Spawner-recruit relationships of demersal marine fishes: Prior distribution of steepness for possible use in SEDAR stock assessments

SEDAR 24−AW−06

June, 2010

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Introduction

In many stock assessments, steepness is a key parameter of the spawner-recruit model. Steepness controls the response of stock productivity to changes in spawning biomass, and thus it heavily influences estimates of management quantities, such as MSY-based benchmarks and related proxies (Brooks et al., 2010). Steepness is also notoriously difficult to estimate (Conn et al., 2010).

One approach to improve estimation is to specify a prior distribution of steepness (Myers et al., 2002). Such distributions 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 et al, 2002; Forrest et al., In press). This study takes the meta-analytic approach to develop a prior distribution of steepness, intended for possible use in stock assessment of reef fishes in the southeast U.S. (Atlantic and Gulf of Mexico waters). It draws together information on steepness from several sources, including Rose et al. (2001), Forrest et al. (In press), and relevant SEDAR assessments.

Steepness

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

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

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).

Data sources

Several data sources were compiled to examine steepness values. 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 steepness as a function of life-history strategy, using three broad categories: equilibrium, opportunistic, and periodic strategists. Because reef fishes in the southeast are generally periodic strategies, this current analysis used only stocks of that strategy, narrowed further to those that are marine and demersal (Table 1).

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

In addition to Rose et al. (2001) and Forrest et al. (In press), previous SEDAR stock assessments were considered as possible sources of data. These comprised all completed benchmark assessments (SEDAR 1 through SEDAR 20) and associated update assessments. To be included here, three criteria had to be met. First, the species had to be a reef-associated finfish. 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 analiysis [i.e., 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 previous SEDAR assessments to be included in the analysis (Table 1).

Distribution of steepness from meta-analysis

Values of steepness from Rose et al. (2001) had a mean (standard deviation) of 0.77 (0.15); values from Forrest et al. (In press), 0.69 (0.12); and values from SEDAR, 0.70 (0.13). Combined across data sets (Fig. 2, Table 1), steepness had a mean of 0.75 (0.15) and median of 0.78. Standard error of the mean was 0.015.

For possible use in stock assessment, prior distributions of steepness were estimated using normal and beta probability density functions (PDFs). Parameter estimates were based on maximum likelihood. Log likelihoods (log *L*), used for parameter estimation and to compute corrected Akaike's Information Criteria ($\mathrm{AIC_c}$), were calculated from PDFs truncated over the range of steepness,

$$\log L = \sum_{i=1}^{n} \ln\left(\frac{f(x_i \mid \theta)}{\int_{0.2}^{1.0} f(x)dx} \right) \tag{2}$$

where x_i are the observed values of steepness (Table 1), f is the PDF (normal or beta), and θ is the parameter set of f.

Normal distribution
For the normal distribution, maximum likelihood estimates of parameters μ and σ are equal to the sample mean and sample standard deviation. The fitted normal distribution had parameter estimates $\hat{\mu} = 0.75$ and $\hat{\sigma} = 0.15$ ($\mathrm{AIC_c} = -97$; Fig. 3).

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

$$f(x \mid \alpha, \beta) = \frac{1}{B(\alpha, \beta)} x^{\alpha-1}(1-x)^{\beta-1} \tag{3}$$

where $0.0 \le x \le 1.0$, $\alpha > 0$, 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,

$$\mathrm{E}X = \frac{\alpha}{\alpha+\beta} \quad \text{and} \quad \mathrm{var}\, X = \frac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)}. \qquad (4, 5)$$

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

$$\hat{\alpha} = \bar{X}\left[\bar{X}(1-\bar{X})/V - 1\right] \quad \text{and} \quad \hat{\beta} = \hat{\alpha}\left[(1-\bar{X})/\bar{X}\right]. \qquad (6, 7)$$

Fitted to data on steepness, the beta distribution had parameter estimates $\hat{\alpha} = 5.50$ and $\hat{\beta} = 1.81$ ($AIC_c = -108$; Fig. 3). The mode occurs at $h = 0.85$.

Application of estimated distributions

For use in stock assessment, a prior distribution of steepness would likely be applied through either Monte Carlo techniques (MCMC or Monte Carlo/Bootstrap) or as a penalty term in a maximum likelihood approach. In some applications, the two approaches are integrated, in the sense that the assessment model does not recognize any difference between a prior and a penalty, providing maximum a posteriori probability (MAP) estimates. In any case, one should be aware that steepness has a narrower range [0.2, 1.0] than the beta range [0, 1] or normal range [−∞, ∞]. In the estimated beta distribution, 0.0006 of its probability mass is below $h = 0.2$. In the estimated normal distribution, 0.0001 is below $h = 0.2$, and 0.0490 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.

Two approaches to maintaining steepness within its bounds are truncation and transformation. The first requires truncating the estimated PDF so that probability mass on [0.2, 1.0] sums to one. The second approach, probably preferable, is to apply a suitable transformation for estimation and then back-transform to steepness space. For example, Mangel et al. (2010) used a beta distribution after transforming steepness onto [0, 1] with,

$$y = 1.25h - 0.25. \qquad (8)$$

After applying this transformation to the data here (Table 1), estimated parameters of the beta distribution are $\hat{\alpha} = 3.52$ and $\hat{\beta} = 1.58$, which could be used to generate beta random numbers ($\tilde{y}$) for back-transformation to steepness space,

$$h = (\tilde{y} + 0.25)/1.25. \qquad (9)$$

To apply the normal distribution, further transformation would be required to operate in the range [−∞, ∞]. This could be achieved with the logit transformation,

$$l = \log\left(\frac{y}{1-y}\right) = \log\left(\frac{h-0.2}{1-h}\right) \tag{10}$$

In logit space, the mean and standard deviation of the transformed data are $\hat{\mu} = 0.95$ and $\hat{\sigma} = 1.00$. However, in this case, the mean of the function exceeds the function of the mean (Jensen's inequality at work), and so back-transformation of $\hat{\mu} = 0.95$ would result in steepness greater than the observed mean of $\bar{h} = 0.75$. Thus it may be more appropriate to apply the logit transformation (eq. 10) to $\bar{h}$ itself. The variance of $\bar{h}$ in logit space could then be computed using the delta approximation,

$$\text{var}\left(l(\bar{h})\right) \approx \text{var}(\bar{h})\left(\frac{\partial l}{\partial \bar{h}}\right)^2 = \text{var}(\bar{h})\left(\frac{0.8}{(1-\bar{h})(\bar{h}-2)}\right)^2 \tag{11}$$

Here, $l(\bar{h}) = 0.803$ and $\text{var}\left(l(\bar{h})\right) = 0.008$.

When used in maximum likelihood, the prior distributions would typically be applied as a penalty term contributing to the overall objective function of a stock assessment model. This penalty increases as the estimate of steepness diverges from the prior distribution's mode (0.75 for normal, 0.85 for beta) at a rate that depends on the variance. Using the formulations of Stock Synthesis (equations in Methot, 2009), the penalty of the beta distribution can be recast to fall within the range of steepness, whereas that of the normal distribution is independent of the range (Fig. 4).

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,

$$h = \frac{\hat{a}}{4+\hat{a}} \qquad \text{or, equivalently,} \qquad \hat{a} = \frac{4h}{1-h}. \tag{12, 13}$$

Here, log($\hat{a}$) has approximately a normal distribution (Shapiro−Wilk normality test: W=0.99, p-value=0.77), with mean 2.68, median 2.68, and standard deviation 0.90 (Fig. 5).

Discussion

By using a prior distribution, estimation of steepness can be informed by auxiliary information, in this case, by estimates from similar stocks. This can be particularly useful if other data sources in the assessment provide only weak information on steepness. 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). In application, truncation or transformation may be necessary to avoid steepness values outside the defined range of [0.2, 1.0].

When 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 0.85, and the mode of the normal distribution was 0.75 (the mean). Although the beta distribution appeared to fit the data better than did the normal distribution (based on AIC_c), the mode of 0.85 might be considered high for some reef fishes, particularly those that are relatively long-lived and slow to mature.

In the Rose et al. (2001) meta-analysis, periodic strategists were found to have a 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, the mean and median of Rose et al.'s data are higher (0.77 and 0.80, respectively), and are quite similar to the central tendencies of this study (mean, 0.75; median, 0.78), which is not surprising given that those data constitute the bulk of this analysis. One could argue that the stocks most similar to reef fishes in the southeast U.S. are other reef fishes from the same region and Pacific rock fishes. Based only on Forrest et al. (In press) and SEDAR data, the mean (s.d.) steepness is 0.69 (0.12) and the median is 0.72.

A prior distribution should be based on species considered to be representative of the focal stock. As we learn more about productivity of reef fishes in the southeastern U.S., the subset of species used to generate a prior could be further refined. Possible criteria for refinement 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). For now, the criteria for selecting species (marine, demersal, periodic strategists) were intentionally general, so as to be as inclusive as possible.

Acknowledgements
Robyn Forrest provided data from the Forrest et al. (in press) study. Kenny Rose provided data from the Rose et al. (2001) study. Paul Spencer provided helpful comments.

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SEDAR1 Update
SEDAR2 Update
SEDAR10
SEDAR12
SEDAR15

Table 1. Estimates of steepness (h) of marine demersal stocks.

Common name	Latin name	Family	Order	Stock	h	Source
Black anglerfish	*Lophius budegassa*	Lophiidae	Lophiiformes	ICES VIIb-k and VIIIa,b	0.95	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	NAFO 2J3KL	0.74	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	NAFO 3NO	0.75	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	NAFO 3Pn4RS	0.84	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	NAFO 3Ps	0.67	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	NAFO 4TVn	0.91	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	NAFO 4VsW	0.74	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	NAFO 4X	0.96	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	NAFO 5Y	0.59	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	NAFO 5Z	0.89	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	Baltic Areas 22 and 24	0.81	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	Baltic Areas 25-32	0.80	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	Celtic Sea	0.85	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	Faroe Plateau	0.82	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	Iceland	0.95	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	Irish Sea	0.81	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	Kattegat	0.91	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	North East Arctic	0.90	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	North Sea	0.93	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	Skagerrak	0.95	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	ICES VIId	0.93	Rose et al. (2001)
Cod	*Gadus morhua*	Gadidae	Gadiformes	ICES VIa	0.87	Rose et al. (2001)
Flounder	*Platichthys flesus*	Pleuronectidae	Pleuronectiformes	Baltic Areas 24 and 25	0.80	Rose et al. (2001)
Greenland halibut	*Reinhardtius hippoglossoides*	Pleuronectidae	Pleuronectiformes	North East Arctic	0.91	Rose et al. (2001)
Greenland halibut	*Reinhardtius hippoglossoides*	Pleuronectidae	Pleuronectiformes	Northwest Atlantic	0.98	Rose et al. (2001)
Greenland halibut	*Reinhardtius hippoglossoides*	Pleuronectidae	Pleuronectiformes	ICES V and XIV	0.80	Rose et al. (2001)
Haddock	*Melanogrammus aeglefinus*	Gadidae	Gadiformes	NAFO 4TVW	0.41	Rose et al. (2001)
Haddock	*Melanogrammus aeglefinus*	Gadidae	Gadiformes	NAFO 4X	0.67	Rose et al. (2001)
Haddock	*Melanogrammus aeglefinus*	Gadidae	Gadiformes	NAFO 5Z	0.75	Rose et al. (2001)

Haddock	*Melanogrammus aeglefinus*	Gadidae	Gadiformes	Faroe Plateau	0.74	Rose et al. (2001)
Haddock	*Melanogrammus aeglefinus*	Gadidae	Gadiformes	Iceland	0.78	Rose et al. (2001)
Haddock	*Melanogrammus aeglefinus*	Gadidae	Gadiformes	North East Arctic	0.84	Rose et al. (2001)
Haddock	*Melanogrammus aeglefinus*	Gadidae	Gadiformes	North Sea	0.75	Rose et al. (2001)
Haddock	*Melanogrammus aeglefinus*	Gadidae	Gadiformes	Rockall Bank	0.73	Rose et al. (2001)
Haddock	*Melanogrammus aeglefinus*	Gadidae	Gadiformes	ICES VIa	0.80	Rose et al. (2001)
Hake	*Merluccius hubbsi*	Gadidae	Gadiformes	Southwest Atlantic Ocean	0.79	Rose et al. (2001)
New Zealand snapper	*Pagrus auratus*	Sparidae	Perciformes	New Zeeland, SNA 8	0.41	Rose et al. (2001)
New Zealand snapper	*Pagrus auratus*	Sparidae	Perciformes	Hauraki Gulf/Bay of Plenty	0.34	Rose et al. (2001)
Pacific hake	*Merluccius productus*	Gadidae	Gadiformes	W. US + Canada	0.62	Rose et al. (2001)
Plaice	*Pleuronectes platessa*	Pleuronectidae	Pleuronectiformes	ICES VIId	0.88	Rose et al. (2001)
Plaice	*Pleuronectes platessa*	Pleuronectidae	Pleuronectiformes	ICES VIIe	0.90	Rose et al. (2001)
Plaice	*Pleuronectes platessa*	Pleuronectidae	Pleuronectiformes	Celtic Sea	0.86	Rose et al. (2001)
Plaice	*Pleuronectes platessa*	Pleuronectidae	Pleuronectiformes	ICES IIIa	0.70	Rose et al. (2001)
Plaice	*Pleuronectes platessa*	Pleuronectidae	Pleuronectiformes	Irish Sea	0.86	Rose et al. (2001)
Plaice	*Pleuronectes platessa*	Pleuronectidae	Pleuronectiformes	Kattegat	0.84	Rose et al. (2001)
Plaice	*Pleuronectes platessa*	Pleuronectidae	Pleuronectiformes	North Sea	0.89	Rose et al. (2001)
Plaice	*Pleuronectes platessa*	Pleuronectidae	Pleuronectiformes	Skagerrak	0.88	Rose et al. (2001)
Pollock or saithe	*Pollachius virens*	Gadidae	Gadiformes	Faroe	0.87	Rose et al. (2001)
Pollock or saithe	*Pollachius virens*	Gadidae	Gadiformes	Iceland	0.80	Rose et al. (2001)
Pollock or saithe	*Pollachius virens*	Gadidae	Gadiformes	North East Arctic	0.78	Rose et al. (2001)
Pollock or saithe	*Pollachius virens*	Gadidae	Gadiformes	North Sea	0.32	Rose et al. (2001)
Pollock or saithe	*Pollachius virens*	Gadidae	Gadiformes	ICES VI	0.90	Rose et al. (2001)
Red snapper	*Lutjanus campechanus*	Lutjanidae	Perciformes	US Gulf of Mexico	0.59	Rose et al. (2001)
Scup	*Stenotomus chrysops*	Sparidae	Perciformes	Cape Cod - Cape Hatteras	0.57	Rose et al. (2001)
Silver hake	*Merluccius bilinearis*	Gadidae	Gadiformes	NAFO 4VWX	0.81	Rose et al. (2001)
Silver hake	*Merluccius bilinearis*	Gadidae	Gadiformes	NAFO 5Ze	0.87	Rose et al. (2001)
Silver hake	*Merluccius bilinearis*	Gadidae	Gadiformes	Mid Atlantic Bight	0.70	Rose et al. (2001)
Sole	*Solea vulgaris*	Soleidae	Pleuronectiformes	Celtic Sea	0.76	Rose et al. (2001)
Sole	*Solea vulgaris*	Soleidae	Pleuronectiformes	ICES IIIa	0.90	Rose et al. (2001)
Sole	*Solea vulgaris*	Soleidae	Pleuronectiformes	Irish Sea	0.79	Rose et al. (2001)
Sole	*Solea vulgaris*	Soleidae	Pleuronectiformes	North Sea	0.57	Rose et al. (2001)

Sole	*Solea vulgaris*	Soleidae	Pleuronectiformes	Bay of Biscay (VIII)	0.96	Rose et al. (2001)
Sole	*Solea vulgaris*	Soleidae	Pleuronectiformes	ICES VIId	0.79	Rose et al. (2001)
Sole	*Solea vulgaris*	Soleidae	Pleuronectiformes	ICES VIIe	0.79	Rose et al. (2001)
Whiting	*Merlangius merlangus*	Gadidae	Gadiformes	Celtic Sea	0.68	Rose et al. (2001)
Whiting	*Merlangius merlangus*	Gadidae	Gadiformes	Irish Sea	0.71	Rose et al. (2001)
Whiting	*Merlangius merlangus*	Gadidae	Gadiformes	North Sea	0.67	Rose et al. (2001)
Whiting	*Merlangius merlangus*	Gadidae	Gadiformes	ICES VIId	0.51	Rose et al. (2001)
Whiting	*Merlangius merlangus*	Gadidae	Gadiformes	ICES VIa	0.69	Rose et al. (2001)
Walleye pollock	*Theragra chalcogramma*	Gadidae	Gadiformes	E. Bering Sea	0.76	Rose et al. (2001)
Walleye pollock	*Theragra chalcogramma*	Gadidae	Gadiformes	Gulf of Alaska, Alaska	0.80	Rose et al. (2001)
Walleye pollock	*Pleuronectes ferrugineus*	Pleuronectidae	Pleuronectiformes	NAFO 5Z	0.94	Rose et al. (2001)
Walleye pollock	*Pleuronectes ferrugineus*	Pleuronectidae	Pleuronectiformes	Southern New England	0.56	Rose et al. (2001)
Black rockfish	*Sebastes melanops*	Sebastidae	Scorpaeniformes	WA, OR	0.72	Forrest et al. (In press)
Bocaccio	*Sebastes paucispinus*	Sebastidae	Scorpaeniformes	W. US	0.50	Forrest et al. (In press)
Canary rockfish	*Sebastes pinniger*	Sebastidae	Scorpaeniformes	W. US	0.76	Forrest et al. (In press)
Chilipepper rockfish	*Sebastes goodei*	Sebastidae	Scorpaeniformes	W. US	0.60	Forrest et al. (In press)
Dusky rockfish	*Sebastes variabilis*	Sebastidae	Scorpaeniformes	Gulf of Alaska	0.74	Forrest et al. (In press)
Northern rockfish	*Sebastes polyspinis*	Sebastidae	Scorpaeniformes	Bering Sea/Aleutian Is.	0.72	Forrest et al. (In press)
Northern rockfish	*Sebastes polyspinis*	Sebastidae	Scorpaeniformes	Gulf of Alaska	0.70	Forrest et al. (In press)
Pacific ocean perch	*Sebastes alutus*	Sebastidae	Scorpaeniformes	W. US	0.43	Forrest et al. (In press)
Pacific ocean perch	*Sebastes alutus*	Sebastidae	Scorpaeniformes	Goose Is. Gully	0.64	Forrest et al. (In press)
Pacific ocean perch	*Sebastes alutus*	Sebastidae	Scorpaeniformes	Gulf of Alaska	0.84	Forrest et al. (In press)
Pacific ocean perch	*Sebastes alutus*	Sebastidae	Scorpaeniformes	Bering Sea/Aleutian Is.	0.88	Forrest et al. (In press)
Rougheye rockfish	*Sebastes aleutianus*	Sebastidae	Scorpaeniformes	Gulf of Alaska	0.75	Forrest et al. (In press)
Widow rockfish	*Sebastes entomelas*	Sebastidae	Scorpaeniformes	W. US	0.60	Forrest et al. (In press)
Yellowtail rockfish	*Sebastes flavidus*	Sebastidae	Scorpaeniformes	W. US	0.72	Forrest et al. (In press)
Black sea bass	*Centropristis striata*	Serranidae	Perciformes	S. US Atlantic	0.62	SEDAR2 update
Gag	*Mycteroperca microlepis*	Serranidae	Perciformes	US Gulf of Mexico	0.79	SEDAR10
Greater amberjack	*Seriola dumerili*	Carangidae	Perciformes	US Atlantic	0.74	SEDAR15
Red grouper	*Epinephelus morio*	Serranidae	Perciformes	US Gulf of Mexico	0.84	SEDAR12
Red porgy	*Pagrus pagrus*	Sparidae	Perciformes	US Atlantic	0.50	SEDAR1 update

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

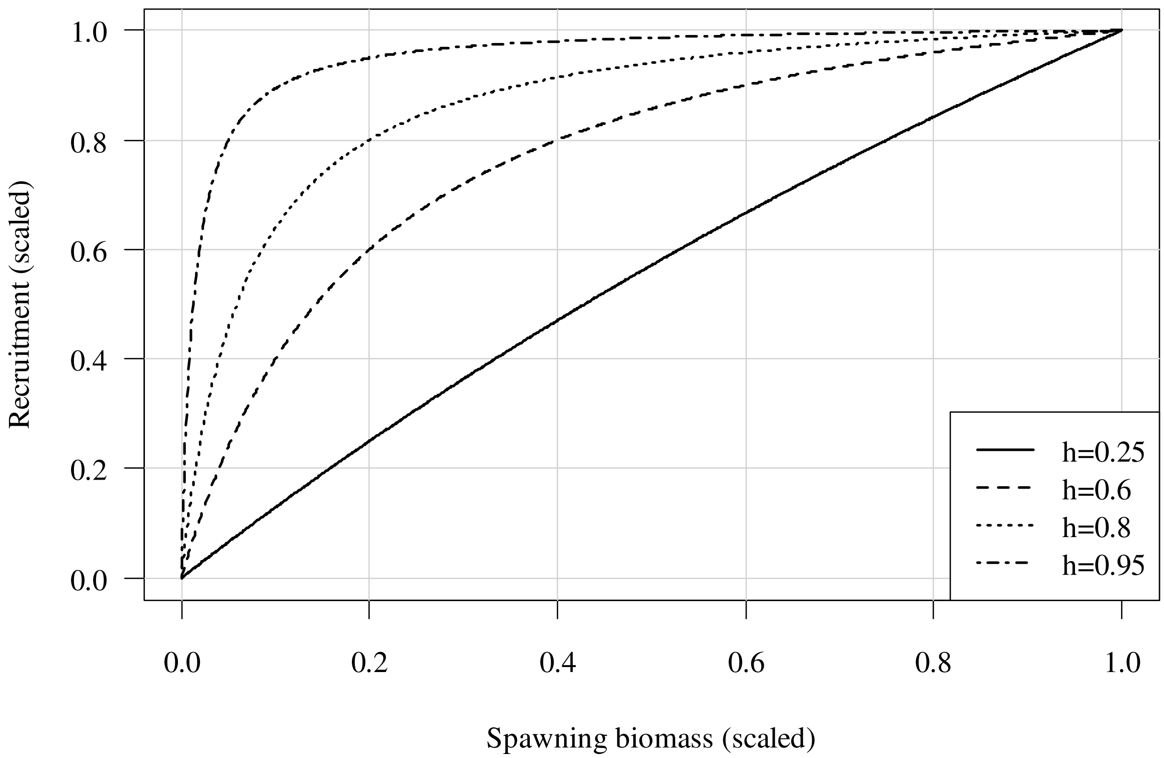

Figure 2. Violin plot of steepness values from Table 1. Gray area outlines a kernel density estimate of the distribution, and the solid black area shows the interquartile range with a white circle indicating the median.

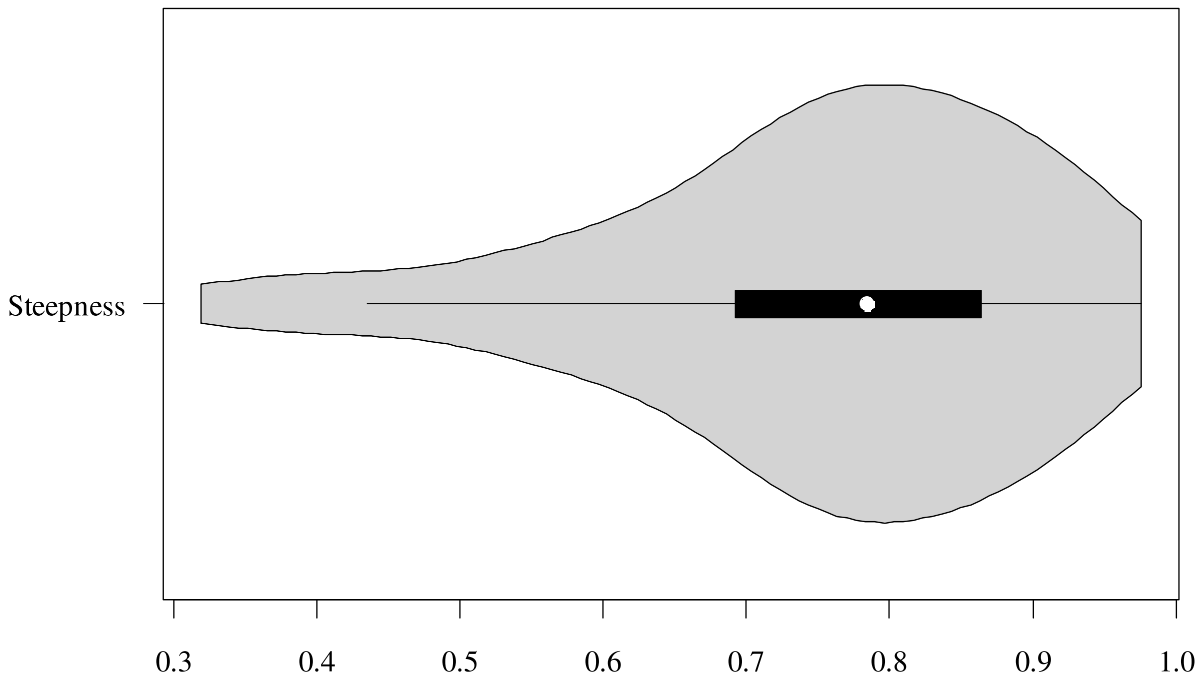

Figure 3. Histogram of steepness values from Tables 1, along with the beta distribution (solid line) and normal distribution (dashed line) fitted by maximum likelihood.

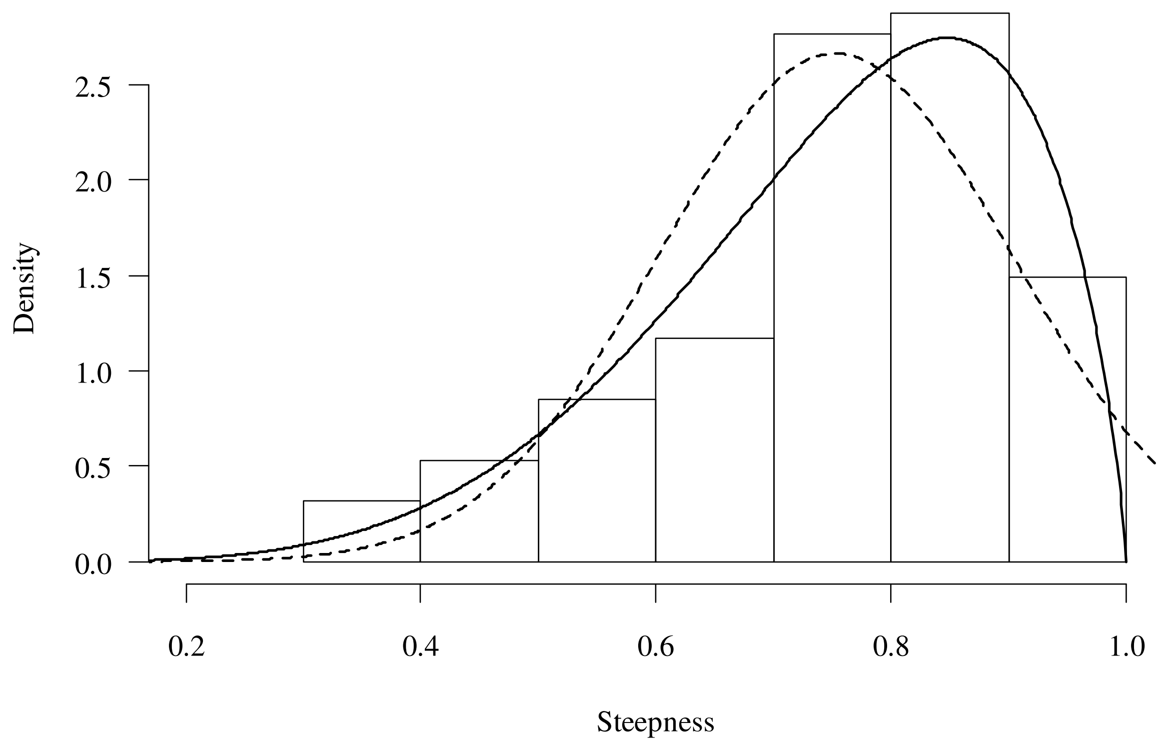

Figure 4. Likelihood contribution of the estimated normal prior distribution (dashed) and beta prior distribution (solid) of steepness. The contribution of the normal distribution is independent of the bounds of steepness [0.2, 1.0], whereas that of the beta distribution is reformulated to fall within those bounds.

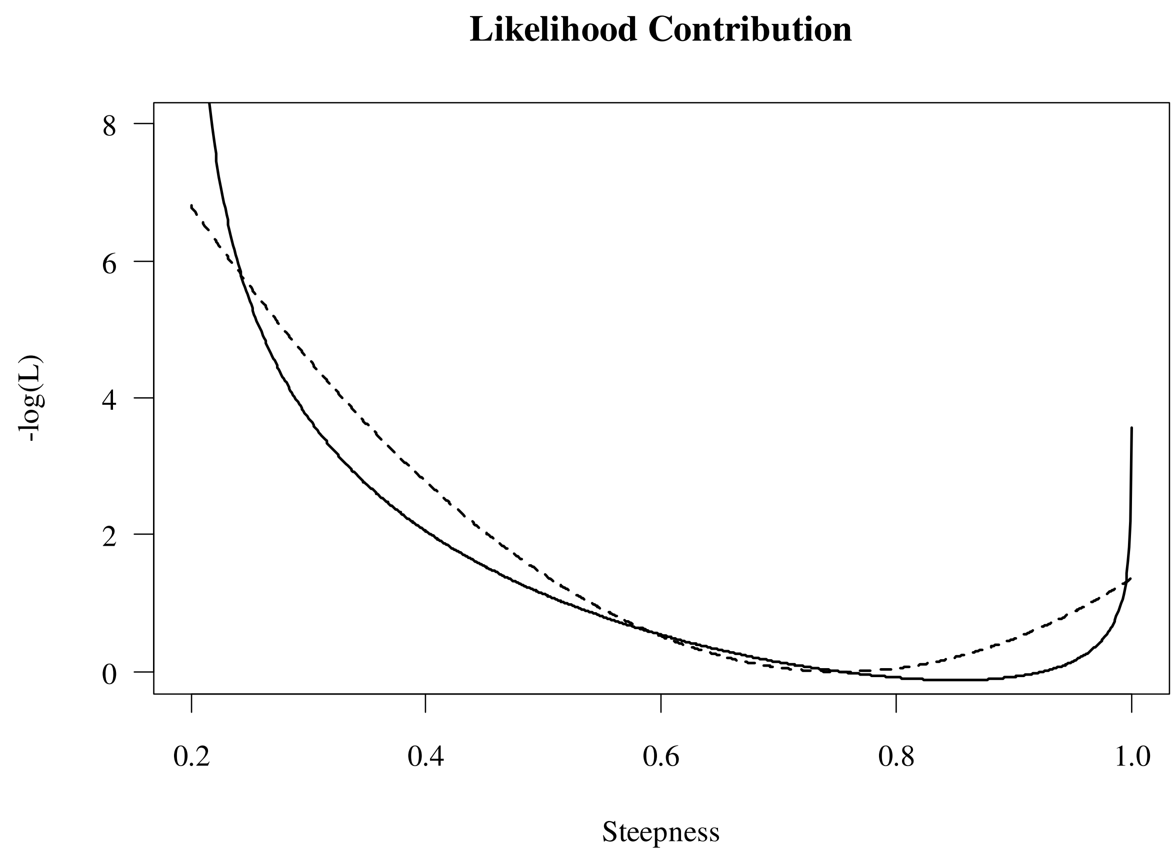

Figure 5. Histogram of log maximum lifetime reproductive rates [$\log(\hat{a})$], translated from steepness values in Tables 1. Overlaid is the normal distribution (solid line) with the same mean and variance as the data.