

## INTERSPECIES SYNCHRONY IN SALMONID DENSITIES AND LARGE-SCALE ENVIRONMENTAL CONDITIONS IN CENTRAL IDAHO

Timothy Copeland and Kevin A. Meyer

Idaho Department of Fish and Game, 1414 East Locust Lane, Nampa, ID 83709, Tel 1-208-465-8404; FAX 1-208-465-8434; tim.copeland@idfg.idaho.gov and kevin.meyer@idfg.idaho.gov

**ABSTRACT** — Abundance of fluvial salmonids varies substantially through time, often due to environmental stochasticity. The extent to which several sympatric species respond coherently to large-scale factors has been investigated rarely in freshwater fishes. We compared correlations among six salmonids at regional and site-specific levels and examined relationships between large-scale environmental variation and changes in salmonid density. Salmonid densities in central Idaho declined from the mid 1980s to the mid 1990s, and then rebounded through 2003. Most correlations in fish density among native salmonids were statistically positive at both regional and site-specific levels. In contrast, nonnative brook trout *Salvelinus fontinalis* were positively correlated to native salmonids at the regional scale but at not the site-specific scale, suggesting that synchrony between native and nonnative species was disrupted at small scales. Streamflow and the number of Chinook salmon *Oncorhynchus tshawytscha* redds (a surrogate for nutrient influx and therefore increased productivity to streams) were correlated with fish densities across the landscape. The importance of environmental conditions differed by species. Our finding that large-scale bioclimatic conditions influence the abundance of several salmonid species is important for fish managers charged with managing entire ecosystems with complex and sometimes sensitive species assemblages.

### INTRODUCTION

Many empirical studies have demonstrated links between environmental variation and the abundance of salmonids in streams (e.g., Bradford 1999; Mote et al. 2003). At the largest scale, population characteristics of fluvial fishes are generally influenced by streamflow, the biological productivity of the system, and thermal regime. However, the interrelationship between fish and their environment is often complex. As an example, anadromous fishes are affected directly by ocean conditions such as upwelling (Scheuerell and Williams 2005) and indirectly because ocean conditions affect the inland environment via weather patterns (Cayan and Peterson 1989). Analyses of the relationships between fish and their environment at large scales provide an opportunity to investigate bioclimatic conditions that might produce correlated abundance patterns (McElhany et al. 2000), yet few studies to date have included multiple species of fluvial fishes.

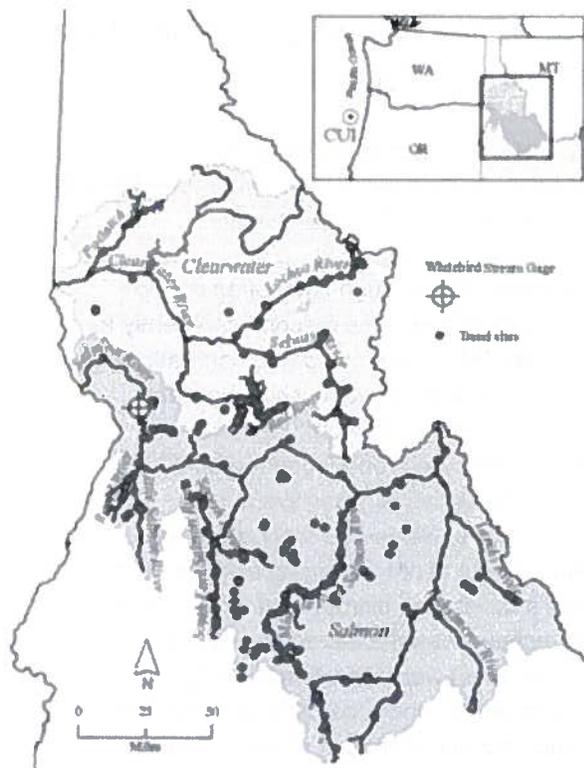
In this study, we explore the synchrony among six salmonid species in central Idaho and examine likely relationships between salmonid abundance

and environmental variables. The large number of observations in our study gave us considerable analytical power to distinguish regional effects, and provided us the opportunity to examine the data at more than one scale. Our objectives were (1) to compare synchrony in the densities of salmonids among spatial scales, (2) to explore the covariations of selected environmental variables to salmonid densities, and (3) to look for commonalities among species. We chose bioclimatic indices that we knew were influential, rather than attempting to include all potential variables.

### METHODS

#### Study Area

The study area consisted of a large contiguous network of stream habitats in the Salmon River and Clearwater River watersheds, excluding the North Fork of the Clearwater River, which is isolated by Dworshak Dam (Figure 1). Land cover is chiefly composed of coniferous forests at higher elevations and sagebrush-grass steppe at lower elevations.



**Figure 1.** Distribution of 367 survey sites within the Salmon and Clearwater basins in Idaho and the location of the Whitebird stream gauging station. The inset displays the position of the study area in the Pacific Northwest and the location from which the coastal upwelling index (CUI) estimate was derived.

Geology is largely granite and is part of the Idaho Batholith. Over 80% of the study area is publicly owned and nearly 25% is designated wilderness, with many large expanses functioning as *de facto* wilderness. Precipitation ranges from 40 to 200 cm annually, depending on elevation, and falls mostly as snow during winter months.

Fluvial native salmonids inhabiting the study area include Chinook salmon *Oncorhynchus tshawytscha*, redband steelhead trout *O. mykiss gairdneri*, bull trout *Salvelinus confluentus*, westslope cutthroat trout *O. clarkii lewisi*, and mountain whitefish *Prosopium williamsoni*. Brook trout *S. fontinalis* were first introduced in Idaho in the late 1800s, and although the stocking of this species has ceased, self-sustaining populations now exist in many parts of the study area.

## Fish Sampling

Since 1985, the Idaho Department of Fish and Game has conducted a large-scale snorkel survey program in central Idaho. Although originally designed to track trends for anadromous species, observations on all resident salmonids have been recorded as well. For logistical reasons, site selection was not random but based on professional judgment regarding habitat quality for juvenile anadromous salmonids and accessibility. Sites averaged 10.6 m in width (range 1.7 – 50.0 m). Petrosky and Holubetz (1986) provide a more detailed description of sampling site selection. Because many sites were not surveyed consistently, we set a criterion of using sites where multiple (i.e., >3) sample events occurred in each decade (1980s, 1990s and 2000s). This resulted in a sample of 367 sites with 4,752 snorkel surveys.

Counts, expressed as number/100 m<sup>2</sup>, were used as an index of abundance for each species. Depending on the stream width and water clarity, from one to five observers snorkeled slowly upstream counting all salmonids. Although rarely encountered, hatchery rainbow trout were distinguishable from wild *O. mykiss* by size and fin condition, and were excluded from our analyses. Visibility was recorded before each survey and averaged 4.3 m; 95% of surveys were conducted when visibility was  $\geq 1.7$  m. Water temperature during snorkel surveys averaged 14.5°C. Total counts were used as minimum abundance estimates with no correction for probability of detection, and thus should not be viewed as accurate estimates of true abundance. However, we assumed that this technique would function adequately as an index of abundance.

Our working hypothesis was that temporal changes in salmonid abundance at the landscape scale are influenced by large-scale bioclimatic variables, chiefly weather and marine nutrient inputs in the form of salmon. We chose five variables on which to focus: streamflow (FLOW), the Palmer drought severity index (PDSI), mean July air temperature (AirT), a coastal upwelling index (CUI), and counts of Chinook salmon redds (REDDS). We obtained estimates of the regressors from several sources. To represent unregulated streamflows in central Idaho, we obtained mean annual discharge (m<sup>3</sup>/s) data on the lower Salmon River near Whitebird from the U.S. Geological Survey. The PDSI and average July air temperatures for central Idaho were

computed by the National Climatic Data Center. The PDSI index is based on balance between moisture supply, soil characteristics, and evapotranspiration. The October CUI at 45°N 125°W was estimated by Scheuerell and Williams (2005) to characterize the ocean conditions that juvenile Chinook salmon from the Snake River encounter during their first season in the ocean. Lastly, we obtained redd counts at trend transects across central Idaho ([www.streamnet.org](http://www.streamnet.org)).

To refine our working hypothesis into a mechanistic explanation for observed fish densities, we correlated each variable against species densities at lags from 0 to 5 years. We assumed the environment would not necessarily affect a species in the year in which the environmental variable was measured but should have a lag effect based on processes such as recruitment. Year 0 was not included for REDDS and CUI because those variables were measured after snorkel surveys were completed. Patterns in the lagged correlations were compared among species and the final form for each variable was chosen based on the largest number of potentially important correlations ( $r^2 > 0.10$ ) in the same direction across the six species (data not shown). We chose to average FLOW at 3- and 4-year lags and PDSI at 4- and 5-year lags. We chose the 2-year lag for CUI and a 1-year lag for REDDS. Correlations were maximized for AirT with no lag.

We used correlation analyses to examine relationships among fish species. All fish densities were log-transformed ( $\log_e[\text{density}+0.01]$ ) before analyses. At the regional scale (Clearwater and Salmon basins), we calculated the annual mean density of each species, then assessed the level of correlation among all species over time. At the site-level scale, we analyzed the relationships between species by correlation, using each snorkeling event as an observation and disregarding the year of sampling. We excluded pair-wise comparisons where density was zero for both species. Correlations were considered statistically significant at  $\alpha = 0.05$ . We conducted separate analyses for the Salmon and Clearwater drainages to discern whether the correlations were consistent between drainages.

To assess the relationship between the five environmental variables and the densities of the six salmonid species, we used canonical correlation. The

canonical correlation was performed on the set of transformed densities averaged within year versus the regressors. We used the variable loadings and redundancies on the first canonical axis, as well as canonical cross loadings, to interpret the canonical correlation. Because correlation matrices were used, interpretation in terms of species density was made in relative terms and each species had equal weight. To clarify interpretation of the canonical correlation, we used information-theoretic model selection techniques to examine the univariate effects of the regressors on individual species densities (Burnham and Anderson 2002).

Univariate model selection for each species was based on Akaike's information criterion corrected for small sample sizes (Burnham and Anderson 2002). All additive combinations of the regressors were fit against transformed density for each species. As a general index of model fit, we used adjusted  $R^2$ . The relative likelihood of each model in the set of models for each species was assessed with Akaike weights (Burnham and Anderson 2002). The weight of evidence for a single regressor is evaluated from the Akaike weight of that regressor versus the others. The relative importance of a particular regressor, given all potential additive combinations of the regressors, was computed as the sum of the Akaike weights of all models containing that regressor (importance value).

## RESULTS

Average densities of all species declined from the 1980s to the mid 1990s, and then rebounded through 2003, although there was much variation about the trends. Bull trout and brook trout had the lowest average densities during the study period (Figure 2). The highest densities were observed for steelhead trout and Chinook salmon. Of all the salmonids, Chinook salmon had the most variable density and the most exaggerated trend. Densities of westslope cutthroat trout and mountain whitefish were intermediate to the other species. Average salmonid densities over time were strongly correlated among species at the regional scale, with 25 of the 30 correlation coefficients for each pair-wise comparison being positive and 13 being statistically significant at  $\alpha = 0.05$  (Table 1).

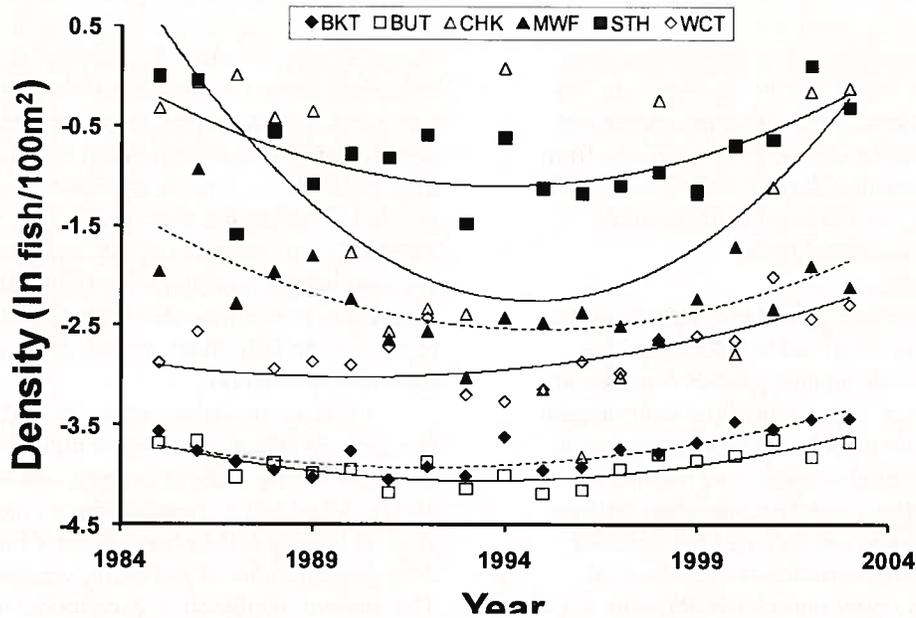


Figure 2. Density of six salmonid species in central Idaho, 1985-2003. Species were steelhead (STH), Chinook salmon (CHK), mountain whitefish (MWF), westslope cutthroat trout (WCT), brook trout (BKT), and bull trout (BUT). Trend lines were fitted using a second-order polynomial.

Table 1. Correlation coefficients among species for annual mean density at snorkel sites in the Salmon River (below the diagonal,  $n = 206$ ) and Clearwater River (above the diagonal,  $n = 161$ ) drainages. Species are brook trout (BKT), bull trout (BUT), Chinook salmon (CHK), mountain whitefish (MWF), steelhead trout (STH), and westslope cutthroat trout (WCT).

Species	BKT	BUT	CHK	MWF	STH	WCT
BKT	--	-0.07	-0.08	0.35	0.33	0.39
BUT	0.81*	--	0.51*	0.63*	0.45	0.52*
CHK	0.35	0.41	--	0.22	-0.05	0.04
MWF	-0.01	-0.01	0.41	--	0.67*	0.54*
STH	0.58*	0.65*	0.61*	0.48*	--	0.66*
WCT	0.23	0.36	0.31	0.54*	0.58*	--

$P < 0.05$

At the site-level scale, correlations among species were also frequent. In fact, 17 of the 30 pairwise comparisons had statistically significant correlations, 14 of which were positive (Table 2). Considering only native salmonids, 16 of the 20 comparisons were positively correlated at a statistically significant level, whereas only 2 statistically significant correlations were negative. However, of the 10 comparisons of nonnative brook trout density to that of native salmonids, only one relationship was statistically significant (brook trout and steelhead trout in the Salmon sub-basin, a negative correlation). In contrast, brook trout were positively

correlated for 7 of 10 comparisons with native salmonids at the regional scale, 2 of which were statistically significant (Table 1).

### Canonical Correlation

The canonical correlation explained a significant amount of the shared multivariate variance between fish densities and environmental variables (Wilks'  $\Lambda = 0.05$ ,  $df_1 = 30$ ,  $df_2 = 34$ ,  $P = 0.0006$ ). The redundancy of the original densities with the first axis of canonical density variate was 51.6% and declined to <10% for the other axes, so we interpreted only the first axis.

**Table 2. Correlation coefficients among species for all pair-wise comparisons from each snorkeling event ( $n = 4,752$ ) in the Salmon River (below the diagonal) and Clearwater River (above the diagonal) drainages. Sample size for each comparison is in parentheses. See Table 1 for species codes.**

Species	BKT	BUT	CHK	MWF	STH	WCT
BKT	--	-0.20 (40)	-0.09 (206)	0.01 (229)	-0.04 (209)	0.04 (167)
BUT	0.05 (161)	--	0.66* (207)	0.50* (208)	0.18* (303)	-0.02 (264)
CHK	0.07 (467)	0.10* (423)	--	0.68* (702)	0.15* (790)	0.17* (628)
MWF	0.00 (296)	0.14* (407)	0.21* (1039)	--	0.28* (852)	0.19* (715)
STH	-0.12* (497)	0.06 (637)	-0.11* (1307)	0.11* (1293)	--	0.08* (961)
WCT	0.04 (137)	0.09 (290)	0.01 (564)	0.15* (738)	-0.10* (791)	--

\* $P < 0.05$

**Table 3. Contributions of individual variables to the canonical correlation between fish densities and selected environmental variables.**

Variable	First axis loading	Canonical cross loading
Fish densities		
BKT	0.735	0.703
BUT	0.848	0.812
CHK	0.766	0.732
MWF	0.664	0.635
STH	0.721	0.689
WCT	0.538	0.515
Regressors		
AirT	0.508	0.486
CUI	-0.608	-0.581
Flow	0.684	0.654
PDSI	0.612	0.586
Redds	0.708	0.678

Contributions to the canonical correlation differed among fish species and environmental variables. All species densities loaded positively onto the first axis of the dependent canonical variate, bull trout most strongly, then Chinook salmon, brook trout, steelhead trout, mountain whitefish, and westslope cutthroat trout, respectively (Table 3). Order by canonical cross-loadings was the same. Of the environmental variables, REDDS loaded most strongly on the first axis, followed by FLOW, CUI, PDSI, and AirT, respectively (Table 3). As with densities, the order by canonical cross loadings was

the same. All the regressors loaded positively on the first axis except for CUI.

### Univariate Model Selection

Akaike weights showed that importance of the regressor variables differed among species (Table 4). For bull trout and brook trout density, FLOW and AirT were the two most important regressor variables (positive effects). For mountain whitefish, CUI was the most important regressor followed by PDSI (both negative relationships). Coastal upwelling index was also the most important regressor for steelhead trout density (negative relationship), but secondarily, AirT was an important regressor (positive relationship). Not surprisingly, REDDS was by far the most important regressor for Chinook salmon density (positive relationship). For westslope cutthroat trout, there was much uncertainty in model selection because no model explained a large amount of variance for this species (maximum adjusted  $R = 0.31$ ). More variance was explained for the other species, with maximum adjusted  $R$  ranging from 0.52 for Chinook salmon to 0.69 for mountain whitefish.

### DISCUSSION

Our results suggest that large-scale temporal trends in abundance were consistent across all study species in central Idaho from the mid 1980s to mid 2000s. The study species were all fluvial salmonids that arguably should react similarly to large-scale

environmental variation. However, these species have disparate thermal optima, spawn and migrate at various times of the year in dissimilar habitats and conditions, prefer different local micro- and meso-habitats for rearing, and make use of resident and

anadromous life history behaviors. Consistent trends in abundance amid such diverse phenotypic characteristics suggest that regionally coherent bioclimatic controls were likely driving the synchronized relationships.

**Table 4. Akaike weights and importance values of regressors explaining observed fish densities by species.**

Variable	Akaike weight	Importance value
<i>Brook trout</i>		
AirT	0.018	0.845
CUI	0.002	0.134
FLOW	0.037	0.944
PDSI	0.004	0.537
REDDS	0.006	0.330
<i>Bull trout</i>		
AirT	0.001	0.727
CUI	0.003	0.577
FLOW	0.078	0.982
PDSI	0.002	0.571
REDDS	<0.001	0.230
<i>Chinook salmon</i>		
AirT	0.001	0.181
CUI	0.005	0.314
FLOW	0.003	0.375
PDSI	0.010	0.401
REDDS	0.098	0.949
<i>Mountain whitefish</i>		
AirT	<0.001	0.182
CUI	0.024	0.946
FLOW	0.004	0.358
PDSI	0.026	0.727
REDDS	<0.001	0.141
<i>Steelhead trout</i>		
AirT	0.009	0.932
CUI	0.022	0.958
FLOW	0.002	0.140
PDSI	0.002	0.199
REDDS	0.006	0.164
<i>Westslope cutthroat trout</i>		
AirT	0.108	0.436
CUI	0.087	0.375
FLOW	0.068	0.413
PDSI	0.044	0.413
REDDS	0.102	0.339

In addition to environmental effects, other potentially synchronizing processes include dispersal and the effects of mobile predators or parasites (Liebhold et al. 2004). We examined interspecies synchrony, not populations *per se*; hence, dispersal cannot explain the patterns we observed (Liebhold et al. 2004). Human predation cannot explain the

interspecies patterns in this study, because there was no fishery for wild steelhead or Chinook salmon during the study period, and because much of the study area is exceedingly rugged and remote with concomitant negligible exploitation rates. Whirling disease *Myxobolus cerebralis* is another potential means of synchronized mortality, but it does not

affect all salmonids equally, it is not found throughout the study area, and resistance to it is unlikely to develop quickly enough to explain the increased densities observed after the mid 1990s. By elimination, we concluded that the most likely synchronizing process in our study was shared correlation to environmental conditions (i.e., the Moran effect, Moran 1953).

### Bioclimatic Effects

Most of the environmental variables included in our analyses logically should have affected salmonid density in subsequent years. For example, CUI was measured in October, at least a month after surveys were conducted in a given year. Only AirT was most strongly related to salmonid densities with no lag. For all other environmental variables, lags of between one and five years were most strongly related to salmonid density, presumably by impacting recruitment (e.g., Tedesco et al. 2004; Zorn and Nuhfer 2007a). We detected these effects in subsequent years through changes in fish densities.

Considering the salmonid community as a multivariate whole, FLOW and REDDS were the most important environmental variables and AirT was the least important. Flow effects on salmonid recruitment (via juvenile survival) are well-documented and can be seasonal in nature, such as redd scour during incubation (Carline and McCullough 2003), displacement of newly emerged fry (Zorn and Nuhfer 2007b), and reduced overwinter survival during low flow years (Mitro et al. 2003). Crozier and Zabel (2006) suggested annual stream flow (dictated by winter/spring snowpack) affected parr-to-smolt survival of Chinook salmon in the Salmon River basin. Hydrographs of almost all streams in central Idaho are driven by snowmelt with flows peaking in May or June. Given this similarity in hydrologic regime, it is plausible that flow would affect stream fishes simultaneously over a large area. In our study, FLOW was of primary importance for bull trout and brook trout, but its effect was positive for all species.

In the multivariate model, REDDS was important largely because of the high loading of Chinook salmon into the canonical variate. It was not surprising that a one-year lag on REDDS was the most influential environmental variable for Chinook salmon because most Chinook (>97%) observed were age 0. We hypothesized that redd counts also might be influential for other species because of the

influence of marine-derived nutrients on stream productivity (Wipfli et al. 1998). The fact that for all species the strongest lag for REDDS was one year suggests that increased numbers of decaying adults led to higher survival (presumably through increased stream productivity) to the next year for all species. However, in the univariate models, REDDS had a minor effect for all species except Chinook salmon, suggesting this influence was weak, at least given the current low abundances of adult Chinook salmon in the system.

Univariate models suggested that CUI was important to steelhead and mountain whitefish. The form of CUI we used was measured in October and was chosen because of its demonstrated impact on Chinook salmon (Scheuerell and Williams 2005). It may have acted as a surrogate for fall stream conditions via influence of ocean conditions on inland weather patterns (Cayan and Peterson 1989). Fall is when steelhead adults are migrating up the Columbia and Snake rivers to Idaho (August-October) and when mountain whitefish spawn. Because CUI was most strongly related to steelhead and whitefish at a lag of four years, it is likely that CUI was related to recruitment of these species, not adult density directly. Alternatively, the relationship between CUI and steelhead or whitefish may have been non-causative. An apparent environmental effect may arise because two species that are correlated to each other such that the first species shows an apparent relationship to that particular environmental variable, even though the direct effect is actually on the second species. There may be other plausible indirect effects as well, providing a good illustration of why it is hard to infer causal mechanisms with large-scale data.

Temperature in the year of observation was an important modifier for all species except Chinook salmon and mountain whitefish. Because there was no lag time for the effect of AirT, we hypothesized this relationship was related to detection probability, not density. Temperature is related directly to the probability of detecting bull trout, cutthroat trout, and rainbow trout with snorkel surveys because fish become less active and more difficult to observe at low temperatures (Thurow et al. 2006). Chinook salmon and mountain whitefish are schooling species, the detection of which may be less affected by temperature because it is easier to observe schools of fish than dispersed individuals. However, temperature was not of primary importance for any species.

The relationship between environmental conditions and fish density was weakest for westslope cutthroat trout. On average, correlations to environmental variables for this species were less than half the values for other species. Model selection results were ambiguous for cutthroat trout; all importance values of the regressors were  $<0.50$ . Further, this species had the lowest loading in the canonical correlation. Westslope cutthroat trout are closely associated with headwater habitats, which are typically more stochastic than downstream reaches and therefore may be less likely to be influenced by the large-scale environmental variables we analyzed.

In spatiotemporal population dynamics, there are two components of variation: environmental correlations and a demographic component, i.e., density-dependence (Liu et al. 2009). In our analyses, the density-dependent component was incorporated only for Chinook salmon (via REDDS), and it was very significant in multivariate and univariate models, as has been found previously in Chinook salmon populations in the study area (Copeland et al. 2008). Similar indices of cohort egg density were not available or were incomplete for the other species, but their inclusion likely would explain more variance in salmonid density.

### Synchrony Among Salmonid Species

High et al. (2008) found that population abundance in salmonid communities in central Idaho fluctuated in synchrony over a multi-decadal time scale, and our study demonstrates that this pattern carries through to smaller scales. Synchrony is common across animal populations and should be expected in multi-population studies (Liebhold et al. 2004; Bjørnstad et al. 2009), including studies of fish communities (Wood and Austin 2009). However, the data needed to discern this phenomenon are extensive in both time and space, and consequently are scarce in freshwater fish ecology. Most previous studies of population synchrony in freshwater fishes have examined only one or two species (e.g., Isaak et al. 2003; Zorn and Nuhfer 2007a). In one of the few studies of synchrony in multiple freshwater fish species, Tedesco et al. (2004) found synchrony in 4 species of African fishes was influenced by regional river discharge the previous year over a 24-year time frame. In comparison, we found synchrony among 6 species over 19 years.

Niche partitioning may allow native salmonids in central Idaho to live sympatrically and fluctuate communally, as demonstrated by synchrony at both the regional and site scales. Such niche partitioning is common among sympatric native salmonids (e.g., Nakano et al. 1992). The presence of exotic salmonids can disrupt this partitioning (Hasagawa and Maekawa 2006) and may explain why the synchrony we observed between nonnative brook trout and native salmonids at the regional scale was absent at the site scale. Indeed, negative interactions between brook trout and native salmonids are ubiquitous in western North America (e.g., Levin et al. 2002; Rieman et al. 2006).

For fishery managers, interspecies synchrony may allow a more powerful multispecies approach to monitoring fish populations. Regional synchrony allows establishment of trend sites that capture the ecological variation over a larger area. By using targeted surveys to describe temporal trends, managers can better interpret findings from individual surveys within a region and be more informed about the effects of management actions (Zorn and Nuhfer 2007a). However, the extent of synchrony should be estimated, because it will vary depending on the study area, the focal group of species, the influential environmental variables, and the range of environmental conditions.

The occurrence of interspecies synchrony suggests that abundances of all salmonids in central Idaho currently are linked. All native species in our study area were formerly more abundant, and may have been less synchronous under such conditions (see Isaak et al. 2003 for an example using Chinook salmon). Synchrony theoretically reduces metapopulation resilience (Heino et al. 1997), and this effect may carry through to community structure.

Studies such as ours serve as an important baseline from which to understand the effects of climate change on stream fishes. There is a mismatch of scales between aquatic ecology and climatology; climate studies are conducted at very large scales (e.g., continental), whereas the typical scale of ecological studies is much smaller. In our data, the clearest climatic influence on fish density was the direct correlation between FLOW and bull trout density, a species that has already been used as an indicator of climate change effects (Rieman et al. 2007). These authors found that bull trout populations in Idaho were sensitive to temperature, but our results suggest that changes to the flow regime also

should be investigated. Effects of various climatic variables on fish populations tend to be interdependent and mechanistically complex. Further, the synchronizing agent may be different from causes responsible for oscillations (Moran 1953; Bjørnstad et al. 2009). However, this study provides an inductive basis for further exploration of likely mechanisms influencing the dynamics and structure of fluvial salmonid communities.

The bioclimatic conditions we included explained 52% of the variation in the abundance of salmonids in central Idaho. Clearly, other factors also were affecting the populations in our study. The relative contribution of the bioclimatic variables to overall variation may provide managers a relative sense of what variation in abundance may be under management control. Such knowledge at large scales may help focus management efforts or shape restoration actions. The influence of climate on fishes is complex and can vary across differing scales in space and time. Causal mechanisms are difficult to infer and require further research. Our study provides a basis for suggesting fruitful avenues for such work.

## ACKNOWLEDGMENTS

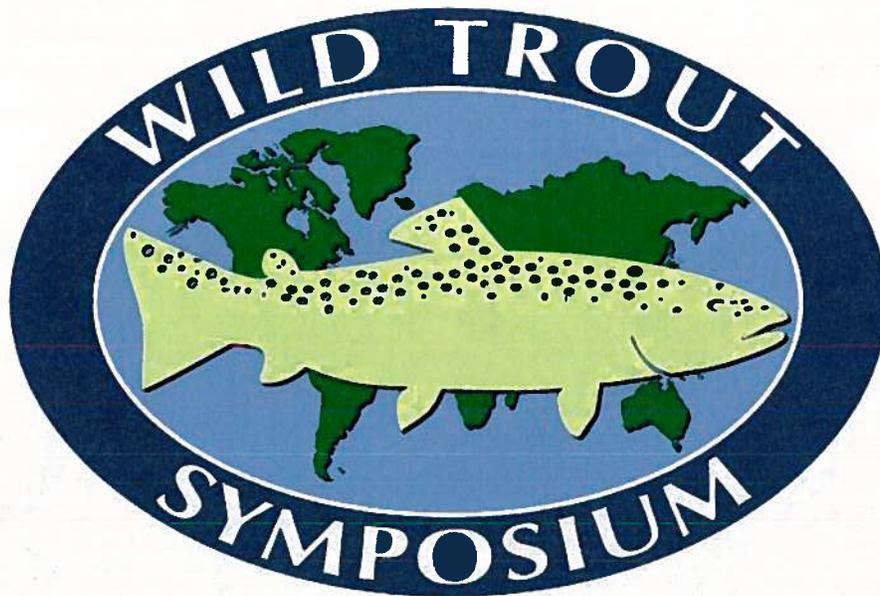
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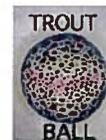
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