# The role of uncertainty in the design of sustainable and precautionary management strategies for fisheries 

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#### Abstract

Environmental variability has a strong influence on marine fish stocks. Thus, management and harvest policies based on deterministic indicators, such as maximum sustainable yield (MSY), may be inappropriate facing such uncertainties. In this study, we investigate the long-term behavior of a singlespecies fishery, whose stock is harvested by several fleets and affected by variability in the recruitment. The dynamics of this population is modeled by a discrete-time stochastic age-structured model. In this context, we introduce the concepts of maximum expected, log expected, and harmonic expected sustainable yield, as biological reference points. We illustrate these concepts with a case study of the Pa tagonian toothfish fishery in Chile and Argentina. Via Monte-Carlo simulations, we verify that high levels of variability have a negative effect on all these maximum expected reference points, which suggests the need to be more cautious when large levels of variability on recruitment impact the fishery. Our simulations show that the deterministic MSY may not be attained in the presence of environmental noise, and therefore its use may lead to a failure of management strategies or rebuilding plans.


## Recommendations for Resource Managers

- For sustainable harvest, proper accounting of stochasticity in recruitment dynamics is necessary. For high levels of volatility, the use of deterministic reference points to develop regulations, such as maximum sustainable yield (MSY), may lead to overexploitation and even a possible extinction of the fishery.
- We extend the MSY to the stochastic age-structured framework by means of maximum expected stationary yield, maximum expected log-sustainable yield, and maximum expected harmonic sustainable yield, which can be used as precautionary reference points.
- These three maximum expected yields and their respective optimal fishing mortalities decrease when the variability of fish recruitment increases. This stresses the need to be more cautious in presence of volatility.


## KEYWORDS

biological reference points, fishery management, optimal sustainable harvesting, stochastic age-structured models

## 1 | INTRODUCTION

Age-structured fish population dynamics models are ubiquitous around the world for integrating the diverse sources of information available with key parameters for describing the factors affecting the dynamics, including natural and fishing mortality and reproduction, along with the fishing process (Quinn \& Deriso, 1999). The basis of these models is a deterministic, linear Leslie matrix formulation (Caswell, 2001; Getz \& Haight, 1989; Horwood \& Shepherd, 1981; Leslie 1945). For biological realism, two modifications are useful: nonlinear dynamics during the early life history stage, and stochastic variation in early life survival to account for the large amount of uncertainty due to environmental conditions.

Stochastic variability in fish population models due to recruitment has already been studied in Brodziak, Rago, and Conser (1998), Getz (1984), Getz, Francis, and Swartzman (1987), Hightower and Grossman (1985), Horwood and Shepherd (1981), and Reed (1983), from a viewpoint of population dynamics and biological reference points. Horwood and Shepherd (1981) studies the sensitivity of an age-structured model with respect to noise in general form, via Fourier analysis. In Reed (1983), a discrete-time nonlinear stochastic age-structured population model, without a plus group, is proposed. To estimate the steady-state variances of the recruitment and yield, equations for approximations of the first and second moments of abundances by age are obtained. A similar analysis is carried out in Getz (1984), with two main
differences: first, the model considers a plus group; second, each year is split into two seasons: during harvesting season the model is given by an ordinary differential equation (ODE), and during spawning season the model is given by a discrete-time equation. Approximate and explicit expressions for the first and second moments of each age-group are obtained. A more practical approach is presented in Getz et al. (1987), where the authors perform Monte-Carlo simulations of a stochastic age-structured model, with a Ricker spawner-recruitment function, to estimate the long term mean yield, for three different fisheries, and conclude that the maximum expected sustainable yield in all the studied fisheries decreases as the coefficient of variation ( $C V$ ) of recruitment increases (considering a range for $C V$ from $0 \%$ to $200 \%$ ). Brodziak et al. (1998) considers a model similar to Reed (1983), with the addition of a plus group, Baranov catches, and a Beverton-Holt spawner-recruitment function with noncentered multiplicative log-normal noise, and performs Monte-Carlo simulations of the obtained model, to generate short-term stochastic projections with different constant values of fishing mortalities based on biological reference points. Regarding bioeconomic analysis, stochastic models considering multispecies, multifleets, and age-structure have been used for ecosystem-based fishery management in Doyen et al. (2012), Gourguet et al. (2013, 2014, 2016), and Lagarde et al. (2018). This analysis was carried out based on coviability of biological, economic, and nontarget species conservation objectives. More specifically, in Doyen et al. (2012) and Gourguet et al. (2013), the variability is presented only in the stock-recruitment relation and is modeled by means of Ockham-Razor functions and normal random variables; in Gourguet et al. (2014, 2016), the authors consider sex-structured population models with a Ricker stock-recruitment function, and environmental uncertainties are modeled by a assuming that the biomass of one of the species is uniform random variable; in Lagarde et al. (2018), the impact of sea temperature on the recruitment is studied. Nevertheless, no explicit formulation for the equilibrium distribution is proposed in the previously cited works.

Regarding risk, Thompson (1999) studies the effect of stochasticity in the optimization of harvesting control rules, and shows the convenience of considering the arithmetic, geometric, and harmonic mean yields as indicators of the state of the catch. According to Thompson (1999), these quantities are related to the attitude towards risk from the point of view of an agent that needs to design fishing control policies. For example, a limit control rule might be defined by the decisiontheoretic optimum derived under a risk-neutral stance, while a target control rule might be defined by the decision-theoretic optimum derived under a risk-averse stance. A simple way to characterize this difference is as follows: the risk-neutral solution maximizes the expectation of stationary yield, while the risk-averse solution maximizes the expectation of log-sustainable yield. The harmonic mean is also used as a part of a precautionary control value for biomass-based control rules used by the North Pacific Fishery Management Council (2016). Due to the inherent nonlinearity of the models, it is not easy to compute these quantities, nor to obtain explicit expressions of the stationary distribution associated with these models. This can be done in onedimensional biomass models, such as in Bousquet, Duchesne, and Rivest (2008) and Ewald and Wand (2010), where the authors study respectively a discrete- and continuous-time Schaefer population model with multiplicative noise for the biomass, for specific probability distributions of the noise. The authors derive explicit formulas for the stationary distribution and prove that the expected sustainable yield decreases as the variance of the noise increases. The drawback of this formulation is that the age-structure information disappears; the discussion in Tahvonen (2009) illustrates the interest of considering an age-structured approach over a biomass approach.

In this article, we are interested in the long term behavior of a single-species fishery harvested by several fleets and subject to environmental randomness that affects the recruitment.

More specifically, we want to derive optimal constant fishing strategies that maximize the expected long term yield. To this purpose, we model the dynamics of the fishery by a discretetime nonlinear stochastic age-structured population model with a plus group, where the recruitment is given by a Beverton-Holt spawner-recruitment function. We introduce the concepts of maximum expected stationary yield (MESY), maximum expected log-sustainable yield (MELSY), and maximum expected harmonic sustainable yield (MEHSY), and illustrate the results with the case of the Patagonian toothfish population in Chilean and Argentinean fisheries. We compare the different reference points and the deterministic maximum sustainable yield (MSY). Via numerical simulations, we show that the uncertainty has a negative effect on every maximum expected reference point, which suggests the need to be more cautious where large levels of variability on recruitment affect the fishery, and that the deterministic MSY cannot be attained in the presence of environmental noise. These results confirm the theoretical results obtained in Bousquet et al. (2008) for biomass-based models.

This article is organized as follows: In Section 2.1, we define the deterministic agestructured model and investigate the properties of its equilibrium values depending on fishing mortality. In Section 2.2, we introduce a stochastic term to the recruitment function, leading to a stochastic age-structured model, and we define the mentioned expected yield measures. In Section 3, we show the results of numerical simulations for both the deterministic and stochastic models, and we give estimates of these yield measures, showing the relevance of accounting for variability in the model.

## 2 | MATERIALS AND METHODS

## 2.1 | Preliminaries and deterministic model

Consider a model of a fishery composed of $n$ fleets $f=\{1, \ldots, n\}$. The fish population contains individuals of ages $a \in\{1, \ldots, A-1, A\}$, in which $A$ is the age category of individuals of $A$ or more years, called a plus group. The proportion of mature individuals at age $a$ is denoted $m_{a}$. The population within each age group is subject to mortality, that is composed of natural mortality and the effect of fishing exerted by the fleets. We denote by $M_{a}$ and $F_{a}$ the natural and fishing mortality rates at age $a$, respectively. $F_{a}$ can be written as $F_{a}=\sum_{f=1}^{n} F_{f, a}$, where $F_{f, a}$ is the fishing mortality rate at age $a$ by fleet $f$. This mortality rate is a linear function of the fullrecruitment fishing mortality $F$, that is, $F_{f, a}=P_{f} S_{f, a} F$, where $P_{f}$ is the proportion of fishing mortality exerted by fleet $f$, and $s_{f, a}$ is the selectivity of fish of age $a$ by fleet $f$ (Quinn \& Deriso, 1999). The fishing mortality rate $F_{f, a}$ is also related to the fishing effort $e_{f}$ of fleet $f$ (in number of days at sea) by $F_{f, a}=q_{f, a} k_{f} e_{f}$, with $q_{f, a}$ the catchability coefficient by fleet $f$ at age $a$, and $k_{f}$ is the number of vessels of fleet $f$ (Doyen et al., 2012). By convention, $\max _{a} S_{f, a}=1$. The total mortality rate at age $a$ is $Z_{a}=M_{a}+F_{a}$ (Table 1 summarizes the parameters and variables of the model). Notice that fishing mortality $F$ (and consequently $F_{a}$ ) depends on time $t$. However, since we are only interested in reference points at equilibrium, this dependence on time is not used and, consequently, it is omitted.

Let us define $N_{t}=\left(N_{t, 1}, \ldots, N_{t, A-1}, N_{t, A}\right)^{\top}$ the state vector, containing in each component $N_{t, a}$ the abundance of fish belonging to age-class $a$ at the beginning of year $t$. Total abundance is considered as the sum of all individuals of ages $r$ or more, where $r$ corresponds to the age of recruitment (often the starting age at which data are collected, when the young fish become vulnerable to capture in a fishery, or when the number of fish in a cohort can be reliably

TABLE 1 Notation used in the age-structured population model

| Symbol | Description | Range/unit |
| :--- | :--- | :--- |
| $f$ | Fleet type | $1, \ldots, n$ |
| $a$ | Age category | $1, \ldots, A-1, A$ |
| $M_{a}$ | Natural mortality at age $a$ | $[0, \infty)$ |
| $P_{f}$ | Proportion of fishing mortality of fleet $f$ | $[0,1]$ |
| $S_{f, a}$ | Selectivity of fish of age $a$ by fleet $f$ | $[0,1]$ |
| $F$ | Full-recruitment fishing mortality | $[0, \infty)$ |
| $F_{f, a}=P_{f} S_{f, a} F$ | Fishing mortality rate at age $a$ by fleet $f$ | $[0, \infty)$ |
| $F_{a}=\sum_{f=1}^{n} F_{f, a}$ | Fishing mortality rate at age $a$ | $[0, \infty)$ |
| $Z_{a}=M_{a}+F_{a}$ | Total mortality rate at age $a$ | $[0, \infty)$ |
| $m_{a}$ | Maturity at age $a$ | $[0,1]$ |
| $W_{a}$ | Weight at age $a$ | $[0, \infty)$, kg |
| $N_{t, a}$ | Abundance of fish of age $a$ at beginning of year $t$ | $[0, \infty)$, millions |
| $R_{t}$ | Recruitment (at age $a=r)$ in year $t$ | $[0, \infty)$, millions |
| $\mathrm{SSB}_{t}$ | Spawning stock biomass in year $t$ | $[0, \infty)$, tons |
| $Y_{t}$ | Yield of year $t$ | $[0, \infty)$, tons |

estimated by a stock assessment). The spawning stock biomass (SSB) in the year $t$ is composed of the individuals from the beginning of the year $t$ that have survived the proportion $\tau$ of the year until they spawn:

$$
\begin{equation*}
\mathrm{SSB}_{t}=\sum_{a=r}^{A} m_{a} W_{a} N_{t, a} e^{-\tau Z_{a}} \tag{1}
\end{equation*}
$$

Recruitment to the population occurs at age $r$, and depends on the SSB of $r$ years before

$$
\begin{equation*}
R_{t}=\varphi\left(\mathrm{SSB}_{t-r}\right) . \tag{2}
\end{equation*}
$$

The function $\varphi(\cdot)$ represents a spawner-recruit function, of which the asymptotic Beverton-Holt and the dome-shape Ricker are the most common. The Beverton-Holt recruitment function is given by

$$
\begin{equation*}
\varphi(\mathrm{SSB})=\frac{\alpha \mathrm{SSB}}{\beta+\mathrm{SSB}} \tag{3}
\end{equation*}
$$

(see, for instance, Quinn \& Deriso, 1999). The individuals of age $a+1$ at the beginning of a given year $t+1$ correspond to the individuals of age $a$ that survived the year $t$. With the previous assumptions, the equations for the age-structured deterministic population model are

$$
\begin{align*}
N_{t+1,1} & =\varphi\left(\mathrm{SSB}_{t}\right) ; \quad N_{t+1, a+1}=N_{t, a} e^{-Z_{a}}, \quad a=1, \ldots, A-2 ; \\
N_{t+1, A} & =N_{t, A-1} e^{-Z_{A-1}}+N_{t, A} e^{-Z_{A}} . \tag{4}
\end{align*}
$$

The yield of year $t$ is given by the Baranov catch in weight formula

$$
\begin{equation*}
Y_{t}=\sum_{a=r}^{A} W_{a} \frac{F_{a}}{Z_{a}}\left(1-e^{-Z_{a}}\right) N_{t, a} . \tag{5}
\end{equation*}
$$

The previous equations can be put in matrix form as

$$
\left\{\begin{array}{l}
N_{t+1}=A(F) N_{t}+B \varphi\left(\mathrm{SSB}_{t}\right),  \tag{6}\\
Y_{t}=C(F) N_{t},
\end{array}\right.
$$

where $A(F)$ is an age-structured Leslie matrix in which the first row has null entries and the off-diagonals contain survival rates $\exp \left(-Z_{a}\right)$. To use this matrix formulation, we place recruitment at $r$ years after their spawning. Following Quinn and Deriso (1999, Section 7.4) we consider the natural mortalities of the first $r-1$ groups of juvenile individuals to be null, that is, $M_{1}=\cdots=M_{r-1}=0$, and the selectivities $s_{f, 1}=\cdots=s_{f, r-1}=0$ for all fleets $f=1, \ldots, n$. To handle the plus group, the matrix is further modified to take into account the survival rate of the individuals that belong to the plus group $A$, or,

$$
\begin{equation*}
A(F)_{a+1, a}=e^{-Z_{a}(F)}, \quad a=1, \ldots, A-1 ; \quad A(F)_{A, A}=e^{-Z_{A}(F)}, \tag{7}
\end{equation*}
$$

and

$$
\begin{equation*}
B=(1,0, \ldots, 0)^{\top}, \quad C(F)=\left(W_{1} \frac{F_{1}}{Z_{1}}\left(1-e^{-Z_{1}}\right), \ldots, W_{A} \frac{F_{A}}{Z_{A}}\left(1-e^{-Z_{A}}\right)\right) \tag{8}
\end{equation*}
$$

A key role in the analysis of population dynamics is the concept of equilibrium. For the standard Leslie matrix without including the plus group, the equilibrum formulas are presented in Quinn and Deriso (1999, Section 7.4). For this analysis, we consider constant mortality rates $M_{a}$, selectivities $S_{f, a}$, proportions of fishing mortalities $P_{f}$, and fishing mortality $F$. Denote by $N^{\star}=\left(N_{1}^{\star}, \ldots, N_{A}^{\star}\right)^{\top}, \mathrm{SSB}^{\star}$, and $Y^{\star}$ the abundances of fish by age class, the spawning-stock biomass level, and the yield at equilibrium, respectively. These quantities depend of $F$, and satisfy the following relations with respect to $N^{\star}$ (from (1) and (5)):

$$
\begin{equation*}
\mathrm{SSB}^{\star}(F)=\sum_{a=r}^{A} m_{a} W_{a} N_{a}^{\star} e^{-\tau Z_{a}}, \quad Y^{\star}(F)=\sum_{a=r}^{A} W_{a} \frac{F_{a}}{Z_{a}}\left(1-e^{-Z_{a}}\right) N_{a}^{\star} . \tag{9}
\end{equation*}
$$

Definition 1. We define the MSY as the maximum yield at equilibrium, as a function of the full-recruitment fishing mortality $F$

$$
\begin{equation*}
\text { MSY }:=\max _{F \geq 0} Y^{\star}(F) . \tag{10}
\end{equation*}
$$

We denote by $F_{\text {MSY }}$ the fishing mortality that attains the MSY, that is, MSY $=Y^{\star}\left(F_{\text {MSY }}\right)$.

The quantities at equilibrium $N^{\star}, \mathrm{SSB}^{\star}, Y^{\star}$, can be computed in terms of $N_{1}^{\star}$ and the spawning potential ratio $\mathrm{SPR}^{\star}=\operatorname{SPR}^{\star}(F)$, defined as

$$
\mathrm{SPR}^{\star}:=\sum_{a=r}^{A-1} W_{a} m_{a} \mathscr{L}_{a} e^{-\tau Z_{a}}+\frac{W_{A} m_{A} \mathscr{L}_{A}}{1-e^{-Z_{A}}} e^{-\tau Z_{A}},
$$

where $\mathscr{L}_{a}=\mathscr{L}_{a}(F)$ is the cumulative survival at age $a$ given by

$$
\mathscr{L}_{a}:=\exp \left\{-\sum_{x=1}^{a-1} Z_{x}\right\}, \quad a=2, \ldots, A, \quad \mathscr{L}_{1}:=1
$$

As in Getz (1984), the population at equilibrium can be characterized by the equations

$$
\begin{equation*}
N_{1}^{\star}=\varphi\left(N_{1}^{\star} \operatorname{SPR}^{\star}\right), \quad N_{a}^{\star}=N_{1}^{\star} \mathscr{L}_{a}, \quad a=2, \ldots, A-1, \quad N_{A}^{\star}=N_{1}^{\star} \frac{\mathscr{L}_{A}}{1-e^{-Z_{A}}} . \tag{11}
\end{equation*}
$$

(a detailed deduction of previous formulas is stated in Appendix A). Thus, the yield at equilibrium has the following explicit formula (depending on $N_{1}^{\star}$ ):

$$
\begin{equation*}
Y^{\star}=Y^{\star}(F)=N_{1}^{\star}\left(\sum_{a=r}^{A-1} W_{a} \frac{F_{a}}{Z_{a}}\left(1-e^{-Z_{a}}\right) \mathscr{L}_{a}+W_{A} \frac{F_{A}}{Z_{A}} \mathscr{L}_{A}\right) . \tag{12}
\end{equation*}
$$

Thus, for the deterministic case, the MSY corresponds to the maximum value of $Y^{\star}(F)$ given by (12). From Quinn and Deriso (1999) and Reed (1980), a sufficient condition for stability of the equilibrium point is

$$
\begin{equation*}
\left|\operatorname{SPR}^{\star} \frac{\partial \varphi}{\partial \mathrm{SSB}^{2}}\left(\mathrm{SSB}^{\star}\right)\right|<1 . \tag{13}
\end{equation*}
$$

For the particular case of the Beverton-Holt recruitment function (as given in (3)), we have

$$
\begin{equation*}
N_{1}^{\star}=\alpha-\frac{\beta}{\mathrm{SPR}^{\star}}, \quad \mathrm{SSB}^{\star}=\alpha \mathrm{SPR}^{\star}-\beta \tag{14}
\end{equation*}
$$

Thus, a condition for the equilibrium points $N^{\star}, \mathrm{SSB}^{\star}, Y^{\star}$ to have ecological meaning is $\mathrm{SPR}^{\star} \geq \frac{\beta}{\alpha}$. Also, the condition for stability (13) is equivalent to $\mathrm{SPR}^{\star}>\frac{\beta}{\alpha}$, that is, the positivity of the equilibrium $\mathrm{SSB}^{\star}$ or, equivalently, the positivity of $N_{1}^{\star}$.

## 2.2 | Stochastic model and optimal yield measures

Fluctuations on fish populations naturally appear as effect of environmental variations such as temperature, food availability, or reproductive success (Shepherd and Horwood, 1979). As in Doyen et al. (2012), Getz (1984), Gourguet et al. (2013, 2014, 2016), Hightower and Grossman (1985), Lagarde et al. (2018), and Reed (1980), we consider that the variability affects the stockrecruitment relation, by introducing a modification in the recruitment function given by a
log-normal random variable at each time (see Hightower \& Grossman, 1985, for the discussion about this particular choice of noise). The generalized model is

$$
\left\{\begin{array}{l}
N_{t+1}=A(F) N_{t}+B \varphi\left(\mathrm{SSB}_{t}\right) \omega_{t} e^{-\frac{1}{2} \sigma^{2}}, \quad t \in \mathbb{N}, t \geq t_{0}  \tag{15}\\
Y_{t}=C(F) N_{t},
\end{array}\right.
$$

with $A(F), B, C(F)$ as in (7)-(8), $\mathrm{SSB}_{t}$ as in (1). Here $\left(\omega_{t}\right)_{t \in \mathbb{N}}$ is a sequence of independent and identically distributed log-normal random variables, defined on a probability space ( $\Omega, \mathscr{F}, \mathbb{P}$ ), with parameters $\mu=0$ and $\sigma>0$, and independent of $N_{t_{0}}$. The term $\exp \left(-\sigma^{2} / 2\right)$ corrects for bias, that is, the mean value of the noise term is $\mathbb{E}\left(\omega_{t} e^{-\sigma^{2} / 2}\right)=1$, for all $t \geq t_{0}$ (where $\mathbb{E}(\cdot)$ denotes the expectation operator associated with $\mathbb{P}$ ). As usual, $\sigma$ is called standard deviation. Under this context, for each $t$, the yield $Y_{t}$ is a random variable.

As in the previous section, we aim to study the concept of MSY, now in the stochastic framework. Denote by $f_{Y}(\cdot \mid F)$ the stationary probability density of the yield (as a function on $F$ ), corresponding to the limiting probability distribution of process $\left(Y_{t}\right)_{t \in \mathbb{N}}$ (Meyn \& Tweedie, 2012), that is, given a constant value of $F, f_{Y}(\cdot \mid F)$ is the nonnegative integrable function satisfying that

$$
\begin{equation*}
\lim _{t \rightarrow \infty} \mathbb{P}\left(Y_{t}(F) \in B\right)=\int_{B} f_{Y}(y \mid F) d y, \quad \forall B \in \mathscr{B}, \tag{16}
\end{equation*}
$$

where $\mathscr{B}$ denotes the Borel $\sigma$-algebra on $[0, \infty$ ) (a detailed survey on stationary distributions of recursive distributional equations can be found in Aldous \& Bandyopadhyay, 2005 and Diaconis \& Freedman, 1999). Following Thompson (1999), we introduce the following definitions.

Definition 2. Define $\operatorname{ESY}(F)$ (resp. $\operatorname{ELSY}(F), \operatorname{EHSY}(F)$ ) as the expected sustainable (resp. log-sustainable, harmonic sustainable) yield with respect to the stationary yield distribution

$$
\begin{align*}
\operatorname{ESY}(F) & :=\int_{0}^{\infty} y f_{Y}(y \mid F) d y \\
\operatorname{ELSY}(F) & :=\exp \left\{\int_{0}^{\infty} \log (y) f_{Y}(y \mid F) d y\right\},  \tag{17}\\
\operatorname{EHSY}(F) & :=\left(\int_{0}^{\infty} y^{-1} f_{Y}(y \mid F) d y\right)^{-1} .
\end{align*}
$$

We define the maximum expected sustainable (resp. log-sustainable, harmonic sustainable) yield MESY (resp. MELSY, MEHSY) as

$$
\begin{equation*}
\operatorname{MESY}:=\max _{F \geq 0} \operatorname{ESY}(F), \quad \text { MELSY }:=\max _{F \geq 0} \operatorname{ELSY}(F), \quad \text { MEHSY }:=\max _{F \geq 0} \operatorname{EHSY}(F) . \tag{18}
\end{equation*}
$$

We denote by $F_{\text {MESY }}$ (resp. $F_{\text {MELSY }}, F_{\text {MEHSY }}$ ) the fishing mortality that attains the maximum expected sustainable (resp. log-sustainable, harmonic sustainable) yield MESY (resp. MELSY, MEHSY).

Remark 1. For any fixed $F \geq 0$, we have the inequality $\operatorname{EHSY}(F) \leq \operatorname{ELSY}(F) \leq \operatorname{ESY}(F)$. Indeed, both inequalities are a consequence of Jensen's inequality for concave functions (Kallenberg, 1997, Lemma 2.5). This shows that the sustainable expected
yield measures, previously defined, capture different degrees of risk aversion. Consequently, MEHSY $\leq$ MELSY $\leq$ MESY.

Remark 2. It is usually difficult to obtain an explicit expression of the stationary distribution $f_{Y}(\cdot \mid F)$. Consequently, it is even rarer to find analytical expressions for MESY, MELSY, and MESHY. Thus, the previously defined reference points are typically estimated via Monte-Carlo methods (Spall, 2003). Indeed, since $f_{Y}(\cdot \mid F)$ is the stationary density of the process $\left(Y_{t}\right)_{t \in \mathbb{N}}$, the distribution of $Y_{t}$ (which depends on $F$ ) is a good approximation of $f_{Y}(\cdot \mid F)$ provided that $t$ is large enough. Then, a large number of several independently generated replications of $N_{t}$ allow computing several replications of $Y_{t}$ (via (15)), which in turns are used to compute an empirical distribution that approximates $f_{Y}(\cdot \mid F)$. Consequently, the arithmetic, geometric, and harmonic means of these replications of $Y_{t}$ are used to estimate $\operatorname{ESY}(F)$, $\operatorname{ELSY}(F)$, and $\operatorname{ESHY}(F)$, respectively. Finally, the maximum of these three quantities, with respect to $F$, are then used to estimate MESY, MELSY, and MESHY, respectively.

## 3 | ILLUSTRATION: PATAGONIAN TOOTHFISH

Patagonian toothfish (Dissostichus eleginoides) is a fish species that lives in the southern Pacific and Atlantic oceans (Figure 1). It was first researched as a potential fishery resource in Chile in


FIGURE 1 Distribution of Patagonian toothfish and Antarctic toothfish in the southern Pacific and Atlantic Oceans. Source: ccamlr.org
the 1950s by exploratory fishing at great depths (Guerrero \& Arana, 2009; Moreno, 1991). Thirty years later, this resource began to be caught as bycatch in trawl fisheries developed around Kerguelen islands, the Patagonian shelf, and the South Georgia Islands. In the mid-1980s, the development of longline gear that could be operated at great depths led to fishing in Chilean waters directed toward adult toothfish. Fishing activity quickly expanded to the Patagonian shelf, the South Georgia Islands, and Kerguelen Islands. The high price of this product in the international market led to large increases in catch and the exploration of new fishing grounds. According to FAO, and including only legal catches, landings in Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) convention area and territorial waters increased from $<5,000$ tons in 1983 to over 40,000 tons in 1992 (Tascheri \& Canales, 2015).

In Argentina, the Patagonian toothfish fishery followed a similar development, starting as bycatch in trawl fisheries, and subsequently developing as longline fisheries in Argentina as well as in the Falkland islands. The Argentinean fishery started in the 1990s and reached its peak in 1995 with a total catch of 19,225 tons; since then, catches have decreased. Longline fishing started in the Falkland islands as an experimental fishery in 1992, and became established in 1994 (Laptikhovsky \& Brickle, 2005). The catch reached a maximum of 2,733 tons in 1994, and then it became stable in the range of $1,200-1,800$ tons.

Based on recomendations of the Instituto Nacional de Investigación y Desarrollo Pesquero de Argentina (INIDEP), since the year 2000, hooks size is regulated, catches are documented, a minimum size limit is in place, there are minimum depths of operation, and there is a protected area for juvenile toothfish.

The Chilean Patagonian toothfish fishery is divided mainly in two zones. The northern zone, between the northern limit of the country $\left(18^{\circ} 21^{\prime}\right)$ and $47^{\circ}$, is reserved exclusively for the artisanal fleet. The southern zone $\left(47^{\circ} S-57^{\circ} S\right)$ is open to the industrial fleet.

The Argentinean Patagonian toothfish fishery is comprised of two fleets distinguished by their rigging/fishing gear used: the longline fleet started operating in 1990 and since its inception, has been a directed fishery with an area of operation involving almost the entire ranges of the resource along the Argentinean shelf. The longline fishery is responsible for the largest historic landing registered in 1995, from which catches were significantly reduced by this fleet. The number of ships that make up the longline fleet has been on a gradual decline from a peak of 25 in 1996 to 4 in 2013 (Wöhler, 2013). The second fleet operates with bottom trawl gear and began in the late 1980s. Because of the differential size distribution with depth exhibited by toothfish, and because most of the trawl sets are made between 400 and 500 m deep, the trawl fleet mainly impacts the juvenile fraction of the population. The catches of trawlers showed an increasing trend from 1999, which is related to the exploration of new fishing areas and not to an increase in the resource abundance. Currently, this fleet is composed of five trawlers (Wöhler, 2013).

In Chile, the new General Law of Fisheries and Aquaculture (Ley General de Pesca y Acuicultura, LGPA) took effect in the year 2013. Regarding fisheries, the modifications to the law covered five fundamental aspects: sustainability, industrial and artisanal fishery regulations, research, and audit. One of the main aspects will be to keep or to rebuild the fishery to the MSY, considering the biological characteristics of the exploited resources. It is important to have good estimate of MSY, to use as a target or limit for the harvest control policy.

The aim of this section is to illustrate, for the case of the Patagonian toothfish fishery, how the introduction of the uncertainty in the recruitment affects the reference points typically used for the management of this fishery. This is done via the numerical estimation of the values

MESY, MELSY, and MEHSY, introduced in this study, and their comparison with the wellknown MSY.

## 3.1 | Simulation parameters and procedure

We model the Patagonian toothfish population as an age-structured population with a plus group at age $A=30$ years, and the age of recruitment $r=3$ years. Spawning occurs at $\tau=7 / 12$ of the way through the year. There are four fleets: Chilean industrial fleet, Chilean artisanal fleet, Argentinean longline fleet, and Argentinean artisanal fleet.

For the numerical simulations, we consider data of the landings from 1978 to 2014 and the parameters estimated from stock assessment obtained from IFOP webpage (more details in Tascheri \& Canales, 2015). The parameter values, obtained from Tascheri and Canales (2015), are $M=0.15$, $h=0.6$ (steepness of stock-recruit relationship), $B_{0}=214,009$ tons (virgin biomass), $R_{0}=5,309$ tons (virgin recruitment), $\alpha=4 h R_{0} /(5 h-1)=6370.8, \beta=B_{0}(1-h) /(5 h-1)=42801.8$. The proportions of fishing mortality of the different fleets are $P=(50.23 \%, 23.57 \%, 16.44 \%, 9.76 \%)$, so that the Chilean industrial fleet currently takes a majority of the fish, followed by the Chilean artisanal fleet, the Argentinean longline fleet and, lastly, the Argentinean artisanal fleet. Selectivities are shown in Table S1, weight and maturity by age are shown in Table S2, and initial conditions for the simulations (with baseline year 2014) are shown in Table S3 in Appendix B.

We consider a time horizon $T_{\text {end }}=500$ years (time in which we can observe a steady behavior for the deterministic trajectories). As a first step, we run simulations of the deterministic process (4). We define a meshgrid in the interval [ 0,1 ] with a step $h_{d}=10^{-5}$, and for each value $F_{j}$ in this meshgrid we compute the theoretical equilibrium values $N^{\star}\left(F_{j}\right), \operatorname{SSB}^{\star}\left(F_{j}\right)$, and $Y^{\star}\left(F_{j}\right)$ as given in Equations (11), (14), and (12). The obtained value $F=F_{\text {MSY }}$ that maximizes the sustainable yield is $F_{\mathrm{MSY}}=0.132$, the corresponding maximum yield is $\mathrm{MSY}=$ 7323 tons, and the stationary SSB is 69,929 tons (see Figures $2-3$ ). The simulated values match the theoretical values.

As described in Remark 2, the yield measures MESY, MELSY, and MEHSY are computed via Monte-Carlo simulations by using a large number of several independently generated replications of $N_{t}$. We search the optimal values $F_{\text {MESY }}, F_{\text {MELSY }}$, and $F_{\text {MEHSY }}$, in the interval [ $\left.0, F_{\text {ext }}\right]$ (with $F_{\text {ext }}=0.41$ the maximum fishing mortality that allows a non-null sustainable yield in the deterministic case) by defining a meshgrid of 100 points, and for each value $F_{j}$ in the meshgrid we compute $\nu=500,000$ replications of time trajectories, for different values of $\sigma$ in the mesh $(0.25,0.5,0.75,1.0,1.25,1.5,1.75,2.0,2.25,2.5,2.75,3.0)$. This number of replications is large enough to ensure that the confidence interval at $95 \%$ for MESY is at most $1 \%$ with respect to the mean value. The values of yield at the final time for each replication $k$ (for fixed $\sigma$ and $F_{j}$ ) are denoted $y_{T_{\text {end }}}^{k}$. We estimate the values $\operatorname{ESY}(F), \operatorname{ELSY}(F)$, and $\operatorname{EHSY}(F)$ by the arithmetic, geometric, and harmonic means of the final values of yield:

$$
\operatorname{ESY}(F)=\frac{1}{\nu} \sum_{k=1}^{\nu} y_{T_{\text {end }}}^{k}, \quad \operatorname{ELSY}(F)=\exp \left\{\frac{1}{\nu} \sum_{k=1}^{\nu} \log \left(y_{T_{\text {end }}}^{k}\right)\right\}, \quad \operatorname{EHSY}(F)=\left(\frac{1}{v} \sum_{k=1}^{\nu} \frac{1}{y_{T_{\text {end }}}^{k}}\right)^{-1} .
$$

We search the value MESY as the maximum among the computed values $\operatorname{ESY}\left(F_{j}\right)$ (we proceed analogously for MELSY and MEHSY).


FIGURE 2 Deterministic equilibrium yield as a function of fullrecruitment fishing mortality. MSY, maximum sustainable yield

## 3.2 | Simulation results

The results of the numerical simulations explained in the previous section are shown in Tables 2 and 3. The case $\sigma=0$ corresponds to the deterministic case. Consequently, the two values in the first line of Table 2 correspond to MSY and $F_{\text {MSY }}$, respectively, and they are included only for comparison purposes.

The maximum expected yield (in any of its possible measures) decreases as the variability of fish recruitment increases. Also, the fishing mortality that produces the maximum expected sustainable yield decreases, which can be taken as a sign to be more cautious when there is stochasticity in recruitment present (see Table 2 and Figures 4-5). Also, for small values of $\sigma$, the values $F_{\text {MESY }}, F_{\text {MELSY }}$, and $F_{\text {MEHSY }}$ are close (and also close to $F_{\text {MSY }}$ ), but for large values of $\sigma$, they become clearly different. The most conservative measure is $F_{\text {MEHSY }}$, and the least conservative is $F_{\text {MESY }}$, as expected from deterministic theory. Nevertheless, as Table 3 shows, this


FIGURE 3 Deterministic equilibrium $\operatorname{SSB}$ as a function of fullrecruitment fishing mortality. SSB, spawning stock biomass

TABLE 2 Values of MESY, MELSY, MEHSY (in tons), and maximum full recruitment fishing mortalities associated, for different values of $\sigma$

| $\boldsymbol{\sigma}$ | MESY | MELSY | MEHSY | $\boldsymbol{F}_{\text {MESY }}$ | $\boldsymbol{F}_{\text {MELSY }}$ | $\boldsymbol{F}_{\text {MEHSY }}$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 0.00 | 7,323 | 7,323 | 7,323 | 0.132 | 0.132 | 0.132 |
| 0.25 | 7,309 | 7,293 | 7,276 | 0.132 | 0.132 | 0.127 |
| 0.50 | 7,264 | 7,195 | 7,126 | 0.127 | 0.127 | 0.127 |
| 0.75 | 7,178 | 7,002 | 6,836 | 0.127 | 0.123 | 0.123 |
| 1.00 | 7,016 | 6,663 | 6,342 | 0.123 | 0.119 | 0.119 |
| 1.25 | 6,756 | 6,136 | 5,619 | 0.119 | 0.115 | 0.110 |
| 1.50 | 6,370 | 5,399 | 4,678 | 0.110 | 0.102 | 0.098 |
| 1.75 | 5,846 | 4,478 | 3,592 | 0.102 | 0.093 | 0.083 |
| 2.00 | 5,136 | 3,404 | 2,455 | 0.089 | 0.076 | 0.068 |
| 2.25 | 4,273 | 2,313 | 1,425 | 0.076 | 0.064 | 0.051 |
| 2.50 | 3,252 | 1,319 | 619 | 0.064 | 0.047 | 0.034 |
| 2.75 | 2,125 | 552 | 135 | 0.047 | 0.034 | 0.017 |
| 3.00 | 1,106 | 124 | 0.034 | 0.017 | 0.004 |  |

Abbreviations: MESY, maximum expected stationary yield; MELSY, maximum expected log-sustainable yield; MEHSY, maximum expected harmonic sustainable yield.

TABLE 3 Values of expected yields and spawning stock biomass (in tons) under the optimal fishing mortalities $F_{\text {MSY }}, F_{\text {MESY }}, F_{\text {MELSY }}, F_{\text {MEHSY }}$, for different values of $\sigma$

| $\sigma$ | $\mathbf{E S Y}_{F_{M S Y}}$ | $\mathbf{E S Y}_{F_{M E S Y}}$ | $\mathbf{E S Y}_{F_{M E L S Y}}$ | $\mathbf{E S Y}_{\boldsymbol{F}_{M E H S Y}}$ | $\mathbf{S S B}_{F_{M S Y}}$ | $\mathbf{S S B}_{F_{M E S Y}}$ | $\mathbf{S S B}_{F_{M E L S Y}}$ | $\mathbf{S S B}_{F_{M E H S Y}}$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 0.00 | 7,323 | 7,323 | 7,323 | 7,323 | 69,929 | 69,929 | 69,929 | 69,929 |
| 0.25 | 7,309 | 7,309 | 7,309 | 7,309 | 69,790 | 69,790 | 69,790 | 72,123 |
| 0.50 | 7,263 | 7,264 | 7,264 | 7,264 | 69,352 | 71,688 | 71,688 | 71,688 |
| 0.75 | 7,174 | 7,178 | 7,175 | 7,175 | 68,501 | 70,842 | 73,264 | 73,264 |
| 1.00 | 7,003 | 7,016 | 7,011 | 7,011 | 66,887 | 71,657 | 74,171 | 74,171 |
| 1.25 | 6,719 | 6,756 | 6,753 | 6,741 | 64,166 | 71,468 | 74,082 | 76,794 |
| 1.50 | 6,274 | 6,370 | 6,346 | 6,319 | 59,917 | 72,562 | 78,312 | 81,358 |
| 1.75 | 5,624 | 5,846 | 5,823 | 5,752 | 53,681 | 72,111 | 78,345 | 85,100 |
| 2.00 | 4,656 | 5,138 | 5,063 | 4,938 | 44,512 | 72,458 | 83,278 | 91,307 |
| 2.25 | 3,342 | 4,273 | 4,189 | 3,930 | 31,905 | 70,197 | 82,490 | 96,604 |
| 2.50 | 1,729 | 3,252 | 3,104 | 2,726 | 16,520 | 64,138 | 83,315 | 100,425 |
| 2.75 | 478 | 2,125 | 2,001 | 1,374 | 4,554 | 56,952 | 73,615 | 100,786 |
| 3.00 | 72 | 1,106 | 885 | 303 | 685 | 40,646 | 64,867 | 88,655 |

[^0]monotone behavior with respect to $\sigma$ is not observed in the expected SSB at the optimal fishing mortalities.

From Table 3, we can directly confirm that the values at stationarity of the expected yield, as well as of the expected SSB, are much smaller when we use the (deterministic) fishing mortality $F_{\text {MSY }}$ than when their stochastic variants are considered. Actually, this difference is more evident for larger values of recruitment volatility. For instance, under a highly cautious behavior ( $F_{\text {MEHSY }}$ ), the expected SSB under high variability is by far larger than the deterministic SSB (for instance, for $\sigma=2.0$, it is $30.6 \%$ larger).

In Figure 6, we show the behavior of the estimators of the expected sustainable yield ESY $(F)$ as a function of $F$, for different values of $\sigma$. We can see that for each fixed $F$, the estimated expected sustainable yield values are decreasing with respect to $\sigma$, and extinction of biomass occurs for a larger range of fishing mortality than in the deterministic case. The same type of behavior can be observed for the estimator of the mean value of SSB, as Figure 7 shows.

Figure 8 shows the comparison of the probability density functions of the yield (at the corresponding $F_{\text {MESY }}$ ) for different values of $\sigma$. In this figure, the empirical probability density function is shown. As the figure shows, if $\sigma$ increases, the yield distribution becomes flatter and more spread out, and moves to the left, and so do its mean values. The size of the confidence intervals also increases with $\sigma$, showing the necessity to consider more conservative yield measures under high volatility.

In Figure 9, we compare the deterministic, expected sustainable, log-sustainable, and harmonic sustainable yields as functions of the fishing mortality $F$. For small values of $\sigma$, the differences are small, but for large values of $\sigma$, the differences are substantial, both in the optimal mean values and in the optimal fishing mortalities.

In Table 4 the behaviors of the yield and SSB are shown for different values of $\sigma$, when the fishing mortality of year 2017 is used as an stationary fishing effort (i.e., $F=F_{2017}:=0.292$ ). Figure 10 compares the behavior, for different values of $\sigma$, of MESY, MELSY and the yield obtained after applying the 2017 fishing mortality level $F_{2017}=0.292$. When this fishing mortality is maintained, it leads to small values of equilibrium yield compared to the maximum expected sustainable yield; this situation becomes critical the recruitment is impacted by high volatility (large values of $\sigma$ ), as shown in Figures 11-12. Indeed, Figure 11 emphasizes that any


FIGURE 4 Comparison of reference points MESY, MELSY, MEHSY with MSY, as functions of $\sigma$. MSY, maximum sustainable yield; MESY, maximum expected stationary yield; MELSY, maximum expected log-sustainable yield; MEHSY, maximum expected harmonic sustainable yield

FIGURE 5 Comparison of optimal mortalities $\mathrm{F}_{\text {MESY }}$, $\mathrm{F}_{\text {MELSY }}$, $\mathrm{F}_{\text {MEHSY }}$ with $\mathrm{F}_{\text {MSY }}$, as functions of $\sigma$. MSY, maximum sustainable yield; MESY, maximum expected stationary yield; MELSY, maximum expected log-sustainable yield; MEHSY, maximum expected harmonic sustainable yield

FIGURE 6 Expected sustainable yield as a function of fishing mortality, for different values of $\sigma$. ESY, expected stationary yield

FIGURE 7 Spawning stock biomass as a function of fishing mortality, for different values of $\sigma$. SSB, spawning stock biomass



Expected SSB as function of $F$


Stationary yield probability density

(a)
(b) ESY, ELSY, EHSY as functions of $F$ for $\sigma=2.0$


FIGURE 8 Probability density function of stationary yield, for different values of $\sigma$

FIGURE 9 Comparison between deterministic, expected sustainable, log-sustainable and harmonic
sustainable yields. On (a), $\sigma=0.5$; on (b), $\sigma=2$. ESY, expected stationary yield; EHSY, expected harmonic sustainable yield; ELSY, expected logsustainable yield

TABLE 4 Equilibrium values of yield and SSB (in tons) for fishing mortality $F_{2017}=0.292$ and different values of $\sigma$

| $\sigma$ | Mean yield | Mean SSB |
| :---: | :---: | :---: |
| 0.00 | 4,226 | 17,710 |
| 0.25 | 4,198 | 17,593 |
| 0.50 | 4,091 | 17,146 |
| 0.75 | 3,888 | 16,290 |
| 1.00 | 3,552 | 14,888 |
| 1.25 | 3,024 | 12,684 |
| 1.50 | 2,305 | 9,676 |
| 1.75 | 1,518 | 6,377 |
| 2.00 | 847 | 3,558 |
| 2.25 | 380 | 1,604 |
| 2.50 | 134 | 570 |
| 2.75 | 42 | 182 |
| 3.00 | 7 | 29 |

of the optimal constant fishing mortalities studied in this paper has a better performance in the equilibrium than the current fishing mortality for large levels of volatility. The same can be checked for the time evolution of SSB (Figure 12). In both cases, the application of the current fishing mortality leads to a slight but constant decrease of the yield and SSB levels, concluding that overexploitation can lead to extinction, whereas the application of an optimal fishing mortality can maintain acceptable population levels even in scenarios with high volatility.

FIGURE 10 Yield (in tons) as a function of $\sigma$ for fishing mortality $F_{2017}=0.292$, compared with the optimal yield measures. ESY, expected stationary yield; EHSY, expected harmonic sustainable yield; ELSY, expected log-sustainable yield



FIGURE 11 Mean yield for different optimal fishing mortalities, for $\sigma=2.0$. Baseline year 2017. ESY, expected stationary yield; EHSY, expected harmonic sustainable yield; ELSY, expected log-sustainable yield

## 4 | DISCUSSION AND CONCLUSIONS

MSY is an important biological reference point that can be used to assess the status of fisheries and develop regulations as well as harvest control rules. Its estimation can be highly affected by the age structure of a fish population, as well as by multiple types of uncertainty. So, biomassbased models and deterministic models may not be accurate enough to compute the biological reference points associated with the respective fishery. In this study, we propose to consider a mathematical model consisting in a discrete-time stochastic single-species age-structured model for fisheries composed of several fleets, that take into account environmental and biological variability. We extend the concept of MSY to this framework by means of three new stochastic indicators: maximum expected sustainable, log-sustainable, and harmonic sustainable yields (denoted by MESY, MELSY, and MEHSY, respectively). These new values can thus be used as reference points provided that some degree of volatility is witnessed in the catches. We illustrate the application of this approach via the study of the Patagonian toothfish fishery (Chilean and Argentinean stock), computing via numerical simulations the respective maximum (constant)


FIGURE 12 Mean SSB for different optimal fishing mortalities, for $\sigma=2.0$. Baseline year 2017. ESY, expected stationary yield; EHSY, expected harmonic sustainable yield; ELSY, expected log-sustainable yield; SSB, spawning stock biomass
fishing mortalities $F_{\text {MESY }}, F_{\text {MELSY }}, F_{\text {MEHSY }}$ for small and large volatility levels, and comparing them with the optimal deterministic fishing mortality $F_{\text {MSY }}$ (theoretically obtained). This analysis leads to the following conclusion:

- Yield is more variable, and its mean value decreases when the variability of fish recruitment increases. This fact needs to be considered when constructing confidence intervals for the three maximum expected sustainable yields introduced in this study.
- These three maximum expected yields and their respective optimal fishing mortalities decrease when the variability of fish recruitment increases. This establishes the need to be more cautious in presence of stochasticity in recruitment.
- For small volatility levels, the differences between MESY, MELSY, and MEHSY are at most negligible, whereas, for high levels of volatility, they become substantial. The same applies to their respective optimal fishing mortality. This has important implications. Indeed, for high levels of volatility, to use deterministic reference points, such as MSY, may lead to an overexploitation and even to a possible extinction of the fishery.

In conclusion, for sustainable and precautionary harvest to occur, proper accounting of stochasticity in recruitment dynamics is mandatory. Conversely, not accounting for stochasticity in recruitment dynamics can, in the worst case, lead to extinction.

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## AUTHOR CONTRIBUTIONS

All authors conceived of the presented idea. V. R. performed the simulations for the Patagonian toothfish fishery under the supervision of T. Q and H. R. All authors discussed the results. The manuscript was mainly written by V. R.

## CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

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## SUPPORTING INFORMATION

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

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## APPENDIX A: ADJUSTMENT OF EQUILIBRIUM EQUATIONS FOR A PLUS GROUP

Consider the equations for an age-structured dynamic with a plus group as in system (4), written in short form as in Equation (6). For the computation of the equilibrium we solve the equation

$$
\begin{equation*}
N^{\star}=A(F) N^{\star}+B \varphi\left(\mathrm{SSB}^{\star}\right), \tag{A1}
\end{equation*}
$$

which translates to the equations

$$
N_{1}^{\star}=\varphi\left(\mathrm{SSB}^{\star}\right), \quad N_{a+1}^{\star}=N_{a}^{\star} e^{-Z_{a}}, \quad a=1, \ldots, A-2, \quad N_{A}^{\star}=N_{A-1}^{\star} e^{-Z_{A-1}}+N_{A}^{\star} e^{-Z_{A}},
$$

with

$$
\begin{equation*}
\mathrm{SSB}^{\star}=\sum_{a=r}^{A} m_{a} W_{a} N_{a}^{\star} e^{-\tau Z_{a}} . \tag{A2}
\end{equation*}
$$

A recurrence formula for the abundances $N_{a+1}^{\star}$ can be derived, which depends on $N_{1}^{\star}$, for $a=2, \ldots, A-1$

$$
\begin{equation*}
N_{a}^{\star}=N_{a-1}^{\star} e^{-Z_{a-1}}=N_{a-2}^{\star} e^{-Z_{a-2}} e^{-Z_{a-1}}=\cdots=N_{1}^{\star} \prod_{x=1}^{a-1} e^{-Z_{x}} \tag{A3}
\end{equation*}
$$

For the plus group, we have

$$
\begin{equation*}
N_{A}^{\star}=\frac{e^{-Z_{A-1}}}{1-e^{-Z_{A}}} N_{A-1}^{\star}=\frac{\prod_{x=1}^{A-1} e^{-Z_{x}}}{1-e^{-Z_{A}}} N_{1}^{\star} \tag{A4}
\end{equation*}
$$

Define the cumulative survival $\mathscr{L}_{a}$ and the spawning potential ratio $\mathrm{SPR}^{\star}$ as

$$
\begin{align*}
\mathscr{L}_{a} & =\prod_{x=1}^{a-1} e^{-Z_{x}}=\exp \left\{-\sum_{x=1}^{a-1} Z_{x}\right\}, \quad \mathscr{L}_{1}=1  \tag{A5}\\
\mathrm{SPR}^{\star} & =\sum_{a=r}^{A-1} W_{a} m_{a} \mathscr{L}_{a} e^{-\tau Z_{a}}+\frac{W_{A} m_{A} \mathscr{L}_{A}}{1-e^{-Z_{A}}} e^{-\tau Z_{A}} . \tag{A6}
\end{align*}
$$

Replacing (A3) and (A4) in (A2), we obtain

$$
\begin{equation*}
\mathrm{SSB}^{\star}=N_{1}^{\star} \mathrm{SPR}^{\star} \tag{A7}
\end{equation*}
$$

where $N_{1}^{\star}$ solves the nonlinear equation

$$
\begin{equation*}
N_{1}^{\star}=\varphi\left(N_{1}^{\star} \mathrm{SPR}^{\star}\right) \tag{A8}
\end{equation*}
$$

Summarizing, the abundances at equilibrium solve

$$
N_{1}^{\star}=\varphi\left(N_{1}^{\star} \operatorname{SPR}^{\star}\right), \quad N_{a}^{\star}=N_{1}^{\star} \mathscr{L}_{a}, \quad a=2, \ldots, A-1, \quad N_{A}^{\star}=N_{1}^{\star} \frac{\mathscr{L}_{A}}{1-e^{-Z_{A}}} .
$$

With the previous values for $N^{*}$, the yield at equilibrium is function of the number of recruits $N_{1}^{\star}$

$$
\begin{equation*}
Y^{\star}=\sum_{a=r}^{A} W_{a} \frac{F_{a}}{Z_{a}}\left(1-e^{-Z_{a}}\right) N_{a}^{\star}=N_{1}^{\star}\left(\sum_{a=r}^{A-1} W_{a} \frac{F_{a}}{Z_{a}}\left(1-e^{-Z_{a}}\right) \mathscr{L}_{a}+W_{A} \frac{F_{A}}{Z_{A}} \mathscr{L}_{A}\right) . \tag{A9}
\end{equation*}
$$

Remark 3. The spawning potential ratio SPR* represents the quantity of SSB produced by one unit of recruits.

We can write SPR $^{\star}$ in a simpler form. Defining

$$
\tilde{M}_{a}=\sum_{x=1}^{a-1} M_{x}+\tau M_{a}, \quad \text { and } \quad \tilde{S}_{a}=\sum_{f=1}^{n} P_{f}\left(\sum_{x=1}^{a-1} s_{f, x}+\tau s_{f, a}\right)
$$

we have

$$
\begin{equation*}
\mathrm{SPR}^{\star}(F)=\sum_{a=r}^{A-1} W_{a} m_{a} e^{-\tilde{M}_{a}} e^{-\tilde{S}_{a} F}+W_{A} m_{A} \frac{e^{-\tilde{M}_{A}} e^{-\tilde{S}_{A} F}}{1-e^{-M_{A}} e^{-\sum_{f=1}^{n} P_{f} S_{f, A} F}} \tag{A10}
\end{equation*}
$$

Proposition 1. The function $F \mapsto \operatorname{SPR}^{\star}(F)$ is decreasing and converges to 0 as $F$ goes to infinity.

Proof. The derivatives of $Z_{a}$ and $\mathscr{L}_{a}$ with respect to $F$ are

$$
\begin{equation*}
\frac{\partial Z_{a}(F)}{\partial F}=\sum_{f=1}^{n} s_{f, a} P_{f}, \quad \frac{\partial \mathscr{L}_{a}(F)}{\partial F}=-\mathscr{L}_{a} \sum_{f=1}^{n} \sum_{x=1}^{a-1} s_{f, x} P_{f} \tag{A11}
\end{equation*}
$$

We compute the derivative of $\mathrm{SPR}^{\star}$ (given in (A10)) with respect to $F$, using (A11)

$$
\begin{aligned}
\frac{\partial \mathrm{SPR}^{\star}(F)}{\partial F}= & -\sum_{a=r}^{A-1} W_{a} m_{a} \mathscr{L}_{a} e^{-\tau Z_{a}}\left[\sum_{f=1}^{n} P_{f}\left(\tau S_{f, a}+\sum_{x=1}^{a-1} s_{f, x}\right)\right] \\
& -\frac{W_{A} m_{A}}{\left(1-e^{-Z_{A}}\right)^{2}} \mathscr{L}_{A} e^{-\tau Z_{A}}\left\{\sum_{f=1}^{n} P_{f}\left[\left(\tau s_{f, A}+\sum_{x=1}^{A-1} s_{f, x}\right)\left(1-e^{-Z_{A}}\right)+e^{-Z_{A}} S_{f, A}\right]\right\}
\end{aligned}
$$

which is negative for all values of $F$, thus proving that $F \mapsto \operatorname{SPR}^{\star}(F)$ is decreasing. For the second statement, we take limits in (A10) when $F \rightarrow \infty$ and we see that both terms of the right-hand side converge to zero.

The equilibrium spawning potential ratio $\mathrm{SPR}^{\star}$ is maximized in $F=0$ :

$$
\begin{equation*}
\operatorname{SPR}^{\star}(0)=\sum_{a=r}^{A-1} W_{a} m_{a} e^{-\tilde{M}_{a}}+W_{A} m_{A} \frac{e^{-\tilde{M}_{A}}}{1-e^{-M_{A}}} \tag{A12}
\end{equation*}
$$

This value is important for the existence of a positive equilibrium value of the equilibrium abundances. For the particular case of a Beverton-Holt spawner-recruit function of the form

$$
\begin{equation*}
\varphi(\mathrm{SSB})=\frac{\alpha \mathrm{SSB}}{\beta+\mathrm{SSB}} \tag{A13}
\end{equation*}
$$

the equilibrium $\mathrm{SSB}^{\star}$ and abundance $N_{1}^{\star}$ are

$$
\mathrm{SSB}^{\star}=\alpha \mathrm{SPR}^{\star}-\beta, \quad N_{1}^{\star}=\alpha-\frac{\beta}{\mathrm{SPR}^{\star}}
$$

Then, a condition for the existence of $F \geq 0$ such that the corresponding equilibrium point is positive is that

$$
\begin{equation*}
\operatorname{SPR}^{\star}(0)=\sum_{a=r}^{A-1} W_{a} m_{a} e^{-\tilde{M}_{a}}+W_{A} m_{A} \frac{e^{-\tilde{M}_{A}}}{1-e^{-M_{A}}}>\frac{\beta}{\alpha} \tag{A14}
\end{equation*}
$$

This condition is completely related to the capacity of the fish population to survive in the environment. We conclude the following proposition:

Proposition 2. Suppose that the spawner-recruit function is of the form (A13) and that condition (A14) is satisfied. Then, there exists a value $F_{\mathrm{ext}}>0$ that solves the equation

$$
\begin{equation*}
\operatorname{SPR}^{\star}\left(F_{\mathrm{ext}}\right)=\frac{\beta}{\alpha}, \tag{A15}
\end{equation*}
$$

and then $F_{\mathrm{MSY}}^{\star}$ belongs to the interval $\left[0, F_{\mathrm{ext}}\right]$.
Proof. Consider the function $g(F):=\operatorname{SPR}^{\star}(F)-\frac{\beta}{\alpha}$. This is a continuous and differentiable function, since $F \mapsto \operatorname{SPR}^{\star}(F)$ is continuous and differentiable. Thanks to (A14) we have $g(0)>0$; from Proposition 1 we see that $F \mapsto g(F)$ is decreasing and $\lim _{F \rightarrow \infty} g(F)=-\frac{\beta}{\alpha}<0$. By the intermediate value theorem there exists then a point $F_{\text {ext }}$ such that $g\left(F_{\mathrm{ext}}\right)=0$, or equivalently, (A15) is satisfied. The fact that $F_{\mathrm{MSY}}^{\star} \in\left[0, F_{\mathrm{ext}}\right]$ is concluded because for any $F>F_{\text {ext }}$ the value of equilibrium of $\operatorname{SSB}^{\star}(F)$ and $N_{1}^{\star}(F)$ are negative, leading to negative equilibrium yield from the formula (A9).


[^0]:    Abbreviations: MSY, maximum sustainable yield; MESY, maximum expected stationary yield; MELSY, maximum expected log-sustainable yield; MEHSY, maximum expected harmonic sustainable yield.

