

Maternal age, fecundity, egg quality, and recruitment: linking stock structure to recruitment using an age-structured Ricker model

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Abstract: Understanding the process of recruitment is fundamental to fisheries biology and management. However, recruitment in natural populations is highly variable and rarely well described by classical stock–recruitment relationships (SRRs). Recent analyses suggest that the age composition of the spawning biomass may play an important role in the mismatch between SRRs and data. Here we develop a generalization of the Ricker SRR that incorporates age structure by allowing mortality and fecundity rates to depend on maternal age. We provide a flexible SRR with biologically interpretable parameters that can be estimated from existing fisheries time series and use a Bayesian framework that enables parameters to be informed by experimental data. We apply our method to the Icelandic population of Atlantic cod (*Gadus morhua*) and show models that include age structure effects outperform the classical Ricker SRR that ignores age structure. Our results indicate a strong effect of spawning stock age structure on recruitment dynamics in this population. Our approach provides a biologically interpretable and immediately applicable method for investigating the consequences for spawning stock age structure on recruitment.

Résumé : La compréhension du processus de recrutement est un aspect essentiel de la biologie et de la gestion des pêches. Le recrutement au sein de populations naturelles est toutefois très variable et les relations stock–recrutement (SSRs) classiques en fournissent rarement une description adéquate. Des analyses récentes suggèrent que la composition par âge de la biomasse de frai pourrait être un important facteur explicatif de la non-concordance des SSR et des données. Nous présentons une généralisation de la SRR de Ricker qui intègre la structure par âge en permettant que les taux de mortalité et de fécondité dépendent de l'âge maternel. Nous fournissons ainsi une SRR souple contenant des paramètres pouvant être interprétés d'un point de vue biologique et qui peuvent être estimés à partir de séries chronologiques existantes sur les pêches et nous utilisons un cadre bayésien qui permet la définition des paramètres à partir de données expérimentales. Nous appliquons cette méthode à la population islandaise de morue franche (*Gadus morhua*) et démontrons que les modèles qui intègrent les effets de la structure par âge donnent de meilleurs résultats que la SSR de Ricker classique, qui n'en tient pas compte. Nos résultats indiquent un effet marqué de la structure par âge des stocks reproducteurs sur la dynamique du recrutement dans cette population. Notre approche offre une méthode pouvant être appliquée immédiatement et permettant des interprétations biologiques pour étudier les répercussions de la structure par âge des stocks reproducteurs sur le recrutement.

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Introduction

The fundamental law of population biology is that species cannot increase without bound. When viewed in a single species context, this means that density dependence must act on survival, reproduction, or both. It is common in fisheries science to assume that density dependence acts on reproduction, so that the relationship between recruits, R , and a measure of

spawning biomass, S , is nonlinear. A great deal of effort over the last century was devoted to deriving expressions for recruitment as a function of the spawning biomass in a fish population (collectively referred to as stock–recruitment relationships, SRRs). Classic examples include the Ricker (1954), Beverton–Holt (Beverton and Holt 1957), and Cushing (1971) models. Despite the diversity of potential functional forms, in practice the poor match between fitted

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functions and the data is notable and well known (Hilborn and Walters 1992; Quinn and Deriso 1999). The common approach is then to assume that recruitment deviations from the presumed functional form are some kind of random process, often assumed to be lognormal, so that the stock–recruitment model is $R = f(S) e^{X_\sigma - \frac{1}{2}\sigma^2}$, where X_σ is a normally distributed random variable with mean 0 and standard deviation σ . Understanding the relative contribution of biological, abiotic, and stochastic forces to fish recruitment remains one of the fundamental challenges in fisheries management.

The mismatch between observations of recruitment and the theoretical models has been ascribed to both biological and statistical factors. Biologically, the poor fit suggests that factors in addition to spawning biomass, such as environmental conditions (e.g., ocean temperature) or the abundance of other species, affect the survival of prerecruit individuals and are not incorporated into classical SRRs. Poor fit may also be driven by uncertainty about how density dependence acts in a population. For example, the relative importance of intra-cohort competition, intercohort competition, and cannibalism to density dependence is often poorly understood. Furthermore, the temporal and spatial scales at which density-dependent processes act is important but poorly known. Statistically, short time series, the range of biomass observed during the time series, measurement error of both stock biomass and recruit abundance, and time series biases can all impede or introduce biases in the estimation of parameters (Quinn and Deriso 1999; Needle 2002; Walters and Martell 2004). Taken together, these challenges present a complex problem that have hindered the understanding of recruitment drivers and associated uncertainty.

Classical recruitment models also generally assume that recruitment is a function of total spawning biomass, so that if the reproductive contribution of fish changes with age or size, these models are unlikely to match observed recruitment. Arguments for greater consideration of reproductive biology in studies of recruitment go back decades (e.g., Beverton and Holt 1957; Rothschild and Fogarty 1989), but recent work has increasingly focused on the connection between age and reproductive biology (e.g., Marteinsdottir and Thorarinsson 1998; Morgan 2008). As harvested populations frequently experience dramatic changes in age structure as the oldest (and typically largest) individuals are removed, the age structure of fish populations may play an underappreciated role in recruitment dynamics (reviewed in Berkeley et al. 2004b; Birkeland and Dayton 2005). At least three mechanisms have been hypothesized by which changes in age structure could affect recruitment. First, specific fecundity (eggs per unit biomass) is often an increasing function of the mass of spawning females (Marteinsdottir and Begg 2002; Dick 2009), and so large, old fish may produce more offspring on a per unit mass basis. Second, detailed experimental studies have shown differences in the quality of eggs produced by mothers of different ages (Marteinsdottir and Steinarsson 1998; Vallin and Nissling 2000; Berkeley et al. 2004a), with older mothers typically producing offspring with higher survival probability. Third, large, old fish may senesce (Reznick et al. 2006), and so fecundity or egg quality may decline at very old ages. Thus, the first two mechanisms predict increased production with the age of the population,

while the third predicts a decline in production as fish reach extreme ages.

Several authors have used available fisheries time series to ask if the average age or diversity of age classes present in the spawning population affect recruitment (e.g., Marteinsdottir and Thorarinsson 1998; Venturelli et al. 2009; Brunel 2010). These approaches vary in the details of their statistical approaches but share the characteristic that the parameters are straightforward to estimate. However, model parameters generally lack a mechanistic link between changes in age structure and the consequences for recruitment. Thus the different conclusions about the effect of age structure for recruitment dynamics (e.g., age structure has a strong effect on recruitment (Venturelli et al. 2009) versus age structure has little or no effect on recruitment (Morgan et al. 2007; Brunel 2010)) may arise in part from various statistical models used and the indirect connection between the biology and statistical models.

In this paper, we develop a coherent framework for estimating the effect of age structure on recruitment dynamics that can be explicitly linked to biological mechanisms. We derive a general age-structured version of the Ricker recruitment function that incorporates age-specific fecundity and age-specific egg quality and illustrate special cases of this model that have only age effects on fecundity or egg quality. We then apply a series of models to an exploited fish population (Icelandic cod) with well-documented age effects on recruitment (Marteinsdottir and Thorarinsson 1998; Scott et al. 1999, 2006). We use Bayesian statistical methods to estimate parameters and compare among alternate models. We frame our models in terms of quantities that are likely available or can be estimated from existing data, and therefore our methods can be applied widely.

Materials and methods

We let $N(t)$ denote the number of individuals in a single cohort t time units subsequent to spawning, and S is the biomass of mature individuals in the population that contribute to density dependence. The Ricker SRR is the solution of the ordinary differential equation

$$(1) \quad \frac{dN}{dt} = -(a + bS)N$$

where a is the density-independent mortality rate, and b is the density-dependent mortality rate (Quinn and Deriso 1999). The solution of eq. 1 is

$$(2) \quad N(t) = N_0 e^{-(a+bS)t}$$

where N_0 is the initial number of individuals present in the population (e.g., the number of eggs produced in the population). Assuming that egg production is proportional to the total stock biomass, the initial condition is $N_0 = fS$, where f is the fecundity per unit mature biomass, and T is the age of recruitment, we arrive at the most common parameterization of the Ricker function

$$(3) \quad N(T) = R = (f e^{-aT})S e^{-bST} = \alpha S e^{-\beta S}$$

where $\alpha = f e^{-aT}$ and $\beta = bT$ (Quinn and Deriso 1999). The parameter α combines the density-independent survivorship

and the proportional fecundity of a unit of mature biomass. Note that we have assumed that the biomass contributing to reproduction is identical to the biomass controlling the density-dependent mortality of prerecruit individuals. We first develop a model that relaxes the assumption of the classical Ricker function (eq. 3) that all offspring have identical mortality rates. To do this, we let $N_i(t)$ denote the number of offspring from mothers of age i at time t after spawning, and a_i and b_i denote the density-independent and density-dependent mortality rate for fish from maternal age i , respectively. If S_D denotes the biomass of fish contributing to density-dependent mortality, the generalization of eq. 1 is

$$(4) \quad \frac{dN_i}{dt} = -(a_i + b_i S_D) N_i$$

This formulation assumes that all individuals, regardless of maternal age, experience a shared determinant of density-dependent mortality, S_D . This assumption allows the equation to be solved in closed form. Biologically, this formulation can be interpreted as individuals derived from mothers of different ages to have different traits (e.g., resource provisioning) that affect mortality rates. Integrating eq. 4 we obtain

$$(5) \quad N_i(T) = R_i = E_i e^{-(a_i + b_i S_D)T}$$

where E_i is the initial number of eggs from age i mothers. Then the total number of recruits across the offspring from all parents is $R = \sum_i R_i = \sum_i N_i(T)$:

$$(6) \quad R = \sum_{i=0}^I E_i e^{-(a_i + b_i S_D)T}$$

where I is the maximum age in the population. In this formulation, offspring derived from parents of different ages have distinct density-independent and density-dependent mortality rates and egg production. Thus, eq. 6 is a general and flexible form for incorporating the effects of maternal age; many possible functional forms for a_i , b_i , and E_i are possible, and the appropriate choice of models will depend on the biology of the species of interest (see Discussion).

We begin by assuming that $a_i = g_0 + g_1 i$, and $b_i = h_0 + h_1 i$, so both mortality rates change linearly with age as a function of the parameters g_0 , g_1 , h_0 , and h_1 . These parameters can be understood as the first terms in the Taylor expansion of general nonlinear forms for a and b as a function of age (Venables and Dichmont 2004). For notational simplicity, in subsequent equations we absorb the lag between egg production and recruitment, T , into the parameters g_0 , g_1 , h_0 , and h_1 . We then obtain

$$(7) \quad R = \sum_{i=0}^I E_i e^{-[g_0 + g_1 i + (h_0 + h_1 i) S_D]}$$

Equation 7 allows reproduction and density-independent and -dependent mortality to depend upon maternal age. We will also consider a range of special cases of eq. 7 that includes the standard Ricker without age effects (eq. 3; Table 1). As with the basic Ricker model (eq. 3), where appropriate we combine parameters to ensure parameter identifiability (Table 1). We classify our models based on whether maternal age effects affect density-independent or -dependent mortality

Table 1. List of candidate models that incorporate maternal age effects in fecundity or quality.

Model	Maternal age effect	Statistical model
1	No quality or fecundity effects	$\sum \alpha S_i e^{-\beta S_D}$
Quality only		
2	DI mortality	$\sum \gamma S_i e^{-\beta S_D - g_1 i}$
3	DD mortality	$\sum \alpha S_i e^{-(h_0 + h_1 i) S_D}$
4	DI and DD mortality	$\sum \gamma S_i e^{-g_1 i - (h_0 + h_1 i) S_D}$
Fecundity only		
5	Age-specific fecundity	$\sum \omega E_i e^{-\beta S_D}$
Fecundity and quality		
6	Fecundity and DI mortality	$\sum \kappa E_i e^{-\beta S_D - g_1 i}$
7	Fecundity and DD mortality	$\sum \omega E_i e^{-(h_0 + h_1 i) S_D}$
8	Fecundity, DI, and DD mortality	$\sum \kappa E_i e^{-g_1 i - (h_0 + h_1 i) S_D}$
Parameter combinations		
	$\gamma = f e^{-g_0}$	
	$\kappa = e^{-g_0}$	
	$\omega = e^{-a}$	

Note: Parameter definitions can be found in Materials and methods. Model numbers correspond to numbers in Table 2. The eight models shown were applied to the Icelandic cod data. Abbreviations correspond to age effects on the density-independent mortality rate (DI), density-dependent mortality rate (DD), or both density-independent and -dependent effects (DI+DD). Summation symbols indicate sums across age (i).

rates (referred to as “quality” effects in Table 1) or whether maternal age affects recruitment via the numbers of eggs produced (a “fecundity” effect). Because we absorbed T into the model parameters, g_0 is dimensionless, while g_1 , h_0 , and h_1 have units of age^{-1} , mass^{-1} , and $(\text{mass} \cdot \text{age})^{-1}$, respectively. Recall that because the parameters describe mortality rates, smaller values for g_0 and h_0 correspond to increased survivorship. Negative values of g_1 and h_1 correspond to survivorship increasing with maternal age; and positive values have the converse relationship.

SRRs of the general form (eq. 6) and the specific form with linear mortality rates (eq. 7; Table 1) differ from other analyses that have incorporated maternal age effects on recruitment (e.g., Murawski et al. 2001; Brunel 2010; Morgan et al. 2011). That is, how one includes an effect of maternal age depends critically upon the mechanism hypothesized to produce age effects in recruitment. For example, incorporating age-specific fecundity leads to a different functional form than including age-specific effects on density-dependent mortality, and neither are equivalent to including a summary of the age structure of the population as a covariate (e.g., a Shannon index of age diversity (Marteinsdottir and Thorarinsson 1998) or the mean age of spawning fish (Venturelli et al. 2009)). Including such summaries of age structure may provide a way of improving the fit or predictive power of the SRRs (Marteinsdottir and Thorarinsson 1998; Morgan et al. 2011) and thus may be useful in a management setting, but such analyses are unlikely to be informative about the mechanisms driving age effects because they are difficult to tie to biological processes. Equation 6 also shows how the

two occurrences of spawning stock biomass in the standard Ricker model (eq. 3) are not necessarily equivalent; one arises because it is related to reproductive potential, while the other is related to the per-capita effect of biomass on mortality rates. This is noted in standard texts (e.g., Quinn and Deriso 1999), but is often forgotten in the practical application of the Ricker SRR.

In practice, the usefulness of eq. 6 will depend on the available data for individual stocks. Beyond the obvious limitation that it requires an estimate of age structure for populations, the full model requires estimates of both age-specific egg production and spawning stock biomass. For most species, direct measurements of egg production for each age are not readily available. Instead, estimates of the total biomass of each age class (e.g., from a virtual population analysis) coupled with some information about the reproductive biology of the fish that needs to be combined to provide an estimate of E_i . For example, estimates of size-specific fecundity, proportion of females of a given age (or size) that are mature, and sex ratio can be combined to provide a metric of egg production (e.g., Murawski et al. 2001; Morgan et al. 2011). However, data requirements may limit the complexity of statistical models that can be applied to a given population (see Discussion).

Estimating parameters and comparing models

We combine parameters that cannot be separately identified (Table 1) and generalize eq. 7 to include recruitment deviations by assuming that stochastic variation in recruitment has a lognormal distribution (Quinn and Deriso 1999); if the deviations are independent for each year (y), then eq. 7 on the logarithmic scale is

$$(8) \quad \log R_y = \log \kappa - h_0 S_{D,y} + \log \left[\sum_{i=0}^I E_{i,y} e^{-i(g_1 + h_1 S_{D,y})} \right] + \epsilon_y$$

where $\epsilon_y \sim N(0, \sigma^2)$

An alternate way to include stochasticity is to assume that the deviations from the deterministic function are serially correlated, as might be expected if adjacent recruitment years are similar to one another because of an autocorrelated environment. If the deviations can be assumed to follow a stationary autoregressive process of order 1 (AR(1)), then the model is identical to eq. 8 except $\epsilon_y \sim N(\rho\epsilon_{y-1}, \sigma^2)$. Here, ρ is the autoregression parameter, and for stationary time series, $-1 < \rho < 1$. In writing eq. 8, we assume that the state variables $S_{D,y}$ and $E_{i,y}$ are observed perfectly and all of the stochasticity arises from variation in the recruitment processes (i.e., the state variables are measured without error). Clearly egg production and the biomass are subject to measurement error; methods for explicitly accounting for measurement error involve using state-space methods to simultaneously estimate the model parameters as well as $S_{D,y}$ and $E_{i,y}$. This is a well-known challenge in the estimation of SRRs (Quinn and Deriso 1999), and we defer such analyses to future investigations.

To estimate parameters, we use Bayesian statistical methods (Gelman et al. 2004). Bayesian approaches provide the

distinct advantage of allowing for prior information to be incorporated into the estimate of parameters. We use standard Markov chain Monte Carlo (MCMC) methods to estimate parameters (see Supplementary Appendix S1¹ for details about the prior distributions and model assessment).

To compare among models, we used posterior predictive loss (Gelfand and Ghosh 1998; Clark 2007, pp. 205–209). Posterior predictive loss calculates a goodness-of-fit term, G_m , and a model complexity term, P_m , based on the posterior predictive distribution (see Supplemental Appendix S1¹). In our application, G_m describes the accuracy of the model by calculating the residual sum of squares of the observed data relative to the mean of the posterior predictive distribution. G_m declines as the mean of the predictive distribution approaches the observed data. P_m describes the variance in the posterior predictive distribution; with more model parameters, P_m will generally (but not necessarily) increase (see Clark 2007). Ideally, we wish to find models that provide high accuracy and low variance in their predictions. Therefore, the model that minimizes the sum $D_m = G_m + P_m$ provides the best match between model and data (see Supplemental Appendix S1 for additional details¹).

We initially attempted to use deviance information criterion (DIC) for model selection (Spiegelhalter et al. 2002), but found it to be very sensitive to small numbers of MCMC samples from the tails of the joint posterior distribution. Posterior predictive loss provided a more consistent model selection metric that was far less sensitive to the MCMC sampling procedure. We suspect that the predictive metrics for model selection worked better than DIC because it does not attempt to estimate the dimension of the model (the effective number of parameters, p_d ; Spiegelhalter et al. 2002), an integral component of DIC. Furthermore, we suspect that our problems with DIC arise from the implicit assumption in calculating p_d that the posterior distribution is approximately multivariate-normal distributed. For some of our models, the estimated joint posterior distributions were clearly not multivariate normal and, we suspect, lead to problems implementing DIC (Supplemental Appendix S1¹).

In addition, we calculated the approximate R^2 (i.e., $R^2 = 1 - (SS_{\text{res}}/SS_{\text{tot}})$, where SS_{res} is the residual sums of squares from the mean of the posterior predictive distribution, and SS_{tot} is the standard total sums of squares for each model to provide a familiar metric of model fit). We used R for all analyses (R Development Core Team 2011).

Application to Icelandic cod

To illustrate the approach, we apply our age-structured SRR to the Icelandic population of Atlantic cod (*Gadus morhua*). We chose the Icelandic cod population because it represents one of the longest and highest quality fisheries time series in the world with publicly available age-structured time series of spawning stock biomass and recruitment. Additionally, previous research has demonstrated the effect of maternal age structure on the recruitment of this population (Marteinsdottir and Thorarinnsson 1998; Marteinsdottir and Begg 2002; Scott et al. 2006).

We used the 2009 stock assessment as our source for data (ICES 2009b). For each year between 1955 and 2009, this

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/f2012-082>.

assessment provides estimated numbers at age ($N_{i,y}$), mean mass at age ($W_{i,y}$) in grams, and proportion mature ($p_{i,y}$) for age classes 3 to 14. We combine these to provide a point estimate of the spawning stock biomass ($S_{i,y}$) of each age in each year: $S_{i,y} = N_{i,y}W_{i,y}p_{i,y}$. The stock assessment does not provide estimates of egg production, and to our knowledge empirical data required to estimate egg production is not available for the early years in the time series (Martensdottir and Begg 2002). Thus, we use a published proxy to calculate age-specific egg production in each year (ICES 2009a):

$$(9) \quad E_{i,y} = S_{i,y} \left(0.01 + \frac{W_{i,y}}{20000} \right)$$

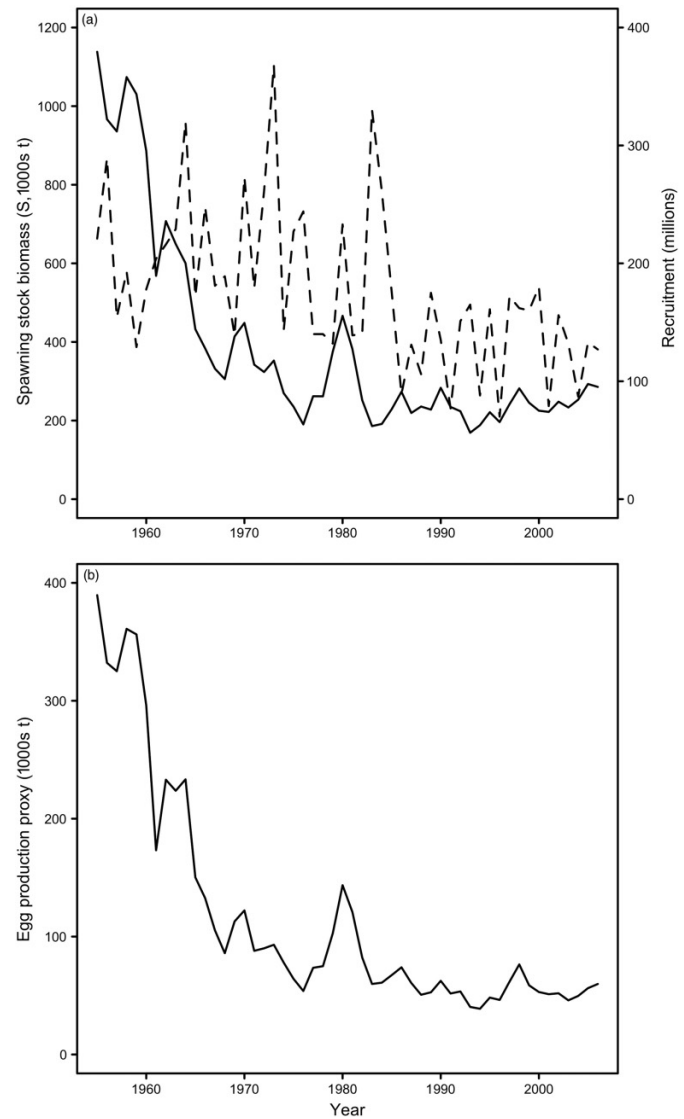
Recruitment occurs at age 3 years in this population (Martensdottir and Thorarinsson 1998; ICES 2009b), and so we used $S_{i,y}$ and $E_{i,y}$ for 1955 to 2006. In Fig. 1, we show the time series of recruitment, spawning stock biomass, and proxy for egg production. Given these data, we estimated parameters for the eight models listed in Table 1 using both independent and autocorrelated errors (16 models in total). In our analysis we consider one model structure for the biomass that contributes to density dependence, $S_{D,y} = \sum_i S_{i,y}$. Thus we assume only spawning biomass contributes to density dependence. This model is consistent with cannibalism being the primary mechanism underlying density dependence and is reasonable given the biology of cod. We emphasize that the choice of S_D is an important aspect of the analyses and note that other forms of S_D are reasonable. For example, $S_{D,y} = \sum_i E_{i,y}$ would be consistent with assuming intracohort competition drives density dependence, while assuming only some portion of the total population contributes to density-dependent mortality (e.g., biomass of age 1 and age 2 fish; Bjørnstad et al. 1999) might be appropriate in other instances. The abundance of age 1 and age 2 cod was not available in the stock assessment (ICES 2009b); thus, we do not consider this model.

Results

The classical Ricker model and models that incorporated only density-independent or only density-dependent (hereafter “DI” and “DD”, respectively) age effects converged to the posterior distribution quickly and had excellent MCMC mixing properties. However, models that include both DI and DD effects exhibited poor MCMC mixing properties, indicating that the parameters had mild identifiability problems. In models with both DI and DD effects (DI+DD models), poor mixing and uncertain model convergence was particularly evident in models that used S as the metric of reproduction. As a result, we had to use longer MCMC chains for DI+DD models to ensure model convergence and obtain sufficient samples from the posterior distribution (see Supplemental Appendix S1¹).

Posterior predictive loss criteria show that models that incorporate an age-dependent mortality rate (DI and (or) DD) or used egg production as the reproductive metric were superior to the standard Ricker model (Table 2). The largest improvement in fit occurred as a result of allowing the biological processes contained in α (eq. 3) in the classic Ricker model to vary among years. This can be achieved by using an estimate of egg production (model 5; Table 1), al-

Fig. 1. (a) Time series for spawning stock biomass (solid line) and 3-year-old recruits (dashed line) for Icelandic cod for year classes 1955 to 2006. (b) Time series for egg production proxy (sum of all ages; see eq. 9).



lowing age to affect the density-independent mortality rates (model 2), or including both processes in various combinations (models 4, 6, 7, 8). This strongly suggests that the primary effect of age in Icelandic cod arises from age-dependent changes in fecundity. However, models that did not allow for a maternal age on offspring quality perform relatively poorly (for example, compare models 1 and 2 or models 5 and 7; Table 2), suggesting that maternal age effects on offspring quality have detectable effects on recruitment. For a given model structure, autocorrelated errors generally produced better results than independent errors, but the improvement to model fit was slight if at all.

The overall preferred model included only a DI age effect on mortality rates and autocorrelated error. Results from this model suggests a strong effect of maternal age on recruitment; years with a larger proportion of old individuals produce more age 3 recruits (Fig. 2a). We show three years that

Table 2. Model comparison among 16 stock–recruitment models.

Model	Reproduction	Error	No. of parameters	G_m	P_m	D_m	Approx. R^2
2. DI	S	AR(1)	5	4.5	5.1	9.6	0.38
4. DI+DD	S	AR(1)	6	4.5	5.3	9.8	0.39
2. DI	S	Indep.	4	4.7	5.2	10.0	0.35
4. DI+DD	S	Indep.	5	4.7	5.3	10.0	0.35
7. DD	E	AR(1)	5	4.8	5.4	10.2	0.34
7. DD	E	Indep.	4	4.9	5.3	10.2	0.33
8. DI+DD	E	AR(1)	6	4.8	5.5	10.3	0.34
8. DI+DD	E	Indep.	5	4.9	5.4	10.3	0.33
6. DI	E	Indep.	4	5.0	5.4	10.4	0.32
6. DI	E	AR(1)	5	4.9	5.5	10.5	0.32
5. Base	E	Indep.	3	5.2	5.6	10.8	0.29
5. Base	E	AR(1)	4	5.2	5.7	10.9	0.29
3. DD	S	Indep.	4	5.8	6.3	12.1	0.21
3. DD	S	AR(1)	5	5.8	6.5	12.2	0.20
1. Base	S	AR(1)	4	6.4	7.0	13.4	0.12
1. Base	S	Indep.	3	6.4	7.1	13.5	0.12

Note: “Model” indicates the corresponding model number in Table 1 and indicates the type of age effects on survival rates and include the standard Ricker with no age effects (Base), age effects on the density-independent mortality rate (DI), density-dependent mortality rate (DD), or both density-independent and -dependent effects (DI+DD). “Reproduction” indicates whether spawning stock biomass (S) or egg production proxy (E) was included as the state variable. “Error” shows whether independent or lag-one autocorrelated errors were used. G_m and P_m are the components of the posterior predictive loss for each model, and $D_m = G_m + P_m$; smaller numbers indicate better match between model and data. For all models, $S_D = \sum_i S_i$.

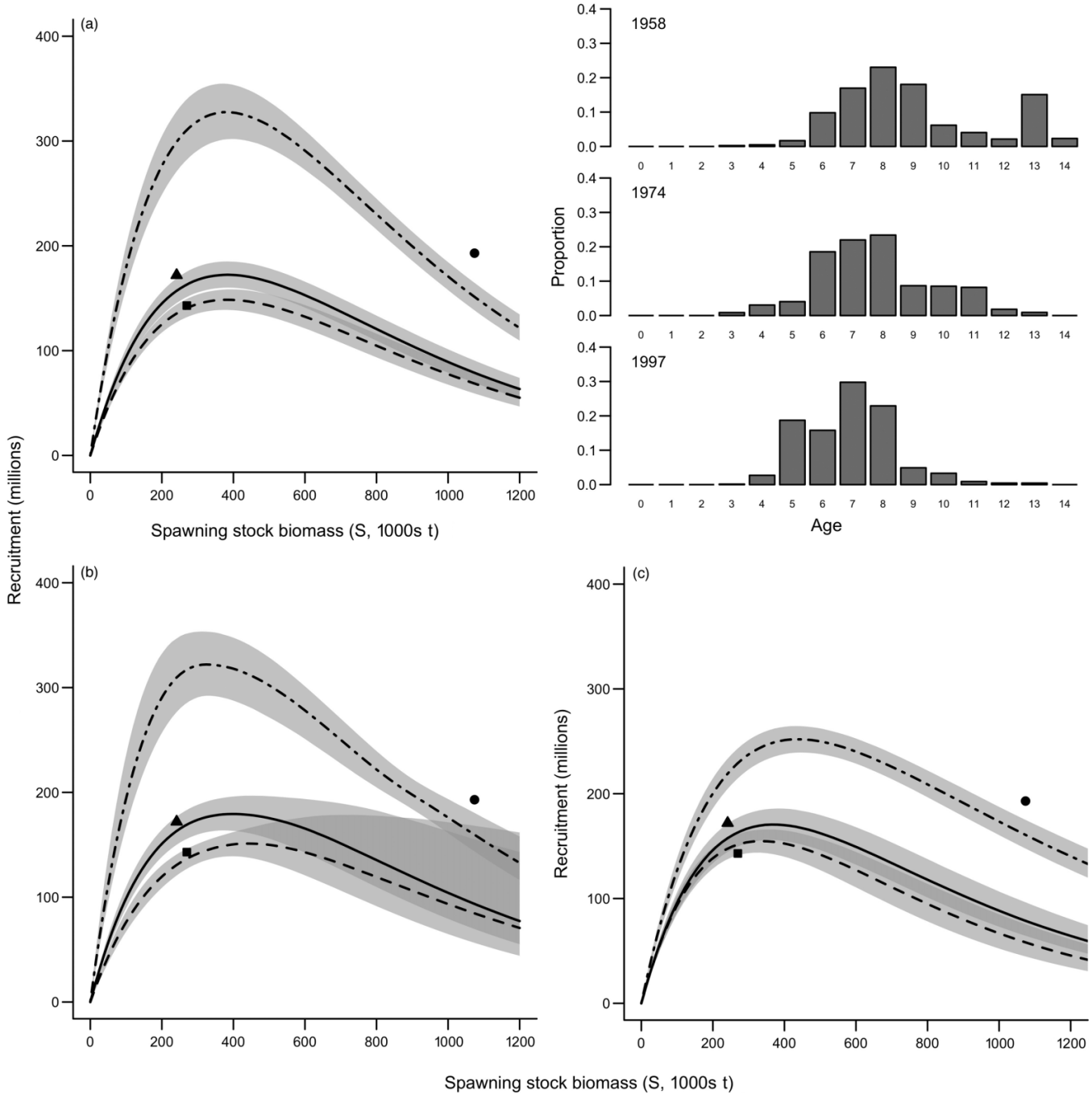
span much of the observed range of age structures during the time series, with many older fish in 1958, many younger fish in 1997, and 1974 being intermediate (Fig. 2). The expected recruitment in a given year can be plotted as a function of S by assuming the relative proportion of biomass in each age is constant but the total S varies (Fig. 2). Note that Fig. 2 illustrates the uncertainty in the expected recruitment curve for each year, not the variation attributable to stochasticity. We present the marginal and joint posterior distributions for model 2 in the Supplemental Appendix (Figs. S1, S2¹). The expected recruitment curve for each year can be plotted for all years in the time series (Fig. 3a); these curves are conditional on the observed $S_{i,y}$ (or $E_{i,y}$) and the observed age structure in each year. The range of curves illustrate the estimated effect of changing age structure on recruitment. The estimated stochastic component of recruitment also declines between the standard Ricker model (model 1; posterior median $\sigma^2 = 0.132$) and the overall preferred model (model 2; posterior median $\sigma^2 = 0.095$) by approximately 20%.

Because many of model structures had similar match to the data (Table 2), we show the top three models that used the AR(1) error structure to illustrate the variation in predicted recruitment that can arise from different assumed model structures (models 2, 4, and 7 in Table 2; Fig. 2; Fig. 3). The first two models use spawning stock biomass for their reproductive value, while the third uses the proxy of egg production. For model 7 (Fig. 2c; Fig. 3c), we plot the predicted recruitment curve assuming that the proportional contribution of each age to total egg production is constant across S . Intuitively, models that allow for maternal age effects in the density-independent mortality term show greater variation in predicted recruitment as spawning biomass declines and approaches the origin (Fig. 3a; Fig. 3b), while model 7 predicts higher variation among years at higher spawning biomass but

lower variation in recruitment at low spawning stock biomass (Fig. 3c). The larger confidence bounds for model 2 (DI+DD) at large stock biomass illustrate the consequences of parameter identifiability issues when attempting to estimate DI+DD models (Fig. 2b; Supplemental Figs. S3, S4¹).

Our methods allow explicit assessment of the value of a unit of old reproductive biomass relative to a unit of young biomass for recruitment. An intuitive way to calculate this is by taking the ratio of the value of a unit of newly recruited reproductive biomass (age 3 cod in this case) relative to the value of biomass of other ages. If we let j indicate age of recruitment and k be the age of interest, then the log-ratio of the relative value of age k relative to age j , $\log(\lambda_{jk})$, is $\log(\lambda_{jk}) = (g_1 + h_1 S_D)(j - k)$ (Fig. 4). A value of 0 indicates no difference in estimated survivorship of offspring produced by newly recruited parents and parents at the age of interest, positive values indicate increased survivorship relative to parents at the recruitment age, while negative values indicate reduced survivorship. As with expected recruitment, we plot this quantity for the top three models with AR(1) errors (models 2, 4, and 7 in Table 2). For models with DD mortality, we plot the relative survivorship at three values of S_D to show the interaction between age-dependent mortality and biomass (Fig. 4). For models 2 and 4, which assume egg production is proportional to spawning stock biomass, the relative survivorship of offspring with older parents is estimated to be very large. In model 2, the median estimate of $\log(\lambda)$ for age 10 mothers is ~ 2 , which corresponds roughly to an 8-fold difference in survivorship between fish from age 3 mothers and age 10 mothers (Fig. 4). In contrast, for model 7, median estimates of $\log(\lambda)$ for age 10 fish range between 0.2 and 0.8, corresponding to a 1.2- and 2.2-fold difference in relative survivorship for S_D of 100 and 500, respectively (Fig. 4).

Fig. 2. Estimated recruitment curves for three illustrative years using the best three models using the AR(1) error structure. Panels *a*, *b*, and *c* correspond to model numbers 2, 4, and 7 in Table 2, respectively. Panels show the expected and interquartile range of recruitment curves in 1958 (dash-dotted line), 1974 (solid line), and 1997 (dashed line) given the proportional age composition of spawning biomass observed in each year (panel at upper right). Points indicate observed data for 1958 (●), 1974 (■), and 1997 (▲).



Discussion

In the past decade, a number of experimental and observational studies have demonstrated differences in both the number of offspring produced by parents of different ages or sizes (Martensdottir and Begg 2002; Sogard et al. 2008) and differences in the quality of offspring (Scott et al. 1999; Vallin and Nissling 2000; Berkeley et al. 2004a). However, it has been difficult to connect the interesting and nuanced work about reproductive biology of fishes with the largely statisti-

cal curve-fitting approaches used to estimate SRRs. Other investigators have used a range of regression and correlative approaches to estimate the effect of age structure on recruitment (e.g., Martensdottir and Thorarinnsson 1998; Morgan et al. 2007; Venturelli et al. 2009). All of these approaches potentially provide valuable information about age effects, but each makes implicit, unstated assumptions about how age affects recruitment. Such assumptions likely contribute to the variety of conclusions about the importance of age structure for recruitment dynamics. More importantly, most of the ap-

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Fig. 3. Estimated recruitment curves for all years using models 2, 4, and 7 (a, b, and c, respectively). Each line represents the expected recruitment curve for each year conditional on the observed age composition. Points show the observed recruitment in each year.

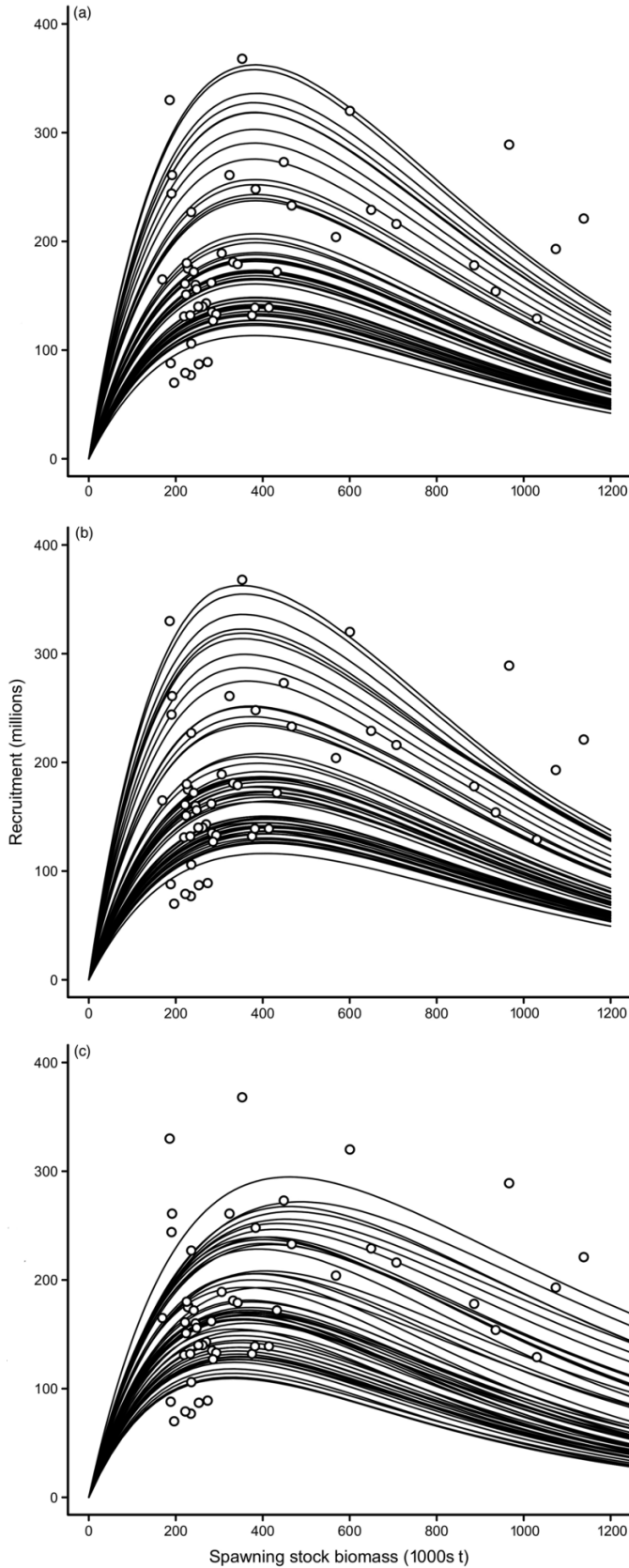
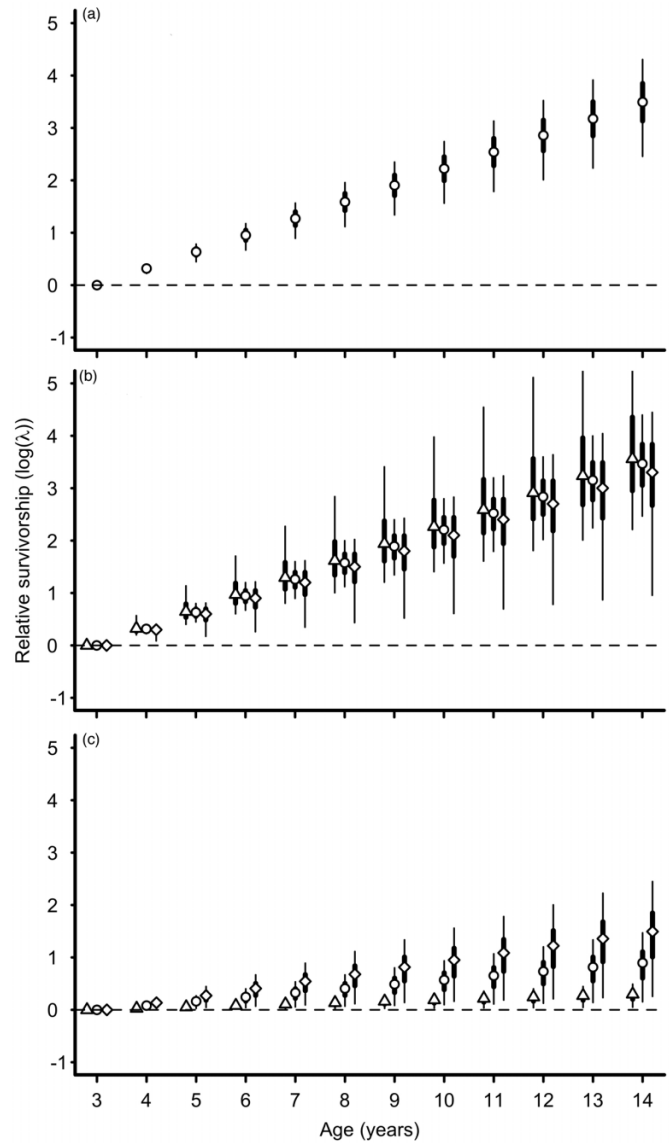


Fig. 4. Estimated survivorship of offspring derived from different maternal ages relative to age 3 fish for models 2 (a), 4 (b), and 7 (c; see Table 2 for model descriptions). Point indicates posterior median, thick line shows interquartile range, and thin line shows 90% credible intervals. For models that incorporate density dependence, we show relative survivorship at three values of S_D : $S_D = 100$ (Δ), $S_D = 300$ (\circ), $S_D = 500$ (\diamond). The units of S_D are thousands of metric tonnes.



proaches are difficult to tie to measurable biological processes, and so results that are biologically unreasonable cannot be easily identified. We advocate a more explicit biological approach; understanding recruitment is a biological problem first and a statistical problem second.

For the example data set explored here, Icelandic cod, model comparison showed that the preferred model used spawning stock biomass as the measure of reproduction. This model structure implies that the reproductive output for a large, old fish per unit mass is the same as that of a young, small fish. This is known to be false for Icelandic cod —

larger fish produce more eggs per unit mass than small fish (Marteinsdottir and Begg 2002; Scott et al. 2006) — and this model produces unreasonable estimates for the effect of age on mortality. That is, it is wholly unreasonable that fish from age 10 mothers have a nearly 10-fold difference in survivorship over age 3 mothers. What is likely happening is that the density-independent parameter is absorbing variation that is really attributable to age-dependent egg production, and thus the estimated effect of maternal age on mortality is overstated. The best-fitting model that incorporates egg production (model 7) supports this conclusion and suggests only a 1- to 2-fold survivorship difference between age 10 and age 3 mothers. If this explanation is correct, a follow-up question is “why are models that use egg production not always preferred?” We suspect that the answer lies in our use of a crude proxy for egg production (eq. 9; ICES 2009a). However, we view our analysis as illustrative, not definitive; we are certain that more detailed measures of egg production can be developed and should be used in future analyses of Icelandic cod (see also Marshall et al. 2004; Morgan 2008; Morgan et al. 2011).

More generally, it is clear that comparing the statistical fits of SRRs will yield relatively few insights into the processes driving variation in recruitment. As noted by many authors, several alternate model formulations can generate similar fits to observed data (Hilborn and Walters 1992; Quinn and Deriso 1999; Morgan et al. 2011). In most cases, the weight of evidence does not provide strong argument for choosing one model over another. Despite the similarity in fit, models with very similar metrics of fit can yield different predictions for recruitment. Our work illustrates this effect in the context of changes in age structure, but the same general principle applies to modeling the effect of other covariates on recruitment (e.g., ocean temperature). New data on recruitment are relatively slow to accumulate — generally one datum each year — and thus simply waiting for more information to arrive is a slow and inefficient way to improve our understanding of recruitment. The challenge is to identify ways to incorporate other experimental or observational data to inform recruitment processes. In a series of important papers, the late R.A. Myers and colleagues showed how recruitment processes could be better understood by using meta-analytic approaches to combine information from multiple fish stocks with shared characteristics (e.g., Myers and Barrowman 1996; Myers et al. 1999). But there are also gains to be made by looking at the smaller-scale details of reproduction within populations. Our use of model structures with interpretable biological parameters and Bayesian approaches that can incorporate prior information provide paths for incorporating age effects on reproduction and survivorship.

Outside information can inform models of recruitment in at least two ways: (i) the parametric form of the model considered and (ii) the inclusion of prior information on the various parameters. For egg production, information about reproductive biology may provide proxies for egg production (Marteinsdottir and Begg 2002; Marshall et al. 2004; Morgan et al. 2011) or may provide road maps for reasonable model structures to consider. Several populations of cod have size-dependent specific fecundity, with larger fish producing more eggs per unit mass than smaller fish (Marteinsdottir and Begg 2002), but this pattern may not be true for all taxa

(Dick 2009). For age-dependent mortality rates, experimental work should strongly inform the functional forms for a_i and b_i . In the example with Icelandic cod, we used a simple functional form — a linear change in both rates as fish age — and showed that including such effects provides a better match to data than models that treat all ages as identical. However, a variety of functional forms are potentially useful. For example, the age dependence of mortality rate may be better described by a curve that approaches an asymptote rather than a curve that increases linearly. In species with little knowledge available about potential parametric forms of age-dependent rates, nonparametric approaches using Gaussian process models are a potentially useful tool (Munch et al. 2005; Rasmussen and Williams 2006). Furthermore, it is not necessary for a_i or b_i to be explicit functions of age; they could be functions of the size of fish in each age class, the relative size of eggs produced by mothers of different ages, or a range of other possibilities.

Considering that there appears to be a substantial effect of age structure of recruitment dynamics, an important point for future investigation will be to understand the generality of the pattern documented here and how models accounting for age-dependent recruitment may make different predictions than models that do not incorporate such age effects. Age-dependent recruitment potentially affects a number of important processes, including fisheries reference points like spawner-per-recruit and yield-per-recruit and the recovery rate of overexploited fish populations. However, despite the apparent large effects of maternal age on recruitment documented here, it is far from certain that predictions from models that incorporate age-dependent recruitment effects will differ substantially from fisheries models that ignore age effects (e.g., O’Farrell and Botsford 2006). This topic deserves further exploration and rigorous testing.

We present a fairly simple model that can be elaborated on to increase our understanding of age effects on recruitment. For example, the Ricker model presented could be modified to explicitly include more biologically realistic descriptions of when compensation occurs during the life cycle (see Brooks and Powers 2007). Alternative models, such as age-structured versions of other SRRs (e.g., the Beverton–Holt model), cannot be derived in a similar manner. One way to write an age-structured version of the Beverton–Holt model would be to replace S_D in eq. 4 with $\sum_i N_i$. Unfortunately, a closed form solution to the ordinary differential equation does not exist except under stringent assumptions, so the differential equation must be solved numerically (see Lucero 2008, 2009). Although it is possible to match recruitment data to such an age-structured Beverton–Holt model, the difficulty in numerically solving the differential equation is likely to dissuade many investigators from applying such methods (Lucero 2008, 2009).

As with all SRRs, the ability to estimate models incorporating age structure will be affected by the information content of recruitment time series — the range of biomass and diversity of age structures observed in a time series and how they have co-occurred with spawning stock biomass — and suffer from the well-known list of potential biases and statistical challenges listed in the Introduction (Quinn and Deriso 1999; Walters and Martell 2004).

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