Metapopulations and ecological communities consist of components whose dynamics vary asynchronously due to unique life histories, local environmental processes, or simply chance. Such asynchrony tends to reduce variability in the dynamics of these ecological aggregates and results in positive diversity-stability relationships, commonly referred to as portfolio effects. The stability conferred by diversity has been associated with a decreased likelihood of extirpation (REF), greater aggregate biomass (REF), healthier ecosystem functioning (REF), and increased availability of ecosystem services (REF). As a result, resource managers are increasingly focused on monitoring and conserving ecological aggregates, rather than single species or component populations. The shift towards managing such aggregates is particularly widespread in fisheries science, where many agencies have a mandate to incorporate multi-stock or ecosystem-based approaches (REF). To sustainably exploit larger assemblages, it is necessary for biologists and managers to better understand how the dynamics of individual components interact to determine aggregate availability.

At the coarsest level, the correlation between diversity and temporal stability is an artifact of statistical averaging, with variability decreasing as the number of components increases (REF). A long-recognized example of this pattern occurs in Bristol Bay, Alaska, where the sheer number of sockeye salmon populations in the region buffers aggregate variability in spawner abundance and fishery yields (REF Hilborn, Schindler). Yet dramatic changes in aggregate variability can occur even as the number of component subpopulations or species remains stable. For example, returns of Central Valley Chinook salmon have simultaneously collapsed and become increasingly variable, reducing the availability of marine subsidies and resulting in frequent fishery closures (REF). REF 2. While the region still exhibits a portfolio effect, in that aggregate variability is reduced relative to component variability, the buffering that occurred historically has been weakened (Carlson and Satterthwaite 2013). Collapsed portfolios such as these are particularly concerning from a management perspective because stakeholders are increasingly unable to shift effort from depleted to relatively abundant components, increasing tension between conservation and socio-economic objectives (REF).

Summary statistics developed in community ecology provide a key tool to understand how interactions among ecological components can shape the dynamics of aggregates and contribute to these collapses. Specifically, Thibaut and Connolly (2013) demonstrate aggregate variability can be decomposed into two metrics representing component variability and synchrony. Although patterns of variance and covariance among subpopulations or species have been widely explored with correlation coefficients, the metrics of Thib and Conn 2013 are uniquely robust to differences in evenness, diversity, and abundance, which allows disparate communities or metapopulations to be compared. Patterns in each metric can guide conservation strategies by providing distinct information about the scale at which destabilizing processes have occurred. If component variability has increased, but synchrony has remained relatively stable, then changes in aggregate dynamics are likely the result of local processes, which may be addressed in isolation. 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, synchronous declines and greater component variability in Central Valley Chinook salmon were not seen in a nearby aggregate, suggesting they may be driven by widespread hatchery releases, rather than shared environmental conditions (Satterthwaite and Carlson 2015). Further analyses in the Sacramento River have demonstrated that conserving specific component aggregates can result in disproportionately large gains to the aggregate (Yamane et al. 2018).

Additionally, changes in component variability as opposed to synchrony may indicate different degrees of conservation risk. Within a component species or population, increased variability may be detrimental to persistence due to an increased likelihood of extirpation (REF). In managed systems such as fisheries, greater temporal variability can also decrease the accuracy of status assessments, potentially resulting in overexploitation (REF). On the other hand, greater synchrony, particularly when paired with downward trends in abundance, may serve as an early warning signal of hysteresis in which the entire aggregate shifts to a fundamentally different state (REF). Intuitively, ecological aggregates in which both processes are occurring simultaneously may be at particularly high risk.

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 on conservation outcomes. 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 other Pacific salmon 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 over evolutionary time scales, dispersal is assumed to be nil from a management perspective, with each CU representing a genetically distinct population assemblage (REF). In the absence of dispersal, synchronous dynamics may be driven by 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 were 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 generated 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.

*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 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* through *j*. We assigned a value of 0.2 for CUs modeled with a Ricker relationship, consistent with evidence of weak autocorrelation in the residuals of these models.

To adequately represent the framework used to manage Fraser River sockeye salmon we modeled four sequential sources of mortality: American fisheries, Canadian mixed-stock fisheries, en route mortality during freshwater migration, and terminal Canadian single-stock fisheries. Total allowable catches in both American and Canadian fisheries were calculated using a harvest control rule (HCR) that replicates the Total Allowable Mortality framework currently in use (REF). Broadly speaking, this HCR uses in-season estimates of recruitment derived from test fisheries to adjust target exploitation rates and meet escapement goals specific to each management unit (MU). If in-season recruitment estimates exceed escapement goals, the HCR switches to a fixed maximum target mortality rate. Escapement goals vary among years due to the cycles present in several CUs and are typically adjusted downwards to account for mortality during upstream migration. Details of the harvest control rule, mortality calculations, and parameter specifications are described in Appendix 1.

*Sources of uncertainty*

The principal drivers of variability in aggregate abundance within the model are deviations from CU-specific stock-recruitment relationships (*w* in Eq. X). To explore the consequences of greater aggregate variability on recruitment potential, we manipulated the strength of recruitment deviations via changes in or , resulting in nine operating models defined by unique variance-covariance matrices (Table 1). Each operating model represents a unique component variability and synchrony “treatment”. We introduced additional stochasticity into the model via interannual variation in age at maturity (lognormal), in-season abundance 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 a suite of performance measures (PMs) to assess how changes in each metric altered the likelihood of achieving different management objectives. Two PMs are driven solely by abundance. Median 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. The second abundance PM, median catch, represents the number of individuals captured in the mixed stock fishery. As a result, median catch integrates the effects of additional uncertainty (e.g. forecast, implementation) relative to 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).

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 8

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 9

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 an abundance at which a CU is at increased risk of extirpation, particularly if additional mortality is introduced by harvest; however Sgen is greater than the abundance that 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.

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.