

AN ABSTRACT OF THE THESIS OF

Justin M. Thorson for the degree of Master of Science in Fisheries Science presented on December 2, 2021.

Title: Factors influencing population density of stream-living Redband Trout in southeast Oregon, USA.

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Fisheries managers often use models of population density to evaluate the status of stream-living fishes, but many of these models have low predictive performance for abundance and density. These models could incorporate several factors that can limit population density, particularly the effect of body size, envisioned by the theory of self-thinning. In addition, constraints imposed on density by physical and biological habitat conditions in streams are important to consider. In this study, we describe a two-phase approach to predict density of stream-living fish. We started by modeling maximum density in relation to body size (length and mass) using quantile regression. We extracted residuals from these models (deviations from maximum predicted density, termed “residual density”). In a second phase of analysis, we applied generalized linear models to predict residual density in relation to habitat factors known to limit abundance of stream-living salmonids (temperature, discharge, and non-native species). Models were based on data from Redband Trout (*Oncorhynchus mykiss* spp.) sampled over 1615 site visits in the Northern Great Basin Region of southeast Oregon, USA. Results in the first phase of the analysis indicated strong evidence for the influence of body size on maximum fish densities in sampled stream reaches. However, in the second phase of the analysis, we found poor predictive capability for

models attempting to correlate limiting habitat factors to residual density. The importance of body size as a predictor of population density is qualitatively consistent with theoretical expectations based on body size and density dependence in stream-living fish, as well as a host of empirical studies reporting inverse relationships between body size and population density. Our inability to predict residual density of Redband Trout in this study is also consistent with a long history of variably successful attempts to predict density based on local environmental variables. Although there are several possible reasons for why density of stream-living fish is so difficult to predict based on environmental variables, body size is a consistently important factor. Given this, additional work to understand environmental drivers of body size may be a more productive route to better understand factors that ultimately drive population density of stream-living fishes.

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Factors influencing population density of stream-living Redband Trout in southeast Oregon,
USA

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Justin M. Thorson, Author

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CONTRIBUTION OF AUTHORS

Ivan Arismendi and Jason B. Dunham assisted with the data analysis and editing of the thesis. During the peer-review of manuscripts considered for publication of this work, these individuals will act as corresponding authors.

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Introduction

Spatial and temporal patterns in the abundance of stream fishes are important factors managers consider when looking at when setting harvest regulations or developing species conservation plans (Isaak et al. 2020, Hubert and Quist 2011). These patterns are the result of physical and biological processes operating at multiple scales including stream discharge, thermal regimes, intra- and interspecific interactions, and stream productivity. Collectively, these factors influence growth, movement, reproduction, and survival in riverine fishes (Poole and Berman 2001, Fausch et al 2002, Rosenfeld 2003, McMillan et al. 2012, Grossman and Simon 2020), and these processes drive abundance. Although the importance of these factors is reasonably well known, attempts to predict the standing stocks of salmonid fishes (e.g., abundance, density, or biomass) have not fully considered them together and often fail to produce accurate predictions (Dunham and Vinyard 1997a, Fausch et al.1988, Van Horne 1983, Muhlfeld et al. 2001).

In this study, we considered abundance of stream-living trout in the context of density-dependence and physical factors that can limit population density. Density dependence is widespread in trout and other salmonids and occurs as a response to intraspecific competition for limited space and energetic resources (Elliott 1994, Rose et al. 2001, Grossman and Simon 2020, Chapman 1966). Often, years of data are required to evaluate the influence of density dependence on many responses (e.g., recruitment, survival, or fecundity), but changes in growth and body size indicating patterns of density dependence and can be explored using observations of body size and population density (Grossman and Simon 2020). In theory, the relationship between body size and population density should be inverse (i.e., lower population density as body size increases) as a result of density-dependent constraints imposed by the capacity of a given location to support trout (Grant 1993, Bohlin et al. 1994). This negative relationship,

referred to as self-thinning, is often observed through time (e.g., cohorts) or space (e.g., locations) and presumably represents constraints imposed by resource requirements (e.g., food or space) associated with individual body size and thus population density (Dunham and Vinyard 1997b, Grant et al. 1998, Rincón and Lobón-Cerviá 2002).

Because of its hypothesized relationship to resource competition, self-thinning is commonly observed in salmonid populations assumed to be at or near carrying capacity, but factors other than space and metabolic needs can also result in self-thinning in salmonid populations (Grant et al. 1998). In some cases, the slopes of self-thinning relationships can differ for smaller fish versus larger fish, presumably due to habitat segregation between different age classes as a potential response to intraspecific competition or thresholds in size-related resource requirements (Rincón and Lobón-Cerviá 2002). In addition to habitat segregation, behavioral differences relationships among larger fish in access to high quality habitats can have a large influence on the presence of self-thinning in stream salmonids. For example, larger and dominant individuals have higher metabolic requirements and may occupy larger spaces than smaller and subordinate individuals (Grossman and Simon 2020). The influence of self-thinning can also differ based habitat availability, particularly differences in discharge and space constraints among years. For example, in years with high discharge, self-thinning may be expressed to a lesser extent than during low flow years, where low flows and reduced habitat volume can significantly increase intraspecific competition (Dunham and Vinyard 1997b).

Whereas body size is clearly an important factor that can limit densities of stream-living salmonids, it is also clear that other factors can limit density below theoretical maximums imposed by body size. As a result, consideration of other potential biotic and abiotic constraints, such a stream temperature, discharge, and competition with non-native species, as possible

limiting factors on fish density may be important (Magnuson et al. 1979, Poff et al. 1997, Miller et al. 2014). In the context of self-thinning, deviations from empirical relations depicting lower than expected densities in relation to body size can indicate the potential influences of these alternative constraints (Figure 1). Limits on population density related to body size can be modeled with statistical techniques such as quantile regression, which are well-suited to such questions (Cade and Noon 2003, Cade and Guo 2000). Deviations or residuals from such relationships may indicate the influences of factors other than body size that constrain local densities (e.g. Cade et. al 1999; Figure 1).

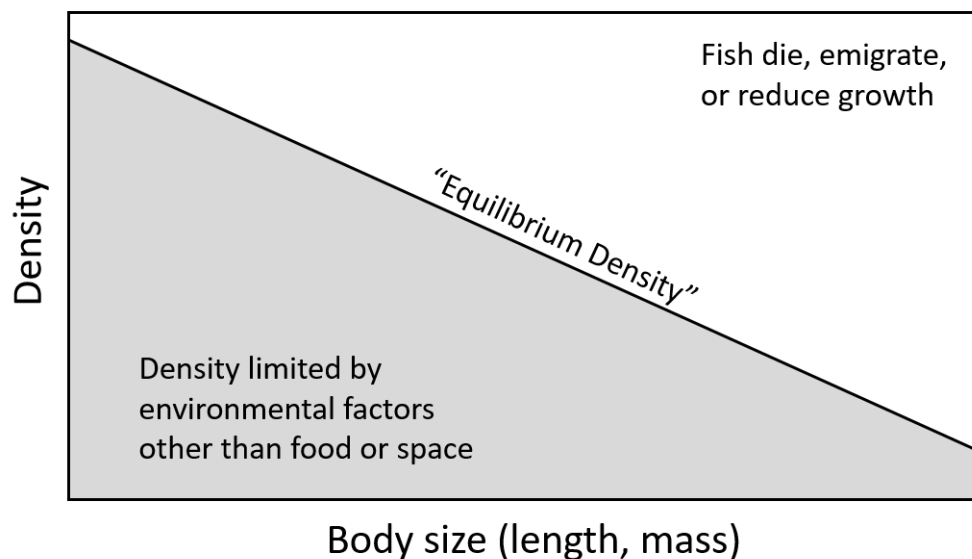


Figure 1. Schematic diagram illustrating self-thinning in salmonid populations, indicating a negative linear relationship between mean body size (by either length, mass, or other measure of size) and population density. Such relationships can be considered on any scale (e.g., logarithmic, or linear). Populations below maximum equilibrium density are limited by other factors other than food or space.

In this study, we used data on body size and density Redband Trout (*Oncorhynchus mykiss* spp.) sampled from 1615 site visits in Southeastern Oregon streams between 2006 and 2012 to test two hypotheses related to density-dependence. First, using data on fish population density (fish/m²) and mean individual body size for both mass (g) and fork length (mm), we

expected to find a negative relationship between population density and mean body size. We also investigated whether several physical and biological conditions can constrain population density using the residuals from the upper predicted quantiles of population density (“residual density”) in this relationship. These included stream temperature (Isaak et al. 2017a) and discharge (Miller et al. 2018), along with the presence of non-native Brook Trout (*Salvelinus fontinalis*), which in previous analyses have been identified as factors that influence the body size and population density of Redband Trout (Zoellick 1999, Meyer et al. 2010, Miller et al. 2014). Collectively, the density-body size relationship can help to understand constraints on population density imposed by alternative physical or biotic factors important to stream-living fishes like Redband Trout.

Methods

Study Location

We studied Redband Trout in the hydrographic Great Basin of Southeastern Oregon (Grayson 1994, Figure 2.), a region that covers ~ 36,600 km² with vegetation primarily composed of high elevation (>1200 m) sagebrush steppe and conifer forest (Minshall et al. 1989). The region contains six major endorheic subbasins, with streams and rivers in the region emptying into terminal and sometimes saline lakes or playas in the lower elevations (Grayson 1994). While currently hydrologically separated, many watersheds within these basins were formerly connected to one another by pluvial lakes during the Pleistocene (Hubbs and Miller 1948 , Bisson and Bond 1971, Minckley et al. 1986). The high degree of topographic and hydrographic variability in the region is paralleled by variation in environmental conditions in streams as indicated by stream flow and temperature regimes. For example, measured average August stream temperatures in 2018 ranged from 7.2 C° to 20.3 C° for 123 monitoring sites in the basin (Thorson et al. 2020) and approximately 84% of stream length in the region are classified as intermittent or ephemeral by National Hydrography Dataset Plus (NHD Plus) stream reaches (US EPA 2021). Stream flow is highly seasonal and dominated by snowmelt (Poff 1996), with flows lowest in late summer through winter and highest during the period of snowmelt and highest precipitation (April-June). For example, measured flows at USGS gage station 10396000 on the Donner und Blitzen River for the period of study ranged from 0.34 m³/s in January 2007 to 35.31 m³/s in May 2011.

Species of Interest

Redband trout includes diverse lineages of inland *O. mykiss* found in watersheds east of the Cascade Mountains and includes the populations we studied in the Northern Great Basin region

(Behnke 1992, Currens et al. 2009). For management purposes, populations are delimited into six Species Management Units (SMUs) that align with the major hydrological basins in the regions (Meeuwig and Clements 2015) (Fig. 2., Table 1.). These SMUs represent distinctive geographic locations and corresponding patterns of genetic divergence as a result of past connections to other basins (Meeuwig and Clements 2015). Redband Trout generally occupy cold water ($< 18\text{ }^{\circ}\text{C}$), with growth potentially lowered at temperature conditions above this threshold and mortality increasingly likely as temperatures exceed $24\text{ }^{\circ}\text{C}$ (Gamperl et al. 2002, Rodnick et al. 2004).

Fish Dataset

To evaluate relationships between the population density (fish/m²) of Redband Trout and habitat features (stream flows and temperatures) within our study area, we used data on fish collected by ODFW crews at 1,212 sites between May 2006 and October 2012 (Figure 2.). A total of 1615 surveys of Redband Trout were conducted at the sites, with 490 surveys representing 102 sites surveyed multiple years. (2-6 years of repeated surveys at these 102 sites). Sampling efforts were centered on major basins across years (Table 1.), and thus location and year of sampling could be confounded from a statistical perspective. Surveys were conducted using backpack electrofishing units using multi-pass depletion methods, with a subset (102) of surveys also employing mark-recapture methods (Dunham et al. 2009). Trout representing year-of-young (fork length $< 60\text{ mm}$) were excluded from the analysis (Meeuwig and Clements 2014). In addition to the fish capture data, the survey reach was measured to find stream length, and measurements of stream width and depth were collected from five equally spaced transects along the survey reach. Surface area was then calculated by multiplying the average transect width by the total length of the survey site.

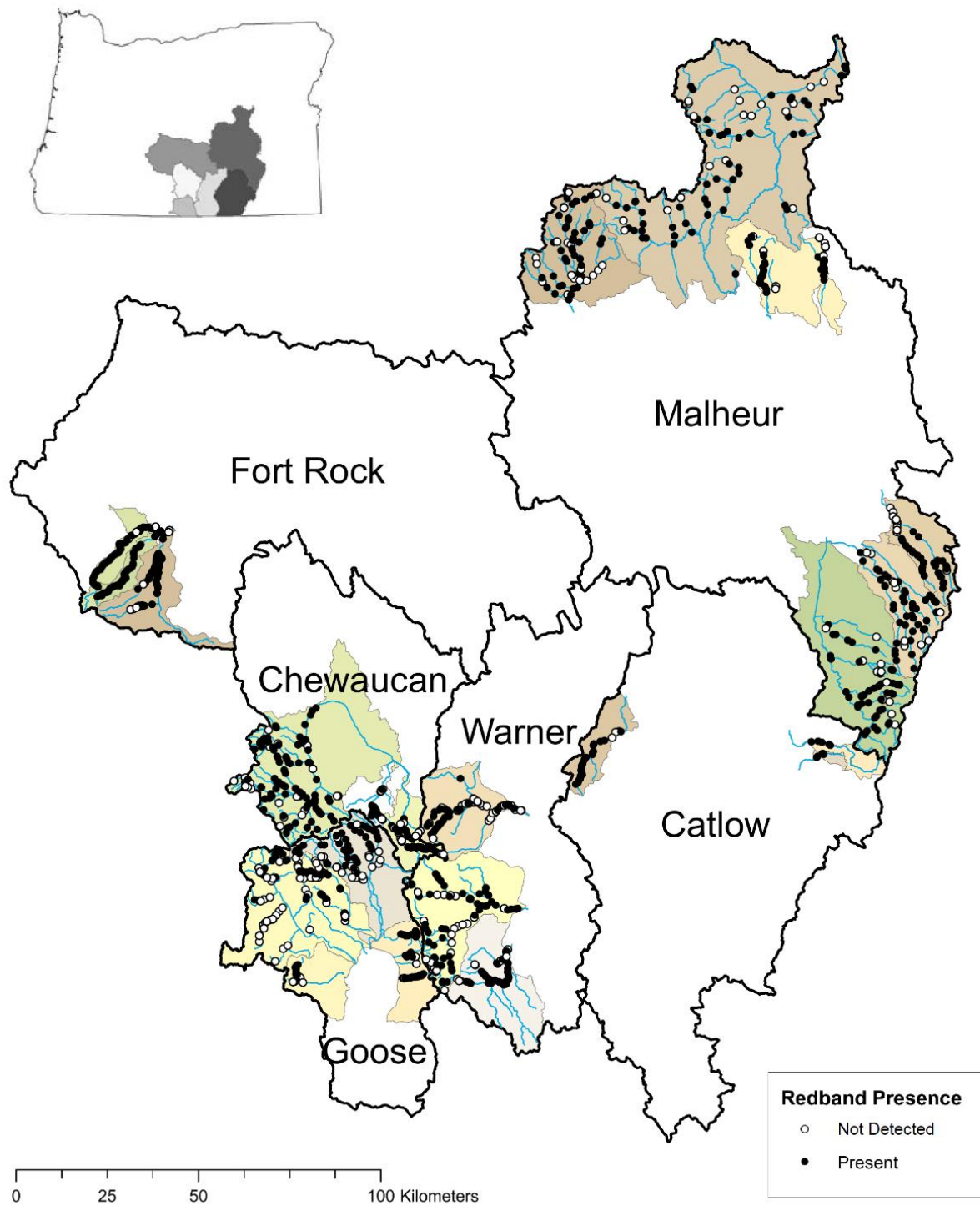


Figure 2. Map of Species Management Units (SMUs) for Redband Trout in southeast Oregon (outlined with black lines) Within SMUs, fish sampling locations within shaded HUC10 watersheds and major streams sampled are indicated, with survey sites indicated by dots. Survey sites with Redband Trout present or not detected are indicated by black or white dots, respectively.

Table 1. Number of surveys per year and Species Management Unit (SMU) for all visits in the study

SMU	2006	2007	2008	2009	2010	2011	2012
Catlow	0	8	0	11	13	19	7
Chewaucan	32	33	25	69	30	29	65
FortRock	0	30	24	61	28	25	83
Goose	0	94	24	29	87	29	29
Malheur	0	39	139	33	37	158	39
Warner	0	96	24	31	79	30	26

Standing stock of Redband Trout was summarized for each visit in terms of numerical density (fish/m²). Depending on how fish were sampled, mean population size estimates \pm SD for Redband Trout were estimated using the K-pass depletion method and Lincoln-Peterson mark-recapture methods (Rosenberger and Dunham 2005). We used the *FishR* package (Ogle et al. 2021) and the R code in their *FishR* Vignette to estimate fish population size. Among the depletion estimates, 54 surveys had inadequate data for proper estimates, which included surveys with a larger number of fish encountered on subsequent passes or negative population estimates for the lower 95% confidence interval. A regression analysis relating mark-recapture as the response and depletion estimates as the predictor for the 102 sites that used both methods yielded a slope of 1.58 and an $R^2 = 0.73$. To find the mean fish mass for each survey, a length/mass equation for Rainbow Trout referenced in Railsback et al. (2005) was used to estimate the mass of each captured Redband Trout caught during the depletion passes. To account for the differences in surface area between survey reaches, population estimates were divided by the surface area of the site to calculate to number of fish per square meter.

Predicting Population Density of Redband Trout

We initially predicted maximum density of Redband Trout within sites based on the size of conspecifics across all sites and years sampled, based on the theory of self-thinning in space

across all cohorts of fish older than age 1 (Dunham and Vinyard 1997a). For this, we used data from 1129 unique surveys to determine the influence of body size on maximum fish densities, two quantile regression models were fit between $\log_{10}(\text{Mean Mass})$ and $\log_{10}(\text{Estimated Density})$, and Mean Length and $\log_{10}(\text{Estimated Density})$ using the `quantreg` package (Koenker et al. 2018) on R (Version 3.6.0). Residuals for the linear regression equations at the upper edge of the distribution (i.e., quantiles 95th, 90th, 80th, and 70th) were then extracted for each site visit.

We considered body size to impose a primary limitation on maximum population density of Redband Trout. Residual deviations from predicted maximum densities could indicate the presence of alternative limiting factors (Cade et al. 1999). We considered three alternative factors (in addition to body size) as limiting density of Redband Trout in our study sites including the presence of nonnative Brook Trout and two primary physical environmental features: stream temperature and discharge. We determined presence of nonnative Brook Trout using the capture data for each survey (numbers of Brook Trout were not quantified). To quantify these environmental features, the latest coordinates for each site were used to create a point shapefile in ArcMap (Version 10.7.1). To predict the impact of stream temperature on Redband Trout density, mean predicted August stream temperature from NorWeST (Isaak et al. 2017) was used. Modeled stream temperature data used was available for each year of the study. Predicted discharge estimates from Miller et al. (2018) were also used to predict the influence of mean annual discharge on fish density. The stream discharge data was aggregated to calculate the mean annual discharge for each National Hydrography Dataset (NHD) COMID, which was then joined to the NHD shapefile (USGS 2021). Both stream datasets were spatially joined into one stream shapefile using the flowlines from the NHD Plus (US EPA 2011). The site points

were then snapped to the combined stream shapefile to extract the relevant reach data (i.e., mean annual discharge and mean summer stream temperature) used in the analysis.

With data on alternative limiting factors assembled, we employed multiple linear regression to determine their potential influences on population density of Redband Trout on residual densities at sites (the value of residuals from quantile regression model predicting maximum density from conspecific body size). To reduce co-linearity among variables a correlation matrix was employed, and any variables with >70% correlation were removed. Population density and mean body mass were \log_{10} transformed to account for non-linearity and non-normality.

Because we expected the response of Redband Trout to temperature to be quadratic (Isaak et al. 2017b), we included a squared term for mean August temperature in addition to the linear value for mean August temperature. A \log_{10} transformation was also applied to mean yearly discharge to correct for the non-normality in the data. To avoid issues with 0 log, 1 was added to discharge before log transformation. To account for variation between years and basins on fish density, site visit year and SMU were used as random effects.

Results

Self-Thinning Analysis

A negative relationship between mean fish size and estimated density was found for both $\log_{10}(\text{Mean Mass})$ and Mean Length for all quantile regression lines (Figure 3, Table 2). For both $\log_{10}(\text{Mean Mass})$ and Mean Length, the regression slope was lowest and least significant for the 95th quantile. All the remaining quantile regression lines were significant at the 95th percentile. Quantile regression slopes appeared to better fit the upper bounds of the distribution for the Length/logDensity than the logMass/logDensity relationship. Overall, variability in densities was greater for locations with smaller sized fish (Figure 3)

Table 2. Quantile regression statistics for the relationship between Fish Density ($\log_{10}\text{Density}$ (Fish/m²) and (a.) Mean Length (mm) and (b.) $\log_{10}\text{Mean Mass}$ (g).

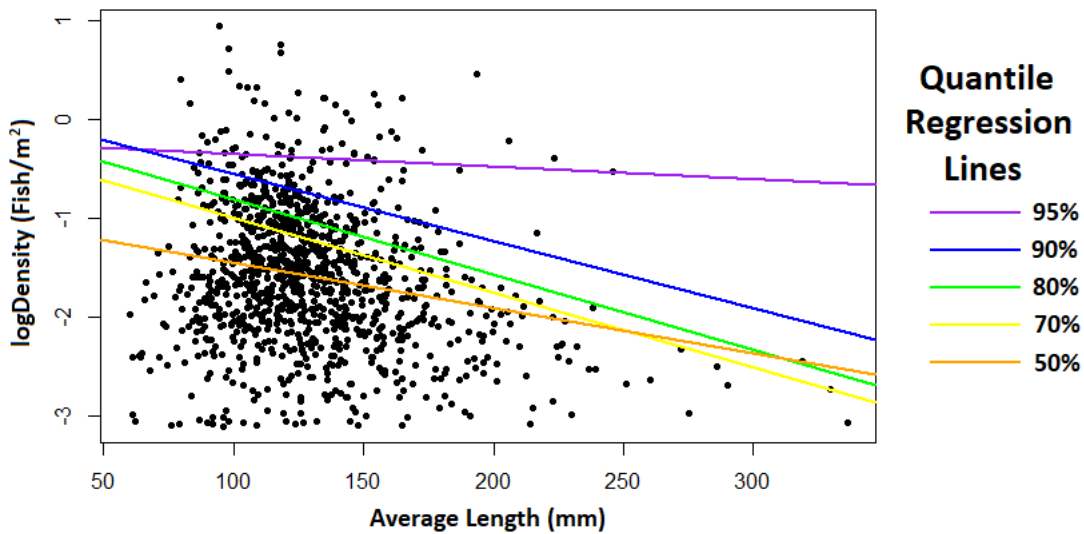
a.

Quantile	Slope	Intercept	T (slope)	p (slope)
95	-0.0013	-0.2181	-0.588	0.5569
90	-0.0068	0.1218	-4.685	< 0.001
80	-0.0076	-0.0530	-9.915	< 0.001
70	-0.0076	-0.2415	-13.437	< 0.001
50	-0.0046	-0.9869	-7.457	< 0.001

b.

Quantile	Slope	Intercept	T (slope)	p (slope)
95	-0.3462	-0.0175	-0.105	0.9167
90	-0.3836	-0.1790	-5.213	< 0.001
80	-0.4898	-0.2935	-5.870	< 0.001
70	-0.5550	-0.4163	-6.076	< 0.001
50	-0.2067	-1.2819	-3.131	0.0018

a.



b.

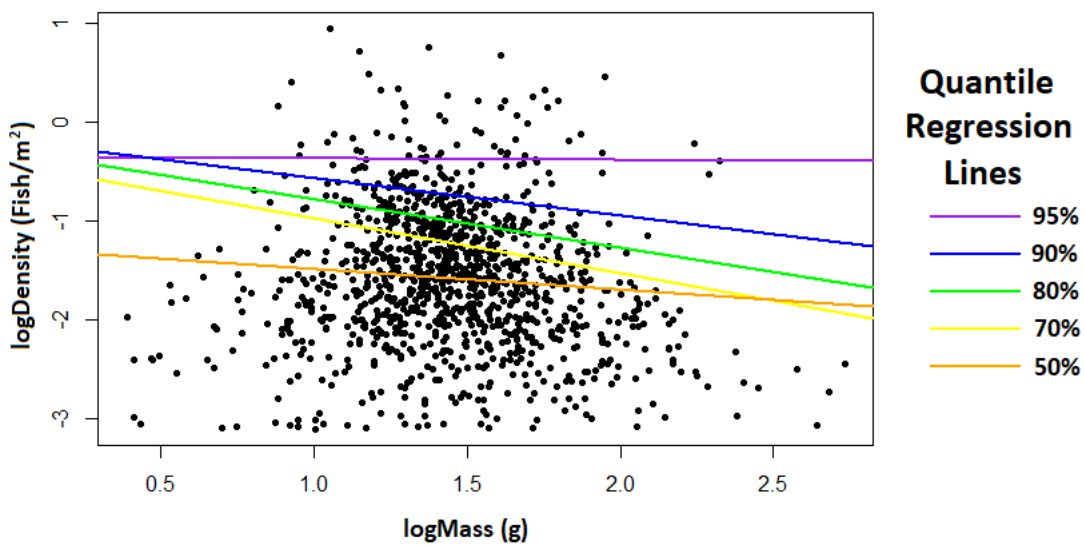


Figure 3. Scatter plot of \log_{10} population densities (Fish/m²) for site visits in the study in relation to (a.) Mean Length (mm) and (b.) \log_{10} Mean Mass (g) with regression lines used in the analysis for reference

Multiple Linear Regression

Multiple linear regression model fits for the quantile residuals from both \log_{10} (Mean Mass) and Mean Length and the limiting habitat variables (Aug Temp, Sq Aug Temp, Brook Trout, and \log_{10} Mean Yearly Flow, SMU, and Year of Survey) was poor ($R^2 < 0.1$) for all quantiles (Table 3,

Figure 4). The best model fits for both the Mean Length and Mean Mass models were for the 95th quantile, while the lowest fits were those for the 90th quantile model.

Table 3. Full model fits for (a.) Mean Length (mm) and (b.) \log_{10} Mean Mass (g) of residual density as explained by potential limiting factors (Aug Temp, Sq Aug Temp, Brook Trout, \log Mean Yearly Flow, SMU, and Year of Survey).

a.				b.			
Quantile	df	F	R ²	Quantile	df	F	R ²
95	1113	4.182	0.05336	95	1113	4.372	0.05564
90	1113	4.059	0.05186	90	1113	4.088	0.05222
80	1113	4.154	0.05301	80	1113	4.103	0.0524
70	1113	4.15	0.05297	70	1113	4.134	0.05277

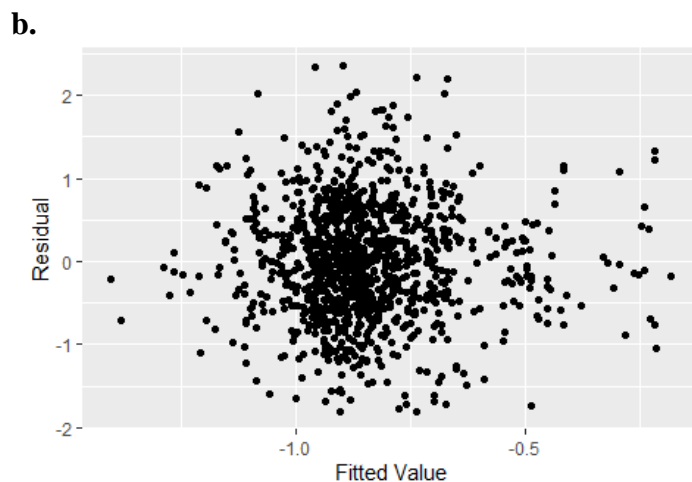
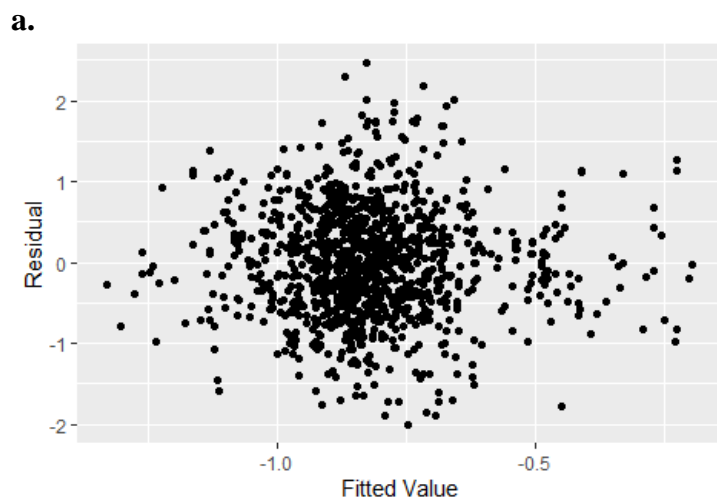


Figure 4. Residual plots for 90% quantile models for (a.) Mean Length (mm) and (b.) \log Mean Mass (g) to display model fits.

After accounting for the effect of self-thinning on fish density, coefficients for model variables did not appear to differ between models for each quantile (Appendix Table 1). While overall the models showed poor predictive capacity, the large sample size included in the study did show significant slopes for some predictor variables. Mean August temperature was positively associated with fish density residuals, with a negative association to quadratic term for Mean August Temperature and the fish density residuals. Residual fish density was positively associated with Mean Yearly Discharge. Brook Trout presence was negatively associated with residual fish density. Mean August Temperature, Squared Mean August Temperature, and Mean Yearly Discharge all had slopes significantly different from zero at $p = 0.001$ confidence level, while Brook Trout presence was significant at the $p = 0.1$ level. Despite the confounding of Year and SMU to site visits, there was evidence to suggest that residual densities differed between years at the $p = 0.05$ confidence level for all years except 2007. No differences in residual density were found between SMU's at the $p = 0.05$ level.

Discussion

For decades, fisheries biologists have sought to find models capable of predicting standing stock of salmonids with variable success (Platts and Nelson 1988, Fausch 1988, Rosenfeld 2003). In this study we evaluated relationships between population density (fish/m²) of Redband Trout and two sets of factors hypothesized to influence density including: body size and environmental variables (stream discharge, temperature, and presence of non-native Trout). Using quantile regression to predict maximum density of Redband Trout, we show that both mass and length were effective predictors. Sites at or above the 90th quantile of the logMean Mass/Mean Length and logDensity relationship were at or near maximum predicted density, but most sites were well below this threshold. To potentially explain these deviations from maximum predicted density, we extracted residuals from values predicted by the 90th quantile regression based on body size (“residual densities”), and modeled them as a function of stream discharge, temperature, and presence of non-native Brook Trout. This analysis indicated that none of these factors could explain residual densities, even though they are often cited as important drivers of salmonid populations in streams (Magnuson et al. 1979, Poff et al. 1997, Dunham et al. 2002). Based on these findings, we discuss implications for future studies to better predict standing stock of salmonids in streams.

Based on the prevalence of density dependence in stream-living salmonids (Grossman and Simon 2020) and widespread observation of inverse relationships between body size and population density of these species (Chapman 1966, Grant 1993, Bohlin et al. 1994, Elliott 1994, Dunham and Vinyard 1997, Hughes and Grand 2000) we expected a negative relationship between body size and population density. Indeed, such relationships can emerge due to intraspecific competition for limited energetic resources and space for populations near carrying

capacity (Chapman 1966, Grant 1993, Bohlin et al. 1994). In this study we did not seek to identify which of these factors or others potentially associated with body size were important, as they can be extremely difficult to identify with such observational data alone (Dunham and Vinyard 1997a). In a purely predictive context, we found that quantile regression was particularly useful in modeling possible limits to maximum density constrained by body size.

One important finding from this work is that deviations from predicted maximum density were greater for smaller fish (< ~150 mm) versus larger fish. This could indicate that factors other than body size are more likely to influence numerical densities of smaller fish. Similar studies have also noted this, offering a range of potential explanations (Rincón and Lobón-Cerviá 2002, Elliott 1994). In natural stream settings, larger individual salmonids may differ in their vulnerability to predators (Penaluna et al. 2021, Harvey and White 2017), are typically competitively dominant to smaller individuals (Young 2004). Larger individuals also have greater per-capita resource requirements (Hughes and Grand 2000) and since they are more likely to be mature, their patterns of resource use may also reflect more than just the need to grow or survive, but also to reproduce (Kendall et al. 2015). Although we were unable to evaluate these processes in this work, we suspect variability in their influences among locations was likely important and is an important area for future work to better understand variability in body size itself, with implications for expected density of Redband Trout in streams.

Although we observed considerable deviations from maximum densities predicted by body size, especially for locations with smaller sized individuals, we were unable to link this residual density to stream discharges, temperatures, or the presence of nonnative Brook Trout. Although temperature is known to be important for salmonids for many reasons (McCullough et al. 2009), we were unable to detect associations with summer (August mean) temperatures. This

may be because for many stream salmonids, stream thermal regimes outside of the summer season can also be important, particularly in the context of growth opportunities that vary across thermal regimes and potentially drive body sizes (Railsback et al. 1999, Hayes et al. 2000, Benjamin et al. 2020, Armstrong et al. 2021). Similarly, discharge has been shown to be an important factor in predicting fish abundance (Isaak et al. 2020), likely due to its association with processes and patterns influencing productivity in lotic systems (Vannote et al. 1980). Stream productivity (both instream and riparian or allochthonous subsidies) can also interact with temperature and drive food availability, growth, and ultimately body size of salmonids (Wipfli and Baxter 2010, Whitney et al. 2020). To address these interactions, more detailed studies of spatial and temporal variability in thermal regimes, productivity and growth of Redband Trout would be needed.

Productivity in partially migratory species such as Redband Trout is not only limited by local conditions at the time of survey, but by conditions in adjacent locations or ecological neighborhoods, particularly for adult fish (Schlosser 1995, Wiens 2002, Rosenfeld 2003). For example, adult Redband Trout may migrate long distances (>50 km), in streams with strong longitudinal environmental gradients and migratory connectivity (Anderson et al. 2011, Hahlbeck 2021). While movement patterns in smaller fish are generally more limited, studies have suggested that they can migrate within local watersheds to minimize exposure to warm water temperatures during the summer and to maximize growth potential in the fall (Tattum et al. 2013, McMillan et al. 2012). Accounting for this spatial and temporal variability and habitat complementation may be important in predicting density of Redband Trout in this region.

Despite previous studies demonstrating lower densities of Redband Trout in relation to Brook Trout presence (Miller et al. 2014) we did not find sufficient evidence in this analysis that

Brook Trout presence was important in predicting residual densities in Redband Trout. Unlike other species, such as Bull Trout (*Salvelinus confluentus*) and Cutthroat Trout (*O. clarkii* ssp.), negative impacts from interactions between Redband Trout and Brook Trout may be limited due to habitat partitioning among the two species limiting interspecific competition that can result in lower species abundance, as was hypothesized by Miller et al. (2013). These spatial patterns may occur on large scales, such as differences in suitable thermal regimes between species (Benjamin et al. 2016) or may occur on local scales within stream reaches where species may differ in microhabitat usage or feeding strategies (Nakano and Furukawa-Tanaka 1994). More mechanistic studies that identify patterns of habitat use within sites and species interactions may be required to better understand impacts of non-native species, particularly Brook Trout, on Redband Trout abundance (Peterson et al. 2004).

There may also be differences between juveniles and adults in terms of what factors influence abundance, particularly in migratory Redband Trout populations. Studies of juvenile salmonids have had much greater success in predicting abundance using habitat variables, even without considering the influence of self-thinning on density. For example, Isaak et al. 2020 used many similar limiting habitat metrics ($R^2 = 0.57$) as this study (Mean August Stream temperature, mean yearly discharge, and Brook Trout abundance) to predict abundance of juvenile *O. mykiss* in the Columbia Basin. Density is also heavily determined by spawning location, particularly for juvenile fish. Studies of anadromous *O. mykiss* in the nearby John Day basin found high prediction ($R^2 = 0.79$) of juvenile occurrence in relation to spawning habitat and neighborhood habitat characteristics to important juvenile rearing (Falke et al. 2013).

There were some facets of the survey design that limited the analysis of population density to habitat attributes in this study despite the relevance of the habitat factors included in

the analysis. First, site visits were not randomly distributed between years and basins, which limited both analysis of the impact of different yearly conditions on fish density. This also limited analysis of variability that could be attributed to spatial factors ranging from intrinsic (e.g. phenotypic differences in a region with a high degree of genetic and phenotypic diversity between populations; Currens et al. 2009, Meeuwig and Clements 2015, Gamperl et al. 2002) or extrinsic (e.g., environmental modifiers that act independently or interactively with temperature, discharge, or nonnative Brook Trout) factors that influence population density. Much of the yearly differences may be accounted for by variation in flow and temperature but a longer time series of observations and analysis design to account for spatial and temporal variability would be needed to elucidate these potential influences. For example, lagging effects related to flow and cohort growth can be more easily detected with multiple visits when compared to single visit sites (Kovach et al. 2016, Elliott 1994, Leasure et al. 2020). Finally, while our study included a relatively long period (7 individual years), this still may not be long enough to fully account for variability among populations of Redband Trout in the region given their maximum lifespan of at least 6-7 years (Kendall et al. 2015). Longer term studies, while difficult to execute, might help determine the influence of environmental conditions on density on multiple generations of Redband Trout and help better understand how such variability influences population dynamics in fishes (Leasure et al. 2019).

Given the large number of sites and long duration of the period of study it can be inferred that maximum density of Redband Trout in Northern Great Basin streams are limited by mean body size. While understanding the influence of habitat factors on limiting fish densities requires additional analyses, the influence of body size is well established in this study. Determining the extent of this self-thinning and what factors influence it (territoriality, food availability) could be

a valuable next step in any future analyses. Furthermore, although there are many factors we were not able to consider to more effectively predict density in this work, it may be more important to consider body size itself as a response. Further understanding the full suite of processes that influence both body size and population density of Redband Trout can better inform conservation of this species in the face of climate change and further environmental variability.

Bibliography

- Anderson, M., G. Giannico, & S. Jacobs. 2011. Seasonal migrations of adult and sub-adult redband trout in a high desert basin of Eastern Oregon, USA. *Ecology of Freshwater Fish*, 20(3):409-420.
- Armstrong, J. B., A. H. Fullerton, C. E. Jordan, J. L. Ebersole, J. R. Bellmore, I. Arismendi, B. E. Penaluna, & G. H. Reeves. 2021. The importance of warm habitat to the growth regime of cold-water fishes. *Nature Climate Change*, 11(4):354-361.
- Benjamin, J. R., J. M. Heltzel, J. B. Dunham, M. Heck, & N. Banish. 2016. Thermal regimes, nonnative trout, and their influences on native bull trout in the Upper Klamath River Basin, Oregon. *Transactions of the American Fisheries Society*, 145(6):1318-1330.
- Benjamin, J. R., D. T. Vidergar, & J. B. Dunham. 2020. Thermal heterogeneity, migration, and consequences for spawning potential of female bull trout in a river–reservoir system. *Ecology and Evolution* 10(9):4128-4142.
- Behnke, R. J., 1992. Native trout of western North America.
- Bisson, P. A. & Bond, C.E., 1971. Origin and distribution of the fishes of Harney Basin, Oregon. *Copeia*, 268-281.
- Bohlin, T., C. Dellefors, U. Faremo, & A. Johlander. 1994. The energetic equivalence hypothesis and the relation between population density and body size in stream-living salmonids. *The American Naturalist*, 143(3):478-493.
- Cade, B. S., J. W. Terrell, & R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology*, 80(1):311-323.
- Cade, B. S. & Q. Guo. 2000. Estimating effects of constraints on plant performance with regression quantiles. *Oikos*, 91(2):.245-254.
- Cade, B. S. & B R. Noon, 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, 1(8):412-420.
- Chapman, D. W., 1966. Food and space as regulators of salmonid populations in streams. *The American Naturalist*, 100(913), pp.345-357.
- Currens, K. P., C. B. Schreck, and H. W. Li. 2009. Evolutionary ecology of redband trout. *Transactions of the American Fisheries Society* 138:797-817.
- Currens, K. P., C. B. Schreck, & H. W. Li. 2009. Evolutionary ecology of redband trout. *Transactions of the American Fisheries Society* 138:797-817.
- Dunham, J. B., & G. L. Vinyard. 1997a. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. *Transactions of the American Fisheries Society* 126(2):323-329.
- Dunham, J. B. & G. L. Vinyard. 1997b. Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(5):1025-1030.
- Dunham, J. B., S. B Adams, R. E. Schroeter, & D. C. Novinger. 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. *Reviews in Fish Biology and Fisheries*, 12(4), pp.373-391.
- Dunham, J. B., A. E. Rosenberger, R. F. Thurow, C. A. Dolloff, & P. J. Howell. 2009. Coldwater fish in wadeable streams. In *Standard methods for sampling North American freshwater fishes*. Edited by S.A. Bonar, W.A. Hubert, and D.W. Willis. American Fisheries Society, Bethesda, Md, 119–138.

- Elliott, J. M., 1994. Quantitative ecology and the brown trout. Oxford University Press.
- Falke J. A., J. B. Dunham, C. E. Jordan, K. M. McNyset, & G. H. Reeves. 2013. Spatial Ecological Processes and Local Factors Predict the Distribution and Abundance of Spawning by Steelhead (*Oncorhynchus mykiss*) across a Complex Riverscape. *PLoS ONE* 8(11):e79232-42
- Fausch, K. D. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-85 (Vol. 213). US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, & H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes: a continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat. *BioScience*. 52(6):483-498.
- Gamperl, A.K., K. J. Rodnick, H. A. Faust, E. C. Venn, M. T. Bennett, L. I. Crawshaw, E. R. Keeley, M. S. Powell, & H. W. Li. 2002. Metabolism, swimming performance, and tissue biochemistry of high desert redband trout (*Oncorhynchus mykiss* ssp.): evidence for phenotypic differences in physiological function. *Physiological and Biochemical Zoology* 75(5):413-431.
- Grant, J.W., 1993. Self-thinning in stream-dwelling salmonids. *Canadian Special Publication of Fisheries and Aquatic Sciences*, pp.99-102.
- Grant, J. W., S. O. Steingrímsson, E. R. Keeley, & R. A. Cunjak. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(S1), pp.181-190.
- Grayson, D.K. 1994. *The Desert's Past. A Natural Prehistory of the Great Basin*. Smithsonian Institution Press, Washington, DC
- Grossman, G. D. & T. N. Simon. 2020. Density-dependent effects on salmonid populations: A review. *Ecology of Freshwater Fish*, 29(3):400-418.
- Hahlbeck, N. J. 2021. *How Behavior, Physiology, and Ontogeny of Klamath Redband Trout Shape the Functionality of Habitats in a Landscape of Temperature Extremes*. Ph.D. Dissertation, Oregon State University, Corvallis, OR.
- Harvey, B. C. & J. L. White. 2017. Axes of fear for stream fish: water depth and distance to cover. *Environmental Biology of Fishes*, 100(5):565-573.
- Hayes, J. W., J. D. Stark, & K. A. Shearer. 2000. Development and test of a whole-lifetime foraging and bioenergetics growth model for drift-feeding brown trout. *Transactions of the American Fisheries Society*, 129(2):315-332.
- Hubbs, C. L., & R. R. Miller. 1948. The Great Basin, with emphasis on glacial and postglacial times. II. The zoological evidence: correlation between fish distribution and hydrographic history in the desert basins of western United States. *Bull. Univ. Utah* 38:18-166.
- Hubert, W. A., & M. Quist. 2011. Inland fisheries management in North America. *Fisheries*, 36(2).
- Hughes, N. F. & T. C. Grand. 2000. Physiological ecology meets the ideal-free distribution: predicting the distribution of size-structured fish populations across temperature gradients. *Environmental Biology of Fishes*, 59(3):285-298.
- Isaak, D. J., S. J. Wenger, E. E. Peterson, J. M. Ver Hoef, D. E. Nagel, C. H. Luce, S.W. Hostetler, J. B. Dunham, B. B. Roper, S. P. Wollrab, G. L. Chandler, & S. Parkes-Payne. 2017a. The NorWeST summer stream temperature model and scenarios for the western US: A crowd-sourced database and new geospatial tools foster a user community and

- predict broad climate warming of rivers and streams. *Water Resources Research* 53(11):9181-9205.
- Isaak, D. J., S. J. Wenger, & M. K. Young, M.K. 2017b. Big biology meets microclimatology: defining thermal niches of ectotherms at landscape scales for conservation planning. *Ecological Applications*, 27(3):977-990.
- Isaak, D. J., E. E. Peterson, J. M. Ver Hoef, D. Nagel, S. Wollrab, G. Chandler, D. Horan, & S. Parkes-Payne. 2020. Analysis of Spatial Stream Networks for Salmonids. 77234:77246. Technical report to the Bonneville Power Administration, BPA Contract.
- Kendall, N. W., J. R. McMillan, M. R. Sloat, T. W. Buehrens, T. P. Quinn, G. R. Pess, , K. V. Kuzishchin, M. M. McClure, & R. W. Zabel. 2015. Anadromy and residency in steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of the processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(3):319-342.
- Koenker, R., S. Pin Tian Ng, A. Zeileis, P. Grosjean, & B. D. Ripley. 2018. Package 'quantreg'. Cran R-project. org.
- Kovach, R. P., C. C. Muhlfeld, R. Al-Chokhachy, J. B. Dunham, B. H. Letcher, & J. L. Kershner. 2016. Impacts of climatic variation on trout: a global synthesis and path forward. *Reviews in Fish Biology and Fisheries*, 26(2):135-151.
- Leasure, D.R., Wenger, S.J., Chelgren, N.D., Neville, H.M., Dauwalter, D.C., Bjork, R., Fesenmyer, K.A., Dunham, J.B., Peacock, M.M., Luce, C.H. and Lute, A.C., 2019. Hierarchical multi-population viability analysis. *Ecology*, 100(1):p.e02538.
- Magnuson, J. J., L. B. Crowder, & P. A. Medvick. 1979. Temperature as an ecological resource. *American Zoologist*, 19(1):331-343.
- McCullough, D. A., J. M. Bartholow, H. I. Jager, R. L. Beschta, E. F. Cheslak, M. L. Deas, J. L. Ebersole, J. S. Foott, S. L. Johnson, K. R. Marine, & M. G. Mesa. 2009. Research in thermal biology: burning questions for coldwater stream fishes. *Reviews in Fisheries Science*, 17(1):90-115.
- McMillan, J.R., J.B. Dunham, G.H. Reeves, J.S. Mills, & C.E. Jordan. 2012. Individual condition and stream temperature influence early maturation of Rainbow and steelhead trout, *Oncorhynchus mykiss*. *Environmental Biology of Fishes*. 93: 343-355.
- Meeuwig, M., & S. Clements. 2014. Use of Electrofishing and a Generalized Random Tessellation Stratified Design to estimate density and abundance of Redband Trout in the Northern Great Basin. ODFW Informational Reports.
- Meeuwig, M., & S. Clements. 2015. Great Basin Redband Trout Genetic Status Assessment.
- Meyer, K. A., J. A. Lamansky, & D. J. Schill. 2010. Biotic and abiotic factors related to redband trout occurrence and abundance in desert and montane streams. *Western North American Naturalist*, 70(1):77-91.
- Minckley, W. L., D. A. Hendrickson, & C. E. Bond. 1986. Geography of western North American freshwater fishes: Description and relationships to intracontinental tectonism. In C. H. Hocutt and E. O. Wiley (editors), *Zoogeography of North American freshwater fishes*, p. 519-613. Wiley Interscience Publications, New York.
- Minshall, G.W., S. E. Jensen, W. S. & Platts. 1989. The ecology of stream and riparian habitats of the Great Basin region: a community profile. Fish and Wildlife Service, US Department of the Interior.
- Miller, S. A., S. L. Gunckel, S. E. Jacobs, & D. R. Warren. 2014. Sympatric relationship between redband trout and non-native brook trout in the Southeastern Oregon Great Basin. *Environmental biology of fishes*, 97(4):357-369.

- Miller, M. P., D. M. Carlisle, D. M. Wolock, & M. Wiczorek. 2018. A database of natural monthly streamflow estimates from 1950 to 2015 for the conterminous United States. *JAWRA Journal of the American Water Resources Association*, 54(6):1258-1269.
- Moore, K. M. & S. V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 45(11):1921-1930.
- Muhlfeld, C. C., D. H. Bennett, & B. Marotz. 2001. Summer habitat use by Columbia River redband trout in the Kootenai River drainage, Montana. *North American Journal of Fisheries Management*, 21(1):223-235.
- Nakano, S. & T. Furukawa-Tanaka. 1994. Intra-and interspecific dominance hierarchies and variation in foraging tactics of two species of stream-dwelling charrs. *Ecological Research*, 9(1):9-20.
- Ogle, D. H., J. C. Doll, P. Wheeler, & A. Dinno. 2021. FSA: Fisheries Stock Analysis. R package version 0.9.1.9000, <https://github.com/droglenc/FSA>.
- Penaluna, B. E., J. B. Dunham, & H. V. Andersen. 2021. Nowhere to hide: The importance of instream cover for stream-living Coastal Cutthroat Trout during seasonal low flow. *Ecology of Freshwater Fish*, 30(2), pp.256-269.
- Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of brook trout on native cutthroat trout. *Ecological Applications*, 14(3):754-772
- Platts, W. S. & R. L. Nelson. 1988. Fluctuations in trout populations and their implications for land-use evaluation. *North American Journal of Fisheries Management*, 8(3):333-345.
- Poff, N.L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, & J. C. Stromberg. 1997. The natural flow regime. *BioScience*, 47(11):769-784.
- Poff, N., 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater biology*, 36(1):71-79.
- Poole, G. C., & C. H. Berman. 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. *Environmental management*, 27(6):787-802.
- Railsback, S. F., R. H. Lamberson, B. C. Harvey, & W. E. Duffy. 1999. Movement rules for individual-based models of stream fish. *Ecological Modelling*, 123(2-3):73-89.
- Railsback, S. F., B. C. Harvey, S. K. Jackson, & R. H. Lamberson. 2005. inSTREAM: The individual-based stream trout research and environmental assessment model. General technical report PSW-GTR-218. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture.
- Rincón, P. A. & J. Lobón-Cerviá. 2002. Nonlinear self-thinning in a stream-resident population of brown trout (*Salmo trutta*). *Ecology*, 83(7):1808-1816.
- Rodnick, K. J., A. K. Gamperl, K. R. Lizars, M. T. Bennett, R. N. Rausch, & E. R. Keeley. 2004. Thermal tolerance and metabolic physiology among redband trout populations in southeastern Oregon. *Journal of Fish Biology*, 64(2):310-335.
- Rose, K. A., J. H. Cowan Jr, K. O. Winemiller, R. A. Myers, & R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries*, 2(4):293-327.
- Rosenberger, A. E., & J. B. Dunham. 2005. Validation of abundance estimates from mark-recapture and removal techniques for rainbow trout captured by electrofishing in small streams. *North American Journal of Fisheries Management*, 25(4):1395-1410.

- Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. *Transactions of the American Fisheries Society*. 132(5):953-968.
- Schlosser, I. J. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. In *American Fisheries Society Symposium*. 17:392-401.
- Tattam, I. A., J. R. Ruzycski, H. W. Li, & G. R. Giannico. 2013. Body Size and Growth Rate Influence Emigration Timing of *Oncorhynchus mykiss*, *Transactions of the American Fisheries Society*, 142(5):1406-1414
- Thorson, J. M., M. P. Heck, J. B. Dunham, & D. P. Hockman-Wert. 2020. Stream Temperature in the Northern Great Basin region of Southeastern Oregon, 2016-2019; U.S. Geological Survey data release, <https://doi.org/10.5066/P924MOCB>
- U.S. Environmental Protection Agency. 2021. National Hydrography Dataset Plus. Accessed at <https://www.epa.gov/waterdata/nhdplus-national-hydrography-dataset-plus>
- US Geological Survey. 2021 National Hydrography Dataset. Accessed at https://www.usgs.gov/core-science-systems/ngp/national-hydrography/national-hydrography-dataset?qt-science_support_page_related_con=0#qt-science_support_page_related_con
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*. 893-901.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, & C. E. Cushing. 1980. The river continuum concept. *Canadian journal of fisheries and aquatic sciences*, 37(1):130-137.
- Whitney, E. J., J. R. Bellmore, J. R. Benjamin, C. E. Jordan, J. B. Dunham, M. Newsom, & M. Nahorniak. 2020. Beyond sticks and stones: Integrating physical and ecological conditions into watershed restoration assessments using a food web modeling approach. *Food Webs*, 25, p.e00160.
- Wiens, J. A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater biology*. 47(4):501-515.
- Wipfli, M. S. & C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. *Fisheries*, 35(8):73-387.
- Young, K. A., 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. *Ecology*, 85(1):134-149.
- Zoellick, B. W. 1999. Stream temperatures and the elevational distribution of redband trout in southwestern Idaho. *The Great Basin Naturalist*. 136-143.

Appendix

Appendix Table 1. Coefficient estimates for response variables used in 90% quantile models for (a.) Mean Length (mm) and (b.) logMean Mass (g). Estimates include difference from 2006 for years and difference from Catlow for SMU's

a.

Variable	Estimate	SE	t value	p
Intercept	-2.0664	0.5200	-3.974	< 0.001
Aug Temp	0.1946	0.0641	3.037	0.002
Square Aug Temp	-0.0058	0.0023	-2.533	0.011
Brook Trout	-0.1341	0.0606	-2.213	0.027
LogMean Flow	3.0230	0.6142	4.922	< 0.001
2007	-0.2897	0.1719	-1.685	0.092
2008	-0.4291	0.1700	-2.525	0.012
2009	-0.4458	0.1689	-2.639	0.008
2010	-0.4540	0.1714	-2.649	0.008
2011	-0.5675	0.1655	-3.429	< 0.001
2012	-0.4603	0.1659	-2.775	0.006
Chewaucan	-0.1332	0.1178	-1.131	0.258
FortRock	-0.1687	0.1230	-1.371	0.171
Goose	-0.1520	0.1182	-1.287	0.199
Malheur	-0.0704	0.1126	-0.625	0.532
Warner	-0.0813	0.1207	-0.674	0.501

b.

Variable	Estimate	SE	t value	p
Intercept	-2.3623	0.5290	-4.466	< 0.001
Aug Temp	0.2514	0.0652	3.858	< 0.001
Square Aug Temp	-0.0083	0.0023	-3.573	< 0.001
Brook Trout	-0.1259	0.0616	-2.043	0.041
LogMean Flow	3.0122	0.6248	4.821	< 0.001
2007	-0.2855	0.1748	-1.633	0.103
2008	-0.4283	0.1729	-2.478	0.013
2009	-0.4678	0.1718	-2.723	0.007
2010	-0.4677	0.1743	-2.683	0.007
2011	-0.5952	0.1683	-3.536	< 0.001
2012	-0.4810	0.1687	-2.851	0.004
Chewaucan	-0.1284	0.1198	-1.071	0.284
FortRock	-0.1712	0.1252	-1.368	0.172
Goose	-0.1294	0.1202	-1.077	0.282
Malheur	-0.0988	0.1146	-0.862	0.389
Warner	-0.0877	0.1227	-0.715	0.475