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Spawning biomass reference points for exploited marine fishes, incorporating taxonomic and body size information

James T. Thorson, Jason M. Cope, Trevor A. Branch, and Olaf P. Jensen

Abstract: Surplus production represents the processes that affect sustainable fishery harvest and is central to the ecology and management of marine fishes. Taxonomy and life history influence the ratio of spawning biomass at maximum sustainable yield to average unfished spawning biomass (SB_{MSY}/SB_0), and estimating this ratio for individual stocks is notoriously difficult. We use a database of published landings data and stock assessment biomass estimates and determine that process errors predominate in this data set by fitting a state–space model to data from each stock individually. We then fit multi-species process-error models while treating SB_{MSY}/SB_0 as a random effect that varies by taxonomic order and maximum length. The estimated $SB_{MSY}/SB_0 = 0.40$ for all 147 stocks is intermediate between the values assumed by the Fox and the Schaefer models, although Clupeiformes and Perciformes have lower and Gadiformes and Scorpaeniformes have higher SB_{MSY}/SB_0 values. Model selection supports the hypothesis that large-bodied fishes for a given taxonomic order have relatively higher SB_{MSY}/SB_0. Results can be used to define reference points for data-poor fisheries or as input in emerging assessment methods.

Résumé : La production excédentaire représente les processus qui ont une incidence sur la récolte de poissons durable et est un élément clé de l'écologie et de la gestion des poissons marins. La taxonomie et le cycle biologique influencent le rapport entre la biomasse féconde correspondant au rendement maximum durable et la biomasse féconde non exploitée moyenne (SB_{MSY}/SB_0), l'estimation de ce rapport pour des stocks donnés étant particulièrement difficile. Nous utilisons une base de données sur les débarquements publiées et des estimations de la biomasse reposant sur des évaluations des stocks et déterminons, en ajustant un modèle d'espace d'états aux données pour chaque stock pris individuellement, que les erreurs de traitement dominent dans cette base de données. Nous ajustons ensuite des modèles multi-espèces d'erreur de traitement en traitant le rapport SB_{MSY}/SB_0 comme s'il s'agissait d'un effet aléatoire qui varie selon l'ordre taxonomique et la longueur maximum. La valeur de $SB_{MSY}/SB_0 = 0{,}40$ estimée pour les 147 stocks est intermédiaire entre les valeurs implicites dans les modèles de Fox et de Schaefer, bien que les SB_{MSY}/SB_0 des Clupéiformes et les Perciformes soient plus faibles et ceux des Gadiformes et des Scorpaeniformes, plus grands. La sélection de modèle appuie l'hypothèse voulant que les poissons à grands corps d'un ordre taxonomique donné présentent un SB_{MSY}/SB_0 relativement plus élevé. Ces résultats peuvent servir à définir des points de référence pour les pêches pour lesquelles peu de données sont disponibles ou comme intrants pour de nouvelles méthodes d'évaluation.

[Traduit par la Rédaction]

Introduction

Surplus production (i.e., production of biomass above what is needed to replace individuals lost to natural mortality) incorporates the combined effects of individual growth, recruitment, predation, and disease (Hilborn 2001; Walters et al. 2008). This process is central to fisheries science because surplus production can be interpreted as the level of fishery harvest that could be maintained without diminishing stock biomass and thus represents the combined effect of all factors that contribute to sustainable fisheries harvest. For any level of fishery harvest to be sustainable, some or all of the biological processes contributing to surplus production must be compensatory (i.e., increasing as stock biomass decreases; Longhurst 2010).

Surplus production models represent a simplified approximation to the surplus production process and, hence, sustainable fishery harvest. The original treatment of the surplus

J.T. Thorson and T.A. Branch. School of Aquatic & Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195-5020, USA.
J.M. Cope. Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112, USA.
O.P. Jensen. Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, NJ 08901-8525, USA.

Corresponding author: James T. Thorson (e-mail: JimThor@uw.edu).

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production process, based on the logistic growth model, assumed that surplus production is maximized at 50% of unfished biomass (Schaefer 1954). By contrast, a later proposal for the surplus production model assumed that surplus production is maximized at approximately 37% of unfished biomass (Fox 1970). Debate has continued since the 1970s regarding the use of one or the other model in any given application (Prager 2002, 2003; Maunder 2003*a*).

As one generalized approximation for the surplus production process, the Pella–Tomlinson model (Pella and Tomlinson 1969) includes a shape parameter that controls the level of biomass as a proportion of unfished biomass at which surplus production is maximized. Given appropriate values for the shape parameter, the Pella–Tomlinson model can exactly replicate either the Schaefer or Fox models, as well as various other possible surplus production relationships. This shape parameter can in theory be estimated from time series data, although in practice, there is generally insufficient information in individual data sets to estimate it with any precision (Prager 2002; Maunder 2003*a*).

To define the surplus production process, age-structured population dynamics and stock assessment models generally assume that compensation arises primarily from recruitment, wherein recruitment per unit spawning biomass (SB) increases as SB decreases (e.g., Methot 2009). Depensatory recruitment (Liermann and Hilborn 1997) is rarely included in this assumed relationship, and density-dependent changes in growth (Lorenzen and Enberg 2002), natural mortality (Walters and Kitchell 2001), and fecundity (Venturelli et al. 2010) could also result in aggregate compensatory or depensatory (decreasing with decreased biomass) surplus production. Each of these biological effects in isolation is difficult to predict, and their net effect is virtually impossible to estimate. This difficulty has led to the widespread assumption that recruitment compensation is the primary determinant of target biomass levels (Beddington and Kirkwood 2005) and is the only form of density dependence allowed for in almost all age-structured model assessments of stock histories or projections of future stock abundance.

Meta-analysis is frequently used to provide information regarding difficult to estimate parameters in ecological and stock assessment models (Hilborn and Liermann 1998; Myers and Mertz 1998). Results from meta-analyses can be included in a given ecological model either by fixing model parameters at their expected values as estimated by meta-analysis or by also including meta-analysis estimates of expected values and predictive errors in a Bayesian prior or likelihood penalty (Punt and Hilborn 1997; Minte-Vera et al. 2005). However, meta-analysis has historically focused on developing priors for recruitment compensation (Clark 1993; Dorn 2002) and is largely absent regarding likely values for the shape of the surplus production relationship. Databases such as the RAM Legacy Stock Assessment Database (Ricard et al., in press), which includes assessed stocks throughout the world but with particularly strong coverage in the USA, Europe, New Zealand, and Canada, represent one possible source of information regarding average and aggregate compensatory factors as approximated by surplus production models.

Fisheries management often involves comparing an estimate of current mature biomass or spawning potential with a target level (Enberg et al. 2010) to ascertain the status of the stock, as well as identifying a harvest level or rate that is appropriate for maintaining an optimal size for a managed population. For good or ill, the level of spawning or total biomass that generates maximum surplus production (SB_{MSY} or TB_{MSY}, respectively) continues to be a common biological reference point (whether target, limit, or otherwise) for fisheries management (Larkin 1977; Smith and Punt 2001; Hilborn and Stokes 2010). When possible, biomass reference points can be calculated from an estimated stock–recruit relationship in addition to estimated or assumed values for natural mortality, fishery selectivity, individual growth, and other effects (Mace 1994). In practice, these additional factors are often unknown or estimated with high variance. In these cases, biomass reference points are often fixed at an ad hoc proxy level by regional fisheries management authorities; proxy values are generally informed by previous meta-analyses of stock–recruit relationships or life history theory for a given taxonomic group (Clark 1993; Brooks and Powers 2007) and may not incorporate information about other compensatory or depensatory processes.

In this study, we use the RAM Legacy Stock Assessment Database in a maximum likelihood mixed-effects model for two related study goals: to identify whether process- or measurement-error models are more suitable for meta-analysis and how taxonomy and life history factors influence SB reference points (SB_{MSY}/SB_0, where SB_0 represents the average spawning biomass of the unexploited stock). Additionally, we try to estimate the expected value and between-stock variability for SB_{MSY} reference points that incorporates taxonomic and life history information. We specifically explore the hypothesis that smaller body size (as a proxy for productivity) will be associated with lower SB_{MSY}/SB_0 and that SB_{MSY}/SB_0 will vary by taxonomic order, where Scorpaeniformes are hypothesized to have relatively high values and Clupeiformes relatively low values of SB_{MSY}/SB_0. We then discuss how our estimates of SB_{MSY}/SB_0 differ from previous theoretical or empirical analyses (as well as possible explanations for these differences) and identify future directions and possible uses for research on biomass reference points.

Materials and methods

Available data

We extracted landings (C_t) and annual estimates of biomass (B_t) for finfishes from the RAM Legacy Stock Assessment Database (Ricard et al., in press). We chose to analyze primarily the surplus production relationship for SB to allow inference to fishery management biomass targets and stock assessment methods that primarily deal with SB. SB_t was then treated as an index of abundance for use in surplus production models, and we calculated "observed" surplus production as the change in biomass plus catch for each year ($SP_t = SB_{t+1} - SB_t + C_t$). Throughout the manuscript, we will generally refer to SB_t, but present results for total biomass (TB_t) in the online Supplementary Information[1].

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[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/f2012-077.

We excluded all stocks where (*i*) less than 20 years of catch and SB were available or (*ii*) a surplus production model was used to estimate the biomass index. We excluded stocks with few years of data, since each additional stock requires the estimation of three additional fixed effect parameters, which would slow the model, without adding much information compared with stocks with longer time series. We also excluded stocks where maximum "observed" surplus production (i.e., $\max(SP_t)$) was more than twice as large as maximum SB ($\max(SB_t)$) because we believe these instances may represent implausible biological effects and (or) errors in previous stock assessment estimates of biomass. This left a total of 147 stocks (average length of 41 years per stock) with landings and stock assessment estimates of spawning stock biomass (listed in Supplementary Table S1[1]). All of these stocks had data regarding maximum length (L_{max}) and taxonomy (order).

We hypothesized that lower values of SB_{MSY}/SB_0 would be associated with higher species productivity (i.e., high capacity to recover if depleted). Species productivity has been estimated previously using a variety of life history characteristics and is correlated with many individual growth and life history parameters (Cheung et al. 2005; Patrick et al. 2009). However, no estimate of productivity was available for all 147 stocks, so we compiled estimates of L_{max} for all stocks and assessed to what degree $\ln(L_{max})$ — a component of productivity (Patrick et al. 2009) — could be used as a proxy for productivity using a set of 74 species collected by Patrick et al. (2009).

In the following "Model development" section, we present the parameterization of the Pella–Tomlinson model that is used for all subsequent models. We then present how biomass is projected forward given this model and use a state–space surplus production model fitted to data from each stock individually to determine whether process or measurement errors have greater magnitude in this stock assessment database. The "Process error meta-analysis modeling" section then explains how the expected value of the Pella–Tomlinson shape parameter depends upon $\ln(L_{max})$ and taxonomic order and the application of empirical Bayes estimation for meta-analysis models using the trapezoid method for integration (Leader 2004).

Model development

Surplus production models approximate population dynamics by modeling annual changes in biomass as a function of current biomass. We focus our model developing, testing, and selection on the Pella–Tomlinson surplus production model because it contains a shape parameter φ that allows it to exactly replicate either the Fox ($\varphi = 1$) or Schaefer ($\varphi = 2$) surplus production models. Each value of φ corresponds to a possible value of SB_{MSY}/SB_0, such that estimating φ is equivalent to estimating SB_{MSY}/SB_0 for a given species, taxonomic order, body size, etc.

We used the Fletcher parameterization of the Pella–Tomlinson model (Fletcher 1978), as provided by Quinn and Deriso (1999), although we reparameterized maximum sustainable yield (MSY) as a proportion of carrying capacity ($y = MSY/SB_0$) to ease selection of biologically plausible starting values for estimated parameters:

$$(1) \quad \widehat{S}_t = \gamma \cdot y \cdot SB_t - \gamma \cdot y \cdot SB_0 \cdot \left(\frac{SB_t}{SB_0}\right)^{\varphi}$$

where

$$(2) \quad \gamma = \frac{\varphi^{\varphi/\varphi-1}}{\varphi - 1}$$

and SB_0 is unfished SB. In these equations, $\widehat{S}_t$ is the estimated surplus production in year t, given parameters SB_0, y, and φ and a state variable SB_t representing SB in year t; γ is an intermediate quantity derived from the shape parameter φ (eq. 2); and other parameters are as defined previously.

The Fletcher parameterization of the Pella–Tomlinson model (eq. 1) has no solution when $\varphi = 1$, although it asymptotically approaches the Fox model as φ approaches 1. In the case that $\varphi = 1$, we used the corresponding parameterization of the Fox model:

$$(3) \quad \widehat{S}_t = e \cdot y \cdot SB_t \cdot \ln\left(\frac{SB_t}{SB_0}\right)$$

These equations generalize to the Fox model when $\varphi \to 1$ and to the Schaefer model when $\varphi = 2$. Note that eqs. 1 and 3 differ from standard notation for Pella–Tomlinson and Fox models because of the definition of y as MSY/SB_0.

Various biological and environmental processes will affect the magnitude of surplus production generated by a population in a given year. Some of these processes are implicit in equations used to calculate surplus production from current stock biomass, including growth, recruitment, and natural mortality. Other factors that are not explicitly modeled can affect surplus production, including changes in age structure; environmental effects on somatic growth, survival, or recruitment; and multispecies interactions (Walters and Kitchell 2001; Lorenzen and Enberg 2002; Kinzey and Punt 2008). These effects will contribute to process errors, which we speculate will have large magnitude. By contrast, measurement errors will arise when stock assessment estimates of SB diverge from the "true" SB that is driving and arising from compensatory factors as approximated by the surplus production relationship.

Parameters in the surplus production relationship can be estimated while assuming that there are process errors, measurement errors, or both (Polacheck et al. 1993; Punt 2003). Process, measurement, and state–space surplus production models all use the following process and observation equations:

$$(4) \quad \widehat{SB}_{t+1} = (\widehat{SB}_t + \widehat{S} - C_t) \cdot \exp(\varepsilon_t)$$

$$(5) \quad SB_t = \widehat{SB}_t \cdot \exp(\tau_t)$$

where ε_t and τ_t are process and measurement errors, respectively, in year t. All models include the assumption that the catchability coefficient was equal to one, because stock assessment estimates of SB were used as indices of true SB. Process and measurement errors are both multiplicative and lognormal, although exploratory analysis showed that results are similar when using additive and normally distributed errors. This error structure implies that estimated and observed biomass is always positive, while surplus production (i.e., $SB_{t+1} - SB_t + C_t$) may be either positive or negative. Process-error models assume that $\tau_t = 0$, and measurement-error models assume that $\varepsilon_t = 0$, while state–space models estimate both simultaneously.
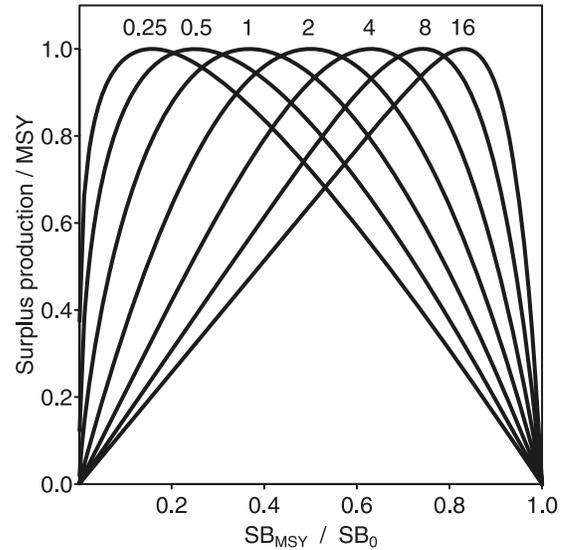
Simultaneously estimating both process and measurement errors requires a state–space modeling framework (Punt 2003) and is not computationally feasible for all species simultaneously within a single meta-analysis. We therefore fitted state–space surplus production models (Punt 2003; Ono et al. 2012) to data for each species individually to explore the plausible ratio of process and measurement errors. Exploratory analysis showed that convergence generally required specifying φ at a fixed value (i.e., $\varphi = 2$) and that resulting estimates of process and measurement errors were not sensitive to this value. The marginal likelihood for the state–space model was calculated as

Fig. 1. Surplus production as a function of biomass using the Pella–Tomlinson model given different values of φ, from left to right: 0.25 ($SB_{MSY}/SB_0 = 0.157$), 0.5 ($SB_{MSY}/SB_0 = 0.25$), 1 ($SB_{MSY}/SB_0 = 0.367$), 2 ($SB_{MSY}/SB_0 = 0.5$), 4 ($SB_{MSY}/SB_0 = 0.630$), 8 ($SB_{MSY}/SB_0 = 0.743$), 16 ($SB_{MSY}/SB_0 = 0.831$), showing that φ is symmetric around 2 on a logarithmic scale.

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(6) \quad L\left(SB_0, y, \frac{SB_1}{SB_0}, \sigma_p, \sigma_m \mid C_t, SB_t\right)
$$

$$
= \int_\varepsilon \prod_{t=1}^{T-1} \left(\frac{1}{SB_{t+1}\sigma_m\sqrt{2\pi}} \exp\left\{ -\frac{[\ln(SB_{t+1}) - \ln(\widehat{SB}_{t+1})]^2}{2\sigma_m^2} \right\} \cdot \frac{1}{SB_{t+1}\sigma_p\sqrt{2\pi}} \exp\left\{ -\frac{[\ln(SB_{t+1}) - \ln(SB_t + \widehat{S}_t - C_t)]^2}{2\sigma_p^2} \right\} \right) d\varepsilon
$$

where σ_p and σ_m are the standard deviation of process and measurement errors, respectively, and T is the number of years of data for a given stock. The high-dimensional integral across process errors (ε_t) was accomplished using the Laplace approximation as implemented by ADMB-RE (Skaug and Fournier 2006).

Selection between process- and measurement-error models was necessary to decide whether to conduct meta-analysis using process- or measurement-error models, and this model selection cannot be done using common model selection tools such as the Akaike information criterion (AIC; Akaike 1974), because process and measurement error models differ in their assumptions about errors. To decide between process- and measurement-error models, we sought to identify a likely value for the ratio of process to measurement errors (σ_p/σ_m, termed λ). This ratio is important when evaluating the estimation errors that result from ignoring either process or measurement errors; a process-error model is generally appropriate when process errors have much larger magnitude than measurement errors, and vice-versa (Ludwig and Walters 1981; e.g., Thorson and Berkson 2010a). This ratio was estimated by fitting the state–space surplus production model to data for each stock individually, assuming a single fixed value for $\varphi = 2$. Results were discarded for species where either (i) the model did not converge or (ii) the estimated process- and measurement-error standard deviation parameters had not moved from their starting values.

Exploratory data analysis using single-species state–space surplus production models resulted in a single-species estimate of the ratio of measurement to process errors ($\lambda = \sigma_p/\sigma_m$) for 92 of 147 stocks (the model did not converge for the other 55 stocks). The distribution of λ is highly non-normal (as is expected for a ratio statistic), but is strongly skewed towards values greater than one (i.e., process errors > measurement errors). The median value was 3.2, supporting the use of process-error models in subsequent analyses. This supports our hypothesis that process errors have greater magnitude than measurement errors when treating stock assessment estimates of biomass as an index of abundance.

Process error meta-analysis modeling

In meta-analysis, random effects are often used to account for variation among observation units (e.g., fish stocks). Random effect models require specifying an underlying distribution for the random effects and then estimating the parameters (e.g., the expected value and variance) for that distribution (Gelman et al. 2003; Gelman and Hill 2007). Plausible φ values were symmetric on a multiplicative scale around 2 (Fig. 1), so we treated $\ln(\varphi)$ as our parameter of interest (i.e., as a random effect). Treating $\ln(\varphi)$ as a random effect (rather than a fixed effect like other model parameters) provides the benefit that for stocks with little information regarding the Pella–Tomlinson shape parameter, its value is "shrunk" towards the underlying expected value for $\ln(\varphi)$.

This allows the model to determine which stocks are informative about the average shape of the surplus production relationship, without being unduly influenced by stocks with uninformative data. The treatment of $\ln(\varphi)$ as a random effect also acknowledges the biologically plausible variability among stocks in the shape of the surplus production process, and ignoring such variability is likely to obscure any possible conclusions (Clark 2003). However, we refrained from using a fully Bayesian analysis framework given that seemingly "uninformative" priors are frequently informative about derived parameters (Maunder 2003b), and because justifiable priors cannot be feasibly developed for all species in a meta-analysis.

We used a normally distributed hyperdistribution for $\ln(\varphi)$, where the expected value of $\ln(\widehat{\varphi}_s)$ for stock s was affected by taxonomic order and zero-centered, log-scaled body size information, according to one of four hypothesized relationships:

$$(7a) \qquad \ln(\widehat{\varphi}_s) = \beta_I$$

$$(7b) \qquad \ln(\widehat{\varphi}_s) = \sum_{c=1}^{n_{\text{orders}}} I(C_s = c)\beta_{I,c}$$

$$(7c) \qquad \ln(\widehat{\varphi}_s) = \beta_I + \left[\ln(L_{\max,s}) - \frac{1}{n_{\text{stock}}}\sum_{s'=1}^{n_{\text{stock}}}\ln(L_{\max,s'})\right] \cdot \beta_{\ln(L_{\max})}$$

$$(7d) \qquad \ln(\widehat{\varphi}_s) = \sum_{c=1}^{n_{\text{orders}}} I(C_s = c)\beta_{I,c} + \left[\ln(L_{\max,s}) - \frac{1}{\sum_{s'=1}^{n_{\text{stock}}} I(C_s = C_{s'})}\sum_{s'=1}^{n_{\text{stock}}} I(C_s = C_{s'})\ln(L_{\max,s'})\right] \cdot \beta_{\ln(L_{\max})}$$

where β_I is the intercept when not including taxonomic class, $\beta_{I,c}$ is the intercept for taxonomic class c when including taxonomic class, $I(C_s = c)$ is an indicator function that equals 1 when the class C_s of stock s equals c and 0 otherwise, $L_{\max,s}$ is $L_{\max}$ (in cm) for stock s, $\beta_{\ln(L_{\max})}$ is the estimated coefficient representing the linear effect of $\ln(L_{\max})$ on $\ln(\widehat{\varphi}_s)$, and $I(C_s = C_{s'})$ is an indicator function that equals 1 when the taxonomic class C of stock s and s' are the same and 0 otherwise. Equation 7a represents a model without taxonomic class or $\ln(L_{\max})$. Equation 7b includes taxonomic order without $\ln(L_{\max})$, while eq. 7c includes $\ln(L_{\max})$ without order. Equation 7d includes both taxonomic order and class. Equation 7c represents the effect of $\ln(L_{\max})$ on $\ln(\widehat{\varphi}_s)$ both within- and between-class, while eq. 7d represents the effect of $\ln(L_{\max})$ only within-class (i.e., while controlling separately for the impact of taxonomic class).

We used maximum likelihood estimation to fit an "empiri-cal Bayes" mixed-effects model (de Valpine 2009). The integral across $\ln(\varphi)$ used in empirical Bayes mixed-effects models was evaluated using the trapezoid method (Leader 2004) with 50 evaluations that were evenly spaced in log-space ranging from $\ln(0.1)$ to $\ln(40)$, where exploratory analysis and model diagnostics showed that this number of evaluations was a sufficient approximation to the full integral. We use the trapezoid method rather than the Laplace approximation as implemented in ADMB-RE because the trapezoid method is likely to be more accurate than the Laplace approximation for low-dimensional integrals such as this (Bolker et al. 2009), and because it allows easy calculation of confidence intervals for random effects at the maximum likelihood estimate. We use the trapezoid method instead of Gaussian–Hermite quadrature for simplicity of presentation.

The marginal likelihood for the process-error model when using the trapezoid method was calculated as

$$(8) \qquad L\left(\text{SB}_0, y, \sigma_{\text{process}}, \beta_I, \beta_{L_{\max}}, \sigma_{\ln(\varphi)} \mid C_{s,t}, \text{SB}_{s,t}\right) = \prod_{s=1}^{n_{\text{stock}}} \sum_{i=1}^{n_{\text{trap}}} w_i \prod_{t=1}^{T_s - 1}$$

$$\left(0.95\frac{1}{\text{SB}_{s,t+1}\sigma_{\text{process},s}\sqrt{2\pi}}\exp\left\{-\frac{[\ln(\text{SB}_{s,t+1}) - \ln(\text{SB}_{s,t} + \widehat{S}_t - C_t)]^2}{2\sigma_{p,s}^2}\right\}\right.$$

$$\left. + 0.05\frac{1}{\text{SB}_{s,t+1}20\sigma_{\text{process},s}\sqrt{2\pi}}\exp\left\{-\frac{[\ln(\text{SB}_{s,t+1}) - \ln(\text{SB}_{s,t} + \widehat{S}_t - C_t)]^2}{40\sigma_{p,s}^2}\right\}\right) \cdot \frac{1}{\sigma_{\ln(\varphi)}\sqrt{2\sigma}}\exp\left\{-\frac{[\ln(\widehat{\varphi}_s) - \ln(\varphi)_i]^2}{2\sigma_{\ln(\varphi)}^2}\right\}$$

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where $\ln(\varphi)_i$ is the value of $\ln(\varphi)$ for evaluation i of the trapezoid method, w_i is a corresponding weight, T_s is the number of years of data for stock s, and $\sigma_{\ln(\varphi)}$ is the estimated between-stock variability in $\ln(\varphi)$. Process-error models require estimating SB_0, y, process-error standard deviations (σ_p), and $\ln(\varphi)$. Evaluations for the integral, $\ln(\varphi)_i$, are evenly spaced between $\ln(0.1)$ and $\ln(40)$, with weights w_i equal to the distance between evaluation points. This equation involves a "robust normal" error distribution for process errors, which is implemented as a mixture where 5% of process errors have 20 times greater standard deviation than the other 95% of process errors. This robust normal distribution was specified to ensure that the model was robust to outliers in the surplus production process that may not be informative about its average value, and exploratory analysis showed that it decreased the sensitivity of model results to small changes in data or model assumptions.

Maximization of the marginal log-likelihood for process-error models was accomplished using the Automatic Differentiation Model Builder (ADMB) software (Fournier et al. 2012), called from within the R statistical platform (R Development Core Team 2009). Standard errors for all parameters were estimated from the inverse Hessian matrix as calculated using ADMB. Diagnostics for model convergence and fit included plotting estimated and observed surplus production while fixing random effects at their modes conditional on fixed effect maximum likelihood estimate (MLE) values. We also plotted the log-likelihood for species-specific $\ln(\varphi)$ conditional on fixed effect MLE values, both to explore the assumption that $\ln(\varphi)$ was normally distributed and to inspect the width of the 95% confidence interval for $\ln(\varphi)$ for each stock conditional on the MLE.

Objective 1: model selection and life history effects

We sought to identify the effect of taxonomic order and maximum length on the ratio SB_{MSY}/SB_0 for each stock. Data on taxonomic order and maximum length were available globally and did not require restricting the set of stocks. Taxonomic order has been used to explain differences in the stock–recruit relationship in previous meta-analyses (Myers and Barrowman 1996; Myers 2001), and sufficient data were available to distinguish Pleuronectiformes (e.g., flatfishes), Gadiformes (e.g., codfishes), Scorpaeniformes (e.g., rockfishes), Clupeiformes (e.g., anchovies), and Perciformes (e.g., perches). An additional group was assembled from all stocks that did not fall in one of these orders. Taxonomy was hypothesized to affect the expected value for $\ln(\varphi)$, where Scorpaeniformes was hypothesized to have relatively high values for SB_{MSY}/SB_0 owing to relatively low levels of recruitment compensation, and Clupeiformes was hypothesized to have relatively low values of SB_{MSY}/SB_0 (Myers 2001; Dorn 2002). Body size was hypothesized to be correlated with increased SB_{MSY}/SB_0 because increased size is associated with decreased productivity (Patrick et al. 2009).

The 2×2 cross arising from either including or excluding maximum length and taxonomic group were fitted for process-error random effects models. AIC (Akaike 1974) was used to select among different life history models for the process-error model. AIC has been extensively tested for selection of fixed effects in a mixed effects model (Pinheiro and Bates 2009).

Objective 2: estimating SB_{MSY} reference points

We seek to characterize the average shape of the surplus production process for marine fishes, which could be used either (i) as a likely value or Bayesian prior for future surplus production models (i.e., using the Pella–Tomlinson parameter φ) or (ii) as a likely value for SB_{MSY}/SB_0, which can be used to inform biological reference points for fisheries management. We therefore transform estimates of β_I and $\beta_{I,c}$ (from eq. 7) to give mean and standard deviation values for φ and SB_{MSY}/SB_0, using the delta method and the following relationship between the shape parameter φ and B_{MSY}/B_0 (McAllister et al. 2001):

$$(9) \quad \frac{SB_{MSY}}{SB_0} = \left(\frac{1}{\varphi}\right)^{\frac{1}{\varphi-1}}$$

Results (including standard errors) could be used as a Bayesian prior in future stock assessments involving surplus production models, where values for this prior can be conditioned on known characteristics of the target stock (e.g., taxonomic order). Bayesian priors are generally used to synthesize information from meta-analyses (Hilborn and Liermann 1998; Minte-Vera et al. 2005; Thorson and Berkson 2010b) and can be readily applied in many types of stock assessment models.

Results and discussion

Objective 1: model selection and the effect of taxonomy and body size

We found an R^2 of 43% (p value < 0.001 using a randomization test) when explaining productivity obtained by Patrick et al. (2009) using $\ln(L_{max})$. Thus, we concluded that $\ln(L_{max})$ could serve as a proxy for species productivity and assessed the impact of $\ln(L_{max})$ and taxonomic group on SB_{MSY}/SB_0. The model with greatest AIC support (Table 1) includes both taxonomic order and $\ln(L_{max})$, indicating that taxonomy is an important predictor of SB_{MSY}/SB_0 and that differences in length within a given taxonomic order are important for predicting SB_{MSY}/SB_0 for at least one of the taxonomic groups included in this study. Models that included $\ln(L_{max})$ had greater AIC support than corresponding models without $\ln(L_{max})$, either with or without taxonomic order. Support both with and without taxonomic order is important because results from life history studies will often vary depending upon whether associations are sought within (i.e., when controlling for) or between (i.e., when not controlling for) taxonomic order (Stearns 1983; Dunham and Miles 1985). The identified impact of $\ln(L_{max})$ on SB_{MSY} reference points is consistent with previous studies that demonstrate an increased rebuilding time for large-bodied, K-selected species (Adams 1980), because a high SB_{MSY}/SB_0 implies reduced surplus production at low levels of SB.

Objective 2: estimating SB_{MSY} reference points

The expected value for SB_{MSY}/SB_0 for all stocks pooled is 0.40 (standard error (SE) = 0.015; Table 2). Ranking among taxonomic groupings (Fig. 2) shows the highest SB_{MSY}/SB_0 for Scorpaeniformes ($SB_{MSY}/SB_0 = 0.46$, SE = 0.032). The high SB_{MSY}/SB_0 for Scorpaeniformes is unsurprising given that species from this order have been shown previously to

Table 1. Akaike information criterion (AIC) comparison among models with different taxonomic groupings (i.e., orders) and including or excluding the natural logarithm of maximum length ($\ln(L_{max})$) as a linear predictor of $\ln(\varphi)$ for process-error models, along with estimated value and standard error (SE) for the linear predictor.

Configuration name	Order	$\ln(L_{max})$	ΔAIC	$\beta_{\ln(L_{max})}$	SE $(\beta_{\ln(L_{max})})$
1a	No	No	10.9	—	—
2a	Yes	No	2.5	—	—
1b	No	Yes	2.6	0.461	0.148
2b	Yes	Yes	0.0	0.388	0.186

Table 2. Proposed priors for SB_{MSY}/SB_0.

	SB_{MSY}/SB_0 (estimated average value)	SD (between-stock variability in SB_{MSY}/SB_0)	SE (standard error for SB_{MSY}/SB_0)	$\sqrt{SD^2 + SE^2}$ (predictive error for SB_{MSY}/SB_0)
Pooled				
All	0.404	0.135	0.015	0.136
Taxonomic groupings				
Pleuronectiformes	0.395	0.119	0.029	0.122
Gadiformes	0.439	0.122	0.028	0.125
Perciformes	0.353	0.114	0.036	0.120
Clupeiformes	0.261	0.097	0.040	0.105
Scorpaeniformes	0.463	0.122	0.032	0.126
Other	0.405	0.120	0.044	0.127

Note: "Pooled" results are from process-error model configuration 1a; "Taxonomic groupings" results are from process-error model configuration 2a. SD, standard deviation; SE, standard error.

have relatively little recruitment compensation (Dorn 2002). Next in decreasing order is Gadiformes ($SB_{MSY}/SB_0 = 0.44$, SE = 0.028) and Pleuronectiformes ($SB_{MSY}/SB_0 = 0.40$, SE = 0.029). By contrast, Perciformes ($SB_{MSY}/SB_0 = 0.35$, SE = 0.036) and Clupeiformes ($SB_{MSY}/SB_0 = 0.26$, SE = 0.040) have lowest values for SB_{MSY}/SB_0. This is unsurprising for Clupeiformes because species from this taxonomic order often have high variability in abundance and appear to be capable of rapid population recovery given suitable environmental conditions (Hutchings 2000). For completeness, we present results for the "Other" category, which are intermediate relative to the orders that are estimated separately ($SB_{MSY}/SB_0 = 0.41$, SE = 0.044). Also included is a recommended value for predictive error in SB_{MSY}/SB_0, composed of both estimation errors and estimated between-stock variability in SB_{MSY}/SB_0 (Table 2). These values range from 0.105 to 0.136, representing differences in the predictive accuracy among orders. Exploratory analysis showed that the ranking of SB_{MSY}/SB_0 among taxonomic groups is similar when (*i*) treating SB_{MSY}/SB_0 as a normally distributed random effect (rather than $\ln(\varphi)$), (*ii*) when using a lognormal distribution for errors rather than the robust lognormal as used by default, or (*iii*) when using additive normal process errors rather than the multiplicative lognormal errors presented here. Differences in the distribution of errors or random effects do affect the absolute value of SB_{MSY}/SB_0 for different taxonomic groups (particularly for Scorpaeniformes), and we present results for the robust lognormal model because it is simultaneously least sensitive to outliers and consistent with previous treatment of surplus production errors.

Fig. 2. Range for SB_{MSY}/SB_0 conditional on the maximum likelihood estimate of all fixed effects. The line for each species indicates values where the conditional likelihood is >5% of maximum conditional likelihood for the process-error model using spawning biomass (SB_t) as an index of abundance and including taxonomic order but not maximum length. (*a*) Pleuronectiformes; (*b*) Gadiformes; (*c*) Perciformes; (*d*) Clupeiformes; (*e*) Scorpaeoniformes; (*f*) Other.

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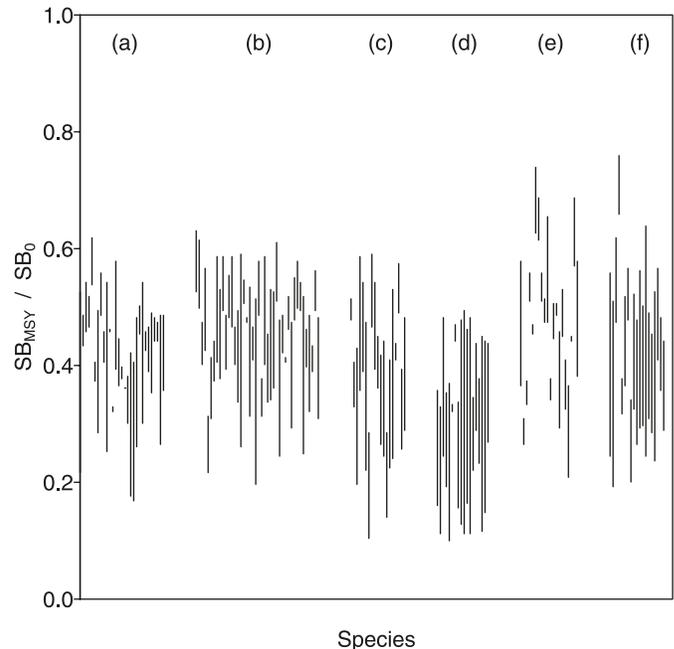
Table 3. Hyperparameter estimates for process-error models.

	φ (estimated average value)	SD (between-stock variability in φ)	SE (standard error for φ)	$\sqrt{SD^2 + SE^2}$ (predictive error for φ)
Pooled				
All	1.478	0.844	0.094	0.849
Taxonomic groupings				
Pleuronectiformes	1.353	0.715	0.176	0.736
Gadiformes	1.729	0.913	0.210	0.937
Perciformes	1.064	0.562	0.179	0.590
Clupeiformes	0.599	0.316	0.131	0.342
Scorpaeniformes	1.970	1.040	0.268	1.074
Other	1.431	0.756	0.277	0.805

Note: "Pooled" results are from process-error model configuration 1*a*; "Taxonomic groupings" results are from process-error model configuration 2*a*. SD, standard deviation; SE, standard error.

Results for the process-error model with all stocks pooled yields an expected value for φ ($\varphi = 1.48$, SE = 0.094; Table 3) that is intermediate between the assumed value for the Schaefer ($\varphi = 2$) and Fox ($\varphi = 1$) models. However, the estimated value of φ is lower than the Fox model for Clupeiformes and close to the Schaefer model for Scorpaeniformes. This indicates that the suitability of different conventional surplus production models varies by taxonomic order. Alternatively, future surplus production studies could use estimates of φ, either with a fixed value or with the estimated predictive error as the standard deviation of a Bayesian prior.

Estimated values for TB_{MSY}/TB_0 and φ given TB (rather than SB) are presented in the Supplemental Information[1]. These values show similar trends to SB_{MSY}/SB_0, although the estimated TB_{MSY}/TB_0 for all stocks pooled is somewhat higher (0.44), and Scorpaeniformes has an appreciably higher estimate of TB_{MSY}/TB_0 than of SB_{MSY}/SB_0 ($TB_{MSY}/TB_0 = 0.57$, SE = 0.052). J. Cope (unpublished data) applied simplified age-structure models to 36 species of rockfishes (*Sebastes* spp.) and four flatfishes and found a mean ratio of SB_{MSY}/SB_0 to TB_{MSY}/TB_0 of 84% (i.e., that biomass reference points for TB are generally higher than biomass reference point for SB when using age-structured modeling methods). This difference arises because fishing is generally directed at older individuals. Thus, the mature individuals contributing to recruitment will often be depleted proportionally greater than immature individuals, and at MSY, TB will be a greater fraction of unfished levels than SB. However, the value and even relative magnitude of SB and TB ratios will vary depending on specifics of each fishery, including the age- or length-selective properties of fishing gear.

As comparison with SB targets for one particular fisheries management region, $SB_{MSY}/SB_0 = 40.4\%$ is nearly identical to the $SB_{40\%}$ proxy for SB_{MSY} (i.e., the assumption that MSY occurs when $SB_{MSY}/SB_0 = 40\%$) used by the Pacific Fisheries Management Council (PFMC) for all stocks prior to 2009. The SB target proxy for flatfishes (i.e., Pleuronectiformes) was changed to $SB_{25\%}$ in 2010 by the PFMC, and this revised value is considerably lower than the $SB_{MSY}/SB_0 = 40\%$ estimated for Pleuronectiformes in this analysis. An important reason for differences between this and past analyses may be that biomass reference point analyses have generally been based on stock–recruit meta-analysis (e.g., Dorn 2002), and these may not account for other types of compensatory or depensatory processes, including changes in individual growth rates, maturity, trophic interactions, maternal effects, or other processes. Future theoretical and empirical research could therefore explore the imprecision and (or) bias that may occur when using an incorrect parametric model for the stock–recruit relationship in age-structured models and (or) failing to account for other compensatory or depensatory processes, as well as the impact of this when analyzing resulting biomass estimates in a meta-analysis.

The value for SB_{MSY}/SB_0 estimated in this study for all orders pooled represents the value when averaging across the frequency of selecting each taxonomic order (and other factors that influence SB_{MSY}/SB_0, such as fecundity at age and selectivity at age) in the RAM database. Given that the RAM Legacy Stock Assessment Database represents an opportunistic selection of assessed species for which data is publically available, we believe that an unbiased estimate of SB_{MSY}/SB_0 for a given species requires controlling as much as possible for confounding effects such as taxonomic order. In a similar vein, the "Other" category represents a value for SB_{MSY}/SB_0 when averaging across all other taxonomic groups (besides the five that we estimated individually) in their relative frequency in the opportunistic RAM database. The sampling frequency of orders in the "Other" category is unlikely to correspond to a desired "sampling population" for any given application, so we recommend against using the estimated SB_{MSY}/SB_0 for the "Other" category for orders besides those used here. Instead, we recommend using the average SB_{MSY}/SB_0 value for all stocks pooled for orders besides the five we estimated individually.

Prior understanding of the SB_{MSY}/SB_0 relationship has direct application to surplus production stock assessment models such as ASPIC (Prager 1992) and other surplus production model applications (e.g., Ono et al. 2012). SB_{MSY}/SB_0 is also an important parameter in many recently developed approaches to managing species in data-limited situations. Examples include SB_{MSY} or TB_{MSY} reference points when using a relative index of abundance that starts at a relatively unexploited state (Porch et al. 2006) or when using local depletion ratios to manage fishery harvest near marine protected areas (McGilliard et al. 2011). SB_{MSY}/SB_0 is also used as one of four inputs while calculating sustainable catch levels in depletion-corrected average catch (MacCall

2009) and depletion-based stock reduction analysis (Dick and MacCall 2011). Current assumptions about SB_{MSY}/SB_0 used in depletion-based stock reduction analysis are based on the target biomass reference points for the US Pacific Fishery Management Council, mainly 0.40 and 0.25 for groundfishes and flatfishes, respectively, with an a priori standard deviation of 0.05. These values are informed by assumptions about the value of recruitment compensation (i.e., the steepness parameter of the stock–recruit relationship) for these groups. Results from this study can help update such prior distributions to better inform species-specific productivity rates, although our results will conflict somewhat with current assumptions about steepness for flatfishes (Pleuronectiformes) in particular.

Other theories for calculating SB_{MSY}/SB_0

The conflict between priors on steepness and priors on SB_{MSY}/SB_0 estimated in this study arises because there is a direct correspondence between recruitment compensation (i.e., the steepness parameter of the stock–recruit relationship) and SB_{MSY}/SB_0 in age-structured models that use a two-parameter stock–recruit relationship, such as the Beverton–Holt or Ricker models (Mangel et al. 2010). Such a link allows calculation of the shape parameter from the stock–recruit steepness parameter, and vice-versa, given information or assumptions regarding individual growth, mortality, and fecundity and the assumption that all compensation occurs in recruitment. This link provides an alternative method for determining a plausible range of values for the surplus production shape parameter given minimum or maximum plausible values for steepness (He et al. 2006 and Brooks et al. 2010, respectively). Such calculations could be used to corroborate or refine the SB_{MSY}/SB_0 priors developed in this study. Alternatively, three-parameter stock–recruit models do not have a direct correspondence between steepness and SB_{MSY}/SB_0 (E. Dick, National Marine Fisheries Service (NMFS) – National Oceanic and Atmospheric Administration (NOAA), Southwest Fisheries Science Center, Santa Cruz, CA 95060, USA, personal communication, 2012), so we recommend the use of three-parameter stock–recruit models when simultaneously using priors on both steepness and SB_{MSY}/SB_0 to avoid a situation where priors on different parameters represent conflicting information about the shape of aggregate surplus production.

Life history theory has previously highlighted the binary trade-off between opportunistic (*r* type) and equilibrium (*K* type) species (Adams 1980) or an expanded life history pyramid (Winemiller and Rose 1992; Cortés 2000; Rose et al. 2001). Such theory has repeatedly lead to the assertion that long-lived species will tend to maintain population sizes near environmental carrying capacity and will optimize individual fitness (i.e., per capita reproductive output and survival) when population size is near carrying capacity. Such *K*- or equilibrium-selected species are hypothesized to have maximum net production near carrying capacity (i.e., high SB_{MSY}/SB_0), while other *r*- or opportunistic-selected species would have maximum net production during phases of scramble competition (i.e., low SB_{MSY}/SB_0; Fowler 1981). This theory is supported by Fowler's (1988) meta-analysis showing a negative relationship between SB_{MSY}/SB_0 and ln ($r \cdot T$) where $r \cdot T$ is population growth rate per generation, because a decreased growth rate per generation (as expected for

equilibrium-type species) is correlated with an increased SB_{MSY}/SB_0. However, empirical evidence remains mixed for the hypothesis that opportunistic species have lower SB_{MSY}/SB_0 than equilibrium-type species (Sibly et al. 2005). As one explanation for this mixed evidence, Williams and Shertzer (2003) point out that a weak link between population dynamics and life history theory can be explained either by data sets with weak power to detect life history relationships or by population dynamics strongly driven by environmental conditions.

Other studies have attempted to deduce information regarding SB_{MSY} reference points from demographic information (Thompson 1992; Garcia-Saez 1997; McAllister et al. 2001). Such studies combine life history theory with assumptions about individual growth parameters, fishery selectivity, and other relevant age-structured effects to provide bounds on plausible values for SB_{MSY} reference points. However, the use of such strategies to inform the shape of the surplus production relationship remain highly contested (Prager 2002, 2003; Maunder 2003a), in part because of the strong assumptions implied by conventional age-structured population dynamics models (e.g., natural mortality being age- and time-invariant, stock–recruit relationship being fixed at a single parametric model, selectivity being time-invariant and parametric, etc.).

Future studies

There are many possible next steps for the current work, including (*i*) estimating fishing mortality reference points (e.g., F_{crash}, F_{MSY}) for data-poor stocks; (*ii*) testing different possible life history covariates to explain between-species variability in SB_{MSY} reference points; (*iii*) simulation testing the performance of the Bayesian priors developed in this study; (*iv*) identifying any selection biases caused by using data from assessed stocks to characterize population dynamics of marine fishes in general; and (*v*) exploring the consequences of using stock assessment estimates of total abundance as an index of abundance. We point these out as suggestions for future research.

At first glance, the present analysis might appear to provide F_{MSY} estimates for multiple species, which could perhaps be summarized to provide advice for F_{MSY} reference points by taxonomic grouping, similar to how single-species estimates have been summarized in previous meta-analysis of the recruitment process (Myers 2001). However, many authors have noted that the Pella–Tomlinson model (in either differential equation or Fletcher-form difference equations as used here) has positive surplus production even when total abundance is at zero when $\varphi < 1$ (i.e., $SB_{MSY}/SB_0 < 0.37$; McAllister et al. 2001). Such a property makes the Fletcher parameterization of the Pella–Tomlinson model unattractive for estimating F_{MSY} reference points, thus encouraging use of the reparameterization of the Pella–Tomlinson curve proposed by McAllister et al. (2001) or Dick and MacCall (2011). Additionally, F_{MSY} reference points estimates differ from SB_{MSY} reference points estimates in that they do not depend upon estimation of B_0 (i.e., the descending limb of the surplus production curve). This implies that parametric forms are unnecessary and has given rise to the variety of empirical, nonparametric methods for estimating F reference points (O'Brien 1999; Bravington et al. 2000). Finally, F_{MSY} may

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be particularly sensitive to species-specific life history parameters (e.g., natural mortality; Zhou et al. 2012), and therefore summarizing F_{MSY} in a meta-analysis may require an expanded set of life history traits to achieve reasonable predictive accuracy.

Further investigation into life history covariates for SB_{MSY} reference points (such as fecundity or the von Bertalanffy growth coefficient) could also help refine species-specific estimates of SB_{MSY}/SB_0. The productivity measure of Patrick et al. (2009, 2010) is particularly appealing because it combines 10 life history traits into one composite measure and is easy to score. Adding this metric to analysis of surplus production patterns would offer new insight into the interplay of life history traits and invariants (Charnov 1993), taxonomy, and population response to fisheries removals (Jennings et al. 1998).

All proposed stock assessment methods require simulation testing to explore their performance when model assumptions are violated. Additionally, management learning and feedback mechanisms will allow management to be robust to some types of model failures, complicating the prediction of management outcomes given different possible model assumptions (Sainsbury et al. 2000). For these reasons, we suggest that future research could identify the relative costs and benefits of overestimating or underestimating SB_{MSY}/SB_0 when using different management strategies, as well as the benefits of estimating the shape parameter versus using a fixed value as implied by the Fox or Schaefer models. Such work would presumably include estimating the yield lost from overly conservative fisheries management, as well as the increased risk of stock collapse due to underestimating B_{MSY}/B_0 (Hilborn et al. 2012; Maunder 2012).

Selection biases may also influence the results of this study, because the RAM Legacy Stock Assessment Database represents a subset of valuable stocks, drawn primarily from a few intensively managed areas of the world's oceans (Sethi et al. 2010; Thorson et al. 2012), and may not be representative of the population dynamics of marine fishes in general. Life history characteristics have previously been shown to differ between stocks in the RAM database and the set of stocks included in the FAO landings database (FAO 2010; Pinsky et al. 2011). However, the RAM database contains a wide set of life history and taxonomic types and represents the largest existing database available for fish population dynamics studies such as this one. We therefore believe that our results are a useful description of fish population dynamics, while recommending future research that would characterize the selection characteristics of stocks included in the RAM database as well as possible consequences of this selection.

Finally, we note that all results are estimated using stock assessment model output (i.e., estimated time series of SB or TB). The use of model output is necessary, given that it is not computationally feasible to run 147 age-structured stock assessment models simultaneously using random effects. Any biases, however, in stock assessment estimates of biomass will consequently be propagated into the present results. For this reason, we interpret our results as a "consensus summary" of stock assessment estimates of surplus production. This should not limit its utility when informing the surplus production shape parameter or target biomass levels in future stock assessments, especially given that the impact of reusing information from any individual stock in this case is ex-

tremely small (Minte-Vera et al. 2005). This does, however, leave room for future studies to explore the likely impacts of using stock assessment estimates of biomass as a surplus production index of abundance, including the impact of using biomass estimates that are derived from a model using a parametric stock–recruit model. We also recommend the development of generic age-structured meta-analysis methods, which can facilitate the development of meta-analysis models that incorporate selective fishing, individual growth, and the other age-structured processes that are routinely incorporated into stock assessment models.

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