In many ecological systems diversity can increase the availability and stability of ecosystem services. Diversity-stability relationships typically arise due to the dynamics of individual species or populations varying asynchronously with one another. As a result, the temporal variability of an aggregate is reduced relative to its components. Increasingly, resource managers are explicitly recognizing these benefits and moving towards managing ecological aggregates, rather than single species or component populations. For example, several government agencies 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 simply an artifact of statistical averaging (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 even though their diversity 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.

Decomposing aggregate temporal variability into trends in synchrony and component variability can inform conservation or management strategies in multiple ways. First, it can provide information critical to identifying destabilizing processes. If the variability of a subset of abundant component populations 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 versus synchrony may indicate different levels of conservation risk. Increased variability is considered detrimental to population persistence and may serve as an early warning signal of hysteresis or regime shifts in ecological aggregates. Evidence suggests that many ecological systems are exhibiting increasingly variable and synchronized dynamics (REF), which intuitively should be associated with negative conservation outcomes; however the long-term risks associated with these trends are rarely explicitly quantified.

In this study, we identify the processes that underpin aggregate variability in a Pacific salmon metapopulation and then construct stochastic, closed-loop simulation models to explore the consequences of component variability and synchrony on a suite of conservation metrics. 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 strong impact of exploitation on the dynamics of these populations, the closed-loop simulation incorporates 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, management actions are structured around conservation units (CUs) – 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 most 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 in particular years. 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 maturation grounds, presumably due to a combination of natural mortality (thermal stress, pathogen infection, predation) and unreported harvest. 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.

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 are commonly 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 driven by synchrony. Therefore, as synchrony increases, CVA becomes increasingly 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 the same age-structured models described above (i.e. a Ricker model for most CUs and Larkin models for those with evidence of cyclicity), with process variance generated via random deviations in recruitment and age-at-maturity. 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). These models also generated estimates of stock-recruit deviations; however we parameterized sigma within the closed-loop simulation depending on the aggregate variability scenario that was being explored (details below).

Each year we calculated exploitation rates using a harvest control rule (HCR) that replicates the Total Allowable Mortality framework currently used to regulate Fraser River sockeye salmon fisheries. Briefly, this rule adjusts target exploitation rates to meet escapement goals when in-season forecasts of recruitment are moderate relative to fishery reference points. When in-season forecasts of recruitment exceed the upper fishery reference points, the HCR switches to a fixed 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 salmon abundance at the MU level, we simulated the forecast process as

Equation 6

where is the forecasted abundance of recruits from management unit *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.

As noted above, each MU’s total allowable catch (TAC) was determined by the MU’s forecast relative to two fishery reference control points (Table A1). The TACs were used to calculate an MU-specific target harvest rate 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 two benchmarks that are 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 be consistent with a healthy population status, where the CU can sustain moderate harvest, and provide its fully suite of ecosystem service, indefinitely. Sgen, as a lower benchmark, is intended to be precautionary. Therefore, it represents an increased risk of extirpation that can be exacerbated by additional mortality introduced by harvest, but is typically still greater than the abundance which triggers protection under at-risk species legislation. Within the Wild Salmon Policy framework, CUs with an average abundance greater than SMSY are assigned a green status, those with an abundance 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 is 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 φ (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.