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Differences in population size variability among populations and species of the family Salmonidae

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Summary

1. How population sizes vary with time is an important ecological question with both practical and theoretical implications. Because population size variability corresponds to the operation of density-dependent mechanisms and the presence of stable states, numerous researchers have attempted to conduct broad taxonomic comparisons of population size variability.

2. Most comparisons of population size variability suggest a general lack of taxonomic differences. However, these comparisons may conflate differences within taxonomic levels with differences among taxonomic levels. Further, the degree to which intraspecific differences may affect broader inferences has generally not been estimated and has largely been ignored.

3. To address this uncertainty, we examined intraspecific differences in population size variability for a total of 131 populations distributed among nine species of the Salmonidae. We extended this comparison to the interspecific level by developing species level estimates of population size variability.

4. We used a jackknife (re-sampling) approach to estimate intra- and interspecific variation in population size variability. We found significant intraspecific differences in how population sizes vary with time in all six species of salmonids where it could be tested as well as clear interspecific differences. Further, despite significant interspecific variation, the majority of variation present was at the intraspecific level. Finally, we found that classic and recently developed measures of population variability lead to concordant inferences.

5. The presence of significant intraspecific differences in all species examined suggests that the ability to detect broad taxonomic patterns in how population sizes change over time may be limited if variance is not properly partitioned among and within taxonomic levels.

Key-words: ecological stability, extinction risk, temporal variability

Introduction

The degree to which population size varies with time is tied to several key questions in ecology (Connell & Sousa 1983). For example, population size variability is intrinsically related to the role of density-dependent vs. density-independent processes and whether populations possess stable equilibria (May 1973; Connell & Sousa 1983; Peterson 1984; Hanski 1990). Population size variability is also often associated with the operation of density-dependent mechanisms (Hanski 1990) and is known to influence the probability of extinction for a population (Pimm, Jones & Diamond 1988; Bengtsson & Milbrink 1995; Vucetich *et al.* 2000; Fagan *et al.* 2001; Inchausti & Halley 2003).

For these reasons, considerable attention has been directed towards describing broad taxonomic patterns in how population sizes vary temporally. Differences among taxa are of ecological and evolutionary interest because they may reflect differences in the relative role of density-dependent and density-independent processes (Connell & Sousa 1983). For example, Connell & Sousa (1983) suggest there is no evidence of general taxonomic differences in population size variability as various taxa (e.g. plants, insects, parasites and birds) exhibit a comparable range of variability. More recently, Inchausti & Halley (2001, 2002) found no evidence for taxonomic differences in temporal variability, suggesting that density-dependent mechanisms are not specific to particular taxa; although Reed & Hobbs (2004) suggested that birds may exhibit somewhat more stable populations. This greater stability may suggest that density-dependent mechanisms are more prevalent in birds. Unfortunately, comparing

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population size variability among taxa is difficult due to potential biases in variability indices, correlations with density, scale of sampling and data reliability (McArdle, Gaston & Lawton 1990).

Differences in population fluctuation over time among populations of conspecifics as well as among congeners are important for two reasons: First, many of the broad taxonomic patterns – or absence thereof – have been described based on only a few populations of a species. Thus, high or low environmental stochasticity experienced by single populations may bias estimates of population variability for a species. Differences within taxa may therefore obscure differences among taxa. Secondly, because of the relationship between population size variability and extinction risk, identifying differences between populations of the same species may help to elucidate underlying causal mechanisms of variability, either natural or anthropogenic derived, which in turn can be used to fine tune conservation strategies (Marsh 2001).

Here, we describe a jackknife method for examining intra- and interspecific population size variability. We used this method to first characterize population size variability for five populations of Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*), a threatened inland salmonid subspecies of cutthroat trout endemic to the northwestern Great Basin region in western North America, over a 5-year period. We extended the jackknife method to the estimation of population size variability of another 126 populations distributed among eight species of salmonids. We obtained data for these populations from the Global Population Dynamics Database (GPDD; NERC Centre for Population Biology 1999) and tested whether or not among population differences were common for salmonid species. If population size variability differs among populations of the same species, it would suggest that efforts to test for taxonomic patterns may inadvertently conflate intra- and interspecific differences.

Next, we estimated the proportion of variation explained at inter- vs. intraspecific levels. Finally, we conducted a demonstrative test of interspecific differences between Lahontan cutthroat trout and a steelhead population, the anadromous form of rainbow trout (*Oncorhynchus mykiss*), located in the Keogh River, Canada. Steelhead is the most closely related salmonid available in the GPDD. Because the Lahontan cutthroat trout populations studied here are restricted to small isolated regions with high levels of environmental variability, we predicted that Lahontan cutthroat trout populations would exhibit greater temporal size variability than the anadromous steelhead population.

Materials and methods

LAHONTAN CUTTHROAT TROUT

Study populations

Lahontan cutthroat trout are currently listed as threatened under the United States Endangered Species Act with a greatly restricted and fragmented range relative to a once widespread distribution (Coffin & Cowan 1995; Dunham & Vinyard 1997). Historically populations of Lahontan cutthroat trout lived in large multiple order stream networks but the majority of populations including those in this study are now isolated into single stream reaches (Dunham *et al.* 1999; Neville, Dunham & Peacock 2006). Neville *et al.* (2006) suggest that both landscape and metapopulation processes played a role in long term population persistence of Lahontan cutthroat trout populations in these large interconnected stream systems. The re-creation of such large stream networks is unlikely, thus, understanding the potential risk of extinction for different populations and understanding and differentiating between the extrinsic and intrinsic factors affecting temporal variability will allow proper direction of conservation efforts.

We studied the population dynamics of five populations of Lahontan cutthroat trout from 1996 to 2000. These populations were located in the Mohawk, Tierney, Indian, Abel and 3-Mile creeks. These creeks are all first- or second-order tributaries of the Humboldt River and are located in the eastern portion of the greater Lahontan hydrographic basin (Fig. 1). Populations in these creeks are isolated into headwater reaches due to downstream barriers disrupting stream interconnectedness. Barriers include water diversions, unsuitable water temperature and manmade barriers designed to minimize hybridization and competition threats posed by non-native salmonids (Dunham *et al.* 1999; Peacock & Kirchoff 2004).

Population sampling

From 1996 to 2000 the five creeks were sampled during late summer, low-flow conditions. This length of sampling represents a complete

Fig. 1. The Lahontan hydrographic basin, which Lahontan cutthroat trout are endemic to, spans four states in the western United States.

population turnover for Lahontan cutthroat trout (Ray, Peacock & Dunham 2007). A creek's population size was estimated using a multiple-pass with depletion sampling approach at seven sites spaced along the occupied reach within a creek. Sampling sites were 25 m in length and separated by 300 m (as per standard sampling protocols for the species, e.g. Dunham & Vinyard 1996, 1997; Dunham, Cade & Terrell 2002). Prior to sampling, sites were blocked at down and upstream ends with mesh seines to prevent fish escaping during sampling. A site was sampled using backpack electro-fishing units while moving downstream to upstream between the block-nets, which constituted a 'sampling pass'. Electro-fishing units shock individual fish temporarily stunning them with little effect on immediate survival (Mitton & McDonald 1994), although some affects on growth have been suggested (Dwyer, Shepard & White 2001). Passes continued until no new fish were detected. The mass (g) and standard lengths (mm) were recorded for each individual trout sampled.

The number of Lahontan cutthroat trout within each site was estimated using MicroFish (Van Deventer & Platts 1989), a maximum-likelihood approach that estimates the number of fish present based on the number of fish captured during each sampling pass. If all individuals sampled were caught during the first pass, we used the total number captured as our estimate. The population size of a creek was then estimated by extrapolating the density of fish at sites across the occupied length of the creek (Dunham *et al.* 1999).

Although we sampled Lahontan cutthroat trout at multiple locations within each creek, the data structure (specifically, the presence of zero counts) were not amenable to the variance partitioning approach suggested by Stewart-Oaten, Murdoch & Walde (1995). Also the population size variability of other salmonids (see below) could not be partitioned into spatial and temporal components. Thus, partitioning spatial variance for the Lahontan cutthroat trout would have made comparisons with other species uninformative.

OTHER SALMONIDAE

We extended our analysis of patterns of differences in population size variability to other species in the Salmonidae family based on those populations available in the GPDD.

GPDD data

We used populations in the GPDD for which population size estimates were determined yearly and based on individual counts. Populations were included in our analysis without consideration for 'data quality'. This approach is consistent with other uses of GPDD data (e.g. Fagan *et al.* 2001; Inchausti & Halley 2002, 2003) and forces the assumption that data quality does not *directionally* affect population size estimates. We did not, however, include data sets with gaps in year to year estimates greater than one sampling period. In addition to the five populations of Lahontan cutthroat trout, this resulted in the inclusion of an additional 126 populations distributed among eight more species (Appendix S1, Supporting information). However, the number of populations included and the length of sampling varied by species (Table 1).

DATA ANALYSIS

Intraspecific differences in population size variability

To examine intraspecific differences in population size variability, we calculated three indices of temporal variability to determine differences among populations. We first calculated the coefficient of variation of population abundances (CoefVar) and the standard deviation of log-transformed abundances (StdLog). These are the two most common indices of population variability but both are sensitive to violations of underlying assumptions such as the underlying

Table 1. Species level estimates of population size variability based on a jackknifing approach for each of the three indices: Heath's PV, the coefficient of variation (CoefVar) and the standard deviation of log transformed abundances (StdLog). We also determined whether species exhibited intraspecific differences in magnitude of population size variability

Common name	Species	No. populations	Years of sampling	Intraspecific differences	Species population variability		
					Heath's PV (SE)	CoefVar (SE)	StdLog (SE)
Lahontan cutthroat trout	*Oncorhynchus clarkii henshawi*	5	5	Yes[b,c] ($F_{4,20} = 19{\cdot}59$; $P \ll 0{\cdot}01$)[b]	0·240 (0·046)	0·236 (0·050)	0·242 (0·050)
Steelhead	*Oncorhynchus mykiss*	1	7	n/a	0·507	0·643	0·661
Atlantic salmon	*Salmo salar*	9	11–111	Yes[a,b,c,*] ($F_{8,257} = 4{\cdot}48$; $P \ll 0{\cdot}01$)[a]	0·416 (0·046)	0·533 (0·102)	0·661 (0·146)
Brook trout	*Salvelinus fontinalis*	7	6–7	Yes[b,c] ($F_{6,41} = 38{\cdot}81$; $P \ll 0{\cdot}01$)[b]	0·410 (0·030)	0·472 (0·048)	0·528 (0·051)
Coho salmon	*Oncorhynchus kisutch*	1	10	n/a	0·531	0·625	0·896
Chum salmon	*Oncorhynchus keta*	8	14–38	Yes[a,b,c,*] ($F_{7,201} = 4{\cdot}35$; $P \ll 0{\cdot}01$)[a]	0·648 (0·107)	0·904 (0·163)	1·498 (0·501)
Chinook salmon	*Oncorhynchus tshawytscha*	1	26	n/a	0·197	0·201	0·201
Pink salmon	*Oncorhynchus gorbuscha*	57	7–44	Yes[a,b,c,*] ($F_{56,958} = 5{\cdot}50$; $P \ll 0{\cdot}01$)[a]	0·590 (0·038)	0·841 (0·108)	1·151 (0·165)
Sockeye salmon	*Oncorhynchus nerka*	42	10–67	Yes[a,b,c,*] ($F_{41,1462} = 18{\cdot}94$; $P \ll 0{\cdot}01$)[a]	0·517 (0·051)	0·705 (0·174)	0·838 (0·236)

[a]Heath's PV, [b]CoefVar or [c]StdLog differed significantly between populations; [a] or [b] or then [c]ANOVA results are presented. *These intraspecific differences are conflated with the effects of time series length.

distribution of population sizes (McArdle & Gaston 1995; Heath 2006). Thus we also calculated a nonparametric index of temporal variability proposed by Heath (2006). Heath's population variability (Heath's PV) calculates variability as the average proportional differences between all measured abundances. Simulations suggest that Heath's PV is less sensitive to non-normal distributions and more accurately estimates long-term variability from short-term data sets (Heath 2006). We used all three indices to allow greater generality and because Heath's PV may not be immediately comparable to previously published estimates. We did not calculate spectral reddening as it addresses questions different from those we are asking here.

To compare point estimates between groups – in this case population size variability indices among populations – we used a 'delete-one jackknife' approach (Roff 2006). The jackknife procedure generates a 'pseudovalue' for each year of sampling for each population and index. For example, if a population had been sampled on 20 occasions, 20 pseudovalues would be calculated for each index being estimated. Pseudovalues are calculated by first estimating a particular parameter (i.e. $\hat{\Theta}$) for the entire data set. For example, $\hat{\Theta}$ could be the mean abundance for a population, or as was the case here, one of the three indices of population size variability. Next a single value from the data set is removed and $\hat{\Theta}$ is recalculated from the remaining values ($\hat{\Theta}_{-1}$), followed by the calculation of a 'pseudovalue', S_1:

$$S_1 = n\hat{\Theta} - (n-1)\hat{\Theta}_{-1},$$

where n is the sample size. The removed value is then returned to the data set and the next observation is removed to calculate a second psuedovalue (S_2). This delete, estimate and replace procedure is continued 'n' times, once for each data point. The average of the pseudovalues is then the jackknife estimate of the parameter of interest ($\tilde{\Theta}$). Likewise, the standard error of the psuedovalues is the standard error of the jackknife estimate (Roff 2006). In addition to calculating the standard error for an estimate, pseudovalues can also be used for hypothesis testing (Roff 2006). This is particularly useful for population size variability estimates as it allows the quantitative comparison of one population to another.

Using this jackknife approach (an R script for the jackknife estimation of size variability indices is provided in Appendix S2, Supporting information), we calculated pseudovalues for each of the three indices of population size variability for each of the 131 populations. Pseudovalues were then used for intraspecific comparisons of populations using analyses of variance with each index as a response variable. However, this approach potentially conflated intraspecific differences with the tendency for population variability to increase with the length of sampling (Pimm & Redfearn 1988). Thus, we also conducted analyses on subsets of the data with comparable time scales of sampling (see below).

To determine whether intraspecific variation was present, the size variability among populations of species for which sampling was conducted on the same time scale frame using either analyses of variance or t-tests. For example, seven populations of Pink Salmon (*Oncorhynchus gorbuscha*) were each sampled over a 13-year period. For these populations, three analyses of variance were conducted using the jackknife estimates for each index with population as an independent factor. This general approach was repeated for Atlantic salmon (*Salmo salar*), Chum salmon (*Oncorhynchus keta*) and Sockeye salmon (*Oncorhynchus nerka*) The specific populations and lengths of sampling are reported in Table 2.

Interspecific differences in population size variability

To produce species level estimates of population size variability and allow interspecific comparisons, we used several different approaches. Which approach should be used differs based on the data available.

Single populations. For species where only a single population has been sampled, the jackknife estimate for a particular index can be used for each of the three population size variability indices. While a standard error can be calculated for this estimate, we do not report it here and do not recommend its use because these standard errors are estimated in a different manner for other data combinations (see sections Multiple populations, same sampling length and Multiple populations, variable sampling length below). We used this approach for steelhead trout (*O. mykiss*), Coho salmon (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) (Table 1).

Table 2. When population size variability was calculated for populations of varying length, intraspecific differences were conflated with an observed tendency for population size variability to increase with the length of observations (Table 1 differences labelled '*'). We evaluated intraspecific differences in these populations based on subsets of the data of comparable lengths using either one-way ANOVAS (with population as a fixed factor) or two-way t-tests

Common name	Species	No. populations	Years of sampling	Intraspecific differences		
				Heath's PV (SE)	CoefVar (SE)	StdLog (SE)
Atlantic salmon	*Salmo salar*	4	10–13	$F_{3,42} = 3{\cdot}14$ $P = 0{\cdot}04$	$F_{3,42} = 296{\cdot}74$ $P \ll 0{\cdot}01$	$F_{3,42} = 736{\cdot}11$ $P \ll 0{\cdot}01$
Chum salmon[a]	*Oncorhynchus keta*	4 (2 by 2)	14	$t_{19} = 3{\cdot}1$ $P < 0{\cdot}01$	$t_{19} = 23{\cdot}64$ $P \ll 0{\cdot}01$	$t_{14} = 43{\cdot}8$ $P \ll 0{\cdot}01$
			30	$t_{56} = 0{\cdot}43$ $P = 0{\cdot}67$	$t_{56} = 8{\cdot}77$ $P \ll 0{\cdot}01$	$t_{56} = 21{\cdot}35$ $P \ll 0{\cdot}01$
Pink salmon	*Oncorhynchus gorbuscha*	7	13	$F_{6,45} = 4{\cdot}02$ $P < 0{\cdot}01$	$F_{6,45} = 69{\cdot}21$ $P \ll 0{\cdot}01$	$F_{6,45} = 7{\cdot}32$ $P \ll 0{\cdot}01$
Sockeye salmon	*Oncorhynchus nerka*	14	45–47	$F_{13,625} = 20{\cdot}17$ $P \ll 0{\cdot}01$	$F_{13,625} = 376{\cdot}33$ $P \ll 0{\cdot}01$	$F_{13,625} = 89{\cdot}57$ $P \ll 0{\cdot}01$

[a]For Chum Salmon, we compared two pairs of populations: one pair had been monitored for 14 years (top row) and the other pair for 30 (bottom row).

Multiple populations, same sampling length. For species where multiple populations have been sampled but the populations were each sampled for the same length of time, we first calculated each population's jackknife estimated index. The average index among populations and its standard error were then used as species level estimates of population size variability. We used this approach for Lahontan cutthroat trout (each of the five populations was monitored for 5 years) and for brook trout (*Salvelinus fontinalis*) (Table 1). For six of the seven brook trout populations available in the GPDD were sampled for 7 years. The last population was sampled for 6 years. As the majority of the populations were sampled for the same time span and one was sampled for just one less year, we ignored this difference for the species. Because this approach to calculating species estimates also produces an estimate of variance, interspecific differences can be tested.

Multiple populations, variable sampling length. For species where multiple populations were sampled but with varying length of sampling period, determining species level estimates was more complicated because population size variability increases with the number of sampling iterations (Lawton 1988; Pimm & Redfearn 1988; Ariño & Pimm 1995; Inchausti & Halley 2002). To address this concern, we calculated jackknife estimates for each index for each population. We then regressed these population estimates against the length of the time series. Each regression models' intercept and standard error was then used as a species level estimate of population size variability with the effects of time series length removed. We used this approach for Atlantic salmon (*S. salar*), Chum salmon (*O. keta*), Pink salmon (*O. gorbuscha*) and Sockeye salmon (*O. nerka*). Among these species, the length of time population sizes were estimated ranged from 7 to 111 years (Table 1).

We consider this approach to be the most applicable for interspecific comparisons as different species may exhibit different time : variability relationships. Thus, the intercept estimates allow comparisons without the possible confounding relationship of sampling length. Indeed, these estimates can perhaps be considered the basal variability for a species. However, it is important to note that while estimates produced in this manner can be compared with each other, they cannot be directly compared with estimates from either methods 'Single populations' or 'Multiple populations, same sampling length' described above.

Inter- vs. intraspecific patterns and between species comparisons. To identify the general presence of intra- and interspecific differences, we used linear models to estimate the proportion of variability explained by intraspecific differences. Species was included as a factor and census length as a continuous variable and size variability estimated via jackknife at the population level was used as the dependent variable. Because we lacked sufficient phylogenetic information we assumed a star phylogeny in this analysis with all species being equally related to one another (Garland, Bennett & Rezende 2005). Thus, we used this analysis only to calculate the variation explained at the species level vs. the variation remaining due to intraspecific variation. For any two species, standard statistical approaches make the appropriate phylogenetic assumptions so we also demonstrate the testing of interspecific differences using estimated population size variabilities for Lahontan cutthroat trout and steelhead trout.

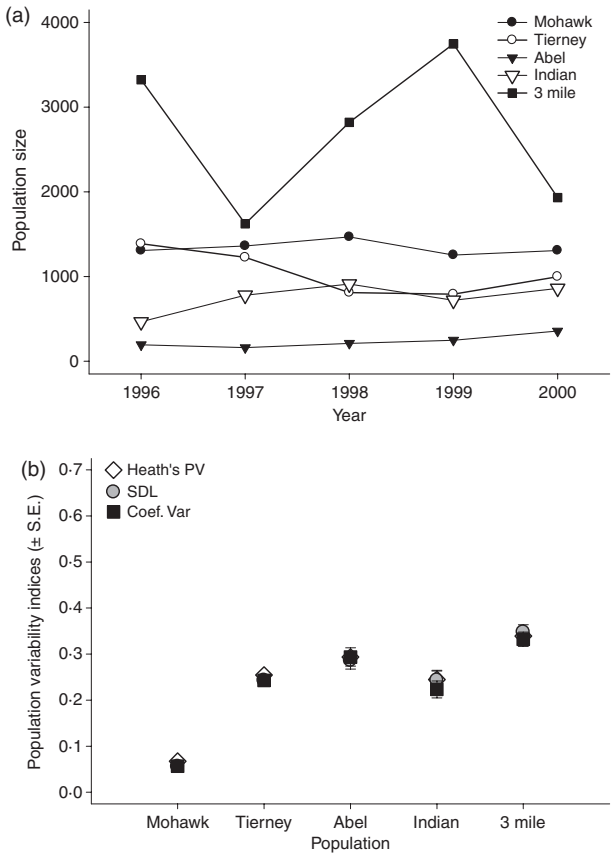

Fig. 2. (a) Size estimates for five Lahontan cutthroat trout populations estimated for 5 years. All populations are located in the eastern portion of the Lahontan Basin and are isolated to headwater reaches with no immigration among them. Population sizes were estimated using MicroFish (Van Deventer & Platts 1989). (b) Population size variability estimates for the five populations of Lahontan cutthroat trout. Variability estimates were generated for Lahontan cutthroat trout based on 5 years of sampling and a jackknife approach.

Results

LAHONTAN CUTTHROAT TROUT

We compared abundances among populations of Lahontan cutthroat trout using population/creek as a random factor and year as a covariate. Abundances were log-transformed after which they were normally distributed (Shapiro-Wilk's $W = 0{\cdot}941$; $P = 0{\cdot}16$). We estimated that on average more than 6000 total Lahontan cutthroat trout were present among the combined populations at Mohawk, Tierney, Abel, Indian and 3-Mile creeks during each year of sampling (excluding young-of-the-year; Fig. 2a). However, Lahontan cutthroat trout were not distributed equally among populations. Populations differed in abundance ($F_{4,19} = 55{\cdot}7$, $P \ll 0{\cdot}01$; Fig. 2a) but population abundance did not differ consistently by year ($F_{1,19} = 0{\cdot}52$, $P = 0{\cdot}48$). In general 3-Mile Creek had the greatest population size while Abel and Indian creeks had the lowest (Fig. 2a).

The Lahontan cutthroat trout populations also differed in temporal variability. Sites differed significantly in StdLog

($F_{4,20}$ = 20·21; $P \ll 0{\cdot}01$; Fig. 2b); CoefVar ($F_{4,20}$ = 19·59; $P \ll 0{\cdot}01$; Fig. 2b) but not when temporal variability was estimated using Heath's PV ($F_{4,20}$ = 1·66; P = 0·20; Fig. 2b). *Post-hoc* (Tukey) comparisons were conducted between populations for all three measurements. 3-Mile exhibited greater variability than all creeks based on StdLog and all creeks except Abel based on CoefVar. Mohawk Creek exhibited lower variability than all other creeks for both StdLog and CoefVar. Indian Creek exhibited lower variability than Abel based on CoefVar.

SALMONID INTRASPECIFIC DIFFERENCES

As was the case for Lahontan cutthroat trout, all species where it could be tested exhibited intraspecific differences in population size variability (Table 1). For Atlantic, Chum, Pink and Sockeye salmon, actual population differences were potentially conflated with the effects of differences in the length of sampling. To test for intraspecific differences in these species, we used subsets of the data with comparable lengths of sampling. This subset analysis demonstrated the presence of intraspecific variation for all four species (Table 2). However, for Chum salmon, Heath's PV did not indicate that the two populations sampled over 30 years differed from one another (Table 2).

INTERSPECIFIC DIFFERENCES

Linear models identified significant species differences for all three indices of population size variability (Table 3). Despite statistical significance, species and time only accounted for 22% of the variation present on average. Thus for the three indices 78% of the variation in population size variability remained at the intraspecific level.

To demonstrate the ability of using jackknife estimates to conduct interspecific comparisons, we tested for the presence of differences between Lahontan cutthroat trout and steelhead trout. Jackknifed population estimates calculated for Lahontan cutthroat trout were tested vs. the jackknifed species estimate for steelhead trout using a t-test [H_0 = 0·507 (Heath's PV), 0·643 (CoefVar), 0·661 (StdLog)]. Lahontan cutthroat trout populations exhibited significantly less variability in abundance than did steelhead (Heath's PV: $t_4 = -5{\cdot}78$, P = 0·004; CoefVar: $t_4 = -8{\cdot}43$, P = 0·001; StdLog: $t_4 = -8{\cdot}42$, P = 0·001).

Overall, the three different indices of population size variability were concordant in how they ranked the different species with regard to population size variability. Spearman rank correlations ranged between 0·95 and 1 for the three different indices (Fig. 3) suggesting that the indices measure the same population dynamic properties.

Table 3. Linear model results estimating the contribution of intraspecific variation to differences in population size variability and testing the presence of interspecific differences. After statistically controlling for the effects of series length and species, the remaining variation can be attributed to intraspecific differences among populations

	d.f.	F	P-value	Adjusted R^2	Remaining variation (%)
Heath's PV				0·324	67·6
Series length	1	0·75	0·388		
Species	8	8·84	< 0·001		
Residual	121				
CoefVar				0·195	80·5
Series length	1	4·11	0·045		
Species	8	4·54	< 0·001		
Residual	121				
StdLog				0·145	85·5%
Series length	1	0·30	0·587		
Species	8	3·85	< 0·001		
Residual	121				

Discussion

Most studies of variability in population sizes among *populations* of a single species have focused on differences in the context of the vulnerability of particular populations to extinction (Schoener & Spiller 1992; Lima, Marquet & Jaksic 1998; Vucetich *et al.* 2000; Marsh 2001; Inchausti & Halley 2003; Reed & Hobbs 2004; Legendre *et al.* 2008). This differs from our goal here which was to quantify the magnitude and prevalence of intrapopulation differences. Our results show that there are significant differences in abundance fluctuations among populations of different salmonid species.

Differences in population size variability among *species* can be difficult to properly determine due to methodological problems. These problems certainly extend to among *population* differences within a species and include issues with both the measures used to quantify temporal variation (McArdle *et al.* 1990; McArdle & Gaston 1992, 1995) and the conflation of different sources of variation (Stewart-Oaten *et al.* 1995). Mathematical concerns about indices of population size variability seem to be relatively unimportant for the salmonid data presented here because estimates of population size variability were highly consistent for each of the three measures variability (StdLog, CoefVar and Heath's PV). All three measures led to the same general inferences both at the conspecific and congener level; however, there were some qualitative differences.

Of the three measures of population size variability, Heath's PV is thought to be generally robust to large but rare population size fluctuations (Heath 2006). We found support for this pattern with the data analysed here. If rare and extreme events strongly affect the estimate of a particular index, the addition or removal of values during the jackknife process would lead to an increased standard error. In all cases, the jackknife estimated standard error was lower for Heath's PV than it was for any of the other measures. However, in two cases among population differences identified using CoefVar and StdLog were not identified based on Heath's PV. Future work should determine whether this inconsistency is due to problems with the alternative index or a general conservative tendency in the index.

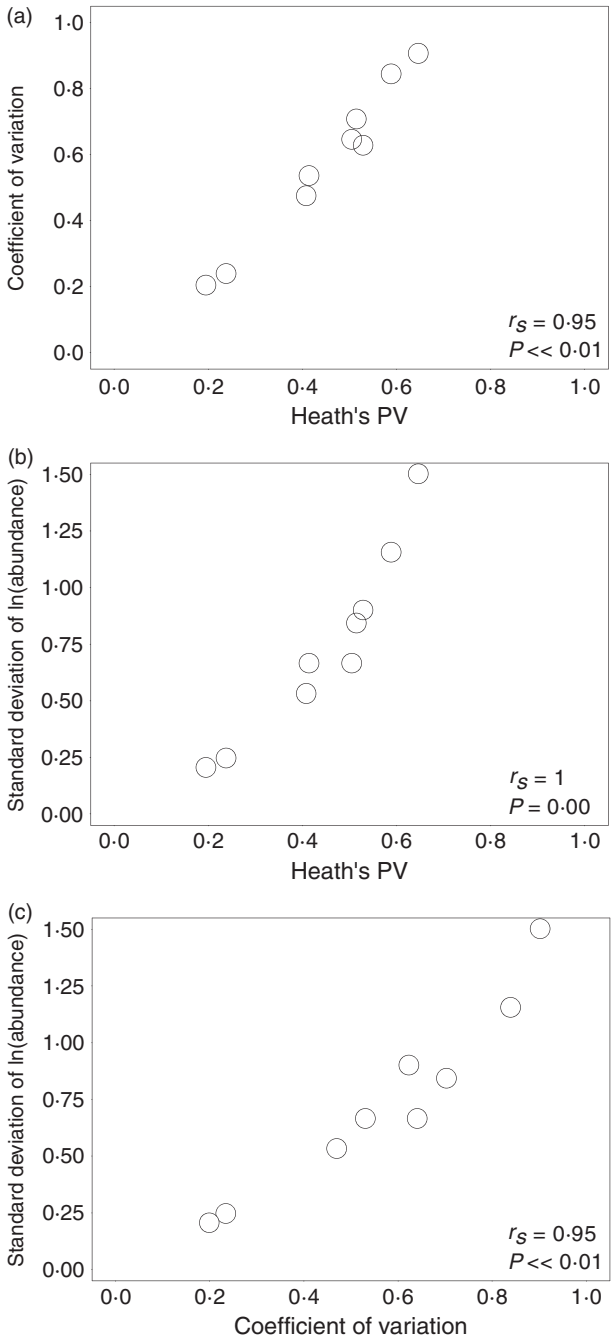

Fig. 3. The correlation between Heath's population variability (Heath's PV) and the coefficient of variation (CoefVar) for species abundances (a); between Heath's PV and the standard deviation of log-transformed species abundances (StdLog) (b) and between CoefVar and StdLog (c). Based on Spearman rank correlations, all three indices were highly correlated.

Population size variability in general is affected by a variety of different factors including extrinsic factors such as resource availability (Trzcinski, Walde & Taylor 2005) and intrinsic factors such as individual variation in survival and fecundity (Uchmanski 1999, 2000). For the majority of the species discussed here the specific factors affecting population size variability are not clear. However, the Lahontan cutthroat trout data provides greater resolution regarding the factors leading to intraspecific variation.

For the Lahontan cutthroat trout, differences in population size variability among populations are likely due to extrinsic factors such as differences in watershed characteristics including elevation, stream gradient and riparian plant communities (Dunham *et al.* 1999). Using regression quantile models, Dunham *et al.* (2002) showed that variation in fish density among populations was inversely related to the width : depth ratio of streams. These variables contributed to the amount of available habitat during base flow conditions (i.e. suitable water temperatures; Dunham, Schroeter & Rieman 2003). Because environmental conditions in the Great Basin are highly variable, variability in width : depth ratio due to precipitation differences between years may also contribute to the size variability of individual populations and extinction risk.

Regardless of the extrinsic factors responsible for intraspecific differences between populations, the lower variability of Lahontan cutthroat trout compared to that of a steelhead population is quite surprising. We had predicted that because the Lahontan cutthroat trout populations, we studied were restricted to isolated headwater reaches they would exhibit higher population size variability due to greater exposure to environmental stochasticity. In contrast, individual steelhead might be able to select favourable habitats despite environmental stochasticity and this access to a greater range of environmental conditions could result in more stable population sizes. Life-history differences between the two species may help explain this difference. Steelhead trout populations are typically anadromous and semelparous with less per-egg investment than cutthroat trout (Crespi & Teo 2002). This relatively greater investment by Lahontan cutthroat trout may buffer their populations against large fluctuations (Winemiller 2005).

Unfortunately, interspecific comparisons between just two species are limited in the degree to which they allow generalizable ecological or evolutionary inferences (Garland & Adolph 1994). Thus, we do not consider the differences demonstrated here between steelhead and Lahontan cutthroat trout to necessarily be representative of differences between anadromous and potamodromous salmonids. Instead this comparison should be viewed as an example of how jackknife estimates can be used to generate species level estimates of population size variability and allow interspecific comparisons without conflating within species differences with among species differences.

The identification of significant intraspecific variation among Lahontan cutthroat trout populations was mirrored in our findings for other Salmonids. In all cases where multiple populations were monitored, significant intraspecific variation was identified (Table 1). We also identified significant intraspecific variation even where such differences would not be conflated with differences in sampling length (Table 2). Moreover, despite significant differences among species, more variation in how greatly population sizes fluctuated was present at the intra- than interspecific level (Table 3).

These results are consistent with those for other taxa. For example, Schoener & Spiller (1992) demonstrated considerable inter- and intraspecific differences in population size variability for spiders. Marsh (2001) similarly demonstrated that amphibians exhibit large differences in population size variability between taxonomic families. Unfortunately in neither of these cases were intraspecific differences explicitly of interest.

Using the GPDD, Fagan *et al.* (2001) found that estimated population growth rates of fish exhibited variation (δ) comparable to that of mammals and lepidopterans but higher than that of birds. In their analysis, δ corresponded to population size variability and so while fish may generally exhibit higher variability than birds, the relationship between the population size variability of salmonids vs. that of other fish is not currently clear. However, Winemiller (2005) provides some basis on which to generate predictions as to how salmonids may differ from other species: species with lower fecundity, greater egg size and parental care would be expected to have relatively dampened population size variability. Our results appear generally consistent with these expectations. For example, Chinook salmon have relatively larger eggs and lower fecundity than Sockeye salmon (Crespi & Teo 2002) and also exhibit lower population size variability (Table 1). Thus life-history attributes may allow some general predictions as to how fish species differ, although this may be complicated by the migratory status (e.g. anadromous vs. potadromous) of the species or populations.

Despite the demonstration of intra- and interspecific differences, the role that sampling periods of different lengths can have on species level estimates requires further study. Because of the well-established relationship between the length of sampling and population size variability, it seems possible that variability may be underestimated for species for which the majority of sampling has been conducted over short periods of time. The degree to which this is true and to which this bias can be statistically removed should be the target of further research.

The presence of taxonomic patterns in how population sizes vary with time has been hotly debated within the ecological literature (Connell & Sousa 1983; Schoener 1985; Inchausti & Halley 2002). Based on an increased availability of long-term data, population size variability now seems to be generally independent of major taxonomic groupings (Inchausti & Halley 2002) but conflicting reports remain (e.g. Reed & Hobbs 2004). However, assessment of large-scale taxonomic patterns may rely on only a few populations of a species or a few species of a genus. As our results demonstrated, population size variability can differ greatly among populations of single species. Thus any actual large-scale taxonomic patterns may be obscured due to variation within taxa. For example, despite significant differences among salmonid species, considerable variation remained at the intraspecific level. In conventional analyses, this variation would remain in the residual denominator of F-values which could obscure taxonomic differences. The assertion or dismissal of broad taxonomic patterns should be reassessed after accounting for these concerns. One potential approach to resolving this concern is the jackknife-linear model approach used here for multiple populations sampled at varying lengths. This approach generates species estimate that could be used in broad taxonomic comparisons.

Equally important, approaches where taxa are organized into broad groupings (e.g. birds or mammals) inappropriately assuming a 'star phylogeny' of equal evolutionary relatedness within these groups, inflates type-I error rates (Garland *et al.* 2005). To properly assess whether large scale patterns exist, species level estimates jackknife estimates can be made and compared between or among species, as we did here in our comparison of Lahontan cutthroat trout populations with steelhead. However, when well-resolved phylogenetic trees are available, broad taxonomic patterns in population variability should be evaluated using the jackknifing method described here along with new approaches combining phylogenetic methods and meta-analyses (Adams 2008; Lajeunesse 2009).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. GPDD identifying call numbers for the datasets used in this study.

Appendix S2. Annotated R script for bootstrap estimation of population size variability indices.

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