In many ecological systems diversity increases the availability and stability of ecosystem services. Such diversity-stability relationships typically arise due to the dynamics of individual species or populations varying asynchronously with one another, resulting in reduced temporal variability of the aggregate relative to its components. To maximize stability, resource managers are increasingly focused on monitoring and conserving ecological aggregates, rather than single species or component populations. For example, many government agencies tasked with managing multispecies fisheries have transitioned from single-species stock assessments to ecosystem-based approaches that evaluate the status of multiple trophic levels (REF).

At the coarsest level, the correlation between diversity and temporal stability, commonly referred to as the portfolio effect, is an artifact of statistical averaging, i.e. stability is directly related to the number of components in the system (REF). Yet aggregate variability is clearly driven by processes beyond the number of component species or populations. For example, many ecological aggregates exhibit evidence of increased temporal variability in recent years even though the number of components they contain is unchanged. Example 1. Example 2. Such aggregates, often referred to as “collapsed portfolios”, are of particular conservation concern because they are less capable of providing essential ecosystem services and may be at higher risk of extirpation. Recent work in community ecology has provided a framework to explore changes in aggregate variability in greater detail. Thib and Conn 2013 demonstrate that aggregate variability can be quantified as a function of the mean variability of each component (weighted by its abundance) and synchrony among components. These metrics are robust to differences in evenness, diversity, and abundance among communities or metapopulations, allowing disparate systems to be directly compared. Although component variability and synchrony can have complex knock-on effects on population dynamics (REF), analyses that simultaneously evaluate both metrics in ecological aggregates are relatively rare.

We believe that decomposing aggregate variability into trends in synchrony and component variability can guide conservation and management strategies in multiple ways. First, changes in each metric provide distinct information about the scale at which destabilizing processes have occurred. If the component variability has increased, but synchrony has remained relatively stable, then apparent changes in metapopulation dynamics are likely the result of local, perhaps isolated, processes. Conversely, coherent increases in both synchrony and aggregate variability would suggest that regional drivers have become increasingly dominant, as well as destabilizing. These patterns can in turn guide directed management actions. For example, targeted interventions to stabilize the dynamics of specific populations (e.g. reducing mortality rates) are much more likely to improve the status of the aggregate in the former scenario than in the latter.

Second, changes in component variability as opposed to synchrony may indicate different categories of conservation risk. Within an individual component species or population, increased variability may be detrimental to persistence due to an increased likelihood of extirpation (REF). Greater synchrony, paired with downward trends in abundance, is often viewed as an early warning signal of hysteresis or regime shifts in ecological aggregates (REF). Evidence suggests that many ecological systems are exhibiting both increasingly variable and synchronized dynamics (REF), which intuitively should be associated with particularly dire conservation outcomes.

In this study, we decompose aggregate temporal variability in a Pacific salmon metapopulation into component variability and synchrony then use stochastic simulations to evaluate the long-term consequences of these changes to conservation goals. We focus our analysis on Fraser River sockeye salmon, an abundant and diverse Pacific salmon metapopulation located in southern British Columbia. Fraser River sockeye salmon are commercially exploited in mixed-stock fisheries, but component populations vary in their abundance and conservation status. Furthermore, many populations have experienced declines in recent years (REF) and the aggregate has exhibited recurring periods of high synchrony (REF). The optimal management strategy would allow abundant populations to be harvested while simultaneously allowing depleted populations to recover. Given that changes in aggregate variability may complicate this goal, we used statistical and closed-loop simulation models to test two hypotheses. 1) To what extent are observed trends in aggregate variability associated with changes in the variability of component populations, as opposed to changes in synchrony among component populations? 2) Are increases in aggregate variability associated with an increased likelihood of negative conservation outcomes and, if so, do changes in synchrony versus component variability have differential effects on those outcomes? Given the impact of human exploitation on the dynamics of these populations, the closed-loop simulation incorporate multiple sources of mortality, as well as a realistic proxy of the current harvest control rule used to determine total allowable catch.

**Methods**

*Sockeye salmon biology, fisheries and data sources*

Sockeye salmon is an anadromous, semelparous fish distributed throughout the northern Pacific. Populations in southern British Columbia typically rear as juveniles in freshwater lakes for one-two years, mature in the Gulf of Alaska, and return to spawn as two-five year olds. Pacific salmon populations exhibit local adaptations and are typically managed to conserve life history diversity (REF). In Canada, Pacific salmon status is assessed at the scale of conservation units (CUs) – groups of spawning populations with a common life history strategy, adult migration phenology, genetic history, and juvenile rearing habitat. Sockeye salmon CUs typically contain fewer spawning populations and are more spatially restricted than the CUs of other species due to their dependence on nursery lakes. The Fraser River sockeye salmon aggregate is composed of 24 CUs, which are grouped into four management units (MUs) based on adult migration timing. Like many Pacific salmon, Fraser River sockeye salmon are only targeted by commercial fisheries as they move through nearshore areas relatively close to their natal river. As a result, shifting marine fishery openings to coincide with a given migration phenology can be used to constrain effort at the MU, but not the CU, level. The Fraser River sockeye salmon MUs, along with their respective run timings and the component CUs included in our analysis, are described in Table 1 and Fig. 1.

Although the majority of Fraser River sockeye salmon were historically harvested in Canadian marine fisheries, mortality from at least three other sources can be substantial. First, American commercial fisheries in Juan de Fuca Strait off the coast of Washington harvest returning sockeye salmon before they reach Canadian waters. Second, individuals that pass through American and Canadian marine fisheries can experience high rates of en route mortality before reaching their spawning grounds, presumably due to a combination of natural mortality (thermal stress, pathogen infection, predation) and unreported harvest (REF). En route mortality, which can exceed 60% in certain years (REF), appears to be correlated with migration phenology, in-river temperatures (REF), and freshwater flow (REF). Finally, Fraser River sockeye may be harvested in a range of in-river fisheries (e.g. food, social and ceremonial First Nations fisheries, terminal demonstration fisheries), which are closer to spawning grounds and therefore more stock-specific.

A range of ecological processes may underpin changes in variability and synchrony in Fraser River sockeye salmon. Component variability (i.e. within CU temporal variation) may increase due to changes in local environmental conditions, such as loss of spawning habitat (REF), high levels of mortality during incubation (e.g. scouring events (REF), high water temperatures (REF)), or changes in competition and predation during juvenile freshwater stages (REF). Synchrony among components within metapopulations is often associated with connectivity (i.e. dispersal). Although Fraser River sockeye salmon likely function as a metapopulation on long, evolutionary time scales, from a management perspective dispersal is assumed to be nil, with each CU representing a genetically distinct population assemblage (REF). In the absence of dispersal, synchrony is linked with a common response to shared environmental drivers (i.e. Moran effect), competitors, or predators. In the case of Fraser River sockeye salmon, such mechanisms may be more likely to occur during marine residence, when populations from throughout North America migrate to the Gulf of Alaska.

The time series of salmon abundance we used for this analysis are derived from estimates of spawner abundance and recruitment (age-specific catch plus escapement minus an adjustment for en route mortality) for 19 relatively data-rich CUs (Grant et al. 2011). Depending on the CU, these time series began between 1948 and 1973. Escapement estimates have been generated using a variety of techniques including fence counts, mark-recapture and visual surveys, and passive sonar methods (Grant et al. 2011). Catch is estimated in marine and freshwater fisheries for each CU and age class. Methods for estimating escapement and catch are reviewed in detail in Grant et al. (2011).

*Synchrony metrics*

We examined temporal changes in three metrics of metapopulation variability (Loreau and de Mazancourt 2008; Thibaut and Connolly 2013). Synchrony (Equation 1) reflects the relative degree of similarity in the dynamics of an aggregate’s components. It is defined as the total temporal variance of an aggregate’s components (i.e. sum of all elements of the variance-covariance matrix), divided by the variance of a hypothetical aggregate with the same component variances, but perfect covariance.

Equation 1

Here *v* denotes variance (over time) for populations *i* through *j* making up an aggregate. Thus the simplified numerator represents the variance of the total abundance of the aggregate consisting of *n* populations. The denominator is the variance of a hypothetical population aggregate with the same population-level variances, but perfectly synchronized (Loreau and de Mazancourt 2008; Thibault and Connolly 2013). This synchrony index () is analogous to comparing mean pairwise correlation coefficients, which have been used in similar analyses (e.g. Peterman and Dorner 2012), but makes no distributional assumptions, is normalized (i.e. ranges between 0 and 1 rather than -1 and 1), and explicitly accounts for unequal variances among components.

The second metric is the mean of the component populations’ coefficients of variation (CVc), weighted by each component’s mean abundance.

Equation 2

where *mpop*(*i*) is the mean abundance (through time) of population *i* and *magg* is the mean abundance of the aggregate. Finally, we calculated the coefficient of variation for the aggregate (CVA) as a function of the first two metrics following Thibaut and Connolly (2013).

Equation 3

This metric defines CVA as linearly proportional to CVC, with a constant of proportionality related to synchrony. As synchrony increases, CVA becomes more similar to CVC and CVA is dampened when components are asynchronous.

*Retrospective analysis*

To explore changes in aggregate variability of Fraser River sockeye salmon, we calculated continuous time series of , CVC, and CVA using 10-year moving windows of both spawner abundance and per capita productivity. We used the residuals from CU-specific spawner-recruit models as an index of productivity. For most CUs this model was defined as:

Equation 4

where *i* represents a CU, *y* is a given year, *R* the number of recruits (number of offspring that return to spawn or are captured in the fishery), and *S* the number of spawners. The parameter represents the number of recruits produced per spawner at low abundance and the density-dependent parameter, the reciprocal of the number of spawners that produce maximum recruits. To incorporate normally distributed process error , we linearized Equation 4:

Equation 5

The productivity of a subset of CUs with cyclic dynamics (Table 1) was estimated using a Larkin model, a modified version of the Ricker model that accounts for delayed density-dependent effects (details in supplement). Whether we estimated productivity for a given CU using a Ricker or Larkin model followed assignments made in the most recent Wild Salmon Policy assessment (REF). We examined trends in per capita productivity, rather than spawner abundance alone, because this metric accounts for density dependent processes and cyclicity, as well as changes in en route mortality and exploitation rate that moderate spawner abundance. While managers and stakeholders are most directly impacted by spawner abundance, increased variability or synchrony in productivity is potentially more concerning since recovery may be compromised even if harvest is dramatically reduced.

We next tested for linear increases in , CVC, and CVA by regressing each index against time. We then tested whether changes in CVA were more strongly correlated with or CVC by comparing correlation coefficients.

*Forward simulation*

We used a stochastic, closed-loop simulation model to explore how differences in aggregate variability may influence conservation outcomes for Fraser River sockeye salmon. The model includes CU-specific population dynamics and harvesting, while incorporating process, observation, and management implementation uncertainty. The dynamics of salmon CUs were simulated using age-structured models equivalent to Equation 5. To parameterize each CU’s stock-recruit relationship we used median estimates of and generated from an external, CU-specific Bayesian stock recruit analysis (ref to FRSSI). To account for autocorrelation and incorporate covariation among CUs we simulated deviations from the stock-recruitment relationship as

Where represents the previous year’s recruitment deviation, represents an AR1 autocorrelation coefficient, and represents random error drawn from a multivariate normal distribution with mean 0 and standard deviation defined by the variance-covariance matrix between CUs *i* and *j*.

Each year we calculated exploitation rates using a harvest control rule (HCR) that replicates the Total Allowable Mortality framework currently used to manage Fraser River sockeye salmon fisheries (REF). Broadly speaking, this HCR uses in-season forecasts of recruitment to adjust target exploitation rates to meet escapement goals. If in-season forecasts of recruitment exceed escapement goals, the HCR switches to a fixed maximum target mortality rate. Details of the harvest control rule are described in Appendix 1. Since target exploitation rates in mixed stock marine fisheries are adjusted based on abundance at the management unit (MU) level, we simulated the forecast process as

Equation 6

where is the forecasted abundance of recruits from MU *m.* Mean forecast error was parameterized using deviations between in-season and post-season estimates of salmon abundance from 2007-2011 (Fraser River Panel reports). In order to produce realistic deviations in forecast error, the normal distribution was truncated at 0.

We calculated an MU-specific target harvest rate (based on relative to escapement goals) and we calculated a realized exploitation rate for each CU by adjusting its target harvest rate to incorporate outcome uncertainty (details below). Outcome uncertainty is intended to represent processes such as underreporting, insufficient enforcement, by-catch of non-target MUs, or changes in catchability, which lead to deviations between target and realized exploitation rates.

Biological benchmarks are commonly used to assess population status relative to a desired state (REF). In this study, we calculated benchmarks derived from stock-recruit relationships and referenced in Canada’s Wild Salmon Policy (REF). The upper benchmark is the estimated spawner abundance necessary to achieve maximum sustainable yield (*S*MSY), estimated using the Lambert W function following Scheuerell (2016)

Equation 7

The lower benchmark is the estimated spawner abundance necessary to recover to *S*MSY in one generation in the absence of fishing mortality (*S*gen), which was solved numerically according to the following equation (Holt et al. 2009)

Equation 8

SMSY is intended to represent an abundance at which a CU can sustain harvest and provide its full suite of ecosystem services indefinitely. Sgen is intended to be precautionary lower benchmark. Therefore, it represents abundance at which a CU is at increased risk of extirpation, which can be exacerbated by additional mortality introduced by harvest; however Sgen is typically greater than the abundance which would trigger protection under at-risk species legislation. Within the Wild Salmon Policy framework, CUs with an abundance greater than SMSY are considered green status, those with abundances below SMSY and above Sgen are amber, and those below Sgen are red.

*Sources of uncertainty*

The principal driver of aggregate variability in the simulation model are deviations from CU-specific stock-recruitment relationships (*w* in Eq. X). To explore the consequences of greater aggregate variability on long-term metapopulation dynamics we manipulated the strength of recruitment deviations by increasing CVC or (via changes in sigma and phi, respectively). We represented each CVC or φ “treatment” with a different operating model (i.e. the component of a closed-loop simulation representing a biological hypothesis (REF)), defined by a unique variance-covariance matrix

INSERT EXAMPLE MATRIX HERE

Recruitment deviations were estimated each year by drawing from a multivariate normal distribution with mean 0 and a standard deviation defined by this variance-covariance matrix. CU-specific estimates of sigma in Fraser River sockeye salmon are relatively large (mean = 0.97, range = 0.76 – 1.39). Therefore, we varied sigma between 0.75 and 1.5 across CVC treatments. To increase φ, we varied the correlation among CUs from 0 to 1. We completed a full factorial comparison to test the relative influence of independent changes in CVC and φ, as well as interactions between the two, resulting in 16 distinct operating models (Table 2).

We introduced additional stochasticity into the model via interannual variation in age at maturity (lognormal), forecasting error, en route mortality, and outcome uncertainty (Table 2). Although the parameters for these variables did not change across the tested operating models, we increased and decreased each in a series of sensitivity analyses to ensure that our results were robust to assumptions. Details of how each process was parameterized, as well as the results of the sensitivity analyses, are provided in the online supplement.

*Evaluating model performance*

We first confirmed that each operating model produced the predicted changes in CVC,φ and CVA. We then used four performance measures (PMs) to assess how changes in CVA altered the likelihood of achieving different management objectives. Mean recruit abundance represents the temporal mean number of individuals (at the aggregate level, i.e. summed across CUs) that are available to harvest or escape to spawning grounds each year. Mean catch represents the temporal mean number of individuals captured in the mixed stock fishery. As a result, mean catch integrates the effects of additional uncertainty (e.g. forecast, implementation) relative to mean recruit abundance and provides a proxy for socio-economic factors that may influence fisheries management decisions. The last two PMs incorporate biological benchmarks based on stock-recruit analyses, providing a more nuanced estimate of population status than absolute abundance. The first is the proportion of years the aggregate was above its lower benchmark (∑*S*Gen, k), while the second is the proportion of CUs within the aggregate that were above their individual lower benchmarks (*S*Gen, k).

We focused the majority of our analysis on performance metrics that represent the status of the metapopulation because CVC,φ, and CVA reflect characteristics of the aggregate, rather than individual CUs. However, we present CU-specific PMs for a subset of CUs that often dominate management discussions. Since we were interested in both short- and long-term changes in population dynamics, we calculated each PM over two time frames – eight or 40 years after forward simulations began (two and ten generations, respectively).

Instead of priming the simulation with initial abundance sampled from random distributions, we used CU-specific time series of recruit and spawner abundance (i.e. the same data that were used in the retrospective analysis). We used these time series to ensure that each CU’s abundance reflected the best estimate of its current status and to seed cyclic CUs with representative levels of variation among cycle lines. The length of the simulation period was set at 40 years and each OM was simulated 1000 times (a supplementary analysis indicated variation in output metrics stabilized at 500-700 iterations). To evaluate differences in performance between OMs, we present median outputs among simulations, as well as 10th and 90th percentiles.