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Spatiotemporal patterns of mountain whitefish (*Prosopium williamsoni*) in response to a restoration of longitudinal connectivity

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Abstract

To examine the role of longitudinal connectivity on the spatial and temporal dynamics of mountain whitefish (*Prosopium williamsoni*), we quantified movement and population dynamics following installation of the Landsburg Dam fishway, Cedar River, WA, USA. Mountain whitefish is widely distributed, poorly studied, and not the focus of restoration. Before the fishway, mountain whitefish were not observed above the dam. Here, we focus on snorkel counts collected at reach and mesohabitat (e.g. pools) scales over 11 summers on the 20-km above-dam segment following restoration. A camera within the ladder provided number, size, and movement timing, thereby informing on behavior and recolonization. Segment scale abundance increased following fish passage reaching an asymptote in 7 years, and mountain whitefish were detected throughout the main stem in 10 years. Annual movement through the ladder increased over time, was positively correlated with instream abundance and discharge, but negatively correlated with water temperature. About 60 % of fish movements occurred in spring and early summer, potentially for foraging opportunities. Reach-scale abundance peaked between 7 and 10 km from the dam; these reaches were characterized by deep, cool (~10.6 to 11.6 °C) conditions. At the mesohabitat scale, mountain whitefish detection increased with depth and velocity after accounting for distance from the dam. Our results show how restoring longitudinal connectivity allowed this non-target species to colonize newly available habitat. Their response supports the critical roles of longitudinal connectivity and environmental conditions, that manifest at different spatial scales, in dictating how freshwater fish respond to habitat disturbance.

Key words: barriers; colonization; fish passage; longitudinal connectivity; mountain whitefish; spatial and temporal dynamics

Introduction

Fishes are one of the most threatened vertebrates worldwide, and a large portion spend part of their lives in freshwater (Fausch et al., 2002; Darwall & Freyof, 2016). In

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ivers, a variety of anthropogenic factors contribute to these declines such as invasive species, pollution, and habitat disturbance including impacts to longitudinal connectivity. Road crossings (Valentine-Rose & Layman, 2011), culverts (MacPherson et al., 2012), and dams (Couto & Olden, 2018) can constrain both upstream and downstream movement of riverine fish (Calles & Greenberg, 2009). How riverine fish respond to artificial barriers depends on a variety of factors such as location and permeability of the barrier, and fish life history traits especially size and mobility (Cooney & Kwak, 2013). While we have a relatively strong understanding of the effects of artificial barriers on highly mobile diadromous fish like Pacific salmon (*Onchorynchus* spp.) (Fullerton et al., 2010), our understanding is not as strong for less mobile or poorly studied non-diadromous species.

To address the effects of artificial barriers on a non-diadromous and less studied freshwater fish, we examined the response of mountain whitefish (Salmonidae: *Prosopium williamsoni*) to restoration of longitudinal connectivity at Landsburg Dam on the Cedar River, WA, USA. This low-head (~ 6 m high), run-of-the-river dam blocked the upriver migration of multiple fish species after construction in 1901. To mitigate the negative effects on upstream fish passage, a fishway or ladder was installed at the dam in 2003, restoring access for multiple target species of threatened diadromous Pacific salmon to historic, high quality spawning and rearing habitat for the first time in over 100 years (Anderson & Quinn, 2007). While allowing for natural recolonization by Pacific salmon, the ladder also provided a migratory pathway for non-target, potamodromous species occurring below the dam, including mountain whitefish.

Mountain whitefish is a relatively large (adults range from 200 – 600 mm), long-lived (up to 25 years), abundant, and widely distributed salmonid of clear, cold freshwater systems of western North America (Davies & Thompson, 1976; Northcote & Ennis, 1994; Meyer, Elle, & Lamansky, 2009). They consume almost exclusively aquatic invertebrates by feeding on drift or directly off the benthos (Baxter, 2002; Wydoski & Whitney, 2002). Furthermore, while some individuals within a population are relatively stationary (Davies & Thompson, 1976; Northcote & Ennis, 1994), others can be

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migratory. Available evidence indicates these migratory individuals require access to different portions of the river network for foraging, reproduction, and overwintering (Pettit & Wallace, 1975; Davies & Thompson, 1976; Baxter, 2002; Benjamin et al., 2014).

Despite their widespread distribution, abundance, and potential to have ecosystem effects (Flecker et al., 2010; Lance & Baxter, 2011), mountain whitefish, particularly populations inhabiting coastal rivers (Starr & Torgersen, 2015), are poorly studied (Meyer et al. 2009). For instance, relatively little is known regarding the influence of anthropogenic disturbance on mountain whitefish populations including effects on movement (Baxter, 2002; Benjamin et al., 2014), population dynamics, or how abiotic and biotic factors modify these processes (Meyer et al., 2009; Starr & Torgersen, 2015). Our study provides a unique opportunity to address some of these gaps and learn more about this poorly studied species by quantifying recolonization over multiple spatial scales and across an 11-year period following restoration of longitudinal connectivity via the fishway.

We examine three processes fundamental to the ecology and management of mountain whitefish and stream fish in general: dispersal, population dynamics, and habitat selection (Schlosser, 1991). Dispersal is an essential process affecting stream fish populations including how they respond to disturbance (Radinger & Wolter, 2014). However, studying dispersal and factors modifying it, like season, water temperature, and discharge, is challenging (Fausch et al., 2002). Gaining this knowledge may inform on the mechanism (foraging, overwintering, reproduction) causing movement, how movement affects seasonal changes in fish assemblages, and how movement is modified by environmental conditions (Baxter, 2002). Long-term studies of stream fish populations are also rare (e.g. Milner et al., 2008), yet invaluable in developing effective fisheries and ecosystem management (Ricker, 1946; Pikitch et al., 2004).

Forming effective conservation strategies also depends on the identification of abiotic and biotic factors influencing stream fish populations at relevant spatial scales (Fausch et al., 2002). For example, water temperature can modify the spatial distribution

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of stream fish, especially at large spatial scales (Lawrence et al., 2012), by acting on metabolic processes (Isaak et al., 2012; Fenkes et al., 2016). Yet, results from the few studies examining the effects of large-scale spatial variation in water temperature on mountain whitefish are mixed indicating the need for further study (Torgersen et al., 2006; Meyer et al., 2009). At smaller spatial scales, like the mesohabitat scale (e.g. pools), water depth and velocity, in concert with body size and morphology, can regulate fish assemblage composition and density, predation risk, and food acquisition (Power, 1984; Harvey, White & Nakamoto, 2005; Rosenfeld & Taylor, 2009). Depth and velocity may also be important predictors of mountain whitefish abundance, yet there are conflicting accounts for how they respond to these conditions (Northcote & Ennis, 1994; Baxter, 2002; Meyer et al., 2009; Starr & Torgersen, 2015).

We used two complementary sources of data to examine the temporal and spatial dynamics of mountain whitefish in the Cedar River above Landsburg Dam in northwestern Washington state following restoration of longitudinal connectivity at the dam. The first source of data is habitat and snorkel surveys conducted at multiple spatial scales spanning about 33 km of main stem and tributary habitat, three years before (2000-2002) and 11 years (2004-2015) following provision of fish passage. Here, we focus on post restoration data from the main stem because mountain whitefish were not detected before the ladder and post-ladder surveys indicated that they were rare or not detected in tributaries. The second source is a time series (2008-2014) of mountain whitefish pictures taken by a camera system inside the ladder as they recolonized above the dam.

With these data, we address the following questions regarding the temporal and spatial dynamics of mountain whitefish following restoration of longitudinal connectivity:

- Does abundance and distribution increase over time following restoration of longitudinal connectivity?
- Does upstream movement rate increase over time and is it correlated with in-stream abundance?
- Does upstream movement vary seasonally?

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- Do mountain whitefish track environmental conditions that manifest at the reach and mesohabitat scales?

Methods

Study system

■ The Cedar River originates at the crest of the Cascade Mountains at about 1700 m in elevation within Seattle's 164 km² protected municipal watershed 47 km from the city. The watershed acts as a de facto conservation area to protect the water source for over 1 million people. The river flows southwest through the watershed, then through rural residential and urban landscapes before flowing into Lake Washington near Seattle (Figure 1). Landsburg Dam, located at the western boundary of the watershed, was constructed in 1901 at river kilometer 35 (distance from Lake Washington) to divert drinking water for the city. The dam was originally built without fish passage, blocking the upriver dispersal of multiple diadromous and potamodromous salmonids denying them access to the relatively high-quality habitat above the dam (see Kiffney, Volk, & Hall, 2002; Kiffney et al., 2006 and Anderson & Quinn, 2007 for additional site details).

The river above the dam flows through dense, coniferous-dominated forests (primarily ~90-100 years old) and is typical of clean, cool, nutrient-poor, rocky-bottomed mountain tributaries to the Pacific Ocean (Naiman, Bilby & Bisson 2000). The weather is also typical of coastal tributaries with wet (~1.4 m of precipitation per year) and mild conditions (mean monthly air temperature ranges from 4 to 15 °C). Most precipitation falls as rain or snow during fall and winter months, while July and August are relatively dry (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?waland>). Highest river flows occur between November and March when heavy precipitation leads to large runoff, while lowest flows occur in August and September.

Before the fish ladder was constructed, the above-dam main stem fish assemblage consisted of multiple species of sculpin (Cottidae), resident rainbow (*O. mykiss*) and coastal cutthroat trout (*O. clarkii clarkii*), western brook lamprey (*Lampetra richardsonii*), and an occasional bull trout (*Salvelinus confluentus*) (Casne, 1975; Kiffney

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et al., 2002; Kiffney et al., 2006). While mountain whitefish were not observed during above-dam surveys prior to installation of the ladder, they have been observed or captured below the dam (Casne, 1975; Drs. R. Peters, U.S. Fish and Wildlife Service and D. Beauchamp, U. S. Geological Survey). We recognize that failure to observe mountain whitefish above the dam does not demonstrate absence (MacKenzie et al., 2002), but our pre-ladder surveys indicate they were either absent or rare. Because the area above the dam has been closed to the public to protect the city's water supply, the fish populations are entirely unexploited, though regulated recreational fishing is allowed in the Cedar River below the dam.

Data sources

Habitat and snorkel surveys- Habitat and fish surveys were conducted during low flow, summer conditions on the main stem Cedar River and associated tributaries. We applied a stratified sampling design to capture the longitudinal, hierarchical structure of river systems (Frissell et al., 1986) by sampling at multiple, nested scales (i.e. mesohabitat or habitat unit [$10^0 - 10^2$ m] nested within reach [$10^1 - 10^1$ km] nested within segment [$10^1 - 10^2$ km]), with reaches defined by changes in gradient, valley confinement, and dominant substratum (Baxter, 2002; Kiffney et al., 2002; Wolter, Buijse & Parasiewicz, 2016) (Table 1). Samples collected at these spatial scales provide insight into environmental filters controlling a species' distribution, such as identifying 'biological hotspots'. Furthermore, the larger spatial scales (i.e., reach, segment) are appropriate for conservation and management of stream fishes (Fausch et al., 2002).

The 20-km main stem segment (Wolter et al., 2016), from about 200 m above the dam to an upstream natural barrier at Cedar Falls, was divided into 10 geomorphic reaches (CR1-CR10, with CR1 closest to the dam) that varied in length from ~300 to 3500 m. The entire length of short reaches was surveyed (CR4, CR9 and CR10) and ~600 - 800 m sections of longer reaches. The length of these longer sections was about 30 to 40× the river's wetted width; studies indicate this length represents habitat conditions for the reach as a whole (Kaufmann et al., 2003). The same approach was used in tributaries. Within each reach, we categorized individual mesohabitat units (~ 20 – 800

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m²) based on methods in Hawkins et al. (1993) (Appendix A, Table A1 for description of these units). These mesohabitats - pools, step-pools, runs, riffles, cascades and depositional habitats - correspond to the scale commonly used to determine environmental requirements of stream fishes (Wolter et al., 2016).

A laser range finder (Model Laser Impulse, Laser Technology Inc., Centennial, CO, USA) measured length and width of each mesohabitat and reach. We also used a range finder, stadia rod, and surveyor's level to measure gradient, or changes in stream elevation, between the bottom and top of each reach. Average water velocity (Swoffer Model # 3000 flow meter, Tukwila, WA, USA), and mean and maximum depth (stadia rod) were quantified by point measurements taken in the thalweg at the bottom, middle, and end of each mesohabitat. Water velocity was measured at 60 % of the water depth at each location. In exceptionally deep or fast habitats, these measurements were taken as close to the thalweg as possible. We also estimated the dominant and sub-dominant substrata (bedrock, boulders, cobbles, pebbles, gravel, sand/silt; Williams et al., 2006) within each mesohabitat based on the proportion of stream bottom they covered.

Because of the main stem's large size, depth, gradient and exceptional water clarity, snorkeling was the most effective method to quantify fish populations, almost exclusively salmonids. Following protocols described in Thurow (1994) and Lance & Baxter (2011), each mesohabitat was surveyed for fish during daylight hours (i.e. between 09:00-16:00) in the upstream direction by trained observers who relayed identity and abundance of all water-column species to a recorder on the bank.

Using the paired snorkel and physical habitat data, we estimated number of mountain whitefish per linear km (fish·km⁻¹); frequency of occurrence (p , or the proportion of mesohabitats where fish were detected relative to total number of that particular habitat type in each reach); and occurrence or detection (1 = detected, 0 = not detected). These responses were estimated in each mesohabitat within each reach and year surveyed. A description of response variables is presented in Appendix A, Table A2. *Camera system-* A *Vaki Riverwatcher* underwater camera (Aquaculture Systems Ltd., Kópavogur, Iceland), located inside the ladder, provided details on mountain whitefish

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upstream movement including timing and body size. Fish swimming upstream through the ladder triggered the camera, which took five photographs, recorded time and date of each image captured, and estimated total fish length (mm). It can be difficult to distinguish salmonids of similar size and shape (e.g. rainbow trout and cutthroat trout), but mountain whitefish have a distinct body shape, with a slender caudal peduncle, sub-terminal mouth, and large, reflective scales. These features facilitate positive identification, even under sub-optimal conditions of water clarity and lighting. Camera data were available from 27 February 2008 to 31 December 2014.

Owing to maintenance of the facility, the camera, and other operational events, the camera did not function on all days in all years. The amount of time the camera was not operating ranged from a low of 0 % in 2012 to 33 % in 2014. Therefore, to estimate temporal changes, annual totals were normalized within each year by calculating the count of mountain whitefish per day of camera operation. Monthly patterns were estimated by summing counts per month in each year and averaging those values using only years when there were counts for that month. Appendix A, Table A3 provides details on response variables based on camera images.

Water temperature and discharge- Along with variables hypothesized to influence mountain whitefish at the mesohabitat unit scale (e.g. depth), we hypothesized that their distribution would co-vary with water temperature at the reach scale. We assumed reach-scale water temperature to be invariant because there were no major geologic or anthropogenic events during the course of the study. Therefore, in our analysis of mountain whitefish spatial distribution (see **Data analysis**), we used water temperature measured at the mid-point of each reach hourly from 1 March to 31 July 2005 with data loggers fixed to log jams by wire and a concrete weight (Onset Hobo, Model #U22, Bourne, MA, USA).

We also expected that annual rates of upstream movement through the ladder would co-vary with water temperature (Benjamin et al., 2014) and discharge (Bret et al., 2016); therefore, these predictors were used in our statistical analysis with data measured at the dam during the spring-summer period between 2008 and 2014 (WSDOE 2016) (see

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Appendix A, Table A4 for list of predictor variables). The reach-scale spring-summer period was used in our analyses as this period coincided with peaks in upstream movement through the ladder and abundance estimates from snorkel surveys.

Data analysis

Temporal dynamics

Snorkel surveys – Data from snorkel surveys were used to model the temporal dynamics of the mountain whitefish population following habitat reconnection in three ways. First, we quantified temporal change at the segment scale (~20 km) by averaging estimates of linear abundance (fish·km⁻¹) and frequency of occurrence (p), first across mesohabitats in a reach and then across reaches within a year using data collected between 2004-2015.

Exploratory scatter plots of abundance with time indicated little support for a random or exponential response; therefore, yearly estimates were used in an information-theoretic model selection framework to test whether abundance or occurrence increased linearly, indicative of a growing population, or asymptotically indicating density dependence (Madenjian, Schoesser & Krieger, 1998). Using the JMP platform (Sall, Creighton & Lehman, 2005), model selection was based on the AIC_c statistic (lower score indicates a superior model) and the change in AIC_c or ΔAIC_c ($\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$), model weights (w_i , higher score indicates more support), and the coefficient of determination (R^2) (Burnham & Anderson, 2002).

Second, the reach-scale mountain whitefish time series was used to estimate the annual rate of spatial expansion above the dam. Specifically, spatial expansion was determined by regressing the distance (rkm, or river kilometers) between the dam and the mid-point of the most upstream reach where mountain whitefish were observed each summer with time.

Third, we calculated cumulative frequency of occurrence, which was based on the number of years' mountain whitefish were observed in a reach relative to the total years that reach was surveyed. For example, mountain whitefish were detected in CR1 every summer between 2004 and 2015; thus, the cumulative frequency of occurrence at CR1 was 1. We used model selection as described above to determine the relative support for

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linear and logistic models in predicting how cumulative frequency of occurrence varied across reaches. To provide an estimate of reach-scale sampling effort, the number of years each reach was surveyed is shown in Appendix A, Table A5.

Camera data- To quantify temporal changes in mountain whitefish migrating upstream through the ladder, daily camera counts averaged within a year were regressed vs. time ($n = 7$ years, 2008-2014). Pearson's correlation coefficient was used to examine the direction and strength of associations between annual upstream movement rates, abundance estimates from snorkel surveys, and discharge and water temperature measured at Landsburg Dam (2008-2014).

Spatial dynamics

Analysis of habitat use by mountain whitefish at the reach and mesohabitat scales used snorkel and habitat data collected between 2010 and 2015, because segment scale analysis indicated the population reached an asymptote by about 2009. By focusing this analysis on data collected after 2009, we aimed to minimize the confounding effects of temporal autocorrelation of the growing population on patterns of habitat selection.

Reach-scale patterns- Under the assumption that the dam was a barrier to upriver migration by mountain whitefish, we predicted abundance/occurrence could display a variety of spatial patterns. Based on our understanding of the system and the species, we focus our analysis on three. First, if habitat suitability and/or propensity to move declined with distance from the dam, we would expect mountain whitefish abundance to peak in reaches closest to the dam then decline upstream. Second, if movement is relatively unconstrained and preferred environmental conditions are patchily distributed at the reach scale, mountain whitefish might display distinct peaks where abundance increases from the dam to a point or points indicating potential biological hotspots (Fausch et al., 2002; Starr & Torgersen, 2015). Third, if available habitat for mountain whitefish is equally suitable across the main stem segment and upstream movement is unconstrained, we might expect a random reach-scale distribution. Exploratory scatter plots indicated a random distribution did not represent reach-scale spatial patterns; therefore, AIC_c ,

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ΔAIC_c , and model weights were used to determine which response function (exponential, linear, Gaussian peak) best fit the reach-scale patterns of mountain whitefish abundance and frequency of occurrence.

To assess the importance of environmental factors on reach-scale mountain whitefish abundance (averaged across 2010-2015), we used partial least squares regression (PLSR) within the JMP platform (Sawatsky, Clyde & Meek, 2015). This approach, which is similar to principal components regression, is especially useful when sample sizes are small and predictors are highly correlated (Garthwaite, 1994), as was the case in our study (Appendix B, Table B1). To form a relationship between the dependent variable (fish $\cdot \text{km}^{-1}$) and explanatory variables, PLSR constructs new explanatory factors, latent variables or components, where each factor is a linear combination of original predictors (Garthwaite, 1994). This approach uses data from both independent and dependent variables in constructing components, and then standard regression techniques to determine relationships between the dependent variable and new latent factors, (Garthwaite, 1994). Variable importance plots (VIP) were used to determine which factors contributed to variation in both independent and dependent variables. The higher the VIP scores the more influential the variable; traditionally values < 0.8 are considered non-influential (Sawatsky et al., 2015).

The predictor variables used in the PLSR included water temperature, distance from dam to reach mid-point, and channel gradient. Water temperature was examined, because it is a key variable affecting the distribution and abundance of coldwater fish (Isaak et al., 2012). Distance from the dam to reach mid-point was included as a proxy for location of the source population, which is a key predictor of the spatial dynamics of populations recovering from disturbance (Pulliam, 1988; Lubina & Levin, 1988). Channel gradient was included because studies have shown it is a key predictor of stream salmonid population size, biomass, and composition (Hicks & Hall, 2003; Kiffney & Roni, 2007) and other potentially important habitat elements for fish such as water depth.

Mesohabitat scale- Logistic regression was used to analyze the probability of detecting mountain whitefish at the mesohabitat scale ($n = 611$ habitat units surveyed between

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2010-2015). Based on our previous analysis at the reach-scale and exploratory plots, we analyzed the binomial response (1 = detected; 0 = undetected) at the mesohabitat unit scale as a linear and quadratic function of distance from reach midpoint to the dam, (rkm), the linear effects of maximum habitat depth ($\beta_{\text{max.depth}}$) and mean velocity (β_{velocity}), and the interactive effects of depth and distance. We included an interaction between distance and depth, because we expected mountain whitefish to be positively associated with depth in the cooler reaches of CR1 through CR6 relative to CR8 through CR10, which were also further from the hypothetical source population.

The full logistic model, which represented all potentially relevant effects, was of the form:

$$\text{Logit}[(\text{MWF}=1)] = \beta_0 + \beta_{\text{distance}} + \beta_{\text{distance}}^2 + \beta_{\text{max.depth}} + \beta_{\text{velocity}} + \beta_{\text{max.depth}} \times \beta_{\text{distance}}.$$

We constructed plausible alternative hypotheses to the global model including a null model; models that varied the presence of the quadratic coefficient for distance, and linear terms for velocity and maximum depth; and a model without the interaction (R Core Development Team, 2016). Model selection was performed based on differences in the AIC_c statistic (ΔAIC_c) and model weights (w_i) using R version 3.1.3 (Barton, 2016).

The performance of the final logistic regression model in predicting the presence of whitefish was assessed with the following:

- 1) Was the model an improvement over a null model using the likelihood ratio test?
- 2) Was the model's true positive rate of detection (TP) greater than its false positive rate (FP) using receiving operating characteristic (ROC) curve analysis (a standard technique for summarizing classifying performance)?
- 3) Was the model overdispersed (i.e. was residual deviance greater than expected)?

Wald tests were used to test whether coefficients in the final model were equal to zero; coefficient estimates were exponentiated to obtain the predicted odds ratio. The odds ratio describes the factor by which the odds of detecting whitefish at the mesohabitat scale changes when the continuous predictor is increased by one unit while holding other predictors constant.

Results

Environmental conditions

Mean spring-summer (1 March–31 July) water temperature at Landsburg Dam was generally higher at the beginning of the time series than the end, ranging from 8 to 10 °C (Appendix B, Figure B1a). Discharge generally increased over the period, with highest average spring-summer flow in 2012 ($\sim 34 \text{ m}^3 \cdot \text{s}^{-1}$), which was 2.8× higher than the lowest mean flow in 2005 ($\sim 12 \text{ m}^3 \cdot \text{s}^{-1}$) (Appendix B, Figure B1b).

The 20-km main stem segment above the dam displayed marked longitudinal differences in environmental conditions (Table 1). Channel gradient ranged almost 7-fold from 0.5 % at CR1 to 3.3 % at CR9, 19 rkm upstream of the dam. The channel also narrowed in the upstream direction where it went from 22 m wetted width at CR8 to 11 m at CR9. Potentially in response to reach-scale geomorphic changes, the channel was deeper, wood cover was lower, and boulders were more abundant in high gradient (CR3, CR5, CR7, CR9) relative to lower gradient reaches (CR1, CR2, CR4, CR6, CR8, CR10). Mean reach-scale water temperature was warmest in upstream reaches (CR8-CR10), especially CR 8 (12.7 °C), cooling about 1 °C at CR7, and cooling again between CR6 and CR2 (10.8 °C), with a slight warming of 0.4 °C at CR1. Mean maximum temperature showed an even more pronounced upstream warming trend ranging from 13 °C at CR3 and CR6 to 19 °C at CR8.

Temporal dynamics

Snorkel data- The mountain whitefish population above the dam increased asymptotically over time and was best represented by the logistic model ($w_i = 0.99$), which was 1414× more likely than the linear model ($w_i = 0.0007$, $R^2=0.74$) and explained almost 95 % of the total variation in abundance (Figure 2a). The form of the logistic model was:

$$\text{fish} \cdot \text{km}^{-1} \text{ or } p = c/[1 + \exp(-a \times (\text{time}-b))]$$

where a is the growth rate, b is the inflection point, and c is the asymptote (mean (and 95 % CI), $a = 1.8$ (0.58, 3.0), $b = 2009$ (2008, 2009), $c = 62$ (56, 68)). In addition, the

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logistic model was 6× more likely ($w_i = 0.84$) than the linear model ($w_i = 0.14$, $R^2=0.56$) and explained 77 % of the total variation in changes in mountain whitefish occurrence (p) with time. Parameter estimates for predicting changes in the frequency of occurrence were: $a = 3.8$ (1.7, 9.0), $b = 2008$ (2007, 2008) $c = 0.2$ (0.16, 0.23).

To summarize these dynamics: no mountain whitefish were observed in 2000, 2001 or 2003, prior to installation of the fish ladder. Between 2004 - the first summer after the ladder was installed - and 2007, abundance was low (~ 4 fish·km⁻¹). In 2008, segment-scale abundance increased almost fourfold relative to 2007, followed by another fourfold increase in 2009 relative to 2008. Mountain whitefish abundance peaked in 2011 at 80 fish·km⁻¹ or almost 20 times higher than the average between 2004 and 2007. A similar pattern was observed for the relationship between mountain whitefish occurrence (p) and time: mean occurrence at the segment scale ranged from lows of 0-5 % between 2000 and 2007 to highs of 20-25 % in 2008 (data not shown).

In terms of spatial expansion, the mountain whitefish population during summer expanded at a rate of 1.24 rkm·year⁻¹ (MWF upstream extent, rkm = 6.1 + 1.24×(year), Adjusted $R^2 = 0.69$) and they were detected in all reaches by 2013, or 10 years following provision of fish passage.

Cumulative annual frequency of occurrence of mountain whitefish at the reach-scale was high and constant from CR1 (1) to CR6 (0.92) about 12 km from the dam, with a pronounced decline to 0.1 from above CR7 through CR10 (Figure 2b). The logistic model best fit this pattern, and was about 19× more likely than a linear model ($w_i = 0.95$ for logistic model and 0.05 for linear model), explaining about 86 % of the total variance in cumulative occurrence rates relative to 75 % for the linear model.

Camera data- Over the period from March 2008 through December 2014, the camera counted 2,561 mountain whitefish moving upstream through the ladder (Figure 3). The average passage rate at the dam increased approximately fourfold, from 0.66 d⁻¹ in 2008 to 2.68 d⁻¹ during the period of 2012-2014 (fish·camera day⁻¹ = -852 + 0.42×(year), adjusted $R^2 = 0.69$). Annual variation in fish·camera day⁻¹ was positively correlated with estimates of fish·km⁻¹ from snorkeling ($r = 0.56$, $n = 7$) and spring-summer discharge

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measured at the dam ($r = 0.56$, $n = 7$), but negatively related to water temperature ($r = -0.54$, $n = 7$) (Appendix B, Table B2).

In addition to this annual variation, two seasonal modes of movement were evident (Figure 4). About 60 % of the annual total moved in March and April, with a second, smaller mode in November and December: (~14 % of the annual total), declining to a **minimum** in February. The camera recorded virtually no mountain whitefish migrating through the ladder in September and October. Upstream movements also showed a very distinct diel pattern. Over all months, 57.3 % of the movements were from 15:00 to 19:00 h, and 74.4 % were between 14:00 and 20:00 h.

Consistent with snorkel observations, most images of mountain whitefish moving through the ladder were sub-adults or adults; estimated lengths ranged from 150 to 480 mm and 92 % of all observed fish were between 210 and 340 mm (mean \pm sd, 270.3 \pm 44.6 mm; Figure 5).

Spatial dynamics

Reach-scale patterns- The mountain whitefish population above the dam exhibited a pronounced peak in abundance at the reach scale: a Gaussian peak model ($w_i = 0.99$, $R^2=0.93$) was 495 \times more likely than the 2nd ranked, linear model ($w_i = 0.002$, $R^2=0.56$) in predicting the reach-scale relationship between mountain whitefish abundance and distance from the dam (Figure 6a). Similarly, the peak model ($w_i = 0.80$, $R^2=0.78$) was about 6 \times more likely than a linear model ($w_i = 0.14$, $R^2=0.40$) in predicting the frequency of occurrence, explaining 78 % of total model variance. The Gaussian peak model has the following form:

$$\text{fish}\cdot\text{km}^{-1} \text{ or } p = a \times \exp[-(0.5 \times ((\text{year}-b/c))^2)],$$

where a is the peak value, b the critical point, and c the growth rate (mean (and 95 % CI), $a = 89$ (66, 112), $b = 8.7$ (7.4, 10), $c = 3.9$ (2, 5.3) for $\text{fish}\cdot\text{km}^{-1}$; $a = 0.37$ (0.24, 0.51), $b = 8.4$ (6.7, 10), $c = 3.7$ (1.9, 5.4) for p). The distinct peak in abundance and habitat occupancy between 7 and 10 rkm from the dam corresponded to reaches CR3 to CR5.

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This spatial pattern first appeared in 2008, and was evident through the remainder of the time series (data now shown).

Partial least squares regression indicated that both water temperature and distance from the dam were important predictors (VIP = 1.1 for temperature and 0.93 for distance; negative slopes for both) of reach-scale mountain whitefish abundance, while channel gradient was not (VIP < 0.8). The two extracted factors, or components, in the final model explained about 79 % of the variance in abundance.

The role of water temperature in predicting the reach-scale distribution of mountain whitefish was supported by the negative relationship between mean maximum water temperature and mountain whitefish abundance (Figure 6b). Because water temperature and distance from the dam were correlated ($r = 0.83$), we also assessed the partial correlation coefficients between water temperature, distance from dam, and mountain whitefish abundance. This analysis showed that water temperature was negatively ($r = -0.72$) related with mountain whitefish abundance after controlling for distance from the dam, whereas distance ($r = -0.05$) was not after controlling for temperature.

Mesohabitat patterns- Mountain whitefish abundance and frequency of occurrence were highest in the deepest mesohabitats of pools and step pools ($\sim 80 \text{ fish}\cdot\text{km}^{-1}$, Table 2) and lowest in shallow, depositional habitats ($\sim 1.8 \text{ fish}\cdot\text{km}^{-1}$) located along channel margins. Their apparent preference for deep mesohabitats may have been partially determined by the body size of observed fish: 92 % of all fish detected were over 190 mm in estimated length.

The logistic model providing the best fit for predicting mountain whitefish occurrence (presence/absence) at the mesohabitat scale included linear and quadratic terms for distance, and linear terms for maximum depth and velocity. This model was about $4.9\times$ ($w_i = 0.84$) more likely than the full model ($w_i = 0.17$), and all coefficients differed from zero (Table 3). In terms of performance, the final model provided a better fit than the null and there was no evidence of overdispersion. Furthermore, the area under the ROC curve indicated the best fit model correctly predicted mountain whitefish

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presence 84 % of the time. In terms of predictors, the odds of detecting whitefish increased by a factor of 9.4 per one-unit increase in velocity and 5.3× per unit increase in maximum depth, while holding other coefficients constant. Moreover, the odds ratio (0.98) for the quadratic term of distance from the dam supported the observation of curvature in the relationships between mountain whitefish presence and distance from the source population.

Discussion

This study adds to our understanding of freshwater fish ecology in general and mountain whitefish ecology specifically by examining how this species responds to restoration of longitudinal connectivity via movement behavior, population dynamics, habitat selection, and, in some cases, how these processes influenced one another. Below, we discuss our results within the context of our original research questions.

Does abundance and distribution increase over time following restoration of longitudinal connectivity?

There are few long-term, spatially extensive studies of unassisted fish recolonization (Pess et al., 2014); here we attempt to address this discrepancy by measuring the long-term population-level response of mountain whitefish following restoration of longitudinal connectivity. We found a logistic model best represented the dynamics of mountain whitefish at the segment scale, with abundance reaching an asymptote in about seven years indicating geographic limits on summer population size, a result consistent with some studies on stream salmonid populations (e.g. Jenkins et al., 1999). However, most studies of freshwater fish recolonization are of relatively short duration (< 2 yrs) (e.g. Bayley & Osborne, 1993), with some exceptions. Following dam removal on the Rappahannock River, VA, USA, American eel (*Anguilla rostrata*) abundance in distant tributary streams increased over time (Hitt et al., 2012), as did abundance of spawning adult pink salmon (*O. nerka*) colonizing an Alaskan coastal stream following glacial recession (Milner et al., 2008). Yet, neither of these studies

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evaluated whether the rate of population growth slowed over time indicating density dependence. Although our analysis suggests geographic limits, we acknowledge the dynamics of the above-dam population could also be a reflection of temporal changes in mountain whitefish abundance below the dam, with the two linked by dispersal through the ladder. Addressing these linkages, will be part of future research efforts.

- In addition to population dynamics, range expansion is of considerable conservation importance because of the need to predict where a species will be in the future (Lubina & Levin, 1988), while also providing a measure of recovery following disturbance. We found that mountain whitefish were detected in the uppermost reaches of the main stem 10 years following habitat reconnection, though their occurrence in these reaches was infrequent. Measurement of range expansion by freshwater fish is rare except for studies of invasive species (Adams, Frissell & Rieman, 2002; Rubenson & Olden, 2016). For example, the upstream expansion of Idaho mountain streams by adult, non-native brook trout (*Salvelinus fontinalis*) was one to two orders of magnitude slower (estimated range: $\sim 0.009\text{-}0.12 \text{ km}\cdot\text{yr}^{-1}$) than what we observed for mountain whitefish (Adams et al., 2002).

Variation in the rate of spatial expansion by freshwater fish as they colonize new or historic habitat depends on a variety of factors including: presence, location, and permeability of barriers; differences in the propensity to migrate; population size; how the species uses the new habitat (rearing, foraging, reproduction); and habitat quantity and quality (Detenbeck et al., 1992; Bayley & Osborne, 1993; Pess et al., 2014). For example, invading brook trout failed to establish in some Idaho streams, indicating that local habitat conditions, including natural migration barriers, hindered spatial expansion (Adams et al., 2002). Furthermore, the upstream expansion of smallmouth bass (*Micropterus dolomieu*) invading the North Fork John Day River, OR, USA was constrained by cold water temperatures and high-gradient sections (Lawrence et al., 2012). We also observed that spatial expansion by mountain whitefish was potentially constrained by local environmental conditions, as they were rare in the warmer, more distant upper reaches of the 20-km main stem and small, relatively shallow tributaries.

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The observed rate of mountain whitefish recolonization of the Cedar River above Landsburg Dam supports the view that stream salmonids are capable of establishing self-replacing populations in newly available or historic freshwater habitat within 5-30 years (Milner et al., 2008; Pess et al., 2014). Much of this research has focused on anadromous fish, however (Pess et al., 2014). We suggest that to increase the effectiveness of freshwater fish conservation, there is a need for more long-term studies that assess rates of population recovery following anthropogenic or natural disturbance of species representing other migratory strategies, and how local environmental conditions influence this response. Such knowledge will improve our ability to predict how freshwater fish assemblages respond to future environmental change.

Does upstream movement rate increase over time and is it correlated with in-stream abundance?

Relatively little is known about how mountain whitefish movement behavior responds to changes in longitudinal connectivity or how their movement influences local fish populations (Baxter, 2002). The camera system within the fish ladder coupled with snorkel surveys provided insight into these questions. We observed that the annual rate of mountain whitefish movement through the ladder increased over time and was positively correlated with abundance estimates from snorkeling suggesting that mountain whitefish population growth above the dam was partly a reflection of spring-summer upriver movement rates. This supports the observation that the proximity and supply of colonizers are fundamental to the population dynamics of species spreading into new, historic, or recently disturbed habitat (Pulliam, 1988; Radinger & Wolter, 2014). Our results also support the fundamental importance of riverine longitudinal connectivity, because it facilitates the movement of multiple life stages to access points in the 'riverscape' that provide habitat critical to the successful completion of life history events (Schlosser, 1991; Baxter, 2002; Fausch et al., 2002).

Does upstream movement vary seasonally?

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We speculate that upriver movement was largely a pursuit of improved foraging opportunities, because 60 % of all movement occurred in spring/early summer and consisted primarily of sub-adult to adult-sized individuals (> 200 mm total length); these attributes are consistent with observations from other studies (Davies & Thompson, 1976; Baxter, 2002; Benjamin et al., 2014). Baxter (2002) hypothesized that the spring upriver migration of adult-sized mountain whitefish in tributaries to the Grand Ronde River, OR, USA was to access foraging conditions energetically superior to those available in downstream portions of the study system. In addition, most of the migrants moving through the ladder were relatively large, which is consistent with the positive effect of body size on movement observed in multiple families of stream fish (Radinger & Wolter, 2014).

Although the majority of upriver movements in our study occurred in spring, there was a second, smaller mode in late fall and early winter (November through January), coinciding with spawning migrations of the species elsewhere (Davies & Thompson, 1976; Northcote & Ennis, 1994). However, we have yet to observe a juvenile mountain whitefish during summer snorkel surveys indicating that reproduction was likely limited and/or juveniles moved downstream prior to surveys as observed in other systems (Davies & Thompson, 1976).

We also observed that annual variation in movement rates through the ladder co-varied with spring-summer discharge and temperature, possibly acting in concert with the physiological status of migrants (Skov et al., 2010; Taylor & Cooke, 2012; Radinger & Wolter, 2014). Consistent with the positive relationship between discharge and mountain whitefish movement we observed, upriver movement of adult coho salmon through the Landsburg Dam fish ladder during their spawning migration was positively associated with river flow and with change in flow from the previous day in two of three study years (Anderson & Quinn, 2007).

In contrast to the positive effects of river flow, annual variation in spring-summer water temperature was negatively associated with annual rates of mountain whitefish movement, which may be especially responsive to changes in water temperature

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(Benjamin et al., 2014). In autumn, the proportion of mountain whitefish departing from the Methow River, WA to the main stem Columbia River increased with mean summer water temperature. While in early spring, the proportion returning from the main stem to the Methow River increased with main stem mean winter water temperature (Benjamin et al., 2014). These authors hypothesized that the influence of water temperature on mountain whitefish movement was related to food acquisition. We are unsure of the mechanism behind the negative correlation between annual movement and water temperature we observed, but perhaps higher spring-summer temperature also acted on metabolic processes to inhibit dispersal above the dam.

Collectively, these results support the importance of discharge and temperature in modifying stream fish movement (Taylor & Cooke, 2012; Fenkes et al., 2016), including mountain whitefish. However, additional research is needed on the movement ecology of mountain whitefish and other non-diadromous species, to understand how they use river networks and the consequences of this use. If possible, this research should track the physiological status of marked individuals and how movement behavior is modified by changes in ambient environmental conditions, such as water temperature and discharge (Cooke et al., 2012). Such efforts are particularly important given climate change models predict disruptions to riverine thermal and flow regimes, which may, individually and through interactions with other factors (e.g. discharge, food), alter migratory behavior of stream fish (Cooke et al., 2012; Benjamin et al., 2014; Fenkes et al., 2016).

Management of riverine connectivity for fish has largely focused on maintaining upriver spawning migrations of anadromous species (Baxter, 2002; Calles & Greenberg, 2009). Our results, in conjunction with other studies (Baxter, 2002; Benjamin et al., 2014; Radinger & Wolter, 2014), highlight the importance of longitudinal connectivity for mobile non-diadromous fish by allowing them to migrate for purposes other than reproduction. Therefore, we recommend a holistic approach, that considers bi-directional movement, multiple fish migratory behaviors and life stages, in addition to ecosystem processes (e.g. sediment flux), when assessing the effects of natural and artificial obstructions on the longitudinal connectivity of river ecosystems (Calles & Greenberg,

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2009; Moore, 2015; van Leeuwen et al., 2017).

Do mountain whitefish track environmental conditions that manifest at the reach and mesohabitat scales?

Consistent with other large-scale studies of riverine fish populations, we found a variety of factors, including stream size, and water depth, velocity, and temperature, that manifest at different scales, influenced the above dam spatial distribution of mountain whitefish. Others have observed that mountain whitefish abundance increases with stream size indicating they are mainly a large river species (Baxter, 2002; Meyer et al., 2009; Starr & Torgersen, 2015). For example, mountain whitefish in southern Idaho streams were almost always detected in channels greater than 15 m, but rarely in channels less than 10 m (Meyer et al., 2009). Supporting these results, we found that mountain whitefish were most abundant in the wider and deeper reaches of the main stem (channel width ~ 20 m) and were rare to absent from narrow upstream reaches and smaller, shallower tributaries that also provided potential summer rearing habitat (i.e. Rock and Taylor creeks, summer wetted width < 10 m). In contrast, more northerly mountain whitefish populations, such as in British Columbia, Canada, have been observed in smaller tributary streams (McPhail & Troffe, 1998). Meyer et al. (2009) speculated there is a latitudinal shift in the occupancy of small streams by mountain whitefish, but the mechanism(s) (channel morphology, water temperature, migratory behavior, body size) accounting for these latitudinal differences are unknown.

In addition to stream size, our results suggest water temperature was also influential in determining the reach-scale distribution of mountain whitefish. Research on the effects of water temperature on mountain whitefish is sparse and generally inconclusive; however, a recent experiment focusing on early life stages showed mountain whitefish were sensitive to warm thermal regimes (e. g. maximum growth rate occurred at 13.8 °C), a sensitivity which may contribute to recent population declines in portions of their range (Brinkman et al., 2013). Another experiment exposing wild, sub-adult and adult mountain whitefish to different temperature regimes in the laboratory

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found their thermal preference ranged from 11.1 to 16.4 °C when acclimated between 7 and 15 °C (Ihnat & Bulkley, 1984). Partially supporting these experimental results, the large mountain whitefish we observed were rare in the warmer upstream reaches of CR8 through CR10 where maximum temperatures ranged from 16 to 19 °C, while abundance peaked in the cooler reaches of CR3 through CR5 (maximum temperature ~14 °C). The negative relationship between reach-scale water temperature and mountain whitefish abundance was correlative; hence, we cannot discount the influence of channel gradient and distance from the dam, in addition to unmeasured factors (e.g., prey availability), in shaping the reach-scale spatial distribution of mountain whitefish.

At the mesohabitat scale, the probability of detecting mountain whitefish was higher in deep, high velocity habitats, a finding consistent with some (Meyer et al., 2009; Starr & Torgersen, 2015) but not all studies of the species (Northcote & Ennis, 1994; Baxter, 2002; Torgersen et al., 2006). Habitat volume or size has been shown to be key predictor of fish distribution, species diversity, and trophic structure in other freshwater ecosystems (Post et al., 2000; Harvey, White & Nakamoto, 2005). Predator avoidance is often cited as determining this relationship for stream fish; for example, armored catfish (Locariidae) avoided predation from birds and mammals by occupying deep stream habitats (Power, 1984).

In addition to predator avoidance, we hypothesize that energetic factors played a role in determining the mesohabitat scale distribution of mountain whitefish. First of all, most individuals were relatively large and likely able to avoid most predators including rainbow and cutthroat trout and piscivorous birds (e.g. Belted kingfisher, *Megaceryle alcyon*) in our system. Second, deep, swift habitats have been shown to support high invertebrate prey productivity and availability (Townsend & Hildrew, 1976). And, bioenergetic modeling predicts higher energy intake in deeper habitats, especially for larger fish (Rosenfeld & Taylor, 2009). In fact, Rosenfeld & Taylor noted that higher energy intake in pools by stream fish was sufficient to account for differential use of these mesohabitats, regardless of other demonstrated functions of pool habitat.

Our continued monitoring of this system will provide additional insights into the

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relative importance of multiple environmental factors, including stream gradient, water temperature and velocity, and prey availability, found to affect the spatial distribution of resident and anadromous fish (Hicks & Hall, 2003; Rosenfeld & Taylor, 2009; Starr & Torgersen, 2015). This information will be useful in characterizing the habitat requirements for these fishes, thereby contributing to their conservation and management (Fausch et al., 2002).

Although we showed that mountain whitefish demonstrated clear temporal and spatial changes in abundance and distribution in response to restoration of longitudinal connectivity at the dam, we recognize several limitations to our study. A key limitation was establishing whether mountain whitefish were absent from above the dam at the time it was modified for fish passage. Our observations and surveys by others (e.g. Casne, 1975) detected none; thus, the population would have been at most very small. Reasons for this absence remain unknown. Presumably, mountain whitefish were either absent above the dam when it was constructed, moved below the dam and could not return after construction over a century ago, or were locally extirpated.

Regardless, our study highlights the benefits of restoring riverine longitudinal connectivity and simultaneously increasing availability of high quality habitat for a native potamodromous fish that was not the target of the restoration action. This finding is in contrast to recent studies that found artificial barriers were generally not important in explaining the distribution of riverine fish in some study systems (Branco et al., 2012; Radinger & Wolter, 2015). We speculate this discrepancy partially reflects the permeability and location of the barrier within the river network, fish life history, habitat quality and quantity, confounding effects of other stressors (e.g. hatchery supplementation), lack of pre-restoration data, and short-term duration of most river restoration effectiveness studies (Kail et al., 2015).

Interestingly, the response of mountain whitefish, a non-target species, was similar in concept to the positive effects of corridors in terrestrial ecosystems where some restorations have provided benefits beyond the boundaries of the targeted ecosystem (Brudvig et al., 2009). While our study showed the benefits of restoration to a non-target,

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native species, it is essential to also point out that restoration can benefit non-natives if they are part of the local species pool (Fausch et al., 2009).

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1 Table 1. Mean (and 95 % CI when applicable) environmental conditions during summer in the 10 study reaches of the Cedar
 2 River above Landsburg Dam, WA, USA.

3

Reach	Distance	Channel	Channel	Maximum		Water		Total		Mean (min, max) water	Boulder temperature (°C) ¹
	from dam to reach midpoint (rkm)			wetted width (m)	gradient (%)	depth (m)	95% CI	velocity (m·s ⁻¹)	95% CI		
CR1	2.5	21	0.5	0.9	(0.8-0.9)	0.42	(0.37-0.47)	44	(8-60)	1	11.3 (9, 14)
CR2	5.5	23	0.6	1.0	(1.0-1.1)	0.43	(0.38-0.48)	22	(14-30)	9	10.9 (9, 14)
CR3	8.0	24	1.2	1.1	(1.0-1.1)	0.54	(0.45-0.62)	2	(0.5-4)	30	10.6 (9, 13)
CR4	9.9	24	0.5	1.1	(1.0-1.3)	0.39	(0.34-0.43)	19	(10-28)	1	10.8 (9, 14)
CR5	11.0	23	0.9	1.2	(1.1-1.3)	0.36	(0.30-0.43)	1	(0.3-1.4)	23	10.7 (9, 14)
CR6	12.4	23	0.8	0.9	(0.8-0.9)	0.34	(0.30-0.38)	15	(9-21)	4	10.8 (9, 13)
CR7	14.2	22	1.1	0.9	(0.8-0.9)	0.30	(0.27-0.34)	8	(4-13)	10	11.6 (9, 17)
CR8	17.0	22	0.7	1.0	(0.8-1.3)	0.56	(0.41-0.72)	13	(2-24)	2	12.7 (8, 19)
CR9	19.1	11	3.3	1.4	(1.3-1.5)	0.41	(0.31-0.52)	2	(0.1-4)	42	12.3 (8, 17)
CR10	19.9	13	1.5	1.3	(1.1-1.5)	0.35	(0.30-0.40)	0.5	(0-1.0)	6	11.3 (8, 16)

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Table 2. Mountain whitefish abundance (fish·km⁻¹) and frequency of occurrence (*p*), maximum habitat depth and velocity, and sample size (*n*) of each mesohabitat type surveyed in the main stem Cedar River above Landsburg Dam, WA, USA between 2005 and 2015.

Habitat Type	Mean (± 1se) fish·km ⁻¹	Mean (± 1se) <i>p</i>	Mean (± 1se)		<i>n</i>
			maximum depth (m)	velocity (m·s ⁻¹)	
Cascade	13 (12.5)	0.05 (0.05)	0.99 (0.07)	0.72 (0.07)	20
Depositional	2 (1.9)	0.006 (0.004)	0.72 (0.02)	0.14 (0.01)	353
Pool	67 (9.1)	0.20 (0.02)	1.30 (0.04)	0.30 (0.01)	606
Riffle	24 (5.3)	0.15 (0.02)	0.72 (0.03)	0.63 (0.02)	248
Run	28 (7.5)	0.13 (0.02)	0.94 (0.03)	0.41 (0.03)	248
Step pool	52 (12.0)	0.28 (0.04)	1.33 (0.04)	0.48 (0.04)	149

Table 3. Covariate estimates from the ‘best’ logistic model predicting mountain whitefish occurrence during summer in each mesohabitat surveyed (*n* = 611) of the Cedar River above Landsburg Dam, WA, USA between 2010 and 2015.

Variable	Mean odds ratio	
	(97.5 % CI)	Wald-test
Intercept	0.008 (0.002, 0.02)	
Distance (rkm) ^a	1.4 (1.2, 1.8)	13.9*
Distance × distance	0.98 (0.97, 0.98)	23.2*
Velocity (m·s ⁻¹) ^b	9.4 (4.2, 21.0)	29.2*
Max depth (m) ^b	5.3 (3.3, 8.6)	48.6*

^a Distance (rkm) between the dam and the midpoint of the reach surveyed.

^b Average of three current velocity measurements taken at 60 % depth in each

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mesohabitat.

^c Deepest point of mesohabitat surveyed.

* p -value < 0.001.

Figure captions

Figure 1. Map of the Cedar River, WA, USA above Landsburg Dam including 10 study reaches (CR1-CR10) represented by black lines with natural migration barriers represented by red lines.

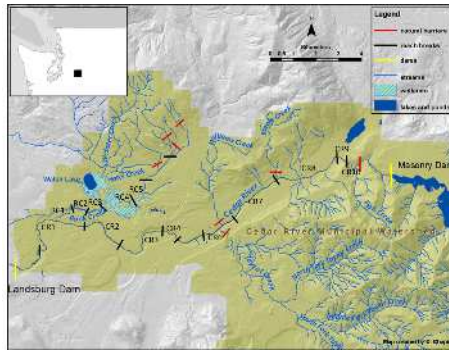
Figure 2. Best fit lines (and 95 % CI) describing the relationship between a) mean annual mountain whitefish (MWF) abundance ($\text{fish}\cdot\text{km}^{-1}$) at the segment scale above Landsburg Dam, Cedar River, WA and time (2004-2015) and b) MWF cumulative occurrence rate (number of MWF observed relative to years surveyed) and the distance (rkm) between the reach mid-point and the dam.

Figure 3. Number of mountain whitefish (MWF) counted by the Vaki camera within the Landsburg Dam fishway, Cedar River, WA divided by the number of days each year that the camera was operational, 2008-2014.

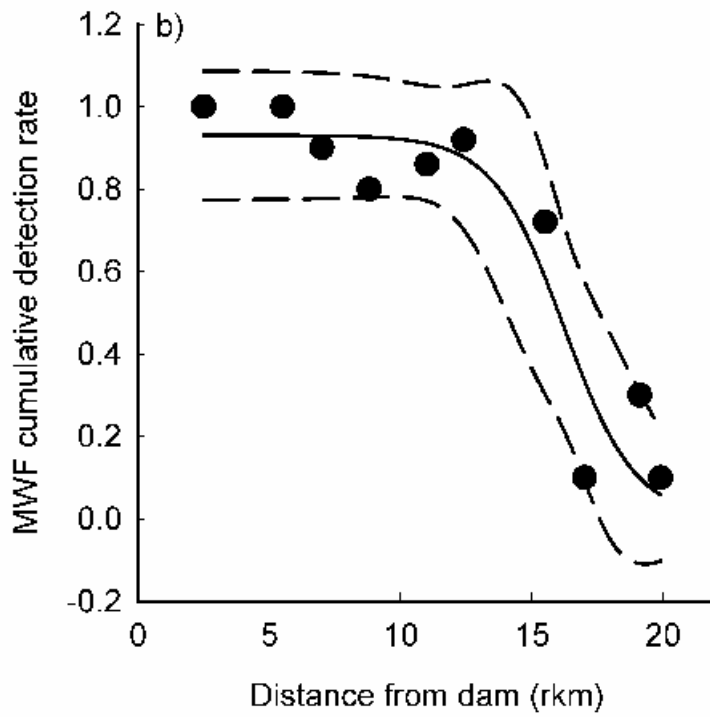
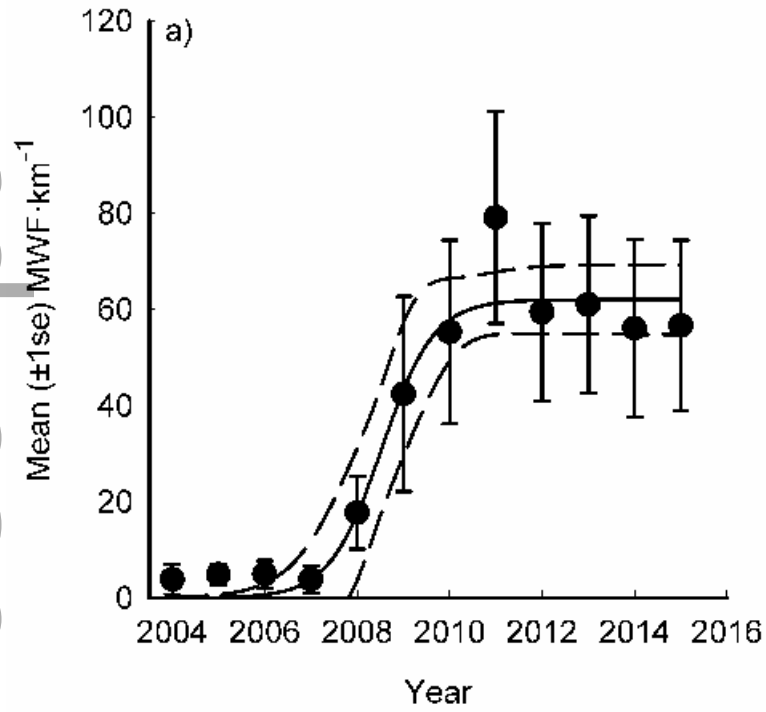
Figure 4. Mean monthly percentage of annual upstream mountain whitefish (MWF) migrants captured by the Vaki camera within the Landsburg Dam fishway, Cedar River, WA based on total annual number observed between 2008 and 2014.

Figure 5. Histogram of estimated length (mm) for mountain whitefish detected by the camera located in the fish passage facility, Landsburg Dam, Cedar River, WA between 2008 and 2014.

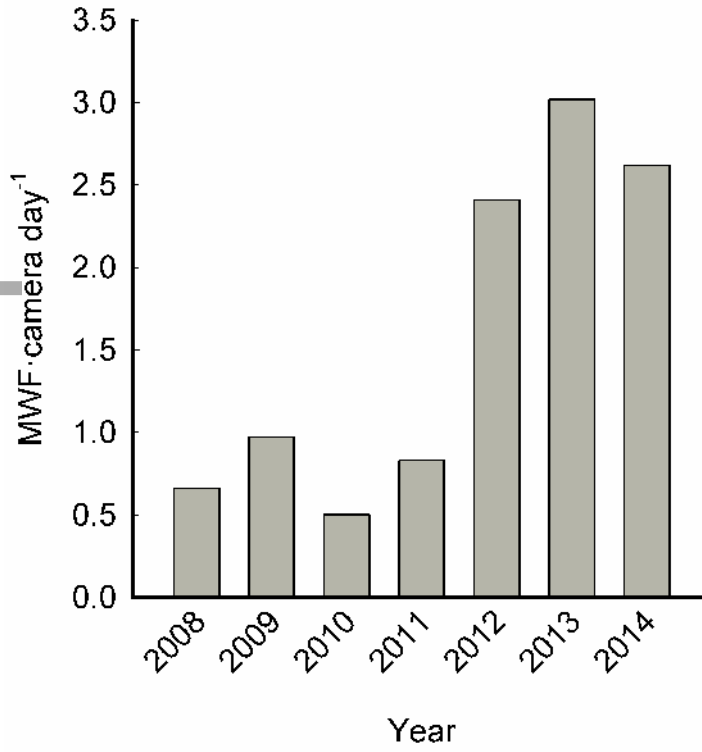
Figure 6. Best fit lines (and 95 % CI) describing the relationship between a) mountain whitefish (MWF) abundance ($\text{fish}\cdot\text{km}^{-1}$) above Landsburg Dam, Cedar River, WA averaged across 2010-2015 relative to the distance (rkm) between the dam and reach mid-point and b) reach-scale MWF abundance ($\text{fish}\cdot\text{km}^{-1}$) vs. spring-summer water temperature ($^{\circ}\text{C}$) above Landsburg Dam.



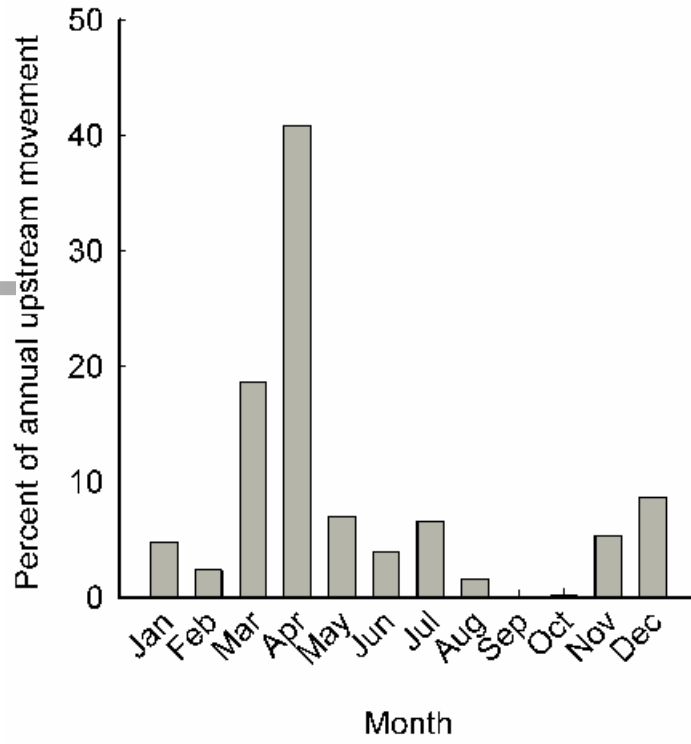
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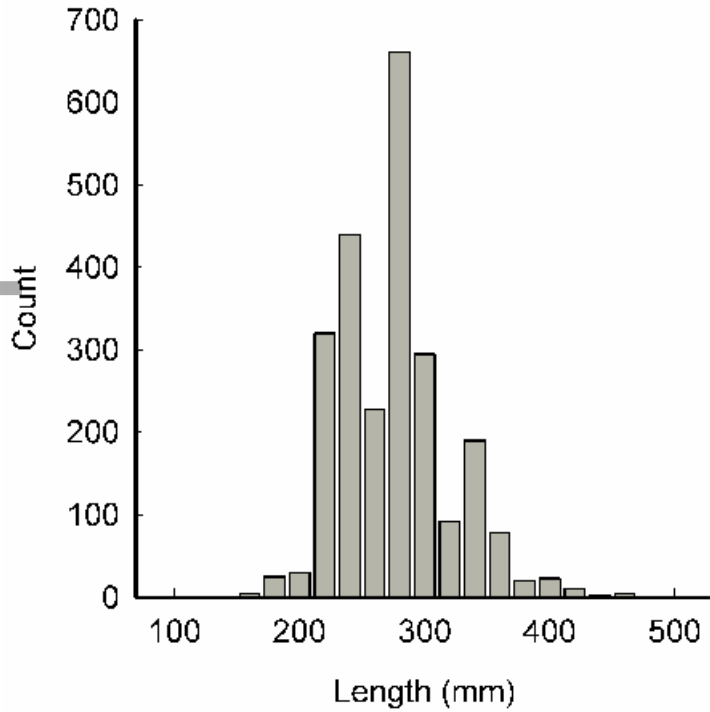
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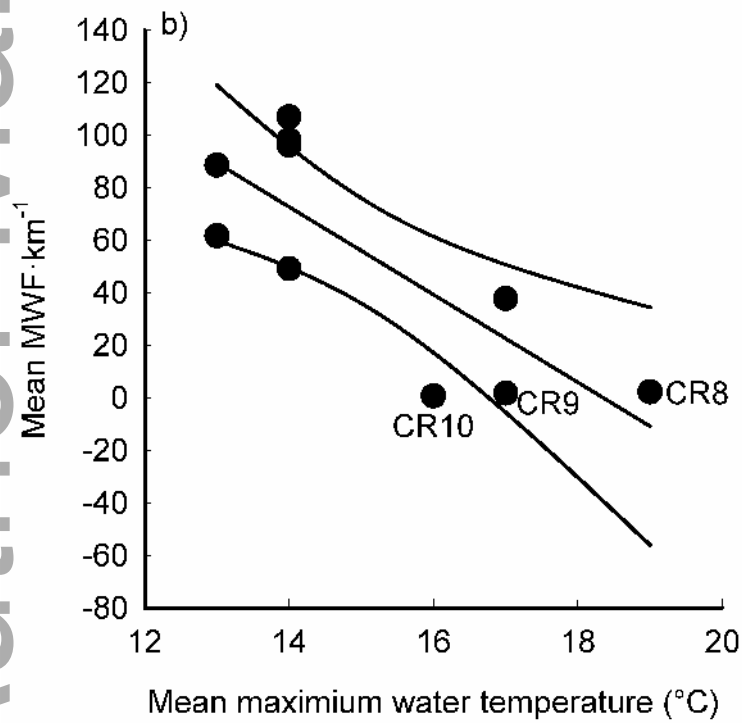
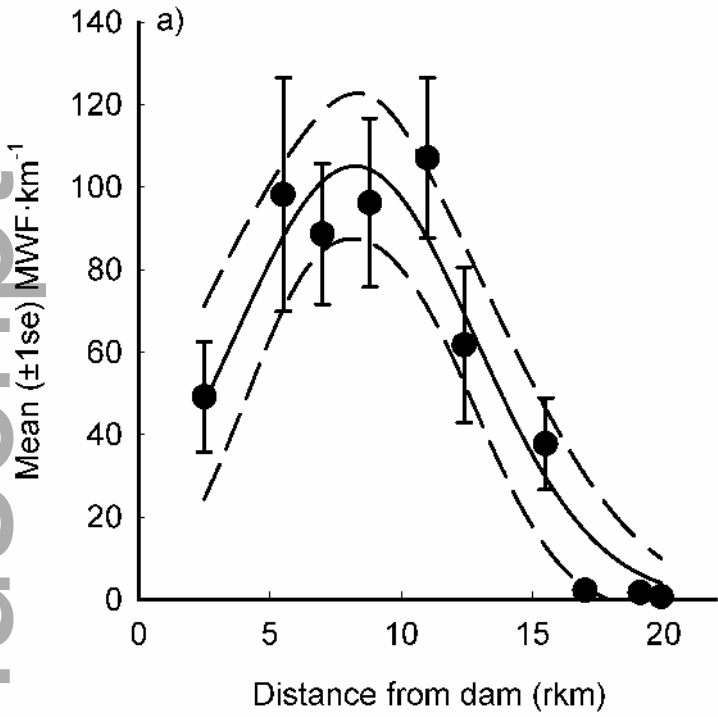
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