

1 Seasonal growth in juvenile steelhead

2

3

4 Article – Ecology of Freshwater Fish – special issue

5

6 **Seasonal variation in growth, consumption, and growth efficiency in overwintering juvenile**  
7 **steelhead**

8

9

10 Knut Marius Myrvold<sup>1\*</sup>; knut.marius.myrvold@gmail.com

11 Brian Patrick Kennedy<sup>2</sup>; kennedy@uidaho.edu

12

13 <sup>1</sup> Norwegian Institute for Nature Research (NINA), Vormstuguvegen 40, 2624 Lillehammer, Norway

14 <sup>2</sup> Department of Fish and Wildlife Sciences, Department of Biological Sciences, and Department of  
15 Geological Sciences, University of Idaho, Moscow, ID, USA 83844-1136

16

17

18 \* Correspondence author: Knut Marius Myrvold, email: knut.marius.myrvold@gmail.com, phone:  
19 (+47) 920 64 963, fax: (+47) 73 80 14 01

20

21 **Abstract**

22 Food availability and thermal regimes can largely govern growth opportunities in fishes. In temperate  
23 regions, streams can exhibit summer temperatures that exceed the optima for coolwater-adapted  
24 species relative to the amount of available food, and there, spring and fall may confer better growing  
25 conditions, especially for larger size classes. We examined the relationship between growth,  
26 consumption, and growth efficiency across seasons in juvenile steelhead (*Oncorhynchus mykiss*) in  
27 their natal streams in Idaho, USA. Subyearling (0+) growth rates were higher in summer, whereas  
28 yearlings exhibited no statistically significant difference in growth between seasons. Consumption  
29 rates were overall lower in winter-spring but constituted a higher proportion of maximum  
30 consumption compared to summer and fall, indicating better food availability relative to metabolic  
31 demands. Net growth efficiencies were higher in winter-spring, but substantially more so than the  
32 proportion of maximum consumption. This suggests that overwinter growth performance was driven  
33 at least partly by higher growth efficiency, and the effect was most pronounced for yearling  
34 steelhead. The low proportions of maximum consumption for both age classes suggest that food was  
35 an overall limiting factor to growth, especially in summer when metabolic demands were highest. We  
36 discuss how temperature-based models can overestimate growth in the warmest parts of the year,  
37 and develop a simple conceptual model for the seasonal timing of juvenile growth. In anadromous  
38 populations, the outmigration of presmolts in spring can reduce the level of competition. For the  
39 individuals that remain in the river, growth in this period can be particularly important.

40

## 41 Introduction

42 Early growth performance can have important consequences for life-history expression and lifetime  
43 fitness in fishes (Rose et al., 2001; Thorpe, 2007; Satterthwaite et al., 2010; Kendall et al., 2015). For  
44 anadromous salmonids, growth during the first years in freshwater can influence the timing of  
45 outmigration (Ward et al., 1989; Busby et al., 1996; Hartson & Kennedy, 2015), survival in freshwater  
46 and at sea (Bond et al., 2008; Duffy & Beauchamp, 2011), and age at maturation (Vøllestad, Peterson,  
47 & Quinn, 2004). Identifying the timing of juvenile growth can therefore give important insights into  
48 the ecology of a population because it is shaped by life histories, environmental conditions,  
49 community composition, and food availability (Thompson & Beauchamp, 2016; Quinn, 2018).

50 Factors that influence individual growth rates act directly or indirectly on the relationship between  
51 energy intake and expenditure, and range from intrinsic individual characteristics such as physiology  
52 and behavior (Metcalf, 1998; Reid, Armstrong, & Metcalf, 2011) to intraspecific competition,  
53 environmental conditions, and food availability (Yamamoto, Ueda, & Higashi, 1998; Van den Avyle &  
54 Hayward, 1999; Myrvoold Kennedy, 2015a; Spanjer et al., 2018). Which factor is more influential  
55 depends on its magnitude and rank relative to the other factors under a given range of conditions  
56 (Uthe, Al-Chokhachy, Shepard, Zale, & Kershner, 2019). For example, appetite in fishes generally  
57 increases with water temperature up to some species-specific threshold (Wootton, 1999). Given  
58 unlimited access to food, the temperature for which the scope for growth is optimal (i.e. the largest  
59 difference between maximum consumption and energy expenditures) is relatively close to the  
60 species' thermal tolerance (Brett, 1971; Wootton, 1999). However, food is most often limited in  
61 natural settings due to fluctuating production and competition over what is available (Keeley, 2001;  
62 Letcher et al., 2015; Myrvoold & Kennedy, 2015a). When the amount of food is limited and the  
63 availability is unpredictable, the optimal temperature for growth is much lower because basal  
64 metabolism and costs associated with processing the food also increase with temperature (Elliott,  
65 1975; Hewett & Kraft, 1993).

66 Translated to geography, in cold environments (northern regions or high-altitude locations with a  
67 short ice-free season) the summer temperatures may never exceed the optimal temperature under  
68 an unpredictable and limited food supply. Consequently, there may be a positive relationship  
69 between temperature, consumption, and growth over the restricted range of observed temperatures  
70 in those areas because the effects of food limitation are less visible. In contrast, prolonged periods of  
71 high water temperatures (> 18°C) typical of summers in lowland or temperate regions can prove  
72 challenging for juvenile salmonids in streams, both directly through energetic stress and in  
73 combination with other factors (Xu, Letcher, & Nislow, 2010; Letcher et al., 2015; Myrvoold &  
74 Kennedy, 2015b; Ayllón et al., 2019; Kelson & Carlson, 2019). High water temperatures in the early  
75 summer often coincide with the onset of summer baseflow conditions and the emergence of a new  
76 cohort, so that increased competition and elevated metabolism may further decrease energy intake  
77 and elevate energy expenditures (Nicola & Almodovar, 2004; McCarthy, Duda, Emlen, Hodgson, &  
78 Beauchamp, 2009; Spanjer et al., 2019). Therefore, while the ice-free summer months (June, July,  
79 and August) are important for growth performance at high latitudes and elevations (Borgstrøm &  
80 Museth, 2005), spring and fall seasons may confer better conditions for growth in warmer climates  
81 (Nicola & Almodovar, 2004; McCarthy et al., 2009; Tattam, Li, Giannico, & Ruzycki, 2017; Kelson &  
82 Carlson, 2019). The optimal conditions for growth therefore depend critically on the seasonal timing

83 of temperature and prey availability, both of which are affected by landscape-scale features such as  
84 climate, elevation, and latitude.

85 Here, we study the growth performance of juvenile steelhead across seasons in the Lapwai Creek  
86 watershed in the Inland Pacific Northwest, USA. We have previously documented depressed growth  
87 rates due to intraspecific competition and high metabolic demands during the dry season from June  
88 to October (Myrvold & Kennedy, 2015a, b). Despite limited growth in summer and fall, overwintering  
89 yearling cohorts begin the subsequent summer substantially larger than expected based on summer  
90 and fall growth performance. Our first objective is to estimate the growth trajectories for  
91 overwintering juvenile steelhead to identify the timing of the mass accrual using a bioenergetics  
92 model. Next, we compare growth rates, consumption rates, and growth efficiency across seasons to  
93 elucidate the extent to which seasonal variation in growth performance was the result of high  
94 consumption rates or efficient use of energy. Finally, we develop a conceptual model for individual  
95 growth in relation to temperature, density, food availability, and stream area for anadromous  
96 populations in a similar physiographic setting.

97

98

## 99 **Methods**

### 100 Study area

101 The study was conducted in the 694 km<sup>2</sup> Lapwai Creek watershed of North-Central Idaho, United  
102 States (Figure 1). The study area and methods for obtaining data have been described in previous  
103 works (e.g. Myrvold and Kennedy 2015b, c), and will be briefly described here. Lapwai Creek is  
104 located between the Columbia River Plateau and Northern Rockies ecoregions (McGrath et al., 2002).  
105 The four tributaries drain through steep canyons before opening up to wider floodplains at their  
106 successive confluences. Coniferous forest dominates the high elevation (max. elevation 1530 m) and  
107 grassland and grain crops dominate the middle and lower elevations towards the confluence with the  
108 Clearwater River (elevation 237 m). The substrate is chiefly cobble-sized, and wetted channel widths  
109 during sampling ranged from 3 m in the upper study sites to 9 meters in the downstream sites. Mean  
110 annual precipitation is 490 mm, primarily from October through May (Myrvold & Kennedy, 2015c),  
111 and the mean annual discharge (1975 – 2018) was 2.2 m<sup>3</sup>s<sup>-1</sup> (obtained from USGS gauge 13342450).  
112 The hydrograph follows a typical snowmelt-driven pattern with a few rain-on-snow events occurring  
113 in spring, and stable baseflow conditions with very few rain-driven spates from mid-June through  
114 October (Myrvold & Kennedy, 2015a). The upper parts of the anadromous reaches freeze over during  
115 the coldest periods, whereas the mainstem remains mostly ice-free (K.M. Myrvold, *personal*  
116 *observation*). However, with predicted shifts in the form, amount, and timing of precipitation (Mote  
117 & Salathe, 2010; Vano, Nijssen, & Lettenmaier, 2015) it is likely that streams will enter baseflow  
118 earlier in the summer, and that periodic drying of stream beds will occur more frequently (Myrvold &  
119 Kennedy, 2018).

120

### 121 Steelhead growth data

122 Lapwai Creek is a tributary to the Clearwater River and is designated as critical habitat for a wild  
123 steelhead population (NMFS, 2010). As part of a monitoring program to assess individual  
124 performance and population dynamics, we established an array of study sites representative of the  
125 physiographic variation in the watershed (Hartson & Kennedy, 2015; Myrvold & Kennedy, 2015b,c).  
126 Each study site was approximately 100m long, and key characteristics have been presented in  
127 previous publications (e.g., see Table 1 in Myrvold & Kennedy, 2015c). We visited each study site  
128 monthly from June to October in 2010, 2011, and 2012. In addition, we visited six of the uppermost  
129 study sites in May 2012. Fish were captured via three-pass depletion electrofishing using a Smith-  
130 Root LR-24 backpack electrofisher (Smith-Root Inc., Vancouver, Washington, USA). We measured  
131 fork length in millimeters and mass to the nearest 0.1g and tagged individuals larger than 65mm with  
132 a Passive Integrated Transponder (PIT). This allowed us to calculate the specific growth rates  
133 (referred to as *growth rate* in this article) of recaptured individuals between encounters (in the same  
134 year or in the subsequent year), expressed as the percent change in body mass per day.

135 Juvenile steelhead spend on average two years in their natal streams in the Lapwai Creek system but  
136 there is consistent variation among sites and some individual variation (Hartson & Kennedy, 2015;  
137 Caisman, 2015). Fish inhabiting the uppermost sites in each tributary tend to grow slower and  
138 outmigrate at a higher age than do fish in downstream sites, and fast-growing individuals tend to  
139 outmigrate earlier than their cohorts. In this paper we were interested in quantifying the growth  
140 rates of fish that remained in the study sites over winter (Figure 2). We tagged 3986 juvenile  
141 steelhead in 2010 and 2011, of which 133 were recaptured in subsequent years, i.e. had  
142 measurements of overwinter growth rates. Because we did not sample between October and May or  
143 June, we modeled the growth trajectories of these individuals using a bioenergetics model.

144

#### 145 Temperature data

146 Stream temperatures were recorded every 30 minutes in each study site from 01 May 2010 through  
147 2012 using HOBO TidbiT v2 temperature loggers (Onset Computer Corporation, Pocasset,  
148 Massachusetts, USA). The data were used in the bioenergetics modeling.

149

#### 150 Bioenergetics model

151 We used Fish Bioenergetics 3.0 (“Wisconsin model”; Hanson, Johnson, Kitchell, & Schindler, 1997) to  
152 calculate consumption rates necessary to achieve a certain growth in a given thermal regime, and to  
153 simulate the growth trajectories on a daily time step during the period between encounters. Myrvold  
154 & Kennedy (2015b) used field data from the Lapwai Creek watershed to parameterize the model, and  
155 we use this model in the following analyses. The model was specified with Thornton & Lessem’s  
156 (1978) consumption equation, Kitchell et al.’s (1977) respiration equation, Elliott’s (1976) waste  
157 losses equation, predator energy density equation number 2 (Hanson et al., 1997), and subsequent  
158 improvements of the parameter set (Railsback & Rose, 1999). We used an energy density of 4324 J/g  
159 wet weight for the invertebrate prey (the main diet; Myrvold and Kennedy 2015b), and an energy  
160 density of 5763 J/g wet weight for steelhead (Glova & McInerney, 1977) – these values were used for  
161 all individuals in the current analysis. We used site-specific temperature data for each period and

162 specified the mass of the fish at the start and the end of the simulation run. For a given change in  
163 body mass between encounters, the bioenergetics model simulates the growth trajectory over the  
164 time period on daily time steps and outputs parameter values relevant to the energy budget for the  
165 fish. We note, however, that predator energy density tends to be overestimated for juveniles, which  
166 in turn leads to underestimates of consumption rates (Trudel, Tucker, Morris, Higgs, & Welch, 2005).

167

#### 168 Consumption rates and growth efficiency

169 We were particularly interested in an individual's relative consumption rate, expressed as the  
170 proportion of maximum consumption ("P-value"; Hanson et al., 1997), and its growth efficiency. The  
171 P-value is the quotient between the modeled ration from a simulation and the maximum theoretical  
172 ration in a given time interval, such as the period between capture and recapture. An individual's  
173 growth efficiency in the same time interval is the quotient between the amount of energy allocated  
174 towards somatic growth and the total energy consumption. To obtain the amount of energy  
175 allocated towards growth we ran two simulations: one simulation reflecting the actual weight gain  
176 between capture and recapture to calculate the total ration, and one without any growth (by setting  
177 the end weight equal to the start weight) to calculate the ration necessary just to maintain its mass  
178 (Hewett & Kraft, 1993; Myrvold & Kennedy, 2015b). The difference between the two is the amount  
179 of energy allocated to growth. To calculate the growth efficiency we divided the ration allocated  
180 towards growth by the total ration.

181

#### 182 Modeling overwinter growth trajectories

183 To assess the timing of mass accrual under a bioenergetics framework we simulated the average  
184 growth trajectories from October 15 to June 15 (as denoted in Figure 3). Subyearlings grew, on  
185 average, from 7.1g ( $n = 36$ ,  $SD = 2.3g$ ) on the last sampling visit in year 1 to 25.8g ( $SD = 10.9g$ ) on the  
186 first regular sampling visit in June the following year, whereas the yearlings for which we had  
187 recapture data grew from 19.8g ( $n = 9$ ,  $SD = 8.5g$ ) to 49.5g ( $SD = 23.5g$ ). The discrepancy in mean  
188 body mass between one-year old fish in June and in October owes to movement and migration:  
189 some of the fast-growing one-year old fish outmigrate in the fall following their second summer and  
190 would hence not be recaptured the following summer, and due to considerable movement  
191 throughout the year the composition of individuals in a given site is dynamic (Hartson & Kennedy,  
192 2015). We specified the bioenergetics model with the same parameters as described above and  
193 conducted simulations for an example site (site UMU; mean = 4.5 °C,  $SD = 3.4$  °C) for both age  
194 classes.

195

#### 196 Statistical analyses

197 The study design was clustered in both a longitudinal sense (observations nested within known  
198 individuals over time) and cross-sectional sense (comparison of individuals at given points in time,  
199 nested in discrete study sites). To account for the multilevel structure, we used linear mixed models  
200 (Raudenbush & Bryk, 2002). To find the average growth rate of subyearlings and yearlings and to

201 partition the variance among the different levels we first specified a variance components model  
 202 (Raudenbush & Bryk, 2002). Here we have observations of growth rates nested within individuals  
 203 taken at subsequent points in time:

$$204 \quad \text{growth}_{ij} = \gamma_{00} + u_{0j} + r_{ij},$$

205 where growth rate  $i$  of fish  $j$  is related to a grand mean growth rate for all the individuals ( $\gamma_{00}$ ), an  
 206 individual-level variance ( $u_{0j}$ ) around this mean, and a residual error within each individual ( $r_{ij}$ ), with  
 207  $u_{0j} \sim N(0, \tau_{00})$  and  $r_{ij} \sim N(0, \sigma^2)$ . We also assessed whether a three-level model structure was necessary  
 208 by adding study site as a random effect in the variance components model (Myrvold & Kennedy,  
 209 2015a). There was no clustering at the level of study sites, and we consequently proceeded with the  
 210 two-level model (Table 1).

211 We tested whether individual growth rates and growth efficiency differed between seasons. We  
 212 defined summer as June-July, June-August, and July-August; fall as August-September, September-  
 213 October, and August-October; and winter-spring as the period between October in one year and May  
 214 or June the following year. To account for the paired observations within each individual we specified  
 215 a mixed effects model with season as a categorical predictor variable with three fixed levels  
 216 (summer, fall, and winter-spring) and individual as a random effect:

$$217 \quad (\text{eq. 1}) \quad \text{growth}_{ij} = \beta_{0j} + \beta_{1j}\text{season}_{ij} + r_{ij}$$

218 To allow for individual-specific intercepts we can write

$$219 \quad \beta_{0j} = \gamma_{00} + u_{0j} \text{ and } \beta_{1j} = \gamma_{10}$$

220 Substituting into equation 1, this becomes a linear mixed effects model

$$221 \quad \text{growth}_{ij} = \gamma_{00} + \gamma_{10}\text{season}_{ij} + u_{0j} + r_{ij}$$

222 where  $u$  and  $r$  are random effects.  $r_{ij}$  is assumed  $N(0, \sigma^2)$  for growth rate  $i$  in fish  $j$ , and is the residual  
 223 of growth rate  $i$  from the mean growth rate in fish  $j$  after controlling for season. Because of the  
 224 categorical predictor variable, the value for the intercept was used to decode the values for the three  
 225 levels of seasons. We conducted the same analysis for proportion of maximum consumption and  
 226 growth efficiency.

227 All models were specified with the Kenward & Roger (1997) approximation of denominator degrees  
 228 of freedom, an unstructured covariance matrix to allow for individual variation in growth trajectories,  
 229 and maximum likelihood as the estimator. We used SAS v.9.4 Proc MIXED (SAS Institute, Cary, North  
 230 Carolina, USA) for all the analyses. Finally, we assessed that model assumptions were met by visually  
 231 examining the residual plots for all the models, obtained with the *ods graphics* command. Even  
 232 though the proportion of maximum consumption and net growth efficiency are bound between 0  
 233 and 1, we only encountered a limited range of values for which a linear model was appropriate.

234

## 235 Results

236 The 133 individuals with overwinter growth histories were found in 10 sites (Appendix 1). These  
237 individuals were encountered 518 times and yielded 385 growth estimates (i.e. from one sampling  
238 visit to another), partitioned into 202 subyearling and 183 yearling growth histories. Only one  
239 individual moved between sampling sites (a subyearling tagged in site ULL in the summer of 2010  
240 was recaptured in site ULU in July 2011). The individuals were primarily found in the uppermost  
241 study sites in each tributary (Figure 1), which corroborate earlier findings of later outmigration and  
242 greater site fidelity in the upper sites (Hartson & Kennedy, 2015).

243

#### 244 Overwinter growth trajectories

245 The simulated growth trajectories for the average subyearlings and yearlings in example site UMU  
246 are shown in Figure 4. Some growth occurred in the remainder of October in both years and was  
247 relatively stagnant between the beginning of November and mid March both years. Most of the  
248 growth happened in the last month of the simulation. Subyearlings reached their average mass  
249 (16.5g) on May 15<sup>th</sup> (average for all simulations), and yearlings reached their average mass (34.7g) on  
250 May 14<sup>th</sup>, at which time 86% of the period had lapsed. The P-values (i.e. the proportion of maximum  
251 consumption) necessary to achieve this growth over the entire period were 0.372 in 2010-2011 and  
252 0.363 in 2011-2012 for subyearlings and 0.376 and 0.367 for yearlings.

253 To show how temperature affected the growth trajectory in the bioenergetics model we plotted the  
254 thermograph and the specific growth rate together with the simulated subyearling mass (Figure 5).  
255 The simulated daily weight increments were closely, and positively, related to temperature in this  
256 temperature range.

257

#### 258 Growth, consumption, and growth efficiency

259 We plotted the average values and associated standard deviations for specific growth rates (% body  
260 mass per day), P (proportion bound by 0 and 1), and growth efficiency (proportion bound by 0 and 1)  
261 for all the periods ( $n = 133$  individuals with 385 growth measurements; Figure 3). Qualitatively,  
262 subyearlings achieved the highest growth rates in their first summer and fall, and overall lower  
263 growth rates in the winter-spring period. Growth efficiency was consistently higher in the winter-  
264 spring period. Yearling growth rates were more variable throughout the different periods but were  
265 generally higher in the winter-spring period, and lower in summer and fall. Growth efficiency was  
266 substantially higher in the winter-spring period for both age classes.

267 In order to focus on the difference between seasons, we considered individuals with growth  
268 measurements within the narrow definitions of summer (June-July, June-August, and July-August),  
269 fall (August-September, August-October, September-October), and winter-spring (October-May and  
270 October-June). Sixty-three subyearlings yielding 118 growth histories and 60 yearlings yielding 125  
271 growth histories satisfied these criteria. The discrepancies between numbers of individuals and  
272 growth histories owe to multiple growth histories for some individuals in summer (e.g. from June to  
273 July and July to August).

274 Subyearling growth rates were consistently higher in summer (mean 0.83% body mass per day) than  
275 in fall (mean 0.70% per day) and winter-spring (0.52% per day;  $n = 118$ ,  $F = 5.5$ ,  $d.f. = 118$ ,  $P = 0.005$ ).  
276 Inclusion of season as a factor in the model explained some 9% of the variance in growth rates (Table  
277 2). For yearling steelhead there was no statistically significant difference in growth rates between  
278 summer (mean 0.24% body mass per day), fall (mean = 0.27%), and winter-spring (0.36% per day;  $n =$   
279  $125$ ,  $F = 0.35$ ,  $d.f. = 125$ ,  $P = 0.70$ ). Inclusion of season as a factor variable in the model explained only  
280 1% of the variance in yearling growth rates (Table 2). All the variance in the growth rates came from  
281 variation in an individual's growth rates, not from consistent variation among individuals.

282 Growth efficiency for subyearlings was highest in winter-spring ( $n = 118$ ,  $F = 91$ ,  $d.f. = 97$ ,  $P <$   
283  $0.0001$ ). Inclusion of season explained 60% of the total variance in the data for subyearlings (64% of  
284 which at the residual level; Table 2). Similarly, yearling growth efficiency was higher in winter-spring  
285 (mean = 53%) than in fall (mean = 16%) and summer (mean = 9%;  $n = 125$ ,  $F = 14.5$ ,  $d.f. = 125$ ,  $P <$   
286  $0.0001$ ). Inclusion of season explained 19% of the total variance, all of which at the residual level  
287 (Table 2).

288 Finally, we tested how the corresponding values for daily consumption rates and proportion of  
289 maximum consumption ("P-values") related to the pattern of higher growth efficiency in winter-  
290 spring. Daily average yearling consumption rates were significantly higher in summer (mean = 184  
291 J/g/d,  $SE = 16$ ) than in fall (mean = 146 J/g/d,  $SE = 17$ ) and winter-spring (mean 91 J/g/d,  $SE = 15$ ;  $n =$   
292  $125$ ,  $F = 22.5$ ,  $d.f. = 125$ ,  $P < 0.0001$ ). The corresponding proportions of maximum consumption were  
293 0.202 ( $SE = 0.019$ ) in summer, 0.209 ( $SE = 0.020$ ) in fall, and 0.311 ( $SE = 0.018$ ) in winter-spring, which  
294 were significantly different ( $n = 125$ ,  $F = 17$ ,  $d.f. = 125$ ,  $P < 0.0001$ ). Hence, an overall lower absolute  
295 consumption rate in winter-spring constituted a higher proportion of maximum consumption and  
296 yielded higher growth efficiencies than in summer and fall. For subyearlings, daily average  
297 consumption rates were significantly higher in summer (mean = 321 J/g/d,  $SE = 5$ ) than in fall (mean  
298 234 J/g/d,  $SE = 8$ ) and winter-spring (mean 110 J/g/d,  $SE = 7$ ;  $n = 118$ ,  $F = 135$ ,  $d.f. = 118$ ,  $P < 0.0001$ ).  
299 The corresponding proportions of maximum consumption were 0.198 ( $SE = 0.015$ ) in summer, 0.211  
300 ( $SE = 0.0059$ ) in fall, and 0.328 ( $SE = 0.0056$ ) in winter-spring, which were significantly different ( $n =$   
301  $118$ ,  $F = 203$ ,  $d.f. = 90.7$ ,  $P < 0.0001$ ). The higher consumption rates in summer yielded significantly  
302 higher growth rates, despite constituting a lower proportion of maximum consumption in summer  
303 relative to fall and winter-spring.

304 In discerning the extent to which consumption levels or growth efficiency were driving the observed  
305 variation in seasonal growth, our results show two main patterns. First, even though absolute  
306 consumption rates in winter-spring were overall lower, they constituted a higher P compared to that  
307 in summer for both age classes (Table 3). Similarly, the net growth efficiencies were higher in winter-  
308 spring than in summer and fall, but substantially more so than for P. For example, whereas yearling P  
309 was 54% higher in winter-spring than in summer, the net growth efficiency was 471% higher. This  
310 suggests that overwinter growth was driven chiefly by higher growth efficiency and to some extent  
311 by higher proportions of maximum consumption. Secondly, this manifested unequally among the age  
312 classes in terms of growth rates (Table 3). Whereas subyearlings grew faster in summer, there were  
313 no significant difference between seasons for yearlings. This could be due to high metabolic demands  
314 for larger fish in summer, that is, because the absolute demands could not be met as easily as for  
315 smaller individuals. Furthermore, the overall low proportions of maximum consumption for both age

316 classes in summer suggest that food is a limiting factor to summer growth under the prevailing  
317 thermal regime.

318

319

## 320 Discussion

321 Seasonal growth patterns varied between age classes in the Lapwai Creek watershed. Whereas  
322 subyearling steelhead grew faster in their first summer and fall than in winter-spring, there was no  
323 statistically significant difference between seasons for yearling fish. Because we did not sample  
324 during the winter and spring, we did not have any growth measurements on regular intervals;  
325 however, bioenergetics simulations suggested that most of the body mass was accrued during May  
326 and early June. This owes partly to more efficient energy use over the entire winter-spring period,  
327 when fish were able to allocate a much higher fraction of their ration towards somatic growth. This  
328 suggests that spring might be particularly important for annual growth in areas where stream  
329 temperatures are high relative to the availability of food in the summer, especially for larger  
330 individuals.

331 Most studies on stream salmonid growth are conducted in summer and fall. There exist a handful of  
332 studies on the seasonal growth patterns in juvenile steelhead in temperate regions (Merz, 2002;  
333 Hayes et al., 2008; McCarthy et al., 2009; Thompson & Beauchamp, 2016; Tattam et al., 2017). Hayes  
334 et al. (2008) studied seasonal growth and life history of steelhead in a small coastal watershed in  
335 California. The watershed is characterized by mild winters (minimum average daily water  
336 temperature of 5.6 °C) and dry, mild summers (average temperatures 14-18 °C). Yearling fish  
337 achieved the highest growth rates in spring (0.50% body mass per day) and the lowest in summer  
338 and fall (0.0-0.20% body mass per day). These findings were similar to that of other studies on  
339 steelhead growth in California (Railsback & Rose, 1999; Merz, 2002). McCarthy et al. (2009) studied  
340 steelhead and rainbow trout growth and consumption in Northern California and reported overall  
341 fast growth in spring (March to May), and weight loss in summer. They attributed the pattern to  
342 overall higher consumption rates and closer-to-optimal temperatures for growth in spring than in  
343 summer. Recently, Tattam et al. (2017) documented the highest growth rates of the year in spring in  
344 juvenile steelhead in Central Oregon, an area with a similar temperature regime as the Lapwai Creek  
345 watershed. The average temperature in the spring season was 9 °C, which is lower than the reported  
346 optimal temperatures for growth (22 °C; Railsback & Rose 1999), suggesting that optimal  
347 temperatures for growth may depend on the season.

348 The same pattern of rapid growth in spring and slower growth in subsequent seasons has also been  
349 reported across species and genera in temperate rivers. Ebersole et al. (2006) found that juvenile  
350 coho in Oregon grew significantly faster in the spring (mean 0.84% body mass per day from mid-  
351 March through June) than winter (mean 0.58% body mass per day, December to March), and that  
352 spring growth rates did not differ among tributaries and mainstem rearing locations. Similar findings  
353 have been reported in Eastern North America. Horton, Letcher, Bailey, & Kinnison (2009) found that  
354 Atlantic salmon (*Salmo salar*) growth rate in Massachusetts was highly seasonal for all cohorts. The  
355 highest growth rates occurred in spring for age 1+ and 2+ fish, then decreasing through the  
356 subsequent seasons. Carlson, Hendry, & Letcher (2007) found that growth of sympatric brook trout

357 (*Salvelinus fontinalis*) and introduced brown trout (*Salmo trutta*) in West Brook, Massachusetts  
358 peaked in spring. This could result from higher drift densities in the spring and a sharp decline in  
359 drifting invertebrates in the subsequent seasons (Grade & Letcher, 2006).

360 Several field studies have compared seasonal growth rates with predictions from temperature  
361 models derived from laboratory studies of growth and consumption. Nicola & Almodovar (2004)  
362 found that brown trout in streams in Spain achieved their highest growth rates in spring. They  
363 compared these empirical growth rates with modeled growth rates from Elliott, Hurley, & Fryer's  
364 (1995) temperature-based growth model, which was based on ad libitum laboratory studies in  
365 Northwest England. Despite a limited and dynamic food supply, growth rates under natural  
366 conditions in Spain surpassed the modeled growth. It is uncertain whether this was because of a  
367 seasonal effect (for example that the laboratory studies were conducted in summer, when the  
368 optimal temperature for growth was higher; see discussion below), or genetic factors (e.g. that  
369 selection favors growth earlier in the year in Spanish populations). Similarly, Bacon, Gurney, Jones,  
370 McLaren, & Youngson (2005) studied the seasonal growth patterns of juvenile Atlantic salmon in  
371 Scotland and compared their field results to two temperature-based growth models for the species  
372 (Elliott & Hurley, 1997; Forseth, Hurley, Jensen, & Elliott, 2001). Bacon et al. found that most of the  
373 growth happened in a 10-week period in the spring at temperatures that were lower than what the  
374 models deemed necessary to achieve that level of growth.

375 Apart from misapplication of temperature-based growth models to systems for which they were not  
376 developed, the discrepancy between model predictions and field measurements of salmonid growth  
377 in temperate regions could result from two main factors. First, temperature-based models do not  
378 take into account the dynamic effects of season on growth efficiency. In a series of experiments,  
379 Averett (1969) investigated the effects of season on juvenile coho growth, consumption, and growth  
380 efficiency. He found that the optimal temperature for growth and growth efficiency depended upon  
381 season: fish achieved higher growth efficiencies at lower temperatures in April and May (range 5 – 14  
382 °C) than in June-July (range 11 – 14 °C) and August-September (range 14 – 17 °C). At the lowest  
383 temperature treatments in the April-May experiment the growth efficiencies were high at low  
384 consumption rates, and declined sharply with increasing consumption rates, presumably due to a  
385 combination of increased costs of systemic dynamic action and increased activity costs (Averett,  
386 1969). In other words, fish achieved no growth benefit from increasing their consumption rates, but  
387 grew well on a limited ration due to lower temperature-induced energy losses. In summer and fall,  
388 this relationship was shifted towards higher growth efficiency at higher temperatures, which were  
389 consistent with the thermal regime in their natal streams (Averett, 1969). The effects of thermal  
390 adaptation in local populations has received variable support. Jonsson, Forseth, Jensen, & Næsje  
391 (2001) and Forseth et al. (2009) found no evidence of growth-related adaptation to the prevailing  
392 thermal regimes in populations of Atlantic salmon and brown trout, respectively. However, Narum et  
393 al. (2013) found some evidence for thermal adaptation between populations of redband rainbow  
394 trout in Idaho. When subjected to high temperatures (from 17.0 to 28.5 °C), fish from relatively  
395 warmer desert environments exhibited lower heat shock protein response than fish from relatively  
396 colder mountain environments. This suggests that desert fish have maintained or developed  
397 mechanisms to cope with thermal stress (high temperatures in this case), but the relation to growth  
398 performance was not investigated.

399 Secondly, there is evidence that there is more food of higher quality available in spring. Grade &  
400 Letcher (2006) found the highest density of drift in April and June, and substantially lower densities  
401 in summer and fall. Benthic density showed an opposite pattern, with the highest values in summer  
402 and fall, and the lowest in winter and spring (Grade & Letcher 2006). Nakano & Murakami (2001)  
403 reported higher amounts of aquatic insects from December to July, and greater amounts of  
404 terrestrial invertebrates from July to September in Japan. Li, Gerth, Driesche, Bateman, & Herlihy  
405 (2016) reported a similar pattern in a coastal watershed in Oregon, and found that juvenile steelhead  
406 relied more on terrestrial invertebrates in summer. We do not have data on drift densities in the  
407 spring in Lapwai Creek. However, even if the amount of food were constant throughout the year, the  
408 lower metabolic demands during the typical temperatures in spring, and potentially the higher  
409 growth efficiency in this period, could explain why yearling growth rates in this period were  
410 comparable to those of summer (Myrvold & Kennedy 2015b).

411 In order to decouple the effect of season from temperature it is useful to compare growth rates  
412 between seasons with similar temperatures and photoperiods. Xu et al. (2010) provided a strong test  
413 of the effect of temperature and stream discharge on brook trout growth rates at different times of  
414 the year over 8 years in Massachusetts. Growth rates generally increased with water temperature in  
415 spring and winter but decreased with temperature in summer and fall within the same temperature  
416 range. Stream flow had a modulating effect through its control over temperature, but these effects  
417 were dynamic: growth increased with flow in cool summers but had no effect in the warmest  
418 summers. The effects of flow were not strong enough to affect the direction of the relationship  
419 between temperature and growth, but flow did affect the strength of the relationship (i.e. the slope  
420 of the regression). The effects of density on individual growth rates were also higher in summer than  
421 in spring (Xu et al., 2010).

422 Our simulations of overwinter growth trajectories suggested that most of the body mass was accrued  
423 at the end of the spring period (15. May to 15. June; figure 4). However, there is uncertainty in how  
424 well the temperature-dependent function of the bioenergetics model represents the ecology in the  
425 Lapwai Creek watershed. Given the results from other studies (Railsback & Rose, 1999; Merz, 2002;  
426 Hayes et al., 2008; McCarthy et al., 2009; Tattam et al., 2017) that have measured steelhead growth  
427 rates in spring we suspect that the modeled growth in our study was shifted more towards the end of  
428 the winter-spring period than what was actually the case. We attribute this to the distinct dry season,  
429 which represents metabolically stressful conditions in Lapwai Creek (Myrvold & Kennedy, 2015b).

430 Seasonality in food availability, temperature, and optimal temperatures for growth have been shown  
431 to affect size classes differently. Connolly & Petersen (2003) investigated the effects of overwinter  
432 temperature on different size classes of subyearling steelhead reared at different temperatures (3, 6,  
433 and 9 °C). All size classes grew faster at the highest temperature, but the small individuals benefited  
434 the most. The proportion of lipids decreased in the largest fish but increased overall in the smallest  
435 fish. Finally, Fulton's condition factor decreased for all size classes at the highest temperature but  
436 increased for all size classes at the lowest temperature. Relatively higher winter temperatures in  
437 concert with limited food availability could hence be physiologically more challenging for larger  
438 individuals (Connolly & Petersen, 2003). During high temperature conditions in summer, Breau,  
439 Cunjak, & Peake (2011) found physiological and behavioral differences between age classes of  
440 Atlantic salmon. Whereas subyearlings were feeding up to the highest temperature (28 °C) in the  
441 experiment, older fish experienced lactate buildup and ceased feeding at 24 °C. This shows that the

442 interactions between temperature, food, and fish size are complex, and that selection for certain  
443 traits and behaviors (e.g. movement between seasonal habitats) may vary throughout the species'  
444 range.

445 The level of competition for food and space can largely control individual growth opportunities  
446 (Quinn, 2018). During summer and fall, Myrvold & Kennedy (2015a) found evidence of density-  
447 dependent growth rates in subyearling steelhead in the Lapwai Creek watershed, whereas Myrvold &  
448 Kennedy (2015b) found that yearling growth was largely limited by food and high metabolism.  
449 However, winter mortality and the emigration of steelhead smolts during snowmelt in March and  
450 April (Hartson & Kennedy, 2015) will reduce the level of competition for the fish that remain in the  
451 rivers (Figure 2) at a time when food may be plentiful and growth efficiency is high. Hartson &  
452 Kennedy (2015) found that the probability of an individual outmigrating increased with density and  
453 the size of the individual relative to its conspecifics. Juvenile steelhead are territorial, and occupation  
454 of good feeding stations is to some extent linked to size (Keeley, 2001; Rundio & Lindley, 2019). This  
455 suggests that when the largest individuals outmigrate, the smaller individuals that remain in the river  
456 gain access to better feeding territories and can capitalize on the lower levels of exploitative and  
457 interference competition.

458 Because the release from competition coincides with a greater stream area, closer-to-optimal  
459 temperatures for growth efficiency, and potentially more food, the period between the start of  
460 spring runoff and summer baseflow might therefore be particularly important to yearling growth in  
461 locations such as Lapwai Creek. Based on these coinciding events we suggest a conceptual model for  
462 seasonal growth in juvenile steelhead that applies to temperate rivers with cold winters and long, dry  
463 summers (Figure 6). The model is clearly an oversimplification; however, it can be useful to help  
464 visualize the interrelationships between the main ecological components that can govern temporal  
465 growth patterns in juvenile stream salmonids.

466 With global climate change and increasing pressures on stream ecosystems, the suite of  
467 environmental conditions experienced by most steelhead populations will likely shift (Thompson &  
468 Beauchamp, 2016; Spanjer et al., 2018; Kelson & Carlson, 2019). Historically, the summer and fall  
469 discharge in the Lapwai Creek watershed has been influenced by gradual snowmelt and surface  
470 runoff until late June, and groundwater and spring releases until the return of precipitation in  
471 October. However, there is substantial inter-annual variation in the form of precipitation and timing  
472 of the runoff because the watershed lies in a transitional climatic zone and is topographically  
473 complex (Elsner et al., 2010; Mote & Salathe, 2010), and in addition, the changes in snow storage  
474 capacity due to logging and grazing have likely contributed to earlier snowmelt. Forecasting future  
475 streamflow and temperature is therefore complicated. The Lapwai Creek region showed some of the  
476 greatest sensitivity of streamflow to forecasted changes in precipitation and temperature in the  
477 Inland Northwest (Vano et al., 2015). The greatest decline in runoff was forecasted to occur in the  
478 warm season, which was largely driven by changes in the form of precipitation in the winter and an  
479 earlier runoff (Vano et al. 2015). In predicting the effects of climate change on the growth  
480 performance, life history choices, and population dynamics of salmonids it is important to have  
481 realistic models (Ayllón et al., 2019). As has been shown by others (Nicola & Almodovar, 2004; Bacon  
482 et al., 2005), this paper suggests that temperature-based growth models derived from trials in  
483 northern regions should be used with caution in temperate streams, which exhibit great annual  
484 temperature ranges and where summers pose energetically stressful conditions.

485

486

**487 Acknowledgements**

488 This work was funded by the United States Bureau of Reclamation, the United States Geological  
489 Survey, and the Norwegian Institute for Nature Research. The field data were obtained through the  
490 hard work of numerous people, and we thank Emily Benson, Rick Hartson, Tim Kuzan, Johanna Nifosi,  
491 Jeff Caisman, Alifia Merchant, and Nick Chuang for their tremendous efforts. Discussions with Austin  
492 Anderson and Natasha Wingerter were helpful in framing the question and the analyses. Comments  
493 by six anonymous reviewers improved earlier versions of the manuscript. Finally, we thank the  
494 Lewiston Orchards Irrigation District, the Nez Perce Tribe, and landowners for access to their  
495 properties.

496

**497 Ethical approval**

498 The sampling procedures were permitted as part of the Section 7 consultation for the Lewiston  
499 Orchards Biological Opinion (NMFS 2010). The procedures were reviewed and approved by the Idaho  
500 Department of Fish and Game and the University of Idaho Institutional Animal Care and Use  
501 Committee.

502

**503 Data availability statement**

504 The data that support the findings of this study are available from the corresponding author upon  
505 reasonable request.

506

**507 References**

508 Averett, R. C. (1969). *Influence of temperature on energy and material utilization by juvenile coho*  
509 *salmon*. Oregon State University.

510 Ayllón, D., Railsback, S. F., Harvey, B. C., Quirós, I. G., Nicola, G. G., Elvira, B., & Almodóvar, A. (2019).  
511 Mechanistic simulations predict that thermal and hydrological effects of climate change on  
512 Mediterranean trout cannot be offset by adaptive behaviour, evolution, and increased food  
513 production. *Science of the Total Environment*, *693*, 133648.  
514 <https://doi.org/10.1016/j.scitotenv.2019.133648>

515 Bacon, P. J., Gurney, W. S. C., Jones, W., McLaren, I. S., & Youngson, A. F. (2005). Seasonal growth  
516 patterns of wild juvenile fish: partitioning variation among explanatory variables, based on individual  
517 growth trajectories of Atlantic salmon (*Salmo salar*) parr. *Journal of Animal Ecology*, *74*, 1–11.  
518 <https://doi.org/10.1111/j.1365-2656.2004.00875.x>

- 519 Bond, M. H., Hayes, S. A., Hanson, C. V., & MacFarlane, R. B. (2008). Marine survival of steelhead  
520 (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. *Canadian Journal of Fisheries and*  
521 *Aquatic Sciences*, 65(10), 2242–2252. <https://doi.org/10.1139/F08-131>
- 522 Borgstrøm, R., & Museth, J. (2005). Accumulated snow and summer temperature - Critical factors for  
523 recruitment to high mountain populations of brown trout (*Salmo trutta* L.). *Ecology of Freshwater*  
524 *Fish*, 14(4), 375–384. <https://doi.org/10.1111/j.1600-0633.2005.00112.x>
- 525 Breau, C., Cunjak, R. A., & Peake, S. J. (2011). Behaviour during elevated water temperatures: can  
526 physiology explain movement of juvenile Atlantic salmon to cool water? *Journal of Animal Ecology*,  
527 80, 844–853. <https://doi.org/10.1111/j.1365-2656.2011.01828.x>
- 528 Brett, J. R. (1971). Energetic responses of salmon to temperature. A study of some thermal relations  
529 in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *American*  
530 *Zoologist*, 11, 99–113.
- 531 Busby, P. J., Wainwright, T. C., Byant, G. J., Lierheimer, L. J., Waples, R. S., Waknitz, F. W., &  
532 Lagomarsino, I. V. (1996). *Status review of West Coast steelhead from Washington, Idaho, Oregon,*  
533 *and California*. Seattle, WA.
- 534 Caisman, J. (2015). *Partial migration in steelhead (Oncorhynchus mykiss): identifying factors that*  
535 *influence migratory behavior and population connectivity across a watershed*. University of Idaho.
- 536 Carlson, S. M., Hendry, A. P., & Letcher, B. H. (2007). Growth rate differences between resident  
537 native brook trout and non-native brown trout. *Journal of Fish Biology*, 71, 1430–1447.  
538 <https://doi.org/10.1111/j.1095-8649.2007.01615.x>
- 539 Connolly, P. J., & Petersen, J. H. (2003). Bigger is not always better for overwintering young-of-year  
540 steelhead. *Transactions of the American Fisheries Society*, 132, 262–274.
- 541 Duffy, E. J., & Beauchamp, D. A. (2011). Rapid growth in the early marine period improves the marine  
542 survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian*  
543 *Journal of Fisheries and Aquatic Sciences*, 68(2), 232–240. <https://doi.org/10.1139/F10-144>
- 544 Ebersole, J. L., Wigington Jr., P. J., Baker, J. P., Cairns, M. A., Church, M. R., Hansen, B. P., ... Leibowitz,  
545 S. G. (2006). Juvenile coho salmon growth and survival across stream network seasonal habitats.  
546 *Transactions of the American Fisheries Society*, 135, 1681–1697.
- 547 Elliott, J. M. (1975). The growth rate of brown trout (*Salmo trutta* L.) fed on reduced rations. *Journal*  
548 *of Animal Ecology*, 44, 823–842.
- 549 Elliott, J. M. (1976). Energy losses in the waste products of brown trout (*Salmo trutta* L.). *Journal of*  
550 *Animal Ecology*, 45, 561–580.
- 551 Elliott, J. M., & Hurley, M. A. (1997). A functional model for maximum growth of Atlantic salmon parr  
552 from two populations in northwest England. *Functional Ecology*, 11, 562–563.
- 553 Elliott, J. M., Hurley, M. A., & Fryer, R. J. (1995). A new, improved growth model for brown trout,  
554 *Salmo trutta*. *Functional Ecology*, 9, 290–298.

- 555 Elsner, M. M., Cuo, L., Voisin, N., Deems, J. S., Hamlet, A. F., Vano, J. A., ... Lettenmaier, D. P. (2010).  
556 Implications of 21st century climate change for the hydrology of Washington State. *Climatic Change*,  
557 *102*(1–2), 225–260. <https://doi.org/10.1007/s10584-010-9855-0>
- 558 Forseth, T., Hurley, M. A., Jensen, A. J., & Elliott, J. M. (2001). Functional models for growth and food  
559 consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian river. *Freshwater Biology*, *46*(2),  
560 173–186. <https://doi.org/10.1046/j.1365-2427.2001.00631.x>
- 561 Forseth, T., Larsson, S., Jensen, A. J., Jonsson, B., Näslund, I., & Berglund, I. (2009). Thermal growth  
562 performance of juvenile brown trout *Salmo trutta*: No support for thermal adaptation hypotheses.  
563 *Journal of Fish Biology*, *74*(1), 133–149. <https://doi.org/10.1111/j.1095-8649.2008.02119.x>
- 564 Glova, G. J., & McInerney, J. E. (1977). Critical swimming speeds of coho salmon (*Oncorhynchus*  
565 *kisutch*) fry to smolt stages in relation to salinity and temperature. *Journal of the Fisheries Research*  
566 *Board of Canada*, *34*, 151–154.
- 567 Grade, M., & Letcher, B. H. (2006). Diel and seasonal variation in food habits of Atlantic salmon parr  
568 in a small stream. *Journal of Freshwater Ecology*, *21*, 503–517.  
569 <https://doi.org/10.1080/02705060.2006.9665028>
- 570 Hanson, P., Johnson, T., Kitchell, J., & Schindler, D. E. (1997). *Fish bioenergetics [version] 3.0*.  
571 Madison, WI: University of Wisconsin Sea Grant Institute.
- 572 Hartson, R. B., & Kennedy, B. P. (2015). Competitive release modifies the impacts of hydrologic  
573 alteration for a partially migratory stream predator. *Ecology of Freshwater Fish*, *24*, 276–292.  
574 <https://doi.org/10.1111/eff.12145>
- 575 Hayes, S. A., Bond, M. H., Hanson, C. V., Freund, E. V., Smith, J. J., Anderson, E. C., ... MacFarlane, R. B.  
576 (2008). Steelhead growth in a small Central California watershed : Upstream and estuarine rearing  
577 patterns. *Transactions of the American Fisheries Society*, *137*, 114–128.
- 578 Hewett, S. W., & Kraft, C. E. (1993). The relationship between growth and consumption: Comparisons  
579 across fish populations. *Transactions of the American Fisheries Society*, *122*, 814–821.
- 580 Horton, G. E., Letcher, B. H., Bailey, M. M., & Kinnison, M. T. (2009). Atlantic salmon (*Salmo salar*)  
581 smolt production: the relative importance of survival and body. *Canadian Journal of Fisheries and*  
582 *Aquatic Sciences*, *66*, 471–483. <https://doi.org/10.1139/F09-005>
- 583 Jonsson, B., Forseth, T., Jensen, A. J., & Næsje, T. F. (2001). Thermal performance of juvenile Atlantic  
584 salmon, *Salmo salar* L. *Functional Ecology*, *15*, 701–711.
- 585 Keeley, E. R. (2001). Demographic responses to food and space competition by juvenile steelhead  
586 trout. *Ecology*, *82*(5), 1247–1259.
- 587 Kelson, S., & Carlson, S. M. (2019). Do precipitation extremes drive growth and migration timing of a  
588 Pacific salmonid fish in Mediterranean-climate streams? *Ecosphere*, *10*, e02618.  
589 <https://doi.org/10.1002/ecs2.2618>
- 590 Kendall, N. W., McMillan, J. R., Sloat, M. R., Buehrens, T. W., Quinn, T. P., Pess, G. R., ... Zabel, R. W.  
591 (2015). Anadromy and residency in steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of

- 592 the processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, *342*, 319–342.  
593 <https://doi.org/10.1139/cjfas-2014-0192>
- 594 Kenward, M. G., & Roger, J. H. (1997). Small sample inference for fixed effects from restricted  
595 maximum likelihood. *Biometrics*, *53*, 983–997.
- 596 Kitchell, J. F., Stewart, D. J., & Weininger, D. (1977). Applications of a bioenergetics model to yellow  
597 perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research*  
598 *Board of Canada*, *34*, 1922–1935.
- 599 Letcher, B. H., Schueller, P., Bassar, R. D., Nislow, K. H., Coombs, J. A., Sakrejda, K., ... Dubreuil, T. L.  
600 (2015). Robust estimates of environmental effects on population vital rates: An integrated capture-  
601 recapture model of seasonal brook trout growth, survival and movement in a stream network.  
602 *Journal of Animal Ecology*, *84*(2), 337–352. <https://doi.org/10.1111/1365-2656.12308>
- 603 Li, J. L., Gerth, W. J., Driesche, R. P. Van, Bateman, D. S., & Herlihy, A. T. (2016). Seasonal and spatial  
604 fluctuations in *Oncorhynchus* trout diet in a temperate mixed-forest watershed. *Canadian Journal of*  
605 *Fisheries and Aquatic Sciences*, *73*, 1642–1649.
- 606 McCarthy, S. G., Duda, J. J., Emlen, J. M., Hodgson, G. R., & Beauchamp, D. A. (2009). Linking habitat  
607 quality with trophic performance of steelhead along forest gradients in the South Fork Trinity River  
608 watershed, California. *Transactions of the American Fisheries Society*, *138*, 506–521.
- 609 McGrath, C. L., Woods, J. A., Omernik, J. M., Bryce, A. A., Edmondson, M., Nesser, J. A., ... Plocher, M.  
610 D. (2002). Ecoregions of Idaho (map scale 1:1,350,000).
- 611 Merz, J. E. (2002). Seasonal feeding habits, growth, and movement of steelhead trout in the lower  
612 Mokelumne River, California. *California Fish and Game*, *88*(3), 95–111.
- 613 Metcalfe, N. B. (1998). The interaction between behavior and physiology in determining life history  
614 patterns in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*,  
615 *55*(suppl.1), 93–103.
- 616 Mote, P. W., & Salathe, E. P. (2010). Future climate in the Pacific Northwest. *Climatic Change*, *102*,  
617 29–50. <https://doi.org/10.1007/s10584-010-9848-z>
- 618 Myrvold, K. M., & Kennedy, B. P. (2015a). Density dependence and its impact on individual growth  
619 rates in an age-structured stream salmonid population. *Ecosphere*, *6*(12), 281.
- 620 Myrvold, K. M., & Kennedy, B. P. (2015b). Interactions between body mass and water temperature  
621 cause energetic bottlenecks in juvenile steelhead. *Ecology of Freshwater Fish*, *24*, 373–383.
- 622 Myrvold, K. M., & Kennedy, B. P. (2015c). Variation in juvenile steelhead density in relation to  
623 instream habitat and watershed characteristics. *Transactions of the American Fisheries Society*, *144*,  
624 577–590.
- 625 Myrvold, K. M., & Kennedy, B. P. (2018). Increasing water temperatures exacerbate the potential for  
626 density dependence in juvenile steelhead. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*,  
627 897–907. <https://doi.org/10.1139/cjfas-2016-0497>

- 628 Nakano, S., & Murakami, M. (2001). Reciprocal subsidies: dynamic interdependence between  
629 terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences*, *98*, 166–170.
- 630 Narum, S. R., Campbell, N. R., Meyer, K. A., Miller, M. R., & Hardy, R. W. (2013). Thermal adaptation  
631 and acclimation of ectotherms from differing aquatic climates. *Molecular Ecology*, *22*(11), 3090–  
632 3097. <https://doi.org/10.1111/mec.12240>
- 633 Nicola, G. G., & Almodovar, A. (2004). Growth pattern of stream-dwelling brown trout under  
634 contrasting thermal conditions. *Transactions of the American Fisheries Society*, *133*, 66–78.  
635 <https://doi.org/10.1577/T02-169>
- 636 NMFS. (2010). *Endangered Species Act - section 7 formal consultation Biological Opinion and*  
637 *Magnuson-Stevens Fishery Conservation Act Essential Fish Habitat consultation for the operation and*  
638 *maintenance of the Lewiston Orchards Project*. Seattle, WA: National Marine Fisheries Service.
- 639 Quinn, T. P. (2018). *The behavior and ecology of Pacific salmon and trout* (2<sup>nd</sup> ed). Bethesda, MD:  
640 American Fisheries Society in association with University of Washington Press.
- 641 Railsback, S. F., & Rose, K. A. (1999). Bioenergetics modeling of stream trout growth: Temperature  
642 and food consumption effects. *Transactions of the American Fisheries Society*, *128*, 241–256.
- 643 Raudenbush, S. W., & Bryk, A. S. (2002). *Hierarchical linear models* (2<sup>nd</sup> ed.). Thousand Oaks,  
644 California: Sage Publications.
- 645 Reid, D., Armstrong, J. D., & Metcalfe, N. B. (2011). Estimated standard metabolic rate interacts with  
646 territory quality and density to determine the growth rates of juvenile Atlantic salmon. *Functional*  
647 *Ecology*, *25*, 1360–1367.
- 648 Rose, K. A., Cowan Jr, J. H., Winemiller, K. O., Myers, R. A., & Hilborn, R. (2001). Compensatory  
649 density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish*  
650 *and Fisheries*, *2*, 293–327.
- 651 Rundio, D. E., & Lindley, S. T. (2019). Diet variability of steelhead / rainbow trout in a coastal basin in  
652 Central California: relative importance of seasonal, spatial, and ontogenetic variation. *Transactions of*  
653 *the American Fisheries Society*, *148*, 88–105. <https://doi.org/10.1002/tafs.10121>
- 654 Satterthwaite, W. H., Beakes, M. P., Collins, E. M., Swank, D. R., Merz, J. E., Titus, J. E., ... Mangel, M.  
655 (2010). State-dependent life history models in a changing (and regulated) environment: steelhead in  
656 the California Central Valley. *Evolutionary Applications*, *3*, 221–243.
- 657 Spanjer, A. R., Moran, P. W., Larsen, K. A., Wetzel, L. A., Hansen, A. G., & Beauchamp, D. A. (2018).  
658 Juvenile coho salmon growth and health in streams across an urbanization gradient. *Science of the*  
659 *Total Environment*, *625*, 1003–1012. <https://doi.org/10.1016/j.scitotenv.2017.12.327>
- 660 Tattam, I. A., Li, H. W., Giannico, G. R., & Ruzycski, J. R. (2017). Seasonal changes in spatial patterns of  
661 *Oncorhynchus mykiss* growth require year-round monitoring. *Ecology of Freshwater Fish*, *26*(3), 434–  
662 443. <https://doi.org/10.1111/eff.12287>

- 663 Taylor, T. N., Myrvold, K. M., & Kennedy, B. P. (2016). Food habits of sculpin spp. in small Idaho  
664 streams: no evidence of predation on newly emerged steelhead alevins. *Northwest Science*, *90*(4),  
665 484–490. <https://doi.org/10.3955/046.090.0408>
- 666 Thompson, J. N., & Beauchamp, D. A. (2016). Growth of juvenile steelhead *Oncorhynchus mykiss*  
667 under size-selective pressure limited by seasonal bioenergetic and environmental constraints.  
668 *Journal of Fish Biology*, *89*(3), 1720–1739. <https://doi.org/10.1111/jfb.13078>
- 669 Thornton, K. W., & Lessem, A. S. (1978). A temperature algorithm for modifying biological rates.  
670 *Transactions of the American Fisheries Society*, *107*, 284–287.
- 671 Thorpe, J. E. (2007). Maturation responses of salmonids to changing developmental opportunities.  
672 *Marine Ecology Progress Series*, *335*, 285–288. <https://doi.org/10.3354/meps335285>
- 673 Trudel, M., Tucker, S., Morris, J. F. T., Higgs, D. A., & Welch, D. W. (2005). Indicators of energetic  
674 status in juvenile coho salmon and Chinook salmon. *North American Journal of Fisheries*  
675 *Management*, *25*(1), 374–390. <https://doi.org/10.1577/M04-018.1>
- 676 Uthe, P., Al-Chokhachy, R., Shepard, B. B., Zale, A. V., & Kershner, J. L. (2019). Effects of climate-  
677 related stream factors on patterns of individual summer growth of cutthroat trout. *Transactions of*  
678 *the American Fisheries Society*, *148*, 21–34. <https://doi.org/10.1002/tafs.10106>
- 679 van den Avyle, M. J., & Hayward, R. S. (1999). Dynamics of exploited fish populations. In C. C. Kohler  
680 & W. A. Hubert (Eds.), *Inland fisheries and management in North America* (2nd ed., pp. 127–166).  
681 Bethesda MD: American Fisheries Society.
- 682 Vano, J. A., Nijssen, B., & Lettenmaier, D. P. (2015). Seasonal hydrologic responses to climate change  
683 in the Pacific Northwest. *Water Resources Research*, *51*, 1959–1976.
- 684 Vøllestad, L. A., Peterson, J., & Quinn, T. P. (2004). Effects of freshwater and marine growth rates on  
685 early maturity in male coho and Chinook salmon. *Transactions of the American Fisheries Society*, *133*,  
686 495–503.
- 687 Ward, B. R., Slaney, P. A., Facchin, A. R., & Land, R. W. (1989). Size-biased survival in steelhead trout  
688 (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at  
689 the Keogh River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*, 1853–  
690 1858.
- 691 Wootton, R. J. (1999). *Ecology of teleost fishes*. Dordrecht, The Netherlands: Kluwer Academic  
692 Publishers.
- 693 Xu, C., Letcher, B. H., & Nislow, K. H. (2010). Context-specific influence of water temperature on  
694 brook trout growth rates in the field. *Freshwater Biology*, *55*, 2253–2264.
- 695 Yamamoto, T., Ueda, H., & Higashi, S. (1998). Correlation among dominance status, metabolic rate  
696 and otolith size in masu salmon. *Journal of Fish Biology*, *52*, 281–290.

697 **Tables**

698 Table 1. Variance partitioning among the two levels (within individuals and among individuals) for 63  
 699 subyearlings and 60 yearlings with recapture histories in both summer (June, July, and August), fall  
 700 (August, September, and October) and the subsequent winter-spring season (October to May or  
 701 June).  $\rho$  is the intraclass correlation coefficient, i.e. the proportion of the total variance which is  
 702 attributable to each level. The P-value refer to the test  $H_0$ : estimate = zero. Also shown is the mean  
 703 value for growth rate, consumption, and growth efficiency for both age classes.

Response and age class	Level	Variance term	Estimate (SE)	$\rho$	P-value
<b>SPECIFIC GROWTH RATE</b>					
Subyearlings	Mean $\gamma_{00}$		0.642 (0.029)		<0.0001
	Residual	$\sigma^2$	0.100 (0.013)	100	<0.0001
	Individual	$\tau_{00}$	0.0 (-)	0	n/a
Yearlings	Mean $\gamma_{00}$		0.249 (0.038)		<0.0001
	Residual	$\sigma^2$	0.177 (0.022)	100	<0.0001
	Individual	$\tau_{00}$	0.0 (-)	0	n/a
<b>PROPORTION OF MAXIMUM CONSUMPTION</b>					
Subyearlings	Mean $\gamma_{00}$		0.253 (0.0063)		<0.0001
	Residual	$\sigma^2$	0.0046 (0.0006)	100	<0.0001
	Individual	$\tau_{00}$	0 (-)	0	n/a
Yearlings	Mean $\gamma_{00}$		0.212 (0.0054)		<0.0001
	Residual	$\sigma^2$	0.0036 (0.0005)	100	<0.0001
	Individual	$\tau_{00}$	0	0	n/a
<b>GROWTH EFFICIENCY</b>					
Subyearlings	Mean $\gamma_{00}$		0.437 (0.018)		<0.0001
	Residual	$\sigma^2$	0.0396 (0.005)	100	<0.0001
	Individual	$\tau_{00}$	0.0 (-)	0	n/a
Yearlings	Mean $\gamma_{00}$		0.146 (0.023)		<0.0001
	Residual	$\sigma^2$	0.066 (0.008)	92.2	<0.0001

	Individual	$\tau_{00}$	0.0 (-)	7.8	0.33
704					
705					

---

706 Table 2

707 Table 2. Parameter estimates for the effect of season on growth rates, consumption, and growth  
 708 efficiency. Shown for each age class are the growth rate estimates and standard errors for each  
 709 season and the estimates for the variance components.  $\rho_{\text{growth period}}$  shows how much of the  
 710 explainable variation at the residual level was explained by the inclusion of season as a factor, and  
 711 similarly,  $\rho_{\text{individual}}$  shows the effect on the individual level.

Response and age class	Variable	Parameter estimate (SE)	$\rho_{\text{growth period}}$	$\rho_{\text{individual}}$
<b>SPECIFIC GROWTH RATE</b>				
Subyearlings	Season_Summer $\gamma_{10}$	0.825 (0.035)		
	Season_Fall $\gamma_{10}$	0.697 (0.059)		
	Season_Winter-Spring $\gamma_{10}$	0.523 (0.047)		
	Random intercept $\tau_{00}$	0.0 (-)		n/a
	Residual $\sigma^2$	0.092 (0.0012)	8.5	
Yearlings	Season_Summer $\gamma_{10}$	0.240 (0.15)		
	Season_Fall $\gamma_{10}$	0.275 (0.15)		
	Season_Winter-Spring $\gamma_{10}$	0.356 (0.14)		
	Random intercept $\tau_{00}$	0.0 (-)		n/a
	Residual $\sigma^2$	0.176 (0.027)	0.6	
<b>PROPORTION OF MAXIMUM CONSUMPTION</b>				
Subyearlings	Season_Summer $\gamma_{10}$	0.198 (0.015)		
	Season_Fall $\gamma_{10}$	0.211 (0.0059)		
	Season_Winter-Spring $\gamma_{10}$	0.328 (0.0056)		
	Random intercept $\tau_{00}$	0.00024 (0.0006)		0
	Residual $\sigma^2$	0.0013 (0.0007)	83.5	
Yearlings	Season_Summer $\gamma_{10}$	0.202 (0.017)		
	Season_Fall $\gamma_{10}$	0.209 (0.020)		
	Season_Winter-Spring $\gamma_{10}$	0.311 (0.016)		
	Random intercept $\tau_{00}$	0 (-)		n/a

	Residual $\sigma^2$	0.0025 (0.0003)	32	
GROWTH EFFICIENCY				
Subyearlings	Season_Summer $\gamma_{10}$	0.310 (0.055)		
	Season_Fall $\gamma_{10}$	0.325 (0.024)		
	Season_Winter-Spring $\gamma_{10}$	0.642 (0.020)		
	Random intercept $\tau_{00}$	0.0017 (0.0023)		n/a
	Residual $\sigma^2$	0.0014 (0.0027)	64	
Yearlings	Season_Summer $\gamma_{10}$	0.093 (0.082)		
	Season_Fall $\gamma_{10}$	0.159 (0.085)		
	Season_Winter-Spring $\gamma_{10}$	0.531 (0.078)		
	Random intercept $\tau_{00}$	0.0 (-)		n/a
	Residual $\sigma^2$	0.054 (0.0068)	19	

712

713

714 Table 3

715 Table 3. Proportional differences between seasons for mean growth and consumption components.  
 716 Asterisks denote statistical significance ( $P < 0.05$ ) from the mixed-effects model.

<i>Age class</i>	<i>Component</i>	<i>Proportional difference</i>		
		<i>Winter/spring - summer</i>	<i>Winter/spring - fall</i>	<i>Fall - summer</i>
Subyearling	Specific growth rate (%BM per day)*	-37%	-25%	-16%
	Proportion of max. consumption (P) *	66%	55%	7%
	Net growth efficiency (%) *	101%	92%	5%
Yearling	Specific growth rate (%BM per day)	48%	29%	15%
	Proportion of max. consumption (P) *	54%	49%	3%
	Net growth efficiency (%) *	471%	234%	71%

717

718 **Figure captions**

719

720

721 Figure 1. Map showing the location of the study sites in the Lapwai Creek watershed. Overwintering  
722 juvenile steelhead with recapture histories were found in sites ULL, ULM, ULU, UML, UMM, UMU,  
723 USM, USU, UWM, and UWU.

724

725

726 Figure 2. Conceptual figure showing the fate of a steelhead cohort through three age classes in the  
727 Lapwai Creek watershed. The figure starts with the emergence of a new 0+ cohort (dotted line) in  
728 mid May (Taylor, Myrvold, & Kennedy, 2016). After a period of mass mortality, the cohort enters  
729 their first summer and begin establishing territories (Myrvold & Kennedy, 2015a). As individual  
730 demands for food and space increase, the cohort thins throughout summer and fall. The cohort (solid  
731 line) then enters the first outmigration period during the spring runoff in mid March to mid April.  
732 Few and only the fastest growing individuals outmigrate as subyearlings (Hartson & Kennedy, 2015).  
733 The cohort then begins its second summer (the first summer as 1+ yearlings), with less mortality than  
734 in its first summer (Caisman, 2015). A small fraction of the cohort will outmigrate in the fall (Hartson  
735 & Kennedy, 2015). There is less mortality in the cohort's second winter (dashed line) leading up to  
736 the main outmigration period. Fish leave the watershed on the main spring runoff, the same  
737 discharge event their parents ascended upon approximately two years earlier (Caisman, 2015). This  
738 paper concerns the growth performance and energy allocation in those individuals that did not  
739 outmigrate or die, and that were encountered in two subsequent years.

740

741

742 Figure 3. Relationships between growth rate, P-value (the proportion of maximum consumption),  
743 and growth efficiency for a) subyearling and b) yearling steelhead recaptured at different time  
744 intervals. Periods with captures and recaptures in the same calendar year (e.g. from July to August,  
745 2011) are denoted "same", whereas periods with captures in one year and recaptures the following  
746 year (e.g. from October 2011 to May 2012) are denoted "next". Asterisks indicate the periods used in  
747 the comparison between summer, fall, and winter-spring.

748

749 Figure 4. Simulated overwinter growth trajectories for average yearling (top) and subyearling  
750 (bottom) steelhead at site UMU (chosen as an example site) in two winter and spring seasons. Solid  
751 lines denote 2010-2011 and dashed lines denote 2011-2012. The start and end weights were the  
752 same across years, and the primary factor varying between the scenarios is the temperature regime.  
753 For example, yearling steelhead weighed 25.2g on 01 March 2011. On 01 March 2012 the same fish  
754 would have weighed 22.9g (9.1% less) due to a different thermal regime.

755

756

757 Figure 5. Simulated growth trajectory (solid black line) of an average subyearling steelhead in  
758 example site UMU from October 2010 to June 2011, growing from 7.1g to 25.8g. Most of the growth  
759 happened after early April and continued until the end on 15. June. Note the negative growth rate  
760 (dashed line, displayed on the secondary axis) during the cold periods in winter (temperature as solid  
761 grey line).

762

763

764 Figure 6. Schematic showing the relationships between the typical Lapwai Creek wetted stream area  
765 in a snowmelt year (blue line), the abundance of the steelhead cohort that enters their second or  
766 third summer (grey dashed line), the abundance of insect larvae in the drift (green line), the water  
767 temperature profile (red line), and the specific growth rates of the average overyearling individual  
768 (black dashed line). It highlights the saddle-shaped pattern of specific growth rates (percent change  
769 in body mass per day) as it relates to changes in abundance of steelhead and wetted area (proxies for  
770 intraspecific competition), food, and temperature (which controls appetite and metabolic demands)  
771 throughout a typical year. Based on our findings in the Lapwai Creek watershed we hypothesize that  
772 the best growing conditions for juvenile salmonids in temperate regions with a marked dry season  
773 occur in the spring and fall.

774

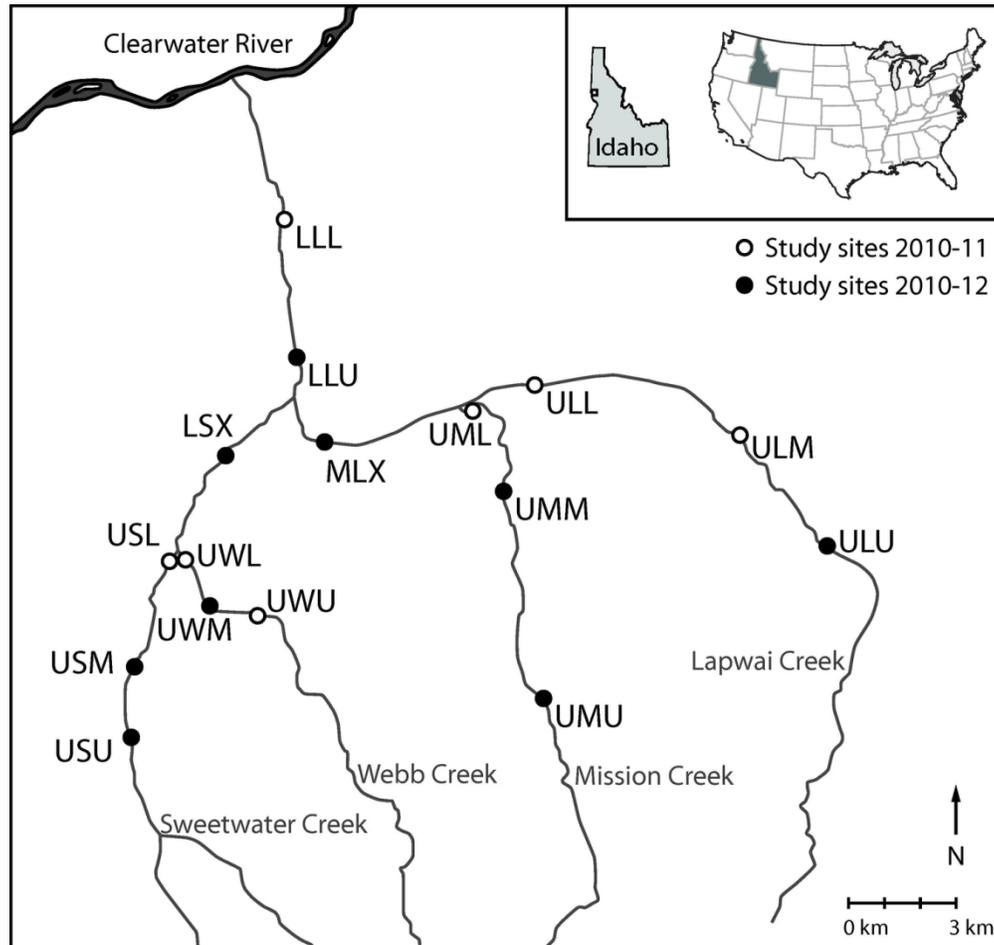
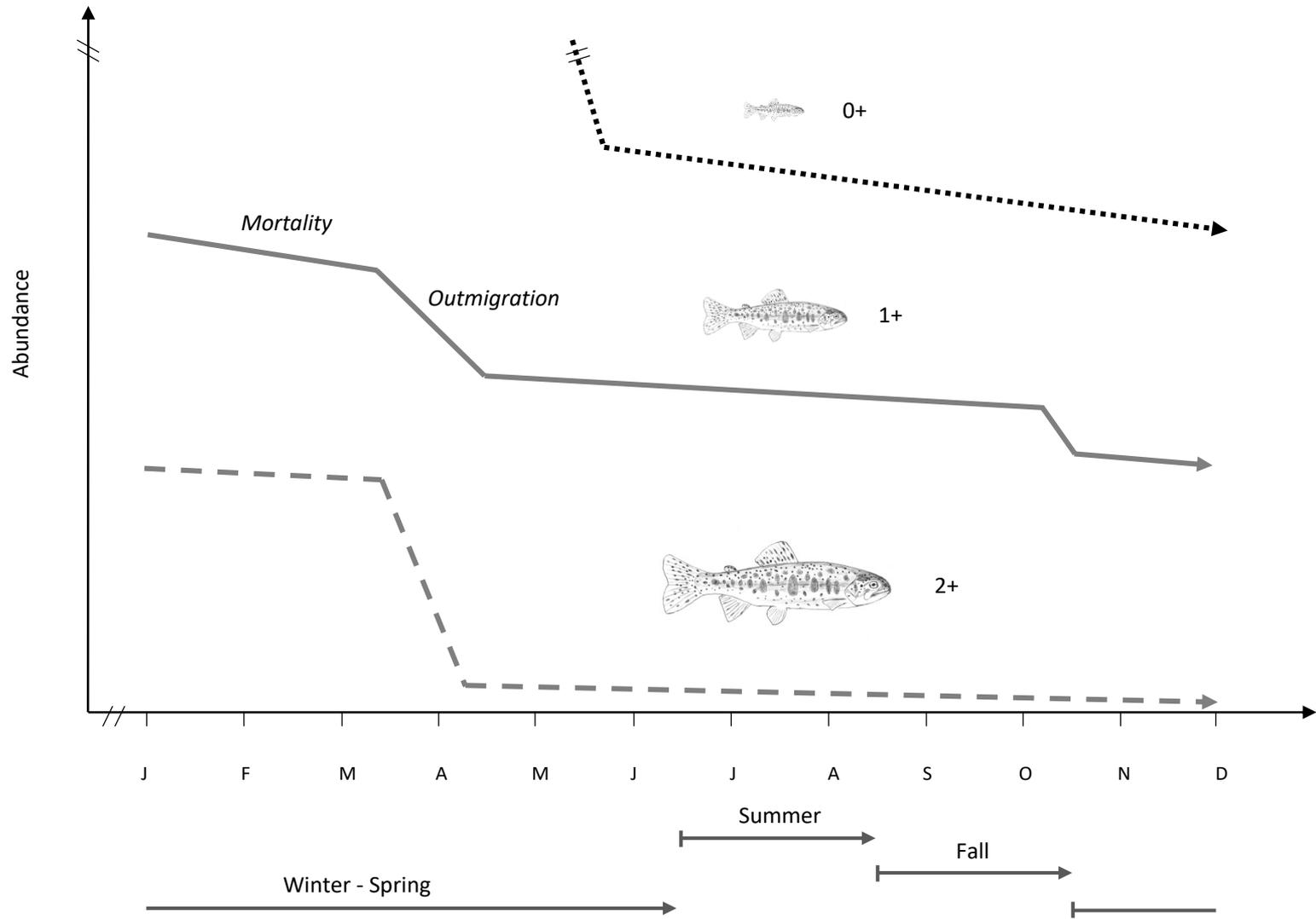
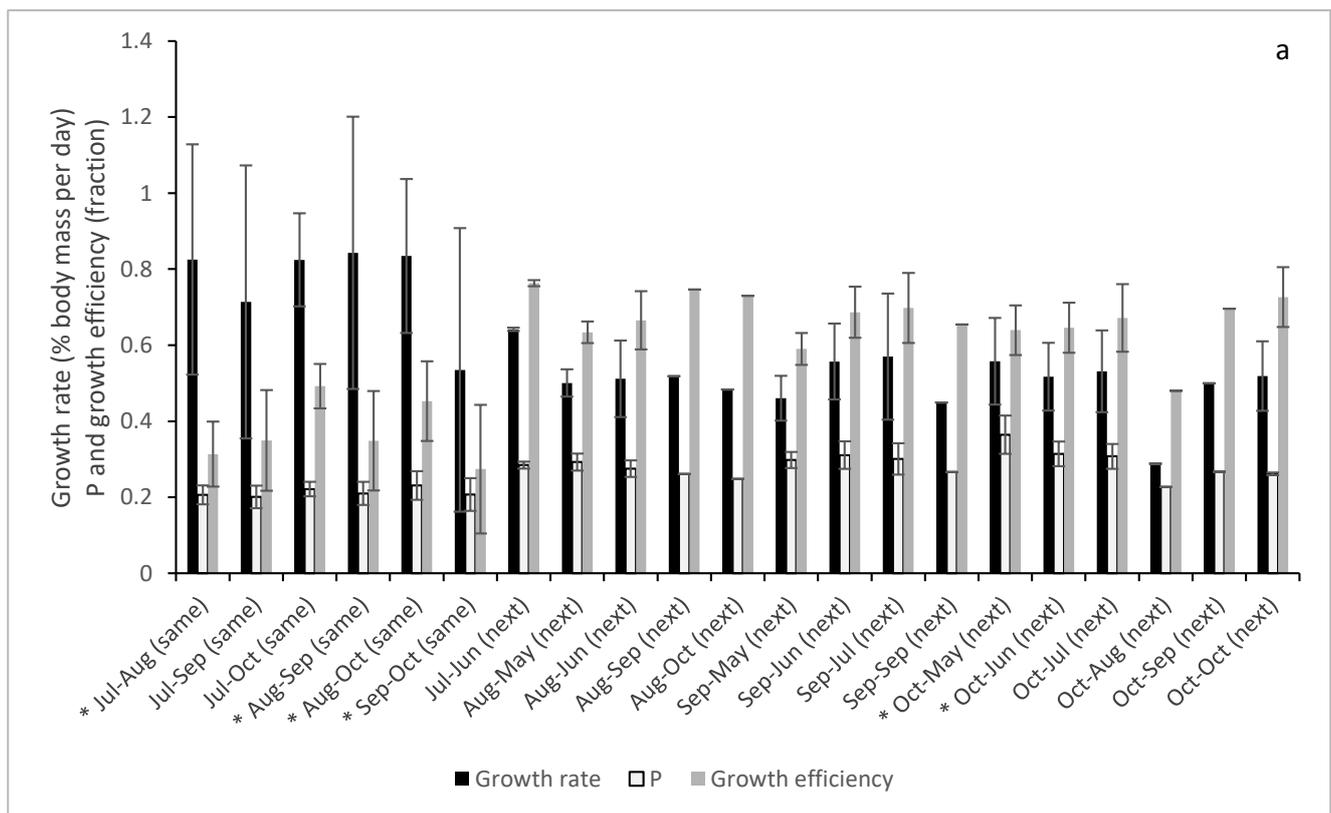
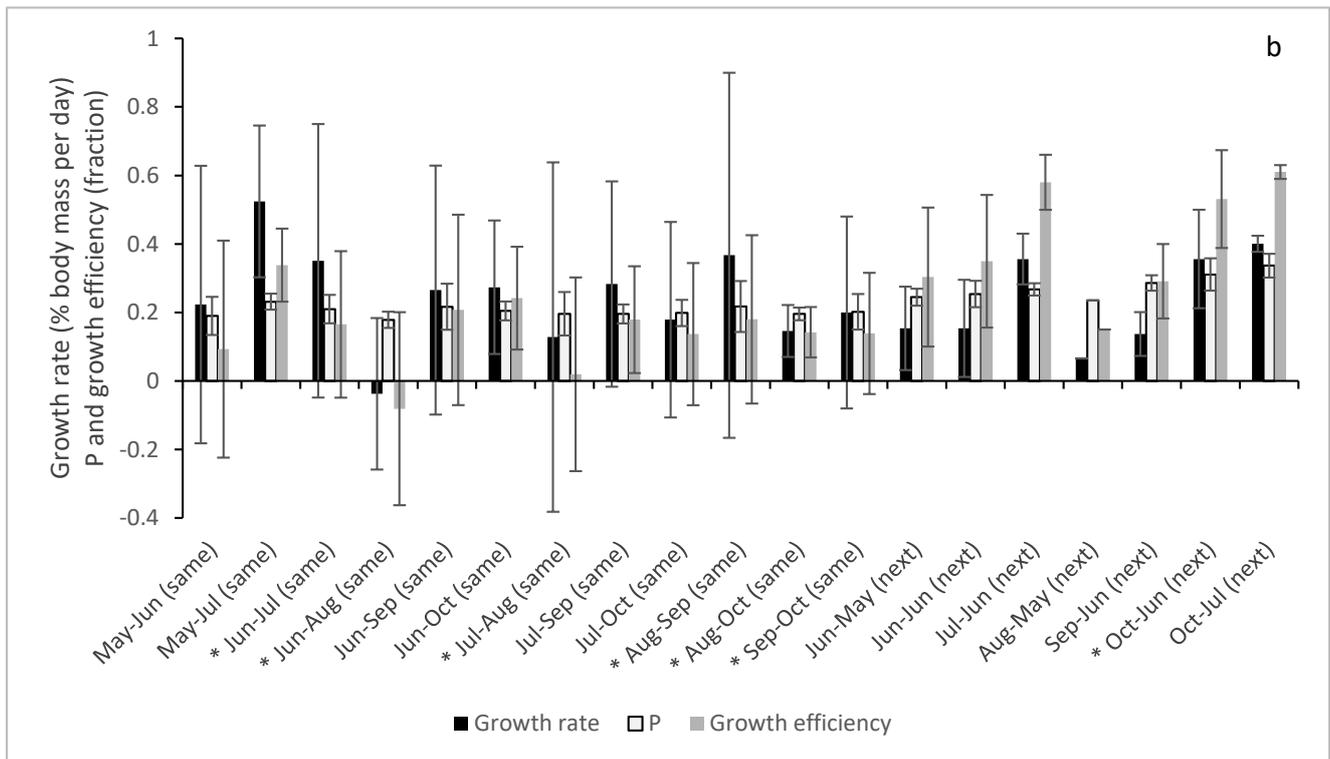


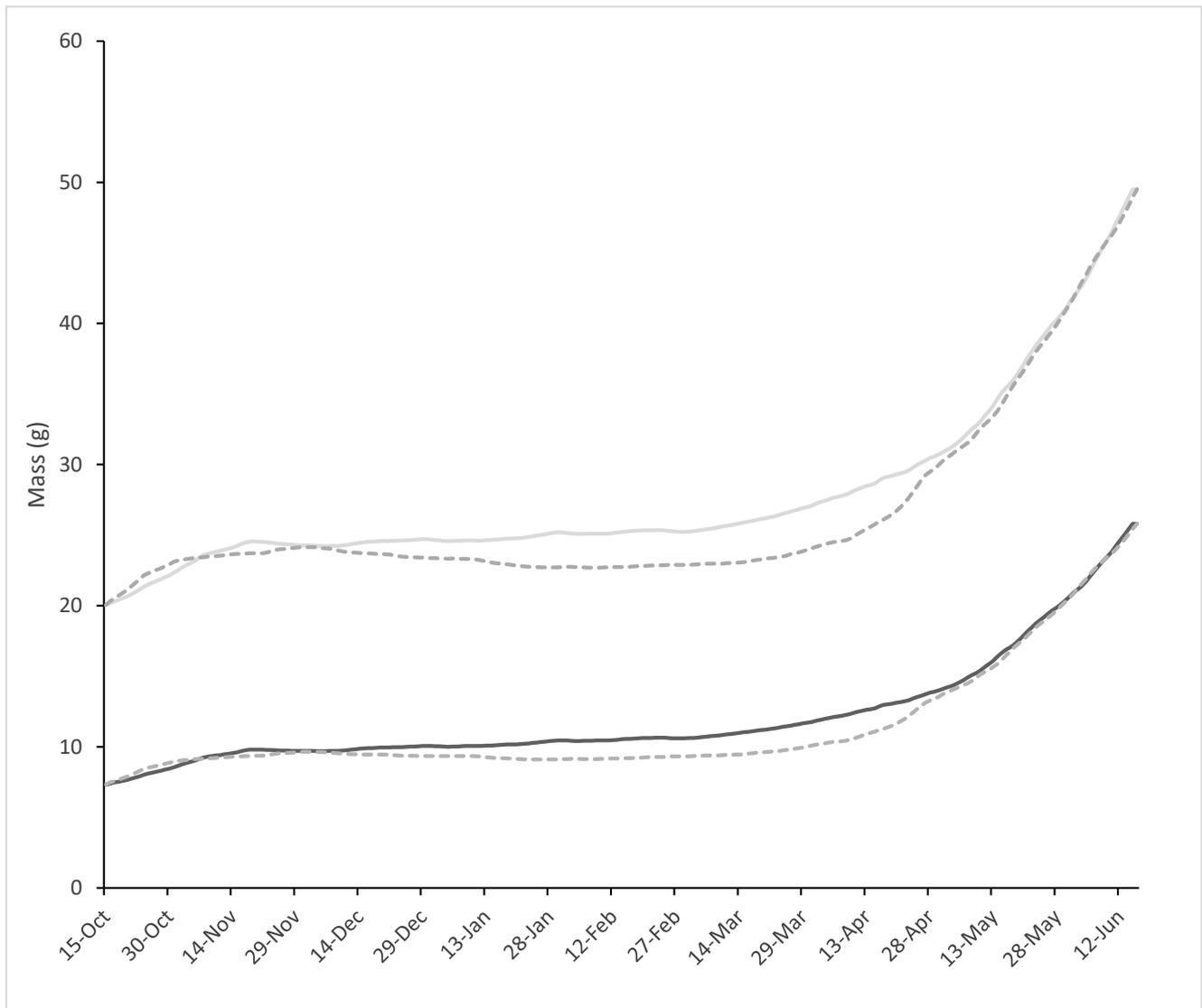
Figure 1. Map showing the location of the study sites in the Lapwai Creek watershed. Overwintering juvenile steelhead with recapture histories were found in sites ULL, ULM, ULU, UML, UMM, UMU, USM, USU, UWM, and UWU.

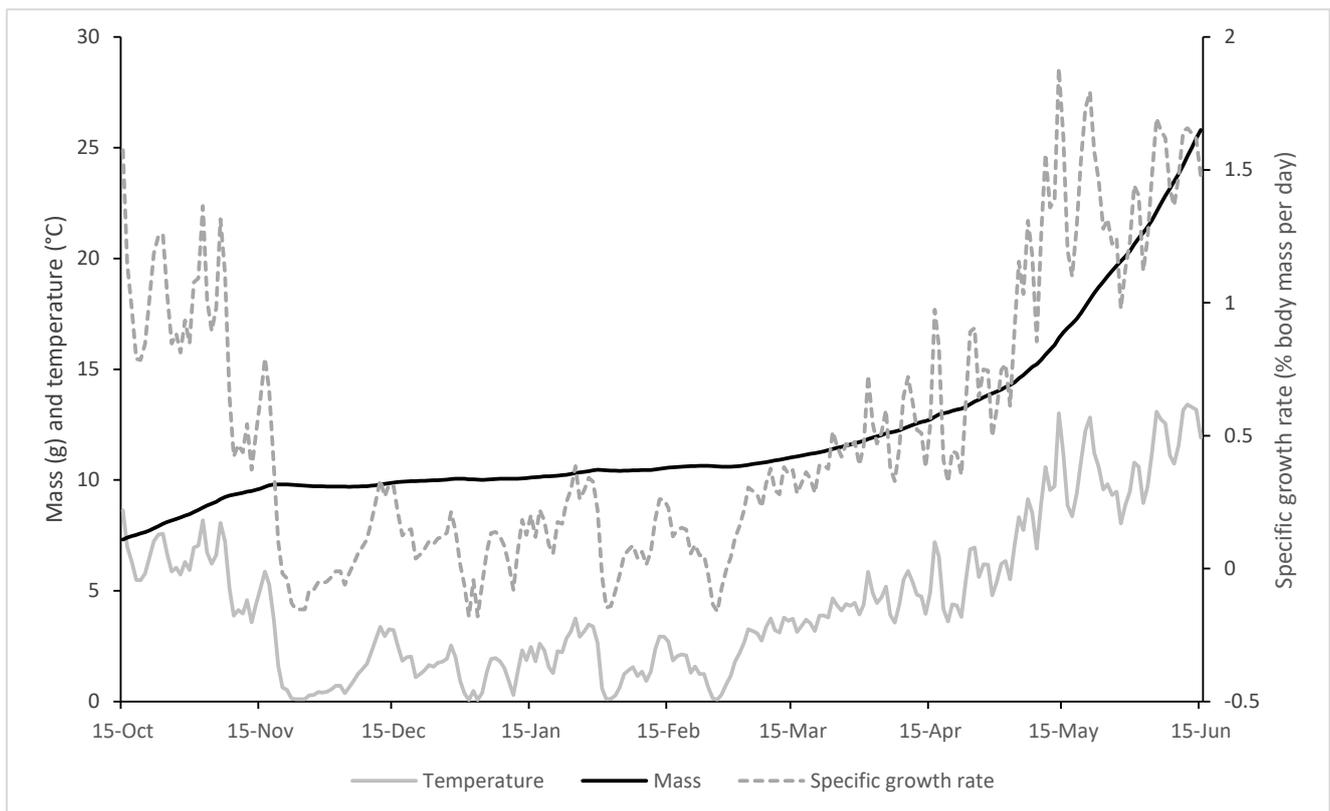
126x120mm (300 x 300 DPI)

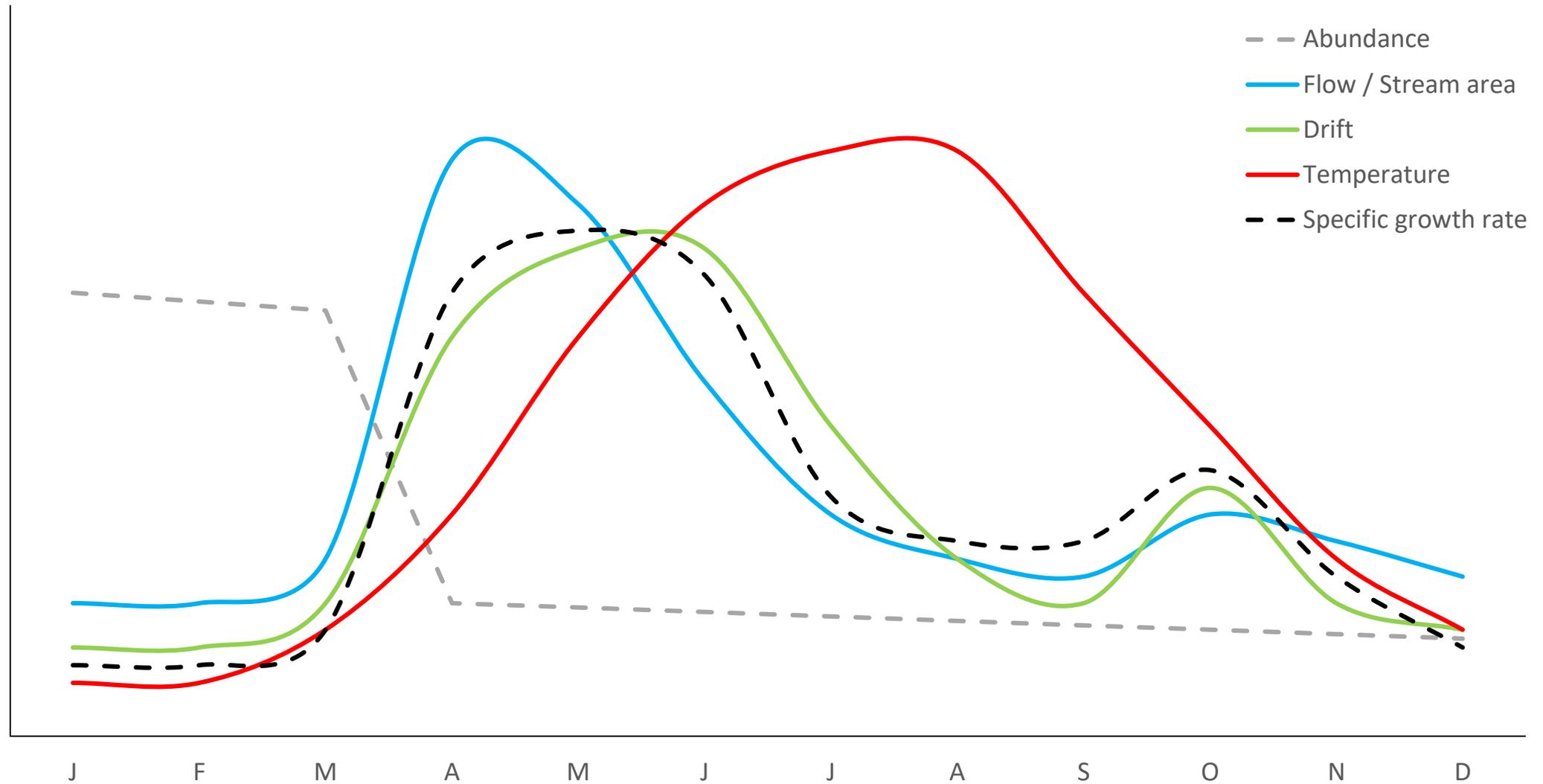












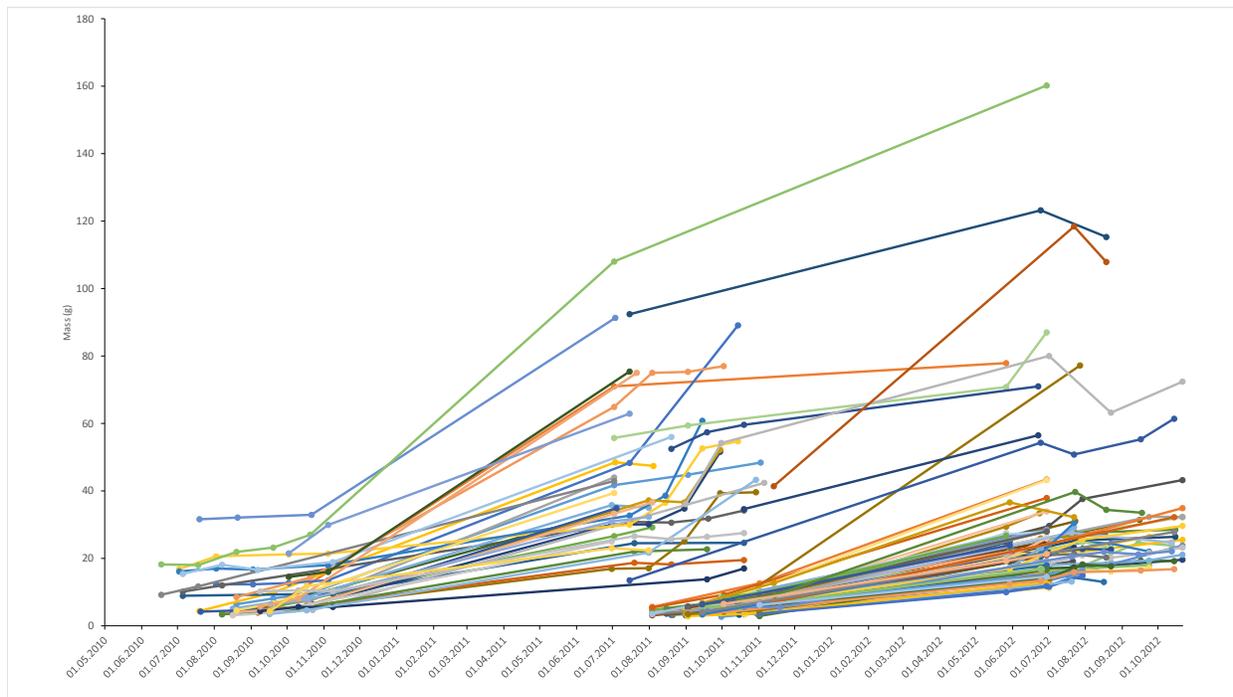


Figure A1. Raw data for the 133 individuals with overwinter recapture histories.