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Original research article

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

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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.

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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

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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).