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DR. MARISA NORMA CHANTAL LITZ (Orcid ID : 0000-0001-7336-7151)

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Energy dynamics of subyearling Chinook salmon reveal the importance of piscivory to short-term growth during early marine residence

MARISA N.C. LITZ¹, JESSICA A. MILLER¹, RICHARD D. BRODEUR², ELIZABETH A. DALY³, LAURIE A. WEITKAMP⁴, ADAM G. HANSEN⁵, and ANDREW M. CLAIBORNE⁶

¹*Department of Fisheries and Wildlife, Coastal Oregon Marine Experiment Station, Oregon State University, Hatfield Marine Science Center, 2030 SE Marine Science Dr. Newport, OR 97365*

²*Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, Newport Research Station, 2032 SE Marine Science Dr. Newport, OR 97365*

³*Cooperative Institute for Marine Resources Studies, Hatfield Marine Science Center, Oregon State University, 2030 SE Marine Science Dr. Newport, OR*

⁴*Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, Newport Research Station, 2032 SE Marine Science Dr. Newport, OR 97365*

⁵*Colorado Parks and Wildlife, 317 W. Prospect Rd., Fort Collins, CO 80526*

⁶*Washington Department of Fish and Wildlife, 1111 Washington St. SE, Olympia, WA 98501*

*Corresponding Author

Email: marisa.litz@dfw.wa.gov

Current address: *Washington Department of Fish and Wildlife, 1111 Washington St. SE, Olympia, WA 98501*

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30 Running Title: Ocean growth of subyearling Chinook salmon

31 **ABSTRACT**

32 Variation in prey quantity and quality can influence growth and survival of marine predators,
33 including anadromous fish that migrate from freshwater systems. The objective of this study was
34 to examine the energy dynamics of subyearling Chinook salmon (*Oncorhynchus tshawytscha*)
35 following freshwater emigration. To address this objective, a population of Chinook salmon and
36 their marine prey were repeatedly sampled from June–September over two years in coastal
37 waters off Oregon and Washington. Subyearlings from the same population were also reared
38 under laboratory conditions. Using a bioenergetics model evaluated in the laboratory, we found
39 that growth rate variability in the field was associated more with differences in northern anchovy
40 (*Engraulis mordax*) consumption and less with variation in diet energy density or ocean
41 temperature. Highest growth rates (2.43–3.22% body weight d⁻¹) occurred in months when
42 anchovy biomass peaked, and the timing of peak anchovy biomass varied by year. Our results
43 support a general pattern among subyearling Chinook salmon occurring from Alaska to
44 California that feeding rates contribute most to growth rate variability during early marine
45 residence, although dominant prey types can differ seasonally, annually, or by ecosystem. In the
46 northern California Current, faster growth appears to be associated with the availability of age-0
47 anchovy. Identifying factors that influence the seasonal development of the prey field and
48 regulate prey quantity and quality will improve understanding of salmon growth and survival
49 during early marine residence.

50

51 **Keywords:** Chinook salmon, northern anchovy, subyearling, diet, growth, bioenergetics, feeding
52 rate

53

54 **INTRODUCTION**

55 Given the highly dynamic nature of marine ecosystems, interactions between predator and prey
56 can be incredibly complex (Steele, 1991; Lima, 1998; Hunsicker *et al.*, 2011). Environmental
57 variability, which can influence the timing, abundance, availability, or quality of prey can impact
58 the feeding success, growth, behavior, and survival of a predator (Österblom *et al.*, 2008).
59 Among fish populations, a match/mismatch between prey resources and consumers during
60 critical life stages has been recognized as a potential mechanism affecting survival to adulthood

61 for over a century (Hjort, 1914; Cushing, 1990; Houde, 2008). Trophic interactions in marine
62 environments can be measured directly, by quantitatively sampling predator diets, but this
63 approach is limited temporally to the last meal, and predator-prey relationships can change over
64 time. A more informative approach is sampling predator and prey repeatedly over time, which
65 can clarify the consequences of prey variability on predator consumption over periods of weeks
66 to months. Understanding how energy is transferred between predator and prey through time also
67 leads to better estimates of the predator's growth.

68 For Pacific salmon (*Oncorhynchus* spp.), research has focused on the early marine phase
69 following freshwater emigration, when mortality rates are highly variable (Parker, 1968; Bax,
70 1983; Welch *et al.*, 2011). There is some evidence that mortality may be size-selective during
71 this time, especially in juvenile life history types that migrate to sea as 0-age fish, or subyearlings
72 (Neilson and Geen, 1986; Miller *et al.*, 2013; Woodson *et al.*, 2013). A positive relationship
73 between early marine growth and subsequent adult survival has been demonstrated using otoliths
74 (Tomaro *et al.*, 2012; Miller *et al.*, 2014). Larger size and faster growth are attributes
75 hypothesized to benefit juvenile salmonids through the first few months of ocean entry when
76 predation rates are high as well as through the first ocean winter when prey abundances may
77 decrease and fish may starve (Beamish and Mahnken, 2001).

78 During the early marine phase, juvenile Chinook (*O. tshawytscha*), and coho (*O. kisutch*)
79 salmon undergo an ontogenetic shift in diet when invertebrate prey is gradually replaced by
80 marine fish prey, with piscivorous salmonids typically larger than those that feed primarily on
81 invertebrates (Brodeur, 1991; Schabetsberger *et al.*, 2003; Daly *et al.*, 2009). The size and timing
82 of freshwater emigration varies by species and stock group (Weitkamp *et al.*, 2015), therefore
83 stocks with different outmigration timing are likely to encounter different prey fields. Because
84 seasonal variability in the prey field could affect growth and survival rates of juvenile salmonids
85 differently depending on their timing of ocean entry, understanding seasonal variability in the
86 prey field could help fisheries ecologists to better predict future adult returns. Prey resources
87 have been shown to vary seasonally based on upwelling intensity and other nearshore
88 oceanographic processes (Litz *et al.*, 2017a); hence a better understanding of the prey field can
89 also help illustrate mechanistic linkages between the environment and the prey community and
90 serve as an early indicator of salmon growth and survival.

91 Since 1998, NOAA Fisheries and Oregon State University have measured the biomass
92 and species composition of potential fish prey (ichthyoplankton) sampled biweekly from January
93 through March in bongo nets at five stations along the Newport Hydrographic (NH) line off
94 Newport, Oregon, USA (44°40' N). Information generated from these cruises is used as an
95 indicator of prey resources available to salmonids following freshwater emigration two to three
96 months later (Burke *et al.*, 2013; Daly *et al.*, 2013; Daly *et al.*, 2017). Ichthyoplankton indicators
97 are strongly correlated with adult returns of yearling migrant populations, but weakly correlated
98 with returns of subyearlings, who typically migrate from freshwater later in the year than
99 yearlings. Moreover, subyearlings may be more gape-limited than yearlings when they arrive in
100 the ocean, meaning that winter ichthyoplankton resources may grow to be too large by the time
101 subyearlings enter the ocean to be available as prey. Ichthyoplankton indicators have also been
102 criticized because of the temporal lag between when samples are collected (winter) and when
103 salmonids enter the ocean (spring and summer), during which time environmental forces may
104 render prey unavailable. Concurrent sampling of salmon and their prey provides an alternative
105 sampling strategy for direct measurements of predator (size, abundance, diet, etc.) and prey
106 (composition, density) that is more insightful for trying to understand predator-prey interactions
107 (Litz *et al.*, 2017a).

108 Previous bioenergetics models showed that juvenile salmon growth is most sensitive to
109 changes in prey energy density or feeding rate when ocean temperatures range from 8–18 °C
110 (Trudel *et al.*, 2002; Beauchamp *et al.*, 2007). The objective of the current study was to examine
111 the energy dynamics of a population of subyearling Chinook salmon following outmigration. To
112 this end, we constructed a bioenergetics model that was tested in the laboratory, and then applied
113 it to field data to estimate salmon consumption and feeding rates during early marine residence
114 over two years. We then conducted a sensitivity analysis to determine whether salmon growth
115 was most affected by variations in estimated feeding rate, prey energy density, or observed
116 temperature during field observations. We wanted to determine if variability in juvenile salmon
117 growth rates during their initial summer reflected changes in the abundance or quality of
118 common prey. This work provides novel insight into the seasonal energy dynamics of
119 subyearling Chinook during early marine residence that may be useful in determining growth
120 potential during contrasting years of prey abundance and composition.

121

122 **METHODS**

123 We conducted our analysis of growth and energy dynamics on upper Columbia River summer-
124 fall (UCSF) subyearling Chinook salmon. Salmon from this population spawn in main-stem and
125 tributary habitats east of the Cascade Mountains, USA with hatchery and natural production
126 occurring in both the mid- and upper-Columbia River (Miller *et al.*, 2013; Teel *et al.*, 2014).
127 Subyearlings from the UCSF stock group enter the ocean throughout the summer, peaking in
128 July (Weitkamp *et al.*, 2015), but remain concentrated nearshore along the Oregon and
129 Washington coasts during their first few months at sea (Fisher *et al.*, 2014; Teel *et al.*, 2015).
130 The protracted ocean entry period, along with the limited ocean dispersal by this group during
131 their first few months at sea make UCSF subyearlings a suitable stock group for repeated
132 sampling of early marine diet and growth.

133

134 *Bioenergetics Model*

135 Bioenergetics models are important tools for examining the effects of environmental variability
136 on Pacific salmon populations and have been used to determine subyearling Chinook salmon
137 energy dynamics in the ocean in many regions (MacFarlane, 2010; Marin Jarrin, 2012; Gamble,
138 2016). The model is based on the principle of thermodynamics (Kleiber, 1975) and contains
139 mass- and temperature dependent functions for maximum daily consumption and metabolism,
140 and a temperature- and ration-dependent function for waste (Beauchamp, 2009). Bioenergetics
141 models can account for changing thermal and food conditions explicitly and are valuable
142 analytical tools for isolating and evaluating the relative contribution of different factors (e.g.,
143 food quality, feeding rate, and temperature) on growth during different life stages.

144 To investigate the energy dynamics of UCSF subyearlings, we used the Wisconsin
145 bioenergetics model (Hanson *et al.*, 1997) parameterized for Chinook salmon (Stewart and
146 Ibarra, 1991) and coded to run in the R statistical package (R Core Team, 2015). To assess model
147 error, we first used the model to predict consumption based on growth observed in the laboratory
148 over four weeks, and then used the model to predict growth based on total laboratory
149 consumption over the same period. Error was evaluated as the percent difference from observed
150 and modeled growth and consumption. Next, we fit the model to observed growth based on
151 repeated field collections to calculate consumption and feeding rate over three months in two
152 separate years. Each field simulation lasted approximately one month. Finally, to determine

153 which factor (prey energy density, salmon feeding rate, or temperature) contributed most to
154 growth rate variability over the duration of our study, we conducted a sensitivity analysis using
155 parameter values representative of field conditions.

156 157 *Laboratory rearing of subyearlings*

158 To evaluate performance of the Wisconsin bioenergetics model in juvenile Chinook salmon,
159 subyearlings from the UCSF group were obtained from Priest Rapids Hatchery in May 2013 and
160 transported for, but not used in, a related study at the Hatfield Marine Science Center in
161 Newport, Oregon (Litz *et al.*, 2017b). A total of 80 fish were transferred to a 568-l round
162 aquaculture tank with a constant current speed of 0.2 m s⁻¹, a continuous flow of charcoal-
163 filtered freshwater (mean = 14.8 ± 0.5 °C standard deviation SD), and air supply. Salmon were
164 allowed to acclimate for 4 weeks before being gradually introduced to seawater from Yaquina
165 Bay, Oregon over one week. Seawater was sand filtered to 50 µm and sterilized using ultraviolet
166 light before entering the lab. Water quality parameters were measured daily, and throughout the
167 duration of the experiment temperature averaged 12.1 ± 2.1 °C, salinity was 32.5 ± 0.5, and
168 dissolved oxygen concentrations were 7.1 ± 0.6 ml l⁻¹.

169 To determine growth of laboratory-reared fish, all salmon were measured for fork length
170 (FL, mm) and mass (g) at the start of the study in late June and at the end of weeks 4, 8, and 12
171 in late July, August, and September. At the start of the experiment, seven fish were inserted with
172 a passive integrated transponder (PIT) tag to track individual growth for comparison with tank-
173 averaged growth. Specific growth rates (SGR, g, % body weight [BW] d⁻¹) were calculated from
174 the difference between initial and final mass according to the following formula:

$$SGR = \frac{(\ln[W_f] - \ln[W_i])}{(t_f - t_i)} \times 100,$$

176
177 where W_f is final mass at time t_f and W_i is initial mass at t_i . A maintenance diet of commercial
178 hatchery feed (Otohime Fish Diet® extruded pellets; 11.8% lipid and 13,709 J g⁻¹ by wet
179 weight) was offered once daily at 2% of the total fish weight in the tank based on size
180 measurements. Fish were observed until all food was consumed, which typically took <2 min.
181 Ration was adjusted weekly between measurements by assuming an approximate increase of

182 1.5% BW d⁻¹ according to the temperature-dependent growth formula of Iwama and Tautz
183 (1981).

184 Predator energy density is a required input into the Wisconsin bioenergetics model
185 (Hanson *et al.*, 1997) and for Chinook salmon, is estimated from an allometric relationship
186 between size and energy density previously determined for adults (Stewart and Ibarra, 1991).
187 However, as noted by Trudel *et al.* (2005), energy density determined by this method tends to
188 overestimate juvenile salmon values and can result in model error. To evaluate this issue, we
189 compared model output using salmon energy densities estimated both by the Stewart and Ibarra
190 (1991) adult method and by using juvenile data to estimate energy density. For the juvenile
191 method, we fit a regression model based on 44 measurements of juvenile Chinook salmon mass
192 and energy density (Appendix Table A1) collected in summer off southern British Columbia (M.
193 Trudel pers. comm.) that had the following form:

$$ED = 1.76w + 4218.54,$$

195
196 where ED is salmon energy density (J g⁻¹) and *w* is the wet mass (g) of the salmon. The model
197 had an *R*² value of 0.46 and *p* < 0.01.

198 To evaluate error in the bioenergetics model, we ran simulations to estimate the change in
199 mass (Δ g) and total consumption (g) in individual PIT-tagged fish and the tank average over
200 three months. For each 4-week period between measurements, percent error was calculated from
201 the difference between observed and modeled output. For each simulation, we compared results
202 using both the adult and juvenile methods for calculating salmon energy density (Stewart and
203 Ibarra, 1991; Trudel *et al.*, 2005). A one-way analysis of variance (ANOVA) with method as the
204 factor was used to compare percent error in growth and consumption using a logit
205 transformation.

206 207 *Field Collections*

208 Juvenile salmon were collected from the field in three separate coastal surveys (Teel *et al.*, 2015;
209 Weitkamp *et al.*, 2015; Litz *et al.*, 2017a) from June through September 2011 and 2012 (Fig. 1).
210 Sampling for the main study occurred from the lower Columbia River estuary (46° 10') north to
211 Willapa Bay, Washington (46° 40'). Supplementary otolith samples were collected from salmon

212 in September 2011 between La Push, Washington (47° 55') and Newport, Oregon (44° 40'). We
213 also collected potential salmon prey in 36 surface trawls from July through September of each
214 year using a 264 Nordic rope trawl (NET Systems, Bainbridge Island, Washington) with 3-mm
215 mesh in the cod end (Litz *et al.*, 2017a). Juvenile salmon used in the study (n=514) were
216 assigned to the UCSF genetic stock based on genotyping of 13 microsatellite DNA loci
217 following Teel *et al.* (2015) and classified as subyearlings based on FL (Weitkamp *et al.*, 2015;
218 Litz *et al.*, 2017a).

219

220 *Salmon ocean growth rates and diet composition*

221 Monthly estimates of ocean growth (SGR) were determined by subtracting mean size (mass; g)
222 and timing of fish sampled in the estuary from mean size and timing of fish sampled in the ocean
223 approximately one month later (e.g., mass in ocean July – mass in estuary June = growth in
224 month 1). To determine growth uncertainty, Monte Carlo simulations (5,000 per month) were
225 conducted using mean size and size variation given the sample size for each time period. This
226 approach assumed that fish captured in the ocean between consecutive months were distinct
227 cohorts of fish entering the ocean and potentially introduced bias into growth estimates. Growth
228 uncertainty determined from Monte Carlo simulations was used to estimate error in consumption
229 and feeding rate in bioenergetics model simulations.

230 Ocean growth rates of UCSF subyearlings based on mean size and timing of capture may
231 be biased due to uncertainty about how long fish have been in the marine environment. To
232 address this issue, we used an independent method to calculate ocean growth using otoliths
233 sampled for another study (Claiborne *et al.*, 2014). Growth was estimated using an approach that
234 combined otolith chemistry, microstructure analysis, and back-calculation. Otoliths from 56
235 UCSF subyearlings were prepared using standard methods for determining timing and size of
236 freshwater emigration (Miller *et al.*, 2011; Tomoro *et al.*, 2012) described in Claiborne *et al.*
237 (2014). Otolith trace element ratios of Sr:Ca are typically lower in freshwater than in marine
238 waters and can be used to identify transitions to marine environments (Secor *et al.*, 1995; Miller
239 *et al.*, 2011). Values of ⁸⁶Sr and ⁴³Ca were measured along the dorsal-ventral otolith axis using a
240 Thermo X series II inductively coupled mass spectrometer (LA-ICPMS) coupled with a Photon
241 Machines G2 193 nm excimer laser at the Keck Collaboratory for Plasma Mass Spectrometry in
242 Corvallis, Oregon. We determined otolith width at freshwater emigration based on the increase

243 in otolith Sr:Ca to marine levels near otolith edges (Claiborne *et al.*, 2014). Fish size (fork length
244 in mm, FL) at freshwater emigration was determined from the positive linear relationship
245 between FL and otolith width (Claiborne *et al.*, 2014) and converted to mass based on a linear
246 relationship between FL and ln-mass determined from 254 UCSF subyearlings (FL 79-154 mm
247 FL) collected in 2011 ($R^2 = 0.99$ and $p < 0.01$):

$$\ln Mass = 0.03 FL - 0.48.$$

249
250 Counts of otoliths daily increments after freshwater emigration were used to determine total
251 number of days since freshwater emigration. For each individual, marine growth was the
252 difference between size at freshwater emigration and size at capture.

253 Stomach contents of 208 UCSF subyearlings were examined from July–September in
254 2011 and 2012 and are presented in Litz *et al.* (2017a). For this analysis, we assumed stomach
255 contents represented prey consumed over the previous month (i.e. stomach contents measured in
256 July 2011 represented diet from June–July 2011), an assumption that was necessary due to the
257 sampling schedule. Stomach fullness was determined as the percent of stomach content weight
258 relative to whole fish weight minus the stomach content (Weitkamp and Sturdevant, 2008). Prey
259 taxa that contributed $\geq 2\%$ of salmon diets by weight were grouped into 13 categories that
260 included insects (Insecta), pteropods (Pteropoda), cladocerans (Cladocera), ostracods
261 (Ostracoda), copepods (Copepoda), isopods (Isopoda), amphipods (Amphipoda), mysids
262 (Mysidacea), krill (Euphausiidae), shrimp larvae (Pandalidae), crab megalopae (*Metacarcinus*
263 *magister* and *Cancer* spp.), northern anchovy (*Engraulis mordax*), and unidentified fish
264 (Osteichthyes). Stomach contents of all individuals within a month were averaged and presented
265 as the proportion of total stomach content wet mass, excluding unidentified digested material or
266 non-food items (Fig. 2; Appendix Table A2). For further analysis, diet proportions were
267 aggregated into periods when salmon were mostly piscivorous (i.e., $\geq 50\%$ of their diet was
268 comprised of fish; August–September 2011 and July–August 2012) and when they fed mostly on
269 invertebrates (June–July 2011 and 2012, July–August 2011, and August–September 2012).

270 To determine prey energy density, we relied on measurements obtained from the
271 literature (Beauchamp *et al.*, 2007; Boldt and Haldorson, 2002; Marin Jarrin, 2012), as well as
272 proximate analysis of four prey samples (krill, shrimp larvae, crab larvae, and northern anchovy)

273 collected throughout the sampling period (Appendix Table A3). For this analysis, we measured
274 percent water, lipids, and nitrogen (N) in each prey sample based on wet mass. Water content of
275 samples was measured by drying samples in an oven at 60 °C for 48 h. Lipids were extracted in
276 chloroform and methanol according to Copeman *et al.* (2016), and % N was determined using
277 mass spectrometry (Litz *et al.*, 2017a). For calculation of the % protein in each sample, the % N
278 was multiplied by a conversion factor of 5.8 (Gnaiger and Bitterlich, 1984; Clarke *et al.*, 1992;
279 Doyle *et al.*, 2007). Carbohydrate fraction, which is often a negligible (<2%) component of prey
280 (Lawson *et al.*, 1998), was determined from the remainder. Quantities of lipid, protein, and
281 carbohydrates were expressed in joules (J) based on published energy equivalents (Schmidt-
282 Nielsen, 1997), with lipid equal to 39,300 J g⁻¹, protein equal to 17,800 J g⁻¹, and carbohydrates
283 equal to 17,600 J g⁻¹. Apparent digestibility estimates were determined from the literature and
284 assumed to be 90% for lipids, 85% for protein, and 40% for carbohydrates, although these values
285 may be quite variable (Hajen *et al.*, 1993; Hillestad *et al.*, 1999; Krogdahl *et al.*, 2005).

286

287 *Thermal environment*

288 The thermal environment experienced by UCSF subyearlings from late June through late
289 September 2011 and 2012 was estimated from daily measurements of sea surface temperature
290 (SST) collected by four buoys in coastal waters from the mouth of the Columbia River to Grays
291 Harbor, Washington. The buoys were station 46243 (Clatsop Spit, Oregon; 46°12' N, 124°7' W),
292 station 46029 (Columbia River Bar 20 nautical miles west of Columbia River Mouth; 46°9' N,
293 124°30' W), station 46248 (Astoria Canyon, Oregon; 46°8' N, 124°38' W), and station 46211
294 (Grays Harbor, Washington; 46°51' N, 124°14' W), and data were obtained from the National
295 Data Buoy Center (<http://www.ndbc.noaa.gov/>). Daily averages from the four stations were
296 compiled for input into the bioenergetics model (Appendix Figure A1). We assumed that buoy
297 temperatures reflected the thermal environment experienced by subyearlings in the coastal ocean
298 even though juvenile salmon may migrate vertically into cooler water during part of the day
299 (Emmett *et al.*, 2004). To further investigate this issue, we compared buoy data with surface (1
300 m) and vertically-integrated (1 to 15 m) temperatures measured *in situ* with a Seabird SBE 25
301 conductivity, temperature, and depth (CTD) profiler at 13 stations sampled 81 times along the
302 Columbia River and Willapa Bay transects from June through September in 2011 and 2012. We
303 found that the average difference between CTD and buoy SST was 0.5 °C, indicating strong

304 coherence between these two datasets. We also found that on average, surface temperatures were
305 1.5 °C warmer than the vertically integrated temperatures. To account for this difference, we
306 adjusted daily buoy SST by 1.5 °C and used these values in all bioenergetics simulations,
307 yielding temperatures that ranged from 10.9–16.0 °C.

308

309 *Bioenergetics models*

310 Bioenergetics model simulations to estimate consumption and feeding rate in field-caught
311 salmon were run from June–July, July–August, and August–September of each year. For each
312 period, we relied on empirical measurements of growth, along with growth uncertainty
313 determined from Monte Carlo simulations (growth SD), fixed diet proportions determined from
314 monthly averaged stomach contents and diet energy densities, and temperature. Models
315 calculated total consumption ($\text{g} \pm \text{SD}$), average daily consumption (g d^{-1} , J d^{-1} , and $\% \text{ BW d}^{-1} \pm$
316 SD), and feeding rate (proportion [p] of the maximum theoretical daily consumption rate [C_{max}]
317 $\pm \text{SD}$). Aggregate diet energy densities were calculated for each month by multiplying diet
318 proportions with prey energy densities and indigestible fractions summed across all prey types.
319 The average number of crab megalopae and anchovy consumed per day was calculated by
320 dividing average daily consumption (g d^{-1}) of these prey types by their average mass, which was
321 determined from 66 field-caught crab megalopae and 557 anchovy collected from July–
322 September in 2011 and 2012.

323 To address potential bias in the size-based method for determining growth, we also
324 conducted bioenergetics model simulations using each of the 56 UCSF subyearlings collected in
325 September 2011 whose growth was determined using otolith chemistry, microstructure analysis,
326 and back-calculation. It was determined that these fish entered marine waters in June ($n=1$), July
327 ($n=31$), and August ($n=24$), which generated growth rates (SGR) that roughly corresponded with
328 the size-based growth periods. For each time period (June–July, July–August, and August–
329 September) covered by our simulations, initial and final size was adjusted based on otolith
330 growth rates to match the temporal period covered for size-based bioenergetics model
331 simulations. Estimates ($\pm \text{SD}$) of average daily consumption and feeding rate were calculated for
332 visual comparison with size-based growth model outputs.

333 To evaluate the effects of piscivory on juvenile Chinook salmon growth, we compared
334 specific growth rates (SGR), biomass of potential prey, diet energy densities, consumption, and

335 feeding rates during periods when fish comprised $\geq 50\%$ of the diet (August – September 2011
336 and July–August 2012) with periods when subyearlings fed mostly on invertebrates (June–July
337 2011 and 2012, July–August 2011, and August–September 2012) using one-way ANOVA. For
338 these comparisons, SGR and consumption based on body size (% body weight d^{-1}) were
339 modeled using a logit transformation. Prey biomass data, diet energy densities (J) and
340 consumption based on daily energy ($J g^{-1}$) were ln-transformed.

341 To quantify the effects of diet energy density, feeding rate, and temperature on
342 subyearling Chinook salmon growth, we conducted a sensitivity analysis constrained by field
343 observations made in 2011 and 2012. Across years, we determined minimum, average, and
344 maximum diet energy densities (2,894, 3,257, and 3,394 $J g^{-1}$), feeding rates (43%, 64%, and
345 90% of C_{max}), and temperatures (10.9, 13.6, and 16.0 °C), then ran 135 four-week simulations of
346 growth in UCSF subyearlings with starting masses of 5, 10, 15, 20, and 25 g, by changing one
347 variable across the range at a time. The starting weights represented the observed range in
348 salmon mass upon ocean entry from June through August. Across simulations, minimum
349 (maximum) values corresponded with a decrease (increase) in diet energy density of 11% (4%),
350 feeding rate of 33% (41%), and temperature of 20% (18%) relative to average conditions.

351

352 **RESULTS**

353 *Evaluation of bioenergetics model*

354 Subyearling Chinook salmon from the UCSF group increased in mass in the laboratory from an
355 average of 9.8 g in June to 21.8 g in September (Fig. 3a). There were no significant differences
356 between the average mass of PIT-tagged fish and the average mass of all fish in the tank over the
357 course of the experiment (ANOVA, $F_{1,6} = 0.003$, $p = 0.96$). Therefore, we used the average mass
358 of all fish measured each month to calculate growth. Specific growth rates ($g, \% BW d^{-1}$)
359 increased from 0.85 to 1.14 over the three months. When fit to growth, the bioenergetics model
360 overestimated consumption (g Otohime consumed $fish^{-1}$) by $13.2 \pm 1.3\%$ SD if the adult method
361 was used to estimate salmon energy density. Model error was only $0.70 \pm 1.4\%$ SD using the
362 juvenile method. Error in consumption was significantly higher (ANOVA, $F_{2,3} = 14.67$ $p = 0.02$)
363 using the adult method compared to the juvenile method. When fit to consumption, growth was
364 underestimated by $5.7 \pm 0.6\%$ SD if the adult method was used, whereas growth was only
365 underestimated by $0.4 \pm 0.8\%$ SD using the juvenile method. Error in growth using the adult

366 method was also significantly (ANOVA, $F_{2,3} = 12.7$ $p = 0.02$) greater than using the juvenile
367 method. Given that model error was $<1\%$ for both growth and consumption based on the juvenile
368 method, we used this method for all further simulations.

369 370 *Field data*

371
372 Field results are detailed in Litz *et al.* (2017a) and briefly summarized here. Individual size
373 variation of UCSF subyearling Chinook salmon sampled in the field in 2011 and 2012 was high,
374 ranging from 4.9 g in June to 118.8 g in September (Fig. 3b–c), yielding mean (\pm SD) specific
375 growth rates that varied from 0.97 ± 0.31 to $3.22 \pm 0.14\%$ BW d^{-1} among months (Table 1).
376 Mean growth rates were highest from August to September 2011 ($3.22 \pm 0.14\%$ BW d^{-1}) and
377 July to August 2012 ($2.43 \pm 0.36\%$ BW d^{-1}), when salmon were piscivorous compared to when
378 they fed mostly on invertebrates, but these rates were not significantly (ANOVA $F_{1,4} = 4.7$ $p =$
379 0.10) faster than during periods when salmon fed mostly on invertebrates (Fig. 4a). Prey biomass
380 was also highest $>350 \mu\text{g m}^{-3}$ during periods of piscivory, but values (ln-transformed) were not
381 significantly higher (ANOVA $F_{1,4} = 5.8$ $p = 0.07$) compared to months when salmon consumed
382 mostly invertebrates (Fig. 4b). Anchovy comprised $>97\%$ of the total prey biomass when growth
383 was fastest (Litz *et al.*, 2017a).

384 We used stomach content data and prey energy densities to aggregate diet energy
385 densities by month for bioenergetics model simulations. Of the four taxa collected for this study
386 that were measured for energy density (krill, shrimp larvae, crab megalopae, and juvenile
387 northern anchovy), we noted seasonal variation in crab megalopae and juvenile anchovy, which
388 accounted for 3–50% of diet through time. There were too few samples to detect seasonality in
389 krill and shrimp larvae energy density, which collectively accounted for 0–22% of diet through
390 time. We found crab megalopae to be the most energetically dense prey ranging from 3,295 to
391 $5,027 \text{ J g}^{-1}$, and anchovy to be the least energetically dense prey ranging from 2,345 to $3,257 \text{ J g}^{-1}$.
392 However, mean overall diet energy densities (\pm SD) were similar across months and years
393 ($2,894 \pm 373$ to $3,394 \pm 327 \text{ J g}^{-1}$; Fig. 4c). We found that diet energy densities (ln-transformed)
394 did not significantly vary (ANOVA, $F_{1,4} = 1.7$, $p = 0.27$) during periods when salmon were
395 mostly piscivorous (fish represented $\geq 50\%$ of the diet) compared to when they fed mostly on

396 invertebrates, indicating that growth rate variability was probably not due to differences in prey
397 quality.

398 The thermal environment experienced by UCSF subyearlings ranged from 10.9 to 16.0
399 °C across years. Within-year variability in SST reflected northwesterly wind patterns typical of
400 the northern California Current in summer when upwelling and relaxation events fluctuate over
401 periods of days to weeks (Hickey and Banas, 2003). Juvenile salmon temperature-dependent
402 growth rates tend to vary little within the range of temperatures experienced by salmon in this
403 study (Beauchamp, 2009).

404

405 *Bioenergetics models*

406 It was determined that UCSF subyearlings consumed, on average (\pm SD) 0.77 ± 0.11 to $2.53 \pm$
407 0.16 g d^{-1} , equivalent to $2,804 \pm 385$ to $9,133 \pm 582 \text{ J d}^{-1}$, and 6.0 ± 0.6 to $10.2 \pm 0.3\% \text{ BW d}^{-1}$
408 (Fig. 4d–f). While consumption rates based on prey mass (g d^{-1}) and prey energy (J d^{-1}) were
409 similar across months, consumption based on body weight ($\% \text{ BW d}^{-1}$) was significantly higher
410 during times of piscivory ($F_{1,4} = 12.3, p = 0.02$). Likewise, feeding rates were significantly
411 higher (ANOVA $F_{1,4} = 15.0, p = 0.02$) when salmon were piscivorous, which occurred from
412 August to September 2011 ($90 \pm 3\%$ of C_{max}) and from July to August 2012 ($80 \pm 8\%$ of C_{max} ;
413 Fig. 4g). The lowest feeding rates occurred from June to July in both years when salmon
414 consumed mostly amphipods (44–49% of diet by wet mass) and fed at rates $<50\%$ of C_{max} . To
415 illustrate the potential difference in foraging costs between feeding on fish compared to
416 invertebrates, model simulations indicated that salmon consumed 1–2 anchovy per day when
417 anchovy comprised 39% of diet by wet mass (August – September 2011), and 30 crab megalopae
418 when crab comprised a similar amount of the diet (33% in August – September 2012; Table 2).

419 We fit bioenergetics models to salmon growth using both the size- and otolith-based
420 methods, from June through July, July through August, and August through September 2011
421 (Fig. 5). We found that otolith-based growth rates ($\% \text{ BW d}^{-1}$) were highest later in the summer,
422 but in September 2011 (3.00) were 0.22 lower than size-based estimates (3.22), or about 7%
423 lower (Table 1). This was the only overlapping temporal period when growth determined using
424 the two independent methods could be compared, and suggests that the size-based method may
425 not be biased. Bioenergetics model simulations of individual fish whose growth was determined
426 using otoliths consumed, on average (\pm SD) 1.29 ± 0.45 to $2.20 \pm 1.13 \text{ g d}^{-1}$, equivalent to 4,619

427 ± 1591 to $7,949 \pm 4,087 \text{ J d}^{-1}$, and 9.49 ± 1.42 to $9.82 \pm 2.27\% \text{ BW d}^{-1}$. These fish had average
428 ($\pm \text{SD}$) feeding rates that ranged from 66 ± 11 to $83 \pm 23\% \text{ C}_{\text{max}}$.

429

430 *Sensitivity analysis*

431 The factor that contributed most to growth rate variability across all 135 simulations was feeding
432 rate (Fig. 6). Overall, growth rates varied from -0.13 to $4.66\% \text{ BW d}^{-1}$ in response to observed
433 variation in feeding rate (min = 43%, average = 64%, max = 90% C_{max}), diet energy density
434 ($2,894, 3,257, 3,394 \text{ J g}^{-1}$), temperature ($10.9, 13.6, 16.0 \text{ }^\circ\text{C}$), and starting weight ($5\text{--}25 \text{ g}$).
435 Negative growth (-0.07 and $-0.13\% \text{ BW d}^{-1}$) was determined from two simulations for salmon
436 with initial mass of 20 and 25 g feeding on the lowest quality diet ($2,894 \text{ J g}^{-1}$), at the lowest
437 feeding rate (43% of C_{max}), and the highest temperature ($16.0 \text{ }^\circ\text{C}$). Fastest growth ($4.66\% \text{ BW d}^{-1}$)
438 was calculated for salmon with an initial mass of 5 g feeding for 4 weeks on the highest
439 quality prey ($3,394 \text{ J g}^{-1}$), at the highest feeding rate (90% of C_{max}), and average temperature
440 ($13.6 \text{ }^\circ\text{C}$).

441

442 **DISCUSSION**

443 Results from two years of field data determined that early marine growth rates of
444 subyearling Chinook salmon off the Washington coast were positively associated with the
445 biomass of juvenile northern anchovy (Litz *et al.*, 2017a). Using a bioenergetics approach, we
446 determined that relative differences in salmon growth were related to variation in consumption
447 ($\% \text{ BW d}^{-1}$) and feeding rate (proportion of C_{max}) more than prey quality (in terms of energy
448 density) or temperature (given the range observed). Additionally, there appears to be tight
449 coupling between estimated feeding rate and the presence of juvenile anchovy biomass in our
450 surveys. The dominance of anchovy as a prey species for subyearlings in marine waters off
451 Oregon and Washington has been demonstrated over multiple years (1998–2012) (Dale *et al.*,
452 2017). Anchovy also make up a large proportion of the adult Chinook salmon diet (Thayer *et al.*,
453 2014) indicating that the availability of this prey type is important during all life stages in coastal
454 waters of the northern California Current.

455 Size of subyearling Chinook salmon during early marine residence can be highly variable
456 (Miller *et al.*, 2013; Claiborne *et al.*, 2014; Gamble *et al.*, 2018). In this study, we used mean size
457 and time of capture to estimate growth following freshwater emigration. We assumed field

458 estimates of growth were both accurate and precise, and that bias was not introduced based on
459 factors such as uncertainty about the amount of time spent in the marine environment, size-
460 selective mortality, or size-based emigration. Supporting evidence from otoliths about growth
461 during the early marine residence period in 2011 indicate that our growth assumptions were
462 likely reasonable. MacFarlane (2010) found subyearling growth increased from 0.98 to 5.24 %
463 BW d⁻¹ as salmon transitioned from the estuary to the ocean, which was very similar to our
464 reported values ranging from 0.97 during the early outmigration period to 3.22 by late summer.

465 We found that subyearlings feeding mostly on anchovy had ocean growth rates and
466 feeding rates that were on average 2-fold faster than fish feeding mostly on invertebrates. In our
467 study, piscivorous salmon consumed prey at ≥80% of their daily digestive capacity.
468 Consumption rates obtained in this study (6.0 ± 0.6 to 10.2 ± 0.3% BW d⁻¹) were in general
469 agreement with values published elsewhere for subyearlings feeding on fish (McFarlane, 2010;
470 Haskell *et al.*, 2017), but were up to 3-fold higher than estimates presented for field-caught
471 Chinook based on laboratory observations (2.0 to 4.3 BW d⁻¹, Benkwitt *et al.*, 2011). The
472 difference may indicate that the laboratory-derived values, based on juvenile Chinook feeding on
473 invertebrates, were biased low. Piscivorous bull trout (*Salvelinus confluentus*) exceeded
474 bioenergetically sustainable consumption rates over short periods when fish prey availability was
475 high (Furey *et al.*, 2016), and it has been suggested that binge-feeding on fish prey may be an
476 adaptive response by salmonids to capitalize on patchy prey resources and maximize growth
477 during vulnerable life history phases (Armstrong and Schindler, 2011). High feeding rates during
478 prey pulses, and the subsequent increase in growth may be one way juvenile salmon increase
479 survival through early marine phases, consistent with the stage-duration hypothesis, which is the
480 idea that fast-growing fish require less time to transit through stages when they are most
481 vulnerable to predators (Houde, 2008).

482 We used prey energy density as a metric for prey quality and our modeling approach
483 assumed prey energy density estimates were accurate. Seasonal differences were detected in two
484 important prey types (crab and anchovy), but the extent of seasonal variation for other prey
485 remains unknown. More extensive work determining seasonal estimates of prey energy density
486 could improve our ability to detect seasonal variation in prey quality and may or may not support
487 the conclusion that subyearling ocean growth rates are most related to feeding rate. The energy
488 density of crab megalopae measured during several time periods in our study exceeded that of

489 northern anchovy, yet subyearlings feeding on anchovy displayed higher growth rates (>2.4%
490 BW d⁻¹). It should be noted that if invertebrates like crab megalopae are abundant enough for
491 subyearlings to feed on at high rates, salmon could achieve the same amount of growth as if
492 feeding on anchovy at a high rate. In Puget Sound, subyearling Chinook salmon grew up to 3%
493 BW d⁻¹ in habitats where they were able to feed on crab megalopae at relatively high rates
494 (Gamble, 2016). High marine survival (12.5%) of juvenile coho salmon (*O. kisutch*) feeding
495 intensely on crab megalopae has also been documented in Southeast Alaska (Weitkamp and
496 Sturdevant, 2008).

497 The Wisconsin bioenergetics model used in this study accounted for some of the
498 variability in predator size, predator energy density, predator diet, diet energy density, and
499 temperature, but likely not all possible variation. The assumption that all inputs were accurate
500 and precise is false, although many attempts were made to minimize introduced error and bias.
501 For example, salmon energy density values were adjusted for juveniles based on laboratory
502 observations, growth rates compared using two independent methods, prey energy density values
503 adjusted seasonally for two important prey types, and temperatures adjusted to reflect the range
504 of salmon habitat utilized in the ocean. Still, other factors could contribute to model error. For
505 instance, the Wisconsin model does not account for its variation in predator activity level (Trudel
506 and Rasmussen, 2006). Adjustments to the activity multiplier to reflect energy expenditure, if
507 known or estimated, could improve model performance.

508 An aspect of foraging that was not investigated in this study was the effect of prey size on
509 feeding rates. Work on other species such as lake trout (*Salvelinus namaycush*) and yellow perch
510 (*Perca flavescens*) showed that growth rates are strongly influenced by prey size (Bosclair and
511 Leggett, 1989; Pazzia *et al.*, 2002), with growth differences associated with the foraging costs of
512 capturing few versus many prey. In particular, Kerr (1982) argued that foraging costs increased
513 with feeding rates in actively foraging fish, and used laboratory experiments conducted on cod
514 (*Gadus morhus*) to illustrate this concept. Modifications to the Wisconsin model to account for
515 variation in foraging costs may be useful to determine trade-offs between feeding rate and prey
516 quality. In addition, better understanding of the energetic costs of pursuing, capturing, handling,
517 and digesting various prey types relative to their overall size could help determine whether
518 highly abundant, low quality prey offer more to growth potential than less abundant, high quality

519 prey. This may be particularly important to during years when forage fish abundance is low and
520 subyearlings feed more heavily on invertebrates.

521 Chinook salmon are generalist predators (Gregory and Northcote, 1993) and consume
522 both invertebrate and fish prey during early marine residence, although fish prey typically
523 comprise a larger proportion of the diet over time. During all months of sampling, both prey
524 types were represented in the prey field, although biomass of fish prey ($290 \mu\text{g m}^{-3}$) was 100
525 times greater than invertebrate prey ($2.9 \mu\text{g m}^{-3}$). While this might have been an accurate
526 reflection of prey availability, it could also have been due to a bias in our sampling gear whereby
527 we were unable to adequately sample all invertebrate prey types. A sampling design that utilizes
528 multiple gear types (zooplankton nets in addition to trawling) to quantify the salmon prey field
529 could better assess whether fish prey were actually more available to foraging subyearlings than
530 smaller invertebrates. More accurate estimates of prey availability, while useful, would not
531 change our conclusions from the bioenergetics model that feeding rate contributed most to
532 growth rate variability in subyearlings over the years examined.

533 Previous work showed that salmon may revert back to feeding on invertebrates in fall
534 after becoming mostly piscivorous and that this did not negatively impact growth (Litz *et al.*,
535 2017a). In fact, mean salmon growth rates were $>2\% \text{ BW d}^{-1}$ from August to September 2012
536 (the third fastest growth rate measured during the study) while feeding mostly on invertebrates
537 after previously feeding on anchovy. The availability of invertebrates as alternative prey may be
538 important for growth and survival during fall and the first winter at sea (Wells *et al.*, 2012; Dale
539 *et al.*, 2017), although few studies have sampled marine diets during this time. In one instance
540 where data are available, Hertz *et al.* (2017) found that Chinook salmon supplemented their
541 mostly fish diet by consuming more krill during the winter compared to fall, suggesting that the
542 abundance and distribution of krill may be important as a winter prey resource. Alternatively, if
543 overwinter survival of subyearlings depends on a critical size attained by fall, as indicated by the
544 “critical size, critical period” hypothesis (Beamish and Mahnken, 2001), perhaps an earlier onset
545 of piscivory offsets future energetic deficits by allowing subyearlings to invest more heavily in
546 growth when fish prey are available.

547 Adult survival of subyearlings examined in this study (fish that entered the ocean in 2011
548 and 2012 and returned three years later to Priest Rapids Dam) was relatively high ($>165,000$
549 salmon in each year) compared to 50-year mean (54,110). Other studies have shown that during

550 years of high survival, subyearlings tend to consume proportionally more invertebrates in
551 September of their first ocean year (Dale *et al.*, 2017). This may be because certain prey are
552 more abundant during high survival years, or that competition for fish prey is greater during
553 years of high survival, supported by observations that body condition in September is inversely
554 related to survival (Miller *et al.*, 2013). Another explanation, based on observations from 2011
555 and 2012, is that subyearlings might survive better in years when anchovy are highly abundant
556 early in the summer. In these years, high anchovy consumption and growth rates in July and
557 August may accelerate salmon through a phase when they are most vulnerable to predation.
558 Abundant anchovy in summer could also serve as alternative prey for other predators that might
559 otherwise prey upon juvenile salmon just arriving in the marine environment.

560 Our analysis determined that the Wisconsin bioenergetics model, when salmon energy
561 densities were corrected to reflect more reasonable juvenile values, accurately predicted growth
562 and consumption of subyearling Chinook salmon reared at low rations in the laboratory with less
563 than one percent error. This result highlights the importance of testing bioenergetics models in
564 the laboratory prior to applying them to field observations, and for using caution when
565 borrowing bioenergetics parameters from other species or life history stages (Hansen *et al.*,
566 1993; Ney, 1993; Chipps and Wahl, 2008). It also questions whether the numerous bioenergetics
567 studies that used adult parameters values for juvenile Chinook salmon overestimated
568 consumption, particularly studies where successful corroboration of the Wisconsin model for
569 Chinook salmon is presented (e.g. Brodeur *et al.*, 1992). Evaluating growth and consumption
570 across a range of temperatures, diet energy densities, and rations could help quantify the
571 magnitude of error in consumption and growth estimates related to juvenile predator energy
572 values based on the Stewart and Ibarra (1991) model. Inappropriate biological assumptions
573 leading to error in bioenergetics models have been recognized for some time (Trudel *et al.*, 2004;
574 Madenjian *et al.*, 2012; Canale and Breck, 2013), especially for juvenile Chinook salmon, whose
575 oxygen consumption rates likely differ from adults (Trudel and Welch, 2005). Differences in
576 activity may also result from differences in oceanographic currents among years, which could
577 influence ocean growth and migration rates (Burke *et al.*, 2016). Laboratory studies can help
578 identify systematic error in bioenergetics models, even though consumption rates and activity
579 may differ considerably between the laboratory and the field (Madenjian *et al.*, 2004).

580 Results from multiple bioenergetics modeling studies on the feeding ecology and growth
581 of Chinook salmon, from Southeast Alaska (Weitkamp, 2004) to the central coast of California
582 (MacFarlane, 2010), including different parts of the Salish Sea (Gamble, 2016), surf zones and
583 estuaries in Oregon (Marin Jarrin, 2012), and coastal waters of the Pacific Northwest (Brodeur *et*
584 *al.*, 1992; Beauchamp, 2009), consistently point towards the importance of high prey availability
585 and high feeding rates for salmon growth and survival across a wide range of temperatures,
586 especially for subyearlings. We found fastest growth occurred when feeding rates on anchovy
587 were highest. Our results contribute to a broader knowledge base on the foraging plasticity of
588 subyearling Chinook salmon that is emerging from work examining energy dynamics during
589 early marine residence across ecosystems. Dominant prey types may vary seasonally, annually,
590 and across different ecosystems, but if the feeding rate on that prey type is high enough,
591 subyearling growth rates should increase.

592 There are key opportunities to address the limited information on prey abundance, prey
593 energy density, and predator feeding and activity levels in the field. In the coastal marine waters
594 of the northern California Current examined in this study, anchovy appears to be the dominant
595 prey type. In British Columbia and other parts of the Salish Sea, Pacific herring (*Clupea pallasii*)
596 appears to be the dominant forage (Hertz *et al.*, 2015), whereas in Puget Sound and Southeast
597 Alaska, crab megalopae seem particularly important, at least during the early marine phase.
598 Young-of-the-year rockfish (*Sebastes* spp.), crab megalopae, and krill dominate the prey field in
599 central California (Wells *et al.*, 2016). Better understanding of juvenile salmon and prey
600 abundance, prey size, and prey quality will help to better understand foraging success relative to
601 ocean conditions and could help predict early marine growth and survival of juvenile salmonids.

602

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616

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923 **Table 1** Top values show average mass (g) and standard deviation (SD) of subyearling Chinook

924 salmon (*Oncorhynchus tshawytscha*) from the upper Columbia summer-fall genetic stock group

925 collected in the lower estuary and ocean. Sample sizes, days before capture in the ocean after

926 ocean entry, and average specific growth rates (SGR; g, % body weight d⁻¹) with error (± SD)

927 based on Monte Carlo simulations, are also presented. Bottom values show average (± SD) size

928 and ocean growth rates in 2011 determined from otoliths of 56 subyearlings collected in

929 September.

Year	Mass in	n	Mass in	n	Days in	SGR
------	---------	---	---------	---	---------	-----

	estuary (g)		ocean (g)		ocean	
Size Method						
2011						
Jun/Jul	11.3 (3.9)	31	14.4 (4.2)	38	25	0.97 (0.31)
Jul/Aug	10.5 (3.9)	26	21.3 (7.9)	33	36	1.96 (0.29)
Aug/Sep	11.5 (2.8)	30	46.0 (17.5)	98	43	3.22 (0.14)
2012						
Jun/Jul	10.7 (8.1)	6	16.2 (4.8)	48	32	1.30 (0.49)
Jul/Aug	11.1 (3.9)	33	27.3 (5.9)	3	37	2.43 (0.36)
Aug/Sep	14.7 (4.0)	27	34.9 (11.3)	53	41	2.11 (0.18)
Otolith Method						
2011						
Jun/Sep	13.2	1	99.7	1	105	1.92
Jul/Sep	10.1 (2.8)	31	57.4 (37.1)	31	64 (7)	2.55 (0.64)
Aug/Sep	11.6 (3.8)	24	45.9 (25.7)	24	44 (8)	3.00 (0.89)

930 **Table 2** Diet proportions, sample sizes, average (\pm standard deviation SD) mass, and amount of northern anchovy (*Engraulis*
 931 *mordax*) and crab megalopae (*Metacarcinus magister* and *Cancer* spp.) consumed by subyearling Chinook salmon (*Oncorhynchus*
 932 *tshawytscha*).

Date	2011			2012		
	Jun-Jul	Jul-Aug	Aug-Sep	Jun-Jul	Jul-Aug	Aug-Sep
<i>Northern anchovy</i>						
Diet proportion	0	0.025	0.394	0	0.254	0.034
n =	0	120	239	97	90	11
Average mass (g)	0	0.25 \pm 0.05	0.64 \pm 0.45	0.15 \pm 0.03	0.35 \pm 0.14	0.27 \pm 0.21
Consumption (g d ⁻¹)	0	0.03 \pm 0.004	1.00 \pm 0.07	0	0.48 \pm 0.08	0.06 \pm 0.01
Consumption (no. d ⁻¹)	0	0.1	1.6	0	1.4	0.2
<i>Crab megalopae</i>						
Diet proportion	0.176	0.003	0.109	0.124	0	0.329
n =	47	3	1	14	0	1
Average mass (g)	0.04 \pm 0.02	0.04 \pm 0.01	0.04	0.03 \pm 0.05	0	0.02
Consumption (g d ⁻¹)	0.14 \pm 0.02	0.004 \pm 0.001	0.28 \pm 0.02	0.11 \pm 0.03	0	0.60 \pm 0.05
Consumption (no. d ⁻¹)	3.5	0.1	7.0	3.7	0	30

933 **Appendix Table A1** Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) mass (g) and energy
934 density (J g⁻¹) determined using bomb calorimetry on fish collected off southern British
935 Columbia in 1999 and 2002 (modified from Trudel *et al.*, 2005).

g	ED	g	ED	g	ED	g	ED
690	4,761	287	4,572	128	4,470	79	4,507
640	6,231	256	4,790	118	4,767	73	4,334
590	5,015	250	4,448	115	4,276	72	4,013
464	4,622	235	4,529	115	4,388	72	4,325
412	4,946	226	4,522	109	4,308	70	4,135
323	5,280	208	4,799	109	4,093	56	4,561
316	4,926	205	4,816	103	4,185	54	3,975
313	4,158	173	4,937	101	4,623	53	4,360
313	5,262	139	4,268	100	4,194	47	4,637
304	5,136	138	4,225	100	4,537	34	4,258
296	4,814	131	4,153	81	4,205	34	4,583

936 **Appendix Table A2** Diet proportions by month based on stomach contents (n=208) of subyearling Chinook salmon (*Oncorhynchus*
 937 *tshawytscha*) modified from Litz *et al.* (2017a).

Diet		2011			2012		
Common name	Scientific name	Jun-Jul	Jul-Aug	Aug-Sep	Jun-Jul	Jul-Aug	Aug-Sep
Insect	Insecta	0.160	0.276	0.085	0.143	0.019	0.183
Pteropod	Pteropoda						0.015
Cladoceran	Cladocera					0.297	
Ostracod	Ostracoda	0.001					
Copepod	Copepoda	0.022					0.003
Isopod	Isopoda						0.014
Amphipod	Amphipoda	0.490	0.306	0.142	0.436	0.157	0.066
Mysid	Mysidacea	0.097			0.033		
Krill	Euphausiidae		0.216		0.119		0.032
Shrimp larvae	Pandalidae	0.053				0.019	0.169
Crab megalopae	<i>Metacarcinus magister</i> and <i>Cancer productus</i>	0.176	0.003	0.109	0.124		0.329
Northern anchovy	<i>Engraulis mordax</i>		0.025	0.394		0.254	0.034
Unidentified fish	Osteichthyes		0.175	0.270	0.144	0.254	0.155

938

939 **Appendix Table A3** Energy density ($J g^{-1}$) of prey for input into the bioenergetics model, including % indigestible, and references.

Diet	Energy Density	2011			2012			% Indigestible	Reference
Common name		Jun-Jul	Jul-Aug	Aug-Sep	Jun-Jul	Jul-Aug	Aug-Sep		
Insect		3,511	3,511	3,511	3,511	3,511	3,511	3.33	3

Pteropod	2,612	2,612	2,630	2,612	2,612	2,630	8.50	2
Cladoceran	2,514	2,514	2,514	2,514	2,514	2,514	10.00	1
Ostracod	2,586	2,586	2,586	2,586	2,586	2,586	10.00	1
Copepod	2,623	2,623	2,623	2,623	2,623	2,623	9.00	3
Isopod	2,460	2,460	2,460	2,460	2,460	2,460	50.00	3
Amphipod	3,606	3,606	3,606	3,606	3,606	3,606	15.12	3
Mysid	4,208	4,208	4,208	4,208	4,208	4,208	11.83	3
Krill	3,190	3,190	3,190	3,190	3,190	3,190	NA*	4
Shrimp larvae	3,959	3,959	3,959	3,959	3,959	3,959	NA*	4
Crab megalopae	3,658	4,343	5,027	3,733	3,514	3,295	NA*	4
Northern anchovy	2,345	3,257	2,892	2,345	2,764	3,103	NA*	4
Unidentified fish	4,104	4,104	4,104	4,104	4,104	4,104	13.67	3
Total Diet	3,314	3,274	3,367	3,298	2,894	3,394		

940 *Indigestibility fraction accounted for in proximate analysis equation

941 ¹ Boldt and Haldorson 2002

942 ² Beauchamp *et al.*, 2007

943 ³ Marin Jarrin 2012

944 ⁴ This study

945 **Figure Legends**

946

947 **Figure 1.** Map of study area where subyearling Chinook salmon (*Oncorhynchus tshawytscha*)
948 and their potential prey were sampled in 2011 and 2012 (estuary = triangles, ocean = circles).
949 Prey samples were collected in the stations indicated by filled circles; temperature data were
950 collected at buoys indicated by stars; salmon collected for otoliths indicated by a cross.

951

952 **Figure 2.** Average diet composition of subyearling Chinook salmon (*Oncorhynchus*
953 *tshawytscha*) as a proportion of wet mass, with an emphasis on northern anchovy (*Engraulis*
954 *mordax*). Invertebrates are shown in grayscale; fish categories are in solid (modified from Litz et
955 al. [2017a]).

956

957 **Figure 3.** Mass (g) of salmon a) reared in the laboratory from June through September 2013, or
958 captured in the estuary and ocean from June through September in b) 2011 and c) 2012. Colored
959 symbols indicate laboratory fish marked with a passive integrated transponder (PIT) tag.
960 Averages used to calculate growth denoted by solid lines.

961

962 **Figure 4.** Average (\pm standard deviation SD) a) salmon growth rate, b) prey biomass, c) diet
963 energy density, d–f) consumption, and g) feeding rate of salmon measured for each sampling
964 period of the study. Prey biomass values are ln-transformed and error bars for these values
965 represent standard error (SE).

966

967 **Figure 5.** Comparison of otolith-based and size-based a) growth, and resultant values from
968 bioenergetics model simulations including b-d) consumption, and e) feeding rate. Error (\pm
969 standard deviation SD) determined for otolith-based measurements based on individuals (n=56),
970 and for size-based measurements based on model outputs using growth error estimates
971 determined from Monte Carlo simulations (n=5,000 replications).

972

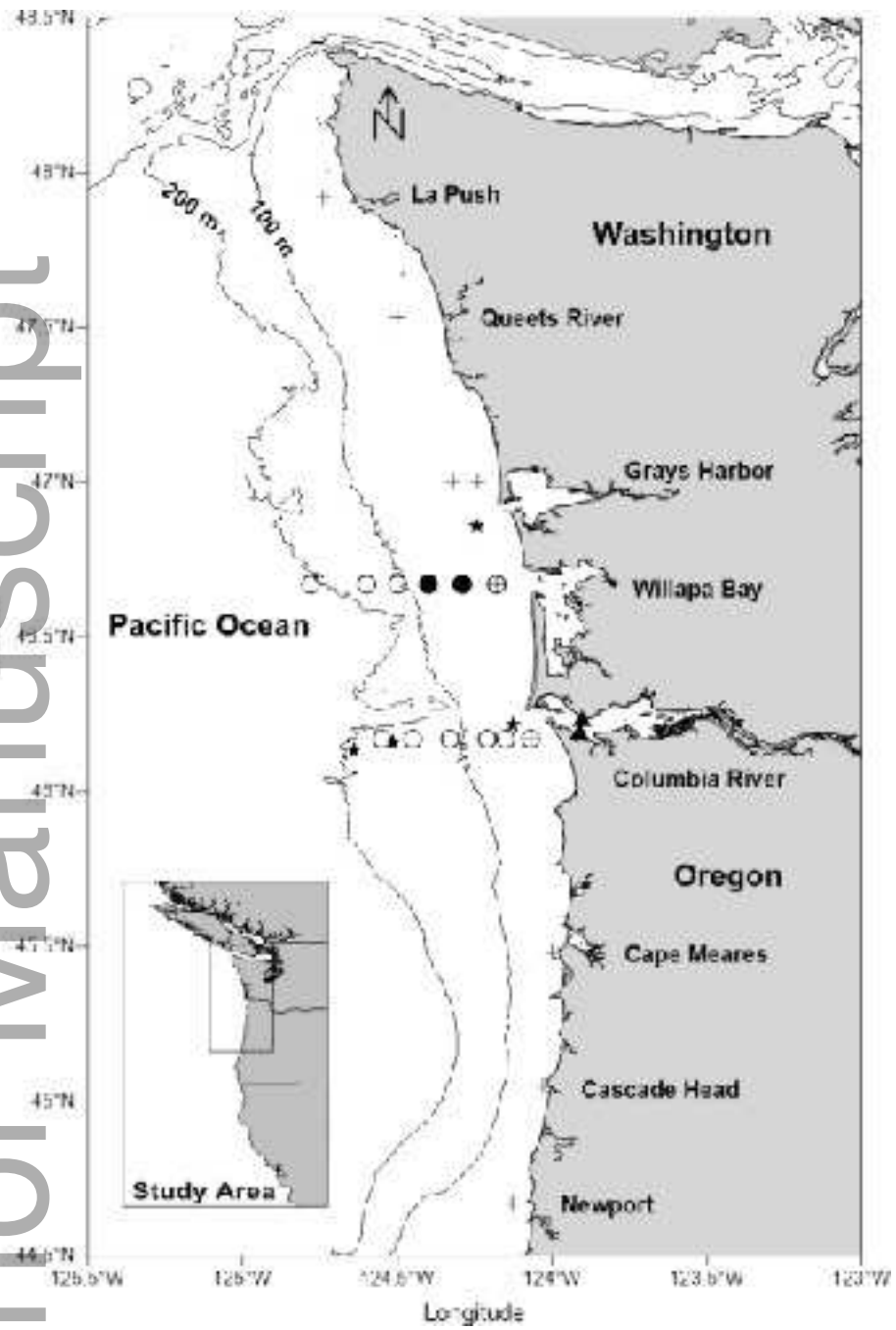
973 **Figure 6.** Average (\pm standard deviation SD) specific growth rates (SGR; g, % body weight d⁻¹)
974 of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) ranging from 5–25 g (a–c) feeding
975 at the minimum, average, and maximum observed feeding rates (% of maximum consumption

976 C_{\max}), diet energy densities ($J g^{-1}$), and temperatures ($^{\circ}C$) measured during the field study. Also
977 shown (d–f) are average percent change in growth relative to average conditions.

978

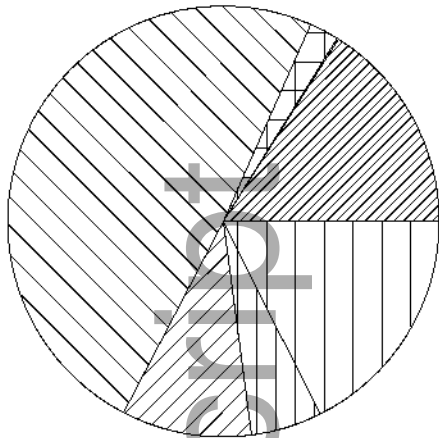
979 **Appendix Figure A1.** Daily average sea surface temperatures (SSTs) measured at 30-minute
980 intervals from station 46243 (Clatsop Spit, Oregon), station 46029 (Columbia River Bar 20
981 nautical miles west of Columbia River Mouth), station 46248 (Astoria Canyon, Oregon), and
982 station 46211 (Grays Harbor, Washington) June through October 2011 and 2012. Solid
983 horizontal line is mean SST; dotted lines represent minimum and maximum SSTs for the entire
984 sampling period.

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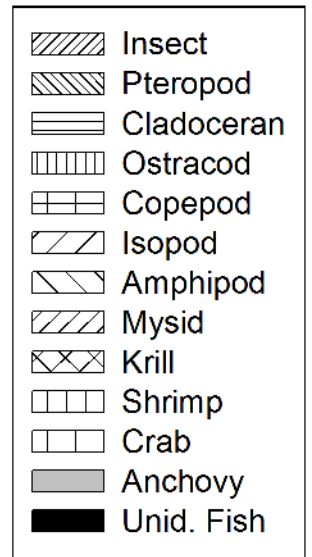
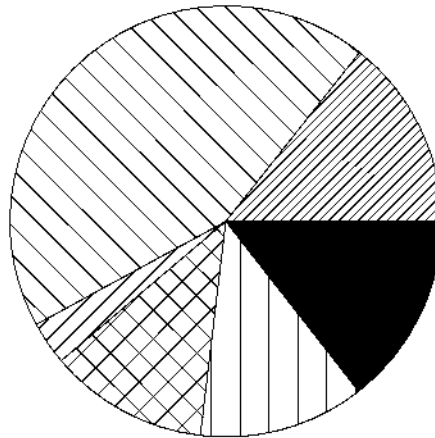


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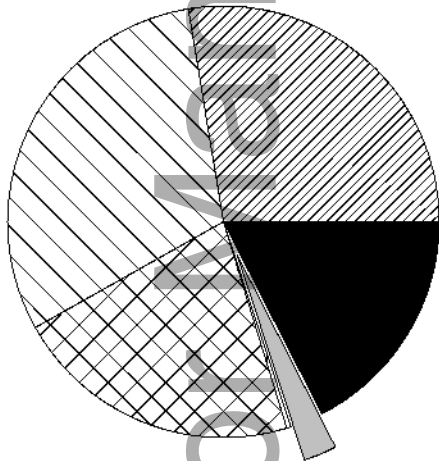
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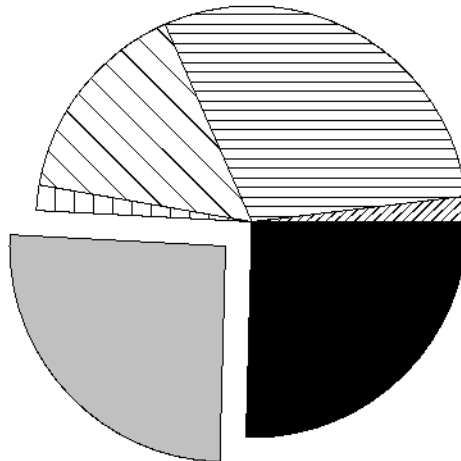
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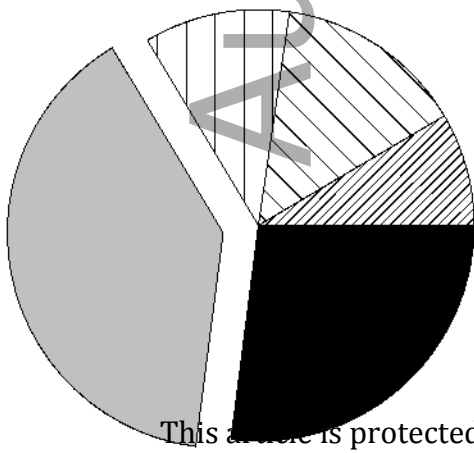
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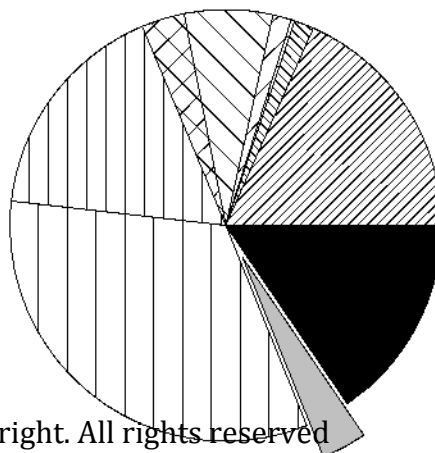
e. Jul-Aug 2012



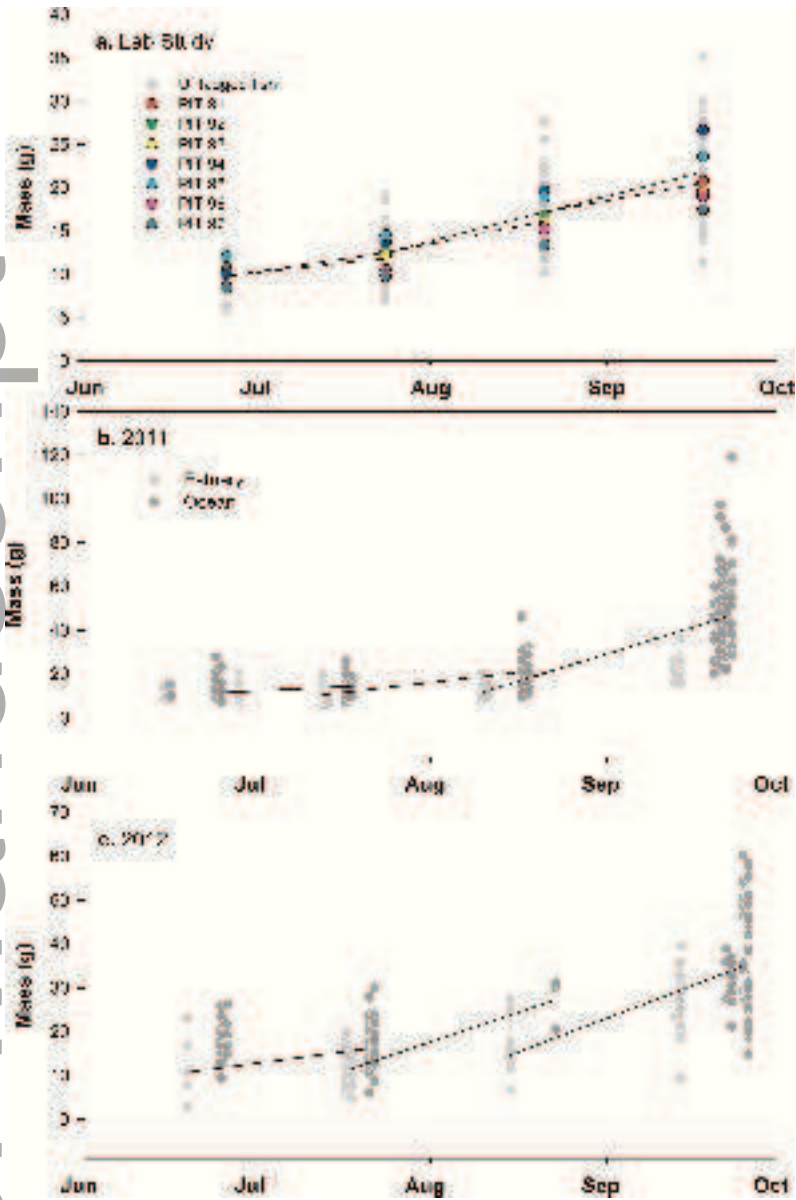
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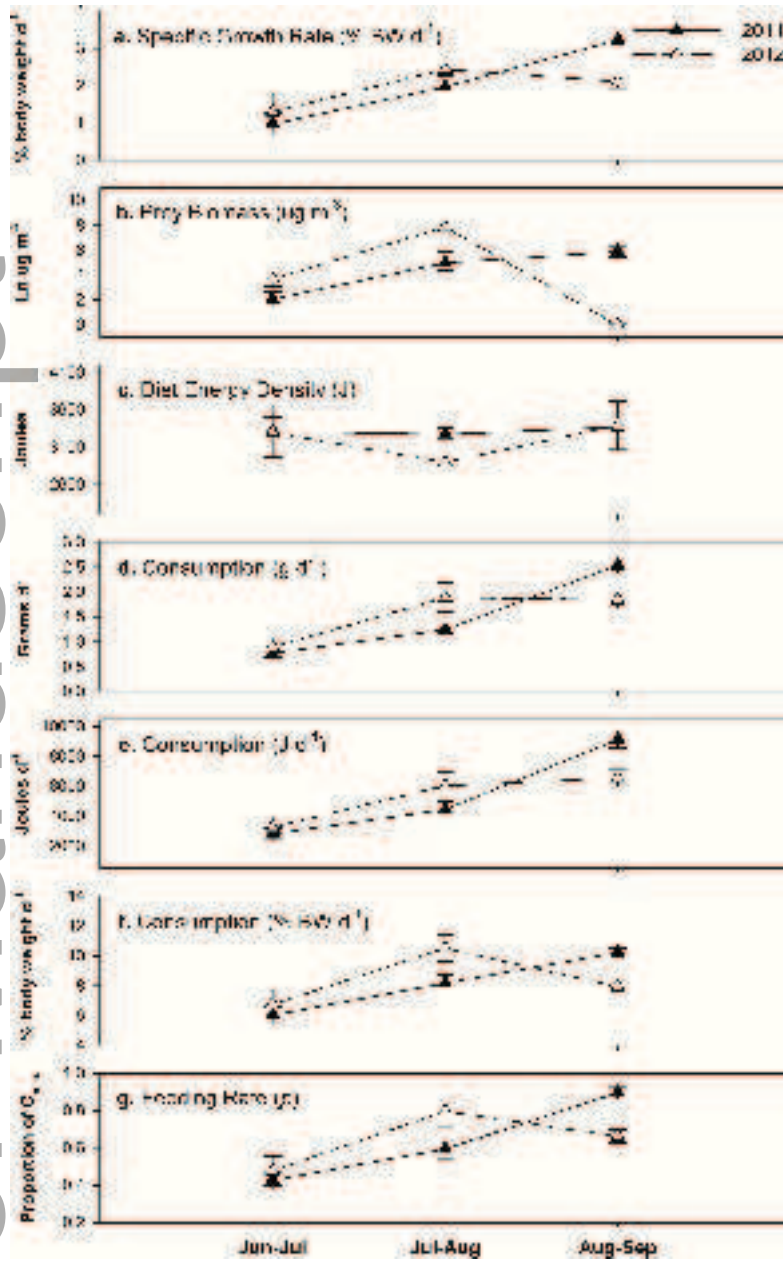
f. Aug-Sep 2012



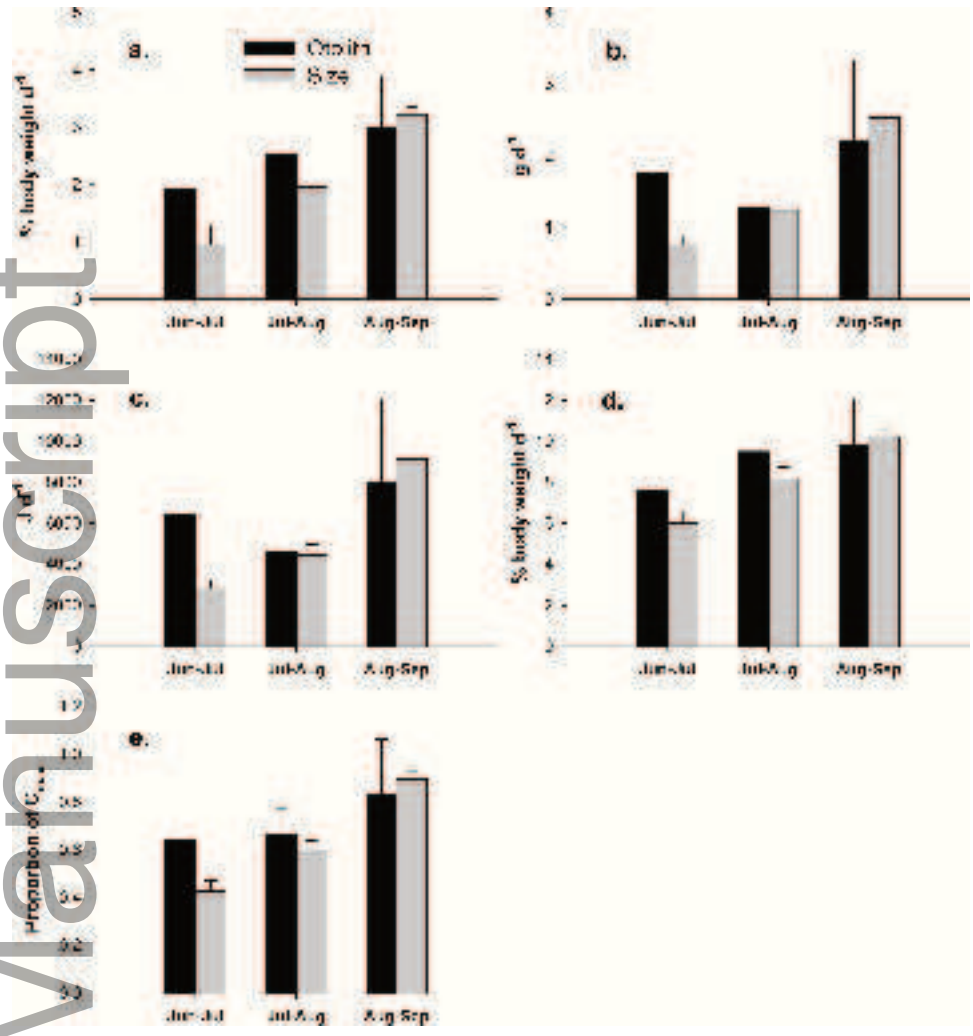
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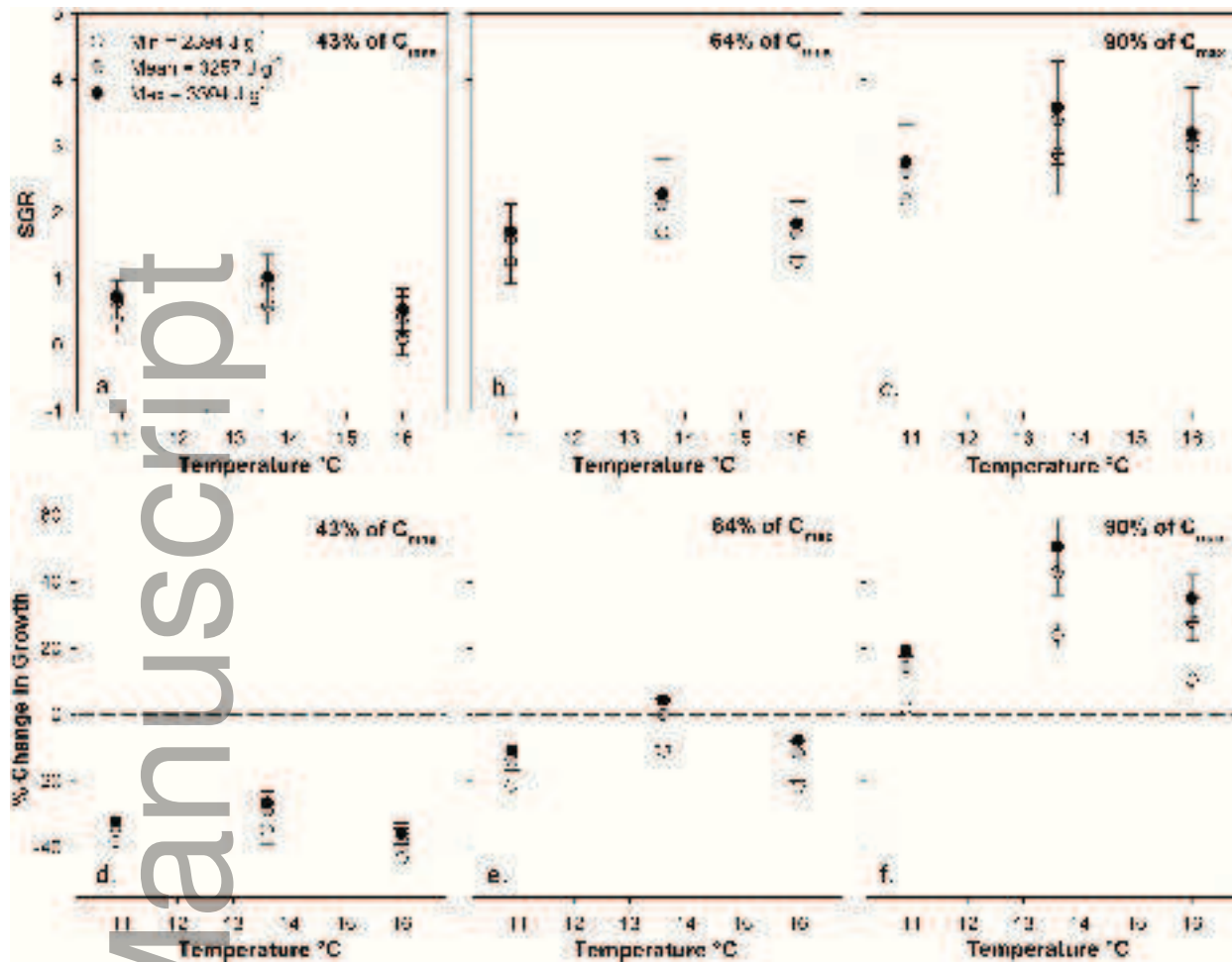
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fog_12407_f4.tif



fog_12407_f5.tif



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