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

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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 (\textit{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-SD = 0.55) is approximately equal in magnitude to synchronous temporal variability (log-SD = 0.67), but much lower than spatial variability (log-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 particular, 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;
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:

$$\hat{r}_{i,y,p} = \frac{A_{i,y,p} \cdot s_{y,p} \cdot a_{y,p}}{1 + \left(\frac{a_{y,p}}{C_0}\right) \cdot \frac{b_{y,p}}{a_{y,p}}}$$

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 \(p\), \(a_{y,p}\) is the maximum per capita recruitment rate, \(b_{y,p}\) measures the strength of density dependence (in units recruits per hectare) and maximum expected recruitment per hectare is \(a_{y,p} / (a_{y,p}/C_0) \cdot b_{y,p}\). Alternatively, the expected count can be specified using the Ricker model:

$$\hat{r}_{i,y,p} = A_{i,y,p} \cdot s_{y,p} \cdot a_{y,p} \cdot \exp\left[-\frac{s_{y,p}}{b_{y,p}}\right]$$


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

Random effects are also bias corrected (mean equals parameters is proportional to the probability of observed parameter). The Bayesian statistical paradigm. The posterior distribution of model parameters is equal to zero and zero otherwise, and zero otherwise, and hence have an expected count of zero, and hence have an expected count of zero), and $(all derived parameters) have a mean equal to $\exp(x)$ and $\exp(b)$, respectively (i.e. the intercepts $x$ and $b$ can be interpreted as the log-mean across all years and populations). Random effects are specified in log-space such that $x_{p} = \exp(x_{p} + a_{p}r_{p} + a_{y}y_{p} + a_{y,p}y_{p} + a_{y,p}y_{p})$.

Productivity parameters $a_{p}$ and $b_{p}$ 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:

$$a_{p} = \exp(x + a_{y}y_{p} + a_{y,p}y_{p} + a_{y,p}y_{p})$$

and

$$b_{p} = \exp(y + b_{y}y_{p} + b_{y,p}y_{p} + b_{y,p}y_{p})$$

where $x$ and $b$ are intercepts for $a_{p}$ and $b_{p}$, $a_{y}$, $a_{y,p}$ and $a_{y,p}y_{p}$ are random effects for $a$ accounting for the effect of year, population and their interaction, respectively, and $b_{y}$, $b_{y,p}$ and $b_{y,p}y_{p}$ are random effects for $b$ 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 $\sigma_{a_{y}}$, $\sigma_{b_{y}}$ and $\sigma_{a_{y,p}}$ are the standard deviation for $a_{y}$, $b_{y}$ and $a_{y,p}y_{p}$, respectively, and $\sigma_{b_{y,p}}$, $\sigma_{b_{y,p}y_{p}}$ and $\sigma_{b_{y,p}y_{p}}$ are the standard deviation for $b_{y}$, $b_{y,p}$ and $b_{y,p}y_{p}$, respectively. Random effects are also bias corrected (mean equals $-\sigma^{2}/2$, where $\sigma^{2}$ is the random effect variance) such that $x_{p}$ and $b_{p}$ (and all derived parameters) have a mean equal to $\exp(x)$ and $\exp(b)$, respectively (i.e. the intercepts $x$ and $b$ can be interpreted as the log-mean across all years and populations). Random effects are specified in log-space such that $x_{p}$ and $b_{p}$ remain positive for all years and populations.

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

$$Pr[R = r_{i,j,p} = \rho \cdot I(R = 0) + (1 - \rho) \cdot \binom{n}{R} \cdot p^{R} \cdot (1 - p)^{n-R}]$$

$$n = \frac{r_{i,j,p}}{1 + \frac{1}{\rho} \cdot r_{i,j,p}}$$

$$p = \frac{1}{1 + \frac{1}{\rho} \cdot r_{i,j,p}}$$

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 $a_{y}$ and $b_{y}$ are variance-inflation parameters such that the variance for the non-zero-inflated component is $\sigma^{2} r_{i,j,p} + b^{2} r_{i,j,p}$ (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 parameters, 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 50 000 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 ($\beta \rightarrow \infty$, $b_{y,p} = b_{y} = 0$), constant among years and populations ($\sigma_{b_{y,p}} = \sigma_{b_{y}} = 0$), or variable among populations ($\sigma_{b_{y,p}} = \sigma_{b_{y}} = 0$, $\sigma_{b_{y,p}} = \sigma_{b_{y}} = 0$);
3. The Population × Year interaction was either absent ($a_{y,p}y_{p} = b_{y,p} = b_{y} = 0$) or only estimated for the density-independent parameter ($\sigma_{a_{y}} = \sigma_{b_{y},y_{p}} = \sigma_{a_{y},y_{p}}$ = 0). However, the Ricker and Beverton–Holt models are indistinguishable in the absence of density dependence, such that this $2 \times 2 \times 2$ cross resulted in fourteen configurations total. In all models, density-independent productivity was parameterized to include variability among populations ($\sigma_{a_{y}}$ and $\sigma_{b_{y}}$) as well as synchronous temporal variability ($\sigma_{a_{y},y_{p}}$ and $\sigma_{b_{y},y_{p}}$), 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, $\sigma_{a_{y}}$ is the standard deviation of synchronous temporal variability ($\sigma_{a_{y}}$) while $\sigma_{a_{y},y_{p}}$ is the magnitude of asynchronous temporal variability ($\sigma_{a_{y}}$). 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 $a_{y,p}y_{p} = b_{y,p} = b_{y} = 0$ 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 the specification of the random effects distribution in intrinsic productivity for all models that include both synchronous ($\sigma_{a_{y}}$) and asynchronous ($\sigma_{a_{y},y_{p}}$) temporal variability. By
assumption of independence between these two random effects, the total temporal variance for any given population is $\sigma^2_{a,year} + \sigma^2_{a,year-pop}$, while the covariance between any pair of populations is $\sigma^2_{a,year}$ and their expected correlation is thus $\sigma^2_{a,year} / (\sigma^2_{a,year} + \sigma^2_{a,year-pop})$, 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 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 × Year interaction; $\Delta$DIC $\geq$ 67-6), and the estimated magnitude of asynchronous variability ($\sigma^2_{a,year} = 0.55$) is comparable to synchronous temporal variability ($\sigma^2_{a,year} = 0.67$). 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 $\sigma^2_{a,year} / (\sigma^2_{a,year} + \sigma^2_{a,year-pop})$, 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 ±1 standard deviation: 850–2500) at low spawning density.

The estimated magnitude of spatial variability in productivity ($\sigma^2_{a,year} = 1.11$) 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 ($\Delta$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 ($\Delta$DIC = 7.3). Finally, the Beverton–Holt model is supported over the Ricker model ($\Delta$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 × Year combinations, and either the Ricker or Beverton-Holt (B-H) model for juvenile survival.

<table>
<thead>
<tr>
<th>Model structure</th>
<th>Random effect variability</th>
<th>Derived productivity parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Synchrony</td>
<td>Maximum RPS</td>
</tr>
<tr>
<td></td>
<td>σ_{a,year}</td>
<td>σ_{a,pop}</td>
</tr>
<tr>
<td>None No</td>
<td>NA</td>
<td>0.502</td>
</tr>
<tr>
<td>None Yes</td>
<td>NA</td>
<td>0.373</td>
</tr>
<tr>
<td>Constant No</td>
<td>Ricker</td>
<td>0.539</td>
</tr>
<tr>
<td>Constant No</td>
<td>B-H</td>
<td>0.670</td>
</tr>
<tr>
<td>Constant Yes</td>
<td>Ricker</td>
<td>0.405</td>
</tr>
<tr>
<td>Constant Yes</td>
<td>B-H</td>
<td>0.542</td>
</tr>
<tr>
<td>By year No</td>
<td>Ricker</td>
<td>0.634</td>
</tr>
<tr>
<td>By year No</td>
<td>B-H</td>
<td>0.956</td>
</tr>
<tr>
<td>By year Yes</td>
<td>Ricker</td>
<td>0.39</td>
</tr>
<tr>
<td>By year Yes</td>
<td>B-H</td>
<td>0.521</td>
</tr>
<tr>
<td>By pop. No</td>
<td>Ricker</td>
<td>0.547</td>
</tr>
<tr>
<td>By pop. No</td>
<td>B-H</td>
<td>0.916</td>
</tr>
<tr>
<td>By pop. Yes</td>
<td>Ricker</td>
<td>0.411</td>
</tr>
<tr>
<td>By pop. Yes</td>
<td>B-H</td>
<td>0.594</td>
</tr>
</tbody>
</table>

For each model, we list ΔDIC (the difference in the Deviance Information Criterion between models, where the selected model has ΔDIC = 0), the analytic estimate of synchrony, that is, the ratio of shared to total variance (\(\sigma_{a,year}^2/(\sigma_{a,year}^2 + \sigma_{a,pop}^2)\)), the standard deviation of random effects (a: maximum productivity; b: density-dependent productivity parameter) by year, population and the Population × 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 ±1 standard deviation (i.e. the 15.9 and 84.1 percentiles of the posterior distribution), where models with ΔDIC < 10 are shown in bold (the range for synchrony and standard deviation of random effects is shown in Appendix B).
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
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 Elmqvist 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 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 Liebold, 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 & Seddon 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 redds counts and thereby account for this and other potential errors and biases (De Valpine & Hilborn 2005).

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Supporting Information

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

Appendix S1. JAGS code for model with lowest DIC.

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