

# Spatial variation buffers temporal fluctuations in early juvenile survival for an endangered Pacific salmon

James T. Thorson<sup>1\*</sup>, Mark D. Scheuerell<sup>1</sup>, Eric R. Buhle<sup>1</sup> and Timothy Copeland<sup>2</sup>

<sup>1</sup>National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Blvd. East, Seattle, WA 98112, USA; and <sup>2</sup>Idaho Department of Fish and Game 1414 East Locust Lane, Nampa, ID 83686, USA

## Summary

1. Spatial, phenotypic and genetic diversity at relatively small scales can buffer species against large-scale processes such as climate change that tend to synchronize populations and increase temporal variability in overall abundance or production. This portfolio effect generally results in improved biological and economic outcomes for managed species. Previous evidence for the portfolio effect in salmonids has arisen from examinations of time series of adult abundance, but we lack evidence of spatial buffering of temporal variability in demographic rates such as survival of juveniles during their first year of life.

2. We therefore use density-dependent population models with multiple random effects to represent synchronous (similar among populations) and asynchronous (different among populations) temporal variability as well as spatial variability in survival. These are fitted to 25 years of survey data for breeding adults and surviving juveniles from 15 demographically distinct populations of Chinook salmon (*Oncorhynchus tshawytscha*) within a single metapopulation in the Snake River in Idaho, USA.

3. Model selection identifies the most support for the model that included both synchronous and asynchronous temporal variability, in addition to spatial variability. Asynchronous variability ( $\log\text{-SD} = 0.55$ ) is approximately equal in magnitude to synchronous temporal variability ( $\log\text{-SD} = 0.67$ ), but much lower than spatial variability ( $\log\text{-SD} = 1.11$ ). We also show that the pairwise correlation coefficient, a common measure of population synchrony, is approximated by the estimated ratio of shared and total variance, where both approaches yield a synchrony estimate of 0.59. We therefore find evidence for spatial buffering of temporal variability in early juvenile survival, although between-population variability that persists over time is also large.

4. We conclude that spatial variation decreases interannual changes in overall juvenile production, which suggests that conservation and restoration of spatial diversity will improve population persistence for this metapopulation. However, the exact magnitude of spatial buffering depends upon demographic parameters such as adult survival that may vary among populations and is proposed as an area of future research using hierarchical life cycle models. We recommend that future sampling of this metapopulation employ a repeated-measure sampling design to improve estimation of early juvenile carrying capacity.

**Key-words:** Chinook salmon, hierarchical model, juvenile survival, portfolio effect, random effects

## Introduction

Ecologists have long hypothesized that spatial, behavioural and genetic diversity can buffer against variability in population abundance (MacArthur 1955; May 1986). In particu-

lar, temporal fluctuations that are not synchronized among local populations will be 'averaged out' when aggregating measures of abundance or productivity to the metapopulation level, whereas synchronous temporal fluctuations will persist in the aggregate. This 'portfolio effect' (Doak *et al.* 1998) within a single species is analogous to the stabilizing effects of species diversity in communities (Elton 1958;

\*Correspondence author. E-mail: James.Thorson@noaa.gov

Tilman 1999) and can have positive impacts on regional persistence and the economic outcomes arising from species harvest. Conversely, spatially structured population models show that synchronous local fluctuations can increase overall variability and extinction risk at the metapopulation scale (Heino *et al.* 1997; Earn 2000; Engen, Lande & Sæther 2002). The degree of correlation in local population dynamics is thus one of the key determinants of the strength of the portfolio effect (Tilman, Lehman & Bristow 1998; Thibaut & Connolly 2013).

Spatial and temporal variability in demographic rates such as survival and fecundity has been much discussed in the ecological literature (Clark 2003) and has also been demonstrated using high-quality data in several high-profile cases (e.g. Coulson *et al.* 2001; Barrowman *et al.* 2003; Clark, LaDeau & Ibanez 2004). Juvenile survival is a particularly important demographic rate for many populations, as it contributes to growth rates for re-introduced species, the rate of spread for invasive species and the observed variability in harvested species (Nichols *et al.* 1992; Walters & Kitchell 2001; Govindarajulu, Altwegg & Anholt 2005). Therefore, the degree of spatial synchrony and the potential for portfolio effects in demographic rates such as juvenile survival have important implications for the conservation and management of many aquatic and terrestrial species. Both theoretical (Heino *et al.* 1997; Doak *et al.* 1998; Tilman, Lehman & Bristow 1998; Earn 2000) and empirical (Hanski & Woiwod 1993; Myers, Mertz & Bridson 1997; Thibaut, Connolly & Sweatman 2012; Cavanaugh *et al.* 2013) studies have commonly measured synchrony as the temporal correlation between pairs of populations in either abundance (or density) or population growth rate (i.e. interannual change in abundance). However, juvenile survival is highly variable and difficult to measure for many species (Anders *et al.* 1997; Gaillard, Festa-Bianchet & Yoccoz 1998), and this perhaps contributes to the dearth of information for most species regarding the synchrony or asynchrony of temporal variation in juvenile survival.

Anadromous salmonid fishes have provided some of the clearest illustrations of the within-species portfolio effect (Rogers & Schindler 2008; Greene *et al.* 2010; Moore *et al.* 2010; Schindler *et al.* 2010; Carlson & Satterthwaite 2011), but previous research has focused on time series of adult abundance or productivity (i.e. population growth rate per generation) rather than stage-specific demographic rates. Nevertheless, variability in juvenile survival is more logistically feasible to study in anadromous fishes such as Pacific salmon (*Oncorhynchus* spp.) than in many other taxa. First, salmon have a per capita reproductive output, measured by eggs per female that is approximately constant among years (although changes in age-structure of the spawning population will cause some variability in fecundity). Thus, changes in the number of juveniles per adult (whether among populations or years) can be attributed largely to changing juvenile survival. Secondly, a nearly complete census of

spawning adults can be achieved during migration from saltwater to freshwater, making these species an excellent candidate for estimating the relative magnitude of spatial, synchronous and asynchronous temporal variability in demographic rates. Finally, there is little risk of misidentifying juvenile ages, which tends to complicate studies of juvenile survival in marine fishes (Punt *et al.* 2008).

Over the past century, however, a wide variety of human drivers (e.g. construction of dams, overharvesting) has interacted with natural forces (e.g. climate variability) to cause massive population declines in Pacific salmon populations, such that many stocks are now listed as threatened or endangered under the U.S. Endangered Species Act (Good, Waples & Adams 2005). Moreover, for Chinook salmon (*O. tshawytscha*) populations in the Snake River basin of Idaho, USA, previous analyses have shown that synchrony among populations in reproductive adult abundance (Isaak *et al.* 2003) has increased from the 1960s to the present, potentially increasing extinction risk by reducing the variance-dampening portfolio effect. Despite very low numbers, density-dependent survival has been observed in Chinook salmon (*O. tshawytscha*) populations within the freshwater portion of their life cycle (Achord, Levin & Zabel 2003; Walters, Copeland & Venditti 2013). Theory suggests that local density dependence may weaken the synchrony among populations driven by either dispersal or correlated environmental forcing (i.e. the 'Moran effect'), particularly if the strength of density dependence varies spatially (Liebhold, Koenig & Bjørnstad 2004).

We are therefore interested in whether and to what degree spatial variation can buffer populations at low abundance against years of poor juvenile productivity (i.e. fecundity and juvenile survival). Spatial variability will buffer populations if temporal fluctuations are not synchronized among populations, but will have little benefit if temporal fluctuations are synchronous. Thus, we estimate the relative magnitude of spatial, synchronous and asynchronous temporal variability in juvenile productivity using counts of breeding Chinook salmon and their offspring over 25 years from 15 populations in central Idaho, USA. We additionally explore whether there is evidence for density-dependent productivity in these heavily depleted populations, and, if so, whether density dependence varies spatially or temporally.

## Materials and methods

### DATA

Chinook salmon in our study are 'stream-type', that is, juveniles usually spend one full year in freshwater before migrating to sea. Adults breed in August and September, and eggs are deposited in a nest ('redd') dug into the streambed where they incubate over winter before juveniles hatch and emerge the following spring. During the summer, stream-dwelling juveniles ('parr') can then be

observed via snorkelling. Our data consist of 2651 snorkel surveys from 1984 to 2008 (conducted primarily in June–August) in the Salmon River basin of central Idaho (Copeland & Meyer 2011). This study area encompasses portions of a distinct population complex, the Snake River spring–summer Evolutionarily Significant Unit (ESU; Waples 1995). This ESU comprises multiple populations, which have little demographic connectivity via migration (that is, little ‘straying’ of returning adults) and are hence largely demographically decoupled. Our data come from 15 such populations (Fig. 1). Snorkel survey data have uneven sampling intensities among populations, but approximately even sampling intensities among years within a given population starting in the early 1990s.

Each observation includes counts of parr as well as survey area swept, calculated as the product of wetted channel width and transect length. More details regarding sampling methodology can be obtained from Copeland & Meyer (2011). We obtained spawner abundance for each population and year as estimated using redd counts and correcting for redds per spawner and other spatially varying factors (Good, Waples & Adams 2005). Spawner abundance was divided by suitable spawning area in hectares (accounting for drainage area, habitat type and other variables) to calculate spawners per hectare, which was used to predict parr counts.

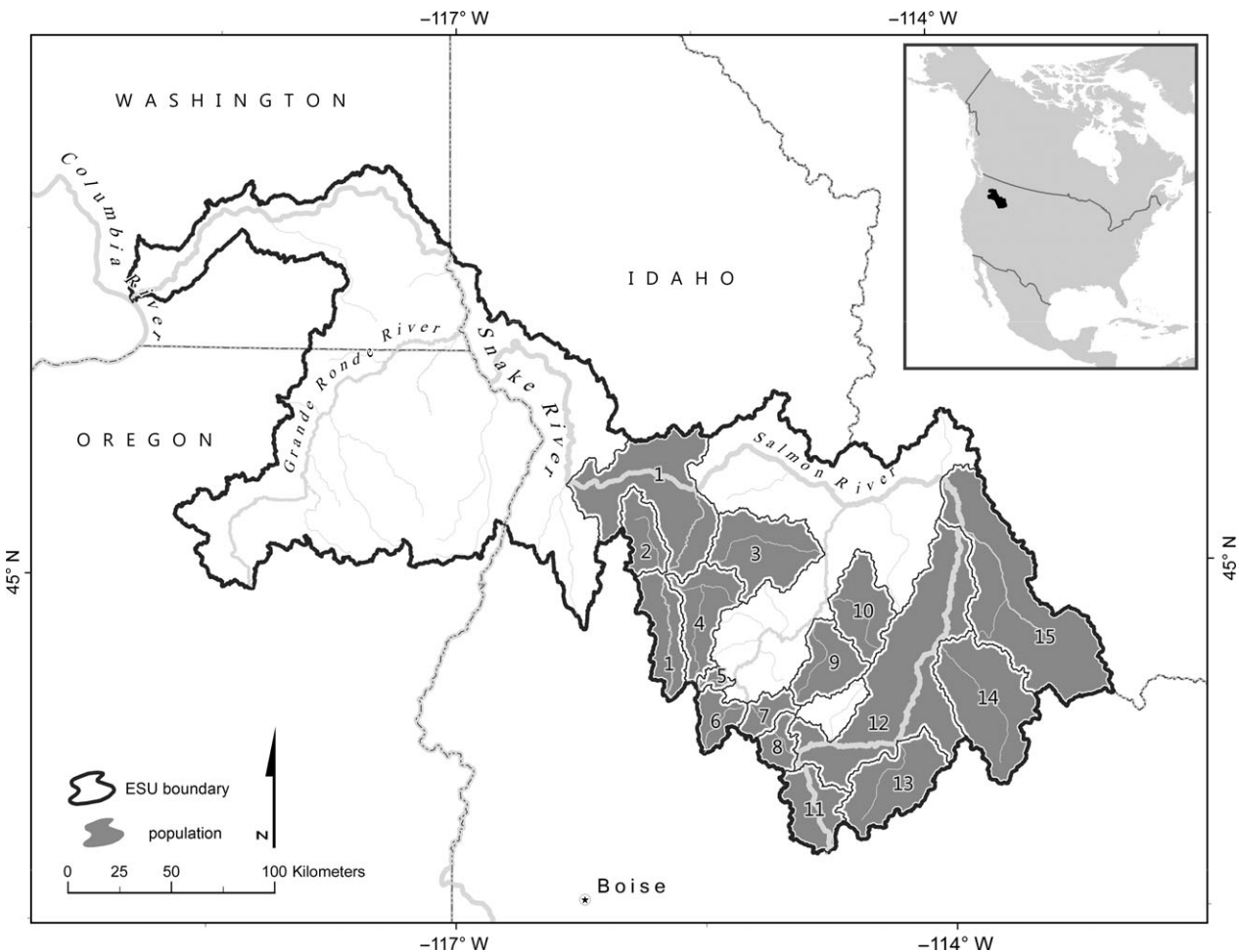
MODEL

We hypothesize that the number of age-0 Chinook parr observed on each snorkel survey sampling occasion will be a function of survey area swept and adult spawners. Specifically, we considered two discrete-time population dynamics models that have been used for many species, including salmonids (e.g. Turchin 2003). The Beverton–Holt model gives the expected parr count as:

$$\hat{r}_{i,y,p} = A_{i,y,p} \cdot \frac{s_{y,p} \cdot \alpha_{y,p}}{1 + (\alpha_{y,p} - 1) \cdot \frac{s_{y,p}}{\beta_{y,p}}} \tag{eqn 1}$$

where  $\hat{r}_{i,y,p}$  is the expected number of parr for sample  $i$  of year  $y$  and population  $p$ ,  $A_{i,y,p}$  is area swept (in hectares),  $s_{y,p}$  is the observed spawners per hectare for the year  $y$  and population  $p$ ,  $\alpha_{y,p}$  is the maximum per capita recruitment rate,  $\beta_{y,p}$  measures the strength of density dependence (in units recruits per hectare) and maximum expected recruitment per hectare is  $\alpha_{y,p}/(\alpha_{y,p} - 1) \cdot \beta_{y,p}$ . Alternatively, the expected count can be specified using the Ricker model:

$$\hat{r}_{i,y,p} = A_{i,y,p} \cdot s_{y,p} \cdot \alpha_{y,p} \cdot \exp\left[-\frac{s_{y,p}}{\beta_{y,p}}\right] \tag{eqn 2}$$



**Fig. 1.** Map with ESU (heavy black line) and each population outlined (1: South Fork Salmon R. Mainstem; 2: Secesh R.; 3: Big Cr.; 4: South Fork Salmon R. – East Fork; 5: Sulphur Cr.; 6: Bear Valley Cr.; 7: Marsh Cr.; 8: Valley Cr.; 9: Loon Cr.; 10: Camas Cr.; 11: Salmon R. – Upper Mainstem; 12: Salmon R. – Lower Mainstem; 13: Salmon R. – East Fork; 14: Pahsimeroi R.; 15: Lemhi R.).

where  $\alpha_{y,p}$  is again the maximum per capita recruitment rate for year  $y$  and population  $p$ ,  $\beta_{y,p}$  is the spawning density that maximizes recruitment (in units of spawners per hectare) and maximum expected recruitment per hectare is  $\alpha_{y,p}\beta_{y,p}/e$ .

Productivity parameters  $\alpha_{y,p}$  and  $\beta_{y,p}$  in (1) and (2) are calculated from parameters representing their average value for all populations and years, as well as a multiplicative offset representing the specific effect of a given population, year and the interaction of population and year:

$$\alpha_{y,p} = \exp[\alpha + a_{\text{year},y} + a_{\text{pop},p} + a_{\text{year} \times \text{pop},y,p}] \quad \text{eqn 3}$$

$$\beta_{y,p} = \exp[\beta + b_{\text{year},y} + b_{\text{pop},p} + b_{\text{year} \times \text{pop},y,p}] \quad \text{eqn 4}$$

where  $\alpha$  and  $\beta$  are intercepts for  $\alpha_{y,p}$  and  $\beta_{y,p}$ ,  $a_{\text{year}}$ ,  $a_{\text{pop}}$  and  $a_{\text{year} \times \text{pop}}$  are random effects for  $\alpha$  accounting for the effect of year, population and their interaction, respectively, and  $b_{\text{year}}$ ,  $b_{\text{pop}}$  and  $b_{\text{year} \times \text{pop}}$  are random effects for  $\beta$  accounting for the effect of year, population and their interaction, respectively (lower-case Roman characters  $a$  and  $b$  are used for random effects). All random effects were normally distributed, where  $\sigma_{a,\text{pop}}$ ,  $\sigma_{a,\text{year}}$  and  $\sigma_{a,\text{year} \times \text{pop}}$  are the standard deviation for  $a_{\text{year}}$ ,  $a_{\text{pop}}$  and  $a_{\text{year} \times \text{pop}}$ , respectively, and  $\sigma_{b,\text{pop}}$ ,  $\sigma_{b,\text{year}}$  and  $\sigma_{b,\text{year} \times \text{pop}}$  are the standard deviation for  $b_{\text{year}}$ ,  $b_{\text{pop}}$  and  $b_{\text{year} \times \text{pop}}$ , respectively. Random effects are also bias corrected (mean equals  $-\sigma^2/2$ , where  $\sigma^2$  is the random effect variance) such that  $\alpha_{y,p}$  and  $\beta_{y,p}$  (and all derived parameters) have a mean equal to  $\exp(\alpha)$  and  $\exp(\beta)$ , respectively (i.e. the intercepts  $\alpha$  and  $\beta$  can be interpreted as the log-mean across all years and populations). The random effects are specified in log-space such that  $\alpha_{y,p}$  and  $\beta_{y,p}$  remain positive for all years and populations.

The observation process for the number of recruits  $R$  given its expected value  $\hat{r}_{i,y,p}$  is approximated using a zero-inflated negative binomial likelihood:

$$\Pr[R = r_{i,y,p} = \rho \cdot I(R = 0) + (1 - \rho) \cdot \frac{\Gamma(R + n)}{R! \Gamma(n)} p^n (1 - p)^R] \quad \text{eqn 5}$$

$$n = \frac{\hat{r}_{i,y,p}}{\omega - 1 + \theta \cdot \hat{r}_{i,y,p}} \quad \text{eqn 6}$$

$$p = \frac{1}{\omega + \theta \cdot \hat{r}_{i,y,p}} \quad \text{eqn 7}$$

where  $I(R = 0)$  is an indicator variable that equals one if  $R$  is equal to zero and zero otherwise,  $\rho$  is the zero-inflation parameter (i.e. the proportion of samples that occur in unsuitable habitat and hence have an expected count of zero), and  $\omega$  and  $\theta$  are variance-inflation parameters such that the variance for the non-zero-inflated component is  $\omega \cdot \hat{r}_{i,y,p} + \theta^2 \cdot \hat{r}_{i,y,p}^2$  (Lindén & Mäntyniemi 2011). This zero-inflated negative binomial distribution implies that some sampled locations have an expected count of zero (in particular for years with low spawning numbers), and that heterogeneous habitat among sampling locations causes variability greater than expected for evenly and independently distributed individuals.

To ease computation given several random effects, we use a Bayesian statistical paradigm. The posterior distribution of model parameters is proportional to the probability of observed parr

counts, random effects and the prior probability of parameters. Standard deviation parameters were given independent and uniform prior distributions (which we selected such that the bounds were never approached), as were the variance-inflation and zero-inflation parameters. Samples from the posterior distribution were obtained using Markov chain Monte Carlo (MCMC) sampling, as implemented with JAGS (Plummer 2003), called from the R statistical platform (R Development Core Team 2011) using the package ‘R2jags’ (Su & Yajima 2012) and parallelized using the package ‘snowfall’ (Knaus 2010). We specifically used five chains, each with a burn-in of 100 000 samples followed by 100 000 monitored samples, and this resulted in 5000 retained samples per model given a thinning rate of 100. Convergence was checked using trace plots and the Gelman–Rubin  $R$  statistic (Gelman & Rubin 1992), and we confirmed that the highest  $R$  statistic for each model was lower than 1.01 (and generally lower than 1.001).

We fit this model with multiple configurations, representing a full cross of the following model options:

- 1 The stock-recruit function was specified using either the Ricker or Beverton–Holt model;
- 2 Density dependence was either excluded ( $\beta \rightarrow \infty$ ,  $b_{\text{pop}} = b_{\text{year}} = 0$ ), constant among years and populations (estimate  $\beta$ ;  $b_{\text{pop}} = b_{\text{year}} = 0$ ), variable among years (estimate  $\beta$ ,  $b_{\text{year}}$ , and  $\sigma_{b,\text{year}}$ ;  $b_{\text{pop}} = 0$ ), or variable among populations (estimate  $\beta$ ,  $b_{\text{pop}}$  and  $\sigma_{b,\text{pop}}$ ;  $b_{\text{year}} = 0$ );
- 3 The Population  $\times$  Year interaction was either absent ( $a_{\text{year} \times \text{pop}} = b_{\text{year} \times \text{pop}} = 0$ ) or only estimated for the density-independent parameter (estimate  $a_{\text{year} \times \text{pop}}$  and  $\sigma_{a,\text{year} \times \text{pop}}$ ;  $b_{\text{year} \times \text{pop}} = 0$ ).

However, the Ricker and Beverton–Holt models are indistinguishable in the absence of density dependence, such that this  $2 \times 4 \times 2$  cross resulted in fourteen configurations total. In all models, density-independent productivity was parameterized to include variability among populations ( $a_{\text{pop}}$  and  $\sigma_{a,\text{pop}}$ ) as well as synchronous temporal variability ( $a_{\text{year}}$  and  $\sigma_{a,\text{year}}$ ), because we expect *a priori* that productivity will vary among populations and years. Standard deviation parameters can be interpreted as the magnitude of the corresponding effect, that is,  $\sigma_{a,\text{year}}$  is the standard deviation of synchronous temporal variability ( $a_{\text{year}}$ ) while  $\sigma_{a,\text{year} \times \text{pop}}$  is the magnitude of asynchronous temporal variability ( $a_{\text{year} \times \text{pop}}$ , Gelman 2005). This set of models was selected to span a biologically plausible range while also being estimable without specifying informative priors for any random effect variance parameter. We selected among models using the Deviance Information Criterion (DIC, Spiegelhalter *et al.* 2002). Selection of the asynchronous temporal variability parameter  $a_{\text{year} \times \text{pop}}$  is interpreted as evidence that the data exhibit both synchronous and asynchronous variability (Burnham & Anderson 2002). For illustration purposes, we include the JAGS code for the DIC-selected model as Appendix S1.

Various metrics have been used to quantify synchrony in population variables of interest (Liebhold, Koenig & Bjørnstad 2004). For comparison with existing literature, we report estimates of the most common metric, the pairwise Pearson’s product-moment correlation coefficient averaged across pairs of populations. This average pairwise correlation can be approximated from our specification of the random effects distribution in intrinsic productivity for all models that include both synchronous ( $\sigma_{a,\text{year}}$ ) and asynchronous ( $\sigma_{a,\text{year} \times \text{pop}}$ ) temporal variability. By

assumption of independence between these two random effects, the total temporal variance for any given population is  $\sigma_{a,\text{year}}^2 + \sigma_{a,\text{year} \times \text{pop}}^2$ , while the covariance between any pair of populations is  $\sigma_{a,\text{year}}^2$ , and their expected correlation is thus  $\sigma_{a,\text{year}}^2 / (\sigma_{a,\text{year}}^2 + \sigma_{a,\text{year} \times \text{pop}}^2)$ , or simply the proportion of the total temporal variance that is shared between populations. Note that we cannot calculate a corresponding synchrony metric for the density dependence parameter because none of our models include a shared temporal random effect on  $\beta$ .

We report the estimated maximum per capita recruitment rate per hectare and the maximum parr per hectare. We report these derived parameters after including lognormal bias-correction for random effect variances, and thus, reported parameters represent the value for the average year, population and stream. However, we present estimates using the posterior median for all estimated and derived parameters. This is carried out to prevent the estimation errors in random effect variance from having excessive influence over derived parameter estimates, which would in turn imply a high sensitivity to the specification of prior probabilities for these variance parameters.

## Results

### MAXIMUM PRODUCTIVITY

We find support for a Beverton–Holt model with spatial and temporal variability in productivity (i.e. maximum parr per spawner), where temporal variability includes both synchronous and asynchronous components (Table 1). Model selection identifies very strong support for a model that includes asynchronous temporal variability (i.e. a Population  $\times$  Year interaction;  $\Delta\text{DIC} \geq 67.6$ ), and the estimated magnitude of asynchronous variability ( $\sigma_{a,\text{year} \times \text{pop}} = 0.55$ ) is comparable to synchronous temporal variability ( $\sigma_{a,\text{year}} = 0.67$ ). The resulting posterior distribution for the pairwise correlation synchrony index (Fig. 2) has a median of 0.587, which is close to the 0.594 calculated from the estimated variance parameters  $\sigma_{a,\text{year}}^2 / (\sigma_{a,\text{year}}^2 + \sigma_{a,\text{year} \times \text{pop}}^2)$ , and the range of both pairwise correlation and variance-ratio estimates of synchrony is also similar (Fig. 2, Appendix S2). The resulting model estimates a maximum parr per spawner of approximately 1350 for the average population and year (68% credible interval, corresponding approximately to  $\pm 1$  standard deviation: 850–2500) at low spawning density.

The estimated magnitude of spatial variability in productivity ( $\sigma_{a,\text{pop}} = 1.11$ ) is greater than either the synchronous or asynchronous temporal component. This can be seen in the relatively low variability in the spawner-recruit curve among years for a given population (Fig. 3) compared with the relatively higher variability among populations for a given year (Fig. 4). Inspection of the production curve by population and year shows that the Pahsimeroi population always has the highest maximum parr per spawner (Fig. 3: red line), but the relative productivity of other populations varies among years (Fig. 3: other lines). The production curve for an average population in a given year (Fig. 3: dashed black line) is

also considerably less variable than the production curve for each particular population. Hence, the relative contribution of different populations to overall parr production varies among years, and retaining multiple viable populations helps to buffer against random temporal variability in early juvenile survival within the Salmon River basin as a whole.

### DENSITY DEPENDENCE

Model selection indicates strong evidence of density dependence in juvenile survival ( $\Delta\text{DIC} = 10.4$ ). Variation in density dependence among populations or years is also supported by these data, where variation among populations is favoured over variation among years ( $\Delta\text{DIC} = 7.3$ ). Finally, the Beverton–Holt model is supported over the Ricker model ( $\Delta\text{DIC} = 19.2$ ), and hence, we do not find support for overcompensation (i.e. a decline in total production at high spawner densities). The resulting model estimates a maximum number of recruits per hectare of approximately 5200 for the average population and year (68% credible interval: 2780–14 360).

## Discussion

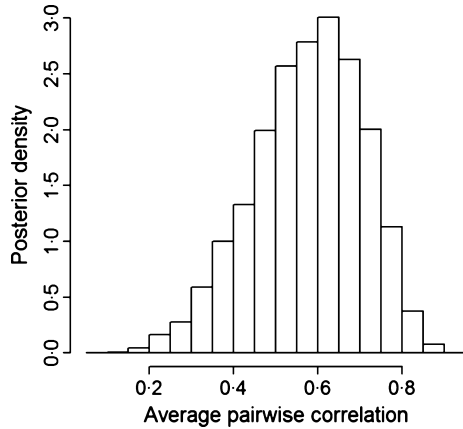
Temporal variability in population variables (e.g. abundance) or demographic parameters (e.g. early juvenile survival) is likely to occur in many terrestrial, marine and freshwater populations (Bjørnstad, Ims & Lambin 1999; Clark, LaDeau & Ibanez 2004, p. 200; Liebhold, Koenig & Bjørnstad 2004; Saether *et al.* 2008), and this variability will buffer aggregate productivity as long as it is not synchronized among local populations (Doak *et al.* 1998; Tilman, Lehman & Bristow 1998; Thibaut & Connolly 2013). We have shown that different populations of Chinook salmon in the Salmon River respond asynchronously to temporal variability, and that asynchronous variability among populations and years has a similar magnitude to synchronous variability. We therefore conclude that the diversity of population responses to temporal fluctuations in this salmon ESU helps to buffer a substantial portion of overall interannual variability in productivity.

Investigation of synchrony within and among species has a rich history in ecology (reviewed by Bjørnstad, Ims & Lambin 1999; Koenig 1999; Liebhold, Koenig & Bjørnstad 2004). Investigations of population synchrony have often focused on the spatial scale of synchrony in an effort to distinguish among potential hypotheses for population synchrony, such as the Moran effect, dispersal and coupling via interspecific interactions such as predation. Among-population synchrony in abundance or population growth rates will presumably arise from correlations in underlying demographic rates such as age-specific survival and fecundity. Studies in fishes and birds have reported levels of synchrony ranging from weak to strong in stage-specific survival (Grenouillet *et al.* 2001;

**Table 1.** Model selection and parameter estimate results for each of 14 models with different density dependence (absent, constant for all populations and years; different by year; and different by population), either with or without variation in maximum juvenile survival for all Population  $\times$  Year combinations, and either the Ricker or Beverton–Holt (B-H) model for juvenile survival

Model structure			Random effect variability					Derived productivity parameters							
Density dependence	Pop $\times$ year	Model	$\Delta$ DIC	Synchrony	$\sigma_{a,y}$	$\sigma_{a,pop}$	$\sigma_{a,y} \times \text{pop}$	$\sigma_{b,y}$	$\sigma_{b,pop}$	Maximum RPS		Maximum RPH			
										Median	Lower	Upper	Median	Lower	Upper
None	No	NA	139.8	–	0.502	1.117	–	–	–	674	466	1121	–	–	–
None	Yes	NA	18.2	0.243	0.373	1.090	0.661	–	–	720	502	1182	–	–	–
Constant	No	Ricker	113.4	–	0.539	0.934	–	–	–	756	561	1117	3251	2318	5054
Constant	No	B-H	122.5	–	0.670	1.128	–	–	–	1058	698	1860	4218	3481	5307
Constant	Yes	Ricker	12.0	0.293	0.405	0.990	0.633	–	–	784	559	1185	5658	3292	15896
Constant	Yes	B-H	11.9	0.429	0.542	1.159	0.627	–	–	1182	751	2121	3268	2461	4931
By year	No	Ricker	93.7	–	0.634	0.85	–	0.997	–	960	702	1367	3801	2298	7291
By year	No	B-H	68.2	–	0.956	1.591	–	1.142	–	8051	3275	37670	2151	1504	3447
By year	Yes	Ricker	15.5	0.280	0.39	1.000	0.631	0.888	–	778	554	1177	14348	4510	628673
By year	Yes	B-H	19.4	0.439	0.521	1.255	0.589	0.924	–	1771	1002	4217	2909	1834	5865
By pop.	No	Ricker	71.4	–	0.547	0.931	–	–	0.998	882	647	1306	4788	2647	12302
By pop.	No	B-H	80.7	–	0.916	1.062	–	–	0.852	1748	1059	3258	3487	2547	5631
By pop.	Yes	Ricker	15.6	0.339	0.411	0.997	0.575	–	1.224	815	586	1247	14592	4823	199752
<b>By pop.</b>	<b>Yes</b>	<b>B-H</b>	<b>0</b>	<b>0.594</b>	<b>0.663</b>	<b>1.111</b>	<b>0.550</b>	–	–	<b>1353</b>	<b>866</b>	<b>2562</b>	<b>5204</b>	<b>2867</b>	<b>18771</b>

For each model, we list  $\Delta$  DIC (the difference in the Deviance Information Criterion between models, where the selected model has  $\Delta$  DIC = 0), the analytic estimate of synchrony, that is, the ratio of shared to total variance ( $\sigma_{a,y}^2 / (\sigma_{a,y}^2 + \sigma_{a,y} \times \text{pop}^2)$ ), the standard deviation of random effects ( $a$ : maximum productivity;  $b$ : density-dependent productivity parameter) by year, population and the Population  $\times$  Year interaction, and derived productivity parameters (RPS: recruits per spawner; RPH: recruits per hectare) with the median and a lower and upper range representing approximately  $\pm 1$  standard deviation (i.e. the 15.9 and 84.1 percentiles of the posterior distribution), where models with  $\Delta$  DIC < 10 are shown in bold (the range for synchrony and standard deviation of random effects is shown in Appendix B).



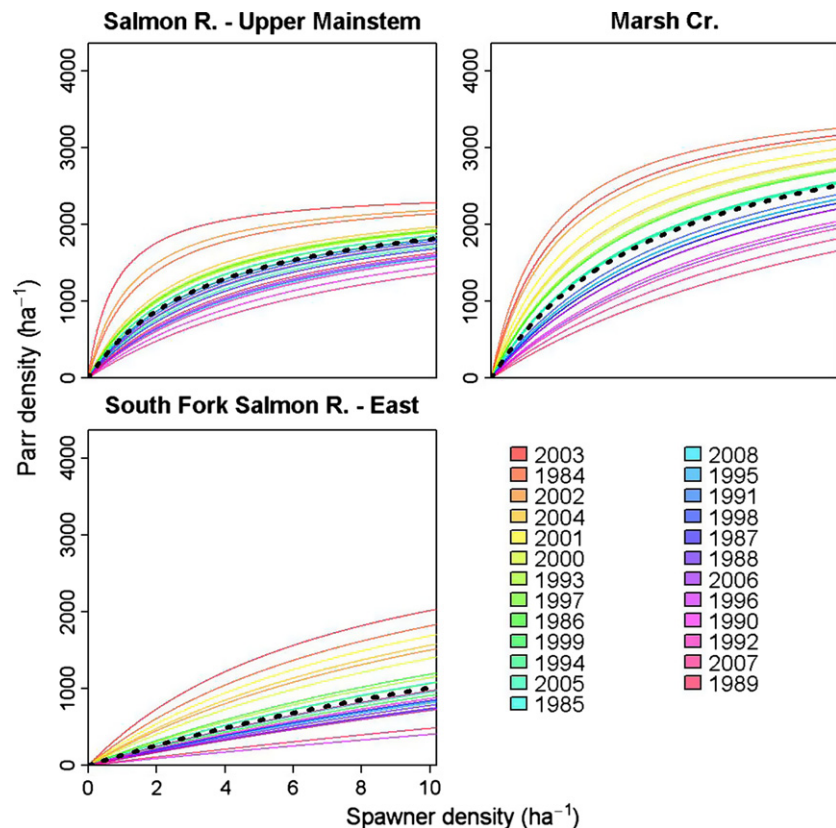
**Fig. 2.** Posterior distribution for synchrony in juvenile productivity, calculated using the pairwise Pearson's product-moment correlation coefficient averaged across pairs of populations (Liebhold, Koenig & Bjørnstad 2004).

Ringsby *et al.* 2002; Crozier & Zabel 2006; Tavecchia *et al.* 2008), fecundity (Tavecchia *et al.* 2008), sex ratio (Koizumi *et al.* 2008) and growth. However, there is little general theory linking synchrony in vital rates to synchrony in abundance at a population or metapopulation level.

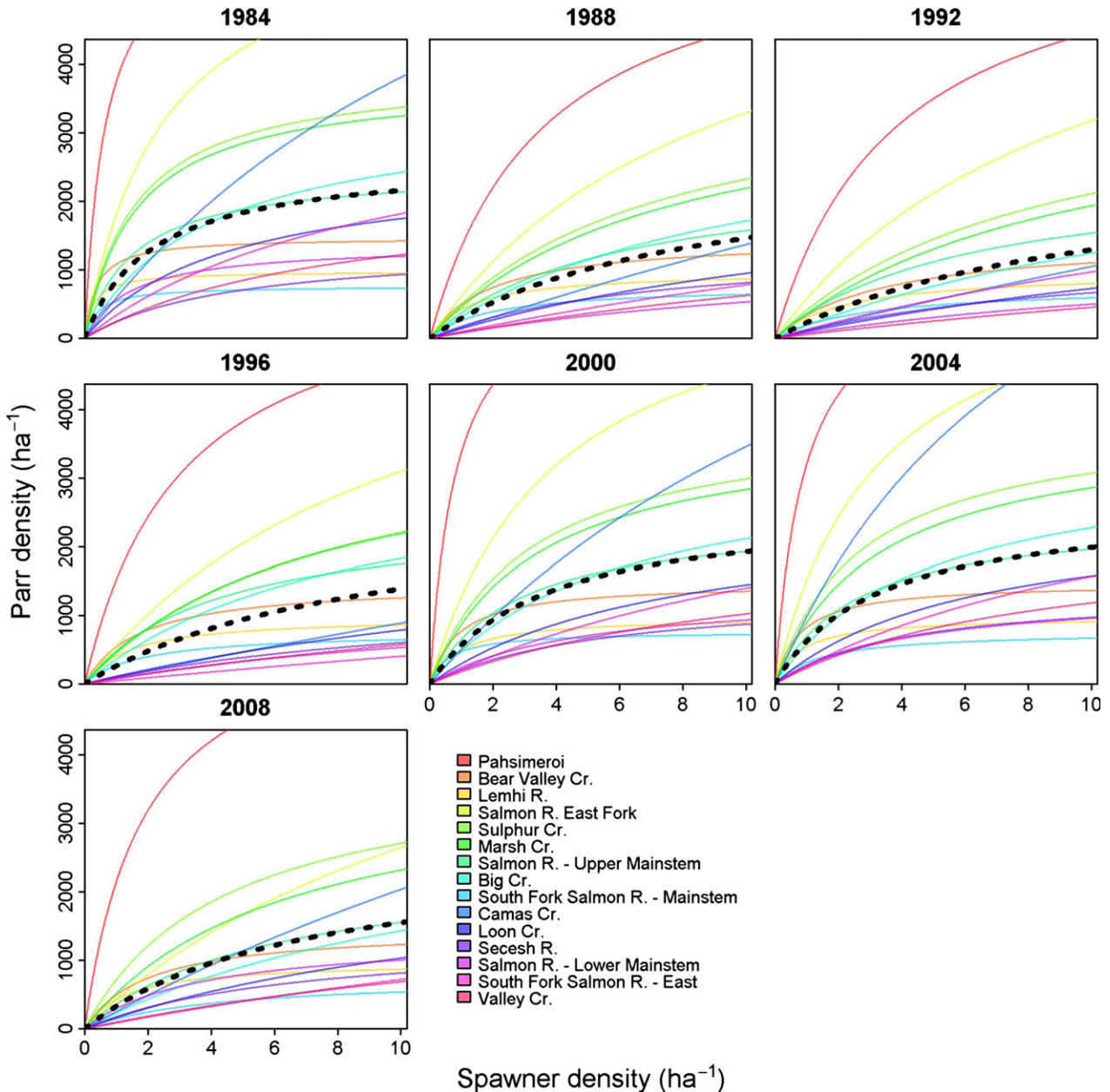
The exact degree to which variability in juvenile productivity is buffered at the scale of the Salmon River metapopulation depends upon both temporal asynchrony and the average within-population temporal variability

(Carlson & Satterthwaite 2011; Thibaut & Connolly 2013). In turn, the degree to which asynchrony in juvenile productivity translates into a portfolio effect in either adult abundance or overall adult-to-adult productivity will depend upon population-specific demographic rates during other life cycle stages and hence awaits analysis using a life cycle model. For example, many of the parr in the Pahsimeroi River are on a life-history trajectory that currently cannot be completed (Copeland & Venditti 2009). A life cycle analysis would also facilitate comparison between our estimates of synchrony in juvenile productivity and the results of previous studies of synchrony in Salmon River Chinook salmon using different metrics, such as spawner abundance (Isaak *et al.* 2003) or residuals from spawner-recruit models (Moore *et al.* 2010).

Asynchrony in demographic rates such as juvenile productivity could serve as a mechanism for generating asynchrony in population variables such as spawning abundance. Recent studies have found that the magnitude of temporal synchrony in spawning abundance has increased over time for Chinook salmon in the Salmon River basin (Isaak *et al.* 2003; Moore *et al.* 2010), perhaps caused by common effects of oceanographic conditions and hydropower dams (Pyper, Mueter & Peterman 2005; Scheuerell & Williams 2005; Moore *et al.* 2010). Our results suggest that these populations retain the potential to regain some of the lost variability if some of the synchronizing factors in the adult phase are relaxed. For example, Crozier & Zabel (2006) found a



**Fig. 3.** The expected number of recruits per hectare ( $y$ -axis; >99% of recruit per hectare records are between the  $y$ -axis limits of 0 and 4000) given spawners per hectare ( $x$ -axis; >98% of spawners per hectare records are between the  $x$ -axis limits of 0 and 10) for each of the years 1984–2008 (coloured lines), for the three populations with greatest data availability, that is, Salmon River Upper Mainstem (top panel), Marsh Creek (middle panel) and South Fork Salmon River East (lower panel), with the average across years also shown (black dashed line). Years are colour coded to show the years with a high (red) or low (purple) productivity on average, and deviations away from this spectrum show the effect of asynchronous variability (i.e. a Population  $\times$  Year interaction).



**Fig. 4.** The expected number of recruits per hectare ( $y$ -axis; >99% of recruit per hectare records are between the  $y$ -axis limits of 0 and 4000) given spawners per hectare ( $x$ -axis; >98% of spawners per hectare records are between the  $x$ -axis limits of 0 and 10) for all populations, for every fourth year ranging from 1984 to 2008, with the average across years also shown (black dashed line). Populations are colour coded to show the populations with a high (red) or low (purple) productivity on average, and deviations away from this spectrum show the effect of asynchronous variability (i.e. a Population  $\times$  Year interaction).

diversity of relationships between parr-to-smolt survival and climatic drivers such as stream discharge and temperature among Salmon River Chinook salmon populations. Differential responses to climate were associated with differences in life-history phenology (run timing) and physical characteristics of streams (e.g. elevation and width). Similar response diversity (*sensu* Elmquist *et al.* 2003) in the spawner-to-parr stage could explain the levels of asynchrony in productivity parameters that we observed. These mechanisms could lead to asynchrony in population variables such as total spawning

abundance given sufficient time and protection from the synchronizing effects of habitat loss, harvest and invasive species. However, we do not have sufficiently long time-series data to attempt estimating any trend in the relative magnitudes of synchronous and asynchronous variability in juvenile survival. Trends in the magnitude of variability have important implications for the projecting future abundance, including the risk of population extirpation.

We found that spatial variability in the density-independent productivity parameter generally has greater



magnitude than either synchronous or asynchronous temporal variability. This suggests that intrinsic productivity for spring–summer Chinook salmon differs among these populations, which could be caused by a variety of habitat characteristics including differences in average temperature, stream flow and the presence of invasive brook trout (Levin *et al.* 2002; Crozier *et al.* 2009; Copeland & Meyer 2011). The larger magnitude of spatial variability implies that, while the existence of multiple populations is helpful to buffer temporal variability, there still remain particular populations that are especially important for Salmon River early juvenile production. The identity of these productive populations may have changed during the last several hundred years as it has with Bristol Bay sockeye salmon (Schindler *et al.* 2010), although we do not have sufficient years of data to account for decadal-scale changes in population-specific demographic parameters.

Future study of these populations would benefit from changes in the sampling design for salmon parr, specifically if it implemented a repeated-measures sampling design. Repeated measures can be achieved by surveying the same site several times during a given year, using a tag-resighting design in randomly selected populations, or by including samples from complementary sampling gears (Walters, Copeland & Venditti 2013). This repeated-measures design would support the assumption of a partially closed population at each sampled site and would allow estimation of detectability (Royle & Nichols 2003; Royle & Dorazio 2008). Imperfect detection contributes to additional sampling variance among sites (Royle & Wikle 2005), and hence explicitly accounting for this can decrease residual errors and result in tighter estimates of productivity and density dependence. We have instead accounted for sampling variance caused by spatial heterogeneity and imperfect detection using a sampling distribution with three overdispersion parameters (i.e. zero-inflation and two types of variance inflation). Although our three-parameter model accounts for overdispersion, it does not allow us to estimate detectability. Naturally, any modifications to future sampling designs will require a balance between statistical ideals and logistical practicalities.

That being said, our estimate of 1350 parr per spawner is strikingly similar to an independent estimate of 1360 parr per spawner derived by assuming 4300 eggs per spawner (Bradford 1995) with egg-to-smolt survival of 5.9% (Bradford 1995) and parr-to-smolt survival of 18.6% (Zabel *et al.* 2006). Further, contrasting our parr-per-spawner estimate with the independent smolt-per-redd estimate from Walters, Copeland & Venditti (2013) yields a parr-to-smolt survival of 20.3%, which is consistent with Zabel *et al.*'s (2006) estimate. Our estimate is subject to several potential errors, including imperfect detectability in parr samples, nonrandom selection of sampling locations and errors in spawning density information (Copeland & Meyer 2011). Having a less-than-one probability of detecting each parr will result in a negative bias in estimating parr densities,

while nonrandom selection of sampling locations will have the opposite effect (e.g. by only surveying sites with higher than average parr densities). Similarly, the estimate of 1360 parr per spawner derived from parr-to-smolt survival fails to account for density-dependent survival during the parr-to-smolt stage, which has previously been observed (Achord, Levin & Zabel 2003). However, the similar answer from these independent estimates supports the interpretation that our parr survey counts are reasonable estimates of parr densities.

Interestingly, these Chinook salmon populations in the Salmon River also exhibit evidence of density-dependent early juvenile survival despite very large reductions in the number of spawning adults compared with historical estimates. Much of the freshwater habitat in this region is relatively intact, but losses of nutrient and energy subsidies from spawning adults (e.g. Schindler *et al.* 2003; Moore, Schindler & Scheuerell 2004) as well as impacts from invasive brook trout (Levin *et al.* 2002) could have reduced habitat quality (Achord, Levin & Zabel 2003). Previous work has shown that the timing and magnitude of density dependence is central to predictions regarding salmon restoration efforts (Greene & Beechie 2004). Density dependence has previously been documented for salmonids in migration, growth and survival (Bjornn 1971, 1978; Sekulich 1980; Walters, Copeland & Venditti 2013), and its strength has been shown to vary among populations (Barrowman *et al.* 2003), although our study is the first to our knowledge to quantify the degree of variability in density dependence among both years and populations. We estimate that parr carrying capacity is approximately 5000 per hectare ( $\pm 1$  standard deviation: 2800–14 400) for the average population and year, with the caveat again that this could be somewhat biased due to imperfect detectability and/or estimates of spawning numbers. Some theoretical models of spatially structured population dynamics (reviewed by Liebhold, Koenig & Bjørnstad 2004) suggest that heterogeneity among populations in the strength of density-dependent regulation can weaken temporal synchrony. The interplay between spatial and temporal variation in density dependence, environmental stochasticity and synchrony (or conversely, portfolio effects) would be a fruitful avenue for future research.

Captive breeding and reintroduction programmes have been used world-wide to support at-risk populations of animals including mammals (Bright & Morris 1994), birds (Hirzel *et al.* 2004) and amphibians (Kraaijeveld-Smit *et al.* 2006), but potential limitations to their effectiveness are often not well understood (Seddon, Armstrong & Maloney 2007; Armstrong & Seddon 2008). Supplementation of imperiled salmon populations through hatchery programmes has been, and continues to be, used as a means for increasing abundance of wild fish (Brannon *et al.* 2004; Naish *et al.* 2008; Hess *et al.* 2012). Our results regarding density-dependent juvenile survival imply that hatchery supplementation efforts seeking to increase

parr abundance above 5000 parr per hectare will often not increase production in many populations and years. Similarly, density-dependent juvenile mortality is likely to result in an upper bound on useful supplementation of juveniles for other taxa and systems. The effect of supplementation using smolts may avoid this type of density dependence, but may be subject to other density-dependent effects that are not quantified here. Nonetheless, we note that this result should be interpreted cautiously, due to the well-known effect of measurement errors in spawners causing an increased perception of density dependence in stock–recruit relationships (Ludwig & Walters 1981). Improved estimates of variability in the magnitude of density-dependent effects should await a full life cycle model for these populations, which can use a state-space model to incorporate observation-level data on redd counts and thereby account for this and other potential errors and biases (De Valpine & Hilborn 2005).

## Acknowledgements

We gratefully acknowledge R. Hovel and P. Lisi, who contributed to ideas to this manuscript, and D. Holzer, who provided Fig. 1. We also thank K. See for editorial suggestions. Bonneville Power Administration provided funding for field work (Project 1991-073-00), and Paul Bunn compiled the data for this analysis. The manuscript would be incomplete without acknowledgement of the biologists who supervised the snorkel crews over the years (in alphabetical order): Kim Apperson, Arnie Brimmer, Tom Curet, Jon Flinders, Russ Kiefer, Eric Leitzinger, Jeff Lutch, Charlie Petrosky, Bruce Rich and Bill Schrader. Finally, we are grateful for helpful comments from three anonymous reviewers.

## References

- Achord, S., Levin, P.S. & Zabel, R.W. (2003) Density-dependent mortality in Pacific salmon: the ghost of impacts past? *Ecology Letters*, **6**, 335–342.
- Anders, A.D., Dearborn, D.C., Faaborg, J. & Iii, F.R.T. (1997) Juvenile survival in a population of neotropical migrant birds. *Conservation Biology*, **11**, 698–707.
- Armstrong, D.P. & Seddon, P.J. (2008) Directions in reintroduction biology. *Trends in Ecology & Evolution*, **23**, 20–25.
- Barrowman, N.J., Myers, R.A., Hilborn, R., Kehler, D.G. & Field, C.A. (2003) The variability among populations of coho salmon in the maximum reproductive rate and depensation. *Ecological Applications*, **13**, 784–793.
- Bjornn, T.C. (1971) Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. *Transactions of the American Fisheries Society*, **100**, 423–438.
- Bjornn, T.C. (1978) *Survival, Production, and Yield of Trout and Chinook Salmon in the Lemhi River, Idaho*. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, Idaho, USA.
- Bjornstad, O.N., Ims, R.A. & Lambin, X. (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution*, **14**, 427–432.
- Bradford, M.J. (1995) Comparative review of Pacific salmon survival rates. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1327–1338.
- Brannon, E.L., Amend, D.F., Cronin, M.A., Lannan, J.E., LaPatra, S., McNeil, W.J. et al. (2004) The controversy about salmon hatcheries. *Fisheries*, **29**, 12–31.
- Bright, P.W. & Morris, P.A. (1994) Animal translocation for conservation: performance of dormice in relation to release methods, origin and season. *Journal of Applied Ecology*, **31**, 699–708.
- Burnham, K.P. & Anderson, D. (2002) *Model Selection and Multi-Model Inference*, 2nd edn. Springer, New York, New York, USA.
- Carlson, S.M. & Satterthwaite, W.H. (2011) Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 1579–1589.
- Cavanaugh, K.C., Kendall, B.E., Siegel, D.A., Reed, D.C., Alberto, F. & Assis, J. (2013) Synchrony in dynamics of giant kelp forests is driven by both local recruitment and regional environmental controls. *Ecology*, **94**, 499–509.
- Clark, J.S. (2003) Uncertainty and variability in demography and population growth: a hierarchical approach. *Ecology*, **84**, 1370–1381.
- Clark, J.S., LaDeau, S. & Ibanez, I. (2004) Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs*, **74**, 415–442.
- Copeland, T. & Meyer, K.A. (2011) Interspecies synchrony in salmonid densities associated with large-scale bioclimatic conditions in central Idaho. *Transactions of the American Fisheries Society*, **140**, 928–942.
- Copeland, T. & Venditti, D.A. (2009) Contribution of three life history types to smolt production in a Chinook salmon (*Oncorhynchus tshawytscha*) population. *Canadian Journal of Fisheries and Aquatic Sciences*, **66**, 1658–1665.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H. et al. (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**, 1528–1531.
- Crozier, L.G. & Zabel, R.W. (2006) Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. *Journal of Animal Ecology*, **75**, 1100–1109.
- Crozier, L.G., Zabel, R.W., Hockersmith, E.E. & Achord, S. (2009) Interacting effects of density and temperature on body size in multiple populations of Chinook salmon. *Journal of Animal Ecology*, **79**, 342–349.
- De Valpine, P. & Hilborn, R. (2005) State-space likelihoods for nonlinear fisheries time-series. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 1937–1952.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'malley, R.E. & Thomson, D. (1998) The statistical inevitability of stability-diversity relationships in community ecology. *The American Naturalist*, **151**, 264–276.
- Earn, D.J.D. (2000) Coherence and conservation. *Science*, **290**, 1360–1364.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. et al. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, **1**, 488–494.
- Elton, C.S. (1958) *The Ecology of Invasions by Plants and Animals*. Methuen & Co., London.
- Engen, S., Lande, R. & Sæther, B. (2002) The spatial scale of population fluctuations and quasi-extinction risk. *The American Naturalist*, **160**, 439–451.
- Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, **13**, 58–63.
- Gelman, A. (2005) Analysis of variance—why it is more important than ever. *The Annals of Statistics*, **33**, 1–53.
- Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical science*, **7**, 457–472.
- Good, T.P., Waples, R.S. & Adams, P. (2005) *Updated Status of Federally Listed ESUs of West Coast Salmon and Steelhead*. NOAA Tech. Memo. NMFS-NWFSC-66., U.S. Department of Commerce, Washington, DC.
- Govindarajulu, P., Altwegg, R. & Anholt, B.R. (2005) Matrix model investigation of invasive species control: bullfrogs on Vancouver Island. *Ecological Applications*, **15**, 2161–2170.
- Greene, C.M. & Beechie, T.J. (2004) Consequences of potential density-dependent mechanisms on recovery of ocean-type chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 590–602.
- Greene, C.M., Hall, J.E., Guilbault, K.R. & Quinn, T.P. (2010) Improved viability of populations with diverse life-history portfolios. *Biology Letters*, **6**, 382–386.
- Grenouillet, G., Hugué, B., Carrel, G.A., Olivier, J.M. & Pont, D. (2001) Large-scale synchrony and inter-annual variability in roach recruitment in the Rhône River: the relative role of climatic factors and density-dependent processes. *Freshwater Biology*, **46**, 11–26.
- Hanski, I. & Woiwod, I.P. (1993) Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology*, **62**, 656–668.
- Heino, M., Kaitala, V., Ranta, E. & Lindstrom, J. (1997) Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society B-Biological Sciences*, **264**, 481–486.
- Hess, M.A., Rabe, C.D., Vogel, J.L., Stephenson, J.J., Nelson, D.D. & Narum, S.R. (2012) Supportive breeding boosts natural population abundance with minimal negative impacts on fitness of a wild population of Chinook salmon. *Molecular Ecology*, **21**, 5236–5250.
- Hirzel, A.H., Posse, B., OGGIER, P.-A., Cretienand, Y., Glenz, C. & Arlettaz, R. (2004) Ecological requirements of reintroduced species and the

- implications for release policy: the case of the bearded vulture. *Journal of Applied Ecology*, **41**, 1103–1116.
- Isaak, D.J., Thurow, R.F., Rieman, B.E. & Dunham, J.B. (2003) Temporal variation in synchrony among chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 840–848.
- Knaus, J. (2010) *Snowfall: Easier Cluster Computing (Based on Snow)*. <http://CRAN.R-project.org/package=snowfall>.
- Koenig, W.D. (1999) Spatial autocorrelation of ecological phenomena. *Trends in Ecology & Evolution*, **14**, 22–26.
- Koizumi, I., Yamamoto, S., Nomoto, K. & Maekawa, K. (2008) Synchrony in local population dynamics of stream-dwelling Dolly Varden: do genetically similar groups show similar demography? *Population Ecology*, **50**, 367–377.
- Kraaijeveld-Smit, F.J.L., Griffiths, R.A., Moore, R.D. & Beebee, T.J. (2006) Captive breeding and the fitness of reintroduced species: a test of the responses to predators in a threatened amphibian. *Journal of Applied Ecology*, **43**, 360–365.
- Levin, P.S., Achord, S., Feist, B.E. & Zabel, R.W. (2002) Non-indigenous brook trout and the demise of Pacific salmon: a forgotten threat? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **269**, 1663–1670.
- Liebold, A., Koenig, W.D. & Bjørnstad, O.N. (2004) Spatial synchrony in population dynamics. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 467–490.
- Lindén, A. & Mäntyniemi, S. (2011) Using negative binomial distribution to model overdispersion in ecological count data. *Ecology*, **92**, 1414–1421.
- Ludwig, D. & Walters, C.J. (1981) Measurement errors and uncertainty in parameter estimates for stock and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 711–720.
- MacArthur, R. (1955) Fluctuations of animal populations and a measure of community stability. *Ecology*, **36**, 533–536.
- May, R.M. (1986) The search for patterns in the balance of nature: advances and retreats. *Ecology*, **67**, 1115–1126.
- Moore, J.W., Schindler, D.E. & Scheuerell, M.D. (2004) Disturbance of freshwater habitats by anadromous salmon in Alaska. *Oecologia*, **139**, 298–308.
- Moore, J.W., McClure, M., Rogers, L.A. & Schindler, D.E. (2010) Synchronization and portfolio performance of threatened salmon. *Conservation Letters*, **3**, 340–348.
- Myers, R.A., Mertz, G. & Bridson, J. (1997) Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1400–1407.
- Naish, K.A., Taylor, J.E., Levin, P.S., Quinn, T.P., Winton, J.R., Huppert, D. *et al.* (2008) An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology*, **53**, 61.
- Nichols, J.D., Bart, J., Limpert, R.J., Sladen, W.J.L. & Hines, J.E. (1992) Annual survival rates of adult and immature eastern population tundra swans. *The Journal of Wildlife Management*, **56**, 485–494.
- Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*. March, pp. 20–22.
- Punt, A.E., Smith, D.C., KrusicGolub, K. & Robertson, S. (2008) Quantifying age-reading error for use in fisheries stock assessments, with application to species in Australia's southern and eastern scalefish and shark fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 1991–2005.
- Pyper, B.J., Mueter, F.J. & Peterman, R.M. (2005) Across-species comparisons of spatial scales of environmental effects on survival rates of northeast Pacific salmon. *Transactions of the American Fisheries Society*, **134**, 86–104.
- R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Development Core Team, Vienna, Austria.
- Ringsby, T.H., Sæther, B.-E., Tufto, J., Jensen, H. & Solberg, E.J. (2002) Asynchronous spatiotemporal demography of a house sparrow metapopulation in a correlated environment. *Ecology*, **83**, 561–569.
- Rogers, L.A. & Schindler, D.E. (2008) Asynchrony in population dynamics of sockeye salmon in southwest Alaska. *Oikos*, **117**, 1578–1586.
- Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities*, 1st edn. Academic Press, London.
- Royle, J.A. & Nichols, J.D. (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology*, **84**, 777–790.
- Royle, J.A. & Wikle, C.K. (2005) Efficient statistical mapping of avian count data. *Environmental and Ecological Statistics*, **12**, 225–243.
- Saether, B.-E., Lillegård, M., Grotan, V., Drever, M.C., Engen, S., Nudds, T.D. *et al.* (2008) Geographical gradients in the population dynamics of North American prairie ducks. *Journal of Animal Ecology*, **77**, 869–882.
- Scheuerell, M.D. & Williams, J.G. (2005) Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*). *Fisheries Oceanography*, **14**, 448–457.
- Schindler, D.E., Scheuerell, M.D., Moore, J.W., Gende, S.M., Francis, T.B. & Palen, W.J. (2003) Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment*, **1**, 31–37.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A. *et al.* (2010) Population diversity and the portfolio effect in an exploited species. *Nature*, **465**, 609–612.
- Seddon, P.J., Armstrong, D.P. & Maloney, R.F. (2007) Developing the science of reintroduction biology. *Conservation Biology*, **21**, 303–312.
- Sekulich, P.T. (1980) The carrying capacity of infertile forest streams for rearing juvenile Chinook Salmon. Ph.D., University of Idaho, Moscow, Idaho, USA.
- Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & van der Linde, A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society. Series B (Statistical Methodology)*, **64**, 583–639.
- Su, Y.-S. & Yajima, M. (2012) *R2jags: A Package for Running Jags from R*. <http://CRAN.R-project.org/package=R2jags>
- Tavecchia, G., Minguez, E., De León, A., Louzao, M. & Oro, D. (2008) Living close, doing differently: small-scale asynchrony in demography of two species of seabirds. *Ecology*, **89**, 77–85.
- Thibaut, L.M. & Connolly, S.R. (2013) Understanding diversity–stability relationships: towards a unified model of portfolio effects. *Ecology Letters*, **16**, 140–150.
- Thibaut, L.M., Connolly, S.R. & Sweatman, H.P. (2012) Diversity and stability of herbivorous fishes on coral reefs. *Ecology*, **93**, 891–901.
- Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**, 1455–1474.
- Tilman, D., Lehman, C.L. & Bristow, C.E. (1998) Diversity-stability relationships: statistical inevitability or ecological consequence? *The American Naturalist*, **151**, 277–282.
- Turchin, P. (2003) *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton, New Jersey, USA.
- Walters, A., Copeland, T. & Venditti, D. (2013) The density dilemma: limitations on juvenile production in threatened salmon populations. *Ecology of Freshwater fish*, **22**, DOI: 10.1111/eff.12046
- Walters, C. & Kitchell, J.F. (2001) Cultivation/densation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 39–50.
- Waples, R.S. (1995) Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. *American Fisheries Society Symposium*, **17**, 8–27.
- Zabel, R.W., Scheuerell, M.D., McClure, M.M. & Williams, J.G. (2006) The interplay between climate variability and density dependence in the population viability of Chinook salmon. *Conservation Biology*, **20**, 190–200.

Received 16 January 2013; accepted 28 June 2013

Handling Editor: Corey Bradshaw

## Supporting Information

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

**Appendix S1.** JAGS code for model with lowest  $\Delta DIC$ .

**Appendix S2.** Credible intervals for estimated variance parameters and the synchrony index.