

Conservation risks and portfolio effects in mixed-stock fisheries

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Abstract

Fish biodiversity sustains the resilience and productivity of fisheries, yet this biodiversity can be threatened by overharvest and depletion in mixed-stock fisheries. Thus, the biodiversity that provides benefits may also make sustainable resource extraction more difficult, a key challenge in fisheries management. We simulated a mixed-stock fishery to explore relationships between different dimensions of biodiversity and fishery performance relative to conservation and fishery objectives. Different dimensions of biodiversity (number of stocks, evenness, asynchrony among stocks, heterogeneity in stock productivity) exacerbated trade-offs between fishery and conservation objectives. For example, fisheries targeting stock-complexes with greater asynchrony, and to a lesser extent richness, had greater stability in harvest through time but also greater risks of overfishing weak stocks and reduced yield compared to less biodiverse stock-complexes. These trade-offs were ameliorated by increasing management control—the capacity of fishery managers to harvest specific stocks. To explore these trade-offs in real-world fisheries, we contrasted the fishing and population status of individual stocks within three major mixed-stock sockeye salmon (*Oncorhynchus nerka*, Salmonidae) fisheries—Bristol Bay, Fraser River, and Skeena River. In general, the fisheries with lower management control had individual stocks that were more often being over- or under-fished, compared with those with higher management control, though variation among regions in biodiversity, scale of management, and magnitude of habitat alteration likely also contribute to these relationships. Collectively, our findings emphasize that there is a need to extract less or regulate better in order to conserve and benefit from biodiversity in fisheries and other natural resource management systems.

KEYWORDS

diversity-stability, ecological portfolio effects, mixed-stock fishery, Pacific salmon, resilience, sustainable fisheries

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1 | INTRODUCTION

The sustainability and resilience of fisheries and the ecosystems that support them is a global management challenge. Fish are a key contributor to global food security, providing over 4.5 billion people with at least 15% of their protein (Bene et al., 2015), and are remarkably biodiverse—there are more than 32,000 fish species, more than all other vertebrate species combined (Wiens, 2015). Fish biodiversity within and across species can contribute to stable and resilient fisheries (Cline et al., 2017; Kasperski & Holland, 2013; Nesbitt & Moore, 2016; Schindler et al., 2010; Sethi, 2010). Here we focus on stability as the lack of temporal variation in aggregate processes (Doak et al., 1998), such as interannual variation in fishery catches. Such stability in fishery catches arise from portfolio effects, whereby fisheries that harvest multiple fish populations or species can benefit from the statistical averaging of their asynchronous dynamics (Doak et al., 1998; Figge, 2004; Markowitz, 1952; Schindler et al., 2015). If stocks also respond differently to specific perturbations, such biodiversity can also provide ecosystem resilience (Cline et al., 2017; Doak et al., 1998; Gunderson, 2000). Accordingly, biological diversity is increasingly viewed as a foundation of sustainable and resilient resource management systems (Biggs et al., 2012; Carpenter et al., 2009; Robinson et al., 2020). Yet, fisheries that catch multiple stocks within a stock complex, whether they be specific populations (Hilborn et al., 2003; Hutchinson, 2008) or species (Hilborn et al., 2012), may over-exploit the less productive stocks within that complex (Burgess et al., 2013; Connors, Staton, et al. 2020; Matsuda & Abrams, 2006; Ricker, 1958). Such “mixed-stock” over-fishing is one of the foundational challenges to fisheries sustainability and can compromise fishery yield and increase risks of depletion to undesirable levels or even potential extinction (Hilborn et al., 2015; Link, 2018; Okamoto, Hessing-Lewis, et al., 2020; Ricker, 1958). Thus, the biodiversity that provides benefits may also make sustainable resource extraction more difficult.

Different aspects of biodiversity control different ecosystem processes (Cardinale et al., 2013; Hooper et al., 2005; Loreau et al., 2001; Naeem et al., 2012; Pasari, et al., 2013) and the benefits that humans derive from them, like the performance of mixed-stock fisheries (Cline et al., 2017; Nesbitt & Moore, 2016; Schindler et al., 2010). For instance, portfolio effects and resultant stability in aggregate processes are a function of multiple dimensions of biodiversity: (a). Richness—the number of assets in the portfolio, such as the number of species or populations in a fishery; (b). Evenness—the distribution of biomass or abundance among the assets; (c). Variation—the temporal change in the asset performance or abundance through time, often measured by the coefficient of variation (CV); and (d). Correlation—or synchrony among the assets in their dynamics, linked to response diversity (Elmqvist et al., 2003). Multiple dimensions of biodiversity can also, via different mechanisms, promote other attributes such as productivity. For example, aggregate productivity is often positively associated with biodiversity in systems that range from grasslands (Cardinale et al., 2013; Hooper et al., 2005) to marine ecosystems (Dee et al., 2016; Greene

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et al., 2010; Worm et al., 2006). Given these positive effects of biodiversity, there have been calls for natural resource management systems, such as fisheries, to try to maximize diversity within harvests (Robinson et al., 2020).

Numerous dimensions of fisheries performance could be influenced by stock diversity. Fisheries could harvest only a single stock or many stocks (Bieg et al., 2018), and in the latter case, those stocks could vary in their productivity, evenness, and asynchrony. The objectives and metrics used to assess fisheries performance may be associated with harvest, such as the average annual yield of catch or the inter-annual stability of catch (Hilborn, 2020; Hilborn et al., 2015). Alternatively, fishery performance can be based on biologically-based objectives such as reducing conservation risks, with metrics such as the probability that a stock is overfished to depletion or extinction (Hilborn, 2020; Hilborn et al., 2015). Biodiversity may influence fisheries performance via different processes. Many predictions should follow standard ecological theory of the relationships between diversity and ecological function. As noted above, portfolio theory predicts that fisheries that harvest more stocks may have more stable catches (Griffiths et al., 2014; Nesbitt & Moore, 2016; Schindler et al., 2010). However, unlike other ecological and economic portfolios that benefit from their assets without influencing their dynamics, fisheries inherently modify fish populations and so may complicate predictions. For example,

biodiversity could exacerbate trade-offs among fisheries objectives (Connors, Staton, et al. 2020; Okamoto, Hessing-Lewis et al., 2020), with greater richness, asynchrony, or unevenness potentially increasing risk of overfishing and depletion. Fisheries performance is also commonly assessed based on the status of individual stocks within a fishery. For example, fisheries often aim to achieve harvest rates and abundances of individual stocks that are predicted to maximize sustainable harvest over time thereby avoiding lost catch potential from under- or overfishing as well as depletion to undesirably low levels of abundance such as those that pose extinction risks (e.g., Kobe plots of status of each stock relative to their theoretically optimal harvest rate and abundance). Within biodiverse fisheries, it may be challenging to avoid overharvesting less productive (“weaker”) stocks unless harvest rates are reduced below those expected to maximize yield for the most productive (“stronger”) stocks (Burgess et al., 2013; Connors, Staton, et al. 2020; Hilborn, 1985; Hilborn et al., 2012; Matsuda & Abrams, 2006; Ricker, 1958). Thus, the performance of fisheries, whether it is assessed based on aggregate or individual components, is expected to be strongly influenced by different aspects of biodiversity.

Here we explore how different aspects of biodiversity influence fishery performance and trade-offs through simulations and analyses of major mixed-stock sockeye salmon (*Oncorhynchus nerka*, Salmonidae) fisheries in the eastern North Pacific. First, we use simple simulation models of mixed-stock fisheries to examine how different aspects of biodiversity (richness, evenness, synchrony, and differences in stock productivity) (Burgess et al., 2013; Doak et al., 1998; Figge, 2004) influence three metrics of fishery performance and conservation objectives: inter-annual catch stability, over-fishing risk, and catch. We also examine how fishery performance is influenced by two key management levers: fishing intensity and management control—the capacity of the management system to allocate harvest to specific stocks (Hilborn, 1985; Hilborn et al., 2012). Second, we evaluated the fishing and conservation status of individual stocks within three globally-important mixed-stock sockeye salmon fishery complexes. Collectively, our results integrate key concepts from biodiversity-ecosystem functioning and mixed-stock fisheries theory to explore the benefits and challenges posed by multiple dimensions of biodiversity in fisheries. Further, our study reveals that to avoid overharvest of weak stocks, managers can decrease harvest rates or improve management control to conserve biodiversity and its associated benefits.

2 | MATERIALS AND METHODS

2.1 | Modeling biodiversity and mixed-stock fishery performance

We simulated an age-structured, multi-stock fish population complex that is exploited by a mixed-stock fishery with varying degrees

of management control and overfishing tolerance (base parameterizations are described in Table S1). We then used the simulation model to explore how different aspects of diversity (number of stocks, synchrony among stocks, evenness, differences in productivity among stocks), fishery management control (the ability of the managers to control and allocate harvest), and risk tolerance to overfishing weak stocks, influence the ability of fisheries to be (a) productive (maximize yield of catch from the system), (b) biologically-sustainable (lower biological risk of stock extirpation), and (c) provide stable catches over time.

2.1.1 | Stock sub-model

We simulated a stock complex comprised of n stocks whose dynamics were governed by autocorrelated Ricker-type stock recruitment relationships:

$$R_{y,n} = \alpha_n S_{y,n} e^{-\beta_n S_{y,n} + \phi \log(R_{y-1,n}/\hat{R}_{y-1,n}) + r_{y,n}} \quad (1)$$

where $R_{y,n}$ is recruitment for stock n that spawned in year y , α_n and β_n are stock-specific intrinsic rates of growth (productivity) and within-stock density dependence, $S_{y,n}$ is spawner abundance, ϕ is the degree of temporal correlation in recruitment from one brood year to the next, $\hat{R}_{y-1,n}$ is the expected recruitment in the previous brood year, and $r_{y,n}$ is variation in recruitment that is correlated among stocks according to ρ following a multivariate normal distribution:

$$r_{y,n} \sim \text{MVN}(0, \mathbf{V}),$$

$$\mathbf{V} = \begin{bmatrix} \sigma_1 \sigma_1 & \cdots & \sigma_1 \sigma_n \rho \\ \vdots & \ddots & \vdots \\ \sigma_n \sigma_1 \rho & \cdots & \sigma_n \sigma_n \end{bmatrix} \quad (2)$$

Stock specific combinations of α_n and β_n determine equilibrium stock size ($\log(\alpha_n)/\beta_n$) which we allowed to vary as a function of an overall evenness index J' ; Pielou's evenness index (Pielou, 1966) calculated as $H'/\log[\max(n)]$ where H' is the Shannon Diversity Index ($-\sum_{i=1}^n p_i \ln p_i$) and p is the proportional contribution of stock i to aggregate equilibrium stock complex size ($\sum_{i=1}^n \log(\alpha_i)/\beta_i$).

Returns in a given year, $N_{y,n}$, are a function of the proportion of individuals that return to spawn at each age:

$$N_{y,n} = \sum_{a=4}^7 R_{y-a,n} \pi_{a-3} \quad (3)$$

where π is a maturity schedule common to all stocks and comprised of four age classes (i.e., fish maturing at ages 4–7). To incorporate the effects of small stock size on reproductive success (e.g., Allee effects and depensation), we set a quasi-extinction threshold at 20 spawners such that if spawner abundance fell below this threshold recruitment from that brood year was assumed to be zero.

2.1.2 | Harvest sub-model

We simulated a mixed-stock fishery with varying degrees of management control. Under perfect management control the harvest rate, U , experienced by stock n in year y was:

$$U_{y,n} = \begin{cases} 0 & \hat{N}_{y,n} - E_n \leq 0 \\ (N_{y,n} - E_n)/N_{y,n}, & \hat{N}_{y,n} - E_n > 0 \end{cases} \quad (4)$$

where $\hat{N}_{y,n}$, the forecasted run size, is equal to the true run size ($N_{y,n}$) plus forecast error ϵ_n which was lognormally distributed with a mean of zero and variance equal to σ_f^2 , where the f subscript differentiates this variance from other variance terms in the simulation. The escapement goal for a given stock, E_n , is the spawner abundance expected to produce maximum sustainable yield based on the stock specific α_n and β_n (Scheuerell, 2016), such that "surplus" production above the escapement goal is harvested when the forecasted run size is larger than it. Total harvest by stock, $H_{y,n}$, is then:

$$H_{y,n} = U_{y,n} N_{y,n} \quad (5)$$

and total escapement, by stock, is:

$$S_{y,n} = N_{y,n} - H_{y,n} \quad (6)$$

To simulate a range of management control, and tolerance for risk of overfishing, we allowed the harvest rate experienced by each stock, $H_{y,n}$, to be modified by C^* and P^* , respectively:

$$H_{y,n} = (U_{y,n} C^* + U_y (1 - C^*)) P^* N_y \quad (7)$$

where U_y is the mixed-stock harvest rate calculated as per Equation (4) but with E equal to the sum of E_n , and N_y equal to the sum of $N_{y,n}$. Under Equation (7), when management control is perfect C^* is equal to 1, and when the fishery system seeks to maximize yield from the stock complex as a whole, C^* is equal to 0. To allow for a range in tolerance for the risk of overfishing weak stocks we allowed the realized harvest rate to be further modified by P^* ; when P^* is equal to 1 risk tolerance is relatively high (i.e., harvest rates are at those expected to maximize yield), and values less than 1 indicate increasingly less tolerance for the risk of overfishing weak stocks (i.e., harvest rates are proportionally less than those predicted to maximize yield).

2.1.3 | Performance measures

For each simulation we calculated three performance measures over the last 20 years of each 50 year simulation:

- *fishery yield*: median aggregate harvest relative to the maximum harvest possible,
- *fishery stability*: one over the coefficient of intra-annual variation in harvest, and
- *biological risk*: the proportion of stocks whose median spawner

abundance over the last 20 years of the simulation fell below 5% of their equilibrium size.

Each simulation was repeated over 300 Monte Carlo trials (unless stated otherwise) and parameterized with biologically-realistic parameters (Table S1). We examined fishery performance across a range of the numbers of stocks (n ; 6–31), synchrony among stocks (ρ ; 0–1), productivity among stocks (α ; 1.5–8), evenness (J' ; 0.03–1), degrees of fishery management control (C^* ; 0–1), and risk tolerance to overfishing weak stocks (P^* ; 0–1). For more details of the justification for range of values considered see Table S1.

2.2 | Case study of sockeye salmon fisheries

To explore how stock diversity, management control, and fishing intensity interact to shape the status of individual stocks in real-world mixed-stock fisheries, we analysed stock status through time in three of the largest sockeye salmon (*O. nerka*) fishery complexes in the world: Bristol Bay, Alaska, USA; Fraser River, British Columbia (BC), Canada; and Skeena River, BC, Canada (Table 1). These fisheries integrate harvest across numerous salmon stocks as they migrate back to their natal waters to spawn (Greene et al., 2010; Griffiths et al., 2014; Schindler et al., 2010). All three fishery complexes target a diversity of stocks (at least 8 stocks) that are relatively asynchronous and exhibit a range of stock productivities (Table 1). Accordingly, portfolio effects have been observed to dampen inter-annual catch variability in all three systems: Bristol Bay (Schindler et al., 2010), Skeena (Price et al., 2021), and Fraser (Freshwater et al., 2019). From a qualitative perspective, management control across these systems, at the scale at which it occurs, varies from high (Bristol Bay), intermediate (Fraser), to low (Skeena) due to factors such as spatial configuration of the fishery complex (multiple rivers vs. single river), run-timing diversity, and the extent to which in-season management occurs (Table 1). However, it is important to note that fishery management occurs at a finer biological scale in the Skeena and Fraser than in Bristol Bay. While some stocks (usually representing individual lake systems) within the Skeena and Fraser are comprised of numerous spawning populations (e.g., Stuart-Takla), within each of the eight stocks (representing major river systems) in Bristol Bay there are hundreds of locally-adapted populations (Hilborn et al., 2003; Rogers & Schindler, 2008; Schindler et al., 2010). Thus, while management control at these aggregate levels (what we call the "management unit") is higher in Bristol Bay than in the other systems, there is more unaccounted biodiversity in Bristol Bay. We also note the Skeena and Fraser Rivers have more degraded freshwater habitat than Bristol Bay (Griffiths et al., 2014), and have, in general, experienced depressed productivity over the last several decades (Peterman & Dorner, 2012). Management priorities have also shifted over time in each system (Table 1). Thus, we quantify stock status across these systems that vary in management control, as well as the biological scale at which management occurs, biodiversity, and habitat quality.

TABLE 1 Attributes of sockeye salmon case study fisheries

Fishery	Stock biodiversity	Management
Bristol Bay	Richness ^a = 8 Synchrony ^b = 0.31, 0.087 to 0.57 Range of productivity ^c = 2.70 to 5.62 Autocorrelation ^d = 0.43, 0.22 to 0.61 Recruitment variability ^e = 0.78, 0.58 to 1.06 Evenness ^f = 0.866 Portfolio effect ^g = 1.55 Age at maturity = [0,0.25, 0.62, 0.13] ^h Watershed area = 82,254 km ²	High control Fisheries target different river systems and thus managers can control harvest rates on specific stocks through spatial and temporal differences in migration, additionally controlled by in-season test fisheries with associated rapid genetic stock identification (Dann et al., 2013). Fairly consistent management priorities across time (Cunningham et al., 2019).
Skeena	Richness = 11 Synchrony = 0.15, -0.68 to 0.63 Range of productivity = 2.75 to 8.37 Autocorrelation = 0.33, 0.017 to 0.68 Recruitment variability = 0.80, 0.41 to 1.41 Evenness = 0.532 Portfolio effect = 1.19 Age at maturity = [0.02, 0.46, 0.5, 0.2] Watershed area = 54,400 km ²	Low control Major fisheries occur in the marine approaches to, and lower portion of, a single large river. The enhanced Babine lake stock constitutes ~80% of total sockeye returns to the Skeena. Abundance-based management control rule, limited in-season management for specific stocks though harvest rates on aggregate returns take wild stocks into consideration (Fisheries and Oceans Canada, 2019a). Management priorities had generally shifted from fishery yield to protection and recovery of weak stocks in recent decades (Walters et al., 2018).
Fraser	Richness = 16 Synchrony = 0.23, -0.18 to 0.62 Range of productivity = 1.99 to 8.57 Autocorrelation = 0.22, -0.072 to 0.57 Recruitment variability = 1.29, 0.67 to 2.82 Evenness = 0.714 Portfolio effect = 1.92 Age at maturity = [0.01, 0.91, 0.08,0] Watershed area = 220,000 km ²	Medium control Major fisheries occur in the marine approaches to, and lower portion of, a single large river and target co-migrating stocks. In-season management based on test-fisheries and rapid genetic stock identification, but harvest can only be allocated by four major run-timing groups that each contain multiple stocks (Fisheries and Oceans Canada, 2019b). Management priorities had generally shifted from fishery yield to protection and recovery of weak stocks in recent decades (Walters et al., 2018).

^aNumber of stocks for which their status can be assessed across the study periods.

^bAverage and range in correlation coefficient among pairs of substocks in recruitment residuals (natural log of recruits per spawner) over the study periods, using years where pairs have data.

^cRange of observed productivities (alpha parameters) over the study periods; note for all stocks a single alpha was estimated and thus these numbers do not reflect annual productivities that may drop below these estimates.

^dAverage and range lag1 autocorrelation within stocks from acf() function in R, not including lag1 values with an NA for discontinuous time series.

^eAverage and range of CV of recruitment for substocks within a region.

^fPielou's evenness index using averaged run sizes across the entire time series.

^gPortfolio effect across the entire time series as expected CV of run size for the entire system (weighted sum of CVs by subpopulation) divided by the realized CV for the entire system (CV of system when summed by year).

^hAverage age at maturity across 3, 4, 5, and 6 year old adults; calculated across all years and stocks.

To characterize stock status we fit Ricker stock-recruit relationships for each stock independently (no shared parameters across stocks within the system) using the linear version of Equation (1) in a Bayesian estimation framework. For each stock, the entire time series of data was used and only stocks with a minimum of 20 years of stock-recruitment data, and data for the most recent decade (the year 2000 or later) were considered. We assigned a uniform prior probability distribution for $\ln(\alpha)(U(0, 4))$, a uniform prior on process error ($U(0.05, 10)$) and informative lognormal prior probability distributions based on habitat carrying capacity for β (details on β priors for each system and stock are provided below).

Our analysis was conducted using Just Another Gibbs Sampler (JAGS) through the package R2jags (Su & Yajima, 2015), from the

R statistical computing software (R Core Team, 2019). Posterior distributions were generated for the parameters based on models fit with four chains for 100,000 iterations and thinned every tenth iteration with a burn in of 50,000. Model convergence for each stock was examined using traceplots of posterior estimates on α and β , and the Gelman-Rubin convergence statistic (Gelman & Ubrin, 1992).

We calculated the spawner abundances ($S_{MSY,n}$) and harvest rates ($U_{MSY,n}$) for each population, n , that correspond to those predicted to maximize yield under equilibrium conditions using the method described by Scheuerell (Scheuerell, 2016). Stock status based on spawner abundance and harvest rate was then calculated for each decade, y , using management targets estimated from the entire time series, as $S_{n,y}/S_{MSY,n}$ and $U_{n,y}/U_{MSY,n}$, respectively. We

used Kobe plots to illustrate the distributions of individual stock status based on harvest rates (U) and abundances (S) relative to those predicted to maximize long-term sustainable yield (MSY) ($U/U_{MSY} \sim 1$; $S/S_{MSY} \sim 1$). Following the Food and Agricultural Organization (FAO) of the United Nations (Hilborn, 2020), we considered stocks to have achieved harvest rate and abundance management targets if they were within 20% of these values ($U/U_{MSY} = 0.8 - 1.2$; $S/S_{MSY} = 0.8-1.2$).

2.2.1 | Bristol Bay

In Bristol Bay, we considered eight stocks which corresponded to the major salmon bearing rivers in the system: Igushik, Wood, Nushagak, Kvichak, Alagnak, Naknek, Egegik, and Ugashik. We note that there are multiple sub-stocks within each of these major river systems; given that management occurs at the scale of major river system we did not estimate stock status at this finer spatial scale. All of these rivers have estimates of escapement and recruitment continuously across the time series for brood years 1963–2009 (Cunningham et al., 2018). Priors on the mean historical stock size were used to inform β for seven of these systems from paleolimnological data using lake cores collected from nursery lakes (Rogers et al., 2013; Schindler et al., 2005, 2006). However, there was no paleolimnological data for the Nushagak, and so we used a minimally informative prior (inverse of average historical abundance with a CV equal to 10). While we could have used an uninformative prior for in the Nushagak, or estimated parameters with Maximum Likelihood (Cunningham et al., 2019) we chose to use a minimally informative prior to be consistent in our use of prior information (regardless of type) across stocks.

2.2.2 | Fraser

In the Fraser, we considered 16 stocks with time series of escapement and recruitment that spanned the time periods of focus (1980s–2000s): Early-Stuart, Late-Stuart, Stellako, Bowron, Raft, Quesnel, Chilko, Late-Shuswap, Birkenhead, Portage, Weaver, Fennell, Gates, Nadina, Pitt, and Harrison. All stocks had continuous time series beginning as early as the 1952 brood year and as late as 1973 brood year and ended in the 2010 or 2011 brood year. For 14 of the stocks there were habitat-based estimates of maximum stock size (Grant et al., 2011) which we used as a prior on β . For Fennell and Harrison, habitat-based estimates of capacity were not available and so, as in the Bristol Bay, we used a minimally informative prior (inverse of average historical abundance with a CV equal to 10). The posteriors were minimally influenced by the priors because of the amount of data available; this was tested for Fennell and Harrison by using the maximum historical average (Grant et al., 2011), and found the same trend in the results.

2.2.3 | Skeena

In the Skeena, we considered 11 stocks: Alastair, Babine-enhanced, Baine-early-wild, Babine-mid-wild, Babine-late-wild, Kitsumkalum, Lakelse, Mcdonnell, Morice, Stephens, and Swan. Time series of escapement and recruitment were sparser for the Skeena compared to the other two systems and so there was insufficient data to consider the numerous other stocks in the watershed. We used photosynthetic-based estimates of (inverse) capacity as priors for these stocks following previous work in the system (Korman & English, 2013), with a moderately informative CV (0.3) used for all stocks other than those in the Babine system where a minimally informative CV (1) was used. As the data is much sparser for the Skeena system, decadal estimates of spawner abundances ($S_{n,y}$) and harvest rates ($U_{n,y}$) were averaged across the data available for each decade considered (1980s, 2000s) but they not always the same years for each stock and often did not include a full 10 years of data.

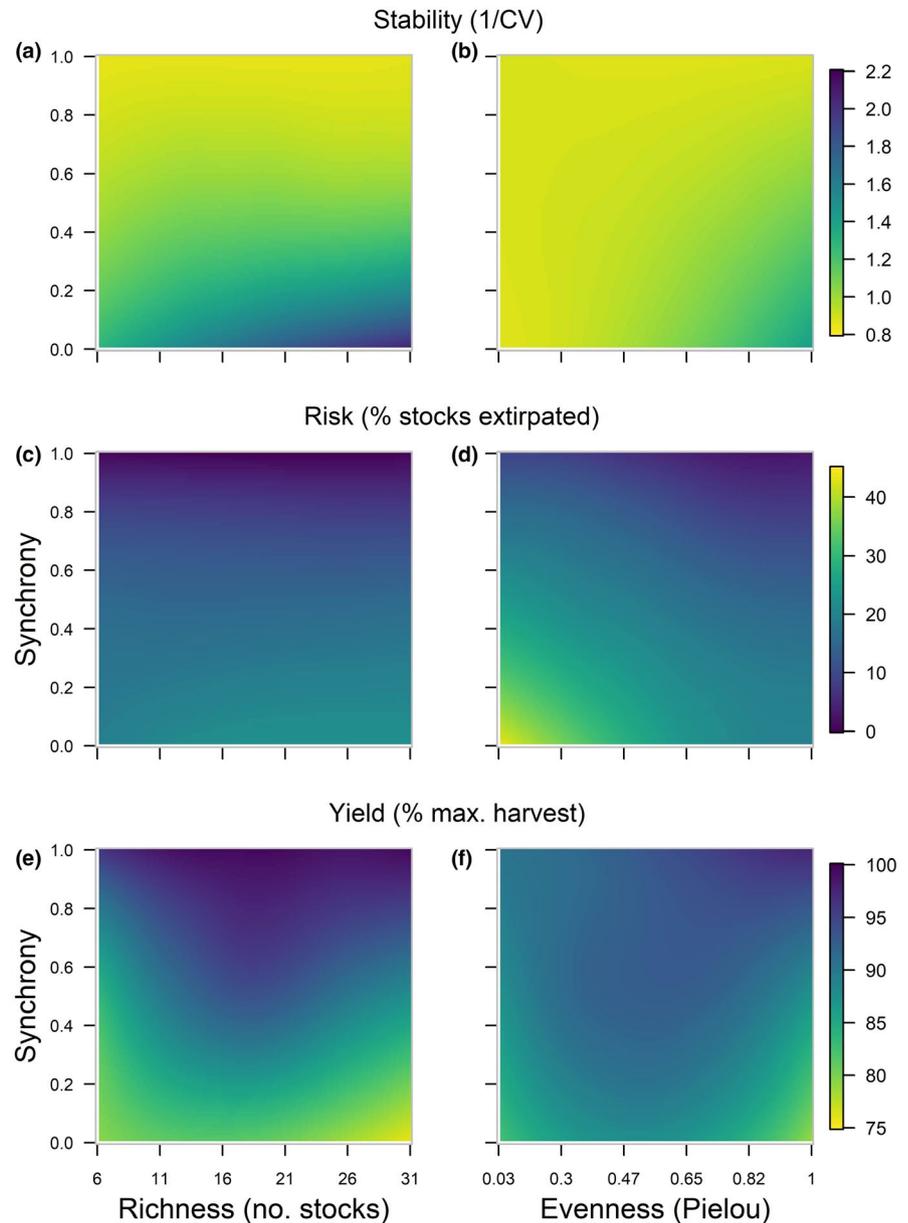
3 | RESULTS

3.1 | Simulations of mixed-stock fisheries

In the simulated mixed-stock fishery with low management control, biodiversity mediated trade-offs between catch stability, total yield, and overfishing risks (Figures 1 and 2). As predicted from statistical averaging in economic portfolio theory (Doak et al., 1998; Figge, 2004; Markowitz, 1952) and empirical studies (Carlson & Satterthwaite, 2011; Cline et al., 2017; Greene et al., 2010; Griffiths et al., 2014; Nesbitt & Moore, 2016; Schindler et al., 2010; Sethi et al., 2014), catch stability was over two times greater in fisheries with high richness and low synchrony compared to fisheries with low richness and high synchrony (Figure 1a). Thus, stock richness and asynchrony increase the stability of fisheries catches through portfolio effects. Yet, under this base case of low management control, conservation risks from overfishing also increased with lower synchrony. Specifically, the probability of extirpating weak stocks increased from 0% in fisheries with high synchrony to ~15% in fisheries with low synchrony (Figure 1c). Fisheries over-harvested less productive populations to pseudo-extinction. Further, under the base case of low management control, total yield generally decreased by as much as 25% with increasing stock richness and decreasing synchrony (Figure 1e). Thus, higher stock richness and lower synchrony in mixed-stock fisheries can increase catch stability but decrease overall yield and increase risks to biodiversity (Figure 2).

Additional dimensions of biodiversity further modulate these trade-offs in fishery performance in complex ways (Figure 1, Figures S2 and S3). Greater evenness in stock size within the simulated stock complex increased catch stability, particularly when stocks exhibited weakly synchronous dynamics; in these

FIGURE 1 Fishery and conservation consequences of stock diversity, in terms of: (a–b) inter-annual stability in total harvest, (c–d) proportion of stock extirpated, and (e–f) percent of maximum potential harvest realized, across a range synchrony in survival (y -axis) and either (a, c, d) number of stocks in the stock complex or (b, d, f) evenness in stock size (x -axes). Under the scenario shown all stocks ranged in productivity from 3.25 to 6 recruits per spawner, richness was equal to 10 stocks in the evenness panels, there is no management control ($C^* = 0$), and high overfishing tolerance ($P^* = 1$)



cases, stability increased by as much as 60% as evenness increased (Figure 1b). Lower evenness also strongly exacerbated extirpation risk, and this relationship was exacerbated by lower synchrony among stocks. Extirpation risk was as high as 40% in mixed-stock fisheries with extreme unevenness in stock size (i.e., a single stock constitutes 99% of total production) and asynchronous dynamics, and near 0% when the stock complex was made up of stocks of equal size with synchronous dynamics (Figure 1d). Mixed-stock yield also tended to be greatest when stocks were synchronous and even in size (Figure 1f). In addition, when heterogeneity in stock productivity among stocks was large (e.g., spanning 1.5–8 recruits-per-spawner) risk of biodiversity loss due to over-exploitation were further exacerbated for the weakest, least productive stocks, but had little impact on fishery yield or stability (Figure S2, S3). For example, fisheries that target a mixture of species with slow and fast life-histories with different productivities

pose greater conservation risks (Burgess et al., 2013). Thus, different dimensions of biodiversity strongly alter fishery stability, yield, and risk (Figure 3).

If fisheries managers are interested in moderating the risks of overfishing weak stocks, they can, most simply, decrease harvest rates. In our simulations, fishing below maximum sustainable yield (P^* , see Equation (7)) decreased overfishing risks and stock extinction, but at the obvious cost of decreases in catch (Figure 2b,d), following previous analyses (Connors, Staton, et al. 2020; Hilborn, 1985). The scope for decreasing risk was largest in the stock complexes with the greatest stability and biodiversity—those with high stock richness and low synchrony where a 6-fold reduction in risk (from 18% to 3%) can at the cost of a ~ 50% reduction in harvest (from 50% to 25% of maximum yield) (Figure 2b,d).

The optimal method, however, in terms of minimizing extinction risk and maximizing fishery yields in mixed-stock fisheries was

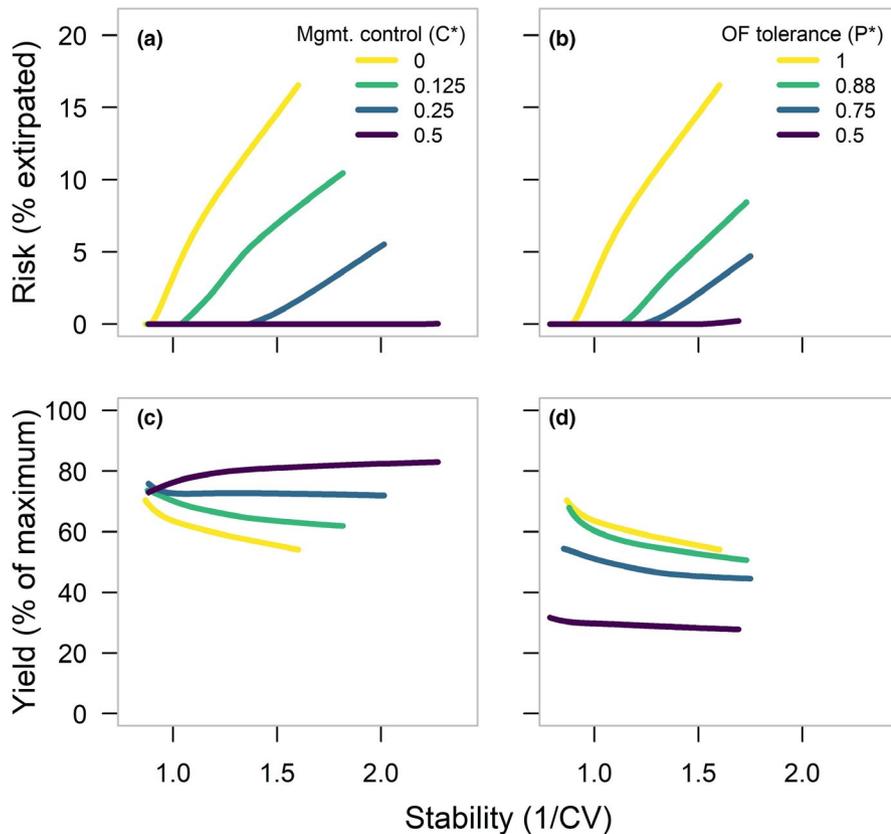


FIGURE 2 Risk – stability trade-offs. Relationships between risk (a and b) or yield (c and d) and stability across a range of (a and c) management control (C^*) and (b and d) overfishing (OF) tolerance (P^*). Each relationship is generated across a range of synchrony (0–1) in recruitment among stocks ($n = 12$) which range in productivity from 3.25 to 6 recruits per spawner. The lines are different lengths as there is an interaction between management control and catch stability

to have high management control (high C^*). Management control is the allocation of effort and harvest to individual management units (e.g., stock) with high precision such as through space or time closures or gear restrictions. If there was no management control at the individual stock scale (e.g., no information or capacity to target individual stocks), then the harvest rates predicted to maximize yield are based on the stock aggregate. Under a scenario of low management control, there is a higher risk of over-exploitation and stock extirpation, as noted above (Figure 1). In contrast, if there was perfect knowledge and harvest rates can be allocated to maximize yield of each individual stock (complete management control; $C^* = 1$), risks to individual stocks are low to non-existent even when fishing catches are prioritized above biological conservation (overfishing risk tolerance; high P^*). Even relatively small changes in the degree of management control dramatically decreased conservation risks; for example, increasing management control from 0% to 25% (where 25% of the harvest rate decision is informed by stock-specific abundance), cut the risks of extirpation by at least half (Figure 2a). Higher management control also increased fishery yield, particularly in simulated stock complexes with high richness and low synchrony and associated high catch stability (Figure 2c). Collectively, these results indicate that high management control is particularly impactful in diverse fisheries and enables fisheries to have higher catches that are stable with minimal risk of overfishing biodiversity (Figure 2). Broadly, fisheries of biodiverse stocks therefore need to regulate better or harvest less in order to conserve biodiversity. In contrast, systems with high synchrony benefited less from stock-specific harvest control as all stocks

fluctuated from year to year in a similar manner thereby reducing the chance that a good year for one stock occurred during a year with poor returns for another.

The status of individual stocks within our simulations further illustrates the trade-offs between conservation and fishing in biodiverse fisheries (Figure 4). When biodiverse stock complexes were fished under low management control and prioritization of fishing (high tolerance for biological risk; high P^*), individual stocks were often either depleted by over-fishing or were under-fished (Figure 4a). Specifically, only 21% of stocks achieved fishery targets ($U/U_{MSY} = 0.8-1.2$; $S/S_{MSY} = 0.8-1.2$), 24% were overfished ($S/S_{MSY} < 0.8$), and 25% could be sustainably fished at a higher rates ($U/U_{MSY} < 0.8$ and $S/S_{MSY} > 1.2$), representing missed harvest opportunities. In contrast, when biodiverse stock complexes were fished with high management control (C^*) and high tolerance for overfishing (P^* ; Figure 4b), 84% of stocks achieved fishing and abundance targets ($U/U_{MSY} = 0.8-1.2$; $S/S_{MSY} = 0.8-1.2$), with no stocks overfished and experiencing overfishing ($U/U_{MSY} > 1.2$; $S/S_{MSY} < 0.8$), and minimal lost fishing opportunities (0% of stocks with $U/U_{MSY} < 0.8$ and $S/S_{MSY} > 1.2$).

In simulations where managers prioritized conservation over fisheries by reducing overfishing risk tolerance (lower P^*), stocks generally achieved abundance objectives ($S/S_{MSY} > 0.8$) but at the cost of substantial missed harvest opportunities (Figure 4d,e). Specifically, under low management control, 80% of stocks could be sustainably fished at a higher rate ($U/U_{MSY} < 0.8$ and $S/S_{MSY} > 1.2$), while there were still 10% of stocks that were depleted ($S/S_{MSY} < 0.8$). With increased management control under this conservation-priority

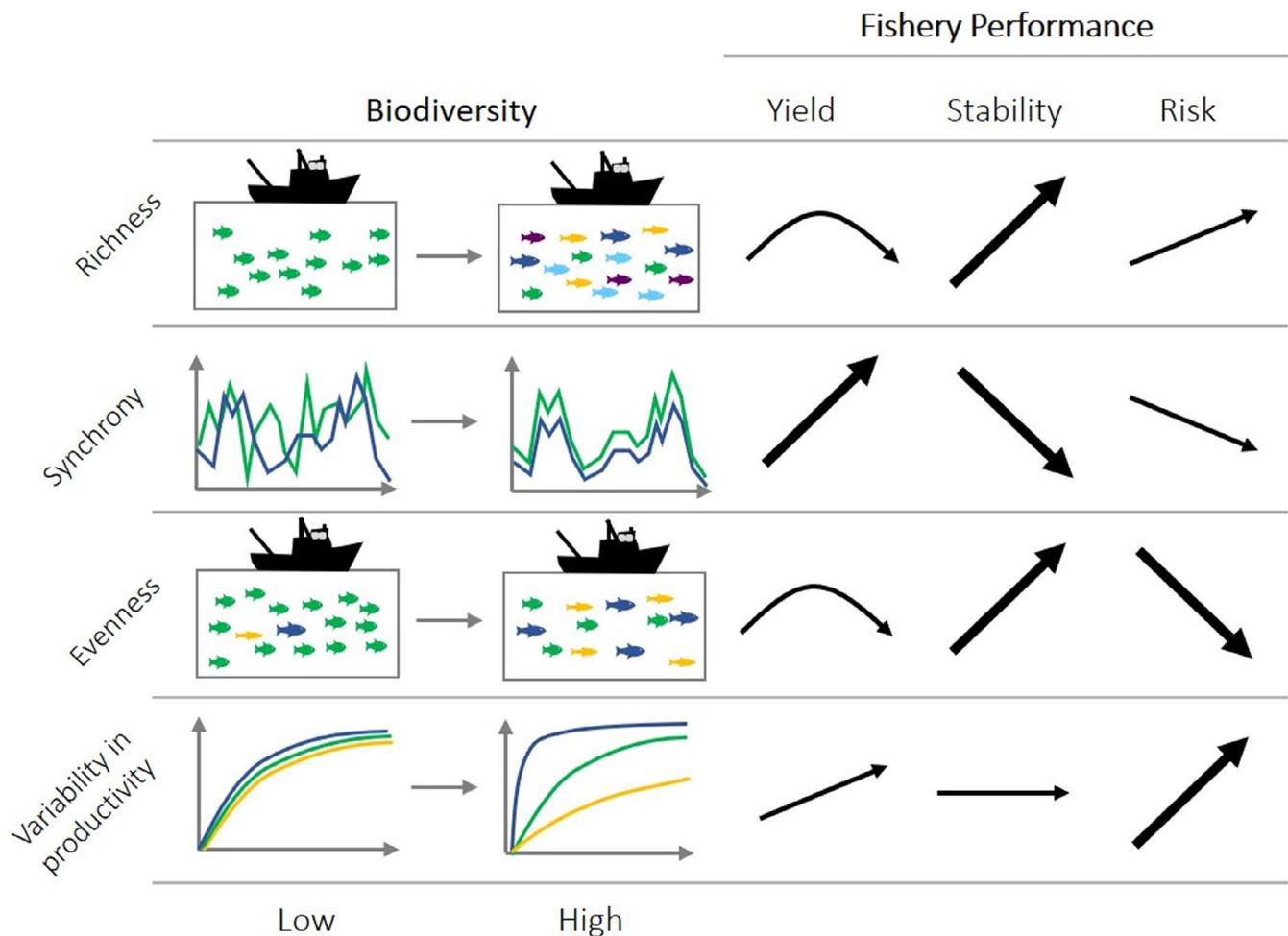


FIGURE 3 Illustrative synthesis of relationships between dimensions of biodiversity and fisheries performance under the base case simulations (see Figure 1 and Figure S1). These relationships are further influenced by harvest intensity and management control (see Figure 2). Arrows indicate the direction, approximate shape, and magnitude (arrow weight) of the relationship between increasing biodiversity (x axis) and fishery performance (y axis)

scenario, risks of depleted abundance were eliminated (0% of stocks were depleted with $S/S_{MSY} < 0.8$) and 80% of stocks could be sustainably fished at a higher rate ($U/U_{MSY} < 0.8$ and $S/S_{MSY} > 1.2$). Thus, mixed-stock fisheries lead to variable conservation and fishery performances for individual stocks, from over-fished to depletion to under-fished, unless managers can effectively allocate harvest to specific stocks that can sustain it.

3.2 | Case study sockeye salmon fisheries

Exploring three major sockeye salmon fisheries (Bristol Bay, Alaska; Fraser River, BC; Skeena River, BC; Table 1) revealed both trade-offs and opportunities in mixed-stock fisheries. As previously shown (Freshwater et al., 2019; Price et al., 2021; Schindler et al., 2010), all three systems benefit from portfolio effects, where aggregate catches were more stable than would be expected based on observed variation in the individual stock abundances (Table 1). Further, as predicted by simulations (Figure 1) and theory (Doak

et al., 1998), this portfolio effect was smaller in the Skeena where there was substantially lower evenness (Table 1).

Following our simulation results (Figure 4), we expected differences in stock status (and among stock variation in it) across the three case study systems. For Bristol Bay, the system with the highest management control at the level of the management unit, we expected sockeye salmon stocks to be closer to fishery and abundance targets and exhibit less among stock variation in status relative to the other systems (e.g., Figure 4b). This low expected spread in values in both abundance and harvest metrics is the most indicative of fisheries being able to target specific stocks, thus exhibiting high control. In contrast, we expected that Fraser River and Skeena River sockeye salmon stock status to be more variable due to lower management control at the level of the management unit (e.g., Figure 4d,e). In addition, due to changes over time from a focus on fishery yield to conservation in the Canadian stock complexes (Walters et al., 2018), we expected the status of many individual Canadian stocks would shift from being overfished to being under-fished, but that there would still be a few weak stocks at or below fishing and abundance targets.

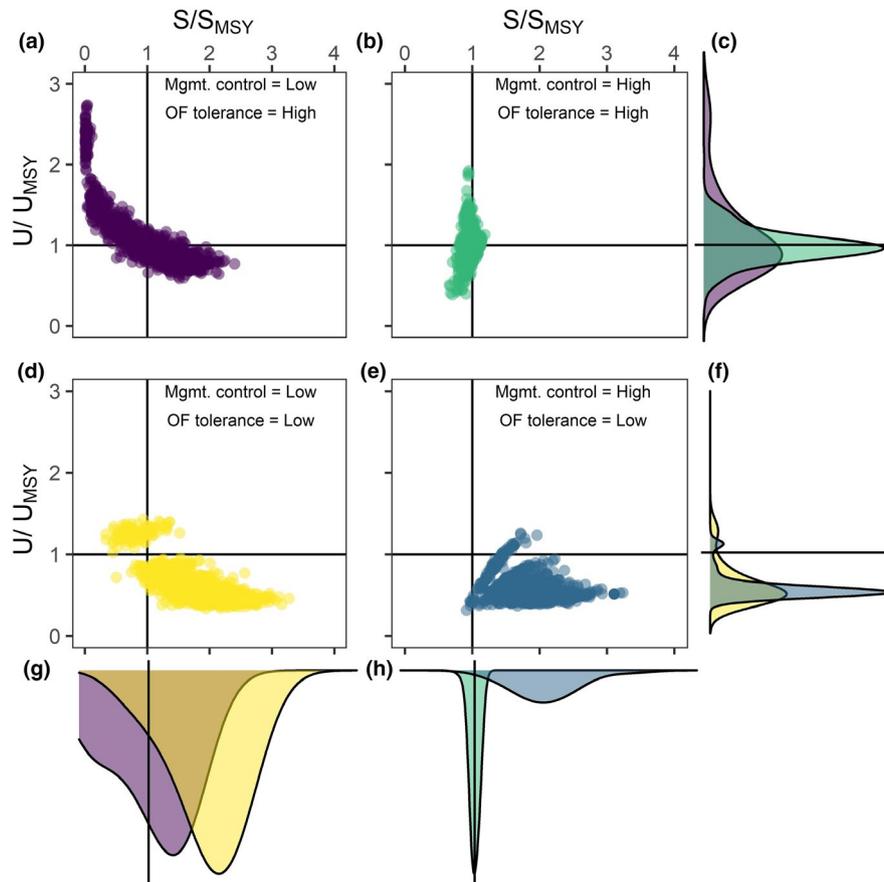


FIGURE 4 Stock consequences of variation in management control and risk tolerance. The four quadrants of the Kobe plot correspond to (clockwise from top left): over-fished and experiencing overfishing, under-fished but experiencing overfishing, under-fished and not experiencing overfishing, and over-fished but not experiencing overfishing. $U/U_{MSY} = 1$ and $S/S_{MSY} = 1$ represent fishing and abundance targets. a, b, d and e average spawner abundance and harvest rate for individual stocks (circles) relative to the spawner abundance (S_{MSY} ; x-axis) and harvest rate (U_{MSY} ; y-axis) expected to maximize yield. Each point is the average of the last 10 time steps of a 50 year simulation, and points are generated across 12 stocks and 100 simulations. c, f, g and h distribution of outcomes across each combination of management control and overfishing (OF) tolerance. High and low management control correspond to $C^* = 0.85$ and 0, respectively. High and low overfishing tolerance correspond to $P^* = 1$ and 0.5, respectively. The simulations were parameterized with values that were similar to the empirical case studies (Figure 5): range in productivity (α_n ; 1.7–7.8), lag-one correlation in survival (ϕ ; 0.3), recruitment variability (σ ; 0.4), correlation in recruitment variation among stocks (ρ ; 0.25) and maturity schedules (π ; [0, 0.7, 0.3, 0])

TABLE 2 System-wide reference point status across stocks for each case study system, including mean and standard deviations for spawning stock biomass and fishing rate relative to MSY values in the 1980s and 2000s

System	Year	S/S_{MSY} mean (SD)	U/U_{MSY} mean (SD)
Bristol Bay	1980s	0.83 (0.32)	1.02 (0.19)
Bristol Bay	2000s	1.00 (0.81)	0.96 (0.29)
Skeena River	1980s	1.05 (0.60)	0.89 (0.28)
Skeena River	2000s	1.62 (1.13)	0.71 (0.23)
Fraser River	1980s	0.40 (0.37)	1.30 (0.36)
Fraser River	2000s	0.62 (0.69)	0.56 (0.16)

The sockeye salmon fishery with greater management control at the level of the management unit, Bristol Bay, Alaska, as predicted, had mean abundance and fishery harvest performance metrics

closer to 1 than the other two systems, with lower variability, for the most part (Table 2, Figure 5a,b). Bristol Bay management targets are actually below S_{MSY} at what is called the Sustainable Escapement Goal (SEG) (Cunningham et al., 2019), so a system average of $S/S_{MSY} < 1$ would not be surprising, but overall the suite of stocks was expected to be closer to the target than the other systems and with low variability. Over the past 30 years, the status of Bristol Bay sockeye salmon stocks tended to be tightly clustered around fishing and abundance objectives that are expected to maximize long-term yield (Figure 5a,b). There was only one exception in the recent time period that had relative spawner abundance far above 1 (Alagnak, Figure S4) (Schindler et al., 2006), but the other stocks were consistently close to or just below 1. This pattern is similar to our simulation of a high management control and high risk scenario (Figure 4b). Thus, the Bristol Bay sockeye salmon fishery appears to be achieving multiple management objectives even though it integrates high biological diversity (Figure 5) (Schindler et al., 2010).

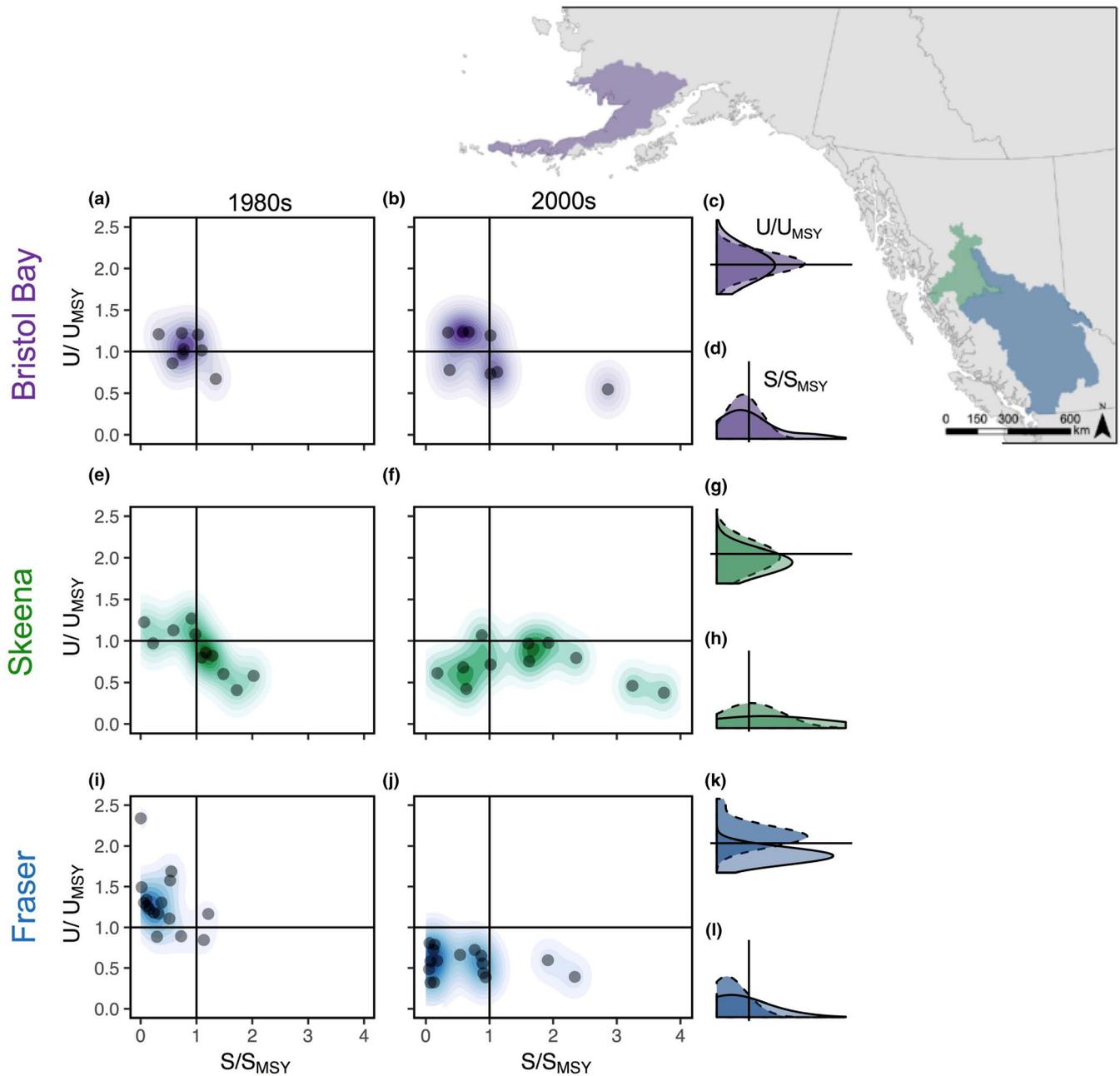


FIGURE 5 Performance of mixed-stock sockeye salmon fisheries that vary in management control and risk tolerance (Table 1). Panels are ordered from North to South in line with locations on watershed map. a, b, e, f, i, and j average spawner abundance and harvest rate for individual stocks relative to the spawner abundance (S_{MSY} ; x-axis) and harvest rate (U_{MSY} ; y-axis) expected to maximize yield. Shown are historical (1980s) (left column) and contemporary (2000s) periods (middle column). Points indicate the median posterior probability estimate and the probability surfaces for these parameters are denoted with colour. Values for U and S represent an average over a 10-year time period (or less if time series were not continuous). c, d, g, h, k, and l are the distributions of U/U_{MSY} and S/S_{MSY} for the two time periods with same axes as primary plots, 1980s (dashed line) and 2000s (solid line)

In contrast, the Fraser River, a system with intermediate management control at the management unit level due to some run-timing differentiation and in-season genetic stock identification (Beacham et al., 2004), had numerous stocks that were both overfished ($S/S_{MSY} < 1$) and experiencing overfishing ($U/U_{MSY} > 1$) in the 1980s (Figure 5i). By the 2000s, with a shift in management towards more conservation objectives, stocks were no longer subject to overfishing (shift in average U/U_{MSY} from 1.30 to 0.56) but few had increased

in their average abundance (shift in average S/S_{MSY} from 0.4 to 0.62) (Figure 5i), likely as a result of persistent declines in productivity for many stocks due to changes in survival (Peterman & Dorner, 2012). With reductions in harvest rates, among stock variability in overfishing status decreased, but variability in stock status increased with lost harvest opportunities for some stocks (Table 2; Figure 5i,j).

Lastly, the Skeena, with lower management control and the lowest evenness of the stock complexes we considered, had the

highest among-stock variability in abundance status (S/S_{MSY}) relative to the other systems in both time periods (Table 2; Figure 5e,f). This among-stock variability in abundance status increased from the 1980s to the 2000s as average fishing rates declined relative to those expected to maximize yield, likely to recover depleted stocks as ocean survival declined. Although the mean abundance increased in the 2000s, there were still lost opportunities for fishing as three stocks had $S/S_{MSY} > 2$ (Figure 5e,j).

One property that we would expect to influence variability in status would be the range stock productivities, where the most productive stocks (i.e., high α values; Equation 1) would be expected to show the most foregone fishing opportunity. This was largely the case as the stocks with abundance status well over 1 had higher relative productivities as compared to other stocks in the same system (Figure S4). This is exemplified in the 2000s time period by Stephens in the Skeena, Alagnak in Bristol Bay and Pitt in the Fraser (Figure S4).

Overall, following our simulations (Figure 4a,d), the Fraser and Skeena sockeye fisheries are illustrative of biodiverse systems with relatively lower management control at the management unit, albeit additionally challenged by lower survival in recent years as well (Peterman & Dorner, 2012), that create challenges with achieving stock-specific management objectives for fisheries and conservation (Figure 5). More generally, comparisons across time and the three salmon fisheries indicate trade-offs among conservation and fishery objectives that can be shifted by management priorities or ameliorated by increased management control (Figure 5).

4 | DISCUSSION

We explored how biodiversity in mixed-stock fisheries contributes to interannual stability in harvest, but also exacerbate overfishing risks, and influence maximum harvests that can be sustained (Figure 3). Our findings bring together two large bodies of research related to fisheries sustainability. First, building on examinations of risks in mixed-stock fisheries (Cheung & Sumaila, 2008; Connors, Staton, et al. 2020; Hilborn et al., 2012; Ricker, 1958; Freshwater et al., 2019; Okamoto, Hessing-Lewis, et al. 2020), we illustrate how different aspects of biodiversity (asynchrony, evenness, richness, productivity) exacerbate trade-offs among conservation and fishery objectives. Second, building on research on biodiversity and fisheries performance (Schindler et al., 2010; Worm et al., 2006) and more general research on biodiversity and ecosystem functioning (Cardinale et al., 2013; Hooper et al., 2005; Loreau et al., 2001; Naeem et al., 2012; Pasari et al., 2013), we explore how these same dimensions of biodiversity influence fishery performance. Following the statistical averaging of economic portfolio theory (Doak et al., 1998; Figge, 2004) and results from empirical studies (Carlson & Satterthwaite, 2011; Greene et al., 2010; Griffiths et al., 2014; Moore et al., 2010; Nesbitt & Moore, 2016; Schindler et al., 2010), variance was dampened by higher richness, evenness, and greater asynchrony among stock assets. However, greater asynchrony and

richness was also associated with lower catches and greater risks of extirpation. Thus, multiple dimensions of biodiversity control the trade-offs among conservation risk, inter-annual catch stability, and catches in mixed-stock fisheries (Figure 3). These trade-offs can be ameliorated through greater management control—if managers can effectively allocate fishing effort among component stocks, then fisheries can better benefit from and conserve biodiversity.

4.1 | Biodiversity, management, and the performance of salmon fisheries

Our comparisons of conservation and harvest status of stocks within three major sockeye salmon fisheries provided an empirical examination of how mixed-stock fisheries confront the trade-offs associated with biodiversity. The fisheries we considered are globally important—Bristol Bay supports the largest sockeye salmon fishery in the world, and the Fraser and Skeena are the two largest sockeye salmon fisheries in Canada. The fishery with greatest management control at the scale of the management unit, Bristol Bay, tended to have stocks that were closer to fishing and abundance targets associated with maximizing long-term fishery yield. Indeed, Bristol Bay sockeye salmon are an archetype of biodiversity and fishery sustainability (Hilborn et al., 2003; Schindler et al., 2010). In contrast, the two Canadian sockeye fisheries have relatively lower management control, with management control in the Fraser focusing on four main run-timing groups and some in-season management using genetic stock identification (Beacham et al., 2004) and the Skeena having even less management control due to the inter-mingling of co-migrating stocks. Both the Fraser and Skeena stocks exhibited more broadly distributed abundance and fishing statuses relative to Bristol Bay. In these two systems, stock statuses increased closer to S_{MSY} as management priorities shifted from catch maximization towards conservation/recovery of weak stocks. In the 1980s, an era where catch was a management priority, a few stocks were close to abundance and fishery targets, while many stocks were experiencing over-fishing and became severely depleted (Figure 4). In contrast, in the 2000s, harvest rates were reduced, leading many stocks to be “under-fished”, evidence of lost fishing opportunities. Depressed productivity, likely due to changing ocean conditions and degraded freshwater habitat, has likely kept many Canadian sockeye stocks from recovering in abundance (Connors, Staton, et al. 2020; Peterman & Dorner, 2012) resulting in some stocks being assessed as at risk of extinction (COSEWIC, 2017). Thus, biodiverse mixed-stock fisheries with little management control will be challenged by lost harvest opportunities or over-fishing risks.

The three focal sockeye salmon fishery complexes differ in many ways, such as exhibiting a high degree of hierarchical biodiversity that is managed differently. Management of BC sockeye salmon generally considers each sockeye rearing lake as its own “Conservation Unit”, or stock, to be managed for harvest and conservation, following Canada's Wild Salmon Policy (Fisheries & Oceans, 2005). Thus, while some of the stocks within the Skeena and Fraser consist of

multiple spawning populations (e.g., Stuart-Takla), in general this scale of management is finer-grained than that of Bristol Bay. Thus, while management control is higher in Bristol Bay due to the spatial arrangement of major river systems, these units of management (stocks) in Bristol Bay are much coarser-grained than those in the Skeena and Fraser River. Within each of the eight major river systems in Bristol Bay that can be targeted by fisheries (stocks), there are hundreds of locally-adapted populations that spawn and rear in different locations, have different morphological, physiological, or life-history adaptations, experience different habitat dynamics, and exhibit asynchronous dynamics (Hilborn et al., 2003; Rogers & Schindler, 2008; Schindler et al., 2010). Thus, there is enormous biodiversity within each Bristol Bay “stock”. Accordingly, it is likely that there is a wide range of specific population statuses within each stock; some less productive populations may be depleted and experiencing over-fishing while more productive populations could be sustainably fished at higher levels. Perhaps non-stationarity in productivities, meta-population processes, and intact habitat complexes enable temporarily over-fished and depleted populations to recover or persist and contribute to the apparent biological and fishery sustainability of Bristol Bay. Additional processes also likely contribute to the different stock statuses across the three sockeye fisheries (Table 1); for instance, southern sockeye salmon such as from the Fraser and Skeena have exhibited large-scale declines in marine survival and population productivity over the last several decades (Connors, Malick, et al., 2020; Peterman & Dorner, 2012) and have greater human alteration of freshwater and coastal habitats compared with Bristol Bay (Griffiths et al., 2014). Regardless, our analyses emphasize the importance of the spatial scale of fishery management for both defining and achieving the multiple objectives of fisheries (Okamoto, Poe, et al., 2020; Riddell, 1993; Waples, 1991).

Variation in productivity and unevenness in abundance among stocks were key elements of biological diversity that elevated conservation risks in our simulated mixed-stock fisheries (Figure 2), as has also been shown in previous work (Burgess et al., 2013; Connors, Malick, et al., 2020; Connors, Staton, et al. 2020; Hilborn, 1985; Ricker, 1958), a result with important management implications for salmon and other fishes. In particular, salmon management activities such as hatcheries or other supplementation practices aim to enhance the productivities of select stocks to increase fisheries harvest (Amoroso et al., 2017; Naish et al., 2007). Thus, hatcheries can introduce a highly productive population that often reduces evenness within a stock complex—both factors that we highlight as posing risks to fisheries sustainability. Unless fisheries can avoid populations with low productivity (e.g., wild populations) and target high productivity ones (e.g., enhanced populations), such enhancement will increase over-fishing risks to less productive wild stocks unless harvest rates are curtailed (which would undermine the intended benefit provided by hatcheries), and also mask potential declines of wild stocks (McClure et al., 2003). Such hatchery propagation has been increasing across the North Pacific over the last several decades (Ruggerone & Irvine, 2018). For example, enhancement of Babine sockeye salmon in the Skeena River system which

exacerbated the unevenness in abundance among stocks has likely exacerbated trade-offs among fisheries objectives and decreased the strength of portfolio effects (Price et al., 2021; Walters et al., 2008). Previous studies have found that hatcheries are associated with decreased salmon portfolio performance (Griffiths et al., 2014; Moore et al., 2010; Satterthwaite & Carlson, 2015) and decreased population productivities of wild populations (Amoroso et al., 2017; Naish et al., 2007). Thus, our work further underscores the challenges of incorporating hatcheries and other enhancement activities into sustainable wild salmon fisheries.

4.2 | General implications for fisheries management

Our findings explore how different dimensions of biodiversity influence trade-offs and risks to biological and fishery sustainability (Figure 3). Some dimensions of diversity, namely higher richness and asynchrony, tended to increase catch stability. However, asynchrony among stocks, while contributing to stability via portfolio effects and linked to response diversity that can foster resilience (Elmqvist et al., 2003), also exacerbated risks of overfishing in mixed-stock fisheries, following recent findings (Connors, Staton, et al. 2020; Okamoto, Hessing-Lewis, et al., 2020). In contrast with previous correlative studies (Worm et al., 2006), we found that richness (when paired with asynchrony) can actually decrease fisheries yield. In addition, we found that variability in productivity can simultaneously increase risks of overfishing to extinction. Previous work has long-recognized that differences in stock productivities or sensitivities will decrease sustainable harvest rates and increase conservation risks in mixed-stock fisheries (Burgess et al., 2013; Hilborn, 1985; Ricker, 1958; Schindler et al., 2002). We also found that unevenness, especially paired with low synchrony, can decrease stability and increase overfishing risk. Across these different relationships, there may be different magnitudes, functional forms, and nonlinearities (Figure 3), leading to a complex trade-offs. Thus, our findings collectively provide general insight into how different dimensions of biodiversity are a key property of fisheries systems that influence their sustainability (Link, 2018).

Our study also emphasizes that the degree of spatio-temporal structure in biodiversity acts as an additional property linked to sustainability that can enable, or hinder, management control (Hilborn, 2017). For instance, in our case studies, we compared performance in sockeye salmon fisheries that differed in their spatial structure—Bristol Bay Alaska has different sockeye stocks that can be targeted in different locations so that harvest can be more easily allocated to specific management units (though this is not the case at a finer scales in the region). In contrast, there is less intrinsic potential for effective spatial management control on the Fraser and the Skeena Rivers as the fisheries harvest salmon on their return migrations through a single river mouth (Moore et al., 2015). Similarly, temporal variation in migration timing can be used to target specific stocks (Beacham et al., 2005; Okamoto, Poe, et al., 2020). Thus, the degree of spatial and temporal structure of biodiversity will be a key dimension of mixed-stock fishery sustainability (Link, 2018).

While we used sockeye salmon mixed-stock fisheries to explore these ideas, we expect that the concepts and our findings apply broadly to mixed-stock fisheries across the globe. Other mixed-stock fisheries range from trawl-caught bottom fish assemblages (Hilborn et al., 2012) to tuna and billfish caught with purse seines and long-line gear (Burgess et al., 2013; Kitchell et al., 2002; Schindler et al., 2002) to fisheries in tropical freshwaters for hyper-diverse species complexes (McCann et al., 2016) to herring fisheries that target multiple populations (Okamoto, Poe, et al., 2020). Given that some of these fisheries target many species that may have enormous variability in life-histories and productivities (Bieg et al., 2018), the mixed-stock fishery challenges in many of these other fisheries are likely even greater than we explore for salmon. Moreover, based on fishing methods, these systems will exhibit more or less management control similar to our scenarios and case studies.

Even in the face of highly diverse fisheries, however, there are a variety of management options that can improve harvest control to both conserve and benefit from fish biodiversity (Hilborn et al., 2020). These management options can be considered across linked hierarchical scales of organization. First, the fishery management or governance system can influence harvest control. For example, the natural diversity in the fleet such as in terms of gear types or target system can enable fishers to shift from one fishery to another avoid collapse of fishing economies (Burgess, 2014; Cline et al., 2017). Alternatively, management control will also presumably be higher in more localized fisheries, in line with recent suggestions to shift towards terminal fisheries for salmon that can reduce mixed-stock fishing risks but may come at a cost of decreased fish quality and necessitate transfer of access (Atlas et al., 2021; Gayeski et al., 2018). Second, fisheries regulations can improve harvest control. Seasonal or spatial closures and openings are also common approach for harvest control. These range from static marine protected areas that can protect contain key habitats for less productive fish stocks (Hastings et al., 2017) to in-season management of fisheries through approaches such as genetic stock identification (Beacham et al., 2004; Dann et al., 2013; Garcia-Vazquez et al., 2012). Third, the behaviour of fishers, often coupled with new technologies, incentive programs, or regulations such as mentioned above, can influence harvest control. In different systems, fishery managers or fishers can benefit from knowledge of diversity in habitat use across space and time by targeted fish stocks (Hilborn, 2017), use selective gear types, or use spatial mapping analyses to map risks associated with harvest of weaker stocks (Hazen et al., 2018). Thus, there are options for increasing harvest control across the scales of organization of fishery systems.

If such management options do not exist in mixed-stock fisheries, then managers will need to confront difficult trade-offs among fishery yields and biodiversity conservation (Ricker, 1958). For example, decreasing fishing rates below those predicted to maximize yield, such as at "pretty good yield" (Hilborn, 2010), can decrease risks to weak stocks. Regardless, a key step toward making informed decision about how to balance trade-offs between fishery yields

and weak stock protection is to explicitly quantify the trade-offs where possible (e.g., (Connors, Staton, et al. 2020; Pestes et al., 2008; Walters et al., 2008a)). Ultimately, the opportunities and relative merits of different approaches will depend on the fishery and priorities of fishery managers and stakeholders. In general, more knowledgeable fisheries management can benefit fish and fisheries (Hilborn et al., 2020).

5 | CONCLUSIONS

Natural resource management systems often integrate across biological diversity, both benefiting and extracting from it. While recent papers have called for diversifying fisheries (Robinson et al., 2020), here we caution that such diversification will also generally increase conservation risks unless it co-occurs with increased management control. With an increasing global human population and many communities that depend on fisheries both economically and for sustenance (Bene et al., 2015), there is a need for fisheries to be both resilient and productive. Climate change and regime shifts will pose novel additional challenges to the resilience of fisheries. Fishery resilience and fish biodiversity conservation are intertwined global challenges. Yet, the enormous biodiversity of fish (Wiens, 2015) can support fisheries that are resilient to environmental perturbations (Cline et al., 2017). Here we have illuminated how biodiversity creates strong trade-offs among conservation and fishery objectives within mixed-stock fisheries. We reveal that to best inform fishing practices and ensure a long future of access to a diversity of fish species and populations, there is a need for continued investment in characterizing and managing for the biodiversity in fishery systems.

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AUTHOR CONTRIBUTIONS

J.W.M., B.M.C., and E.E.H. designed and performed research; B.M.C., and E.E.H. analysed data; and J.W.M., B.M.C., and E.E.H. wrote the paper.

DATA AVAILABILITY STATEMENT

All data and code required to reproduce the analyses and figures in this manuscript are archived and available at <https://doi.org/10.5281/zenodo.4724357>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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