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Running Head: Thermal impacts on early marine Steelhead

Title: Two anomalously warm years in the northern California Current: impacts on early marine Steelhead diet composition, morphology, and potential survival

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<A>Abstract

Juvenile Steelhead *Oncorhynchus mykiss* enter the northern California Current ecosystem from the Columbia River and other Northwest coastal rivers and include several populations listed under the US Endangered Species Act. However, relatively little is known about the response of these populations to interannual variability in ocean conditions. In 2015 and 2016, anomalous

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30 ocean conditions, called the warm ‘Blob’, persisted in the northern California Current, increasing
31 ocean temperatures by $>2.5^{\circ}\text{C}$. To determine how Steelhead respond to such major shifts in
32 temperature, we compared juvenile Steelhead diet composition, stomach fullness, size, and body
33 condition from 2015 and 2016 to a subset of Steelhead collected from previous surveys (2001,
34 2002, 2004, 2006-2011) that included warm, cool, and neutral ocean years. In addition, we used
35 bioenergetics models to assess the importance of the marine environment in contributing to
36 changes in Steelhead condition under different ocean temperature scenarios. Steelhead from
37 2015 and 2016 exhibited some of the poorest body conditions but were the largest sizes across all
38 years evaluated. Steelhead diet composition varied between warm and cold years and between
39 warm and average years, with Steelhead consuming more insects, juvenile rockfishes, and rare
40 and unidentified fish in warm years. Unusual taxa including gelatinous salps (2015 and 2016)
41 and juvenile smelts (2016) were consumed during Blob-influenced years. Bioenergetics models
42 indicated that interannual variability in growth is influenced by changes in temperature and
43 feeding conditions in the marine environment, with significant differences in growth between
44 warm and cold ocean years apparent by day two of the simulated marine residence. These
45 findings highlight the potential for warm ocean years to influence the diet composition and
46 morphology of Columbia River Steelhead populations and may lead to a better understanding of
47 factors influencing survival of juvenile Steelhead in the early marine residence.

48

49 <A>Introduction

50 Anadromous Steelhead *Oncorhynchus mykiss* are salmonids with a diverse life history that is
51 heavily mediated by the marine environment (Kendall et al. 2017). Steelhead travel rapidly
52 through the estuarine and coastal environment as juveniles (Weitkamp et al. 2012; Daly et al.
53 2014) and then migrate directly to offshore habitats in the North Pacific where they mature
54 (Hayes and Kocik 2014; Myers 2018). Evidence suggests that mortality of salmonid smolts is
55 high during their first year in the marine environment (Pearcy 1992; Quinn 2005), yet the marine
56 phase of the Steelhead life history remains understudied in comparison to its freshwater phase
57 (Daly et al. 2014). Steelhead are widely distributed across the Columbia River Basin of the
58 Pacific Northwest and serve many important ecological, economic, and cultural roles within the
59 region (Pearcy et al. 1990; Myers 2018). However, numerous Columbia River Steelhead
60 populations are listed as threatened or endangered under the US Endangered Species Act (ESA).

61 An understanding of the marine life history of these populations is critical to ensure their
62 persistence in the future.

63 Columbia River populations of Steelhead enter the northern California Current (NCC)
64 ecosystem as smolts in late spring (Weitkamp et al. 2012). This ecosystem is highly productive
65 due to intense seasonal upwelling, and interannual and interdecadal variability in the NCC is
66 closely coupled with salmon survival in the region (Burke et al. 2014; Daly and Brodeur 2015).
67 Unlike other salmonids which generally spend months in coastal waters of the Northeast Pacific
68 Ocean, juvenile Steelhead from the Columbia River spend relatively little time in nearshore
69 waters as they migrate directly offshore to oceanic waters (Myers 2018). In coastal surveys off
70 Washington and Oregon, they are found mainly at the offshore stations in May and are almost
71 entirely absent from coastal waters by the end of June (Daly et al. 2014). Despite the short
72 period within this coastal environment (<10 days), Steelhead feed extensively when prey
73 resources are sufficiently available, and grow rapidly, especially compared to their short
74 residence in the Columbia River estuary (Daly et al. 2014). Juvenile Steelhead in coastal waters
75 feed on a variety of prey, consuming mainly crustaceans, insects, and small fishes, and appear to
76 feed mainly in the near-surface or even neustonic part of the water column (Pearcy et al. 1990;
77 Brodeur et al. 2013; Daly et al. 2014). Previous juvenile Steelhead food habits studies in this
78 region showed some interannual variability in their diets (Pearcy et al. 1990; Daly et al. 2014;
79 Myers 2018).

80 Interannual and decadal variability in the California Current upwelling region can lead to
81 changes in ocean conditions that may impact the Steelhead prey field. Sea surface temperature
82 (SST) in the NCC is influenced by a variety of climatic phenomena including the El Niño
83 Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre
84 Oscillation (NPGO). Together, these climatic patterns influence the amount and type of prey
85 that will persist in the water column each year (Daly et al. 2013; Sydeman et al. 2013).
86 Steelhead require sufficient nutrition within a relatively short window of time in order to grow
87 and develop at sea. If food resources are suboptimal, size-selective mortality can occur
88 (Thompson and Beauchamp 2014). Steelhead first return to freshwater to spawn after one to
89 three years in the ocean, so high mortality during their first few months in the ocean can suppress
90 subsequent adult returns (Daly et al. 2014).

91 Climatic data suggests that the NCC has experienced extreme variability with respect to
92 physical ecosystem properties (including temperature, oxygen levels, and salinity) during the last
93 several decades (Sydeman et al. 2013; Garcia-Reyes and Sydeman 2018). In the most recent
94 decade, the ENSO and the PDO have shown anomalously positive phases and the NPGO has
95 shown extreme negative phases, impacting SST within the region (Peterson et al. 2007; Brodeur
96 et al. 2019a). In addition to this long-term climatic variability, the North Pacific began to
97 experience anomalously weak atmospheric forcing during the winter of 2013-2014, leading to a
98 lack of deep-water mixing and lower-than-normal rates of heat loss from the subarctic Pacific
99 Ocean (Bond et al. 2015). The anomalously warm water mass in the North Pacific that formed
100 as a result of these events was termed the ‘Blob’ and produced SST anomalies of $>2.5^{\circ}\text{C}$ (Bond
101 et al. 2015; Di Lorenzo & Mantua 2016; McClatchie et al. 2016), which moved on the NCC shelf
102 in September 2014 (Peterson et al. 2017). This warm water mass persisted in the NCC
103 throughout much of 2015. In 2016, these unusual conditions continued with the NCC
104 experiencing the strongest El Niño event on record in the tropical Pacific (Jacox et al. 2016).
105 Together, these warm water temperatures have exceeded the magnitude and duration of any other
106 recent warming events off the Pacific Northwest coast (Peterson et al. 2017; Auth et al. 2018;
107 Brodeur et al. 2019a).

108 The combined environmental perturbations associated with the ‘Blob’ and El Niño in
109 2015 and 2016 have contributed to unprecedented shifts within the region’s biological
110 community (Cavole et al. 2016; Sakuma et al. 2016; Peterson et al. 2017; Auth et al. 2018;
111 Brodeur et al. 2019a,b). Studies conducted during this time observed changes across many
112 trophic levels including increases in harmful algal blooms, changes in distribution and phenology
113 of important fish stocks, and mass mortalities of marine mammals and seabirds (Leising et
114 al. 2015; Cavole et al. 2016; Piatt et al. 2020). These ecosystem changes have the potential to
115 modify the Steelhead prey field by altering the distribution, phenology, and abundance of
116 traditional prey taxa and by increasing the number of unusual taxa within the region (Sakuma et
117 al. 2016; Auth et al. 2018). In the winters of 2015 and 2016, overall larval fish concentrations
118 were the highest observed since 1998 and included unusually large amounts of warm-water taxa
119 such as rockfishes (*Sebastes* spp.) and northern anchovy (*Engraulis mordax*) (Daly et al. 2017;
120 Auth et al. 2018). It has been suggested that a warm water taxa-dominated prey field is
121 associated with poor returns of Chinook salmon (*Oncorhynchus tshawytscha*), and the

122 prevalence of warm water prey in the NCC in 2015 and 2016 may have implications for the adult
123 returns of other species of Pacific salmonids including Steelhead (Daly and Brodeur 2015; Dale
124 et al. 2017; Daly et al. 2017).

125 The purpose of our study is to examine shifts in the diet composition and overall
126 morphology of early marine Columbia River Steelhead that entered the ocean during the ‘Blob’
127 and El Niño-influenced years and to compare these results to those of other warm, cold, and
128 average temperature years within the NCC. In addition, we assess the importance of the marine
129 environment in influencing interannual differences in Steelhead growth using bioenergetics
130 models. We analyzed juvenile Steelhead caught in May of 2015 and 2016 and compared their
131 diet and condition metrics to those found in nine other survey years (2001, 2002, 2004, 2006-
132 2011). By examining the effects of the 2015-2016 anomalously warm ocean conditions on
133 juvenile Steelhead, we hope to evaluate the impact of changing ocean conditions on these
134 populations to help predict marine survival and thus inform management in projected future
135 warm-ocean years.

136

137 <A>Methods

138 *Sample collection.*-- Juvenile Steelhead were collected from Columbia River-influenced coastal
139 nearshore waters during surface-trawl surveys in May 2015-2016. These surveys occurred as part
140 of the long-term Bonneville Power Administration (BPA) Plume Survey. Fish caught in 2015-
141 2016 were compared to a subset of Steelhead collected from previous May BPA Plume Surveys
142 (2001, 2002, 2004, 2006-2011; Daly et al. 2014). The survey design prior to 2015 was broader in
143 geographic scope. For direct comparison with 2015-2016 samples, we limited the earlier data set
144 to a subset of fish captured in the region from Willapa Bay, WA (46.68 °N) to the Columbia
145 River, OR (46.14 °N).

146 We collected all juvenile salmon with a Nordic 264 pelagic rope trawl (mouth opening:
147 30 m wide and 20 m deep; cod-end liner: 0.8 cm). The rope trawl was towed for 30 min during
148 daylight hours at a ship speed of ~ 6 km/hr (3.2 knots) within 1 m of the surface (see Daly et al.
149 2014 for more detailed methodology). All captured juvenile salmon were identified to species,
150 measured (fork length, FL, nearest 1 mm), individually labeled, and then frozen immediately. In
151 the laboratory, field identification of salmonids was verified, fin clips were taken, and each fish
152 was re-measured and weighed. Stomachs were removed and placed in a non-formaldehyde

153 fixative [Prefer, Anatech Ltd.] for trophic analysis. Genetic analysis on fin clips were performed
154 according to methods in Van Doornick et al. (2019).

155

156 *Diet.*-- Stomach contents were analyzed under a dissecting microscope, and prey were classified
157 to the lowest possible taxonomic category, quantified, and weighed to the nearest 0.001 g. In
158 preparation for data analysis, we calculated Steelhead diet composition by weight of prey
159 consumed using 19 prey groups: rockfishes (*Sebastes* spp.), cottids, osmerids, hexagrammids,
160 sablefishes, Pacific sand lance, salmonids, unidentified/rare fishes (fish that made up < 5% of
161 diet composition in any year), *Cancer* spp. crab larvae, salps, euphausiids, shrimp larvae,
162 polychaetes, isopods, pteropods, cirripede larvae, insects, unidentified gelatinous material, and
163 other (including amphipods, non-*Cancer* crab larvae, and copepods). A prey taxon was
164 determined to be a prey group if in any given year, they were at least five percent of the diets by
165 weight of prey consumed. Juvenile Steelhead diets were averaged at each station to eliminate
166 auto-correlation between individual fish at stations where Steelhead fed concurrently on the prey
167 that was present, resulting in most individuals having similar diets.

168

169 *Data analysis.* -- Ocean regime was determined by ecosystems indicator data compiled in
170 Peterson et al. (2014) for 1998-2013 and updated for 2014-2016 at
171 <https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/g-forecast.cfm#TableSF-02>;
172 last accessed July 2, 2018). The ocean ecosystem indicator table was developed for juvenile
173 salmon in the Northern California current ecosystem. Using the rank of the means from the
174 ocean ecosystem indicator table, we divided the years into the lowest one-third ranked years and
175 classified them as cold years, the middle-third as average, and the top-third as warm ocean years.
176 In 2001, fish were captured in warmer Columbia River Plume waters, but overall ocean
177 conditions for that year were considered cool (Table 1).

178 Community diet relationships were visually represented with a Nonmetric
179 Multidimensional Scaling (NMDS) ordination of 2 dimensions and statistically analyzed using a
180 Multi-Response Permutation Procedure (MRPP). A random starting location was used for the
181 NMDS with up to 200 iterations per run. The environmental data in our analysis included year
182 and ocean regime (warm, cold, or average). We visualized community diet data during each year
183 or ocean regime with a dispersion ellipse of 95% confidence intervals of the average spatial

184 scores (Oksanen et al. 2012). The MRPP tested the null hypothesis that diet did not differ
185 between groups and used a Bray-Curtis distance measure (McCune and Grace 2002). We used an
186 A statistic value of >0.02 and a p value of < 0.05 to determine significant associations between
187 groupings. All multivariate statistics for juvenile Steelhead diet composition were conducted
188 with the *vegan*, *MASS*, *labdsv*, and *indicpecies* packages in R v. 3.1.2. (e.g. Hill et al. 2015) and
189 verified using PC-ORD v. 6.22 (McCune and Mefford 1999).

190 We used an Indicator Species Analysis (ISA) to describe the primary prey species
191 contributing to significant differences in Steelhead diet composition between ocean regimes.
192 (Dufrene and Legendre 1997). ISA examines significant occurrences of prey species within
193 ocean regimes. The analysis is a combined proportional measure of prey abundance within a
194 group relative to all groups and includes percent frequency of that prey species for each group
195 (see Brodeur et al. (2019b) for more detailed methods). Statistical significance was determined
196 by a Monte Carlo test.

197 Stomach fullness was calculated as: (Weight [g] of prey consumed / (Total fish weight –
198 Weight of prey consumed). Due to the proportional nature of Steelhead stomach fullness [0-1],
199 we used a beta regression with a logit link function to examine the relationships between year
200 captured and Steelhead fork length on overall stomach fullness, which tested the null hypothesis
201 that stomach fullness did not change between years or between fish of different sizes. Our
202 observed data (y_i) included zeros, and as a result, we transformed the data by

$$203 \quad y = \frac{[y_i(n - 1) + 0.5]}{n}$$

204 where n is the sample size, to allow inclusion of these extreme values in the beta regression
205 model (Smithson and Verkuilen 2006). Empty stomachs were classified when overall stomach
206 fullness was < 0.05% of the Steelhead's body weight. We used a logistic regression with a logit
207 link function to assess the number of Steelhead with empty stomachs across study years.

208 In order to provide an index of Steelhead growth, we examined Steelhead fork length
209 (mm), weight (g), and overall condition. We used length-weight condition residuals from the
210 regression analysis of $\ln(\text{weight [g]})$ to $\ln(\text{FL [mm]})$ to determine if Steelhead were fat (positive
211 residual) or thin (negative residual) for their size using the following regression: $\ln(\text{Wt}) = -$
212 $4.73417 + 2.84966 * \ln(\text{L}); P = 0.0001; R^2 = 90.6\%$. We tested for significant interannual
213 differences in Steelhead fork length, weight, and condition using the Kruskal-Wallis

214 Nonparametric test, as the fork length, weight, and condition residuals were not normally-
215 distributed (Shapiro-Wilk Test; $P < 0.05$). When there were significant differences in size or
216 condition, we used a Bonferonni-corrected Dunn pairwise comparison test to determine specific
217 differences.

218 Our two largest sample years were 2006 ($n = 122$) and 2015 ($n = 176$). We used these
219 years to assess variability in diet composition among different sizes of juvenile Steelhead within
220 a single year. We divided 2006 and 2015 into five or six different size classes based on the most
221 even division of samples in the dataset (**2006:** <190mm, 190-210mm, 210-230mm, 230-250mm,
222 > 250mm; **2015:** <180mm, 180-200 mm, 200-220 mm, 220-240 mm, 240-260mm, >260mm).
223 We analyzed community diet relationships between size classes with an MRPP, and if results
224 were significant, we used an ISA analysis to determine specific differences.

225
226 *Bioenergetics simulations.*-- The influence of the marine environment in determining interannual
227 variability in Steelhead growth was assessed using bioenergetics models. Bioenergetics models
228 quantify fish growth based on thermodynamic principles where energy from food consumption is
229 partitioned into three components: energy required for metabolism, waste removal, and growth
230 (Deslauriers et al. 2017). Bioenergetics models can be parameterized to include water
231 temperature to provide insight into how warming water temperatures impact Steelhead food
232 consumption (as a proportion p of maximum consumption) and growth (Beauchamp 2009;
233 Railsback & Rose 1999). We examined five different growth scenarios where Steelhead fed at
234 different consumption rates in warm and cold ocean years in order to assess changes in growth
235 across the first twelve days of marine residence. Fish fed at rates of 100% and 50% of maximum
236 consumption in cold years, and 100%, 50%, and 20% of maximum consumption in warm years.
237 Feeding rates of 20% maximum consumption were unlikely for fish in cold year scenarios
238 because ocean productivity and prey abundance during cold ocean conditions are likely more
239 favorable than in warmer ocean conditions (Piatt et al. 2020). Each simulation was
240 parameterized with average daily temperatures between May 10th and 21st from NOAA buoys
241 along the Oregon and Washington Coasts in warm and cool years. The date range is
242 representative of the timing and temperatures experienced by the fish in this study (Daly et al.
243 2014). The bioenergetics model evaluated specific growth rate over twelve days and used
244 weight measurements instead of length measurements. When food conditions are sufficient,

245 salmon specific growth rate will increase under warmer water temperatures up to a temperature
246 maximum and then decline (Beauchamp 2009). All fish were set at 90 g at day 0 of the
247 simulations based on average weight of Steelhead across all survey years.

248 Bioenergetics simulations were conducted in Fish Bioenergetics 4.0 in the Shiny interface
249 of the R computing environment (Deslauriers et al. 2017). The model was parameterized using
250 values obtained for juvenile Rainbow Trout (non-anadromous form of Steelhead; Tyler and
251 Bolduc 2008). Steelhead energy density was set to 4967 J/g (Myers 2018), and average marine
252 prey energy density and average proportion of indigestible prey were determined from Davis et
253 al. (1998) and Marin Jarrin (2012). Marine prey energy density was elevated by 30% in cold
254 ocean years to illustrate the temperature-influenced trends in prey energy density observed by
255 Daly and Brodeur (unpublished data) and compared to simulations run at a constant marine prey
256 energy density. Warm and cold years were determined based on a combination of Ocean
257 Indicator Data compiled in Peterson et al. 2014 (1998-2013) and
258 <https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/g-forecast.cfm#TableSF-02>;
259 last accessed July 2, 2018 (2014-2016). Five years of the time series were assigned as warm
260 years and five years were assigned as cold years. We did not create an “average” year category
261 for this analysis. Using the rank of the means from the ocean ecosystem indicator table, we
262 divided the years into the lowest half ranked years and classified them as cold years, and the top
263 half as warm ocean years. Within each warm and cold year temperature assignment, temperature
264 values from individual years were averaged together in pairs of three to obtain a total of ten data
265 points per temperature treatment. Average daily May temperatures were determined from
266 NOAA buoys located approximately 23 km offshore from the mouth of the Columbia River, OR
267 and Grays Harbor, WA (https://www.ndbc.noaa.gov/maps/Columbia_River.shtml) at depths of 1
268 and 0.46 m, respectively.

269 Bioenergetics simulations were compared using a 2-way ANOVA where final weight
270 was compared between different growth scenarios and between days of each simulation. When
271 there were significant differences between growth scenarios, a Tukey HSD pairwise comparison
272 was used to determine specific differences. Final size after 12 days of the bioenergetic
273 simulations were compared to actual size of Steelhead in warm and cool years using a 2-way
274 ANOVA. Specific Growth Rate (g/g*d) was also calculated and compared between different
275 growth scenarios using a 2-way ANOVA and associated pairwise comparisons.

276

277 <A>Results

278 Between 2001 and 2016, 606 juvenile Steelhead were caught during May surveys between the
279 Columbia River and Willapa Bay. In 2015, 176 Steelhead were captured, and in 2016, 28 were
280 captured. Within our study years, 2006 and 2015 represented the two largest sample sizes (122
281 and 176 individuals, respectively), whereas 2004, 2007, 2009, and 2011 all had sample sizes less
282 than 20 individuals (Table 1).

283

284 Diet composition by year and ocean regime

285 Steelhead from warm ocean years (2004, 2006, 2010, 2015, 2016) consumed significantly
286 different prey communities than Steelhead from average temperature years (MRPP; $A = 0.023$; P
287 $= 0.002$), or Steelhead from cold temperature years (MRPP; $A = 0.033$; $P < 0.001$; Figure 1).

288 Analysis of individual study years further illustrated interannual variation in diet (MRPP; $A =$
289 0.095 ; $P < 0.001$ Figure 2). Steelhead diets in 2015 were significantly different from all cold
290 years except 2007, while 2016 Steelhead exhibited more moderate differences in diet compared
291 to other study years (significant diet differences between just 2001, 2006, and 2009). 2001 and
292 2006 also exhibited significant differences in diets compared to most other study years.

293 Steelhead diet composition varied both interannually and between ocean regimes (Figure 3). In
294 cold ocean regimes, especially in 2009, polychaetes were common prey (ISA; $P = 0.016$). In
295 warm years, juvenile and larval rockfishes (*Sebastes* spp.) and insect prey were eaten in
296 significantly higher amounts (ISA; $P < 0.001$; $P = 0.025$, respectively). In warm years, we
297 observed a significant increase in the percentage of unidentified and rare fish in Steelhead diet
298 (ISA; $P = 0.022$). Interestingly, several unusual taxa appeared in Steelhead diets in 2015 and
299 2016. Smelt (Osmeridae) were common prey in 2016 but were rare in all other ocean years
300 (ISA; $P = 0.011$). In addition, salps (Class Thaliacea) appeared in Steelhead diet in both 2015
301 and 2016. Though salps did not represent a significant proportion of Steelhead diet, these
302 represented the first observations of salp predation by juvenile Steelhead in our time series.

303

304 Diet variation by predator size and genetic stock (2006 and 2015)

305 Steelhead diet composition varied significantly by size class in 2006 (MRPP; $A = 0.03$; $P <$
306 0.001). Euphausiid prey dominated in all size classes except the 230-250 mm fork length

307 grouping (ISA; $P < 0.001$). Barnacle cyprids dominated the 230-250 mm and the < 190 mm size
308 classes. In contrast, 2015 yielded no significant size-specific diet variations. There were no
309 significant diet differences among any of the four stock groups (Clearwater and Salmon Rivers in
310 Idaho, Mid and Upper Columbia River/Lower Snake River, and Lower Columbia River summer
311 and winter runs) that had a sufficiently large sample size in either 2006 or 2015 (MRPP; $P >$
312 0.05).

313

314 Stomach fullness by year

315 Average Steelhead stomach fullness varied significantly with overall fish length (Beta
316 Regression; log-odds = -0.0031; $Z = -2.901$; $P = 0.004$). There was significant interannual
317 variability in stomach fullness among years, with stomach fullness significantly lower than
318 average during most warm years (Figure 4; Beta Regression; $P < 0.01$ for 2015, 2016, and 2006).
319 Stomach fullness in May 2010, a warm year, exhibited significantly higher average stomach
320 fullness than any other study year (Beta Regression; log-odds = 1.0918; $Z = 8.415$; $P < 0.001$).
321 Stomach fullness in 2002 and 2008, two cool years, had high variability in overall stomach
322 fullness and lower mean fullness than average (Beta Regression; $P < 0.01$ for 2002 and 2008).
323 There was no significant variability in the number of Steelhead with empty stomachs between
324 study years (Logistic Regression; $Z = -1.154$; $P = 0.248$).

325

326 Size and condition by year

327 May 2015 and 2016 Steelhead exhibited moderately longer fork length size relative to other
328 study years (Kruskal-Wallis; $\chi^2 = 47.78$; $P < 0.001$; Figure 5). Two other warm years, 2004 and
329 2006, also demonstrated higher mean fork lengths than average across the study period. In
330 contrast, 2007 and 2010 fish were the shortest in the time series. Steelhead weight varied
331 significantly between study years ($\chi^2 = 42.75$; $P < 0.001$), with fish in 2001, 2007, and 2010
332 exhibiting the lowest weights of the time series. Steelhead in May 2015 and 2016 were, on
333 average, the thinnest of all study years (Kruskal-Wallis; $\chi^2 = 174.64$; $P < 0.001$). The fattest
334 Steelhead in the time series appeared in 2002, 2008, 2010, and 2011.

335

336 Bioenergetics simulations

337 Cool temperature scenarios with elevated prey energy density were significantly different than
338 warm temperature scenarios without elevated prey energy density (Figure 6; $P < 0.001$). There
339 was a significant interaction between fish growth scenarios and the day of the simulation (2-way
340 ANOVA; $F_{44, 540} = 387.76$; $P < 0.001$; partial $\eta^2 = 0.96$), so interpretations are limited by the
341 interaction. By the end of day one, all simulated fish weights between the different growth
342 scenarios were significantly different with the exception of the fish feeding at 100%
343 consumption rates during a cold year and the fish feeding at 100% consumption rates during a
344 warm year ($P > 0.05$). By the end of day two, simulated fish weight was significantly different
345 between all five temperature/feeding scenarios with elevated prey energy density. Scenarios
346 where cool temperature years were not accompanied with a 30% elevation in prey energy density
347 were not significantly different than warm temperature years ($P > 0.05$), although fish weight
348 remained significantly different across the variable consumption rates (Figure 6). Changes in fish
349 weight between all scenarios became more extreme towards the end of the simulation period.
350 Simulated fish weight for warm and cool ocean conditions was not significantly different than
351 actual fish weight in warm and cool years (2-way ANOVA; $F_{1, 751} = 0.0151$; $P > 0.05$; partial η^2
352 < 0.001). Specific growth rate of Steelhead was significantly different between scenarios, with
353 highest specific growth in scenarios with cooler temperatures and higher feeding rates (2-way
354 ANOVA; $F_{4, 590} = 31.86$; $P < 0.001$; partial $\eta^2 = 0.99$).

355

356 <A>Discussion

357 Based on plankton and micronekton sampling occurring during anomalous conditions in
358 2015 and 2016, the prey field available to juvenile Steelhead in coastal waters was likely altered
359 compared to normal conditions. Adult euphausiid abundance in the water column appeared to be
360 exceptionally low, and they seemed to be replaced by several offshore or southern gelatinous
361 taxa (Peterson et al. 2017, Brodeur et al. 2019a). Juvenile rockfishes were also available in
362 higher abundance on the shelf compared to cooler years, similar to what was observed during the
363 El Niño of 2010 (Adams et al. 2017; Auth et al. 2018). Similar to juvenile Chinook salmon
364 *Oncorhynchus tshawytscha* (Daly et al. 2017) and several forage fish species (Brodeur et al.
365 2019b), juvenile Steelhead exhibited some plasticity in their feeding, consuming these alternate
366 prey taxa in lieu of euphausiids and other cold-water prey taxa. This plasticity resulted in normal
367 stomach fullness levels during anomalous conditions in 2015-2016. However, this tradeoff may

368 not be beneficial to the consumer. It is likely that the energetic and lipid content of these prey
369 may be much lower than the prey normally available in cold years (Daly et al. 2010; Daly and
370 Brodeur unpublished data), leading to reduced growth and poorer body condition.

371 We acknowledge high variability in sample size across our study years, especially in
372 regards to the four years with juvenile Steelhead catch per unit effort less than twenty individuals
373 (2004, 2007, 2009, and 2011). To ensure NMDS analyses were robust to low sample size, we
374 ran ordinations on both our actual data and on randomized data. In instances of low sample size,
375 NMDS ordinations can find solutions with artificially low stress, and checking actual stress
376 against randomized stress is a way to assess robustness of the ordination to small sample sizes
377 (McCune & Grace 2002). Actual stress was greater than randomized stress in our analysis,
378 suggesting that the ordination was selecting the correct solution despite low sample size in
379 several years. Our sample size was sufficient in 2006 and 2015 to examine other factors which
380 may affect diet. We observed differences in diet based on the size of Steelhead for 2006 but not
381 2015, suggesting that factors other than predator size may play a larger role in diet composition
382 determination. We also examined subsets of the data based on the genetically-determined stock
383 composition (Van Doornik et al. 2019). None of the four stock groups present in sufficient
384 sample size were significantly different from each other in terms of diet composition, suggesting
385 similar ocean habitat and prey utilization patterns among these stocks.

386 Our bioenergetics simulations suggest that many of the size-specific differences observed
387 between Steelhead in warmer and cooler ocean years are manifested during the late estuarine and
388 early marine residence. In addition, we demonstrate that a 30% elevation of marine prey energy
389 density values in cool ocean conditions, similar to that observed by Daly and Brodeur
390 (unpublished data), can help drive patterns in simulated growth that are comparable to actual
391 growth observed in the marine environment. Salmon growth can increase under warmer water
392 temperatures if there are enough food resources available (Beauchamp 2009). However, low
393 prey availability in 2015 and 2016 suggest that fish were not feeding at maximum consumption
394 rates (Piatt et al. 2020), and juvenile Steelhead grew in length but lost weight. In our
395 simulations, fish that were the same weight upon entering the marine environment experienced
396 significant changes in their weight by only the second day in the ocean based upon the different
397 temperatures, prey energy densities, and consumption rates characteristic of warm and cool
398 ocean conditions. By day 6 in the marine environment, fish feeding at 50% of their maximum

399 consumption rate under warm year conditions were 11.7% lighter than fish that experienced high
400 consumption rates in cooler conditions. This is comparable to the 17.6% reduction in weight
401 observed in spring Chinook salmon in 2015, a Blob-influenced year, compared to 2008, a
402 relatively cool ocean year (Daly et al. 2017). Similar to previous work on early marine stage
403 Chinook salmon (Wells et al. 2012; Litz et al. 2019), our bioenergetics models suggest that
404 juvenile Steelhead growth at this life history stage is strongly influenced by their feeding rate in
405 their late-estuarine and early marine residence. In addition, ocean temperature and prey energy
406 density appear to influence Steelhead growth in the marine environment. Out-migrating
407 Steelhead smolts in the Columbia River Estuary have been shown to exhibit relatively consistent
408 size ranges and condition at ocean entry across highly contrasting ocean years (Weitkamp et al.
409 2015), further supporting our hypothesis that interannual variability in size is largely driven by
410 conditions experienced in the late estuarine and early marine residence.

411 It is uncertain at this time what effect these poor feeding conditions might have on
412 Steelhead survival as they pass through warm and apparently less productive coastal waters.
413 Daly and Brodeur (2015) have shown that juvenile Chinook salmon generally consume higher
414 rations (based on fuller stomachs) during warm years compared to cool years, but this does not
415 necessarily translate to higher survival rates. This is likely due to increased metabolism
416 occurring at higher temperatures but could also be a result of poorer prey quality (Daly and
417 Brodeur unpublished data), necessitating higher rations to fulfill energetic needs. This may have
418 been the situation observed in 2010 Steelhead, which had a substantially higher amount of food
419 in their stomachs compared to average or cool years.

420 Stomach fullness was below average in 2015 and 2016, similar to the levels seen in other
421 warm years such as 2004 and 2006, which may have been caused by extremely low food
422 availability. Piatt et al. (2020) found many ectothermic forage fishes had poor body condition
423 during the marine heatwave of 2015 and 2016 due to their diet consisting of low-quality prey,
424 leading to mass starvation and reproductive failure in piscivorous seabirds throughout the
425 Northeast Pacific Ocean. Several forage fishes off Oregon and Washington shifted their diets
426 from their typical crustacean-based prey to one dominated by gelatinous zooplankton (mainly
427 salps) during 2015 and 2016, resulting in reduced body condition compared to normal or cool
428 years (Brodeur et al. 2019b). Although the amount of food in the Steelhead stomachs may reflect
429 food availability, other factors can affect stomach fullness (time of day, size of predator, location

430 of capture) that make this indicator a somewhat imprecise metric. For example, Steelhead that
431 entered the ocean in 2010 showed the highest proportions (46.7%) of lower Columbia River
432 stocks of any year we examined. These stocks tend to enter the ocean most quickly of all
433 populations. 2007 also had high proportions of lower Columbia River stocks, and both years had
434 low mean fork lengths (see Figure 5; Van Doornik, et al. 2019). In addition, smaller salmon
435 have larger stomachs relative to their length than larger salmon (Brodeur et al. 2007). Steelhead
436 in the warm ocean conditions of 2010 were different than the Steelhead from other warm years
437 because of their small size (stock related), high condition, and high stomach fullness, all during a
438 warm ocean condition that had relatively high prey conditions (Daly et al. 2013), and subsequent
439 adult returns were relatively high compared to other warm years. This anomaly is reflected in our
440 bioenergetic model, but runs counter to other warm years such as 2015-2016.

441 Steelhead typically spend 1-2 years in the ocean before returning as adults (Quinn 2005)
442 and the counts of adult Steelhead returning past Bonneville Dam in 2016, 2017, 2018, and 2019
443 were some of the lowest numbers in the last 30 years (Columbia River Data Access in Real Time
444 [Dart]; www.cbr.washington.edu/dart/query/adult_daily/; last access February 18, 2020; Figure
445 7). Steelhead diets in warm ocean conditions, such as 2015-2016, were significantly different
446 from cooler ocean condition years, and the juvenile Steelhead were also thin for their size during
447 2015-2016. Similar differences in diet and body condition corresponding with low adult fish
448 returns several years later have been previously documented for yearling Chinook salmon,
449 another spring out-migrant from the Columbia River (Daly et al. 2017). Additionally, both Coho
450 *Oncorhynchus kisutch* and fall Chinook salmon had poor adult returns from the population that
451 out-migrated in 2015 and 2016 (Columbia River Data Access in Real Time [Dart];
452 www.cbr.washington.edu/dart/query/adult_daily/; last access June 6, 2019).

453 Overall, our findings suggest that the NCC ecosystem had diminished potential to support
454 salmon populations in the Warm Blob (2015-2016) and subsequent El Niño (2016) conditions
455 (Leising et al. 2015, McClatchie et al. 2016, Piatt et al. 2020). Due to the prolonged existence of
456 Steelhead in the ocean compared to other salmon, a major environmental perturbation such as the
457 2015-2016 marine heatwave may not impact this species as much as other salmonids that return
458 to spawn after only 1-3 years in the ocean. As marine heatwaves are projected to occur with
459 more frequency and higher intensity in the coming decades in the Northeast Pacific Ocean
460 (Oliver et al. 2019), southern populations of Steelhead may become increasingly vulnerable to

461 these anomalous conditions. Through long-term monitoring of Steelhead in their early ocean
462 existence, we are able to provide potential insights into environmental effects on their feeding
463 and potential survival in the ocean, which may serve as a baseline against which to measure
464 future changes. However, since Steelhead migrate relatively rapidly into the Subarctic Pacific
465 Ocean, conditions occurring later during their open ocean existence that we have not examined
466 may also play a role in overall ocean survival (Atcheson et al. 2012; Myers 2018).

467

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483

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652

653 <A> Figure Captions

654 **Figure 1:** Nonmetric multidimensional scaling biplot (NMDS) of early marine Columbia River
655 Steelhead *Oncorhynchus mykiss* diet composition during warm ocean years (red crosses), cold
656 ocean years (blue circles), and average temperature years (grey triangles). Study years include
657 2001, 2002, 2004, 2006-2011, 2015 and 2016. Individual Steelhead stomach contents are
658 grouped by sampling station and are indicated as points color-coded by ocean regime. Ellipses
659 represent 95% confidence intervals in the two major axes. Vectors indicate significant prey
660 species correlations ($p < 0.05$) with the two major axes.

661

662 **Figure 2:** Non-metric multidimensional scaling biplot of early marine Columbia River Steelhead
663 *Oncorhynchus mykiss* diet composition by year for major taxonomic prey categories. Study years
664 include 2001, 2002, 2004, 2006-2011, 2015, 2016. Year averages are represented by points
665 color-coded by ocean regime for that year: cold (blue), warm (red), and average (grey)
666 temperatures.

667

668 **Figure 3:** May diet composition by percentage of prey weight for early marine Steelhead
669 *Oncorhynchus mykiss* by year (2001, 2002, 2004, 2006-2011, 2015, 2016) for fish prey and
670 invertebrate prey. The “other invertebrates” category includes amphipods, non-*Cancer* crab
671 larvae, and copepods. The “other fish” category includes Clupeids, Pleuronectiformes,
672 *Engraulis mordax*, *Microgadus proximus*, and unidentified Osteichthyes.

673

674 **Figure 4: (Top)** Average annual stomach fullness for early marine Columbia River Steelhead
675 *Oncorhynchus mykiss* in May surveys: 2001, 2002, 2004, 2006-2011, 2015, 2016. Boxplots

676 include the median (lines in boxes), 25th and 75th percentiles (lower and upper ends of boxes), 1.5
677 times the interquartile range (error bars), and outliers (points) for each year. Mean proportional
678 stomach fullness of 0.7101 is represented by the solid line. Ocean regime for the year is
679 represented by blue (cold years), red (warm years), or grey (average temperature years).
680 **(Bottom)** Annual percentage of empty stomachs for early marine steelhead. Percentage of
681 empty stomachs are represented by black triangles. Mean percent empty stomachs of 12.6237 is
682 represented by the solid line.

683
684 **Figure 5: (Top)** Average annual fork length for early marine Columbia River Steelhead
685 *Oncorhynchus mykiss* during May surveys: 2001, 2002, 2004, 2006-2011, 2015, 2016. Mean
686 fork length of 220.2 mm is represented by the solid line. Ocean regime for the year is
687 represented by blue (cold), red (warm), or grey (average temperature). Boxplots include the
688 median (lines in boxes), 25th and 75th percentiles (lower and upper ends of boxes), 1.5 times the
689 interquartile range (error bars), and outliers (points) for each year. **(Center)** Average annual
690 weight for early marine Steelhead. Mean weight of 93.37 g is represented by the solid line.
691 **(Bottom)** Average annual length-weight condition residuals for early marine Columbia River
692 Steelhead. Mean condition residual of 0.00 is represented by the solid line. Positive condition
693 denotes fatter fish while negative condition denotes thinner fish.

694
695 **Figure 6:** Simulated Columbia River Steelhead *Oncorhynchus mykiss* weight during the first 12
696 days of marine residence given different ocean temperatures and consumption rates associated
697 with warm and cold ocean years. **(Left)** Energy density is elevated by 30% in cool ocean years.
698 **(Right)** Energy density is constant across warm and cool years. All fish in this simulation were
699 set at 90 g at day 0 of the simulations.

700
701 **Figure 7:** Adult Steelhead *Oncorhynchus mykiss* count anomalies from fish returning to the
702 lower Bonneville Dam from 2000 to 2019. Trends for adult Steelhead with an unclipped adipose
703 fin are represented in dark blue, and trends for the entire population are represented in light blue.
704 Data accessed from Columbia River Data Access in Real Time [Dart];
705 www.cbr.washington.edu/dart/query/adult_daily/; last access February 18, 2020.

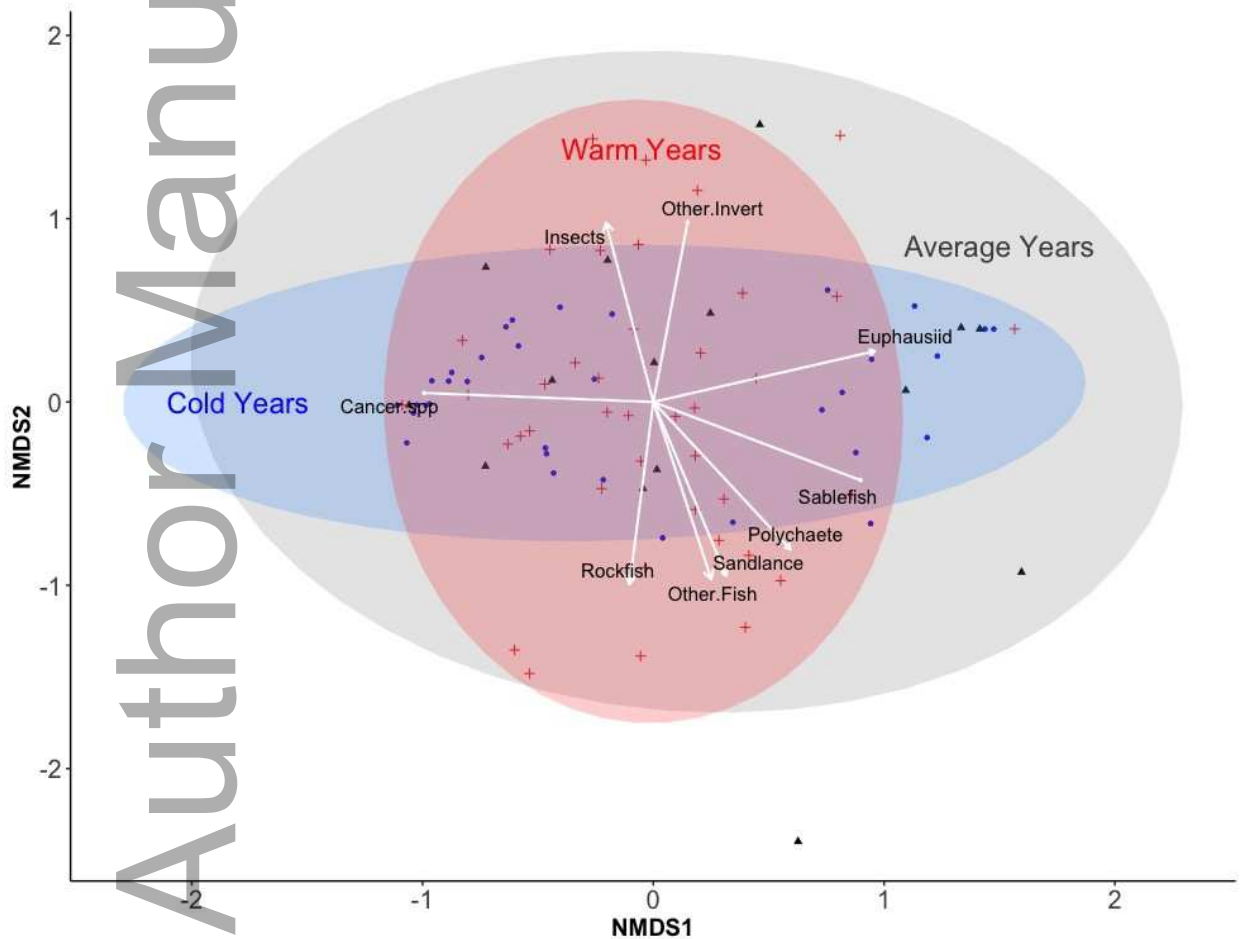
706

707 **Table 1:** Annual cruise dates, sample size, number of sampling stations, average temperature at
708 station, and ocean regime classification for juvenile Columbia River Steelhead *Oncorhynchus*
709 *mykiss*. Ocean regime was determined by the rank of means for ecosystems indicator data
710 compiled in Peterson et al. 2014 (1998-2013) and 2014-2016 at
711 <https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/g-forecast.cfm#TableSF-02>;
712 last accessed July 2, 2018). In 2001, fish were captured in warmer Columbia River Plume
713 waters, but overall ocean conditions for that year were considered cool. Blanks: no cruises or
714 Steelhead were available.

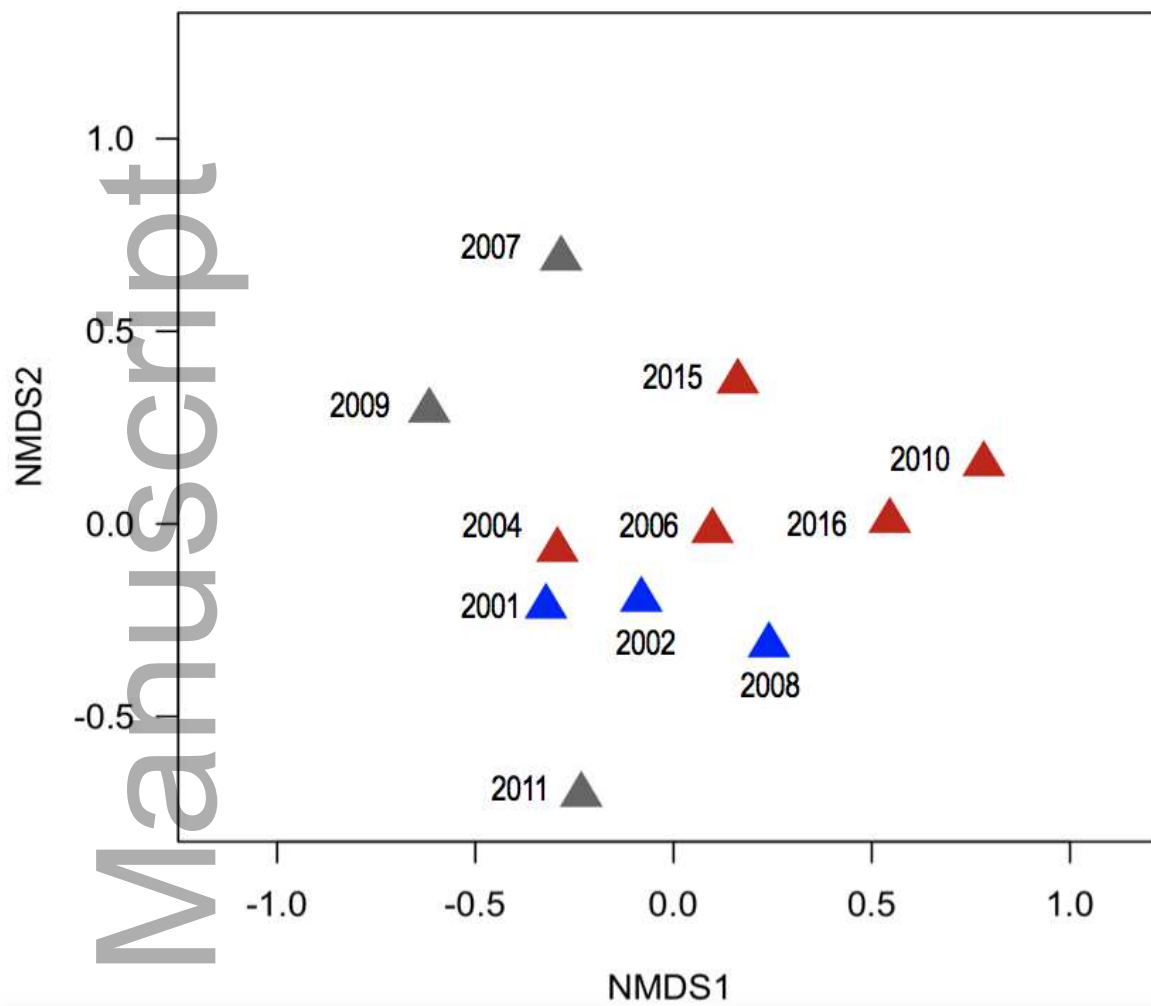
715 <A>Figures

716

717 **Figure 1**



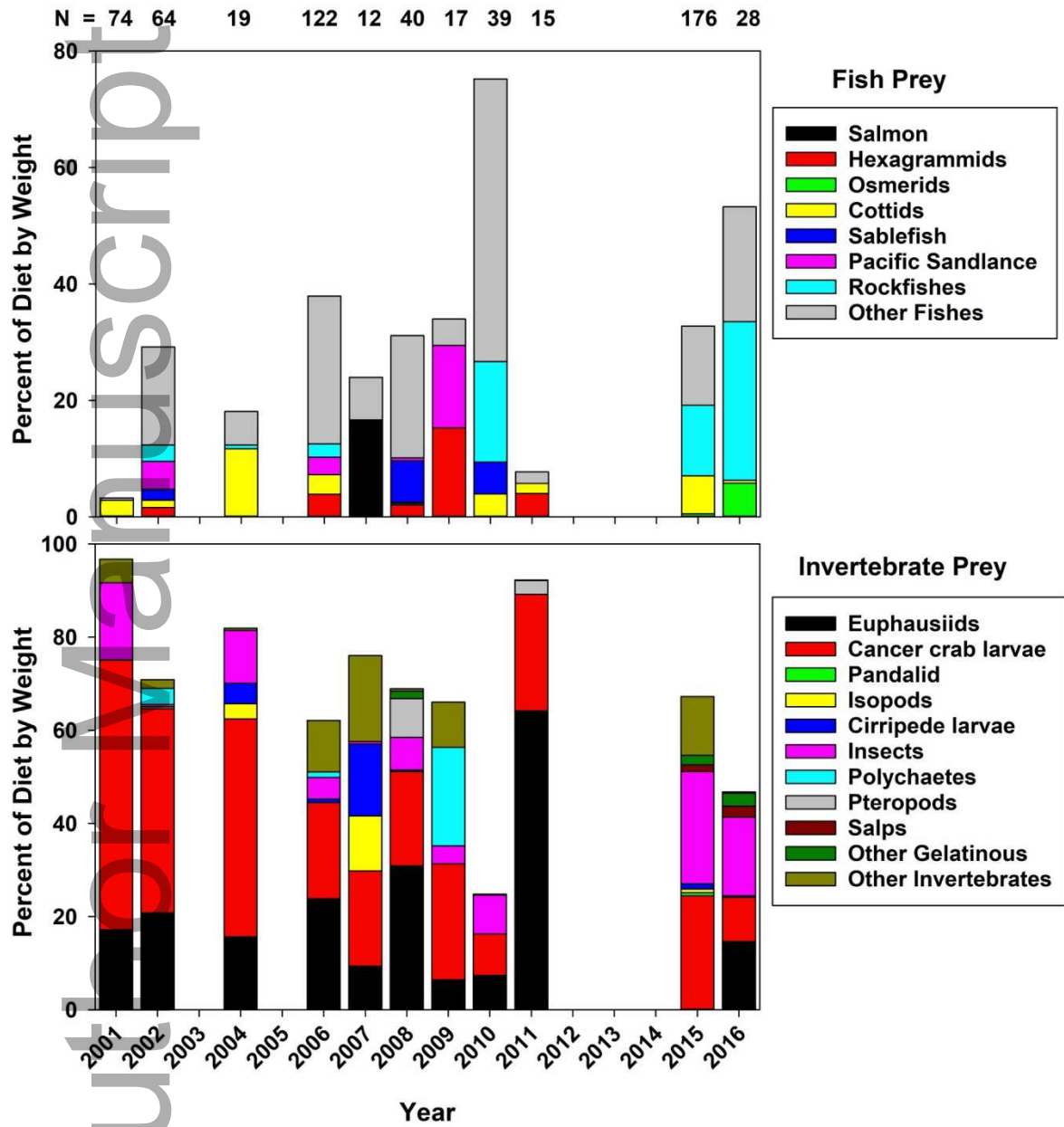
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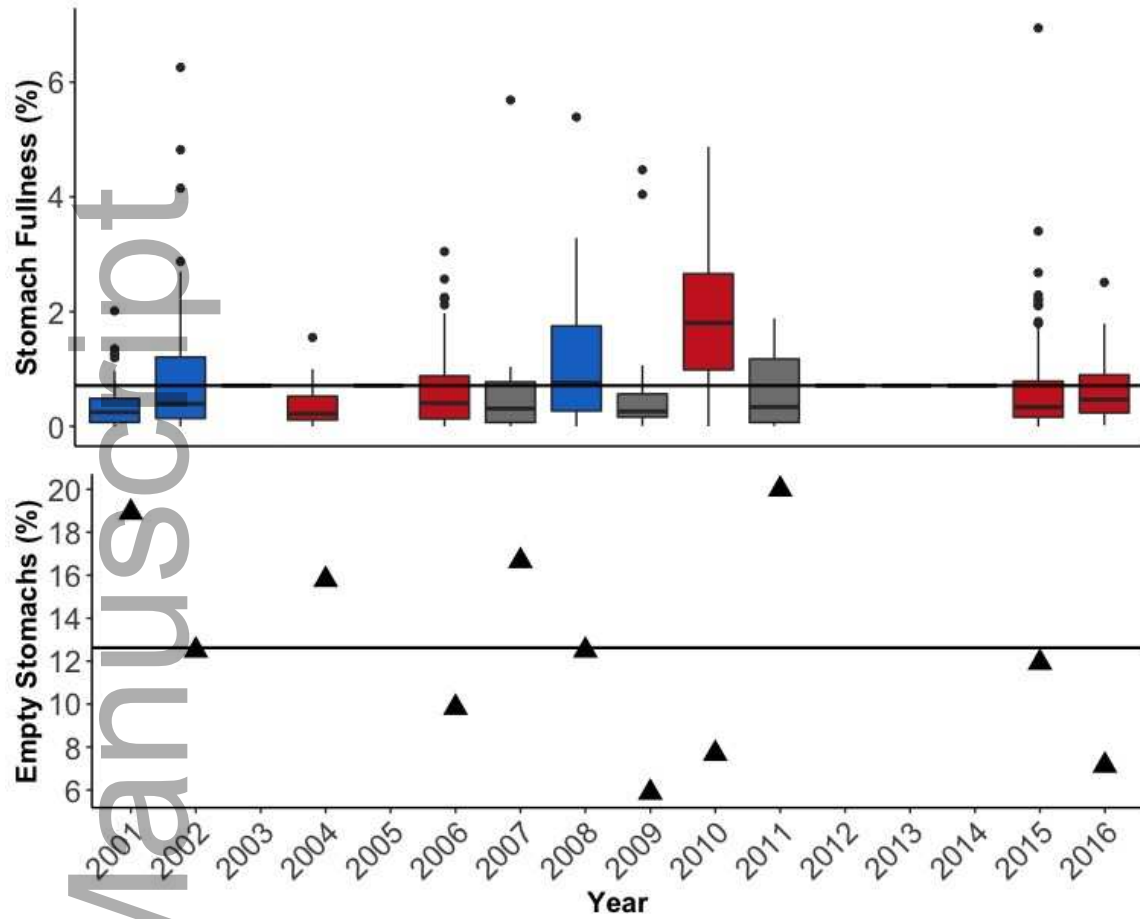
720

Figure 2



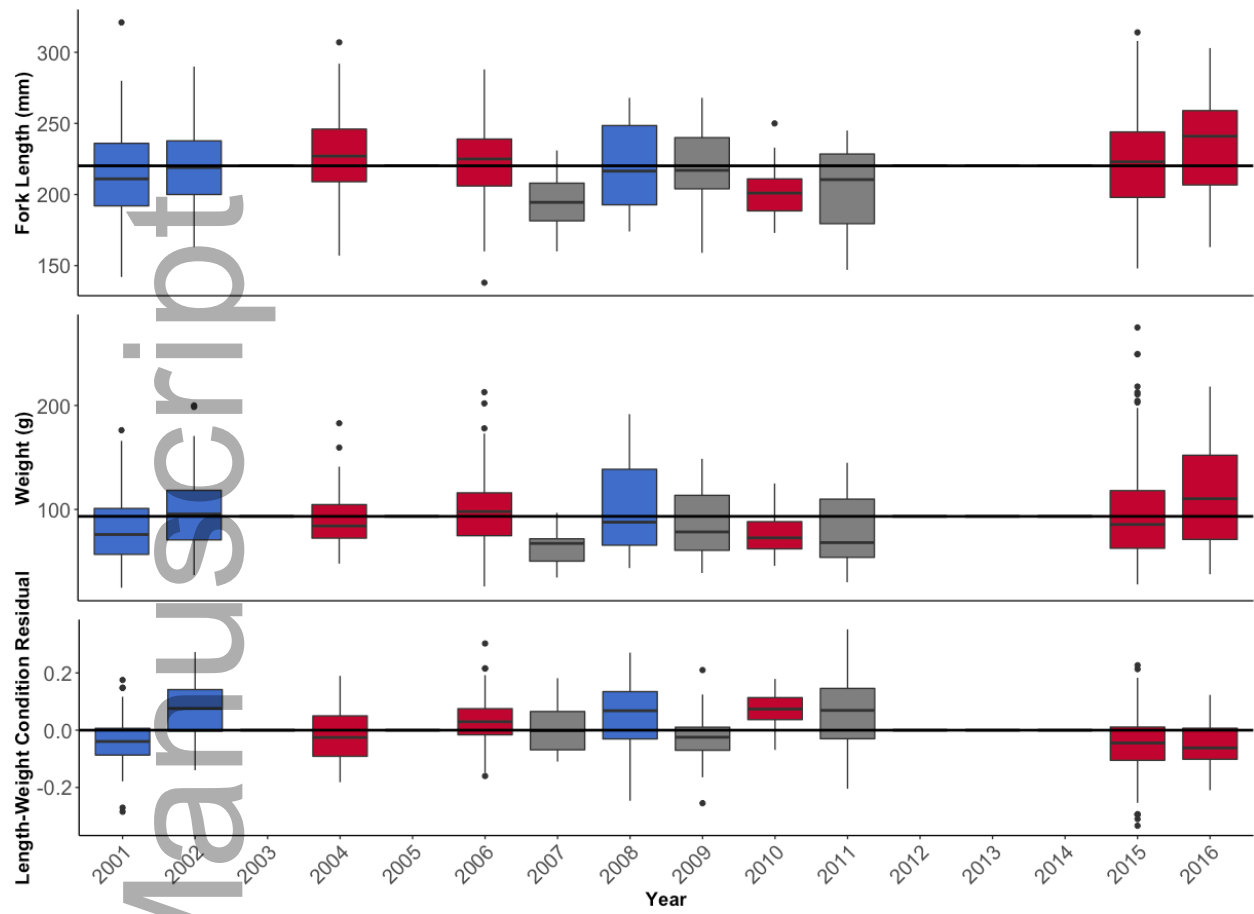
721

722 **Figure 3**



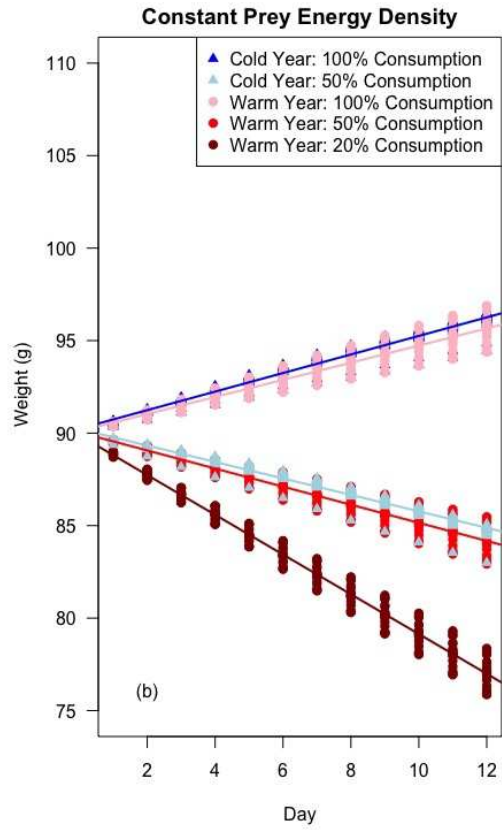
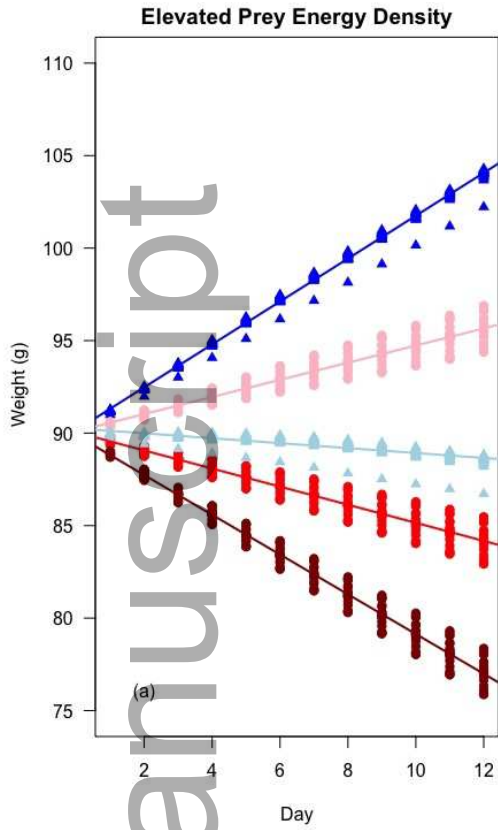
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Figure 4



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Figure 5

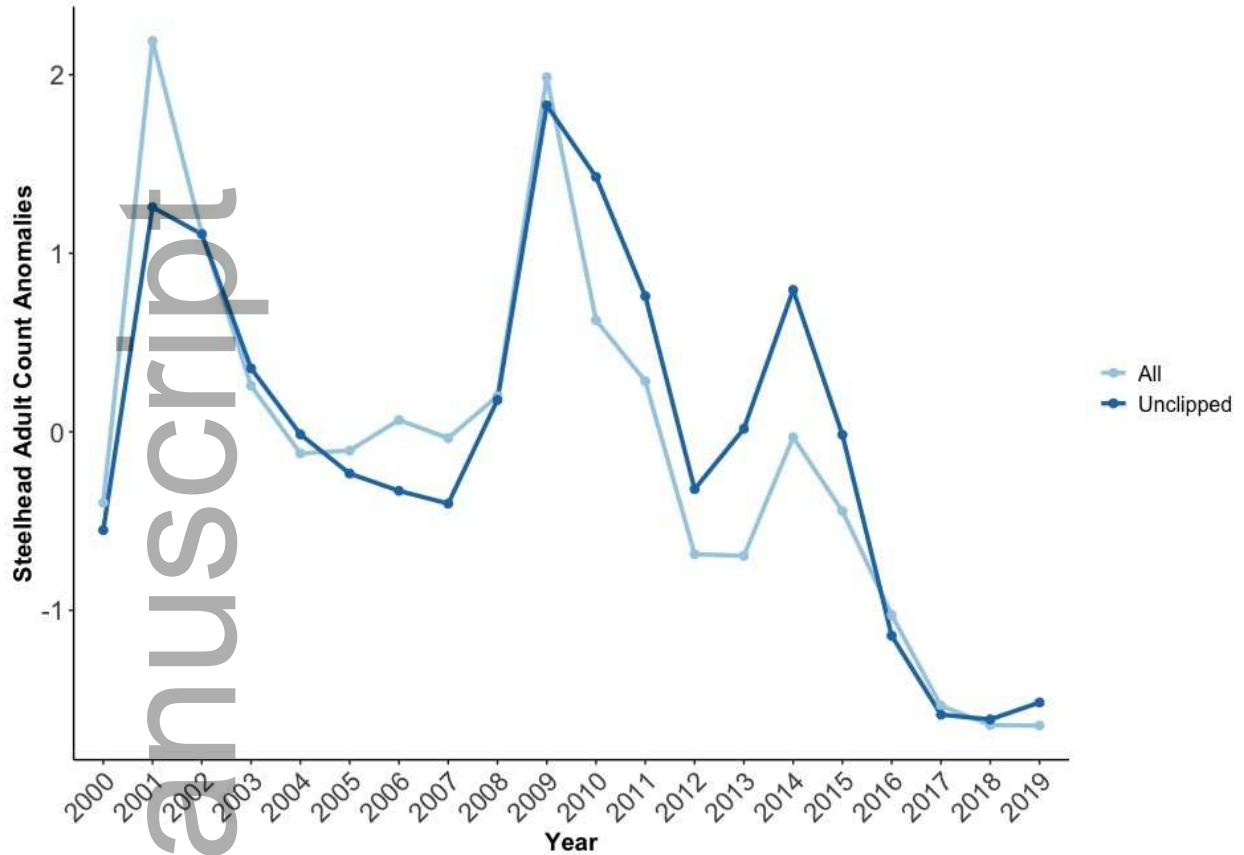


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Figure 6

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Figure 7

Year	Sampling Dates	No. Samples	No. Stations	Station Average Temperature	Ocean Regime
2001	May 20-28	74	16	11.48143	Cold
2002	May 21-29	64	10	10.21321	Cold
2003					
2004	May 23-29	19	4	12.70288	Warm
2005					
2006	May 24-30	122	7	12.25981	Warm
2007	May 25-30	12	6	10.90427	Average
2008	May 24-29	40	10	10.01113	Cold
2009	May 24-29	17	6	10.41852	Average
2010	May 22-27	39	4	10.94434	Warm
2011	May 19-27	15	4	10.51671	Average
2012					

2013

2014

2015 May 24-27 176 21 11.41073 Warm

2016 May 24-26 28 7 12.53416 Warm

734

735 **Table 1**

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