**Introduction**

Ecological aggregates, such as metapopulations or communities, consist of components whose dynamics vary due to life history, unique environmental interactions, or simply chance. Such asynchrony tends to reduce variability in the dynamics of these ecological aggregates and results in positive diversity-stability relationships (Hooper REF), commonly referred to as portfolio effects (Tilman 1999 REF; Schindler 2015 REF). The stability conferred by biodiversity is often associated with greater productivity and biomass, as well as increases in the availability of ecosystem services (Tilman, Isbell & Cowles 2014; Schindler, Armstrong & Reed 2015). Increased recognition of these ecological benefits has resulted in a greater emphasis on the monitoring and conservation of aggregates, rather than component species or populations.

Accounting for portfolio effects via systems-based approaches may be particularly useful in disciplines such as fishery science, where managers are often tasked with sustainably harvesting aggregates of distinct stocks. At the coarsest level the relationship between diversity and stability is strongly influenced by statistical averaging (Doak *et al.* 1998). Thus there are tangible benefits to simply insuring that a relatively large number of stocks contribute to a fishery. Indeed one of the most commonly cited examples of ecological portfolios is the Bristol Bay sockeye salmon fishery, where the sheer number of distinct populations in the region reduces aggregate variability in spawner abundance (Hilborn et al. 2003; Schindler et al. 2010). Since stock diversity is also correlated with fewer fishery closures, there are clear incentives to distribute fishing effort in such a way that the maximum number of populations is maintained.

Yet the presence of an ecological portfolio does not guarantee stability indefinitely. For example, aggregate Chinook salmon returns to California’s Central Valley have simultaneously collapsed and become increasingly variable (Carlson & Satterthwaite 2011; Satterthwaite & Carlson 2015), even though the number of component stocks within the system has remained the same. Reduced productivity coupled with decreased stability at the aggregate level has resulted in substantial ecological (e.g. reduced marine subsidies) and socio-economic costs (e.g. more frequent fishery closures). While the region technically still exhibits a portfolio effect because aggregate variability is reduced relative to that of individual stocks, the buffering conferred by its diversity is substantially weaker than it was historically (Carlson & Satterthwaite 2011).

The drivers and consequences of changes in aggregate variability can be better understood by decomposing it into two subordinate components. The first of these, component variability, represents temporal variation in individual populations (species) within a metapopulation (community), while the second, synchrony, describes the relative degree of similarity among components (Thibaut & Connolly 2013). Each metric provides intuitive information about the scale at which destabilizing processes have occurred, clarifying how aggregate dynamics have changed through time. For example, a scenario where component variability has increased, while synchrony has remained relatively low and stable, suggests changes in aggregate dynamics are likely the result of local processes that could potentially be addressed in isolation. Conversely, coherent increases in both synchrony and component variability might suggest that shared drivers have become increasingly dominant, as well as destabilizing. Indeed patterns in synchrony among watersheds suggest changes in hatchery practices, rather than reduced marine survival, may have led to reduced stability within Central Valley Chinook salmon (Satterthwaite & Carlson 2015).

While patterns of covariance among populations have been frequently identified in ecological systems, and particularly in Pacific salmon (Peterman & Dorner 2012; Griffiths *et al.* 2014; Satterthwaite & Carlson 2015), links between covariance and the recovery or persistence of metapopulations are less certain. Generally, the benefits of portfolio effects are quantified by testing the effects of sequentially removing component populations (Schindler *et al.* 2010; Yamane, Botsford & Kilduff 2018)(Moore et al. 2010 REF compares synchrony and diversity interactions). Though less dramatic, changes in component variability and synchrony may result in similarly strong negative effects. For example, high levels of component variability are likely to increase the probability of fishery closures or the probability of overharvest if management targets fail to track changes in stock abundance. These issues may be exacerbated if periodic years of high abundance create perverse incentives to maintain harvesting capacity, increasing the likelihood of overharvest when abundance declines. High levels of synchrony should intuitively magnify the negative effects of increased component variability. Instead of the dynamics of component populations buffering one another, changes in abundance will increasingly occur in unison and prevent harvesters from shifting effort between stocks. INSERT SENTENCE ON PRODUCTIVITY DECLINES HERE

In this study, we explore how patterns of variability and synchrony influence trade-offs between conservation and management objectives using Fraser River sockeye salmon as a case study. Sockeye salmon are an anadromous, semelparous species and the Fraser River aggregate is composed of populations that spawn throughout southern British Columbia. Sockeye salmon have been harvested in the region by commercial marine fisheries for over a century and by indigenous communities for thousands of years (REF). Despite the historical abundance of Fraser River sockeye salmon, the aggregate’s productivity strongly declined in the 1990s, resulting in frequent fishery closures and an emergency federal inquiry (REF). While there have been signs of recovery in recent years, recruitment continues to be highly variable and several populations within the aggregate continue to be assessed as at risk (REF). Since Fraser River sockeye salmon fisheries, like most Pacific salmon fisheries, are largely mixed-stock, abundant and depleted populations are inevitably harvested simultaneously (REF). Altogether these factors create a delicate framework, where managers must balance conservation goals with the desire to sustain economically and culturally significant fisheries, particularly during periodic years of high abundance. Changes in patterns of variability and synchrony may increase tension between these trade-offs if the fishery becomes increasingly concentrated on a smaller number of abundant years.

We first conduct a retrospective analysis to demonstrate that aggregate temporal variability within the Fraser River has recently increased due to changes in both component variability and synchrony. We then use stochastic simulations to test whether increases in component variability and synchrony are associated with negative outcomes across a suite of performance metrics.

**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 (Holtby 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 (Grant REF; Holtby REF). Sockeye salmon CUs typically contain fewer spawning populations and are more spatially restricted than other Pacific salmon due to their dependence on nursery lakes (Holtby REF). The Fraser River sockeye salmon aggregate is composed of 24 CUs, which are grouped into four management units (MUs) based on adult migration timing (Grant REF). 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 rivers. 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 included in our analysis, along with their component CUs, are listed in Table 1.

The time series of salmon abundance we used for this analysis are derived from estimates of spawner and recruit (age-specific catch plus escapement minus an adjustment for en route mortality) abundance for 19 CUs (Grant et al. 2011), with individual time series beginning between 1948 and 1973 (Table 1). 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).

Table 1. Relevant sockeye salmon management units and component conservation units within the Fraser River aggregate.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| MU | CU | Stock | Status† | SR Model | Time Series |
| Early Stuart | Takla-Trembleur | Early Stuart | Red | Larkin |  |
| Early Summer | Bowron | Bowron | Red | Ricker |  |
| Shuswap-ES | Seymour | Amber | Larkin |  |
| Scotch | Amber | Ricker |  |
| North Barriere | Fennel | Amber | Ricker |  |
| Anderson-Seton | Gates | Amber/Green | Ricker |  |
| Nadina-Francois | Nadina | Amber/Green | Ricker |  |
| Pitt | Upper Pitt River | Green | Ricker |  |
| Summer | Takla-Trembleur | Late Stuart | Red/Amber | Larkin |  |
| Francois-Fraser | Stellako | Amber/Green | Ricker |  |
| Kamloops-ES | Raft | Amber | Ricker |  |
| Quesnel | Quesnel | Red/Amber | Larkin |  |
| Chilko | Chilko | Green | Ricker |  |
| Harrison (river-type) | Harrison | Green | Ricker |  |
| Late Summer | Shuswap-L | Late Shuswap | Amber/Green | Larkin |  |
| Lillooet-Harrison | Birkenhead | Amber | Ricker |  |
| Cultus | Cultus | Red | Ricker |  |
| Seton | Portage | Red | Ricker |  |
| Harrison (upstream) | Weaver Creek | Red | Ricker |  |

*Synchrony metrics and retrospective analysis*

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 ecological aggregate’s components. It is defined as the total temporal variance of the 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 aggregate abundance, consisting of *n* populations, and the denominator is the variance of a hypothetical, perfectly synchronized population aggregate (Loreau and de Mazancourt 2008; Thibault and Connolly 2013). The 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. As a result, it can be readily used to directly compare disparate systems.

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 (Thib and Connolly 2013). Thus as synchrony increases, CVA becomes more similar to CVC and CVA is dampened when components are asynchronous.

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 per capita productivity, log(recruits/spawner). Since Fraser River CUs vary in the length of their spawner-recruit time series, we generated trends in these metrics using two datasets. The primary dataset consisted of 11 CUs with data extending back to the 1948 brood year, while the second contained 18 CUs with data beginning in the 1973 brood year (Table 1). To place these changes in a broader management context we also present temporal changes in aggregate spawner abundance and aggregate catch.

*Forward simulation*

*Process submodel*

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, as well as process and management implementation uncertainty. The dynamics of each CU were simulated using age-structured, stock recruit models which typically took the form of the Ricker model (Ricker REF)

Equation 3

where *i* represents a CU, *R* the number of recruits (number of offspring that return to spawn or are captured in the fishery), and *S* the number of spawners in year *y*. 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. This model can be arranged to account for normally distributed process error as

Equation 4

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 interactions among brood years, i.e. delayed density-dependent effects (Larkin ref; details in Appendix). 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; Table 1).

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

Equation 5

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 **V** for *n* CUs. 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 (results not shown). Note that recruitment deviations in Larkin models did not include an autocorrelation component because AR1 processes have not been validated in these models and the inclusion of delayed density dependence parameters, to some extent, accounts for such effects.

We also incorporated a second productivity scenario in our analysis intended to represent a period of broadly unfavorable environmental conditions for sockeye salmon, which could magnify the relative effects of changes in CVC or synchrony. Decreases in productivity are commonly modeled by shrinking relative to reference values (REF); however, rather than manipulate per capita productivity directly, we sampled recruitment deviations from a skewed, multivariate Student *t* distribution (heavy-tailed) in a subset of years. Thus deviations were fit with the following distribution

Equation 6

where **V** is defined as above, *v* represents the degrees of freedom parameter, and the skewness parameter. Lower values of *v* corresponding to heavier tails and as *v* approaches infinity, the *t* distribution approaches the normal distribution (Anderson ref). When is negative the distribution is left-skewed, when it is positive it is right-skewed. We assigned relatively moderate values to both parameters that are consistent with weak evidence of heavy tails generally (Anderson ref) and the mean estimate of skewness from models fit to CU-specific stock-recruitment residuals (not shown). In the low productivity scenario we sampled from the Student *t* distribution with a mean frequency of 0.3 and a multivariate normal distribution in all other years, resulting in an increased likelihood of recruitment failures in approximately one third of the simulation period.

We also tested the effect of an alternative scenario where average productivity is directly reduced during the simulation period by using smaller values of . Specifically we used estimates from the 10th percentile of the posterior distribution, rather than the median, to represent a persistently low productivity regime. This model produced declines in performance metrics that were more severe, relative to the reference productivity scenario, than the skewed scenario described above (results presented in Appendix).

*Management submodel*

The closed-loop simulation incorporated two sources of mortality. The first mortality mechanism simulated harvest in mixed stock fisheries. Total allowable catch (TAC) in this fishery was calculated each year using a harvest control rule (HCR) that replicates the Total Allowable Mortality framework currently used by fisheries management (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 persistent cycles present in several CUs and are typically adjusted upwards (i.e. TACs reduced) to account for mortality during upstream migration and spatial overlap between abundant and depleted MUs. The second simulated source of mortality represented en route mortality that occurs after fish enter freshwater due to a combination of natural mortality (thermal stress, pathogen infection, predation) and unreported harvest (REF). We modeled en-route mortality as a stochastic, CU-specific process because it appears to be correlated with migration phenology (REF), in-river temperatures (REF), and freshwater flow (REF). Details of the harvest control rule, mortality calculations, and parameter specifications are described in the Appendix.

*Component variability and synchrony “treatments”*

The principal drivers of variability in aggregate abundance within the model are deviations from CU-specific stock-recruitment relationships (i.e. *w* in Equation 5). To explore the consequences of greater aggregate variability on recruitment potential, we manipulated the strength of recruitment deviations to create nine operating models defined by unique variance-covariance matrices **V**, with each representing a distinct component variability and synchrony “treatment” (Table 2). Specifically, we created component variance treatments by adjusting CU-specific estimates of process variance up or down by 25%. We selected these adjustments because they were sufficient to produce changes in CVC, but constrained to values that are plausible for sockeye salmon. We parameterized synchrony treatments by adjusting the correlation coefficient to values consistent with 10-year moving window estimates of mean pairwise correlations in log(R/S) among CUs from historical observations, current observations, or values moderately higher than present.

We introduced additional stochasticity into the model via interannual variation in: age at maturity, in-season abundance estimates error, en route mortality, and outcome uncertainty (Table A1). The results we present in the main text are based on simulations with the reference value for each parameter only; however, we tested the effect of alternative values in a series of sensitivity analyses to ensure that our results were robust to this assumption. Details of how each process was parameterized are described in the Appendix and results of sensitivity analyses are provided in an online supplement.

Table 2. Parameterization of component variability and synchrony operating models.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Low CVC | Moderate CVC | High CVC |
| Low |  |  |  |
| Moderate |  |  |  |
| High |  |  |  |

*Evaluating model performance*

We first confirmed that each operating model produced the predicted changes in CVC and. We then used a suite of performance measures (PMs) to assess how changes in each metric altered the likelihood of achieving conservation- and catch-based management objectives. The first conservation-based PM we generated was recruit abundance, calculated as the temporal median number of individuals (at the aggregate level, i.e. summed across CUs) that were available to be harvested or to escape to their spawning grounds each year. The second and third conservation-based PMs incorporate biological benchmarks based on stock-recruit analyses, providing a more nuanced estimate of population status than absolute abundance. These were calculated as the mean proportion of CUs within the aggregate that were above their individual upper (*S*MSY) and lower (*S*Gen) biological benchmarks during the simulation period. SMSY is defined as the estimated spawner abundance necessary to achieve maximum sustainable yield, while SGen is the estimated spawner abundance necessary to recover to *S*MSY in one generation in the absence of fishing mortality (WSP ref, Holt ref). The equations used to estimate these metrics are presented in the Appendix. Finally, we calculated the proportion of CUs extirpated at the end of the simulation period.

Catch-based PMs included median catch, a measure of interannual catch stability, and three PMs associated with fishery benchmarks. We quantified interannual catch stability as

Equation 7

where *C* is aggregate catch in year *t*. We defined the first of the benchmark PMs as the mean proportion of MUs with recruit abundance greater than the minimum escapement target (i.e. the lower fishery reference point specified by the harvest control rule). The other two catch-based PMs are calculated as the proportion of years during the simulation period where total allowable catch (TAC) across all MUs was greater than 500,000 and 1,000,000 fish. When aggregate TAC is below the smaller value, managers struggle to allocate sufficient quota to priority stakeholders (i.e. food, social, and ceremonial harvest for various First Nations) and when it is above the larger value managers are able to allocate some degree of catch to the commercial sector. Note that while the proportion of fisheries open is based on “true” recruit abundance, representing a hypothetical omniscient manager, the PMs based on TAC levels incorporate uncertainty associated with the in-season forecast process.

Instead of priming the simulation with initial abundances 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 (approximately 10 sockeye salmon generations) and each OM was simulated 1000 times (a supplementary analysis indicated variation in output metrics stabilized after 500-700 simulation runs). To evaluate differences in performance between OMs, we present median outputs among simulations, as well as 10th and 90th percentiles. We stress, however, that this study is not intended to accurately forecast the dynamics of Fraser River CUs or to predict the trajectory of the aggregate as a whole. Rather our goal is to demonstrate relative differences in projected performance associated with differences in component variability and synchrony.

**Results**

*Retrospective analysis*

Mean Fraser River sockeye salmon productivity, log(recruits/spawner), declined from the late 1980s through 2005, the brood year which was predominantly responsible for producing the poor return in 2009. Subsequently the aggregate exhibited several years of higher productivity, but the trend has remained variable and productivity has recently declined again (Fig. 2a). Mean CVC (i.e. the temporal variability of the “average” CU’s productivity) was relatively stable for most of the time series before showing an increase in the 1990s that steepened over several years (Fig. 2b). Productivity was relatively highly synchronized in the first decade of the time series, followed by a variable, but generally asynchronous period. In the early 2000s, approximately when CVC reached unusually high levels, synchrony increased again (Fig. 2c). Unsurprisingly, changes in CVA mirror these patterns, showing a dramatic increase in the early 2000s (Fig. 2d).

Figure 1. Observed trends in Fraser River sockeye salmon productivity (log (recruits per spawner)), aggregate spawner abundance, and aggregate catch (top row). 10-year moving window estimates of the mean component coefficient of variation (CVC), synchrony index (), and aggregate variability (bottom row). Solid black lines represent trends for 11 CUs with time series extending back to 1948, lighter red lines represent trends for 18 CUs beginning in 1973.

*Forward simulation*

By specifying low, medium, and high values for and we were able to generate scenarios that consistent with historical, current, and moderately elevated trends in CVC and the synchrony index (Figure 2).

Changes in CVC and synchrony interacted to produce relatively strong impacts on certain conservation-based performance metrics, but had negligible effects on others. For example, increases in CVC led to increased median recruit abundance, as long as synchrony remained low; however as synchrony increased, the likelihood that median abundance would decline rose (Figure 3). Conversely, higher levels of CVC were associated with a smaller proportion of CUs being above their lower biological benchmark (Sgen), while increasing synchrony only increased variability among trials. Interestingly neither the proportion of CUs above their upper biological benchmark (SMSY) nor the proportion of CUs that were extant was strongly influenced by CVC or synchrony under the reference productivity scenario.

The negative effects of high CVC and synchrony were notably stronger when the biological model included intermittent recruitment failures (generated by skewed process variance). For example, when both processes were increased simultaneously median aggregate recruit abundance declined from approximately 8 million individuals to less than 6, while the mean proportion of CUs above their lower benchmark declined from 0.68 to 0.55, and the mean number of extirpations rose from 0 to 5%. Additionally, high levels of synchrony, but not CVC, were associated with fewer CUs being above their upper biological benchmark.

**Discussion**

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.

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