Synchronization and portfolio performance of threatened salmon

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Abstract

Interpopulation variation in dynamics can buffer species against environmental change. We compared population synchrony in a group of threatened Chinook salmon in the highly impacted Snake River basin (Oregon, Washington, Idaho) to that in the sockeye salmon stock complex of less impact Bristol Bay (Alaska). Over the last 40 years, >90% of populations in the Snake River basin became more synchronized with one another. However, over that period, sockeye populations from Alaska did not exhibit systemic changes in synchrony. Coincident with increasing Snake River population synchrony, there was an increase in hatchery propagation and the number of large dams, potentially homogenizing habitats and populations. A simulation using economic portfolio theory revealed that synchronization of Snake River salmon decreased risk-adjusted portfolio performance (the ratio of portfolio productivity to variance) and decreased benefits of population richness. Improving portfolio performance for exploited species, especially given future environmental change, requires protecting a diverse range of populations and the varied habitats upon which they depend.

Introduction

Spatial coherence in population dynamics is recognized as an important issue in conservation science (e.g., Earn *et al.* 2000). For a group of spatially distinct populations, synchrony in population dynamics can increase the risk of simultaneous and global extinction (Heino *et al.* 1997; Earn *et al.* 2000; Engen *et al.* 2002). In contrast, asynchronous population dynamics decrease extinction risk and may increase sustainability of long-term production from groups of populations (Hilborn *et al.* 2003; Schindler *et al.* in press).

Three main mechanisms—both naturally and anthropogenically driven—cause synchrony in population dynamics: (1) spatial coherence in environmental drivers (i.e., Moran effect), (2) dispersal among populations, and (3) interactions with other species that are synchronized (Liebhold *et al.* 2004). In contrast, population asynchrony can be maintained by a diversity of phenotypes and variation among local environmental conditions (e.g., Hilborn *et al.* 2003, Crozier & Zabel 2006, Ruzzante *et al.* 2006).

Pacific salmon exhibit fine-scale population structure and local adaptations to their natal habitats (e.g., Achord *et al.* 2007), which likely contributes to asynchrony in population dynamics (Hilborn *et al.* 2003; Rogers & Schindler 2008; Greene *et al.* 2009). Indeed, proximate salmon populations are often only moderately correlated (e.g., Pyper *et al.* 2005; Rogers & Schindler 2008). This correlation decreases as distance increases among populations, likely due to decreases in shared environmental conditions (e.g., Peterman *et al.* 1998; Pyper *et al.* 2005). However, human activities can impact salmon population diversity and synchrony. For example, artificial propagation programs may increase dispersal among populations, eliminating locally adapted life history variation (Ayllon *et al.* 2006; McClure *et al.* 2008). There has been little evaluation of human-induced homogenization of salmon population structure or its consequences for sustainability.

Economic portfolio theory provides a framework to explore the consequences of synchronization. Units of biodiversity (e.g., species or populations) within

ecosystems can be analogous to stock assets within portfolios. Asynchronous dynamics of assets can increase portfolio performance by buffering against temporal variability in individual assets, thereby increasing portfolio stability (Markowitz 1952). Economic theory can predict performance of a portfolio based on the number of assets, their performance, and the degree to which their performance is correlated (Markowitz 1952; Sharpe 1994; Koellner & Schmitz 2006). Performance of a portfolio of salmon populations could be the provisioning of indirect or direct services such as nutrient import and harvest. The portfolio model is particularly relevant here because fisheries simultaneously exploit many populations, thereby integrating across the stock (Hilborn *et al.* 2003; Schindler *et al.* 2008; Schindler & Rogers 2009).

Here, we document increased demographic synchrony among Chinook salmon (*Oncorhynchus tshawytscha*) populations within the Snake River region over the last 40 years, concurrent with increased intensity of human impacts. In contrast, sockeye salmon (*O. nerka*) populations in the lightly impacted region of Bristol Bay, Alaska, have not become more synchronized. We acknowledge that the differences between these systems (i.e., location and species) might complicate this comparison. Simulations using economic portfolio theory demonstrate that the synchronization of Snake River salmon has compromised its performance. Management of spatially structured species can benefit from explicit consideration of population diversity.

Methods

Snake River basin

The Snake River spring/summer Chinook salmon Evolutionarily Significant Unit contains 21 extant populations with time series of abundance extending to the 1960s. This system is highly altered by habitat degradation, dams, invasive species, and hatcheries (McClure *et al.* 2003). These fish generally spend at least 1 year rearing in natal streams before migrating to the ocean where they spend 1–3 years before returning to spawn.

Data consist of spawner abundance based on redd (salmon nest) counts and counts of total live fish for each of the 21 populations (Good *et al.* 2005). We calculated recruits per spawner for each brood year from 1959 to 1998. We used brood-year specific-residuals (ε_t) from the Ricker model as an index of population productivity that incorporates density feedback. Specifically, we fit a Ricker model to each population,

$$\log_e \left(\frac{R_t}{S_t} \right) = \log_e \alpha - \beta S_t + \varepsilon_t$$

where R_t is the number of recruits produced by S_t spawners in a given brood year, by minimizing the total squared error. Due to poor and decreasing returns, fishery harvest rates on these populations have been low and decreasing over the study period. Specifically, the median annual harvest rate was 0.09, ranged from 0.00 to 0.64, and has been below 0.15 since 1974, with one exception. Thus, we did not incorporate fisheries catches into estimates of population productivity.

To examine temporal changes in synchrony for each pair of populations, we calculated correlation coefficients for a 10-year moving window (i.e., correlation coefficients were calculated among all pairs of populations for 1963–1972, 1964–1973, etc.). To assess temporal trends in correlations (synchronization rate), we examined the slope of the relationship between the correlation coefficient and year for each pair of populations. All pair-wise rates were averaged for each population to produce a single value.

Bristol Bay, Alaska

We conducted similar analyses for sockeye salmon from streams and rivers in Bristol Bay, Alaska, as a comparison to the highly altered Snake River region. Like Snake River Chinook salmon, these fish generally rear 1 or 2 years in freshwater, and spend 1 to 3 years in the ocean. This group of sockeye populations has supported high but sustainable levels of commercial fishing for over a century. Other anthropogenic impacts are negligible—habitat is essentially intact and there is no artificial propagation.

As above, we analyzed population productivity (ε_t) and correlations between populations between 1963 and 1998 based on age structure and counts from eight streams within the Wood River system and eight major river systems across Bristol Bay (Rogers & Schindler 2008). Due to the heavy fishing pressure on these stocks, the fishery catch was added back into the returns based on the age composition of spawning populations and the fishery harvest (Rogers & Schindler 2008).

While the methods used to estimate abundance have inherent sampling error, which can be exacerbated by erroneous age structure data (e.g., Zabel & Levin 2002), there have been no significant changes in the methods used for either set of time series that would be likely to bias estimates of synchronization.

Comparison of rates of synchronization

We used linear hierarchical modeling to assess synchronization across populations and regions. Specifically, we used WinBUGS v1.04 to estimate the mean and variance in synchronization rate for each population, assuming

that the population-specific means and variances were drawn from a normally distributed regional hyper-mean and hyper-variance. We ran a single chain of 100,000 iterations with a burn-in period of 500 iterations; repeat model runs with different initial runs revealed model convergence. Priors were uninformative, either through a wide uniform distribution (on means and hyper-mean) or a vague gamma distribution (on variance and hyper-variance). We ran this model for Wood River populations associated with individual streams, Bristol Bay stocks associated with major rivers, and Snake River populations. These models estimated mean and variance in synchronization rates for each population and the hyper-distribution of these parameters for each region based on pair-wise correlations, so the data are not fully independent.

Portfolio analysis

To explore the consequences of synchronization of population dynamics, we used simulations based on economic portfolio theory. Our simulations examined portfolio performance as a function of synchrony and the number of populations.

In this application, the portfolio is the Snake River Evolutionarily Significant Unit and the assets are populations. We use productivity of the portfolio as the performance metric given its importance for the sustainability of populations; we use variance in the portfolio productivity as the risk metric given the importance of temporal stability for sustainability. Specifically, the performance of population j of salmon was considered to be population productivity (ε_t) averaged across years (μ_j), with the ε_t being rescaled so that they were all above 0 by adding the minimum observed ε_t to all. The variance in ε_t of population j over the time period is σ^2_j and COV_{jk} is the covariance in population productivity between populations j and k over the time period. The proportional contribution (X_j) of each population to the portfolio was the number of spawners in population j divided by the number of spawners in the entire Evolutionarily Significant Unit over the time period. These X_j were normalized so that they summed to 1 for each iteration, the conservative approach that portfolio size (abundance) does not vary across simulations. Simulations examined portfolio performance across different levels of synchrony and across a range ($n = 1–21$) of the number of populations in the portfolio. A first set of simulations used the population productivities, variances, and covariances estimated for early (1963–1972) and late (1989–1998) periods to evaluate the effect of the combination of productivity and synchrony on portfolio performance. A second set used the average (1963–1998) population productivities and

variances, but the decade-specific covariances to isolate the effect of synchronization on portfolio performance.

These simulations assume that selection of populations for inclusion in the portfolio is random. However, management and conservation of salmon stocks has often focused on the most productive and largest stocks (Price *et al.* 2008). Therefore, we ran simulations to examine how selection strategy influenced portfolio performance. We compared portfolio performance for the late period (1989–1998) based on three different selection strategies: random (described above), historic contribution, and current contribution. For the latter two strategies, the probability of selection was proportional to the relative contribution of that population (X_j) during either the early period (1963–1972), or the most recent period (1989–1998).

For each iteration, n populations ($n = 1–21$) from the Snake River were selected without replacement to comprise the portfolio. The variance in portfolio performance (σ^2_P) was calculated as the average of the individual variances plus covariances among n populations in the portfolio, weighted by the proportional contribution (X_j) of each asset

$$\sigma_P^2 = \sum_{j=1}^{n} X_j^2 \sigma_j^2 + \sum_{j=1}^{n} \sum_{\substack{k=1 \\ k \neq j}}^{n} X_j X_k COV_{jk}$$

The average performance of the portfolio (μ_p) was calculated as the average performance of the individual assets j

$$\mu_P = \sum_{j=1}^{N} X_j \mu_j.$$

We use the ratio of performance to variance, a derivation of the Sharpe index (Sharpe 1994), following Koellner & Schmitz (2006), as an index of risk-adjusted yield (θ)

$$\theta = \frac{\mu_p}{\sigma_p}.$$

We ran 200 iterations for each period, simulation set, selection strategy, and portfolio size.

Results

Synchrony in salmon population dynamics

Snake River spring/summer Chinook salmon populations have become increasingly synchronized over the last four decades. From 1970 to 1979, the average correlation among populations was only 0.26—similar to the mean value of 0.3 seen in Pyper *et al.* (2005). Since then, populations have become more synchronized, and the average correlation most recently reached 0.63 (Figure S1).
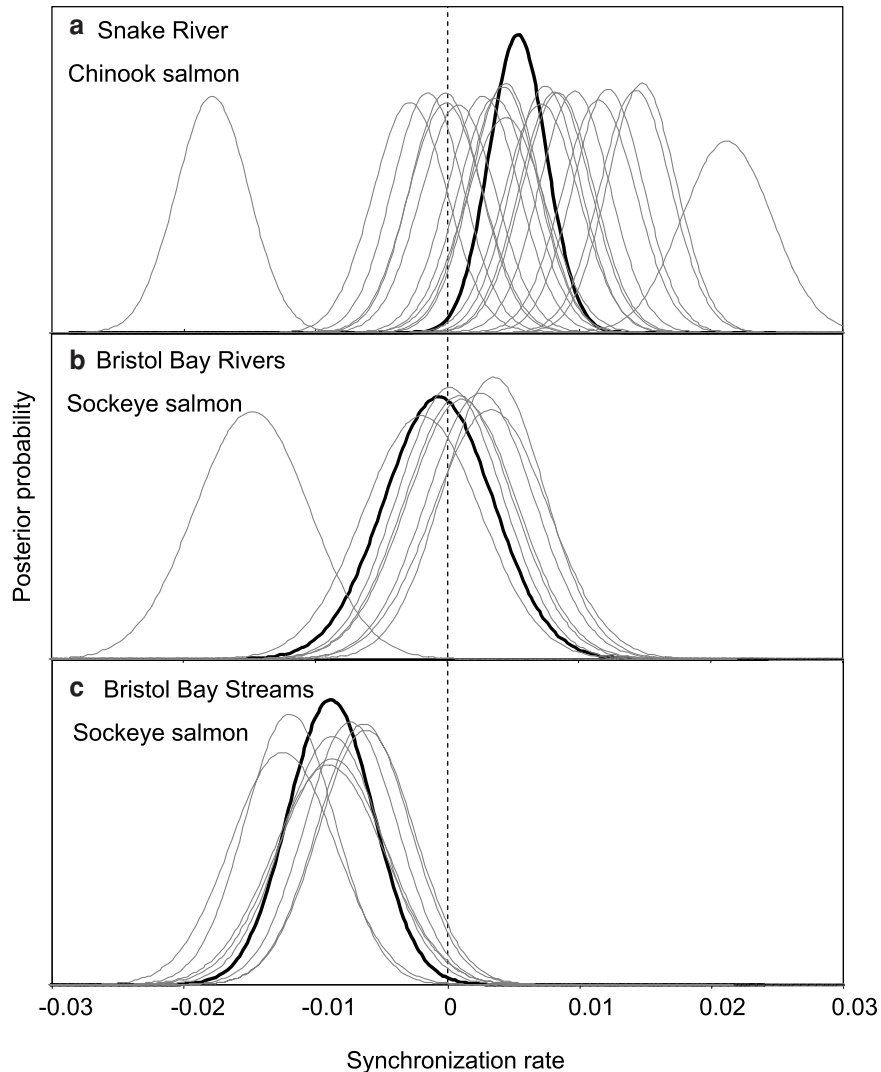
Figure 1 Distributions of the rate of change in the degree of population synchrony for salmon from stream populations and river stocks from Bristol Bay, Alaska and populations from the Snake River Evolutionary Significant Unit. Shown are the posterior probability distributions of mean rates of synchronization, estimated for specific populations (thin gray lines) and for the hyper-distributions (thick black lines). Values reflect the slope in the relationship between year and average correlation for a population. The dotted line references a synchronization rate of 0, where there was not a change in the degree of synchronization. Thus, for example, values above the dotted line refer to a population that became more synchronized, on average, with all other populations in the group over the period.

Hierarchical modeling of synchronization rates revealed differences among populations and regions (Figure 1). The highest probability synchronization rate was positive (increasing synchrony) for 16 of 21 Snake River populations. Furthermore, in 10 populations the 95% probability distribution of synchronization rates was above 0. Similarly, the probability distribution of the hyper-distribution of synchronization rate for all populations within the Snake River region was positive and nonoverlapping with 0, indicating that this group of populations is generally increasing in synchrony (Figure 1a). In contrast, at the scale of river systems in Bristol Bay, sockeye populations both increased and decreased in synchrony, and the hyper-distribution of synchronization rates was centered on 0 (Figure 1b). At the scale of stream populations within the Wood River system, populations tended to become less synchronized (Figure 1c).
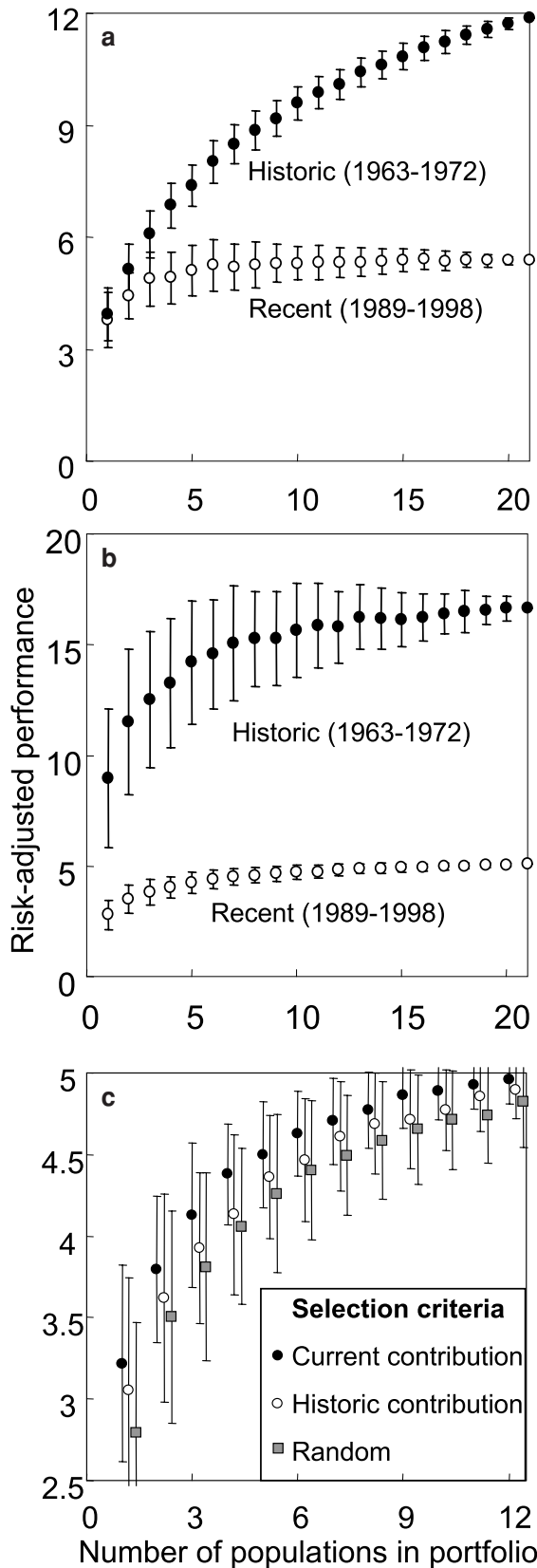
Portfolio analysis

Simulations revealed that the synchronization among Snake River Chinook salmon populations decreased the portfolio performance of this stock (Figure 2). Increasing the number of populations decreases variability (risk), increasing average performance, but the pattern of increase differed under different levels of synchrony (Figure 2). During the historic period, population dynamics were asynchronous; increasing the number of populations increased performance even when the portfolio contained many populations. In contrast, during the recent period, populations have such high covariance that the benefits of population richness are achieved quickly, and increasing the number of populations does little to improve average portfolio performance (Figure 2a). Across the study period, there was not only an increase in synchronization, but there was also a decrease in population productivity, further reducing portfolio performance (Figure 2b).

To a lesser degree, selection criteria for inclusion of populations also influenced performance (Figure 2c). Selecting populations based on historic and current population size resulted in higher average portfolio performance than random inclusion, but only slightly. For example, in a portfolio with four populations, using historic and current population size to guide inclusion only increased portfolio performance by 1.8% and 7.8% when compared to random selection, respectively. This low influence of inclusion criteria on portfolio performance is likely due to the temporal inconsistency of population characteristics and the weak relationship between population size and population productivity.

Figure 2 Performance of a portfolio of salmon populations as a function of time period, number of populations, and selection criteria. The *y*-axis portrays the predicted performance of the portfolio, based on the Sharpe index and data drawn from 21 Chinook salmon populations from the Snake River Evolutionary Significant Unit (see text for methods). The symbols reflect the average performance across 200 simulations and error bars are ± 1 standard deviation. (a) Simulations where the covariance was the only difference between the time periods. The population characteristics were held constant over the periods and the population-specific productivity and variance were calculated and used for the entire period (1963–1998). (b) Simulations where both the population characteristics and covariances were used for the specified decade. (c) Simulations of the recent period that examined different population inclusion scenarios based on: current contribution (filled black circles), historic contribution (white circles), or random (gray squares). Note different *x* and *y* axes scales on the different panels.

Discussion

Chinook salmon populations within the Snake River Evolutionarily Significant Unit have become more synchronized; over 75% of the populations increased in synchrony over the last four decades (Figure S1). Isaak *et al.* (2003) analyzed redd counts from a subset of the populations (Middle Fork Salmon River) and also observed increased population synchrony. Our results suggest that the synchronization is occurring over a larger area and for more populations than previously described.

In this system, there are several possible mechanisms underlying the observed increase in synchrony. First, changes in population abundance can affect correlations between populations (Bolker & Grenfell 1996; Paradis *et al.* 1999). However, the observed decreases in population abundance (Figure 3a) should decrease interpopulation synchrony due to an increase in demographic noise. This is in contrast to our observed results. Second, climate change could be driving the synchronization of salmon populations, especially as abiotic factors approach the limits of physiological tolerances (e.g., water temperatures approach thermal maxima). Indeed, some locations in the Snake River region exhibited increased air temperatures and earlier discharge peaks (see appendix S1) and these populations are closer to their southern range limit. Third, over the last century, anthropogenic activities in the Snake River basin may have homogenized
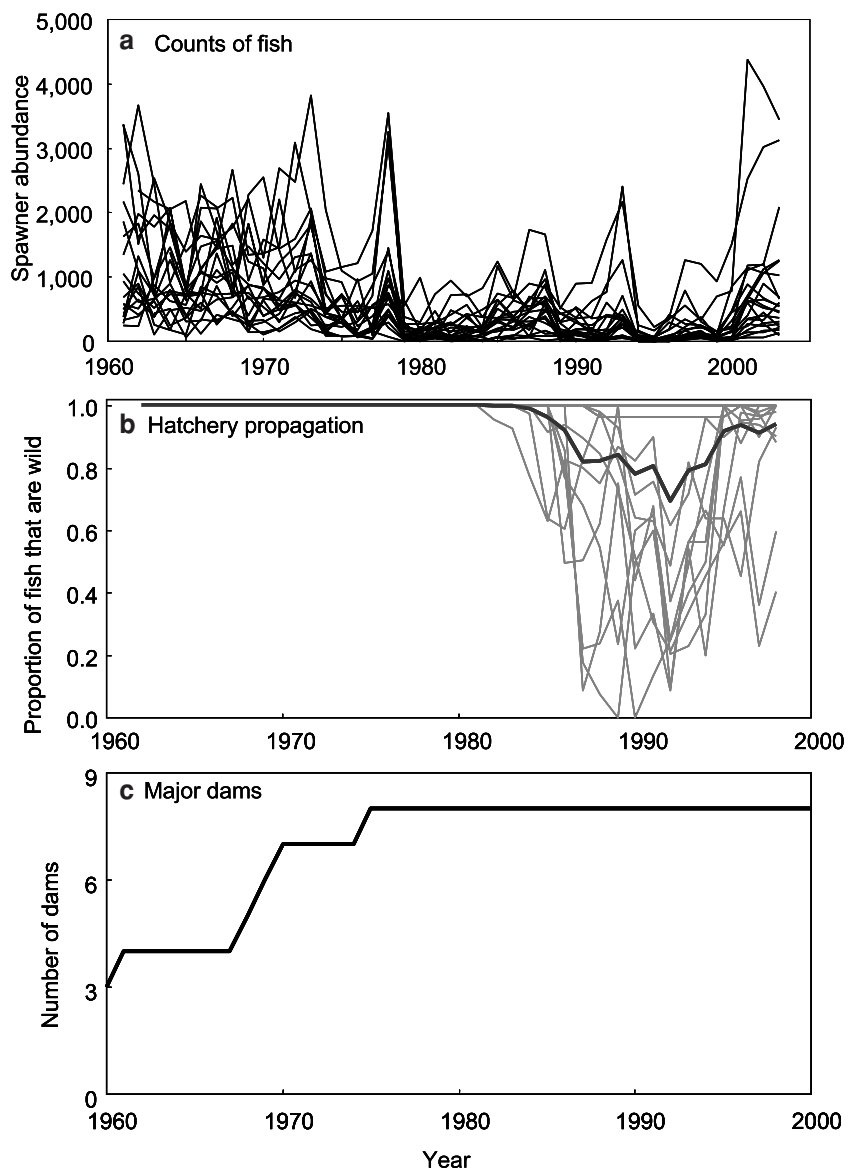

Figure 3 Time series data from the Snake River Evolutionary Significant Unit. (a) Numbers of spawning adult Chinook salmon in 21 populations. (b) Estimates of the proportion of returning fish that have wild parents. Gray lines show single populations from the Snake River Evolutionary Significant Unit, and the solid black line portrays the average across the 21 populations. (c) Cumulative number of major dams on the migration route for salmon populations in the Snake River Evolutionary Significant Unit. Note the differences in *x*-axis.

environments and reduced genetic diversity. Hatchery releases, which increased substantially during the study period (Figure 3b), are associated with increased straying and decreased population structure (Ayllon *et al.* 2006; McClure *et al.* 2008). In addition, dams homogenize habitats and flow regimes (Poff *et al.* 2007), leading to the loss of habitat variability that maintains salmonid population diversity (e.g., Beechie *et al.* 2006). There was an increase in the number of major dams during the study period (Figure 3c). These anthropogenic influences are likely contributing to the observed synchronization of salmon population dynamics.

The comparison between Snake River populations and Bristol Bay populations is not ideal; they differ in location and species. However, the two species do have roughly similar life histories with similar periods of freshwater and ocean residency. Unfortunately, unimpacted reference systems in the U.S. Pacific Northwest do not exist, and Chinook salmon are not well-documented in Alaska.

Regardless of the underlying mechanisms, the observed increase in population synchrony has major conservation implications. First, theory predicts that increased synchrony will increase extinction risk for the entire meta-population (Heino *et al.* 1997; Earn *et al.* 2000; Engen *et al.* 2002), which has already been identified as having a substantial risk of extinction (McClure *et al.* 2003). In addition, Chinook salmon populations are now fluctuating more similarly, no longer buffering the portfolio against change. Our simulations revealed that this increased synchrony has compromised the performance of this portfolio. Specifically, increased synchrony decreases portfolio performance and reduces the benefit of population richness. Thus, the stock is now more vulnerable to temporal fluctuations—synchronization is likely to increase the probability of synchronous crashes of populations with serious consequences for their conservation and use in fisheries. These analyses not only apply to the small subsistence fishery operating on the remaining Snake River Chinook salmon, but also provide a useful example for understanding the consequences of diversity loss in other exploited stocks.

Population asynchrony can be considered as high levels of "response diversity" of populations (sensu Elmqvist *et al.* 2003). We offer the following suggestions for incorporating this response diversity into management strategies:

1. Include population diversity as a goal for recovery. Indeed, habitat, genetic, and phenotypic diversity within and among populations have been included as a component of goals used in management plans for Pacific salmon in the United States and Canada (McElhany *et al.* 2000; DFO 2005).

2. Preserve the diverse habitats and natural processes that maintain response diversity. Preserving variable landscapes and the physical processes that maintain habitat variation (Stanford *et al.* 2005) will help maintain the different environmental conditions supporting adaptation and response diversity of phenotypic traits such as timing of migration and spawning (Hilborn *et al.* 2003; Rogers & Schindler 2008; Schindler *et al.* 2008).

3. Adjust artificial propagation programs to manage for response diversity. Reducing artificially inflated straying rates, using locally derived brood stock, and ensuring that hatchery-origin spawners are not overly represented on spawning grounds, are all changes that would reduce impacts of artificial propagation on response diversity (Mobrand *et al.* 2005).

4. Manage harvest in mixed-origin fisheries to avoid depleting low productivity populations that are harvested simultaneously with more productive populations (e.g., Hilborn 1985). Given that population productivities will change through time, protecting the amalgamation may eventually pay off to fishery production as some low productivity populations become more productive, and vice versa.

5. Given that population productivities change through time, monitoring should not just focus on currently productive populations but also include lower productivity populations (e.g., Walters & Cahoon 1985; Price *et al.* 2008).

Conserving population diversity and the associated asynchrony in population dynamics could be critical for long-term production and sustainability of any spatially structured species. While there has been much attention devoted to species extinction, there have been calls for increased focus on biodiversity loss on the population level (Ehrlich & Daily 1993; Balmford *et al.* 2003; Luck *et al.* 2003), especially for exploited populations (e.g., Walters & Cahoon 1985; Hutchinson 2008). Managing for this population diversity and associated response diversity will likely necessitate changing monitoring, management, and conservation strategies to maintain networks of intact habitat and the associated stocks of locally adapted populations (DFO 2005; Schindler *et al.* 2008).

Acknowledgments

Supporting Information

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

Figure S1: Temporal changes in the correlation among populations in Snake River Chinook populations.

Appendix S1: Temporal changes in Snake River flow regime and temperature.

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References

Achord, S., Zabel R.W., Sandford B.P. (2007) Migration timing, growth, and estimated parr-to-smolt survival rates of wild Snake River spring-summer Chinook salmon from the Salmon River Basin, Idaho, to the Lower Snake River. *Trans Am Fish Soc* **136**, 142–154.

Ayllon, F., Martinez J.L., Garcia-Vazquez E. (2006) Loss of regional population structure in Atlantic salmon, *Salmo salar* L., following stocking. *ICES J Mar Sci* **63**, 1269–1273.

Balmford, A., Green R.E., Jenkins M. (2003) Measuring the changing state of nature. *Trends Ecol Evol* **18**, 326–330.

Beechie, T., Buhle E., Ruckelshaus M., Fullerton A., Holsinger L. (2006) Hydrologic regime and the conservation of salmon life history diversity. *BiolConser* **130**, 560–572.

Bolker, B.M., Grenfell B.T. (1996) Impact of vaccination on the spatial correlation and persistence of measles dynamics. *Proc Natl Acad Sci* **93**, 12648–12653.

Crozier, L.G., Zabel R.W. (2006) Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. *J Anim Ecol* **75**, 1100–1109.

DFO (Fisheries and Oceans Canada). (2005) Canada's policy for conservation of wild Pacific salmon. Available from: http://www.pac.dfo-mpo.gc.ca/publications/pdfs/wsp-eng.pdf. Accessed 19 February 2010.

Earn, D.J.D., Levin S.A., Rohani P. (2000) Coherence and conservation. *Science* **290**, 1360–1364.

Ehrlich, P.R., Daily G.C. (1993) Population extinction and saving biodiversity. *Ambio* **22**, 64–68.

Elmqvist, T., Folke C., Nyström M. *et al.* (2003) Response diversity, ecosystem change, and resilience. *Front Ecol Environ* **1**, 488–494.

Engen, S., Lande R., Sæther B.-E. (2002) The spatial scale of population fluctuations and quasi-extinction risk. *Amer Natur* **160**, 439–451.

Good, T.P., Waples R.S., Adams P., editors. (2005) *Updated status of federally listed ESUs of West Coast salmon and steelhead. U.S. Dept. Commer., NOAA Tech.* Memo. NMFS-NWFSC-66, 598 p. Available from: http://www.nwr.noaa.gov/Publications/Biological-Status-Reviews/upload/SR2005-allspecies.pdf. Accessed 19 February 2010.

Greene, C.M., Hall J.E., Guilbault K.R., Quinn T.P. (2009) Improved viability of populations with diverse life-history portfolios. *Biol Lett*doi:10.1098/rsbl.2009.0780.

Heino, M., Kaitala V., Ranta E., Lindstrom J. (1997) Synchronous dynamics and rates of extinction in spatially structured populations. *Proc Roy Soc London B* **264**, 481–486.

Hilborn, R. (1985) Apparent stock recruitment relationships in mixed stock fisheries. *Can J Fish Aquat Sci* **42**, 718–723.

Hilborn, R., Quinn T.P, Schindler D.E., Rogers D.E. (2003) Biocomplexity and fisheries sustainability. *Proc Natl Acad Sci* **100**, 6564–6568.

Hutchinson, W.F. (2008) The dangers of ignoring stock complexity in fishery management: the case of the North Sea cod. *Biol Lett* doi:10.1098/rsbl.2008.0443.

Isaak, D.J., Russell F.T., 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. *Can J Fish Aquat Sci* **60**, 840–848.

Koellner, T., Schmitz O.J. (2006) Biodiversity, ecosystem function, and investment risk. *BioScience* **56**, 977–985.

Liebhold, A., Koenig W.D., Bjørnstad O.N. 2004. Spatial synchrony in population dynamics. *Annu Rev Ecol Evol System* **35**, 467–490.

Luck, G.W., Daily G.C., Ehrlich P.R. (2003) Population diversity and ecosystem services. *Trends Ecol Evol* **18**, 331–336.

Markowitz, H. (1952) Portfolio selection. *J Finance* **7**, 77–91.

McClure, M.M., Holmes E.E., Sanderson B., Jordan C.E. (2003) A large-scale, multispecies status assessment: anadromous salmonids in the Columbia River basin. *Ecol Appl* **13**, 964–989.

McClure, M.M., Utter F.M., Baldwin C. *et al.* (2008) Evolutionary effects of alternative artificial propagation programs: Implications for the viability of endangered anadromous salmonids. *Evol Appl* **1**, 356–375.

McElhany, P., Ruckelshaus M.H., Ford M.J., Wainwright T.C., Bjorkstedt E.P. (2000) Viable salmon populations and the recovery of evolutionarily significant units. U.S. Dept. of Commerce, NOAA Tech. Memo., NMFS-NWFSC-42, 156 p. Available from: http://www.nwfsc.noaa.gov/assets/25/5561_06162004_143739_tm42.pdf. Accessed 19 February 2010.

Mobrand, L.E., Barr J., Blankenship L. *et al.* (2005) Hatchery reform in Washington state: principles and emerging issues. *Fisheries* **30**, 11–23.

Paradis, E., Baillie S.R., Sutherland W.J., Gregory R.D. (1999) Dispersal and spatial scale affect synchrony in spatial population dynamics. *Ecol Lett* **2**, 114–120.

Peterman, R.M., Pyper B.J., Lapointe M.F., Adkison M.D., Walters C.J. (1998) Patterns of covariation in survival rates of British Columbia and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Can J Fish Aquat Sci* **55**, 2503–2517.

Poff, N.L., Olden J.D., Merritt D.M., Pepin D.M. (2007) Homogenization of regional river dynamics by dams and global biodiversity implications. *Proc Natl Acad Sci* **104**, 5732–5737.

Price, M.H.H., Darimont C.T., Temple N.F., MacDuffee S.M. (2008) Ghost runs: management and status assessment of Pacific salmon (*Oncorhynchus* spp.) returning to British Columbia's central and north coasts. *Can J Fish Aquat Sci* **65**, 2712–2718.

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. *Trans Am Fish Soc* **134**, 86–104.

Rogers, L.A., Schindler D.E. (2008) Asynchrony in population dynamics of sockeye salmon in southwest Alaska. *Oikos* **17**, 1578–1586.

Ruzzante, D.E., Mariani S., Bekkevold D. *et al*. (2006) Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. *Proc R Soc B* **273**, 1459–1464.

Schindler, D.E., Augerot X., Fleishman E. *et al*. (2008) Climate change, ecosystem impacts, and management for Pacific salmon. *Fisheries* **33**, 502–506.

Schindler, D.E., Hilborn R., Chasco B. *et al*. (in press) Population diversity and the portfolio effect in an exploited species. *Nature*.

Schindler, D.E., Rogers L.A. (2009) Responses of salmon populations to climate variation in freshwater ecosystems. Pages 1127–1142 in C.C. Krueger, C.E. Zimmerman, editors. *Pacific Salmon: ecology and management of western Alaska's populations. Symposium 70*. American Fisheries Society, Bethesda, MD.

Sharpe, W.F. (1994) The Sharpe ratio. *J Portf Manage* **Fall**, 49–58.

Stanford, J.A., Lorang M.S., Hauer F.R. (2005) The shifting habitat mosaic of river ecosystems. *Verh Internat Verin Limnol* **29**: 123–136.

Walters, C.J., Cahoon P. (1985) Evidence of decreasing spatial diversity in British Columbia salmon stocks. *Can J Fish Aquat Sci* **42**, 1033–1037.

Zabel, R.W., Levin P.S. (2002) Simple assumptions on age composition lead to erroneous conclusions on the nature of density dependence in age-structured populations. *Oecologia* **133**, 349–355.