Original Article

A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries

Adrian Hordyk[1]*, Kotaro Ono[2], Sarah Valencia[3], Neil Loneragan[1], and Jeremy Prince[1,4]

[1]*Centre for Fish, Fisheries and Aquatic Ecosystems Research, Murdoch University, 90 South Street, Murdoch, WA 6150, Australia*
[2]*School of Aquatic and Fisheries Science, University of Washington, Seattle, WA, USA*
[3]*Bren School of Environmental Science and Management, University of California, Santa Barbara, CA, USA*
[4]*Biospherics, P/L South Fremantle, Western Australia, Australia*

Corresponding author: tel: +61 893606685; e-mail: a.hordyk@murdoch.edu.au

The spawning potential ratio (SPR) is a well-established biological reference point, and estimates of SPR could be used to inform management decisions for data-poor fisheries. Simulations were used to investigate the utility of the length-based model (LB-SPR) developed in Hordyk *et al.* (2015). Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. ICES Journal of Marine Science, 72: 204–216.) to estimate the SPR of a stock directly from the size composition of the catch. This was done by (i) testing some of the main assumptions of the LB-SPR model, including recruitment variability and dome-shaped selectivity, (ii) examining the sensitivity of the model to error in the input parameters, and (iii) completing an initial empirical test for the LB-SPR model by applying it to data from a well-studied species. The method uses maximum likelihood methods to find the values of relative fishing mortality (F/M) and selectivity-at-length that minimize the difference between the observed and the expected length composition of the catch, and calculates the resulting SPR. When parameterized with the correct input parameters, the LB-SPR model returned accurate estimates of F/M and SPR. With high variability in annual recruitment, the estimates of SPR became increasingly unreliable. The usefulness of the LB-SPR method was tested empirically by comparing the results predicted by the method with those for a well-described species with known length and age composition data. The results from this comparison suggest that the LB-SPR method has potential to provide a tool for the cost-effective assessment of data-poor fisheries. However, the model is sensitive to non-equilibrium dynamics, and requires accurate estimates of the three parameters (M/k, L_∞, and $CV_{L\infty}$). Care must be taken to evaluate the validity of the assumptions and the biological parameters when the model is applied to data-poor fisheries.

Keywords: Beverton–Holt invariants, cost-effective, fish growth, life-history ratios, size composition.

Introduction

Measurements of the length composition of an exploited stock are relatively cheap and simple to collect, and are one of the most common forms of data available to fisheries researchers (Quinn and Deriso, 1999). For small-scale and data-poor fisheries, where the collection of age data is often restricted by lack of technical expertise and expense, length composition data are often the only form of information available to researchers and managers. This is especially so for many tropical species, where the lack of clearly defined annual growth rings in otoliths or other hard parts make the task of ageing individuals very difficult. As a result of the ready availability of length data for many stocks, a number of length-based methods have been developed and applied to estimate biological parameters and to understand the dynamics of fish populations (e.g. Beverton and Holt, 1957; Pauly and Morgan, 1987; Basson *et al.*, 1988; Gulland and Rosenberg, 1992). Many of

these size-based techniques were developed to estimate the growth and mortality rates of fish without the need for expensive and difficult to obtain age data (e.g. see Pauly and Morgan, 1987). Other length-based techniques aim to use the length structure of the population to estimate the stock status and provide useful management advice (e.g. Ault *et al.*, 2005; O'Farrell and Botsford, 2005; Gedamke and Hoenig, 2006; O'Farrell and Botsford, 2006; Klaer *et al.*, 2012).

Recent work has demonstrated that, under equilibrium conditions (i.e. constant F and no recruitment variability) and assuming von Bertalanffy growth, constant natural mortality for all age classes, no variability in length-at-age, and knife-edge selectivity, the standardized length composition of two stocks with the same ratio of natural mortality to growth rate (M/k) and the same ratio of fishing mortality to natural mortality (F/M) will be identical (Hordyk *et al.*, 2015). The extension of this model to incorporate variability in length-at-age and logistic selectivity confirmed that, at equilibrium, the expected length composition of the catch of an exploited stock is primarily determined by the ratios of M/k and F/M. The analytical models developed in Hordyk *et al.* (2015) suggest that with knowledge of the von Bertalanffy asymptotic length L_∞ and the coefficient of variation in L_∞ (CV_{L_∞}), the ratio of total mortality to the von Bertalanffy growth coefficient (Z/k) for a particular stock can be estimated from a representative sample of the length structure of the catch. If M/k is also known (from meta-analysis, life-history theory, expert judgement, or biological studies of a stock), then the results of Hordyk *et al.* (2015) suggest that it is possible to estimate F/M from the size composition of the catch. When M is unknown, i.e. only the ratio M/k is known, it is not possible to estimate F using this method. However, the ratio of F/M has often been used as a biological reference point, with $F_{MSY} = 0.87M$ considered a reasonable approximation for teleosts (Zhou *et al.*, 2012).

The ratio of F/M can be misleading, however, if not interpreted with care, as the selectivity of the fishery is also important. For example, perhaps a highly selective fishery could target only a few of the oldest year classes in a stock. Under this scenario, even if F/M is exceptionally high, the fishery is likely to be sustainable, but the yield is likely to be very low. Conversely, even a relatively low F/M can reduce the spawning per recruit drastically if the fishery catches a large proportion of immature individuals (Walters and Martell, 2004; Hordyk *et al.*, 2015).

A persistent challenge for length-based methods has been to provide indicators of stock status that can be compared against predefined biological reference points. The spawning potential ratio (SPR) of a stock is defined as the proportion of the unfished reproductive potential left at any given level of fishing pressure (Goodyear, 1993; Walters and Martell, 2004) and is commonly used to set target and limit reference points for fisheries. By definition, the SPR equals 100% in an unexploited stock, and zero in a stock with no spawning (e.g. all mature fish have been removed, or all female fish have been caught). The $F_{40\%}$, i.e. the fishing mortality rate that results in SPR = 40%, is considered risk adverse for many species (Clark, 2002), and suitable SPR-based reference points for fisheries management can be derived from assumptions about the steepness of the stock–recruit relationship (Brooks *et al.*, 2010). Hordyk *et al.* (2015) demonstrate that, under the assumptions of knife-edge selectivity-at-length at L_c, and knife-edge maturity at L_m, the SPR is determined by the ratios of M/k, F/M, L_m/L_∞, and L_c/L_∞.

The aims of the current study were to evaluate the utility of the models developed in Hordyk *et al.* as a methodology for assessing data-poor and small-scale stocks. This has been achieved by (i) testing some of the main assumptions of the length-based SPR (LB-SPR) model, including recruitment variability and dome-shaped selectivity, (ii) examining the sensitivity of the model to error in the input parameters, and (iii) empirically testing the prediction from the LB-SPR model by applying it to data from a well-studied species (*Sillago schomburgkii*, Coulson *et al.*, 2005) and comparing the results with those from a conventional age-based technique. The LB-SPR model requires the following parameters: an estimate of the ratio M/k (i.e. the individual values of the M and k parameters are unknown), L_∞, CV_{L_∞}, and knowledge of maturity-at-size, and uses data on the length composition of the catch to estimate the SPR. A simulation model was used to test the performance of the LB-SPR model for four species with a diverse range of life histories. These life histories where chosen based on the M/k ratios, varying from 0.53 for a species with a length composition dominated by large individuals to 3.05, representing a species with an unfished length distribution dominated by smaller fish (see Hordyk *et al.*, 2015; Prince *et al.*, 2015).

Methods

The LB-SPR method requires as input length composition data of the catch, as well as the three parameters: M/k, L_∞, and CV_{L_∞}. The model estimates the selectivity-at-length and the ratio F/M, which in turn are used to calculate the SPR. To test the utility and sensitivity of the estimation model to a range of issues likely to be encountered in the real world, an age-structured operating model (OM) was developed to generate length composition data for a range of life-history types. All simulation modelling was done using the open-source statistical software R (R Development Core Team, 2012).

Operating model

The population dynamics were modelled with a female-only, age-structured OM, assuming a population closed to immigration and emigration. In general, the OM used annual time-steps; however, for short-lived species (i.e. species with lifespan ≤10 years), monthly time-steps were used. The conversion from annual to monthly time-steps was necessary to ensure the construction of smooth length compositions for short-lived species, and was achieved by scaling the rate parameters appropriately. For example, an annual M is converted to a monthly rate by dividing by 12. For the short-lived species, recruitment was assumed to be continuous and occurred on the first day of every month.

The abundance, N, at age a at time t is given as:

$$N_{a,t} = \begin{cases} R_t & \text{if } a = 0 \\ N_{a-1,t-1}e^{Z_{a-1}} & \text{if } 0 < a \leq a_{max} \end{cases}, \qquad (1)$$

where R_t is the number of recruits at time t, Z_a the instantaneous total mortality-at-age a, and a_{max} the maximum age. Total mortality-at-age a is given by:

$$Z_a = M + S_a F, \qquad (2)$$

where M is the annual instantaneous rate of natural mortality, S_a the selectivity at age a, and F the annual instantaneous rate of fishing mortality. The catch-at-age (C_a) was calculated using the Baranov

equation:

$$C_{a,t} = \frac{F_a}{Z_a} N_{a,t}(1 - e^{-Z_a}). \tag{3}$$

Maximum age ($a_{\max}$) was determined as the first age class where the number of surviving individuals was $\leq 1\%$ of initial recruitment (Quinn and Deriso, 1999), so that:

$$a_{\max} = \frac{-\ln(0.01)}{M}. \tag{4}$$

Natural mortality was assumed to be constant and independent of size or age, and fishing mortality was assumed to be constant for all t. Recruitment at time t (R_t) was related to the spawning biomass by the Beverton–Holt stock–recruit relationship with multiplicative lognormal error:

$$R_t = \frac{SB_{t-1}}{\delta + \rho SB_{t-1}} e^{\epsilon_t - (\sigma_R^2/2)}, \tag{5}$$

where SB_t is the spawning-stock biomass at time t, δ and ρ are parameters of the stock–recruit function, and ϵ_t the recruitment residual at time t that is normally distributed by $N(0, \sigma_R^2)$, where σ_R is the standard deviation of the recruitment.

The δ and ρ parameters of the stock–recruit relationship were re-parameterized in terms of steepness (h), which is defined as the fraction of virgin recruitment (R_0) obtained when spawning biomass is 0.2 of the unfished spawning biomass (i.e. $0.2SB_0$).

Growth was modelled with the three-parameter von Bertalanffy function:

$$L_a = L_\infty(1 - e^{-k(a-t_0)}), \tag{6}$$

where L_∞ is the asymptotic length, k the growth coefficient, and t_0 the theoretical age when length is zero. Variation of length-at-age was assumed to be normally distributed, with variance increasing with increased mean length (Sainsbury, 1980):

$$\sigma_{L_a}^2 = \sigma_{L_\infty}^2 \left(1 - e^{-k(a-t_0)}\right)^2, \tag{7}$$

$$\sigma_{L_\infty} = CV_{L_\infty} L_\infty. \tag{8}$$

Maturity was assumed to be size-dependent, and was modelled with the two-parameter logistic function:

$$Mat_l = \frac{1}{1 + e^{-\ln(19)(l-L_{50})/L_{95}-L_{50}}}, \tag{9}$$

where Mat_l is the maturity at length l, and L_{50} and L_{95} are lengths at 50 and 95% maturity, respectively. Maturity-at-length was converted to maturity-at-age (Mat_a):

$$Mat_a = \int_{l=0}^{l=\infty} Mat_l \frac{1}{\sigma_{L_a}\sqrt{2\pi}} e^{-(l-L_a)^2/2\sigma_{L_a}^2}, \tag{10}$$

where $\sigma_{L_a}^2$ is the variance of length-at-age a. Spawning-stock biomass was calculated as:

$$SB_t = \sum_a N_{a,t} Mat_a W_a, \tag{11}$$

where W_a is the weight-at-age a, which was calculated as:

$$W_a = \alpha L_a^\beta, \tag{12}$$

where α and β are constants. Egg production at age a was assumed to be proportional to weight:

$$E_a \propto Mat_a W_a. \tag{13}$$

For most cases, selectivity was assumed to be asymptotic and size dependent, and was modelled by replacing L_{50} and L_{95} in Equation (9) with the lengths at 50 and 95% selectivity (L_{S50} and L_{S95}). The sensitivity of the model to dome-shaped selectivity was also examined. For these cases, selectivity-at-length (S_l) was modelled as a two-sided curve:

$$S_l = \begin{cases} e^{[-(l-L_1)^2/2s_1^2]} & \text{for } l < L_1 \\ e^{[-(l-L_2)^2/2s_2^2]} & \text{for } l \geq L_1 \end{cases}, \tag{14}$$

where L_1, L_2, s_1, and s_2 are the mean and standard deviations of the two normal curves. Selectivity-at-length was converted to selectivity-at-age (S_a) in the same manner as Equation (10).

SPR was calculated following Goodyear (1993), by calculating the ratio of the average lifetime production of eggs per recruit (EP) at equilibrium for the fished and unfished states, assuming no density-dependent suppression of maturation or fecundity:

$$SPR = \frac{EP_{Fished}}{EP_{Unfished}}, \tag{15}$$

where

$$EP_{Fished} = \sum_a \begin{cases} E_a & \text{for } a = 0 \\ e^{-Z_{a-1}a}E_a & \text{for } 0 < a \leq a_{\max} \end{cases}, \tag{16}$$

where $Z_a = M + S_a F$, and

$$EP_{Unfished} = \sum_a E_a e^{-Ma}. \tag{17}$$

An age–length transition matrix (Hilborn and Walters, 1992) was constructed from the assumptions of mean length-at-age and variation of length-at-age, where the probability of an individual at age a being in length class i is given by:

$$P_{i,a} = \begin{cases} \phi\left(\dfrac{l_{i+1}^{lo} - L_a}{\sigma_{L_a}}\right) & \text{if } i = 1 \\[2ex] \phi\left(\dfrac{l_{i+1}^{lo} - L_a}{\sigma_{L_a}}\right) - \left(\dfrac{l_i^{lo} - L_a}{\sigma_{L_a}}\right) & \text{if } 1 < i \leq I, \\[2ex] 1 - \left(\dfrac{l_i^{lo} - L_a}{\sigma_{L_a}}\right) & \text{if } i = I \end{cases} \tag{18}$$

where ϕ is the standard normal cumulative distribution, l_i^{lo} the upper bound of length class i, and I the total number of length classes. The age–length probability matrix was modified for the expected age–length distribution of the catch (p) to account for the selectivity-at-length by multiplying the age–length transition matrix by the selectivity at length class i (S_i):

$$p_{i,a} = P_{i,a} S_i. \tag{19}$$

The age–length transition matrix for the catch was standardized, so that the probability of an individual in the catch-at-age a being in one of the I length classes was 1:

$$\dot{p}_{i,a} = \frac{p_{i,a}}{\sum_a p_{i,a}}.$$ (20)

The length composition of the catch (N_i) was then constructed by multiplying the vector of catch-at-age by the transpose of the matrix $\dot{p}$:

$$N_i = C_a \dot{p}^T.$$ (21)

Estimation model

The estimation model was based on the analytical derivations developed in Hordyk *et al.* (2015), but for completeness, it is described fully here. To ensure that there was no possibility of cross-contamination of parameter values between the OM and the estimation model, the estimation model was coded separately in ADMB (Fournier *et al.*, 2012). Hordyk *et al.* (2015) demonstrated that, once standardized (to L_∞, or some other standardization, e.g. L_{max}), the expected length composition of the catch is determined by the interaction of selectivity and Z/k. If M/k is known, from meta-analysis or some other method, then there is the potential to estimate F/M and selectivity-at-length from length frequency data of the catch. In turn, these estimated parameters can be used to calculate the SPR, which can be used as an indicator of the status of the stock for management of the fishery.

To make the problem numerically tractable, the estimation model was constructed from a modified age-structured model, with "age" defined in arbitrary units. Let X be the number of discrete "age" classes in the estimation model, where X is a fixed parameter of the estimation model. The vector x is then defined as a sequence of "ages" in an arbitrary temporal scale from 0 to $X - 1$ (i.e. maximum "age" $= X - 1$), and $\tilde{x}$ is a vector of relative "ages" defined between 0 and 1:

$$\tilde{x} = \frac{x}{X}.$$ (22)

It is important to remember that the units of x are undefined, and that any ages in the estimation model are only meaningful in relative terms. The mean standardized length ($\tilde{l}$) at age x can then be given in terms of M/k (Hordyk *et al.*, 2015):

$$\tilde{l}_x = 1 - 0.01^{\tilde{x}(1/M/k)}.$$ (23)

Assuming that length-at-age is normally distributed with constant CV, the standard deviation of $\tilde{l}_x$ is (Hordyk *et al.*, 2015):

$$\sigma_{\tilde{l}_x} = CV(1 - 0.01^{\tilde{x}(1/M/k)}).$$ (24)

If there are I length classes in the observed length composition of the catch, and the length composition is standardized to L_∞, then the probability of an individual at age x being in length class i ($\tilde{P}$) can be calculated by using Equation (18). Assuming a logistic selectivity pattern, selectivity at standardized length $\tilde{l}$ ($\tilde{S}$) can be calculated by substituting $\tilde{l}$ into Equation (9) and standardizing the L_{S50} and L_{S95} parameters to asymptotic size. Using Equation (19), the matrix

$\tilde{P}$ can be modified to account for the selectivity-at-length, to calculate the probability that an individual in the catch-at-age x is in size class i ($\ddot{C}$). The matrix $\tilde{C}$ must be standardized so that there is a probability of 1 that an individual in the catch-at-age x is in one of the I length classes:

$$\ddot{C}_{i,x} = \frac{\tilde{C}_{i,x}}{\sum_x \tilde{C}_{i,x}}.$$ (25)

Hordyk *et al.* (2015) demonstrated that it is possible to calculate the number of individuals at age x in terms of M/k and F/M by using the assumed relationship between longevity and natural mortality. If X is the number of discrete age classes, then the corresponding M can be calculated from Equation (4): $M = -\ln(0.01)/t_{max} = -\ln(0.01)/X - 1$. The unit of time relating to t_{max} (and therefore M) is not known, so let this M be referred to as $\dot{M}$ to identify it as a generic parameter with unknown time-scale. The value of the X parameter (and hence the value of $\dot{M}$) is fixed, and determined by the analyst. Although the value of $\dot{M}$ will depend on the value of X chosen by the analyst, the ratio of M/k remains fixed, and $\dot{k}$ scales accordingly so that $\dot{M}/\dot{k} = M/k$. We conduct sensitivity tests to the value of X (see below), but in general, the model is insensitive to this parameter and it can remain fixed at some arbitrary value (e.g. $X = 100$; see Hordyk *et al.*, 2015 for further discussion). A vector of total mortality-at-age x can then be given as:

$$\dot{Z}_x = \dot{M} + \dot{M}\frac{F}{M}\tilde{S}_x,$$ (26)

where $\tilde{S}_x$ is the selectivity at age x (in unknown units of time) determined by multiplying the matrix $\tilde{P}$ by the vector $\tilde{S}_i$:

$$\tilde{S}_x = \tilde{S}_i \tilde{P}.$$ (27)

The relative number of individuals at age x can then be calculated using the traditional fisheries model:

$$\tilde{N}_x = \begin{cases} 1 & \text{if } x = 0 \\ \tilde{N}_{x-1}e^{-\dot{Z}_{x-1}} & \text{if } 0 < x \leq X \end{cases}.$$ (28)

The expected proportion of individuals in the catch in length class i is then calculated by multiplying the age structure of the vulnerable portion of the population ($\tilde{N}_x \tilde{S}_x$) by the transpose of the catch age–length transition matrix ($\ddot{C}$), and standardizing:

$$\tilde{P}_i^{\text{Catch}} = \frac{(\tilde{N}_x \tilde{S}_x) \ddot{C}^T}{\sum_i (\tilde{N}_x \tilde{S}_x) \ddot{C}^T}.$$ (29)

With the assumptions of constant CV of length-at-age, logistic selectivity, and constant natural mortality, the above algorithm gives the expected proportion of the catch in length class i in terms of M/k, F/M, and selectivity at relative length (l_{S50} and l_{S95}). When the observed length composition of the catch is standardized to L_∞, then the two selectivity parameters are equal to L_{S50}/L_∞ and L_{S95}/L_∞, respectively. Given knowledge of M/k, the parameters F/M, L_{S50}/L_∞, and L_{S95}/L_∞ can be estimated from the standardized length composition of the catch by minimizing the following

multinomial negative log-likelihood function (NLL):

$$\text{NLL} = \operatorname*{argmin}_{F/M, L_{S50}/L\infty, L_{S95}/L\infty} \sum_i O_i \ln \frac{\tilde{P}_i^{\text{Catch}}}{O_i^P}, \qquad (30)$$

where O_i and O_i^P are the observed number and proportion of the catch, respectively, in length class i.

Hordyk et al. (2015) demonstrated that, with the simplifying assumptions of no variation of length-at-age, and knife-edge selectivity, SPR is invariant with respect to the ratios M/k and F/M. They extended the model further to relax some of the assumptions and showed the relationship between SPR and M/k and F/M holds with logistic selectivity and variable length-at-age. Using the generic age-structure of the estimation model, and given estimates of maturity-at-age and the size-fecundity relationship, SPR can be calculated from the estimated parameters. Assuming that maturity is a logistic function of length, then maturity at relative length $\tilde{l}$ can be calculated by substituting the relative lengths at maturity, $\tilde{l}_{50}$ and $\tilde{l}_{95}$ for 50 and 95% maturity, respectively, into Equation (9). Similarly to selectivity-at-length, maturity-at-length can be converted to maturity-at-age x by multiplying the vector Mat_i by the age–length transition matrix $\tilde{P}$:

$$\text{Mat}_x = \text{Mat}_i \tilde{P}, \qquad (31)$$

where Mat_i is the probability that an individual in length class i is mature. Assuming that fecundity is linearly related to weight, and that weight is a cubic function of length, the relative egg production ($\tilde{E}$) at relative age x is:

$$\tilde{E}_x = \text{Mat}_x \tilde{l}_x^3. \qquad (32)$$

Total relative egg production for the fished state ($\tilde{E}P_{\text{Fished}}$) and unfished ($\tilde{E}P_{\text{Unfished}}$) states can then be calculated by substituting $\tilde{E}_x$ and $\dot{Z}_x$ into Equation (16) and $\dot{M}$ into Equation (17). SPR can then be calculated using Equation (15).

Simulation and evaluation

The utility of the LB-SPR method was evaluated by using the OM to generate length data, and comparing the estimates of F/M, selectivity-at-length, and SPR from the estimation model with the true values of the OM. Biological parameters for the simulated data were based on four species with a range of life histories: (I) sand sole (*Psettichthys melanostictus*), (II) Puget Sound rockfish (*Sebastes emphaeus*), (III) yellowtail flathead (*Platycephalus endrachtensis*), and (IV) Pacific saury (*Cololabis saira*) (Hughes, 1974; Watanabe et al., 1988; Beckmann et al., 1998; Pearson and Mcnally, 2005; Coulson et al., 2007). These species were chosen because of the range of life histories that they represented. The t_0 of these species were all set to 0 to test the sensitivity of the model to variation in this parameter, CV_{L_∞} was set to 0.1, steepness set to 0.7 for all species, and the selectivity-at-length parameters were arbitrarily set lower than maturity-at-length for each species (Figure 1). Hence, hereafter these species are referred to as Species I, II, III, and IV (Table 1).

The utility of the LB-SPR model was tested using a number of robustness tests to understand the sensitivity of the model to various assumptions, values of the input parameters, and life histories (Table 2). The assessment model was parameterized with the "true" value of the M/k, L_∞, CV_{L_∞} parameters, except in the cases
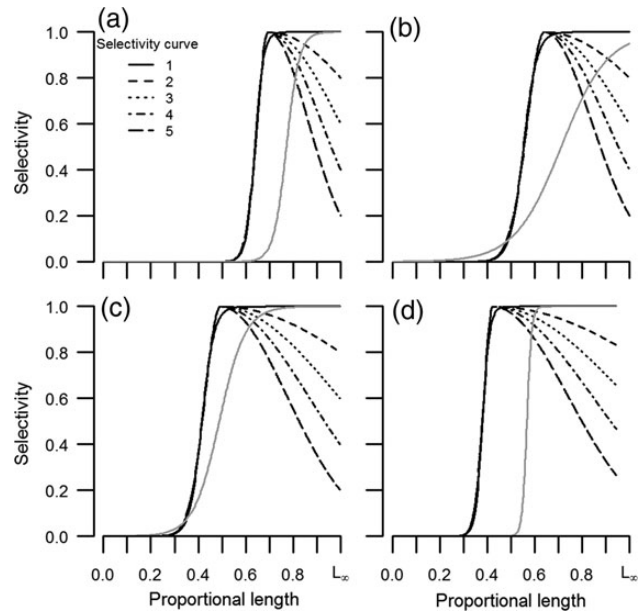

Figure 1. The five selectivity curves used to assess the sensitivity of the LB-SPR model to length data from a fishery with dome-shaped selectivity for Species I, II, III, and IV (a–d, respectively, Table 1). Curve 1 (solid line) is the asymptotic selectivity curve used in all base case scenarios, and curves 2–5 are two-sided selectivity curves with increased doming. For reference, the maturity curve for each species is represented as a solid grey line.

Table 1. The biological and selectivity parameters for the four test species used in the robustness tests of the LB-SPR model.

| Parameter | Species | | | | Definition |
	I	II	III	IV	
L_∞ (mm)	376	170	530	342	Asymptotic size
CV_{L_∞}	0.1	0.1	0.1	0.1	Coefficient of variation of L_∞
M	0.42	0.44	0.63	1.25	Natural mortality
k	0.79	0.535	0.41	0.41	Growth coefficient
t_0	0	0	0	0	Theoretical age at zero length
M/k	0.53	0.82	1.54	3.05	M/k ratio
L_{50} (mm)	290	121	259	194	Length at 50% maturity
L_{95} (mm)	320	170	344	204	Length at 95% maturity
L_{S50} (mm)	240	94	220	130	Length at 50% selectivity
L_{S95} (mm)	260	108	260	145	Length at 95% selectivity

Biological parameters are based on (I) sand sole (*P. melanostictus*) (Pearson and Mcnally, 2005); (II) Puget Sound rockfish (*S. emphaeus*) (Beckmann et al., 1998); (III) yellowtail flathead (*P. endrachtensis*) (Coulson et al., 2007); and (IV) Pacific saury (*C. saira*) (Hughes, 1974; Watanabe et al., 1988).

where sensitivity to those parameters was being tested (i.e. Tests 1–3 and 11). Similarly, the entire catch was sampled except in Test 5. Fishing mortality was set equal to natural mortality for all cases except Test 7. For Tests 1–7, σ_R was set to 0 (i.e. no variability in recruitment), and the OM was projected forward until the stock was at fished equilibrium. The X parameter of the estimation model was set at 100 for all cases except Test 4.

Tests 1–3 examined the sensitivity of the estimation model to misspecification of the M/k, L_∞, and CV_{L_∞} parameters, respectively (Table 2). For each test, the estimation model was run 100 times with the assumed value of the relevant parameter arbitrarily allowed to

Table 2. Description of the 12 tests to understand the robustness and sensitivity of the LB-SPR model to a range of parameter misspecification and assumption violations for the four test species of Table 1.

Test	Description
1	Assumed M/k parameter ranging $\pm 25\%$ of true value
2	Assumed L_∞ parameter ranging $\pm 25\%$ from true value
3	Assumed CV_{L_∞} parameter ranging $\pm 25\%$ from true value
4	X (the length of vector x in the estimation model) ranging from 10 to 208
5	Sample size reduced to 100, 500, 1000, 5000, and 10 000 individuals
6	Length-at-birth (L_0) ranging $0 - 0.25L_\infty$
7	True F/M ranging $0.01 - 5$
8	Recruitment variability with $\sigma_R = 0.1, 0.3, 0.6,$ and 0.9
9	Same as Test 8, with autocorrelated recruitment variability
10	Same as Test 8, with episodic recruitment failure
11	M/k, L_∞, and CV_{L_∞} drawn from triangle distributions, and $\sigma_R = 0.6$
12	Increasing levels of dome-shaped selectivity, and $\sigma_R = 0.6$

range from -25 to $+25\%$ of the true value. Results for these tests were summarized as the relative error in F/M and the resulting SPR for the range of the assumed parameters. The relative error (RE) was calculated as:

$$\frac{\text{RE} = \hat{\lambda} - \lambda}{\lambda,} \tag{33}$$

where λ and $\hat{\lambda}$ are the true and estimated parameters, respectively.

Test 4 determined the sensitivity of the estimation model to changes in X, the temporal resolution of the estimation model. For this test, the estimation model was run 100 times with X in Equation (22) ranging from 10 to 208. The results of this test were summarized as the relative error in F/M and the resulting SPR as a function of X.

Although samples of the length composition of the catch are relatively cheap and simple to obtain, it is unlikely that the entire catch would be measured usually. Test 5 examined the impact of sample size on the effectiveness of the LB-SPR method. Five levels of sampling coverage were examined, with sample sizes of 100, 500, 1000, 5000, and 10 000 individuals, respectively. For each case and test species, length compositions were generated from 200 Monte Carlo simulations by randomly sampling with replacement from the age composition of the catch, with the probability proportional to that in the true age composition of the catch. The estimation model was run on each generated length composition, and results were summarized as boxplots of the relative error in the estimated parameters for each sample size.

The estimation model assumes that length at birth (L_0) is zero [Equation (23)] which, for the purposes of this model, is probably a reasonable assumption for many species of fish. However, in some species, for example, live-bearing teleosts and many sharks, L_0 is considerably larger than zero. When modelling fish growth with the von Bertalanffy function, this is accounted for with the inclusion of the t_0 parameter, which is the theoretical age at which the length of the animal would be 0. Usually, the t_0 is ≤ 0, which indicates that $L_0 \geq 0$. In cases where $t_0 > 0$, L_0 is < 0 which is biologically impossible, and the von Bertalanffy growth function may not be the most appropriate model to use in these situations. The sensitivity of the estimation model to $L_0 > 0$ was examined in Test 6. For this test,

the length compositions were generated with L_0 ranging from 0 to $0.25L_\infty$ for each species. To generate the length compositions, the appropriate t_0 parameter was calculated in the OM by manipulating Equation (6):

$$t_0 = \frac{\ln(1 - (L_0/L_\infty))}{k}. \tag{34}$$

Test 7 investigated the sensitivity of the assessment model to variation in the value of F/M. For this test, length compositions were generated from 100 Monte Carlo simulations with the true F/M ranging from 0.01 to 5, and the estimated F/M was compared against the true value.

Like many length-based methods, the LB-SPR technique is an equilibrium-based method, which compares the observed length composition of the catch with the expected length composition in equilibrium conditions. In reality, an exploited stock is rarely at equilibrium. Even if exploitation rates are held constant for some time, a stock is still likely to be at disequilibrium due to variability in recruitment. The last three tests examined the sensitivity of the estimation model to population disequilibrium by generating length compositions from stocks with variable recruitment. For Test 8, the number of Monte Carlo simulations was increased to 200, with the OM projected forward under four levels of lognormally distributed recruitment variability, with σ_R set at 0.1, 0.3, 0.6, and 0.9, respectively. For each of the Monte Carlo simulations, a length composition of the catch was generated from the last year. Test 9 repeated a similar test to Test 8, but with the addition of autocorrelated recruitment variability, with a lag of 1 year and an autocorrelation coefficient of 0.6. Test 10 further extended the examination of recruitment variability by investigating the impact of episodic recruitment failure. For this test, there was a 15% chance in any given time-step (usually yearly, but monthly for short-lived species) of recruitment failure. Two hundred Monte Carlo simulations were conducted for each of the four species types (Table 1) for the same range of recruitment variability as Tests 8 and 9 (Table 2).

While Tests 1–3 evaluated the impact of misspecification of the parameters of the LB-SPR model, all three input parameters may be uncertain and the equilibrium assumptions may not hold. For Test 11, we conducted 5000 Monte Carlo simulations for each test species, with recruitment variability ($\sigma_R = 0.6$), and, for each simulation, selected each of the three LB-SPR input parameters from a triangle distribution, with the mode at the true value, and the same range as that used in Tests 1–3. The results from Test 11 are presented as boxplots of the estimated SPR and the relative error in the estimated F/M. The results from Test 2 indicated that when the L_∞ parameter was specified to be too low, the model hit the lower bound on F/M ($F/M = 0$), and returned estimates of SPR of 1 (see Figure 2b and below for discussion). In reality, such an extreme underestimate of the L_∞ parameter would be unlikely, and the poor model fit would raise suspicions about the validity of the LB-SPR estimate of SPR ≈ 1. To address this issue, for Test 11, we discarded the LB-SPR estimates where SPR ≥ 0.99, which occurred in 20, 12, 4, and 4% of the simulations for Species I, II, III, and IV, respectively.

A common problem with many fishing gears, such as gillnets and trawls, is dome-shaped selectivity, where large fish are not caught by the fishery. The LB-SPR model assumes asymptotic selectivity, and it is expected that the method will overestimate F/M and underestimate SPR when confronted with data from a fishery with dome-shaped selectivity. To test the performance of the LB-SPR
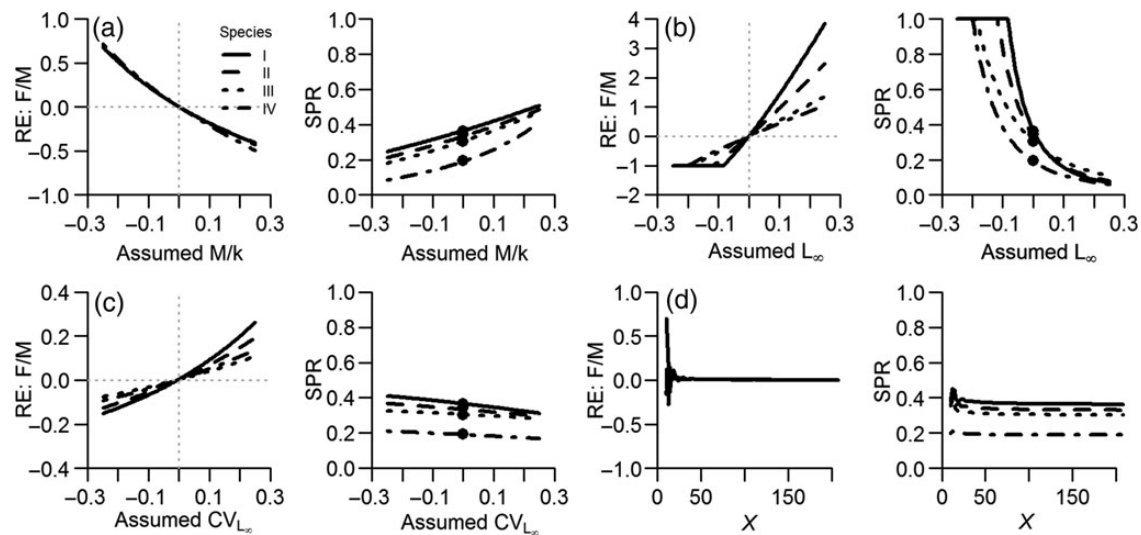
Figure 2. The relative error (RE) in the estimated F/M and resulting estimate of the SPR for the four simulated species for (a) Test 1: misspecification of M/k, (b) Test 2: misspecification of L_∞, (c) Test 3: misspecification of CV_{L_∞}, and (d) Test 4: resolution of the age-structured estimation model (X). The solid black points in the SPR panels of (a–c) indicate the true SPR for each species.

model where selectivity is dome-shaped, we ran 200 Monte Carlo simulations, with recruitment variability ($\sigma_R = 0.6$), for a range of increasingly dome-shaped selectivity patterns for each species. The dome-shaped selectivity curves were modelled as a two-sided function, with one asymptotic curve (the base case) and four curves with increasing doming (Figure 1). The results from Test 12 are presented as a series of boxplots showing the relative error in the SPR estimates for the five different selectivity curves and the four test species.

Preliminary empirical test
An empirical test of the LB-SPR method was carried out using detailed biological data for the temperate yellowfin whiting (*S. schomburgkii*, Sillaginidae) in Shark Bay, Western Australia (Coulson *et al.*, 2005). We used the data on the female length composition as a case study for the LB-SPR method. Currently, there is no stock assessment for the Shark Bay *S. schomburgkii* and Coulson *et al.* (2005) did not estimate natural or fishing mortality for the species. However, unpublished work suggests that *S. schomburgkii* is lightly exploited in Shark Bay (Coulson 2013, Murdoch University, pers. comm.), and we used the maximum age of female fish in the Coulson *et al.* (2005) study (10 years; $n = 997$) with the Hoenig method (Hoenig, 1983) to estimate natural mortality ($M = 0.42$). We used the catch-curve method with the age composition data to estimate total mortality ($Z = 0.55$), resulting in an estimate of $F = 0.13$ and $F/M = 0.31$. The female length composition data were also used to estimate F/M and SPR with the LB-SPR model, parameterized with the female biological parameters ($L_\infty = 345.97$ mm, $k = 0.477$ year^{-1}, $L_{50} = 223$ mm, $L_{95} = 259$ mm Coulson *et al.*, 2005, and assumed that $CV_{L_\infty} = 0.1$). The results from this estimation of SPR were compared with those based on conventional age-based techniques, i.e. Z estimated using a catch curve and F calculated as $F = Z - M$. We evaluated the sensitivity of the LB-SPR model to alternative values for the L_∞ and M/k parameters by re-running the model with a combination of different L_∞ and M/k parameters ($L_\infty = 330, 345, 360$ and $M/k = 0.60, 0.88, 1.15$. CV_{L_∞} was held constant at 0.1). This

empirical test provides an indication of the performance of the LB-SPR model, and comprehensive testing of the model is now being carried out by applying the LB-SPR model to empirical data from a wide range of species (Prince *et al.*, Murdoch University, unpublished data).

Results
The sensitivity tests revealed that, for all four species, the accuracy of the estimated F/M and the assumed values of the parameters for the LB-SPR method was closely related (Figure 2a–c). When the three parameters of the LB-SPR model were set equal to the true values, the estimation model returned estimates of F/M, the selectivity parameters, and SPR that were equal to the true values (Figure 2a–c). The model had similar behaviour for all four species when M/k was misspecified (Test 1), with F/M overestimated by ~70% when M/k was assumed to be 25% lower than the true value, and underestimated by ~40% when M/k was assumed to be 25% higher than the true value (Figure 2a). The estimates of the selectivity parameters L_{S50} and L_{S95} were insensitive to the assumed M/k. The exact relationship between F/M and SPR depends on the selectivity pattern; however, in general, SPR decreases as F/M increases. As expected, the relationship between estimated SPR and the degree of misspecification in the assumed M/k parameter is the reverse to the pattern observed between the estimated F/M and assumed M/k, with SPR being increasingly overestimated as the M/k parameter is assumed to be higher than the true value (Figure 2a).

The estimation model was most sensitive to the assumed L_∞, with considerable overestimation in F/M when the assumed L_∞ was specified to be higher than the true value, particularly when >0.1 of the true L_∞ (Test 2; Figure 2b). Sensitivity to the assumed L_∞ increased with decreasing M/k, with Species I the most sensitive to misspecification of L_∞ (F/M overestimated by ~400% when L_∞ assumed to be 25% higher than the true value) and Species IV the least (F/M overestimated by ~100% when L_∞ assumed to be 25% higher than the true value). The model underestimated F/M when L_∞ was assumed to be lower than the true value, with F/M estimated

to be 0 (i.e. $F = 0$) when the assumed L_∞ was specified to be 10–20% lower than the true value. As with Test 1, the selectivity-at-length parameters were well estimated and were not sensitive to the misspecification of the assumed L_∞ parameter (Figure 2b). However, SPR showed the same sensitivity as F/M, with the estimated SPR rapidly increasing as the assumed L_∞ was decreased below the true value, and rapidly decreasing when the assumed L_∞ was increased above the true value (Figure 2b).

The estimation model was relatively insensitive to variation in the assumed CV_{L_∞} for all four life-history types, although species with low M/k appeared the most sensitive to this parameter (Figure 2c). The model was also completely insensitive to the temporal scale of the estimation model when X was above ~25 (Figure 2d). Below this value, the model behaved somewhat chaotically and often did not fit the data well.

As expected, the variability in the estimates of F/M, selectivity-at-length, and SPR increased when the number of measurements decreased, particularly at a sample size of 100 individuals. However, even with the error in these parameters, the estimates of SPR were relatively consistent across all sample sizes (Figure 3). The median relative error in F/M was close to 0 for all sample sizes, and SPR was well estimated, particularly for sample sizes of 1000 individuals or greater (Figure 3).

Species with higher M/k appear to be the most sensitive to the assumption that $L_0 = 0$ (i.e. $t_0 = 0$); however, the estimation model was relatively insensitive to $L_0 > 0$, with F/M being overestimated by 5–10% when $L_0 = 0.25L_\infty$ (Test 6; results not shown). The estimation model was not sensitive to the true F/M of the OM and returned accurate estimates for the entire range of F/M (Test 7; results not shown).

The relative error in the estimates of L_{S50} and L_{S95} was consistent over the range of recruitment variability, $\sigma_R = 0.1 - 0.9$, for all four species (Test 8; Figure 4). Not unexpectedly, the relative error in the selectivity parameters increased with increasing recruitment variability; however, usually, the selectivity parameters were estimated within 10% of the true values. A similar pattern was observed in the estimated F/M for all four species, with variance increasing with increased recruitment variability (Figure 4). However, except the scenarios with high recruitment variability ($\sigma_R = 0.9$) where the estimates were positively biased, the median relative error in the estimated F/M for all four life-history types was centred on 0, indicating that on average the method was successful in correctly estimating the parameters (Figure 4). The variability in the estimates of F/M and the selectivity parameters directly translates through to the estimates of SPR; however, SPR appeared to be consistently well estimated for all four life-history types and four levels of recruitment variability (Figure 4).

The inclusion of autocorrelated recruitment variability resulted in increased variance in the four estimated parameters, particularly when σ_R was 0.6 or 0.9 (Test 9; Figure 5). Although the estimates of the selectivity parameters were consistent, the relative error in F/M was often quite large. While the median relative error in F/M was centred on 0, F/M was sometimes considerably overestimated, which resulted in SPR being considerably underestimated (Figure 5). In addition, F/M was also occasionally underestimated by close to 100%, resulting in SPR being greatly overestimated (see 95 and 5 percentiles of F/M and SPR, respectively, in Figure 5). There appeared to be little extra impact from the inclusion of episodic recruitment variability, with the estimation model appearing to behave in a similar manner to Test 8 (Test 10; results not shown). As with the other tests involving recruitment variability,

the relative error in the estimated parameters increased with increasing recruitment variability, with F/M being occasionally overestimated and underestimated by up to 100% when $\sigma_R = 0.9$.

The variability in the model estimates increased as simultaneous error in the three LB-SPR parameters was introduced, with the model tending to overestimate F/M and underestimate SPR, particularly for Species I and II (Test 11; Figure 6). Species I ($M/k = 0.53$) was most sensitive to misspecification in the three parameters (Figure 6), with the median relative error in the estimated F/M positively biased $\sim36\%$, and in some cases, F/M was overestimated by up to four times the true value and in others underestimated by nearly 100%. The median estimates of SPR were negatively biased by some 20%, and the estimates ranged from close to 1 to essentially 0 (Figure 6). The sensitivity of the model decreased with the increasing M/k of the other three species, with the median relative error in the estimated F/M positively biased by 18, 6, and 5% for Species II ($M/k = 0.82$), III ($M/k = 1.54$), and IV ($M/k = 3.05$), respectively. Species IV was the least sensitive to error in the assumed parameters, with the resulting estimate of SPR ranging from 0 to ~0.6, and the median estimated SPR close to the true value of 0.19.

The LB-SPR model underestimated SPR for all four test species when provided with length data from a fishery with dome-shaped selectivity (Figure 7). Species I and II (Figure 7a and b) were the most sensitive to dome-shaped selectivity, with SPR significantly underestimated by over 50% for curves 4 and 5. Species III and IV (Figure 7c and d) were less sensitive to the dome-shaped selectivity, especially for the curves with only slight doming (curves 2 and 3).

Although the length frequency distribution of the female *S. schomburgkii* was bimodal, with one group from 165 to 215 mm total length, and the other from 255 to 295 mm, the LB-SPR model appeared to fit to the data fairly well (Figure 8). The LB-SPR model estimates of $F/M = 0.55$ and SPR = 0.44 were more conservative than the estimates from the age-based catch curve ($F/M = 0.42$ and SPR = 0.62). The LB-SPR model was sensitive to the various combinations of M/k and L_∞, with the resulting SPR varying from 0.18 ($L_\infty = 360$, $M/k = 0.6$) to 1.00 ($L_\infty = 330$, $M/k = 1.15$) (Table 3).

Discussion

The length-based technique developed in this study offers an alternative method to estimate F/M, selectivity-at-length, and the SPR for an exploited stock based only on length frequency data. Length frequency data are one of the easiest and most affordable metrics to collect, and for many small-scale, data-poor fisheries, may be the only data available. Our technique provides a means of estimating the biological reference points, F/M and SPR, which previously required expensive and technically challenging catch-at-age analyses.

In this study, we simulated length data from four species with diverse life histories, spanning the range of M/k (0.53 to 3.05) in the meta-analysis of Prince *et al.* (2015). The M/k values correspond to species that mature and reach their maximum length relatively early in life ($M/k = 0.53$), and those that continue growing throughout life ($M/k = 3.05$). The results from the simulations showed that the LB-SPR method appeared to work well, especially for species with $M/k > 0.53$. However, it is likely that the model will be increasingly biased for species with $M/k < 0.53$, as the method relies on detecting the signal of fishing mortality in the right-hand side of the length composition. Species with low M/k are expected to have an unfished length composition very strongly skewed to the left, with the length composition consisting of
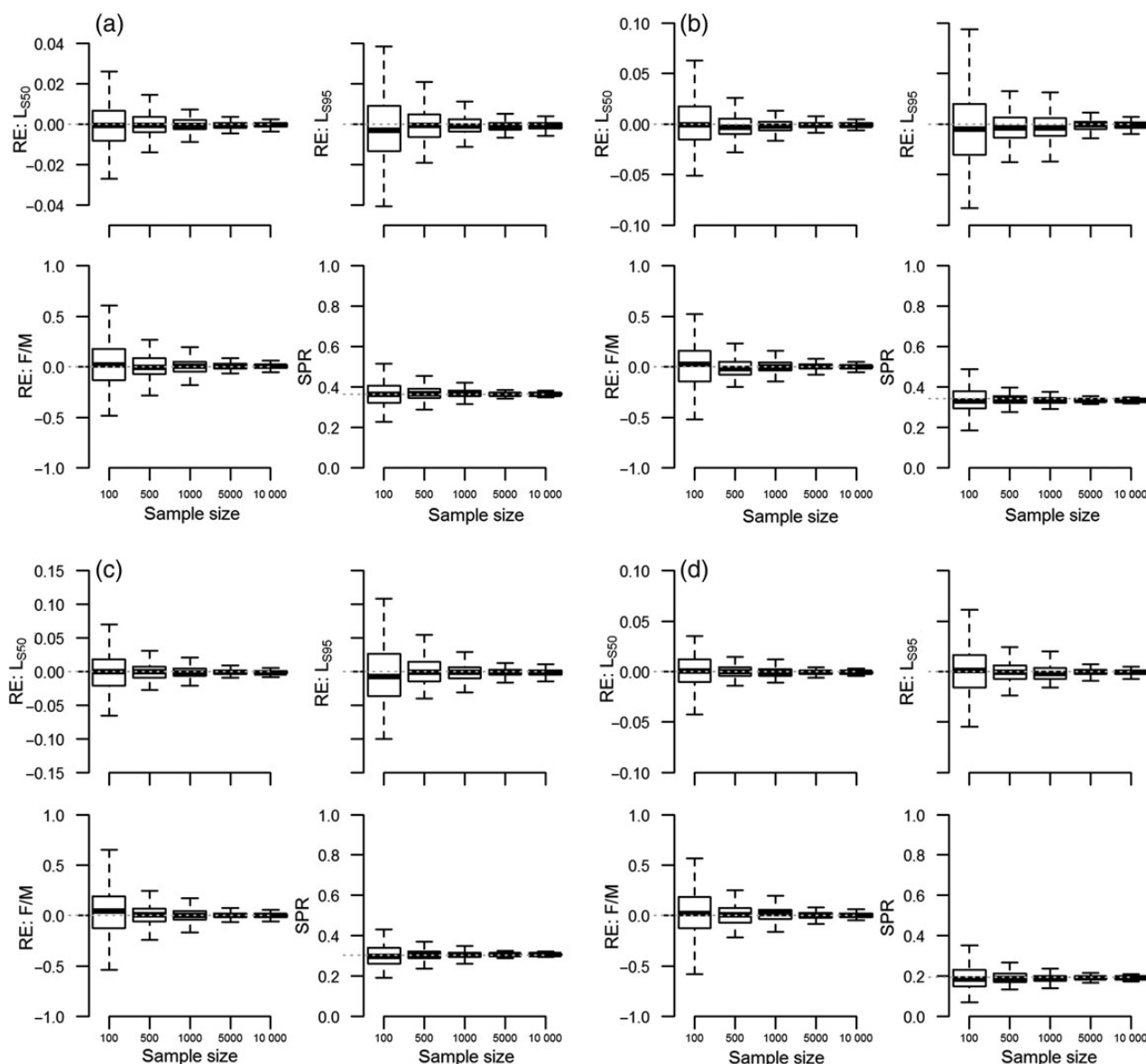
Figure 3. Boxplots showing the 5th, 25th, 50th, and 95th percentiles of the relative error (RE) in the estimated F/M, L_{S50}, L_{S95} and resulting estimate of the SPR for a range of sample sizes (Test 5) for (a) Species I, (b) Species II, (c) Species III, and (d) Species IV. The biological attributes for the test species are given in Table 1.

adults of widely varying age, but at a similar (near asymptotic) size (Figure 1 of Hordyk *et al.*, 2015). Consequently, fishing is not likely to have a visible impact on the length composition until fishing mortality is very high and SPR is very low.

As modelled here, the LB-SPR method assumes that length-at-age is normally distributed with a constant coefficient of variation (*CV*), an assumption that does not always appear to hold (Erzini, 1994; Bowker, 1995). Detailed costly ageing studies are required to test this assumption, research that is not feasible for small-scale, data-poor fisheries. However, meta-analyses of existing length-at-age studies are likely to provide a cost-effective way to determine whether the assumption of normally distributed length-at-age is commonly violated, or if there are predictable violations of this assumption among some species. The impact of violating the assumption of normally distributed length-at-age has not

been investigated in this study, but knowledge of the distribution of length-at-age could be incorporated into the LB-SPR method for specific species.

Influence of variation in parameters on estimating SPR

The simulation tests involving uncertainty in all three parameters showed clearly that the accuracy of the estimated SPR from the LB-SPR method depends on the precision of the parameters M/k, $CV_{L_{\infty}}$, and L_{∞} (Figure 6). When tested empirically for a species with known age and length composition, the LB-SPR model returned a more conservative estimate of SPR than the age-based catch curve. However, it must be emphasized that the catch-curve method is also an equilibrium method, and these estimates do not necessarily reflect the "true" status of the stock. Furthermore, depending on the assumed values for the M/k and L_{∞} parameters,
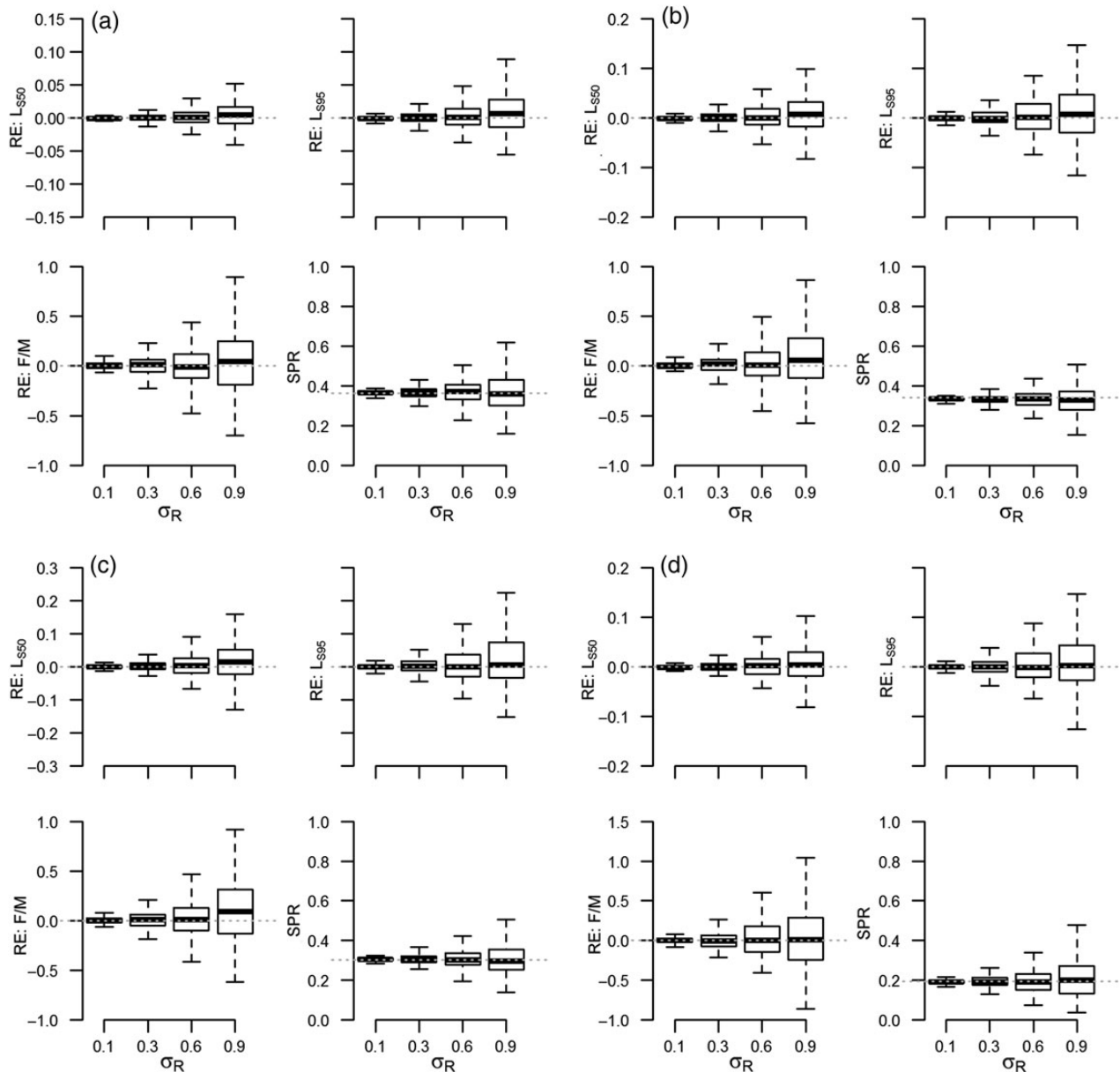
Figure 4. Boxplots showing the 5th, 25th, 50th, and 95th percentiles of the relative error (RE) in the estimated F/M, L_{S50}, L_{S95} and resulting estimate of the SPR with recruitment variability (Test 8) for (a) Species I, (b) Species II, (c) Species III, and (d) Species IV. The biological attributes for the test species are given in Table 1.

the LB-SPR suggests that the status of the *S. schomburgkii* stock ranges from unfished (SPR = 1) to a fully or heavily exploited (SPR < 0.2, Table 3), which reinforces the importance of accurate and reliable estimates of the biological parameters for the LB-SPR model. The research required to estimate these three parameters directly from the stock is time-consuming, somewhat complex, and expensive; precisely the factors that limit age-based population modelling from being applied to data-poor and small-scale fisheries. Without relatively expensive ageing studies, it is difficult to obtain reliable estimates of the individual parameters M and k. A number of length-based methods exist which aim to estimate k from size frequency or tagging studies (e.g. Pauly and Morgan, 1987; Smith *et al.*, 1998; Siegfried and Sansó, 2006). Estimating M is often more difficult, even with data-rich techniques (Lee *et al.*, 2011), especially for stocks with a long history of exploitation. However, the ratio of M/k

is known to be often less variable between species than either of the individual parameters in the ratio (Beverton, 1992; Prince *et al.*, 2015).

Many rules-of-thumb have been developed to estimate L_∞ in data-poor stocks. For example, Taylor (1958) suggested that the lifespan of a fish species could be estimated as the age at which fish reach 95% of their asymptotic length; i.e. the mean length of the cohort is $0.95L_\infty$ at a_{max}. Assuming that a cohort is at its mean maximum length (L_{max}) at a_{max}, L_∞ can be estimated by: $L_\infty = L_{max}/0.95$ (Pauly, 1984). If a stock is exploited only relatively lightly, L_{max} could be approximated by the maximum observed length. However, as demonstrated by Hordyk *et al.* (2015, their Figure 1), the assumption that fish are $0.95L_\infty$ at a_{max} does not hold for species where M/k diverges away from the Beverton–Holt Life History Invariant value of 1.5. For example, a species with an M/k
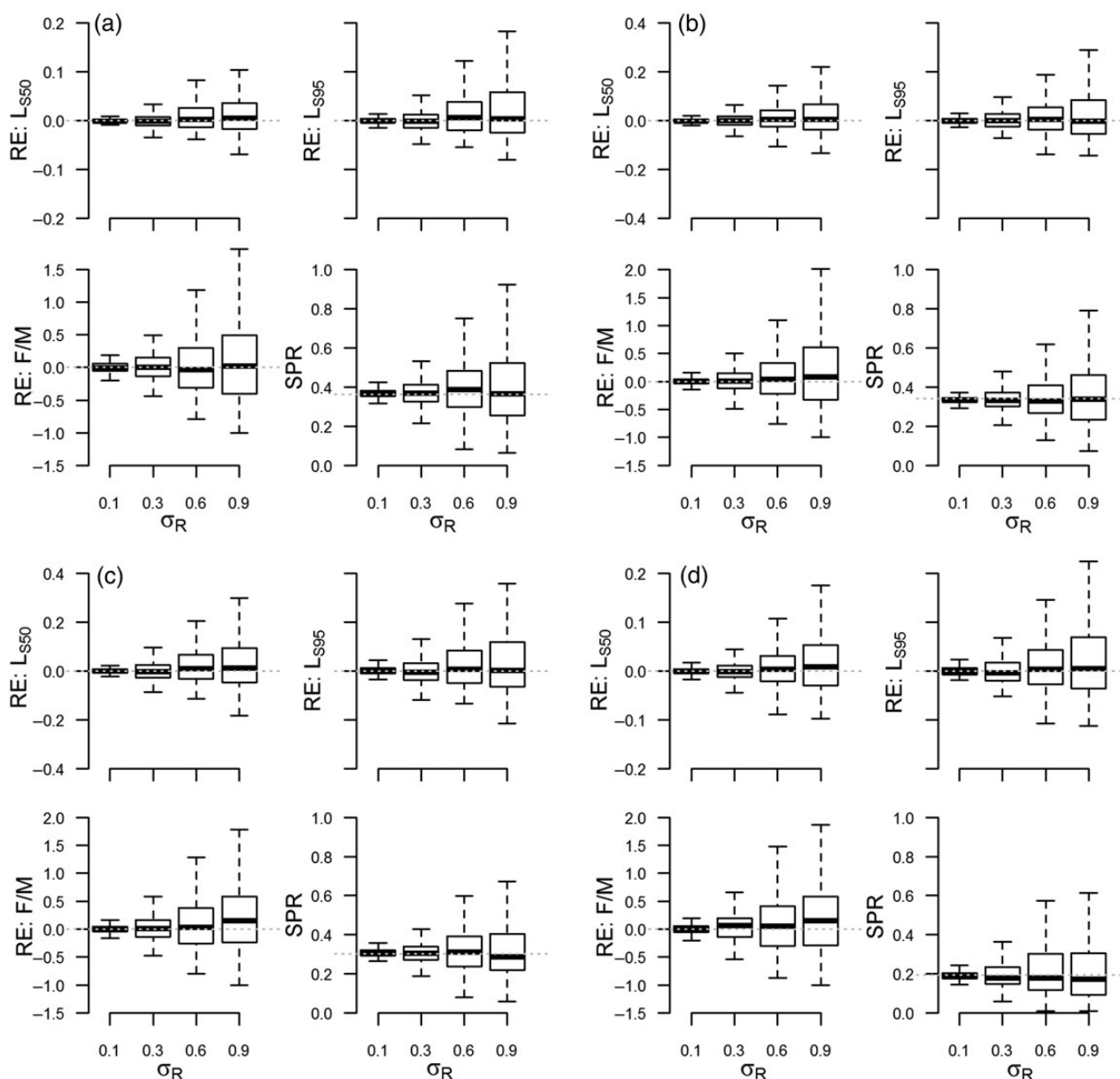
Figure 5. Boxplots showing the 5th, 25th, 50th, and 95th percentiles of the relative error (RE) in the estimated F/M, L_{S50}, L_{S95} and resulting estimate of the SPR with autocorrelated recruitment variability (Test 9) for (a) Species I, (b) Species II, (c) Species III, and (d) Species IV. The biological attributes for the test species are given in Table 1.

ratio of 0.7, i.e. species where individuals reach maximum size relatively early in life, would be expected to reach L_∞ at $\sim 0.7a_{max}$ (i.e. $L_{max} = L_\infty$). In contrast, a species with an M/k ratio of 2.3, i.e. a species that has indeterminate growth, would be expected to only reach $0.8L_\infty$ at the end of its life (i.e. $L_{max} = 0.8L_\infty$) (see Figure 1 in Hordyk *et al.*, 2015). If an estimate of the ratio M/k is known, then the equations derived in Hordyk *et al.* (2015) could be used to estimate L_∞ from L_{max} and M/k, which could then be used to as an estimate of L_∞ for the LB-SPR model developed in the current study.

Beverton (1992) demonstrated that a relationship between M/k and the ratio of size at maturity to asymptotic size (L_m/L_∞) can be derived analytically for teleosts. Hordyk *et al.* (2015) and Prince *et al.* (2015) confirm this relationship from an empirical analytical approach with a meta-analysis of these ratios for 123 species in the

literature. They suggest that the co-varying ratios can be predicted for species based on taxonomic relationships and a species' life-history strategy. Meta-analysis and life-history theory appear to offer a way of estimating these parameters for small-scale and data-poor stocks (Prince *et al.*, 2015). Assuming that other closely related species, or nearby stocks, have a similar life history and are well studied, the ratio L_m/L_∞ from these stocks could be used as a starting estimate for use in the LB-SPR model for estimating SPR for the data-poor stock of interest (Prince *et al.*, 2015).

Representative length data

Hilborn and Walters (1992) warn against using length-based methods, and note that length compositions are often not representative of the whole stock. Unrepresentative samples would cause bias in any stock assessment method and the resulting
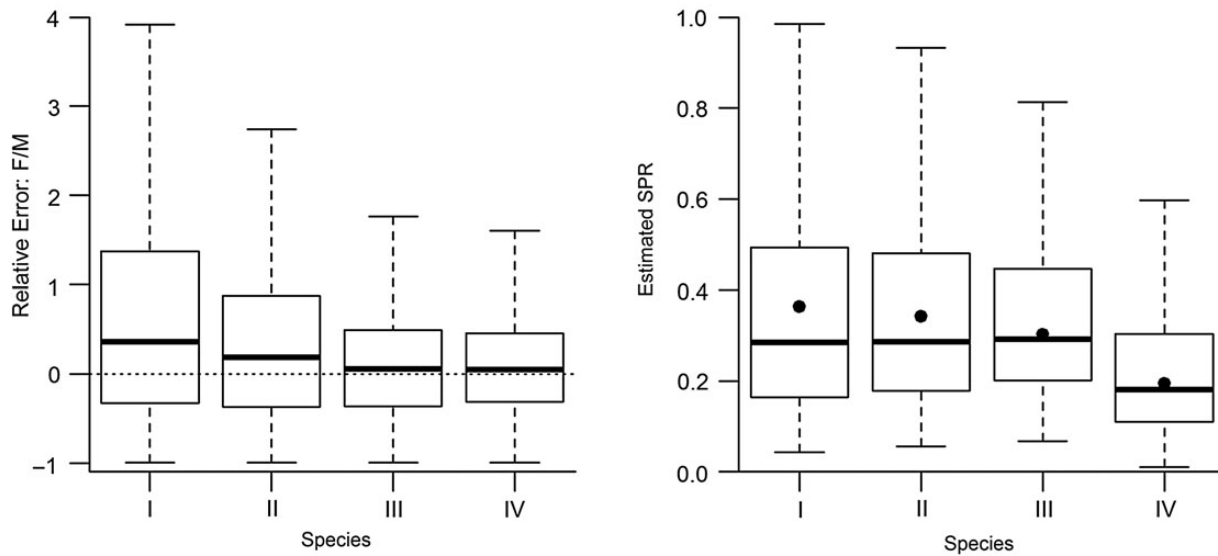
Figure 6. Boxplots showing the 5th, 25th, 50th, and 95th percentiles of the relative error in the estimated F/M and the resulting estimates of the SPR for the four test species from 5000 Monte Carlo simulations with simultaneous error in the three parameters of the LB-SPR method and recruitment variability ($\sigma_R = 0.6$). The solid black points indicate the true SPR for the four species. The biological attributes for the test species are given in Table 1.
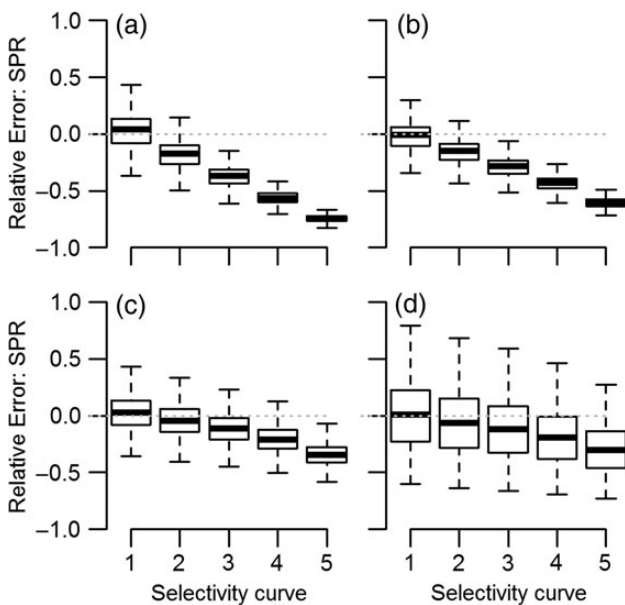

Figure 7. Boxplots showing the 5th, 25th, 50th, and 95th percentiles of the relative error in the estimated SPR for the five different selectivity curves (one asymptotic and four with increasing doming) for Species I, II, III, and IV (a–d, respectively). The biological attributes for the test species are given in Table 1.
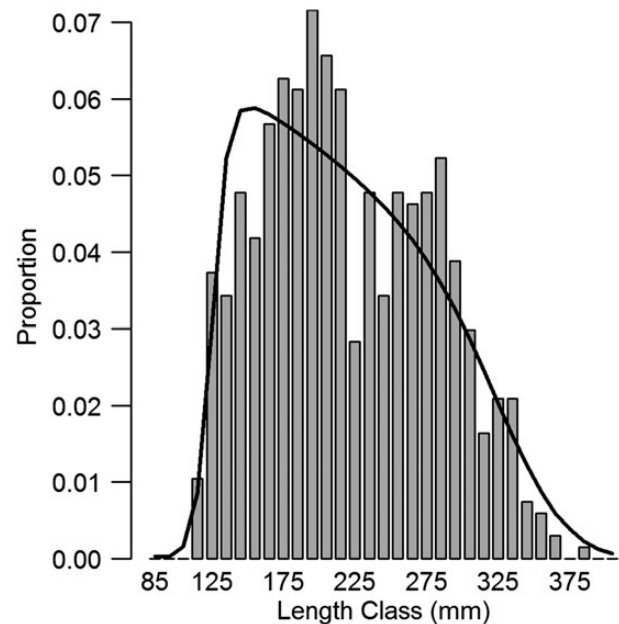

Figure 8. The female length frequency distribution of *S. schomburgkii* (Coulson 2013, Murdoch University, unpublished data) with the fit from the LB-SPR model overlaid as a black solid line. When parameterized with the biological parameters from Coulson *et al.* (2005), the LB-SPR model estimated $F/M = 0.55$ and SPR = 0.44. For comparison, the F/M estimated from the age data was 0.42, which corresponds to an SPR of 0.62.

evaluation of the condition of the stock. Consequently, ensuring that high quality, representative length data are collected for the stock should be an important research priority, and care must be taken in designing a rigorous sampling programme to collect length data. Since the LB-SPR method assumes that any large fish that are missing from the data have been removed by fishing, if the large fish are underrepresented in the length sample for any reason, the LB-SPR method will overestimate F/M and underestimate the SPR (Figure 7).

The precision of the estimated SPR from the length composition data can be increased by simply increasing the sample size of the length measurements (Figure 3). Gerritsen and McGrath (2006) recommend a rule-of-thumb where the minimum sample size is ten times the number of length classes in the sample. Our results and those from other simulation studies suggest that sample sizes of

Table 3. The estimated SPR from the LB-SPR model for the *S. schomburgkii* data (Coulson *et al.,* 2005) for the combination of three different values for the L_∞ and M/k parameters.

	M/k		
L_∞(mm)	0.60	0.88	1.15
330	0.31	0.62	1.00
345	0.23	0.44	0.78
360	0.18	0.34	0.58

1000 length measurements are required to sufficiently capture the features of a length composition (Erzini, 1990). We found that the variation in the estimated SPR was reduced greatly when 1000 measurements were taken (Figure 3). In addition to measuring an adequate number of fish to increase the precision of the estimated SPR, the sampling design should consider the temporal and spatial distribution of the fished stocks to ensure that the sample is a true representation of the length structure of the stock (Gerritsen and McGrath, 2006). For example, if 1000 samples are taken from a single vessel that targeted a spawning aggregation, the effective sample size would be much lower than 1000 and the length data are unlikely to be representative of the stock.

Not surprisingly, the LB-SPR model is particularly sensitive to length composition data from a fishery with dome-shaped selectivity. In particular, species with low M/k (<0.8) are especially sensitive to dome-shaped selectivity. Such species are expected to have a large proportion of the individuals at or near L_∞ (Hordyk *et al.,* 2015), and the LB-SPR model interprets the absence of the large individuals from the size structure as evidence for a high level of exploitation. Species with higher M/k are less sensitive to dome-shaped selectivity, as even in the unfished state, few individuals live long enough to reach asymptotic size, and a smaller fraction of the population is affected by the size-based dome-shaped selectivity. It is often difficult to detect the presence of dome-shaped selectivity, especially when the length composition of the catch are the only available data. If there are multiple fleets targeting the same stock, the LB-SPR model should be applied to the data from the fleet that target the adult portion of the stock, and data that are suspected to come from a fishery with dome-shaped selectivity should be used cautiously. Furthermore, the effects of any recent management changes should also be considered. For example, if there has been a recent change in mesh size, or another form of management that influences the selectivity of the fishery, the length structure of the catch will be affected which may introduce bias into the LB-SPR estimates.

Dynamic effects on estimating SPR

The model developed in this study assumes that the stock is in equilibrium, which means that the current size composition of the stock is assessed against the expected size composition if the stock had experienced a constant level of fishing pressure and constant recruitment. The small-scale fisheries that are the focus of this methodology often experience high levels of fishing pressure. For example, experience with artisanal fisheries of the western Pacific has shown that uncontrolled and unmanaged fisheries are often heavily exploited. Fishing pressure in such fisheries often changes relatively slowly in response to economic forces, rather than in response to management changes which can cause changes on a faster time-scale. The second assumption of constant recruitment, however, is unlikely to hold for many stocks (Myers, 2001). The

simulation of variation in recruitment examined in this study ranged from low, where the standard deviation of recruitment = 0.1 (i.e. $\sigma_R = 0.1$); and the difference between the strongest and weakest year classes is $\approx 1.5 : 1$, to reasonably high, where $\sigma_R = 0.9$ and the difference in magnitude between the strongest and weakest year classes is $\approx 30 : 1$. Not unexpectedly, the results of the LB-SPR model are most variable when the annual recruitment variability is high. The results from our simulations showed that high recruitment variability is likely to cause considerable variation in the estimates from the LB-SPR method, especially when σ_R is ≥ 0.6 (difference in years class strength $\approx 10 : 1$), and the model performed the worst when the recruitment variability was autocorrelated. At low levels of recruitment variability ($\sigma_R = 0.1$) and constant F, the stock is essentially at equilibrium, and F/M, the selectivity parameters, and the SPRs are estimated with minimal error (Figures 4 and 5). However, as the recruitment variation was increased ($\sigma_R = 0.6$ and 0.9), the estimated F/M in any given year could be underestimated by close to 100% ($F/M = 0$, SPR = 1), or overestimated by over 100% (Figures 4 and 5). The relative error in the estimated parameters in the simulations with recruitment variability, however, was centred on 0, and SPR was estimated reasonably well, i.e. within 30% of the real value, in most of the Monte Carlo simulations for all four species. Occasionally, particularly for high recruitment variability ($\sigma_R = 0.9$), the estimates of F/M and the selectivity parameters were very biased, resulting in large over- or underestimates of SPR.

As the LB-SPR model is an equilibrium-based method, and assumes constant recruitment, it cannot fit multimodal length compositions well. Modes in length compositions often occur from a disparity in year-class strength, and following the progression of these modes through time is the foundation for many length-based techniques used to estimate growth and mortality (Pauly and Morgan, 1987). If the length frequency of a population is highly multimodal, the LB-SPR model will not fit the data well, and any estimates of F/M, selectivity and SPR are likely to be unrealistic. This is demonstrated in the poorer performance of the LB-SPR model in the simulations with highly variable, and autocorrelated, recruitment trends. While a good fit of the LB-SPR model does not necessarily imply that the estimates are accurate (the model can potentially fit the data very well even if M/k or L_∞ are misspecified), a poor fit of the model to multimodal length data indicates that the results are likely to be untrustworthy. If the year-classes are clearly identified as modes in the length data, the LB-SPR method may not be the most suitable technique for estimating the status of the stock and other, more traditional, length-based methods may be more applicable. Alternatively, collecting data at a higher temporal resolution (e.g. monthly for short-lived species) and then aggregating the data over a year may provide a means of constructing a length composition more representative of the equilibrium size composition. Furthermore, perfect knowledge of the biological parameters, M/k, L_∞, and CV_{L_∞}, is unlikely, especially for data-poor stocks. Therefore, it must be emphasized to carefully evaluate the results of a single "snapshot" approach using the LB-SPR method, and the validity of the model assumptions and parameter estimates should be examined before implementing the method.

In this study, we did not examine the influence of temporal variability in F. A time-varying F implies that SPR also varies temporally, and the equilibrium-based LB-SPR model will undoubtedly not track the true SPR during this transitional period. A full examination of the dynamic effects (i.e. time-varying F and recruitment

variability) on estimating SPR with the LB-SPR model is outside the scope of this study. A separate study is attempting to develop a harvest control rule to incorporate the LB-SPR model, and evaluate the performance of the LB-SPR model in iteratively driving the stock to a target level of SPR. However, management strategy evaluation modelling conducted by Wayte and Klaer (2010) and Prince et al. (2011) on harvest control rules based on equilibrium-based catch-at-age and SPR-based size targets shows that while individual assessments of size composition may be imprecise due to the transitory dynamics of a population's size structure, smoothed trends estimated over several years provided an accurate basis for harvest control rules. Additionally, Klaer et al. (2012) demonstrate a length-based harvest control rule that iteratively manages catch to drive to stock to a target level. Prince et al. (2011) noted that size composition is often far from equilibrium, and affected by recent recruitment trends, and they included other forms of data (i.e. catch rates) to calibrate the size data. Without these other sources of data, the LB-SPR-based harvest control rule is likely to be less stable. However, our observations support their finding, in that some of the transitory size dynamics we simulated gave LB-SPR estimates that were quite variable, but the median error across estimates was close to zero.

When confronted with a data-poor fishery with only data on the length frequency distribution of the stock, the LB-SPR model may be an effective tool to providing an initial estimate of the stock status, and inform preliminary management advice. However, it must be emphasized that the assumptions and sensitivities of the LB-SPR model are considered carefully when interpreting the estimates of SPR from this method. Furthermore, the application of the LB-SPR model will highlight important research needs, e.g. a better understanding of the growth or maturity schedule, and efforts should be made to collect additional data required for more comprehensive assessment methodologies (e.g. Prince et al., 2011).

Acknowledgements

References

Ault, J., Smith, S., and Bohnsack, J. 2005. Evaluation of average length as an estimator of exploitation status for the Florida coral-reef fish community. ICES Journal of Marine Science, 62: 417–423.

Basson, M., Rosenberg, A. A., and Beddington, J. R. 1988. The accuracy and reliability of two new methods for estimating growth parameters from length-frequency data. ICES Journal of Marine Science, 44: 277–285.

Beckmann, A. T., Gunderson, D. R., Miller, B. S., Buckley, R. M., and Goetz, B. 1998. Reproductive biology, growth, and natural mortality of Puget Sound rockfish Sebastes emphaeus (Starks, 1911). Fishery Bulletin, 96: 352–356.

Beverton, R. J. H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. Journal of Fish Biology, 41: 137–160.

Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations, 19. Fishery Investigation Series II, London, UK. 533 pp.

Bowker, D. W. 1995. Modelling the patterns of dispersion of length at age in teleost fishes. Journal of Fish Biology, 46: 469–484.

Brooks, E. E. N., Powers, J. J. E., and Cortés, E. 2010. Analytical reference points for age-structured models: application to data-poor fisheries. ICES Journal of Marine Science, 67: 165–175.

Clark, W. G. W. 2002. $F_{35\%}$ revisited ten years later. North American Journal of Fisheries Management, 22: 251–257.

Coulson, P. G., Hesp, S. A., Potter, I. C., and Hall, N. G. 2005. Comparisons between the biology of two co-occurring species of whiting (Sillaginidae) in a large marine embayment. Environmental Biology of Fishes, 73: 125–139.

Coulson, P. G., Potter, I. C., Hesp, S. A., and Hall, N. 2007. Biological parameters required for managing western blue groper, blue morwong and yellowtail flathead. Tech. rep., FRDC Project 2004/057, Centre for Fish and Fisheries Research, Murdoch University, Murdoch, Western Australia

Erzini, K. 1990. Sample size and grouping of data for length-frequency analysis. Fisheries Research, 9: 355–366.

Erzini, K. 1994. An empirical study of variability in length-at-age of marine fishes. Journal of Applied Ichthyology, 10: 17–41.

Fournier, D. A., Skaug, H. J., Ancheta, J., Magnusson, A., Maunder, M. N., Nielsen, A., and Sibert, J. 2012. Optimization Methods and Software AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software, 27: 233–249.

Gedamke, T., and Hoenig, J. M. 2006. Estimating mortality from mean length data in nonequilibrium situations, with application to the assessment of goosefish. Transactions of the American Fisheries Society, 135: 476–487.

Gerritsen, H. D., and McGrath, D. 2006. Precision estimates and suggested sample sizes for length frequency data. Fishery Bulletin, 106: 116–120.

Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. In Risk Evaluation and Biological Reference Points for Fisheries Management, 120, pp. 67–81. Ed. by S. J. Smith, J. J. Hunt, and D. Rivard. Canadian Special Publications of Fisheries Aquatic Sciences.

Gulland, J. A., and Rosenberg, A. A. 1992. A review of length-based approaches to assessing fish stocks. FAO Fisheries Technical Paper, 323, Rome. 100 pp.

Hilborn, R., and Walters, C. J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York. 570 pp.

Hoenig, J. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin, 82: 899–903.

Hordyk, A. R., Ono, K., Sainsbury, K., Loneragan, N. R., and Prince, J. D. 2015. Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. ICES Journal of Marine Science, 72: 204–216.

Hughes, S. E. 1974. Stock composition, growth, mortality and availability of Pacific saury, Cololabis saira, of the northwestern Pacific Ocean. Fishery Bulletin, 72: 121–131.

Klaer, N. L., Wayte, S. E., and Fay, G. 2012. An evaluation of the performance of a harvest strategy that uses an average-length-based assessment method. Fisheries Research, 134–136: 42–51.

Lee, H-H., Maunder, M. N., Piner, K. R., and Methot, R. D. 2011. Estimating natural mortality within a fisheries stock assessment model: an evaluation using simulation analysis based on twelve stock assessments. Fisheries Research, 109: 89–94.

Myers, R. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. ICES Journal of Marine Science, 58: 937–951.

O'Farrell, M. R., and Botsford, L. W. 2005. Estimation of change in lifetime egg production from length frequency data. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1626–1639.

O'Farrell, M. R., and Botsford, L. W. 2006. Estimating the status of near-shore rockfish (Sebastes spp.) populations with length frequency data. Ecological Applications, 16: 977–986.

Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews, 8: 1–325.

Pauly, D., and Morgan, G. P. R. 1987. Length-based methods in fisheries research. ICLARM Conference Proceedings 13, Manila.

Pearson, D. E., and Mcnally, S. V. G. 2005. Age, growth, life history, and fisheries of the sand sole, *Psettichthys melanostictus*. Marine Fisheries Review, 67: 9–18.

Prince, J. D., Dowling, N. A., Davies, C. R., Campbell, R. A., and Kolody, D. S. 2011. A simple cost-effective and scale-less empirical approach to harvest strategies. ICES Journal of Marine Science, 68: 947–960.

Prince, J., Hordyk, A., Valencia, S. R., Loneragan, N., and Sainsbury, K. 2015. Revisiting the concept of Beverton–Holt life-history invariants with the aim of informing data-poor fisheries assessment. ICES Journal of Marine Science, 72: 194–203.

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

R Development Core Team. 2012. R: a Language and Environment for Statistical Computing.

Sainsbury, K. J. 1980. Effect of individual variability on the von Bertalanffy growth equation. Canadian Journal of Fisheries and Aquatic Sciences, 37: 241–247.

Siegfried, K. I., and Sansó, B. 2006. Two bayesian methods for estimating parameters of the von Bertalanffy growth equation. Environmental Biology of Fishes, 77: 301–308.

Smith, B. D., Botsford, L. W., and Wing, S. R. 1998. Estimation of growth and mortality parameters from size frequency distributions lacking age patterns: the red sea urchin (*Strongylocentrotus franciscanus*) as an example. Canadian Journal of Fisheries and Aquatic Sciences, 55: 1236–1247.

Taylor, C. C. 1958. Cod growth and temperature. Journal du Conseil International Pour L'Exploration de la Mer, 23: 366–370.

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

Watanabe, Y., Butler, J. L., and Mori, T. 1988. Growth of the Pacific saury, *Cololabis saira*, in the northeastern and northwestern Pacific Ocean. Fishery Bulletin, 86: 489–498.

Wayte, S. E., and Klaer, N. L. 2010. An effective harvest strategy using improved catch-curves. Fisheries Research, 106: 310–320.

Zhou, S., Yin, S., and Thorson, J. 2012. Linking fishing mortality reference points to life history traits: an empirical study. Canadian Journal of Fisheries and Aquatic Sciences, 69: 1292–1301.

Handling editor: Emory Anderson