**Introduction**

Metapopulations, communities, and other ecological aggregates consist of components whose dynamics vary due to life history, unique environmental interactions, or simply chance. Asynchrony among components, commonly referred to as portfolio effects, reduces temporal variability of the aggregate resulting in greater productivity, increased availability of ecosystem services, and improved resilience (Tilman, Isbell & Cowles 2014; Schindler, Armstrong & Reed 2015). Portfolio effects have been identified as key stabilizing processes in a number of ecosystems and have been used as justification for systems-based approaches, which emphasize monitoring and conserving ecological aggregates, rather than individual components (Link 2018). The broad goal of systems-based approaches is to increase the stability of ecosystem services, while avoiding the difficulties associated with accurately forecasting the dynamics of single populations (Link 2018).

Systems-based approaches and portfolio effects are particularly relevant to management-oriented disciplines such as conservation biology and fisheries science. A common way to quantify a portfolio’s performance is via aggregate variability, the temporal coefficient of variation of multiple populations. An emergent property of ecological portfolios is that, due to statistical averaging alone, aggregate variability decreases as the number of components increases (Doak et al. 1998). For example, the Bristol Bay sockeye salmon (*Oncorhynchus nerka*) fishery encompasses an aggregate of nine major river systems, each containing tens to hundreds of spawning populations (Schindler et al. 2010). This population diversity reduces aggregate variability in spawner returns and catches, as well as the probability of fishery closures, relative to a hypothetical fishery containing fewer stocks (Hilborn et al. 2003; Schindler et al. 2010). Thus maintaining biodiversity across ecological scales is a way to promote resilience, particularly when future environmental conditions are uncertain (Anderson et al. 2015).

Even when population diversity is stable and extirpations do not occur, ecological portfolios can exhibit changes in aggregate variability that compromise their performance. Although the number of stocks within California’s Central Valley Chinook salmon (*O. tshawytscha*) aggregate has not declined, aggregate returns to the fishery have collapsed and become increasingly variable in recent decades (Carlson & Satterthwaite 2011; Satterthwaite & Carlson 2015). In this case, decreased stability appears to be associated with three distinct processes: greater variability in the returns of individual stocks, greater synchrony among stocks, and reduced productivity (Satterthwaite & Carlson 2015). While the region technically still exhibits a portfolio effect (i.e. 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). Ultimately increased aggregate variability has resulted in substantial socio-economic costs with the probability of fishery closures increasing by more than 10-fold relative to historic levels (Yamane et al. 2018).

Aggregate variability is driven by the variance and covariance of component populations. Thus it can be decomposed into two metrics – the weighted mean coefficient of variation among components (CVc) and an index of synchrony (φ) (Loreau and de Mazancourt 2008; Thibaut and Connolly 2013). While increases in either CVC or φ will decrease an aggregate’s stability and weaken its portfolio effect, each process can produce unique challenges to systems-based management. For instance, the dynamics of individual populations become chaotic as CVC increases, raising the risk of overharvest if managers are unable to respond to rapid changes in abundance. In a healthy portfolio with sufficient diversity and relatively low levels of synchrony, divergent dynamics among populations will reduce the impact of these changes at the aggregate level. However, as synchrony increases, otherwise localized boom-and-bust cycles will become more widespread and harvesters will be less able to shift effort among component stocks, leading to reduced profits (Cline et al. 2017).

Aggregate variability can be associated with substantial negative ecological and socio-economic outcomes, as demonstrated by the decline of the Central Valley Chinook salmon fishery (Satterthwaite and Carlson 2015). However, it is unclear to what extent these outcomes are driven by increased component variability, increased synchrony, or reduced population productivity. The latter is particularly relevant because declines in abundance and productivity appear to be particularly widespread among exploited fishes (Peterman and Dorner 2012; Britten et al. 2016). Furthermore, the impacts of productivity declines on management strategies are likely to increase due to persistent stressors such as climate change (Oliver et al. 2015) and may be magnified by changes in aggregate variability.

An additional source of uncertainty is how changes in aggregate variability will influence various indicators of ecosystem health. Previous analyses of portfolio effects have typically examined changes in metrics such as abundance or catch (Moore et al. 2010; Schindler et al. 2010). Yet management actions often respond to a range of control points (e.g. whether abundance is above or below a value that provides maximum sustainable yield), which may vary in their sensitivity to changes in aggregate variability. The performance of systems-based approaches will be improved by a better understanding of how portfolio effects interact with various productivity regimes to influence different management objectives.

In this study, we explore how increased aggregate variability influences the probability of achieving a range of conservation and management objectives using Fraser River sockeye salmon as a case study. We first present a retrospective analysis that reveals aggregate temporal variability within the Fraser River has increased in recent years due to greater component variability, as well as greater synchrony among components. We then use stochastic, closed-loop simulations to evaluate how changes in component variability and synchrony influence the likelihood of meeting a suite of conservation- and catch-based performance metrics. Finally we repeat the simulations under a range of productivity scenarios to clarify how aggregate variability interacts with changes in productivity to shape dynamics. This multi-step approach allows us to assess changes in ecosystem functioning along a gradient of scenarios from historically observed levels of high asynchrony and productivity to heavily synchronized, unproductive dynamics consistent with degraded systems.

**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 (Burgner 1991). Under Canada’s Wild Salmon Policy, 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 (Holtby & Ciruna 2007; Grant *et al.* 2011). 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 *et al.* 2011).

Fraser River sockeye salmon have been harvested in the region by commercial fisheries for over a century and by indigenous communities for thousands of years (Cohen 2012)., productivity declined in the 1990s, resulting in frequent fishery closures and an emergency federal inquiry (Cohen 2012). While there have been signs of recovery for some CUs in recent years, recruitment continues to be highly variable with some recent declines (ref). Fraser River sockeye salmon are targeted by commercial fisheries as they move through nearshore areas on their return migration to their natal rivers for spawning. Shifting marine fishery openings to coincide with a given migration phenology can be used to constrain effort at the MU-level. However, , at the CU level…. Fraser River sockeye salmon CUs vary in conservation status from abundant with stable or increasing population trends (i.e. healthy) to depleted with declining trends (critical). A recent assessment under Canada’s Wild Salmon Policy concluded that nine CUs were within the critical zone, 11 were within the cautious zone, and three were healthy (WSP 2017). The Fraser River sockeye salmon MUs included in this analysis, along with their component CUs, are listed in Table 1.

We used annual estimates of spawner abundance and recruit abundance (i.e. the number of spawning fish and catch produced by a spawners in a given brood year, minus an adjustment for en route mortality) for 19 CUs (Grant et al. 2011), with individual time series beginning between 1948 and 1973 (Table 1). Spawner abundance 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 spawning abundance 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** | **Time Series Start** | **Stock Recruit Model & Parameters** | | | |
| Model |  |  |  |
| Early Stuart | Takla-Trembleur | Early Stuart | 1948 | Larkin | 1.80 | 1.49 | 0.77 |
| Early Summer | Bowron | Bowron | 1948 | Ricker | 1.60 | 25.96 | 0.81 |
| Shuswap-ES | Seymour | 1948 | Larkin | 1.98 | 3.58 | 0.82 |
| Scotch | 1980 | Ricker | 1.50 | 4.83 | 1.11 |
| North Barriere | Fennel | 1967 | Ricker | 2.14 | 97.82 | 0.96 |
| Anderson-Seton | Gates | 1968 | Ricker | 1.73 | 12.88 | 0.92 |
| Nadina-Francois | Nadina | 1973 | Ricker | 1.40 | 6.31 | 0.87 |
| Pitt | Upper Pitt River | 1948 | Ricker | 1.50 | 22.39 | 0.76 |
| Summer | Takla-Trembleur | Late Stuart | 1948 | Larkin | 2.03 | 1.01 | 1.28 |
| Francois-Fraser | Stellako | 1948 | Ricker | 1.84 | 3.96 | 0.83 |
| Kamloops-ES | Raft | 1948 | Ricker | 1.51 | 21.59 | 0.79 |
| Quesnel | Quesnel | 1948 | Larkin | 2.05 | 0.39 | 0.83 |
| Chilko | Chilko | 1948 | Ricker | 1.83 | 1.23 | 0.80 |
| Harrison (river-type) | Harrison | 1948 | Ricker | 1.49 | 2.79 | 1.39 |
| Late Summer | Shuswap-L | Late Shuswap | 1948 | Larkin | 2.17 | 0.30 | 0.95 |
| Lillooet-Harrison | Birkenhead | 1948 | Ricker | 1.90 | 6.75 | 0.98 |
| Cultus\* | Cultus | 1948 | Ricker | 1.23 | 18.05 | 1.18 |
| Seton | Portage | 1965 | Ricker | 2.06 | 35.98 | 1.12 |
| Harrison (upstream) | Weaver Creek | 1966 | Ricker | 2.21 | 5.89 | 0.91 |

\*Cultus spawner abundance and catch estimates extend to 2011, but the population has been heavily managed since 2000 using a captive breeding program. As a result, population parameters were estimated only using data collected prior to this change.

*Synchrony metrics and retrospective analysis*

We examined temporal changes in three metrics of metapopulation variability (Loreau & de Mazancourt 2008; Thibaut & Connolly 2013). The synchrony index () reflects the relative degree of similarity in the dynamics of an ecological aggregate’s components (put references here). It is defined as the total temporal variance of the components (i.e. sum of all elements of the variance-covariance matrix **V**), divided by the variance of a hypothetical aggregate with the same component variances, but perfect covariance.

Equation 1

Here denotes temporal covariance in abundance for populations *i* and *j* within the aggregate of *n* populations. Thus the numerator of the synchrony index represents the variance of aggregate abundance, consisting of *n* populations, and the denominator is the variance of a hypothetical, perfectly synchronized population (Loreau & de Mazancourt 2008; Thibaut & 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 regardless of the number of components), and explicitly accounts for unequal variances among components (Thibaut & Connolly 2013).

The second metric is the mean temporal coefficient of variation among components (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. Thus as synchrony increases CVA becomes more similar to CVC, while CVA is dampened when components vary asynchronously. Note, however, that CVA is identical to the temporal coefficient of variation of summed aggregate abundance.

To explore changes in aggregate variability of Fraser River sockeye salmon, we generated time series of , CVC, and CVA using 12-year moving windows of recruit abundance. **Insert blub on Bayesian sampling or TMB for intervals**. We used estimates of recruit, rather than spawner, abundance to account for large changes in exploitation rate over the past 70 years. Since Fraser River CUs vary in the length of their spawner-recruit time series, we generated trends in these metrics using a subset of CUs with data extending back to the 1948 brood year; however, a supplementary analysis analyzing a shorter time series that contained 18 CUs exhibited similar trends. To place these changes in a broader management context, we also present temporal changes in observed productivity (log(R/S)), aggregate spawner abundance, and aggregate catch.

*Forward simulation*

*Structure of biological and management submodels*

We used a stochastic, closed-loop simulation model of the Fraser River sockeye salmon management system 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 variance and deviations between target and realized catches (i.e. outcome uncertainty). The dynamics of each CU were simulated using age-structured, Ricker stock recruit models (Ricker 1975)

Equation 3

where *i* represents a CU, *R* the number of recruits, 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 maximizes recruitment. This model is commonly arranged to account for normally distributed process error as

Equation 4

A subset of sockeye salmon CUs exhibit persistent cycles in spawner abundance with highly abundant returns occurring every four years (DFO. This dominant cycle line is followed by one subdominant and two weak return years. Although the specific mechanism that drives these cycles remains unclear, ecological interactions among cycle lines are likely a factor (e.g. predator abundance tracking juvenile sockeye salmon abundance at a one-two year lag (Ricker 1997)). The productivity of CUs with cyclic dynamics is generally estimated with an extended version of the Ricker model (the Larkin model; Larkin 1971), which accounts for interactions between brood years. For these cyclic CUs, we used the Larkin model to forward simulate the dynamics of cyclic CUs (details of model structure and simulations in Appendix). Whether we simulated dynamics for a given CU using a Ricker or Larkin model followed assignments made in the most recent Wild Salmon Policy assessment (DFO *in press*; Table 1).

To parameterize each CU’s stock-recruit relationship we used median estimates of , , and generated with a 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). Recruitment deviations in Larkin models did not include an autocorrelation component because AR1 processes because inclusion of delayed density dependence parameters, to some extent, accounts for such effects.

We incorporated two alternative productivity scenarios in our analysis intended to represent an increased likelihood of poor recruitment events, which could magnify the relative effects of changes in CVC or synchrony. Decreases in productivity are commonly modeled by shrinking relative to its reference value (e.g. Dorner et al. 2009, Holt & Folkes 2015), representing a change to a less favourable productivity regime. Rather than manipulate per capita productivity in this way, we chose to create scenarios where mean productivity remained the same, but the relative frequency of recruitment failures increased. These could represent, for example, intermittent periods of poor marine survival that are thought to regularly result in synchronous, poor returns of Pacific salmon (Mueter, Pyper & Peterman 2005; Peterman & Dorner 2012).

To simulate this process we sampled recruitment deviations from one of two skewed distributions. In the “moderate decline” scenario, we used a skewed multivariate normal distribution that was identical to the distribution in equation 5, but included a skewness parameter = 0.65, representing moderate, left skew (when = 1 the distribution is symmetrical). Our parameterizaton of skewness is moderately more extreme than estimates from the historical dataset using CU-specific stock recruit models that included this additional parameter (median among all CUs = 0; 90th percentile interval = 0.51-1.19). To simulate a scenario with greater probability of low productivity events (“severe decline” scenario), we sampled recruitment deviations from a skewed multivariate Student *t* distribution. The heavy-tails of this distribution increase the probability that extreme values will be sampled (Anderson *et al.* 2018). Deviations were fit with

Equation 6

where **V** is defined as in Equation 5, *v* represents the degrees of freedom parameter which affects the spread of the distribution and the proportion within the tails. Lower values of *v* correspond to heavier tails and as *v* approaches infinity, the *t* distribution approaches the normal distribution (Anderson *et al.* 2017). For this “severe decline” scenario, we used the same value for the skewness parameter as above and set = 3, which allows for an event three SDs beyond the mean to occur once every 18 years, rather than once every 435 years using a normal distribution (Figure 1).



Figure 1. Distributions used to generate recruitment deviations in different productivity scenarios. All distributions have mean = 0 and standard deviation = 1. Both skewed distributions include parameter = log(0.65). The Student *t* distribution includes a fourth parameter = 3.

In addition the natural mortality implicitly incorporates in the stock-recruitment model, two additional source sources of mortality were included. 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 approximates the Total Allowable Mortality framework currently used to manage the Fraser River sockeye salmon fishery (Pestal, Huang & Cass 2011). Broadly speaking, this HCR uses in-season estimates of recruitment derived from test fisheries to adjust TAC and meet escapement goals specific to each 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 adjusted upwards (i.e. TACs reduced) to account for mortality during upstream migration (en route mortality), as well as spatial overlap between abundant and depleted MUs. The second simulated source of mortality represented en route mortality that occurs after fish enter freshwater prior to spawning due to a combination of natural mortality (thermal stress, pathogen infection, predation) and unreported harvest (Grant *et al.* 2011). We modeled en-route mortality as a stochastic, CU-specific process because it appears to be correlated with migration phenology, in-river temperatures, and freshwater flow (Macdonald 2000; Cooke *et al.* 2004; Crossin *et al.* 2008). Details of the harvest control rule, mortality calculations, and parameter specifications are described in the Appendix.

We introduced additional stochasticity into the model via interannual variation in age at maturity, error associated with in-season abundance estimates (forecast error), en route mortality, and deviations between target and realized exploitation rates (implementation uncertainty). We parameterized using literature-derived values from studies of Sockeye Salmon, or Pacific salmon if species-specific values were not available (Table A1, move to main text). We tested the effect of alternative values that bound the ranges of observed values in a series of sensitivity analyses to asses if our results were robust to these assumptions. Sensitivity analyses are provided in supplement S1.

We used CU-specific time series of recruit and spawner abundance to initiate the simulation model (i.e. the same data that were used in the retrospective analysis). The length of the simulation period was set at 40 years (approximately 10 sockeye salmon generations) and each OM was simulated 1000 times to ensure representative posterior distributions.

*Component variability and synchrony “treatments”*

To explore the consequences of greater aggregate variability on management objectives, 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). We created component variance treatments by adjusting CU-specific estimates of variance in recruitment up or down by 25%. which were within plausible ranges for sockeye salmon (the maximum estimated mean value for across three sockeye salmon studies was 1.64 (Korman et al. 1995, Peterman et al. 2003, Holt and Peterman 2008) and the maximum here was 1.73). 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 during periods of when productivity was weakly ( = 0.05; 1980s and 1990s) or moderately correlated ( = 0.50; 1950s, 1960s, and present). We specified a third high correlation treatment ( = 0.75) to represent a hypothetical scenario where synchrony increases.

Table 2. Parameterization of component variability (CVc) and synchrony () operating models.

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

*Evaluating model performance*

We used a suite of performance measures (PMs) to assess how changes in CVC and impact the likelihood of achieving conservation- and catch-based management objectives (Table 3). Conservation-based PMs included the proportion of CUs with spawner abundances being greater than an upper biological benchmark delineating sustainable population sizes, 80% of spawner abundances at maximum sustainable yield , averaged over years (reword to match text of WSP) (DFO 2007).. Catch-based PMs included proportion of years when aggregate TAC was equal to or greater than 1,000,000 fish as a proxy for healthy fisheries since at this level of abundance managers are able to allocate quota to each major stakeholder group (i.e. First Nations, commercial, and recreational fisheries). We present median outputs among simulations for each PM, and the 10th and 90th percentiles.

Table 3. Conservation- and catch-based performance metrics (PMs). PMs are presented as median values among trials.

|  |  |  |
| --- | --- | --- |
|  | Performance Metric | Definition |
| Conservation | Median recruitment | Median aggregate recruit abundance over years and MC trials (where aggregate is summation of recruits across all CUs within a return year) |
| Proportion of CUs above upper benchmark | The temporal mean proportion of CUs within a return year with spawner abundance greater than 0.8\*SMSY. |
| Proportion of CUs extant | The proportion of CUs with spawner abundances above the extinction threshold at the end of the simulation period. |
| Catch | Median catch | Median aggregate catch (i.e. summed across all CUs within a return year) during the simulation period. |
| Catch stability | The inverse of the temporal coefficient of variation in aggregate catch (i.e. ). |
| Proportion of years above catch threshold | The proportion of years during the simulation period when aggregate TAC was greater than 1,000,000. |

Although we focused our analyses on performance at the aggregate level (across all CUs) because CVC and synchrony are relevant at the metapopulation scale, the consequences of increased aggregate variability may vary among components due to intrinsic differences in productivity or carrying capacity, as well as their exposure to harvest in mixedCU fisheries. An exhaustive analysis of CU-specific differences was beyond the scope of this paper, however to illustrate potential differences we present simulated changes in median spawner abundance across CVC and synchrony treatments for two CUs: a low abundance, red status CU within the Early Summer Run MU (Bowron) and an abundant green status CU within the Summer Run MU (Chilko).

The goal of this study was to demonstrate relative differences in projected performance associated with trends in component variability and synchrony and not to provide status or forecast the dynamics of individual Fraser River CUs or the aggregate as a whole (as described in Grant et al. ).

**Results**

*Retrospective analysis*

Mean Fraser River sockeye salmon productivity (loge(recruits/spawner)) declined from the late 1980s through 2005, the brood year predominantly responsible for producing the poor return in 2009. Althoughwere on average, productivity was moderate after brood year 2005 until 200?, it has recently declined again with high temporal variablilty (Figure 2a). Aggregate spawner abundance and aggregate catch increased until the early 1990s before declining (Figure 2b,c), coincident with declines in productivity and exploitation rate. However, there is substantial interannual variability in both metrics due to several abundant, cyclic CUs. Particularly large returns were observed in 2010 and 2014. Catches for 2014 are not shown because ….

Mean component coefficient of variation, CVC was low in the 1970s and 90s, but was elevated at the beginning of the time series (1950s) and has increased by approximately 50% since the early 2000s (Figure 2d). Similarly, synchrony in recruit abundance was relatively high in the 1950s, low and stable for approximately from 1960-1980, and increased through the 1990s, leading to a recent peak in 201? (Figure 2e.) As expected, changes in aggregate coefficient of variability, CVA mirror these patterns, showing a gradual increase from 1960 to 2010 followed by a jump to particularly high levels in the early 2010s (or late in the first decade of the 2000s) (Figure 2f).



Figure 2. Observed trends in (a) CU-specific productivities (loge (recruits per spawner)) (grey lines) and average of CU-specific productivities (black line), (b) aggregate recruit abundance, and (c) aggregate catch. 12-year moving window estimates of the mean component coefficient of variation (CVC), synchrony index (), and aggregate coefficient of variability (CVA) (d-f) of 11 CUs with time series extending back to 1948. Black lines represent median estimates and grey bands represent 90th percentile intervals.

*Forward simulation*

By specifying low, medium, and high values for CU-specific variability in recruitment residuals, and lag-1 year autocorrelation in CU-specific recruitment residuals, we were able to generate a range of CVC and synchrony scenarios (Figure 3). We use as a proxy for CVC and as a measure of synchrony in subsequent results. Due to stochasticity within the model, median trends in CVC and were lower than recently observed values, even when and were maximized. However, individual Monte Carlo trials exhibited temporal variation in CVC and consistent with the historical time series (Figure S1).



Figure 3. Trends in recruitment component variability and synchrony as a function of and , respectively. 12-year moving window Trends in the observed stock-recruitment dataset are shown in black, the dashed line represents the beginning of the simulation period, and colored lines represent different CVC and synchrony operating models. Lines represent medians across 250 trials.



Figure S1. Trends in recruitment synchrony as a function of and , respectively. The median trend among trials is shown in the top left and other panels represent a random subset of Monte Carlo trials.

The effects of aggregate variability on conservation-based PMs were strongly dependent on productivity scenario. When productivity was simulated at its reference value (i.e. median retrospective estimates of productivity and normally distributed process error) effects of changing CU-specific SD and autocorrelation coefficients on performance metrics were relatively minor (Fig. 4 a,b,c). Increases in synchrony led to moderate declines in recruit abundance, while increases in component variability led to moderate increases (Figure 4a). The increase in median recruitment with increasing variance is due…. 0). The proportion of CUs above their biological benchmark and the proportion of CUs extant at the end of the simulation period were stable across all scenarios (Figure 4b,c).

Unsurprisingly, conservation-based PMs declined under alternative productivity scenarios. However, the relative magnitude of these declines was moderated by synchrony. Under our low productivity scenario, median recruit abundance declined by approximately 50% when synchrony was moderate or high, compared to the reference productivity scenario (purple and green symbols Figure 4d vs a). The proportion of CUs above their biological benchmark exhibited similar declines at higher synchrony levels (Figure 4e vs a). Increases in CVC were associated with declines in recruit abundance and conservation status, but only when they co-occurred with moderate or high levels of synchrony under low productivity scenarios (Figure 4d,e). The interaction between component variability and synchrony was most noticeable with regards to extirpation risk. The median proportion of extant CUs was stable as long as synchrony was low, but declined by ~5% when synchrony increased to moderate levels and by ~10% when both component variability and synchrony were at their maximum values (Figure 4f). Conservation outcomes declined or deteriorated? when extreme events were more frequent (“name of scenario”), but the overall patterns were similar (Figure 4g-i).



Figure 4. Effects of component variability and synchrony on conservation-based performance measures. Points represent medians and whiskers 90% posterior interval among 250 simulation runs.

Similar to conservation-based PMs, for catch-based PMs the effects of component variability and synchrony also differed among PMs and productivity scenarios. Under the reference productivity scenario median catch size displayed a similar pattern to median recruit abundance, declining moderately at high levels of synchrony (Figure 5a). Increasing synchrony and component variability simultaneously also led to moderate declines in the proportion of years the target TAC was achieved, as well more severe declines in catch stability (Figure 5b,c). As with the conservation-based PMs, the impacts of aggregate variability on catch-based PMs were more severe under pessimistic productivity scenarios. When process variance was simulated with a skewed normal distribution median catches declined by 45-65% as aggregate variability increased (Figure 5d). Similarly the proportion of years that target TAC was achieved declined from 93% when component variability and synchrony were minimized to 43% at their maximum (Figure 5e). While declines in catch stability with aggregate variability were similar between the reference and skewed normal productivity scenarios, they were much more severe when extreme productivity events were more frequent (“name of this scenario”) (Figure 5c,f,i). Differences between the two pessimistic productivity scenarios were relatively minor for the remaining catch-based PMs (Figure 5g,h).



Figure 5. Effects of component variability and synchrony on catch-based performance measures. Points represent medians and whiskers 90% posterior interval among 250 simulation runs.

CU-specific median spawner abundances declined with greater component variability, although these effects were dwarfed by declines associated with alternative productivity scenarios. Counterintuitively, shifts in median abundance relative to biological benchmarks associated with increasing variance or declines in productivity or both? were more severe in relatively healthy CUs (e.g. Chilko) because depleted CUs (e.g. Bowron) had a low likelihood of recovery even when dynamics were simulated with relatively high productivity and low component variance (Figure 5). Median spawner abundance within CUs also declined with increasing levels of synchrony, but only under the two pessimistic productivity scenarios (Figure S2).



Figure 6. Distributions of CU-specific median spawner abundance (among 250 trials) across different levels of component variability (shading) and three productivity regimes for Bowron and Chilko CUs. The vertical dashed line represents each CU’s upper biological benchmark (0.8\*Smsy). Simulations included moderate synchrony among CUs ( = 0.5). Note that y-axes differ between CUs.



Figure S2. Distributions of CU-specific median spawner abundance (among 250 trials) across different levels of synchrony (shading) and two productivity regimes for Chilko (top) and Cultus (bottom) CUs. The vertical dashed line represents each CU’s upper biological benchmark (Smsy). Simulations included moderate synchrony among CUs (1.0). Note that x-axes differ between CUs.

**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 that cannot recolonize within a reasonable timeframe such as a human lifetime (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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