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8 **Title** Climate and conspecific density inform phenotypic forecasting of juvenile Pacific salmon

9 body size.

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11 **Running title** Phenotypic forecasting of salmon body size

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27 **Author's contributions**

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28 PW, HF, and AB conceived the ideas and PW, AB, and MU designed methodology; MU

29 collected and analyzed the data; MU led the writing of the manuscript. All authors contributed

30 critically to the drafts and gave final approval for publication.

31

35

36 **Abstract**

37 1. Predicting effects of climate on fitness-linked phenotypic traits, such as body size, is

38   important for the management and conservation of species in the face of global change.

39   During sensitive life stages, small changes in mean trait values can have large effects on

40   survival and population productivity.

41 2. The transition from freshwater to saltwater by migrating anadromous fishes such as

42   Pacific salmon (genus *Oncorhynchus*) is a critical life history transition, where survival is

43   mediated by the size of migrating individuals. For salmon that spend extended periods

44   rearing in freshwater, the size at ocean entry (i.e., smolt length) may be sensitive to

45   changes in freshwater conditions shaped by biotic and abiotic factors, yet long-term

46   phenotypic time series for exploring these responses are rare.

47 3. We reconstructed a four-decade time series of smolt length from archives of returning

48   adult scales to quantify population-specific responses to climate and conspecific density

49   in a small watershed.

50 4. Dynamic linear modeling found that the relationship between a proxy for cohort density

51   and smolt length at ocean entry was consistently negative, suggestive of competition. In

52   contrast, there was a positive, yet dynamic, relationship between a proxy for density of

53   emerging fry during the second summer of growth and smolt length.

54 5. The effect of temperature on smolt length was not consistent between two populations of

55   sockeye salmon *O. nerka* that likely use distinct habitats within the watershed. A positive

56   relationship between smolt length and temperature was only detected for the less

57   abundant, early returning population.

58   6. Predictions of smolt length showed variable responses under scenarios of increasing
59   temperature and high and low densities of conspecifics. Collectively, these results reveal
60   population-specific responses to temperature and density, suggesting that local habitat
61   conditions may filter larger-scale climate drivers.

62

63   **Introduction**

64   Freshwater species are particularly vulnerable to effects of climate change, especially in
65   regions of northern high latitudes that are warming at over twice the global rate (IPCC, 2014;
66   Woodward, Perkins, & Brown, 2010). In addition to increases in water temperature, changes in
67   growing season and ice cover are likely to have large effects on freshwater ectothermic
68   organisms of northern regions (Magnuson et al., 2000). The hydrologic regimes of streams and
69   rivers are expected to change due to shifts in precipitation and decreased snowpack (Ficke,
70   Myrick, & Hansen, 2007; King, Shuter, & Zimmerman, 1999). Effects on lentic systems may
71   include eutrophication and changes in the onset and duration of lake stratification. The
72   dependence of water temperature on climate, species' limited dispersal abilities, and numerous
73   other anthropogenic stressors contribute to the susceptibility of freshwater species to alterations
74   in temperature and other climate effects.
75   Effects of climate change on fresh waters may disproportionately affect fishes, as their
76   entire life cycle is contained in fresh water. However, responses to regional climate will vary
77   among species and habitats due to trophic dynamics, variation in the physical landscape, and
78   species' thermal tolerances (Magnuson, Meisner, & Hill, 1990; O'Gorman et al., 2016). Air
79   temperatures can affect the onset, duration, and intensity of lake stratification, thereby affecting
80   the growth of fish positively or negatively depending on where they are distributed in the water
81   column (King et al., 1999). If rising temperatures do not exceed the physiological tolerance of a
82   fish species, they may be favorable given availability and quality of prey to meet metabolic
83   demands. However, decreases in growth rates would be expected if rising temperatures are
84   coupled with food limitation (Magnuson et al., 2000; McDonald, Hershey, & Miller, 1996).
85   Similarly, local differences in the density of competitors can cause asynchronous effects of
86   climate on populations in close geographic proximity (Rogers & Schindler, 2011). The physical
87   landscape also filters regional climate variation such that environmental conditions fishes

88   experience are a result of local habitat features (Griffiths, Schindler, Ruggerone, & Bumgarner,
89   2014).

90   For anadromous fishes that spend part of their life cycle in freshwater and part in the
91   ocean, climate effects on fresh waters can shift key phenotypic traits that predict survival in the
92   marine environment. For example, the early period following ocean entry of anadromous Pacific
93   salmon (genus *Oncorhynchus*) is a well-known survival bottleneck, presumably due to predation
94   (Healey, 1982; Parker, 1971). Body size at this life-history stage has been identified as a key trait
95   in determining marine survival (Foerster, 1954; Koenings & Geiger, 1993; Ward, Slaney,
96   Facchin, & Land, 1989). Although the ecological agents of selection are not fully described,
97   higher survivability of larger smolts is presumably linked to increased escape ability, faster
98   growth, and a shorter time to attain a size less susceptible to predation and starvation (Heintz &
99   Vollenweider, 2010; Sogard, 1997; Ulaski, Finkle, & Westley, 2020). Therefore, the conditions
100 mediating growth that juvenile salmon experience in freshwater may have direct consequences
101 for marine survival.

102   Effects of climate change on growth and survival of juvenile salmon rearing in freshwater
103 can depend on features of the landscape and local habitat (Crozier & Zabel, 2006; Griffiths et al.,
104 2014). Thus, the response of salmon smolt size to changing environmental conditions can be
105 highly variable in space and time and population-specific predictions are necessary to determine
106 the potential consequences of a warming climate for growth and marine survival. Yet, due to a
107 lack of time series data on smolt length for most salmon populations, it is difficult to understand
108 how this trait has been historically related to factors such as temperature and density. In contrast,
109 records of adult salmon returning to freshwater are abundant, including sex and length
110 information. Scales of returning adults have been collected over long periods of time for many
111 populations and individual growth of juveniles during freshwater residence can be inferred from
112 scale patterns (Ruggerone, Nielsen, & Bumgarner, 2007). Therefore, smolt length-at-age can be
113 determined using back-calculation methods to reconstruct time series of smolt length, allowing
114 for opportunities to understand effects of climate and density on smolt length over time.

115   The objectives of this study were to use a long-term archive of adult scales to reconstruct
116 juvenile salmon body length to 1) quantify responses of smolt length at ocean entry to air
117 temperature and conspecific density for two populations that occupy distinct habitats within the
118 same watershed and 2) conduct a phenotypic prediction of smolt length at ocean entry with

119   varying climate and density scenarios. We hypothesized that temperature and density would be

120   important in predicting smolt length for both populations, though the relative effects of

121   temperature may vary between populations. In addition, we hypothesized that smolt length

122   would be predicted to increase with scenarios of low escapement and increasing temperature.

123

124   **Materials and methods**

125

126   *Study area*

127   The South Olga lakes system on the southern end of Kodiak Island, Alaska, USA

128   supports one of the largest sockeye salmon *Oncorhynchus nerka* runs in the Kodiak Archipelago

129   and has a long-term average sockeye salmon combined return of approximately half a million

130   fish (Finkle & Loewen, 2015; Jackson, Dinnocenzo, Spalinger, & Keyse, 2012). South Olga

131   lakes includes Upper Olga Lake, an oligotrophic lake with a maximum depth of 70 m, and Lower

132   Olga Lake, a mesotrophic lake with a maximum depth of 2 m (see Ulaski et al. 2020). Adult

133   sockeye salmon have been enumerated and sampled for age and length at the Upper Station weir

134   since 1928 (Finkle & Loewen, 2015). Run reconstructions based on escapement and scale pattern

135   analysis are available beginning in 1969 for the Early run and 1970 for the Late run. As such, the

136   collection of archived adult scales begins in 1969-1970 and continues on an annual basis by

137   ADF&G. The South Olga lakes system has two temporally and genetically (Gomez-Uchida,

138   Seeb, Habicht, & Seeb, 2012) distinct sockeye salmon populations that are managed as separate

139   stocks. Early run sockeye salmon return from late May through mid-July and spawn in tributaries

140   of Upper Olga Lake, while late run sockeye salmon return from mid-July through September and

141   spawn in the shoals and creek between the two lakes (Finkle & Loewen, 2015).

142

143   *Time series of smolt length at ocean entry*

144   Archived scales sampled by ADF&G from returning adult fish during 1970–2012 were

145   preserved as impressions in acetate cards and mid-eye to fork length, age, and sex of each fish

146   were recorded. Acetate scale impressions were digitized using a Z-Scan 46-II microfiche reader

147   (Indus International Inc., West Salem, Wisconsin) attached to a 19.3 mm zoom lens and images

148   were exported at high resolution (3352 x 4425 pixels) to Image-Pro software (Media Cybernetics

149   Inc., Rockville, Maryland). We included adult scale impressions if 1) we agreed with age

150   determination by ADF&G staff (Foster, 2014), 2) annuli were clearly defined and not affected by

151   regeneration or reabsorption of the scale, and 3) the shape of the scale indicated it was taken

152   from the preferred area, which is immediately above the lateral line and slightly forward of the

153   adipose fin (Koo, 1962; Ruggerone et al., 2007). Following the approach of Ruggerone et al.

154   (2007), a random sample of up to 25 scales from a single age-class of adult females (age 2.2) was

155   selected from each population and each year of ocean entry from 1971–2010 (Table S1). Age-2.2

156   females were chosen because this age class was present in high abundance for both the early and

157   late run returns in most years. Adult scales were not available for age-2.2 adults that entered the

158   ocean in 1975.

159   Back-calculated smolt length was estimated from scales of returning adults by measuring

160   the distance (mm) on the longest axis from the focus of the scale to the last circulus of the end of

161   freshwater growth. In addition, we measured the total distance from the focus of the scale to the

162   edge of the scale (Ruggerone et al., 2007). Random checks between two trained readers occurred

163   for approximately 5% of adults scales (see Ulaski et al., 2020). We used the Fraser-Lee equation

164   (Fraser, 1915; Lee, 1920) to back-calculate smolt length from scales of returning adults:

$$L_i = a + (L_c - a) \times \left(\frac{S_i}{S_c}\right), \tag{1}$$

165   where L_i is the length of the fish at ocean entry, L_c is the length of the adult fish when the scale

166   was collected, S_i is the radius of the scale at ocean entry, and S_c is the total radius of the scale.

167   Smolts were collected downstream of Lower Olga lake with a Canadian fan trap (see Barrett,

168   Swanton, & Nelson, 1993). Smolt scales were collected from 1990–1993 and included in

169   regression of scale radius on fork length to estimate the constant, *a*, used in the Fraser-Lee

170   equation.

171   *Potential predictors of smolt length at ocean entry*

172   Densities of adult salmon that produced the smolts at ocean entry in year *y* (escapement

173   at *t* - 3; Fig. 1) was the first factor hypothesized to affect smolt length. Densities of adult salmon

174   that spawned in the system before the second summer of growth (escapement at *t* - 2) was the

175   second factor hypothesized to affect smolt length. The density of juvenile sockeye salmon is

176   likely to be non-linearly related to the number of spawning adults due to density-dependent

177   effects (Rich, Quinn, Scheuerell, & Schindler, 2009). Therefore, we used the natural log of

178   escapement as a proxy for juvenile density. Escapement was pooled for both the early and late

179 run since juveniles likely have overlapping rearing habitat and mix with conspecifics of both

180 populations. Spring temperature during the second summer of growth (spring temperature at $t -$

181 1) was the third factor hypothesized to affect smolt length. We used mean air temperature from

182 March–June, as recorded by the Kodiak Airport, as an index of water temperature. Air

183 temperature has been shown to be a good predictor of water temperature (Livingstone & Lotter,

184 1998; Stefan & Preud'homme, 1993) though lake depth has a strong influence on thermal inertia

185 (Toffolon et al., 2014). We compared mean air temperature in spring to mean water temperature

186 in summer (May–August) for 15 years from 1990–2016 when data were available. We explored

187 model performance of several combinations of temperature before the temperature index was

188 selected including temperatures from June–September and from March–September.

189

190 *Time series analysis*

191   We used dynamic linear models (DLM) to quantify the relative effects of three factors on

192 smolt length at ocean entry: escapement at $t - 3$, escapement at $t - 2$, and spring temperature at $t -$

193 1. This technique has been used effectively to identify abiotic and biotic drivers of growth and

194 survival for salmon while accounting for autocorrelation (Scheuerell & Williams, 2005;

195 Schindler, Rogers, Scheuerell, & Abrey, 2005). A major advantage of a DLM approach is that

196 the model structure allows regression coefficients of predictor variables to vary through time. In

197 contrast, more typical GLM or GAM approaches assume stationary (i.e., temporally static)

198 relationships with predictor variables. Accounting for non-stationarity of regression parameters

199 is important, as the processes linking climate and population parameters may not be static

200 (Litzow et al., 2018). The DLM structure can be described by two equations. First, the

201 observation equation can be written as,

202 $y_t = \boldsymbol{F}_t^{\mathrm{T}} \boldsymbol{\theta}_t + v_t$ $\qquad\qquad\qquad v_t \sim N(0, r)$ (1)

203 where smolt length y_t at time t is modeled as a function of $\boldsymbol{F}_t$, a column vector of potential

204 predictor variables, $\boldsymbol{\theta}_t$ is a column vector of fitted regression parameters, and v_t is a vector of

205 normally distributed observation errors with mean 0 and variance r. The second, the process

206 equation, allows regression parameters to vary over time through an autoregressive process via a

207 Kalman filter and smoother (Elizabeth E Holmes, Ward, & Wills, 2012),

208 $\boldsymbol{\theta}_t = \boldsymbol{\theta}_{t-1} + \boldsymbol{w}_t$ $\qquad\qquad \boldsymbol{w}_t \sim MVN(0, \boldsymbol{Q_t})$ (2)

209   where $\boldsymbol{w_t}$ is a vector of process errors and $\boldsymbol{Q_t}$ is the system variance matrix. The variance of $\boldsymbol{w_t}$ is

210   stored in the diagonal with zeroes elsewhere. All models were fitted using the MARSS package

211   (Holmes et al., 2012) in the R programming language (www.r-project.org).

212   Models were fit separately to early and late run smolt length. We used a random-walk

213   model as a means to evaluate the relative performance of more complicated models containing

214   predictor variables (Rich et al., 2009). Alternative models for each population were compared

215   using the Akaike Information Criterion, bias-corrected for small sample sizes (AICc; Table 1).

216   The relative effects of each predictor on smolt length were estimated as the product of the

217   regression coefficient and the value of the independent variable in each year of the time series

218   (Rich et al., 2009; Schindler et al., 2005). Effect sizes were expressed in the units of the response

219   variable in order to provide a simple interpretation of the effect of independent variables on

220   smolt length of South Olga lakes sockeye salmon.

221

222   *Phenotypic forecasting of smolt length at ocean entry*

223   Predictions for smolt length at ocean entry were estimated using data from 1971–2010

224   and four climate and escapement scenarios from 2011–2050. Four future scenarios were

225   characterized as 1) relatively large increases in temperature (hereafter, 'high temperature

226   forecast') and high escapement, 2) high temperature forecast and low escapement, 3) relatively

227   small temperature increases (hereafter, 'low temperature forecast') and high escapement, and 4)

228   low temperature forecast and low escapement. Spring temperatures from 2011–2050 were

229   simulated using down-scaled global climate models (GCMs) from Scenarios Network for Arctic

230   Planning (SNAP; https://www.snap.uaf.edu). High and low temperature predictions were based

231   on high and low CO_2 emission scenario global climate models, respectively (Walsh et al., 2018).

232   For each year, spring temperature at t - 1 was sampled from a normal distribution of

233   temperatures with a mean of the predicted GCM temperature for that decade and a standard

234   deviation of 0.1°C. Predictor variables for high and low escapement scenarios were sampled

235   from observed escapement greater than the 75% quantile and within the 25% quantile,

236   respectively.

237   We evaluated the accuracy of model predictions by estimating one-step forecasts from

238   1971–2010 using observed escapement and mean spring air temperatures (March–June) from

239   1970–2010. One-step forecasts of the parameters at time t were estimated via the Kalman filter

240   algorithm where the predictive distributions of the regression parameters are conditioned on

241   previous observations ($\theta_t|y_{1:t-1}$) and are updated as new information is incorporated into the

242   model (Holmes & Ward, 2011). MARSS estimates the states at $t = 0$ (θ_0), which allowed us to

243   compute a forecast for the first time point. Prediction intervals of forecasts are computed from

244   the variance of parameter estimates calculated as part of the Kalman filter and observation

245   variance. We compared one-step forecasts from 1971–2010 to observed smolt length during the

246   same period.

247

248   **Results**

249

250   *Time series of smolt length at ocean entry*

251   Smolt length for the early run varied during the 40-year time series (1971–2010) from

252   105–139 mm (Table S1, Fig. 2). Late run smolt length also varied during the time series from

253   106–135 mm. Early and late run smolt length were correlated (*cor* = 0.72), though the mean

254   smolt length of age-2.2 early run cohorts were 2.8 mm larger, on average, than their late run

255   counterparts (ANOVA, $F_1 = 28.7$, $p < 0.001$).

256

257   *Predictors of smolt length at ocean entry*

258   Mean air temperature in spring (March–June) was significantly correlated with mean

259   water temperature in summer (May–August; $r^2 = 0.55$, $p = 0.0015$). Early run smolt length was

260   best explained by proxies for conspecific density and spring air temperature. The top-performing

261   model for the early run (ΔAICc < 2) included escapement at t - 3, escapement at t - 2, spring

262   temperature at t -1, and an interaction between escapement at t - 2 and spring temperature at t - 1

263   (Table 1). Limited evidence supports the effect of spring air temperature on early run smolt

264   length (ΔAICc < 2); however, the Akaike weight for the model that does not include spring air

265   temperature ($w = 0.27$) was much lower than the model that includes temperature as an

266   explanatory variable ($w = 0.47$). The values fitted using density and spring air temperature

267   showed general agreement with observed data ($r^2 = 0.69$) and the model performed substantially

268   better than the reference model (ΔAICc = 32.2; Fig. 3). The proxy for cohort density

269   (escapement at t -3) was negatively associated with smolt length, as the mean regression

270   parameter was -2.1 ($SD = 0.005$) throughout the time series. The proxy for density of emerging

271   fry during the second summer of growth (escapement at t - 2) was positively associated with

272   smolt length after 1990, with a mean regression parameter of 5.0 ($SD = 5.2$; Fig. 4). In general,

273   spring air temperature during the second summer of growth (spring temperature at $t – 1$) was

274   positively associated with smolt length with a mean regression parameter of 1.1 ($SD = 0.01$). The

275   interaction between spring air temperature and the proxy for density of emerging fry was

276   negatively associated with smolt length with a mean regression parameter of -4.1 ($SD = 0.002$).

277   Thus, smolts were larger when either temperatures were high or density of emerging fry was

278   high, but smolts were smaller if both temperature and density were high or both were low. The

279   mean effect of conspecific density was -3.7×10^{-6} mm (range = -4.0–5.4 mm) and the mean

280   effect of density of emerging fry was 1.05 mm (range = -10.6–7.0 mm; Fig. 3). The mean effect

281   of spring air temperature was -2.9×10^{-3} mm (range = -2.5–2.0 mm) and the mean effect of the

282   interaction between spring temperature at density of emerging fry was 4.0×10^{-4} mm (range = -

283   8.6–9.2 mm).

284   Late run smolt length was best explained by proxies of conspecific density and there was

285   little evidence supporting an effect of spring air temperature. The model including escapement at

286   t - 3 and t - 2 performed much better than the reference model (ΔAICc = 29.5; Table 1). The

287   fitted values using density matched the observed data relatively well ($r^2 = 0.67$; Fig. 3). The

288   proxy for cohort density (escapement at $t – 2$) was negatively associated with smolt length with a

289   mean regression parameter of -2.9 ($SD = 0.01$). The proxy for density of emerging fry during the

290   second summer of growth (escapement at $t – 2$) had a dynamic effect on smolt length throughout

291   the time series with a mean regression parameter of 5.5 ($SD = 4.7$). Unlike the early run, the

292   parameter for density of emerging fry was significantly positive from 1971–1973, significantly

293   negative during the year 1979, and became increasingly positive from 1993–2010 (Fig. 4). The

294   mean effect of cohort density was 6.2×10^{-3} mm (range = -9.2–6.7) and the mean effect of

295   density of emerging fry was 1.03 mm (range = -5.6–7.4).

296

297   *Forecasting smolt length at ocean entry*

298   Forecasts of smolt length varied among the four different climate and escapement

299   scenarios. In general, both scenarios with high escapement showed decreases in smolt length

300   from 2011–2050, with a mean length of 117.0 mm ($SD = 3.3$ mm) at higher temperatures and a

301   mean length of 119.4 mm ($SD = 1.8$ mm) at lower temperatures (Fig. 5). With low escapement

302   and lower temperatures (rcp 4.5), smolt length was forecasted to increase to a mean of 127.4 mm

303   (SD = 2.4 mm); whereas with higher temperatures (rcp 8.5) smolt length was predicted to

304   decrease slightly with a mean of 121.1 mm (SD = 5.1 mm). Prediction intervals were similar

305   among scenarios, except smolt length predicted with low escapement and high temperature had a

306   wider prediction interval compared to the other scenarios (Figure S1). One-step forecasts

307   matched the observed trends from 1971–2010 reasonably well (r^2 = 0.47).

308

309   **Discussion**

310   Consistent with the role of within-watershed climate filtering, we show distinct responses

311   of smolt length to temperature and density within a small watershed. In addition, we demonstrate

312   that smolt length can be forecasted with reasonable model certainty using a dynamic linear

313   model framework. Forecasts indicate rising temperatures may be favorable as smolt length is

314   predicted to increase if conspecific density is low. However, if temperatures increase to levels

315   predicted by high emission GCMs or conspecific density is high, smolt length is predicted to

316   decrease and may have consequences for marine survival. Overall, our results demonstrate that

317   future responses to abiotic and biotic drivers in expression of key phenotypic traits, such as body

318   size, should be considered when managing species facing global change.

319

320   *Predictors of smolt length at ocean entry*

321   We hypothesized that spring temperature and conspecific density would be important

322   factors explaining variation in smolt length, though the relative effects of each may vary among

323   populations (Griffiths et al., 2014; Rich et al., 2009; Schindler et al., 2005). Spring temperature

324   and conspecific density appeared to be relatively important for early run smolt length, providing

325   support for this hypothesis. In contrast, the relative weight of evidence only identified

326   conspecific density as an important predictor variable for late run smolt length. Corroborating

327   findings from others, we have shown that two distinct populations occupying the same small

328   watershed may have different responses to climate and competition. Griffiths et al. (2014) found

329   two populations of sockeye salmon at the sub-watershed scale had opposite growth responses to

330   spring and fall air temperatures, likely due to climate drivers being mediated by differences in

331   lake morphometry. Upper and Lower Olga lakes are morphometrically dissimilar. Lower Olga

332   Lake is characterized as warm, with temperatures sometimes exceeding 15 °C which may

333 increase metabolic stress for juveniles (Finkle & Loewen, 2015; Griffiths & Schindler, 2012).

334 Although the population-specific distribution of juveniles in Olga lakes is not well known, it is

335 possible that juveniles from the early and late run would be segregated in this small watershed.

336 Density dependent effects for late run juveniles may also overshadow temperature effects since

337 they are more numerically abundant than the early run population. Differences in phenology

338 could contribute to observed patterns, where early run sockeye salmon emerge earlier and may

339 be more susceptible to changes in the onset of zooplankton blooms that are driven by

340 temperature and timing of ice breakup (Schindler et al., 2005). The mechanisms for these

341 differences, however, remain unknown.

342   Overall, our findings add additional evidence to the general understanding that

343 conspecific density can negatively affect juvenile sockeye salmon freshwater growth in some

344 systems (Rich et al., 2009; Schindler et al., 2005). The overall effects of density on growth

345 appear to be of a lower magnitude than in previous studies. Differences may be a result of

346 several factors. For example, the present study relates conspecific density to the total

347 accumulated freshwater growth of age-2 sockeye salmon. Previous studies have quantified the

348 growth of fry in the first summer (Rich et al., 2009; Schindler et al., 2005). In addition, smolt

349 length was back-calculated from returning adults in this study and is survivor-biased. Significant

350 size-selective mortality of smolts after they enter the ocean (Ulaski et al., 2020) could make

351 strong density-dependent effects more difficult to detect.

352   We detected a positive effect of escapement at t - 2 on smolt length at ocean entry,

353 contrary to previous findings. The positive effect of escapement at t - 2 was significant after

354 1990, when parent escapements were relatively low. Since we are not using a direct measure of

355 juvenile density, given the lack of those data, this positive effect may be evidence of nutrient

356 subsidies introduced from parent carcasses. Formal escapement goals for the early and late run

357 were established in 1988, which likely contributed to stabilizing parent escapements and may

358 have contributed to the positive effect of escapement at t-2 that was observed after 1990 (Finkle

359 and Loewen 2015). Though it has been shown that marine-derived nutrients (MDN) from salmon

360 carcasses can increase algal productivity in coastal lakes, the links between MDN and salmon

361 population productivity are less clear (Schindler, Leavitt, Brock, Johnson, & Quay, 2005). In

362 systems that are spawning limited, it is likely that the effect of nutrient supplementation is hard

363 to detect over long time periods (> 100 years). The input of pink salmon carcasses increased

364   juvenile coho salmon *O. kisutch* growth in streams, where increasing the density of salmon

365   carcasses increased growth up to a saturation point (Wipfli, Hudson, Caouette, & Chaloner,

366   2003). The effect of MDN on juvenile salmon growth and survival in shallow lakes, such as

367   Lower Olga Lake, that rely on a different prey base (i.e., aquatic insects) is poorly understood

368   and may more closely resemble that of stream-dwelling salmonids (Richardson, Beaudreau,

369   Wipfli, & Finkle, 2017). Further, as juveniles increase in length (> 60 mm) they undergo an

370   ontogenetic shift in their diet to even higher compositions of aquatic insects compared to

371   zooplankton. Further investigation into the role of MDN in sockeye salmon systems with shallow

372   nursery lakes and an older age structure (age 2+) is necessary to understand the role of nutrient

373   input in similar systems.

374   The present study design has a few limitations and caveats regarding estimation of smolt

375   length at ocean entry. Back-calculation methods from returning adults can inflate variance

376   (Wilson, Vigliola, & Meekan, 2009) and, as previously mentioned, lengths are survivor-biased.

377   However, back-calculated smolt length of the early and late run were highly correlated,

378   suggesting that it is unlikely variation in mean smolt length is explained by spurious variation in

379   sub-sampling and back-calculation methods. In addition, it appears that selection on size for age-

380   2 smolts is relatively consistent among years (Ulaski et al., 2020); therefore, growth patterns of

381   surviving adults should represent relative trends in smolt length. We have demonstrated that

382   despite the ecological noise of size-selective survival and a relatively small sample size per year,

383   the effects of climate and density on juvenile growth can still be detected and potentially used to

384   inform management of these populations. For example, as we continue to observe unprecedented

385   climate warming, the interaction of temperature and density on growth may be important to

386   consider when setting escapement goals that influence the levels of adult density in a system.

387

388   *Phenotypic forecasting of smolt length at ocean entry*

389   By using a dynamic linear model framework, we were able to forecast smolt length using

390   varying future climate and escapement scenarios from 2011–2050. We hypothesized that smolt

391   length would increase if future escapement was low and temperatures increased. According to

392   model predictions it appears that smolt length for early run sockeye salmon is predominantly

393   controlled by density dependent effects with smolt length generally predicted to decrease with

394   high densities. Though, it is clear temperature can mediate the magnitude of those effects. For

395   example, smolt length was forecasted to increase with low densities, but only if temperatures

396   increased at lower magnitudes.

397   Though predicting smolt length may be useful for management, it is important to

398   consider the limitations that arise from this approach. First, the model does not account for

399   several factors that could affect smolt length over time. McDonald et al. (1996) predicted a

400   decrease in young-of-the-year lake trout when zooplankton food resources did not increase with

401   increasing temperatures. An earlier and more robust stratification of freshwater lakes could result

402   in a reduced food supply due to an intense nutrient deficit in the epilimnion that results in lower

403   plankton production. However, Upper Olga Lake appears to have consistent productivity in

404   recent years (Finkle & Loewen, 2015; Healey, 2011). Although unknown in Olga Lakes, climate

405   effects on predator structure and behavior may also have implications for sockeye salmon growth

406   in freshwater (Petersen & Kitchell, 2001). Inter-specific competition with three-spine stickleback

407   *Gasterosteus aculeatus* can increase as stickleback breeding is more frequent with warm summer

408   temperatures (Hovel, Fresh, Schroder, Litt, & Quinn, 2018). Dramatic changes in temperature

409   and density could partially result in shifts in age rather than size, where juvenile sockeye salmon

410   enter the ocean predominantly as age-0 or age-1 smolts (Finkle & Loewen, 2015; Tillotson &

411   Quinn, 2016). In addition, our model cannot predict the influence of carryover effects (Tattam et

412   al., 2015; Wilson et al., 2021) or evolutionary changes over time (Crozier et al., 2008).

413   Moreover, changes in trait-means, albeit from plastic or genetic influences, can alter ecological

414   effects and species interactions (Des Roches et al., 2018). Therefore, this framework may be

415   useful to explore general trends in smolt length in response to warming temperatures or changes

416   in escapement goals, but it does not represent a complete understanding of the various and inter-

417   connected factors that determine smolt length at ocean entry in this system.

418   *Conclusion*

419   Salmon populations can have different responses to climate and density whether they are

420   geographically proximate or otherwise. Therefore, drivers of smolt size for many populations are

421   unknown. By utilizing archived scales from returning adult scales to reconstruct smolt length,

422   there may be many more opportunities to understand the factors that influence freshwater growth

423   and subsequent marine survival for salmon across their geographic range. As conditions for

424   growth in freshwater continue to change from shifts in climate and anthropogenic disturbances it

425   will become increasingly important to understand how salmon smolt size will respond (Finstad,

426   Einum, Forseth, & Ugedal, 2007; Hyatt, McQueen, Shortreed, & Rankin, 2004; Schindler et al.,

427   2005). Since smolt size mediates the outcomes of marine survival, the conditions that smolts

428   experience in freshwater can have implications for overall population productivity and resilience

429   (Henderson & Cass, 1991; Koenings & Geiger, 1993). Moreover, population-specific responses

430   to climate and competition at the sub-watershed scale highlights the significance of collecting

431   population-specific data to effectively manage populations in the face of continuing

432   environmental change.

433   **Data Availability Statement**

434   *Data for this study are available at https://doi.org/10.5061/dryad.6djh9w12c.*

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601 Table 1 Summary of dynamic linear models (DLM) to explain variation in age-2.2 female

602 sockeye salmon *Oncorhynchus nerka* smolt length from South Olga lakes, Alaska. Top-ranked

603 models are in bold.

Rank	Model	AICc	ΔAICc
Early run			
1	**$\log(\text{esc})_{t-3}$ + spring temp$_{t-1}$ + spring temp$_{t-1}$ * $\log(\text{esc})_{t-2}$**	271.7	0.0
2	$\log(\text{esc})_{t-2}$ + $\log(\text{esc})_{t-3}$	272.8	1.1
3	$\log(\text{esc})_{t-2}$	273.8	2.1
4	$\log(\text{esc})_{t-3}$	275.9	4.2
5	$\log(\text{esc})_{t-2}$ + spring temp$_{t-1}$	278.9	7.2
6	$\log(\text{esc})_{t-3}$ + spring temp$_{t-1}$	279.1	7.4

7	spring temp$_{t-1}$	297.8	8.2
8	log(esc)$_{t-2}$ + log(esc)$_{t-3}$ + spring temp$_{t-1}$	284.0	12.3
9	reference	303.8	32.2
Late run			
1	**log(esc)$_{t-2}$ + log(esc)$_{t-3}$**	257.4	0.0
2	log(esc)$_{t-2}$	262.1	4.7
3	log(esc)$_{t-3}$ + spring temp$_{t-1}$	262.6	5.2
4	log(esc)$_{t-3}$ + log(esc)$_{t-2}$ * spring temp$_{t-1}$ + spring temp$_{t-1}$	262.8	5.4
5	log(esc)$_{t-3}$	265.8	8.4
6	spring temp$_{t-1}$	266.5	9.1
7	log(esc)$_{t-2}$ + spring temp$_{t-1}$	267.2	9.8
8	log(esc)$_{t-2}$ + log(esc)$_{t-3}$ + spring temp$_{t-1}$	269.5	12.1
9	reference	285.0	27.6

604
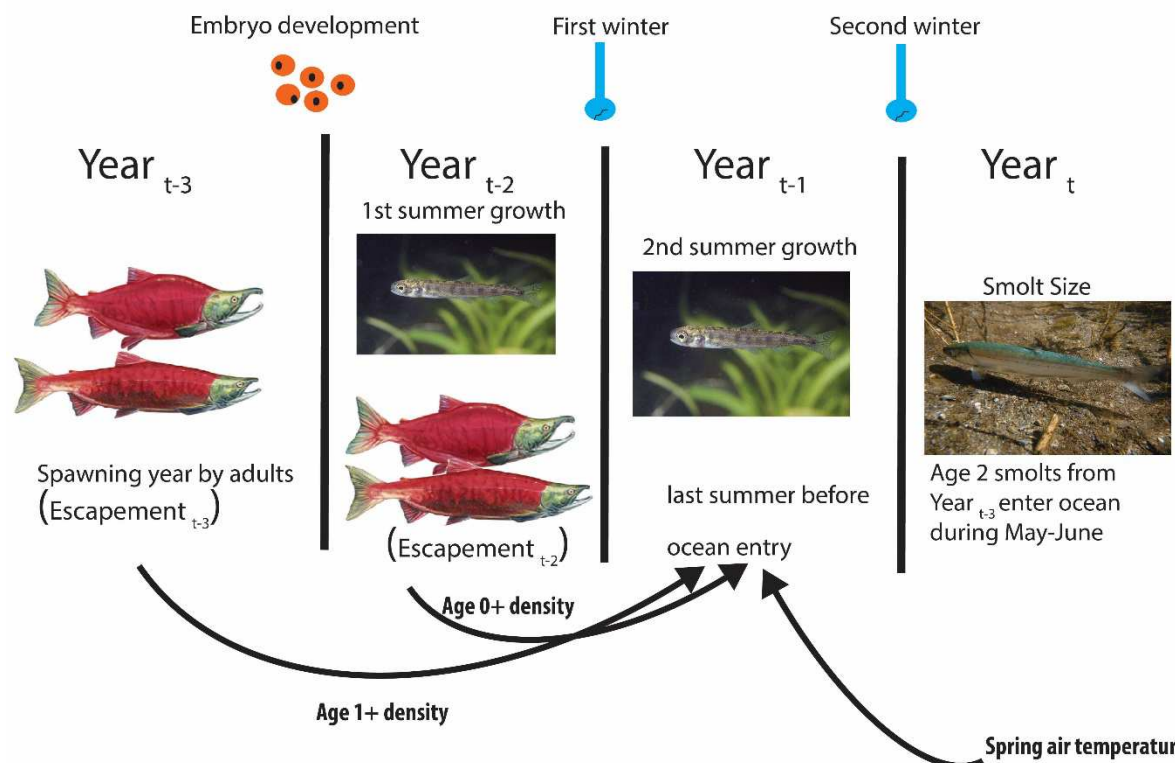
605

606 **Figure 1** Diagram of freshwater life-history of age-2 smolts produced by adults that spawn in

607 year t - 3 in relation to timing of predictor variables. Predictor variables include escapement at t -

608 3 as a proxy for cohort density (age-1+ density), escapement at t - 2 as a proxy for density of

609 emerging fry during the second summer of growth (age-0+ density), and spring air temperature

610 at t - 1.
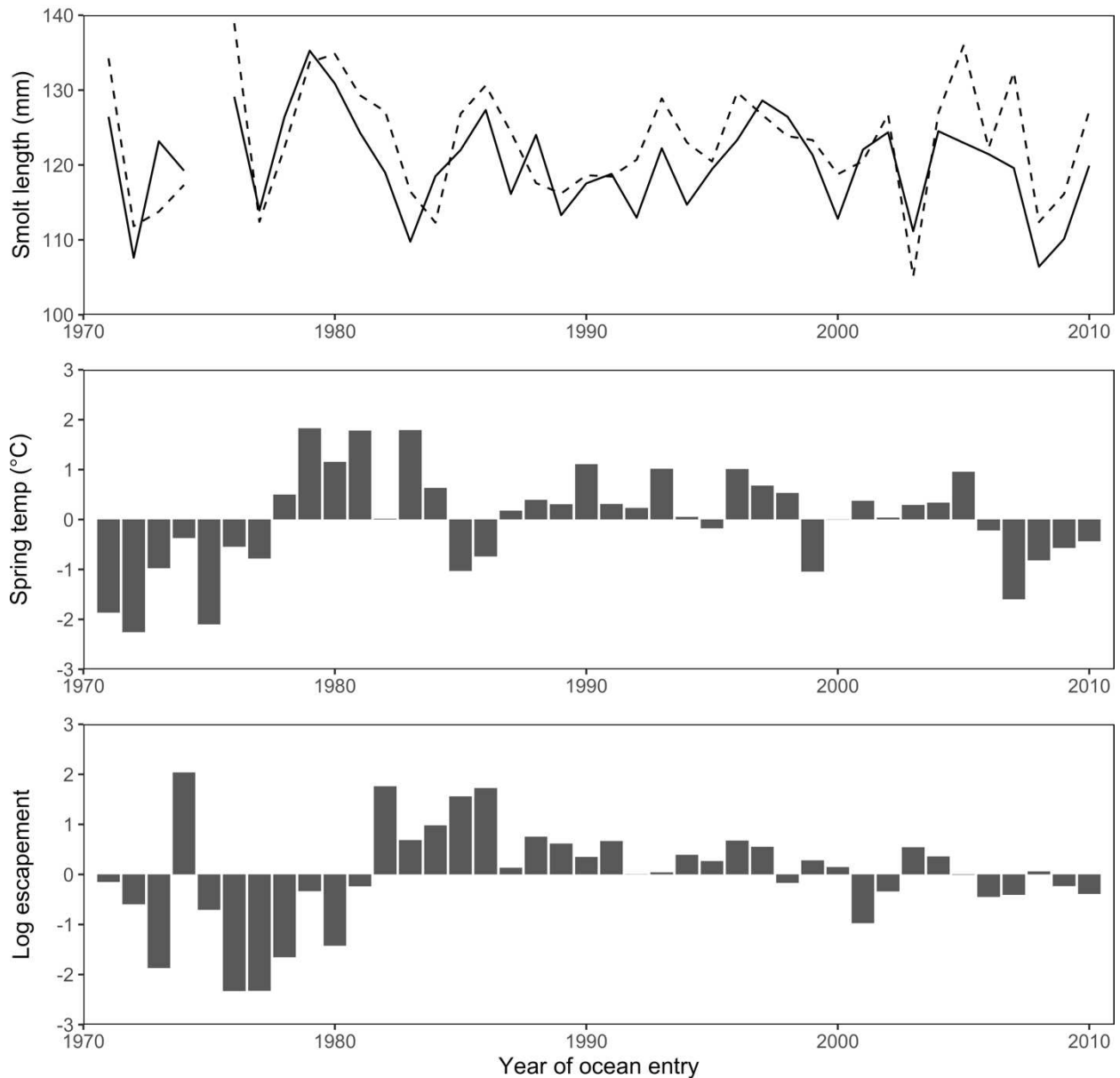
611

612 **Figure 2** Top panel shows time series of back-calculated smolt length (mm) of age-2.2 females

613 from the early run (solid) and late run (dashed). Middle panel shows time series of mean spring

614 temperature (May–June) and bottom panel shows log of early and late run combined escapement.

615 Both spring temperature and escapement were standardized to a mean of zero and standard

616 deviation of one.

617
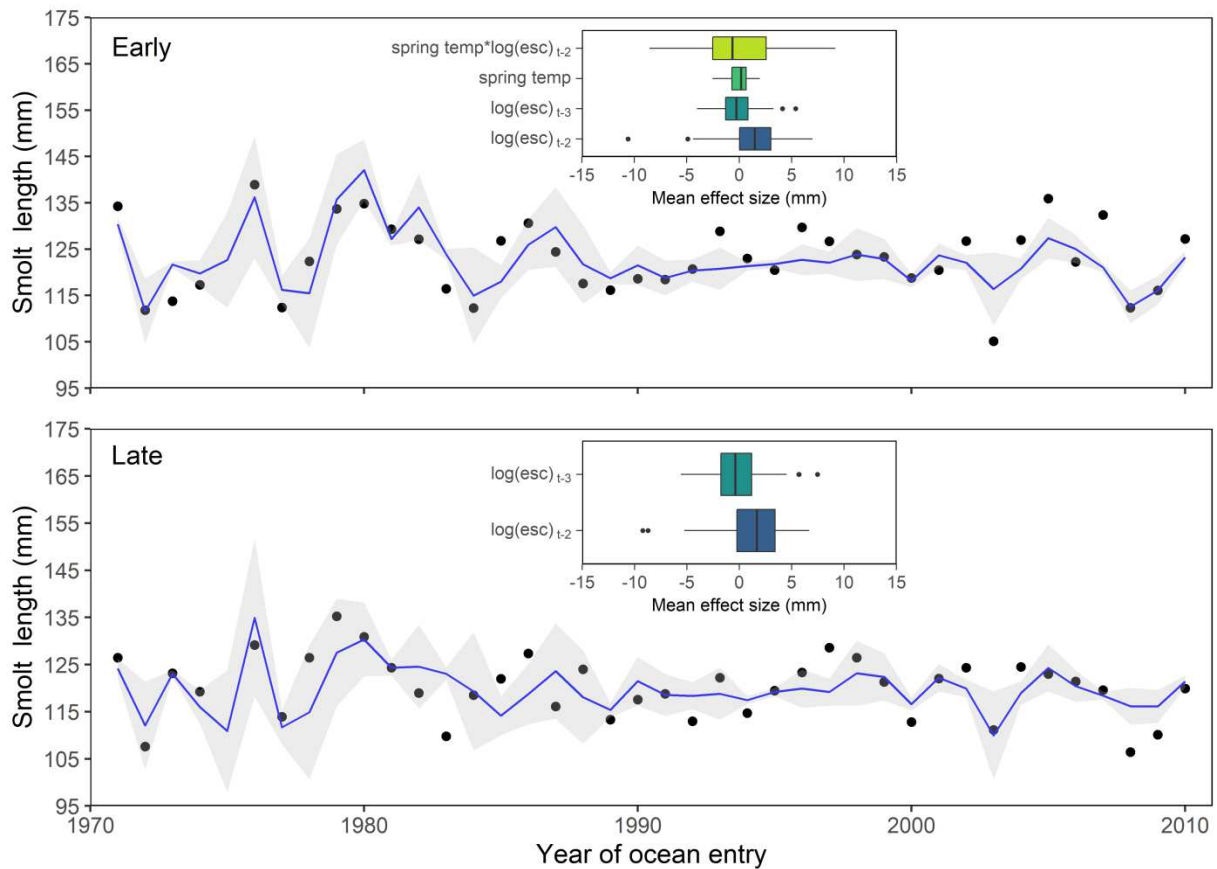
Figure 3 Top-ranked model fits for the early and late run back-calculated smolt length (black dots), where the blue line indicates fitted values and shaded area depicts 95% confidence intervals. Inset plots illustrate mean effect size (mm) for predictor variables.

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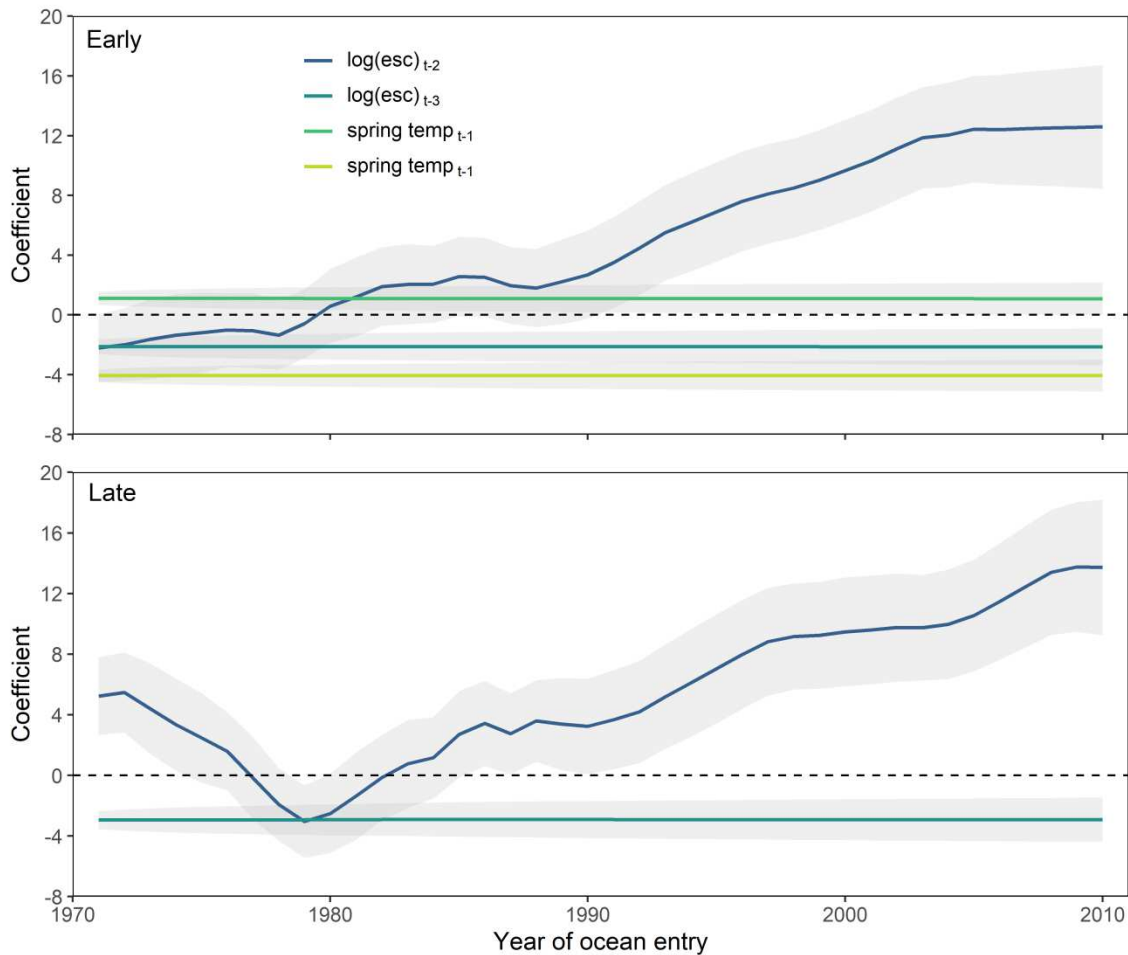
Figure 4 Regression coefficients of predictor variables at time *t* (i.e., year of ocean entry) for top-ranking early and late run models. Shaded area indicates 95% confidence intervals and black dashed line is located at zero.

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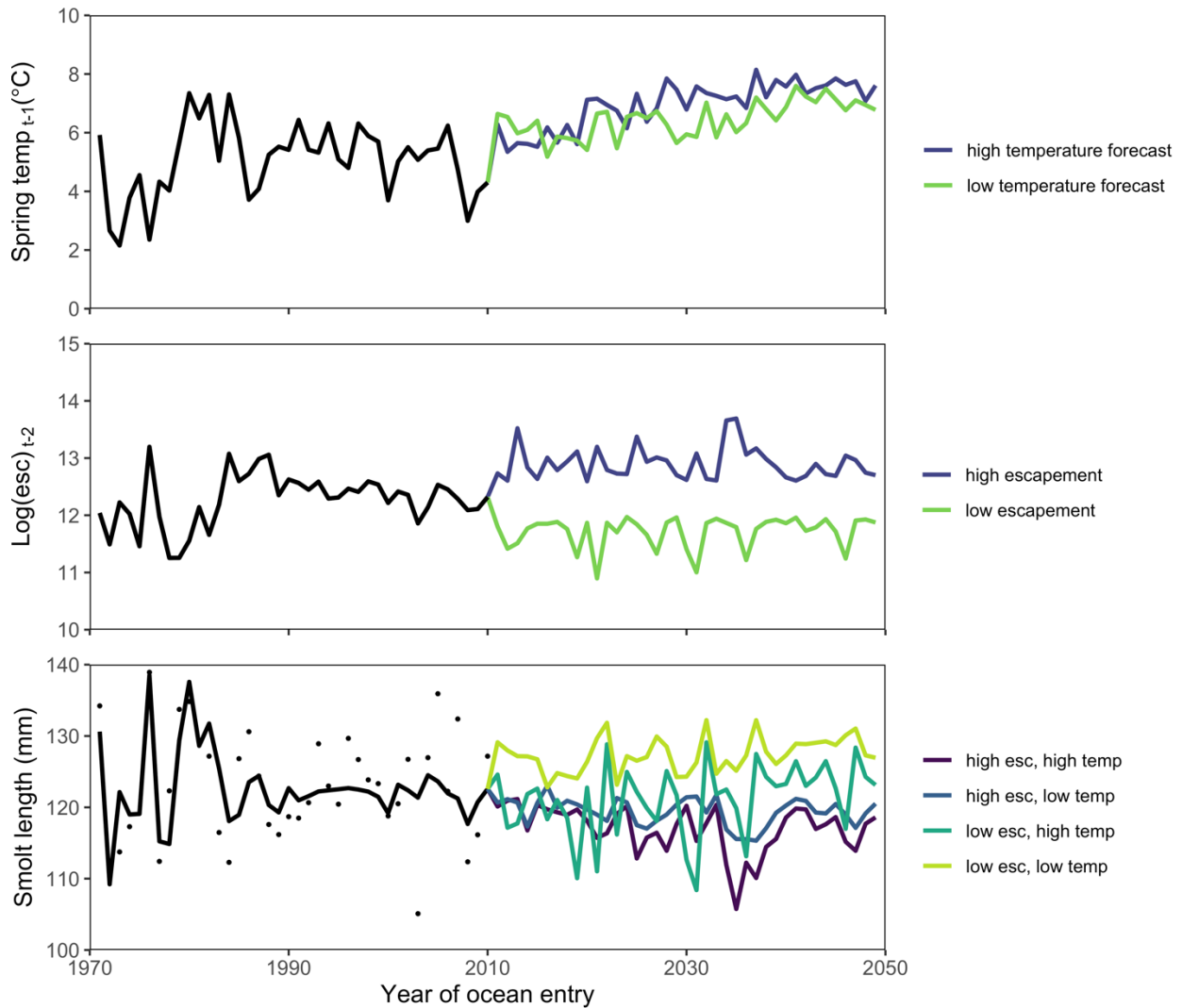
Figure 5 Top panel shows mean spring temperature (May–June) at t - 1 observed at Kodiak
Airport, Kodiak, AK from 1971–2010 (black line) and two future scenarios (colored lines) of
mean spring temperature from 2011–2050. Temperatures predicted by two down-scaled global
climate models with low (rcp 4.5) and high (rcp 8.5) CO_2 emissions from SNAP
(https://www.snap.uaf.edu). Middle panel shows observed escapement at t - 2 of Olga lakes
sockeye salmon *Oncorhynchus nerka* from 1971–2010 (black line) and two scenarios of high (>
75% quantile) and low (< 25% quantile) escapement (colored lines). Bottom panel shows one-
step forecasts of early run smolt length from 1971–2010 predictions of early run smolt length
from 2011–2050 with four scenarios of high and low escapement and temperature predictions
(colored lines) Black points indicated observed smolt length from 1971–2010.

Embryo development

First winter

Second winter

Year $_{t-3}$

Year $_{t-2}$
1st summer growth

Year $_{t-1}$
2nd summer growth

Year $_{t}$

Smolt Size

Spawning year by adults
(Escapement $_{t-3}$)
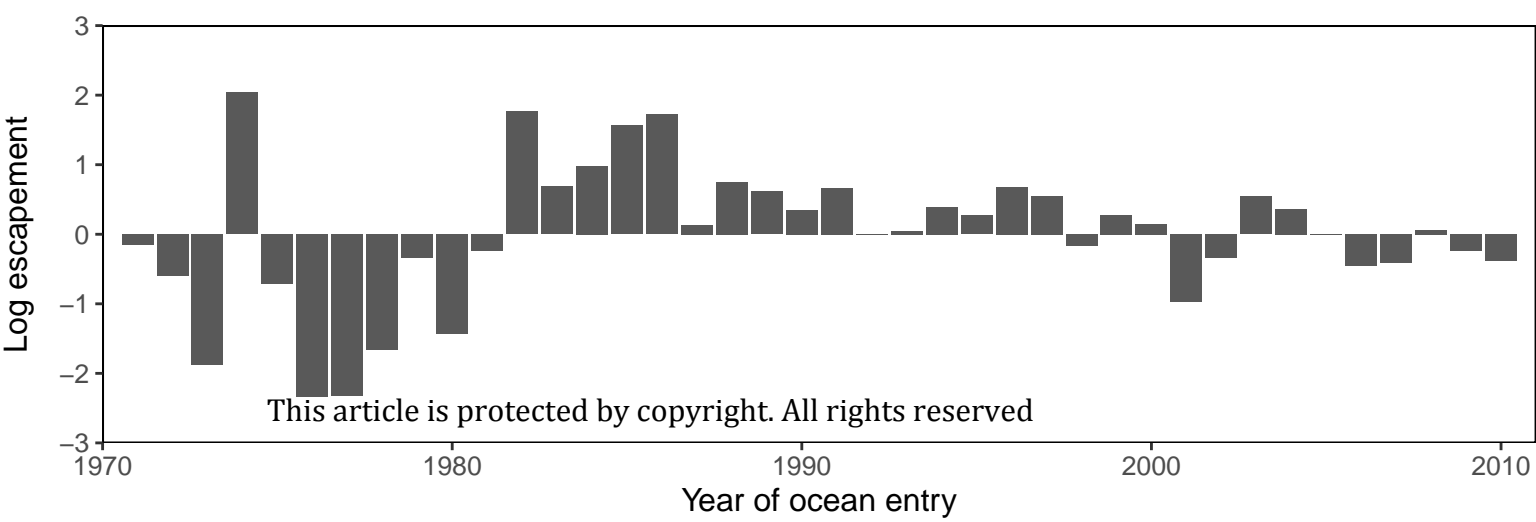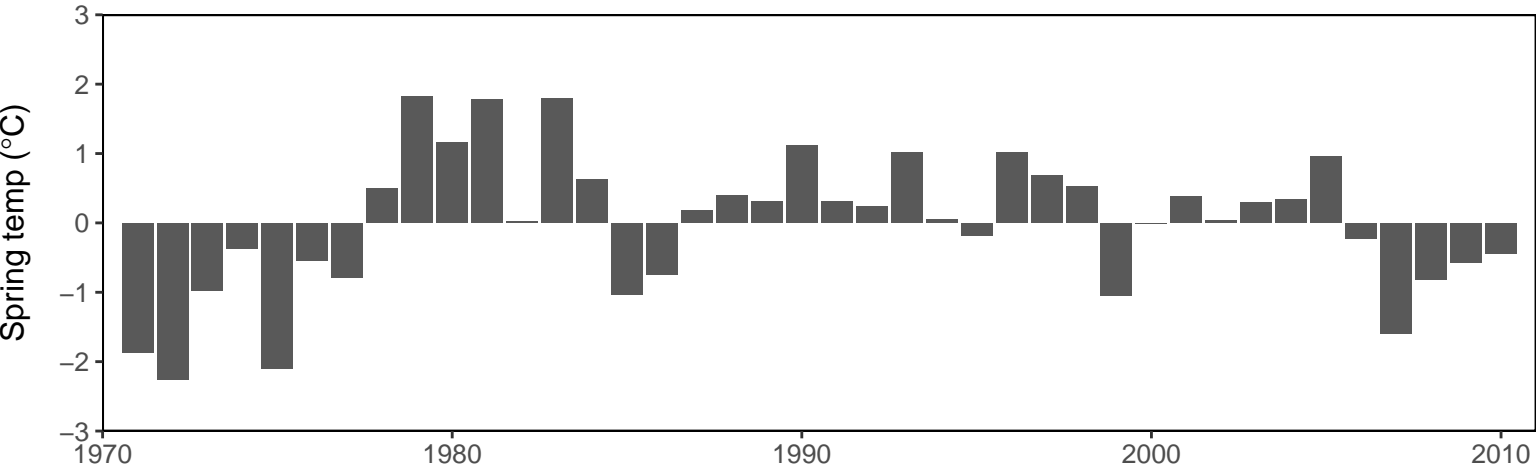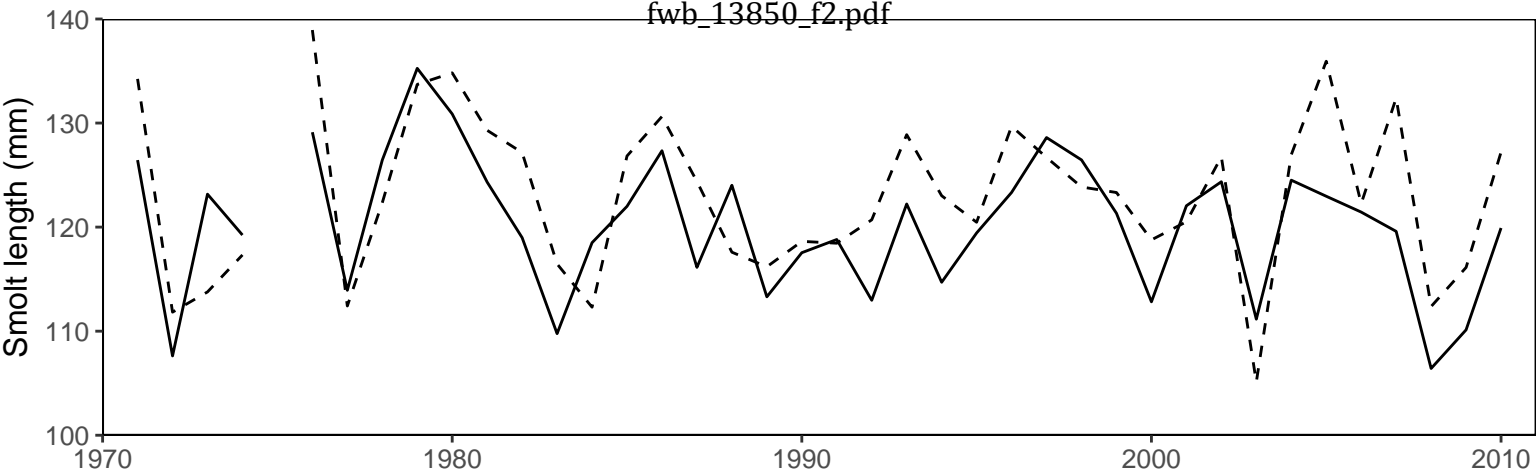
(Escapement $_{t-2}$)

last summer before

ocean entry

Age 2 smolts from
Year $_{t-3}$ enter ocean
during May-June

Age 0+ density

Age 1+ density

Spring air temperature

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