

1 Warming exacerbates density dependence

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4 **Increasing water temperatures exacerbate the potential for density dependence in juvenile steelhead**

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15

16 **Abstract**

17 We study the potential effects of predicted climate change on the energetic demands of juvenile
18 steelhead (*Oncorhynchus mykiss*) and their consequences for local population size and structure in
19 Idaho, USA. Projected increases in water temperature incurred on average a 10% higher energetic cost
20 by 2040 (range 7.0%-12.5% among study reaches in the watershed), and a 16% increase (range 8.5%-
21 21.3%) by 2080 following the A1B scenario. The predicted increase in energetic cost was largest in the
22 coolest stream reaches, where the proportional increases in energetic cost exceed that of temperature.
23 Energetically, and in absence of increases in food supply, local densities were consequently expected to
24 decline. We examined which factors best described the shape of current size distributions to explore
25 future size distributions as temperatures increase. Mass distribution skewness was best explained by
26 local biomass (positive relationship) and water temperature (negative relationship). The results suggest
27 that local steelhead cohorts will approach a platykurtic, slightly negatively skewed distribution with
28 increasing temperatures, and demonstrate that temperature can exacerbate demographic density
29 dependence in fish populations.

30

31

32 Introduction

33 In the face of global warming, local environments are changing at a rapid pace. In turn, the shifts in
34 habitat conditions can influence the ecology and phenotypic expression in the species inhabiting those
35 environments (Parmesan 2006; Rijnsdorp et al. 2009; Crozier and Hutchings 2014). Because fishes are
36 ectotherms they are sensitive to changes in temperature (Rijnsdorp et al. 2009; Crozier et al. 2010). A
37 number of studies have investigated the potential impacts of climate change on salmonids
38 (*Oncorhynchus*, *Salmo*, and *Salvelinus*) in the northern hemisphere, where most freshwater systems are
39 expected to become warmer (Beer and Anderson 2013; Chang and Psaris 2013). Salmonids are
40 coolwater species and may therefore show early responses to warming water temperatures (Wenger et
41 al. 2011; Kovach et al. 2016). Potential impacts on salmonids and their habitats due to warming water
42 temperatures include increased levels of physiological stress and disease (Cooke et al. 2012; Al-
43 Chokhachy et al. 2013), changes in life-history expression (Crozier et al. 2008; Rich et al. 2009; Benjamin
44 et al. 2013; Hegg et al. 2013), range shifts (Ruesch et al. 2012; Cheung et al. 2015; Isaak et al. 2016),
45 concurrent changes in disturbance regimes (Isaak et al. 2010), and altered interactions among species
46 (Wenger et al. 2011).

47 Importantly, abiotic factors can modulate how demographic density dependence is manifested in
48 populations (Lundberg et al. 2000; Buckley et al. 2010; Crozier et al. 2010; Myrvold and Kennedy 2015a).
49 For example, Crozier et al. (2010) found that the average size of juvenile Chinook salmon (*Oncorhynchus*
50 *tshawytscha*) was positively related to water temperature at low population densities, but negatively
51 related to temperature at high population densities. At the population level, Myrvold and Kennedy
52 (2015a) found that cohorts of juvenile steelhead (*O. mykiss*) exhibited steeper self-thinning curves in
53 locations with higher temperatures, demonstrating that temperature exacerbated density-dependent

54 regulation of the cohorts. Here, increased energetic demands due to higher temperatures were
55 reflected in higher mortality rates (Myrvold and Kennedy 2015a), a pattern that can be expected from
56 metabolic theory (Brown et al. 2004). The interacting effects of temperature and density dependence
57 can hence be particularly important in fishes, whose energetic demands scale predictably with
58 temperature and body mass (Brett 1971).

59 Most natural populations exhibit skewed size frequency distributions (Pfister and Stevens 2002; Begon
60 et al. 2006). Individual size disparities (which lead to skewness in size distributions) can be particularly
61 visible in fishes because they exhibit flexible and indeterminate growth (Rubenstein 1981; Nakano 1995;
62 Rose et al. 2001). Importantly, the shape of the size distributions, particularly when hatch dates are
63 synchronized, can provide information about the intensity of intraspecific competition in the population
64 relative to the constraints of their environment (Lomnicki et al. 1999; Pfister and Stevens 2002; Begon et
65 al. 2006; Connolly and Brenkman 2008; Ohlberger et al. 2013). Greater competition typically leads to
66 greater size inequality and positively skewed distributions, whereas less competition relative to the
67 direct constraints of the environment leads to lesser size inequality and negatively skewed distributions
68 (Figure 1; Pfister and Stevens 2002; Begon et al. 2006). For example, most individuals in a sparse
69 population of territorial fishes may be able to fulfill their resource demands without much interference
70 competition, but the larger individuals can be limited by total resource availability relative to their
71 energy expenditure. Here, food availability, and not an individual's ability to acquire food, might create a
72 negatively skewed size distribution. Hence, by comparing size distributions across gradients of
73 environmental conditions and population density (a proxy for competition) at equal points in time, it can
74 be possible to detect the patterns of skewness, and subsequently infer the processes responsible (Figure
75 1).

76 In this article, we demonstrate how predicted temperature increases can elevate individual energetic
77 demands during the warmest period of the year, and in turn, investigate how this may influence
78 population size and structure in juvenile steelhead rearing in the Snake River Basin, United States.
79 Steelhead spend their first years in their natal streams where they compete for food and space, and
80 migrate to the ocean once they reach a certain size (Keeley 2001; Quinn 2005; Kendall et al. 2015).
81 Previous work in the system has shown that temperatures in the summer can approach the thermal
82 tolerance of steelhead, and thus pose an important constraint on individual performance and
83 population dynamics (Myrvold and Kennedy 2015a, b). Our first objective is to quantify the added
84 energetic cost for individuals as incurred by projected warming of water temperatures across the entire
85 size range of juvenile steelhead in their natal rearing habitats. Secondly, we calculate the total energetic
86 demands of local populations across the observed water temperature range in the watershed, and
87 impose the temperature increases to quantify the added energetic requirements associated with
88 predicted climate change. Finally, we compare the shapes of the size distributions across the naturally
89 occurring gradient of population densities and temperature, and discuss how local size distributions
90 might shift in the face of predicted climate change.

91

92 **Methods**

93 *Study area*

94 The study took place in the 694 km² Lapwai Creek watershed, Idaho, United States. The watershed is
95 located at the transition between the Columbia River Plateau and the Northern Rockies ecoregions
96 (McGrath et al. 2002), and spans a gradient of land cover and land use from its headwaters on Craig

97 Mountain (elevation 1530m) to its confluence with the Clearwater River (elevation 237m). The four
98 main tributaries are designated as critical habitat for a wild steelhead population (NMFS 2010), for
99 which no hatchery supplementation exists. As part of a monitoring program to identify drivers of
100 individual performance and population dynamics (Hartson and Kennedy 2015; Myrvold and Kennedy
101 2015b, c), we established an array of randomly selected study sites representative of the physiographic
102 variation in the watershed (Figure 2). The study sites were approximately 100m long, and key
103 characteristics are given in Table 1 and in Myrvold and Kennedy (2015a). Historically the hydrograph has
104 predominantly resembled a snowmelt-driven pattern, by which most of the precipitation came in the
105 form of snow in the winter and a gradual snowmelt in the spring-early summer (Mote et al. 2003). With
106 predicted climatic change, the region is expected to experience substantial warming over the next
107 decades, due to higher air temperatures and shifts in the amount, form, and timing of precipitation
108 (Mote et al. 2003; Mote and Salathe 2010).

110 *Steelhead data*

111 Data on the size distribution of juvenile steelhead were obtained monthly from each study site from
112 June to October 2011. We captured fish via three-pass depletion electrofishing using a Smith-Root LR-24
113 backpack electrofisher (Smith-Root Inc., Vancouver, Washington, USA). We measured fork length in
114 millimeters and mass to the nearest decigram. We considered sampling visits where we caught eight or
115 more individuals, and the frequency distribution was binned by 1 g increments. Individuals were
116 classified as *subyearling* (hatched in May the same year) or *overyearling* (hatched in a previous year)
117 based on size frequency histograms at the sampling visit. To separate out effects of ontogenetic changes

118 and life-history decisions (Benjamin et al. 2013) we focused primarily on subyearlings in this analysis. We
119 estimated the size of the subyearling cohort using Carle and Strub's (1978) maximum weighted
120 likelihood estimator for removal data. We then multiplied the estimate with the average mass of
121 subyearlings to obtain the standing biomass present at the sampling visit. To allow for comparison
122 between sampling sites we divided the population estimate and the biomass by the area sampled to
123 obtain density (number/m²) and biomass per unit area (g/m²). All sampling and handling procedures
124 were permitted as part of the Section 7 consultation for the Lewiston Orchards Biological Opinion
125 (NMFS 2010), and reviewed by the Idaho Department of Fish and Game and the University of Idaho
126 Institutional Animal Care and Use Committee.

127

128 *Temperature data*

129 Stream temperatures were recorded every 30 minutes in each study site from 2010 through 2012 using
130 HOBO TidbiT v2 temperature loggers (Onset Computer Corporation, Pocasset, Massachusetts, USA). The
131 temperature data were used 1) to inform climate projections with the observed spatial heterogeneity in
132 the watershed, and 2) to explain variation in the shape of the size distributions of steelhead in each
133 study site.

134

135 *Temperature projections*

136 We used the NorWeST Regional Database and Modeled Stream Temperature model (Isaak et al. 2010)
137 to predict the future temperatures in the study sites in the Lapwai Creek watershed. The stream

138 temperature model is based on an extensive grid of temperature measurements, and creates
139 continuous temperature profiles (expressed as the average temperature for the month of August) for
140 streams in the region using spatial statistical network models. Between locations where water
141 temperature measurements were made the model interpolates predictions based on characteristics
142 such as elevation, stream order, and discharge (Isaak et al. 2010). The projections are based on the
143 commonly used A1B scenario (Isaak et al. 2010), which emphasizes a balance between fossil- and non-
144 fossil based energy sources (IPCC 2000). The model captures the temperature profile patterns well on
145 the scale of kilometers, but does not account for thermal heterogeneity on smaller spatial extents, e.g.
146 due to spring inputs or groundwater exchange (Snyder et al. 2015). The concordance between the
147 predicted current temperature and our own temperature measurements in the Lapwai Creek watershed
148 was overall very good (average August temperatures of 17.30°C and 17.31°C, respectively), but with
149 local discrepancies (average 0.026°C, SD=0.51; Table 1). We therefore adjusted the projections for the
150 study sites with our local temperature measurements, that is, the temperature increases (predicted
151 future temperature minus predicted current temperature) were added to our measured data, not to the
152 predicted current temperature from the Isaak et al. (2010) model. We considered the projected August
153 temperatures for the 2040s (midpoint for the 2030-2059 period) and 2080s (midpoint for the 2070-2099
154 period).

155

156 *Bioenergetic model*

157 We used Fish Bioenergetics 3.0 (Hanson et al. 1997) to model the energetic cost incurred by the water
158 temperature on juvenile steelhead. Bioenergetic models consist of a set of mass-balance equations,

159 which link fish physiology with the environment (Hewett and Kraft 1993; Hanson et al. 1997). Myrvoid
160 and Kennedy (2015b) parameterized a detailed bioenergetics model with field values for the Lapwai
161 Creek system, and the following analyses draw on this model. Energetic cost was calculated as the daily
162 energetic demand under a given temperature with no somatic growth, i.e. the cost of maintaining
163 standard metabolism (Hewett and Kraft 1993; Myrvoid and Kennedy 2015b). Two main patterns are
164 important for the following analysis (Figure 3). First, standard metabolism is nonlinearly related to
165 temperature, and, secondly, mass-specific metabolism ($J \cdot g^{-1} \cdot d^{-1}$) decreases with fish mass (Myrvoid and
166 Kennedy 2015b).

167

168 *Total energetic demands in local populations*

169 We selected three study sites (USU, ULL, and UML) which spanned the gradient of current temperatures
170 (the lowest, mid, and highest water temperatures in the watershed, respectively), and characterized the
171 population size and structure in each. We then calculated the current and future ration (g prey with an
172 energy density of 4324 J/g; Myrvoid and Kennedy 2015b) for maintenance metabolism for each
173 individual for the month of August 2011 in each site. We then compared the sites with regards to the
174 total energy demands necessary to maintain body mass.

175 To identify the temperature at which metabolic demands start to decrease on the margin (i.e. a change
176 in concavity) we fit a third order polynomial function to the relationship between maintenance
177 consumption rate and temperature up to the maximum predicted temperature for the 2080s scenario
178 (22.45°C). We then took the second-order derivative to find the inflection point, and solved for
179 temperature by setting the function equal to zero.

180

181 *Shape of subyearling size distributions*

182 We focused the analysis on subyearling steelhead in their first summer (June – October) to avoid the
 183 confounding effects of migration. In the Lapwai Creek watershed, steelhead outmigrate at ages 1-3
 184 depending on local factors such as density and habitat productivity (Hartson and Kennedy 2015).
 185 Following emergence from the redds (typically the month of May in this system; Taylor et al. 2016) fry
 186 disperse in search for suitable shelter habitat, and later establish feeding territories. Mortality is high
 187 during this time, and the analysis concerned the period after fry dispersal. We calculated the skewness
 188 of the size distribution using the adjusted Fisher-Pearson standardized moment coefficient in SAS 9.2
 189 Proc Univariate (SAS Institute, Cary, North Carolina, USA). The coefficient is unbound and measures the
 190 tendency of the deviations to be larger in one direction than in the other. For example, a normal
 191 distribution of individuals has a skewness of zero, whereas a distribution with a positive skew (long tail
 192 on the right) indicates that there are many small and a few, larger individuals. To quantify how much of
 193 the variation in sample skewness attributable to the different levels in the data (sampling visit and study
 194 site) we performed a one-way analysis of variance (Raudenbush and Bryk 2002). The model for the
 195 variance components for the site- and visit levels (also known as the empty or unconditional model) is
 196 expressed as

$$197 \quad skewness_{ij} = \gamma_{00} + u_{0j} + r_{ij} \text{ (eq. 1),}$$

198 where γ_{00} is the grand mean skewness of all sampling visits, u_{0j} is the random site effect, i.e. the
 199 deviation of site j from the grand mean, and r_{ij} is the random sampling visit effect, i.e. the deviation of
 200 visit ij from the site mean. Because sites and sampling visits were randomly sampled from a larger

201 statistical population of potential sites and visits we can assume that $u_{0j} \sim N(0, \tau_{00})$ and $r_{ij} \sim N(0, \sigma^2)$
 202 (Raudenbush and Bryk 2002). The variance decomposition revealed substantial clustering by study site
 203 (as indicated by the intraclass correlation coefficient ρ - Table 2), and we hence modeled the skewness
 204 under a mixed-effects framework (Raudenbush and Bryk 2002). We investigated the effects of density,
 205 biomass, average mass, and water temperature on skewness as these factors have been shown to affect
 206 both individual growth and cohort regulation in the system (Hartson and Kennedy 2015; Myrvold and
 207 Kennedy 2015a, c, d). A visit-level model of skewness as a function of a visit-level variable X (i.e. density,
 208 biomass, average mass, and temperature) can be written as

$$209 \quad \text{skewness}_{ij} = \beta_{0j} + \beta_{1j}X_{ij} + r_{ij} \text{ (eq. 2)}$$

210 To allow for site-specific intercepts, we can write

$$211 \quad \beta_{0j} = \gamma_{00} + u_{0j} \text{ and } \beta_{1j} = \gamma_{10}$$

212 Combining into eq. 2, this model structure becomes a random intercept model

$$213 \quad \text{skewness}_{ij} = \gamma_{00} + \gamma_{10}X_{ij} + u_{0j} + r_{ij} \text{ (eq. 3)}$$

214 Adding more variables to equation 3 expands the model linearly. In addition to the skewness, we were
 215 interested in understanding how biomass affected the height of the central peak in the size distribution.
 216 We modeled the kurtosis of the size distributions as a function of biomass, using the same framework.
 217 We used SAS 9.2 Proc MIXED specified with the Kenward and Roger (1997) approximation of
 218 denominator degrees of freedom and maximum likelihood as the estimator in all the analyses. Models
 219 were ranked using the small-sample corrected version of Akaike's Information Criterion (Akaike 1973;
 220 Hurvich and Tsai 1989); the model with the lowest $AICc$ value is the best approximating model of the

221 data (Burnham and Anderson 2002). We report on models with substantial relative support, i.e. within
222 2.0 $AICc$ points from the best model, and present their Akaike weight, which is the relative support for a
223 given model in the candidate set (Burnham and Anderson 2002).

224

225 **Results**

226 *Objective 1: Increases in energetic cost*

227 Stream temperatures in the Lapwai Creek watershed were estimated to increase on average by 1.81°C
228 by the 2040s (the midpoint of the period 2030-2059), and by 3.11°C by the 2080s (the period 2070-
229 2099) following the A1B scenario (Table 1). On a site-by-site basis, the predicted percent increase from
230 the current temperature decreased with higher current temperature (Table 1).

231 We predicted the associated increases in August energetic cost for a size range of juvenile steelhead for
232 each study site (Table 3). Compared to current conditions, the projected temperature increases would
233 on average lead to a 10% higher standard metabolic cost by the 2040s, and a 16% increase by the 2080s.
234 The variation among the study sites in the watershed ranged from 7.0% to 12.5% in the 2040s
235 projection, and from 8.5% to 21.3% in the 2080s projection.

236 The predicted increase in energetic cost was negatively related to current temperature (Figure 4). In
237 other words, fish in the warmest reaches in the watershed were predicted to have the lowest rate of
238 *increase* in standard metabolism. The reason is that the maintenance metabolic cost decreases more
239 rapidly on the margin at higher temperatures within the thermal tolerance levels (Figure 3). The
240 projected temperature increases (absolute values) in all the study sites were within 2.0% of each other

241 for the 2040s (range 9.5%-11.4%; Table 1), whereas the associated increases in metabolic cost were
242 7.0% to 12.5% (Table 3, Figure 4). The largest predicted increases in metabolic cost were therefore
243 found in the currently coolest sites. Hence, even though the range of temperature increases were subtle
244 across the study sites (range 1.78°-1.86°C), the energetic impacts of these increases depended upon the
245 actual temperature, present and future (Figure 5). The same pattern, but with larger absolute increases,
246 was visible for the predicted 2080s situation. The inflection point for the temperature-metabolic cost
247 relationship was at 18.0°C (range 17.9°-18.1°C) across the size range of juvenile steelhead.

248

249 *Objective 2: Total energetic demands in local populations*

250 We calculated the maintenance ration (total mass of prey) necessary for the individuals in three local
251 populations to maintain their body mass. The three study sites (USU, ULL, and UML; Table 4) spanned
252 the observed temperature gradient in the watershed, and included both subyearling and overyearling
253 fish. For example, in order to maintain the body mass for the 61 individuals in USU a total of 1026 g prey
254 was needed for the month of August (Table 4). If the abundance were the same in 2040, this amount
255 would be 1153 g, an increase of 12.4% due to the increases in water temperature. It follows that if the
256 temperature increase were compensated by a 12.4% increase in food availability (in caloric terms) there
257 would be no change in steelhead numbers through mortality or emigration, or reduction in average
258 mass through individual weight loss. This is equivalent to an additional 127 g, or 549 kJ (i.e. 127 g × 4324
259 J/g) of prey for the month of August. The largest predicted increase in metabolic demands was in the
260 coolest site (USU) and the smallest predicted increase was in the warmest site (UML), consistent with
261 the above reported results for the size range.

262 In absence of a proportional increase in prey availability, fewer individuals would be supported by the
263 environment due to the increased individual energetic demands. The reduction would be larger in the
264 relatively cooler sites. We further quantified the shape of the size distributions in all the study sites to
265 explore how this would manifest in local abundance and size structure.

266

267 *Objective 3: Shape of subyearling size distributions*

268 The shape of the size distributions of subyearling steelhead was overall positively skewed (longer tail on
269 the right). Summary statistics for the month of August are given in Table 5. The overall skewness in the
270 size distribution data (all visits combined) was 0.617 (SE=0.092), with 70% of the variance attributable to
271 factors on the visit (residual) level and 30% attributable to factors on the site level (Table 6, top half).

272 When modeling the factors that could explain the variation in skewness we found that biomass (positive
273 relationship) was the best approximating model (Akaike weight=0.38), with some additional support to
274 water temperature (negative relationship, Akaike weight=0.16). Biomass explained some 28% of the
275 site-level variance and 3% of the visit-level variance. This means that sites with relatively higher biomass
276 and cooler temperatures had positively skewed size distributions, i.e. with longer tails on the right. This
277 corresponds to a situation with many small and a few large individuals (see below). Sites with relatively
278 higher temperatures and lower biomass approximated a normal distribution or had negative skew. In
279 the negatively skewed populations there were relatively more large individuals and fewer small
280 individuals (Figure 6).

281 Biomass is a composite measure of density and average mass. However, it can be desirable to separate
282 out the relative contribution of these constituents. Using the same approach as described for skewness,

283 we modeled the relationship between biomass and density and average mass, respectively. We found
284 that biomass was largely driven by variation in density (estimate=3.9, $SE=0.41$, $d.f.=28.4$, $P(|t|)<0.0001$,
285 $AICc=23.5$) and less by average mass (estimate= 0.022, $SE=0.013$, $d.f.=58.8$, $P(|t|)=0.089$, $AICc=67.6$).
286 Finally, there was a positive effect of biomass on the kurtosis of the size distribution with site as a
287 random effect (estimate=0.975, $SE=0.45$, $d.f.=51.2$, $P(|t|)=0.033$). This means that the mass distributions
288 in high-density sites tended to be more leptokurtic (narrowly peaked), and conversely, that mass
289 distributions in low-density sites were more platykurtic (flatter and wider; Figure 6).

290

291

292 Discussion

293 In order to forecast the effects of climate change on fish populations there is a need to identify the
294 potential mechanisms that link the physical environment with biological processes (Brown et al. 2004;
295 Rijnsdorp et al. 2009; Wenger et al. 2011; Crozier and Hutchings 2014; Kovach et al. 2016). The goal of
296 this study was to highlight the increase in individual energetic cost associated with a warming climate as
297 a mechanism regulating in part the size and structure of local populations of juvenile steelhead in their
298 natal streams. Water temperature is an important factor which influences individual performance and
299 population dynamics in the studied population (Myrvold and Kennedy 2015a, b, d), and we hence
300 expected that further increases in water temperature due to climate change can be important.
301 Predicting a future situation based on a single variable can be speculative, however, as other changes
302 may occur simultaneously (Beer and Anderson 2013). For example, it can be expected that climatic
303 change will also result in altered streamflow, changes in stochastic events, and shifts in stream

304 productivity and community structure (Isaak et al. 2010; Wenger et al. 2011; Al-Chokhachy et al. 2013),
305 all with the potential to modulate the effects of greater metabolic demands associated with elevated
306 water temperatures. Nevertheless, metabolic demands scale directly and predictably with water
307 temperature in fishes (Brett 1971; Hewett and Kraft 1993; Hanson et al. 1997; Brown et al. 2004), and it
308 is thus likely that a warming trend will result in elevated individual energetic demands (Rijnsdorp et al.
309 2009). The extent to which this is ultimately manifested in population size will depend on concurrent
310 changes in the stream ecosystem (Wenger et al. 2011; Al-Chokhachy et al. 2013; Beer and Anderson
311 2013) as well as plastic and adaptive shifts in the life-history expression of steelhead (Benjamin et al.
312 2013; Kendall et al. 2015; Phillis et al. 2015). This article concerns the energetic consequences of
313 warming water temperatures during a period of the summer when rearing steelhead experience the
314 highest water temperatures of the year.

315 The predicted temperature increase was relatively uniform across the watershed (average 1.8°C by the
316 2040s), as the area we considered is relatively small compared to the scale at which the warming trend
317 is expected to affect the region (Mote and Salathe 2010). However, because of the temperature
318 gradient and local heterogeneity within the watershed, the percent increase varied considerably among
319 the study sites. Relatively cooler sites were predicted to experience the highest proportional increases in
320 temperature, whereas relatively warmer sites had a smaller proportional increase. Because the
321 proportional temperature increase was larger, and because the inflection point in the relationship
322 between temperature and maintenance consumption rate was approximately at 18°C, the increases in
323 energetic cost were also higher in the cooler sites. Importantly, the proportional increase in energetic
324 cost exceeded that of the increase in temperature in these sites due to the nonlinear relationship
325 between these variables in the parameter range experienced by fish in this system, where August mean

326 temperatures ranged from 15.1°C to 19.3°C (Figures 3 and 5). The currently cooler sites were predicted
327 to approach the current temperatures observed in the warmer sites. These reaches are located within a
328 similar physiographic setting, and the shape of the current size distributions of juvenile steelhead across
329 this temperature gradient may therefore be used to inform the future state under a warming trend.

330 In discussing how increases in energetic cost can be manifested in population numbers it is necessary to
331 also consider the structure of the population. Most populations of plants and animals exhibit skewed
332 size distributions. Pfister and Stevens (2002) proposed that asymmetric competition (resource
333 acquisition, growth, and survival) is the most important mechanism responsible for generating size
334 variability within cohorts, i.e. when individuals experience the same conditions. Asymmetric competition
335 can be detected by studying individual growth performance over time (Lomnicki 1999; Pfister and
336 Stevens 2002). If resources are distributed unevenly among individuals in a consistent manner, size
337 disparities are thought to increase over time (a pattern known as growth autocorrelation), but more
338 often, trade-offs between the ability to acquire resources and avoid risk can change throughout
339 ontogeny. In other words, growth and survival on the long term depend on other factors than
340 momentary size alone. Larger size might therefore not always confer a growth advantage, which is why
341 initially small individuals could experience growth compensation at a later stage (Pfister and Stevens
342 2002).

343 In heterogeneous environments, abiotic factors interact with density dependence to influence individual
344 performance (Buckley et al. 2010; Crozier et al. 2010; Myrvold and Kennedy 2015a). The impact of
345 environmental factors can be detected when individuals from multiple populations are followed
346 simultaneously (Myrvold and Kennedy 2015b). Myrvold and Kennedy (*in press*) studied size – growth
347 relationships in the same steelhead population. They found a positive correlation between an

348 individual's relative size and its growth rate (i.e. larger individuals grew faster), but importantly, this
349 relationship was context dependent: during periods of high water temperatures and in relatively
350 warmer streams reaches the positive effect of a relatively large body size diminished. This finding
351 indicates that abiotic conditions can exert an important control over biotic interactions and individual
352 performance (Crozier et al. 2010).

353 Several studies have investigated the genetic and behavioural causes of individual variation and
354 asymmetric competition. There can be considerable variation in metabolic rate among individuals within
355 a population, and the expression of these traits vary depending on the context. A commonly observed
356 pattern in juvenile salmonids is the correlation between aggressive behaviour and growth rate whereby
357 aggressive individuals can better compete for resources (Abbott and Dill 1989; Nakano 1995). However,
358 if the supply of prey is dynamic in space and time, the selection for these traits can be counterbalanced
359 by the relatively higher energetic cost of such behaviour (Vøllestad and Quinn 2003; Biro and Stamps
360 2010; Robertsen et al. 2014; Sloat and Reeves 2014). Sloat and Reeves (2014) experimentally tested how
361 the spatial predictability of food influenced behaviour and demography in juvenile steelhead in artificial
362 channels. When food availability was predictable, there was a positive selection for individuals exhibiting
363 a high standard metabolic rate, and conversely, a negative directional selection for this trait under low
364 food predictability. These energetic controls are likely to be stronger with increasing temperatures
365 (Hewett and Kraft 1993), which suggests that temperature can act as an important mediator of the
366 profitability of aggression in wild populations. Our study did not investigate the individual-level basis for
367 size disparities in the population, but merely focused on documenting the shape variation in size
368 distributions; however, we note that as the body of literature which examines the genetic and
369 behavioural basis for individual variation in aggression and behaviour is growing, it becomes increasingly

370 clear that the patterns of social interactions and competition are complex and context-dependent
371 (Millidine et al. 2009; Reid et al. 2012, Adriaenssens and Johnsson 2013; Sloat and Reeves 2014).

372 Comparing the shapes of the size distributions in multiple local populations allowed us to simultaneously
373 quantify the effects of temperature and density on the size variation in local cohorts. Although the local
374 populations are located within a relatively small watershed, they experience a range of abiotic
375 conditions and exist at varying densities (Myrvold and Kennedy 2015d). Few studies have compared the
376 shape variation of fish cohorts in space or time, but Ohlberger et al. (2013) investigated the shape
377 variation in European perch (*Perca fluviatilis*) in Lake Windermere, United Kingdom. Factors both
378 extrinsic and intrinsic to the population explained the variation in the skewness of cohort size
379 distributions. Notably, food availability related positively to the skewness of the size distributions.
380 Temperature related positively to mean length in the perch and decreased distribution skewness,
381 presumably due to concurrent eutrophication in the lake (Ohlberger et al. 2013). Connolly and
382 Brenkman (2008) examined size distributions in rainbow trout in the Elwha River, Washington, both
383 upstream and downstream of a dam. They could not discern whether the overall smaller sizes in the
384 lower section owed to higher density, less food due to disrupted flows, or some combination of the
385 factors (Connolly and Brenkman 2008). However, the water temperatures were also higher downstream
386 of the dam. Energetic demands in concert with competition likely contributed strongly to the smaller
387 overall size in the lower section.

388 The variation in size distribution skewness across the gradients of density and temperature hence
389 suggests that individual size might be influenced by temperature in addition to competition. The
390 negative skewness in the warmer sites indicates that most individuals were able to meet their resource
391 demands due to low densities, but that high temperatures may create an upper size threshold above

392 which the absolute energetic demands become too great (Myrvold and Kennedy 2015b). Although mass-
393 specific energetic demands decrease with fish mass, the absolute demands increase (Myrvold and
394 Kennedy 2015b). We therefore hypothesize that the direct effects of temperature were more important
395 than competition in limiting the size of the largest fish in the relatively warmer sites, and conversely,
396 that asymmetric competition was more important in the cooler, denser sites where dominance
397 hierarchies were established and a few dominant individuals could competitively displace their
398 conspecifics (Figure 6). This hypothesis is supported by Myrvold and Kennedy (*in press*) who
399 demonstrated how temperature can modulate the outcome of asymmetric competition, and by Crozier
400 et al. (2010) who documented that the average size of juvenile Chinook salmon was positively related to
401 water temperature at low population densities, but negatively related to temperature at high
402 population densities.

403 Could the observed patterns be used to predict the future abundance and size distribution in reaches
404 across the watershed? In absence of a proportional increase in food availability, fewer individuals can be
405 supported by the environment because of elevated metabolic demands. This would likely be manifested
406 in increased emigration- and mortality rates, depressed growth opportunities for individuals, and an
407 altered size distribution (Nakano 1995; Keeley 2001; Einum et al. 2011; Hartson and Kennedy 2015;
408 Myrvold and Kennedy 2015a). Because study reach characteristics (stream order, physical habitat and
409 biotic communities) were relatively similar across the temperature range (Myrvold and Kennedy 2015a,
410 d), we expect that the abundance and size distribution in the currently cool sites will approach those of
411 the currently warmer sites, i.e. a flatter and wider size distribution that is slightly negatively skewed. The
412 effects on currently warmer sites are more difficult to elucidate beyond that of energetics, because the
413 predicted temperatures lie beyond the parameter space we have yet observed. In addition to direct

414 energetic effects, future conditions in these sites could see altered community structure, habitat
415 configuration, and water quality, with potentially important consequences for rearing steelhead (Hicks
416 et al. 1991; Tinus and Reeves 2001; Waples et al. 2009; Reed et al. 2011; Benjamin et al. 2013).
417 Important to note is that the density of subyearlings may ultimately depend on the distribution and
418 abundance of adult spawners (Einum et al. 2011) so that higher initial densities occur closer to spawning
419 grounds.

420 Could the greater energetic demands be compensated by increased food availability, e.g. through
421 increased production of aquatic invertebrates? From a strictly caloric perspective, increased
422 consumption could compensate for higher temperature-induced metabolic costs, everything else being
423 equal. However, the relationship between consumption and food availability is more complex, and
424 depend on concurrent shifts in the physical environment and the biota (Boughton et al. 2007; McCarthy
425 et al. 2009; Benjamin et al. 2013). For example, streamflows are predicted to decrease due to climate
426 change in the Inland Northwest (Mote et al. 2003; Mote and Salathe 2010). On one hand, this might
427 increase the ability of the fish to detect drifting prey (Hughes and Dill 1990), but on the other hand,
428 fewer prey items might enter the drift in response to lower flows (Harvey et al. 2006). Taxonomic shifts
429 in the invertebrate community might further influence the amount and type of prey in the drift. In other
430 words, predicting changes to the food resources in the face of climatic change and, in turn, how this will
431 affect consumption rates is largely tentative.

432 Plastic and adaptive changes, as well as behavioral adjustments, can also buffer the population size
433 against climate change (Crozier and Hutchings 2014). Due to their wide distribution, *O. mykiss* exhibits
434 considerable diversity and plasticity in life-history expression and habitat use, which permit the species
435 to persist across a wide range of environments (Sogard et al. 2012; Moore et al. 2014; Kendall et al.

436 2015). For example, the number of life-history types present in a given watershed reflects an adaptation
437 to the prevailing environmental regimes (Sogard et al. 2012; Kendall et al. 2015), and because these
438 expressions can be dynamic it ensures resilience at the population level (Moore et al. 2014). Given
439 examples from other systems (Benjamin et al. 2013; Moore et al. 2014) and the large adaptive potential
440 in *O. mykiss*, we expect both plastic and adaptive shifts in response to an altered selection pressure with
441 climate change in the Lapwai Creek watershed (Crozier and Hutchings 2014; Sloat and Reeves 2014;
442 Kendall et al. 2015).

443 In summary, our findings can help unravel how climate change can manifest in fish populations, and
444 more fundamentally, how abiotic factors can exacerbate demographic density dependence. Future
445 studies should consider concurrent changes to streamflow and productivity as these are often strongly
446 associated with temperature in running waters (Beer and Anderson 2013; Kovach et al. 2016). For
447 example, could increases in stream productivity compensate for increased metabolic demands and less
448 habitat? Climate change will likely lead to altered temperature regimes throughout the entire year. For
449 example, winter temperatures might increase and provide better growing conditions (Sogard et al.
450 2012) but increased levels of stress associated with ice movement and other hydraulic shifts might
451 offset these thermal advantages. An interesting avenue for future research is to quantify the energetic
452 consequences of changes to the flow and temperature regimes in different environmental settings
453 (Thompson and Beauchamp 2016). Finally, it would be interesting to quantify the variation in expression
454 of behavioural and physiological traits across the range of temperature regimes (Biro and Stamps 2010;
455 Reid et al. 2012; Adriaenssens and Johnsson 2013). This would provide important insights into the
456 operation of selective forces which could prove increasingly important under rapid environmental

457 change, particularly in populations which periodically experience stressful abiotic conditions (Rijnsdorp
458 et al. 2009; Crozier and Hutchings 2014).

459

460

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662 **Tables**

663

664 Table 1. Temperature (°C) predictions for the month of August under the A1B scenario (“balanced scenario”; IPCC 2000) for the study sites in the
 665 Lapwai Creek watershed, ID. The table shows, from left, the elevation (m) of the study site and August discharge (m³/s), the projected current
 666 and future temperatures (Isaak et al. 2010), field data measured at each study site and the difference from the predicted temperature, and the
 667 corrected predictions for 2040 and 2080 (right panel).

Site	Physical site characteristics		Projected mean August temperature (°C)			Field data 2010-2012 (°C)		Corrected mean August temperature (°C)			% increase from current	
	Elevation (m)	Discharge (m ³ s ⁻¹)	Current	2040	2080	Measure	Correction	Current	2040	2080	2040	2080
	LLL	280	0.37	18.27	20.12	21.45	18.41	0.14	18.41	20.26	21.59	10.0
LLU	324	0.25	18.63	20.49	21.83	18.14	-0.49	18.14	20.00	21.34	10.3	17.6
LSX	390	0.26	17.40	19.21	20.51	17.24	-0.16	17.24	19.05	20.35	10.5	18.0
MLX	357	0.13	18.70	20.57	21.91	19.15	0.45	19.15	21.02	22.36	9.80	16.8

ULL	449	0.053	17.47	19.29	20.59	17.02	-0.45	17.02	18.84	20.14	10.7	18.3
ULM	585	0.054	17.33	19.14	20.44	17.62	0.29	17.62	19.43	20.73	10.3	17.7
ULU	693	0.058	17.03	18.82	20.12	16.62	-0.41	16.62	18.41	19.71	10.8	18.6
UML	411	0.067	17.92	19.75	21.08	19.29	1.37	19.29	21.12	22.45	9.50	16.4
UMM	472	0.053	17.71	19.54	20.85	18.55	0.84	18.55	20.38	21.69	9.90	16.9
UMU	629	0.034	16.73	18.51	19.80	16.57	-0.16	16.57	18.35	19.64	10.7	18.5
USL	448	0.18	16.73	18.52	19.81	16.52	-0.21	16.52	18.31	19.60	10.8	18.6
USM	531	0.13	15.77	17.52	18.78	15.62	-0.15	15.62	17.37	18.63	11.2	19.3
USU	575	0.14	15.07	16.79	18.03	15.11	0.04	15.11	16.83	18.07	11.4	19.6
UWL	438	0.10	17.63	19.45	20.77	17.38	-0.25	17.38	19.20	20.52	10.5	18.1
UWM	490	0.10	17.54	19.36	20.67	16.84	-0.70	16.84	18.66	19.97	10.8	18.6

UWU	525	0.11	16.83	18.62	19.91	16.27	-0.56	16.27	18.06	19.35	11.0	18.9
Average	475	0.13	17.30	19.11	20.41	17.31	-0.026	17.27	19.08	20.38	10.5	18.1
St.dev.	112	0.09	0.92	0.96	0.99	1.16	0.51	1.13	1.16	1.18		

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669 Table 2

670 Table 2. Candidate models to explain variation in skewness in size distributions of subyearling steelhead. Also shown is the empty model. *Density*
671 refers to the estimated number of subyearlings at a sampling visit (no. per m²); *biomass* refers to the biomass of subyearlings encountered at a
672 sampling visit (g/m²); *temperature* refers to the average monthly temperature (°C) in a study site, and *avg. mass* refers to the average
673 subyearling mass (g) during the sampling visit. Shown in parentheses behind each variable is the direction of its influence on the skewness of the
674 distribution. Bolded *AICc* values indicate the best approximating models.

Model	Predictor variable(s)	Random term	K	AICc	Random effects P(Z)	
					Intercept	Residual
0	No predictors (empty model)	intercept	3	88.5	0.045	<0.0001
1	Density (+)	intercept	4	89.0	0.057	<0.0001
2	Biomass (+)	intercept	4	86.5	0.066	<0.0001
3	Temperature (-)	intercept	4	89.8	0.039	<0.0001
4	Avg. mass (+)	intercept	4	89.8	0.042	<0.0001
5	Density (+), Temperature (-)	intercept	5	89.7	0.043	<0.0001
6	Biomass (+), Temperature (-)	intercept	5	88.2	0.057	<0.0001

7	Avg. mass (+), Temperature (-)	intercept	5	91.7	0.039	<0.0001
8	Density (+), Avg. mass (+), Temperature (-)	intercept	6	90.8	0.052	<0.0001
9	Biomass (+), Avg. mass (+), Temperature (-)	intercept	6	90.5	0.061	<0.0001

675

676 Table 3

677 Table 3. Estimated energetic demand for maintenance metabolism ($J \cdot g^{-1} \cdot d^{-1}$) for different sizes of juvenile steelhead in the study sites under the
 678 current temperature regime (2011) and future temperature regime (2040 and 2080) for the month of August. The columns to the right refer to
 679 the change in energetic demands for a 10g steelhead from the current situation to the future regimes.

Site	2.5g			5g			10g			20g			40g			80g			% chg.	
	'11	'40	'80	'11	'40	'80	'11	'40	'80	'11	'40	'80	'11	'40	'80	'11	'40	'80	'40	'80
LLL	289	316	327	249	271	281	214	234	242	184	201	208	159	173	179	136	149	154	9	13
LLU	285	312	326	245	269	280	211	231	241	182	199	208	156	171	179	134	147	154	10	14
LSX	270	299	317	232	257	272	200	221	234	172	191	202	148	164	173	127	141	149	11	17
MLX	301	323	329	259	278	283	223	239	243	192	206	209	165	177	180	142	152	155	7	9
ULL	266	296	314	229	255	270	197	219	233	170	189	200	146	162	172	126	140	148	11	18
ULM	276	305	321	238	262	276	205	225	237	176	194	204	152	167	176	130	144	151	10	16
ULU	260	289	309	223	249	265	192	214	228	165	184	197	142	159	169	123	136	145	11	19
UML	303	324	329	260	279	283	224	240	243	193	207	209	166	178	180	143	153	155	7	9
UMM	292	317	328	251	273	282	216	235	243	186	202	209	160	174	179	138	150	154	9	12

UMU	259	288	308	223	248	265	192	213	228	165	184	196	142	158	169	122	136	145	11	19
USL	258	288	307	222	248	264	191	213	227	164	183	196	141	158	168	122	136	145	11	19
USM	243	272	293	209	234	252	180	202	217	155	173	187	133	149	161	114	128	138	12	21
USU	234	263	284	201	226	244	173	195	210	149	168	181	128	144	156	110	124	134	12	21
UWL	272	301	318	234	259	274	202	223	236	173	192	203	149	165	175	129	142	150	11	17
UWM	263	293	312	227	252	268	195	217	231	168	187	199	144	161	171	124	138	147	11	18
UWU	254	284	304	218	244	261	188	210	225	162	181	193	139	156	166	120	134	143	12	20
Avg.	270	298	314	233	257	270	200	221	232	172	190	200	148	163	172	128	141	148	10	16
% chg.		10	16		10	16		10	16		10	16		10	16		10	16		

680

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682 Table 4

683 Table 4. Calculated maintenance ration (i.e. standard metabolism only) for the actual size distribution of juvenile steelhead in the coolest (USU),
 684 average (ULL), and warmest (UML) study site for the month of August under the current and future temperature regimes. The ration is given as
 685 total prey biomass over the month based on a prey energy density of 4324 J/g prey (Myrvold and Kennedy 2015b).

Site	Age class	Abundance	Biomass current (g)	Ration (g prey in August)					Temperature rank
				Current	2040	2080	% increase to 2040	% increase to 2080	
USU	Total	61	1092	1026	1153	1244	12.4	21.2	Coolest
	Subyearling	39	118	189	213	229	12.4	21.3	
	Yearling	22	975	837	941	1014	12.4	21.2	
ULL	Total	59	352	552	613	651	11.1	17.9	Average
	Subyearling	59	352	552	613	651	11.1	17.9	
	Yearling	0	0	-	-	-	-	-	
UML	Total	55	659	915	980	993	7.1	8.5	Warmest
	Subyearling	47	256	465	497	504	7.1	8.5	

	Yearling	8	403	451	483	489	7.1	8.6
<i>All sites</i>		175	2103	2493	2747	2888	10.2	15.8

686

687

688 Table 5

689 Table 5. Summary statistics for the subyearling size distributions for the month of August. CV refers to
 690 the coefficient of variation.

Site	Area (m ²)	Abund ance	Avg. mass (g)	Media n mass (g)	SD mass (g)	CV	Biomass s (g/m ²)	Skewne ss	Kurtosi s	Rang e
LLL	747	20	16.7	15.1	7.5	44.6	0.55	0.29	-1.25	23.1
LLU	677	53	12.2	11.1	3.8	30.8	1.1	0.89	1.06	18.3
MLX	624	31	9.6	9.1	2.8	29.5	0.49	1.27	2.49	13.6
ULL	482	59	7.9	7.7	2.8	35.7	0.78	0.79	0.98	13.2
ULM	439	101	4.3	4.2	1.3	30.2	1.1	0.99	1.65	8.1
ULU	551	146	4.5	4.3	1.5	33.6	1.2	0.28	-0.35	7.5
UML	478	47	7.8	8.1	3.8	48.9	0.34	0.99	1.30	14.9
UMM	438	106	5.4	5.0	1.9	36.1	1.4	1.20	2.74	11.2
UMU	363	29	3.8	3.8	0.8	21.0	0.33	0.20	-0.27	3.1
USL	311	18	10.8	10.9	3.0	27.5	0.73	-0.24	-0.41	10.3
USM	390	13	8.2	8.4	2.0	24.2	0.32	0.00	-1.19	6.3
USU	395	39	4.5	4.3	1.4	31.9	0.74	0.46	0.30	6.8
UWL	286	10	2.2	2.2	0.3	13.7	0.16	-0.32	0.20	1.0
UWM	370	80	4.3	4.0	1.3	31.5	0.96	0.84	0.01	5.9
UWU	353	63	3.2	2.9	1.1	33.5	0.63	0.74	0.02	4.9

691

692 Table 6

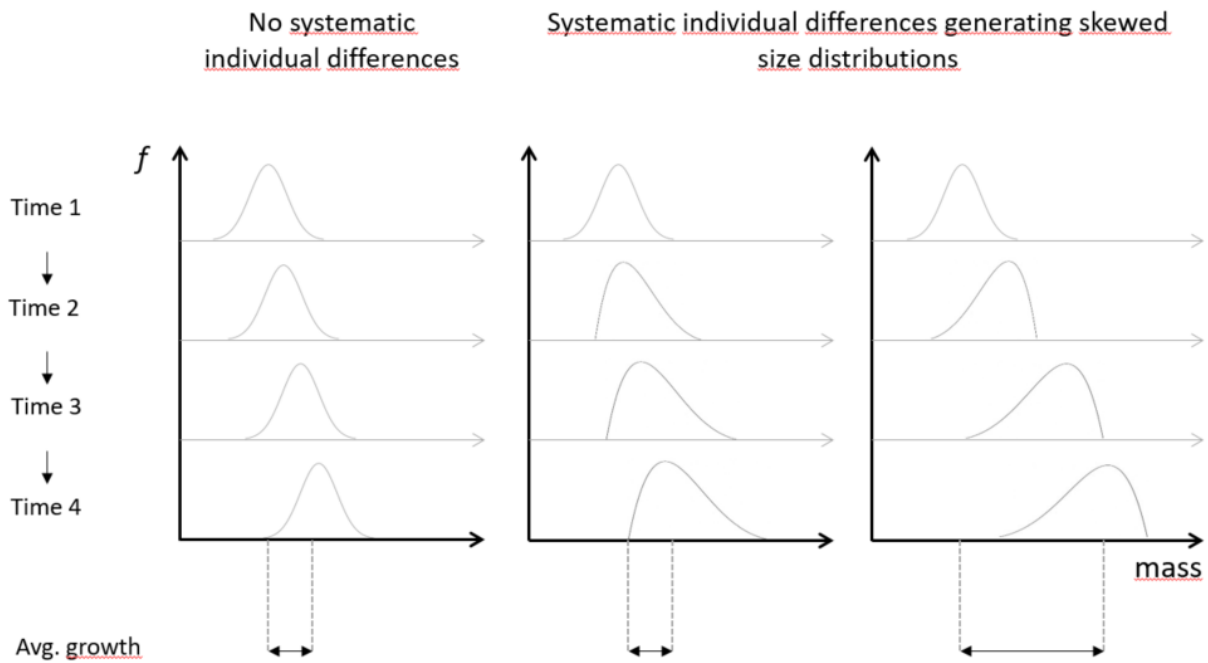
693 Table 6. Parameter estimates for the variance components model and the best approximating models
 694 for skewness in the size distribution of subyearling steelhead. Standard errors are given in parentheses.
 695 ρ (unconditional) refers to the proportion of variance attributable to the two levels (site and visit), and
 696 ρ (unconditional) refers to the proportion of the variance explained by the covariates in the model.

Model and variables	Parameter estimate (SE)	ρ (unconditional)	ρ (conditional)
Variance components (0)			
Intercept γ_{00}	0.617 (0.092)		
Random intercept (site) τ_{00}	0.0786 (0.046)	30%	
Residual (visit) σ^2	0.183 (0.039)	70%	
Best model (2, $w=0.38$)			10.3%
Intercept γ_{00}	0.408 (0.13)		
Biomass γ_{10}	0.316 (0.15)		
Random intercept τ_{00}	0.0563 (0.037)		28.4%
Residual σ^2	0.179 (0.038)		2.6%
Second best model (6, $w=0.16$)			10.1%
Intercept γ_{00}	0.706 (0.356)		

Biomass γ_{10}	0.306 (0.153)	
Temperature γ_{20}	-0.0197 (0.022)	
Random intercept τ_{00}	0.0628 (0.0398)	20.0%
Residual σ^2	0.173 (0.0366)	5.8%

697

698

699 **Figures**700 **Figure 1**

What is causing the variation in current size distribution skewness? Can this be used to inform future size distributions in a changing climate?

701

702

703 Figure 1. Conceptual figure showing the size distributions of juvenile steelhead in a single cohort at four

704 time points. The left panel shows a situation with no systematic individual differences, whereas the

705 middle and right panels show systematic individual differences, which generate skewed size

706 distributions. While the pattern depicted in the left panel may represent random variation in individual

707 growth rates over time, the middle panel shows a situation with asymmetric competition. Here, a few

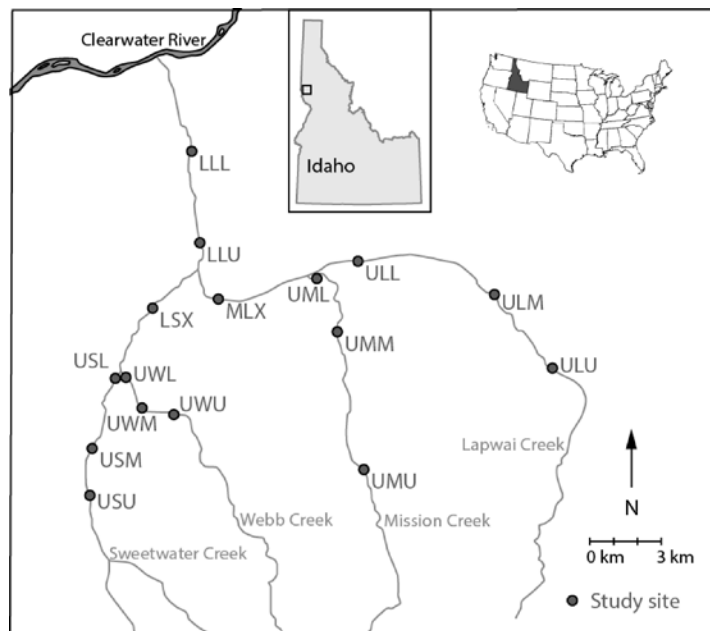
708 individuals capture most of the resources and grow amply, whereas the average individuals in the

709 cohort grow less. In the right panel there is less competition for the available resources, and most
710 individuals can grow fast. Here, the direct constraints of the environment may pose an upper limit to the
711 size of the largest individuals. This study aimed at identifying the factors that generate skewed size
712 distributions in present day in order to predict the potential shifts associated with climate change.

713

714

715 Figure 2



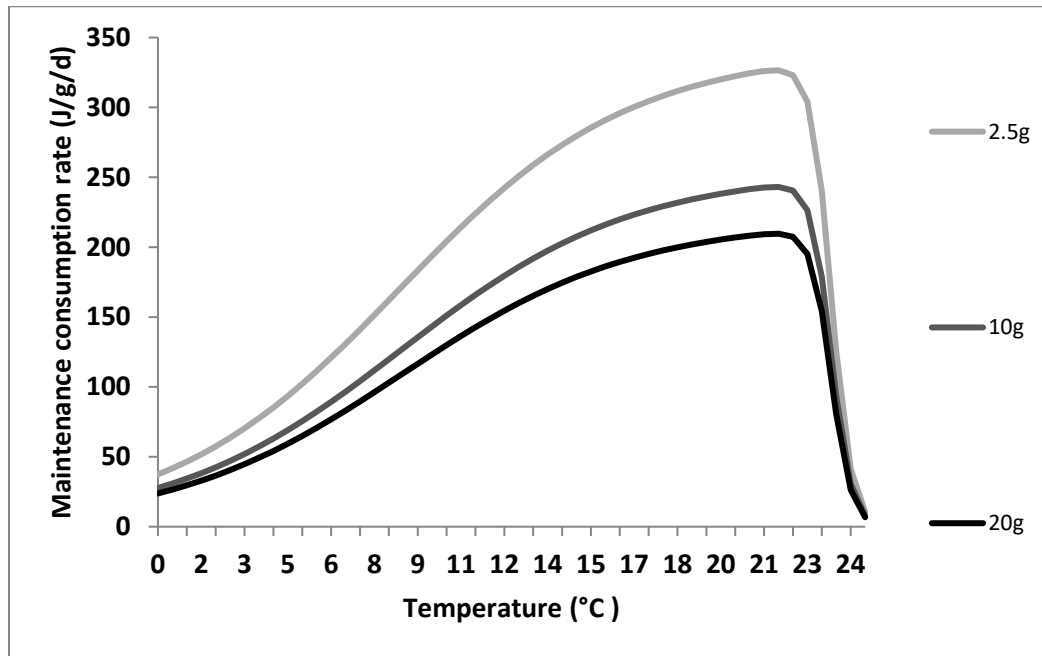
716

717 Figure 2. Map of the study watershed (center at $46^{\circ}17'N$, $116^{\circ}44'W$) and its location in Idaho, United
 718 States (inset). Modified from map data provided by DigitalGlobe, Inc., Westminster, Colorado, USA.

719

720

721 Figure 3

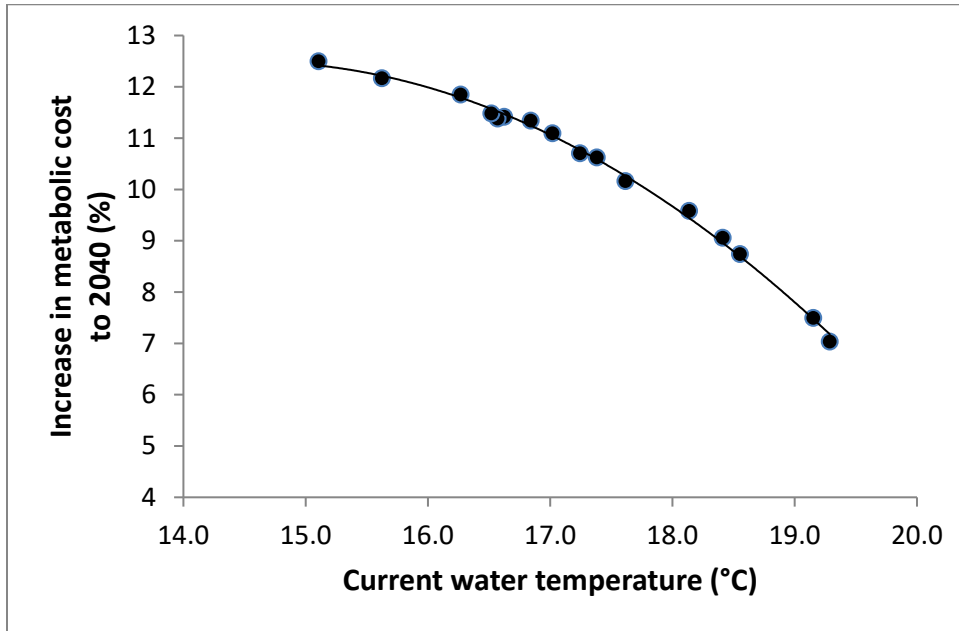


722

723 Figure 3. Daily mass-specific consumption rates ($J \cdot g^{-1} \cdot d^{-1}$) necessary to maintain standard metabolism as
724 a function of temperature for three sizes of juvenile steelhead.

725

726 Figure 4



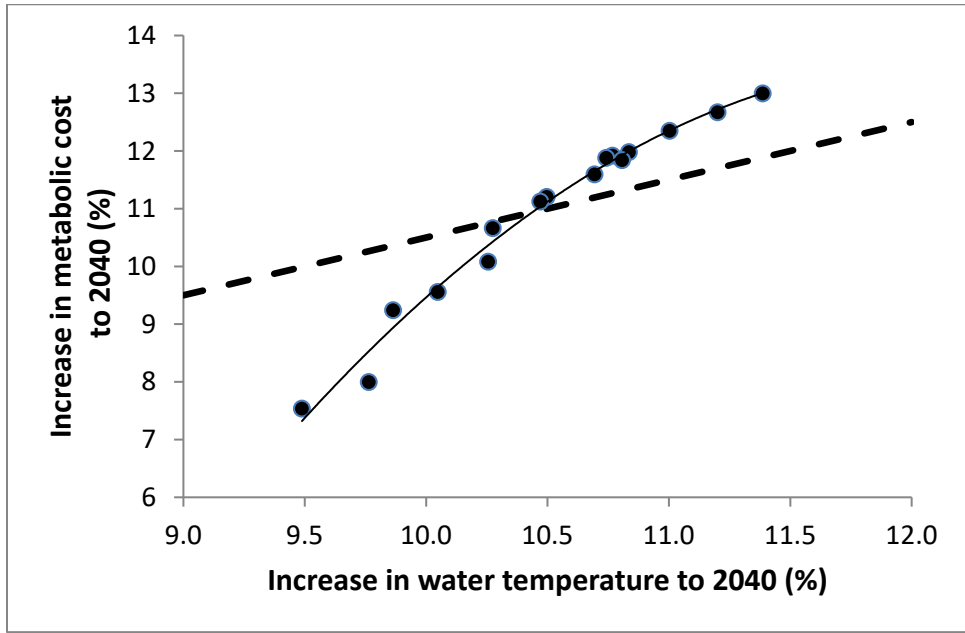
727

728 Figure 4. Predicted increase in maintenance metabolic cost (%) to the 2040s as a function of current
 729 temperature (°C) for a 10g juvenile steelhead in the 16 study sites in the Lapwai Creek watershed. The
 730 equation for the second-order polynomial regression is $y = -0.236x^2 + 6.87x - 37.5$.

731

732

733 Figure 5



734

735 Figure 5. Relationship between the predicted increase in temperatures (%) to 2040 in each of the 16
736 study sites and the associated predicted increase in energetic cost (%) for a 10g juvenile steelhead.

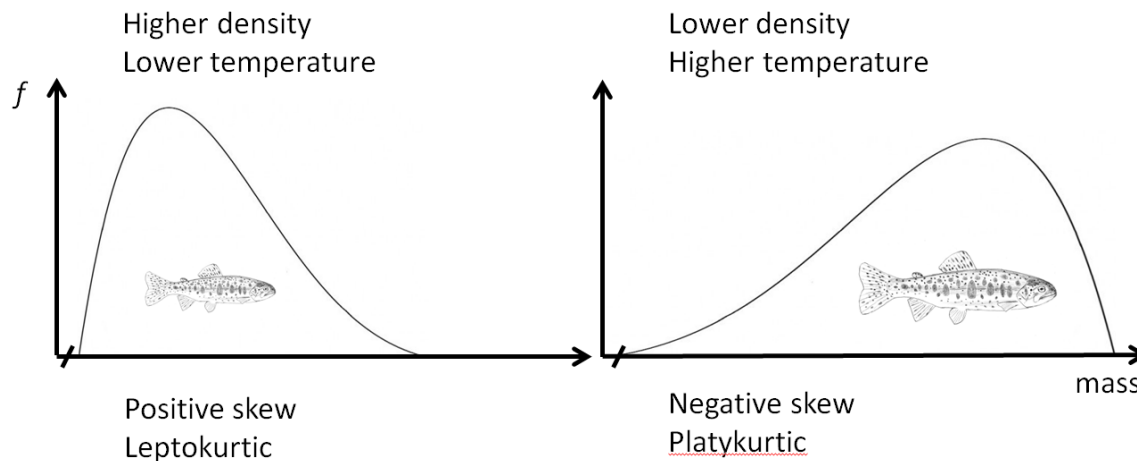
737 Dashed line indicates 1:1. Differential increases owe to the nonlinear relationship between maintenance
738 consumption rate and temperature in the 15.0°C to 19.5°C region, which is why a certain increase in
739 water temperature does not yield a similar increase in energetic cost. The equation for the second-order
740 polynomial is $y = -0.86X^2 + 21.1x - 115$.

741

742

743 Figure 6

744



745

746 Figure 6. Conceptual figure showing size distributions of subyearling steelhead. Sites with high densities

747 and low temperatures were positively skewed (left), whereas sites with low abundances and high

748 temperatures were negatively skewed (right). With a warming trend due to climate change, we

749 hypothesize that currently positively skewed populations will approach a negatively skewed size

750 distribution.

751