WILEY

FISH and FISHERIES

ORIGINAL ARTICLE

Accounting for Salmon Body Size Declines in Fishery Management Can Reduce Conservation Risks

Jan Ohlberger[1,2] | Daniel E. Schindler[1] | Benjamin A. Staton[3]

[1]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA | [2]Fish Program, Washington Department of Fish and Wildlife, Olympia, Washington, USA | [3]Fishery Science Department, Columbia River Inter-Tribal Fish Commission, Portland, Oregon, USA

Correspondence: Jan Ohlberger (jan.ohlberger@dfw.wa.gov)

ABSTRACT

Changes in population demographic structure can have tangible but unknown effects on management effectiveness. Fishery management of Pacific salmon is often informed by estimates of the number of spawners expected to produce maximum sustainable yield (S_{MSY}), implicitly assuming that reproductive output per spawner does not change over time. However, many salmon populations have experienced long-term trends in age, sex and length compositions that have resulted in smaller body sizes of mature fish. We present an empirically based simulation approach for evaluating management implications of declining reproductive output resulting from shifting demographics. We simulated populations with or without demographic trends, selective or unselective harvests, and harvest policies based on assessment methods that did or did not account explicitly for demographic trends when estimating S_{MSY}. A management strategy evaluation showed reduced expected harvests and run sizes when populations exhibited negative demographic trends. Reduced abundances and increased conservation risks (higher probability of falling below an abundance threshold) could be partially mitigated by using stock-recruitment analyses based on total egg mass instead of spawner abundance, or via precautionary management where target escapements were higher than S_{MSY}, especially in fisheries that selectively removed large fish. Explicit accounting of demographic trends in stock-recruit analyses resulted in up to 25% higher run sizes and up to 20% lower conservation risks compared to traditional methods when trends toward smaller, younger and male-biased runs were present in the population. Conservation of population demographic structure may be critical for sustaining productive fish populations and their benefits to ecosystems and people.

1 | Introduction

Pacific salmon (*Oncorhynchus* spp.) are keystone species in freshwater and marine ecosystems and are economically and culturally valuable to people living around the North Pacific Rim. Many populations of Pacific salmon that spawn in freshwater systems of western North America have experienced long-term declines in the average body size of mature fish since at least the 1970s (Bigler, Welch, and Helle 1996; Jeffrey et al. 2017; Losee, Kendall, and Dufault 2019; Oke et al. 2020). Size declines are particularly pronounced in Chinook salmon (*O.*

tshawytscha; Lewis et al. 2015; Ohlberger et al. 2018, 2019), with differences among populations linked to life-history and ocean distribution (Buckner et al. 2023). Changes in the mean body size of mature fish are a major concern because they may have negative impacts on fishery catches and freshwater ecosystems (Oke et al. 2020). Further, reductions in average reproductive output associated with declines in mean body size (Ohlberger et al. 2020; Malick et al. 2023) have the potential to undermine the effectiveness of current management practices for achieving sustainable fisheries because salmon management is typically focused on the numerical abundance of spawners and does

not account explicitly for their demographic composition. The conservation and management implications of demographic changes that result from body size declines of salmon remain poorly understood. Importantly, when demographic shifts that lead to smaller mean body size are present in a population, it may be critical if and how they are accounted for in assessment models used in fishery management.

Trends in population demographic characteristics can occur due to changing ecological and environmental conditions as well as intense size-selective exploitation. It is well known that exploited fish populations typically show higher short-term variability in abundance compared to unexploited populations because harvesting can lead to age/size truncation and reduced body sizes (Hsieh et al. 2006; Anderson et al. 2008; Sharpe and Hendry 2009), which can destabilise population dynamics by increasing sensitivity to environmental impacts (Anderson et al. 2008; Botsford et al. 2014; Stige et al. 2017). While various mechanisms can lead to changes in population demography, in this study we focus on the consequences of shifts in age, sex and length compositions—and different ways of accounting for them in assessments—regardless of the ultimate or proximate causes of these demographic shifts.

The demographic structure of a population, which integrates the effects of external drivers on individual growth and survival, reflects many of the short- and long-term impacts of ecological and environmental changes on populations. Previous work showed that demographic trends can affect the recruitment and productivity of populations (Shelton et al. 2015; Ohlberger, Langangen, and Stige 2022; Feddern et al. 2024) and that integrating demographic information into stock-recruit analyses can improve the estimation of reference points used in fishery management (Murawski 2001; Wang et al. 2005). The age, sex and length composition of spawners matters for recruitment because large females have higher reproductive output (Hixon, Johnson, and Sogard 2014; Barneche et al. 2018).

In Chinook salmon, large females produce more and larger eggs than small individuals (Healey and Heard 1984; Beacham and Murray 1993). Consequently, recent declines in mean body size of Chinook salmon are associated with declines in spawner reproductive potential (Ohlberger et al. 2020; Malick et al. 2023). Maternal effects that result in better offspring survival may also contribute to higher recruitment when the spawning population is composed of older (larger) females (Green 2008; Ohlberger, Langangen, and Stige 2022). Changes in reproductive output due to trends in demographic characteristics may, therefore, need to be considered when developing management reference points (Heino et al. 2013; Staton et al. 2021) that aim to optimise harvest opportunity and conservation benefits.

Fishery management of Pacific salmon in North America is commonly informed by the principle of maximum sustainable yield (MSY) and management goals are often expressed in terms of escapement goals for achieving the number of spawners on the spawning grounds that maximise long-term yield (Ricker 1954; Beverton and Holt 1957; ICES 1993; Clark, Bernard, and Fleischman 2009). Similarly, salmon management may use a limit reference point that equals spawners at MSY (S_{MSY}) or is directly proportional to S_{MSY} (ICES 2002;

Crozier et al. 2003). Thus, salmon management is typically focused on the numerical abundance of fish on the spawning grounds and implicitly assumes that each spawner contributes equally to population replenishment and that stock-recruit relationships are stationary such that the mean and variance in recruitment produced by a given number of spawners are constant over time (Walters and Martell 2004). This is evidenced by the rarity with which the demographic composition of spawners is considered when setting management goals. In addition to apparent trends in the demographic composition of the spawning population, stock-recruit relationships may also vary over time due to changes in environmental conditions. Earlier work on Pacific salmon showed that including time-varying parameters in stock-recruitment models can reduce parameter bias and uncertainty (Peterman, Pyper, and Grout 2000). However, these analyses were concerned with cyclic changes in productivity due to climate variability, yet long-term trends in population productivity have become increasingly apparent in many populations of Pacific salmon (Peterman and Dorner 2012; Ruggerone and Connors 2015; Malick and Cox 2016).

Here, we use a simulation approach to evaluate the consequences of shifting age, sex and length (ASL) composition on fishery management performance when informed by models that differ in how they account for demographic trends when estimating biological reference points. The data-driven simulation model quantifies how reproductive output and the number of spawners needed to produce maximum sustainable yield change when trends in average body size (and sex ratios) of mature fish are present in the population. We quantify bias in the estimation of escapement at MSY when using traditional spawner-recruit analyses that are based on spawner abundance and, therefore, do not account for trends in demographic characteristics. We then use a management strategy evaluation approach to quantify the effect of different estimation methods on long-term fishery management performance. To evaluate conservation risks, we calculated probabilities of falling below certain abundance thresholds, which were based on biological reference points (Punt et al. 2016) but could reflect population-specific recovery goals (e.g., populations listed under the U.S. Endangered Species Act). Our general approach to evaluating implications of changing demographics for fishery management is illustrated in Figure 1 and all scenarios that were explored as part of our management strategy evaluation are summarised in Table 1.

Our model was parameterised using life-history characteristics and observed demographic trends for Chinook salmon. This species has experienced the most pronounced changes in age-sex-length characteristics of mature fish among all species of Pacific salmon (Ohlberger et al. 2018; Losee, Kendall, and Dufault 2019; Oke et al. 2020). Mean body lengths of adult Chinook salmon in North America have declined by nearly 10% since the 1970s due to changes in age structure and size-at-age (Ohlberger et al. 2019; Oke et al. 2020) which translates into significant declines in reproductive output (Ohlberger et al. 2020). In addition, sex ratios of some populations have shown trends toward lower proportions of females among mature fish (Staton et al. 2021), likely as a result of changes in the relative survival of males and females during ocean residence (Olsen et al. 2006).

The analysis presented explores the management implications of declines in mean age, sex ratios and length-at-age of mature fish and is relevant to the conservation of Pacific salmon throughout their range.

2 | Methods

We considered various scenarios of harvest selectivity, management strategies and methods for estimating biological reference points that do or do not account for demographic trends (Table 1). We used closed-loop simulations based on an operating model to generate stochastic population data with or without demographic trends, paired with one of three possible estimation models used to fit stock-recruit models to estimate the reference points. Observations of the simulated data from the operating model were passed to the estimation model for assessment every 10 years, which used either spawner abundance or total egg mass (aggregate mass of eggs across all individuals) as the metric of spawning stock in a stock-recruit model. The estimated biological reference point from the assessment model (escapement at MSY) was periodically used to set a new management target. Simulations were run over multiple periodic assessments and the performance of the fishery management was evaluated at the end of the simulations after 100 years according to multiple metrics intended to index harvest and conservation objectives.

2.1 | Simulating Population Dynamics (Operating Model)

We simulated stochastic Chinook salmon population data using a Ricker stock-recruit relationship, where the population was modelled to include trends in the age composition and sex ratio of recruits and the length-at-age of returning mature fish. Recruitment in our simulation model describes the expected number of fish from a given brood year (i.e., cohort of spawners) that survive to mature and return to rivers from the ocean. Adult recruits are partitioned into calendar year returns (adult abundances) based on an assumed age composition. Harvest is then taken each calendar year and fish that escape the fishery are assumed to reach the spawning grounds to reproduce.

We simulated observations of fishery catches and escapements with error and used those observations in an estimation model to derive estimates of biological reference points as described in the subsequent section. Fishery catches and escapement were based on an escapement goal, set as the estimated escapement at MSY for most scenarios. Harvests were taken using a specified size selectivity (e.g., in gill net fisheries), which was varied as an additional dimension of the analyses given a recent study found sensitivity of reference point estimates to different fishing gears (Staton et al. 2021). The following section provides a detailed description of the stochastic simulations that generated the time series data used in the stock-recruit analyses of the estimation model.

2.1.1 | Recruitment

We used a Ricker stock-recruit relationship to simulate the expected recruitment given spawner abundance:

$$R_y = \alpha S_y e^{-\beta S_y + \epsilon_y} \tag{1}$$
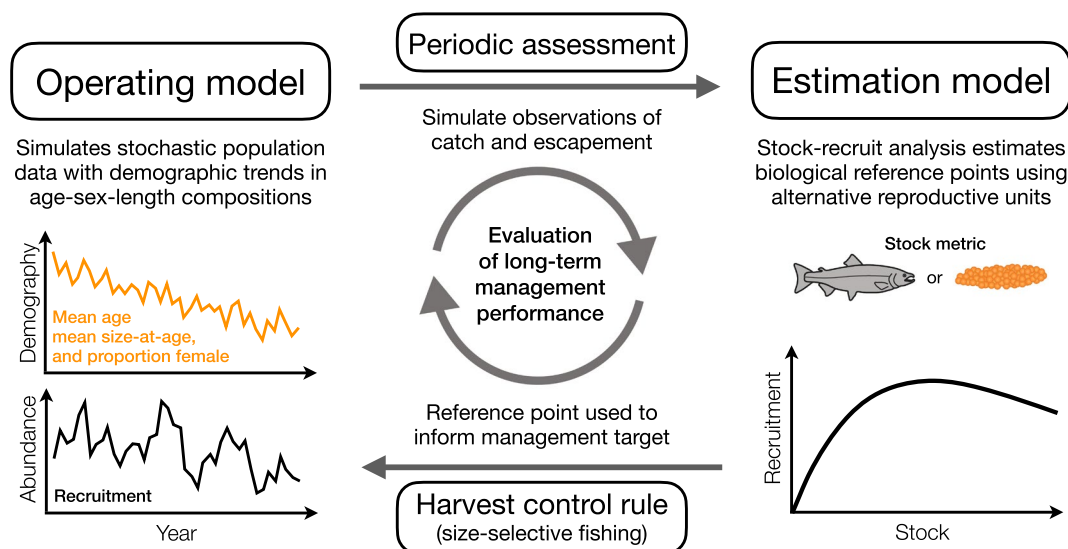
FIGURE 1 | Conceptual illustration of the approach. An operating model was used to simulate stochastic population data with demographic trends in the age-sex-length compositions of recruits that are harvested by a potentially size-selective fishery. Observations of the catch and escapement were then made with error from the simulated recruitment outcomes and passed periodically to an estimation model that used a stock-recruit analysis to estimate biological reference points, in particular the escapement at MSY, using different estimation methods that did or did not account for trends in demographic trends. The estimates inform the harvest control rule via a management target (e.g., escapement goal), by using the reference point estimate directly or a more liberal or precautionary strategy based on its value. The long-term performance of the fishery management, relative to quantitative utility measures, was evaluated under different scenarios of demographic trends, harvest selectivity, methods for estimating reference points and management strategies (see Table 1).

TABLE 1 | Scenarios explored in the management strategy evaluation, including simulated ASL (age-sex-length) trends in the operating model, estimation methods used in the stock assessment, size selectivity of the harvest and the type of fishery management (liberal to precautionary).

Variable	Scenarios	Aim
Demographic trends	• No ASL trends • ASL trends stabilised • ASL trends continued	Model populations with demographic trends based on observed/past trends and compare to typically made assumption of no trends
Estimation method	• Traditional Ricker model • Dynamic Linear Model • Yield-per-recruit approach	Understand the management implications of accounting – or not – for demographic trends in the stock assessment model
Size selectivity of the harvest	• Unselective • Small mesh • Large mesh	Understand how fishery selectivity affects management performance when ASL trends are present in the population
Type of fishery management	• MSY • Liberal • Precautionary	Understand how liberal (more harvest) and precautionary (more escapement) approaches affect fishery catches and conservation risks

where R_y is the estimated recruitment arising from spawner abundance S_y in brood year y, α represents recruits per spawner as spawner abundance approaches zero, and β represents the strength of density dependence. The parameter α was drawn from a lognormal distribution:

$$\log(\alpha) \sim \text{Normal}\left(\log(\alpha_r), \sigma_\alpha\right) \quad (2)$$

where α_r is the default parameter value and σ_α is the log-scale standard deviation. The density-dependence parameter β was also drawn from a lognormal distribution:

$$\log(\beta) \sim \text{Normal}\left(\log(\beta_r), \sigma_\beta\right) \quad (3)$$

where β_r is the default parameter value and σ_β is the log-scale standard deviation. The Ricker parameters were adjusted using previously estimated ratios when using egg mass as the stock metric and were applied annually based on the estimated annual reproductive output of spawners (see section 'Parameter values' and Staton et al. 2021).

The error term ϵ_y was modelled as autocorrelated residuals (Thorson, Jensen, and Zipkin 2014):

$$\epsilon_y = \phi_r \epsilon_{y-1} + \sqrt{1 - \phi_r^2} \delta_y \quad (4)$$

where ϕ_r represents first-order autocorrelation, ϵ_y and ϵ_{y-1} are recruitment residuals in years y and $y - 1$, respectively. The first-year residual was assumed to be zero. Further, δ_y are normally distributed errors with bias correction for the mean:

$$\delta_y \sim \text{Normal}\left(-0.5\,\sigma_r^2, \sigma_r\right) \quad (5)$$

such that σ_r is the standard deviation of the random component of the recruitment variation. The bias correction ensures that the expected mean value is zero based on a lognormal error variance (Quinn and Deriso 1999).

Recruits (R_y) from brood year y were apportioned to adult abundances in calendar year t by age and sex ($N_{a,s,t}$) based on the expected sex-specific age-at-maturity proportions of the recruitment ($\pi_{a,s,y}$):

$$N_{a,s,t} = R_{y=t-a,s}\, \pi_{a,s,y=t-a} \quad (6)$$

We assumed the proportion of recruits of sex s from brood year y that returned at age a followed a normal curve with peak age-of-return $A_{s,y}$ and standard deviation σ_a. This normal curve gave densities for all possible ages-of-return, which were then normalised to sum to 1 (Equation 8) to give the expected proportion returning by age. To add among-brood year variability in the simulation, we drew the realised proportion of recruits returning by age, sex and brood year ($\pi_{a,s,y}$) from a Dirichlet distribution:

$$\pi_{a,s,y} \sim \text{Dirichlet}\left(\gamma_{a=1,s,y,\ldots}, \gamma_{a=a_{\max},s,y}\right) \quad (7)$$

where the vector of concentration parameters $(\gamma_{a=1,s,y,\ldots}, \gamma_{a=a_{\max},s,y})$ was equal to the normalised densities from the normal distribution (probability density function denoted by f) times an inverse dispersion parameter (d; set to 50, smaller numbers would give more variability; Fleischman et al. 2013):

$$\gamma_{a,s,y} = d\, \frac{f\left(a, A_{s,y}, \sigma_y\right)}{\sum_{a=1}^{a_{\max}} f\left(a, A_{s,y}, \sigma_y\right)} \quad (8)$$

This variability in age-at-maturity reflects variation resulting from environmental impacts during both freshwater and ocean residence.

Total abundance in calendar year t was taken as the sum of the age- and sex-specific abundances:

$$N_t = \sum_{s=1}^{2} \sum_{a=1}^{a_{\max}} N_{a,s,t} \quad (9)$$

2.1.2 | Harvest and Escapement

Fishery management was guided by an escapement goal. Because escapement goals are not achieved precisely in salmon

management due to practical challenges related to run forecasts, run timing uncertainty, mixed-stock considerations, fishing effectiveness, processor capacities and market dynamics, we assumed that the realised escapement in a given year could differ from the escapement goal target. Spawner escapement in year t (S_t) was calculated based on the escapement goal (S_{goal}) and a lognormal implementation error:

$$S_t = \begin{cases} S_{goal} \, e^{\epsilon_i}, & S_{goal} \, e^{\epsilon_i} < N_t \\ N_t, & S_{goal} \, e^{\epsilon_i} \geq N_t \end{cases} \qquad (10)$$

where $\epsilon_i \sim \text{Normal}(0, \sigma_i)$ are normally distributed errors. This formulation ensures that the escapement cannot be larger than the total run size in a given year.

The harvest control rule used in the simulations was a *constant escapement* rule (*sensu* Free et al. 2022) which attempts to maintain a fixed level of escapement across run sizes (total abundance). We thus assumed that all fish above the realised spawner escapement were harvested. Total harvest was calculated as the difference between run size and spawner escapement:

$$H_t = N_t - S_t \qquad (11)$$

We assume that pre-spawn mortality is negligible and that all returning fish that are not caught in the fishery survive to spawn.

Harvest selectivity was modelled using the Pearson gillnet selectivity model developed for Chinook salmon (Bromaghin 2005), which expresses selectivity as a function of the ratio between fish size and mesh perimeter such that a single set of parameters explains fishery selectivity for all mesh sizes:

$$
\begin{aligned}
v(x) = {} & \left(1 + \frac{\lambda^2}{4\theta^2}\right)^{\theta} \left(1 + \frac{\left(x - \frac{\sigma\lambda}{2\theta} - \tau\right)^2}{\sigma_s^2}\right)^{-\theta} \\
& \exp\left(-\lambda\left(\tan^{-1}\left(\frac{x - \frac{\sigma\lambda}{2\theta} - \tau}{\sigma_s}\right) + \tan^{-1}\left(\frac{\lambda}{2\theta}\right)\right)\right)
\end{aligned}
\qquad (12)
$$

where x is the ratio between fish length and mesh perimeter and $\lambda, \theta, \sigma_s, \tau$ are species-specific parameters (Bromaghin 2005; Staton et al. 2021).

Harvest was removed from the run using unequal probability sampling without replacement, based on probabilities of being harvested given age, year and mesh size ($\varpi_{a,t,m}$):

$$\varpi_{a,t,m} = v\left(\frac{L_{t,a}}{m}\right) \qquad (13)$$

where $L_{t,a}$ is mean length of age a in year t, and m indicates the mesh size of the fishing gear. Note that heterogeneity in this vector leads to escapement having a different ASL composition than the run. Using the unequal probability sampling H_t was always achieved exactly.

2.1.3 | Demographic Trends

We simulated demographic trends without making assumptions about the causes of these trends. We set default values for the initial mean age, size-at-age, and the proportion of females in the population at the beginning of the simulation based on empirical data for Chinook salmon in western Alaska rivers (Ohlberger et al. 2018, 2020; Staton et al. 2021), and added trends in these demographic characteristics that roughly matched the recent history of these populations. The mean age, mean size-at-age and proportion female in a given year were drawn from respective distributions to reflect annual variation in demographic characteristics.

Mean age (A_y) of returns from a given brood year y was drawn from a normal distribution with a mean depending on the initial mean age (A_0) and the change in mean age over time (δ_a), and a standard deviation (σ_a) describing annual variation around the deterministic trend:

$$A_y \sim \text{Normal}(A_0 + y\,\delta_a, \sigma_a) \qquad (14)$$

Mean age of female recruits was given by $A_{f,y} = A_y + 0.5\,\Delta A$, and mean age of male recruits was given by $A_{m,y} = A_y - 0.5\,\Delta A$, where ΔA is the mean age difference between the two sexes (females tend to return as older fish compared to males, see parameter values).

The proportion of females ($\psi_{f,y}$) from a given run year was drawn from a logit-normal distribution with a mean depending on the initial proportion female ($\psi_{f,0}$) and change in the log-odds of being female over time (δ_f), and a standard deviation (σ_f) describing annual variation around the deterministic trend:

$$\text{logit}(\psi_{f,y}) \sim \text{Normal}(\text{logit}(\psi_{f,0}) + y\,\delta_f, \sigma_f) \qquad (15)$$

Growth was not modelled explicitly such that size-at-age was provided by run (i.e., calendar) year. Mean length-at-age ($L_{a,t}$) in a given run year was drawn from a normal distribution with a mean depending on the initial mean length-at-age ($L_{a,0}$) and a change in mean length-at-age over time (δ_l), and a standard deviation (σ_l) describing annual variation around the deterministic trend:

$$L_{a,t} \sim \text{Normal}(L_{a,0} + y\,\delta_{l,a}, \sigma_l\,L_{a,0}) \qquad (16)$$

Setting δ_a, $\delta_{l,a}$ and δ_f to zero resulted in simulations without any demographic trends (one of the examined scenarios). In addition to simulated changes in demographic characteristics, selective harvest affected the age and size composition of the escapement, though it did not affect the sex composition at a given age, because growth and thus size-at-age are not sex-specific in the model.

2.1.4 | Reproductive Output

Our model assumes that reproduction is limited by females such that total reproductive output across all spawners can be

calculated solely from female abundance and their size distribution. Reproductive output (z) as a function of female length (L) was modelled according to:

$$\log(z) = \log\left(a_z\right) + b_z \log(L) \qquad (17)$$

where z is reproductive output measured as total egg mass, and a_z and b_z are the intercept and slope of the relationship on the log scale, or the scalar and exponent of the allometric relationship on the arithmetic scale, respectively. The size-scaling of reproduction was assumed to be time-invariant.

Based on the average reproductive output per female spawner by age and year ($z_{a,y}$), the age-specific proportion of female spawners ($\psi_{f,a,y}$), and the age-specific spawner abundance ($S_{a,y}$) that year, we calculated the total annual reproductive output of all female spawners as:

$$Z_y = \sum_{a=1}^{a_{\max}} S_{a,y}\psi_{f,a,y}z_{y,a} \qquad (18)$$

2.1.5 | Model Observations

We assumed that annual observations of harvest and escapement abundances were made with error. Observed escapement (E_t) was modelled based on true escapement (S_t) and lognormal errors:

$$E_t = S_t e^{\epsilon_e} \qquad (19)$$

where the error term was bias-corrected just as the white noise portion of recruitment variability in Equation (4) [$\epsilon_e \sim \text{Normal}\left(-0.5\,\sigma_e^2, \sigma_e\right)$]. Similarly, observed catch (C_t) was modelled based on true harvest (H_t) and lognormal errors:

$$C_t = H_t e^{\epsilon_h} \qquad (20)$$

where $\epsilon_h \sim \text{Normal}\left(-0.5\,\sigma_h^2, \sigma_h\right)$.

We assumed that the age compositions of escapement and harvest were observed without error.

2.1.6 | Parameter Values

Parameter values for the stock-recruitment relationship, harvest selectivity, allometric scaling of reproduction, age-sex-length compositions and demographic trends over time were based on literature values for Chinook salmon. However, different salmon life histories can easily be implemented by adjusting these values accordingly and estimates for most parameters are available for other species of Pacific salmon.

2.1.6.1 | Stock-Recruitment Function.
To reflect uncertainty in the underlying stock-recruit relationship, Ricker parameters were drawn randomly for each stochastic simulation from lognormal distributions. The parameter α is interpreted as the maximum adult recruits produced by one unit of reproductive output and β is the inverse of the number of reproductive units expected to produce maximum

recruitment. We used mean $\alpha_r = 5$ and standard deviation $\sigma_\alpha = 0.2$ for the productivity term and mean $\beta_r = 5e^{-5}$ (i.e., 20,000 spawners produce maximum recruitment) and standard deviation $\sigma_\beta = 0.2$ for the density-dependence term, based on previous work on Chinook salmon (Fleischman et al. 2013). However, these values only apply to stock-recruit relationships based on spawner abundance, whereas our simulations used total egg mass as the stock metric. We, therefore, converted parameter values using estimates from a recent empirical study that fitted Ricker models based on spawner abundance (N) or total egg mass (E) and accounted for demographic trends (Staton et al. 2021):

$$\alpha = \frac{\alpha_E}{\alpha_N}\alpha_r \text{ and } \beta = \frac{\beta_E}{\beta_N}\beta_r \qquad (21)$$

where previously estimated parameter values were $\alpha_N = 5.07$ or $\alpha_E = 0.01036$ for productivity and $\beta_N = 8.6e^{-6}$ or $\beta_E = 1.7e^{-8}$ for the density-dependence term (Staton et al. 2021).

Values for the autocorrelation ($\phi_r = 0.4$) and standard deviation ($\sigma_r = 0.35$) of recruitment residuals were based on previous stock-recruit analyses on Chinook salmon (Staton et al. 2021). However, stronger residual autocorrelation has previously been reported for Chinook salmon (Fleischman et al. 2013), and other species of Pacific salmon may exhibit lower autocorrelation and higher variation in recruitment (Thorson, Jensen, and Zipkin 2014), presumably owing to their less diverse spawner age distributions.

2.1.6.2 | Age Composition.
We modelled Chinook salmon from total age 1–9. We assumed that the youngest age group returning to spawn was age 3, after freshwater and ocean residence. The overall mean age at the start of the simulation was set to $A_0 = 5.5$ years, and the difference between sexes was $\Delta A = 1$, such that the average age of males and females without trends was 5 and 6 years, respectively. Concentration parameters of the Dirichlet distribution were based on normal probability densities (gamma, Equation 7) around the mean age by sex using a standard deviation of $\sigma_a = 0.6$. Consequently, the majority of the return from a given brood year was initially composed of total ages 4, 5, 6 and 7, with males primarily returning at ages 4–6 and females at ages 5–7. The proportional contributions of all other age groups were typically below 1%. This age distribution was representative of high latitude Chinook salmon populations in the 1970/1980s (Ohlberger et al. 2018). When included in scenarios, the trend in mean age was set to $\delta_a = -0.008$, i.e., a decline of -0.4 over 50 years, consistent with empirical data on Chinook salmon (Ohlberger et al. 2018; Staton et al. 2021).

2.1.6.3 | Size-At-Age.
Size-at-age distributions at the start of the simulation were based on von Bertalanffy growth parameters describing the marine growth of the fish. We used an average asymptotic length (mm) of $L_{\inf} = 1200$, a growth rate coefficient of $k = 0.325$ and an ocean entry length (mm) of $S_e = 150$, yielding initial mean lengths-at-age ($L_{a,0}$) at $t = 0$ of 650, 800, 910 and 990 mm for fish that return after 4, 5, 6 and 7 years, respectively (typical ocean ages 2–5; Ohlberger

et al. 2018, 2019). Changes in length-at-age compositions over time were then modelled using assumed trends based on empirical observations and thus did not emerge from an explicit growth model. Mean length-at-age in a given run year was drawn from a normal distribution with standard deviation σ_l equal to 0.1 times the initial mean length-at-age (Equation 16). When included in scenarios, the default trends in mean length-at-age ($\delta_{l,a}$) over time differed by age group, with younger ages slightly increasing and older ages declining in length-at-age. Changes in mean lengths for return ages 4, 5, 6 and 7 were set to 0.2, −0.6, −1.2 and −2 mm per year, respectively, which is equivalent to total changes of 10, −30, −60 and −100 mm over a period of 50 years. These values are consistent with an empirical analysis that estimated changes in the average lengths-at-age of Chinook salmon since the 1970s of 3%, −5%, −7% and −9% for ocean ages 2, 3, 4 and 5, respectively (Ohlberger et al. 2018). Similarly, changes in mean lengths of these age groups over that time period were 5%, −6%, −8% and −10% for female Chinook salmon in the Kuskokwim River, Alaska (Staton et al. 2021).

2.1.6.4 | Mean Body Size.
The resulting overall decline in mean body size due to shifts in age composition and length-at-age, when included in the simulated scenarios, was on average about 65 mm or 8% (a typical mean length in years prior to demographic changes was roughly 800 mm). Depending on the selectivity of the fishing gear, these trends translate into changes in mean length in the escapement (after harvest) of about 60–80 mm or 7.5%–10%. The simulated trends match observed declines of 70–80 mm or nearly 10% in the mean body size of Chinook salmon in North America (Ohlberger et al. 2019; Oke et al. 2020).

2.1.6.5 | Sex Composition.
The proportion of females from a given brood year at the beginning of the simulations was set to $\pi_{f,0} = 0.45$ (Ohlberger et al. 2020; Staton et al. 2021). When included in scenarios, we used a trend in the proportion female of $\delta_f = -0.008$ per year on the logit scale, which is equivalent to a proportional decline of 0.1 over a period of 50 years, i.e. $\pi_{f,50} = 0.35$ (Staton et al. 2021).

2.1.6.6 | Reproduction.
The length-scaling exponent and scalar (slope and intercept on log–log scale) of total egg mass as a function of female length were set to $a_z = 8.71e^{-12}$ and $b_z = 4.8$, based on previous work on Yukon River Chinook salmon (Ohlberger et al. 2020). Because body mass scales roughly to length cubed ($b \sim 3.4$), total egg mass per female scales hyperallometrically with body mass in Chinook salmon (Ohlberger et al. 2020). We standardised this allometric relationships to a typical female length of 800 mm with a mean egg mass of 916 g at that size.

2.1.6.7 | Fishery Parameters.
Species-specific values for the parameters of the selectivity function were taken from the literature. We used values of $\lambda = -0.547$, $\theta = 0.622$, $\sigma = 0.204$, $\tau = 1.920$ for Chinook salmon (Bromaghin 2005). To simulate unselective fishing, we set $\sigma = 10$. The implementation error of the fishery was assumed to be $\sigma_i = 0.3$.

2.1.6.8 | Observations.
We assumed that observations of escapement were less certain than observations of harvest.

While fishery catches may be misreported, escapement estimates are often based on space and time extrapolations that can introduce considerable error. We used observation errors of $\sigma_e = 0.2$ for annual escapements and $\sigma_h = 0.1$ for annual harvests. Parameters and their values are listed in Table 2.

2.2 | Estimating Biological Reference Points (Estimation Model)

Estimation of biological reference points using the Ricker stock-recruit model was based on the observed harvest and escapement and their age, sex and length compositions. However, we did not account for observation error in the harvest and escapement in the estimation model because fitting a state-space population model (e.g., Fleischman et al. 2013; Staton et al. 2021) to thousands of stochastic simulations was computationally impractical. We, therefore, used a regression-based approach to estimate parameters of the stock-recruit relationships, which implicitly assumes that spawner and recruit data are independent and observed with negligible error in addition to the aforementioned assumptions about stationarity and repeatability. While regression-based approaches can suffer from bias in estimates of biological reference points (Walters 1985; Walters and Martell 2004), our preliminary analyses indicated little bias in model parameters and estimated reference points when comparing estimates from stock-recruit models fit to simulated true values to estimates from models fit to observations of the simulated data, within the range of observation error values used in the simulations. We used three different regression-based approaches for estimating biological reference points that varied in how they accounted for demographic time trends: a traditional linearised stock-recruit model (no accounting), a dynamic linear model (implicit accounting) and a yield-per-recruit approach (explicit accounting). These methods were used to estimate the S_{MSY} reference point (spawner escapement at maximum sustainable yield) which was used to update the escapement goal (S_{goal}). This process was repeated periodically every 10 years (Figure 1).

2.2.1 | Traditional Ricker Stock-Recruit Model

A maximum-likelihood estimation of the linearised Ricker stock-recruitment model based on spawner abundance was used as the *traditional* approach to estimating biological reference points used in salmon management. The traditional Ricker model (TRM) assumed time-invariant parameters such that the demographic characteristics of the population are averaged across all years of the assessed time series. It is important to note, however, that using the time-invariant Ricker model did not imply that the management policy was constant through time because management goals were assessed periodically, which allowed the management to adjust to changes in population productivity as new data become available, even when the assessment model is assumed stationarity.

Stock-recruit parameters were estimated by fitting the linearised version of the Ricker model using maximum-likelihood

TABLE 2 | Parameter values for simulating stochastic population data with demographic trends.

Symbol	Description	Value	Source
Ricker stock-recruitment relationship			
α_r	Mean Ricker productivity parameter	5	1, 2
β_r	Mean Ricker density-dependence parameter	5e^{-5}	1, 2
σ_r	Standard deviation in recruitment residuals	0.35	1, 2
ϕ_r	Autocorrelation in recruitment residuals	0.4	2
σ_α	Standard deviation in α (log scale)	0.2	2
σ_β	Standard deviation in β (log scale)	0.2	2
Demographic characteristics and trends			
A_0	Mean age at beginning of simulation	5.5	3
σ_a	Standard deviation in mean age (log scale)	0.6	3
δ_a	Annual trend in mean age	-0.008	3
ΔA	Difference in mean age between sexes	1.0	3
$\pi_{f,0}$	Initial proportion female	0.45	1, 5
δ_f	Annual trend in proportion female (logit scale)	-0.008	1, 5
L_{inf}	Average asymptotic length (mm)	1200	4
k	Growth rate coefficient	0.325	4
L_s	Length at ocean entry (mm)	150	4
σ_l	Standard deviation multiplier mean size-at-age	0.01	3
$\delta_{l,a}$	Trends in mean size-at-age (mm • yr.$^{-1}$)	0.2, 0.6, -0.6, -1.2, -1.8	3
b_z	Slope of allometric relationship (egg mass)	4.8	5
a_z	Intercept of allometric relationship (egg mass)	8.71e^{-12}	5
Fishery			
λ	Harvest selectivity parameter	0.547	6
θ	Harvest selectivity parameter	0.622	6
τ	Harvest selectivity parameter	1.920	6
σ	Harvest selectivity parameter	0.204 or 10	6
m	Mesh size in inches	6.0 or 8.5	6
σ_i	Fishery implementation error	0.3	—
Observations			
σ_e	Observation error on escapement	0.2	—
σ_h	Observation error on harvest	0.1	—

Note: Sources: (1) Fleischman et al. (2013); (2) Staton et al. (2021); (3) Ohlberger et al. (2018); (4) Ohlberger et al. (2019); (5) Ohlberger et al. (2020); (6) Bromaghin (2005).

estimation. The reconstructed brood year recruitment (R_y) was:

$$\ln(R_y) = \ln(\alpha') + \ln(S_y) - \beta' S_y + \varphi \omega_{t-1} + \varepsilon \qquad (22)$$

where S_y is spawner abundance in brood year y, ω_{y-1} is the recruitment residual in year $y-1$, φ is an autocorrelation parameter, and $\varepsilon \sim \text{Normal}(0, \sigma_r)$ are normally distributed random errors.

The productivity parameter was corrected for the difference between the median and the mean of a lognormal error distribution with a first-order autocorrelation process (Fleischman et al. 2013):

$$\ln(\alpha_R) = \ln(\alpha') + \frac{\sigma_r^2}{2(1 - \varphi^2)} \tag{23}$$

where φ is the autocorrelation and σ_r is the standard deviation of the random recruitment error, as described above. Following Hilborn and Walters (1992), the density-dependence parameter was corrected as:

$$\beta_R = \beta' \frac{\alpha}{\alpha'} \tag{24}$$

We calculated the escapement that is expected to produce maximum sustainable yield based on the estimated stock-recruit parameters using the explicit solution (Scheuerell 2016):

$$S_{MSY} = \frac{1 - W(e^{1-\alpha_R})}{\beta_R} \tag{25}$$

where W is the Lambert function and α_R and β_R are the corrected Ricker parameters.

2.2.2 | Dynamic Linear Model

A Dynamic Linear Model (DLM) was used to allow for time-varying parameters of the linearised Ricker stock-recruitment model. Here, the α and β parameters can vary over time to reflect changes in population productivity and density dependence due to trends in the population age, sex and length compositions. The productivity and density-dependence parameters of the linearised Ricker function can be modelled as a function of time as follows:

$$\ln(R_y) = \ln(\alpha'_y) + \ln(S_y) - \beta'_y S_y + \varphi \omega_{t-1} + \varepsilon \tag{26}$$

where the time-varying α'_y and β'_y parameters were estimated using maximum-likelihood estimation with added Kalman filtering and backward recursive smoothing as implemented in the R package *dlm* (Petris 2009). The estimated productivity parameter was corrected for the difference between the median and the mean of a lognormal error distribution (see Equation 23).

Escapement at MSY estimates for the DLM were based on the time-varying stock-recruit parameters as follows:

$$S_{MSY} = \frac{1 - W(e^{1-\overline{\alpha}})}{\overline{\beta}} \tag{27}$$

where $\overline{\alpha}$ and $\overline{\beta}$ are average parameter values for the most recent 5 years prior to assessment.

2.2.3 | Equilibrium Calculations for Alternative Reproductive Units

To explicitly account for demographic trends, we used a yield-per-recruit (YPR) approach based on equilibrium calculations to obtain estimates of escapement at MSY (Botsford 1981; Walters and Martell 2004). Here, total reproductive output is used as the stock metric in the Ricker stock-recruit model, instead of

spawner abundance. The fishing mortality that maximises equilibrium harvest is then determined using an optimisation algorithm (e.g., Staton et al. 2021) and the resulting equilibrium escapement is taken as the escapement that produces maximum sustainable yield. This yield-per-recruit analysis assumes that the allometric relationship between reproductive output and body size is known and that data on the size composition of spawners are available, such that the expected average reproductive output per spawner can be calculated.

The equilibrium calculations for alternative reproductive units were performed according to equations (13–17) in Staton et al. (2021), see Data S1. An optimisation algorithm was used to determine the fishing mortality associated with the highest equilibrium harvest, and to calculate the total equilibrium escapement, which was taken as S_{MSY}. Equilibrium escapement depends on the mesh size used in the fishery because selectivity affects the age-specific probability of escaping harvest. Our reference period for setting new management targets was the last 5 years of the assessed time series. This means that the equilibrium escapement was based on the average reproductive output per recruit over the 5 years prior to the assessment.

2.2.4 | Fishery Management Targets

We used the estimated escapement at MSY to update the escapement goal (S_{goal}) used in the fishery unless the new estimate was not within 0.5–2 times the previous escapement target. These limits were set to avoid unrealistic targets, especially early in the time series when few years were available to inform the estimation model. We further explored more liberal and precautionary management strategies by using either 0.75 S_{MSY} or 1.5 S_{MSY} as the new management target, respectively. These scenarios were implemented to represent systems in which the managers favour a liberal approach (0.75), i.e. more harvest, or a precautionary approach (1.5), i.e. more escapement. The precautionary approach of using 1.5 S_{MSY} is similar to using an upper target of S_{MAX}, the spawner abundance that maximises recruitment (S_{MAX} equals about 1.5 S_{MSY} across all scenarios in our analysis). S_{MAX}-based escapement goals are sometimes used in fishery management and are deemed more appropriate where the fishery is dominated by subsistence and sport fisheries that wish to harvest a fixed number of fish each year and are attempting to minimise the effort needed to harvest (Liller and Savereide 2022). The escapement target (S_{goal}) was then updated with the new estimate of S_{MSY}, which was subsequently used to dictate fishery catches until the next periodic assessment was performed.

2.3 | Assessing Fishery Management Performance

We assessed several different scenarios as part of a management strategy evaluation, each of which included different assumptions about demographic trends, fishery selectivity, estimation method and the management strategy (Table 1). Each of these scenarios was evaluated by using 1000 stochastic replicates. We evaluated differences in estimates of the escapement at MSY for alternative estimation methods that accounted for demographic trends compared to the traditional time-invariant method after 50 years of simulations for which trends were parameterised

using observed trends in the age-sex-length compositions of North American Chinook salmon (Ohlberger et al. 2018).

We evaluated the performance of the fishery management during the following 50 years (after 100 years of simulations), with either (i) no demographic trends, (ii) trends in ASL compositions that stabilised after the historical period for the remaining 50 years or (iii) ASL trends that continued at the historical rate for the entire simulation period. We used the latter two scenarios to bracket the most likely range of future demographic trends, where stabilised and continued trends in age, sex and length compositions were considered the most optimistic and pessimistic scenarios, respectively. A scenario where ASL compositions reverse to their historical values was considered unlikely and thus not included. An example of simulated demographic trends and population abundances for a scenario with ASL trends that stabilise after 50 years using a large-mesh selective fishery and a traditional Ricker stock-recruit analysis is shown in Figure S1.

Fishery management performance was evaluated for the last 50 years of the simulations. Metrics used to evaluate management performance were mean annual harvest, mean annual run size and the probabilities that recruitment and escapement were above certain conservation thresholds. Mean harvest and mean run size were calculated as the average harvest and run size over the simulated time period. We used abundance thresholds to assess potential conservation risks. First, we calculated the fraction of years that the recruitment (R_y) was above 50% of the maximum recruitment of the population (R_{max}):

$$P_{0.5R_{max}} = P(R_y > 0.5\,R_{max}) \tag{28}$$

where R_{max} depends on the stock-recruit parameters as follows (Hilborn and Walters 1992):

$$R_{max} = \frac{\alpha}{\beta}e^{-1} \tag{29}$$

Second, we calculated the fraction of years that the spawner escapement (S_y) was above 50% of the equilibrium spawner abundance (S_0):

$$P_{0.5S_0} = P(S_y > 0.5\,S_0) \tag{30}$$

where S_0 depends on the stock-recruit parameters as follows (Hilborn and Walters 1992):

$$S_0 = \frac{\log(\alpha)}{\beta} \tag{31}$$

We considered higher mean harvests, higher mean run sizes and a higher probability of abundance above the conservation thresholds as desirable fishery management objectives.

3 | Results

3.1 | Changes in Reproductive Output Over Time

Average reproductive output, measured as mean egg mass per spawner, declined over time due to trends in spawner age-sex-length compositions (Figure S2). Declines in mean egg mass per spawner over 50 years were in the 30%–45% and 40%–55% range (median values) for simulated age-length trends and age-sex-length trends, respectively, depending on the selectivity of the fishery. A large-mesh fishery (8.5-in. gillnets) caused ~15% stronger declines in body sizes of fish in the escapement than a small-mesh fishery (6-in. gillnets), due to the selective removal of larger individuals. For reference, the estimated median decline in reproductive output was zero for a population without demographic trends that experienced an unselective fishery. The estimation method had a negligible effect on changes in reproductive output.

3.2 | Estimated Escapement at MSY

Differences in estimates of the escapement that produces MSY (S_{MSY}) among the alternative estimation methods depended on the interaction between demographic trends and the selectivity of the fishery (Figure 2). When demographic trends were present in the population, the Dynamic Linear Model (DLM) resulted in median S_{MSY} estimates that were similar to or slightly lower than the traditional Ricker model (TRM), whereas the yield-per-recruit analysis (YPR) resulted in higher estimates of S_{MSY}, with the exception of a small-mesh selectivity where estimation method had little effect. For a large-mesh selective fishery, the YPR method resulted in S_{MSY} estimates that were about 24% higher for simulations with age-length trends and about 30% higher for simulations with age-sex-length trends (median values) compared to the TRM. For an unselective fishery, the median % difference was about 11% and 18% for age-length and age-sex-length trends, respectively. Under a small-mesh selective fishery, the YPR method resulted in S_{MSY} estimates that were lower than estimates of the TRM, especially when no demographic trends were present in the population.

3.3 | Fishery Management Performance

The performance of fishery management depended on the estimation method, selectivity of the fishery and the presence of demographic trends (Figure 3). Mean harvest, mean run size and the probability that the recruitment was above 50% of the maximum recruitment all declined when demographic trends were present. This overall performance decline is attributable to the reduced reproductive output and associated decline in population productivity. In addition, the probability that the escapement was above 50% of the equilibrium spawner abundance (S_0) declined unless demographic trends were explicitly accounted for using the YPR approach. Compared to the TRM, the YPR method increased the probability that escapement was above 50% of S_0 by up to 0.2, which implies a reduction in the risk of falling below that abundance threshold of 20%. All performance metrics further tended to be lower for a large-mesh selectivity because a fishery that selectively removes large individuals further exacerbates the decline in mean reproductive output per spawner. Moreover, the method used for estimating S_{MSY} had a relatively small effect on harvest such that the three estimation methods resulted in similar mean annual harvests.

The YPR approach outperformed both the TRM and DLM estimation methods in terms of mean run sizes and the probabilities
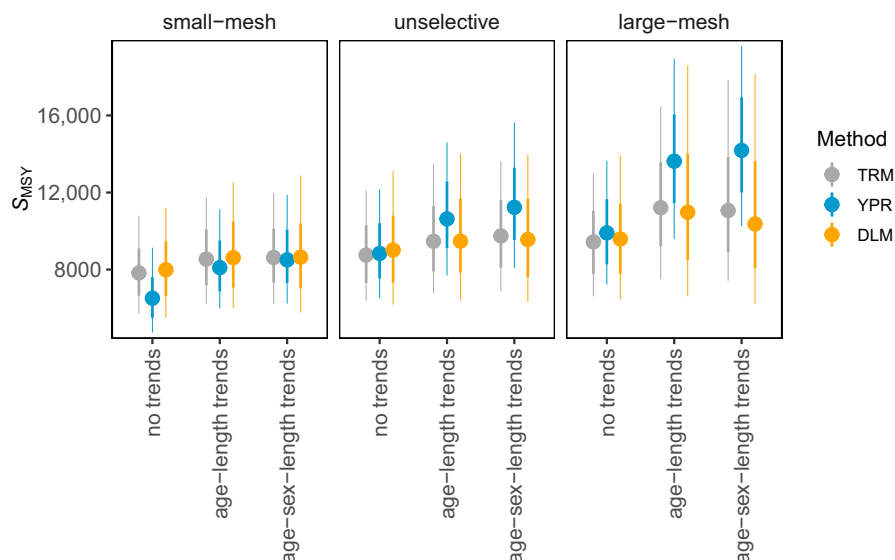
FIGURE 2 | S_{MSY} estimates by estimation method. Shown are median values (circles) with 50% quantiles (thick bars) and 80% quantiles (thin bars) for the traditional Ricker model (TRM, grey), the yield-per-recruit analysis (YPR, blue) and the Dynamic Linear Model (DLM, yellow). S_{MSY} estimates were evaluated at the end of the historical period after 50 years of demographic trends.

that recruitment and escapement were above the conservation thresholds. Specifically, when assuming continued age-sex-length trends, the median percent difference in mean run abundances between the YPR and TRM was about 8%, 17% and 25% for a small-mesh, unselective and large-mesh fishery, respectively (Figure 4). These differences between the alternative approaches and the traditional model became more pronounced over time (Figure 5). Furthermore, differences in mean run size were mostly attributable to differences in the mean escapement, rather than differences in mean harvest (Figure 6).

3.4 | Precautionary Management

Differences between estimation methods were less pronounced when using a more precautionary management strategy where the escapement target was set to 1.5 times the estimated escapement at MSY (Figure 7). By contrast, when using a more liberal management strategy where the escapement target was set to 0.75 times the estimated escapement at MSY, differences between estimation methods were more pronounced. When assuming continued age-sex-length trends and an unselective fishery, for example, the median percent difference in mean run sizes between the YPR and TRM approaches was 17% and 25% for the precautionary and liberal management strategies, respectively. For comparison, the ratio of the estimated S_{MSY} for the YPR over the TRM approach reached a factor of 1.5 or higher only in case of a large-mesh selective fishery. Median values were within the 0.8–1.25 range across all scenarios, which suggests that a slightly lower S_{MSY} multiplier may be sufficiently precautionary (Figure S3).

4 | Discussion

We investigated fishery management implications of demographic trends in age, sex and length compositions of salmon populations using a broadly applicable data-driven simulation approach. We found that compared to a traditional Ricker stock-recruitment model (TRM) based on spawner abundance and compared to a dynamic linear model (DLM) with time-varying Ricker parameters, an alternative yield-per-recruit (YPR) approach that explicitly accounts for changes in spawner reproductive output results in higher estimates of S_{MSY} in the presence of negative demographic trends. The estimation method affected fishery management performance when escapement targets were directly based on S_{MSY} estimates. Mean run sizes were higher and conservation risks were lower when using the explicit YPR method, while fishery catches remained unaffected by the choice of model. This pattern was apparent when fishing was unselective and was most pronounced for a large-mesh fishery, in line with previous results (Staton et al. 2021). Further, we found that lower mean run sizes and higher conservation risks due to demographic trends could be mitigated by using a precautionary management strategy where the escapement target was higher than the estimated S_{MSY}. Taken together, our results show that accounting for declines in spawner reproductive output in stock-recruit analyses, or using a precautionary management strategy, can partially mitigate declines in reproductive potential and reduce conservation risks, especially in fisheries that selectively remove large fish. These conclusions generally apply to other species and taxa, in particular species exposed to climate change and intense harvesting that are expected to show similar demographic trends, although the fishery management implications are likely most pronounced where demographics are traditionally not accounted for in the stock assessment.

4.1 | Simulated and Observed Demographic Trends

The demographic trends in age and length compositions used in our simulations are based on observations for Chinook salmon populations along the west coast of North America (Ohlberger et al. 2018, 2019), and trends in sex ratio are based
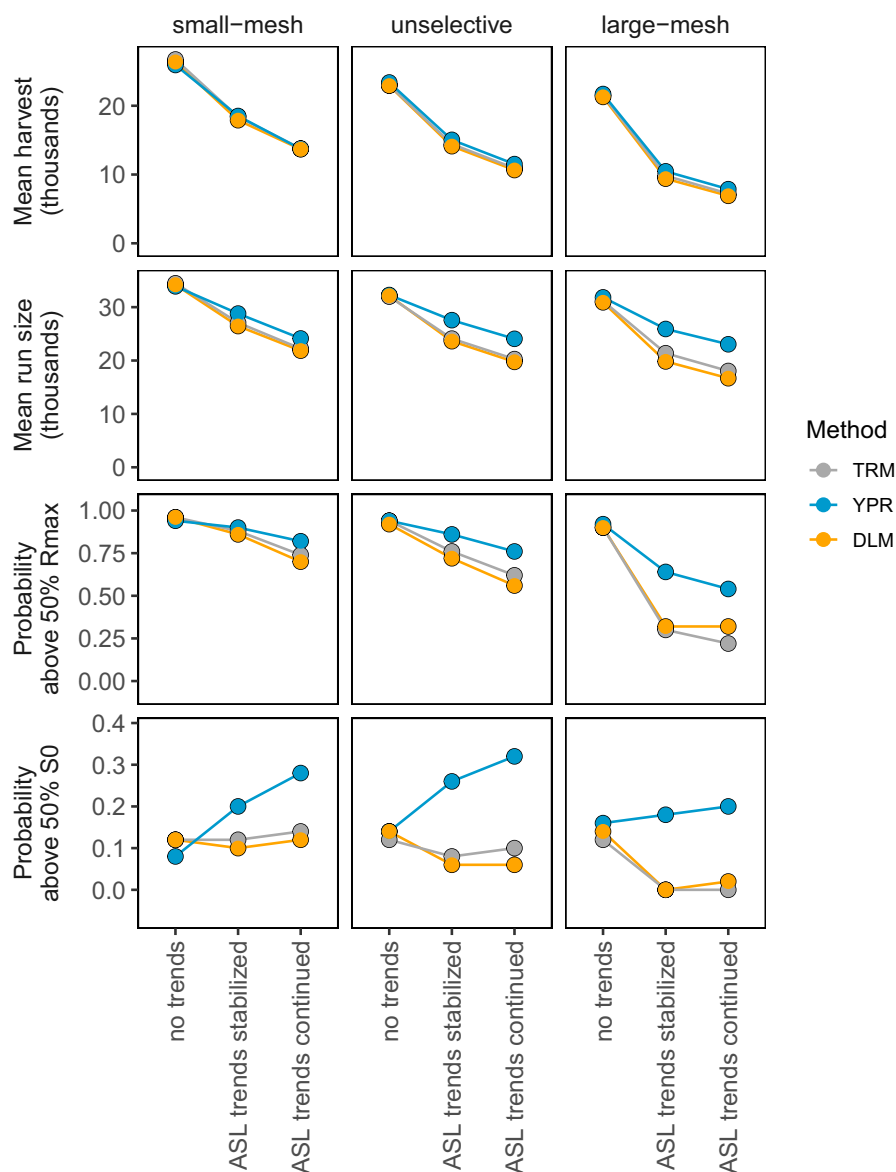
FIGURE 3 | Evaluation of fishery management performance under different scenarios. Shown are median values of four performance metrics (rows) under three different selectivity regimes (columns) for each estimation method (colours) as a function of the demographic trends. Evaluated performance metrics were mean harvest, mean run size, probability that recruitment was above 50% of the maximum recruitment (R_{max}), and the probability that the spawner escapement was above 50% of the equilibrium spawner abundance (S_0). Simulated selectivity regimes were a small-mesh (6-in.), unselective or large-mesh (8.5-in.) fishery. The three estimation methods were the traditional Ricker model (TRM, grey), the yield-per-recruit analysis (YPR, blue) and the Dynamic Linear Model (DLM, yellow). Age-sex-length (ASL) trends were either not included, stabilised after 50 years or were assumed to continue into the future (x-axis). Simulations were run for 100 years, and fishery performance was evaluated for the last 50 years.

on one of the historically largest populations in North America (Staton et al. 2021). The associated declines in average spawner reproductive output in our simulations (Figure S2) are in line with available empirical estimates for Chinook salmon populations. Reproductive output declined by about 28% for the Yukon River population based on age-length trends (Ohlberger et al. 2020), and by about 49% for the Kuskokwim River population based on trends in age, sex and length compositions (Staton et al. 2021). While demographic trends over the past few decades have been most pronounced in Chinook salmon, weaker trends toward younger and smaller fish at maturation have also been reported for other species of Pacific salmon, including chum (*O. keta*), coho (*O. kisutch*), sockeye

(*O. nerka*) and pink (*O. gorbuscha*) salmon (Jeffrey et al. 2017; Losee, Kendall, and Dufault 2019; Oke et al. 2020; Ohlberger et al. 2023).

Shifts in population demographic structures have been linked to changes in environmental and ecological conditions in the ocean such as climate change, intensified predation on maturing fish and competition with other salmon (Ohlberger et al. 2019; Oke et al. 2020; Manishin et al. 2021). In this study, we did not make specific assumptions about the causes of demographic trends. This implies potential evolutionary change in traits related to growth and maturation in response to (size-selective) fishing was not accounted for in the simulations. Several studies
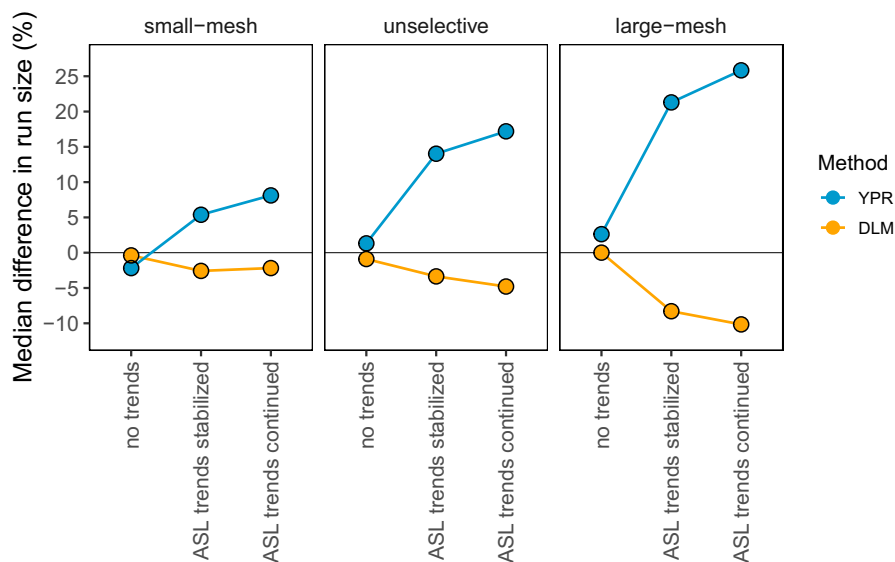
FIGURE 4 | Median % difference in average total run size from the time-invariant model. Shown are differences for the two alternative estimation methods, the yield-per-recruit analysis (YPR, blue) and the Dynamic Linear Model (DLM, yellow), compared to the time-invariant Ricker model for three different fishery selectivities (columns) given the simulated demographic trends (x-axis). This figure is based on numbers presented in the second row of Figure 3.
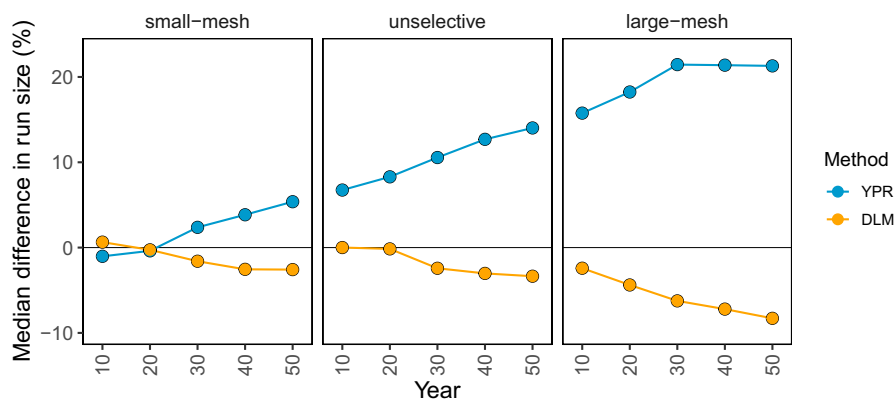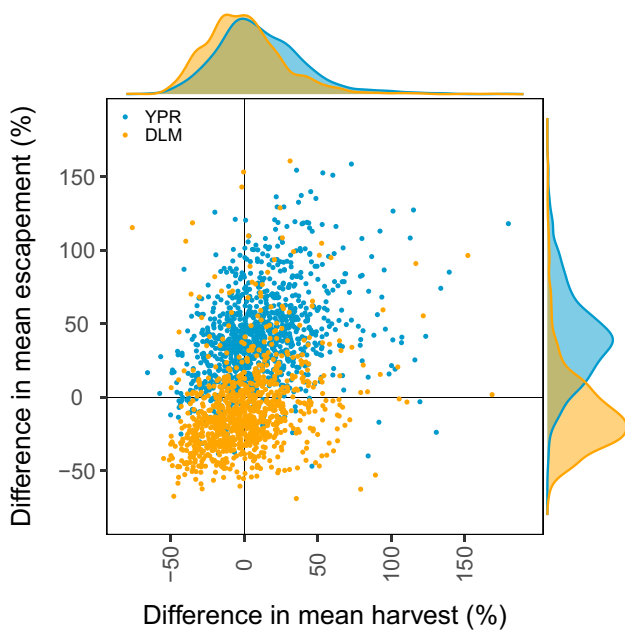

FIGURE 5 | Median % difference in run size from the time-invariant model across years. Shown is the median difference for the yield-per-recruit analysis (YPR, blue) and the Dynamic Linear Model (DLM, yellow) compared to the time-invariant Ricker model in each decade starting after the historical period (e.g., year 10 is the difference for future years 1–10) assuming continued ASL trends.

have concluded that fisheries were not a major driver of recent size declines in Pacific salmon (Kendall et al. 2014; Lewis et al. 2015; Jeffrey et al. 2017; Oke et al. 2020), although they may have caused significant size declines during earlier periods (Ohlberger et al. 2019). Finally, we note that the model does not account for intraspecific density effects on individual growth and length-at-age as was shown for numerically abundant sockeye salmon (Ohlberger et al. 2023, 2022), although effects of intraspecific competition on survival are accounted for via the stock-recruit relationship.

4.2 | Time-Varying Productivity Models

Previous work that explored time-varying productivity in Ricker stock-recruit models suggested that estimates of S_{MSY}

decrease when population productivity declines and vice versa (Peterman, Pyper, and Grout 2000; Peterman, Pyper, and MacGregor 2003). Management targets based on such estimates may thus not be consistent with conservation goals as these models suggest lowering escapement targets when population productivity declines (Holt and Michielsens 2020). However, estimates of S_{MSY} may not necessarily decline with productivity when density dependence in the stock-recruit relationship also changes over time. For example, assuming a constant maximum recruitment instead would imply an increase in S_{MSY} with declining population productivity. To avoid the implicit assumption of stationarity in density dependence, the DLM used in this study allowed for both Ricker parameters to vary over time. This approach nevertheless tended to estimate a lower S_{MSY} compared to the time-invariant model (consistent with Peterman, Pyper, and Grout 2000; Peterman,

FIGURE 6 | Difference in mean harvest and mean escapement from time-invariant model. Shown is the % difference in harvest and escapement in each stochastic run (circles) for the yield-per-recruit analysis (YPR, blue) and the Dynamic Linear Model (DLM, yellow) compared to the time-invariant Ricker model for a large-mesh fishery assuming continued ASL trends. Marginal plots along the secondary axes show the respective density distributions.

Pyper, and MacGregor 2003). Accordingly, our results suggest that conservation risks may in fact increase when adjusting management targets based on a time-varying Ricker model, which may misinterpret declining reproductive potential as declining productivity.

By contrast, explicitly accounting for declining average reproductive output using the YPR method resulted in higher estimates of escapement at MSY and thus leads to management that is more aligned with conservation goals. The YPR method resulted in the highest escapement at MSY estimates and the best management performance in terms of mean run sizes and the probability of that run abundance was above the conservation threshold. Notably, average harvest was not affected with the use of the YPR approach.

4.3 | Assumptions and Limitations of the YPR Approach

The YPR method has limitations and makes important assumptions about the biology of the population and the data available to the stock assessment. First, this approach assumes that total reproductive output is limited by the number of females but not males. Female spawners are thought to limit population recruitment because eggs are more costly to produce than sperm, spawner sex ratios are often male-biased due to their shorter ocean residence and higher marine survival rates (Olsen et al. 2006; Holtby and Healey 1990), and females defend their nest sites with negligible assistance from males (McPhee and Quinn 1998). Second, this approach assumes that the length

composition of the spawners is known. Such information is available for some but not all salmon populations. Third, the YPR approach also assumes that the relationship between female size and reproductive output is known. While this assumption may seem limiting due to lack of population-specific data in some systems and potential differences in the allometry of reproductive output among populations (Healey and Heard 1984), such variation is small compared to the implicit assumption of a traditional abundance-based stock-recruitment model that reproductive output does not depend on body size. The length-scaling exponent used in this study was 4.8, which is roughly equivalent to a mass scaling exponent of 1.3 in Chinook salmon (Ohlberger et al. 2020). This value is typical for marine fishes and reflects the commonly found hyper-allometric relationship between reproductive output and body size (Barneche et al. 2018). A recent study on Chinook salmon in Alaska found that varying the allometric exponent of the reproductive output in a YPR analysis, such as the one used in this study, had a relatively small effect on estimates of biological reference points within the range of observed size-scaling relationships (Staton et al. 2021, Supplement A therein). However, adaptive changes in life-history trade-offs that lead to long-term shifts in how fish allocate energy to somatic versus reproductive growth could alter the size-fecundity relationship of a population and partially compensate for the effects of declining mean body size on average spawner reproductive output. Egg mass was used in this study as a proxy of female reproductive output because it tightly correlates with egg energy content (Ohlberger et al. 2020). Total egg mass may be a better proxy for female reproductive output than egg number, because a trade-off between egg number and egg mass likely evolved to maximise reproductive success in the environment experienced by a population (Heath et al. 2003). Large females produce not only more but also larger eggs compared to small females (Healey and Heard 1984; Ohlberger et al. 2020). Despite the demands of the YPR method, it was the only approach among those tested that allowed explicit accounting of demographic trends and translating them into biological reference points used in fishery management. It should also be noted that we assumed non-retention mortality from small-mesh gillnets was negligible for larger fish that interact with the gear but are not captured, yet studies have indicated that gillnet injuries may cause substantial non-retention mortality in salmon (e.g., Baker and Schindler 2009). We further did not assume compensatory increases in survival and thus spawner abundance, which could partially offset declines in reproductive output per spawner, because observational data did not indicate that marine survival of Chinook salmon has increased over the examined period. Finally, we used a Ricker stock-recruit model because it has been extensively used to model population dynamics of Pacific salmon (Peterman 1981; Hilborn and Walters 1992; Fleischman et al. 2013), and we did not explore the sensitivity of our findings to the structural form or parameterisation of the stock-recruit relationship, which could be assessed in future extensions of this work.

4.4 | Implementation Uncertainty of the Fishery

Differences in the performance of fishery management among estimation methods used in the assessment model may be partially masked by uncertainties in the harvesting process (e.g.,
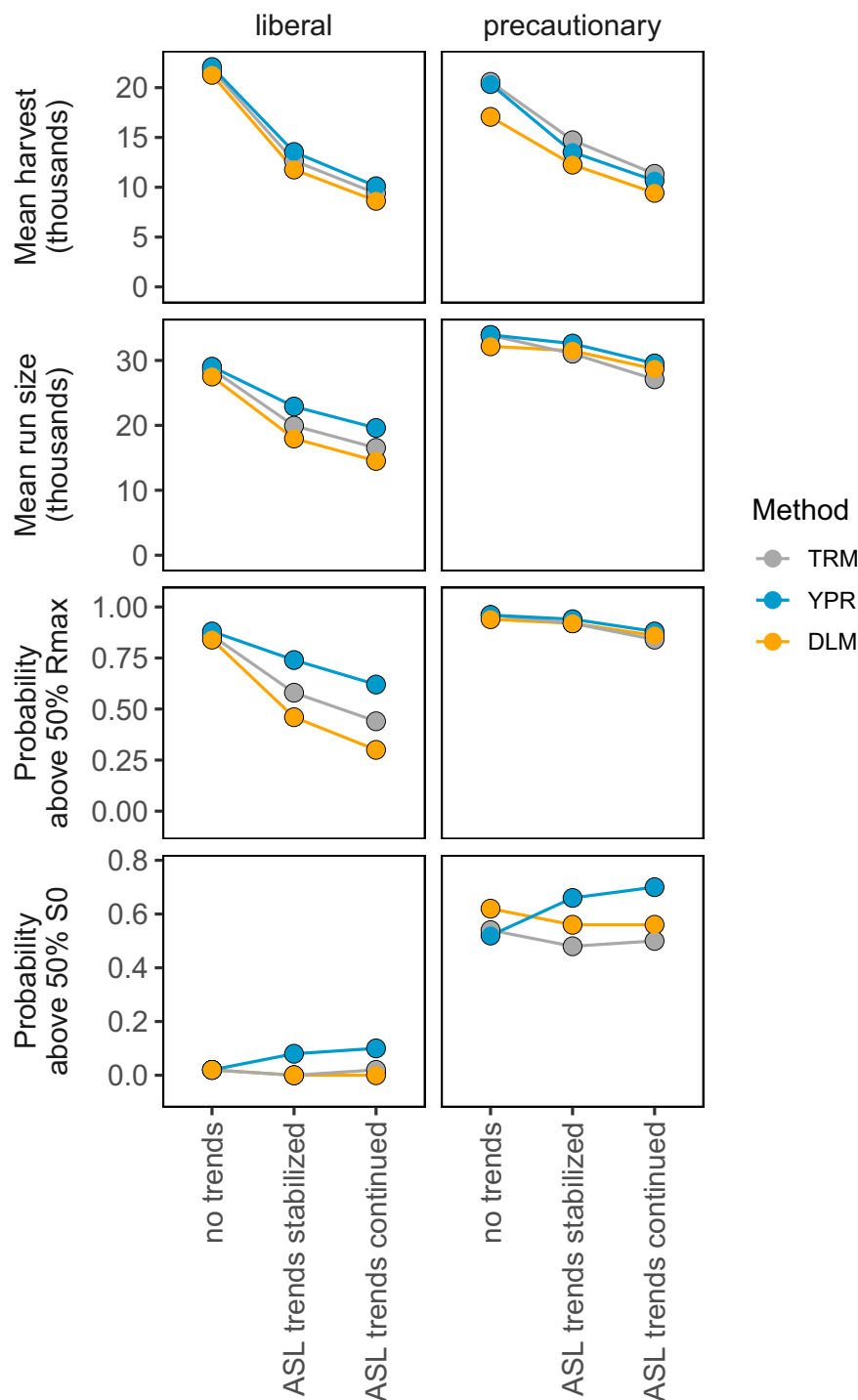
FIGURE 7 | Performance metrics for liberal and precautionary management strategies. Shown are median values of four performance metrics (rows) for each estimation method (colours) using management targets of either 0.75 S_{MSY}, (left, liberal) or 1.5 S_{MSY}, (right, precautionary), assuming unselective fishing. Details on the performance metrics, the estimation methods, and time period are provided in the caption to Figure 3.

implementation error) that cause the achieved harvest and escapement to deviate substantially from the management target (Eggers and Rogers 1987; Dorner, Peterman, and Su 2009; Collie, Peterman, and Zuehlke 2012). Such outcome uncertainty may stem from multiple interacting processes, including errors in pre-season or in-season forecasts of run abundance, changes in catchability, non-compliance of harvesters to regulations, and slow adjustments in the capacity of the fishing fleet or processors to changes in population abundance (Dorner,

Peterman, and Su 2009; Holt and Peterman 2006; Holt and Folkes 2015). Previous simulation studies showed that this uncertainty can have large effects on the expected management performance when population productivity varies over time (Dorner, Peterman, and Su 2009). Our simulations assume random lognormal error around the escapement target to account for outcome uncertainty. However, we did not include an implementation bias (Peterman, Pyper, and Grout 2000), and the uncertainty associated with the harvesting process

likely varies among fisheries, species and regulatory frameworks. Stock-specific applications of assessment models that incorporate information on changes in spawner reproductive potential should thus consider historical patterns in outcome uncertainty of the fishery or investigate how reducing that uncertainty could affect the expected management performance. Briefly, we found that reducing the implementation error (σ_i, from 0.3 to 0.15) did not affect the relative performance of the estimation methods (Figure S4) and hence would not alter any of our conclusions.

5 | Conclusions

Salmon management is commonly governed by the principle of sustainable yield and quantities such as the escapement at MSY assume that all spawners contribute equally to recruitment. Under this approach, long-term declines in average reproductive output per spawner produce continuously declining escapement goals when goals are assessed periodically. Using methods that estimate time-varying productivity, abundance-based assessments further accelerate the process and thus increase conservation risks. In contrast, explicit accounting for reduced spawner reproductive output in salmon stock assessments by using alternative reproductive units, or implicit accounting by implementing a precautionary management strategy, can partially mitigate the increased conservation risks due to trends toward younger, smaller and male-biased returns. However, because such strategies cannot fully compensate for expected declines in run abundances and associated risks, preserving population demographic structure may be an important conservation strategy for sustaining productive salmon populations and their benefits to ecosystems and people.

To conserve population demographic structure, we need a better understanding of the causes of demographic change, which requires monitoring populations for shifts in age, sex and length compositions, or average reproductive output. The YPR approach assumes that data on size compositions are available to calculate the expected average reproductive output per spawner. In the absence of such data needed to explicitly account for changes in demographic parameters, managing harvest in a more precautionary manner can ameliorate much of the reductions in management performance. The precautionary approach we considered (using 1.5 times S_{MSY}) showed little effect on long-term average harvests but improved conservation outcomes. While we did not consider effects of precautionary management on other conservation goals such as maintaining population diversity in large rivers (Connors et al. 2020), such an approach would also work to improve the chance of satisfying those outcomes.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Code for this analysis is available at https://github.com/janohlberger/SizeShiftsImplications.

References

Anderson, C. N., C. H. Hsieh, S. A. Sandin, et al. 2008. "Why Fishing Magnifies Fluctuations in Fish Abundance." *Nature* 452: 835–839.

Baker, M. R., and D. E. Schindler. 2009. "Unaccounted Mortality in Salmon Fisheries: Non-retention in Gillnets and Effects on Estimates of Spawners." *Journal of Applied Ecology* 46: 752–761.

Barneche, D. R., D. R. Robertson, C. R. White, and D. J. Marshall. 2018. "Fish Reproductive-Energy Output Increases Disproportionately With Body Size." *Science* 360: 642–644.

Beacham, T. D., and C. B. Murray. 1993. "Fecundity and Egg Size Variation in North American Pacific Salmon (*Oncorhynchus*)." *Journal of Fish Biology* 42: 485–508.

Beverton, R. J. H., and S. J. Holt. 1957. *On the Dynamics of Exploited Fish Populations. Fishery Investigations Series.* London, UK: Ministry of Agriculture, Fisheries and Food.

Bigler, B. S., D. W. Welch, and J. H. Helle. 1996. "A Review of Size Trends Among North Pacific Salmon (*Oncorhynchus* spp.)." *Canadian Journal of Fisheries and Aquatic Sciences* 53: 455–465.

Botsford, L. W. 1981. "The Effects of Increased Individual Growth Rates on Depressed Population Size." *American Naturalist* 117: 38–63.

Botsford, L. W., M. D. Holland, J. C. Field, and A. Hastings. 2014. "Cohort Resonance: A Significant Component of Fluctuations in Recruitment, Egg Production, and Catch of Fished Populations." *ICES Journal of Marine Science* 71: 2158–2170.

Bromaghin, J. F. 2005. "A Versatile Net Selectivity Model, With Application to Pacific Salmon and Freshwater Species of the Yukon River, Alaska." *Fisheries Research* 74: 157–168.

Buckner, J. H., W. H. Satterthwaite, B. N. Nelson, and E. J. Ward. 2023. "Interactions Between Life History and the Environment on Changing Growth Rates of Chinook Salmon." *Canadian Journal of Fisheries and Aquatic Sciences* 80: 648–662.

Clark, R. A., D. R. Bernard, and S. J. Fleischman. 2009. "Stock-Recruitment Analysis for Escapement Goal Development: A Case Study of Pacific Salmon in Alaska." *American Fisheries Society Symposium* 70: 743–757.

Collie, J. S., R. M. Peterman, and B. M. Zuehlke. 2012. "A Fisheries Risk-Assessment Framework to Evaluate Trade-Offs Among Management Options in the Presence of Time-Varying Productivity." *Canadian Journal of Fisheries and Aquatic Sciences* 69: 209–223.

Connors, B. M., B. Staton, L. Coggins, et al. 2020. "Incorporating Harvest-Population Diversity Trade-Offs Into Harvest Policy Analyses of Salmon Management in Large River Basins." *Canadian Journal of Fisheries and Aquatic Sciences* 77: 1076–1089.

Crozier, W. W., P.-J. Schön, G. Chaput, E. C. E. Potter, N. Ó. Maoiléidigh, and J. C. MacLean. 2003. "Managing Atlantic Salmon (*Salmo salar* L.) in the Mixed Stock Environment: Challenges and Considerations." *ICES Journal of Marine Science* 61: 1344–1358.

Dorner, B., R. M. Peterman, and Z. Su. 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.

Eggers, D. M., and D. E. Rogers. 1987. "The Cycle of Runs of Sockeye Salmon (*Oncorhynchus nerka*) to the Kvichak River, Bristol Bay, Alaska: Cyclic Dominance or Depensatory Fishing?" *Canadian Special Publication in Fisheries and Aquatic Sciences* 96: 343–366.

Feddern, M., R. Shaftel, E. Schoen, et al. 2024. "Body Size and Early Marine Conditions Drive Changes in Chinook Salmon Productivity Across Northern Latitude Ecosystems." *Global Change Biology* 30, no. 10: e17508.

Fleischman, S. J., M. J. Catalano, R. A. Clark, and D. R. Bernard. 2013. "An Age-Structured State-Space Stock-Recruit Model for Pacific Salmon (*Oncorhynchus* Spp.)." *Canadian Journal of Fisheries and Aquatic Sciences* 70: 401–414.

Free, C. M., T. Mangin, J. Wiedenmann, C. Smith, H. McVeigh, and S. D. Gaines. 2022. "Harvest Control Rules Used in US Federal Fisheries Management and Implications for Climate Resilience." *Fish and Fisheries* 24: 248–262.

Green, B. S. 2008. "Maternal Effects in Fish Populations." *Advances in Marine Biology* 54: 1–105.

Healey, M. C., and W. R. Heard. 1984. "Inter- and Intra-Population Variation in the Fecundity of Chinook Salmon (*Oncorhynchus tshawytscha*) and Its Relevance to Life History Theory." *Canadian Journal of Fisheries and Aquatic Sciences* 41: 476–483.

Heath, D. D., J. W. Heath, C. A. Bryden, R. M. Johnson, and C. W. Fox. 2003. "Rapid Evolution of Egg Size in Captive Salmon." *Science* 299: 1738–1740.

Heino, M., L. Baulier, D. S. Boukal, et al. 2013. "Can Fisheries-Induced Evolution Shift Reference Points for Fisheries Management?" *ICES Journal of Marine Science* 70: 707–721.

Hilborn, R., and C. J. Walters. 1992. *Quantitative Fisheries Stock Assessment*. New York: Chapman and Hall.

Hixon, M. A., D. W. Johnson, and S. M. Sogard. 2014. "BOFFFFs: On the Importance of Conserving Old-Growth Age Structure in Fishery Populations." *ICES Journal of Marine Science* 71: 2171–2185.

Holt, C. A., and M. J. P. Folkes. 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.

Holt, C. A., and C. G. J. Michielsens. 2020. "Impact of Time-Varying Productivity on Estimated Stock–Recruitment Parameters and Biological Reference Points." *Canadian Journal of Fisheries and Aquatic Sciences* 77: 836–847.

Holt, C. A., and R. M. Peterman. 2006. "Missing the Target: Uncertainties in Achieving Management Goals in Fisheries on Fraser River, British Columbia, Sockeye Salmon (*Oncorhynchus nerka*)." *Canadian Journal of Fisheries and Aquatic Sciences* 63: 2722–2733.

Holtby, L. B., and M. C. Healey. 1990. "Sex-Specific Life History Tactics and Risk-Taking in Coho Salmon." *Ecology* 71: 678–690.

Hsieh, C. H., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006. "Fishing Elevates Variability in the Abundance of Exploited Species." *Nature* 443: 859–862. https://doi.org/10.1038/nature05232.

ICES. 1993. "Report of the North Atlantic Salmon Working Group." ICES Document, CM 1993/ACFM:10.

ICES. 2002. "Report of the Working Group on North Atlantic Salmon." ICES Document, CM 2002/ACFM:14.

Jeffrey, K. M., I. M. Côté, J. R. Irvine, and J. D. Reynolds. 2017. "Changes in Body Size of Canadian Pacific Salmon Over Six Decades." *Canadian Journal of Fisheries and Aquatic Sciences* 74: 191–201.

Kendall, N. W., U. Dieckmann, M. Heino, A. E. Punt, and T. P. Quinn. 2014. "Evolution of Age and Length at Maturation of Alaskan Salmon Under Size-Selective Harvest." *Evolutionary Applications* 7: 313–322.

Lewis, B., W. S. Grant, R. E. Brenner, and T. Hamazaki. 2015. "Changes in Size and Age of Chinook Salmon *Oncorhynchus tshawytscha* Returning to Alaska." *PLoS One* 10: e0130184.

Liller, Z. W., and J. W. Savereide. 2022. "Escapement goal review for select Arctic–Yukon–Kuskokwim Region salmon stocks, 2023." Alaska Department of Fish and Game, Fishery Manuscript No. 22-08, Anchorage.

Losee, J. P., N. W. Kendall, and A. Dufault. 2019. "Changing Salmon: An Analysis of Body Mass, Abundance, Survival, and Productivity Trends Across 45 Years in Puget Sound." *Fish and Fisheries* 20: 934–951.

Malick, M. J., and S. P. Cox. 2016. "Regional-Scale Declines in Productivity of Pink and Chum Salmon Stocks in Western North America." *PLoS One* 11: e0146009-23.

Malick, M. J., J. P. Losee, G. Marston, et al. 2023. "Fecundity Trends of Chinook Salmon in the Pacific Northwest." *Fish and Fisheries* 24: 454–465.

Manishin, K. A., C. J. Cunningham, P. A. H. Westley, and A. C. Seitz. 2021. "Can Late Stage Marine Mortality Explain Observed Shifts in Age Structure of Chinook Salmon?" *PLoS One* 16: e0247370.

McPhee, M. V., and T. P. Quinn. 1998. "Factors Affecting the Duration of Nest Defense and Reproductive Lifespan of Female Sockeye Salmon, *Oncorhynchus nerka*." *Environmental Biology of Fishes* 51: 369–375.

Murawski, S. 2001. "Impacts of Demographic Variation in Spawning Characteristics on Reference Points for Fishery Management." *ICES Journal of Marine Science* 58: 1002–1014.

Ohlberger, J., T. J. Cline, D. E. Schindler, and B. Lewis. 2023. "Declines in Body Size of Sockeye Salmon Associated With Increased Competition in the Ocean." *Proceedings of the Royal Society B* 290: 20222248.

Ohlberger, J., Ø. Langangen, and L. C. Stige. 2022. "Age Structure Affects Population Productivity in an Exploited Fish Species." *Ecological Applications* 32: e2614.

Ohlberger, J., D. E. Schindler, R. J. Brown, et al. 2020. "The Reproductive Value of Large Females: Consequences of Shifts in Demographic Structure for Population Reproductive Potential in Chinook Salmon." *Canadian Journal of Fisheries and Aquatic Sciences* 77: 1292–1301.

Ohlberger, J., D. E. Schindler, E. J. Ward, T. E. Walsworth, and T. E. Essington. 2019. "Resurgence of an Apex Marine Predator and the Decline in Prey Body Size." *Proceedings of the National Academy of Sciences of the United States of America* 116: 26682–26689.

Ohlberger, J., E. J. Ward, D. E. Schindler, and B. Lewis. 2018. "Demographic Changes in Chinook Salmon Across the Northeast Pacific Ocean." *Fish and Fisheries* 19: 533–546.

Oke, K. B., C. J. Cunningham, P. A. H. Westley, et al. 2020. "Recent Declines in Salmon Body Size Impact Ecosystems and Fisheries." *Nature Communications* 11: 4155.

Olsen, J. B., S. J. Miller, K. Harper, J. J. Nagler, and J. K. Wenburg. 2006. "Contrasting Sex Ratios in Juvenile and Adult Chinook Salmon *Oncorhynchus tshawytscha* (Walbaum) From South-West Alaska: Sex Reversal or Differential Survival?" *Journal of Fish Biology* 69: 140–144.

Peterman, R. 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, R. M., and B. Dorner. 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.

Peterman, R. M., B. J. Pyper, and J. A. Grout. 2000. "Comparison of Parameter Estimation Methods for Detecting Climate-Induced Changes in Productivity of Pacific Salmon (*Oncorhynchus* spp.)." *Canadian Journal of Fisheries and Aquatic Sciences* 57: 181–191.

Peterman, R. M., B. J. Pyper, and B. W. MacGregor. 2003. "Use of the Kalman Filter to Reconstruct Historical Trends in Productivity of Bristol Bay Sockeye Salmon." *Canadian Journal of Fisheries and Aquatic Sciences* 60: 809–824.

Petris, G. 2009. "Dlm: An R Package for Bayesian Analysis of Dynamic Linear Models." University of Arkansas.

Punt, A. E., D. S. Butterworth, C. L. de Moor, J. A. De Oliveira, and M. Haddon. 2016. "Management Strategy Evaluation: Best Practices." *Fish and Fisheries* 17: 303–334.

Quinn, T. J., and R. B. Deriso. 1999. *Quantitative Fish Dynamics*. New York: Oxford University Press.

Ricker, W. E. 1954. "Stock and Recruitment." *Journal of the Fisheries Research Board of Canada* 11: 559–623.

Ruggerone, G. T., and B. M. Connors. 2015. "Productivity and Life History of Sockeye Salmon in Relation to Competition With Pink and Sockeye Salmon in the North Pacific Ocean." *Canadian Journal of Fisheries and Aquatic Sciences* 72: 818–833.

Scheuerell, M. D. 2016. "An Explicit Solution for Calculating Optimum Spawning Stock Size From Ricker's Stock Recruitment Model." *PeerJ* 4: e1623.

Sharpe, D. M. T., and A. P. Hendry. 2009. "Synthesis: Life History Change in Commercially Exploited Fish Stocks: An Analysis of Trends Across Studies." *Evolutionary Applications* 2: 260–275.

Shelton, A. O., J. A. Hutchings, R. S. Waples, D. M. Keith, H. R. Akçakaya, and N. K. Dulvy. 2015. "Maternal Age Effects on Atlantic Cod Recruitment and Implications for Future Population Trajectories." *ICES Journal of Marine Science* 72: 1769–1778.

Staton, B. A., M. J. Catalano, S. J. Fleischman, and J. Ohlberger. 2021. "Incorporating Demographic Information Into Spawner-Recruit Analyses Alters Biological Reference Point Estimates for a Western Alaska Salmon Population." *Canadian Journal of Fisheries and Aquatic Sciences* 78: 1755–1769.

Stige, L. C., N. A. Yaragina, Ø. Langangen, B. Bogstad, N. C. Stenseth, and G. Ottersen. 2017. "Effect of a Fish stock's Demographic Structure on Offspring Survival and Sensitivity to Climate." *Proceedings of the National Academy of Sciences of the United States of America* 114: 1347–1352.

Thorson, J. T., O. P. Jensen, and E. F. Zipkin. 2014. "How Variable Is Recruitment for Exploited Marine Fishes? A Hierarchical Model for Testing Life History Theory." *Canadian Journal of Fisheries and Aquatic Sciences* 71: 973–983.

Walters, C. J. 1985. "Bias in the Estimation of Functional Relationships From Time Series Data." *Canadian Journal of Fisheries and Aquatic Sciences* 42: 147–149.

Walters, C. J., and S. J. D. Martell. 2004. *Fisheries Ecology and Management*. Princeton, NJ: Princeton University Press.

Wang, S.-P., C.-L. Sun, A. E. Punt, and S.-Z. Yeh. 2005. "Evaluation of a Sex-Specific Age-Structured Assessment Method for the Swordfish, *Xiphias gladius*, in the North Pacific Ocean." *Fisheries Research* 73: 79–97.

Supporting Information

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