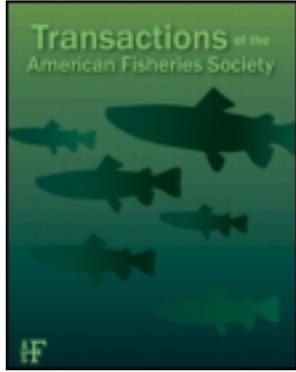


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ARTICLE

Interspecies Synchrony in Salmonid Densities Associated with Large-Scale Bioclimatic Conditions in Central Idaho

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Abstract

The abundance of lotic salmonids varies substantially through time, but the extent to which several sympatric species respond coherently to large-scale bioclimatic conditions has rarely been investigated for freshwater fishes. We compared correlations in salmonid density in central Idaho and examined the relationships between changes in salmonid density and the variation in large-scale bioclimatic conditions as indexed by stream flow, air temperature, drought, coastal upwelling, and the number of Chinook salmon *Oncorhynchus tshawytscha* redds (a surrogate for nutrient influx and therefore increased stream productivity). The average densities of six stream-dwelling salmonid fishes were highly synchronous, with declines from the mid-1980s to the mid-1990s followed by a rebound through 2003. All pairwise correlations were positive and 8 of 15 were statistically significant. Stream flow and Chinook salmon redds were correlated with fish densities as a group, but the importance of bioclimatic indices differed by species and varied by the lag times applied. Stream flow 3 and 4 years previous was most important for brook trout *Salvelinus fontinalis* and bull trout *S. confluentus*. The presence of Chinook salmon redds from the previous year was most important for Chinook salmon. The coastal upwelling index 4 years previous was most important for mountain whitefish *Prosopium williamsoni* and steelhead *O. mykiss*. No variable captured much of the variation in the density of westslope cutthroat trout *O. clarkii lewisi*. Models based on data from 1985 to 2003 correctly predicted the synchronous declines in fish density observed for all species from 2004 to 2009, suggesting that the bioclimatic indices we chose were useful surrogates for large-scale factors influencing the temporal changes in salmonid densities in central Idaho. For fishery managers, interspecies synchrony may allow a more powerful multispecies approach to monitoring and reveal the tractability of large systems to management control. However, causal mechanisms are hard to infer and require further research (e.g., the effects of ocean conditions). Our study provides a basis for such work.

The abundance of lotic salmonids often varies substantially through time (Bradford 1999; Carline 2006; High et al. 2008). Because fluctuations can affect population characteristics such as viability, life history behaviors (e.g., dispersal), and harvestable surplus, understanding the causes of fluctuations in abundance is important for fisheries managers (Milner et al. 1993). Unless harvest varies substantially, managers assume that population fluctuations are caused by environmental stochasticity (Strange et al. 1992).

Many empirical studies have demonstrated links between environmental variation and the abundance of salmonids in streams (e.g., Rieman and McIntyre 1995; Bradford 1999; Mote et al. 2003). At the watershed scale, population characteristics

of lotic fishes are generally influenced by stream flow, the biological productivity of the system, and thermal regime. However, the relationship between fish and their environment is often complex. As an example, ocean upwelling directly influences juvenile salmon abundance through bottom-up forcing of the marine food web (Nickelson 1986; Scheuerell and Williams 2005), but upwelling in the ocean also affects inland weather patterns (Cayan and Peterson 1989), which could indirectly affect premigratory salmon parr. Analyses of the relationships between fish and their environments at large scales provide an opportunity to investigate bioclimatic conditions that might produce synchronous abundance patterns (Wiley et al. 1997; Kendall et al. 2000; McElhany et al. 2000), yet

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few such studies to date have included multiple species of lotic fishes.

Many native salmonids in the interior of the Pacific Northwest have experienced substantial long-term declines in distribution and abundance (Thurow et al. 1997), and several species have been listed or proposed for listing under the U.S. Endangered Species Act. This commonality likely is not a coincidence but rather an indication of a coherent response to large-scale disturbances and changes. For anadromous salmon the largest disturbance in the region has clearly been the construction and operation of dams on the Columbia and Snake rivers (Raymond 1988; Petrosky et al. 2001; Yuen and Sharma 2005). All native salmonids have been negatively affected by nonnative species introductions and invasions (e.g., Levin et al. 2002; Rieman et al. 2006), overharvest (Young 1995; Lichatowich 1999), and alteration of habitat (see review in Hicks et al. 1991). Global climate change looms as a potentially overarching impact on all species (Battin et al. 2007; Rieman et al. 2007; Rahel et al. 2008), but we wished to assess the specific components of climate and other influential factors to which fish might have been reacting in the recent past. Because much of central Idaho is in a relatively undeveloped condition, and anthropogenic changes to physical stream habitats in recent decades have been minimal, the likelihood of other factors obscuring relationships between bioclimatic variability and salmonid abundance is minimized.

In this study, we explored the synchrony among six salmonid species in central Idaho and examined likely relationships between salmonid abundance and bioclimatic variables. The large number of observations in our study gave us considerable analytical power to distinguish regional-level annual effects. Our objectives were to (1) test for synchrony in the densities of salmonids in central Idaho and (2) explore the covariation of selected bioclimatic indices to salmonid densities. As part of the first objective, we conducted preliminary analyses to estimate the amount of variance in fish densities related to coherent annual variation. To address the second objective, we chose a few broad-scale bioclimatic indices that have been linked to fish populations in the study area, rather than attempt to include all potential variables. Our initial analysis was on data collected during 1985–2003. To confirm the temporal patterns in the data, we used the most recent 6 years of data (2004–2009) to validate both the interspecific synchrony in densities and the species-specific models that related those densities to the selected bioclimatic indices.

STUDY AREA

The study area consisted of a large contiguous network of stream habitats that included the Salmon and Clearwater river basins, excluding the North Fork of the Clearwater River, which is isolated by Dworshak Dam (Figure 1). The Clearwater and Salmon rivers drain a combined 61,000 km² of mountainous terrain in central Idaho. The area lies within the Idaho Batholith and Northern Rockies ecoregions (Omernik 1995),

which are characterized as mountainous and rugged with coniferous forests at higher elevations (up to 3,800 m in elevation) and sagebrush–grass steppe at lower elevations. The geology is largely Cretaceous granite and thick volcanic ash deposits. Over 80% of the study area is publicly owned, and nearly 25% is designated wilderness, with many large expanses functioning as de facto wilderness. Annual precipitation ranges from 40 to 200 cm, depending on elevation, and falls mostly as snow during winter months.

Native lotic salmonids inhabiting the study area include Chinook salmon *Oncorhynchus tshawytscha*, steelhead/redband 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. These six species were the focus of this investigation.

METHODS

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 of all resident salmonids have been recorded as well. For logistical reasons, site selection was not random but rather was based on existence of established sites, professional judgment regarding quality of habitat for juvenile anadromous salmonids, and accessibility. Petrosky and Holubetz (1986) provide a more detailed description of sample site selection.

Snorkeling counts of all salmonids observed were used as an index of abundance for each species, which was expressed as a density (number/100 m²). Depending on the stream width and water clarity, from one to five observers snorkeled slowly upstream counting all salmonids greater than 75 mm total length (TL) and binning them in 25-mm size-classes, except for Chinook salmon, which were counted as either age-0 or age-1 fish (based on easily distinguishable size differences). Although rarely encountered, hatchery rainbow trout *O. mykiss* of catchable size were distinguishable from their wild counterparts by fish size and fin condition, and were excluded from our analyses. Visibility (i.e., distance to distinguish patterns on an object [e.g., boot or tape measure] as a surrogate for spotting patterns on fish) was measured before each survey and averaged 4.3 m; 95% of surveys were conducted when visibility was at least 1.7 m. Water temperature during snorkel surveys averaged 14.5°C and ranged from 5°C to 28°C, but less than 1% of the surveys occurred at temperatures less than 8°C, the temperature at which salmonids typically initiate concealment behavior (e.g., Chapman and Bjornn 1969; Meyer and Gregory 2000). Total counts were used as minimum abundance estimates with no correction for probability of detection, and thus should not be viewed as

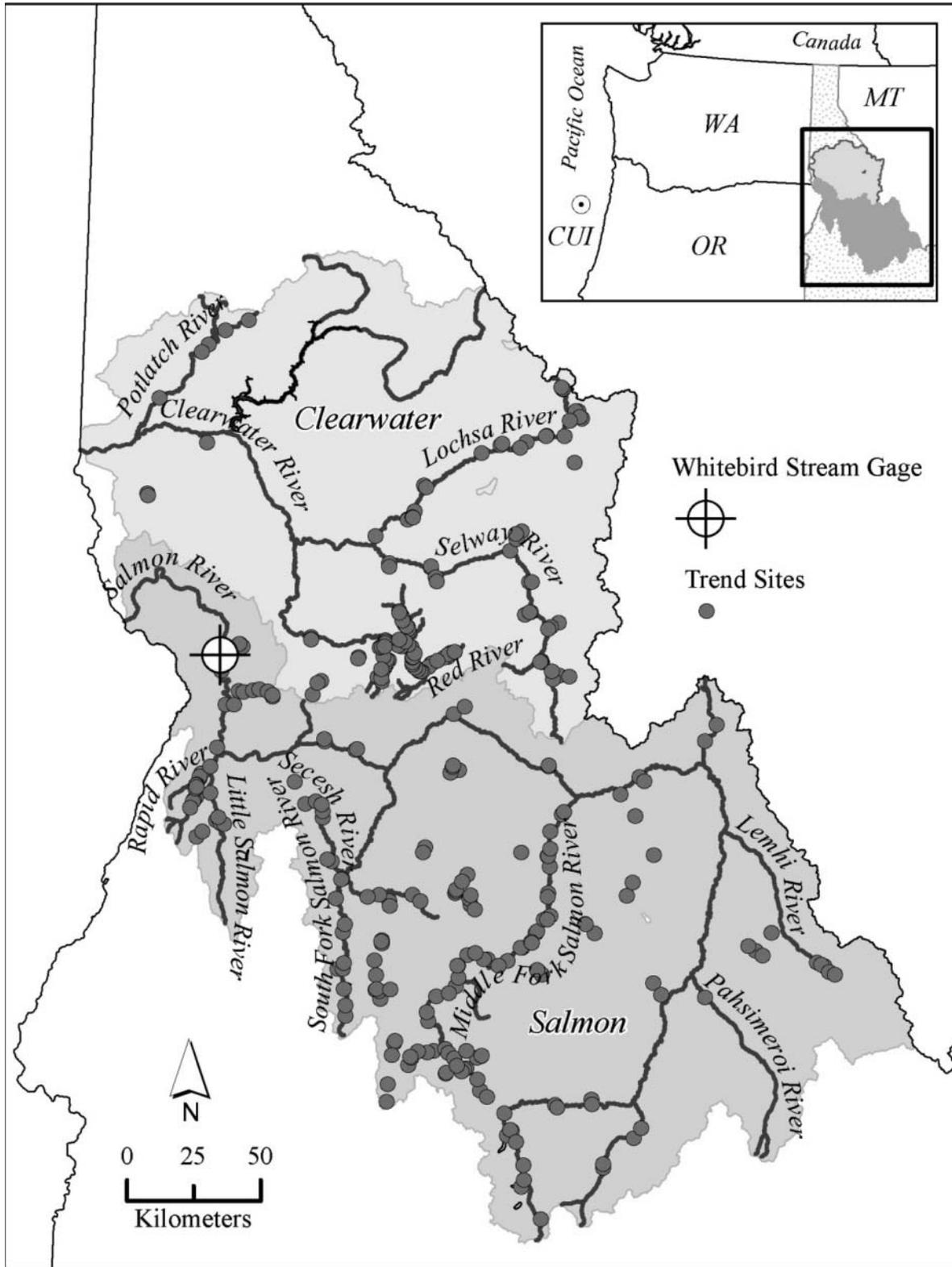


FIGURE 1. Distribution of the 367 survey sites within the Salmon and Clearwater river basins in Idaho and the location of the Whitebird stream gauging station. The inset shows the location from which the coastal upwelling index (CUI) estimate was derived.

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TABLE 1. Percentile distributions of selected survey and site characteristics in central Idaho.

Percentile	Survey characteristics		Site characteristics		
	Surveys per site	Surveys per year	Mean width (m)	Stream order	Site elevation (m)
5th	5	110	4.5	2	600
25th	9	196	6.9	3	1,004
50th	13	245	9.6	4	1,289
75th	16	276	13.6	4	1,698
95th	18	302	22.1	6	2,023

accurate estimates of true abundance. However, snorkel surveys yield repeatable estimates of abundance that are usually well correlated with other estimates of abundance (Thurow 1994).

A total of 15,627 snorkel surveys at 7,965 sites were conducted during 1985–2003. However, many sites were not surveyed consistently. To detect trends in density instead of sampling effort variability, we set a criterion of using sites where multiple (i.e., >3) sample events occurred in each decade (1980s, 1990s, and 2000s). This reduced the number of sample sites to 367, but there were 4,600 snorkel surveys conducted at these sites. For this set of sites, most were surveyed 9–16 times during 1985–2003 (Table 1). Surveys occurred most often in third- to fourth-order streams (Strahler 1964), with mean wetted widths of 7–14 m and elevations from 1,000 to 1,700 m. These sites were broadly distributed in the study area, encompassed a wide variety of physical conditions, and, hence, should be minimally biased in regards to spatial coverage despite nonrandom selection (Kadmon et al. 2003; Wagner et al. 2007).

Bioclimatic Variables

Our working hypothesis was that temporal changes in stream salmonid abundance at the landscape scale would be influenced by large-scale bioclimatic variables affecting thermal experience, hydrologic regime, and biological productivity. We chose five variables on which to focus: stream flow, temperature, drought, coastal upwelling, and counts of Chinook salmon redds.

Stream flow.—In recent decades, stream flow in the U.S. Pacific Northwest has declined (Luce and Holden 2009; Clark 2010) and shifted to earlier spring runoff timing (Stewart et al. 2004). Presumably, these changes will be exacerbated as the climate continues to warm. Considering that stream flow is important for nearly every salmonid life stage, including migration, spawning, and rearing (see review in Bjornn and Reiser 1991), altered stream flow over the long term may have profound effects on stream-dwelling salmonids. For example, occupancy may change if stream reaches become uninhabitable owing to elevated stream temperature or channel desiccation (Zoellick 1999; Matthews and Marsh-Matthews 2003). Migratory pattern and timing may shift for anadromous and resident salmonids as winter freshets increase, spring runoff decreases, and summer

low flows are prolonged (see review in Mote et al. 2003). Lower stream discharge may increase predation risk (Heggenes and Borgström 1988), resulting in reduced carrying capacity. Based on abundant information from the literature, we hypothesized that changing stream flows would broadly affect salmonids in central Idaho streams.

We used data from the gauge on the lower Salmon River near Whitebird (U.S. Geological Survey station 13317000; <http://waterdata.usgs.gov/id/nwis/rt>) because it covers the largest drainage area of all the gauges within the study area, is centrally located, and is well correlated to flows in the Clearwater River at Orofino ($r^2 = 0.83$). We calculated annual mean discharge (m³/s) to characterize stream flow (hereafter FLOW) because the six species in our study spawn, hatch, and migrate at different times of the year.

Temperature.—Given the requirement of salmonids for cold water temperatures, recent increases in global temperature and predicted increases over the rest of the century (IPCC 2007) probably will have a strong effect on the distribution and abundance of stream-dwelling salmonids (Keleher and Rahel 1996; Rieman et al. 2007). However, empirical studies directly relating changing water temperature to changes in salmonid abundance are generally lacking because long-term water temperature data across the landscape are virtually nonexistent (Isaak et al. 2010). Instead, air temperature is often used as a surrogate for water temperature (Rahel 2002) because air and water temperatures in general are strongly correlated (Isaak and Hubert 2001; Crisp and Howson 2006). Because long-term water temperature data in central Idaho were lacking, and July air temperature (hereafter AirT) can be correlated to the distribution and abundance of salmonids in Rocky Mountain streams (Dunham et al. 1999; Rahel and Nibbelink 1999), we used the average July AirT for central Idaho (estimated by the National Climatic Data Center, www.ncdc.noaa.gov) to characterize stream temperature.

Drought.—Drought conditions may be coupled with warmer water temperature and reduced streamflow in ways that are not completely captured by the temperature and flow indices discussed above. As a measure of drought, we used the Palmer Drought Severity Index (PDSI), which is based on balance between moisture supply, soil characteristics, and evapotranspiration (Palmer 1965). Negative PDSI values 0 to –0.5 are

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normal, -0.5 to -1 indicate incipient drought, -1 to -2 indicate mild drought, -2 to -3 moderate drought, -3 to -4 indicate severe drought, and less than -4 indicate extreme drought. Positive PDSI values follow a similar qualitative categorization for wet weather. Paulsen and Fisher (2001) found that lower July–December PDSI values were related negatively to survival of Chinook salmon parr from their natal streams to Lower Granite Dam on the lower Snake River, and resident salmonids also can be negatively related to drought conditions (Elliott 2000; Hakala and Hartman 2004; White and Rahel 2008). The PDSI for central Idaho was computed by the National Climatic Data Center (Heddinghaus and Sabol 1991; www.ncdc.noaa.gov). We averaged the monthly values during July to December.

Coastal upwelling.—Salmon production in the Pacific Northwest is related to ocean temperatures and the strength of upwelling currents (Nickelson 1986). Scheuerell and Williams (2005) examined correlations of coastal upwelling index (CUI) to smolt-to adult return rate (SAR) of Snake River spring–summer Chinook salmon; this relationship was strongest in October. Petrosky and Schaller (2010) found that October was the only month in which CUI was significantly correlated to SAR for both Chinook salmon and steelhead. Ocean conditions affect inland weather (Cayan and Peterson 1989; Mote et al. 2003) and thus could affect inland fishes via variables such as FLOW, AirT, and PDSI. To incorporate variation in ocean climate and additional inland effects, we used October CUI at 45°N , 125°W estimated by the Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov).

Numerous studies have linked the dominant pattern of North Pacific sea surface temperature variability, termed the Pacific Decadal Oscillation (PDO), to Pacific salmon stock productivity (e.g., Mantua et al. 1997; Francis et al. 1998). The mechanisms for this relationship are not well known, but are presumed to be related to ocean nutrient levels (in the form of phytoplankton and zooplankton) available to juvenile salmon early in their marine life (Francis et al. 1998), and these levels appear to persist over several years (Mote et al. 2003). However, as with CUI, PDO is correlated to inland weather patterns, which could affect stream-dwelling salmonids. A warm PDO phase is usually associated in the Pacific Northwest with above-average fall and spring air temperatures, below-average fall and spring precipitation, and below average snowpack, summer rainfall, and stream flow (Cayan 1996; Mantua et al. 1997; Hamlet and Lettenmeier 1999; Nigam et al. 1999). The PDO was in the warm phase from 1977 to 1998 and from 2002 to 2006, and was in a cool phase from 1999 to 2001 and from 2007 onward (Mantua et al. 1997; N. Mantua, University of Washington, personal communication). Since FLOW, AirT, and PDSI were used to account for these factors, and CUI was used to account for ocean productivity, the inclusion of PDO in our analyses was deemed redundant.

Chinook salmon redd counts.—Salmon are the chief vector for the transfer of marine-derived nutrients to inland ecosystems (Cederholm et al. 1999). Marine-derived nutrients can be particularly important for biological production in areas with

unproductive geologies, such as central Idaho (Kohler et al. 2008; Sanderson et al. 2008). The influx of nutrients from spawning salmon can influence stream productivity and subsequently the growth and survival of premigratory parr (Wipfli et al. 1998, 2003). However, the response of resident fish populations to marine-derived nutrients remains largely unverified by data and constitutes a critical knowledge gap in salmon research (Janetski et al. 2009).

Historical levels of salmon carcasses in the study area are hard to estimate. Total spring–summer Chinook salmon production in the Snake River was probably in excess of 1.5 million during the late 1800s (Matthews and Waples 1991). This number includes production from areas now inaccessible to salmon; the study area is approximately 27% of the historical salmon habitat in the Snake River basin but includes some of the most productive areas in the Columbia River basin (Matthews and Waples 1991). Run size declined to about 70,000 by the late 1960s and to about 12,000 by the mid-1980s. During our study, wild adult returns averaged about 27,000 annually and ranged from 1,000 to 92,000. These fish disperse across central Idaho, northeast Oregon, and southeast Washington; accessible habitat in the Clearwater and Salmon rivers is approximately 66% of this area (NPPC 2000), but 80% of the redds counted in the basin in recent years were located in Idaho (T. Copeland, unpublished data). It is clear that current numbers of salmon carcasses in the study area have been reduced from historical amounts, but estimation of the reduction is complex and laden with unverifiable assumptions.

Despite the currently depressed levels of salmon returns, and the concomitant loss of nutrient imports (Gresh et al. 2000), there is empirical evidence that marine-derived nutrients continue to affect freshwater productivity in central Idaho (Scheuerell et al. 2005). Therefore, we suspected that the nearly two orders of magnitude fluctuation during our study period could provoke a response in the resident fish community. We used counts of Chinook salmon redds (REDDS) as an index of this potential effect. Steelhead redd counts were not available, and dam counts of wild steelhead are incomplete and highly correlated to Chinook salmon redd counts ($r^2 = 0.93$, T.C., unpublished data), so we deemed steelhead adult abundance would not add substantially more information. We obtained redd counts at trend transects across central Idaho (www.streamnet.org).

Determining Bioclimatic Time Lags

To refine our working hypothesis into a mechanistic explanation for observed fish densities, we correlated each bioclimatic variable with species densities at various time lags. We obtained time series for each variable for the years 1975–2003 but focused on lags from 0 to 5 years because most fish observed were less than 6 years old. We assumed the environment would not necessarily affect a species in the year in which a bioclimatic index was measured, but rather might have a lag effect based on processes such as survival and recruitment. Year 0 was not included for REDDS or CUI because those

variables were measured after snorkel surveys were completed in each year. 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.

Model Development

We decomposed the variance in fish densities into temporal and spatial components using the factorial analysis of variance (ANOVA) approach outlined by Wiley et al. (1997) to address several questions that were preliminary to the main analysis, such as the following: How much variance was due to temporal changes that were coherent across the entire data set as opposed to being caused by geographic location? How much variance was due to temporal changes that were unique to the major basins (Clearwater versus Salmon river basins)? How much variance was due to local geographic factors below the major basin scale? The main factors in this analysis were year and basin with a year \times basin interaction. Because of the highly unbalanced number of surveys per site (5–19), we aggregated sites to the subbasin level to discern local effects using fourth-level hydrologic unit codes (HUC4) as the local units, which were nested within basin. The HUC4s are hydrologically distinct watersheds. All previous factors were treated as categorical fixed effects because all possible levels were sampled by the data (i.e., there were no other major basins and all but one HUC4 was included in the data set). The random variation truly due to site-level effects was treated as part of the residual error. Formally stated, the model was

$$\text{Var}(\log_e \text{ density}_i) = \text{Var}_{\text{year}} + \text{Var}_{\text{basin}} + \text{Var}_{\text{HUC4}(\text{basin})} + \text{Var}_{\text{year} \times \text{basin}} + \text{Var}_{\text{site} + \text{residual}}$$

where the variance of the transformed densities of species i was decomposed into temporal and spatial elements. Note that the residual term also includes variance due to unspecified interactions as well as site effects.

We used correlation analyses to examine the relationships among bioclimatic indices and among fish species. All fish densities were log transformed [$\log_e(\text{density} + 0.01)$] before analyses. To address the first objective, we calculated the annual mean density of each species (average of all sites sampled during each year), then assessed the level of correlation among species over time. To address the second objective, we explored covariations with all six species as a group using a multivariate approach, and then focused on each species individually using a regression approach to clarify interpretation of the multivariate analysis. Lastly, we used data from 2004 to 2009 to validate the relationships seen in the 1985–2003 data.

To assess the relationship between the five bioclimatic indices and the densities of the six salmonid species as a group, we used canonical correlation, which has the fewest data restrictions of multivariate statistical techniques (Hair et al. 1998).

The canonical correlation was performed on the set of transformed densities averaged within year versus the set of bioclimatic variables. 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. This is a useful property to clarify interpretation because variances in density were widely disparate among species (Rencher 1995).

To clarify interpretation of the canonical correlation, we used information-theoretic model selection techniques to examine the effects of the bioclimatic parameters on individual species densities using multiple linear regression (Burnham and Anderson 2002). Selection for models of annual mean density of each species was based on Akaike’s information criterion (AIC) as corrected for small sample sizes. All additive combinations of the bioclimatic parameters (31 models) were fit against transformed density for each species. As a general index of model fit, we used adjusted R^2 (Montgomery and Peck 1992). The relative likelihood of each model i in the set of models (M) for each species was assessed with Akaike weights (w_i , Burnham and Anderson 2002) as follows:

$$w_i = \frac{\exp(-0.5(\text{AIC}_i - \text{AIC}_{\min}))}{\sum_{m=1}^M \exp(-0.5(\text{AIC}_m - \text{AIC}_{\min}))}$$

The relative importance of a particular bioclimatic variable, given all potential additive combinations of the variables, was computed as the sum of the Akaike weights of all models containing that variable (importance value).

Validating the model: 2004–2009 data.—The validation exercise was performed in two steps. We obtained data from the next six years (2004–2009) for snorkel surveys conducted at the same 367 sites used in the previous analyses. During 2004–2009, over 90% of the original sites were revisited at least once; most were surveyed two to four times. For the first step, we computed the correlation matrix of species densities using the 1985–2003 data and compared it with that computed using all of the data (1985–2009) to see whether addition of the new data changed the original correlations. We inspected both matrices and noted any changes in the significance of correlations. For the second step, we used the regressions relating densities to the bioclimatic variables from 1985 to 2003 to predict the 2004–2009 densities for each species. We averaged the predictions of all models with a substantial level of empirical support (i.e., $\text{AIC}_i - \text{AIC}_{\min} < 2$, Burnham and Anderson 2002) as weighted by each model’s w_i . We computed the mean percent prediction bias based on the back-transformed densities for all predictions together and for each species.

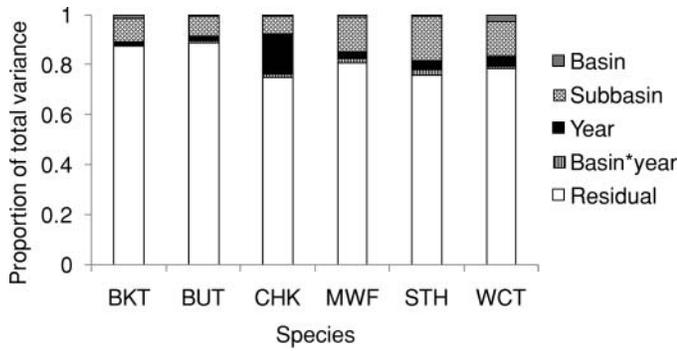


FIGURE 2. Proportions of the variance in transformed density explained by temporal and spatial factors, by species. Species are brook trout (BKT), bull trout (BUT), Chinook salmon (CHK), mountain whitefish (MWF), steelhead (STH), and westslope cutthroat trout (WCT).

RESULTS

Variance Decomposition

The preliminary variance decomposition showed that much of the variance in the density data was not explained by the temporal or spatial factors specified (residual variance, among-species mean = 80.8%; Figure 2). Most of the explained variance was related to local watershed factors (HUC4, among-species mean = 11.8%). The year effect was still distinguishable (among-species mean = 4.8%). Chinook salmon exhibited the greatest amount of coherent yearly variation (15.7%). In every species, year effects were greater than basin \times year interactions. Effects due to major basin were the smallest of all the factors because most of the spatial variance was explained by HUC4.

Synchrony among Species

The average densities of all species declined from the 1980s to the mid-1990s and 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 3). The highest densities were observed for steelhead and Chinook salmon. Of all the salmonids, Chinook salmon had the most variable density and the most exaggerated trend. Of all Chinook salmon counted, 97.4% were age 0. Densities of westslope cutthroat trout and mountain whitefish were intermediate to the other species.

During 1985–2003, average salmonid densities were synchronous among all species (Figure 3). All 15 correlation coefficients for each pairwise comparison were positive, eight of which were statistically significant (Table 2, above the diagonal). Bull trout were the species with the most significant correlations (i.e., with all other species) and Chinook salmon the least (only with bull trout).

Bioclimatic Indices

The five selected bioclimatic indices fluctuated widely over time. The variable FLOW was lowest in 1977 and had peaks in 1982 and 1997. There were periods of low flows during

1987–1994 and again during 2000–2003. The variable PDSI had similar patterns to flow, with peaks in the early 1980s and again in the late 1990s. There were 8 years of severe drought. July mean AirT went from a low of 13.3°C in 1993 to a high of 20.7°C in 1998. The July mean exceeded 20°C in 1975, 1985, 1998, 2002, and 2003. The October CUI had a very different pattern: two extreme lows in 1975 and 1984 and two peaks in 1991 and 2002. In general, CUI was more negative and variable in the late 1970s and early 1980s than later. Lastly, REDDS showed lower values through the middle of the period of record, being highest in 1978 and 2001–2003 and extremely low in the mid-1990s. In general, correlations among the bioclimatic indices were low, except between FLOW and PDSI ($r = 0.81$; Table 3).

Time Lags

Many of the lagged correlations to the bioclimatic variables were consistent among species, with a 4-year lag appearing frequently (Table 4). There were many positive correlations to FLOW at lags of 3–5 years. We chose to average FLOW at 3- and 4-year lags because this increased correlations in four species above those observed for single-year lags. Similarly, correlations to lagged PDSI were positive and most frequent at lags of 4 and 5 years, and we chose to average these lags as well. For AirT, the number of correlations to fish densities was maximized with no lag. There were negative correlations to CUI at 2 and 4 years. We chose the 4-year lag because correlations were stronger for that lag than for the 2-year lag. The strongest and most consistent correlations to REDDS appeared at lags of 1 year. Within the set of bioclimatic variables, correlations of the final form of the lagged variables were no greater than the original versions (data not shown).

Canonical Correlation

The canonical correlation explained a significant amount of the shared multivariate variance between fish densities and bioclimatic indices (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 less than 10% for the other axes, so we interpreted only the first axis.

Contributions to the canonical correlation differed among fish species and bioclimatic 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, mountain whitefish, and westslope cutthroat trout, respectively (Table 5). Order by canonical cross-loadings was the same. Of the bioclimatic variables, REDDS loaded most strongly on the first axis, followed by FLOW, PDSI, CUI, and AirT, respectively (Table 5). As with densities, the order by canonical cross loadings was the same. All bioclimatic variables loaded positively on the first axis except for CUI.

Model Selection

The importance of the bioclimatic variables differed among species (Tables 6, 7). For bull trout and brook trout density, FLOW and AirT were the two most important variables

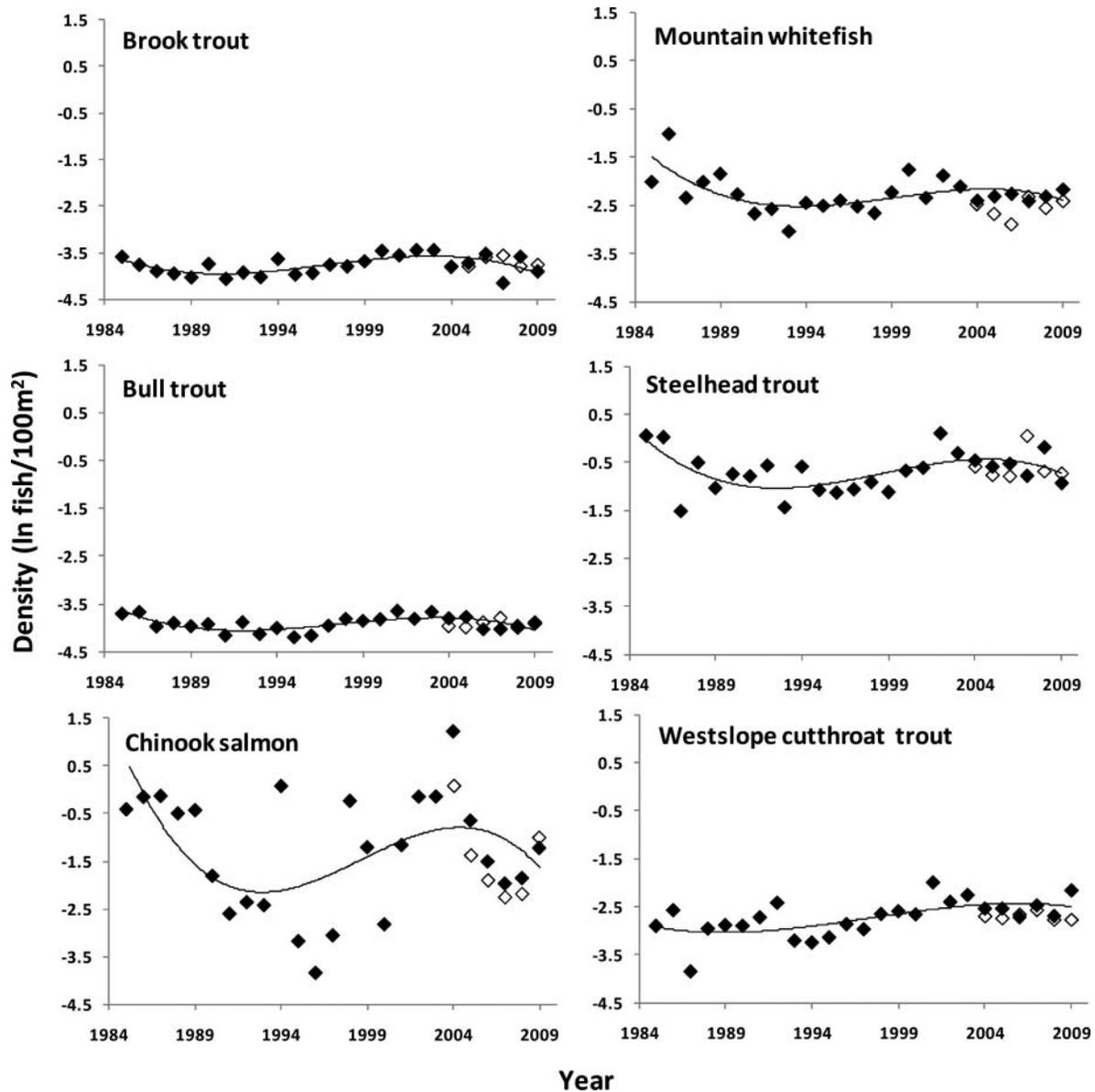


FIGURE 3. Annual mean density of six salmonid species in central Idaho, 1985–2009. Trend lines were fitted with a third-order polynomial. Filled diamonds are observed values; open diamonds are predicted values for 2004–2009. Predictions were made with models relating species density to bioclimatic indices and parameterized with data from 1985 to 2003. Predictions were averaged over the set of models determined to have substantial support by an information-theoretic model selection procedure. See Table 5 for model parameters.

(positive effects). For mountain whitefish density, CUI was the most important variable followed by PDSI (both negative relationships). Coastal upwelling index was also the most important variable for steelhead density (negative relationship), but secondarily, AirT was important (positive relationship). Not surprisingly, REDDS was by far the most important variable 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 $R^2 = 0.31$). More variance was explained for the other species, with maximum adjusted

R^2 ranging from 0.52 for Chinook salmon to 0.69 for mountain whitefish.

Validating the Model

The correlations among species densities in the original data set changed little when the 2004–2009 data were added (Table 2, below the diagonal). The mean correlation in the original matrix was 0.49, compared with 0.43 when the new data were added. In the original data set, 8 of 15 correlations were statistically significant, whereas 9 of 15 correlations were statistically significant in the extended data set.

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TABLE 2. Correlation coefficients (*r*) among species for annual mean fish density at 367 snorkel sites in central Idaho during 1985–2003 (above the diagonal; *n* = 19) and during 1985–2009 (below the diagonal; *n* = 25). Asterisks indicate values for which *P* < 0.05. See Figure 2 for species codes.

Species	BKT	BUT	CHK	MWF	STH	WCT
BKT		0.73*	0.36	0.39	0.59*	0.48
BUT	0.59*		0.61*	0.59*	0.67*	0.60*
CHK	0.28	0.62*		0.42	0.44	0.04
MWF	0.36	0.55*	0.35		0.62*	0.26
STH	0.58*	0.58*	0.41*	0.56*		0.56*
WCT	0.30	0.54*	0.08	0.22	0.48*	

The densities for all six species declined after 2003, and these declines were predicted by the selected models (Figure 3). The overall prediction bias was low (−3.7%) but varied among species. Predictions for Chinook salmon, mountain whitefish, and cutthroat trout were biased low (mean prediction bias = −31.0, −21.3, and −16.1%, respectively), whereas predictions for steelhead, brook trout, and bull trout were biased high (mean prediction bias = 8.6, 31.7, and 5.8%, respectively).

DISCUSSION

Synchrony among Species

The population abundance in salmonid communities in central Idaho fluctuated in synchrony over a multidecadal time scale. Liebhold et al. (2004) and Bjørnstad et al. (2009) argue that synchrony should be expected in multipopulation studies, 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., Cattaneo et al. 2003; Isaak et al. 2003; Zorn and Nuhfer 2007a; Phelps et al. 2008). In one of the few studies of synchrony in multiple freshwater fish species, Tedesco et al. (2004) found synchrony in four species of African fishes was influenced by regional river discharge the previous year over a

TABLE 3. Correlation coefficients (*r*) among bioclimatic indices over time (*n* = 19). Indices are the coastal upwelling index (CUI), Chinook salmon redd counts (REDDS), annual mean July air temperature in central Idaho (AirT), annual mean Salmon River discharge (FLOW), and the Palmer drought severity index (PDSI). The asterisk indicates a value for which *P* = 0.0002.

Index	CUI	REDDS	AirT	FLOW	PDSI
CUI	1.00				
REDDS	−0.31	1.00			
AirT	0.08	0.40	1.00		
FLOW	−0.58	0.19	−0.09	1.00	
PDSI	−0.51	0.18	−0.07	0.81*	1.00

TABLE 4. Correlation coefficients (*r*) for comparisons of bioclimatic indices with salmonid densities at lags of 0 to 5 years. See Figure 2 and Table 3 for species and index codes.

Lag	Species					
	BKT	BUT	CHK	MWF	STH	WCT
AirT						
0	0.49	0.36	0.36	0.14	0.49	0.30
1	0.09	0.32	−0.10	0.33	0.26	0.57
2	0.14	0.05	−0.07	0.04	−0.13	−0.01
3	0.11	0.23	0.18	−0.31	−0.01	0.13
4	−0.02	0.01	0.31	0.09	0.18	0.16
5	0.29	0.02	−0.05	0.07	0.01	0.06
CUI						
1	−0.05	−0.14	−0.19	−0.12	0.06	0.19
2	−0.31	−0.44	−0.27	−0.69	−0.34	−0.13
3	−0.17	−0.34	−0.19	−0.21	−0.14	0.08
4	−0.15	−0.53	−0.5	−0.75	−0.55	−0.27
5	−0.06	−0.09	−0.54	−0.22	0.01	0.42
FLOW						
0	−0.10	−0.18	−0.47	−0.03	−0.24	−0.02
1	0.28	0.22	−0.02	−0.05	−0.13	−0.13
2	0.19	0.45	0.13	0.23	0.10	0.20
3	0.41	0.51	0.39	0.52	0.20	0.11
4	0.50	0.65	0.34	0.63	0.31	0.25
5	0.25	0.30	0.53	0.41	0.28	0.10
PDSI						
0	−0.35	−0.38	−0.52	−0.26	−0.30	−0.19
1	0.07	0.10	−0.12	0.01	−0.03	−0.08
2	0.10	0.31	0.00	0.20	0.02	−0.11
3	0.24	0.50	0.49	0.43	0.12	−0.01
4	0.36	0.44	0.47	0.67	0.24	−0.11
5	0.21	0.37	0.47	0.62	0.31	0.06
REDDS						
1	0.40	0.35	0.67	0.24	0.45	0.29
2	0.23	0.11	0.28	0.15	0.19	0.07
3	−0.31	−0.37	−0.37	0.00	−0.02	0.06
4	−0.34	−0.28	−0.36	−0.28	0.00	−0.01
5	−0.44	−0.27	−0.12	−0.48	−0.15	−0.05

24-year time frame. In comparison, we found synchrony among six species over 25 years.

The spatial scale of the synchrony observed in this study was very large for freshwater fishes. Myers et al. (1997) concluded that the effect of climate on fish recruitment occurred at maximum scales of 50 km for freshwater fishes, whereas Tedesco et al. (2004) found synchrony in abundance at the scale of 160 km. Myers et al. (1997) included five species in their study, with most data originating from lacustrine populations. Our results suggest that regional synchrony in freshwater fish recruitment can occur at an even larger spatial scale (over 330

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TABLE 5. Contributions of individual variables to the canonical correlation between annual mean fish density and selected bioclimatic indices. See Figure 2 and Table 3 for species and index codes.

Variable	First axis loading	Canonical cross-loading
Fish density		
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
Bioclimatic index		
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

aerial km, north to south, in our study). Widespread effects on fish recruitment (e.g., by flow) may be propagated more efficiently in a stream network than in a group of lakes (Grenouillet et al. 2001).

Our results suggest that the level of species synchronization may be related to the intensity or duration of the interactions among the species. For example, all species were correlated, but bull trout were most correlated and Chinook salmon were least correlated with other salmonids. Bull trout are highly predatory and therefore are directly dependent on the abundance of other fish species. In contrast, Chinook salmon spend the least amount of time in freshwater habitat and therefore have the least amount of interaction with other species. There may be other plausible relationships among salmonids in central Idaho as well, providing a good illustration of why it is hard to infer causal mechanisms with large-scale data.

Although the level of correlation varied among species, the overall synchrony we found should not be surprising considering that the study species were all lotic salmonids that arguably should react similarly to large-scale environmental variation.

TABLE 6. Importance values of bioclimatic indices explaining observed fish densities summarized from Akaike weights, by species. See Figure 2 and Table 3 for species and index codes.

Bioclimatic index	Species					
	BKT	BUT	CHK	MWF	STH	WCT
CUI	0.132	0.468	0.318	0.948	0.968	0.356
REDDS	0.329	0.340	0.957	0.132	0.153	0.372
FLOW	0.941	0.983	0.377	0.405	0.137	0.418
PDSI	0.493	0.435	0.369	0.675	0.190	0.419
Air T	0.835	0.618	0.187	0.203	0.936	0.429

However, these species have disparate thermal optima, migrate, spawn, and hatch 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 probably driving the synchronized relationships.

In addition to environmental effects, other potentially synchronizing processes include dispersal and the effects of mobile predators or parasites (Bjørnstad et al. 1999; Liebhold et al. 2004). We examined interspecies synchrony, not populations per se, so dispersal cannot explain the patterns we observed (Liebhold et al. 2004). Human predation cannot explain the interspecies patterns we observed because there was no directed fishery on five of the six species during the study period and mountain whitefish are virtually unexploited by anglers. Whirling disease, caused by the myxosporean parasite *Myxobolus cerebralis*, is another potential means of synchronized mortality, but it does not affect all salmonids equally (El-Matbouli et al. 1992), it is not ubiquitous in the study area (Cavender et al. 2003), and resistance to it is unlikely to develop quickly enough to explain the increased densities observed after the mid-1990s (Rasmussen et al. 2008). 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 bioclimatic indices 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 in year 0. For all other indices, lags of between 1 and 5 years were most strongly related to salmonid density, presumably by affecting recruitment (e.g., Cattaneo et al. 2003; Lobón-Cerviá 2004; Tedesco et al. 2004; Zorn and Nuhfer 2007a). We detected these effects in subsequent years through changes in fish densities.

In the canonical correlation analysis, FLOW and REDDS were the most important bioclimatic indices 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 (Jager et al. 1999; Carline and McCullough 2003), displacement of newly emerged fry (Nehring and Anderson 1993; Lobón Cerviá 2004; 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 Chinook salmon survival from rearing habitats to emigration as smolts. Hydrographs of almost all streams in central Idaho are driven by snowmelt with flows peaking in May or June (Lipscomb 1998). Given this similarity in hydrologic regime, it is plausible that flow would affect stream fishes simultaneously

TABLE 7. Model fit (adjusted R^2), AIC weights (w_i), and estimated coefficients for all models with substantial empirical support ($AIC_i - AIC_{\min} < 2$). See Table 3 for bioclimatic index codes.

Adj R^2	w_i	Intercept	AirT	CUI	FLOW	PDSI	REDDS
Brook Trout							
0.459	0.250	-5.93547	0.02786		0.00003		
0.526	0.249	-6.52585	0.03259		0.00006	-0.05083	
0.572	0.140	-6.28716	0.02703		0.00006	-0.06267	0.00004
Bull trout							
0.681	0.203	-5.93459	0.02234	-0.00652	0.00005	-0.04696	
0.549	0.127	-5.33071	0.01565		0.00004		
0.541	0.107	-4.37556			0.00004		0.00004
0.599	0.098	-5.37111	0.01725	-0.00450	0.00003		
0.478	0.091	-4.33228			0.00004		
Chinook salmon							
0.521	0.205	-3.98292			0.00014		0.00060
0.519	0.200	-2.33641				0.22494	0.00054
0.493	0.122	-2.57822					0.00056
0.428	0.111	-2.54803		-0.03622			0.00065
Mountain Whitefish							
0.687	0.368	-2.34308		-0.01912		0.10463	
0.660	0.169	-3.01126		-0.02136	0.00006		
Steelhead trout							
0.538	0.555	-5.52719	0.07240	-0.02521			
Westslope cutthroat trout							
0.045	0.110	-2.97623					0.00010
0.041	0.106	-5.20946	0.03725				
0.012	0.080	-2.85772		-0.00947			
-0.011	0.064	-3.10708			0.00003		
0.203	0.061	-4.18716			0.00010	-0.16278	0.00014
0.310	0.051	-7.84295	0.06044	-0.01759	0.00009	-0.19776	
0.071	0.050	-5.43338	0.03985	-0.01038			
0.174	0.043	-7.09690	0.04948		0.00010	-0.14712	
-0.058	0.042	-2.80704				-0.00661	
0.052	0.041	-3.74242			0.00008	-0.11206	

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 canonical correlation, REDDS was important because of the high loading of Chinook salmon into the canonical variate and because it was positively correlated to the abundance of all species. It was not surprising that a 1-year lag on REDDS was the most influential bioclimatic index for Chinook salmon because most Chinook salmon (>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, 2003). That there was a positive correlation to REDDS after 1 year for all species, which declines thereafter (Table 4), suggests that increased REDDS led to higher survival (presumably through increased stream productivity) in the next year for all species.

However, in the regression models, REDDS had a minor effect (albeit positive) 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. Scheuerell et al. (2005) showed that nutrient imports by Chinook salmon into the study area declined from the 1960s to the 1980s and 1990s. Although nutrient imports from 2001 to 2004 rebounded to levels not seen in recent decades, Chinook salmon productivity (smolts per spawner) did not rebound, suggesting that the freshwater ecosystem had shifted into a less productive state. Adkison (2010) showed that recovery of nutrient-dependent populations can be slow and they may become trapped in a nutrient-deficient state. Effects of spawning salmon on stream ecosystems can be multifarious and hard to distinguish, but there is much circumstantial evidence supporting their importance to trophic flow (Janetski et al. 2009; Adkison 2010). In this study,

the canonical correlation showed that REDDS was important in the multivariate view, but the regression analysis showed other factors were more important when species were viewed singly. We conclude that other important factors may be easier to detect or, alternatively, it may take sustained high levels of salmon runs to reestablish a more productive ecosystem.

Regression models suggested that CUI was important to steelhead and mountain whitefish. The form of CUI we used was measured in October, and although it was chosen because of its demonstrated effect on Chinook salmon (Scheuerell and Williams 2005) and may have affected ocean survival of early steelhead and subsequently steelhead returns (and thus recruitment) in later years, it may also 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. The CUI was most strongly related to steelhead and mountain whitefish at a lag of 4 years which supports the conclusion that CUI was related to recruitment of these species, not adult density directly. We suggest that ocean conditions are often important for inland fish populations via effects on inland weather, but many effects might be subsumed by more local variables (e.g., FLOW). In this study we focus on effects to recruitment more directly, but ocean conditions are very important to survival of salmon and steelhead to adulthood. Other ocean indices (e.g., sea surface temperature and PDO) also affect Chinook salmon and steelhead in Idaho (Zabel et al. 2006; Petrosky and Schaller 2010). The mechanisms relating ocean climate to inland fishes need to be investigated and other indices may prove more useful than CUI.

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 hypothesize that this effect was on detection probability, not density. Temperature is related directly to the probability of detecting bull trout, cutthroat trout, and rainbow trout with snorkel surveys via influence on fish activity levels (Thurow et al. 2006). Chinook salmon and mountain whitefish are schooling species, the detection of which may be affected less 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 the selected bioclimatic indices for this species were less than half the values for other species. Model selection results were ambiguous for cutthroat trout with all importance values of the bioclimatic variables being less than 0.50. Further, this species had the lowest loading in the canonical correlation. Westslope cutthroat trout are closely associated with headwater habitats (Shepard et al. 2005), which are typically more stochastic than downstream reaches (Richardson et al. 2005) and therefore may be less likely to be influenced by the

large-scale bioclimatic indices we analyzed. Alternatively, other bioclimatic variables that were not included in our data set may have been more influential for this species.

Management Implications

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 (not assumed) because it will vary depending on the study area, the focal group of species, the influential mechanisms, and the range of environmental conditions.

The occurrence of interspecies synchrony suggests that the abundances of all salmonids in central Idaho are currently interconnected. All native species in our study area were formerly more abundant than they are at present, 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; Hilderbrand 2003), and this effect may carry through to community structure. Under a regime of community synchrony, populations of the constituent species would tend to be at low levels simultaneously, potentially leading to correlated extirpations of less common species.

Studies such as ours serve as an important baseline from which to understand the effects of large-scale bioclimatic factors on stream fishes. There is a mismatch of scales between aquatic ecology and climatology; climate studies are usually conducted at very large scales (e.g., continental), whereas the typical scale of ecological studies is much smaller (Walther et al. 2002). In our data, the clearest climatic influence on fish density was the direct correlation between FLOW and bull trout density, a species that has been predicted to be susceptible to the potential effects of climate change (Rieman et al. 2007). Rieman et al. (2007) 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 (Phelps et al. 2008). Further, the synchronizing agent may be different from causes responsible for oscillations (Moran 1953; Bjørnstad et al. 2009). Models based on data from 1985 to 2003 accurately predicted the declines in fish density observed from 2004 to 2009, which suggests the bioclimatic indices we chose were useful surrogates for large-scale factors influencing temporal changes in salmonid densities in central Idaho. However, the linkage between ocean conditions and population dynamics of inland fishes clearly merits further exploration.

Coherent annual variation explained only a small amount of the total variation in salmonid densities, but this was not

unexpected given that many population cycles have low frequencies with much “noise” about them. Instead, the bioclimatic conditions we included in our study explained much of the coherent annual variation in the abundance of salmonids in central Idaho. Nevertheless, other factors such as local habitat conditions and snorkel observation error also inherently added noise to variance in density estimates. The relative contribution of the bioclimatic variables to overall variation in salmonid abundance may provide managers a relative sense of how much variation may be under management control. Such knowledge at large scales may help focus management efforts or shape restoration or protective efforts by revealing the tractability of the system to direct manipulation. However, causal mechanisms are hard to infer and require further research. Our study provides a basis for suggesting fruitful avenues for such work.

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