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SPAWNER-RECRUIT RELATIONSHIPS OF DEMERSAL MARINE FISHES: PRIOR DISTRIBUTION OF STEEPNESS

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ABSTRACT

Stock assessments use spawner-recruit functions to relate the reproductive capacity of a stock (e.g., total fecundity) to subsequent recruitment. The Beverton-Holt spawner-recruit function, perhaps the most widely used, is conventionally parameterized using a "steepness" parameter that describes the stock's productivity. This parameter highly influences predicted population dynamics and responses to exploitation. Unfortunately, steepness can also be difficult to estimate reliably from data typical of stock assessments. In such cases, estimation can be improved by drawing inference from other stocks with similar life-history patterns. In particular, Bayesian prior distributions can formally be incorporated into stock assessments to inform estimation of steepness. In the present study, we used a meta-analytic approach to compute a prior distribution of steepness, focusing on marine demersal fishes. We similarly computed a prior distribution of maximum lifetime reproductive rate, a parameter inextricably related to steepness. In addition, we tested relationships between steepness and two life-history parameters linked to longevity—natural mortality and age at maturity—to examine the common assumption that long-lived, "K-selected" species have lower steepness values. In neither case was steepness significantly related to the life-history parameter. Our results should be directly applicable in stock assessments that apply the Beverton-Holt (or Ricker) function to marine demersal fishes, such as reef-associated species of the southeast United States in Atlantic, Caribbean, and Gulf of Mexico waters.

In marine fish populations, recruitment of new individuals generally increases with spawner abundance (Myers and Barrowman 1996, Myers and Mertz 1998, Myers 2001). Stock assessments often quantify that relationship with the Beverton-Holt spawner-recruit function, which includes steepness as a key parameter (Mace and Doonan 1988). By convention, steepness (h) is defined as the proportion of unfished recruitment (R_0) produced by 20% of unfished population fecundity or spawning biomass (S_0). The Beverton-Holt formulation computes recruitment (R) from spawning biomass (S),

$$R = \frac{0.8 R_0 h S}{0.2 \Phi_0 R_0 (1-h) + (h-0.2) S} \qquad \text{(Eq. 1)}$$

where Φ_0 describes the unfished spawning biomass per recruit. In this formulation, steepness is bounded, $0.2 \leq h \leq 1.0$. A higher value of steepness translates into higher expected productivity, particularly at low levels of spawning biomass (Fig. 1).

Because productivity relates directly to population regulation, steepness heavily influences estimates of management quantities, such as MSY-based biological reference points and related proxies (Brooks et al. 2010). Steepness is also notoriously difficult to estimate (Conn et al. 2010). Estimation difficulties can arise for a host

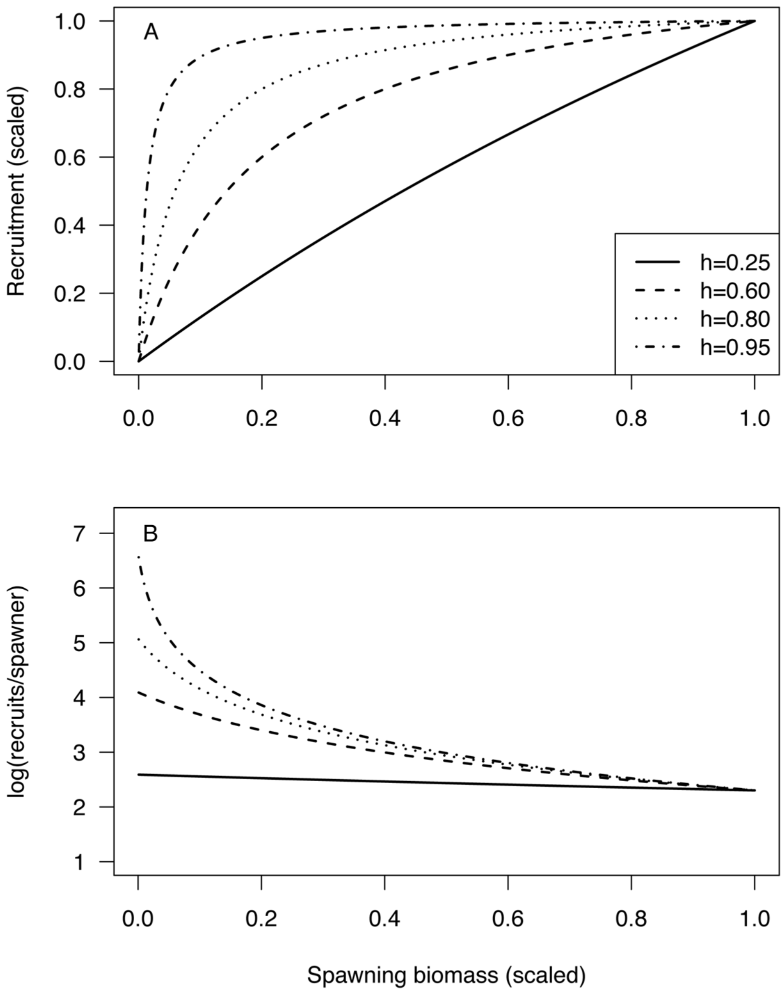

Figure 1. (A) Hypothetical Beverton-Holt spawner-recruit curve for various levels of steepness (*h*), and (B) corresponding levels of density dependence in recruits per spawner.

of reasons, among them: (1) fluctuations in recruitment are magnified at low stock sizes (Myers 2001, Anderson et al. 2008); (2) steepness may change through time, for example, as an adaptive response to exploitation (Enberg et al. 2010); and (3) perhaps most conspicuously, fishery data are often uninformative regarding steepness (Conn et al. 2010).

When other data sources provide weak or no information on steepness, a prior distribution can inform estimation of spawner-recruit curves (Myers et al. 2002). Prior distributions of steepness have been based on evolutionary principles (He et al. 2006), fluctuation or uncertainty in life-history parameters (Mangel et al. 2010), and meta-analysis of ecologically similar species (Dorn 2002, Forrest et al. 2010). The present study takes the meta-analytic approach (Myers and Mertz 1998) to develop a prior distribution of steepness. The analysis draws together information on steepness from several sources, including Rose et al. (2001), Forrest et al. (2010), and relevant

SouthEast Data Assessment and Review (SEDAR) assessments. Using those data, we fit normal and beta distributions to characterize steepness, and we fit generalized additive models to examine relationships between steepness and life-history parameters. Our primary goal is to provide a prior distribution for possible application in stock assessments of demersal marine fishes, with focus on reef-associated species of the southeast United States in Atlantic, Caribbean, and Gulf of Mexico waters.

Methods and Results

Data Sources.—We compiled data from several sources to examine steepness values (point estimates) of 94 stocks. The majority of data were from Rose et al. (2001), who conducted a review of compensatory density dependence and refined the meta-analysis of steepness from Myers et al. (1999). Rose et al. (2001) summarized their data according to three broad categories of reproductive strategies: equilibrium, opportunistic, and periodic (Winemiller and Rose 1992). Because reef fishes in the southeast United States are generally periodic strategists, this current analysis used only stocks of that category, narrowed further to those that are marine and demersal (75 stocks, Table 1).

We also included estimates of steepness derived by Forrest et al. (2010) for 14 stocks of Pacific rockfishes, *Sebastes* spp. (Table 1). Forrest et al. (2010) applied a hierarchical Bayesian meta-analysis built on previous work by Dorn (2002). Values included here were their posterior mean estimates.

In addition to Rose et al. (2001) and Forrest et al. (2010), we examined previous SEDAR stock assessments as possible sources of data. These comprised all benchmark assessments completed before our study (SEDAR 1 through SEDAR 24, most with multiple stocks) and associated update assessments, applied to stocks in southeast United States waters (Atlantic, Caribbean, and Gulf of Mexico). Some stocks have been assessed multiple times, and in those cases, the most recent assessments were considered. For a SEDAR steepness value to be included here, we enforced three criteria. First, the species had to be a reef-associated finfish, to exclude those that are migratory or invertebrate; this criterion left 21 candidate assessments that utilized steepness as a model parameter. Second, the value of steepness had to be estimated (some assessments used values that were fixed). Third, the value must not have been influenced by a prior distribution developed from other data already in this analysis, e.g., from Myers et al. (1999) or Rose et al. (2001). The third criterion was established to avoid double use of data, as cautioned by Minte-Vera et al. (2005). These criteria left steepness estimates from five SEDAR assessments to be included in the analysis (Table 1). The stocks were black sea bass (Atlantic, SEDAR 2005), red porgy (Atlantic, SEDAR 2006a), gag (Gulf of Mexico, SEDAR 2006b), greater amberjack (Atlantic, SEDAR 2008), and red grouper (Gulf of Mexico, SEDAR 2006c).

Distribution of Steepness.—Values of steepness from Rose et al. (2001) had a mean (standard deviation) of 0.77 (0.15); values from Forrest et al. (2010), 0.69 (0.12); and values from SEDAR, 0.70 (0.13). Combined across data sets, steepness had a sample mean of 0.75 (0.15) and median of 0.78 (0.69–0.86 interquartile range). Standard error of the mean was 0.015.

Table 1. Stocks included in meta-analysis. The first set of stocks are from Rose et al. (2001), the second from Forrest et al. (2010), and the third from SEDAR assessments, as indicated in the text.

Species	Common name	Stock(s)
Gadus morhua (Linnaeus, 1776)	Atlantic cod	NAFO 2J3KL; NAFO 3NO; NAFO 3Pn4RS; NAFO 3Ps; NAFO 4TVn; NAFO 4VsW; NAFO 4X; NAFO 5Y; NAFO 5Z; Baltic Areas 22 and 24; Baltic Areas 25-32; Celtic Sea; Faroe Plateau; Iceland; Irish Sea; Kattegat; North East Arctic; North Sea; Skagerrak; ICES VIId; ICES VIa
Lophius budegassa (Spinola, 1807)	Black anglerfish	ICES VIIb-k and VIIIa,b
Micromesistius poutassou (Risso, 1826)	Blue whiting	Northern ICES; Southern ICES
Platichthys flesus (Linnaeus, 1758)	European flounder	Baltic Areas 24 and 25
Reinhardtius hippoglossoides (Walbaum, 1792)	Greenland halibut	North East Arctic; Northwest Atlantic; ICES V and XIV
Melanogrammus aeglefinus (Linnaeus, 1758)	Haddock	NAFO 4TVW; NAFO 4X; NAFO 5Z; Faroe Plateau; Iceland; North East Arctic; North Sea; Rockall Bank; ICES VIa
Merluccius hubbsi (Marini, 1933)	Hake	Southwest Atlantic Ocean
Pagrus auratus (Forster, 1801)	New Zealand snapper	New Zealand, SNA 8; Hauraki Gulf/Bay of Plenty
Merluccius productus (Ayres, 1855)	Pacific hake	West US + Canada
Pleuronectes platessa (Linnaeus, 1758)	Plaice	ICES VIId; ICES VIIe; Celtic Sea; ICES IIIa; Irish Sea; Kattegat; North Sea; Skagerrak
Pollachius virens (Linnaeus, 1758)	Pollock or saithe	Faroe; Iceland; North East Arctic; North Sea; ICES VI
Lutjanus campechanus (Poey, 1860)	Red snapper	US Gulf of Mexico
Stenotomus chrysops (Linnaeus, 1766)	Scup	Cape Cod - Cape Hatteras
Merluccius bilinearis (Mitchill, 1814)	Silver hake	NAFO 4VWX; NAFO 5Ze; Mid Atlantic Bight
Solea vulgaris (Quensel, 1806)	Sole	Celtic Sea; ICES IIIa; Irish Sea; North Sea; Bay of Biscay (VIII); ICES VIId; ICES VIIe
Merlangius merlangus (Linnaeus, 1758)	Whiting	Celtic Sea; Irish Sea; North Sea; ICES VIId; ICES VIa
Theragra chalcogramma (Pallas, 1814)	Walleye pollock	Eeast Bering Sea; Gulf of Alaska, Alaska
Pleuronectes ferrugineus (Storer, 1839)	Yellowtail flounder	NAFO 5Z; Southern New England

Table 1. Continued.

Species	Common name	Stock(s)
Sebastes melanops (Girard, 1856)	Black rockfish	Washington, Oregon
Sebastes paucispinus (Ayres, 1854)	Bocaccio	West US
Sebastes pinniger (Gill, 1864)	Canary rockfish	West US
Sebastes goodie (Eigenmann and Eigenmann, 1890)	Chilipepper rockfish	West US
Sebastes variabilis (Pallas, 1814)	Dusky rockfish	Gulf of Alaska
Sebastes polyspinis (Taranetz and Moiseev, 1933)	Northern rockfish	Bering Sea/Aleutian Is.; Gulf of Alaska
Sebastes alutus (Gilbert, 1890)	Pacific ocean perch	West US; Goose Is. Gully; Gulf of Alaska; Bering Sea/Aleutian Is.
Sebastes aleutianus (Jordan and Evermann, 1898)	Rougheye rockfish	Gulf of Alaska
Sebastes entomelas (Jordan and Gilbert, 1880)	Widow rockfish	West US
Sebastes flavidus (Ayres, 1863)	Yellowtail rockfish	West US
Centropristis striata (Linnaeus, 1758)	Black sea bass	South US Atlantic
Mycteroperca microlepis (Goode and Bean, 1879)	Gag	US Gulf of Mexico
Seriola dumerili (Risso, 1810)	Greater amberjack	US Atlantic
Epinephelus morio (Valenciennes, 1828)	Red grouper	US Gulf of Mexico
Pagrus pagrus (Linnaeus, 1758)	Red porgy	US Atlantic

Prior distributions of steepness were characterized using normal and beta probability density functions (pdf), estimated by maximum likelihood. Because steepness is bounded, log likelihoods (log *L*) were calculated using truncated pdf,

$$\log L = \sum_{i=1}^{n} \log\left(\frac{f(x_i \mid \theta)}{\int_{0.2}^{1.0} f(x \mid \theta)\, dx} \right) \qquad \text{(Eq. 2)}$$

where x_i are the n observed values, f is the pdf (normal or beta), and θ is the parameter set of f. Estimated distributions were compared using Akaike's Information Criteria (AIC$_c$, Burnham and Anderson 2002).

Normal Distribution.—The normal distribution is defined over the interval $(-\infty, \infty)$ by two parameters, the mean (μ) and standard deviation ($\sigma > 0$). Maximum likelihood estimates in truncated space (Eq. 2) were $\hat{\mu} = 0.80$ and $\hat{\sigma} = 0.19$ (AIC$_c = -101.7$; Fig. 2A). For the normal distribution, the mode equals $\hat{\mu}$.

Beta Distribution.—The beta distribution is defined over the interval [0.0, 1.0] by two shape parameters, $\alpha > 0$ and $\beta > 0$. Here, maximizing the truncated log likelihood (Eq. 2) resulted in $\hat{\alpha} = 5.94$ and $\hat{\beta} = 1.97$ (AIC$_c = -108.1$; Fig. 2B). The beta distribution is unimodal when $\alpha > 1$ and $\beta > 1$, with mode equal to $(\alpha - 1)/(\alpha + \beta - 2)$. In this case, the mode occurs at $h = 0.84$.

Uncertainty in Estimated Distributions.—The analyses above were based on point estimates of steepness. Ideally, uncertainty in those estimates would be carried forward in the analyses, but for most values in this data set, characterizations of variance were not available. To examine the likely effect of uncertainty on our estimated distributions, we constructed an ad hoc bootstrap analysis in which we re-fit the normal and beta distributions n = 10,000 times. In each iteration, a new data set of steepness values was created by drawing n = 94 random normal deviates, each centered on a unique point estimate and with an assumed coefficient of variation (CV$_i$ for datum i). The CV$_i$ were drawn anew in each bootstrap iteration from a uniform distribution U (0.05, 0.30). If a normal deviate fell outside the bounds of steepness (i.e., below 0.2 or above 1.0), a new value was drawn to replace it. This analysis provided n = 10,000 sets of parameter estimates for each distribution, and we used the means of those estimates to represent central tendencies.

For the normal distribution, mean parameter estimates were $\hat{\mu} = 0.79$ and $\hat{\sigma} = 0.23$. For the beta distribution, mean estimates were $\hat{\alpha} = 3.89$ and $\hat{\beta} = 1.52$. Thus, uncertainty in the point estimates of steepness had little effect on the modes of the resulting distributions, but did affect the variances (Fig. 2). Although the beta distribution provided a better fit (lower AIC$_c$) in the original data set of point estimates, it did so in only about half of the n = 10,000 bootstrap iterations.

Distribution of Maximum Lifetime Reproductive Rate.—Some stock assessments define steepness in terms of maximum lifetime reproductive rate, $a' = a\Phi_0$, where a is the slope at the origin of the spawner-recruit curve and Φ_0 is the unfished spawning biomass per recruit (as in Eq. 1). Except for a singularity at $h =$

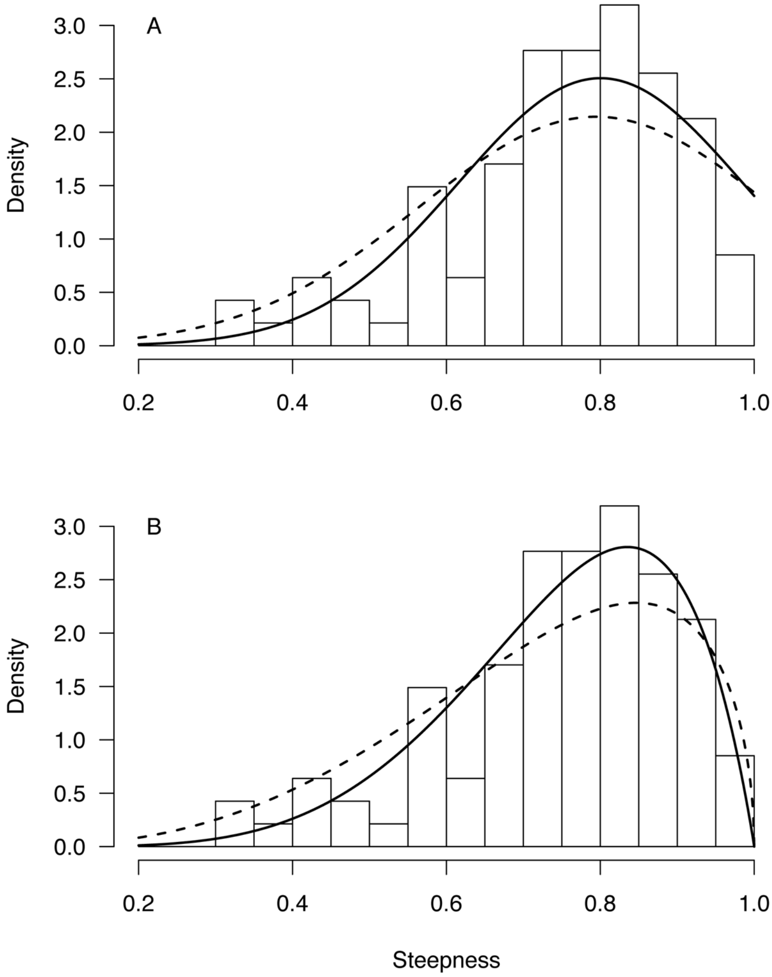

Figure 2. (A) Frequency histogram of steepness values, along with the normal distribution fitted to those data by maximum truncated likelihood (solid curve), and the normal distribution fitted to bootstrapped data (dashed curve). (B) Frequency histogram of steepness values, along with the beta distribution fitted to those data by maximum truncated likelihood (solid curve), and the beta distribution fitted to bootstrapped data (dashed curve).

1, steepness relates nonlinearly to maximum lifetime reproductive rate (Myers et al. 1999),

$$h = \frac{a'}{4 + a'} \qquad \text{or, equivalently,} \qquad a' = \frac{4h}{1 - h} \qquad \text{(Eqs. 3, 4)}$$

Using the data from stocks of Table 1, log(a') conforms approximately to a normal distribution (Shapiro-Wilk normality test: W = 0.99, P = 0.77), with mean 2.68, median 2.68, and standard deviation 0.90. Although log(a') ≥ 0.0 by definition, very little probability mass falls below the bound, and thus maximum truncated likelihood estimates of μ and σ are nearly identical to the sample mean and sample standard deviation.

Relationship Between Steepness and Life-History Parameters.—We used generalized additive models (GAMs) as an exploratory tool to examine the relationship between steepness and approximate age at maturity (A_M), as well as between steepness and natural mortality rate (M). Values of maturity and mortality were taken from the same data sources as the corresponding estimates of steepness. For both life-history parameters, the model included intercept (b_0) and smoothing (s) terms,

$$E(Y \mid h) = b_0 + s(h) \qquad \text{(Eq. 5)}$$

where Y represents either A_M or M, and s is a smoothing spline. The models were fitted using the gam function in R (R Development Core Team 2011), assuming its defaults for smoothing degrees of freedom and error structure (Gaussian family with identity link). We included the smoothing term to detect a relationship, perhaps nonlinear, between predictor and response, without the need to specify a priori any functional form.

In the model to predict age at maturity, the spline function did not contribute significantly to the prediction (F = 1.42; P = 0.24). Similarly, in the model to predict natural mortality, the spline function did not contribute significantly (F = 1.03; P = 0.38). These results indicate that, at least in this data set, the relationships between steepness and A_M or M are described adequately by constants (Fig. 3).

Discussion

The prior distributions we propose are intended to improve estimation in stock assessments. Typical application might be through Bayesian estimation, Monte Carlo simulation, or in maximum composite likelihood as a penalty term. The latter approach, common to standard stock assessment software such as Stock Synthesis (Methot 2011), provides maximum a posteriori probability (MAP) estimates. In any application, analysts should be aware that steepness has a narrower range [0.2, 1.0] than that of the beta or normal distributions ([0, 1] and $(-\infty, \infty)$, respectively). Steepness can be constrained to its range through truncation or suitable transformation (e.g., see Mangel et al. 2010).

Although meta-analysis can reduce uncertainty (Myers and Mertz 1998), we recognize its limitations. Most notably, average relationships across stocks may not well represent each particular stock of interest. Furthermore, our analysis was performed on point estimates of steepness previously estimated in other studies, most of which did not include accompanying measures of precision. As such, the data we analyzed were already subject to an unknown level of estimation error. Our bootstrap analysis, although ad hoc, attempted to quantify effects of estimation error on our results. Knowledge about the true uncertainty in point estimates would have been useful because such uncertainty could be propagated within a Bayesian analysis of steepness. In our view, meta-analysis performed directly on spawner-recruit time series would also be preferable; however, such time series are themselves subject to error, being estimated by stock assessment models. Rerunning the underlying stock assessments would likely provide the best means to carry forward all compounding sources of error, although we acknowledge that doing so for all 94 stocks included here would be a monumental undertaking.

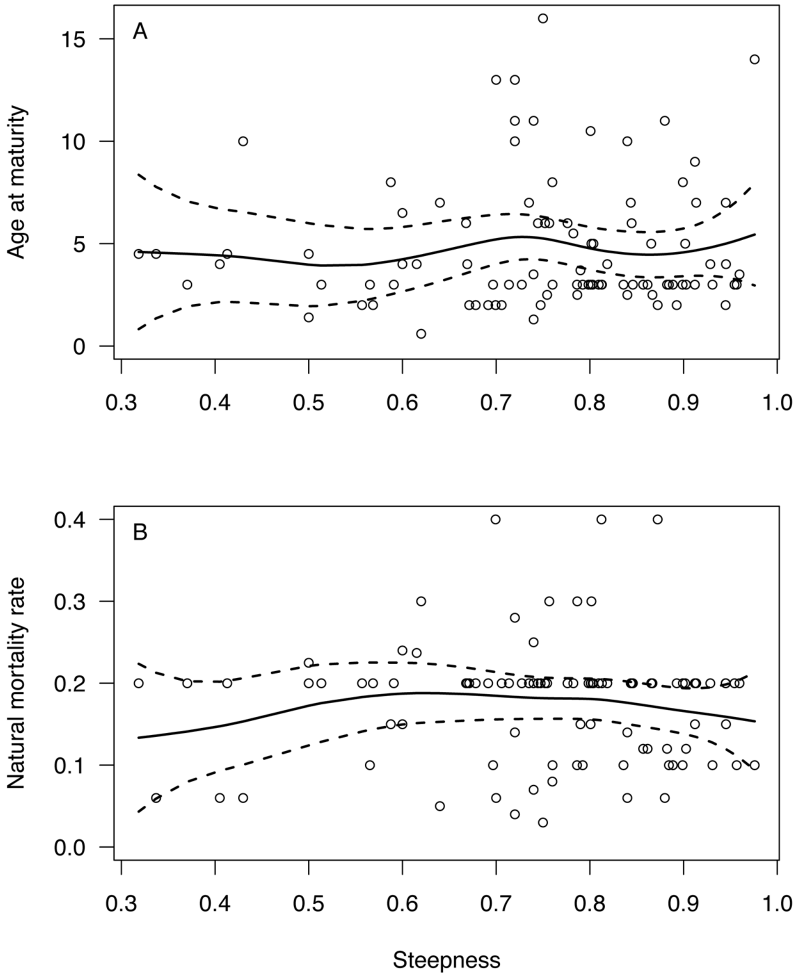

Figure 3. Generalized additive model predictions of (A) approximate age at maturity and (B) natural mortality rate. Solid curves represent predicted responses, dashed curves represent ± 2 standard errors, and open circles represent observations.

Which prior distribution—beta or normal—is more appropriate for describing steepness? The beta distribution fit the data better, based on AIC_c. However, in our bootstrap analysis, the outcome was ambiguous, as each distribution outperformed the other in about half of the bootstrapped data sets. A possible concern about the estimated normal distribution is its sizeable mass near $h = 1$, which could lead to frequent posterior estimates at the upper bound. Thus, the beta distribution might seem to be the better choice for most applications. Either way, a prior distribution informs the estimation process in that the best estimate occurs at the mode (although data may provide counter information), with strength of the prior depending on the shape of the distribution. The mode of the beta distribution was 0.84, and the mode of the normal distribution was 0.80.

The common conjecture that steepness decreases with longevity lacks empirical support. In fact, some studies have found the opposite: that stronger density dependence in recruitment occurs for longer-lived species (Denney et al. 2002, Goodwin et al. 2006). This phenomenon would presumably translate into higher steepness. Our study found no significant relationship between steepness and parameters describing age at maturity or natural mortality, two life-history characteristics linked closely to longevity (longevity–maturity: Winemiller and Rose 1992; longevity–mortality: Hewitt and Hoenig 2005). Although our analyses were intended to be exploratory and were by no means exhaustive, we obtained the same conclusion from linear regressions with and without a quadratic term. We also obtained the same conclusion using GAMs (Eq. 5) applied to only the Forrest et al. (2010) and SEDAR data, which were considered in part to exclude the clusters of apparently assumed M = 0.2 and $A_M = 3$ values found in the Rose et al. (2001) data set. These (negative) results may have occurred because no significant relationship exists, or because the data were not sufficiently precise to allow detection of a relationship. We cannot distinguish between the two, but simply note that we find no evidence in this data set to reject the null hypothesis that steepness is independent of age at maturity or natural mortality rate.

In the Rose et al. (2001) meta-analysis, periodic strategists were found to have a sample mean steepness of 0.70 and a median near 0.75. However, those values include steepness estimates from stocks that are freshwater, anadromous, or pelagic. When restricted to only marine demersal stocks, periodic strategists had higher sample mean and median values (0.77 and 0.80, respectively), similar to central tendencies of our study (mean, 0.75; median, 0.78). The similarity is not surprising given that Rose et al.'s data constitute the bulk of our analysis. Based only on Forrest et al. (2010) and SEDAR data, the sample mean (standard deviation) steepness is 0.69 (0.12) and the median is 0.72. Maximum likelihood (Eq. 2) estimates for the normal distribution were $\hat{\mu} = 0.69$ and $\hat{\sigma} = 0.12$ ($\text{AIC}_c = -22.3$); those for the beta distribution were $\hat{\alpha} = 10.13$ and $\hat{\beta} = 4.59$ ($\text{AIC}_c = -23.7$), resulting in a mode of 0.72.

Our emphasis was on steepness (h) of the Beverton-Holt spawner-recruit function because that model is the most common choice in stock assessments. In the dome-shaped Ricker function, the concept of steepness is less useful because recruitment at 20% of unfished spawning biomass (S_0) can exceed unfished recruitment (R_0), such that steepness is not bounded above (Dorn 2002). Nonetheless, our prior distribution of maximum lifetime reproductive rate [computed on log(a')] may be useful for the standard Ricker parameter a (the slope at the origin), if applied to the log of the product $a' = a\Phi_0$. In our view, the Beverton-Holt function should be the preferred default, unless there is strong evidence for mechanisms that lead to the Ricker function's dome shape.

In some assessments, steepness cannot be well estimated and must be fixed, for example, at the mode of its prior distribution. Fixing steepness determines, in part, MSY-based management quantities. This situation has been used to justify choosing a proxy for F_{MSY}, commonly $F_{X\%}$ (e.g., $F_{30\%}$ or $F_{40\%}$). However, such proxies do not provide biomass benchmarks. Furthermore, choice of X% implies an underlying value of steepness (Brooks et al. 2010), so that in effect, choosing a proxy equates to fixing steepness. It seems preferable to focus on steepness rather than proxies, because steepness is less arbitrary when based on a prior distribution from meta-analysis.

Prior distributions formalize auxiliary information. They can be particularly useful in stock assessments when other data sources provide only weak information for estimating parameters such as steepness. In application, prior distributions of steepness should incorporate information from species considered similar to the focal stock. As we learn more about productivity of reef fishes in the southeast United States, the subset of species used to generate a prior could be further refined. In any region, possible criteria are taxonomy, geographic location, habitat utilization, reproductive characteristics (e.g., gonochoristic or protogynous), or environmental conditions (e.g., prevailing high or low era of productivity). In the present study, the criteria for selecting species were intentionally general, so as to be as inclusive and broadly applicable as possible.

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