

How variable is recruitment for exploited marine fishes? A hierarchical model for testing life history theory

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Abstract: Recruitment often varies substantially in fish populations, and residual variability may have serial autocorrelation due to environmental effects even after accounting for a stock–recruitment relationship. However, the likely magnitude of variability and autocorrelation in recruitment has yet to be formally estimated. We therefore developed a hierarchical model for recruitment variability and autocorrelation and applied it to data for 154 fish populations. Results were similar when using either the Ricker or Beverton–Holt stock–recruitment model, and showed that autocorrelated recruitment has a marginal standard deviation of 0.74 (SD = 0.35) and a mean autocorrelation of 0.43 (SD = 0.28) when predicting for an unobserved taxonomic order. Estimates differed somewhat among taxonomic orders and stocks, and also supported a hypothesized positive relationship between age at maturity and autocorrelation in recruitment. Our results can be used as a Bayesian prior for recruitment variability in models for data-poor stocks and to distinguish recruitment from other process errors in models for data-rich stocks. Estimates can also be used in the design of future simulation models and management strategy evaluations and in theoretical research regarding life history variation.

Résumé : Le recrutement varie souvent beaucoup au sein de populations de poissons, la variabilité résiduelle pouvant présenter une autocorrélation sérielle découlant d'effets ambiants même après la prise en considération de la relation stock–recrutement. La magnitude probable de la variabilité et de l'autocorrélation du recrutement n'a toutefois pas encore été estimée formellement. Nous avons donc mis au point un modèle hiérarchique pour estimer la variabilité et l'autocorrélation du recrutement et l'avons appliqué à des données pour 154 populations de poissons. Les résultats sont semblables à ceux obtenus avec les modèles stock–recrutement de Ricker ou de Beverton–Holt et montrent que le recrutement autocorrélé présente un écart-type marginal de 0,74 (ÉT = 0,35) et une autocorrélation moyenne de 0,43 (ÉT = 0,28) pour la prédiction d'un ordre taxonomique non observé. Les estimations diffèrent quelque peu selon l'ordre taxinomique et le stock et appuient également l'hypothèse d'une relation positive entre l'âge à la maturité et l'autocorrélation dans le recrutement. Nos résultats peuvent être utilisés comme a priori bayésien pour la variabilité du recrutement dans les modèles de stocks pour lesquels peu de données sont disponibles, et pour distinguer le recrutement d'autres erreurs de traitement dans les modèles de stocks pour lesquels les données sont abondantes. Les estimations peuvent également être utilisées pour concevoir de nouveaux modèles de simulation et l'évaluation de stratégies de gestion, ainsi qu'en recherche théorique sur les variations du cycle biologique. [Traduit par la Rédaction]

Introduction

Early research in fisheries science showed that cohorts within a population can have large differences in relative abundance (Hjort 1926). Subsequent research has shown that cohort strength can differ even in the absence of changes in spawning biomass or reproductive output (Morgan et al. 2011), relative cohort size is generally determined when individuals are young, and cohort strength arises primarily owing to variable survival rates of larvae and early juvenile individuals (Cushing 1990). Resulting variability in recruitment to the exploited population is the primary contributor to variability in population growth for many commercially important species (e.g., Pacific hake; Stewart et al. 2012) and is the most common type of stochasticity included in population dynamics and stock assessment models for marine fishes. Marine population models also frequently assume that density dependence occurs primarily during the larval and early juvenile stages (e.g., Brooks et al. 2010). This assumption is justified by a series of classic meta-analyses from the 1990s (Myers and Cadigan 1993; Myers et al. 1999).

Despite this common assumption that variable recruitment is the dominant source of stochasticity in fish population dynamics, there is little theory or analysis of the magnitude of recruitment variability in general. One exception is the study by Mertz and Myers (1996), who used a repository of spawning biomass and recruitment estimates (Myers et al. 1995) to identify a weak positive relationship between recruitment variability and fecundity (also see Rickman et al. 2000). Mertz and Myers (1994) also uncovered weak evidence supporting the hypothesis that a shorter spawning season is associated with increased recruitment variability via an increased probability of temporal mismatch between larvae and preferred foods (Cushing 1990). Finally, Rose et al. (2001) conducted a simple analysis of the Myers et al. (1995) repository to test life history predictions regarding recruitment. However, none of these studies attempted to estimate the distribution of likely values for recruitment variability for different fish taxa. This distribution could be used to guide the design of future simulation modeling experiments and management strategy evaluations (Sainsbury et al. 2000), and could be used as a Bayesian prior in

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population dynamic and stock assessment models (Hilborn and Liermann 1998; Thorson et al. 2014a).

Additionally, concern over the impacts of natural and anthropogenic climate change has resulted in renewed interest in estimating changes in productivity and (or) recruitment in fish populations over time. There are well-studied examples (e.g., Wayte 2013; Szuwalski and Punt 2013) and meta-analytic results (Vert-pre et al. 2013) showing that mean recruitment or productivity may change drastically even in the absence of a change in spawning biomass. Changes in recruitment, and thus productivity, may explain delayed rebuilding for some overexploited fishes (Hutchings 2000; Neubauer et al. 2013). Changes in recruitment are in some cases associated with measurable environmental characteristics (Schirripa and Colbert 2006), although most biological mechanisms for changes in recruitment involve several environmental factors simultaneously (Bailey et al. 2005) and hence are harder to predict using simple models of measured environmental factors. Perhaps for this reason hypothesized relationships between recruitment and the marine environment have tended to lose predictive power over time (Myers 1998).

Given the difficulties in identifying relationships between measurable environmental factors and fish recruitment that (i) improve prediction and (ii) are stable over time, analysts may instead choose to model changes in mean recruitment over time using nonparametric time series methods. One nonparametric model for time-varying parameters is autoregression. Autoregressive models estimate the correlation between residual errors in adjacent time periods (ρ), and autoregressive models reduce to either a conventional “white-noise” (uncorrelated) error when $\rho = 0$ or a random walk when $\rho = 1$. Thus, autoregressive models for recruitment provide a generic approach to including recruitment variability that changes over time over short (uncorrelated) to long (strongly correlated) time scales. Autoregressive models also avoid specifying any environmental relationship a priori, hence avoiding the risk of overfitting to transient environmental relationships. Mechanistically, autocorrelation in recruitment can arise when larval survival is driven by an oceanographic variable that is itself autocorrelated (e.g., Ekman transport for sablefish (Schirripa and Colbert 2006) or temperature for Norwegian spring-spawning herring (Fiksen and Slotte 2002)) or when predation on prerecruits varies owing to changes in predator densities (Walters and Kitchell 2001); autocorrelation may also capture unmodeled changes in spawning output due to maternal effects (Brunel 2010). Autocorrelated recruitment models are likely to be useful when interpreting the relative importance of different data streams and model assumptions (similar to the argument in Deriso et al. (2007) regarding other model components), and can also inform short-term projections of recruitment based on recent recruitment estimates.

We therefore developed a hierarchical model for variability and autocorrelation in recruitment and applied it to recruitment and spawning biomass estimates for 154 populations in an updated version of the Myers et al. (1995) stock–recruitment repository. This model treats all species as having parametric variability (sensu Osenberg et al. 1999) around a mean value for recruitment variability and autocorrelation that is shared among all stocks within a given taxonomic order. We include taxonomic order because some orders (e.g., Salmoniformes) have radically different life histories that are likely to result in different variance and autocorrelation in recruitment. Taxonomic orders are in turn estimated as having a mean recruitment variability and autocorrelation that varies around a mean value for all marine fish orders. This hierarchical approach to meta-analysis allows us to also develop general Bayesian priors for recruitment variability for taxonomic orders that were not included in our dataset.

Methods

Data availability

We used the most recently updated version of the Myers et al. (1995) repository, which compiled spawning biomass and recruitment estimates for several hundred species worldwide, generally using sequential population analysis (SPA). SPA is a family of algorithms for reconstructing abundance at age from catch-at-age and abundance index data, and includes virtual population analysis and cohort analysis. Critically for our purposes, SPA makes few assumptions about fishery selectivity other than that catch at age is known without error. It is more appropriate for meta-analyses of recruitment variability than analyzing recruitment estimates from statistical catch-at-age (SCA) models, because it avoids serial correlations induced whenever a parametric stock–recruitment or selectivity model is specified a priori. It also avoids penalizing recruitment estimates towards a prespecified stock–recruitment relationship as is often done in forward projection models, such as those compiled in the RAM Legacy Stock Assessment Database (Ricard et al. 2012). While others have found that results of stock–recruitment meta-analyses are only weakly influenced by inclusion of data from SCA models (Keith and Hutchings 2012), recruitment variability is likely to be more sensitive, and we reduced the influence of model assumptions by concentrating on recruitment data from SPA models. In addition, we only analyzed data for stocks with more than 20 observations of spawning biomass and recruitment and excluded stocks of pink salmon, which generally have two demographically distinct populations composing each time series. There were 154 stocks from seven taxonomic orders that met these criteria.

Recruitment modelling

We estimate parameters for a hierarchical model that explicitly includes both within-stock variability in relative cohort strength (experimental variation) and between-stock variability in the parameters describing the magnitude of autocorrelation and variability (parametric variation; Osenberg et al. 1999; Thorson et al. 2014a). Standard deviation estimates from a small number of observations will often result in large imprecision. However, hierarchical models generally improve estimation precision when sampling units are exchangeable (Gelman and Hill 2007), and thus we used a hierarchical model for this task. Specifically, we assumed that recruitment follows either the Ricker model (eq. 1) or the Beverton–Holt model (eq. 2) as a function of spawning biomass

$$(1) \quad \hat{R}_{i,t} = \alpha_i S_{i,t} e^{-\beta_i S_{i,t}}$$

$$(2) \quad \hat{R}_{i,t} = \frac{\alpha_i S_{i,t}}{1 + \beta_i S_{i,t}}$$

where $\hat{R}_{i,t}$ is the estimated recruitment arising from spawning biomass $S_{i,t}$ for stock i in year t , α_i represents recruits per unit of spawning biomass as biomass approaches zero, and β_i represents the strength of density dependence per unit spawning biomass for stock i (see Table 1 for a definition of all mathematical symbols). Recruitment is commonly assumed to have stochastic variability that follows a log-normal distribution, and hence working in log space is computationally easier:

$$(3) \quad \begin{aligned} \hat{\ln}_{i,t} &= \ln(\alpha_i) - \beta_i S_{i,t} \\ \hat{\ln}_{i,t} &= \ln(\alpha_i) - \ln(1 + \beta_i S_{i,t}) \end{aligned}$$

where $\hat{\ln}_{i,t}$ is the expected log-recruits per unit of spawning biomass for the Ricker and Beverton–Holt models, respectively.

We also include a first-order autocorrelation model for residuals:

Table 1. List of symbols along with their definitions and type.

Symbol	Definition	Type
$R_{i,t}$	Recruitment for stock i in year t	Data
$S_{i,t}$	Spawning biomass for stock i in year t	Data
$L_{i,t}$	Log-recruits per spawning biomass for stock i in year t	Data
$S_{(min)i}$	Minimum observed spawning biomass for stock i	Data
$S_{(max)i}$	Maximum observed spawning biomass for stock i	Data
a_i	Life history covariate for stock i	Data
O_i	Taxonomic order	
J	Number of taxonomic orders	Data
$\varepsilon_{i,t}$	Residual error in recruitment (in log space) for stock i in year t	Derived
$\delta_{i,t}$	Uncorrelated residual error in recruitment (log space) for stock i in year t	Derived
$\hat{R}_{i,t}$	Estimated recruitment for stock i in year t	
$\hat{L}_{i,t}$	Estimated log-recruits per spawning biomass for stock i in year t	Derived
$R_{(min)i}$	Estimated median recruitment at $S_{(min)i}$ for stock i	Derived
$s_{(S)i}$	Shape parameter for expected standard deviation of residual error for stock i	Derived
$r_{(S)i}$	Rate parameter for expected standard deviation of residual error for stock i	Derived
$s_{(O)j}$	Shape parameter for expected standard deviation of residual error for order j	Derived
$r_{(O)j}$	Rate parameter for expected standard deviation of residual error for order j	Derived
α_i	Maximum recruits per spawning biomass for stock i	Parameter
β_i	Strength of density dependence per spawning biomass for stock i	Parameter
$R_{(max)i}$	Median expected recruitment occurring at $S_{(max)i}$ for stock i	Parameter
Ψ_i	Median expected proportion of $R_{(max)i}$ occurring at $S_{(min)i}$ for stock i	Parameter
σ_i	Standard deviation residual errors in recruitment (in log space) for stock i	Parameter
ρ_i	Autocorrelation in recruitment residuals (in log space) for stock i	Parameter
$\mu_{(S\sigma)j}$	Expected standard deviation of residual error for order j	Parameter
$\nu_{(S\sigma)}$	Coefficient of variation of within-order variation in standard deviation of residual errors	Parameter
$\mu_{(O\sigma)}$	Expected standard deviation of residual error for all orders	Parameter
$\nu_{(O\sigma)}$	Coefficient of variation of among-order variation in standard deviation of residual errors	Parameter
$\mu_{(S\rho)j}$	Central value for distribution of autocorrelations within order j	Parameter
$\tau_{(S\rho)}$	Standard deviation for truncated normal distribution of autocorrelations within a given taxonomic orders	Parameter
$\mu_{(O\rho)}$	Central value for distribution of autocorrelations for all orders	Parameter
$\tau_{(O\rho)}$	Standard deviation for truncated normal distribution of autocorrelations among taxonomic orders	Parameter
λ_σ	Effect of life history covariate on expected standard deviation of residual errors	Parameter
λ_ρ	Effect of life history covariate on expected autocorrelation of residual errors	Parameter
t	Year	Index
i	Stock	Index
j	Taxonomic order	Index

Note: Values are classified into the following categories: Data, numerical quantity; Derived, derived quantity; Parameter, a parameter or hyperparameter (i.e., that requires a Bayesian prior); Index, a bookkeeping index.

$$(4) \quad \varepsilon_{i,t} = \rho_i \varepsilon_{i,t-1} + \sqrt{1 - \rho_i^2} \delta_{i,t}$$

where ρ_i is a coefficient representing first-order autocorrelation for stock i , $\varepsilon_{i,t}$ and $\varepsilon_{i,t-1}$ are observed residuals around the stock-recruitment curve (in log space) in years t and $t - 1$, respectively, and $\delta_{i,t}$ is a normally distributed random variable representing uncorrelated errors (innovations) for stock i in year t . We do not explore higher-order autocorrelation, although a plausible order for autocorrelation in single-species models could be selected via model fit or based on the characteristics of environmental time series in a given region. First-order autocorrelated errors yield the

following estimation equations (Davidson and MacKinnon 2003, p. 286):

$$(5) \quad L_{i,t} = \begin{cases} \hat{L}_{i,t} + \rho_i(L_{i,t-1} - \hat{L}_{i,t-1}) + \sqrt{1 - \rho_i^2} \delta_{i,t} & \text{for } t > 1 \\ \hat{L}_{i,t} + \delta_{i,t} & \text{for } t = 1 \end{cases}$$

where the second equation (for when $t = 1$) is necessary because, at the beginning of the time series for a given stock, there is no previous observation to compute the residual $\rho_i(L_{i,t-1} - \hat{L}_{i,t-1})$. For this first observation, stochastic errors have variance equal to the stationary (marginal) variance of the autocorrelated series (i.e., σ_i^2),

while other observations have errors with variance equal to the conditional variance of the autocorrelated series $(1 - \rho_i^2)\sigma_i^2$. We therefore defined variability in recruitment as deviations away from the stock–recruitment relationship, without attempting to control for any other processes. Our definition of recruitment residuals includes processes that may be predictable using other time series data, e.g., using multispecies data (Minto et al. 2013; Thorson et al. 2013) or environmental variables (Stewart and Martell 2013).

Objective 1: hierarchical modeling

The stochastic error $\delta_{i,t}$ for stock i in year t is modeled as a random variable:

$$(6) \quad \delta_{i,t} \sim \text{Normal}(0, \sigma_i^2)$$

where σ_i^2 is the variance of stochastic errors in recruitment (in log space) for stock i . We specify that the standard deviation of recruitment (in log space) is itself a random variable:

$$(7) \quad \sigma_i \sim \text{Gamma}(s_{(S)i}, r_{(S)i})$$

where $s_{(S)i}$ and $r_{(S)i}$ are the shape and rate parameters, respectively, for stock i from a gamma distribution. These parameters depend upon the taxonomic order of stock i :

$$(8) \quad \begin{aligned} s_{(S)i} &= \sum_{j=1}^J I(O_i = j) \frac{1}{\nu_{(S\sigma)}^2} \\ r_{(S)i} &= \sum_{j=1}^J I(O_i = j) \frac{1}{\mu_{(S\sigma j)} \nu_{(S\sigma)}^2} \end{aligned}$$

where $\mu_{(S\sigma j)}$ is the mean residual standard deviation (in log space) for order j and $\nu_{(S\sigma)}$ is the coefficient of variation of among-stock variability in residual standard deviations (we assumed that this coefficient of variation is constant among orders). The mean standard deviation for each taxonomic order is again given a hierarchical prior:

$$(9) \quad \begin{aligned} \mu_{(S\sigma j)} &\sim \text{Gamma}(s_{(O)j}, r_{(O)j}) \\ s_{(O)j} &= \frac{1}{\nu_{(O\sigma)}^2} \\ r_{(O)j} &= \frac{1}{\mu_{(O\sigma)} \nu_{(O\sigma)}^2} \end{aligned}$$

where $\mu_{(O\sigma)}$ is the mean marginal standard deviation (in log space) for all taxonomic orders.

Similarly, the autocorrelation coefficient ρ_i for stock i is assigned a hyperprior:

$$(10) \quad \rho_i \sim \text{Truncated Normal} \left(\sum_{j=1}^J I(O_i = j) \mu_{(S\rho j)}, \tau_{(S\rho)}^2, \min. = -0.99, \max. = 0.99 \right)$$

where Truncated Normal is a truncated normal distribution centered at $\mu_{(S\rho j)}$ for the taxonomic order corresponding to species i , with dispersion $\tau_{(S\rho)}$ (we again assumed that this parameter is constant for all orders) and truncated to have domain from -0.99 to 0.99 . We used the truncated normal distribution, rather than the commonly used beta distribution, to prevent individual stocks

with high autocorrelation from having undue leverage regarding the expected value for autocorrelation. The center of this truncated normal distribution $\mu_{(S\rho j)}$ for order j is itself given a hierarchical prior:

$$(11) \quad \mu_{(S\rho j)} \sim \text{Truncated Normal}(\mu_{(O\rho)}, \tau_{(O\rho)}^2, \min. = -0.99, \max. = 0.99)$$

where $\mu_{(O\rho)}$ is the central value for autocorrelation of all taxonomic orders and $\tau_{(O\rho)}$ is the dispersion in autocorrelation among orders.

Since we fit the preceding model using a Bayesian approach, we therefore must specify prior distributions for all model parameters. The coefficient of variation of among-stock $\nu_{(S\sigma)}$ and among-order variability $\nu_{(O\sigma)}$, as well as the standard deviation of among-stock $\tau_{(S\rho)}$ and among-order variability $\tau_{(O\rho)}$, are given uniform priors from 0 to 10 (after confirming that sampling never approaches the lower or upper bounds). Recruitment models require priors on maximum recruits per spawning biomass α_i and density dependence per unit spawning biomass β_i . For the Ricker model, we use an improper, uniform prior on β_i given the constraint that it was positive, and an improper uniform prior on $\ln(\alpha_i)$. By contrast, we use a reparameterization of the Beverton–Holt model that improves mixing of the Markov chain Monte Carlo sampling algorithm (discussed in the “Model fitting” subsection). This parameterization involves estimating the median recruitment expected at the maximum observed spawning biomass for species i , $R_{(\max)i}$, which was given an improper, uniform prior in log space. This reparameterization also involves estimating a parameter, Ψ_i , which was used to calculate the median recruitment expected at the minimum observed spawning biomass:

$$(12) \quad R_{(\min)i} = \frac{S_{(\min)i}}{S_{(\max)i}} R_{(\max)i} + \left(1 - \frac{S_{(\min)i}}{S_{(\max)i}} \right) \Psi_i R_{(\max)i}$$

Ψ_i is given a uniform prior from 0 to 1, and these bounds ensure that the estimates of $R_{(\min)i}$ and $R_{(\max)i}$ are consistent with those of the Beverton–Holt model. α_i and β_i are then calculated from $R_{(\max)i}$ and Ψ_i as follows:

$$(13) \quad \begin{aligned} \beta_i &= \frac{R_{(\min)i} S_{(\max)i} - R_{(\max)i} S_{(\min)i}}{S_{(\min)i} S_{(\max)i} (R_{(\max)i} - R_{(\min)i})} \\ \alpha_i &= \frac{R_{(\max)i} (1 + \beta_i S_{(\max)i})}{S_{(\max)i}} \end{aligned}$$

where the formula for β_i was calculated using Wolfram Alpha (<http://www.wolframalpha.com/>).

Posterior distributions for model parameters can then be summarized using standard statistics (i.e., mean and standard deviation). We have also reported predictive distributions for stocks within a given order or for a taxonomic order that has not been included in our analysis. The predictive distribution within a given taxonomic order simulates a single sample from a gamma distribution (for marginal standard deviations) or truncated normal distribution (for autocorrelations) for each retained sample from the posterior distribution (i.e., using eqs. 8 and 10), and then applies summary statistics to these simulated values. The predictive distribution for an unobserved order additionally samples the parameter representing the center of the predictive distribution for that order (i.e., using eqs. 9 and 11), and then simulates the values for stock within that order (eqs. 8 and 10) for each sample from the posterior distribution. Random simulations from a truncated normal distribution are generated using the truncnorm

package (Trautmann et al. 2012) in the R statistical platform (R Development Core Team 2012).

Objective 2: recruitment variability, autocorrelation, and age at maturity

We also explore a previously hypothesized relationship between the magnitude of recruitment variability and species life history. Specifically, Winemiller and Rose (1992) developed a life history theory in which “periodic”, “equilibrium”, and “opportunistic” fish species have different life history strategies for persisting in marine and freshwater environments, and hence have predictable patterns of life history traits. Subsequent developments of this theory have made the following predictions:

1. Age at maturity can be used to distinguish opportunistic species from either periodic or equilibrium species, where opportunistic species will have low age at maturity while other species will have higher age at maturity (Winemiller 2005).
2. Periodic species will have higher autocorrelation in recruitment than opportunistic species (Winemiller 2005).
3. Periodic species will have higher variability in recruitment than equilibrium or opportunistic species (Rose et al. 2001).

To explore these hypotheses, we tested the effect of age at maturity on the expected value for recruitment variability σ_i and the autocorrelation in recruitment residuals ρ_i . To estimate the hypothesized effect of age at maturity on the standard deviation of recruitment variability σ_i , we replaced eq. 8 with

$$s_{(s)i} = \sum_{j=1}^J I(O_j = j) \frac{1}{\nu_{(s)\sigma}^2}$$

$$r_{(s)i} = \sum_{j=1}^J I(O_j = j) \frac{1}{a_i^{\lambda_{(s)\sigma}} \mu_{(s)\sigma} \nu_{(s)\sigma}^2}$$

where $\lambda_{(s)}$ represents the relationship between age at maturity and the variation of recruitment residuals and a_i is the age at maturity for stock i . These equations represent a linear relationship between $\ln(\sigma_i)$ and $\ln(a_i)$, where $\lambda_{(s)}$ is the slope and the intercept differs among taxonomic orders. It reduces to the previous model when $\lambda_{(s)} = 0$, and $\lambda_{(s)} > 0$ indicates that higher age at maturity is associated with increased residual variance. We also replaced eq. 10 with

$$\rho_i \sim \text{Truncated Normal}(\mu_{(s)\rho} + \lambda_{(s)\rho} a_i, \tau_{(s)\rho}^2, \text{min.} = -0.99, \text{max.} = 0.99)$$

where $\lambda_{(s)\rho}$ represents the relationship between age at maturity and the autocorrelation of recruitment residuals. This again reduces to the previous model when $\lambda_{(s)\rho} = 0$, and $\lambda_{(s)\rho} > 0$ indicates that higher age at maturity is associated with increased autocorrelation in recruitment residuals. We hypothesized a positive relationship between age at maturity and both recruitment variability ($\lambda_{(s)\sigma} > 0$) and recruitment autocorrelation ($\lambda_{(s)\rho} > 0$).

Model fitting

All models were estimated using Markov chain Monte Carlo sampling, implemented using the STAN version 1.3 software package (Stan Development Team 2013) as called in R (R Development Core Team 2013) using the rstan package. This software implements Hamiltonian MCMC using the “No U-turn” sampler (Hoffman and Gelman 2014). Each MCMC sample used three sampling chains with 2500 burn-in samples followed by 2500 monitored samples.

We checked for evidence of nonconvergence using trace plots and ensured that all models had an effective sample size of at least 100.

Results

Illustrating model fits

Comparison of results for Beverton–Holt and Ricker models shows very little difference for variance and autocorrelation estimates. We therefore present and interpret the Beverton–Holt results in the main text, while presenting the Ricker results in the Supplementary Materials.¹

Model estimates show a large magnitude of autocorrelation for many individual species (Fig. 1). For example, the lake trout (*Salvelinus namaycush*) from Lake Opeongo, Ontario, has an autocorrelation estimate of 0.95 (SD = 0.03). This autocorrelation is plausible given that log-recruits per spawning biomass is consistently lower than predicted from the Beverton–Holt model for the final 20 years of available data. As a consequence, Beverton–Holt model estimates of recruitment have extremely wide credible intervals (± 1 log-recruit per spawner), while these credible intervals are much smaller for a model that includes autocorrelation. By contrast, Atlantic menhaden (*Brevoortia tyrannus*) off the US Atlantic coast has the median estimate of autocorrelation (0.40, SD = 0.14) for all 154 stocks included in our analysis. This stock has several periods during which recruit estimates are consistently above or below observations (e.g., from years 15 to 22), but has other periods when recruitment residuals are well dispersed around the model estimates. Finally, the chum salmon (*Oncorhynchus keta*) population of northern British Columbia has the lowest autocorrelation of any stock (−0.06, SD = 0.17). In this case, neighboring residuals are slightly more likely to flip from positive to negative, and vice versa, than expected by chance. However, there is relatively little difference between recruitment estimates with and without including autocorrelation.

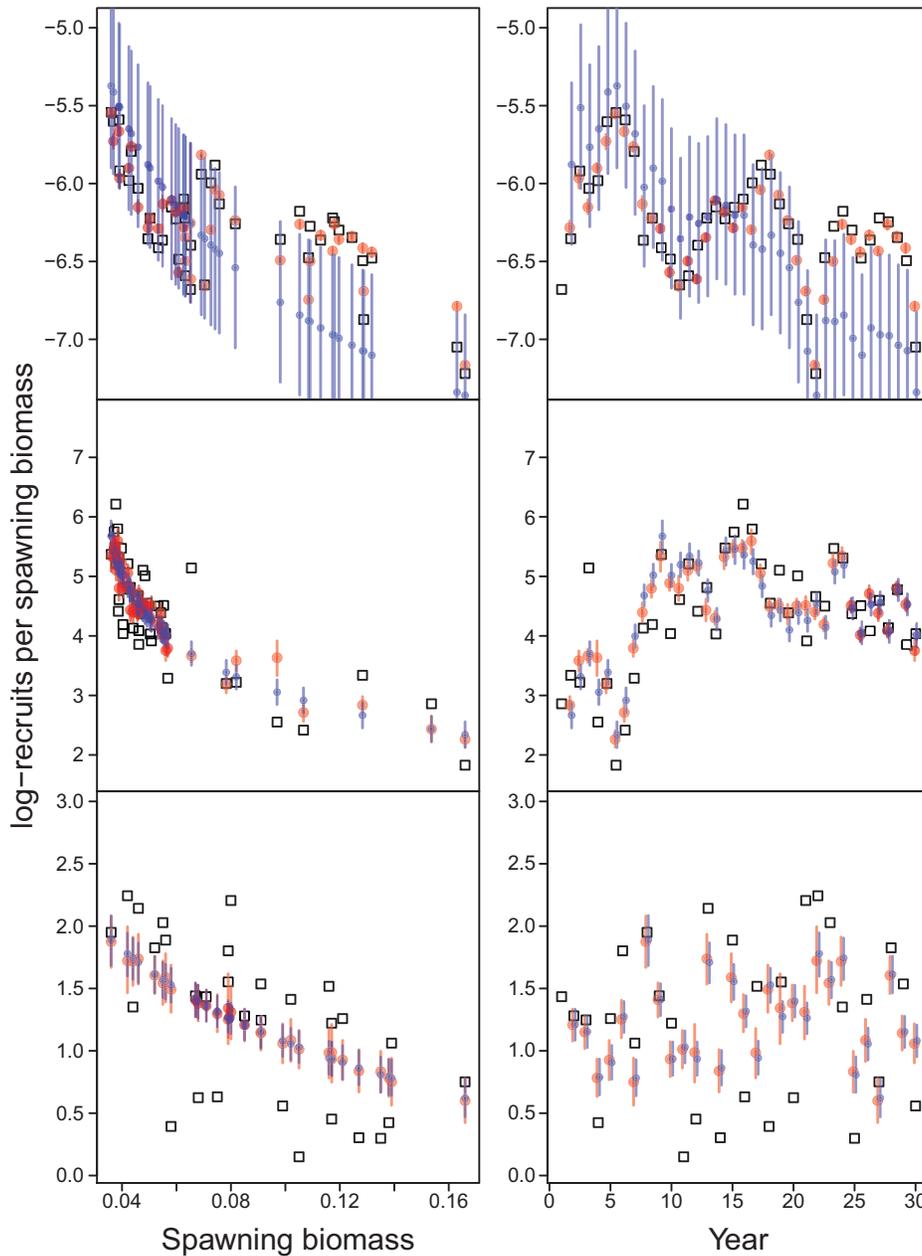
Hierarchical modeling

We next inspected the distribution for the standard deviation of recruitment (Fig. 2; Table 2). The posterior distribution for the expected marginal standard deviation of recruitment residuals across all taxonomic orders is tightly centered around 0.74 (SD = 0.07). However, this posterior distribution does not account for among-stock variability, and the predictive distribution has the same mean (0.74) but considerably larger variability (SD = 0.35). Scorpaeniformes, Clupeiformes, and Perciformes have high residual standard deviations (>0.77), while Pleuronectiformes and Aulopiformes have relatively low residual standard deviation (<0.67). However, there is significant variability among stocks within a given order (among-stock, within-order CV = 0.39), indicating that the majority of variation is explained at the stock level, rather than by taxonomic order.

Similarly, the parameter representing mean autocorrelation among taxonomic orders is significantly positive (0.45, SD = 0.05), and the predictive distribution that contains among-stock variability has a similar mean but is considerably more dispersed (0.43, SD = 0.28). Variation among taxonomic orders (0.08) is again smaller than variation among stocks within a given taxonomic order (0.28), indicating that order explains a small portion of variability among stocks. Predictions of autocorrelation for Salmoniformes (0.37, SD = 0.27) and Gadiformes (0.40, SD = 0.27) are generally lower than for Clupeiformes (0.44, SD = 0.27) and Perciformes (0.47, SD = 0.26).

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0645>.

Fig. 1. Examples of autocorrelated (red, $\hat{L}_{i,t} + \rho_i(L_{i,t-1} - \hat{L}_{i,t-1})$) and nonautocorrelated (blue, $\hat{L}_{i,t}$) estimates of log-recruits per spawning biomass (y axis) for the Beverton–Holt model plotted against spawning biomass (left column) or calendar year (right column), where the black squares are the data, the red and blue circles show the expected recruitment for autocorrelated and nonautocorrelated estimates, and the red and blue lines shows the 80% credible interval for the expected recruitment (the lines do not encompass 80% of points because they do not represent the predictive distribution and hence do not include measurement error). The top row shows results for lake trout (*Salvelinus namaycush*) from Lake Opeongo, Ontario, which had the highest autocorrelation of any stock (0.95, SD = 0.03); the middle row shows results for Atlantic menhaden (*Brevoortia tyrannus*), which had the median observed autocorrelation (0.40, SD = 0.14); the bottom row shows results for northern British Columbia chum salmon (*Oncorhynchus keta*), which had the lowest autocorrelation of any stock (−0.06, SD = 0.17).



Recruitment variability, autocorrelation, and age at maturity

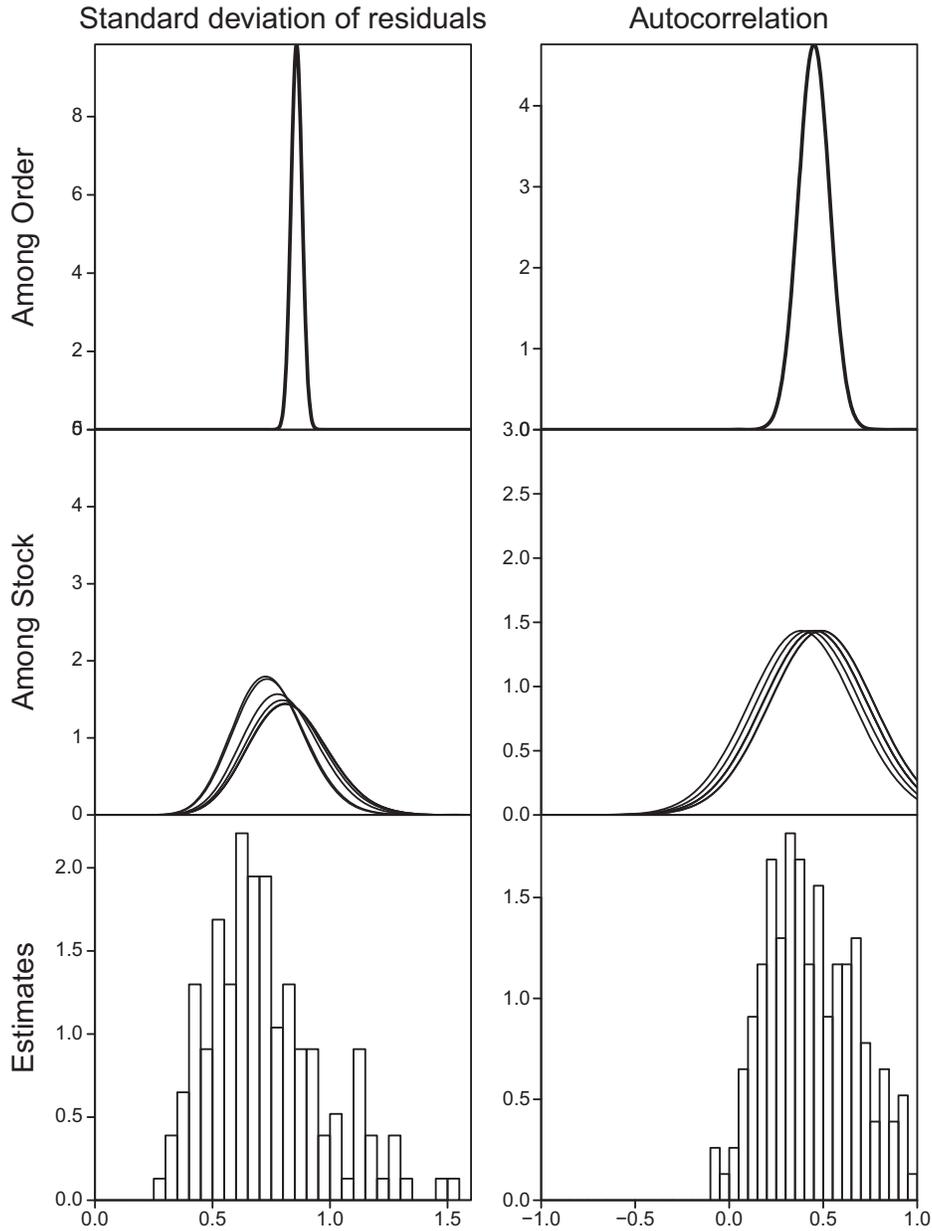
The posterior distribution for the coefficient representing the relationship between age at maturity and the marginal standard deviation of recruitment residuals shows substantial overlap with zero (Fig. 3, top row), indicating little support for this hypothesized relationship. However, the posterior distribution for the relationship between age at maturity and autocorrelation substantially differs from zero and is positive. We therefore conclude that there is evidence that higher autocorrelation in recruitment

variability in marine fishes is associated with increased age at maturity.

Discussion

The current interest regarding changes in fish productivity and its effect on fisheries management recapitulates the old Thompson–Burkenroad debates regarding the cause of decline in population abundance of Pacific halibut in the 1920s (Hilborn and Walters 1992; Smith 2007). For example, recruitment in the anadromous alewife population in Fig. 1 is so strongly autocorrelated

Fig. 2. Estimates for the Beverton–Holt model of the posterior mean of the distribution of residual variance (left column) and autocorrelation (right column) among all orders (top row, i.e., $\mu_{(O\sigma)}$ and $\mu_{(O\rho)}$), among stocks within each order (middle row, i.e., $\mu_{(S\sigma)}$ and $\mu_{(S\rho)}$, where each line represents one of seven estimated orders), and for each of 154 stocks in the stock–recruitment database (bottom row, i.e., σ_i and ρ_i).



that it seems likely to be driven by environmental drivers or some other form of model misspecification. However, modern population models can now incorporate environmental effects in stock–recruitment relationships (Schirripa et al. 2009; Jensen et al. 2010), so population ecologists are no longer faced with an either–or decision between spawning biomass and environmental hypotheses for recruitment. Instead, population ecologists can now entertain both hypotheses in a single model and allow the data to identify the relative magnitude of both effects, as has recently been done in the 2013 Pacific halibut stock assessment (I. Stewart, personal communication). In other cases where an environmental factor has not been identified and verified to have predictive ability for future recruitment, analysts may choose to explain autocorrelated residuals using an explicit correlation parameter, and hence propagate this uncertainty during model estimation and forecasting.

The present study uses a single-stage meta-analysis model (sensu Thorson et al. 2014a) to estimate variability and autocorrelation in recruitment while simultaneously controlling for the stock–recruitment relationship using either the Beverton–Holt or Ricker model. Results can be used as a Bayesian prior on recruitment variability in population dynamics models that do not otherwise have information to estimate the magnitude of recruitment variability. We specifically recommend that researchers match their species to one of the taxonomic orders listed in Table 2a or use the “unobserved order” estimates if their order is not listed. We then encourage future users of this analysis to simulate recruitment deviations as follows:

$$(16) \quad \varepsilon_t = \begin{cases} \rho_s \varepsilon_{t-1} + \sqrt{1 - \rho_s^2} \delta_t & \text{for } t > 1 \\ \delta_t & \text{for } t = 1 \end{cases}$$

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Table 2. Summary of results (values are means with standard deviation (SD) in parentheses) for the Beverton–Holt model.

(a) Posterior distribution of parameters governing the central tendency of marginal SD and first-order autocorrelation.

Order	Central tendency parameters		Predictive distribution		No. of stocks
	Marginal SD	Autocorrelation	Marginal SD	Autocorrelation	
Aulopiformes	0.666 (0.144)	0.492 (0.108)	0.670 (0.298)	0.464 (0.264)	1
Clupeiformes	0.771 (0.054)	0.456 (0.047)	0.766 (0.305)	0.435 (0.266)	32
Gadiformes	0.747 (0.043)	0.420 (0.044)	0.748 (0.293)	0.404 (0.265)	45
Perciformes	0.778 (0.082)	0.490 (0.074)	0.777 (0.313)	0.466 (0.260)	12
Pleuronectiformes	0.639 (0.076)	0.456 (0.065)	0.636 (0.263)	0.437 (0.265)	16
Salmoniformes	0.710 (0.043)	0.383 (0.050)	0.711 (0.282)	0.371 (0.276)	41
Scorpaeniformes	0.778 (0.091)	0.457 (0.074)	0.778 (0.318)	0.439 (0.264)	7
Unobserved order			0.737 (0.353)	0.426 (0.275)	
Mean for all orders	0.736 (0.071)	0.451 (0.052)			154

(b) Posterior distribution for parameters governing the coefficient of variation of marginal SD and the SD of the truncated normal distribution of autocorrelation.

	CV parameter for SD of residuals	SD parameter for autocorrelation
Within-order variability	0.387 (0.028)	0.278 (0.021)
Among-order variability	0.157 (0.129)	0.084 (0.063)

Note: (a) Within-order variation: $\mu_{(S,\rho)_j}$; among-order variation: $\mu_{(O,\rho)_j}$. For first-order autocorrelation: within-order variation: $\mu_{(S,\rho)_j}$; among-order variation: $\mu_{(O,\rho)_j}$. σ_s , marginal standard deviation; ρ_s , autocorrelation for a stock within each order, or a stock in a different order. We also show the number of stocks for each order, and the sum of stocks across all orders. (b) Within-order variation: $\nu_{(S,\rho)_j}$; among-order variation: $\nu_{(O,\rho)_j}$. The standard deviation for the truncated normal distribution of autocorrelation: within-order variation: $\tau_{(S,\rho)_j}$; among-order variation: $\tau_{(O,\rho)_j}$.

where

$$(17) \quad \delta_t \sim \text{Normal}\left(\frac{-\sigma_s^2}{2}, \sigma_s^2\right)$$

and where eq. 17 uses bias correction in the mean, whose magnitude matches the marginal variance of the autocorrelated recruitment. ρ_s and σ_s are either randomly generated samples from the predictive distribution described in Table 2a or the mean of the predictive distribution for each (i.e., for a Gadiformes fish population: (i) simulate σ_s from a normal distribution with a mean of 0.738 and SD of 0.288 (discarding any negative values); (ii) simulate ρ_s from a normal distribution with a mean of 0.401 and SD of 0.262 (discarding any values ≥ 0.99 or ≤ -0.99). Users can alternatively simulate values using the posterior distribution (or its mean) for the actual model parameters (listed in Tables 2a–2b). We also present results for both Ricker and Beverton–Holt stock–recruitment models to facilitate future comparison. We do not present predictions conditional on a given age at maturity, although researchers could compute these predictions using the posterior distributions for parameters presented here. We do not recommend using priors that are calculated using the age at maturity for any single species until this association has been corroborated using other analytic methods.

The recruitment priors developed in this study could be used to estimate recruitment variability in age-structured, data-poor methods such as simple stock synthesis (Cope 2013), where information regarding the recruitment variability is either absent or weak. Models that incorporate both process and measurement stochasticity will often perform better in reconstructing abundance trends than models that only include one or the other (Schnute 1991; Holmes 2001; Punt 2003; Ono et al. 2012), so including recruitment variability will likely be a step forward for these data-poor models. Given that recruitment is the primary form of stochasticity included in many data-rich assessments, recruitment-variability priors will help to “bridge the gap” between data-rich and data-poor assessment methods. Priors can also be combined with mixed-

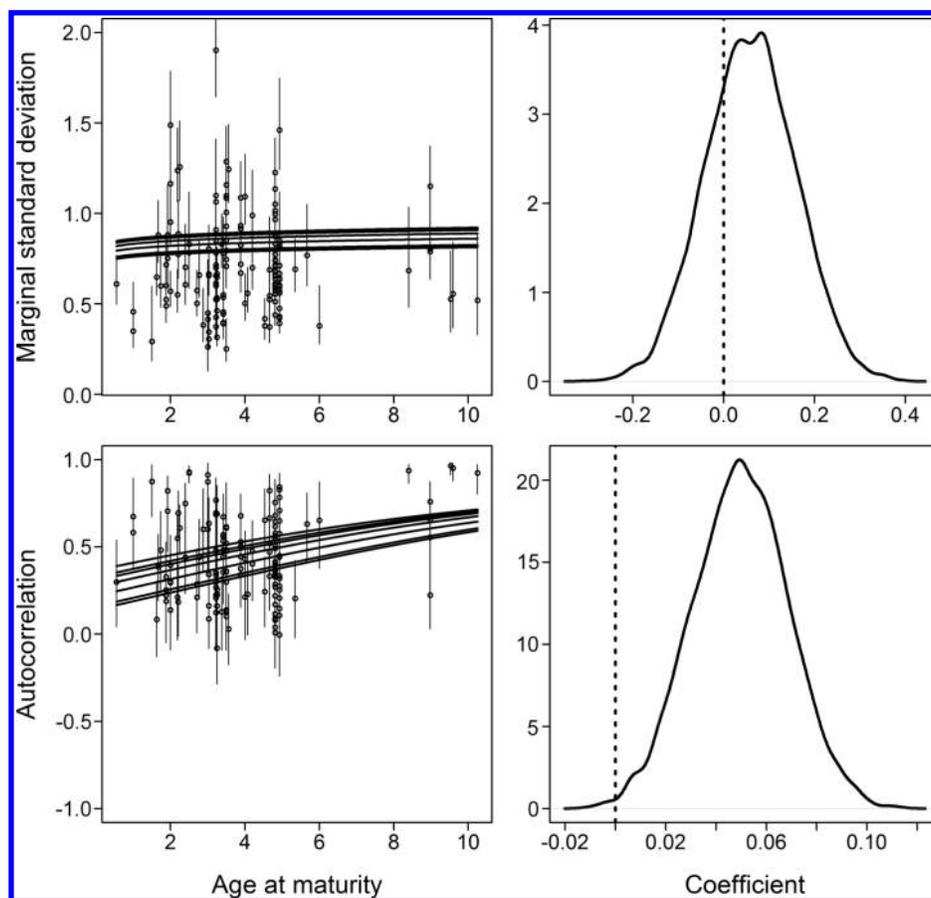
effect estimation methods for data-rich assessments (Thorson et al. 2014b), and may in fact be necessary when simultaneously estimating multiple types of process error (Mäntyniemi et al. 2013). Finally, autocorrelation in recruitment will have important implications for projecting stock recovery during rebuilding plans used for fisheries management, and may help to explain the failure of some species to recover on the expected timeline in certain cases (Neubauer et al. 2013).

Model assumptions

Our hierarchical model for recruitment variability makes two important assumptions. First, it treats taxonomic orders, and stocks within each taxonomic order, as “exchangeable” units (Gelman et al. 2003) from a shared process representing “recruitment variability” for fish in general. This is functionally equivalent to assuming that we have no prior information to distinguish a priori between the variance and autocorrelation in recruitment for each taxon and population. This assumption allows us to specify that residual variance and autocorrelation are shrunk towards a shared mean. Shrinkage allows for improved precision for any estimate (Efron and Morris 1977), but may cause estimates to be biased towards other stocks that are included in the meta-analysis. Future research could explore the sensitivity of model estimates to violations of this assumption and to the sample sizes used in this analysis.

We also assume that sequential population analysis estimates of abundance are an accurate proxy for spawning potential. This assumption is critical, because errors in a variable that is assumed to be “fixed” (i.e., the independent variable in a regression) will lead to biased parameter estimates (Draper and Smith 1998). Similarly, we do not account for the “time series bias” that arises, because spawning biomass is related to previous recruitment rather than being fixed experimentally (Walters 1985; Caputi 1988; Myers and Barrowman 1995). Finally, we note that maximum likelihood estimates of autoregression coefficients have a known asymptotic bias (Shaman and Stine 1988), but the bias of our hierarchical Bayesian estimator remains a topic of future research. In the present case, autocorrelated errors in spawning

Fig. 3. The relationship for the Beverton–Holt model between age at maturity and either the marginal standard deviation of recruitment (top row, σ_i) or autocorrelation in residuals (bottom row, ρ_i). The left column shows each stock with the posterior mean (circles) and 80% credible interval (vertical lines) for its standard deviation or autocorrelation, with the estimated relationship also shown for each taxonomic order (black lines). The right column shows the posterior distribution of the estimated coefficient representing the relationship between age at maturity and either the marginal standard deviation (λ_σ) or autocorrelation (λ_ρ), with the dashed vertical line showing an effect of zero (i.e., age at maturity having no effect). The relationship with autocorrelation is curved because we are plotting the mean of the truncated normal distribution for each value of age at maturity rather than its predicted mode.



biomass may result in autocorrelated residuals for recruitment. Previous analysis of spawner–recruitment data have generally had similar difficulty in dealing with the hypothesis of measurement errors (e.g., Brodziak et al. 2001). One exception, however, is Myers and Cadigan (1993), who used multiple surveys for spawning biomass to simultaneously estimate variability in recruitment and errors in abundance indices. Their study found little evidence of autocorrelation (and, if anything, a negative sign) using data primarily from gadids and pleuronectids. By contrast, Rose et al. (2001) found evidence of autocorrelated recruitment using the same stock–recruitment repository as the one used here, and their recommendation that future studies reanalyze the repository to generate statistically rigorous estimates of the effect inspired the current study.

As always, we hope that these meta-analytic results will be corroborated using alternative scales, data types, and taxa. In particular, future studies may use stock assessment modelling software to replicate this analysis using observation-level data at a regional scale (Thorson et al. 2014c). By fitting directly to stock assessment data — hence avoiding the treatment of biomass estimates as exogenously fixed and known without error — this approach could help to resolve the discrepancy between our results and those of Myers and Cadigan (1993). However, regional-scale analyses of recruitment are likely to be influenced by shared trends in recruitment for sympatric species (Mueter et al. 2002; Thorson

et al. 2013), such that these regional meta-analyses will also have at least one problematic assumption. In the meantime, we see great utility in using our results as a Bayesian prior in data-rich and data-poor models, as well as guidance for the design of future simulation experiments and management strategy evaluations.

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