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.

Historically, the majority of Fraser River sockeye salmon harvest occurred in Canadian marine fisheries; however mortality from three distinct sources can be substantial in particular years. First, American commercial fisheries in Juan de Fuca Strait off the coast of Washington harvest a proportion of returning sockeye salmon each year before they reach Canadian waters. Returning spawners that pass through American and Canadian marine fisheries (i.e. escapement), often experience considerable 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 appears to be correlated with migration phenology, in-river temperatures (REF), and freshwater flow (REF), and can exceed 60% in certain years. Finally, Fraser River sockeye may be harvested in terminal fisheries, which are closer to their spawning grounds and therefore more stock-specific.

We used estimates of spawner abundance and recruitment (age-specific catch plus escapement minus an adjustment for en route mortality; Grant et al. 2011) for Fraser River CUs. Depending on CU, these time series begin in 1948-1973. 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 reflects the relative degree of similarity in the dynamics of an aggregate’s components. It is defined as the total 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.

* + Synchrony – defined as the variance of total metapopulation abundance of *n* components (i.e. sum of all elements of variance-covariance matrix), divided by the variance of a hypothetical metapopulation with same component variances, but perfect covariance (i.e. synchrony)
    - Eq. 2
    - Makes no assumptions about distributions of pairwise correlation coefficients, is normalized (i.e. always varies between 0 and 1), and explicitly accounts for unequal component variances
  + Average component CV weighted by abundance
  + Aggregate variability – sqrt(synch) \* average component CV
    - Component and aggregate variability are linearly proportional to one another, with a constant of proportionality driven by synchrony of components
      * When highly synch, agg perfect tracks components
      * When asynch, agg variability strongly dampened

*Retrospective analysis*

* We first explored metapopulation dynamics by decomposing the variability of a case study aggregate (Fraser River sockeye salmon) into each component’s variability and synchrony among components.
  + Component variability is weighted by the CU’s mean abundance
* We examined these indices in two metrics
  + First, residuals from a basic stock-recruit relationship, providing an index of deviations in per capita productivity.
    - Define model
    - A subset of Fraser River sockeye salmon populations exhibit cyclic dynamics and these CUs’ dynamics were simulated using a Larkin model, an extension of the Ricker that accounts for delayed density dependence among cycle lines
    - Define model
    - Whether CUs were modeled with the Ricker or Larkin was based upon their most recent assessment (WSP 2017 doc)
    - Recruits are enumerated after returning to coastal waters and being captured in fisheries, dying en route to spawning grounds, or successfully reaching spawning habitat.
    - This metric represents trends in metapopulation dynamics independent of two major mechanisms of disturbance in Pacific salmon populations - exploitation in fisheries and en route mortality.
    - By including Larkin model residuals we were also able to account for cyclic dynamics which may confound apparent trends in population dynamics
  + Second we examined trends in absolute spawner abundance, which is simply the number of recruits that successfully reach the spawning grounds
    - By comparing empirical trends in these two metrics we can explore the relative importance of variation in exploitation rate, en route mortality, and cyclic dynamics
* We calculated ten-year moving window averages of each metric and used linear models to test two hypotheses
  + 1) Has there been a significant increase in aggregate variability, consistent with a collapsed portfolio?
  + 2) Is aggregate variability more strongly correlated with component variability or synchrony, consistent with a shift in the dynamics of specific CUs or the metapopulation as a whole.

*Forward simulation*

* To explore the potential consequences of different aggregate variability scenarios, we used a stochastic closed-loop model to forward simulate the dynamics of Fraser River sockeye salmon.
  + The model includes population dynamics and harvesting, as well as process, observation, and management implementation uncertainty.
* Salmon metapopulation dynamics were modeled using the same age-structured Ricker or Larkin models, with demographic stochasticity incorporated with random deviations in recruitment and age at maturity
  + To generate future recruits we used alpha and beta parameters that were estimated from CU-specific stock recruit models.
    - To account for uncertainty in the true underlying stock recruit relationship we sampled with replacement from the posterior distribution of each CU’s estimated parameters each simulation run.
    - Note that although these models provide estimates of stock-recruit deviations, we parameterized sigma independently by drawing CU-specific values from a normal distribution with mu and sigma.
      * Mu varied depending on operating model scenario
* Harvest occurred each year with exploitation rates determined by a harvest control rule replicating the TAM rule that has been used to regulate catch rates on the Fraser River since X
  + A forecast of recruit abundance was made each year at the management unit level, the scale at which harvest typically occurs in mixed stock, marine fisheries.
  + A total exploitation rate was set based whether forecasted abundance was below or above two MU- and cycle line-specific reference points after accounting for losses due to en route mortality.
    - Provide details of TAM rule as supplement
* **Any need to incorporate observation component?**
* To explore the consequences of aggregate variability on long term conservation and economic goals, we ran simulations across a suite of operating models that altered component variability and synchrony via changes in recruitment deviations.
  + To increase component variability we adjusted the mean of the sigma distribution from 0.1 to 0.8.
  + Synchrony among CUs was introduced by drawing annual recruitment deviations from a variance-covariance matrix.
    - The variance-covariance matrix contained CU-specific sigma squared along the diagonal, while the off-diagonal was the product of sigma squared times a correlation coefficient
  + Hence aggregate variability could be increased using either or both variables, while maintaining realistic levels of stochasticity.
  + To explore the relative importance of either process we increased each in isolation, as well as in tandem, resulting in a total of 12 distinct variance scenarios.
* We first confirmed that these scenarios produced realistic patterns in per capita productivity and recruit abundance.
* We then used four performance metrics to assess how changes in aggregate variability influenced long-term conservation outcomes.
  + Mean recruit abundance – indicates how strongly abundance is influenced by variance and covariance
  + Mean catch – indicates how strongly environmental services are impacted by dynamics, while accounting for the realistic buffering effect of harvest control rules
  + Ppn of years aggregate below reference point - provides an estimate of aggregate conservation status that is a useful proxy for total ecosystem health
  + Ppn of CUs above specific reference points at end of sim – provides an index of CU-specific conservation status, which is the focus of most management and conservation interventions
* 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