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Exploring the role of temperature and possible alternative stable states in brook trout (Salvelinus fontinalis) population structure

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Exploring the role of temperature and possible alternative stable states in brook trout (*Salvelinus fontinalis*) population structure

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in

Biology

by

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ABSTRACT OF THE THESIS

Exploring the role of temperature and possible alternative stable states in brook trout (*Salvelinus fontinalis*) population structure

by

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Master of Science in Biology

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Professor Jonathan B. Shurin, Chair

Most organisms undergo ontogenetic changes, leading to complex life histories. An organism's prey and habitat preferences change as they age, as may their responses to the same environmental stressors. Therefore, a changing environment may confer a competitive advantage to a particular life stage, leading to population structures dominated by one stage or another. I used survey data of brook trout (*Salvelinus fontinalis*) in lakes across the Sierra Nevada to investigate if there was evidence for (1) alternative stable states between populations dominated by small or large fish, and (2) trends in population structure across elevation to suggest that temperature plays a key role in determining size structure. I characterized the average fish size, number of size classes, and the evenness of the size class distribution for 42 populations. I found these features by fitting a Bayesian normal mixture model using Markov Chain Monte Carlo simulations. I tested for alternative stable states by looking for bimodality in each feature, and I analyzed each feature's relationship with elevation using Spearman's rank correlation. I found that that populations are most often dominated by small individuals, rarely by large individuals, and most often contain either one or two distinct size classes. If large individual body sizes occur as an alternative population state, my results show that such populations occurred rarely, or were not well sampled by these surveys. High elevation was associated with reduced average size and greater numbers of size classes, suggesting that temperature does affect size distributions.

Introduction

Models of communities typically focus on the interactions between different species. However, most organisms undergo ontogenetic changes throughout their lifespan, and many have complex life histories (Wilbur, 1980), where there are size-specific preferences and size-structured interactions within the same population. Fishes exemplify such complex life histories, with prey and habitat preferences that change as they grow from minute larvae to their adult size. The simplest connections between juvenile and adult stages are the processes of maturation and reproduction; juveniles grow into adults and adults produce more juveniles. In fish that change their diets over time, there can be more complex interactions, such as inter-cohort competition for a shared resource. For piscivorous fish, adult fish may even cannibalize young. Interactions among life history stages can affect recruitment, size structure and population dynamics of fishes.

These intrinsic population dynamics can lead to a rich array of population structures and dynamics. For example, Claessen et al. modeled how varying levels of cannibalism could determine the number of cohorts in a population (Claessen, De Roos, & Persson, 2000). These population structures can even alter community structures. Persson et al. found that a perch (*Perca fluviatilis*) population driven by competition and cannibalism alternated between stunted and gigantic individuals, which led to changing zooplankton and phytoplankton abundances mediated by a trophic cascade (Persson et al., 2003). When large, piscivorous individuals dominated the population, zooplankton were abundant, and phytoplankton were scarce. When small individuals were most numerous, zooplankton were rare and primary productivity was high.

Population and community structures including size-structured species may be altered by environmental drivers. The prominent collapse and failed recovery of the cod fishery is one example of alternative dynamics generated by size structure. Humans overfishing reduced the adult cod population, resulting in a population structure dominated by small juveniles. Adult cod were the major predators of forage fish such as northern sand lance (*Ammodytes dubius*), capelin (*Mallotus villosus*), and Atlantic herring (*Clupea harengus*), which then boomed after they were released from cod predation. This shifted the community from a state dominated by large-bodied benthic fish to one dominated by smaller forage fish (Frank, Petrie, Fisher, & Leggett, 2011). These small, pelagic, planktivorous fishes competed with juvenile cod, reducing their growth rate and inhibiting the recovery of the adult cod population (Neuenhoff et al., 2019).

Environmental factors that determine intrinsic biological rates can also affect the dynamics of size structured populations. In hotter temperatures, fish have higher feeding, activity and metabolic rates (Clarke & Johnston, 1999). If feeding rates or the resource supply cannot satisfy elevated metabolic rates, then populations may decline in higher temperatures. This explanation is size-independent and implies that size structure may not change with temperature. However, because mass-specific metabolic rates decrease with size (Clarke & Johnston, 1999), changes in population structure would likely be size-specific. Since size-specific metabolic rates are lower for larger fish, adults could have a metabolic advantage at higher temperatures. In fish with ontogenetic diet shifts, whether a resource supply is sufficient is also size-dependent, so which stage is at a competitive advantage may also depend on prey availability (Persson, 1987). Lindmark et al. explored how the interaction between the scaling of these rates across size and temperature could lead to a population is dominated by either adults or juveniles (Lindmark, Huss, Ohlberger, & Ardmark, 2017).

One potential outcome of size-structured interactions is alternative stable states in which populations may exist in certain self-enforcing conditions that are separated by unstable equilibria (Scheffer, Carpenter, Foley, Folke, & Walker, 2001). Due to an external stressor, a population may shift suddenly from one state to another, and it cannot recover to its previous state without another stressor. The failed recovery of cod after overfishing is one potential example. Alternative states have important implications for fisheries management, as reducing fishing pressure may fail to result in population recovery. Lindmark et al. (2017) showed that the presence of alternative stable states can depend on environmental conditions including temperature that determine growth, feeding and reproductive rates of both adults and juveniles.

One way to test for the presence of alternative stable states is to test for bimodality in the frequency of different ecosystem or population configurations. For instance, competition between floating plants and phytoplankton may result in alternative stable states as water bodies are characterized most often by little plant cover (<20%) or near-complete plant cover (>80%) (Scheffer et al., 2003). Dynamics between forests and grasslands may also result in ecosystem bistability; where biomes are often characterized by low or high tree cover, and rarely characterized with intermediate tree cover (Staver, Archibald, & Levin, 2011).

The goal of my thesis was to ask whether the intrinsic factor of size and extrinsic factors including temperature and habitat size could lead to alternative stable states of brook trout (*Salvelinus fontinalis*) populations along an elevational gradient in Yosemite National Park, CA. To do so, I used extensive survey data of trout populations distributed among lakes across the Sierra Nevada to answer two questions:

1. Is there evidence for alternative stable states between populations dominated by small or large fish?

2. Are there any trends in population structure across elevation to suggest that temperature plays a key role in determining size structure in these populations?

Methods

Fish length datasets

I analyzed the size structure of 42 brook trout populations in Yosemite National Park, California. Non-native species of trout were introduced throughout Yosemite in the mid-1800's to provide opportunities for recreational fishing (Knapp, 1996). However, these introductions had unintended consequences, such as a decline in native species like the golden trout (*Oncorhynchus aguabonita*) (Knapp, 1996) and the mountain yellow-legged frog (*Rana muscosa*) (Knapp, 2004). Since then, trout stocking has ended within National Parks and trout have even been removed from certain lakes to promote recovery of endangered animals that are eliminated in their presence.

I used two fish length datasets. Both datasets measured the lengths of multiple species of trout over many lakes and years. I filtered the original data to only include brook trout because it was the most common species in both datasets. I assumed that brook trout measured in the same lake at the same time represented one population, so I grouped the fish lengths by a combination of site and year to analyze each population's size structure. Furthermore, I only included populations with at least 25 fish measured. This was an arbitrary decision made to only include populations with enough fish to represent a reasonable sampling of the true population size distribution.

The first dataset I used was provided courtesy of Rob Grasso, Yosemite National Park biologist, who recorded fish lengths during removal campaigns for frog restoration in certain lakes. This subset of data included 12,732 fish measured in 12 lakes between 2007 and 2017

(Table 1). In this dataset, I only included the first year that a lake was sampled because I was only interested in assessing size structure that had not have been altered by intensive removal efforts in previous years. The second dataset was provided courtesy of Roland Knapp, UC Santa Barbara professor, who recorded fish lengths as part of lake-wide ecosystem studies. This subset of data included 1,411 fish measured in 30 lakes between 2000 and 2001 (Table 2).

Analyzing population structure

I investigated three features of population structure: mean fish size (mm), number of size classes, and evenness of the distribution of individuals among size classes. I estimated these features for each population by calculating metrics directly from fish length data, finding peaks in density plots of fish length data, and fitting Bayesian normal mixture models to the fish length data (Figure 1). I calculated additional metrics along the way to inform priors for the mixture models. I completed all analyses in R version 3.5.3 (R Core Team, 2019). I used the dplyr package to combine the original datasets and select brook trout observations (Wickham, François, Henry, & Müller, 2019). I produced figures using packages ggplot (Wickham, 2016) and gridExtra (Auguie, 2017).

To determine the number and distribution of size classes, I first calculated the range of fish lengths for both datasets combined. This informed the possible mean and standard deviation for the mixture models (Table 3). I then calculated the mean fish size for each population, which was one of the three final features of population structure that I analyzed.

Next, I found the number of peaks in density plots of fish length data, assuming that each peak represents a size class. Trout reproduce seasonally but grow continuously, therefore distinct cohorts born in the same year may appear as peaks in the population size distribution. I used this approach to objectively inform the priors of the mixture models. I smoothed the fish length data for each population using the density function in the stats package (R Core Team, 2019). I found the number and locations of peaks and calculated the distance between peak locations using the findPeaks function in the quantmod package (Ryan & Ulrich, 2019) in order to inform the mixture models (Table 3).

Next, in order to estimate the number and locations of peaks in the size distribution of each population, I fit normal mixture models in which each normal component represents a size-class. I wrote models to fit populations with one to five size classes. For each population, multiple models were compared in which the number of normal components is a fixed aspect of each model. I fit two mixture models to each population. I evaluated better model fit with penalized deviance; models with more normal components fit the data better and had a lower deviance, but also received a higher penalty for additional complexity. The model with the lowest penalized deviance was selected as the better fitting model. If the population had *n* peaks in the density plots, then I fit a model with *n* and *n-1* normal components; because the peak-finding method was sensitive to small peaks. If the lake had one peak, then I fit a model with one and two normal components; in case the peak-finding method ignored overlapping size classes. Using Markov Chain Monte Carlo (MCMC) simulations, I estimated the mean of and proportion of data within each normal component. I ran MCMC simulations and calculated penalized deviance using the runjags package (Denwood, 2016). Using the proportion of data within each normal component, I calculated Pielou's evenness index (Pielou, 1966) to evaluate the evenness of each population's size class distribution.

Finally, I combined normal components that had very similar mean sizes. If a population had size classes were less than 50 mm apart, I combined them by averaging their means and adding the proportions of data within them. I then recalculated the number of size classes and the evenness index for all populations this applied to. I chose 50 mm because that was the minimum separation found between peaks in density plots of the fish length data. This retroactive calculation corrected cases in which the mixture model with *n-1* normal components appeared to still overfit the data. In the future, a more streamlined approach could be to fit more models with fewer components (i.e. also fit a model with *n-2, n-3* components), which could correct the poor model fit earlier on.

To test for alternative stable states, I looked for bimodality in population features across lakes. Although it is difficult to detect alternative stable states in the field, one common approach is to look for bimodality (e.g. Scheffer et al., 2003). This suggests that an ecosystem is frequently in one of two stable states, and rarely in intermediate states. To test for relationships between population structure and elevation, I calculated Spearman's rank correlation for each population structure feature with elevation.

Results

The number of size classes exhibits a bimodal distribution while mean fish size and evenness do not (Figure 2). Most populations had a mean fish size between 100 and 250 mm (Figure 2 left). Most populations were bimodal or unimodal, with only one population that was trimodal (Figure 2 middle). Most of the bimodal populations had high evenness indexes, indicating that were evenly distributed (Figure 2 right).

I found a negative and highly significant trend between the average fish size and elevation, indicating that high elevation lakes tend to have smaller fish on average (Table 4, Figure 3 left). There is a positive and significant trend between the number of size classes and elevation (Table 4, Figure 3 middle) and a positive, though not significant, trend between the evenness of size classes and elevation (Table 4, Figure 3 right).

Discussion

Surveys of trout populations in the Sierra Nevada did not find evidence for multi-modality in mean fish size (Figure 2 left). Rather, average size is right-skewed, with a predominance of populations averaging less than 200m in length, and only three populations with much larger fish averaging greater than 300mm. If alternative stable size structures do occur in mountain lake brook trout populations, the state dominated by large fish only occurs in only a small fraction of populations.

I found that most populations contained either one or two size classes, with two size classes being the most frequent state (Figure 2 middle). Thus, trout body size distributions show evidence of discrete cohorts. Finally, I found that most bimodal populations were relatively evenly distributed between two size classes (Figure 2 right), which does not suggest that lakes are dominated by small or large fish, but that fish are equally distributed between those two size classes. Alternate populations states are possible, but perhaps the two alternate states are that one size class is dominant or multiple size classes coexist.

The lack of evidence for alternative stable states between populations dominated by small or large fish may also reflect sampling bias in my study. The few lakes with large fish (Figure 2 left) may reflect populations dominated by larger-bodied fish composed of fewer individuals. I only analyzed lakes with at least 25 individuals measured in a year to represent a population. Since populations with large fish necessarily contain a lower density of individuals, lakes dominated by large individuals may be difficult to adequately sample, and my arbitrary cutoff of 25 individuals could have incidentally excluded populations with larger fish from my analysis.

Lack of clear evidence for alternative states could also indicate that size-structured interactions in trout populations do not lead to alternative size distributions, or that other factors affect growth and the frequency of size classes. Populations with ontogenetic shifts can exhibit a wide variety of dynamics, from transient dynamics (Frank et al., 2011) to chaos (Persson, Leonardsson, de Roos, Gyllenberg, & Christensen, 1998). It is worth considering alternative explanations for these population structures. Their dynamics may also be driven by external factors I did not analyze, such as available prey or habitat availability for each stage, primary productivity, or lake morphometry (e.g. depth, area, perimeter).

I found trends in population structure across elevation to suggest that temperature plays a key role in structuring these fish populations. Mean size and elevation are negatively correlated (Table 4, Figure 3 left) such that high elevation, cold water lakes tend to have smaller fish on average. This finding contradicts the general observation that as temperatures increase, fish body sizes decrease (Ohlberger, 2013). A likely explanation is that these trout are below their optimal temperatures. As with all ectotherms, trout growth rates increase with average temperature up to a thermal maximum, above which growth declines sharply. Most of the lakes in my survey usually experience temperatures below the thermal optimum for trout. The higher elevation lakes may have smaller fish because trout grow more slowly there, and fewer fish survive long enough to reach large adult sizes.

Elevation is positively correlated with the number of size classes in a population (Table 4, Figure 3 middle). Multiple size classes tend to coexist most often in colder, high elevation lakes, while low elevation lakes more often contain only one size class. This pattern could be explained by a combined effect of elevation on growth and inter-cohort interactions. For instance, in warmer temperatures, bigger fish have lower mass-specific metabolic rates than smaller fish (Clarke & Johnston, 1999), conferring a competitive advantage to larger size classes. Large size classes could then exert stronger competitive or cannibalistic effects on small juveniles in warmer, low elevation lakes, resulting in less successful recruitment and fewer size classes in the population. Which stage has a competitive advantage can also be shifted by prey availability (Persson, 1987) though, and varying levels of cannibalism can promote either coexistence or single cohort cycles (Claessen et al., 2000).

Evenness in bimodal populations is not significantly correlated with elevation (Table 4, Figure 3 right). This suggests that other factors determine the distribution between size class and warrants future explanation. It would also be useful to calculate evenness in such a way that incorporates biomass into its interpretation. I calculated Pielou's evenness index based on number of individuals. Therefore, I considered a lake with two size classes with 50% of individuals in either size class as perfectly even. However, the larger-sized individuals would weigh more, and could be considered dominant in terms of biomass. Larger individuals could have stronger ecological impacts, and should be represented accordingly.

My data indicate that mountain brook trout populations are most often dominated by small individuals, rarely by large individuals, and most often contain either one or two distinct size classes. If large individual body sizes occur as an alternative population state, my results show that such populations occurred rarely, or were not well sampled by these surveys. High elevation was associated with reduced average size and greater numbers of size classes, suggesting that temperature, as determined by elevation, affects trout size distributions.

Figures

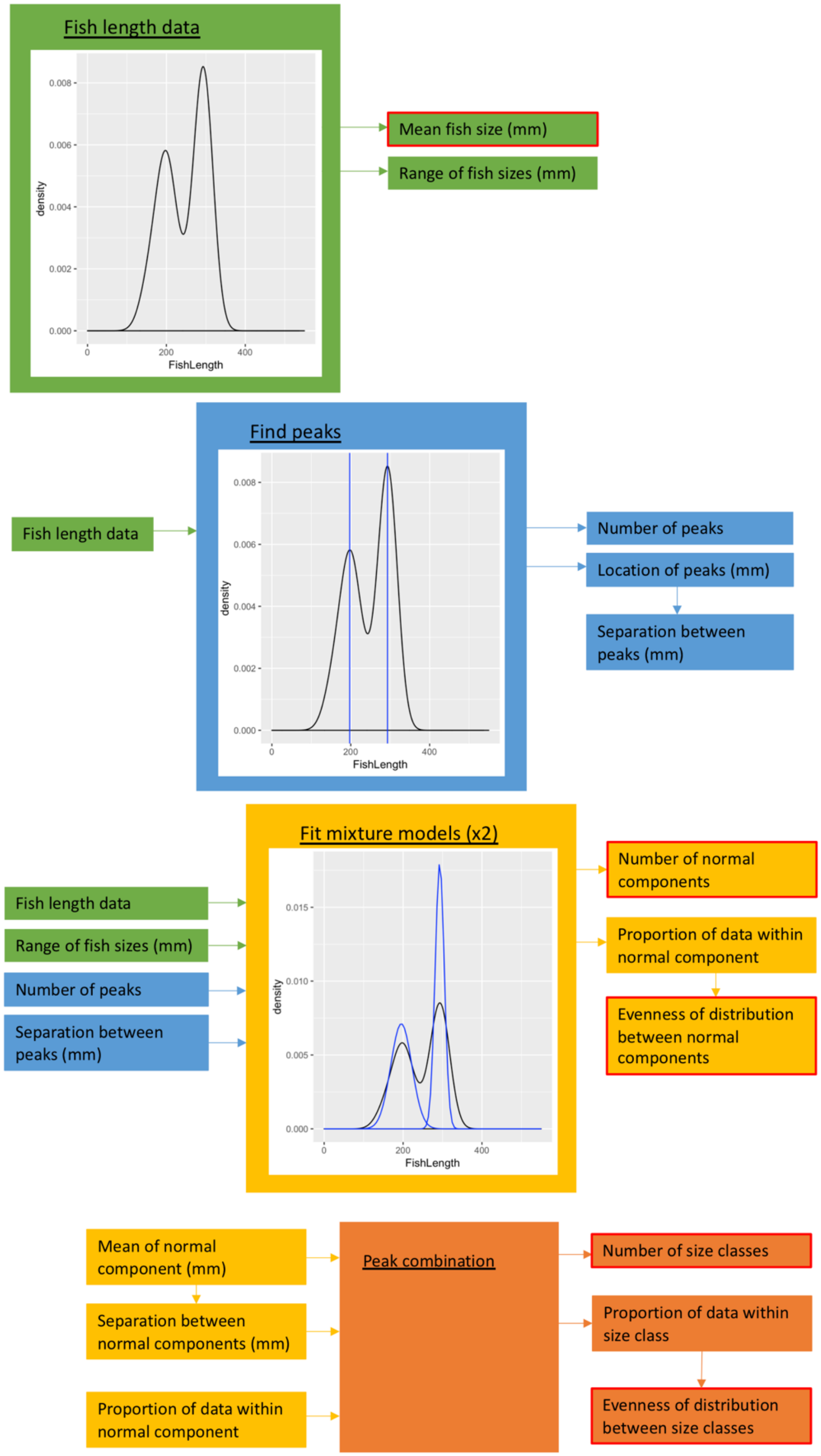

Figure 1: Methods overview. A four-step process to extract structure features from a population's fish length data. Red outline indicates a feature analyzed in the following figures.

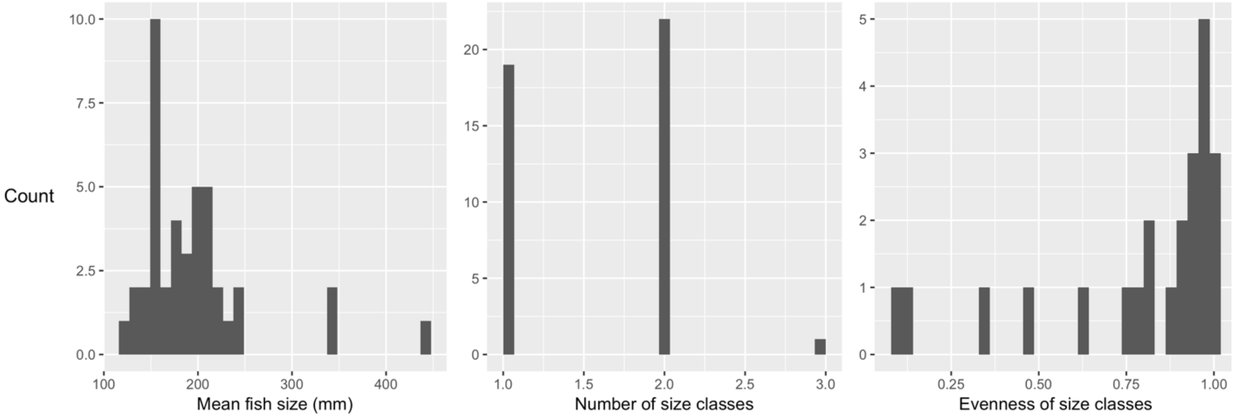

Figure 2: Distribution of population structure features. The mean fish size and number of size class plots show results for all 42 populations analyzed. The evenness of size classes plot shows the evenness for the 22 populations that had two size classes.

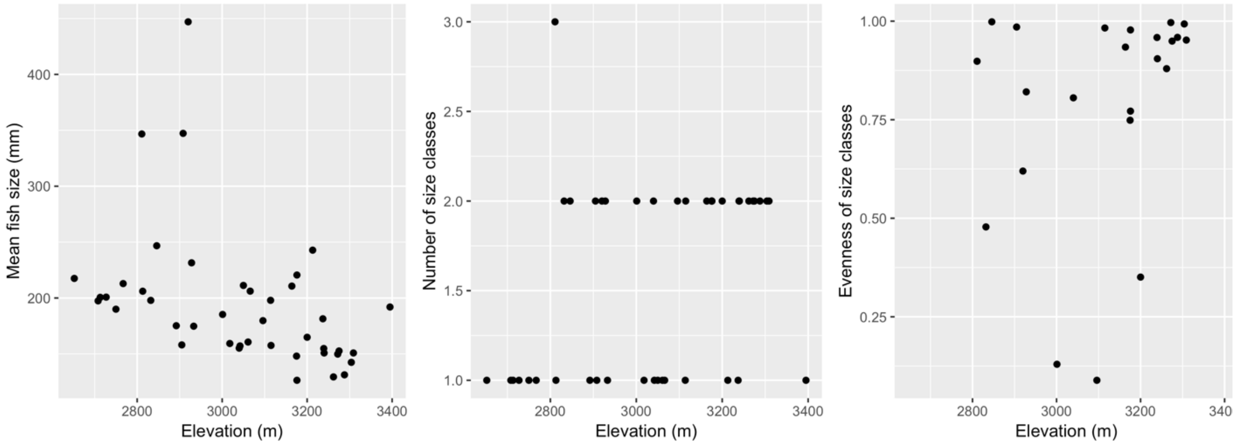

Figure 3: Population structure features plotted against elevation. The mean fish size and number of size class plots show results for all 42 populations analyzed. The evenness of size classes plot shows the evenness for the 22 populations that had two size classes.

Tables

Table 1: Twelve populations in dataset from Rob Grasso. Site lists the lake names in alphabetical order. Year lists the year I included in my analysis. Sample size lists how many fish were measured at each site in its specified year, in descending order.

	Site	**Year**	**Sample size**
1	Budd Lake	2014	4106
2	Marley Lake (Bernice)	2015	2494
3	Gallison Lake	2015	2079
4	Bason Lake (Bernice)	2015	1342
5	Huston Lake (Bernice)	2015	788
6	Boardman Lake (Bernice)	2015	740
7	RASI Pond (Bernice)	2015	441
8	Bennet Lake (Bernice)	2015	372
9	Virginia	2007	250
10	Thompson Lake (Bernice)	2017	60
11	Cold Mtn. Satellite	2007	33
12	Cold Mountain	2007	27

Table 2: Thirty populations in dataset from Roland Knapp. Site lists the lake identifier. Year lists the year I included in my analysis. Sample size lists how many fish were measured at each site in its specified year, in descending order.

	Site	**Year**	**Sample size**
1	70420	2001	113
2	70669	2001	94
3	70484	2001	77
4	70486	2000	75
5	70640	2001	73
6	70489	2001	67
7	70601	2001	58
8	70493	2001	57
9	70633	2000	56
10	70209	2001	46
11	70416	2000	46
12	70367	2000	44
13	70476	2000	43
14	70635	2000	43
15	70527	2001	42
16	70655	2001	42
17	70421	2000	40
18	70456	2000	39
19	70537	2000	37
20	70610	2001	33
21	70618	2000	33
22	70606	2000	32
23	70592	2001	30
24	70582	2000	29
25	70538	2000	28
26	70580	2000	28
27	70630	2000	28
28	70415	2000	27
29	70560	2001	26
30	70485	2001	25

Table 3: Bayesian model framework. Each model was run for a burn-in period of 5000 iterations and a sampling period of 10,000 iterations.

Component feature	How prior was informed	Prior distribution
Mean of first component	Range of fish lengths	Uniform(1, 550)
Standard deviation of component	Range of fish lengths	Uniform(1, 550)
Separation between components$^+$	Range of separation between peaks	Uniform(50, 200)
Proportion of data in a component$^+$	Range from 0 to 1	Categorical Dirichlet(1,…,1)

$^+$ only applicable if there were multiple components

Table 4: Spearman rank correlations between population structure features and elevation. Correlation for number of size classes and mean fish size are for all 42 populations analyzed, evenness is for the 22 populations that had two size classes.

Population structure feature	Correlation coefficient	P-value
Mean fish size (mm)	-0.5888502	5.71E-05
Number of size classes	0.36244802	0.01833025
Evenness of size classes	0.31324111	0.1454923

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