**Abstract**

Ecological diversity is associated with reduced temporal variability at the aggregate level, resulting in portfolio effects. Such relationships, however, may weaken over time due to increases in the variability of component populations or greater synchrony among components. While weakened portfolio effects have been previously documented, the consequence of increased aggregate variability on meeting conservation goals is rarely quantified. Here we demonstrate how changes in component variability, synchrony, and population productivity interact to influence the probability of achieving an array of management objectives. We first present evidence that component variability and synchrony have recently increased in the Fraser River sockeye salmon stock aggregate, consistent with a weakening portfolio effect. We then use these data to parameterize a stochastic, closed-loop model that simulates the population dynamics of each stock, the fishery that harvests the stock aggregate, and the management framework used to establish mixed-CU exploitation rates. We show that when population productivity remains relatively stable, the negative effects of component variability and synchrony on conservation- and catch-based objectives are moderate. However, greater component variability or synchrony can magnify the negative effects of declining productivity. As a result, abundance, catch, and the probability of meeting biological benchmarks are strongly reduced. Such declines are particularly concerning because they occurred even though the Fraser River sockeye salmon aggregate retained high levels of biodiversity and was managed using a relatively sensitive harvest control rule. Our findings clarify that while declines in portfolio effect strength increase the risk that ecological aggregates will decline in abundance, such impacts are moderated by the underlying productivity regime. Given evidence of widespread reductions in per capita productivity, accounting for changes in aggregate variability may be necessary for systems-based approaches to be effective.

**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 such 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).

Yet even when population diversity is stable and extirpations do not occur, ecological portfolios can exhibit changes in aggregate variability that compromise their ability to provide ecosystem services. 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 (referred to here as “component variability” or 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 less predictable 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).

Negative ecological and socio-economic outcomes associated with greater aggregate variability may be exacerbated by changes in other dimensions of population dynamics, particularly declines in productivity. In many fisheries, reduced abundance and lower yields are associated with declines in per capita productivity (Peterman & Dorner 2012; Minto *et al.* 2014; Britten, Dowd & Worm 2016), representing, for example, shifts in survival or fecundity. Furthermore, the negative impacts of productivity declines on managed systems are likely to increase due to persistent stressors such as climate change (Oliver et al. 2015). While changes in either aggregate variability or underlying productivity can negatively impact exploited systems, it is currently unclear how these distinct processes may interact with one another to influence management outcomes.

In this study, we explore how increased aggregate variability, and associated measures of component variability and synchrony, 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 probability of meeting a suite of conservation- and catch-based performance metrics under the current management system in place for Fraser River sockeye salmon. 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 low synchrony and high 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 (WSP), Pacific salmon status is assessed at the scale of conservation units (CUs), “a group of wild salmon sufficiently isolated from other groups that, if lost, is unlikely to recolonize naturally within an acceptable timeframe” (DFO 2005). During WSP assessment a range of criteria are used to assign CUs to three zones (green, amber, and red), which represent increasing degrees of conservation concern and management intervention (DFO 2005; Holt et al. 2005)

As one of Canada’s largest sockeye salmon run, the Fraser River aggregate has considerable ecological, cultural, and economic value; however it is increasingly vulnerable to a range of threats including anthropogenic development, overexploitation, and climate change (Cohen 2012). Furthermore, productivity declined in the 1990s, resulting in frequent fishery closures and an emergency federal inquiry (Cohen 2012). While there have been signs of recovery in recent years for specific CUs, recruitment continues to be highly variable (Grant State of Ocean 2018) and WSP status among CUs ranges from healthy to critical (WSP 2017).

Although WSP status is assessed at the CU level, Fraser River sockeye salmon fisheries are predominantly managed at the scale of management units (MUs) – groups of CUs that share a common return migration phenology, i.e. run timing (REF). Fraser River sockeye salmon are targeted by commercial fisheries as they migrate through nearshore marine areas to spawning rivers. Thus, shifting marine fishery openings to coincide with a given migration phenology can be used to constrain effort at the MU, but not the CU, scale (though some overlap among MUs exists). 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 and recruit abundance for 19 CUs (Grant et al. 2011), with individual time series beginning between 1948 and 1973 (Table 1). Note that throughout this manuscript we distinguish between recruit abundance, defined as the sum of catch and individuals escaping the fishery produced by spawners in a given *brood* year, and return abundance, which is the same, but by *return* year. Escapement is calculated from spawner abundance (estimated using a variety of techniques including fence counts, mark-recapture and visual surveys, and passive sonar methods), plus an adjustment for differences between downstream and up-river estimates (Grant et al. 2011). This latter adjustment is necessary to account for mortality that occurs en route, which can be considerable in certain years. Methods for estimating catch and escapement 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. With the exception of the Cultus CU, all time series end in 2011. Stock recruitment parameters are medians from the posterior distributions of an external analysis (FRSSI REF) and bracketed values for include either a 0.75 or 1.25 scalar (see *Component variability and synchrony “scenarios”* section for details).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **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 (0.58, 0.96) |
| Early Summer | Bowron | Bowron | 1948 | Ricker | 1.60 | 25.96 | 0.82 (0.62, 1.03) |
| Shuswap-ES | Seymour1 | 1948 | Larkin | 1.98 | 3.58 | 0.82 (0.62, 1.03) |
| Scotch1 | 1980 | Ricker | 1.50 | 4.83 | 1.14 (0.85, 1.42) |
| North Barriere | Fennel | 1967 | Ricker | 2.14 | 97.82 | 0.98 (0.73, 1.22) |
| Anderson-Seton | Gates | 1968 | Ricker | 1.73 | 12.88 | 0.93 (0.71, 1.18) |
| Nadina-Francois | Nadina | 1973 | Ricker | 1.40 | 6.31 | 0.89 (0.66, 1.11) |
| Pitt | Upper Pitt River | 1948 | Ricker | 1.50 | 22.39 | 0.78 (0.58, 0.97) |
| Summer | Takla-Trembleur-Stuart | Late Stuart | 1948 | Larkin | 2.03 | 1.01 | 1.28 (0.96, 1.60) |
| Francois-Fraser | Stellako | 1948 | Ricker | 1.84 | 3.96 | 0.85 (0.64, 1.06) |
| Kamloops-ES | Raft | 1948 | Ricker | 1.51 | 21.59 | 0.81 (0.61, 1.01) |
| Quesnel | Quesnel | 1948 | Larkin | 2.05 | 0.39 | 0.83 (0.62, 1.03) |
| Chilko | Chilko | 1948 | Ricker | 1.83 | 1.23 | 0.81 (0.61, 1.02) |
| Harrison (river-type) | Harrison | 1948 | Ricker | 1.49 | 2.79 | 1.42 (1.06, 1.77) |
| Late Summer | Shuswap Complex-L | Late Shuswap | 1948 | Larkin | 2.17 | 0.30 | 0.95 (0.72, 1.19) |
| Lillooet-Harrison | Birkenhead | 1948 | Ricker | 1.90 | 6.75 | 1.00 (0.75, 1.25) |
| Cultus | Cultus2 | 1948 | Ricker | 1.23 | 18.05 | 1.21 (0.91, 1.51) |
| Seton | Portage | 1965 | Ricker | 2.06 | 35.98 | 1.14 (0.86, 1.43) |
| Harrison (upstream) | Weaver Creek | 1966 | Ricker | 2.21 | 5.89 | 0.93 (0.70, 1.16) |

1Although the Seymour and Scotch stocks belong to the same CU, historically they were managed independently. Since stock-recruitment data are available for both, we treated them as distinct “quasi-CUs” for the purposes of this study.

2Cultus 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.

*Retrospective analysis and variability metrics*

To place the retrospective analysis in a broader context, we first calculatedWe then examined temporal changes in annual return abundance using three metrics of metapopulation variability: component variability, synchrony, and aggregate variability (Loreau & de Mazancourt 2008; Thibaut & Connolly 2013). The first metric is the mean temporal coefficient of variation of components (CVc), weighted by each component’s mean abundance.

Equation 1

where *mpop*(*i*) is the mean abundance (through time) of population *i,* *magg* is the mean abundance of the aggregate, and denotes variance.

The second metric, the synchrony index (, reflects the relative degree of similarity in the dynamics of an ecological aggregate’s components. 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). 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 2

Here denotes temporal covariance in abundance for populations *i* and *j* within the aggregate of *n* populations. Thus the numerator of 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).

Finally, for the third metric, 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 historical changes in aggregate variability of Fraser River sockeye salmon, we calculated time series of , CVC, and CVA using 12-year moving windows of return abundance. **Insert blub on Bayesian sampling or TMB for intervals**. We used estimates of return, 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 11 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.

*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, *y* is a given year, *R* the number of recruits, and *S* the number of spawners. The parameter represents the number of recruits produced per spawner at low abundance, while is the density-dependent parameter that represents the reciprocal of the number of spawners that maximizes recruitment. This model is commonly re-arranged so that process error can be estimated as normally distributed (Peterman 1981)

Equation 4

A subset of sockeye salmon CUs exhibit persistent cycles in spawner abundance with highly abundant returns occurring every four years. 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 between cycle lines are likely responsible (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. In this case, we also used the Larkin model to forward simulate the dynamics of cyclic CUs (details of model structure and simulations in Appendix; DFO *in press*; 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, Table 1). To account for temporal 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. represents the correlation coefficient between CU-specific variance terms. 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). Following Holt and Folkes (2015), we also adjusted to account for . 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, which could magnify the relative effects of changes in CVC or synchrony. Declines in productivity are commonly modeled by shrinking the intrinsic productivity parameter relative to a reference value (e.g. Dorner et al. 2009, Holt & Folkes 2015), representing a change to a less favourable environmental regime that supports lower mean productivity. Such a method is consistent with studies that have detected declines in using Kalman filter models (Peterman et al. 2003). In many cases, however, interannual variability in recruitment results in poorly fitting Kalman filter models and is assumed to be stable, even though other techniques may indicate a decline in productivity (e.g. patterns in recruitment residuals, Grant et al. SOPO; dynamic factor analysis, Freshwater, Dorner, Malick). In such instances it may be more realistic to increase the frequency of low productivity events, defined here as negative recruitment deviations, rather than assume that the intrinsic productivity parameter itself has declined. Such an approach reduces mean realized productivity (i.e. recruits per spawners), but also reduces the likelihood of large positive recruitment deviations. In the case of of Fraser River sockeye salmon these positive deviations have been notably absent in recent years (SOPO ref).

To simulate an increase in the frequency of low productivity events we sampled recruitment deviations from one of two left-skewed distributions. Since recruitment deviations are typically assumed to be multiplicative and log-normally distributed, absolute variability in recruitment increases as spawner abundance increases (Peterman 1981). Thus adding a left-skew to these distributions reduces the likelihood of large positive recruitment deviations, particularly at large spawner abundances.

In the first scenario, we used a skewed multivariate log-normal distribution that was identical to the distribution in equation 5, but included a skewness parameter (when = 1 the distribution is symmetrical). To parameterize skewness we estimated using each CU’s time series of recruits and spawners (median = 0.83, 90th percentile interval 0.50-1.19; details of model fitting in Appendix). Thus there is already evidence that recruitment deviations are relatively more likely to be negative than positive in Fraser River sockeye salmon CUs. To represent a “moderate decline” productivity scenario, we selected the 25th percentile for use in forward simulations to represent an increased probability of negative deviations relative to historical observations. which affects the spread of the distribution and the proportion within the tails

In the “severe decline” scenario, we used a skewed multivariate Student *t* distribution, which, as a heavy-tailed distribution, increases the probability that relatively extreme values will be sampled (Anderson *et al.* 2017). Deviations were fit with

Equation 6

where **V** is defined as in Equation 5 and represents the degrees of freedom parameter, which affects the spread of the distribution and the proportion within the tails. Lower values of correspond to heavier tails and as approaches infinity, the *t* distribution approaches the normal distribution (Anderson *et al.* 2017). We used the same value for the skewness parameter as above and set = 2, which allows for an event three SDs below the mean to occur once every 23 years, rather than once every 418 years using a skewed normal distribution or once every 709 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 .

In addition to the natural mortality implicitly incorporated in the stock-recruitment model, we incorporated two additional sources of mortality in the closed-loop simulation. The first mortality mechanism simulated harvest in mixed-CU 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 return abundance derived from test fisheries to adjust TAC and meet escapement goals specific to each MU. If in-season estimates of return abundance 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 en route mortality during upstream migration, 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, but 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 these model components using literature-derived values from studies of sockeye salmon, or Pacific salmon if species-specific values were not available (Table A1). We tested the effect of alternative values that bound the ranges of observed values in a series of sensitivity analyses to assess 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 scenario (described in detail below) was simulated 1000 times to ensure representative posterior distributions.

*Component variability and synchrony “scenarios”*

The principal drivers of variability in aggregate abundance within the model are deviations from CU-specific stock-recruitment relationships (*w* in Equation 5). To explore the consequences of greater aggregate variability on management objectives, we manipulated the strength of recruitment deviations to create nine operating models (the component of a closed-loop simulation model representing a distinct ecological hypothesis (REF)) defined by unique variance-covariance matrices **V**. Each operating model can be considered a distinct component variability (CVC) and synchrony ( “scenario” (Table 2). We created CVC scenarios by adjusting CU-specific estimates of SD in recruitment up or down by 25%, which were within plausible ranges sockeye salmon (Table 1; 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)). We parameterized scenarios 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 when productivity was weakly ( = 0.05; 1980s and 1990s) or moderately correlated ( = 0.50; 1950s, 1960s, and present). We specified a third high correlation scenario ( = 0.75) to represent a hypothetical situation 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 (SMSY), averaged over years (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 return abundance | Median aggregate return over years and MC trials (where aggregate is summation of return abundance across all CUs within a given 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 (100 individuals) 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 (i.e. across all CUs) because CVC and 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 mixed-CU 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 scenarios for two CUs: a low abundance, critical 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 CVC and and not to provide a status assessment or forecast the dynamics of Fraser River sockeye salmon CUs (as described in Grant et al.).

**Results**

*Retrospective analysis*

Mean Fraser River sockeye salmon productivity (log(recruits/spawner)) declined from the late 1980s through 2005, the brood year predominantly responsible for producing the poor return in 2009. Although mean productivity was moderate from 2005 until 2011, it has recently declined again with high temporal variability (Figure 2a). Aggregate spawner abundance and aggregate catch increased until the early 1990s before declining (Figure 2b,c); 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 not shown).

Mean component coefficient of variation ( CVC ; i.e. temporal variability in return abundance, weighted by a CU’s mean abundance) has varied over time, but exhibited notable peaks at the beginning of the time series (1950s) and has increased by approximately 50% since the early 2000s (Figure 2d). Similarly, synchrony ( in return abundance was relatively high in the 1950s, low and stable from 1960-1980, and increased through the 1990s, leading to a recent peak in 2014 (Figure 2e.) As expected, changes in the aggregate coefficient of variability (CVA) mirror these patterns, showing a gradual increase followed by a jump to particularly high levels in the first decade of the 2000s (Figure 2f). Note that trends in variability (Figure 2d-f) are lagged by 12 years.



Figure 2. Observed trends in (a) CU-specific productivity (loge (recruits per spawner)), (b) aggregate spawner abundance, and (c) aggregate catch. 12-year moving window estimates of the mean component coefficient of variation (CVC), synchrony index (), and aggregate coefficient of variation (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. In panel (a), multiple colours are used to show productivity trends for the 11 individual CUs from which the mean was calculated (black line). Analyses were repeated with a larger set of 18 CUs with data ranging from 1973 to 2012, and trends were similar (results not shown).

*Forward simulation*

By specifying low, medium, and high values for CU-specific variability in recruitment residuals, , and the correlation coefficient between CU’s recruitment residuals, , we were able to generate a range of CVC and scenarios (Figure 3).



Figure 3. Trends in 12-year moving averages of component variability and synchrony of return abundance as a function of and , respectively. Black lines show observed values from the retrospective analysis while the coloured lines represent median values over 250 simulation trials for different CVC and synchrony operating models. The dashed vertical line shows the start of the simulation period. Lines represent medians across 250 trials.



Figure S1. Trends in synchrony of returns as a function of , 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 CVC and on conservation-based PMs were dependent on productivity scenario. When productivity was simulated at its reference value (i.e. median retrospective estimates of productivity and normally distributed process error) the effects of greater aggregate variability were relatively minor. Increases in led to moderate declines in return abundance, while increases in CVC led to moderate increases as long as was low (purple symbols Figure 4a). The positive relationship between CVC and aggregate abundance, though initially counterintuitive, is due to individual CUs experiencing large recruitment deviations that increase aggregate abundance in any given year (i.e. the portfolio effect). 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 aggregate variability scenarios (Figure 4b,c).

Unsurprisingly, conservation-based PMs declined as the frequency of poor productivity years increased. However, the relative magnitude of these declines was strongly moderated by aggregate variability in general and in particular. For example, when aggregate variability was low, median return abundance under the low productivity scenario (skewed normal recruitment deviations) declined by approximately 25% relative to the reference productivity scenario (purple circles Figure 4a, 4d); however in simulations where was increased from low to moderate levels, median return abundance declined by more than 50% (green circles Figure 4a, 4d). The proportion of CUs above their biological benchmark exhibited similar declines at higher synchrony levels (Figure 4b, 4e). Increases in CVC were associated with declines in return abundance and conservation status under the low productivity scenario, but only when they co-occurred with moderate or high levels of (Figure 4d,e). The interaction between CVC and was most noticeable with regards to extirpation risk. The median proportion of extant CUs was ~95% as long as was low, but declined to 90% when was increased to moderate levels and to ~85% when both CVC and were at their maximum values (Figure 4f).

Median return abundance and the proportion of CUs above their upper BM deteriorated further under the extreme productivity scenario (i.e. when process variance was simulated from a skewed Student *t* distribution), but the overall patterns were similar to the low productivity scenario (Figure 4g-h). The proportion of extant CUs was one exception, strongly decreasing under the extreme productivity scenario, particularly when was moderate or high (Figure 4i).



Figure 4. Effects of component variability and synchrony on conservation-based performance measures for three different productivity scenarios. Productivity scenarios were associated with distinct distributions from which recruitment deviations were sampled: reference (normal), moderate (skewed normal), and severe (skewed student *t*). Points represent medians and whiskers 90% posterior interval among 250 simulation runs.

Similar to conservation-based PMs, for catch-based PMs the effects of CVC and also differed among PMs and productivity scenarios. Under the reference productivity scenario median catch size displayed a similar pattern to median return abundance, declining moderately at high levels of (Figure 5a). Note that as with return abundance, median aggregate catches increased with greater CVC and low levels of (purple symbols Figure 5a). Increasing and CVC simultaneously also led to moderate declines in the proportion of years the target catch threshold was achieved, as well as severe declines in catch stability (Figure 5b,c).

As with the conservation-based PMs, the impacts of aggregate variability on catch-based PMs were severe under pessimistic productivity scenarios. Under the low productivity scenario, 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 CVC and were at their minimum values to 43% at their maximum (Figure 5e). While declines in catch stability with aggregate variability were similar between the reference and low productivity scenarios, they were much more severe under the extreme productivity 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 for three different productivity scenarios. Productivity scenarios were associated with distinct distributions from which recruitment deviations were sampled: reference (normal), moderate (skewed normal), and severe (skewed student *t*). 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 minor relative to declines associated with alternative productivity scenarios. Counterintuitively, shifts in median abundance relative to biological benchmarks were actually more severe in relatively healthy CUs (e.g. Chilko) because depleted CUs (e.g. Bowron) had a low probability of recovery even when dynamics were simulated with relatively high productivity and low component variability (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**

We present evidence that temporal variability in the abundance of the Fraser River sockeye salmon stock aggregate has recently increased due to greater variability within component stocks (CVC), as well as greater synchrony () among stocks. In theory, simultaneous increases in CVC and , coupled with even moderate declines in productivity, could have severe consequences to management. Greater interannual variability will reduce the accuracy of forecasts and high levels of synchrony will reduce the probability that component populations will buffer one another in years of low abundance. Indeed, aggregate stability and mean population productivity have declined in the Fraser River even as exploitation rates were reduced dramatically, resulting in less consistent catches and substantial socio-economic costs (Cohen 2012; Peterman & Dorner 2012).

Aggregate variability may increase and weaken portfolio effects in Pacific salmon stock aggregates due to a range of ecological processes. Changes in component variability (i.e. within CU temporal variation) reflect dynamics processes at local scales, such as flow regimes or predator abundance, that influence the reproductive success or mortality of specific populations (Connor & Pflug 2004; Crozier & Zabel 2006; Crossin *et al.* 2008; Geist *et al.* 2008). Conversely, greater synchrony suggests shared drivers or dispersal increasingly link the dynamics of component populations (Walter *et al.* 2017). Within Pacific salmon aggregates, synchrony is often associated with anthropogenic disturbance, particularly processes that increase genetic homogenization such as hatchery propagation and hydropower development (Moore et al. 2010, Carlson and Satterthwaite 2015, Yamane et al. 2018).

While Fraser River sockeye salmon inhabit impacted watershed heavily impacted by human development, the specific mechanisms that may have caused stability to decline are unclear. Hatchery contributions to the aggregate are minimal and there are no hydroelectric developments on the Fraser River mainstem (Nelitz *et al.* 2011). Although highly variable, freshwater productivity does not appear to have declined uniformly through the Fraser River and has even increased for certain CUs (DFO 2016). Conversely, survival during marine residence, when sockeye salmon populations from throughout BC rear in the Gulf of Alaska, has been abnormally low in recent years (Peterman & Dorner 2012; Thomson *et al.* 2012). Indeed environmental forcing at relatively large scales appears to have increased synchrony among coho and Chinook populations, presumably due to a common response to changes in the marine ecosystem (Kilduff *et al.* 2015). Interestingly CVC and were elevated early in the Fraser River time series and declined, even though anthropogenic impacts, namely commercial harvest, were stable for several decades. Again, such patterns suggest environmental drivers may produce large increases in aggregate variability independent of anthropogenic disturbance. Fraser River sockeye salmon may be particularly prone to synchrony due to a relatively simple age structure that minimizes buffering within populations by different cohorts.

Declines in aggregate stability have been associated with reduced abundance and substantial socio-economic costs (Satterthwaite and Carlson 2015; Yamane et al. 2018). Yet it is unclear to what extent these impacts are driven by coincident changes in productivity, rather than weakened portfolio effects specifically. We used stochastic, closed-loop simulations to independently manipulate CVC, , and productivity to evaluate how interactions between the three processes influenced the probability of meeting management objectives. Broadly, our simulations demonstrate that the negative effects of greater aggregate variability are dependent on the underlying productivity regime. When population productivity was moderate (i.e. at reference levels), increases in either CVC or resulted in greater uncertainty in median abundance and the probability that biological or catch-based benchmarks would be met, however median status was relatively stable. Unsurprisingly the one performance metric that was sensitive to increased aggregate variability regardless of productivity regime was catch stability. In other words weakened portfolios may produce relatively high catches on average, assuming productivity remains unchanged, but catches will increasingly be driven by boom-and-bust cycles. This result should not be overlooked since greater variability in catches will strongly impact communities that rely on stable sockeye salmon fishing opportunities (Kasperski & Holland 2013).

Conversely, under pessimistic productivity scenarios greater aggregate variability had strong negative impacts on all performance metrics. To some extent these patterns were driven by reduced productivity independently of CVC or . For example, median return abundance declined by approximately X% between the reference (R) and skewed normal (SN) productivity scenarios. Yet increased aggregate variability, and in particular greater synchrony, strongly exacerbated the impacts of lower productivity. Moving from low to moderate synchrony under the SN scenario resulted in a further Y% decline in median return abundance. When high synchrony was paired with high CVC abundance declined an additional Z%. Other conservation- and catch-based benchmarks exhibited similarly severe responses to increased aggregate variability. When simulations incorporated an increased probability of extreme events (i.e. “black swans”) using a skewed Student *t* distribution, the probability of meeting management objectives declined even further. Extirpations in particular became more common, with 25% of CUs going extinct within ten generations under the most pessimistic scenario.

The results of our simulation analysis have important implications for management strategies that seek to incorporate systems-based approaches and leverage stability due to portfolio effects. First, simultaneous declines in productivity and aggregate stability will likely have multiplicative impacts. Management actions that are intended to rebuild populations, but that fail to account for changes in covariance among component populations may underestimate the risk of declines or overestimate the probability of rebuilding. While greater aggregate variability may not significantly increase the probability of negative outcomes unless it is accompanied by reduced productivity, it would be risky to rely on future stability to guide management actions. Many exploited fishes have already exhibited evidence of declines in productivity or carrying capacity in recent years (Peterman & Dorner 2012; Britten, Dowd & Worm 2016). Given evidence that climate change will increase the probability of extreme events in both marine and terrestrial environments (Diffenbaugh *et al.* 2005; Frölicher, Fischer & Gruber 2018), it may be more appropriate to use skewed or heavy-tailed distributions to predict future dynamics, rather than assume stability (Anderson *et al.* 2017). Furthermore, greater aggregate variability may result in negative consequences via management processes we were unable to model here (described in next paragraph). Thus, we echo previous authors in suggesting estimates of portfolio effect strength should augment commonly used metrics, such as trends in abundance or fishing mortality rates, during assessments (Thorson *et al.* 2018).

Second, the consequences of reduced stability will likely be dependent on the characteristics of the aggregate. For example, we observed strong impacts on performance metrics despite the Fraser River sockeye aggregate containing a large number of component stocks. Thus moderately high levels of aggregate variability may compromise even relatively diverse aggregates. Since the strength of potential portfolio effects is strongly influenced by the number of components (Thibaut and Connolly 2013), similar increases in component variability or synchrony in an aggregate with lower richness may result in more severe consequences. Additionally, the risks associated with increased aggregate variability were not uniformly distributed among component stocks. Assemblages that contain a greater proportion of depleted stocks may be particularly sensitive to weakened portfolio effects.

Third, even relatively accurate and precise harvest control rules are unlikely to fully buffer fisheries from reduced stability. Considerable resources are devoted each year to ensuring Fraser River sockeye salmon management targets are met including closely monitored test fisheries, genetic stock identification techniques, and estimates of abundance throughout migration and on spawning grounds (Grant & Pestal 2012). As a result, in-season exploitation rates can be reduced when abundance is lower than expected. Although we replicated the harvest control rule currently used to manage the Fraser River sockeye salmon fishery, including a relatively accurate forecasting procedure and minimal implementation error, biological benchmarks and catch-based reference points were rarely met during pessimistic scenarios. Such resource-intensive management frameworks are uncommon in fisheries and overharvest could exacerbate the effects of greater aggregate variability if management systems fail to accurately assess status. For example, harvest rates are often determined using methods such as pre-season forecasts and estimates of fishing mortality that are based on retrospective relationships (REF). As aggregate variability increases such techniques will likely become less accurate, increasing the probability of overexploitation unless managers are unusually precautionary. Furthermore, intermittent years of high abundance are likely even as aggregate variability increases, resulting in incentives to maintain excess harvesting capacity and further increasing the potential for overexploitation (Holland 1999).

The closed-loop model we created contains several necessary simplifications that could influence the relative effects of aggregate variability. For one, our conclusions are shaped by the performance metrics selected to assess the aggregate’s status. We principally focused on median outcomes (with the exception of catch stability) over approximately ten generations. Alternative metrics that emphasize variability or changes in status over shorter time horizons may indicate more severe impacts of aggregate variability.

We also chose to model alternative productivity regimes via changes in the distribution of process variance. Preliminary analyses suggested that producing a decline in productivity by manipulating alpha directly resulted in weaker effects of aggregate variability. We believe declines associated with process variance are more severe because synchronized negative deviations are less frequently balanced by large positive deviations. Since both processes produce similar declines in median productivity (i.e. observed recruits per spawner) the decision may appear arbitrary; however we believe that generating changes in average productivity via process variance is supported by recent evidence of strong negative recruitment deviations in many Pacific salmon aggregates (Malick & Cox 2016; Dorner, Catalano & Peterman 2018; Grant, Michielsens & MacDonald 2018), uncertainty about future changes in productivity (Britten, Dowd & Worm 2016), and an increased probability of extreme environmental events (Diffenbaugh *et al.* 2005; Frölicher, Fischer & Gruber 2018). Finally, we modeled biological dynamics at a relatively coarse scale. Yet processes occurring during specific life history stages likely drive changes in CVC and . Developing a more complete life cycle model, though beyond the scope of the current study, would provide a means of assessing whether variability in return abundance could be managed using interventions at specific life history stages.

Systems based approaches are increasingly advocated in disciplines, such as fisheries biology, where accounting for portfolio effects can stabilize the availability of ecosystem services (Link 2018). We agree that such approaches have merit and that there is intrinsic value in conserving as many dimensions of biodiversity as possible. We seek to demonstrate, however, that the benefits of focusing management efforts on ecological aggregates will be dependent upon variability within individual components, their covariance, and the underlying productivity regime. Since each process will vary due to environmental and anthropogenic impacts, the strength of a systems portfolio effect is dynamic and may strongly decline through time even if component richness does not. While a sufficiently precautionary approach could buffer management systems from changes in aggregate variability, such reference points will need to be highly conservative unless additional data are collected. As suggested by others, we believe that incorporating estimates of aggregate variability into assessment programs could allow management systems to manage risk (Thorson *et al.* 2018), while allowing exploitation rates to remain higher than under a data-limited precautionary approach.

Anderson, S.C., Branch, T.A., Cooper, A.B. & Dulvy, N.K. (2017) Black-swan events in animal populations. *Proceedings of the National Academy of Sciences*.

Britten, G.L., Dowd, M. & Worm, B. (2016) Changing recruitment capacity in global fish stocks. *Proceedings of the National Academy of Sciences,* **113,** 134-139.

Burgner, R.L. (1991) Life history of Sockeye Salmon (*Oncorhynchus nerka*). *Pacific Salmon Life Histories* (eds C. Groot & L. Margolis).University of British Columbia Press, Vancouver, B.C.

Carlson, S.M. & Satterthwaite, W.H. (2011) Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences,* **68,** 1579-1589.

Cohen, B.I. (2012) The Uncertain Future of Fraser River Sockeye - Part 1. *Cohen Commission,* **1,** 692.

Connor, E.J. & Pflug, D.E. (2004) Changes in the distribution and density of pink, chum, and Chinook salmon spawning in the upper Skagit River in response to flow management measures. *North American Journal of Fisheries Management,* **24,** 835-852.

Cooke, S.J., Hinch, S.G., Farrell, A.P., Lapointe, M.F., Jones, S.R.M., Macdonald, J.S., Patterson, D.A., Healey, M.C. & van der Kraak, G. (2004) Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia. *Fisheries Research,* **29,** 22-33.

Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Patterson, D.A., Jones, S.R.M., Lotto, A.G., Leggatt, R.A., Mathes, M.T., Shrimpton, J.M., Van Der Kraak, G. & Farrell, A.P. (2008) Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. *Canadian Journal of Zoology,* **86,** 127-140.

Crozier, L. & Zabel, R.W. (2006) Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. *Journal of Animal Ecology,* **75,** 1100-1109.

DFO (2016) Supplement to the pre-season run size forecasts for Fraser River Sockeye Salmon (*Oncorhynchus nerka*) in 2016. *DFO Canadian Science Advisory Secretariat Science Response,* **2016/047**.

Diffenbaugh, N.S., Pal, J.S., Trapp, R.J. & Giorgi, F. (2005) Fine-scale processes regulate the response of extreme events to global climate change. *Proceedings of the National Academy of Sciences,* **102,** 15774-15778.

Dorner, B., Catalano, M.J. & Peterman, R.M. (2018) Spatial and temporal patterns of covariation in productivity of Chinook salmon populations of the northeastern Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences,* **75,** 1082-1095.

Dorner, B., Peterman, R.M. & Su, Z. (2009) Evaluation of performance of alternative management models of Pacific salmon (*Oncorhynchus* spp.) in the presence of climatic change and outcome uncertainty using Monte Carlo simulations. *Canadian Journal of Fisheries and Aquatic Sciences,* **66,** 2199-2221.

Frölicher, T.L., Fischer, E.M. & Gruber, N. (2018) Marine heatwaves under global warming. *Nature,* **560,** 360-364.

Geist, D.R., Murray, C.J., Hanrahan, T.P. & Xie, Y. (2008) A model of the effects of flow fluctuations on fall Chinook salmon spawning habitat availability in the Columbia River. *North American Journal of Fisheries Management,* **28,** 1894-1910.

Grant, S.C.H., MacDonald, B.L., Cone, T.E., Holt, C.A., Cass, A., Porszt, E.J., Hume, J.M.B. & Pon, L.B. (2011) Evaluation of uncertainty in Fraser Sockeye (*Oncorhynchus nerka*) wild salmon policy status using abundance and trends in abundance metrics. *Candian Science Advisory Secretariat Research Document,* **2011/087**.

Grant, S.C.H., Michielsens, C.G.J. & MacDonald, B.L. (2018) Fraser River sockeye 2017 update: abundance and productivity trends. *State of the Physical, Biological and Selected Fishery*

*Resources of Pacific Canadian Marine Ecosystems in*

*2017* (eds P.C. Chandler, S.A. King & J. Boldt).Fisheries and Oceans Canada, Nanaimo BC.

Grant, S.C.H. & Pestal, G. (2012) Integrated biological status assessments under the wild salmon policy using standardized metrics and expert judgement: Fraser River sockeye salmon (*Oncorhynchus nerka*) case studies. (ed. C.S.A. Secretariat).

Holland, D.S. (1999) On direct and indirect management of fishing capacity. *Marine Resource Economics,* **14,** 263-267.

Holt, C.A. & Folkes, M.J.P. (2015) Cautions on using percentile-based benchmarks of status for data-limited populations of Pacific salmon under persistent trends in productivity and uncertain outcomes from harvest management. *Fisheries Research,* **171,** 188-200.

Kasperski, S. & Holland, D.S. (2013) Income diversification and risk for fishermen. *Proceedings of the National Academy of Sciences,* **110,** 2076-2081.

Kilduff, D.P., Di Lorenzo, E., Botsford, L.W. & Teo, S.L. (2015) Changing central Pacific El Ninos reduce stability of North American salmon survival rates. *Proceedings of the National Academy of Sciences*.

Larkin, P.A. (1971) Simulation studies of Adams River sockeye salmon (*Oncorhynchus nerka*). *Journal Fisheries Research Board of Canada,* **28,** 1493-1502.

Link, J.S. (2018) System-level optimal yield: increased value, less risk, improved stability, and better fisheries. *Canadian Journal of Fisheries and Aquatic Sciences,* **75,** 1-16.

Loreau, M. & de Mazancourt, C. (2008) Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments *The American Naturalist,* **172,** E48-E66.

Macdonald, J.S. (2000) Mortality during the migration of Fraser River sockeye salmon (*Oncorhynchus nerka*): a study of the effect of ocean and river environmental conditions in 1997. *Canadian Technical Report of Fisheries and Aquatic Sciences,* **2315,** 120 p.

Malick, M.J. & Cox, S.P. (2016) Regional-Scale Declines in Productivity of Pink and Chum Salmon Stocks in Western North America. *PLoS One,* **11,** e0146009.

Minto, C., Mills Flemming, J., Britten, G.L., Worm, B. & Rose, K. (2014) Productivity dynamics of Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences,* **71,** 203-216.

Nelitz, M., Porter, M., Parkinson, E., Wieckowski, K., Marmorek, D., Bryan, K., Hall, A. & Abraham, D. (2011) Evaluating the status of Fraser River sockeye salmon and role of freshwater ecology in their decline. *Cohen Commission Technical Report 3***,** 222 p.

Pestal, G., Huang, A.-M. & Cass, A. (2011) Updated methods for assessing harvest rules for Fraser River sockeye salmon (*Oncorhynchus nerka*). *Canadian Science Advisory Secretariat Research Document 2011/133***,** 175 p.

Peterman, Randall M. (1981) Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. *Canadian Journal of Fisheries and Aquatic Sciences,* **38,** 1113-1119.

Peterman, Randall M. & Dorner, B. (2012) A widespread decrease in productivity of Sockeye Salmon (*Oncorhynchus nerka*) populations in western North America. *Canadian Journal of Fisheries and Aquatic Sciences,* **69,** 1255-1260.

Ricker, W.E. (1975) Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin,* **191**.

Satterthwaite, W.H. & Carlson, S.M. (2015) Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences,* **72,** 1860-1875.

Schindler, D.E., Armstrong, J.B. & Reed, T.E. (2015) The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment,* **13,** 257-263.

Thibaut, L.M. & Connolly, S.R. (2013) Understanding diversity-stability relationships: towards a unified model of portfolio effects. *Ecology Letters,* **16,** 140-150.

Thomson, R.E., Beamish, R.J., Beacham, T.D., Trudel, M., Whitfield, P.H. & Hourston, R.A.S. (2012) Anomalous ocean conditions may explain the recent extreme variability in Fraser River Sockeye Salmon production. *Marine and Coastal Fisheries,* **4,** 415-437.

Thorson, J.T., Scheuerell, M.D., Olden, J.D. & Schindler, D.E. (2018) Spatial heterogeneity contributes more to portfolio effects than species variability in bottom-associated marine fishes. *Proc Biol Sci,* **285**.

Tilman, D., Isbell, F. & Cowles, J.M. (2014) Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics,* **45,** 471-493.

Walter, J.A., Sheppard, L.W., Anderson, T.L., Kastens, J.H., Bjornstad, O.N., Liebhold, A.M. & Reuman, D.C. (2017) The geography of spatial synchrony. *Ecology Letters,* **20,** 801-814.