# Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon

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**Summary**

**1.** We explored differential population responses to climate in 18 populations of threatened spring–summer Chinook salmon *Oncorhynchus tshawytscha* in the Salmon River basin, Idaho.

**2.** Using data from a long-term mark–release–recapture study of juvenile survival, we found that fall stream flow is the best predictor of average survival across all populations.

**3.** To determine whether all populations responded similarly to climate, we used a cluster analysis to group populations that had similar annual fluctuations in survival. The populations grouped into four clusters, and different environmental factors were important for different clusters.

**4.** Survival in two of the clusters was negatively correlated with summer temperature, and survival in the other two clusters was positively correlated with minimum fall stream flow, which in turn depends on snow pack from the previous winter.

**5.** Using classification and regression tree analysis, we identified stream width and stream temperature as key habitat factors that shape the responses of individual populations to climate.

**6.** Climate change will likely have different impacts on different populations within this metapopulation, and recognizing this diversity is important for accurately assessing risks.

*Key-words*: biodiversity, environmental change, freshwater survival, global warming, habitat quality.

## Introduction

Climate change poses a primary threat to species across the globe (Sala *et al*. 2000; Thomas *et al*. 2004). Although it is clear that climate affects species' abundance and distribution, the particular components of climate that most affect animal performance are generally unknown (Lawton 1995), which makes forecasting specific effects of climate change difficult. Both climatic and biological systems are complex, and relationships may appear at multiple spatial and temporal scales. Identifying the scale at which climatic factors best predict population dynamics can help to elucidate specific mechanisms driving the correlations, and potential consequences of climate change.

Recent studies (Hallett *et al*. 2004; Stenseth & Mysterud 2005) have described cases in which global scale

climate phenomena, such as the North Atlantic Oscillation, better explain population dynamics than local weather variables. This counter-intuitive result demonstrates that the appropriate scale at which to describe the impact of climate on populations needs explicit investigation. The question of scale extends further to the population level, because differential responses to particular climatic phenomena can occur within species (Mueter, Peterman & Pyper 2002). Differential responses to climate can result from variation in behaviour or habitat, and often have a genetic component (Hilborn *et al*. 2003; Brannon *et al*. 2004). Understanding these population differences benefits at-risk species because it can help managers understand population fluctuations and trends, and prioritize actions aimed at maintaining diversity within a metapopulation.

Changes in Pacific salmon *Oncorhynchus* spp. abundance are strongly correlated with changes in the weather (Mantua *et al*. 1997; Mueter *et al*. 2002). Previous studies have focused on ocean conditions and broad scale indices such as the Pacific Decadal Oscillation. Here, we instead focus on a much finer

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scale by examining how juvenile survival in freshwater varies in relation to climate among closely related populations. We chose this life stage for several reasons. First, salmon exhibit diverse behaviour and morphology among closely related populations, which is often related to physical variation in freshwater spawning and rearing areas (Taylor 1990). Second, recent studies have identified juvenile survival as the most important stage for recovery of some threatened populations (Kareiva, Marvier & McClure 2000; Zabel *et al*. 2006), so the freshwater stages are crucial from a conservation standpoint. Third, stream temperatures are already approaching critically high levels for some endangered salmonids (Donato 2002), so further increases may have catastrophic effects (Eaton & Scheller 1996). Finally, we have detailed juvenile survival data for 18 populations of threatened Snake River spring–summer Chinook salmon *O. tshawytscha* (Walbaum) over 11 years and corresponding climatological data. We used these data to ask whether natural groups of populations exist in terms of their response to climate and, if so, what factors led to the groupings.

The populations we examined rear in streams primarily fed by snow melt from the neighbouring mountains, which results in stream flow and water temperature that are highly variable from year to year. This led to our primary hypothesis that water temperature and stream flow significantly affect juvenile survival in these populations. Several observations further support this hypothesis. First, as ectotherms, temperature regulates fish development and growth rates (Fry 1967), and has played an important part in the evolution of life-history strategies in salmon (Brannon *et al*. 2004). Second, stream temperature and stream width, which is often correlated with flow, predict salmonid distribution very well in the western United States at both large (Keleher & Rahel 1996) and small spatial scales (Taylor 1988; Torgersen *et al*. 1999). Third, temperature and flow are often linked to salmon production (Bartholow *et al*. 1993; Jager *et al*. 1997), presumably because they affect a variety of habitat characteristics, such as substrate, risk of scouring, oxygen concentration, energetic costs and habitat area. Furthermore, stream temperature and flow are likely to change over this century because they are intimately related to larger-scale processes shown in flux by general circulation models, especially changes in air temperature and precipitation. In the Pacific Northwest, global warming will likely raise stream temperatures (Eaton & Scheller 1996; Mohseni, Stefan & Eaton 2003) and shift the timing and magnitude of stream flows (Hamlet & Lettenmaier 1999; Mote *et al*. 2003).

Here we propose a three-step approach for assessing population variation in response to climate and identifying the best scale at which to describe effects of climate: (1) aggregate survival estimates across all populations, and relate basin-wide survival to prevailing climate patterns at multiple spatial and temporal scales; (2) identify groups of populations that have similar patterns of survival, and relate within-group survival to prevailing climate patterns; and (3) attempt to uncover features within groups that can explain their similar responses.

## Methods

### STUDY SYSTEM

Snake River spring-summer chinook salmon spawn and rear as juveniles in high elevation tributaries in Idaho and Oregon in the Northwestern United States (Fig. 1A). Natal streams studied in this analysis are all within the Salmon River basin, Idaho (Fig. 1B), where juveniles spend a full year before beginning their up to 1500 km migration to the Pacific Ocean. After 1– 4 years in the ocean, they return to their natal streams to reproduce. Fish that spawn in different streams are often differentiated genetically and behaviourally (Interior Columbia Basin Technical Recovery Team 2003), so we refer to them as different populations. Most of the natal streams are in federally protected wilderness areas and are relatively pristine. However, humans have influenced a few sites through grazing practices, water diversions, logging, mining and the introduction of invasive species. Habitat varies across the basin, ranging from arid grasslands to forest (Paulsen & Fisher 2001).

### SURVIVAL DATA

Parr to smolt survival estimates were based on data gathered between 1992 and 2003 from 108,291 individually tagged fish. Each fish had a uniquely coded passive integrated transponder (PIT) tag (Prentice, Flagg & McCutcheon 1990) inserted into its body cavity in July or August of its first year, as described in Achord *et al*. (1996, 2001). When the fish migrate the following spring (April–June), the tags are automatically detected downstream in the juvenile fish bypass systems at hydroelectric dams along the Snake and Columbia Rivers. Using the multiple detection sites to calculate detection rates, survival was estimated to the first dam the fish encounter, Lower Granite Dam (Fig. 1A), as described in Zabel & Achord (2004).

### BASIN SCALE

First we consider survival, parr density, and climate data at the basin scale, and then address the population scale. Population survival ($S$) was estimated by site (s) and year (y) using the capture–recapture program SURPH (Lady, Westhagen & Skalski 2001), resulting in survival estimates for 148 site/year combinations. Annual basin-wide survival was then calculated as 'year effects' using the regression coefficients from a linear model in which site and year are treated as unordered factors, and solving for yearly survival ($S_y$). The model is
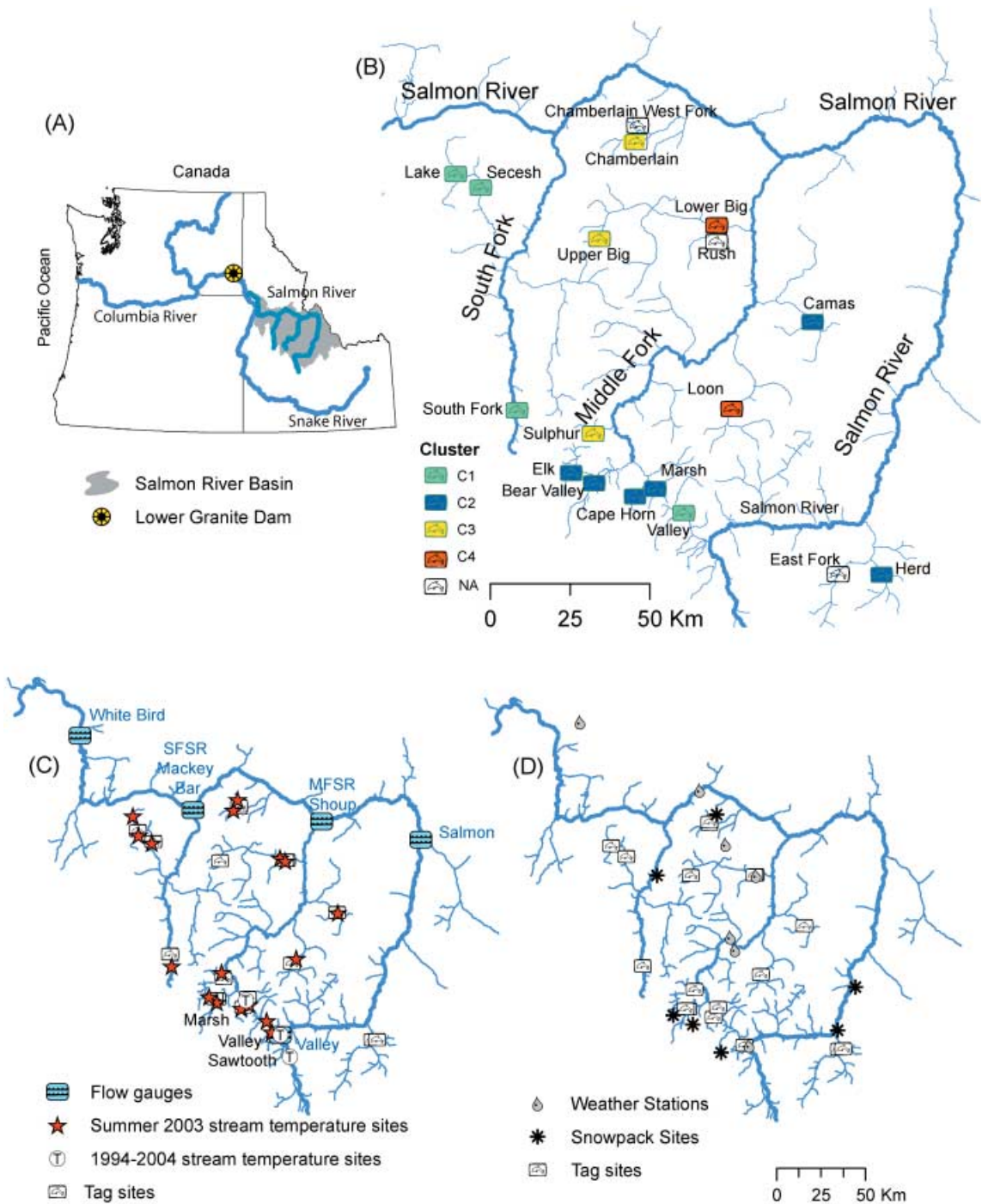
**Fig. 1.** (A) Location of study region in the Pacific Northwest showing the Salmon River Basin and the major tributaries discussed in the text. (B) Fish tagging sites, labelled with creek names, except that South Fork and East Fork refer to the Salmon River itself. Shading of the site icons indicates the cluster to which each site belongs. Sites that were excluded from the cluster analysis are labeled NA. (C) Locations of water temperature and flow gauge monitors. Temperature sites are on Marsh Creek, Valley Creek, and at the Sawtooth Fish Hatchery. Gauge stations are South Fork Salmon River (SFSR) near Mackey Bar, Middle Fork Salmon River (MFSR) near Shoup, Salmon, ID, Valley Creek, and White Bird, ID. (D) Weather stations measuring temperature and precipitation, and Snotel sites measuring snowpack. Weather stations: Grangeville, Yellow Pine Bar, Warren, Stanley, Yellow Pine 7S, Middle Fork Lodge, and Taylor Ranch. Snotel stations: Deadwood Mountain, Mountain Meadows, Big Creek Summit, Mill Creek Summit, Morgan Creek and Secesh Summit.

$$\text{logit}(S_{s,y}) = \beta_0 + \beta_s + \beta_y + \varepsilon.$$

where βs are the regression coefficients for the intercept, site and year, and the error term ε is normally distributed. As in all analyses that follow, survival was logit-transformed because survival data are bounded in the range 0·0–1·0.

Previous analyses found that salmon density has a significant effect on juvenile survival in these fish (Achord, Levin & Zabel 2003), so it was included in

our analysis. Following Achord *et al*. (2003), density indices by site and year ($D_{s,y}$) came from standardized collection procedures at the time of tagging. Basin-wide annual estimates of density were calculated using the same procedure as described above for basin survival. They were log-transformed because of their skewed distribution and to prevent predictions of negative densities for some sites in some years. Although density dependence is typically modelled as a nonlinear function, the linear approximation used here produced comparable fits with a Beverton–Holt model in all our analyses, so we adopted a linear relationship for ease of implementation and interpretation.

### Environmental predictors

Peak stream flows occur in the Salmon River basin when the snow pack melts fastest, in May or June, and low flows usually occur in September or October. Autumn months are also important biologically because juveniles typically migrate to overwintering sites lower in the tributary at this time (Achord *et al*. 2001). To describe interannual variation in flow simply in our models, maximum annual monthly flow and the average of September and October flow on the mainstem Salmon River at its outflow from the basin (at White Bird; USGS 2005) for each year were included.

Seasonal averages (June–August, September–November, December–February, and March–May) of air temperature and precipitation were included in the model. Time series for both variables were highly correlated across weather stations in the Salmon River basin (average $r = 0.70$), so the average of seven stations (locations shown in Fig. 1D; data from WRCC 2004a) effectively described basin-wide patterns between years.

Snow pack depths on 1 April were obtained from six SNOTEL stations (Fig. 1D; WRCC 2004b). This date was selected because it best predicts stream flow over the summer in this basin (Alan Hamlet, Climate Impacts Group, University of Washington, personal communication). Finally, the Palmer Drought Severity Index (PDSI) was used to combine region-wide temperature and precipitation over a longer time period. July–December monthly values for Idaho Climate Division 4 (NCDC 2005) were averaged to reflect the period when flows are lowest.

The largest temporal and spatial environmental indices in our analysis were the Pacific Decadal Oscillation (PDO; Mantua 2005) and the El Niño/Southern Oscillation (ENSO; Wolter 2005). PDO and ENSO monthly indices were averaged from July through June to correspond with the period over which survival was estimated.

### Model selection

A series of alternative models were developed in which survival was a function of parr density and environmental variables. Air temperature and precipitation values from the winter prior to tagging through the spring migration were included to detect the delayed effect of snowmelt as well as rainfall on stream conditions. To simplify the analysis, temperature and precipitation variables were first reduced by using stepwise regression (alternating between step up and step down using the step function in S-Plus 6·1, Insightful Corp., Seattle, WA, USA) based on Mallow's $C_p$ criterion. Then the remaining variables (stream flow, snow pack, PDSI, PDO and ENSO) were added and stepwise regression was completed. The relative utility of the individual environmental predictors was further explored in single-factor regression models and in two-factor models in which one of the factors was density. This allowed the predictors to be ranked, which facilitates interpretation of the single 'best' model produced by multiple regression. Because the one- and two-factor models were used for exploration rather than hypothesis testing, the significance level was not adjusted for multiple comparisons. Several of the environmental factors were strongly correlated with each other and thus were redundant statistically. Only the first factor in each of the following pairs was therefore included: winter precipitation/snow pack ($r = 0.88$), fall stream flow/PDSI ($r = 0.9$), and average/minimum monthly fall flow ($r = 0.98$).

### POPULATION SCALE

After the basin-scale analysis, a similar procedure was applied at the population scale. However, some populations showed very similar changes in survival over time ($r > 0.9$). To reduce statistical redundancy, populations were first grouped by means of cluster analysis (Everitt 1980), and then yearly survival was calculated for each cluster. Euclidean distances between survivals were compared using an agglomerative hierarchical clustering method (S-Plus 6·1, Insightful Corp.). The dissimilarity criterion was based on either average, minimum, or maximum differences between all pairwise combinations of sites in the different clusters. Clusters were defined as the clade for which membership was the same regardless of which method was used to generate the tree. Only sites with at least 4 years of data were included in this part of the analysis (15 sites). Cluster density estimates were the sum of stream densities for each year within each cluster. Yearly mean survival ($S_{c,y}$) and density ($D_{c,y}$) was then calculated using the 'year effects' method described above.

### Basin, cluster and population model comparison

After the cluster analysis, three different units of response variable, survival at the population ($S_{s,y}$), cluster ($S_{c,y}$) and basin-wide level ($S_y$), were used to produce three nested models similar to the form shown in the equation above. The 'best' model was identified by analysis of variance with an *F*-test of significance. Because clustering explained a highly significant portion

of the year-to-year variability among populations and produced a far better fit than the model with individual site effects (see Results), we concluded that populations within clusters were responding to similar environmental factors, and a similar environmental analysis at the single population level was not performed.

*Environmental predictors*

The correlation structure of stream flow from each of the major forks and headwaters of the Salmon River (Fig. 1C; USGS 2005) was analysed to characterize the spatial heterogeneity in flow patterns. Tributary flows were highly correlated with each other ($r \geq 0.96$), so further analyses were limited to the Middle Fork near Shoup gauge station. This station was selected because most of the populations are in the Middle Fork.

Eleven years of stream temperature measurements (1994–2004) from three locations near tagging sites (Fig. 1C) were analysed. For each year, seasonal average daily temperatures during June–August, September–November, December–February and March–May were calculated. A 6000 UPG series multiparameter sonde (YSI Environmental, Louisiana, USA) recorded hourly water temperatures. (Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.) Annual patterns at different sites were correlated ($r \geq 0.72$), so the single record with the fewest missing data points, the Sawtooth Hatchery on the upper Salmon was used. At this site, no data were missing for the summer months, but winter and fall temperatures were missing for 1 and 2 years, respectively. Some streams that were not measured are much smaller than any of the measured streams, and therefore they may track air temperature more closely than larger streams. Air temperature averaged across the basin was therefore included in the analysis, and summer stream and air temperatures are referred to collectively as summer temperature.

*Model selection*

Cluster survival was analysed using annual cluster density, seasonal stream and air temperatures, and minimum fall flow as predictor variables. Temperatures from seasons between summer tagging and spring recapture were included. To select the best overall model for each cluster from all of the variables, step-wise regression was used, followed by $F$-value ranking of predictor variables, as described above.

### LINKING SITE CHARACTERISTICS AND ENVIRONMENTAL DRIVERS

Sites within a cluster shared a primary environmental predictor of variation in survival (see Results). To try to understand why different environmental factors were important for different populations, characteristics shared by sites within each cluster were explored using

classification and regression tree analysis (Breiman *et al.* 1984). This technique is a binary recursive partitioning algorithm that splits the data along coordinate axes of the explanatory variables so as to maximally distinguish clusters at each node. This process produces a decision tree similar to traditional dichotomous keys. Explanatory variables that reflected physical stream characteristics, life history and migration characteristics, and the presence of exotic brook trout were included. Physical characteristics were summer temperatures, stream width, and elevation. The life-history trait was the timing of the adult migration, either spring or summer 'run', as identified by Idaho Department of Fish and Game (StreamNet 2005). Migration characteristics were the distance the fish travelled to Lower Granite Dam where survival was estimated, and the timing of dam passage. Factors related to our methodology were also included: date of tagging and the time period over which survival was measured (passage time minus tagging date).

Our analysis of how site characteristics influence cluster membership required temperature estimates from as many field sites as possible. Stream temperature measurements were obtained from subsets of sites over three summers from 2003 to 2005. The rank order of sites across each of these time periods did not change by more than one position, so the time period that covered the largest set of sites, the 16 sites shown in Fig. 1(C), was selected to characterize site differences. This time frame (the third week of September, 2003) is not necessarily most important biologically, but it reflects characteristic differences between sites. A Tidbit datalogger (Onset Computer Corp., Bourne, MA, USA) recorded temperature every 5 min at these sites, from which we computed the 7-day average.

## Results

### BASIN SCALE

Our regression analysis indicated highly significant year and site effects ($F_{11,108,\text{year}} = 20.4$, $P < 0.0001$, $F_{17,108,\text{site}} = 10.1$, $P < 0.0001$), which were combined to produce annual basin-wide survival estimates. A single-factor model with average fall flow as the predictor was selected by stepwise regression ($F_{1,10} = 10.2$, $P = 0.01$). Exploration of all factors revealed that density was also marginally significant ($P = 0.047$, Table 1), and that precipitation over the previous winter (December–February average) and snow pack on 1 April (prior to tagging), significantly improved model fit when added to density. Temperature, the PDSI, and the PDO and ENSO indices were not significant predictors on their own, nor did they improve model fit over density alone. These results were not due to a lack of variation in the indices: the strong El Niño in 1997–98 and the possible 'regime shift' of the PDO in 1998 (Peterson & Schwing 2003) caused a wide range of index values during the study period. However, the PDO and ENSO

**Table 1.** Single factor regression statistics for predictors of basin-wide annual survival. The * indicates the model chosen by stepwise regression. Snowpack was highly correlated with winter precipitation (ppt), and the Palmer Drought Severity index was highly correlated with fall stream flow; these parameters are therefore not shown

| Predictor | $r^2$ | $F$ | d.f. | $P$ |
|---|---|---|---|---|
| Fall stream flow | 0·5 | 10·2 | 1,10 | 0·01* |
| Density | 0·34 | 5·14 | 1,10 | 0·047 |
| Winter ppt | 0·27 | 3·6 | 1,10 | 0·086 |
| Maximum stream flow | 0·17 | 2·0 | 1,10 | 0·186 |
| Summer air temperature | 0·13 | 1·5 | 1,10 | 0·253 |
| ENSO | 0·03 | 0·3 | 1,10 | 0·597 |
| PDO | 0·00 | 0·0 | 1,10 | 0·982 |

indices were not correlated with local temperature and precipitation, even when various lag times were incorporated.

POPULATION SCALE

The cluster analysis revealed four clusters (Fig. 2) that were robust to the dissimilarity criterion applied, with one exception (the west fork of Chamberlain Creek); this site was removed from later analyses of cluster predictors. There was some spatial structure to the clustering, but factors other than distance were also important. All of the sites on the South Fork clustered together (designated C1), but three clades overlapped on the Middle Fork (designated C2, C3 and C4), and some sites on the upper Salmon grouped with C1 and others with C2 (Fig. 1B). Clustering appeared to capture much of the site by year interaction noted in a previous analysis (Zabel & Achord 2004): clustering significantly improved model fit over site alone ($F = 2·6$, $\Delta Df = 16$, $P = 0·0018$) and over the basin-wide yearly average ($F = 13·8$, $\Delta Df = 13$, $P < 0·0001$).
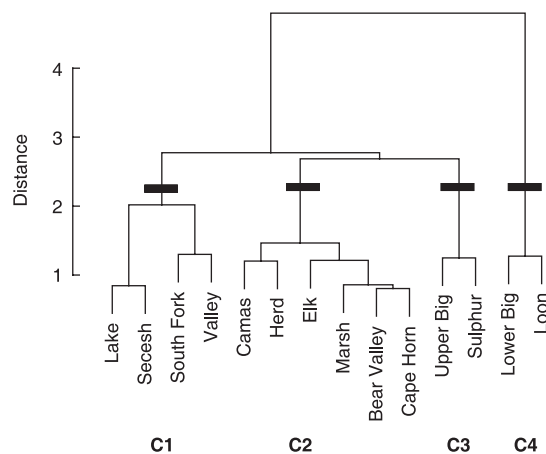


**Fig. 2.** Cluster tree of site survival, based on the average distance between site pairs. The darkened horizontal lines show where the tree was cut to form four clusters. Each cluster is labeled with a code that is used in the text and on other figures.

Survival patterns within each cluster showed a more complex relationship with the environment than revealed at the basin level. Stepwise regression produced a different model for each cluster, indicating that flow, temperature and density are all important (Fig. 3, Table 2). Flow was much more important for clusters C1 and C2 than for the remaining two clusters. Temperature, which was not significant at the basin scale, was very closely related to survival in C3 and C4. Density was most important for C2, although it was quite similar to flow in the amount of variance explained.

Local measurements of flow, temperature, and snow pack were better correlated with survival than basin-wide average measurements (compare Tables 1 and 3). None the less, these measurements can be difficult to attain and forecast in climate change scenarios. Therefore, having identified fall flow and summer temperature as the important local environmental factors, we explored how closely these factors were related to basin-wide patterns in precipitation and air temperature (Table 4). The high correlation values between minimum flow and precipitation and snow pack from the previous winter reflect the direct links between these variables in this snow-fed hydrological system. Stream temperature, on the other hand, is much more responsive to summer air temperature, indicating that both winter and summer weather affect fish survival.

LINKING SITE CHARACTERISTICS AND ENVIRONMENTAL DRIVERS

The classification tree analysis identified a small number of predictors of cluster membership. Each of the clusters fell completely into a single run type: C4 and C1 populations were all summer runs, and C2 and C3 populations were all spring runs. Further classification relied on stream width, stream temperature and elevation (Fig. 4). These three variables covaried to some extent because higher elevation streams are often narrower and cooler. Comparing average stream width and temperature in each cluster with the driving environmental factors in each population revealed that narrower, cooler streams were most sensitive to flow, and the wider, hotter streams were most sensitive to high temperature. Note that other stream characteristics may significantly affect overall survival rates in each stream, but our results suggest that they do not greatly affect interannual variation in survival, and hence cluster identity.

**Discussion**

Our study demonstrates that different aspects of climate appear to be important at different scales of analysis, and consequently, the importance of considering variation among populations when examining the response of species to climate. Although we could identify a significant basin-wide response of Chinook
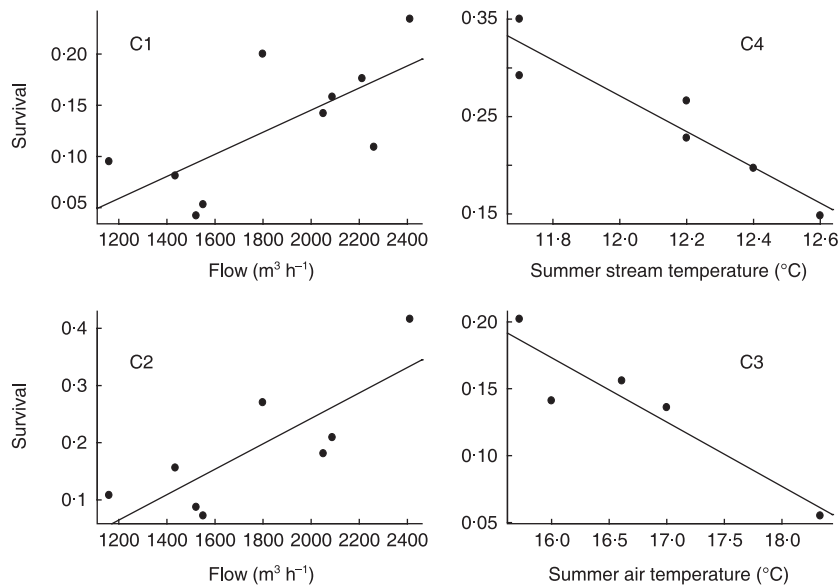
**Fig. 3.** Cluster survival compared with minimum fall flow for the C1 and C2 clusters (left column), and compared with summer air and stream temperature for the C3 and C4 clusters, respectively (right column). Lines show the linear regression.

**Table 2.** Model statistics for predictors of cluster survival. Predictor variables are: basin-wide average summer air temperature, summer stream temperature measured at Sawtooth, fall minimum monthly flow on the Middle Fork Salmon River, and cluster parr density. The model chosen by step-wise regression within each cluster is indicated with an *

| Cluster | Predictor | $r^2$ | F | d.f. | P |
|---|---|---|---|---|---|
| C1 | Temp. (air) | 0·37 | 4·6 | 1,8 | 0·063 |
| | Temp. (stream) | 0·35 | 4·3 | 1,8 | 0·073 |
| | Flow | 0·48 | 7·2 | 1,8 | 0·027* |
| | Density | 0·23 | 2·3 | 1,8 | 0·165 |
| C2 | Temp. (air) | 0·49 | 5·8 | 1,6 | 0·052 |
| | Temp. (stream) | 0·44 | 4·7 | 1,6 | 0·074 |
| | Flow | 0·63 | 10·0 | 1,6 | 0·019 |
| | Density | 0·67 | 12·1 | 1,6 | 0·013* |
| C3 | Temp. (air) | 0·88 | 21·2 | 1,3 | 0·019* |
| | Temp. (stream) | 0·57 | 4·0 | 1,3 | 0·141 |
| | Flow | 0·07 | 0·2 | 1,3 | 0·658 |
| | Density | 0·53 | 3·4 | 1,3 | 0·162 |
| C4 | Temp. (air) | 0·75 | 12·0 | 1,4 | 0·026 |
| | Temp. (stream) | 0·88 | 29·2 | 1,4 | 0·006* |
| | Flow | 0·36 | 2·2 | 1,4 | 0·21 |
| | Density | 0·18 | 0·9 | 1,4 | 0·404 |

salmon to climate indicators, when we examined relationships at the population scale, we found improved fits and revealed striking differential responses to climate. From a conservation standpoint, variation is important because diversity is a critical component of metapopulation stability, and hence, viability (McElhany *et al.* 2000). Distinct ecotypes of Bristol Bay sockeye salmon, for example, have allowed that aggregation of populations to maintain high abundance over several decades, despite wide fluctuations in the abundance of individual populations (Hilborn *et al.* 2003). From a management perspective, it is useful to recognize that certain groups of populations are likely to show similar interannual fluctuations in response to climate. With this information, we can better parameterize population viability models, identify environmental characteristics that should be monitored more closely, assess impacts of potential interventions, and target particular habitat restoration efforts to the populations that will most benefit from them.

When we explored characteristics of individual sites within clusters, we found intrinsic habitat features that

**Table 3.** Correlation coefficients (*r*) between annual cluster survival and environmental variables. The location of each measurement is shown below each variable and in Fig. 1. Environmental variables include minimum monthly flow from gauges throughout the Salmon River (SR) basin, snowpack from the winter prior to tagging (Morgan Creek), and summer stream temperature (Sawtooth). * indicates that the correlation is significant at the $P < 0.05$ level

| | Minimum fall flow | | | | Snowpack upper SR | Temp. upper SR |
|---|---|---|---|---|---|---|
| Cluster | Middle Fork SR | South Fork SR | Upper SR | White Bird | | |
| C1 | 0·75* | 0·69* | 0·64* | 0·55 | 0·6* | −0·59 |
| C2 | 0·87* | 0·83* | 0·76* | 0·74* | 0·76* | 0·66 |
| C3 | 0·2 | −0·11 | −0·05 | 0·29 | 0·34 | 0·76 |
| C4 | 0·67 | 0·53 | 0·31 | 0·35 | 0·08 | 0·94* |
| Basin | 0·78* | 0·68* | 0·69* | 0·63* | 0·72* | −0·59 |

**Table 4.** Correlation coefficients (*r*) between environmental factors. Local variables are minimum fall monthly flow at the Shoup gauge station and mean stream temperature at Sawtooth, on the Upper Salmon River, from June to August in the year of tagging. Basin-wide average variables are mean air temperature from June to August in the year of tagging, total precipitation from December through February from the winter prior to tagging, and snowpack on 1 April. The Palmer Drought Severity Index (PDSI) for Idaho Division 4 was averaged from July–December in the year of tagging, and the Pacific Decadal Oscillation (PDO) and the El Niño Southern Oscillation (ENSO) were averaged from July–June. * indicates that the correlation is significant at the $P < 0.05$ level

|  | Minimum flow | Stream temp. |
|---|---|---|
| Air temperature | −0·5 | 0·7* |
| Winter precipitation | 0·7* | −0·18 |
| Snowpack | 0·87* | −0·5 |
| PDSI | 0·94* | −0·85* |
| PDO | 0·33 | 0·12 |
| ENSO | 0 | 0·31 |
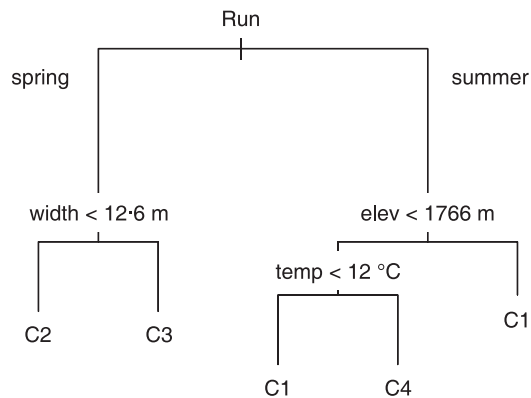


**Fig. 4.** Classification tree of explanatory variables needed to correctly assign each population into the appropriate cluster. Run refers to the timing of adult returns to the Salmon River Basin. Stream width, water temperature in September 2003, and elevation distinguished between clusters with the same run timing. If a stream has a value less than the cutoff shown at the node, then one follows the left branch, and if it is higher then one follows the right branch.

were consistent within the clusters, suggesting that physical, site-specific characteristics may result in populations that respond differentially to climate. In general, juvenile survival in wider and warmer streams was negatively related to temperature, while survival in narrower and cooler streams was positively related to flow. As temperature increases above optimal levels, developmental processes in salmonids are impaired and predation risk increases (Marine & Cech 2004), and prey availability may decline (Bisson & Davis 1976). Flow may act upon survival by several mechanisms. We have observed that as flow decreases in the autumn, streams narrow and potential habitat decreases, which can concentrate predators. Also, these fish typically undergo an autumn migration to overwintering habitat, and reduced flow during this period may alter the timing or reduce success of the migration.
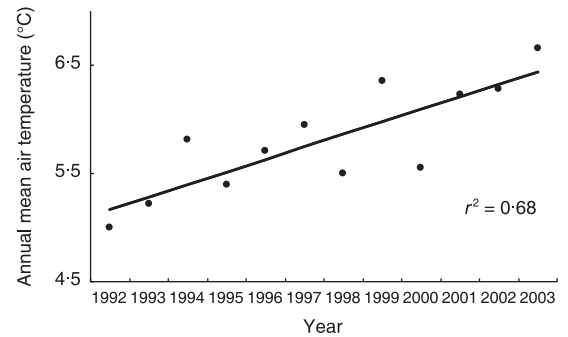


**Fig. 5.** Annual mean air temperature in the Salmon River Basin (average of 7 weather stations), measured from July to June to match periods of estimated survival. Regression line shows a warming rate of 1.2 °C per decade.

Thus it is plausible that juveniles from cooler and narrower streams escape the detrimental effects of summer temperatures but suffer increased mortality due to loss of habitat. Juveniles from warmer and wider streams are not as susceptible to habitat loss, but are potentially more vulnerable to elevated summer stream temperatures.

Climate forecasts clearly indicate that higher summer temperatures and changing hydrological regimes are coming to the Pacific Northwest (Mote *et al.* 2003). These conditions may lower juvenile survival and affect adult migratory behaviour (Quinn & Adams 1996) and fertility (King & Pankhurst 2004). Despite the high elevation, stream temperatures in the Salmon River basin already routinely exceed the 13 °C maximum daily temperature thresholds for salmonids set by the Idaho Department of Environmental Quality (Donato 2002). Alarmingly, annual air temperatures have been climbing steadily at about 1·2 °C per decade since 1992 (Fig. 5). Our results confirm that temperature is negatively correlated with survival, both because winter and spring air temperatures affect the rate at which the snow pack melts and consequently the timing and magnitude of stream flows, and because summer air temperatures affect stream temperatures. Thus, although ocean conditions have improved since 1998 (Zabel *et al.* 2006), the realized benefit may be reduced because of deteriorating freshwater conditions.

As with most endangered species, many factors reduce the long-term viability of these fish (McClure *et al.* 2003). Ecologists have long recognized the importance of maintaining diverse habitats and multiple independent populations, but the added threats from climate change make this goal even more imperative. Managers can sometimes influence stream flow and temperature, for example, by reducing water diversions or encouraging riparian cover, so identifying the most important environmental forcing factors for a particular population can have conservation benefits. However, we still do not know the specific mechanisms by which these factors affect survival, so more study is warranted. Understanding the mechanisms by which

habitat heterogeneity confers stability to existing populations or metapopulations is essential because their stabilizing effects may unravel as the climate changes. In salmon, if temperatures in streams exceed the critical maximum, such streams will become un-inhabitable, leading to the distribution shifts predicted by larger-scale correlation analyses (Eaton & Scheller 1996). Salmon are often considered 'keystone' species because they transfer marine nutrients to otherwise nutrient-poor environments, and provide a crucial food resource for many vertebrates (Willson & Halupka 1995), so their decline or extinction affects both community and ecosystem properties (Scheuerell *et al*. 2005). Many pieces of the puzzle are still unresolved, such as the extent to which behavioural change or thermal adaptation might change the impact of climatic factors over time, and the relative importance of or interactions between density and environmental factors. But clearly, climate change poses a significant risk to this and many other species, and understanding the role of population variation in a diversity of situations is key to understanding these risks.

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