In many ecological systems diversity can increase the availability and stability of ecosystem services. As a result, natural resource disciplines have begun to shift towards managing ecological aggregates, such as communities or metapopulations, rather than single species or component populations. For example, government agencies that manage multispecies fisheries have begun to transition from single-species stock assessments to ecosystem-based approaches that evaluate the status of multiple trophic levels (REF). One of the key benefits of structuring management actions to preserve ecological aggregates is that aggregate variability is typically reduced relative to their components due to individual species or populations varying asynchronously with one another. 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 so that aggregates with a larger number of components will typically be more stable (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 is a function of the mean variability of each component (weighted by its abundance) and their synchrony. These metrics are robust to differences in evenness, diversity, and abundance among communities or metapopulations, allowing for comparisons to be made between disparate systems.

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. For example, if the variability of a subset of abundant component populations has dramatically increased, but synchrony has remained relatively stable, then apparent changes in metapopulation dynamics are likely the result of distinct, local 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. However, it is not immediately clear whether metapopulation dynamics will respond differently to changes in component variability as opposed to synchrony. If the negative consequences of one process are more severe or probable than the other, tracking changes in aggregate variability may be insufficient to assess conservation risk.

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 with a range 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. In Canada, Pacific salmon are managed as conservation units (CUs) – spawning populations with a common life history strategy, adult migration phenology, genetic history, and juvenile rearing habitat. Typically, individual sockeye salmon CUs 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 X 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 we used for this analysis include estimates of spawner abundance and recruitment (age-specific catch plus escapement minus an adjustment for en route mortality; 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 recently defined, 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.

Eq. 1 ADD EQ 2 FROM THIB and CONN

This synchrony index (φ) is approximately equivalent to comparing mean pairwise correlation coefficients, which are commonly used in similar analyses, 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 components’ coefficients of variation (CVc), weighted by each component’s mean abundance.

Eq. 2 Add EQ 4

Finally, we calculated the coefficient of variation for the aggregate (CVA) as a function of the first two metrics following Thibaut and Connolly (2013).

Eq. 3 Add EQ 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 φ, 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:

Ricker Eq.

Where *i* represents a population, *t* a generation time, *R* the number of recruits (number of offspring that return to spawn or are captured in the fishery), *S* the number of spawners, *a* the productivity parameter, and *b* the density-dependent parameter. The term *wi(t)* represents random error with a mean of zero and standard deviation sigma.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 productivity was estimated using a Ricker or Larkin model followed designations in the most recent Wild Salmon Policy assessment (REF). We examined trends in per capita productivity 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 slowed even when harvest is dramatically reduced.

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

*Forward simulation*

We used a stochastic closed-loop model to forward simulate the dynamics of the Fraser River sockeye salmon aggregate and explore how differences in aggregate variability may influence conservation outcomes. 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 Ricker or Larkin models described above, with process variance generated via random deviations in recruitment and age-at-maturity. To parameterize each CU’s stock-recruit relationship we used CU-specific median estimates of *a* and *b* generated from an external stock recruit analysis (ref to FRSSI). While these models generate estimates of stock-recruit deviations, we parameterized sigma within the closed-loop simulation depending on the aggregate variability scenario that was being explored (details below).

We simulated harvest each year, with exploitation rates determined by a harvest control rule (HCR) that replicates the Total Allowable Mortality framework currently used to regulate harvest rates for Fraser River sockeye salmon (details in supplement). Briefly, each year a forecast of recruit abundance was generated at the MU level, the scale at which harvest rates are set in mixed stock marine fisheries. Whether the forecast was above, below, or between two reference control points determined each MU’s total allowable catch (TAC), which were then used to calculate an MU-specific target harvest rate. Finally, we calculated a realized exploitation rate for each CU by adjusting the target harvest rate to incorporate outcome uncertainty (details below). Outcome uncertainty is intended to processes such as underreporting, insufficient enforcement, spatial/temporal overlap between MUs in fisheries, or changes in catchability that may lead to deviations between target and realized exploitation rates.

Biological benchmarks are commonly used to assess population status relative to a target state (REF). We estimated two benchmarks referenced in Canada’s Wild Salmon Policy to provide a more nuanced estimate of changes in each CU’s status through time. The upper benchmark is the estimated spawner abundance necessary to achieve maximum sustainable yield (*S*MSY). *S*MSY was estimated as

INSERT Smsy eq

Where … . 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).

INSERT Sgen eq

*Sources of uncertainty*

A principal driver of stochasticity in the model are deviations from the CU-specific stock-recruitment relationship (*w* in Eq. X). We manipulated this parameter to test the consequences of aggregate variability on long-term metapopulation dynamics by increasing CVC or φ (via changes in sigma and phi, respectively). For the remainder of this manuscript we refer to each CVC or φ “treatment” as an operating model. We defined each operating model using 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 variance defined by the variance-covariance matrix. We completed a full factorial comparison to test the relative influence of independent changes, as well as interactions between both metrics, resulting in 16 distinct operating models (Table 2).

We introduced additional stochasticity into the model via variation in age at maturity (lognormal), forecasting error, en route mortality, and outcome uncertainty (INSERT EQUATIONS). 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 our results were robust to assumptions (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 metrics 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 spawner abundance and provides a proxy for socio-economic dimension. The last two PMs incorporate biological benchmarks, providing a more nuanced estimate of 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 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. 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 realistic 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.

* Simulation specifics
  + Instead of a priming period to initiate the simulation, we used CU-specific observations of recruits and spawners; ensured that populations were at realistic levels of abundance and that cyclic stocks generated realistic patterns
  + The simulation period was set at 60 years (15 sockeye generations) and each synchrony scenario was simulated 1000 times (reference to simulation sensitivity analysis)
  + All output metrics represented by the median value plus/minus 90th/10th percentiles