Steepness of spawner-recruit relationships in reef fishes of the southeastern U.S.: A prior distribution for possible use in stock assessment

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Introduction

In many assessments, steepness is a key parameter of the Beverton-Holt spawner-recruit model. Steepness controls the response of stock productivity to changes in spawning biomass, and as such, heavily influences estimates of management quantities such as MSY-based benchmarks. It is also notoriously difficult to estimate (Conn et al., unpublished manuscript).

One approach to improve estimation is to specify a prior distribution of steepness (Dorn, 2002; Myers et al., 2002), based on meta-analysis of similar species. This study attempts to compute such a prior distribution using information on steepness from several sources, including Myers et al (1999) and relevant SEDAR assessments.

Definition of steepness

Steepness (h) is conventionally defined as the proportion of unfished recruitment (R_0) produced by 20% of unfished spawning biomass (S_0). In the Beverton–Holt spawner-recruit formulation, recruitment (R) is computed from spawning biomass (S),

$$R = \frac{0.8R_0hS}{0.2\Phi_0R_0(1-h)+(h-0.2)S}$$

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

Data sources and treatment

Several data sources were compiled to examine steepness values for species similar to reef fishes in the southeastern United States. The primary source was Myers et al. (1999), who conducted a meta-analysis of many spawner-recruit time series. In Table 1 of Myers et al. (1999), steepness values were reported for species across many families. This current analysis extracted only those species that are marine demersal species (Table 1). Excluded were Scorpaeniformes, because of their low fecundities considered to be uncharacteristic of reef fishes in the southeastern U.S.

In addition to Myers et al. (1999), all previous SEDAR benchmark and update assessments were considered. This included all species from SEDAR 1 through SEDAR 17. For a previous SEDAR steepness value to be included in this analysis, it had to meet three criteria. First, the species had to be a reef-associated finfish. Second, the value had to be estimated (some assessments used values that were fixed). Third, the value must not have been influenced by a prior distribution based on the Myers et al. (1999) data or on the Rose et al. (2001) analysis of those same data. 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 previous SEDAR assessments to be included in the analysis (Table 2).

Distribution of steepness from meta-analysis

For possible use in stock assessment, prior distributions of steepness were estimated using normal and beta probability density functions. In the case of the normal distribution, maximum likelihood estimates of parameters μ and σ are equal to the sample mean and sample standard deviation. Values of steepness (Tables 1 and 2) had a mean of $\hat{\mu} = 0.72$ and standard deviation of $\hat{\sigma} = 0.17$. The median was 0.77.

Alternatively, a prior distribution of steepness could be based on the beta probability density function,

$$f(x \mid \alpha, \beta) = \frac{1}{B(\alpha, \beta)} x^{\alpha-1}(1-x)^{\beta-1}$$

where $0.0 \leq x \leq 1.0$, $\alpha > 0$, and $\beta > 0$. The constant B can be defined in terms of gamma functions, $B(\alpha, \beta) = \Gamma(\alpha)\Gamma(\beta)/\Gamma(\alpha+\beta)$, in which $\Gamma(z) = \int_0^\infty t^{z-1} e^{-t} dt$. In a beta distribution, the mean and variance are defined,

$$EX = \frac{\alpha}{\alpha+\beta} \quad \text{and} \quad VarX = \frac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)}.$$

When $\alpha > 1$ and $\beta > 1$, the distribution is unimodal, with mode equal to $(\alpha-1)/(\alpha+\beta-2)$. Using the sample mean ($\overline{X}$) and sample variance (V), maximum likelihood estimates of α and β can be computed as,

$$\hat{\alpha} = \overline{X}\left[\overline{X}(1-\overline{X})/V - 1\right] \qquad \text{and} \qquad \hat{\beta} = \hat{\alpha}\left[(1-\overline{X})/\overline{X}\right].$$

For the distribution of steepness, $\hat{\alpha} = 4.47$ and $\hat{\beta} = 1.75$, and the mode occurs at $h = 0.82$. The histogram of steepness values and the fitted normal and beta distributions are shown in Fig. 2.

The beta distribution is defined over the interval [0, 1], and the normal distribution is defined over $[-\infty, \infty]$. However, steepness is only defined over the interval [0.2, 1.0]. Thus, for use as a prior distribution, either the beta or normal distributions would require re-normalization to fall within the defined range of steepness. In the estimated beta distribution, 0.0025 of its probability mass is below $h = 0.2$. In the estimated normal distribution, 0.0010 is below $h = 0.2$, and 0.0464 is above $h = 1.0$. Although probability mass for h outside [0.2, 1.0] is small, any application should avoid the possibility of steepness falling outside its defined range, by truncating the estimated beta or normal distribution.

Distribution of maximum lifetime reproductive rate from meta-analysis

Some assessments define steepness in terms of maximum lifetime reproductive rate, $\hat{a} = a\Phi_0$, where a is the slope at the origin of the spawner-recruit curve. As described in Myers et al. (1999), the two quantities relate as,

$$h = \frac{\hat{a}}{4+\hat{a}} \qquad \text{or, equivalently,} \qquad \hat{a} = \frac{4h}{1-h}.$$

Here, log($\hat{a}$) has approximately a normal distribution (Shapiro−Wilk normality test: W=0.97, p-value=0.65), with mean 2.47, median 2.60, and standard deviation 0.91 (Fig. 3). As before, any application of this distribution may require truncation, when transformed back into steepness space.

Discussion

By using a prior distribution, estimation of steepness can be informed by estimates from related stocks. This can be particularly useful if other data sources in the assessment provide only weak information on steepness. As described here, such a prior could take form as a lognormal distribution of lifetime reproductive success, or more directly as a normal or beta distribution of steepness itself, as is used, for example, in Stock Synthesis (Methot, 2009). With any estimated distribution, truncation will be necessary to avoid steepness values outside its defined range of [0.2, 1.0].

Rose et al. (2001) conducted a similar meta-analysis of the Myers et al. (1999) data. In that analysis, species were categorized into one of three general life-history strategies: periodic, opportunistic, or equilibrium spawners. Of the three, reef fishes of the southeastern U.S. would likely be best characterized by the periodic strategy. Rose et al. (2001) found that periodic spawners had a mean steepness of 0.70, with a median near 0.75. Those values are quite similar to the mean (0.72) and median (0.77) steepness values in this analysis.

For choosing between the beta and normal distributions of steepness, one consideration might be the mode of each distribution, because using a prior distribution pushes the posterior estimate toward the mode of the prior. (The strength of that "push" depends on the shape of the distribution.) The mode of the beta distribution was 0.82, and the mode of the normal distribution was 0.72 (the mean). Although the beta distribution appeared to fit the data better than did the normal distribution, the mode of 0.82 might be considered high for some reef fishes, particularly those that are relatively long-lived and slow to mature.

Literature

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SEDAR1 Update
SEDAR2 Update
SEDAR10
SEDAR12
SEDAR15

Table 1. Estimates of steepness (h) from marine demersal species (excluding Scorpaeniformes) reported in Myers et al. (1999). N represents the number of stocks used to estimate the distribution of steepness for a given species, and h20, h50, and h80 represent the 20th, 50th, and 80th percentiles from that distribution.

Common name	Scientific name	N	h20	h50	h80
Gadiforms					
Gadidae		**49**	**0.67**	**0.79**	**0.87**
Blue whiting	*Micromesistius poutassou*	2		0.71	
Atlantic cod	*Gadus morhua*	21	0.76	0.84	0.9
Haddock	*Melanogrammus aeglefinus*	9	0.64	0.74	0.82
Hake	*Merluccius hubbsi*	1		0.82	
Pacific hake	*Merluccius productus*	1		0.32	
Pollock (saithe)	*Pollachius virens*	5	0.78	0.81	0.84
Silver hake	*Merluccius bilinearis*	3	0.31	0.39	0.47
Walleye Pollock	*Theragra chalcogramma*	2	0.53	0.55	0.58
Whiting	*Merlangius merlangus*	5	0.64	0.81	0.91
Lophiformes					
Lophidae		**1**		**0.64**	
Black angler fish	*Lophius budegassa*	1		0.63	
Perciformes					
Sparidae		**3**		**0.95**	
New Zealand snapper	*Pagrus auratus*	2		0.94	
Scup	*Stenotomus chrysops*	1		0.95	
Pleuronectiformes					
Pleuronectidae		**14**	**0.71**	**0.8**	**0.87**
European flounder	*Platichthys flesus*	1		0.57	
Greenland halibut	*Reinhardtius hippoglossoides*	3	0.59	0.79	0.91
Plaice	*Pleuronectes platessa*	8	0.83	0.86	0.88
Yellowtail flounder	*Pleuronectes ferrugineus*	2	0.69	0.75	0.81
Soleidae		**7**	**0.72**	**0.84**	**0.91**
Sole	*Solea vulgaris*	7	0.72	0.84	0.91

Table 2. Estimates of steepness (h) from previous SEDAR assessments of reef fishes that met the criteria (see text) for inclusion.

Common name	Scientific name	h	source	Location
Red porgy	*Pagrus pagrus*	0.50	SEDAR1 Update	Atlantic
Black sea bass	*Centropristis striata*	0.62	SEDAR2 Update	Atlantic
Gag grouper	*Mycteroperca microlepis*	0.79	SEDAR10	GOM
Red grouper	*Epinephelus morio*	0.84	SEDAR12	GOM
Gr. Amberjack	*Seriola dumerili*	0.74	SEDAR15	Atlantic

Figure 1. Hypothetical Beverton–Holt spawner-recruit curve for various levels of steepness.

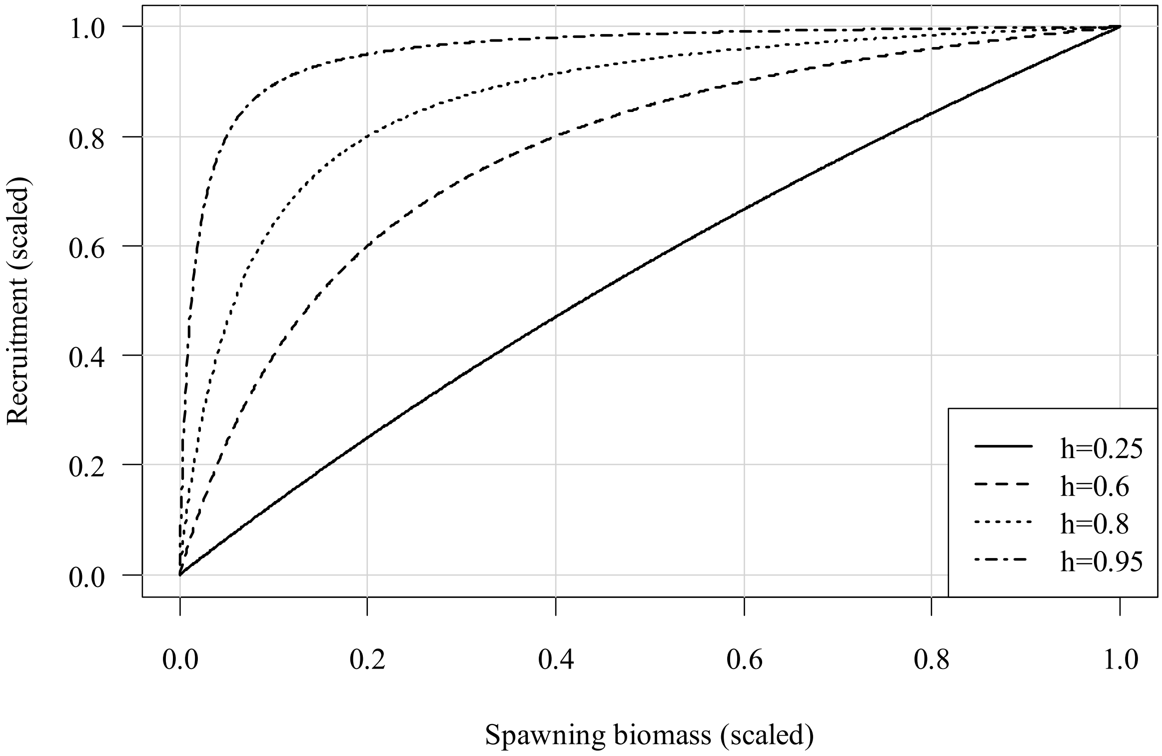

Figure 2. Histogram of steepness values in Tables 1 and 2, along with the beta distribution (solid line) and normal distribution (dashed line) fitted by maximum likelihood.

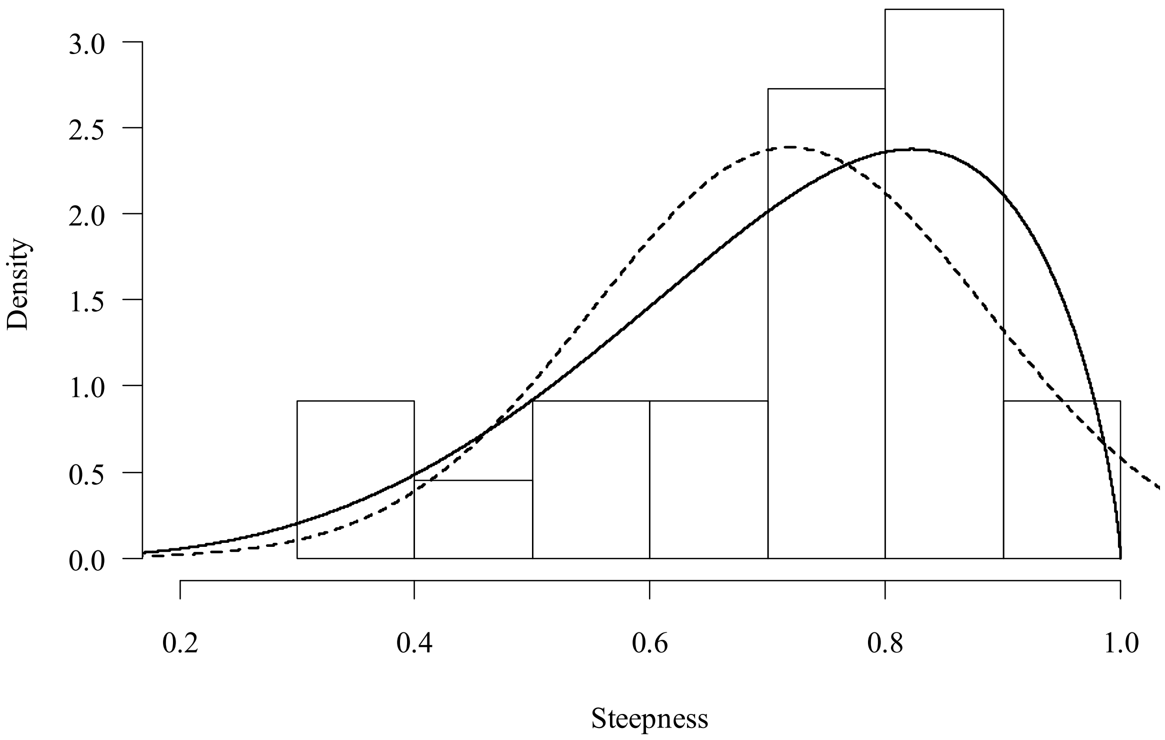

Figure 3. Histogram of log maximum lifetime reproductive rates [$\log(\hat{a})$], translated from steepness values in Tables 1 and 2. Overlaid is the normal distribution (solid line) with the same mean and variance as the data.