, and intra-annual*
640 *growth of Anadyr chum salmon (Oncorhynchus keta) from 1962-2010*. NPAFC Doc. 1330.

641 Zuur, A. F., Ieno, E. N., Walker, N.J., Savaliev, A. A., & Smith, G. M. (2009). *Mixed effects*
642 *models and extensions* in R. Springer.

643

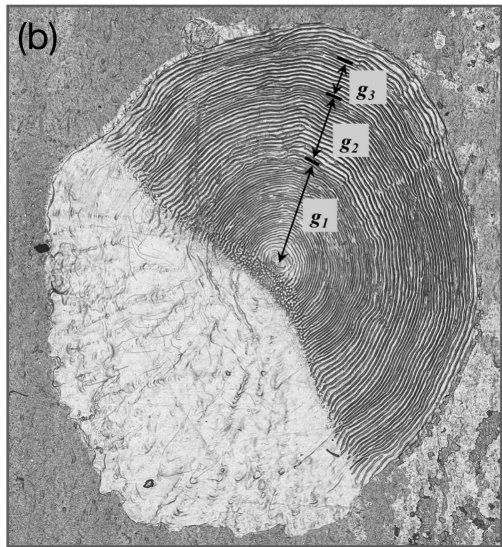
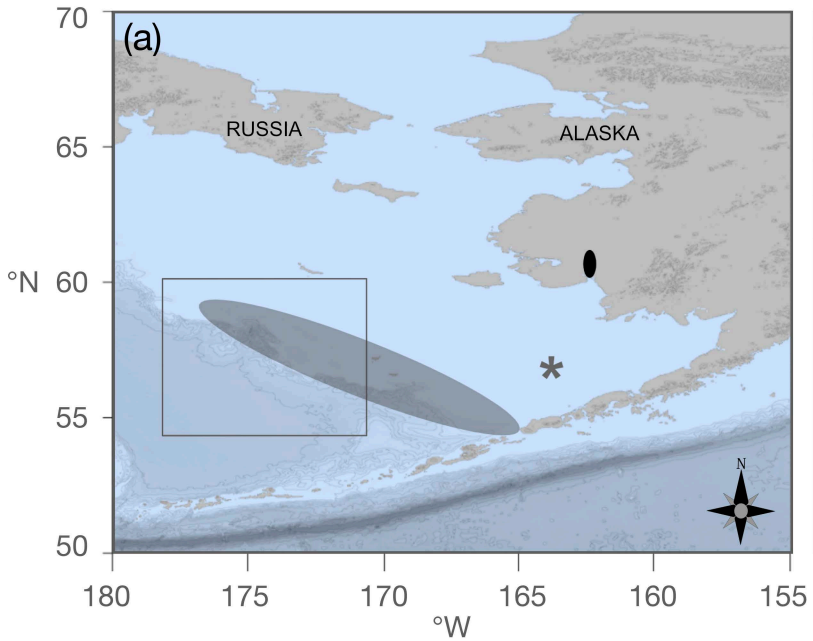
FOG_12505 Figure legends

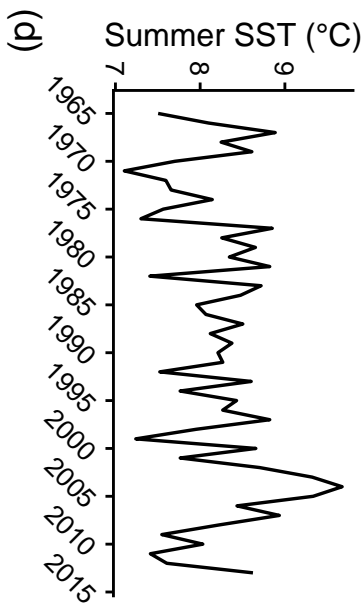
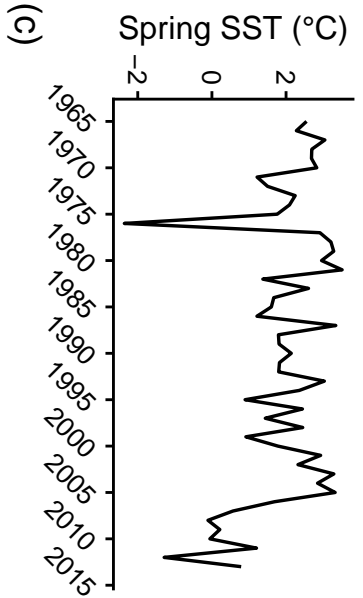
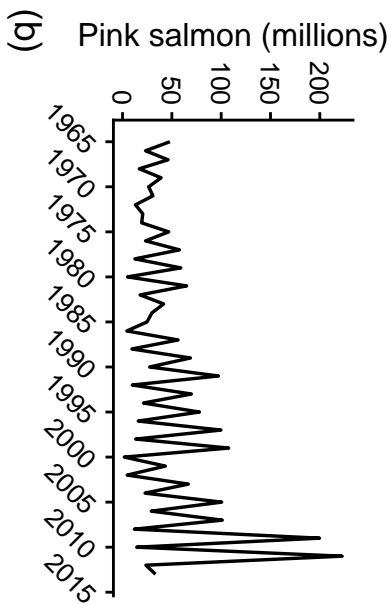
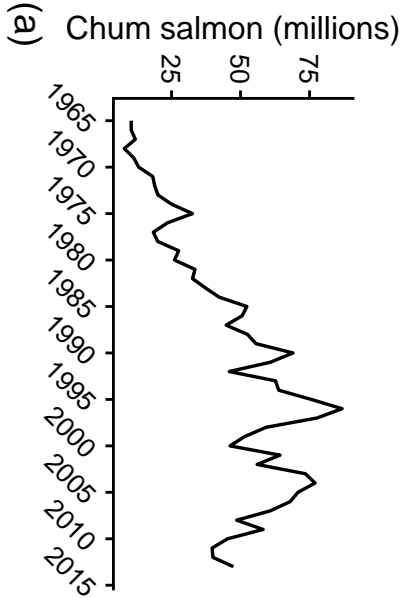
FIGURE 1 Study area (a) and image of chum salmon scale (b). On (a), location of Kuskokwim River chum salmon sampling is shown in black oval, and region of Bering Sea chum salmon bycatch sampling is shown in grey oval. The M2 buoy where spring SST was measured is shown by an asterisk (56.87°N, 164.06°W), and the rectangle shows the region over which summer SST in the central Bering Sea (54.3°-60.0°N, 170.6°-178.1°W) was averaged. On (b) the annual growth increments are shown, depicting the first (g_1), second (g_2), and third (g_3) years of growth at sea; annuli are marked by black bars.

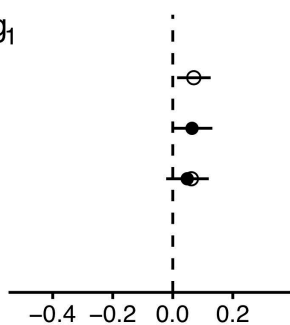
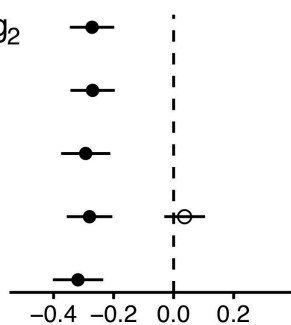
FIGURE 2 Annual variation, 1965-2013, in variables used to model Kuskokwim River chum salmon growth: a) Japanese hatchery chum salmon abundance; b) eastern Kamchatka pink salmon abundance; c) spring SST at M2 buoy; and d) summer SST in the Central Bering Sea.

FIGURE 3 Coefficients and standard errors for salmon abundance indices in best-supported models ($\Delta AIC_c < 2$; see Table 1) for the size of Kuskokwim River chum salmon growth increments $g_1 - g_4$. c In each pane, coefficients are arranged in descending order of model support, with the top model ($\Delta AIC_c = 0$) at the top of each plot pane. Jpn. = Japanese, E. Kam = eastern Kamchatka. The top model for g_1 contained no salmon abundance index.

FIGURE 4 Scale growth of Kuskokwim River chum salmon, averaged over both males and females, versus normalized abundance of Japanese chum salmon by growth increment and age. Solid line and filled circles, four-year olds; dashed line and open circles, five-year olds.



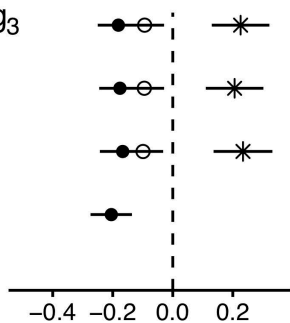
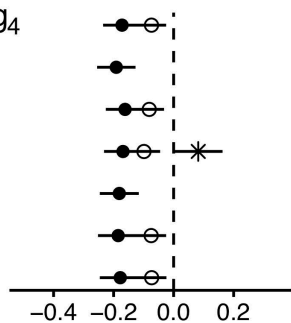


g_1  g_2 

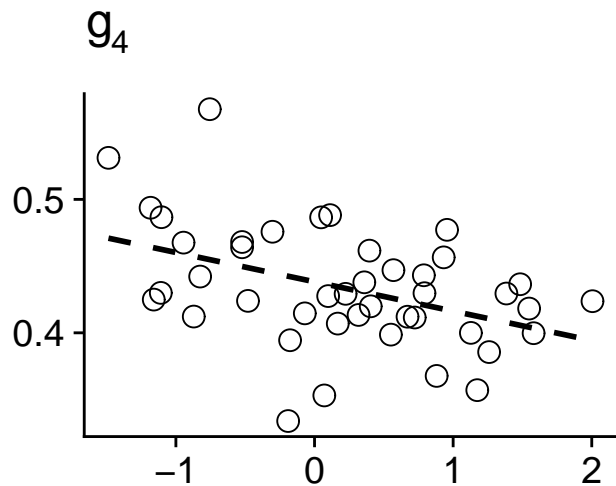
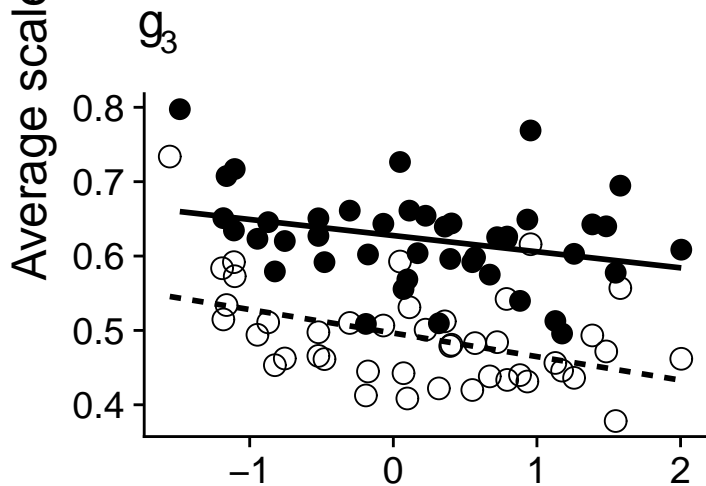
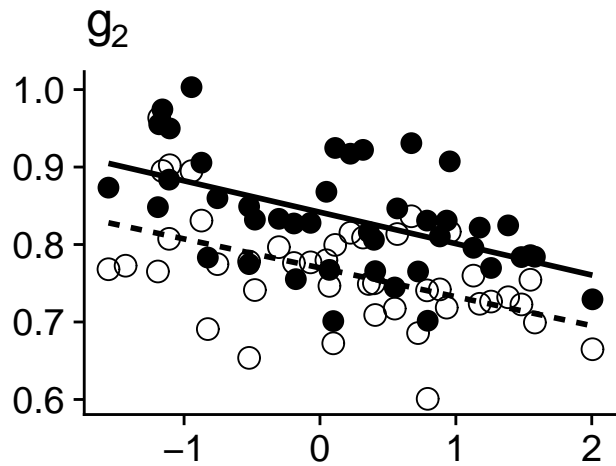
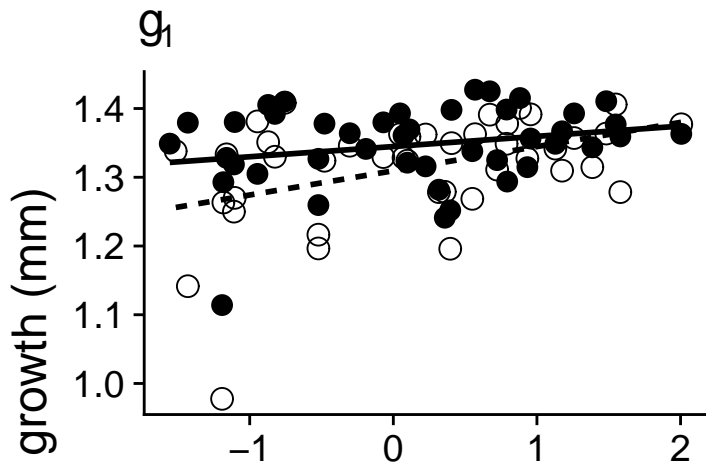
● Jpn. chum

○ E. Kam. pink

* Chum x pink

 g_3  g_4 

Model coefficient



Japanese chum abundance (normalized)

TABLE 1 Coefficients (and their standard errors) from top models for scale growth increments in Kuskokwim River chum salmon. A “—” indicates that a variable was considered in the full candidate model but not included in top model. Variances within (σ^2_W) and among (σ^2_A) calendar year at sea are also reported.

	Growth increment			
	<i>g</i>₁	<i>g</i>₂	<i>g</i>₃	<i>g</i>₄
Intercept	-0.03 (0.06)	0.29 (0.07)	0.35 (0.07)	-0.12 (0.06)
Japanese chum	---	-0.27 (0.07)	-0.18 (0.07)	-0.17 (0.06)
Kamchatka pink	---	---	-0.09 (0.07)	-0.07 (0.05)
Chum * pink	---	---	0.23 (0.10)	---
Sex (male)	---	0.12 (0.03)	0.38 (0.03)	0.45 (0.04)
Age (5)	---	-0.57 (0.03)	-0.97 (0.03)	n/a
Spring SST	---	---	0.09 (0.06)	0.08 (0.05)
Summer SST	0.20 (0.06)	---	---	---
σ^2_W	0.139	0.197	0.148	0.089
σ^2_A	0.857	0.684	0.601	0.844

TABLE 2 Coefficients (and standard errors) from models for growth increments $g_2 - g_4$ in Bering Sea chum salmon, as well as number of individuals (n) and results of likelihood-ratio test (LRT) comparing the model that included the period of reduced hatchery releases (2011-2013; ‘with’) to the model that did not (‘without’). Variances within (σ^2_w) and among (σ^2_A) calendar year at sea are also reported.

Increment/ model	g_2 (n = 1,733)		g_3 (n = 1,451)		g_4 (n = 316)	
	with	without	with	without	with	without
Intercept	0.84 (0.14)	0.82 (0.13)	1.32 (0.19)	1.36 (0.19)	-0.18 (0.14)	-0.08 (0.13)
Reduced release period	0.10 (0.11)		-0.20 (0.10)		-0.30 (0.17)	
Sex (male)	0.09 (0.05)	0.09 (0.05)	0.21 (0.05)	0.21 (0.05)	0.16 (0.11)	0.16 (0.11)
Age (5)	-0.27 (0.04)	-0.27 (0.04)	-0.46 (0.05)	-0.47 (0.05)		
Spring SST	0.16 (0.08)	0.16 (0.07)	0.13 (0.07)	0.13 (0.08)	0.11 (0.12)	0.11 (0.13)
σ^2_w	0.060	0.058	0.050	0.064	0.126	0.152
σ^2_A	0.915	0.915	0.865	0.865		
LRT (χ^2 , <i>df</i> , <i>P</i>)	1.02, 1, <i>P</i> = 0.31		4.40, 1, <i>P</i> = 0.04		3.43, 1, <i>P</i> = 0.06	

TABLE S1 Number of Kuskokwim River chum salmon scales measured from 1963, 1968-2010 by brood year, age at maturity, and sex.

Brood year	Age 4		Age 5		Total
	Male	Female	Male	Female	
1963	5	1	6	3	15
1968	15	17	18	19	69
1969	2	5	1	4	12
1970	18	16	16	1	51
1971	18	22	13	13	66
1972	22	24	19	15	80
1973	21	18	5	19	63
1974	23	23	5	19	70
1976	25	21	25	25	96
1977	25	25	14	19	83
1978	21	18	24	24	87
1979	23	24	21	23	91
1980	24	25	29	28	106
1981	25	28	24	25	102
1982	26	25	25	24	100
1983	25	31	25	25	106
1984	25	25	25	25	100
1985	25	25	25	23	98
1986	25	25	24	25	99
1987	23	24	25	25	97
1988	25	25	25	24	99
1989	22	25	24	25	96
1990	25	25	25	24	99
1991	25	25	24	25	99
1992	25	25	25	25	100
1993	25	25	25	25	100
1994	23	24	23	23	93
1995	22	16	18	23	79
1996	15	22	22	25	84
1997	23	21	20	19	83
1998	18	22	22	24	86
1999	25	24	24	22	95
2000	25	25	25	17	92
2001	25	25	25	25	100
2002	25	26	6	2	59
2003	22	25	25	25	97
2004	25	25	25	26	101
2005	25	25	28	34	112
2006	25	25	31	26	107
2007	25	25	35	25	110
2008	25	28	13	17	83
2009	25	26	33	35	119
2010	33	25	0	0	58

TABLE S2 Number of Bering Sea chum salmon scales measured by brood year, sex, and growth increment. Note that each growth increment is tallied separately, so a 5-year old individual would be represented in each of the columns $g_1 - g_4$.

Brood year	Female					Male					Grand Total
	g_1	g_2	g_3	g_4	Total	g_1	g_2	g_3	g_4	Total	
1996	7	7	7	7	7	8	8	8	8	8	15
1997	21	21	21	6	21	22	22	22	6	22	43
1998	24	24	20	5	24	26	26	23	8	26	50
1999	57	57	49	11	57	69	69	56	10	69	126
2000	29	29	24	4	29	56	56	51	11	56	85
2001	84	84	74	23	84	91	91	81	22	91	175
2002	67	67	48	13	67	49	49	40	9	49	116
2003	32	32	29	6	32	42	42	36	8	42	74
2004	31	31	27	16	31	37	37	33	15	37	68
2005	55	55	51	4	55	72	71	71	8	72	127
2006	54	54	36	19	54	64	64	47	24	64	118
2007	80	80	76	5	80	80	79	72	10	80	160
2008	29	29	14	6	29	41	41	17	10	41	70
2009	58	57	55	8	58	57	57	54	6	57	115
2010	34	34	31	5	34	53	53	50	8	53	87
2011	66	66	57	14	66	68	68	60	16	68	134
2012	104	104	74		104	120	120	95		120	224
2013	21	21			21	36	36			36	57
2014						1				1	1

Table S3. Model selection for counterfactual g_1 and focal growth increments $g_2 - g_4$, for Kuskokwim River chum salmon. Models within 2 ΔAICc units are shown, as well as the null (random effect only) model. SprSST, spring SST; SumSST, summer SST; JpnChum, index of Japanese chum salmon abundance; KamPink, index of Kamchatka pink salmon abundance. Sign of coefficient is indicated by +/- for each of the modeled fixed effects.

Modeled variables	df	logLik	ΔAICc
<i>g₁ (counterfactual)</i>			
<i>SumSST</i>	4	-5065.24	0
<i>SumSST + KamPink</i>	5	-5064.41	0.35
<i>SumSST + JpnChum</i>	5	-5064.77	1.06
<i>SumSST + JpnChum + KamPink</i>	6	-5064.16	1.85
<i>Sex + SumSST</i>	5	-5064.23	1.98
<i>-SprSST + SumSST</i>	5	-5065.24	1.999
<i>Null (random effect only)</i>	3	-5070.90	9.32
<i>g₂</i>			
<i>Sex + Age - JpnChum</i>	6	-4666.56	0
<i>Sex + Age - SprSST - JpnChum</i>	7	-4666.21	1.29
<i>Sex + Age + SumSST - JpnChum</i>	7	-4666.38	1.64
<i>Sex + Age - JpnChum + KamPink</i>	7	-4666.41	1.69
<i>Sex + Age - SprSST + SumSST - JpnChum</i>	8	-4666.43	1.74
<i>Null (random effect only)</i>	3	-4878.61	418
<i>g₃</i>			
<i>Sex + Age + SprSST + (-JpnChum*-KamPink)</i>	9	-4419.48	0
<i>Sex + Age + (-JpnChum*-KamPink)</i>	8	-4420.80	0.64
<i>Sex + Age + SprSST + SumSST + (-JpnChum*-KamPink)</i>	10	-4419.33	1.72
<i>Sex + Age - JpnChum</i>	6	-4423.35	1.73
<i>Null (random effect only)</i>	3	-5096.71	1342
<i>g₄</i>			
<i>Sex + SprSST - JpnChum - KamPink</i>	7	-2422.70	0
<i>Sex + SprSST - JpnChum</i>	6	-2423.95	0.49
<i>Sex - JpnChum - KamPink</i>	6	-2424.09	0.77
<i>Sex + SprSST + (-JpnChum*-KamPink)</i>	8	-2422.10	0.84
<i>Sex - JpnChum</i>	5	-2425.52	1.61
<i>Sex + SumSST - JpnChum - KamPink</i>	7	-2423.53	1.67
<i>Sex + SprSST + SumSST - JpnChum - KamPink</i>	8	-2422.66	1.96
<i>Null (random effect only)</i>	3	-2480.56	108

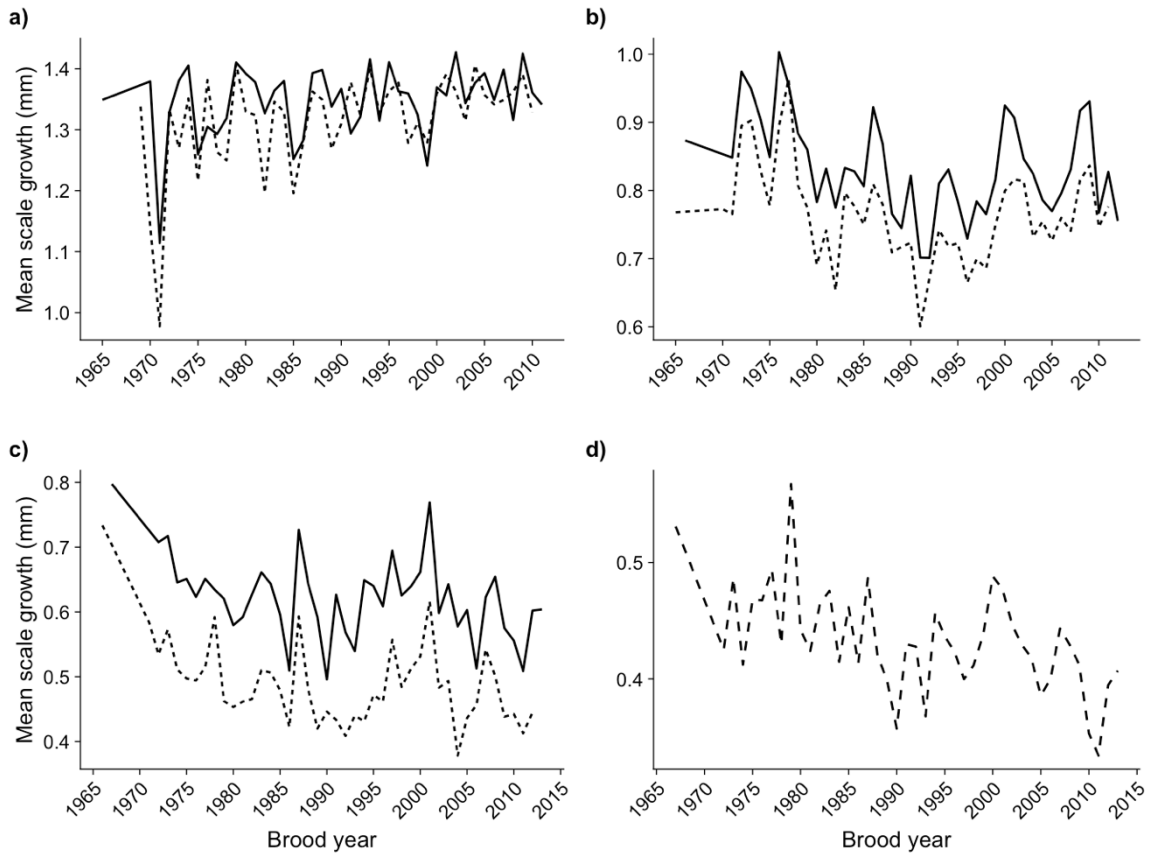


FIGURE S1. Temporal trends in average growth by increment and age for Kuskokwim River chum salmon. a) g_1 ; b) g_2 ; c) g_3 ; d) g_4 . Solid line, four-year olds; dashed line, five-year olds.

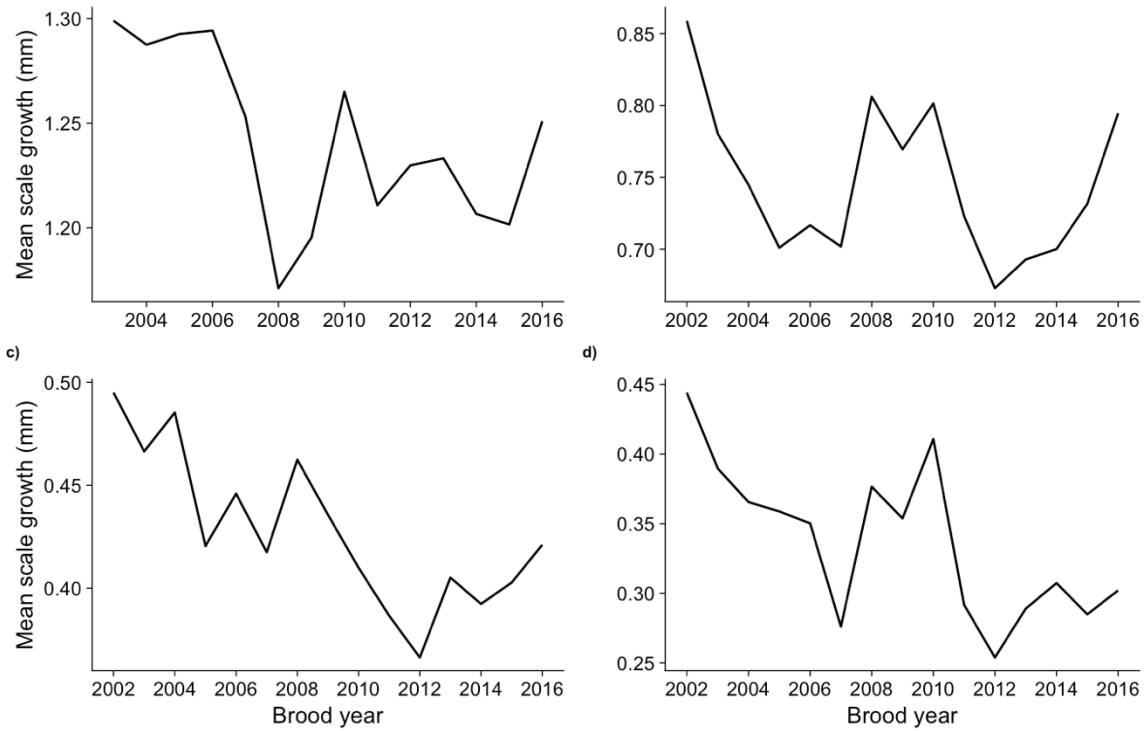


FIGURE S2. Temporal trends in average growth by increment Bering Sea chum salmon. a) g_1 ; b) g_2 ; c) g_3 ; d) g_4 .