



Original Article

Probability of stochastic depletion: an easily interpreted diagnostic for stock assessment modelling and fisheries management

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Marine fish populations have high variation in cohort strength, and the production of juveniles (recruitment) may have persistent positive or negative residuals (autocorrelation) after accounting for spawning biomass. Autocorrelated recruitment will occur whenever average recruitment levels change between oceanographic regimes or due to predator release, but may also indicate persistent environmental and biological effects on shorter time-scales. Here, we use estimates of recruitment variability and autocorrelation to simulate the stationary distribution of spawning biomass for 100 real-world stocks when unfished, fished at F_{MSY} , or fished following a harvest control rule where fishing mortality decreases as a function of spawning biomass. Results show that unfished stocks have spawning biomass (SB) below its deterministic equilibrium value (SB_0) 58% of the time, and below $0.5SB_0$ 5% of the time on average across all stocks. Similarly, stocks fished at the level producing deterministic maximum sustainable yield (F_{MSY}) are below its deterministic prediction of spawning biomass (SB_{MSY}) 60% of the time and below $0.5SB_{MSY}$ 8% of the time. These probabilities are greater for stocks with high recruitment variability, positive autocorrelation, and high natural mortality—traits that are particularly associated with clupeids and scombrids. An elevated probability of stochastic depletion, i.e. biomass below the deterministic equilibrium expectation, implies that management actions required when biomass drops below a threshold may be triggered more frequently than expected. Therefore, we conclude by suggesting that fisheries scientists routinely calculate these probabilities during stock assessments as a decision support tool for fisheries managers.

Keywords: autocorrelated recruitment, fishery collapse, management strategy evaluation, multiannual plan, rebuilding plan, recruitment variability, stationary distribution of abundance, stochastic depletion.

Introduction

Fishery collapse has previously been defined either as catch falling below some fraction of its previous maximum, or as biomass dropping considerably below its average level in an unfished population (Hilborn, 1997; Hutchings, 2000). By either definition, fishery collapse is a global problem that appears to be getting worse through time (Worm *et al.*, 2009; Costello *et al.*, 2012; Thorson *et al.*, 2012). Fishery collapse has historically been associated with severe economic impacts and persistent ecological changes (Walters and Kitchell, 2001; Hilborn *et al.*, 2003), and these effects have encouraged research regarding management instruments and institutions that prevent

overfishing before it leads to severe depletion (Gutiérrez *et al.*, 2011). At the same time, there is a growing appreciation of the limits of our ability to control stock dynamics given the importance of environmental factors and shifts in productivity for individual species over time (Vert-pre *et al.*, 2013; Minto *et al.*, 2014).

Fisheries scientists have long recognized the important role of variation in cohort strength in fish population dynamics (Hjort, 1926). Variability in cohort strength frequently exhibits substantial autocorrelation, where consecutive years will have streaks of positive or negative residuals around the prediction from a stock–recruit model (Pyper and Peterman, 1998; Thorson *et al.*, 2015b).

Recruitment may in some cases have such great variability that it swamps the effect of surviving adult biomass during short-term forecasts of population dynamics (e.g. Pacific hake, Hicks *et al.*, 2014). Therefore, even populations being exploited at target fishing mortality rates may in some cases drop below the associated biomass targets (which are defined for average conditions) due to a series of years with poor recruitment.

Persistent positive or negative residuals in the stock–recruitment relationship may in some cases be interpreted as “regime shifts”, where biological and/or environmental conditions are likely to have changed relative to earlier conditions (Stewart and Martell, 2014; Vert-pre *et al.*, 2013; Wayte, 2013). Climate-related regime shifts with impacts on fish productivity are well documented for many marine ecosystems [e.g. the Pacific Decadal Oscillation, Mantua and Hare (2002) and Atlantic Multidecadal Oscillation, Edwards *et al.* (2013)] and are likely to result in changes in the demographic parameters used to describe population dynamics for marine fish. Regime effects on marine fish are particularly well documented for small pelagics, e.g. the switches between anchovy and sardine in the Pacific Ocean (Chavez *et al.*, 2003; Lindegren *et al.*, 2013), and these switches could be roughly approximated as an autocorrelation parameter near 1.0 for these species. Similarly, analysis of the catch statistics compiled by the FAO showed that nearly 45% of collapses in the recorded harvest (defined by 4 consecutive years after maximum catch where catches are <10% of that maximum) are “erratic”, i.e. showing high variability in catch followed by a prolonged decrease (Mullon *et al.*, 2005). Although there are many mechanisms for changes in harvest (Branch *et al.*, 2011), these patterns are consistent with population dynamics that are driven by stochastic variation in recruitment.

Given this interest in regime shifts and autocorrelated residuals in recruitment patterns, there is continuing research regarding the impact of autocorrelated or environmentally driven recruitment on the performance of management procedures that either do or do not account for time variation (Kell *et al.*, 2005; Haltuch and Punt, 2011; Szuwalski and Punt, 2013). However, there has been little general discussion of the frequency with which recruitment variability alone will cause fish populations to fall below biomass reference points (which we will subsequently call “stochastic depletion”). We therefore use a repository of spawning biomass (SB), recruitment, and life history traits for exploited marine and anadromous fish (Myers *et al.*, 1995), along with recent estimates of the variability and autocorrelation in recruitment in this database (Thorson *et al.*, 2015b), to simulate stochastic trajectories of SB for these species under different fishing treatments, including no fishing. This simulation experiment is used to illustrate how variable SB can be given plausible fish life histories, as well as how this variation changes due to fishing impacts.

Material and Methods

We seek to estimate the distribution of population abundance given the variance and autocorrelation of recruitment, as well as known life history parameters for a large sample of fish stocks. We proceed by extracting estimates of recruitment variance, autocorrelation, and the strength of density-dependent recruitment (i.e. the maximum lifetime spawners per spawner) from a recent meta-analysis of recruitment variability for 154 species globally (Thorson *et al.*, 2015b) using an updated version of the original Myers *et al.* (1995) database. This 1995 database uses extended survival and virtual population analysis, and hence should yield estimates of recruitment that are less influenced by model assumptions than other model types (but see

Dickey-Collas *et al.*, 2014). We then reduce this set down to 100 stocks that have associated information regarding growth rate (individual growth coefficient k), natural mortality (M), and age at maturity (a_{mat}).

Specifically, we follow the following steps for each species:

1. Calculate relative weight at age:

$$W_a = \theta_1(L_\infty(1 - \exp\{-ka + t_0\}))^{\theta_2}$$

while assuming that $t_0 = 0$, and fixing $L_\infty = 1$ and $\theta_1 = 1$ for all species. All statistics derived from the simulation study are ratios that do not depend on the specific value of L_∞ and θ_1 , given the assumption that $t_0 = 0$. Isometric weight at length ($\theta_2 = 3$) is assumed for each species, and this appears approximately accurate for many species (Froese *et al.*, 2014). Values of individual growth rate k vary among species and are taken from the original Myers *et al.* (1995) database.

2. Start the population in deterministic unfished equilibrium at time 1:

$$N_{a,1} = R_0 \exp(-Ma)$$

$$SB_1 = \sum_{a=0}^{a_{max}} N_{a,1} W_a m_a$$

where $N_{a,t}$ is abundance (in numbers) in year t for age a , SB_t is spawning biomass in year t , R_0 is the average recruitment for an unfished population (calculated from stock–recruit parameters introduced below), and m_a is maturity at age, given by knife-edge maturity where $m_a = 1.0$ for all ages greater than a_{mat} and 0 otherwise. Age at maturity again varies among species and is taken from the original Myers *et al.* (1995) database.

3. Determine fishing mortality rates for the next year. We use three alternative treatments of fishing mortality:
 - (a) No fishing, where $F_t = 0$ for all years.
 - (b) Fishing at the rate that produces maximum sustainable yield given deterministic dynamics ($F_t = F_{msy}$), where F_{msy} is the value of F that maximizes catch given equilibrium and deterministic dynamics. This value was calculated using non-linear optimization given fixed values for all other parameters, e.g. given the deterministic spawner–recruit curve and yield-per-recruit relationship.
 - (c) Fishing using a “40-10” harvest control rule, in which fishing occurs at F_{msy} when SB exceeds 40% of unfished levels, fishing is eliminated whenever SB drops below 10% of unfished levels, and varies linearly between these two thresholds:

$$F_t = \begin{cases} 0 & \text{if } SB_{t-1} \leq 0.1SB_0 \\ F_{msy} \frac{SB_t/SB_0 - 0.1}{0.4 - 0.1} & \text{if } 0.1SB_0 < SB_{t-1} < 0.4SB_0 \\ F_{msy} & \text{if } 0.4SB_0 \leq SB_{t-1} \end{cases}$$

where SB_0 is the equilibrium value for SB in an unfished population given deterministic dynamics (i.e. $SB_0 = R_0SPR_{F=0}$, where $SPR_{F=0}$ is SB per recruit in an unfished population).

This 40-10 harvest control rule may in some cases decrease variation in SB for exploited populations (Deroba and Bence, 2008).

These three alternative treatments of fishing mortality are hypothesized to result in different probabilities of exceeding SB levels.

4. Project the population given this level of fishing mortality:

$$N_{a,t} = \begin{cases} R_t & \text{if } a = 0 \\ N_{a-1,t-1} \exp\{-M - F_t\} & \text{if } a \geq 1 \end{cases}$$

where recruitment R_t in year t is generated using stochastic variability around the Beverton–Holt or Ricker stock–recruit curves:

$$R_t = \begin{cases} \frac{\alpha SB_t}{1 + \beta SB_t} \cdot \exp\{\varepsilon_t\} & \text{if using Beverton–Holt} \\ \alpha SB_t \exp\{-\beta SB_t\} \cdot \exp\{\varepsilon_t\} & \text{if using Ricker} \end{cases}$$

and where unexplained residuals ε_t around the stock–recruit curve are derived from a bias-corrected autoregressive process:

$$\varepsilon_t \sim N\left(\rho\varepsilon_{t-1} - \frac{\sigma^2}{2(1-\rho^2)}, \sigma^2\right)$$

Recruitment parameters include maximum recruits per spawner α , density-dependence β , conditional variance σ^2 , and recruitment correlation ρ . All four were estimated for each stock by Thorson et al. (2015b), and we here use the posterior mean for each parameter to simulate data used in this study, while natural mortality rate varies among species and is taken from the original Myers et al. (1995) database.

5. Repeat steps 3 and 4 to project the population for 2000 years, saving SB_t for every tenth year starting at year 1000 (i.e. treating the first 1000 years as burn-in to achieve a stationary distribution for SB).
6. Repeat steps 3–5 for 100 samples from the posterior distribution of recruitment parameters from Thorson et al. (2015b). This results in 10 000 samples from the predictive distribution of SB for each species (i.e. a million samples including all species) given a particular treatment of fishing mortality.
7. Repeat steps 3–6 for each treatment of fishing mortality.

Performance measures

We then compile these simulation results and analyse them to determine the stationary distribution for SB relative to either deterministic SB at maximum sustainable yield (SB_{msy}) or unfished SB (SB_0). Using these estimates, we calculate the proportion of simulated samples from the stationary distribution that were below 100, 50, or 10% of either SB_0 or SB_{MSY} . We also compute the coefficient of variation (C.V.) in the stationary distribution of abundance for each stock, and assess how this C.V. varies for different treatments of fishing mortality.

Finally, we summarize which life history parameters are most predictive of the probability that a stock will drop below these thresholds. To do so, we estimate parameters for a generalized linear mixed model (GLMM) using a binomial distribution for the response and a logit-link function, using the *lme4* library (Bates and Maechler, 2009) in the R statistical environment (R Core Development Team, 2013). The response variable is the number of simulation samples for each species that were below a given threshold, and where stock ID is treated as a random effect to avoid pseudoreplication induced by correlations among simulation replicates within a given stock. Although it is feasible to conduct this analysis for all combinations of three treatments of fishing

mortality (none, F_{MSY} , and a 40:10 harvest control rule), two metrics (SB relative to SB_0 or SB_{MSY}), and three thresholds (100, 50, and 10%), we here focus attention on three representative scenarios:

- (i) No fishing ($F = 0$) and the probability that SB drops below 50% of SB_0 .
- (ii) Fishing at F_{MSY} and the probability that SB drops below 50% of SB_{MSY} .
- (iii) Fishing with a 40 : 10 harvest control rule and the probability that SB drops below 50% of SB_{MSY} .

Results for these illustrate the probability of stochastically exceeding management targets for each taxonomic family, as well as the effect of species traits [i.e. marginal standard deviation of recruitment σ_R , recruitment autocorrelation AR, natural mortality rate M , individual growth rate k , recruitment steepness h , shape of the surplus production curve SB_{msy}/SB_0 , log-transformed recruits per SB $\ln(\alpha)$, log-transformed recruitment density-dependence $\ln(\beta)$, and age at maturity a_{mat} , where each is standardized to have mean zero and standard deviation one] on these probabilities. These life history traits were chosen because they were all used in the population projection (or derived from these parameters), and hence the GLMM summarizes the relative importance of different factors included in each projection.

Results

Recruitment variation, and in particular the autocorrelation in recruitment, is able to drive considerable variation in SB in all three fishing treatments (Figure 1). Species with low variation in recruitment and/or autocorrelation appear to have a lower variation in SB (compare rows 1 and 3 of Figure 1). In particular, the median species in our analysis has a C.V. of 30% for SB in the absence of fishing when simulating dynamics using the Beverton–Holt stock–recruit function, and this increases to 35.5% when fishing at F_{MSY} and decreases to 26.8% when fishing with a 40 : 10 harvest control rule (Figure 2; see Supplementary Materials A for a summary for each individual stock). However, several species have C.V. > 50%, or even 100% (e.g. the Californian stock of chub mackerel) in each treatment. Results are qualitatively similar when simulating dynamics using the Ricker stock–recruit function, although the Ricker model has somewhat increased C.V. for each fishing treatment (see Supplementary Materials B for details).

In general, the standard deviation and autocorrelation in recruitment have the largest effect on the probability of exceeding management targets (Tables 1 and 2), although increased natural mortality rates are also predictive of increased probabilities of exceedance. Computing these average probabilities for each taxonomic family shows that Clupeidae and Scombridae have traits that are associated with increased probabilities of falling below reference points, whereas Scorpaenidae and Soleidae have particularly low probabilities. We also note that, across all families, Scenario 3 (fishing with a 40 : 10 harvest control rule) has greatly reduced the probability of exceedance relative to Scenario 2 (fishing at F_{MSY}).

We depict the stationary distribution of SB in each fishing treatment via its cumulative distribution (Figure 3). Simulated stocks essentially never drop below 10% of SB_0 when unfished (prob < 0.001; Figure 3, Scenario 1), but do occasionally drop below 50% of SB_0 (prob = 5.2%), and spend nearly 58% of the time below SB_0 . The probability of dropping below SB_{MSY} when fishing at F_{MSY} (Figure 3, Scenario 2) is generally larger than that of dropping below SB_0 when unfished, with the probability of dropping below

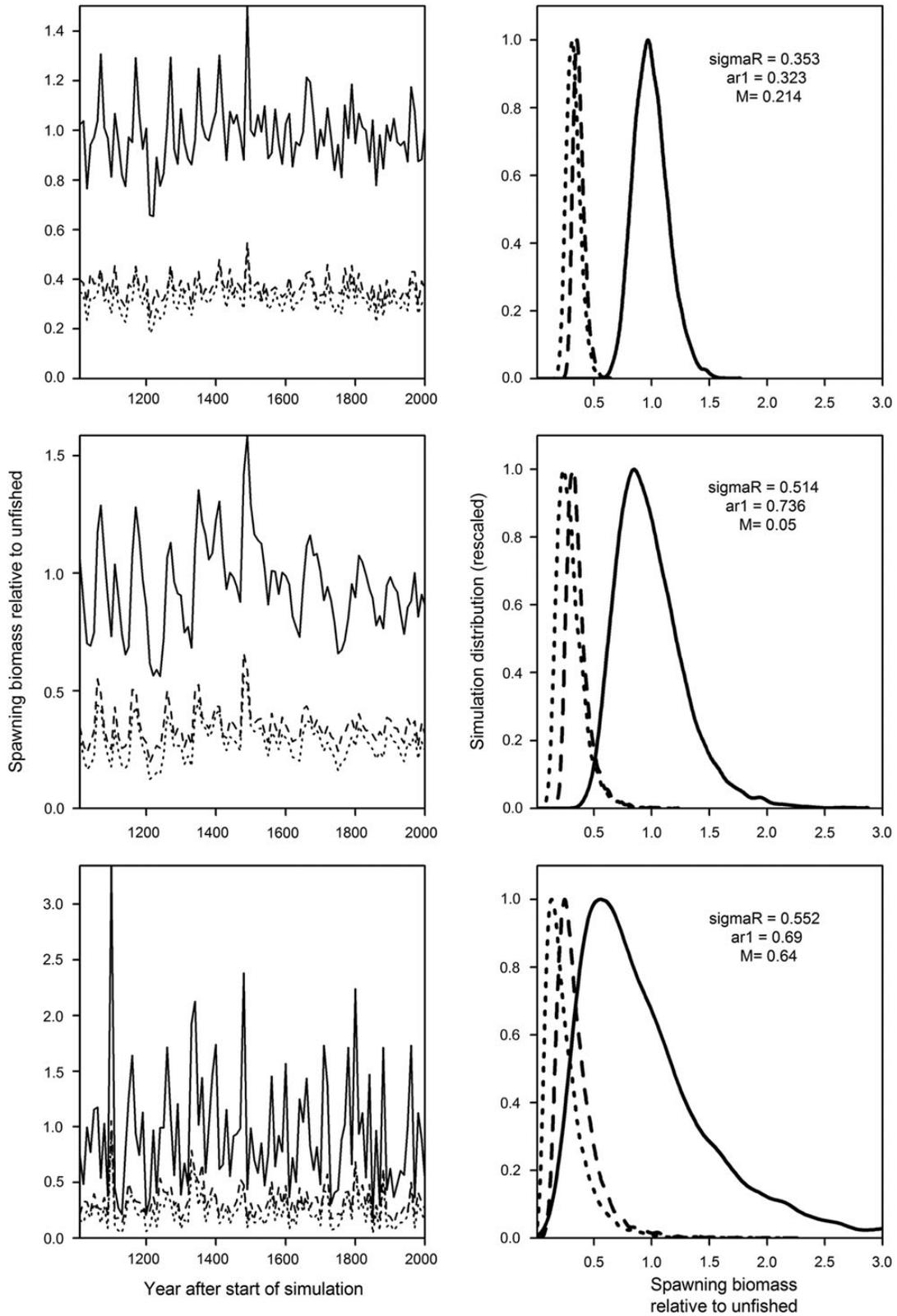


Figure 1. Examples of SB over time (left column) and the distribution of SB relative to its deterministic equilibrium (SB/SB_0 ; right column) for three stocks (chosen as the tenth, 51st, and 90th stocks when ranking stocks from lowest to greatest stationary C.V. in SB relative to unfished) for the Beverton – Holt stock – recruit function, along with their conditional variance of recruitment, recruitment autocorrelation, and natural mortality rate: top: Plaice; middle: Chilepepper rockfish; bottom: Black Sea sprat. In each panel, the solid line is for an unfished population, the dotted line is for fishing at MSY (F_{MSY}), and the dashed line is fishing at a 40 : 10 harvest control rule.

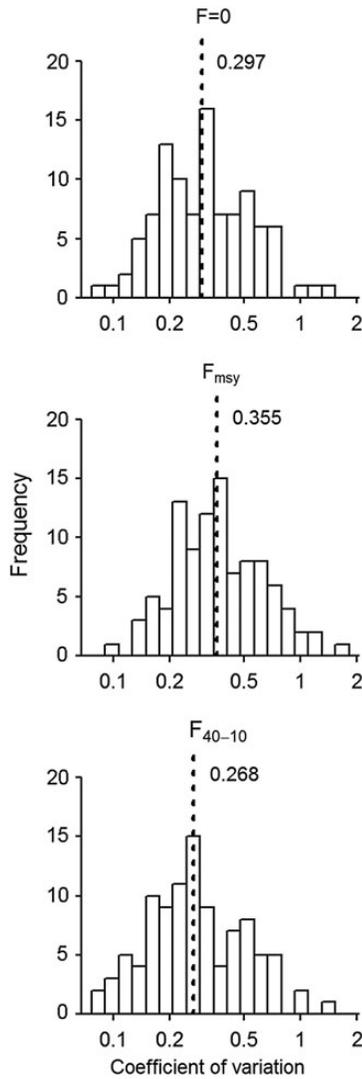


Figure 2. Histograms of the C.V. of the distribution of SB for each stock, given no fishing ($F = 0$), fishing at a level that produces MSY given deterministic dynamics (F_{msy}), and fishing given a 40-10 harvest control rule, along with the average C.V. across all stocks shown as a dashed line with its numeric value listed. Results are based on simulations using the Beverton–Holt stock–recruit model.

50% of SB_{MSY} at 8%. This occurs because the slope of the stock–recruit curve at SB_{MSY} is closer to that of the replacement line than at SB_0 , indicating weaker compensatory recruitment when fishing at F_{MSY} than in an unfished population. However, fishing with a 40 : 10 harvest control rule (Figure 3, Scenario 3) again decreases the probability that SB drops below SB_{MSY} , with <1% chance of dropping below 50%, and >70% of time spent above SB_{MSY} .

Discussion

Our study suggests that even well-managed or unfished populations will spend a substantial portion of time below management targets. In particular, fishing at F_{MSY} results in SB less than SB_{MSY} nearly 60% of time, and no fishing results in SB less than SB_0 58% of the time when simulating dynamics using the Beverton–Holt function (and results are similar for the Ricker function). This discrepancy occurs because SB_{MSY} and SB_0 are defined as the average SB at these levels, while recruitment variability is typically assumed to follow a lognormal distribution (but see Shelton (1992) for a discussion), thus causing the stationary distribution of SB to have positive skewness. Our results therefore support the conclusion that scientists, fisheries managers, and science communicators should not be unduly surprised when SB drops below SB_{MSY} in a well-managed fishery. In contrast, fishing at F_{MSY} results in SB less than 50% of SB_{MSY} less than 10% of the time (and ~9% for clupeids and 12% for scombrids), so dropping below 50% of SB_{MSY} is more justified as cause for concern beyond simple recruitment variability. These probabilities of exceeding management targets and limits when fishing at F_{MSY} due to recruitment variability alone will be increased for more conservative management targets. Lagged responses to assessment results (Kell et al., 2005; Shertzer and Prager, 2007) or misspecified models for stock–recruit dynamics (Haltuch and Punt, 2011) will also lead to greater exceedance probabilities for the scenarios that include fishing than those estimated here.

Our modelling approach includes compensatory increases in juvenile survival as captured by the Beverton–Holt and Ricker stock recruitment models. Both meta-analysis (Myers et al., 1999) and theoretical models (Walters and Korman, 1999) suggest that such compensatory processes in recruitment are likely to be strong. There are, however, other compensatory processes that are not included in this approach which may act to reduce the frequency of stochastic depletion in nature. For example, compensatory increases in somatic growth have been widely observed (Hilborn and Minte-Vera, 2008; Rindorf et al., 2008; Venturelli et al., 2010;

Table 1. Results of a GLMM analysis used to indicate which life history characteristics were most predictive of the probability of a species exceeding a management target for the Beverton–Holt stock–recruit function, showing the estimated coefficient, its estimated standard error, and the estimated probability that this coefficient arises by random chance using a Wald test.

	Estimate	SE	Pr(> z)	Estimate	SE	Pr(> z)	Estimate	SE	Pr(> z)
Intercept	−5.825	0.201	0.000	−4.404	0.143	0.000	−9.997	0.380	0.000
Marginal SD of recruitment (σ_R)	8.862	0.749	0.000	7.076	0.557	0.000	11.229	0.959	0.000
Autocorrelation in recruitment (AR)	7.529	0.914	0.000	4.995	0.679	0.000	8.615	1.165	0.000
Natural mortality rate (M)	4.729	1.035	0.000	2.624	0.797	0.001	5.738	1.154	0.000
Individual growth rate (k)	3.795	4.261	0.373	7.879	3.278	0.016	3.248	5.141	0.528
Recruitment steepness (h)	−2.462	3.801	0.517	0.156	2.955	0.958	−7.746	4.220	0.066
Shape of surplus production curve (SB_{msy}/SB_0)	−5.596	11.177	0.617	3.432	8.745	0.695	−6.644	11.584	0.566
Log max. recruits per spawner ($\ln(a)$)	0.002	0.143	0.988	−0.019	0.110	0.865	0.069	0.183	0.708
Log recruitment density-dependence ($\ln(b)$)	−0.004	0.108	0.969	0.012	0.081	0.887	−0.099	0.131	0.450
Age at maturity (a_{mat})	−0.040	0.204	0.846	0.224	0.157	0.154	−0.176	0.258	0.496

Scenario 1 involves no fishing ($F = 0$) and the probability that SB drops below 50% of SB_0 ; Scenario 2 involves fishing at F_{MSY} and the probability that SB drops below 50% of SB_{MSY} ; Scenario 3 involves fishing at with a 40-10 control rule and the probability that SB drops below 50% of SB_{MSY} . Explanatory variables are given in the order of significance.

Table 2. Results of a generalized linear model (GLM) analysis used to summarize exceedance probabilities for different taxonomic families for the Beverton–Holt stock–recruit function.

Taxonomic family	Number of stocks	Scenario 1 (%)	Scenario 2 (%)	Scenario 3 (%)
Anoplopomatidae	1	2.0	4.0	0.1
Clupeidae	26	7.2	9.2	2.3
Engraulidae	1	4.2	6.5	0.6
Gadidae	43	2.2	4.4	0.0
Pleuronectidae	10	1.6	3.0	0.0
Scombridae	8	8.3	11.9	1.6
Scorpaenidae	6	0.0	0.0	0.0
Soleidae	5	0.2	1.2	0.0

Scenario 1 involves no fishing ($F = 0$) and the probability that SB drops below 50% of SB_0 ; Scenario 2 involves fishing at F_{MSY} and the probability that SB drops below 50% of SB_{MSY} ; Scenario 3 involves fishing at with a 40-10 harvest control rule and the probability that SB drops below 50% of SB_{MSY} .

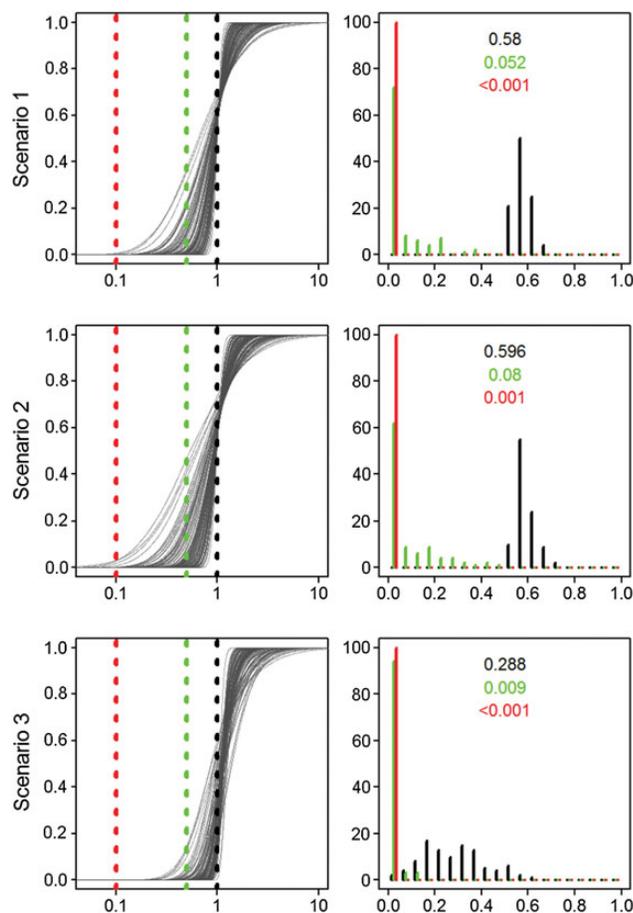


Figure 3. Cumulative distribution of SB for simulations using the Beverton–Holt stock–recruit relationship, either relative to SB_0 (Scenario 1) or SB_{MSY} (Scenario 2–3), as well as the distribution of the proportion of simulations that each stock that is below 100% (black), 50% (green), or 10% (red) of this reference point (see Table 1 for the description of scenarios).

Martino *et al.*, 2012). Compensatory decreases in adult natural mortality may also be important for many forage species, and are implicit in a Type III functional response. Nevertheless, observations of declines in abundance at fishing mortality rates that had previously appeared to be sustainable are common (e.g. butterflyfish NEFSC,

2010). In fact, Mullon *et al.* (2005) found “erratic collapses” to be the most common in their typology of collapse using the FAO landing data.

The potential for depensation in the stock recruitment relationship is also not included in our approach. If depensation were strong, it could result in a substantially higher rate of stochastic depletion as stocks which declined below the depensatory threshold would be more prone to further declines. However, most meta-analyses of depletion in the stock recruitment relationship (Liermann and Hilborn, 1997) or in the biomass–productivity relationship (Hilborn *et al.*, 2014) have found little evidence of strong depensation.

In conclusion, we recommend that assessments calculate the probability of stochastic collapse as a standard diagnostic during stock assessments. This probability could be easily computed by integrated assessment tools such as Stock Synthesis (Methot and Wetzel, 2013) and the state-space assessment model (WGMG, 2009) that include stochastic variability in recruitment. This estimated probability is a simple and easily-interpreted bridge to more complicated management strategy evaluation (Sainsbury *et al.*, 2000), which will frequently incorporate additional stochastic variability including assessment measurement error and implementation errors while simulating annual harvest levels. Computing this probability for every stock remains important, despite its relatively low value overall, because particular stocks can have probabilities of stochastic collapse that are considerably greater than average values. Our study shows that high recruitment variability, positive autocorrelation in recruitment, and high natural mortality rates are associated with stochastic collapse, so fisheries with these traits in particular (e.g. Pacific hake, with $\sigma_R > 1.4$, Thorson *et al.*, 2015a) should develop management thresholds with this possibility in mind. Due to the extreme cost of implementing and monitoring rebuilding plans, stocks with a highly variable stationary distribution for SB may also benefit from a greater buffer between target and limit reference points. These and other decisions regarding management scenarios remain in the purview of fisheries managers, although we believe that knowing the probability of stochastic collapse may in some cases improve the ability to make informed decisions about different combinations of target and limit reference points.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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