Full length article

Extending integrated stock assessment models to use non-depensatory three-parameter stock-recruitment relationships

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ABSTRACT

Stock assessments based on the integrated paradigm often include an underlying stock-recruitment relationship. This, along with estimates of fishery selectivity and biological parameters, allows the biomass and fishing mortality associated with Maximum Sustainable Yield (B_{MSY} and F_{MSY} respectively) to be calculated. However, the estimates of these quantities may differ from the proxies assumed in the harvest control rules that are used to provide management advice. Moreover, the estimated values for B_{MSY} and F_{MSY} are related functionally in population dynamics models based on 2-parameter stock-recruitment relationships such as the commonly used Beverton-Holt or Ricker relationships. Use of 2-parameter stock-recruitment relationships (SRRs) consequently restricts the ability to fully quantify the uncertainty associated with estimating B_{MSY} and F_{MSY} because 2-parameter SRRs restrict the potential range of values for B_{MSY}/B_0. In principle, B_{MSY}/B_0 and F_{MSY} can be more independent if the stock-recruitment relationship is more general than these 2-parameter SRRs. This paper outlines eleven potential 3-parameter stock-recruitment relationships and evaluates them in terms of whether they are able to match a wide range of specifications for B_{MSY} (expressed relative to unfished spawning stock biomass, B_0) and F_{MSY} (expressed relative to natural mortality, M). Of the eleven 3-parameter stock-recruitment relationships considered, the Ricker-Power stock-recruitment relationship is found to best satisfy the characteristics of (a) being able to mimic a wide range of B_{MSY}/B_0 and F_{MSY}/M values, (b) not to lead to negative recruitment for biomasses between 0 and B_0, and (c) not to lead to increasing recruitment while approaching the limit of zero population size. Bayesian assessments of three example groundfish species off the US west coast (aurora rockfish, petrale sole, and cabezon) are conducted using Simple Stock Synthesis based on the Beverton-Holt and Ricker-Power stock-recruitment relationships to illustrate some of the impacts of allowing for a 3-parameter stock-recruitment relationship.

1. Introduction

Many fishery jurisdictions conduct stock assessments in which population dynamics models are fit to monitoring data. These assessments provide various types of information for use in management. For example, they *inter alia* provide estimates of current spawning stock biomass, unfished spawning stock biomass, current spawning stock biomass relative to reference points, and the inputs for harvest control rules selected to provide scientific recommendations regarding limits on catch and effort. Several jurisdictions rely on estimates of the biomass and fishing mortality corresponding to Maximum Sustainable Yield (B_{MSY} and F_{MSY} respectively). B_{MSY} defines the target biomass (e.g., in the USA; Punt et al., 2006), or forms the basis for calculating the target biomass (e.g., in Australia; Rayns, 2007), while the target (or

limit) fishing mortality is often set equal to F_{MSY} or some fraction thereof.

It is well known that the performances of management strategies are not very sensitive to the choice of the proxies for B_{MSY} in harvest control rules (e.g., Clark 1991, 2002; Hilborn, 2010; Punt et al., 2014a). Many of the "integrated" methods of stock assessment (Fournier and Archibald, 1982; Maunder, 1998; Maunder and Punt, 2013) are based on population dynamics models include an underlying stock-recruitment relationship (SRR; Dichmont et al., 2016), and can provide estimates of B_{MSY} and F_{MSY}. However, these estimates are rarely used when applying harvest control rules. This can be concerning to stakeholders, especially when the estimates of B_{MSY} and F_{MSY} from the assessment differ substantially from the proxies used to provide management advice. In principle, it is possible to parameterize population dynamics

models in terms of the value of B_{MSY} (usually expressed relative to the average unfished B_0, i.e., B_{MSY}/B_0) and F_{MSY} (expressed relative to natural mortality M) (i.e., by adopting a "leading parameters" approach (Schnute and Kronlund, 1996; Schnute and Richards, 1998; Martell et al., 2008)).

Martell et al. (2008) show how it is possible to parameterize population dynamics models based on F_{MSY} and MSY when the SRR is of the Beverton-Holt or Ricker form. Unfortunately, simply parameterizing conventional stock assessments in terms of F_{MSY} and MSY (see Dichmont et al., 2016 for a review of the packages on which model-based approaches to stock assessment used in the US are based) will not address several other issues related to how productivity is modelled in the population dynamics models on which stock assessments are based.

- Most integrated stock assessments are based on the Beverton-Holt or Ricker form of the SRR (with constant recruitment a special case of a Beverton-Holt SRR).[1] Unfortunately for these functional forms, specifying B_{MSY}/B_0 is the same as determining the productivity of the population as quantified by F_{MSY} (see Fig. 1 for examples of the relationship between F_{MSY} and B_{MSY}/B_0 for the three example species of this paper; Section 2). Thus, the use of 2-parameter SRRs restricts the potential range of values for B_{MSY}/B_0.
- Methods of assessment wherein the population size at which MSY is achieved relative to the unfished size is pre-specified are often conducted for cetaceans (e.g., de la Mare, 1989; Punt, 1999), and the results of these assessments often suggest that B_{MSY}/B_0 (usually expressed in numbers rather than biomass) is poorly determined when attempts as made to estimate this quantity from monitoring data (e.g., Givens et al., 1995; Punt and Wade, 2012). In contrast, the use of 2-parameter SRRs, as is typically the case for assessments of fish stocks, means that it is inferred that B_{MSY}/B_0 is well-determined by the data if F_{MSY} is well-determined by the data (or that B_{MSY}/B_0 is actually pre-specified if F_{MSY} is pre-specified).
- Many stock assessments, particularly for data-poor scenarios, are now based on methods of stock assessment that quantify uncertainty using Bayesian methods (e.g., Simple Stock Synthesis – SSS: Cope, 2013; Depletion-Based Stock Reduction Analysis – DB-SRA: Dick and MacCall, 2011). Many assessment methods based on age- or size-structured population dynamics models that include integrated SRRs are parameterized in terms of the steepness of the SRR (h: the proportion of unfished recruitment, R_0, when spawning stock biomass is reduced to 20% of B_0: Francis, 1992) and some measure of unfished biomass. However, the relationship between steepness and B_{MSY}/B_0 is non-linear (Fig. 1) so placing (for example) a uniform prior on steepness is not equivalent to the placing such a prior on B_{MSY}/B_0. Moreover, the range for B_{MSY}/B_0 possible for either of the Beverton-Holt or Ricker SRRs is only a subset of the possible U[0,1] range (Punt et al., 2014a; Mangel et al., 2013; Fig. 1).

The issues outlined above suggest the need for stock assessments to include 3- as well as 2-parameter SRRs so a) there are models with no implicit relationship between B_{MSY}/B_0 and F_{MSY}/M, b) it is possible for the population dynamics model to be parameterized in terms of any values of B_{MSY}/B_0 and F_{MSY}/M, and c) priors can be placed on these 'leading parameters'. This paper therefore describes thirteen potential SRRs (two 2-parameter and eleven 3-parameter SRRs), some of which have been proposed in the literature in the past. It then evaluates these relationships in terms of their capacity to achieve a broad range of values for F_{MSY} (expressed in this paper as relative to natural mortality, and thus dimensionless) and B_{MSY}/B_0, and whether they exhibit desirable properties of SRRs, such as being defined for the entire range of

possible values for B/B_0. The paper finally explores the implications of conducting data-poor (catch only) assessments based on the Beverton-Holt SRR and the "best" of the eleven 3-parameter SRRs for three stocks representing contrasting life history types.

2. Example species

The analyses in this paper are based on information for three example species: aurora rockfish (*Sebastes aurora*), petrale sole (*Eopsetta jordani*), and cabezon (*Scorpaenichthys marmoratus*) off the US west coast. These three species cover the range from relatively short-lived and fast growing (cabezon) to very long-lived and slow growing (aurora rockfish). Table 1 lists the values for the biological parameters (growth, natural mortality and fecundity) for these species. Fishery selectivity is assumed to be the same as maturity for consistency with how assessments for data poor species are often undertaken using Simple Stock Synthesis (Cope, 2013).

3. Candidate stock-recruitment relationships

Table 2 lists the thirteen SRRs considered in this paper. It contains two 2-parameter SRRs (Beverton-Holt and Ricker), along with eleven 3-parameter SRRs. The SRRs are parameterized in terms of the average unfished spawning stock biomass, B_0, and the steepness of the SRR. Thus, all of the SRRs in Table 2 satisfy $R_0 = f(B_0)$ and $hR_0 = f(0.2B_0)$, where f denotes the stock-recruitment relationship. The SRRs in Table 2 include ten forms that generalize the Beverton-Holt and Ricker SRRs by raising various functions of spawning stock biomass to a power (γ), and the Pella-Tomlinson SRR, which is commonly used in assessments of cetacean stocks. Most of the SRRs in Table 2 have been introduced to the literature before, but the BH-Power, General-BH-B, Ricker-Power, General-Ricker-A, and General-Ricker-B relationships are (to our knowledge) new to this paper. In principle, SRRs that generalize the 2-parameter Cushing (1971, 1973) SRR could have been considered, but such relationships do not allow include as a special case a SRR for which recruitment asymptotes with increasing spawning biomass, so were not considered as a candidate form for developing generalized SRRs.

Figs. 2 and 3 show the relationships between recruitment and spawning stock biomass for the thirteen SRRs in Table 2 for various choices for h and γ (the Beverton-Holt and Ricker stock-recruitment relationships correspond to $\gamma = 1$ in the center panels of Figs. 2 and 3). All curves pass through the points (B_0, R_0) and $(0.2B_0, hR_0)$ by design.

It is possible to obtain both asymptotic and dome-shaped SRRs depending on the values for the parameters h and γ. All of the SRRs are well behaved when $\gamma = 1$ and h is 0.3 or 0.8 (Figs. 2b,e, 3b,e). Some of the SRRs lead to potentially unrealistic outcomes for other combinations of h and γ. For example, (a) the Shepherd, BH-Power, and Myers et al. SRRs can exhibit a pole at low levels of B/B_0 (i.e., recruitment approaches infinity or negative infinity as biomass approaches a critical value for B/B_0) where the relative biomass at which the pole occurs depends on h and γ (see the right column on Table 2), (b) the Ricker-Power SRR leads to monotonically increasing recruitment when $\gamma \leq 0$ and $0 < B < B_0$ (Fig. 3a,d,g), (c) the BH-Power, Taylor et al. and Gamma SRRs lead to infinite recruitment as $B \to 0$ when $\gamma < 0$, and (d) the BH-Power, Myers et al., General-BH-B, Gamma, General-Ricker-A, and General-Ricker-B SRRs lead to depensation over some or part of their range (critical depensation when steepness is low; e.g. Fig. 3c). Although some of these features suggests that these SRRs may be inappropriate for routine use in stock assessments, it is not clear that the parameter combinations concerned correspond to realistic values for F_{MSY}/M and B_{MSY}/B_0. This is explored in Section 4.

4. Computing MSY

In equilibrium, the fully-selected fishing mortality corresponding to

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[1] An exception is Stock Synthesis (Methot and Wetzel, 2013), which includes the Shepherd SRR and a 3-parameter SRR developed for low productivity species such as sharks (Taylor et al., 2013).
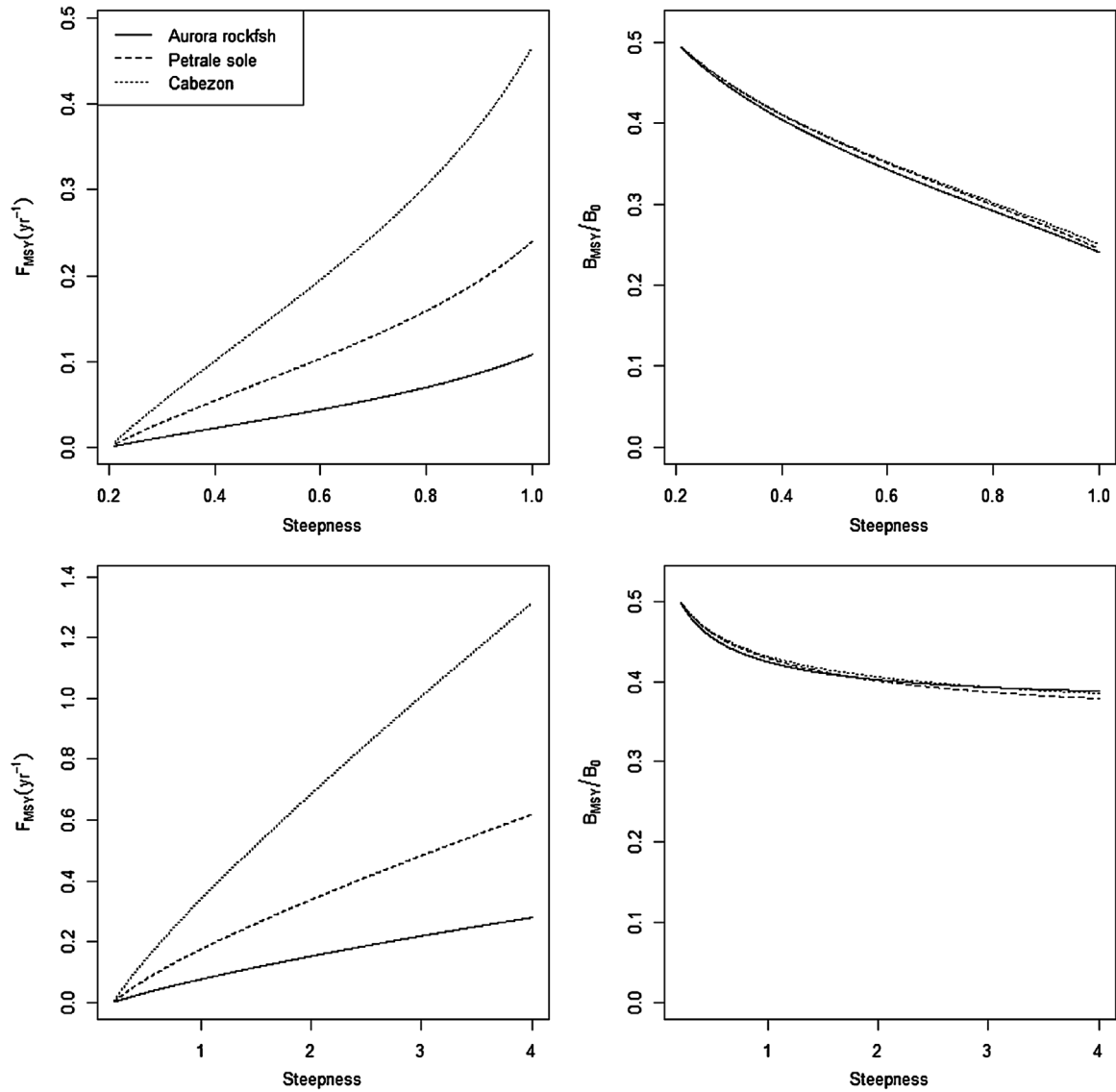
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Fig. 1. Relationship between steepness and F_{MSY} and B_{MSY}/B_0 for the Beverton-Holt (upper row) and Ricker stock-recruitment relationships (lower row). Results are shown for the three example species (lines).

Table 1
Parameters of the population dynamics models for the example species.
sources: Cope et al. (2003); PFMC (2016).

Life history parameter	Aurora rockfish	Petrale sole	Cabezon
Natural mortality (M) (yr^{-1})	0.04	0.15	0.25
Von Bertalanffy Growth			
L_∞ (cm)	31.42	60.38	60.1935
κ (yr^{-1})	0.09	0.13	0.15
t_0 (yr)	−2.32	−0.30	−1.04
CV (age 0)	0.13	0.19	0.10
CV (L_∞)	0.09	0.03	0.18
Weight-length regression			
Intercept (gm/cm$^\psi$)	0.000010	0.0000021	0.0000092
Power, ψ	3.14	3.47	3.19
Maturity			
Length-at-50%-maturity (cm)	25.54	33.10	34.60
Length-at-95%-maturity (cm)	30.29	37.08	38.81

MSY is defined by:

$$\left.\frac{dC(F)}{dF}\right|_{F=F_{MSY}} = 0 \tag{1}$$

where $C(F) = \widetilde{C}(F)R(F)$, $\widetilde{C}(F)$ is yield-per-recruit as a function of fully-selected fishing mortality, and $R(F)$ is recruitment when fully-selected fishing mortality[2] is F (Sissenwine and Shepherd, 1987). The spawning biomass corresponding to MSY is defined as $B(F_{MSY}) = \widetilde{B}(F_{MSY})\,R(F_{MSY})$ where $\widetilde{B}(F_{MSY})$ is spawning biomass-per-recruit as a function of fully-selected fishing mortality. Eq. (1) can be expanded to:

$$R(F_{MSY})\left.\frac{d\widetilde{C}(F)}{dF}\right|_{F=F_{MSY}} + \widetilde{C}(F_{MSY})\left.\frac{dR(F)}{dF}\right|_{F=F_{MSY}} = 0 \tag{2}$$

Computation of $R(F)$ and hence $\frac{dR(F)}{dF}$ for any SRR involves solving the SRR for recruitment as a function of $\widetilde{B}(F)$, recognizing that $R(F) = f(R(F)\widetilde{B}(F))$. It is possible to solve this equation for many of the SRRs (Table 3). However, those SRRs for which recruitment can be

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[2] If there are multiple fleets, the relative fishing mortality among fleets is usually specified, e.g. based on the fully-selected fishing mortality for the last year of the assessment.

Table 2

The candidate stock-recruitment relationships, parameterized in terms of R_0 and h. Note $h > 0.2$ is required for there to be compensation. The sets of values for biomass (B), shape parameter (γ), and steepness (h) where recruitment is undefined or negative is outlined for the stock-recruitment relationships considered for further analysis.

Stock-recruitment relationship	Original	Reparameterized	Undefined (or negative recruitment
2-parameter forms			
Beverton-Holt	$R = \frac{\alpha B}{1+\beta B}$	$R = \frac{R_0 B}{B_0} \frac{4h}{(1-h)+(5h-1)B/B_0}$	$h > 1$ (infinite recruitment at $B_0 \frac{1-h}{5h-1}$)
Ricker	$R = \alpha B e^{-\beta B}$	$R = \frac{R_0 B}{B_0} e^{\ell n(5h)(1-B/B_0)/0.8}$	
3-parameter forms			
Pella-Tomlinson	$R = \alpha B(1+\beta(1-(B/B_0)^\gamma))$	$R = \frac{R_0 B}{B_0}\left(1+\frac{(5h-1)(1-(B/B_0)^\gamma)}{1-0.2^\gamma}\right)$	$B > B_0\left(\frac{5h-0.2^\gamma}{5h-1}\right)^{1/\gamma}$ (negative recruitment) $\gamma < -1$ (increasing recruitment as $B \to 0$)
Shepherd (1982)	$R = \frac{\alpha B}{1+\beta B^\gamma}$	$R = \frac{R_0 B}{B_0}\left(\frac{5h[1-0.2^\gamma]}{1-5h0.2^\gamma+(5h-1)(B/B_0)^\gamma}\right)$	$B < B_0\left(\frac{5h0.2^\gamma-1}{5h-1}\right)^{1/\gamma}$ (negative recruitment) $h > 1/0.2^{\gamma-1}$ & $\gamma < 0$ (there will be a region of negative recruitment)
Deriso (1980)[a]	$R = \frac{\alpha B}{(1+\beta B)^\gamma}$	$R = \frac{R_0 B}{B_0}\left(\frac{(5h)0.8^\gamma}{(1-0.2(5h)^{1/\gamma}+((5h)^{1/\gamma}-1)B/B_0)^\gamma}\right)$	$B < B_0 \frac{0.2(5h)^{1/\gamma}-1}{(5h)^{1/\gamma}-1}$ if $0 < \gamma < 1$ (negative recruitment) $B > B_0\frac{0.2(5h)^{1/\gamma}-1}{(5h)^{1/\gamma}-1}$ $\gamma < 0$ (negative recruitment) $h < 5^{\gamma-1}$ & $\gamma < 1$ (there will be a region of negative recruitment)
Ricker-Power	$R = \alpha B e^{-\beta(1-B/B_0)^\gamma}$	$R = \frac{R_0 B}{B_0} e^{\ell n(5h)(1-B/B_0)^\gamma/0.8^\gamma}$	$\gamma < 0$ (infinite recruitment as $B \to 1$) $B > B_0$ (negative recruitment)
Taylor et al. (2013)	$R = \alpha B e^{-\beta B^\gamma}$	$R = \frac{R_0 B}{B_0} e^{\frac{\ell n(5h)(1-(B/B_0)^\gamma)}{(1-0.2^\gamma)}}$	$\gamma < 0$ (infinite recruitment as $B \to 0$)
BH-Power	$R = \frac{\alpha B^\gamma}{1+\beta B}$	$R = R_0\left(\frac{B}{B_0}\right)^\gamma \frac{0.8h}{0.2^\gamma-0.2h+(h-0.2^\gamma)B/B_0}$	
Myers et al. (1995)	$R = \frac{\alpha B^\gamma}{1+\beta B^\gamma}$	$R = R_0\left(\frac{B}{B_0}\right)^\gamma \frac{(1-0.2^\gamma)h}{0.2^\gamma(1-h)+(h-0.2^\gamma)(B/B_0)^\gamma}$	
General-BH-B	$R = \frac{\alpha B^\gamma}{(1+\beta B)^\gamma}$	$R = =R_0\left(\frac{B}{B_0}\right)^\gamma \frac{4^\gamma h}{1-h^{1/\gamma}+(5h^{1/\gamma}-1)(B/B_0))^\gamma}$	
Gamma	$R = \alpha B^\gamma e^{-\beta B}$	$R = R_0(B/B_0)^\gamma e^{\ell n(h/0.2^{-\gamma})(1-B/B_0)/0.8}$	
General-Ricker-A	$R = \alpha B^\gamma e^{-\beta(1-B/B_0)^\gamma}$	$R = R_0(B/B_0)^\gamma e^{\frac{\ell n(h0.2^{-\gamma})}{0.8^\gamma}(1-B/B_0)^\gamma}$	
General-Ricker-B	$R = \alpha B^\gamma e^{-\beta B^\gamma}$	$R = R_0(B/B_0)^\gamma e^{-\frac{\ell n(h0.2^{-\gamma})}{1-0.2^\gamma}(1-(B/B_0)^\gamma)}$	

[a] Mathematically equivalent to the stock-recruitment relationship used by Schnute (1985).

less than the replacement line, which is a function of fully-selected fishing mortality, (BH-Power, General-BH-B, Myers et al.,[3] Gamma, General-Ricker-A, General-Ricker-B) there are multiple recruitments that satisfy $R(F) = f(R(F)\widetilde{B}(F))$ (see Supplementary Figs. 1 and 2 for analyses for the Gamma SRR). Thus, these SRRs are not considered further in this paper.[4]

Fig. 4 shows yield functions for the five non-depensatory 3-parameter SRRs in Table 2 as well as for the Beverton-Holt and Ricker SRRs. As expected, the yield at $0.2B_0$ is the same for all SRRs given the same value for h. However, the biomass at which MSY is achieved differs among SRRs. In general (the exception being the Ricker-Power SRR), B_{MSY}/B_0 is reduced as γ is reduced, while MSY as a fraction of B_{MSY} (and hence F_{MSY}) increases with increasing steepness.

Eq. (2) can be solved for h using Newton's method given values for F_{MSY} and γ (it is analytical for the Beverton-Holt and Ricker SRRs; Martell et al., 2008). The values for h and γ are therefore found by searching for γ such that $B(F_{MSY})/B_0$ equals the pre-specified value for B_{MSY}/B_0 when steepness is selected such that $\frac{dC(F)}{dF}\big|_{F=F_{MSY}} = 0$. The search process involves a combination of the use of the Nelder-Mead algorithm, on occasion combined with random choices for starting values. However, the Ricker-Power SRR does not exhibit a maximum for $\gamma < 1$ and is undefined for $B > B_0$ for $\gamma < 1$ (except for integers), and the Shepherd and Taylor et al. SRRs achieve maximum yield as $B \to 0$ for $\gamma < 1$.

The values for h and γ were calculated for all combinations of F_{MSY}/

$M \in [0.2, 2]$ and $B_{MSY}/B_0 \in [0.1, 0.9]$ for the three example species for the five non-depensatory 3-parameter SRRs. Supplementary Figs. 3 and 4 plot h and γ vs F_{MSY}/M and B_{MSY}/B_0 for these species. Fig. 5 shows yield curves and SRRs for five combinations of F_{MSY}/M and B_{MSY}/B_0 for each of the five SRRs in Fig. 4 for petrale sole (results for aurora rockfish and cabezon are qualitatively identical; Supplementary Figs. 5 and 6). The yield curves and SRRs for the Pella-Tomlinson and Ricker-Power SRRs are as expected (although recruitment is increasing as $B \to 0$ for the Pella-Tomlinson SRR). The yield curves for $B_{MSY}/B_0 = 0.4$ and 0.9 appear reasonable for the Shepherd, Deriso, and Taylor et al. SRRs, but this is not the case when $B_{MSY}/B_0 = 0.1$. For these SRRs, $B_{MSY}/B_0 = 0.1$ is local minimum rather than global maximum of the yield function and recruitment exhibits a pole for $B > 0$. Fig. 6 provides a summary of the performance of the various SRRs. The Ricker-Power SRR requires the fewest constraints for general use in stock assessments followed by the Pella-Tomlinson. The remaining SRRs lead to results that would preclude their general use in stock assessments.

Fig. 6 indicates the extent to which the SRRs are dome-shaped. The greatest extent of dome-shapedness occurs for high values for F_{MSY}/M and B_{MSY}/B_0, with R_{max} (the maximum recruitment when biomass is between 0 and B_0) often exceeding twice R_0 when B_{MSY}/B_0 exceeds 0.8 and $F_{MSY} > M$.

5. Use in stock assessments

The results in the previous section suggest that the Ricker-Power SRR (and to a lesser extent the Pella-Tomlinson SRR) are able to capture a wide range of possible shapes for the yield function. The Pella-Tomlinson SRR has the undesirable feature that recruitment can increase as $B \to 0$ (i.e., when B_{MSY}/B_0 is low). It also predicts negative recruitment for some values of $B > B_0$ (Table 2). The Ricker-Power appears to exhibit no undesirable properties for $0 < B \le B_0$, but is

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[3] Liermann and Hilborn (1997, 2000) based their analysis of how often stock and recruitment data for fish stocks are depensatory using this relationship.

[4] In principle, rules could be imposed to specify which leg of the relationships (likely upper) in Supplementary Fig. 1 is used when computing recruitment given spawning biomass-per-recruit. However, this would be computationally infeasible in a stock assessment context.
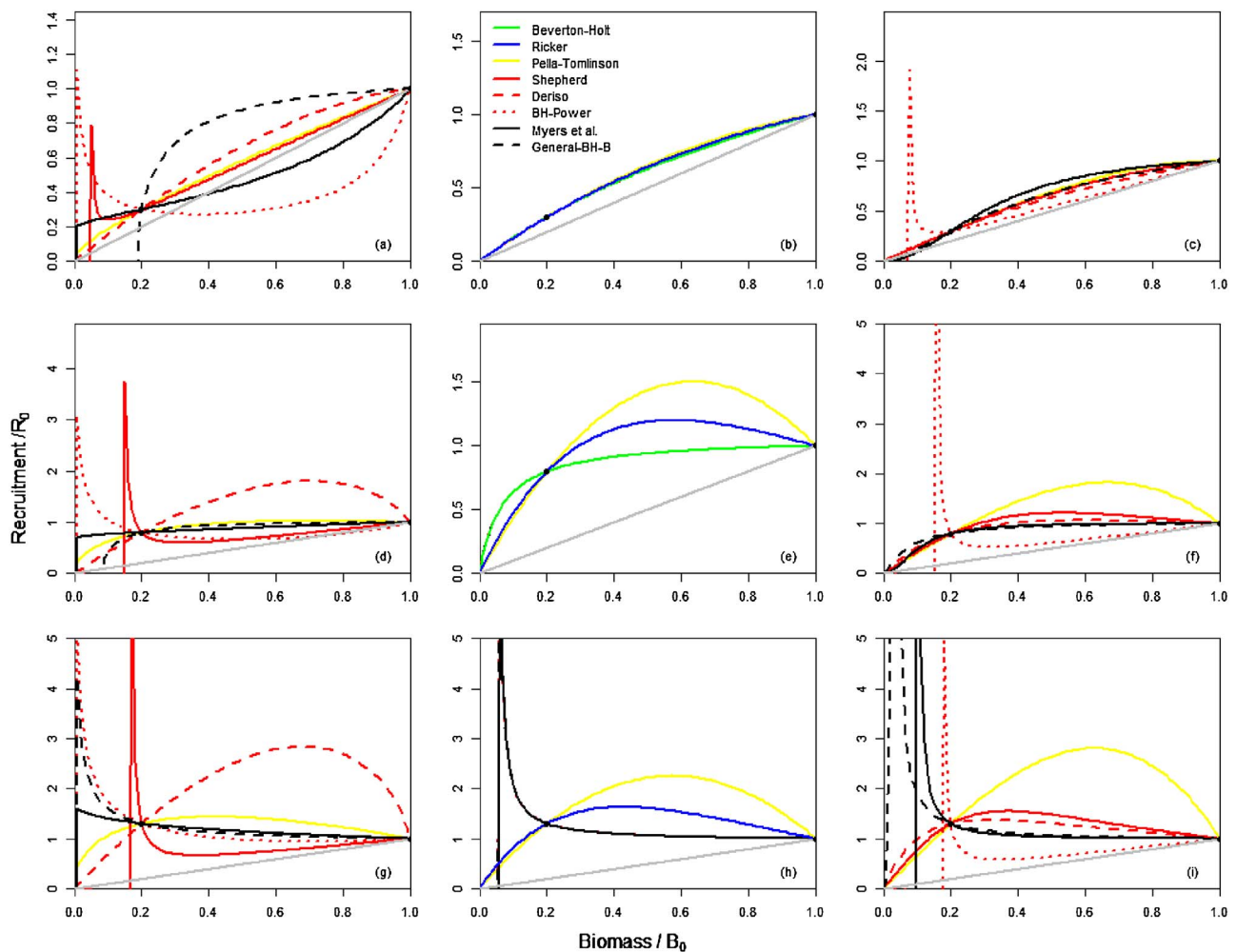
Fig. 2. Relationships between recruitment (expressed relative to R_0) and spawning stock biomass (expressed relative to B_0) for eight of the SRRs. The columns show results for values for γ of -0.5, 1 and 2 and the rows show results for values for h of 0.3, 0.8 and 1.3. Results are shown for the Beverton-Holt, Ricker, and Pella-Tomlinson SRRs and various generalization of the Beverton-Holt SRR. Note that results are only shown for the Beverton-Holt and Ricker SRRs for $\gamma = 1$ as these are 2-parameter forms. The various generalizations of the Beverton-Holt SRRs are the same for $\gamma = 1$. The gray line denotes the replacement line corresponding to zero fishing mortality.

undefined for all values of $B > B_0$ if $\gamma < 1$ and not an integer. However, γ is larger than 1 for few combinations of F_{MSY}/M and B_{MSY}/B_0 in Figs. 5 and 6 so this concern is not likely a major issue for actual stock assessments.

The impact of moving to a general SRR is explored for the data-limited assessment method Simple Stock Synthesis (SSS) (Cope, 2013). This method is based on the Stock Synthesis package (Methot and Wetzel, 2013), but pre-specifies selectivity, natural mortality, growth and steepness, and calculates unfished recruitment (R_0) given a value for depletion (spawning stock biomass relative to B_0) in a pre-specified year. All fixed values are drawn from prior distributions in a Monte Carlo approach to represent uncertainty in model-derived outputs. The SRR in SSS is conventionally taken to be Beverton-Holt, with priors for stock-recruitment steepness that differ between flatfishes, rockfishes, and roundfishes (Cope, 2013). SSS was applied to data for the three example species (see Supplementary Fig. 7 for the catch history for each species) when the SRR is taken to be the Beverton-Holt and Ricker-Power functions. The priors for F_{MSY}/M and B_{MSY}/B_0 (Ricker-Power only), and stock status (Table 4) were based on Zhou et al. (2012), Thorson et al. (2012), and Cope et al. (2015b) respectively.

Supplementary Figs. 8–10 summarize the distributions assumed for F_{MSY}/M and B_{MSY}/B_0, along with a diagnostic that compares the pre-specified values for these parameters with the values computed within Stock Synthesis when the SRR has the Ricker-power form to confirm

that it is indeed possible to achieve the desired distributions for these parameters. Fig. 7 compares the realised distributions for F_{MSY}/M and B_{MSY}/B_0, showing that the two SRRs lead to the same marginal distributions for F_{MSY}/M, but that (as expected) the Ricker-Power SRR covers a broader range of values for B_{MSY}/B_0.

Table 5 compares the distributions for the Overfishing Level (application of F_{MSY} to the exploitable biomass for most recent year) for the three example species for the two SRRs. The results for the two SRRs for aurora rockfish are very similar (see also the upper right panel of Fig. 7). However, the distribution of the OFL for cabezon is shifted to higher values for the Beverton-Holt SRR, while this is also the case for much of the distribution for petrale sole. The only differences between the results for the two SRRs is the form of the SRR and the values for their parameters, but these differences lead to differences in final depletion, even given that year 2000 depletion is the same (Fig. 8a,b,d,e,g,h). The Ricker-Power SRR leads to greater variation about the year 2000 vs final depletion relationship (contrast the center with the left panels of Fig. 8), particularly for the more productive species cabezon and petrale sole; this result is not surprising given the Ricker-Power function has additional parameters and the influence of the SRR is greater for more productive stocks. The relationship between final depletion from the two SRRs is almost exact for the aurora rockfish (Fig. 8c), but there is quite considerable variation about the 1-1 line for the two more productive species (Fig. 8f,g).
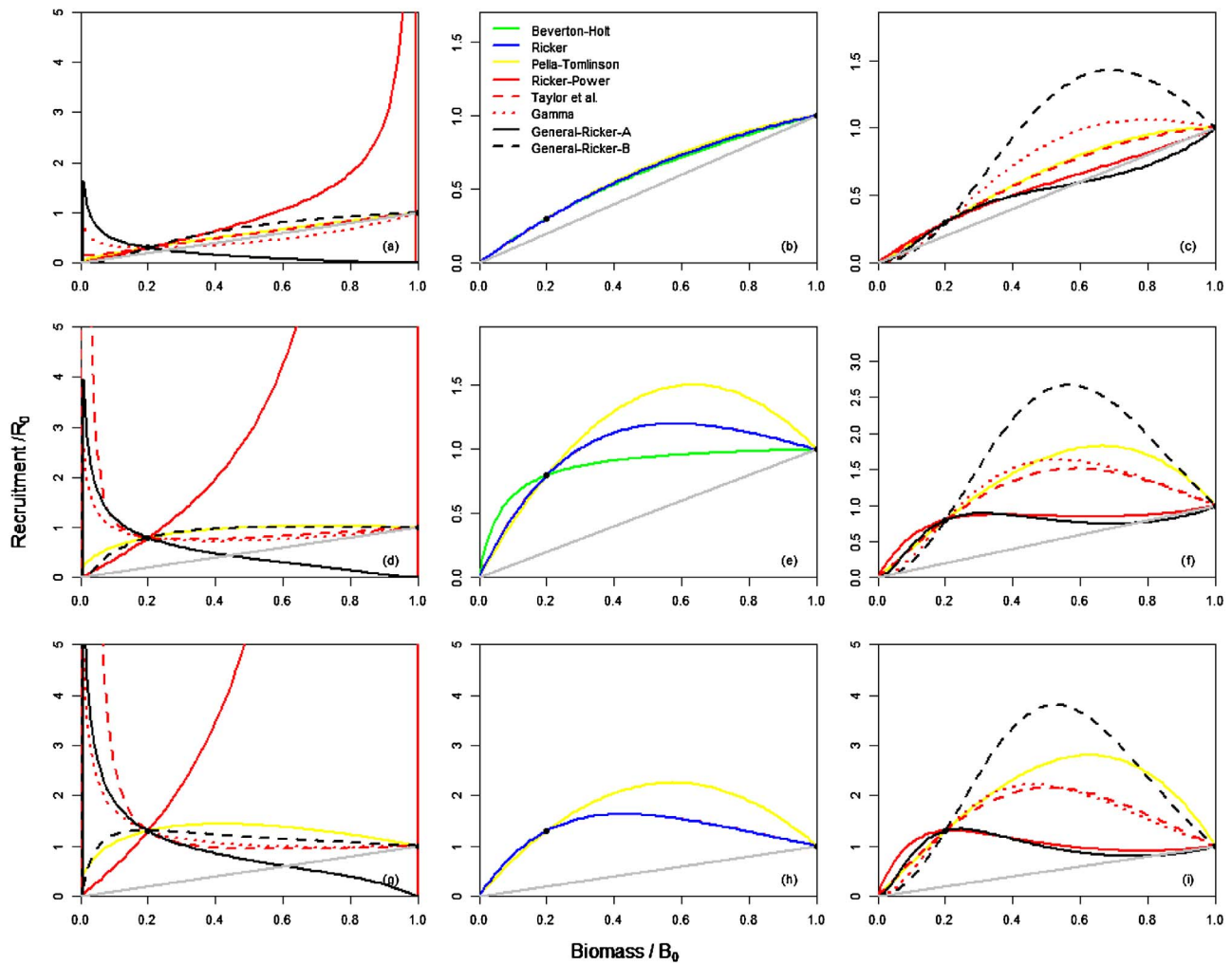
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Table 3

The relationship between expected recruitment and spawning biomass-per-recruit for the seven stock-recruitment relationships for which the relationship between recruitment and spawning biomass-per-recruit is analytical. The SRRs for which this relationship is not analytical are not examined in terms of the MSY calculations in this paper.

Stock-recruitment relationship	Definition
2-parameter forms	
Beverton-Holt	$R = \frac{B_0}{\tilde{B}}\left[\frac{4h\tilde{B}\,/\,\tilde{B}_0 + h - 1}{5h - 1}\right]$
Ricker	$R = \frac{B_0}{\tilde{B}}\left(1 - \frac{0.8\,\ell n(\tilde{B}_0\,/\,\tilde{B})}{\ell n(5h)}\right)$
3-parameter forms	
Pella-Tomlinson	$R = \frac{B_0}{\tilde{B}}\left(1 - \left(1 - \frac{\tilde{B}_0}{\tilde{B}}\right)\frac{1 - 0.2^\gamma}{(1 - 5h)}\right)^{1/\gamma}$
Shepherd (1982)	$R = \frac{B_0}{\tilde{B}}\left[\frac{5h[1 - 0.2^\gamma]\tilde{B}\,/\,B_0 - (1 - 5h0.2^\gamma)}{5h - 1}\right]^{1/\gamma}$
Deriso (1980)	$R = \frac{B_0}{\tilde{B}}\left[\frac{0.8(5h)^{1/\gamma}\tilde{B}^{1/\gamma}\,/\,(\tilde{B}_0)^{1/\gamma} + 0.2(5h)^{1/\gamma} - 1}{(5h)^{1/\gamma} - 1}\right]$
Ricker-Power	$R = \frac{B_0}{\tilde{B}}\left(1 - \left[\frac{0.8^\gamma\,\ell n(\tilde{B}_0\,/\,\tilde{B})}{\ell n(5h)}\right]^{1/\gamma}\right)$
Taylor et al. (2013)	$R = \frac{B_0}{\tilde{B}}\left(1 - \frac{(1 - 0.2^\gamma)}{\ell n(5h)}\ell n(\tilde{B}_0/\tilde{B})\right)^{1/\gamma}$

6. Discussion

6.1. Selection of a SRR

This paper introduced eleven potential 3-parameter SRRs, five of which are newly formulated relationships and not found elsewhere. Six SRRs, including four of the five newly formulated relationships, were excluded because they include depensation over part of the range of biomasses between 0 and B_0, and consequently there is not a one–one relationship between spawning biomass-per-recruit and recruitment, which is needed to calculate γ and h given F_{MSY}/M and B_{MSY}/B_0. Although this problem could be overcome by specifying which legs of the relationships between recruitment and spawning biomass-per-recruit should be used to compute recruitment, it seems unnecessary to add this level of complication given other SRRs are available. However, these six SRRs could be considered for inclusion in future assessment methods when the possibility exists for depensation. For example, Smith and Punt (1998) conducted assessments of gemfish (*Rexea solandri*) off the east coast of Australia using population models that included the Myers et al. SRR, and this form was found to fit the data better than the Beverton-Holt or Ricker SRRs.

Several of the generalizations of the Beverton-Holt SRR (Deriso, Shepherd, and Taylor et al.) exhibit a pole for biomasses between 0 and B_0 for some choices for F_{MSY}/M and B_{MSY}/B_0. In principle, negative (or
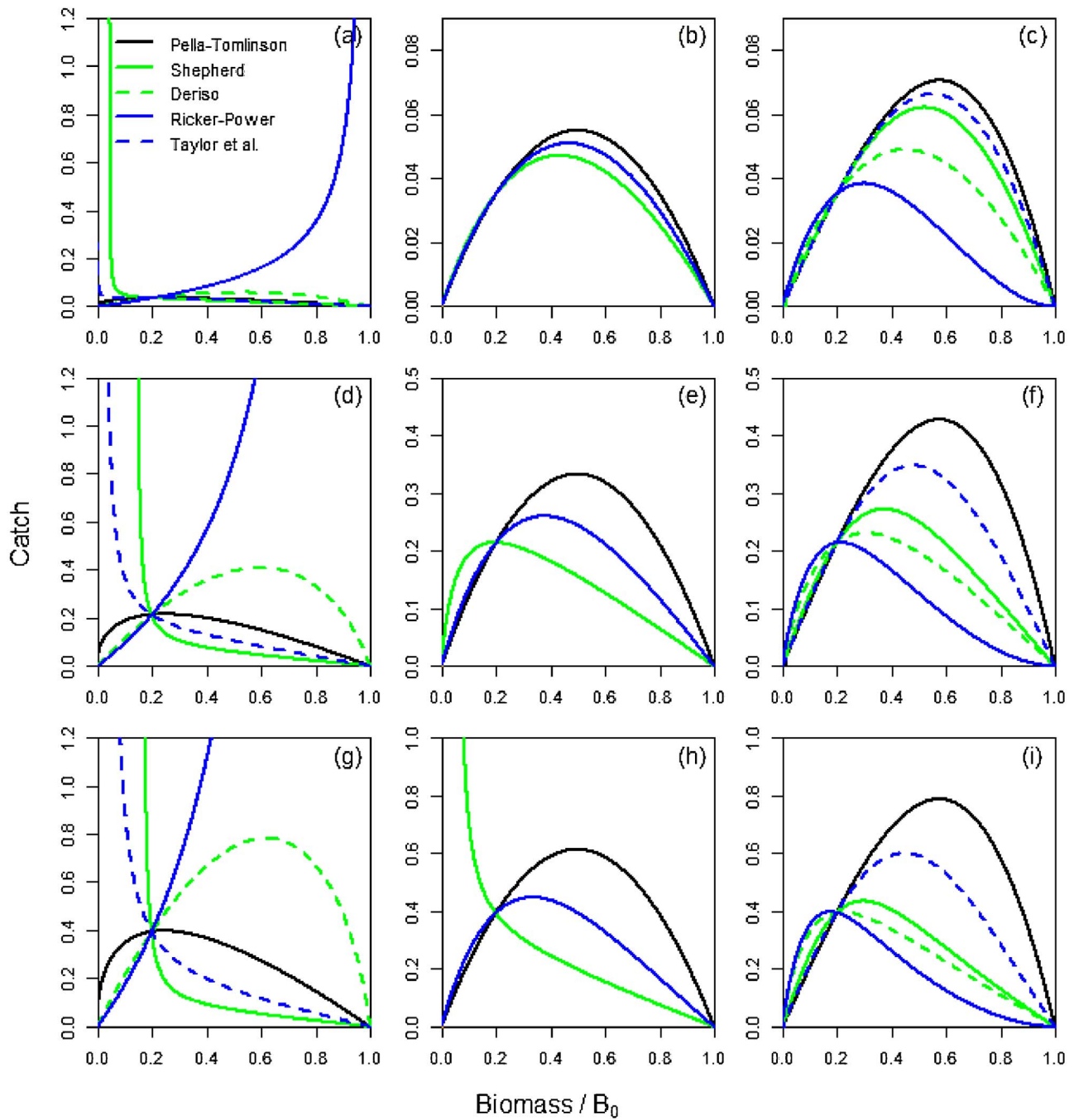
A.E. Punt, J.M. Cope

Fig. 4. Example yield functions for five of the 3-parameter stock-recruitment relationships. The columns show results for values for γ of −0.5, 1 and 3 and the rows show results for values for *h* of 0.3, 0.8 and 1.3. The Beverton-Holt and Ricker stock-recruitment relationships are special cases on the more general forms when γ = 1.

infinite) recruitment could be replaced by 0 (or a large number) when conducting assessments. However, this would lead to loss of differentiability and hence these SRRs are undesirable for inclusion in many stock assessment methods. The Pella-Tomlinson SRR can lead to increasing recruitment as biomass tends to 0 for some combinations for F_{MSY}/M and B_{MSY}/B_0, but recruitment was never infinite for this SRR for any biomass.

The Ricker-Power was selected as "best" in this paper because it satisfies the desirable criteria of (a) being able to mimic a wide range of B_{MSY}/B_0 and F_{MSY}/M values, (b) not leading to negative recruitment for biomasses between 0 and B_0, and (c) not leading to increasing recruitment in the limit of zero population size. This SRR is not defined for $B > B_0$ for non-integer values of γ < 1. γ was always greater than 0 for the applications of this paper, but there are combinations for

F_{MSY}/M and B_{MSY}/B_0 for which the SSR would be undefined. Moreover, the range of values for F_{MSY}/M and B_{MSY}/B_0 for which the SSR may be undefined may depend on the choices for natural mortality, growth, selectivity, and maturity (see Section 6.3). Care therefore needs to be taken when applying the Ricker-Power SSR for stocks which may have exceeded B_0 during the period of assessment.

The Pella-Tomlinson SRR could be considered 'next best', and it has been used extensively in assessments of cetaceans and pinnipeds. It is therefore perhaps surprising then that the Taylor et al. SRR performed poorly because the Pella-Tomlinson SRR is a first-order Taylor series approximation to the Taylor et al. SRR. The reason is that the increase in the impact of the density-dependence term for the Taylor et al. SRR is always more rapid than that of the Pella-Tomlinson SRR because the density-dependence term in the Taylor et al. SRR is based on an
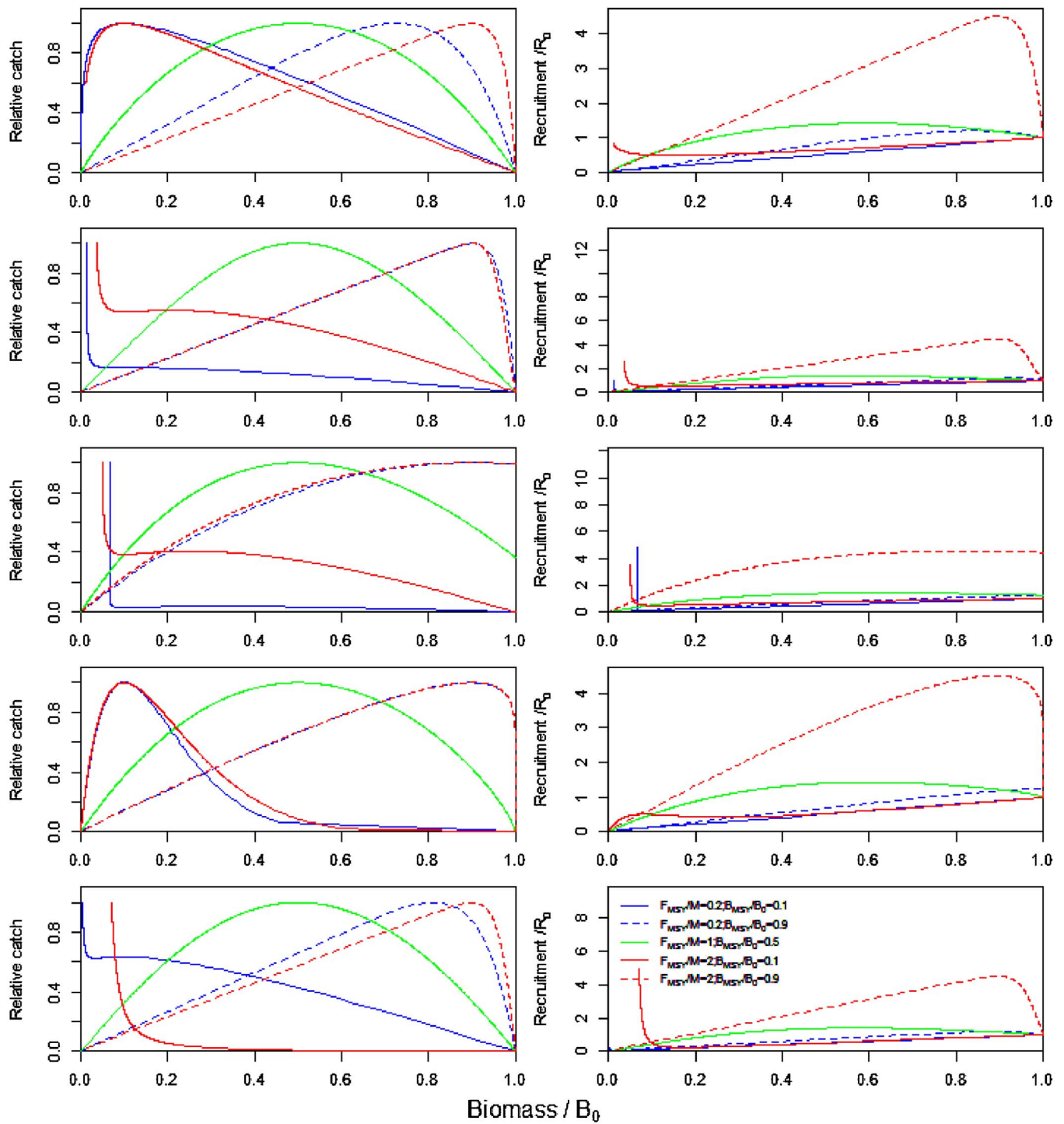
Fig. 5. Yield functions (left panels) and SRRs (right panels) for five choices for (F_{MSY}/M, B_{MSY}/B_0) for petrale sole. Results are shown in the first row for the Pella-Tomlinson SRR, in the 2nd row for the Shepherd SRR, in the 3rd row for the Deriso SRR, in the 4th row for the Ricker-Power SRR, and in the 5th row for the Taylor et al. SRR.

exponential rather than a power function.

6.2. Computation considerations for stock assessment

Many current stock assessment methods are based on AD Model Builder (Fournier et al., 2012), and estimate parameters using maximum likelihood. Thus, the objective function (usually a log-likelihood function with additional components reflecting priors) needs to be differentiable with respect to the parameters of the model. Unfortunately, the process of obtaining the values for γ and h given F_{MSY}/M and B_{MSY}/B_0 is not analytical for the 3-parameter SRRs.

Consequently, it would not be straightforward to move stock assessment methods to a 'leading parameters' approach, i.e. parameterized in terms of F_{MSY}/M and B_{MSY}/B_0 such as those of Martell et al. (2008) and Dick and MacCall (2011) if 3-parameter SRRs were adopted. Rather, it would be necessary to split the model fitting process into two steps (fitting the model conditional on γ and h) and using a second minimization loop to calculate F_{MSY}/M and B_{MSY}/B_0 (and hence γ and h) conditional on the parameters of the model such as selectivity and biological parameters. An alternative to this would be to approximate the relationships between γ and h and F_{MSY}/M and B_{MSY}/B_0 using a differentiable function, and including that in the assessment. However,
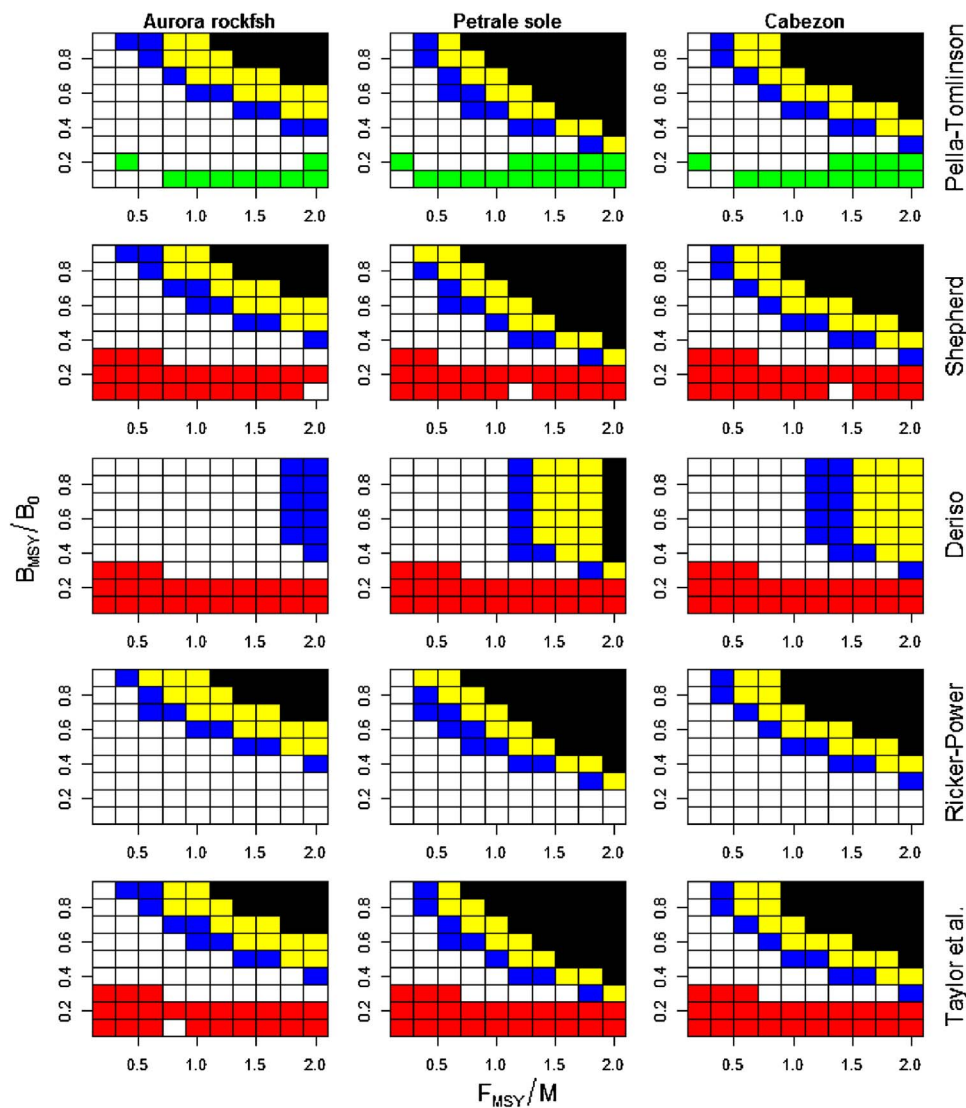
Fig. 6. Summary of the ability to create yield functions versus F_{MSY}/M and B_{MSY}/B_0 (columns and rows respectively) for the three example species. Results are shown in the first row for the Pella-Tomlinson SRR, in the 2nd row for the Shepherd SRR, in the 3rd row for the Deriso SRR, in the 4th row for the Ricker-Power SRR, and in the 5th row for the Taylor et al. SRR. The cells in red indicate combinations of F_{MSY}/M and B_{MSY}/B_0 for which recruitment is negative for $0 < B < B_0$, and the cells in green indicate combinations of F_{MSY}/M and B_{MSY}/B_0 for which recruitment is increasing as $B \to 0$. The blue, yellow and black regions indicate combinations of F_{MSY}/M and B_{MSY}/B_0 for which the maximum recruitment is respectively > 1.25, > 1.5 and > 2 unfished recruitment.

Table 4
The priors on which the applications of SSS are based.

Parameter	Distribution	Input	Species		
			Aurora rockfish	Cabezon	Petrale sole
Natural mortality: female	Lognormal	mean	0.04	0.25	0.15
		sd	0.25	0.25	0.33
Natural mortality: male	Lognormal	mean	0.21	0.30	0.21
		sd	0.25	0.25	0.33
Stock status, B_{2000}/B_0	Beta	mean	0.31	0.51	0.39
		sd	0.17	0.28	0.18
F_{MSY}/M	Lognormal	mean	0.07	0.67	0.72
		sd	0.20	0.20	0.20
B_{MSY}/B_0	Beta	mean	0.46	0.46	0.40
		sd	0.13	0.13	0.12

that function would depend on biological and fishery parameters, in particular fishery selectivity, that are often estimated as part of assessments.

Unlike Bayesian methods, the choice of parameterization is not important for maximum likelihood methods so an alternative would be to treat γ and h as the parameters that are optimized and computing the resulting values for F_{MSY}/M and B_{MSY}/B_0. The approach was taken in Stock Synthesis by Taylor et al. (2013), and by Punt et al. (2014b) for

an assessment of Antarctic minke whales. Estimating the values for γ and h as part of the minimization process would require that constraints be imposed on their values to ensure that the SRR is well defined (right column of Table 2). For the Ricker-Power and Pella-Tomlinson SRRs, these constraints are, however, fairly simple.

Finally, moving to a Bayesian framework imposes little additional computational burden given there is no need for the objective function to be differentiable.[5] Bayesian assessments of the Bering-Chukchi-Beaufort Sea stock of bowhead whales *Balaena mysticetus* and those for the eastern North Pacific stock of gray whales *Eschrichtius robustus* have been based on the Pella-Tomlinson SRR for decades (e.g., Givens et al., 1995; Punt and Wade, 2012). Consequently, methods of stock assessment applied to teleost species that are based on Bayesian methods such as Extended Simple Stock Synthesis (XSSS; Cope et al., 2015a, 2015b) could be modified to include 3-parameter stock-recruitment relationships.

6.3. Additional considerations

This paper is based on the assumption that density-dependence operates via the SRR and that the SRR is a function only of spawning

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[5] Except that the objective function does need to be differentiable if the process of sampling from the posterior is conducted using AD Model builder.
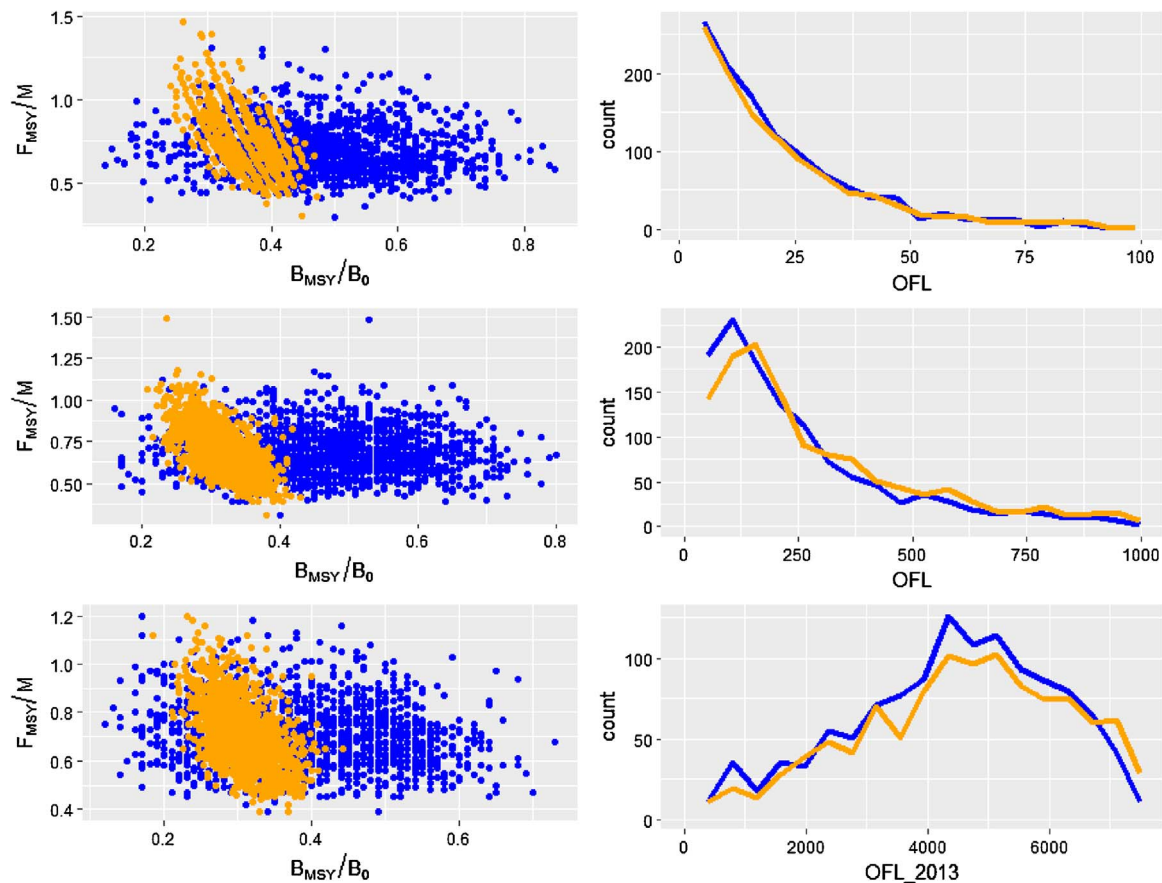
Fig. 7. Sampled values for F_{MSY}/M and B_{MSY}/B_0 (left panels) and the resulting distributions for the Overfishing Level for the Beverton-Holt (orange) and the Ricker-Power SRRs (blue) SRRs. The values for B_{MSY}/B_0 for the Beverton-Holt SRR are not generated from a prior but calculated given the value generated for F_{MSY}/M. Results are shown in the upper panels for aurora rockfish, the center panels for cabezon and the lower panels for petrale sole. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5
Summary of the distributions for the Overfishing Limit by species and stock-recruitment relationship. The analyses assume the same distribution for F_{MSY}/M.

Species	SRR	Overfishing limit (t)		
		5%	50%	95%
Aurora rockfish	Ricker Power	0.02	12	61
	Beverton-Holt	0.02	11	63
Cabezon	Ricker Power	0.01	169	1111
	Beverton-Holt	6	219	1520
Petrale Sole	Ricker Power	617	4903	14,418
	Beverton-Holt	1575	5430	12,173

stock biomass. However, this need not be the case. For example, density-dependence may impact natural mortality, maturity or growth. Few stock assessments have considered these sources of density-dependence, although models with density-dependent natural mortality were used to evaluate the performance of harvest control rules for commercial whaling by Johnson and Punt (2016). It should be noted that moving from density-dependence in recruitment to density-dependence in natural mortality makes the process of calculating γ and h given F_{MSY}/M and B_{MSY}/B_0 much more complicated because recruitment, spawning biomass-per-recruit, and yield-per-recruit are all functions of natural mortality (Punt, 1996). Density-dependence in growth would have similar challenges, but to date no assessment has considered parameterizing density-dependence in growth using a leading parameters approach.

The SSRs of this paper are all based on a parametric relationship between spawning stock biomass and recruitment. In principle, non-parametric relationships between spawning stock biomass and recruitment can be used to characterize the SRR (e.g., Sugeno and Munch, 2013). However, to date, such relationships have not been included in forward projection integrated analysis stock assessments.

The SRRs in Table 2 are based on spawning stock biomass. This is not the only option, and several cetacean assessments are based on the assumption that calf numbers are a function of the number of mature females at low population size while the reduction in fecundity at high population size is a function of the numbers of animals aged 1 and older rather than of mature animals (e.g., Punt et al., 2014b).

6.4. Conclusion

A key 'skeleton in the cupboard' for many stock assessments based on the integrated analysis paradigm is that F_{MSY} and B_{MSY}/B_0 are functionally dependent in 2-parameter SRRs, such that estimating F_{MSY} is equivalent to estimating B_{MSY}/B_0. Consequently, for example, stock assessments based on the Beverton-Holt stock-recruitment relationship imply that high estimated F_{MSY} correspond to low inferred B_{MSY}/B_0 and vice versa The relationship between F_{MSY} and B_{MSY}/B_0 can be weakened by adopting a 3-parameter SRR, and of the eleven 3-parameter SRRs considered in this paper, the Ricker-Power SRR has the most desirable properties. This SRR has been incorporated in a commonly-used data-poor method of stock assessment (SSS) and future work should involve including it in stock assessment packages that, in particular, estimate selectivity and maturity.
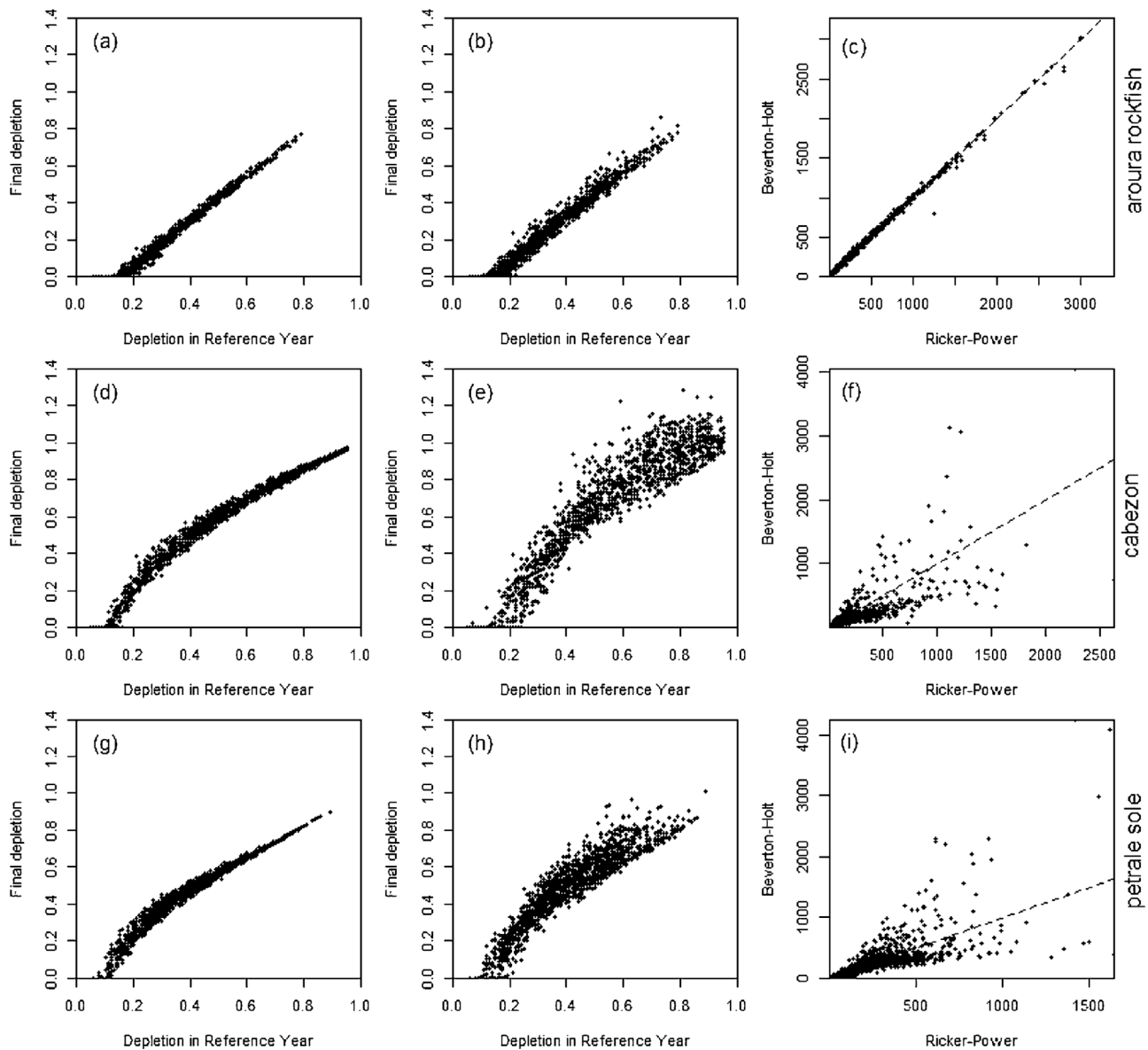
Fig. 8. Relationship between depletion of spawning stock biomass in the reference year (2000) and in the final year of the assessment period (2013 for aurora rockfish and petrale sole and 2009 for cabezon) [left and center panels] and that between spawning stock biomass in the final year from the Beverton-Holt and Ricker-Power models (right panels). Results are shown in the upper, center and lower rows for aurora rockfish, cabezon and petrale sole respectively.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.07.007.

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