Scale and the detection of climatic influences on the productivity of salmon populations

LAUREN A. ROGERS[1] and DANIEL E. SCHINDLER

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA

Abstract

Ecological studies relating population parameters to climate conditions are limited by a lack of experimental control systems and rely instead on correlative evidence to draw inferences about how populations respond to environmental forcing. Consequently, some correlations turn out to be spurious and not ecologically meaningful. To strengthen inferences, multiple populations may be examined simultaneously to confirm whether relationships can be generalized across multiple systems; however, this assumes that populations respond similarly to climate drivers, ignoring the potential for ecological complexity. Using data on eight sockeye salmon populations from southwestern Alaska, we constructed a series of models based on ecological hypotheses, relating salmon population productivity to climate factors experienced at different life stages. We modeled populations at a range of organizational scales, from distinct populations, to populations grouped by common nursery lake, to all populations within a watershed, and determined the relative statistical support for climate drivers at each scale. In general, warmer lake and sea surface temperatures in the summer coincided with increased productivity of these populations, but the most sensitive life-stage for climate effects varied among populations, particularly among nursery lakes. The best model when considering all populations together, despite strong statistical support, failed to represent the complexity which became evident when populations were modeled by common nursery lake, or independently. These results emphasize that the most appropriate organizational scale to model salmon stocks will depend on specific management, scientific, or conservation goals.

Introduction

It is increasingly appreciated that the response of populations to environmental change may vary substantially across the geographic range of a particular species (Planque & Frédou, 1999; Mueter *et al.*, 2002; Sæther *et al.*, 2003; Martinez-Jauregui *et al.*, 2009). This is not surprising, as the constraints on growth and survival may depend on a population's location within the species' range. The potential for populations in close geographic proximity to show differential responses to climate change and variability is less well recognized. A common expectation in ecology is that exposure to shared regional climate conditions synchronizes the dynamics of neighboring populations (Liebhold *et al.*, 2004). However, the synchronizing effects of climate can be reduced by heterogeneity in (a) the local expression of regional climate variation, (b) other extrinsic deter-

minants of population dynamics, such as the density of predators or competitors, and (c) population traits and local adaptations which determine the sensitivity of populations to changes in their environment. While much focus has been placed on the synchronizing effects of climate, less attention has been paid to the possibility that populations may show sensitivity to different climatic drivers, even within the same geographic region, due to genetic and phenotypic heterogeneity among populations and differences in the physical and biotic features of habitats that they occupy (e.g. Ringsby *et al.*, 2002; Hilborn *et al.*, 2003; Crozier & Zabel, 2006; Martins *et al.*, 2011). This study explores variation in how spatially proximate sockeye salmon (*Oncorhynchus nerka*) populations in southwestern Alaska have responded to climate drivers over the past half-century.

Relating recruitment or survival to climate variability is challenging because of temporal confounding of climate drivers with each other and with other environmental changes, and because of a lack of appropriate reference systems. Thus, nearly all climate-population studies rely on correlative evidence from time series data, and are often criticized for finding spurious re-

[1]Present address: Lauren A. Rogers, Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway.

Correspondence: Lauren A. Rogers, tel. + 1 206 221 6884, fax + 1 206 685 7471, e-mail: larogers@u.washington.edu

lationships (Myers, 1998). Such spurious correlations are a consequence of considering many possible relationships, such that some are statistically significant by chance alone and eventually break down as more data accumulate. One analytical strategy to increase the chance of finding meaningful relationships is to consider multiple populations simultaneously and look for commonality in their responses to climatic drivers (Myers & Mertz, 1998; Walters & Martell, 2004). By looking at multiple populations, common climate responses can be more easily isolated from random demographic noise and sampling errors; thus relationships are more likely to represent biological processes rather than statistical flukes (Mueter *et al.*, 2002). However, this multiple-population approach must be implemented carefully in order not to overlook the potential for populations to respond differently to climate variability due to differences in the environments they occupy, and genetic and phenotypic differences among locally adapted populations. We therefore explored the trade-off between the improved confidence in ecological relationships that can be gained from considering multiple populations together, and the subsequent lost potential for detecting ecological complexity characterized by differential responses among populations to changing climate.

Detecting relationships between climate variability and population dynamics also depends on the scale at which both are measured; relationships detected at coarse space and time scales may not match the relationships that ultimately are important at finer space and time scales (Allen & Hoekstra, 1992; Levin, 1992). This is an issue for considering future population responses to climate change because relationships detected at finer scales may not persist at broader scales. Furthermore, relationships detected at broader scales may obscure the underlying mechanisms controlling population dynamics at finer space or time scales (Allen & Hoekstra, 1992; Schindler *et al.*, 2008). To address this, we modeled the relationship between population productivity and several probable climate drivers of production in multiple sockeye salmon (*O. nerka*) populations across a hierarchy of geographic and organizational scales, from individual stream-spawning populations to a large-scale stock consisting of dozens of individual spawning populations, and compared the best models found at each scale.

We addressed three questions relevant to detecting relationships between climate and population productivity. (1) Which climate factors are associated with variation in productivity of sockeye salmon populations in the Wood River system of southwestern Alaska? (2) Do populations differ in their sensitivity to climate drivers? (3) How does the level of aggregation of populations (from individual stream-spawning populations to the Wood River system as a whole) influence the selection of models and our perception of the effects of climate variability on these populations?

Materials and methods

Study system

The Wood River lake system in southwestern Alaska, USA, is a chain of interconnected lakes draining into Bristol Bay and the eastern North Pacific Ocean (Fig. 1). This system has produced an average of 3.2 million adult sockeye salmon per year over the past half-century (Baker *et al.*, 2006), making it one of the most important sockeye salmon watersheds in the world. The spawning and rearing habitat is largely intact, with minimal human impacts, such as roads, development, mining, agriculture, timber harvest, hydropower, or hatcheries. Fishery harvest is relatively high but remains well-managed for long-term sustainability (Hilborn, 2006).

Study populations

Sockeye salmon have a complex life history, spending parts of their lives in both freshwater and marine environments, and they may be sensitive to climate conditions at any stage. Sockeye salmon in Bristol Bay spawn from mid-July to mid-September. They bury their fertilized eggs in the gravel of streams, rivers, and lake beaches, and embryos incubate through the winter. Fry emerge the following spring, and generally move downstream to lakes where they spend 1 or 2 years growing before migrating to the ocean as smolts (Burgner, 1991). These salmon then spend weeks to months in nearshore Bristol Bay and then migrate south through the Aleutian Islands to the Gulf of Alaska by winter (Burgner, 1991). After 1, 2, or 3 years in the North Pacific Ocean, maturing sockeye salmon return to Bristol Bay, and migrate upstream to their natal spawning grounds to reproduce and die. The tendency of sockeye to home to their natal sites to spawn has resulted in reproductive isolation of genetically distinct populations (McGlauflin *et al*, in press), each adapted to local environmental conditions (Dittman & Quinn, 1996). This allowed the examination of multiple distinct populations spawning within a geographic region that experience similar regional climate conditions through at least the freshwater and early marine portions of their lives.

Bristol Bay sockeye salmon are harvested by a terminal fishery, intercepting mature adults on their way into rivers to spawn. Those fish that escape the fishery are counted visually from towers on the rivers, and a proportion of both the catch and escapement are sampled to determine the age composition of returning adults. Brood tables are then constructed for each major river system in Bristol Bay, including the Wood River, using the catch, escapement, and age composition data, attributing returning adults to the year in which they were spawned (Baker *et al.*, 2006). This detailed accounting began in 1956.
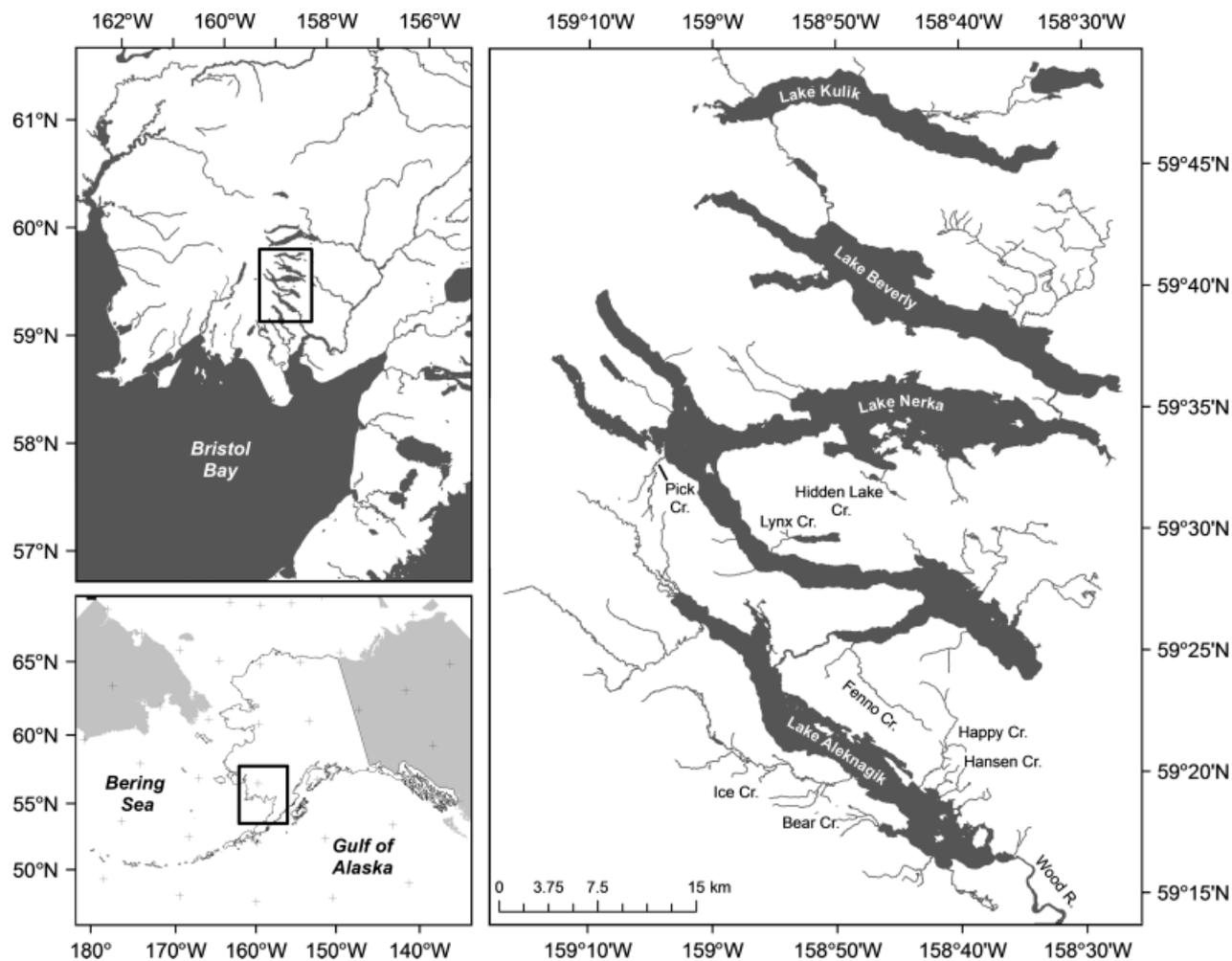
Fig. 1 Map of sockeye salmon spawning streams in the Wood River system, located in the Bristol Bay region of Alaska, USA. The eight streams used for this study are indicated by labels.

Using the catch and escapement data, as well as spawning ground surveys, brood tables were constructed for eight stream-spawning populations within the Wood River system (see Rogers & Schindler, 2008 for details). These populations make up a small (<10%) proportion of the total Wood River stock because most of the stock spawns in large rivers and on lake beaches where the populations are too large to be enumerated precisely. Four of these populations spawn in streams draining to Lake Aleknagik, and four spawn in streams draining to Lake Nerka (Fig. 1). Spawning ground surveys were conducted annually, counting all live and dead fish on the peak date of spawning. Otoliths from approximately 100 males and 100 females were sampled from each stream population each year to determine the age composition of the salmon. We then adjusted the total salmon abundance for each stream by the annual catch-rate for each age class to determine how many fish would have returned to the spawning grounds in the absence of a fishery, assuming that all fish of a given age class are equally vulnerable to the fishery in a given year. Reconstructed numbers of adults were aligned by brood year to determine the total

number of returning adults produced by each generation of parents from each population for the brood years 1961–2002 (i.e., fish returning from 1964 to 2008).

Environmental data

Using available data, we tried to capture the suite of conditions experienced by salmon as they migrate through different habitats at each life stage. This was necessarily complicated by uncertainty in migration timing, location, and variation in the ages at which major life transitions occur. On average, 90% of the sockeye from the Wood River system spend only 1 full year in freshwater as juveniles and migrate seaward the following spring/early summer, rather than residing for 2 full years in a lake; thus the focus was placed upon this dominant life-history pattern when choosing environmental covariates for the models. The environmental factors included are only rough metrics of the multidimensional suite of conditions experienced by migrating salmon, though spatial and temporal autocorrela-

tion in environmental conditions suggest this approach should still capture the relevant variability.

Rearing lake conditions may be important for the growth and survival of sockeye salmon in this system from their first summer through their second summer, before seaward migration. Date of spring ice breakup is an indicator of regional spring climate, and affects the length of the growing season for juvenile sockeye prey items in the lake (Schindler *et al.*, 2005). The timing of ice breakup also constrains the period of outmigration for smolts because substantial seaward migration from the Wood River system does not commence until ice has broken and water temperatures have begun to rise (Burgner, 1962; Rogers, 1988; McGlauflin *et al.*, in press). The date of ice breakup on Lake Aleknagik (Fig. 1) has been recorded annually since 1949, and was included in our models lagged 1 and 2 years from the sockeye brood year ($IceOut_1$, $IceOut_2$) to correspond to the spring of their growing season, and the spring of their smolt migration season, respectively. Lake Aleknagik ice breakup date was used as an indicator of regional climate for all populations because it has been routinely recorded for the length of our study. The date of ice out for Lake Nerka, which is higher in the system, is always later (usually 1–5 days) than for Lake Aleknagik, and limited concurrent observations indicate that interannual variability in the timing is significantly correlated (Pearson's $r = 0.72$, $n = 8$, $P = 0.04$).

Similarly, lake temperature is relevant for sockeye salmon during both the first summer in the lake, and the second summer before migrating to the ocean. Juvenile sockeye salmon grow faster under warmer conditions due to increased physiological scope for growth as well as increased prey abundances (Brett, 1995; Schindler *et al.*, 2005; Rich *et al.*, 2009). During the second summer, yearlings may put on additional growth before migrating to sea, depending on climate conditions and the timing of migration (Burgner, 1962). Lake temperatures in the top 20 m of Lake Aleknagik were measured monthly, June–September, beginning in 1962, and averaged to obtain summer mean lake temperatures. Lake temperature was included in the models lagged to correspond to summers 1 and 2 of the sockeye salmon life cycle ($LakeT_{sum1}$, $LakeT_{sum2}$). Interannual variation in late summer temperatures was highly correlated across the two lakes (Carter, 2010), and so Lake Aleknagik temperatures were used to maximize temporal coverage.

The early marine phase of the salmon life-cycle is considered to be an especially critical period for survival (Pearcy, 1992; Quinn, 2005). The exact factors which regulate survival during this phase are uncertain, and indeed may change from year to year, but likely have to do with distributions and abundances of prey and predators, as well as the size and condition of smolts when entering the sea and the timing of seawater entry (Pearcy, 1992; Koenings *et al.*, 1993; Quinn, 2005). Without data on these specific factors, we used regional sea surface temperatures (SSTs) to characterize the nearshore marine environment. Farley *et al.* (2007) found that warmer nearshore waters were associated with enhanced growth of Bristol Bay sockeye salmon in their first summer at sea, thus temperature may be a reasonable proxy for relevant ecosystem

processes where upwelling is generally not an important controlling mechanism for biological productivity.

SST data were compiled for the Eastern Bering Sea using the NCEP Reanalysis Derived data (Kalnay *et al.*, 1996) provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their website at http://www.cdc.noaa.gov/ for the region defined by 54.3–60°N and 161.2–172.5°W. We used seasonal SST averages, defined as spring (April–June), summer (July–September), and fall (October–December). These were lagged to correspond to the appropriate salmon life stages, beginning with the spring immediately preceding migration of 1-year-old smolts (SST_{spr2}) and continuing through the fall following migration of 2-year-old smolts (SST_{fall3}). After this stage, all Bristol Bay sockeye salmon should have left the Eastern Bering Sea. We avoided using SST reanalysis data for January–March when sea ice coverage in this region changes the interpretation of these values. However, winter sea-ice conditions are important for preconditioning the water column in the Eastern Bering Sea and at least partly control the timing and fate of phytoplankton blooms and zooplankton biomass (Hunt *et al.*, 2002). Measurements of sea-ice extent do not extend back to the 1960s, and therefore we used mean December–March air temperature recorded at St. Paul in the Pribilof Islands ($PribAirT_{win}$) as an index of winter sea-ice extent. Winter air temperatures at St. Paul were significantly correlated ($P < 0.01$) with the Ice Cover Index given at http://www.beringclimate.noaa.gov ($r = -0.69$ for 1979–2008).

In some cases, large-scale climate indices are better predictors of ecological processes than individual local climate variables (Hallett *et al.*, 2004; Stenseth & Mysterud, 2005). The Pacific Decadal Oscillation (PDO) previously has been linked to large-scale salmon productivity trends in the Pacific Ocean (Mantua *et al.*, 1997); therefore, the winter (November–March) index of the PDO was included as an additional covariate, lagged 1–3 years to correspond to the winter of egg incubation (PDO_1), the first winter juveniles are in nursery lakes (PDO_2), and the first winter most Wood River sockeye spend in the NE Pacific ocean (PDO_3).

Modeling approaches

Using brood tables for the eight populations within the Wood River system, combined with the climate data described above, models were constructed to determine how these populations have responded to past climatic variation. This approach incorporated both intrinsic density-dependent effects and extrinsic climate effects on survival.

First, to determine which climate factors the populations were most sensitive to, and whether they differed by population, models were fit for each population independently. For each population, a range of models was considered, incorporating Ricker dynamics and considering climate effects at various life stages:

$$ln\left(\frac{R_t}{S_t}\right) = \alpha + \beta S_t + \gamma E_{j,t+x} + \varepsilon_t, \qquad (1)$$

where R_t is the number of returning adults (both caught and escaped) to the population produced by spawners (S_t) in year

t. α and β are the traditional Ricker (Hilborn & Walters, 1992) stock-recruitment model parameters, E_j is one of *j* time series of environmental/climate conditions experienced in year *x* of the sockeye salmon life cycle, and γ is the population-specific slope term, or sensitivity, to those climate conditions. Because of temporal correlation in the residuals, errors (ε_t) were modeled with an order-1 autoregressive correlation structure (Pinheiro & Bates, 2000). The Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002) was used to compare models with only an intercept, models which incorporated Ricker dynamics, and models which incorporated Ricker dynamics plus any single climate variable. This allowed us to determine which climate variables explained the most variation for each population, whether the most informative variables varied among streams, and whether the models including climate predictors performed better than models with Ricker dynamics alone. Because some of the environmental time series were correlated with one another, and in order to reduce the total number of candidate models, we initially did not consider any models with more than one climate variable. After examination of the initial models, a limited number of more complicated models were considered which included climate effects at multiple lags.

Rogers & Schindler (2008) showed that sockeye salmon populations in Lake Aleknagik were more correlated in productivity through the years with other Lake Aleknagik populations than with Lake Nerka populations, and vice versa. This may be due to exposure to more similar environmental conditions within a lake, or to lake-specific responses to a common environmental driver. If populations using the same rearing lake may be expressing a similar response to climate, they can then be modeled jointly to determine which climate variables are most important for the populations as a group. We built upon the model described above, except that we jointly modeled the populations using a common rearing lake, and considered the climate response (γ) a shared effect across populations. Thus, for each set of four populations using a common rearing lake, we fit the following:

$$\ln \frac{R_{it}}{S_{it}} = \alpha_i + \beta_i S_{it} + \gamma E_{j,t+x} + b_t + \varepsilon_{it},$$
$$\varepsilon \sim N(0, \sigma_i), b \sim N(0, \sigma_0). \tag{2}$$

In this case, the slope parameter, γ, is the same for all populations, but the Ricker parameters (α_i, β_i) are population-specific ($i = 1, \ldots, 4$). A random effect for year (b_t) was included in order to account for the contemporaneous correlation among populations not accounted for by the modeled environmental covariate (Pinheiro & Bates, 2000). Errors (ε_{it}) were assumed to be independently and normally distributed with population-specific variances (σ_i). Models were also fit with a unique γ for each population (γ_i), and it was tested whether this changed the strength of support for the inclusion of particular climate variables. Again, AICc was used to compare the relative support for models including each of the environmental variables, and those which contained only population-specific intercepts and Ricker parameters. Models were fit separately for each rearing lake, and the best models for each set of populations were compared.

Finally, if these eight populations, returning to the same river system and spawning in the same larger watershed, are affected similarly by changes in climate, then modeling them jointly should improve our ability to identify a common climate driver through any noise associated with observation errors. Thus, the same modeling exercise described above was repeated considering all eight populations jointly [$i = 1 : 8$ in Eqn (2)]. In this case, γ was assumed to be the same for the eight populations, and a common series of random year effects was estimated instead of separate series by lake.

At the coarsest scale, we modeled the dynamics of sockeye salmon in the Wood River system as a whole, consisting of dozens of individual populations and over 1 million spawners, on average. The same modeling approach was used as for individual stream spawning populations described previously.

All models were fit using generalized least squares regression or linear mixed effects models in the nlme library of R (Pinheiro *et al.*, 2009). Lagged climate variables were standardized over the period of the study (1961–2002) before modeling to facilitate interpretation of parameter estimates.

Results

The candidate climate variables showed varying degrees of cross-correlation and serial autocorrelation (Table 1). The timing of ice out on Lake Aleknagik was highly correlated with mean summer lake temperatures ($r = -0.73$, $P < 0.01$); earlier ice-free dates corresponded to warmer summer lake temperatures. In addition, correlations between conditions in freshwater and marine environments indicated some regional coherence in climate conditions, especially in the relationship between mean summer temperature of Lake Aleknagik and the mean summer SST for the Eastern Bering Sea ($r = 0.75$, $P < 0.01$). These high correlations made it difficult to distinguish among the factors most important for sockeye survival.

All populations showed evidence of density dependence as given by a non-trivial reduction in AICc with the inclusion of β_i (Table 2). For all populations, β was negative, indicating a reduction in the productivity rate [$\ln(R/S)$] with increasing density. Ricker parameters therefore were included in all subsequent models discussed. Inspection of residuals and random effects estimates from the final models did not reveal any evident outlier observations or strong departures from normality.

Individual population models

When modeled independently, the eight sockeye salmon populations from the Wood River system differed in their sensitivity to climate factors, and particularly in their timing of sensitivity (Table 2). For three

Table 1 Cross-correlations between climate variables for the period 1962–2005

	IceOut	LakeT$_{summer}$	PribT$_{winter}$	SST$_{spring}$	SST$_{summer}$	SST$_{fall}$	PDO
IceOut	*0.13*						
LakeT$_{summer}$	−0.73**	*0.31*					
PribT$_{winter}$	−0.39*	0.35*	*0.28*				
SST$_{spring}$	−0.57**	0.58**	0.67**	*0.33*			
SST$_{summer}$	−0.61**	0.75**	0.43**	0.61**	*0.31*		
SST$_{fall}$	−0.54**	0.41*	0.22	0.47**	0.54**	*−0.03*	
PDO	−0.52**	0.32	0.45**	0.25	0.32	0.18	*0.29*

*$P < 0.05$.

**$P < 0.01$.

Tests of significance for cross-correlations are two-tailed, with the degrees of freedom adjusted to account for autocorrelation in the time series (Pyper & Peterman, 1998). On the diagonal are lag-1 autocorrelations, shown in italics.

SST, sea surface temperature; PDO, Pacific Decadal Oscillation.

populations, Bear, Hansen, and Ice creeks, the strongest model included a positive effect of lake temperature during the second summer (i.e., the smolt year; LakeT$_{sum2}$) as a covariate. This covariate explained an additional 11–17% of the variation in ln(R/S) for these populations over the basic Ricker model. SST during the summer of smolting (SST$_{sum2}$) also was strongly supported and explained nearly as much of the variation as lake temperature, and was the strongest environmental predictor for Fenno and Happy creeks (Table 2). In contrast, the strongest model for Pick and Hidden Lake creeks included a positive effect of lake temperature the previous year, during the first summer as juveniles (LakeT$_{sum1}$), and this was the second ranked model for Fenno Creek. For one population, Lynx Creek, none of the climate variables considered explained enough variation to justify their inclusion and the best model was the basic Ricker stock recruitment model. For some populations, multiple models had strong support (ΔAICc < 2), likely a consequence of the high correlations among some of the climate variables. In all, the total explanatory power of the best environmental models for each stream population ranged from 20% to 59%, not including Lynx Creek (Table 3).

For each population (excluding Lynx Creek; Table 3), the best model indicated increased productivity or survival under warmer conditions (Table 3, Figs 2, 3). However, the relative importance of temperatures experienced during the first and second summers differed among populations. In general, populations from streams draining to Lake Aleknagik (Bear, Hansen, Happy, and Ice creeks) were most sensitive to thermal conditions during the year of smolt migration, whereas populations in Lake Nerka (Hidden Lake and Pick creeks) tended to be more sensitive to thermal conditions during the year of fry growth in freshwater (Table 2).

Joint population models

When populations were grouped by common nursery lake, this pattern of differential timing of sensitivity by lake became more evident. The strongest predictor for Lake Aleknagik populations, when considered jointly, was lake temperature during the second summer (LakeT$_{sum2}$). Again, SST during this same period (SST$_{sum2}$) explained nearly as much variation as lake temperature. Lake Nerka populations, on the other hand, were best modeled by first summer lake temperatures (LakeT$_{sum1}$), with second summer lake temperatures receiving considerably less support (ΔAICc > 2).

Finally, when all eight populations were modeled jointly, and assumed to show similar responses to climate variability, the best predictor was LakeT$_{sum2}$, with SST$_{sum2}$ almost as strong. The model with LakeT$_{sum1}$ had much weaker support (ΔAICc = 9) and was not among the top three models. For the joint models, we also considered the case where the climate response coefficient varied by population (γ_i), allowing for different responses to the same climate driver. In only one case was the improved fit justified by the additional (three or seven) parameters (i.e., the model had a lower AICc), and this was the joint population model for all eight populations with LakeT$_{sum1}$ as a covariate. The estimated response parameters differed considerably by population (γ range: −0.012 to 0.435), being significantly different from zero at the $P = 0.05$ level for three Lake Nerka streams (Fenno, Hidden Lake, and Pick creeks), and not significantly different from zero for the remaining five streams. This is consistent with the results for individual populations models described above.

The Wood River system as a whole, where salmon spawner abundance and total returns were measured on a much coarser scale and integrated across dozens of

Table 2 ΔAICc values for individual population models and joint population models, showing the relative support for each model relative to the others considered for that population or group of populations

Model	Bear (A)	Hansen (A)	Happy (A)	Ice (A)	Fenno (N)	Hidden (N)	Lynx (N)	Pick (N)	Aleknagik (n = 4)	Nerka (n = 4)	All (n = 8)	Wood River
Intercept only	34.9	4.0	6.9	22.8	12.6	6.4	**0.5**	13.4	44.6	18.9	55.0	16.6
Ricker only	11.6	3.4	6.8	10.9	7.5	3.3	**0**	4.8	12.0	5.1	9.7	10.2
Ricker + …												
IceOut$_1$	13.9	4.5	9.4	13.4	8.9	4.7	2.6	6.9	14.3	6.7	11.7	11.3
IceOut$_2$	2.9	5.5	3.7	4.5	7.9	4.9	2.4	6.4	6.8	4.7	5.5	**0**
LakeT$_{sum1}$	14.2	5.9	9.1	13.4	3.3	0	**1.6**	0	13.6	0	9.0	12.6
LakeT$_{sum2}$	**0**	0	**0.5**	0	6.6	3.1	2.3	6.0	0	2.8	0	**1.4**
PribAirT$_{win2}$	14.1	5.8	9.3	13.3	9.1	5.8	2.4	6.8	13.8	6.7	11.3	12.8
SST$_{spr2}$	10.3	5.7	7.9	9.0	5.0	5.5	**0.9**	6.2	10.9	5.2	8.6	7.6
SST$_{sum2}$	3.1	3.0	0	4.1	0	4.3	2.0	5.1	**0.3**	2.9	**1.0**	**1.5**
SST$_{fall2}$	11.5	5.9	4.3	10.7	6.7	5.1	2.5	6.6	12.1	5.9	10.0	3.0
PribAirT$_{win3}$	13.3	5.9	9.4	13.0	10.0	4.2	2.6	7.4	12.9	7.2	11.2	9.9
SST$_{spr3}$	14.2	3.0	8.1	13.3	9.1	5.8	2.6	7.3	13.9	6.9	11.6	12.4
SST$_{sum3}$	13.1	4.7	9.4	13.5	9.6	5.8	2.1	6.5	11.5	6.6	10.4	12.7
SST$_{fall3}$	14.2	3.9	9.0	11.4	8.8	5.7	2.6	7.2	14.4	7.2	12.1	8.7
PDO$_1$	14.2	4.6	9.0	13.5	9.4	5.8	**1.5**	6.1	14.3	7.1	12.0	12.7
PDO$_2$	11.7	5.9	9.3	11.7	9.4	5.2	2.3	6.1	12.5	6.4	10.4	12.5
PDO$_3$	13.2	5.4	8.7	13.3	9.0	5.8	2.6	6.3	13.9	6.7	11.6	9.1

By definition, the most parsimonious model will have a ΔAICc of 0. In general, ΔAICc values lower than 2 (in bold) indicate strong support for that model relative to the other candidate models (Burnham & Anderson, 2002). Nursery lakes are indicated by A (Aleknagik) and N (Nerka). The numbers of populations included in joint population models are indicated in parentheses.

SST, sea surface temperature; PDO, Pacific Decadal Oscillation.

Table 3 The most parsimonious single-covariate model for each population and population group, along with the number of model parameters (k), total data points (n), standardized slope parameter for the climate variable (γ), and standard error for γ

Population unit	Lake	Best model	K	n	γ	SE	R^2 Ricker only	R^2 Best model
Bear	A	LakeT$_{sum2}$	5	41	0.32	0.08	0.42	0.59
Hansen	A	LakeT$_{sum2}$	5	42	0.37	0.15	0.09	0.20
Happy	A	SST$_{sum2}$	5	40	0.44	0.14	0.06	0.24
Ice	A	LakeT$_{sum2}$	5	40	0.52	0.13	0.34	0.54
Fenno	N	SST$_{sum2}$	5	41	0.36	0.10	0.11	0.35
Hidden	N	LakeT$_{sum1}$	5	42	0.39	0.15	0.10	0.26
Lynx	N	–	4	41	–	–	0.09	–
Pick	N	LakeT$_{sum1}$	5	41	0.24	0.09	0.25	0.39
Aleknagik (4)	A	LakeT$_{sum2}$	14	163	0.35	0.09	na*	na
Nerka (4)	N	LakeT$_{sum1}$	14	165	0.25	0.09	na	na
All Streams (8)	A, N	LakeT$_{sum2}$	26	328	0.29	0.08	na	na
Wood River	A, N†	IceOut$_2$	5	41	−0.23	0.06	0.10	0.35

*Analogous goodness-of-fit statistics for the multiple population models are not available because of the inclusion of a random effect for year.

†The Wood River system includes an additional three major sockeye nursery lakes upstream of Lake Nerka (Fig. 1).

Nursery lakes are indicated by A (Aleknagik) and N (Nerka). All models include Ricker stock-recruitment parameters (α, β) plus the climate variable indicated.
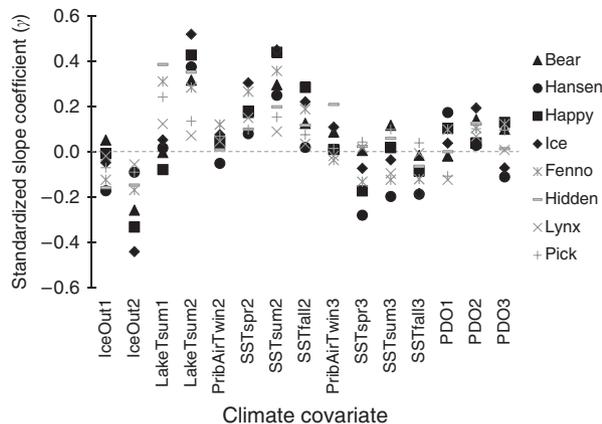
SST, sea surface temperature.

Fig. 2 Standardized slope coefficients for individual population models that include Ricker parameters plus the climate variable indicated on the *X*-axis. Coefficients for populations spawning in streams which drain to Lake Aleknagik are shown by solid black symbols, and for Lake Nerka by open gray symbols.

Fig. 3 Estimated random effects (b_t) for the joint population models given in Table 3, which show the shared patterns of variation in productivity not accounted for by the given climate covariate. Shown are estimates from the joint models given in Table 3 for Lake Aleknagik populations (black triangles), Lake Nerka populations (gray circles), and all populations (light gray squares).

individual populations, including those rearing in lakes Nerka and Aleknagik as well as three other major nursery lakes, was best modeled by second summer temperature metrics, including IceOut$_2$, LakeT$_{sum2}$, and SST$_{sum2}$, in decreasing order of support (Table 2). Models with first summer temperatures were among the least supported (ΔAICc > 11), and the estimated coefficient for LakeT$_{sum1}$ was not significantly different from zero.
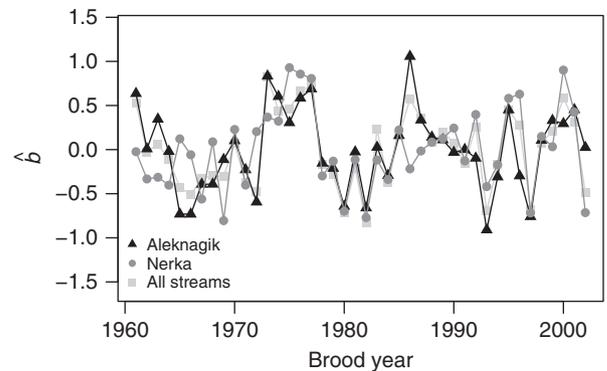
Results from models with single climate covariates indicated that a model with temperature effects in both the first and second summers should be considered. Therefore, models with both LakeT$_{sum1}$ and LakeT$_{sum2}$ were fit and compared with single covariate models at the aggregate lake and Wood River levels. For the joint Lake Aleknagik populations, this model was not an improvement over the model with only LakeT$_{sum2}$

(ΔAICc = 2.4), confirming that Lake Aleknagik populations do not appear to be sensitive to first summer lake temperatures. For the joint Lake Nerka populations, the more complex model received weak support over the model with only first summer lake temperatures (ΔAICc = 0.5), indicating that some additional variance is explained by the inclusion of second summer temperature effects. When considering all populations together, the best model (i.e. with the lowest AICc) remained the model with only second summer lake temperatures.

The inclusion of fall and winter climate variables was never strongly supported, suggesting that, after accounting for density dependence, sockeye salmon survival was determined largely by spring and summer conditions. In addition, an effect of the PDO was never well supported (Table 2), including for the Wood River system as a whole, indicating that salmon population dynamics at the stream and watershed scale are more closely related to local and regional climatic processes than ocean basin-scale climatic patterns. These models incorporated only linear climate responses and examination of plots comparing residuals from the Ricker-only models with climate covariates did not show evidence of nonlinear relationships.

Time series of estimated random effects (b_t) from the joint population models revealed patterns of variation in productivity which were shared among populations and not related to the modeled climate variables (Fig. 3). For each of the best supported joint-population models (Table 3), notable features of these time series were generally low levels of productivity through the 1960s, a sharp increase beginning with the 1973 brood and lasting 5 years, followed by lower levels of productivity until the mid-1980s. After the mid-1980s, the pattern of shared variation was highly variable from year to year. Estimated random effects for Lake Nerka streams varied markedly from Lake Aleknagik streams in some years (Fig. 3). The estimated random effects for the Lake Aleknagik model were moderately autocorrelated (lag-1 autocorrelation = 0.34), violating the assumption of independence for random effects, but this should not affect the relative ranking of models.

Magnitude of climate responses

To assess the magnitude of the climate effects, we modeled how a 2 °C increase in lake temperature would change the expected relationship between spawners and returns (Fig. 4). This model incorporated only the observed relationship between temperature, spawner density and productivity, and did not account for other temperature-dependent processes which could result in nonlinearities at higher temperatures. For populations which demonstrated a temperature response, the expected ratio of returns per spawner increased between 43% (Pick Creek) and 111% (Ice Creek) with a 2 °C increase in temperature. For each population, lake temperature was lagged to correspond to the life stage most sensitive to changes in lake temperature. Over the period of study, observed summer mean lake temperatures ranged from 6.6 to 12.1 °C (mean = 9.4 °C, SD = 1.4 °C).

Discussion

Scale and complexity in ecological systems

We found that the factors affecting the dynamics of individual salmon populations varied over relatively small geographic scales, even within the same river watershed. Populations < 40 km apart from one another varied in their sensitivity to conditions experienced during their first and second summers, while one population (Lynx Creek) showed no detectable response to any of the climate drivers considered. While many studies implicitly assume that climatic effects on populations are spatially invariant at subregional scales, we found that even within a small geographic area, these relationships may differ by population. This demonstrates that the move away from a 'homogeneity paradigm' in ecology towards consideration of spatial heterogeneity in populations, environments, and habitats can further ecological understanding (Wiens, 1997). For Wood River sockeye salmon, this was achieved by modeling climate responses at the population level.

The tradeoff associated with modeling populations independently is that true climate signals may be obscured by observation errors and local stochastic events, increasing the likelihood of detecting spurious relationships and of failing to detect true relationships. For instance, the failure to detect a climate effect on the Lynx Creek population may reflect either poor enumeration of spawner abundance, the dominating influence of local unmeasured variables, or a true lack of sensitivity to any of the drivers we considered. An alternate approach to modeling how populations respond to climate variability takes advantage of possible shared responses among populations in order to increase the likelihood of detecting climate effects (Myers & Mertz, 1998). When all eight Wood River stream populations were considered together, we found strong support for including temperature metrics during the second summer (year of smolt migration) relative to the other candidate models. However, the model with temperature during the first summer of lake residence
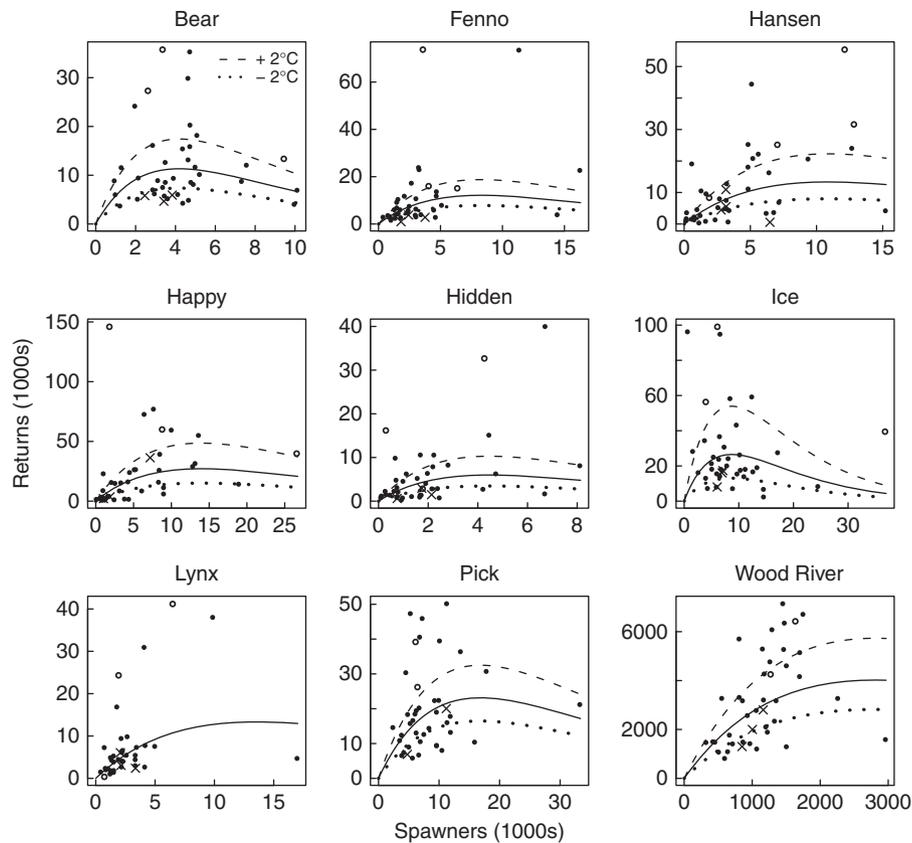
Fig. 4 Numbers of returning sockeye salmon by spawner abundance from brood years 1961 to 2002 for eight study streams in the Wood River system and for the Wood River as a whole. Curves represent the expected spawner/return relationship at average (solid line), 2 °C above average (dashed line), and 2 °C below average (dotted line) temperatures based on the fitted Ricker model with an environmental covariate [Eqn (1)]. Open circles and x's indicate returns associated with warm (2 °C above average) and cold (2 °C below average) temperatures, respectively. For comparison, the model fits shown use lake temperature as the environmental covariate, even if lake temperature was not the best individual predictor for that population unit. Lake temperature was lagged to correspond to the life stage which showed the most sensitivity, either the first summer (Fenno, Hidden, Pick) or second summer (Bear, Hansen, Happy, Ice, Wood River). Lynx Creek did not show evidence of a climate response.

did not even rank among the top three models, despite its strong support for some individual populations. At the level of the Wood River system as a whole, consisting of dozens of individual populations, first summer temperatures had no significant effect on productivity, whereas models with second summer temperature effects received strong support. Thus, had we only considered population responses at this higher level of aggregation, we would have failed to detect differences among populations that became clear at the level of nursery lake and were further demonstrated for individual populations. Therefore, the level at which we choose to model populations can alter our perception of how populations respond to climate variation (Allen & Hoekstra, 1992), demonstrating a tradeoff between seeking generality and allowing complexity in our understanding of how populations respond to climate changes.

In reality, the system is much more complicated than any of these models allow for, and the challenge is choosing a model with an appropriate amount of complexity (Levin, 1992). This is often a concern when considering how many parameters to include in a model. Overparameterized models fit the data well but have little predictive power (Burnham & Anderson, 2002). Underparameterized models may preclude the identification of important ecological relationships and complexity. A similar balance must be found when modeling how populations are affected by environmental/climate change, and the level of spatial complexity or population-specific response diversity allowed into the model should depend on the desired application. For a fishery manager tasked with forecasting total salmon returns to the Wood River system, population- or lake-specific models may be unnecessarily fine-grained to provide good forecasts. On the other hand,

a conservation group concerned with protecting freshwater habitat to support diverse salmon populations may indeed be very interested in differences among populations at the stream or lake level to inform conservation priorities and spending.

Temperature and sockeye salmon productivity

It was not surprising to find that warmer summers, in general, corresponded to improved productivity for sockeye salmon populations from this region of Alaska. This supports previous research which has found that warmer SSTs during the early marine life stage correspond with greater survival (Mueter *et al.*, 2002; Martinson *et al.*, 2009) and growth (Rogers & Ruggerone, 1993; Farley *et al.*, 2007), and that warmer lake temperatures lead to increased growth during freshwater life stages (Schindler *et al.*, 2005; Rich *et al.*, 2009), which can be related to subsequent survival in the marine environment (Koenings *et al.*, 1993). However, the difference in sensitivity by rearing lake was unexpected. The results indicated that Lake Nerka fish appeared more sensitive to lake temperature in the first year, whereas Aleknagik fish seemed more sensitive in the second year. While in both cases, warmer temperatures were associated with improved survival for these populations, the difference in timing suggests that the populations are affected through different mechanisms.

A number of hypotheses may explain how populations using different rearing lakes may differ in the timing of their sensitivity to climate conditions. One difference between sockeye salmon in Lake Nerka vs. Lake Aleknagik is the timing of migration to the ocean. Smolt migration follows the break-up of ice on the lakes, which generally occurs earlier in Lake Aleknagik than in Lake Nerka. This can result in differences in when smolts enter the temporally variable marine environment (Burgner, 1962, 1991). Smolt migration timing can significantly affect survival (Scheuerell *et al.*, 2009), and the temporal match or mismatch between smolt arrival and ocean conditions may lead to differential effects on survival for populations from these two lakes. Because Lake Aleknagik populations appeared to be more sensitive to second summer temperatures than Lake Nerka populations, the match or mismatch between the timing of smolt migration and ocean conditions may be more variable and climate-dependent for smolts from Lake Aleknagik. Later migrating smolts also have the opportunity for additional early summer growth in the freshwater environment (Burgner, 1962), which may buffer Lake Nerka smolts from variable conditions upon entering the marine environment.

A second hypothesis concerns the response to conditions during the first summer in the lake. Productivity of Lake Aleknagik populations appeared to be relatively insensitive to first summer temperatures, whereas Lake Nerka populations showed a strong response to first summer conditions, in general (Fig. 2). Temperatures can affect juvenile sockeye growth and survival in a number of ways. Warmer springs correspond to earlier timing of spring ice breakup, which results in a longer summer growing season for phytoplankton and zooplankton (the primary prey for juvenile sockeye) in the lake (Schindler *et al.*, 2005; Carter, 2010). Warmer waters (up to $\sim 15\,^{\circ}\mathrm{C}$) also increase the metabolic scope for growth given sufficient food densities (Brett, 1995). However, zooplankton densities may be limited by sockeye salmon predation if juvenile salmon densities are high, sometimes even negating the positive effects of temperature on growth (Schindler *et al.*, 2005). Thus, if the relative densities of juveniles differ between the lakes, different responses to increased temperatures could be expected (Burgner, 1962; Rich *et al.*, 2009; Reed *et al.*, 2010). In order for Lake Nerka populations to be more sensitive than Lake Aleknagik populations to thermal conditions in the lake, it is expected that overall juvenile densities have been lower; at high densities, the influence of climate would be masked by density effects (Stige *et al.*, 2010). In fact, based on estimated escapements by lake, juvenile densities have been 1.5–2 times higher in Lake Aleknagik than in Lake Nerka over the last 40 years (D. Schindler, unpublished results). Improved growth does not always correspond to higher survival, although within a year-class, larger individuals tend to have higher survival, in general (Burgner, 1991; Henderson & Cass, 1991; Koenings *et al.*, 1993).

Further study will be required to verify the mechanisms underlying these observed relationships. However, the important point here is that, even within close proximity, populations may be sensitive to different environmental drivers, likely due to features of their life history, local ecology, and the landscape through which climate effects are filtered. It is worth noting that these stream-spawning populations are relatively similar in terms of spawning habitat and life histories compared with the variability expressed in the Wood River system as a whole (Quinn *et al.*, 2001) and across Bristol Bay (Quinn *et al.*, 2009). High quality population data exist for the streams that are small, clear and accessible, and therefore easy to census. Populations spawning in main-stem rivers and on lake beaches are genetically and phenotypically differentiated from stream-spawning populations (Quinn *et al.*, 2001; Lin *et al.*, 2008; McGlauflin *et al.*, in press), and populations spawning in these differing habitats, as well as those rearing in lakes farther inland, would be expected to show an even greater diversity of responses to the climate drivers examined here (Hilborn *et al.*, 2003).

Measurement errors will obscure relationships between climate and salmon productivity, and are difficult to assess in this study. The method of reconstructing brood tables assumed equal vulnerability to the fishery of adults in a given age class, regardless of the population of origin. This is a reasonable assumption given that all the study populations spawned in small streams, showed very little differentiation in migration timing through the fishery (Doctor et al., 2010), and display small differences in size-at-age (Quinn et al., 2001). A detailed analysis of the length-specific vulnerability to the fishery of a subset of Wood River stream populations (including three of the ones used in the present study: Ice, Hansen and Bear creeks) demonstrated only occasional and small differences among streams in age-specific vulnerability (Kendall & Quinn, 2009). However, the brood table reconstructions certainly introduced error into the population data. Further, surveys of spawner abundance provide indices of abundance, but the proportion of salmon counted likely varies among years and among streams depending on the timing of the runs relative to the days the streams are surveyed. While these errors may reduce our ability to detect climatic influences, they should not generate a lake- or stream-specific bias. Finally, the scale at which we can understand how populations respond to climate variability was, in this case, constrained by the scale at which environmental conditions were measured, and this study would be improved by also considering the logistical and statistical tradeoffs of using environmental data at local vs. regional scales. For instance, the temperature metrics we include likely only partly capture the variation experienced by salmon in their specific environments. This concern may be particularly applicable to understanding the effects of marine conditions on survival and productivity of salmon populations. Here, only coarse metrics of ocean thermal conditions or general climate indices (i.e., PDO) were used as potential environmental drivers. More precise mapping of salmon migration patterns in the ocean relative to the spatial and temporal variation in environmental conditions they experience in this phase of their life (Farley et al., 2007) may greatly improve the ability of statistical models to detect the effects of marine conditions on salmon population productivity. However, at present, such data simply do not exist over the time period considered in this study, or at the scale of individual populations.

Conclusions

Projections of future climate impacts on ecosystems and populations are often said to be hindered by the uncertainties associated with downscaling of physical climate models. However, considerable uncertainties lie in the downscaling (and upscaling) of ecological relationships (Levin, 1992; Pettorelli et al., 2005). Climate/species relationships detected at large spatial scales may not hold for individual populations at finer scales, and vice versa. The 'correct' study scale will depend on the research or management objectives as well as data availability. While in this case the observed differences at fine scales may not change long-term population projections in response to global climate change (because summer warming boosts productivity, regardless of which life-stage is most sensitive; Fig. 4), these fine scale differences among stream populations in the timing of sensitivity to warming may drive asynchronous population dynamics on an interannual time scale (Rogers & Schindler, 2008). Diverse responses among populations can stabilize population dynamics in aggregate stocks (Secor et al., 2009; Schindler et al., 2010), suggesting that in this study system, it may be important to manage in ways which maintain population richness even when management or conservation objectives are set at a broader spatial scale.

Acknowledgements

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