ORIGINAL ARTICLE

FISH and FISHERIES **WILEY**

Identifying spawner biomass per-recruit reference points from life-history parameters

Shijie Zhou[1] (iD) | **André E. Punt[2,3]** | **Yeming Lei[1]** | **Roy Aijun Deng[1]** | **Simon D. Hoyle[4]**

[1]CSIRO Oceans and Atmosphere, St Lucia, Brisbane, Queensland, Australia

[2]CSIRO Oceans and Atmosphere, Hobart, Tasmania, Australia

[3]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA

[4]NIWA, Port Nelson, New Zealand

Correspondence
Shijie Zhou, CSIRO Oceans and Atmosphere, 306 Carmody Road, St Lucia, Brisbane QLD 4067, Australia.
Email: Shijie.zhou@csiro.au

Funding information
Commonwealth Scientific and Industrial Research Organisation

Abstract

Analysis of spawning biomass per-recruit has been widely adopted in fisheries management. Fishing mortality expressed as spawning potential ratio (SPR) often requires a reference point as an appropriate proxy for the fishing mortality that supports a maximum sustainable yield—F_{MSY}. To date, a single generic level between $F_{30\%}$ and $F_{40\%}$ is routinely used. Using records from stock assessments in the RAM Legacy Database (RAMLD), we confirm that SPR at MSY (SPR_{MSY}) is a declining function of stock productivity quantified by F_{MSY}. We then use general linear models (GLM) and Bayesian errors-in-variables models (BEIVM) to show that SPR_{MSY} can be predicted from life-history parameters (LHPs, including maximum lifespan, age- and length-at-maturation, growth parameters, natural mortality, and taxonomic *Class*) as well as gear selectivity. The calculated SPR_{MSY} ranges from about 13% to 95% with a mean of 47%. About 64% of the stocks in the RAMLD require $SPR_{MSY} > 40\%$. Modelling SPR_{MSY} reveals that LHPs plus *Class* explain 61% of the deviance in SPR_{MSY}. Faster-growing, low-survival, and short-lived species generally require a high SPR. With equal LHPs, elasmobranchs require about 20% higher SPR_{MSY} than teleosts. When F_{MSY} is estimated from fisheries that harvest older fish, increasing the vulnerable age by one year leads to about an 8% increase in SPR_{MSY}. The BEIVM yields smaller variance and bias than the GLM. The models developed in this study could be used to predict SPR_{MSY} reference points for new stocks using the same LHPs for calculating $F_{x\%}$, but without knowledge of the stock-recruitment parameters.

KEYWORDS

Bayesian measurement error, FishBase, productivity, RAM Legacy database, resilience, spawning potential ratio, steepness

1 | INTRODUCTION

Extensive research has been undertaken to develop biological reference points (BRPs) for fisheries management. Traditionally, management aims to obtain maximum sustainable yield (MSY) from a stock, so MSY-relative quantities have been the most sought-after BRPs and are considered "best practice" (Sainsbury, 2008). MSY-based BRPs can be derived from surplus production models, spawner–recruitment relationships (SRR) for semelparous species,

delay-difference models or age-structured models fitted to monitoring data (Quinn & Deriso, 1999). However, many fish populations do not have sufficient data for reliable population dynamics modelling. This has led to widespread use of proxy reference points for data-poor species.

One group of proxy reference points is based on per-recruit analysis. This approach follows a single cohort through its entire life accounting for growth, maturation, natural and fishing mortality. As the approach focuses on a single cohort, it does not consider a

stock–recruit relationship or population dynamics from one generation to the next.

There are two major types of per-recruit analysis: yield-per-recruit (YPR) and spawning stock biomass per recruit (SSBPR). The most common BRPs from YPR analysis are F_{max} and $F_{0.1}$. F_{max} is the fishing mortality rate at which yield per recruit (Y/R) is maximized. $F_{0.1}$ is the fishing mortality rate at which the slope of the YPR-F curve is 10% of that at the origin. Since YPR analysis ignores potential recruitment reduction due to depletion of the spawning population, the use of F_{max} as a proxy for F_{MSY} could lead to overfishing and overfished stocks. Quinn and Deriso (1999) outlined an extreme scenario in which infinite fishing mortality applied at the critical age maximized YPR, but the maturation age was older than this critical age leading to zero spawning biomass.

The second type of per-recruit analysis, SSBPR, has been used more frequently in recent years because it takes spawning stock size into consideration to some extent. BRPs based on this type of per-recruit analysis are expressed as the ratio between fished and unfished SSBPR (spawning potential ratio; SPR). For example, $F_{x\%SPR}$ or simply $F_{x\%}$ denotes the fishing mortality rate that reduces spawning stock biomass per recruit to x% of the unfished level. SPR reference points are often used for data-poor fisheries (Clarke & Hoyle, 2014; Hordyk, Ono, Prince, & Walters, 2016; Le Quesne & Jennings, 2012; Pope, 2000; Prince, Victor, Kloulchad, & Hordyk, 2015).

Calculation of an SPR-based F reference point, given MSY-based management, requires a relationship between $F_{x\%}$ and F_{MSY}, and the SPR that supports MSY and corresponds to F_{MSY} is SPR_{MSY}. There has been extensive research on the values of x% to use as proxies for F_{MSY}, and various values have been suggested. For example, in a review of biological reference points for precautionary approaches, Gabriel and Mace (1999) recommend that fishing mortality rates in the range from $F_{30\%}$ to $F_{40\%}$ be used as general default proxies for F_{MSY}, in cases where the latter cannot be reliably estimated. In the absence of data and analyses that can be used to justify alternative approaches, they recommended that $F_{30\%}$ be used for species believed to have relatively high resilience, $F_{40\%}$ for species believed to have low to moderate resilience, and $F_{35\%}$ for species with "average" resilience. Similarly, Goodyear (1993) and Clark (1991, 2002) showed that, to maintain the B/B_0 ratio at 20% (or 40%), SPR must be between 20% for more productive species and 70% for less productive species (or between 40% and 80%) depending on their productivities. Based on these recommendations, $F_{45\%}$ is adopted for low productivity species in New Zealand (Ministry of Fisheries, 2011). The suggested values are believed to prevent recruitment overfishing (Gabriel & Mace, 1999). More than one level of x% has been recommended as the basis for management reference points for species with differing levels of productivity in some fisheries (e.g. Clarke & Hoyle, 2014; NFSC, 2008; Punt, 2000). However, in many cases a single constant reference point such as $F_{40\%}$ is advocated for all species regardless their productivity (e.g. Babcock, Tewfik, & Burns-Perez, 2018; Walker, García-Carreras, Le Quesne, Maxwell, & Jennings, 2019).

These diverse recommendations for an appropriate level of SPR indicate that it is well recognized that SPR_{MSY} is not a constant but depends on a species' resilience and productivity. However, there has been no empirical study to show a direct relationship between SPR_{MSY} and F_{MSY} for a wide range of species.

The terms "productivity" and "resilience" quantify different properties of a population. Productivity is generally defined as the total cumulated new biomass produced per biomass unit of a stock (or ecological group) during a given period (Zhou et al., 2019), and resilience is the ability of a stock to return to an equilibrium state after external disturbance such as fishing (adopted from McCann, 2000). Productivity and resilience are basically determined by the same life-history traits. Hence, productivity can also be viewed as resilience against fishing pressure, and species with high productivity will be able to withstand high fishing pressure (Froese, 2005). Species with a higher intrinsic rate of population growth (i.e. the parameter r in a surplus production model) are deemed to have higher productivity and to be more resilient to fishing than species with a lower r (Adams, 1980; Froese, 2005).

In modern fisheries stock assessment, the productivity and resilience of exploited stocks are frequently quantified by the parameter "steepness" (h; Brodziak, Mangel, & Sun, 2015; Conn, Williams, & Shertzer, 2010). h measures the expected reduction in recruitment when spawning biomass declines to 20% of its unfished level (Mace & Doonan, 1988). Using Monte Carlo simulations, Punt, Dorn, and Haltuch (2008) demonstrate that SPR_{MSY} is a function of h, ranging from about 20% for high h to 100% for low h. Brooks, Powers, and Corte (2010) explored the analytical relationship between SPR and the SRR. They investigated the relationship between the slope of an SRR and the maximum excess

recruitment in number of individuals (MER). MER is akin to MSY but is expressed in maximum numbers of fish rather than maximum weight as for MSY. For the Beverton–Holt SRR, the spawning potential ratio at MER is $SPR_{MER} = 1/\sqrt{\hat{\alpha}}$, where $\hat{\alpha}$ is the maximum lifetime reproductive rate at low density (the compensation ratio CR), that is the ratio between the slope at the origin of the SRR and a line drawn between the origin and the unfished point on the SRR (Goodwin, Grant, Perry, Dulvy, & Reynolds, 2006; Goodyear, 1993). F_{MER} (corresponding to SPR_{MER}) is generally greater than F_{MSY}, but both are comparable when steepness and natural mortality are relatively low. CR or $\hat{\alpha}$ is directly linked to steepness. For a Beverton–Holt SRR, $h = \hat{\alpha}/(4 + \hat{\alpha})$ (Brooks et al., 2010; Myers, Bowen, & Barrowman, 1999) leading to a relationship between SPR_{MER} and $\hat{\alpha}$ and h (also see Mangel, Brodziak, & DiNardo, 2010) (Figure 1). Maintaining stock biomass close to B_{MSY} cannot be achieved by the same value of x% for all species. Setting $F_{40\%}$ as the F_{MSY} proxy is equivalent to assuming the stock has a maximum lifetime reproductive rate about 6 (roughly 1 spawner produces 6 recruits in her lifetime when density dependence is negligible), or assuming the stock has a steepness about 0.61 (Figure 1). The relationship between SPR_{MSY} and h or between SPR_{MSY} and $\hat{\alpha}$ and the approximate constants (i.e. $\hat{\alpha} \approx 6$ and $h \approx 0.61$ at $F_{40\%}$) are supported by empirical and simulation studies (Forrest, McAllister, Dorn, Martell, & Stanley, 2010; Punt et al., 2008).

The general guidance to choose default proxies based on species' resilience or productivity (Clark, 2002; Gabriel & Mace, 1999), and the theoretical relationship between SPR_{MER} (or SPR_{MSY}) and h (Brooks et al., 2010; Mangel et al., 2010; Punt et al., 2008) lead to a closely related question: can SPR_{MSY} be determined from life-history traits? In this paper, we refer to life-history parameters (LHPs) as those traits that can be observed or measured from individual fish or a population, including growth parameters (e.g., k, L_{inf}, and t_0 of the Bertalanffy growth function), length- or age-at-maturity (L_m or A_m), maximum age (A_{max}), the parameters of the length–weight relationship (α and β), and natural mortality (M). LHPs differ from stock-recruitment parameters such as h, r, and spawning potential ratio at MSY SPR_{MSY}, which cannot be measured directly (even in principle). Deriving SPR requires life-history information, including k, L_{inf}, L_m or A_m, A_{max}, α, β, and M, as well as fishing mortality F and gear selectivity s. Other information may also be used, for instance, the proportions of fishing and natural mortality that occur before spawning. The required information implies that life-history traits determine SPR_{MSY} (Brooks et al., 2010; Mangel et al., 2010; Myers, Barrowman, Hilborn, & Kehler, 2002; Myers et al., 1999).

It is commonly believed and supported by some evidence that species with a higher r typically have smaller body size, faster growth rate, higher natural mortality, shorter lifespan and earlier maturation age (so-called r-selected species)(Adams, 1980; Froese, 2005; Jennings, Reynolds, & Mills, 1998; Thorson, 2019). Population growth rate r can be linked positively to h as $r = 4Mh/(1-hr)$ (Mangel et al., 2010), but the relationship between h and various life-history traits is more ambiguous than the relationship between r and LHPs. A common belief is that r-selected species

should have a higher h than K-selected species, hence a lower SPR_{MSY}. This perception has been widely adopted in simulation studies in which short-lived species are assigned higher h than long-lived ones (e.g. Wetzel & Punt, 2011; Wetzel & Punt, 2015; Wiedenmann, Wilberg, & Miller, 2013). However, the contrary relationship, that more r-selected species should have lower h than more K-selected ones, is supported by empirical data (Forrest et al., 2010; Myers et al., 2002). As such, some studies have assigned a lower h to short-lived species (Coggins, Catalano, Allen, Pine, & Walters, 2007; Thorson, Monnahan, & Cope, 2015). The relationship between h and LHPs is highly pertinent to this study because SPR_{MSY} is a declining function of h (Brooks et al., 2010; Mangel et al., 2013; Punt et al., 2008).

This paper has two major objectives: (a) to verify that SPR_{MSY} varies among taxonomic groups and that an empirical relationship between SPR_{MSY} and productivity quantified by F_{MSY} can be established; and (b) to develop statistical models using the life-history parameters and empirical data to provide SPR_{MSY} reference points.

2 | MATERIALS AND METHODS

### 2.1 | Relationship between SPR_{MSY} and F_{MSY}

The RAM Legacy Database (RAMLD) contains estimates of F_{MSY} for many stocks. We used LHPs for these stocks to calculate SPR_{MSY}. We obtained LHPs from FishBase for those stocks for which the LHPs required to calculate SPR were not available from the RAMLD. Since F_{MSY} in RAMLD is stock-specific, we averaged values for LHPs that differed between males and females. In total, we identified 185 stocks with estimated F_{MSY} and LHPs to allow calculation of SPR_{MSY}. We followed Gabriel, Sissenwine, and Overholtz (1989) and Goodyear (1993) to derive SPR, as follows. Let the number of fish at age a be N_a, the number of individuals at age $a + 1$ is:

$$N_{a+1} = N_a \exp\left[-\left(M_a + F_a s_a\right)\right] \tag{1}$$

where M is natural mortality, F is fishing mortality, and s is selectivity. Since SPR is a relative quantity between fished and unfished biomass per recruit, number of fish at age 0, N_0, is irrelevant. Because the RAMLD does not provide age-specific M_a, we assumed that M to be constant for all ages. Also, the RAMLD does not have selectivity information so we assumed that it is knife-edge from the first vulnerable age min $[A_v]$. SSBPR changes with selectivity. We focused on the assumption that in most fisheries fishing starts at maturation age A_m, that is $A_v \geq A_m$ (to explore the effect of selectivity, we assumed alternative A_vs; see below). The SSBPR is given by:

$$SSBPR_F = \sum_{a=1}^{A_{max}} N_a W_a m_a \tag{2}$$

FIGURE 1 Relationship between spawning potential ratio at MSY (SPR$_{MSY}$) and productivity measured as the maximum lifetime reproductive rate $\hat{\alpha}$ and steepness h. The circles are estimated values for 16 US west coast groundfish from Forrest et al. (2010). 40% SPR corresponds to $\hat{\alpha} \approx 6$ and $h \approx 0.61$
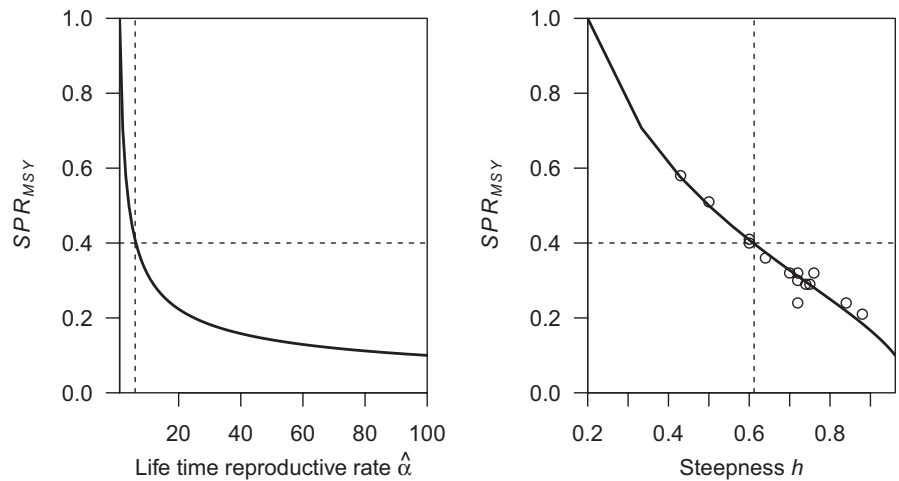
where age-specific body weight is derived from the von Bertalanffy growth parameters and the length–weight relationship parameters α and β:

$$W_a = \alpha \left[L_{inf} \left(1 - e^{-k(a-a_0)} \right) \right]^{\beta} \qquad (3)$$

SPR$_{MSY}$ is then:

$$SPR_{MSY} = \frac{SSBPR_{F=F_{MSY}}}{SSBPR_{F=0}} \qquad (4)$$

where F_{MSY} is taken from the RAMLD.

Multiple methods have been used to estimate F_{MSY} values in the RAMLD, including biomass dynamics models, integrated (or statistical catch-at-age) models and virtual population analysis (Appendix S1). To avoid uncertainty in converting to F_{MSY}, other F-based reference points, such as $F_{MSYproxy}$, $F_{x\%}$, F_{max}, F_{pa} (precautionary approach fishing mortality), F_{target} and F_{lim}, in the RAMDL were not used in our study. Among the 185 stocks, about one third used integrated analysis. We opted to use as many estimates as possible to increase sample size because it was difficult to determine which estimates in the RAMLD were accurate.

Life-history parameters, as well as F_{MSY} in the RAMLD, are not accurate. We conducted a sensitivity analysis to examine how uncertainty in LHPs and F_{MSY} may affect the calculation of SPR$_{MSY}$. Using Monte Carlo simulations, for example assuming LHPs (such as natural mortality M) are log-normal with mean and variance from previous studies (e.g. Hamel, 2015; Munyandorero, 2020; Thorson et al., 2017; Zhou, Yin, Thorson, Smith, & Fuller, 2012) could result in sampled SPR$_{MSY}$ values centring around the mean SPR$_{MSY,i}$ and an increasing variance as the assumed variance in the LHPs increases. However, it is more important to examine the effect of bias in LHPs and F_{MSY} on the calculation of SPR$_{MSY}$. In our baseline analysis, we used fixed values of LHPs and F_{MSY} for each stock. We tested sensitivity to this treatment by applying Equations 1–4 for two scenarios: (a) LHPs and F_{MSY} reduced to 50% of their baseline values for all stocks; and (b) LHPs and F_{MSY} increased by 50% (i.e. 1.5 times) of their baseline values for all stocks.

We used a root-finding algorithm to find the value of F at which SPR equals a given constant (such as 40%). The calculated SPR$_{MSY}$ and $F_{40\%}$ were then compared with F_{MSY} for the 185 RAMLD stocks to reveal the correlation and potential utility of using them as F_{MSY} proxies.

2.2 | Identifying SPR$_{MSY}$ reference points as functions of LHPs using general linear models (GLM)

SPR$_{MSY}$ is a function of lifetime reproduction rate or steepness, but $\hat{\alpha}$ and h are very difficult to estimate (He, Mangel, & Maccall, 2006; Lee, Maunder, Piner, & Methot, 2012) so it is not uncommon to fix the value of h in the SRR (Mangel et al., 2013). We attempted to estimate appropriate SPR reference points from LHPs that are easier to obtain. We examined various potential relationships (e.g. linear, inverse, log-linear) between SPR$_{MSY}$ and the LHPs (A_{max}, A_m, L_m, k, L_{inf} and M) using scatter plots and general linear models (GLMs). We included taxonomic group *Class* as a potential predictor because it is known for all species. The best model was selected using the Akaike information criterion (AIC) and the significance of each LHP (p-value) in the model.

Spawning potential ratio is a function of several LHPs. However, the values of all LHPs may not be available for data-poor stocks. Moreover, LHPs are often correlated (e.g. $\log(A_{max}) \cong 0.5469 + 0.957\log(A_m)$) (Froese & Binohlan, 2000), and natural mortality is proportional to inverse lifespan $M \cong 4.374/A_{max}$ (Hamel, 2015; also see Thorson et al., 2017) so it may be adequate to use a single LHP to predict SPR reference points, which would be useful for providing advice in extremely data-poor situations (noting that several LHPs are required to calculate SPR). Consequently, we estimated relationships between SPR$_{MSY}$ and each of the LHPs (k, L_{inf}, A_{max}, A_m, L_m, and M), that is

$$SPR_{MSY} \sim f(LHP, Class), \qquad (5)$$

where LHP is one of the six life-history parameters, and *Class* is a categorical variable with two values: 0 for teleosts and 1 for elasmobranchs.

To enhance the accuracy of the estimated SPR_{MSY}, we focused on multi-variable models with the same LHPs for calculating SPR. Similar to model (5), we used:

$$SPR_{MSY} \sim f\left(LHPs, Class\right) \tag{6}$$

where "LHPs" indicate more than one life-history parameter and possibly more than one data form for the same parameter (e.g. raw and inverse). We used stepwise regression and again selected the best model in terms of data forms and the number of variables based on AIC.

Equation 1 indicates that selectivity is one of the variables determining SPR. When analysing fishery data where gear type is unknown, it is a common practice to assume knife-edge selectivity (Quinn & Deriso, 1999), although selectivity curves may have varying shapes, including increasing, asymptotic, dome-shaped, and having a saddle, depending on fish species and gear used (Sampson & Scott, 2012). We explored additional three alternative vulnerable ages: $A_v \geq A_m - 1$, $A_v \geq A_m + 1$, and $A_v \geq A_m + 2$, to provide a flexible model for fisheries where the vulnerability ages (A_V) differ from our default assumption of $A_v \geq A_m$. This allowed selectivity s expressed as relative vulnerable age to be included in the model similar to model (6)

$$SPR_{MSY} \sim f\left(LHPs, Class, s\right) \tag{7}$$

Vulnerable ages A_v are relative to the age at first maturation and s has four levels: $s = -1$ for $A_v \geq A_m - 1$, 0 for $A_v \geq A_m$, $s = 1$ for $A_v \geq A_m + 1$, and $s = 2$ for $A_v \geq A_m + 2$.

We used various packages in R for data processing (e.g. extracting from RAMLD and FishBase and merging them) and modelling (R Core Team, 2017).

2.3 | Estimating model parameters using Bayesian errors-in-variables models (BEIVM)

All LHPs and F_{MSY} are subject to measurement error. The presence of measurement errors can mask a true underlying relationship between SPR_{MSY} and LHPs and cause the regression coefficients to be biased (Quinn & Deriso, 1999). To explore the possible effect of measurement errors, we applied Bayesian errors-in-variables models (BEIVM) to the same input data as in models 6 and 7.

$$SPR_{MSY,i} = \theta y_i + \varepsilon_i$$

$$y_i = \exp\left[\log\left(x_i\right) + \varepsilon_{x,i}\right] \tag{8}$$

where θ is a vector of parameters for the predictors (i.e. LHPs, taxonomy $Class$ and selectivity s), y is a vector of true but unobserved predictors, x is a vector of observed predictors (i.e. the input data), ε_x is measurement error for predictor x (except $Class$ and s), and ϵ is the process (model) error. Measurement and process errors were assumed to be normally distributed with a mean zero and precision τ_{ε_x} (=$1/\sigma^2_{\varepsilon_x}$

) and τ_ε (=$1/\sigma^2_\varepsilon$), respectively. Subscript i represents each stock. In this BEIVM, measurement error was assumed to be multiplicative to avoid generating negative values and to be consistent with other studies (Thorson, Cope, & Patrick, 2014; Zhou et al., 2012), whereas the process error was assumed to be additive. The following prior distributions were assumed for the model parameters:

$$\theta \sim N\left(\mu_\theta = 0, \tau_\theta = 0.001\right)$$

$$\tau_{\varepsilon_x} \sim Gamma\left(0.001, 0.001\right)$$

$$\tau_\varepsilon \sim Gamma\left(0.001, 0.001\right)$$

The BEIVM was implemented in WinBUGS (Lunn, Thomas, Best, & Spiegelhalter, 2000). We ran three MCMC chains, with the first 100,000 iterations discarded, and an additional 100,000 iterations used for parameter inference. Chain convergence was verified through visual inspection of the MCMC trace as well as the use of the Gelman–Rubin diagnostic.

3 | RESULTS

3.1 | Correlation between SPR_{MSY} and F_{MSY}

Many of the 185 stocks in the RAMLD (11 Elasmobranchii and 174 Actinopterygii) that have values of F_{MSY} were missing one or more LHPs (and we obtained these missing estimates from FishBase). The calculated SPR_{MSY} values ranged from 12.8% to 94.8%, with an overall mean of 47.5% ($SD = 0.184$). Of these stocks, 63.8% (118 stocks) had a $SPR_{MSY} > 40\%$, while 36.2% had $SPR_{MSY} < 40\%$. This means that SPR_{MSY} was not constant and not equal to the commonly adopted 30% and 40%. For those stocks in the RAMLD, using $F_{40\%}$ as a reference point was equivalent to directly assuming $F = 0.28$ year^{-1} as the F_{MSY} proxy because $F = 0.28$ year^{-1} and $F = F_{40\%}$ resulted in the same number of stocks below (67 stocks) and above (118 stocks) the reference points as $F_{40\%}$. The SPR_{MSY} values had a wide distribution, and their range and density were comparable with empirical F_{MSY} from RAMLD, even though theoretically F_{MSY} can be larger than 1 (Figure 2). Ideally, if SPR_{MSY} in the range 30%–40% was a good proxy for F_{MSY}, most of the stocks should have their SPR_{MSY} centred between 30% and 40% (the grey area in Figure 2) rather than being spread out from 12.8% to 90.8% (less concentrated than F_{MSY}). Maintaining spawning stock biomass per recruit at 40% of the unfished level would ensure that 36.2% of stocks equilibrated above the biomass corresponding to MSY (B_{MSY}) (but with forgone yields) while many other stocks would be overfished.

The relationship between F_{MSY} and $F_{40\%}$ appears to be complicated, and there is a lack of clear linear correlation between the two variables (Figure 3, left panel). F_{MSY} is relatively constant over a wide range of values for $F_{40\%}$ (about 0.3). In fact, using $F_{40\%}$ as an F_{MSY} proxy appears less reliable than simply using natural mortality M (Figure 3, right panel). The linear regression between $F_{40\%}$ and F_{MSY} was weaker

(R^2 = .148) than between M and F_{MSY} (R^2 = .166). Regressions through the origin resulted in F_{MSY} = 0.49 $F_{40\%}$, with mean squared error (MSE) of 0.056, and F_{MSY} = 0.73 M, with MSE of 0.042.

Figure 4 shows that SPR_{MSY} is a declining function of F_{MSY}. Fitting an exponential function to the data results in $SPR_{MSY} = 0.625e^{-1.104F_{MSY}}$. This means that every 0.1 increase in F_{MSY} decreases SPR_{MSY} by about 10%. If we focus only on F_{MSY} values from the integrated age-structured models, the declining pattern is still clear, though it appears less steep than using all datapoints ($SPR_{MSY} = 0.54e^{-0.655F_{MSY}}$, Figure S1).

Summarizing SPR_{MSY} by *Class* and *Order* confirmed the difference between taxonomic groups (Table 1). SPR_{MSY} for the Elasmobranchii was on average 0.26 higher than for Actinopterygii while the pattern for F_{MSY} was approximately opposite (i.e. teleosts can sustain ca. 0.18 year^{-1} higher F_{MSY} than elasmobranchs). The higher SPR_{MSY} required by the Elasmobranchii than by the Actinopterygii is consistent with other studies (e.g. SPR_{MSY} = 0.67 for Elasmobranchii and SPR_{MSY} = 0.30 for Actinopterygii after converting h to SPR_{MSY}; Table 4 in Thorson, 2019). Among all orders, Carcharhiniformes had the highest SPR_{MSY} (mean of 0.788) and Squaliformes the lowest (mean 0.228), but the sample size may be too small for reliable inference for new species (i.e. only one stock for Squaliformes). Together, these results indicate that applying $F_{40\%}$ as a proxy for F_{MSY} could lead to under-exploitation for some stocks but overfishing for many less productive stocks.

Sensitivity of the calculated SPR_{MSY} to potential bias in input variables varied between LHPs (Table 2). SPR_{MSY} was most sensitive to changes in M. For example, reducing M by 50% led to an average reduction of SPR_{MSY} by −40% (ranging from −59% to −6% for the 185 stocks). However, increasing M by 50% only resulted in an average of 28% increase in SPR_{MSY}. Bias in k and A_m had moderate effects on SPR_{MSY}. A 50% reduction in k and A_m led to an average −18% and −16% decline in SPR_{MSY}, respectively, while a 50% increase in k and A_m led to an average 11% and 14% increase in SPR_{MSY}, respectively. SPR_{MSY} was not sensitive to changes in other LHPs, such as A_{max} and L_{inf}. On the other hand, incorrect F_{MSY}, particularly when underestimated, could result in biased SPR_{MSY} estimation. Interestingly, the relative errors in SPR_{MSY} caused by errors in the LHPs and F_{MSY} were smaller than the errors in the input parameter.

3.2 | Modelling SPR_{MSY} as a function of LHPs and identifying their relationships

There was a potential correlation between SPR_{MSY} and the LHPs (Figure 5). Also, the relationships between SPR_{MSY} and A_{max}, A_m, L_m and L_{inf} appeared to be nonlinear whereas the relationships between SPR_{MSY} and k and M were more likely linear. The single-LHP model (Equation 5) confirmed that models using the inverses of A_{max}, A_m, L_m and L_{inf}, and raw k and M had the lowest AIC among the three data forms (Table 3). For these best models, the intercept, LHP and *Class* were all highly significant ($p < .0001$) except invA_m ($p = .005$) (Table 4). The positive coefficients of invA_{max}, invA_m, invL_m, k, invL_{inf} and M indicated that species with short-lived, early-maturing, fast-growing, small body-sized, and high natural mortality traits required a higher proportion of SSBPR than species with opposite traits. The coefficient for *Class* varied between 0.28 and 0.32, suggesting that with the same life-history parameter value elasmobranchs required a SPR_{MSY} about 0.29 higher than equivalent teleosts, which is close to the difference in mean SPR_{MSY} between the Actinopterygii and Elasmobranchii (Table 1).

Based on the stepwise regression, the best multi-variable model had the following structure:

$$SPR_{MSY} = \beta_0 + \beta_{A_m}A_m + \beta_{L_m}L_m + \beta_M M + \beta_{invA_m}\frac{1}{A_m} +$$
$$\beta_{invk}\frac{1}{k} + \beta_{invL_{inf}}\frac{1}{L_{inf}} + \beta_{invM}\frac{1}{M} + \beta_{Class}\text{Class} \qquad (9)$$

All coefficients βs were significant at or below $p < .01$ [except variables invA_m ($p = .06$) and inv$k$ ($p = .05$)], and the model fit had 61% deviance explained (Table 5, Figure 6). The positive coefficients of M and invL_{inf} and negative inv$k$ and inv$M$ were consistent with the results of single-LHP models in Tables 3 and 4, which indicated that r-selected species required a higher SPR_{MSY} than K-selected species. However, the positive coefficients of A_m and L_m and the negative coefficient of invA_m indicated that later-maturing species required a higher SPR_{MSY} than earlier maturing species. This seemingly inconsistency could be caused by high correlation among the LHPs. The coefficient for taxonomic *Class* also suggested that when the values of LHPs were the same, elasmobranchs required about 15% higher SPR_{MSY} than teleosts.

Since natural mortality is very difficult to estimate directly, it is often derived from other life-history parameters. We also modelled the relationship between SPR_{MSY} and the LHPs except M, recognizing that M is needed to calculate SPR. The best model (again based
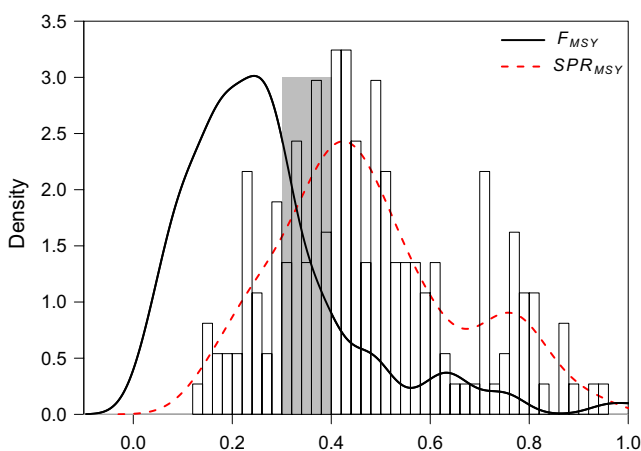

FIGURE 2 Histogram of SPR overlaid with distributions of SPR_{MSY} and F_{MSY} from the RAMDL. The grey area is 30% to 40% SPR, a commonly recommended F_{MSY} proxy. Note that theoretically F_{MSY} can be greater than 1, which is very rare for stocks in the RAMDL. The wide spread of SPR_{MSY} indicates that the range between $F_{30\%}$ and $F_{40\%}$ is a poor F_{MSY} proxy for most stocks [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 Potential correlations between $F_{40\%}$ and F_{MSY} and between M and F_{MSY}. The dark filled circles are Actinopterygii, and the red circles are Elasmobranchii. Box plots based on the same scatter plot data points are overlaid to show a clearer pattern. The lines are regressions through the origin ($F_{MSY} = 0.49$ $F_{40\%}$, $MSE = 0.056$; $F_{MSY} = 0.73$ M, $MSE = 0.042$) [Colour figure can be viewed at wileyonlinelibrary.com]
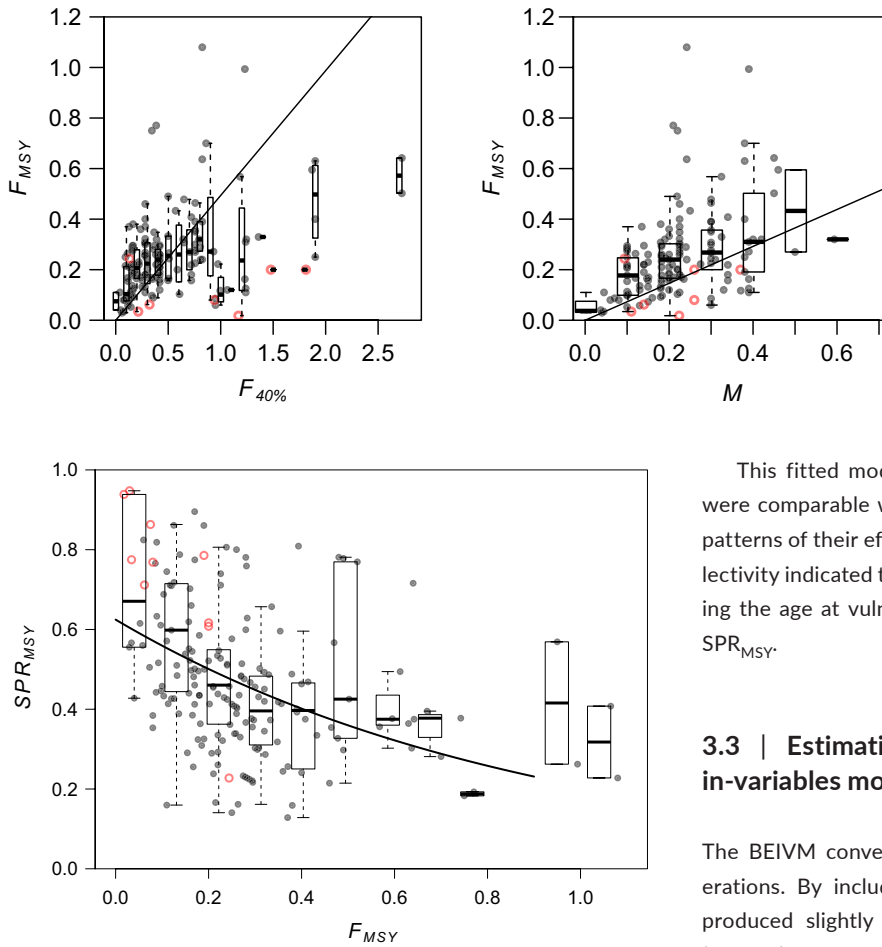

FIGURE 4 Relationship between SPR_{MSY} and F_{MSY} from the RAMLD. Box plots based on the same scatter plot data points are overlaid to show a clearer pattern. The black curve is $SPR_{MSY} = 0.625e^{-1.104F_{MSY}}$. Elasmobranchii is in red and Actinopterygii in black [Colour figure can be viewed at wileyonlinelibrary.com]

on AIC) involved A_m, L_{inf}, $invA_{max}$, $invL_{inf}$ and $invk$, plus *Class* (Table S2). These covariates were all significant at or below $p < .001$ except variable $invL_{inf}$ ($p = .012$) but the fit was poorer (only 43.2% deviance explained) than for the model that included M. This model also implied that species with short-lived and fast-growing but later-maturing traits required a higher SPR_{MSY}. The coefficient for taxonomic *Class* again suggested that on average elasmobranchs required higher SPR_{MSY} (about 23%) than teleosts.

Including selectivity as an additional variable resulted in similar best model as Equation 9, that is A_m, L_m, M, $invA_m$, $invL_m$, $invk$, $invL_{inf}$, $invM$, *Class* and selectivity s all were significant at or below $p < .003$ [except variables $invA_m$ ($p = .1$) and $invL_m$ ($p = .02$), Table 6)]. So the best model is:

$$SPR_{MSY} = \beta_0 + \beta_{A_m}A_m + \beta_{L_m}L_m + \beta_M M + \frac{\beta_{invA_m}}{A_m} + \frac{\beta_{invL_m}}{L_m} + \frac{\beta_{invk}}{k} +$$

$$\beta_{L_{inf}}L_{inf} + \frac{\beta_{invM}}{M} + \beta_{Class}Class + \beta_s s \quad (10)$$

This fitted model had 68.5% deviance explained. Coefficients were comparable with those in Equation 9, which implied that the patterns of their effect remained unchanged. The coefficient for selectivity indicated that when other variables were the same, increasing the age at vulnerability by one year leads to about 8% higher SPR_{MSY}.

3.3 | Estimating parameters using Bayesian errors-in-variables models

The BEIVM converged well and quickly after a few thousand iterations. By including measurement errors in LHPs, the BEIVM produced slightly different parameter estimates for Equation 9 (Table 5). The most obvious difference was predictor $invA_m$ whose 95% CI now barely included zero (−0.329–+0.024). We report the outcomes of this full model because if variable $invA_m$ was removed, the deviation information criteria (DIC) would significantly increase from −290.4 to −278.7. The measurement errors ranged from $\sigma = 0.062$ for A_m (and $invM$) to $\sigma = 0.142$ for L_m. Converting log-scale σ to $cv[x] = \sqrt{\exp(\sigma^2) - 1}$ indicated a coefficient of variation between about 6% and 14%. This was smaller than the model process error of $\sigma_\epsilon = 0.086$. Plotting the estimated SPR_{MSY}^{fit} from both the GLM and BEIVM (Figure 6) showed two clear improvements when the model took measurement errors into account. First, the BEIVM was more accurate as it reduced residual standard error from the GLM's 0.0898 to 0.0573, a 36% reduction, and it increased the adjusted R^2 from the GLM's 0.610 to 0.854. Second, BEIVM reduced the bias in the regression $SPR_{MSY}^{fit} \sim SPR_{MSY}$ by increasing the slope from the GLM's 0.612 to 0.755 so that the ratio between SPR_{MSY}^{fit} and SPR_{MSY} was closer to 1.

Applying BEIVM to Equation 10 resulted in similar improvement over the GLM (Table 6). Again, the BVM produced slightly different estimates from the GLM. The measurement errors were comparable with the BEIVM that did not use selectivity s, except for variables L_m, $invA_m$, and $invk$, which were larger than those in the single-level of s model above. The model process error σ_ϵ was estimated to be 0.089.

The BEIVM with multiple levels of selectivity was also more accurate than the corresponding GLM. It reduced residual standard

TABLE 1 Summary of F_{MSY} and calculated SPR_{MSY} averaged by *class* and *order* for the 185 stocks in the RAMDL

Class	Order	F_{MSY} (year^{-1})			SPR_{MSY}			
		Mean	Median	SD	Mean	Median	SD	N
Actinopterygii	Beryciformes	0.076	0.098	0.038	0.404	0.433	0.146	5
Actinopterygii	Clupeiformes	0.310	0.255	0.186	0.579	0.545	0.188	30
Actinopterygii	Gadiformes	0.291	0.287	0.102	0.443	0.443	0.118	42
Actinopterygii	Lophiiformes	0.228	0.238	0.058	0.711	0.781	0.144	3
Actinopterygii	Ophidiiformes	0.287	0.246	0.122	0.340	0.325	0.048	5
Actinopterygii	Perciformes	0.325	0.230	0.259	0.463	0.427	0.171	59
Actinopterygii	Pleuronectiformes	0.254	0.260	0.086	0.291	0.255	0.113	21
Actinopterygii	Scorpaeniformes	0.118	0.097	0.048	0.528	0.497	0.091	7
Actinopterygii	Zeiformes	0.057	0.057	0.032	0.475	0.475	0.129	2
Actinopterygii		0.284	0.250	0.189	0.459	0.435	0.172	174
Elasmobranchii	Carcharhiniformes	0.103	0.078	0.080	0.788	0.780	0.129	8
Elasmobranchii	Rajiformes	0.062	0.062	0.000	0.712	0.712	0.000	2
Elasmobranchii	Squaliformes	0.244	0.244	NA	0.228	0.228	NA	1
Elasmobranchii		0.109	0.075	0.082	0.723	0.769	0.199	11

TABLE 2 Effect of bias in input life-history parameters and F_{MSY} on calculated SPR_{MSY}

Scenario	Min (%)	Mean (%)	Max (%)
M 50%	−59	−40	−6
M 150%	2	28	62
A_{max} 50%	0	1	16
A_{max} 150%	−11	−2	0
k 50%	−42	−18	−1
k 150%	0	11	35
A_m 50%	−41	−16	0
A_m 150%	2	14	40
F_{MSY} 50%	3	39	103
F_{MSY} 150%	−37	−20	−3

Note: The values (min, mean and max) are summaries for the 185 stocks. For each scenario, a single parameter is decreased or increased from its baseline value while other parameters are kept unchanged.

error from the GLM's 0.0965 to 0.0594, a 38% reduction, and increased the adjusted R^2 from the GLM's 0.685 to 0.890. Second, BEIVM reduced the bias in the regression $SPR_{MSY}^{fit} \sim SPR_{MSY}$ by increasing the slope from the GLM's 0.685 to 0.815.

4 | DISCUSSION

We reaffirm using data from the RAMLD that SPR_{MSY} is a declining function of stock productivity quantified by F_{MSY}. $F_{x\%}$ is a way to express fishing mortality F in terms of SPR, but its relationship with productivity indicates that applying a single x% as an F_{MSY} proxy is not ideal for ensuring stock sustainability or avoiding loss of yields. Our analysis indicates that using a fixed $F_{40\%}$ can be worse

than simply using M as a F_{MSY} proxy. Not only is the model fit of $F_{MSY} \sim F_{40\%}$ poorer than $F_{MSY} \sim M$, but it is also riskier. On average, $F_{40\%}$ is more than double F_{MSY} (1/0.49), whereas $F_{MSY}/M = 0.73$ is more in line with other studies (Thompson, 1992; Zhou et al., 2012). The result showing that SPR_{MSY} differs among taxonomic groups further supports taxonomy-specific reference points (e.g. Thorson, 2019; Zhou et al., 2012). If management is based on SSBPR reference points, x% should be determined for each stock depending on its productivity. We have demonstrated that it is possible to determine SPR_{MSY} from LHPs, including lifespan, age- and length-at-maturation, growth parameters, natural mortality, taxonomic group and selectivity. This study suggests that the practice of applying a single x% for a wide range of species can be improved upon.

Management based on SPR reference points is widely applied. It is relatively simple (compared to a full stock assessment) to calculate $F_{x\%}$ and to convert F into $F_{x\%}$ (note that there are also R-packages, e.g. fishmethods and LBSPR, allowing such calculation if some LHPs are available). As this type of analysis focuses on a single cohort, SPR-based fishing mortality is useless without a benchmark to compare with (note that many data-poor fisheries adopt empirical harvest control rules without defining reference points; in such cases, F is simply used instead of $F_{x\%}$). The challenge is to identify the benchmark—the right $F_{x\%}$ as a F_{MSY} proxy for each species. For example, the F corresponding to $F_{40\%}$ can be calculated for each stock using some life-history parameters. This F, together with estimated biomass, can be used to calculate allowable catch. However, as we have shown, this F is very different from F_{MSY} for most stocks (Figure 3 left panel). The risk to sustainability and the loss in yield from using a constant x% vary among species due to their differing productivity. For instance, $F_{40\%}$ can maintain 40% SPR for a single cohort, but over the long term it may lead to SSB/SSB$_0$ (depletion of true spawning stock biomass) above or below this level depending on the
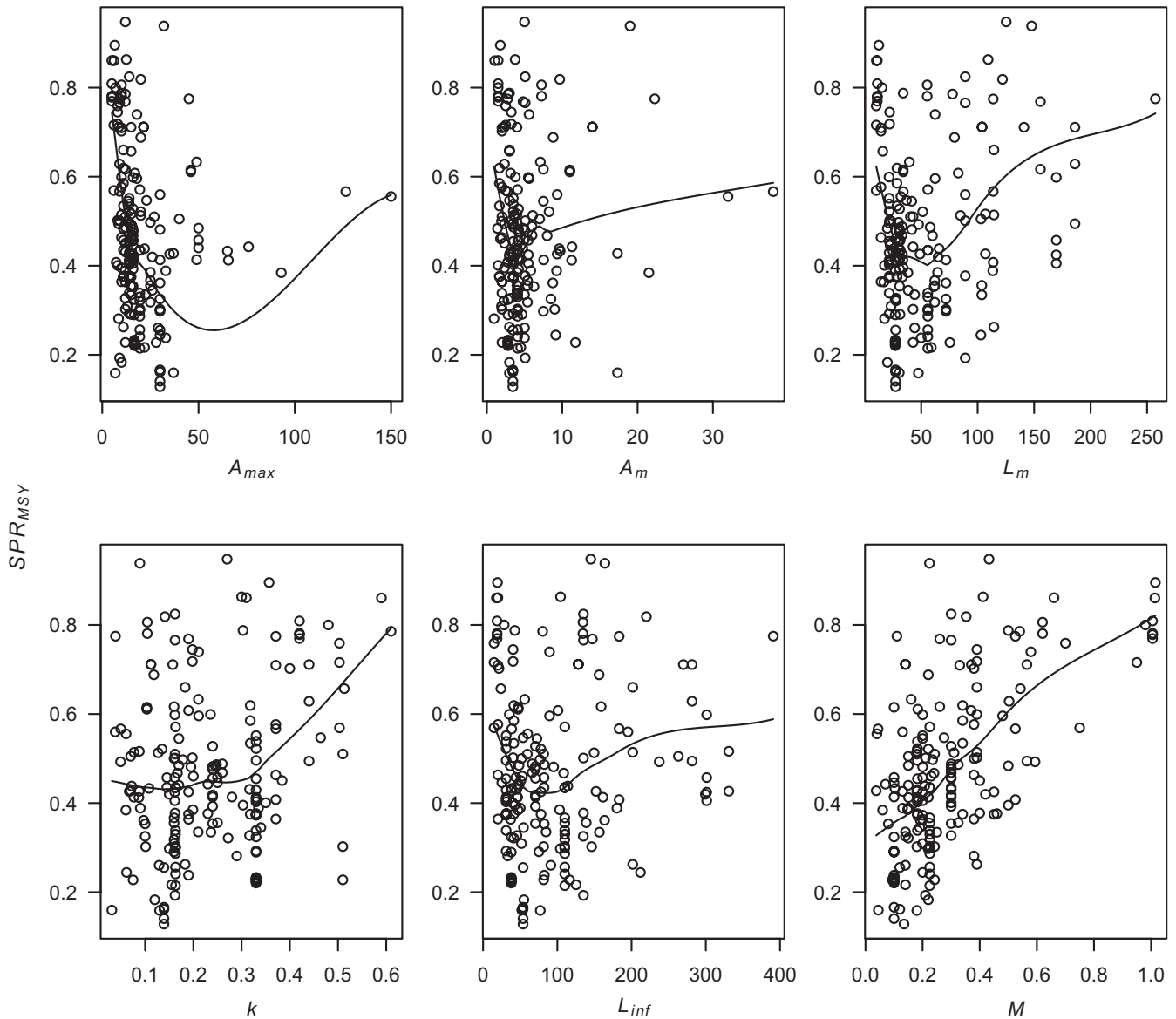
FIGURE 5 Scatter plot of SPR_{MSY} against the values for life-history parameters with superimposed loess (Locally Weighted Smoothing) curves

TABLE 3 Akaike information criteria for three data forms (raw, inverse, and log-transformed) when a single life-history parameter plus *Class* are used as the predictors of SPR_{MSY}

Data	A_{max}	A_m	L_m	K	L_{inf}	M
Linear	−120.7	−117.4	−118.4	**−132.6**	−117.6	**−217.7**
Inverse	**−165.2**	**−125.5**	**−133.3**	−121.8	**−134.1**	−148.1
Logarithm	−141.0	−120.0	−119.1	−127.2	−120.2	−197.5

Note: The bolded numbers are the lowest AIC of the three alternative forms.

stock's productivity. Our analysis shows that $F_{40\%} > F_{MSY}$ for 63.8% of the stocks that we analysed (and $F_{40\%} < F_{MSY}$ for 36.2% of stocks), implying that applying $F_{40\%}$ year after year will eventually drive 63.8% of stocks below B_{MSY}. To validate this deduction, we used the Sissenwine and Shepherd (1987) approach to compute the difference in equilibrium stock biomass status when management is based on F_{MSY} and $F_{40\%}$ for the stocks analysed in this study. The approach cannot be applied to all stocks in this study due to some atypical

and highly uncertain life-history parameters. Assuming a Beverton–Holt SRR, the scheme based on $F_{40\%}$ results in an equilibrium spawning stock biomass $SSB_{eq,F40\%}$ below SSB_{MSY} in 43% of stocks that can be analysed and an average of −43% decline [= ($SSB_{eq,F40\%}$ − SSB_{MSY})/SSB_{MSY}]. The other 57% stocks have a $SSB_{eq,F40\%}$ greater than SSB_{MSY} and on average 55% higher. For these two groups of stocks, one suffers from overfishing and the other one underfishing. Both groups lead to a loss of yield [on average ($C_{F40\%}$ - MSY)/

MSY = −12%]. Clearly, $F_{40\%}$ can be conservative for productive species but too risky for less productive species such as elasmobranchs. A pre-defined $F_{x\%}$ value lacks a theoretical basis.

F_{MSY} is typically estimated from a full stock assessment and takes into account a species' sustainability from generation to generation. Hence, an appropriate proxy for F_{MSY} should be stock-specific and account for both optimal yield and long-term sustainability. Using a generic fixed %SPR as a proxy for SPR_{MSY} avoids the difficulty of defining an SRR but fails to perform the function of true reference points of ensuring stock sustainability or avoiding loss of yields. Although SPR reference points are less sensitive to change in

TABLE 4 Models with the lowest AIC using a single life-history parameter plus *Class* as predictors of SPR_{MSY}, $SPR_{MSY} \sim f\,(\mathbf{LHP}, \mathbf{Class})$. *Class*: 0 for teleosts and 1 for elasmobranchs

Variable	Estimate	SE	Pr(>|t|)
Intercept	0.306	0.024	<2.0E−16
$invA_{max}$	2.137	0.292	7.49E−12
Class	0.290	0.048	6.82E−09
Intercept	0.395	0.026	<2.0E−16
$invA_m$	0.214	0.075	4.97E−03
Class	0.293	0.054	1.69E−07
Intercept	0.381	0.023	<2.0E−16
$invL_m$	2.409	0.597	8.03E−05
Class	0.320	0.054	1.21E−08
Intercept	0.366	0.027	<2.0E−16
K	0.396	0.100	1.14E−04
Class	0.280	0.052	2.25E−07
Intercept	0.388	0.021	< 2.0E−16
$invL_{inf}$	3.650	0.881	5.23E−05
Class	0.307	0.053	2.55E−08
Intercept	0.299	0.017	<2.0E−16
M	0.542	0.047	<2.0E−16
Class	0.277	0.041	2.23E−10

productivity for highly productive stocks (Figure 4), they can vary substantially for low productive stocks that are often the focus of management concern. For example, many elasmobranchs have estimated rates of intrinsic population increase close to zero (Cortés, 2002), indicating that to be sustainable their SPR target should be close to 1. Values in Table 1 and Tables 4–6 indicate that elasmobranchs require about 20% (between 13% and 32%) higher SPR_{MSY} than teleosts, all other adult LHPS being equal. This is interesting because $F_{60\%}$ has been recommended for sharks (Clarke & Hoyle, 2014; Zhou, Deng, Hoyle, & Dunn, 2019) and $F_{50\%}$ for several elasmobranchs on the US West Coast (PFMC, 2014).

The potential problem of using a constant value (usually between $F_{30\%}$ to $F_{40\%}$) as an F_{MSY} proxy has been recognized, and varying levels of x% have been adopted for groundfishes off the US west Coast ($F_{50\%}$ for rockfish and several elasmobranchs, $F_{30\%}$ for flatfish and $F_{45\%}$ for roundfish; PFMC, 2014). However, these assumed values for particular groups of fish are rather arbitrary or based on common beliefs. As pointed out in the introduction, SPR_{MSY} is a function of the SRR steepness ($SPR_{MSY} = \sqrt{1-h/4h}$, Mangel et al., 2013), and both SPR_{MSY} and h are related to life-history traits such as maximum lifespan, maturation age and natural mortality. However, the relationship between h and LHPs is a challenging question and there are currently different perceptions in the literature.

Steepness is the measure of density dependence in a SRR. Density dependence implies that as fishing reduces population density, the population responds with altered life-history traits, including earlier maturation, a faster growth rate, increased fecundity and reduced egg size (Rochet, Cornillon, Sabatier, & Pontier, 2000), that is h and SPR_{MSY} are linked to LHPs. There have been many attempts to define relationships between h or SPR_{MSY} and LHPs, generally using two approaches: analytical and empirical.

The analytical approach involves deriving h or SPR_{MSY} from LHPs by calculating $\hat{\alpha}$, the maximum lifetime reproductive rate at low density. $\hat{\alpha}$ is a product of α and ϕ_0, where α is the slope at the origin of a SRR and ϕ_0 is the spawning biomass per recruit in the absence of fishing mortality (Brooks et al., 2010; Mangel et al., 2013). The

TABLE 5 Estimated parameters for modelling SPR_{MSY} using multiple LHPs (Equation 9) from general linear model (GLM) and Bayesian errors-in-variables model (BEIVM)

	GLM			BEIVM				
Variable	Mean	SE	Pr(>|t|)	Mean	SE	2.50%	97.50%	σ_e
Intercept	0.2884	0.0420	1.1E−10	0.2569	0.0497	0.1586	0.3539	
A_m	0.0180	0.0037	2.6E−06	0.0196	0.0046	0.0109	0.0292	0.0621
L_m	0.0008	0.0003	0.0105	0.0009	0.0004	0.0002	0.0016	0.1421
M	0.4591	0.0750	5.9E−09	0.4537	0.0901	0.2845	0.6343	0.0901
$invA_m$	−0.1594	0.0848	0.0619	−0.1445	0.0910	−0.3293	0.0238	0.0790
Invk	−0.0059	0.0029	0.0457	−0.0067	0.0035	−0.0139	−0.0004	0.0894
$invL_{inf}$	3.3690	1.0860	0.0022	3.9907	1.2447	1.4830	6.4040	0.0647
invM	−0.0144	0.0044	0.0012	−0.0140	0.0048	−0.0236	−0.0048	0.0619
Class	0.1542	0.0420	0.0003	0.1533	0.0495	0.0534	0.2481	

Note: The vulnerable age is assumed to be $A_v \geq A_m$. *Class*: 0 for teleosts and 1 for elasmobranchs.
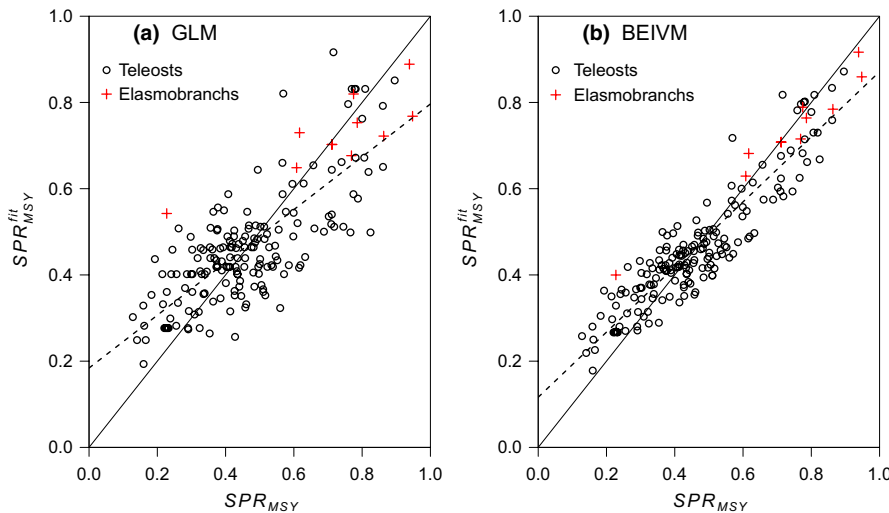
FIGURE 6 Comparison of fitted SPR_{MSY}^{fit} using a general linear model (GLM) and Bayesian errors-in-variables model (BEIVM) for Model 9. The diagonal lines are $SPR_{MSY}^{fit} = SPR_{MSY}$, and the dashed lines are the regressions between SPR_{MSY}^{fit} and SPR_{MSY} [Colour figure can be viewed at wileyonlinelibrary.com]

analytical approach calculates α and ϕ_0 from LHPs, including A_{max}, A_m, M, W_a, s_a, k and L_{inf}. The challenge with this approach is that α and ϕ_0 exhibit opposite trends. The productivity parameter α correlates positively with natural mortality (Denney, Jennings, & Reynolds, 2002; Mangel et al., 2010; Mangel et al., 2013) so short-lived species have a higher value of α. However, ϕ_0 exhibits a strong negative correlation with α (Goodwin et al., 2006). The combined effect leads to the difficulty in detecting the relationship between h and LHPs (Munyandorero, 2020; Thorson, 2019). One of the potential problems with the analytical approach pertains to the LHPs used. By definition, α is determined by LHPs at very low density while ϕ_0 is determined by LHPs at very high density. In addition to uncertainty (measurement error, variation among life stages, and spatial and temporal variation for the same stocks), there is normally only one set of LHPs for each stock and the values are typically collected at various levels of population density and not at the two extreme ends of density spectrum. Applying the same LHPs at intermediate

density ranges to calculate α and ϕ_0 could lead to bias in these parameters and hence in $\hat{\alpha}$, h and SPR_{MSY}.

The second approach involves determining h as the output of a meta-analysis of stock-recruitment data (e.g. Dorn, 2002; Forrest et al., 2010; Shertzer & Conn, 2012; Thorson, 2019). This type of analysis often leads to high uncertainty in parameters, including h. As such, and with a small sample size (e.g. 14 stocks in Forrest et al., 2010) or a narrow range (e.g. M between about 0.03 and 0.4 year^{-1} and A_m between about 1 and 16 years in Shertzer & Conn, 2012), a weak relationship is found between h and LHPs such as M and A_m. Thorson (2019) developed a data-integrated life-history model using LHPs in FishBase and historical records of spawners and recruitment in the RAMLD. This model predicts h and LHPs at various taxonomic levels (e.g. Class, Order, Family, Genus or Species). Thorson (2019) found little correlation between steepness and either natural mortality or asymptotic maximum size (W_∞), but meaningful differences among taxonomic groups. We were able to

TABLE 6 Estimated parameters for modelling SPR_{MSY} using multiple LHPs and including multiple levels of selectivity (Equation 10) from general linear model (GLM) and Bayesian errors-in-variables model (BEIVM). *Class*: 0 for teleosts and 1 for elasmobranchs

	GLM			BEIVM				
Variable	**Mean**	**SE**	**Pr(>|t|)**	**Mean**	**SE**	**2.50%**	**0.975**	**σ_e**
Intercept	0.3139	0.0221	<2.0E−16	0.2954	0.0259	0.2447	0.3455	
A_m	0.0191	0.0019	<2.0E−16	0.0206	0.0023	0.0163	0.0252	0.0998
L_m	0.0005	0.0002	0.0032	0.0007	0.0002	0.0003	0.0011	0.2878
M	0.4530	0.0385	<2.0E−16	0.4528	0.0430	0.3689	0.5385	0.0494
$invA_m$	−0.0734	0.0440	0.0957	−0.0850	0.0422	−0.1736	−0.0149	0.4333
$invL_m$	−2.3467	0.9636	0.0151	−1.5938	0.9589	−3.6071	−0.1081	0.1427
$invk$	−0.0053	0.0015	0.0005	−0.0064	0.0019	−0.0101	−0.0030	0.5296
$invL_{inf}$	5.5925	1.2441	8.1E−06	5.6513	1.2035	3.4890	8.1060	0.0500
$invM$	−0.0176	0.0022	6.1E−15	−0.0180	0.0025	−0.0229	−0.0132	0.0547
Class	0.1328	0.0211	5.4E−10	0.1337	0.0232	0.0886	0.1794	
s	0.0847	0.0039	<2.0E−16	0.0835	0.0040	0.0758	0.0914	

Note: Selectivity s = −1, 0, 1 or 2 when the knife-edge vulnerable age A_v is one-year younger, equal to, 1-year older or 2-year older than the maturation age A_m.

identify correlations between certain LHPs and SPR$_{MSY}$ with a larger sample and a wider range of LHPs, focusing on stock rather than on higher taxonomic ranks.

Recently, Munyandorero (2020) summarized three perceptions in the literature about the relationship between steepness and the life-history traits. (1) h is higher in short-lived than in long-lived species. (2) h is higher in long-lived species than in short-lived ones (Goodwin et al., 2006; Myers et al., 2002). And (3) there are no re-lationships among h and M or other LHPs (Shertzer & Conn, 2012; Thorson, 2019). Our results tend to support Perception 2, which is consistent with a general size- and trait-based theory that predicts h is an increasing function of W_∞(Andersen & Beyer, 2015). The sin-gle-LHP models and the multiple LHP models lead to positive co-efficients for invA_{max}, invA_m, invL_m, k, invL_{inf} and M, and negative coefficients of inv$K$ and inv$M$, implying that short-lived species have a higher SPR$_{MSY}$ than long-lived species. However, the multiple LHP models estimate positive coefficients of A_m and L_m and negative co-efficients of invA_m and invL_m, implying that later-maturing species have a higher SPR$_{MSY}$. The lack of consistency may be caused by high uncertainty in the input data related to both LHPs and the estimated F_{MSY} in the RAMLD. The stronger evidence to support Perception 2 appears to be counterintuitive to some popular beliefs and prac-tice, for example adopting a higher $F_{x\%}$ for long-lived species on the US West Coast, and assuming a higher h for short-lived species in simulation studies (Wetzel & Punt, 2015; Wiedenmann et al., 2013). However, empirical data also support Perception 2; using data from 246 populations, Myers et al., (2002) showed that steepness in-creases with reproductive longevity. Goodwin et al. (2006) analysed 54 stocks of commercially exploited marine fishes in the northeast Atlantic. Their models show that the compensation ratio is strongly and positively correlated with age-at-maturity and generation time for both the Ricker and hockey stick SRRs. These studies suggest that the SPR required to achieve sustainability and a good amount of yield varies among species.

The earlier studies that led to recommendations for target x% levels were based on life histories for commercially important "typ-ical demersal species." As Clark (2002) pointed out, when the $F_{40\%}$ strategy was developed (Clark, 1991), the main concern was obtain-ing a large fraction of the MSY in the long term. Biomass levels were not considered important in themselves. The objectives of those early analyses differed from those of ecosystem-based fisheries management in which biomass status has become a very import-ant factor in defining harvest policies. It is known that a good frac-tion of the MSY can be taken from a wide range of biomass levels from 20% to 60% (Clark, 1991; Hilborn, 2010; Rindorf et al., 2017). However, low levels of biomass are now unacceptable even if that level of biomass can still produce a good fraction (e.g. 75%, Clark, 1991) of MSY.

It is evident from our modelling that stock-specific SPR$_{MSY}$ can be inferred from life-history traits. However, when GLM is used the variance around the relationships can be large (e.g., Figure 6, left panel). This uncertainty may be attributed to several factors:

1. LHPs are subject to high uncertainty (Rudd, Thorson, & Sagarese, 2019; Then, Hoenig, Hall, & Hewitt, 2015; Thorson, 2019; Zhou et al., 2012).
2. F_{MSY} in the RAMLD may also have high uncertainty, due to vari-ous factors including the models used, the (assumed) form of the SRR, and the quantity and quality of data to fit the models.
3. Maturation and selectivity curves are not provided in the RAMLD. These variables have a substantial impact on SPR reference points. Improving data quality can reduce level of uncertainty presented in the paper.
4. The functional relationship between F_{MSY} and SPR$_{MSY}$ does not have the form of Equations 5 and 6.

Of these types of uncertainties, point 1—measurement errors in LHPs—can be addressed using advanced statistical methods and we used BEIVM to take account of this difficulty. The results show that BEIVM reduces both residuals and bias. Therefore, we recommend Model 9 with its BEIVM estimated parameters in Table 5 be used for estimate SPR$_{MSY}$ for new stocks. If selectivity is deemed to differ from the default $A_v \geq A_m$, Model 10 with its BEIVM estimated param-eters in Table 6 can be used instead.

Our analysis is the first attempt to establish a quantitative rela-tionship between SPR$_{MSY}$ and life-history parameters. The models can be and should be enhanced when more data become available and data quality improves. Unlike uncertainty resulting from data quality, the concern with one-size-fits-all %SPR is a conceptual and fundamental issue. The problem does not go away even when the input data are known without error.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available online.

ORCID

Shijie Zhou https://orcid.org/0000-0002-9358-1013

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SUPPORTING INFORMATION

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

How to cite this article: Zhou S, Punt AE, Lei Y, Aijun Deng R, Hoyle S. Identifying spawner biomass per-recruit reference points from life-history parameters. *Fish Fish*. 2020;21:760–773. https://doi.org/10.1111/faf.12459