Global Ecology and Conservation 10 (2017) 93–102

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Life history, population viability, and the potential for local adaptation in isolated trout populations

K.J. Carim [a,b,*], Y. Vindenes [c], L.A. Eby [a], C. Barfoot [d], L.A. Vøllestad [c]

[a] Wildlife Biology Program, University of Montana, 32 Campus Drive, Missoula, MT, 59812, USA
[b] National Genomics Center for Wildlife and Fish Conservation, 800 E. Beckwith Ave, Missoula, MT, 59801, USA
[c] Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, NO-0316, Oslo, Norway
[d] Confederated Salish and Kootenai Tribes, P.O. Box 278, Pablo, MT, 59855, USA

HIGHLIGHTS

- Population growth rates across populations were positively related to stream flow.
- There was no relationship between population growth rates and genetic diversity.
- Lambda was most sensitive to probability of maturity, adult survival, somatic growth.
- Results suggest local adaptation may lead to increase probability of persistence.
- Results suggest genetic rescue in isolated populations should be applied with caution.

ARTICLE INFO

Article history:
Received 1 November 2016
Received in revised form 30 January 2017
Accepted 4 February 2017

Keywords:
Integral projection models
Cutthroat trout (*Oncorhynchus clarkii*)
Genetic diversity
Life history tradeoffs

ABSTRACT

Habitat loss and fragmentation have caused population decline across taxa through impacts on life history diversity, dispersal patterns, and gene flow. Yet, intentional isolation of native fish populations is a frequently used management strategy to protect against negative interactions with invasive fish species. We evaluated the population viability and genetic diversity of 12 isolated populations of *Oncorhynchus clarkii lewisi* located on the Flathead Indian Reservation in Montana, USA. Length-structured integral projection models (IPMs) were used to project population growth rate (lambda) and its sensitivity to underlying vital rates and parameters. We examined relationships between lambda, genetic diversity, and habitat size and quality. Lambda ranged from 0.68 to 1.1 with 10 of 12 populations projected to be in decline. A sensitivity analysis of lambda with respect to projection matrix elements indicated that lambda was generally sensitive to changes in early life history stages (survival/growth), but patterns differed among populations. Another sensitivity analysis with respect to underlying model parameters showed highly consistent pattern across populations, with lambda being most sensitive to the slope of probability of maturity (estimated from published literature), generally followed by adult survival, and the slope of somatic growth rate (directly measured from each population). Lambda was not correlated with genetic diversity. For populations residing in small isolated streams ($\leq$5 km of occupied habitat), lambda significantly increased with base flow discharge ($r^2 = 0.50$, $p < 0.02$). Our results highlight the potential importance of local adaptation for persistence of small, isolated populations. Specifically we saw evidence for higher probability of maturity at smaller sizes in the smallest, coldest isolated systems, increasing probability of persistence for these populations. Climate change threatens to

* Corresponding author at: National Genomics Center for Wildlife and Fish Conservation, 800 E. Beckwith Ave, Missoula, MT, 59801, USA.
E-mail address: kellie.carim@gmail.com (K.J. Carim).

http://dx.doi.org/10.1016/j.gecco.2017.02.001

further fragment populations of aquatic organisms and reduce summertime base flows in much of western North America. Insights from studies such as ours will inform management strategies for long-term persistence of species facing these challenges.

1. Introduction

Across wildlife taxa, habitat loss and fragmentation alter the expression of diverse life history strategies, limit dispersal patterns, and disrupt gene flow, all of which can lead to population decline (Bolger et al., 2008; Morita et al., 2009; Haag et al., 2010; Pavlacky et al., 2012). Stream-dwelling organisms are particularly susceptible to fragmentation due to the dendritic nature of stream networks (Fagan, 2002). For many freshwater species, genetic, phenotypic, and life history diversity, as well as population viability rely on stream connectivity allowing for movement within and dispersal among subpopulations (Green, 2003; Watanabe et al., 2010). For example, populations of salmonids in fragmented habitats suffer from loss of migratory life histories, reduced genetic diversity, and are at increased risk of extirpation (Dunham et al., 1997; Morita et al., 2009; Whiteley et al., 2010; Whiteley et al., 2013).

Nonetheless, many populations of salmonids have persisted in isolation above natural barriers, such as waterfalls, since the last glacial period (Taylor et al., 2003; Wofford et al., 2005; Whiteley et al. 2010). The probability of persistence for isolated salmonid populations likely varies with habitat and demographic characteristics. Habitat size and quality have been identified as strong predictors of salmonid occurrence above natural and man-made barriers (Rieman and McIntyre, 1995; Hastings, 2005; Peterson et al., 2013; Tsuboi et al., 2013). Smaller populations may persist if they can adapt to the demographic pressures and limitations of an isolated environment (Morita and Yokota, 2002; Letcher et al., 2007; Morita and Fukuwaka, 2007; Morita et al., 2009). For example, several studies report that persistence of isolated salmonid populations may rely on faster somatic growth rates, and younger age of maturity (Letcher et al., 2007; Morita et al., 2009). Previous studies support these tradeoffs (Hutchings, 1993; Haugen, 2000) and demonstrate an underlying genetic component associated with the traits involved, including growth and adult body size (Nilsson, 1994; Letcher et al., 2011; Hu et al., 2013). These findings indicate that populations may persist under isolation if there is sufficient genetic diversity to adapt to future environmental and anthropogenic pressures. Yet, genetic diversity can be lost rapidly in isolated populations due to genetic drift and lack of gene flow, potentially leaving populations ill-equipped to adapt to environmental changes and at higher risk of inbreeding depression (Kovach et al., 2015).

In western regions of North America, some populations of *Oncorhynchus clarkii* (Cutthroat Trout) have persisted under isolation above natural barriers, but most have been isolated by anthropogenic disturbances such as road crossings, dams, and stream dewatering in lower reaches (e.g. Dunham et al., 1997; Cook et al., 2010). Reconnecting habitat for these populations comes with tradeoffs because isolation has protected Cutthroat Trout from negative impacts associated with the spread of non-native species. Warming stream temperatures and altered stream flows associated with climate change are predicted to further increase isolation of and reduce available habitat for many isolated inland trout populations (Williams et al., 2009; Wenger et al., 2011). Thus, in order to effectively manage these high-risk populations into the future, we must evaluate the ability of isolation strategies to maintain self-sustaining native populations (Fausch et al., 2009; Rahel, 2013).

We used demographic length-structured models (Easterling et al., 2000) to explore how long-term population growth rate (lambda), a measure of mean fitness and indicator of long-term persistence, is affected by (i) various habitat characteristics; (ii) underlying life history traits; and, (iii) genetic diversity. We studied anthropogenically isolated populations of *O. clarkii lewisi* (Westslope Cutthroat Trout, hereafter "cutthroat") from streams with varying sizes and quality of habitat. We first tested the hypothesis that populations residing in smaller, and/or lower quality habitats would have lower population growth rates. We then identified the vital rates with the largest influence on population growth rates and compared these across all populations. Finally, we examined associations between genetic diversity and abundance and lambda across all populations.

2. Materials and methods

2.1. Study area

This study was conducted on cutthroat populations in first and second order streams in the Lower Flathead River watershed, located on the Flathead Indian Reservation of western Montana (Fig. 1). The Flathead River watershed drains approximately 22,780 km^2 of land, encompassing headwater portions of the Columbia River Basin. The basin is primarily fed by snowmelt runoff, with highest annual flows during spring and then declining to base levels by early August. Streams in the basin flow through a range of habitat types, from high gradient, mountain environments to arid grasslands. Human impacts on streams are common, and generally associated with timber harvest and agricultural and ranching practices (including stream dewatering and cattle grazing). To protect native cutthroat from invasive *Salvelinus fontinalis* (Brook Trout) and *O. mykiss* (Rainbow Trout), managers have chosen to maintain and construct barriers to fish passage on numerous streams throughout the basin. Nonnative Brook Trout are the only salmonid other than genetically pure cutthroat present above barriers in our dataset (see Carim et al., 2016), and were observed in two streams in this study (Revais and Centipede Creeks).

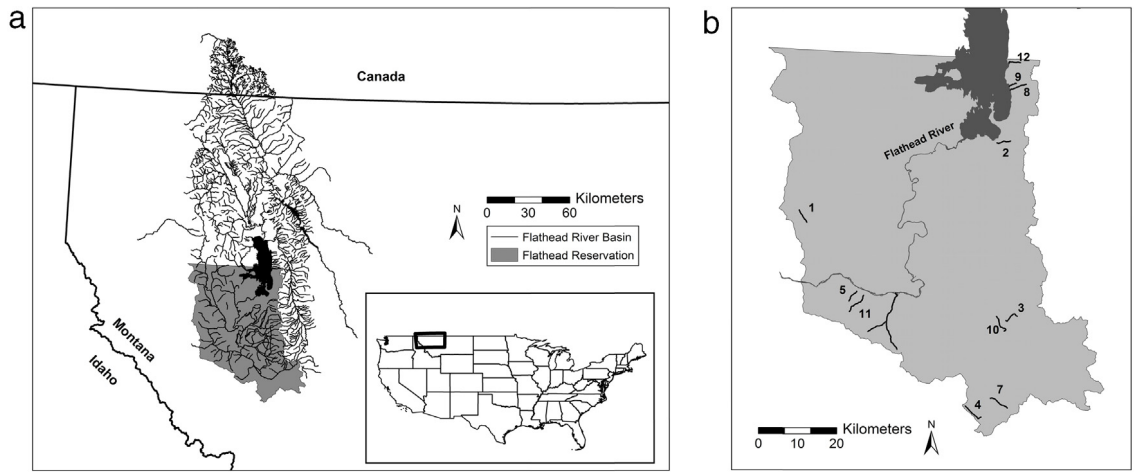

Fig. 1. Map of the study area. Numbers refer to Map ID in Table 1.

Table 1
Habitat characteristics and quality measurements for all 12 anthropogenically isolated populations in this study. Base flow location refers to the location where base flow measurement was taken, measured as kilometers upstream from the isolating barrier. Base flow location was not included as in linear regression analyses.

Map ID	Stream	Habitat length (km)	Base flow	Base flow location (km)	Road density	% leased	GDD
1	Camas	3.5	0.04	1.06	8.78	93.8	1134
2	Centipede	2.7	0.25	1.29	8.35	0	–
3	Cold	4.9	0.62	0.96	0.35	50.7	785
4	Frog	3.7	0.06	2.09	5.54	93.6	912
5	Magpie spring	2.9	0.15	0.39	4.49	83.7	780
6	Revais	14	2.52	3.5	2.35	92.8	970
7	Schley	1.7	0.40	0.57	0.86	91.8	689
8	Talking water	0.6	0.30	0.01	1.01	0	735
9	Teepee	0.4	0.27	0.01	1.26	0	838
10	Thorne	3.5	0.09	1.16	8.24	91.3	919
11	West magpie	4.6	0.14	2.7	4.09	77.3	828
12	Yellow bay	1.4	1.08	0.73	3.89	0	630

2.2. Data collection

We examined 12 cutthroat populations that have been isolated for 12–28 generations (assuming four years per generation) by perched culverts at road crossings or irrigation canals. Barrier assessment, length of occupied habitat above barriers, and date of isolation for each population was previously assessed by Carim et al. (2016).

We estimated cutthroat population density and size using mark-recapture or depletion methods between 2010 and 2013 (Appendix A). Typically we sampled two sites per stream with one located in the upper and one in lower half of the occupied habitat. In three streams (Teepee, Talking Water and Yellow Bay) density estimates were only performed at one site due to short lengths of occupied habitat ($\leq$1.4 km). To calculate population size, we averaged all density estimates and multiplied the average fish density by the total length of occupied habitat in a given stream.

2.3. Habitat measurements

To assess relative habitat quality across streams, we collected information on water temperature, summer base flows, road density, and land use in the watershed upstream of the isolating barrier. We used temperature loggers (HOBO and Tidbit V2 models, Onset Computer Corporation, Pocasset, Massachusetts, $\pm$0.2 °C of accuracy) to record temperature at one-hour intervals from July 1st through September 8th, 2013 (70 days). Temperature was recorded at one location per stream targeting the middle of the known cutthroat trout distribution. We calculated the number of growing degree days (GDD) above 0 °C for the 70 day period in each stream. Base flows were measured as cubic meters per second during 6–8 August, 2013 in the lower half of the cutthroat distribution (Table 1) in each stream using handheld Acoustic Doppler Velocimeters (FlowTracker). We measured road density as total kilometers of road over total watershed area above the barrier for a given stream in Arc GIS using data layers generated by the Confederated Salish and Kootenai Tribes (unpublished data). Similarly, we summarized land use as the total number of square kilometers leased for grazing or agriculture upstream of the barrier, and then used this number to calculate percentage of the watershed leased for these human activities.

Table 2
Vital rate information and sources used in integral population models. In all populations, a majority of fish at age-3 were ≤110 mm in total length (L). Therefore we applied adult survival rates to all fish ≥110 mm in length.

Parameter	Estimate or equation	Notes	Source
Egg to age-0 survival	0.4		Peterson et al. (2004)
Age-0 to age-1	0.318; 0.0247	Survival decreases to 0.0247 in the presence of brook trout	Peterson et al. (2004)
Juvenile survival (<age 2)	0.394	Average of age-1 and age-2 survival estimates	Peterson et al. (2004)
Adult survival	Directly measured from each population	Robson–Chapman method	This study
Length distribution of age-1 fish	Directly measured from each population	Lengths of age-1 fish back-calculated from otoliths	This study
Somatic growth	Directly measured from each population	Estimated from otoliths	This study
Fecundity	$4.4 * \text{Length} - 494.4$		Downs et al. (1997)
Probability of maturity	$\frac{e^{(-20.28+0.13*L)}}{1+e^{(-20.28+0.13*L)}}$		Downs et al. (1997)
Sex ratio (F:M)	1:2.3		Downs et al. (1997)

2.4. Somatic growth and survival estimates

We collected sagittal otoliths from 6 to 26 individuals in each population, taking care not to remove more fish from these populations than necessary (Appendix A). After otoliths were clarified, we aged each fish and back-calculated length-at-age following methods of Corsi et al. (2013). We used back-calculated total length-at-age for all individuals in a population to calculate somatic growth rate as the annual growth increment (length at year t + 1) given current body length (length at t; Appendix A). For each population, we developed age-length keys from otolith length-at-age information and applied these to the size-frequency catch data to create an age-frequency distribution for each population, and then used the Robson–Chapman method to estimate adult survival (Appendices A and B; Chapman and Robson 1960).

2.5. Constructing the integral projection models

We constructed and analyzed integral projection models (IPMs; Easterling et al., 2000) to determine population growth rates of cutthroat in isolated streams. Few studies have applied these models to salmonid populations (but see Bassar et al., 2016). IPMs are the continuous-state analogue to matrix models, and retain all their analytical advantages (Ellner and Rees, 2006) The models were length-structured, female-based and density independent, with a pre-breeding census, adapted from Vindenes et al. (2014). A model was built for each population using all available site-specific demographic information (see Table 2). The long-term population growth rate lambda was calculated as the dominant eigenvalue of the discretized projection kernel constructed from the vital rates, using standard matrix model methods (Caswell, 2001).

2.6. Genetic samples and analysis

All genetic data in this study was obtained from Carim et al. (2016). Briefly, to obtain a representative sample of each population's genetic diversity, tissue samples were collected between late June and early September of 2009–2012 from all density estimate sites, as well as the additional intermediate sampling sites discussed above. All tissue samples were collected from late June through early September of 2009–2012 and stored in 95% ethanol until DNA extraction occurred. We collected and analyzed from 36 to 54 samples across 14 polymorphic microsatellite loci. Genetic diversity was quantified using FSTAT (Goudet, 1995) to calculate allelic richness scaled to the population with the smallest sample size using rarefaction, which was 36 in this study.

2.7. Data and model analyses

To determine the influence of habitat length and quality on population growth rates, we performed individual linear regressions of lambda on length of occupied habitat, GDD, road density, percent of the drainage area leased for grazing and agriculture, and base flow.

To determine the influence of the underlying model parameters (intercepts and slopes of each vital rate function) on the population growth rate, we performed a sensitivity analyses by quantifying the change in population growth rate after perturbing the parameter values one at a time by adding roughly 5% to baseline values. The three parameters with the highest sensitivity values were ranked and compared across all populations. We also calculated the sensitivity and elasticity of population growth rate with respect to projection matrix elements, based on the stable structure and reproductive values (Caswell et al. 2011). Since each projection matrix element is generally determined by multiple vital rates, this analysis reveals the combined impact on lambda from the vital rates in each matrix element. After calculating the sensitivity matrix and the corresponding elasticity matrix for each population, we summarized the elasticities across body length (i.e. the columns in the elasticity matrix) for easier comparison of the contributions of different lengths to the elasticity of lambda.

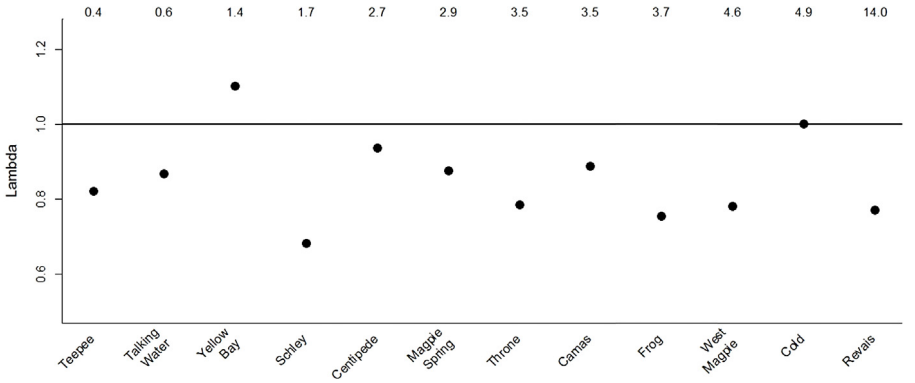

Fig. 2. Estimates of population growth rate (lambda) for each population, ordered by length of habitat. Numbers along the top of the figure show length of occupied habitat in km. Horizontal line 1 indicates stable populations, below which populations are in decline.

Within each model, these elasticities sum up to 1 (Caswell, 2001), allowing for easy comparison of elasticities values between models.

We used linear regression to examine the relationship between genetic diversity and both lambda and population abundance.

All analyses were conducted in program R (R Core Team, 2012). For these analyses we used several R packages specific to analysis of fisheries data including the "FSA" (Ogle, 2012) and "fishmethods" (Nelson, 2012).

3. Results

Across the 12 populations lambda ranged from 0.68 to 1.1, and varied independently from length of occupied habitat (Fig. 2). Temperature information was not successfully collected in Centipede Creek; therefore this population was not included in the linear regression analyses examining the influence of temperature on population growth rate. Regression analyses indicated that there was no relationship between lambda and length of occupied habitat ($r^2 = 0.05$, $p = 0.49$), GDD ($r^2 = 0.09$, $p = 0.37$), or road density ($r^2 = 0.00$, $p = 0.85$; Fig. 3). Lambda was significantly negatively related to percent of the drainage leased ($r^2 = 0.36$, $p = 0.04$; Fig. 3d). Base flow did not emerge as a significant predictor of population growth rate when analyzed using the full dataset ($r^2 = 0.01$, $p = 0.82$). However, the relationship between base flow and population growth rate became significant when Revais Creek (the only population over 5 km of habitat) was removed from the analysis ($r^2 = 0.50$, $p = 0.02$; Fig. 3e).

Across populations, analysis of underlying model parameters indicated that lambda was most sensitive to the slope of the probability of maturity equation. The sensitivity of this parameters was sometimes up to three times greater than the second ranked parameter (Fig. 4, Table A.3). The next two highest ranked parameters most often included the slope of the somatic growth equation (i.e., somatic growth rate) and adult survival. The only exception to this pattern was observed in Yellow Bay Creek where the parameter with the third highest sensitivity was egg to age-1 survival with a value of 1.60. Here, adult survival had the fourth highest sensitivity value at 1.59. Across all streams, trends in elasticities were similar to those observed in the sensitivity analysis (Table A.3).

The summed elasticities of lambda with respect to projection matrix elements showed that lambda was generally sensitive to vital rates in early life stages (growth and survival). However, the degree to which lambda was influenced by vital rates also of lengths corresponding to sub-adult and adults varied between populations, and in some cases these life stages were as influential as those in the juvenile life stage (Fig. 5).

Allelic richness was not associated with lambda ($r^2 = 0.17$, $p = 0.19$), or adult survival ($r^2 = 0.04$, $p = 0.53$), but was positively associated with estimated abundance ($r^2 = 0.46$, $p = 0.01$).

4. Discussion

This study highlights how IPMs can provide insights to demography and population viability in the absence of long-term monitoring data. We developed and analyzed IPMs to evaluate the viability of 12 cutthroat trout populations and used those data to better understand factors affecting persistence of these isolated populations. To construct these models, we combined information directly measured from each population with published data on isolated of cutthroat trout also located in the upper Columbia River basin of southwestern Montana. Incorporating population specific vital rates into demographic models allowed us to better understand the limitations and interpret the outcomes of these data.

Overall, we found no association between length of occupied habitat and population viability for isolated cutthroat populations. In fact, estimates of lambda for the three smallest populations (Teepee, Talking Water, and Yellow Bay Creeks) were higher than for many other populations with more than twice as much habitat. Furthermore, we found no association

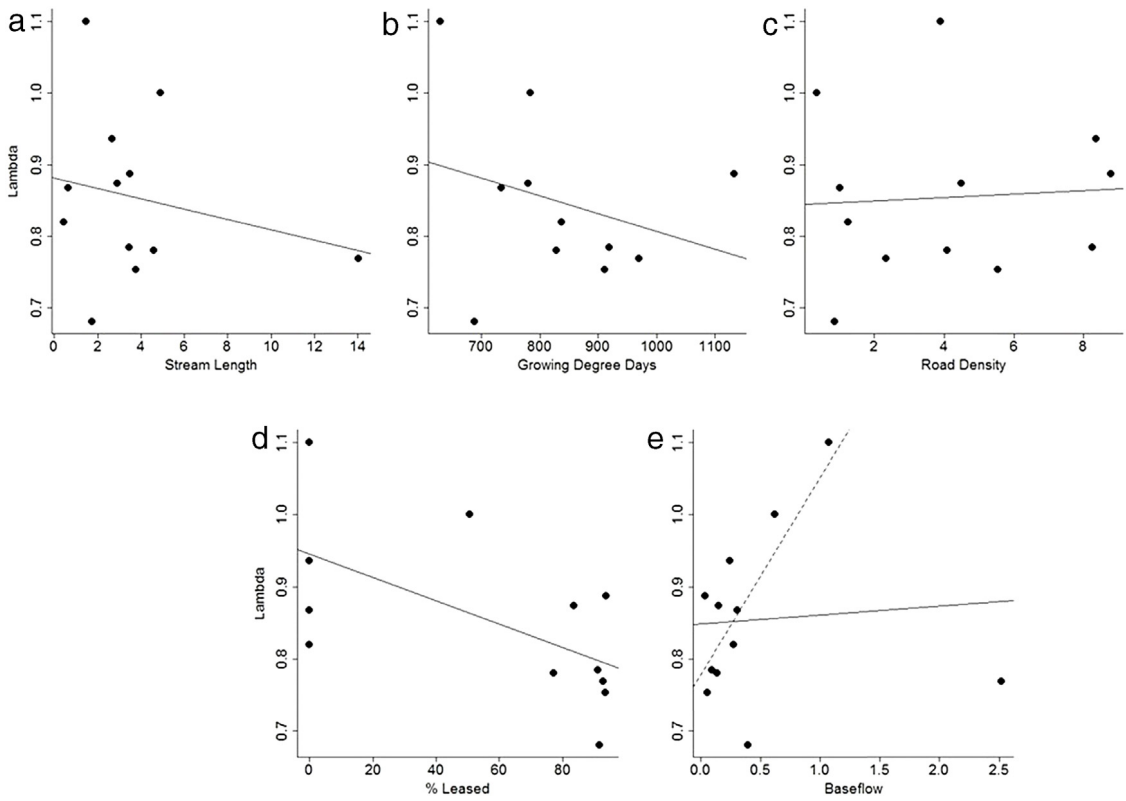

Fig. 3. Population growth rate (lambda) versus (a) length of occupied habitat, (b) stream temperature (as growing degree days), (c) road density (as km of road per km^2), (d) percent of the watershed leased for grazing or agricultural production, and (e) baseflow (as cubic meters per second). Centipede Creek is absent from (b) because temperature information was not collected in this stream. In (e), the dashed line represents the trend line when Revais Creek (14 km, 2.52 CMS), is removed from the dataset.

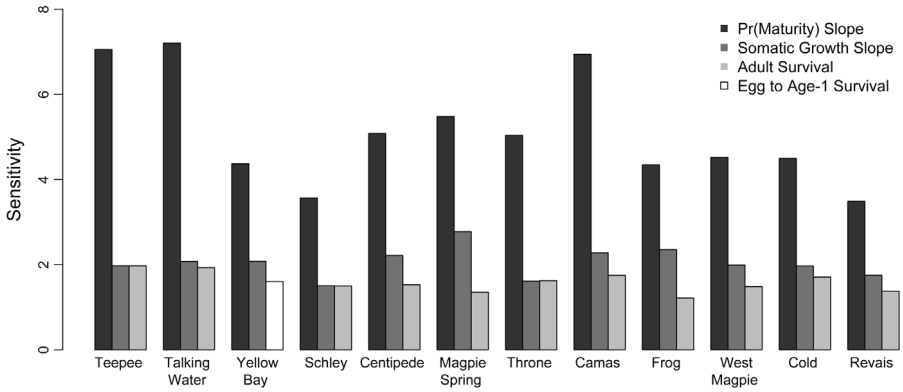

Fig. 4. Ranking of the top three demographic parameters with highest sensitivity values for each population. We have displayed the absolute value of sensitivity values to highlight their relative ranking. The sensitivity value for somatic growth rate is negative because the value of the parameter in the model is negative.

between genetic diversity and population growth rate, suggesting that even populations with the lowest levels of genetic diversity (e.g., Teepee and Talking Water Creeks) are not currently in decline due to inbreeding depression.

Our data suggest that shifts in life history may be necessary for persistence under isolation. For example, in the shortest streams, Teepee and Talking Water (<0.6 km occupied stream length), cutthroat initially grew rapidly with the highest somatic growth rates for fish under 97 mm, but somatic growth rates of larger fish rapidly declined and adults remained relatively small and had low survival rates (adult survival in Teepee and Talking Water Creeks was 0.256 and 0.280 respectively, whereas the median and range for all populations was 0.337 [range = 0.253–0.438]; see Table A.2). This is particularly surprising given that these streams are smaller, steeper, colder, and overall less productive than other study

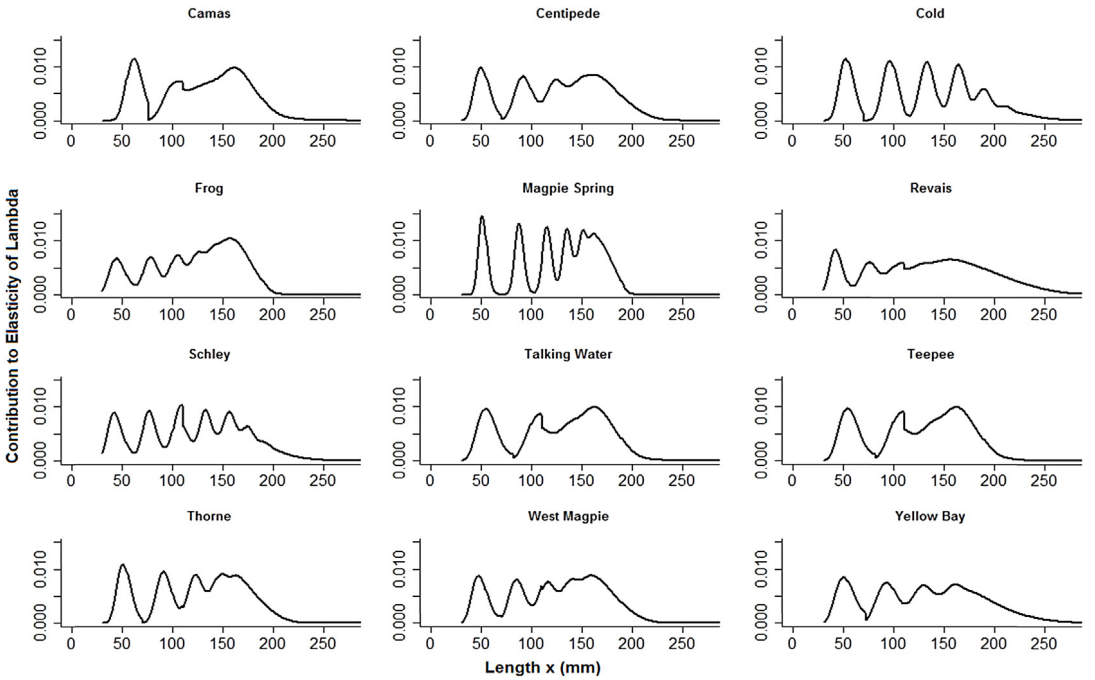

Fig. 5. Summed elasticities of matrix elements for each populations modeled in his study. These elasticity values combine all vital rate information for individuals of a given size to create a summed value for the contribution to elasticity of lambda. Individuals at a given length with a higher contribution have a larger influence on the estimated population growth rate.

streams. Under these conditions, we would expect somatic growth rates to be *lower* in Teepee and Talking Water Creeks relative to other populations. Instead, low adult survival in these streams may have created a selection advantage for individuals that mature early to maximize lifetime fitness. These data support previous work demonstrating that shifts in life history may be necessary for trout to persist under isolation. Letcher et al. (2007) found that persistence of isolated Brook Trout populations was associated with higher survival for smaller size classes and earlier age (and thus smaller size) of maturity compared to connected populations. As a result, populations persisting under isolation in their simulations tended to have a size structure skewed towards smaller individuals compared to connected systems.

Multiple studies spanning various salmonid species demonstrate strong influence of early life stages on population growth and persistence (Elliott, 1994; Peterson et al., 2008a; Bassar et al., 2016). Similarly, analyses of matrix elements for each population in our study demonstrate the impact of survival and growth of early life history stages on population growth rates and persistence (Fig. 5, Fig. A.2). However, the degree to which larger fish (in later life stages) influence lambda varied across populations. In contrast, the sensitivity analysis of lambda with respect to underlying model parameters was more consistent across populations, and lambda was most sensitive to the slope of the probability of maturity, generally followed by slope of somatic growth and adult survival. The adult survival parameter is constant in our model and affects individuals across a large size range, thus a large proportion of the individuals in the model. This explains why lambda was more sensitive to this parameter than to juvenile survival. Changing the slope of somatic growth has a large influence on population growth because a more rapid growth allows individuals to mature earlier, as well as to rapidly reach sizes of higher survival probability and increased fecundity. Changing the slope of the maturity function has an even larger effect on population growth in our models, because only a slight increase allows individuals to mature at smaller sizes and younger age. Being able to reproduce just one year earlier likely has a large impact on the reproductive success of individuals, and therefore on population growth. In more long-lived species where the expected number of reproductive events is high, lambda is not so sensitive to this parameter (e.g. northern pike, Vindenes et al., 2016).

Unlike estimates of somatic growth and adult survival, we obtained estimates of probability of maturity from a previous study on cutthroat in southwestern Montana streams (Downs et al., 1997). In that study, probability of maturity for females 140 mm in length is about 11%. Although we did not conduct quantitative maturity assessments in our study, notes from local sampling records during the 2007 and 2013 spawning seasons in Camas, Centipede, Magpie Spring, Schley, Yellow Bay, and West Magpie Creeks, indicate that gravid females under 140 mm may have been more common than we estimated, with two gravid females as small as 119 mm observed. These observations suggest that some populations in our study are likely maturing at smaller sizes than assumed in our models.

Underestimating the probability of maturity may account for some of our lower than expected predictions of lambda. Only two populations (Yellow Bay and Cold Creeks) were predicted to be stable or increasing. Yet, intermittent monitoring of all

12 cutthroat populations over the last several decades indicates they are not declining as rapidly as our models suggest. For example, with an estimated abundance of 1271 individuals and growth rate of 0.68, the population in Schley Creek would have declined to just 272 individuals over the course of this four-year study. If we increase probability of maturity for a 120 mm female from 1% to 5%, projections of lambda increase 11%–23% across all populations. Additionally, for many populations in this study, early maturation could shorten generation time, increasing life time reproductive output for fish, particularly in systems where adult survival is low. Thus, a shift towards increased maturity at smaller sizes may account for the ability of cutthroat populations in this study to persist under isolation for several decades.

Despite any shifts in life history that may increase viability of isolated populations, isolated salmonids (particularly those in small habitat fragments) will remain at greater risk compared to those in larger, connected habitats. Population occurrence has been positively correlated with habitat size and connectivity in *O. clarkii clarkii* (Coastal Cutthroat Trout), *O. masou* (Masu Salmon), *S. confluentus* (Bull Trout), *S. leucomaenis* (White-spotted Char), and *S. malma* (Doll Varden; Rieman and McIntyre, 1995; Morita et al., 2009; Tsuboi et al., 2013). Smaller habitat fragments provide less refugia from stochastic environmental events, and smaller populations may not be able to rebound from bottlenecks.

The population in Revais Creek had the third lowest projected lambda in this study, despite occupying the largest habitat ($<$14 km). Unlike other populations in our dataset, cutthroat in Revais co-occur with a rapidly increasing population of introduced Brook Trout. Throughout the Intermountain West, invasive Brook Trout have displaced native cutthroat, primarily through competition for resources in juvenile and sub-adult life stages (Dunham et al., 2002). Although the exact rate of population decline for Revais may change with informed adjustments to influential vital rates, population surveys over the last 30 years show sharp declines in cutthroat densities concurrent with increasing densities of Brook Trout in lower stream reaches, supporting our model results (Confederated Salish and Kootenai Tribes, unpublished data). In our viability model, the impacts of Brook Trout would manifest as lower somatic growth rates for cutthroat. Specifically, competition in lower reaches limits resources for cutthroat, while cooler stream temperatures will continue to limit somatic growth for cutthroat relegated to higher elevations. These circumstances in Revais Creek further highlight that isolated populations that are not protected from invasive species will likely require ongoing management efforts for persistence (Peterson et al., 2008b).

Several studies have documented decline and extirpations of cutthroat populations as a result of common dewatering and cattle grazing practices (Thurow et al., 1997; Peterson et al., 2010; Pierce et al., 2013). Similarly, we observed a significant negative association between population growth rate and percent of drainage area leased for agricultural practices. We also observed a significant positive association between population growth rate and base flow in streams with $<$5 km of occupied habitat. Stream flow may be a useful variable for understanding not only habitat size or volume, but also structural habitat components such as pool size. For example Harig and Fausch (2002) found that the number of large pools ($\geq$30 cm deep) at base flow was significantly associated with successful translocations of *O. clarkii virginalis* and *O. clarkii stomias* (Rio Grande and Greenback Cutthroat Trout respectively). The authors suggest that increased numbers of large pools provide overwintering habitat and refuge from high spring flows and summertime drought (Bisson et al., 1982; Behnke, 1992). Additionally, streams with lower base flows may have higher rates of sedimentation (particularly in the presence of grazing) which can reduce recruitment of young cutthroat by decreasing quality and quantity of spawning habitat and embryo survival (Magee et al., 1996). Thus, base flow levels may be a more comprehensive variable representing both the amount of available habitat, as well as generalized habitat quality. Due to climate change and human resource use, current summer base flows have decreased 20% in the upper Columbia River Basin compared to the average for the 1980s, and are projected to decline an additional 10% by 2080 (Wu et al., 2012). The significant associations we observed between population growth rates and both base flow and land use suggest that efforts to find more efficient and less impactful uses of natural resources will play a critical role in maintaining cutthroat populations into the future.

In our study larger cutthroat populations typically had higher levels of genetic diversity. This was not surprising, given that smaller populations are expected to lose genetic diversity through drift more quickly, and may be more likely to suffer from population bottlenecks when faced with stochastic environmental events. Low levels of allelic richness observed in these populations do not directly indicate local adaptation because we analyzed neutral markers. However, if our markers are linked to genes that code for traits such as somatic growth and size-based probability of maturity, it is possible that the low levels of allelic richness observed in these populations are a result of natural selection. More information on the genome-wide location of loci coding for these traits, as well as analyses of diversity at these loci will enhance our understanding of local adaption in these systems.

Similar to our results, Peacock and Dochterman (2012) found no relationship between genetic diversity at neutral makers and extinction risk in Lahontan Cutthroat Trout (*O. c. henshawi*). This contrasts with studies showing that loss of diversity and inbreeding are associated with lower survival and fitness and increased susceptibility to disease (Slate et al., 2000; Höglund et al., 2002; Isomursu et al., 2012; Ruiz-Lopez et al., 2012; Mattey et al., 2013), which can cause population decline (McCallum, 2008; Johnson et al., 2010). The patterns observed in cutthroat may simply mean that these populations have not yet been exposed to emerging selective pressures such that reductions in genetic diversity have led to large-scale population declines. For example, lower diversity may mean less material to adapt to expected environmental changes associated with climate change (Spielman et al., 2004; Meyer-Lucht et al., 2010; Kerstes and Wegner, 2011), and/or decrease the ability to resist disease (Spielman et al., 2004; Meyer-Lucht et al., 2010; Kerstes and Wegner, 2011).

While isolation may be a short-term solution for preventing interactions with many invasive aquatic species, we cannot effectively prevent interactions with organisms that are not limited by the same barriers to movement. As a result, isolated populations maintained for conservation purposes should be closely monitored for declines associated with inbreeding depression and outside factors. If genetic rescue becomes a necessary step, we caution managers to carefully consider which populations they use as donors to avoid outbreeding depression in populations that may have high levels of local adaptation.

Acknowledgments

We thank W. H. Lowe, M.K. Schwartz, D. Patterson, and C. Muhlfeld for feedback on drafts of this work, and F. Allendorf for comments on analysis and interpretation of genetic data. We thank the anonymous reviewers for comments and feedback which improved the manuscript. We also acknowledge our funding sources, including the WestSlope Chapter of Trout Unlimited, P.E.O. Scholars Award, the Confederated Salish and Kootenai Tribes, and Bonneville Power Administration grant # 1991-019-01 to the Confederated Salish and Kootenai Tribes, and National Science Foundation Graduate Research Fellowship Program DGE-0809127. We thank the fisheries and hydrology field crews with the Confederated Salish and Kootenai Tribes field crew for their hard work with data collection.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2017.02.001.

References

Bassar, R.D., Letcher, B.H., Nislow, K.H., Whiteley, A.R., 2016. Changes in seasonal climate outpace compensatory density-dependence in eastern brook trout. Glob. Change Biol. 22, 577–593.
Behnke, R.J., 1992. Native Trout of Western North America. The American Fisheries Society, Bethesda, Maryland.
Bisson, P.A., Nielsen, J.L., Palmason, R.A., Grove, L.E., 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. In: Acquisition and Utilization of Aquatic Habitat Inventory Information. American Fisheries Society, Western Division, Bethesda, Maryland, pp. 62–73.
Bolger, D.T., Newmark, W.D., Morrison, T.A., Doak, D.F., 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecol. Lett. 11, 63–77.
Carim, K.J., Eby, L.A., Barfoot, C.A., Boyer, M.C., 2016. Consistent loss of genetic diversity in isolated cutthroat trout populations independent of habitat size and quality. Conserv. Genet. 17, 1363–1376.
Caswell, H., 2001. Matrix Population Models. John Wiley & Sons, Ltd.
Caswell, H., Neubert, M.G., Hunter, C.M., 2011. Demography and dispersal: invasion speeds and sensitivity analysis in periodic and stochastic environments. Theoret. Ecol. 4, 407–421.
Chapman, D.G., Robson, D.S, 1960. The analysis of a catch curve. Biometrics 16, 354–368.
Cook, N., Rahel, F., Hubert, W.A., 2010. Persistence of Colorado River cutthroat trout populations in isolated headwater streams of Wyoming. Trans. Amer. Fish. Soc. 139, 1500–1510.
Corsi , M.P., Eby , L.A., Barfoot, C.A., 2013. Hybridization with rainbow trout alters life history traits of native westslope cutthroat trout. Canad. J. Fish. Aquat. Sci. 70, 895–904.
Downs, C.C., White, R.G., Shepard, B.B., 1997. Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of westslope cutthroat trout. North Amer. J. Fish. Manag. 17, 85–92.
Dunham, J.B., Adams, S.B., Schroeter, R.E., Novinger, D.C., 2002. Alien invasions in aquatic ecosystems: Towards an understanding of brook trout invasions and potential impacts on inland cutthroat trout in weastern North America. Rev. Fish Biol. Fish. 12, 373–391.
Dunham, J.B., Vinyard, G.L., Rieman, B.E., 1997. Habitat fragmentation and extinction risk of Lahontan Cutthroat Trout. North Amer. J. Fish. Manag. 17, 1126–1133.
Easterling, M.R., Ellner, S.P., Dixon, P.M., 2000. Size-specific sensitivity: Applying a new structured popualtion model. Ecology 81, 694–708.
Elliott, J.M., 1994. Quantitative Ecology and the Brown Trout. Oxford University Press.
Ellner, S.P., Rees, M., 2006. Integral projection models for species with complex demography. Amer. Nat. 167, 410–428.
Fagan, W.F., 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83, 3243–3249.
Fausch, K.D., Rieman, B.E., Dunham, J.B., Young, M.K., Peterson, D.P., 2009. Invasion versus isolation: Trade-offs in managing native salmonids with barriers to upstream movement. Conserv. Biol. 23, 859–870.
Goudet, J., 1995. FSTAT (Version 1.2): A computer program to calculate F-statistics. J. Hered. 86, 485–486.
Green, D.M., 2003. The ecology of extinction: population fluctuation and decline in amphibians. Biol. Cons. 111, 331–343.
Haag, T., Santos, A.S., Sana, D.A., Morato, R.G., Cullen, Jr., L., Crawshaw, Jr., P.G., De Angelo, C., Di Bitetti, M.S., Salzano, F.M., Eizirik, E., 2010. The effect of habitat fragmentation on the genetic structure of a top predator: loss of diversity and high differentiation among remnant populations of Atlantic Forest jaguars (Panthera onca). Mol. Ecol. 19, 4906–4921.
Harig, A.L., Fausch, K.D., 2002. Minimum habitat requirements for establishing translocated cutthraot trout populations. Ecol. Appl. 12, 535–551.
Hastings, K. 2005. Long-term Persistence of Isolated Fish Populations in the Alexander Archipelago. Dissertation. University of Montana.
Haugen, T.O., 2000. Growth and survival effects on maturation pattern in populations of grayling with recent common ancestors. Oikos 90, 107–118.
Höglund, J., Piertney, S.B., Alatalo, R.V., Lindell, J., Lundberg, A., Rintamäki, P.T., 2002. Inbreeding depression and male fitness in black grouse. Proc. R. Soc. Lond. Ser. B: Biol. Sci. 269, 711–715.
Hu, G., Gu, W., Bai, Q.L., Wang, B.Q., 2013. Estimation of genetic parameters for growth traits in a breeding program for rainbow trout (Oncorhynchus mykiss) in China. Genet. Molec. Res. 12, 1457–1467.
Hutchings, J.A., 1993. Adapative life histories effected by age-specific survival and growth-rate. Ecology 74, 673–684.
Isomursu, M., Ratti, O., Liukkonen, T., Helle, P., 2012. Susceptibility to intestinal parasites and juvenile survival are correlated with multilocus microsatellite heterozygosity in the Capercaillie (Tetra urogallus). Ornis Fennica 89, 109–119.
Johnson, W.E., Onorato, D.P., Roelke, M.E., Land, E.D., Cunningham, M., Belden, R.C., McBride, R., Jansen, D., Lotz, M., Shindle, D., Howard, J., Wildt, D.E., Penfold, L.M., Hostetler, J.A., Oli, M.K., O'Brien, S.J., 2010. Genetic restoration of the Florida panther. Science 329, 1641–1645.
Kerstes, N.A.G., Wegner, K.M., 2011. The effect of inbreeding and outcrossing of *Tribolium castaneum* on resistance to the parasite Nosema whitei. Evol. Ecol. Res. 13, 681–696.
Kovach, R.P., Muhlfeld, C.C., Wade, A.A., Hand, B.K., Whited, D.C., DeHaan, P.W., Al-Chokhachy, R., Luikart, G., 2015. Genetic diversity is related to climatic variation and vulnerability in threatened bull trout. Glob. Change Biol. 21, 2510–2524.
Letcher, B.H., Coombs, J.A., Nislow, K.H., 2011. Maintenance of phenotypic variation: repeatability, heritability and size-dependent processes in a wild brook trout population. Evol. Appl. 4, 602–615.
Letcher, B.H., Nislow, K.H., Coombs, J.A., O'Donnell, M.J., Dubreuil, T.L., 2007. Population response to habitat fragmentation in a stream-dwelling brook trout population. Public Library Sci. One 2, e1139.

Magee, J.P., McMahon, T.E., Thurow, R.F., 1996. Spatial variation in spawning habitat of cutthroat trout in a sediment-rich stream basin. Trans. Amer. Fish. Soc. 125, 768–779.
Mattey, S.N., Strutt, L., Smiseth, P.T., 2013. Intergenerational effects of inbreeding in *Nicrophorus vespilloides*: offspring suffer fitness costs when either they or their parents are inbred. J. Evol. Biol. 26, 843–853.
McCallum, H., 2008. Tasmanian devil facial tumour disease: Lessons for conservation biology. Trends Ecol. Evol. 23, 631–637.
Meyer-Lucht, Y., Otten, C., Püttker, T., Pardini, R., Metzger, J., Sommer, S., 2010. Variety matters: Adaptive genetic diversity and parasite load in two mouse opossums from the brazilian atlantic forest. Conserv. Genet. 11, 2001–2013.
Morita, K., Fukuwaka, M., 2007. Why age and size at maturity have changed in pacific salmon. Mar. Ecol. Prog. Ser. 335, 289–294.
Morita, K., Morita, S.A., Yamamoto, S., 2009. Effects of habitat fragmentation by damming on salmonid fishes: lessons from white spotted charr in Japan. Eco. Res. 24, 711–722.
Morita, K., Yokota, A., 2002. Population viability of stream resident salmonids after habitat fragmentation: a case study with white-spotted char (*Salvelinus leucomaenis*) by an individual based model. Ecol. Model. 155, 85–94.
Nelson, G.A. 2012. Fisheries methods and models in R.
Nilsson, J., 1994. Genetics of growth of juvenile Arctic Char. Trans. Amer. Fish. Soc. 123, 430–434.
Ogle, D. 2012. Functions to support simple fisheries stock assement methods. http://www.rforge.net/FSA/.
Pavlacky, D.C., Possingham, H.P., Lowe, A.J., Prentis, P.J., Green, D.J., Goldizen, A.W., 2012. Anthropogenic landscape change promotes asymmetric dispersal and limits regional patch occupancy in a spatially structured bird population. J. Anim. Ecol. 81, 940–952.
Peacock, M.M., Dochtermann, N.A., 2012. Evolutionary potential but not extinction risk of Lahontan cutthroat trout (Oncorhynchus clarkii henshawi) associated with stream characteristics. Canad. J. Fish. Aquat. Sci. 69, 615–626.
Peterson, D.P., Fausch, K.D., Watmough, J., Cunjak, R.A., 2008a. When eradication is not an option: Modeling strategies for electrofishing supression of nonnative brook trout to foster persistence of sympatric native cutthroat trout in small streams. North Amer. J. Fish. Manag. 28, 1847–1867.
Peterson, D.P., Fausch, K.D., White, G.C., 2004. Population ecology of invasion: effects of brook trout on native cutthroat trout. Ecol. Appl. 14, 754–772.
Peterson, D.P., Rieman, B.E., Dunham, J.B., Fausch, K.D., Young, M.K., 2008b. Analysis of trade-offs between threats of invasion by non-native brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). Canad. J. Fish. Aquat. Sci. 65, 557–573.
Peterson, D.P., Rieman, B.E., Horan, D.L., Young, M.K., 2013. Patch size but not sort-term isolation influence occurance of westslope cutthroat trout above human-made barriers. Ecol. Freshwater Fish . http://dx.doi.org/10.1111/eff.12108.
Peterson, D.P., Rieman, B.E., Young, M.K., Brammer, J.A., 2010. Modeling predicts that redd trampling by cattle may contribute to population declines of native trout. Ecol. Appl. 20, 954–966.
Pierce, R., Podner, C., Carim, K., 2013. Response of wild trout to stream restoration over two decades in the Blackfoot River Basin, Montana. Trans. Amer. Fish. Soc. 142, 68–81.
R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Rahel, F.J., 2013. Intentional fragmentation as a management strategy in aquatic systems. Bioscience 63, 362–372.
Rieman, B.E., McIntyre, J.D., 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Trans. Amer. Fish. Soc. 124, 285–296.
Ruiz-Lopez, M.J., Monello, R.J., Gompper, M.E., Eggert, L.S., 2012. The effect and relative importance of neutral genetic diversity for predicting parasitism varies across parasite taxa. PLoS One 7.
Slate, J., Kruuk, L.E.B., Marshall, T.C., Pemberton, J.M., Clutton-Brock, T.H., 2000. Inbreeding depression influences lifetime breeding success in a wild population of red deer (Cervus elaphus). Proc. R. Soc. Lond. Ser. B: Biol. Sci. 267, 1657–1662.
Spielman, D., Brook, B.W., Briscoe, D.A., Frankham, R., 2004. Does inbreeding and loss of genetic diversity decrease disease resistance? Conserv. Genet. 5, 439–448.
Taylor, M., Stamford, D., Baxter, J.S., 2003. Populaiton subdivision in westslope cutthroat trout (*Oncorhynchus clarki lewisi*) at the northern periphery of its range: evolutionary inferences and conservation implications. Mol. Ecol. 12, 2609–2622.
Thurow, R.F., Lee, D.C., Rieman, B.E., 1997. Distribution and status of seven native Salmonids in the interior Columbia River Basin and portions of the Klamath River and Great Basins. North Amer. J. Fish. Manag. 17, 1094–1110.
Tsuboi, J.I., Iwata, T., Morita, K., Endou, S., Oohama, H., Kaji, K., 2013. Strategies for the conservation and management of isolated salmonid populations: lessons from Japanese streams. Freshwater Biol. 58, 908–917.
Vindenes, Y., Edeline, E., Ohlberger, J., Langangen, Ø., Winfield, I.J., Stenseth, N.C., Vøllestad, L.A., 2014. Effects of climate change on trait-based dynamics of a top predator in freshwater ecosystems. Amer. Nat. 183, 243–256.
Vindenes, Y., Langangen, Ø, Winfield, I.J., Vøllestad, L.A., 2016. Fitness consequences of early life conditions and maternal size effects in a freshwater top predator. J. Anim. Ecol.
Watanabe, K., Monaghan, M.T., Takemon, Y., Omura, T., 2010. Dispersal ability determines the genetic effects of habitat fragmentation in three species of aquatic insect. Aquat. Conserv.: Mar. Freshwater Ecosyst. 20, 574–579.
Wenger, S.J., Isaak, D.J., Luce, C.H., Neville, H., Fausch, K.D., Dunham, J.B., Dauwalter, D.C., Young, M.K., Elsner, M.M., Rieman, B.E., Hamlet, A.F., Williams, J.E., 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proc. Natl. Acad. Sci. 108, 14175–14180.
Whiteley , A.R., Hastings , K., Wenburg , J.K., Frissell , C.A., Martin , J.C., Allendorf , F.W., 2010. Genetic variation and effective population size in isolated populations of coastal cutthroat trout. Conserv. Genet. 11, 1929–1943.
Whiteley , A.R., Coombs , J.A., Hudy, M., Robinson , Z., Colton , A.R., Nislow , K.H., Letcher , B.H., 2013. Fragmentation and patch size shape genetic structure of brook trout populations. Can. J. Fish. Aquat. Sci. 70, 678–688.
Williams, J.E., Haak, A.L., Neville, H., Colyer, W.T., 2009. Potential consequences of climate change to persistence of cutthroat trout populations. North Amer. J. Fish. Manag. 29, 533–548.
Wofford, J.E.B., Gresswell, R.E., Banks, M.A., 2005. Influence of barriers to movement on within-watershed genetic variation of costal cutthroat trout. Ecol. Appl. 15, 628–637.
Wu, H., Kimball, J.S., Elsner, M.M., Mantua, N., Adler, R.F., Stanford, J., 2012. Projected climate change impacts on the hydrology and temperature of Pacific Northwest Rivers. Water Resources Research 48:W11530.populations. Canad. J. Fish. Aquat. Sci.