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CATCH-FREE STOCK ASSESSMENTS WITH APPLICATION TO GOLIATH GROUPER (*EPINEPHELUS ITAJARA*) OFF SOUTHERN FLORIDA

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SUMMARY

Many modern stock assessment methods provide the machinery for determining where the stock is in relation to certain reference points and how quickly it can be rebuilt. However, these methods typically require catch data, which are not always available. We introduce a model-based framework for estimating reference points, stock status and recovery times in situations where catch data are unavailable. The specific estimator developed is essentially an age-structured production model recast in terms relative to pre-exploitation levels. A Bayesian estimation scheme is adopted to allow the incorporation of pertinent auxiliary information such as might be obtained from meta-analyses of similar stocks or anecdotal observations. The approach is applied to the population of goliath grouper off southern Florida, for which there are three indices of relative abundance but no reliable catch data. The results confirm anecdotal accounts of a marked decline in abundance during the 1980's followed by a substantial increase after the harvest of goliath grouper was banned in 1990. The ban appears to have reduced fishing pressure to between 50% and 90% of the levels observed during the 1980's. Nevertheless, the predicted fishing mortality rate under the ban remains substantial, perhaps owing to illegal harvest and depth-related release mortality. As a result, the model predicts there is less than a 40% chance that the spawning biomass will recover to a level that would produce a 50% spawning potential ratio.

KEYWORDS

Stock assessment, Population dynamics, Fishing mortality

Introduction

The last decade has witnessed considerable interest in the so-called precautionary approach to resource management, where human activities are curtailed to prevent further environmental degradation without the burden of proving said activities are to blame. Fisheries applications of the precautionary approach typically hinge on the notion that fishing pressure should be reduced in a predetermined fashion as certain ‘limit’ reference points are approached (Caddy 1998, Restrepo et al. 1998). In the United States, for example, the Magnuson-Stevens Fishery Conservation and Management Act (Public Law 94-265) mandates the development of fishery management plans (FMPs) that specify criteria for defining when a stock should be considered overfished and the remedial measures necessary to ensure a timely recovery. The National Standard Guidelines developed by the National Marine Fisheries Service to implement the Act require each FMP to include an “MSY control rule” comprised of two limit reference points known as the maximum fishing mortality threshold (MFMT) and the minimum stock size threshold (MSST). When the abundance of the stock dips below the MSST, special provisions must be made to rebuild the stock to the level that would support the maximum sustainable yield within a time frame that is as short as possible commensurate with the intrinsic productivity of the stock and the needs of the fishing community.

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Many modern stock assessment methods provide the machinery for determining limit reference points as well as appraising where the stock is in relation to them and how quickly it can be rebuilt. However, these methods typically require catch data, which are not always available. In the case of goliath grouper, for example, a recent review panel concluded that the catch statistics were unreliable and not useful for assessment purposes (Anon.[2]). Several *ad hoc* control rules have been developed that try to accommodate such 'data-poor' situations. One approach that is sometimes taken when research surveys or other indices of abundance are available is to set the MSST equal to the survey values observed during an earlier portion of the time series when the stock was presumably close to pre-exploitation or MSY levels. The primary advantage of such an approach is that it is model-free, assuming nothing about the recovery rate of the stock. However, this is a disadvantage with respect to the requirements of the Magnuson-Stevens Act inasmuch as the method cannot be used to estimate recovery times. Moreover, there may be other types of information about the fishery that could influence the perception of the status of the stock and it would be useful to integrate that information formally into the assessment.

The purpose of this paper is to introduce a model-based framework for estimating reference points, stock status and recovery times in situations where catch data are unavailable. The specific estimator developed in this paper is essentially an age-structured production model recast in terms relative to pre-exploitation levels. A Bayesian estimation scheme is adopted to allow the incorporation of pertinent auxiliary information such as might be obtained from meta-analyses of similar stocks or anecdotal observations. The approach is applied to the population of goliath grouper off southern Florida, which is believed to have been severely depleted during the 1980's, but now appears to be rebounding.

Methods

Population dynamics model

The study period begins when the stock was believed to be near virgin levels such that the relative abundance *N* of each age class *a* at the beginning of the first year is given by

$$(1) \qquad N_{a,1} = \begin{cases} 1 & a = a_r \\ N_{a-1,1}e^{-M_{a-1}} & a_r < a < A \,. \\ N_{A-1,1}e^{-M_{A-1}} / (1 - e^{-M_A}) & a = A \end{cases}$$

where a_r is the youngest age class in the analysis, *A* is a 'plus-group' representing age classes *A* and older, and *M* is the natural mortality rate. The relative abundance at the beginning of subsequent years (*y*) is modeled by the recursion

$$(2) \qquad N_{a,y} = \begin{cases} r_y & a = a_r \\ N_{a-1,y-1}e^{-F_{y-1}v_{a-1} - M_{a-1}} & a_r < a < A \\ N_{A-1,y-1}e^{-F_{y-1}v_{a-1} - M_{a-1}} + N_{A,y-1}e^{-F_{y-1}v_A - M_A} & a = A \end{cases}$$

where r_y represents the annual recruitment to age class a_r relative to virgin levels, *F* represents the fishing mortality rate on the most vulnerable age class and v_a represents the relative vulnerability of the remaining age classes (which implicitly

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[2] Anon. 2003. Goliath grouper data workshop report. SEDAR3-DW-1. 11 pp. South Atlantic fishery Management Council, 1 Southpark Circle, Charleston SC 29406.

includes factors such as gear selectivity, size limit regulations, and the fraction of the stock exposed to the fishery).

Relative recruitment (*r*) is modeled as a first-order, lognormal autoregressive process,

(3)
$$\begin{aligned} r_y &= \mu_r e^{\varepsilon_y} \\ \varepsilon_y &= \rho_{r,y}\varepsilon_{y-1} + \eta_{r,y} \end{aligned} ,$$

where m_r is the median expectation, *r* is the correlation coefficient and *h* is a normal-distributed random variate having mean 0 and standard deviation s_r (ostensibly representing the effect on recruitment of fluctuations in the environment). The median level is modeled by the Ricker (1954) or Beverton and Holt (1957) spawner-recruit functions recast in terms of the maximum lifetime reproductive rate a and relative spawning biomass *s*:

(4)
$$\mu_r = \begin{cases} s_{y-a_r}\,\alpha^{1-s_{y-a_r}} & \text{Ricker} \\ \dfrac{\alpha s_{y-a_r}}{1+(\alpha-1)s_{y-a_r}} & \text{Beverton and Holt} \end{cases}$$

$$s_y = \sum_{a=a_r}^{A} E_a e^{-(F_y v_a + M_a)t_s} N_{a,y} \Bigg/ \sum_{a=a_r}^{A} E_a\, e^{-M_a t_s} N_{a,1}$$

where *E* is an index of the per-capita number of eggs produced by each age class (*E*) and t_s is the fraction of the year elapsed at the time of spawning. The shapes of these two curves are essentially the same as the conventional relationships (Figure 1), however their domain is implicitly limited to the interval $0 \leq s \leq 1$ (see Appendix 1 for a derivation).

The fishing mortality rate on the most vulnerable age class *F* is also modeled as a first-order, lognormal autoregressive process,

(5)
$$\begin{aligned} F_y &= \mu_F e^{\delta_y} \\ \delta_y &= \rho_F \delta_{y-1} + \eta_{F,y} \end{aligned} ,$$

where m_F is the median level, r_F is the correlation coefficient and h_F is a normal-distributed random variate having mean 0 and standard deviation s_F. The median is generally assumed to be proportional to an index of fishing effort *f*:

(6) $$F_y = \phi f_y$$

where *f* can vary among three eras of exploitation: a ‘prehistoric’ period, during which little data are available; a ‘modern’ period, when presumably there are some data on abundance or mortality rates; and a ‘future’ period, when fishing mortality rates are controlled (input). The absence of data during the ‘prehistoric era’ generally precludes the estimation of annual deviations in recruitment (e) or fishing mortality rate (d) during that period.

The average weight or fecundity of the plus group is expressed as a function of the average age of the plus-group. Initially, it is assumed that the age composition of the plus-group is in equilibrium consistent with equation (1), in which case the average age of the plus-group at the beginning of the first year is approximately

(7) $$\bar{a}_{A,1} = A + \frac{e^{-M_A}}{1 - e^{-M_A}}$$

Subsequently, the age of the plus-group is updated as

(8) $$\bar{a}_{A,y+1} = \frac{A N_{A-1,y} e^{-F_y v_{A-1} - M_{A-1}} + \left(\bar{a}_{A,y} + 1\right) N_{A,y} e^{-F_y v_A - M_A}}{N_{A,y+1}}$$

Reference points

Equations 1-4 describe the relative dynamics of a population apart from its absolute abundance. As such they are suitable for developing management plans where the fishing mortality rate is controlled directly (e.g., by reducing effort) and the biomass reference points are expressed on a relative scale. When the virgin spawning biomass itself is used as the reference point, the estimated value of s_y is a direct measure of the status of the stock. For example, if the management goal is to maintain spawning biomass at or above 50% of the virgin level, then estimates of s below 0.5 might trigger some action to reduce fishing pressure.

A related reference point is the equilibrium spawning potential ratio (Goodyear, 1993), defined as the expected lifetime fecundity per recruit at a given F (f_F) divided by the expected lifetime fecundity in the absence of fishing (f_0):

(9) $$p = \frac{\phi_F}{\phi_0}$$

$$\phi_F = \sum_{a=0}^{A} E_a e^{-(F_a + M_a) t_s} e^{-\sum_{i=0}^{a-1} F v_i + M_i}$$

As shown in Appendix 2, the corresponding equilibrium level of relative spawning biomass (denoted by a tilde) may be computed as

(10) $$\tilde{s}_p = \begin{cases} 1 + \dfrac{\log_e p}{\log_e \alpha} & \text{Ricker} \\ \dfrac{\alpha p - 1}{\alpha - 1} & \text{Beverton and Holt} \end{cases} .$$

Note that $\tilde{s}_p$ is independent of the vulnerability vector v. Accordingly, MSST definitions based on $\tilde{s}_p$ will have the desirable property of being insensitive to changes in the behavior of the fishery.

Other management plans employ reference points such as F_{max} or $F_{0.1}$, which are based on the yield per recruit statistic

(9) $$\left(\frac{Y}{R}\right) = \sum_{a=0}^{A} w_a F v_a \frac{1 - e^{-(F v_a + M_a)}}{F v_a + M_a} e^{-\sum_{i=0}^{a-1} F v_i + M_i},$$

where w_a is some measure related to the average weight of the catch. Inasmuch as there are no terms involving the absolute abundance of the stock, the calculation of such statistics poses no special problems for the relative framework presented here. Prescriptions based on the maximum sustainable yield (*MSY*) are slightly more complicated because equilibrium yield is the product of equilibrium recruitment $\tilde{R}$ and equilibrium yield per recruit:

(10) $$\tilde{Y} = \tilde{R}_F \sum_{a=0}^{A} w_a F v_a \frac{1 - e^{-(Fv_a + M_a)}}{Fv_a + M_a} e^{-\sum_{i=0}^{a-1} Fv_i + M_i} ,$$

However, the fishing mortality rate that maximizes (8) also maximizes (8) divided by the virgin recruitment R_0 (a constant). Thus, F_{MSY} may be obtained from

(11) $$\max_F \left\{ \frac{F\tilde{s}_p}{p} \sum_{a=0}^{A} w_a v_a \frac{1 - e^{-(Fv_a + M_a)}}{Fv_a + M_a} e^{-\sum_{i=0}^{a-1} Fv_i + M_i} \right\} .$$

where $\tilde{s}_p / p$ has been substituted for $\tilde{R} / R_0$.

The values of p and $\tilde{s}_p$ corresponding to F_{max} , $F_{0.1}$ or F_{msy} may be calculated via equations (9) and (10), respectively. Note however, that p is no longer the target value specified by management, but a derivative of the targeted values of F. This means that MSST definitions based on s_{max} , $s_{0.1}$ and s_{msy} will vary somewhat with the behavior of the fishery. In some cases this could lead to risk prone situations where the perception of stock status changes simply because the fishery targets different age groups (i.e., the definition of MSST changes rather than the abundance of the resource). In the case of MSY, a more stable alternative is to define the MSST in terms of a ‘spawn at least once’ policy where mature animals are regarded as fully available and immature animals regarded as unavailable.

Parameter estimation

The equations above include numerous ‘unknowns’ representing the processes of reproduction, mortality and growth. In the case of “data-poor” stocks like goliath grouper, there are insufficient data to estimate all of these unknown parameters with an acceptable level of precision. However, it is often possible to increase the precision of the estimates through the use of Bayesian prior probability densities constructed to reflect expert opinion (e.g., Wolfson et al. 1996) or the results from meta-analyses involving similar species (e.g., Liermann and Hilborn 1997).

The Bayesian approach to estimation seeks to develop a ‘posterior’ probability density for the parameters **Q** that is conditioned on the data D, P(**Q** | D). By application of Bayes rule it is easy to show that

(12) $$\mathrm{P}(\Theta \mid \mathrm{D}) \propto \mathrm{P}(\mathrm{D} \mid \Theta)\, \mathrm{P}(\Theta) .$$

where P(D | **Q**) is the sampling density (likelihood function) and P(**Q**) is the prior density (in this case the analyst’s best guess of the probability density for **Q**). Estimates for **Q** may be obtained by integrating the posterior (the classical Bayes moment estimator)

(13) $$\bar{\theta}_i = \int \theta_i\, \mathrm{P}(\mathrm{D} \mid \Theta)\, \mathrm{P}(\Theta)\, d\theta_i \quad , \qquad \theta_i \in \Theta .$$

or by minimizing its negative logarithm (the highest posterior density estimator)

(14) $$\min_{\Theta} \left\{ -\log_e \mathrm{P}(\mathrm{D} \mid \Theta) - \log_e \mathrm{P}(\Theta) \right\} .$$

In the present model, a prior needs to be specified for the parameters reflecting recruitment (a and e_y), mortality (M,

F_y v_a), fecundity (E_a) and growth in weight (w_a). It is here assumed that the parameters are statistically independent with respect to prior knowledge such that the joint prior is merely the product of the marginal priors for each parameter. The exceptions are the process error functions for the annual recruitment and fishing mortality rate deviations, e_y and d_y. These are assumed to be autocorrelated lognormal variates with negative log density functions of the form

$$\text{(15)} \qquad -\log \mathrm{P}(\varepsilon) = \frac{1}{2\sigma_r^2}\left[\varepsilon_1^2 + \sum_y (\varepsilon_{y+1} - \rho_r\,\varepsilon_y)^2\right] + \log \sigma_r$$

where w is the last year in the simulation, r_r is the correlation coefficient and σ_r^2 is the variance of $\log_e h_r$. For stability reasons, it is assumed that $e_0 = 0$.

It is possible, at least in principle, to conduct an assessment based on prior specifications alone. However, it may be difficult to develop sufficiently informative priors for some of the parameters, particularly the fishing mortality rates. The preferred approach, of course, is to condition the estimates on data. Use of the present model presumes catch data are either unavailable or unreliable, otherwise a standard age-structured production model would be more appropriate. However, time series of catch per unit effort data or fishery independent surveys are often available even when total catches are not. To the extent that changes in these data (c) are proportional to changes in the abundance of the population as a whole (N), they may be modeled as:

$$\text{(16)} \qquad \begin{aligned} c_{i,y} &= q_i \sum_a v_{i,a} N_{a,y} e^{-\left(F_y v_a + M_a\right)t_i} e^{\gamma_{i,y}} \\ \gamma_{i,y} &\sim Normal(0, \sigma_{c,i}) \end{aligned}$$

where i indexes the particular survey time series, q is the proportionality coefficient scaling the time series to the relative abundance of the population, t_i is the fraction of the year elapsed at the time of the survey, $s_{c,i}$ is the standard deviation of the fluctuations in $\log_e c_i$ owing to observation errors or changes in the distribution of the stock, and v_a and $v_{i,a}$ are the relative vulnerability of each age class to the fishery and the i'th survey, respectively. The corresponding negative logarithm of the sampling density is

$$\text{(17)} \quad -\log \mathrm{P}(\boldsymbol{c}|\Theta) = \sum_i \sum_y \left\{ \frac{1}{2\sigma_{c,i}^2} \left(\log_e(c_{i,y}) - \log_e\left(q_i \sum_a v_{i,a} N_{a,y} e^{-(F_y v_a + M_a)t_i}\right)\right)^2 + \log \sigma_{c,i} \right\}$$

Anecdotal observations may be treated in similar fashion. For example the perceptions of constituents on the abundance of the resource relative to virgin levels (n) can be modeled as

$$\text{(18)} \qquad n_y = \frac{\sum_a \lambda_a N_{a,y} e^{-\left(F_y v_{i,a} + M_a\right)\delta}}{\sum_a \lambda_a e^{-M_a \delta} e^{-\sum_{i=0}^{a-1} M_i}} e^{\gamma_{n,y}}$$

$$\gamma_{n,y} \sim Normal(0, \sigma_n)$$

Here $l_{,a}$ is the relative contribution of each age class in forming the perception of total abundance (e.g., fishermen may never encounter very young fish), d is the time of the year most reflective of the period upon which the perceptions were based (e.g., the peak of the fishing season), and s_n is the standard deviation of the fluctuations in $\log_e n_y$.

It is not generally possible to obtain consistent estimates for all of the elements of the covariance matrix **V** (i.e., $\rho_F, \sigma_F^2, \rho_r, \sigma_r^2, \sigma_{c,i}^2$ and σ_n^2). In the case of survey data, the variances associated with sampling variability are often estimated extraneous to the population model (e.g., during the standardization procedure). However, there may be additional variance owing to fluctuations in the distribution of the stock relative to the survey area (IWC 1994). To accommodate such possibilities, the survey variance parameters are modeled as

$$\sigma_{c,i,y}^2 = \chi_{c,i,y}^2 + \psi_{c,i}\sigma^2 \qquad (19)$$

$$\sigma_{n,y}^2 = \chi_{n,y}^2 + \psi_n\sigma^2$$

where the $\chi_{c,i,y}^2$ and $\chi_{n,y}^2$ are the annual observation variances (estimated outside the model), s^2 reflects some overall process variance (estimated within the model), and the y are constant multipliers (usually fixed by the analyst based on a careful consideration of the inherent variability of the underlying processes). The recruitment variance and correlation coefficient are generally inestimable without a good index of recruitment and may have to be fixed to some moderate values (say $\sigma_r = 0.4$ and $\rho = 0.5$).

The model outlined above was implemented using the nonlinear optimization package AD Model Builder (Otter Research Ltd.[3]), which provides facilities for estimating the mode and shape of the posterior distribution. Confidence intervals for the probability of recovery were generated directly from the posteriors approximated by the likelihood profile method (the accuracy of which was checked by replicating the prior distributions without data and by comparing the modes of the posterior with the HPD estimates). For some quantities confidence limits were computed using normal approximations centered at the HPD estimate with variances obtained by inverting the Hessian matrix. This approach reduced computing time considerably, but the approximations were poor for confidence intervals broader than 80 percent owing to the thick tails and skewed nature of the posterior distributions.

Application to goliath grouper

Goliath grouper are large, long-lived predators found in the tropical western Atlantic and Caribbean Sea. They are among the least wary of reef fishes, easily approached by spearfishers and readily caught in traps or by hook and line gear. Not surprisingly, they have declined considerably throughout much of their range (Sadovy and Eklund 1999). While there are few data on the historic abundance of these animals in southern Florida, anecdotal reports (Figure 2) suggest that they were much more abundant during the 1950's and 60's than they are now. Concerns of overfishing prompted regulators in the U.S. to impose a moratorium on the harvest of goliath grouper that has remained in effect since 1990. To date, the duration of the moratorium has not been specified owing to paucity of information on their potential recovery rates.

Spawner-recruit relationship

There does not appear to be any reliable information on the nature of the spawner-recruit relationship for any grouper species. A Beverton and Holt model is assumed here because it is difficult to envision a mechanism for the strong density dependence in mortality rates required by the Ricker model. A prior for the value of *a* (Figure 3) was constructed from a subset of the values collected by Myers et al (1999) that corresponds to larger, highly fecund fishes with long life spans (the ‘periodic’ strategists of Rose et al. 2001).

Fecundity and growth

To date there are insufficient data for estimating a fecundity-at-age relationship for goliath grouper. We follow

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[3] Otter Research Ltd. 2001. An introduction to AD MODEL BUILDER Version 4.5. Box 2040, Sidney B.C. V8L 3S3, Canada. 141 p.

Legault and Eklund[4] and substitute the weight at age relationship:

(20)
$$E_a = \begin{cases} 0 & a < 6 \\ w_a = 1.31 \times 10^{-5} l^{3.056} & a \geq 6 \end{cases},$$

$$l = 200.6(1 - e^{-0.126(a+0.49)})$$

where w is weight in kg and l is length in cm expressed as a von Bertalanffy function of age (see Bullock et al., 1992).

Natural mortality

The maximum observed age of 37 years (Sadovy and Eklund 1999) suggests a value for M of about 0.11 yr^{-1} according to the method of Hoenig (1984). Legault and Eklund suggested a plausible range of 0.037 yr^{-1} to 0.19 yr^{-1} (midpoint 0.11) based on an analysis of the fraction surviving to various maximum ages. To reflect this uncertainty, a lognormal prior with a median of 0.11 and CV of 0.4 was used (Figure 4a).

Fishing mortality rate and relative vulnerability

A large fraction of the recreational landings of goliath grouper appear to have been from the Ten Thousand Islands area, where most of the animals caught have been between the ages of one and five. However, large animals were often targeted by commercial and recreational fishers in other areas. Accordingly, we assume the vulnerability of goliath grouper generally increased with age according to the sigmoid-shaped logistic curve:

(21)
$$v_a = \frac{1}{1 + e^{-(a - a_{50})/d}}$$

Estimates for the parameters a_{50} and d were obtained by fitting the curve (weighted by cumulative mortality at age) to the relative frequency of ages in two different data sets. The first data set included mostly juveniles animals between the ages of 0 and 5 obtained during creel censuses of recreational catches in the Ten Thousand Islands area of the Everglades National Park (see Porch et al., 2003[5]). The second data set included mostly adult animals obtained opportunistically from recreational and commercial catches in the eastern Gulf of Mexico (Bullock et al. 1992). The resulting curves are contrasted in Figure 5.

The fishing mortality rate on the most vulnerable age class was modeled as follows

(22)
$$F_y = \begin{cases} \phi_1 f_y & 1900 \leq y \leq 1979 \\ \delta_y \phi_2 F_{1979} & 1980 \leq y < 1990 \\ \phi_3 \bar{F}_{1980-89} & 1990 \leq y \end{cases}$$

where f_y is a time series of historical effort and f_1, f_2, f_3, d_y are parameters to be estimated. Here, effort is assumed to

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[4] Legault, C.M. and Eklund, A.-M. 1998. Generation times for Nassau grouper and jewfish with comments on M/K ratios. Sustainable Fisheries Division Contribution SFD-97/98-10A. Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149.

[5] Porch, C. E., A-M. Eklund and G. P. Scott. 2003. An assessment of rebuilding times for goliath grouper. Sustainable Fisheries Division Contribution SFD-2003-0018. Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149.

track the U.S. Census[6] of the number of people living in South Florida coastal counties between 1900 and 1980. From 1980 to 1989 this assumption is no longer required owing to the availability of several time series of relative abundance (see below). Instead, inter-annual variations in fishing mortality modeled according to equation (5) with median $f_2 F_{1979}$, log-scale variance σ_F^2 = 0.15 and correlation coefficient r_F = 0.5, which essentially amounts to a mild constraint on year to year changes in F. Finally, the effect of the harvest moratorium is modeled as a percentage f_3 of the average fishing mortality rate in the 1980-89 era. Relatively uninformative priors were used for f_1 and f_2 (Fig. 4b,c). A somewhat more informative prior with bounds between 0.01 and 0.5 was used for f_2, based on the opinions of members of the SEDAR panel (Figure 4d).

Survey information

Porch and Eklund (in review) have developed relative indices of abundance from two visual surveys: the personal observations of a professional spearfisher (DeMaria[7]) and a volunteer fish-monitoring program administered by the Reef Education and Environmental Foundation (REEF 2000). In addition, Cass-Calay and Schmidt (in review) have standardized catch rate data collected in the Ten Thousand Islands area by the Everglades National Park (ENP). The two visual surveys are assumed to reflect the abundance of mature fish ages 6 and older (based on diver reports of size). The ENP catch rate index, on the other hand, is assumed to reflect the relative abundance of juveniles with relative vulnerabilities given by the dome-shaped gamma function (normalized to a maximum of 1):

$$v_{ENP,a} = \left(\frac{a}{a_{100\%}} e^{1 - a/a_{100\%}} \right)^{cv^{-2} - 1} \tag{23}$$

where $a_{100\%}$ is the most vulnerable age and CV is the coefficient of variation. Estimates for $a_{100\%}$ (3.47) and CV (0.34) were obtained by fitting the mortality-weighted gamma curve to the frequency of ages 0 -7 in the Ten Thousand Islands data mentioned earlier (see Porch et al., 2003[4]).

Anecdotal impressions of stock status

Johannes et al. (2000) point out that local fishers often disagree with the conclusions drawn by scientists in data-poor situations and suggest that many times additional data will prove the fishers correct. As mentioned earlier, expert judgements about the relative abundance of a stock can be treated as data and represented by a ‘prior’ (e.g., Punt and Walker, 1998). We developed a lognormal prior for the value of s at the time moratoriums began (1990) by interviewing fishers and divers who had been active in southern Florida during the 1960's or earlier. Specifically, interviewees were asked to state their perception of the percent reduction in goliath grouper populations from the time they began diving to the time the moratorium on catch was imposed (1990). The average percent reduction reported for large goliath (approximately age 6 and older) was 86% with a standard deviation of about 13% (Figure 2).

Results

The model was able to fit the ENP index for juvenile animals very well, but could not reconcile the recent trends for adults indicated by the DeMaria and REEF indices (Figure 6). The estimated trends in spawning biomass are rather uncertain (Figure 7a), but nevertheless indicate a rapid decline to about 5% of virgin levels by the time the harvest ban was imposed in 1990, followed by a significant increase. The estimates of fishing mortality are also somewhat uncertain, but generally indicate a gradual increase in fishing mortality to moderate levels during the 1970's followed by a rapid increase during the 1980's (Figure 7b). The harvest moratorium is estimated to have been about 83%

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[6] Population of Counties by Decennial Census: 1900 to 1990. Compiled and edited by Richard L. Forstall. Population Division, US Bureau of the Census. Washington, DC 20233

[7] DeMaria, Don. P.O. Box 420975, Summerland Key, FL 33042.

effective in reducing fishing mortality, nevertheless losses owing to human activities (e.g., illegal harvest and release mortality of animals caught at depth) are still estimated to be substantial (F = 0.05 yr^{-1}). If, in accordance with the Gulf of Mexico Management Council's generic Sustainable Fisheries Act amendment, the limit reference point is taken to be the equilibrium spawning biomass corresponding to a spawning potential ratio of 50%, then the model suggests that current fishing mortality rates are near $F_{50\%}$ and that there is less than a 50% chance the stock will recover within 15 years (Figure 8).

Sensitivity runs were conducted to examine the implications of (1) dropping one or more of the indices, (2) increasing the assumed minimum age represented in the REEF and DeMaria indices from 6 to 10, (3) assuming the historical period began in 1950 rather than 1900 while using the anecdotal information as a tuning index and (4) assuming an alternate fishery selection curve where adult animals were much more vulnerable to the fishery than juveniles. Of these, the results were most sensitive to removing the DeMaria index; the projected trends being much more optimistic (Figure 9). This is because the DeMaria index suggests the adult population increased rapidly during the first few years of the harvest ban, but then suffered a set back in 1999 and has since leveled off. In contrast, the REEF index suggests the population continued to increase during that time. Thus, when the DeMaria index is removed, the model allows for a faster post-moratorium increase in the adult population by estimating a low fishing mortality rate of about 0.01 yr^{-1} (i.e., a harvest ban that is 97% effective). The fishing mortality rate estimates for the 1980's are also lower without the DeMaria index inasmuch as the DeMaria index indicates a more precipitous decline during that time than the ENP index (the REEF index does not begin until 1994).

The sensitivity run with the alternate selection curve also produced more optimistic results (Figure 9). Inasmuch as the model now attributes most of the fishing mortality to age classes well beyond the age at first maturity (see Figure 5), the spawning stock biomass is estimated to have been reduced to a lesser extent than the base model (to about 10% of virgin levels by 1990 as compared to 5%). Thus, other things being equal, recovery requires less time. The level of F50% increased with the alternate selection curve because fewer age classes are affected by fishing.

Discussion

All of the model formulations examined depicted the same qualitative patterns: escalating fishing mortality rates and rapidly declining spawning biomass, particularly during the 1980's, followed by a sharp decrease in fishing mortality and strong recovery in spawning biomass after the 1990 harvest ban. These trends are remarkably consistent with the anecdotal observations summarized in Figures 2 and 6 as well as the expert testimony given during the SEDAR stock assessment review. The estimated rapid increase in fishing mortality during the 1980's appears to reflect a real increase in effort that occurred due to elevated demand and selling prices (Sadovy and Eklund, 1999) as well as the widespread use of the LORAN-C navigational system (which made it easier for fishers to relocate productive offshore shipwrecks). Thus, it seems safe to conclude that the population was overfished at the time the harvest ban was imposed and is currently undergoing a substantial recovery. Less clear is the extent to which the population has recovered sice the harvest ban.

The base model estimated that the harvest ban has reduced fishing pressure by more than 50%, but probably less than 90% (Figure 10). Thus, there is a strong chance that the current fishing mortality rate, while greatly reduced as compared to the 1980's, remains greater than $F_{50\%}$ (i.e., above 0.05 yr^{-1}). This in turn translates into less than a 40% chance that the population will recover to levels above $s_{50\%}$ within the next 15 years. Several fishermen have testified that the harvest ban is probably less than 90% effective because goliath grouper are still taken illegally in places and because animals caught and released in deeper water often do not survive[7], so this result does not appear unrealistic.

More optimistic results, implying a 70 to 80% chance of recovery within 15 years, were obtained when the DeMaria index was excluded or when selection was oriented more towards older animals. There does not appear to be a strong *a priori* case for excluding the DeMaria index in favor of the REEF and ENP indices. Although the coverage is rather limited, the trends of the DeMaria index are consistent with those of the ENP index (with a suitable time lag) and with anecdotal accounts of the trends in other areas[8]. The issue of selection is more vexing. It can be argued that the age composition data from the ENP creel census adequately reflects the composition of the juvenile catch inasmuch as it comes from the center of juvenile abundance, however most adults were caught outside this area. Thus, the relative contribution of juveniles and adults to the overall catch is unclear and the directional bias in the fitted logistic selection curve uncertain. The only other age composition information that has come to light comes from the study by Bullock et al (1992), which was not designed to provide a random sample of the catch and is probably biased towards larger animals caught on offshore wrecks. In principle, one could reflect this uncertainty more formally either by developing a prior for the selectivity parameters or else by weighting the results from the two selection models. The SEDAR stock assessment review based their advice on the selection curve derived from the ENP data[7], which is equivalent to placing negligible weight on the curve derived from Bullock et al.'s data, however they recognized it as an important source of uncertainty that is difficult to address without adequate data.

It is important to emphasize that the Bayesian approach adopted here allows one to explicitly model the uncertainty about parameters such as M, for which no data may exist, but a prior distribution covering the plausible range of values may be specified. There is, of course, the potential for introducing bias when one or more of the priors are based on expert opinion or otherwise subjective information. However, the same sorts of bias can be introduced by conducting sensitivity analyses where the unknown parameters are fixed to various values selected by the analysts. Furthermore, if unbiased data are in short supply, analyses based on completely uninformative priors will be useless for generating advice because the range of plausible outcomes is too large. Accordingly, we view the use of subjective priors primarily as a vehicle for providing more realistic limits on uncertainty and prefer to express the model outcomes in terms of probability statements. For example, the point estimate from the base model indicated that the population would never recover to $s_{50\%}$ because the fishing mortality rate under the harvest ban was still slightly above $F_{50\%}$. However, consideration of the uncertainty led to the conclusion that the chance of recovering to $s_{50\%}$ within 15 years was nearly 40%.

Some sources of uncertainty have not been adequately accounted for in the above assessment. For example, the relationship between fecundity and age is unknown. We used weight-at-age as a proxy for the relative fecundity-at-age in our analysis, but it is often the case that fecundity increases with age faster than weight. If this is true for goliath grouper, then our projections would be too optimistic. It should also be remembered that the results apply strictly to the goliath grouper population in South Florida. It is believed that the center of abundance for the population in U.S. waters is southern Florida, particularly the Ten Thousand Islands area, but goliath grouper are known to have occurred throughout the coastal waters of Gulf of Mexico and along the east coast of Florida, and on up through the Carolinas. Inasmuch as goliath grouper are not highly migratory, it is possible it may take some additional time for the species to fully occupy its historical range, thus delaying the overall recovery of the U.S. population.

The primary advantage of the catch-free methodology proposed here is that it does not require knowledge of the total number of removals . In this light it is worth noting that 623 of the 905 stocks included in the 2000 annual report to Congress on the Status of Fisheries were listed as having unknown status, often because catch data were either unavailable or deemed unreliable. Thus we expect the proposed method will become increasingly useful as fishery scientists are more and more frequently being asked to develop FMPs for poorly monitored fisheries. The greatest drawback of the catch-free method is its inability to provide direct estimates of the equilibrium catch levels associated with particular reference points (e.g. MSY). This situation could perhaps be ameliorated by obtaining estimates of absolute abundance from a comprehensive short-term survey covering the entire range of the animal, in which case the relative outputs from the model (including relative catch) could be appropriately scaled. Alternatively, a long-term monitoring program at select sites located throughout the range could be established to detect changes in relative abundance under various closely monitored trial levels of catch.

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[8] Kingsley, M. C. S., ed. 2004. The Goliath Grouper in southern Florida: assessment review and advisory report. Report prepared for the South Atlantic Fishery Management Council, the Gulf of Mexico Fishery Management Council, and the National Marine Fisheries Service. 17 pp. South Atlantic fishery Management Council, 1 Southpark Circle, Charleston SC 29406.

Acknowledgments

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Appendix 1: Reparameterized spawner-recruit relationships

The number of young fish recruiting to a population (R) is often related to the aggregate fecundity of the spawning stock (S) using one of two functional forms:

$$\text{(A.1)} \qquad R = \begin{cases} aSe^{-bS} & \text{Ricker} \\ \dfrac{abS}{b+S} & \text{Beverton and Holt} \end{cases} .$$

The parameter a is the slope of the curve at the origin and the parameter b controls the degree of density dependence. Notice that the domain of both functions extends from zero to infinity, whereas in practice there must be some limitation on S and R even in the absence of fishing owing to environmental constraints (call them S_0 and R_0, respectively). This being so, we obtain

$$\text{(A.2)} \qquad a\frac{S_0}{R_0} = \begin{cases} e^{bS_0} & \text{Ricker} \\ 1 + S_0/b & \text{Beverton and Holt} \end{cases}$$

The ratio S_0/R_0 represents the maximum expected lifetime fecundity of each recruit and a represents the survival of recruits in the absence of density dependence. Accordingly, the product $a = aS_0/R_0$ may be interpreted as maximum possible number of recruits produced by each spawner over its lifetime (Myers et al. 1998).

The dimensionless character of a makes it useful for interspecies comparisons, or for borrowing values from species with similar life history strategies. Solving for b in terms of a one obtains

$$\text{(A.3)} \qquad b = \begin{cases} \log_e \alpha / S_0 & \text{Ricker} \\ S_0 / (1 - \alpha) & \text{Beverton and Holt} \end{cases}$$

Substituting (A.3) into (A.1) gives

$$\text{(A.4)} \qquad R = \begin{cases} aS\alpha^{-S/S_0} & \text{Ricker} \\ \dfrac{aS_0}{1 + (\alpha - 1)S/S_0} & \text{Beverton and Holt} \end{cases}$$

and, since $a = aR_0/S_0$,

$$\text{(A.5)} \qquad R = \begin{cases} R_0 \dfrac{S}{S_0} \alpha^{1-S/S_0} & \text{Ricker} \\ R_0 \dfrac{\alpha S/S_0}{1 + (\alpha - 1)S/S_0} & \text{Beverton and Holt} \end{cases} .$$

Dividing through by R_0 and defining $s = S/S_0$ gives equation (4).

Appendix 2: Formula for equilibrium spawning biomass

The spawning potential ratio (p) is defined as the number of spawners produced by each recruit at equilibrium with a given fishing mortality rate F divided by the number of spawners per recruit under virgin conditions (F=0). This may be written

$$p = \frac{\phi_F}{\phi_0} = \frac{\tilde{S}_F / \tilde{R}_F}{\tilde{S}_0 / \tilde{R}_0} = \frac{\tilde{S}_F / \tilde{S}_0}{\tilde{R}_F / \tilde{R}_0} = \tilde{s} / \tilde{r} \tag{A.6}$$

where the tilde signifies equilibrium values. At equilibrium we also obtain from equation (4)

$$\tilde{r} = \begin{cases} \tilde{s}\,\alpha^{1-\tilde{s}} & \text{Ricker} \\ \dfrac{\alpha\tilde{s}}{\left(1+\tilde{s}(\alpha-1)\right)} & \text{Beverton and Holt} \end{cases} \tag{A.7}$$

Dividing both sides of (A.7) by $\tilde{r}$, substituting p for $\tilde{s} / \tilde{r}$ (A.6) and solving for $\tilde{s}$ gives equation (6).

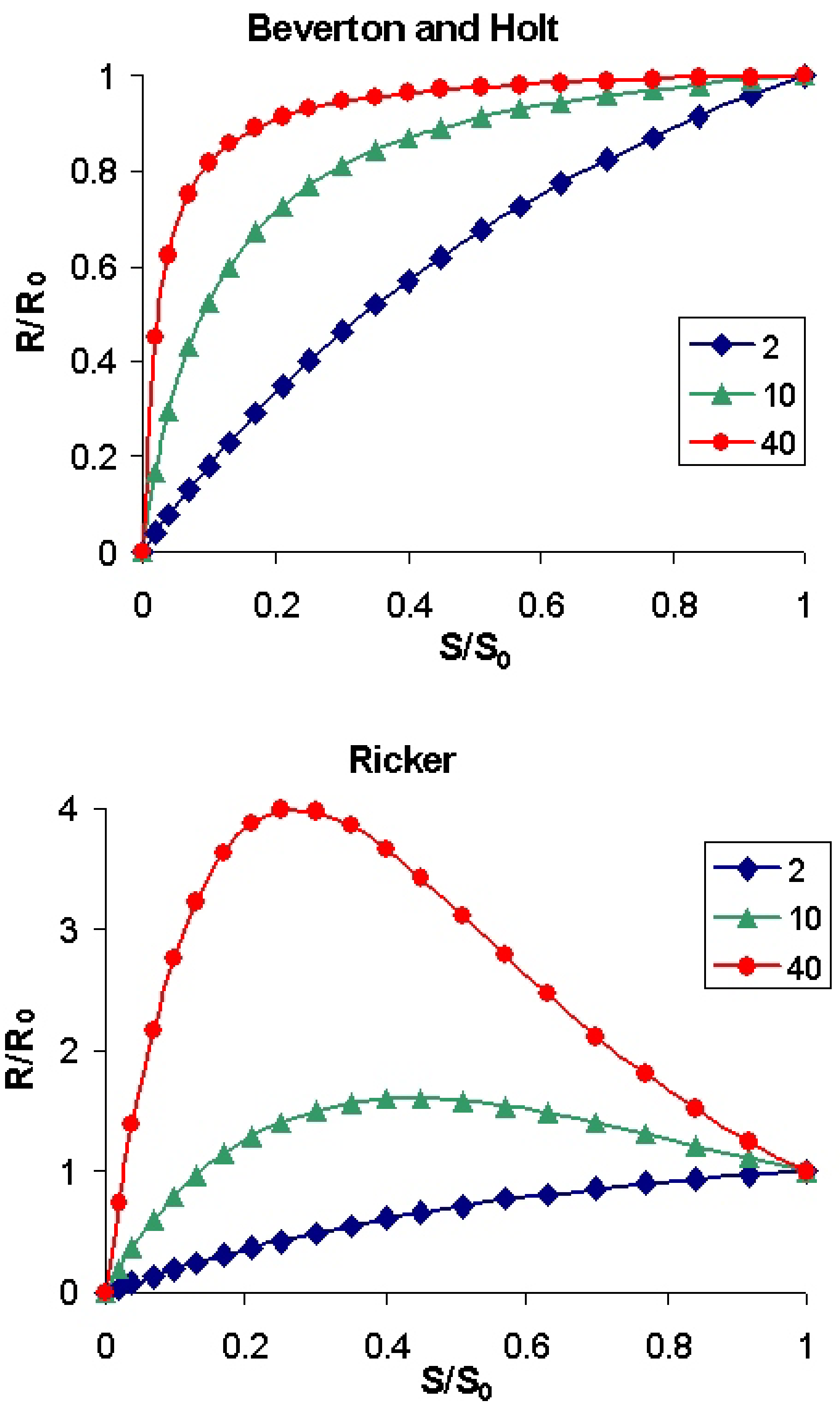


Figure 1. Examples of scaled Beverton-Holt and Ricker spawner-recruit relationships for various values of α.

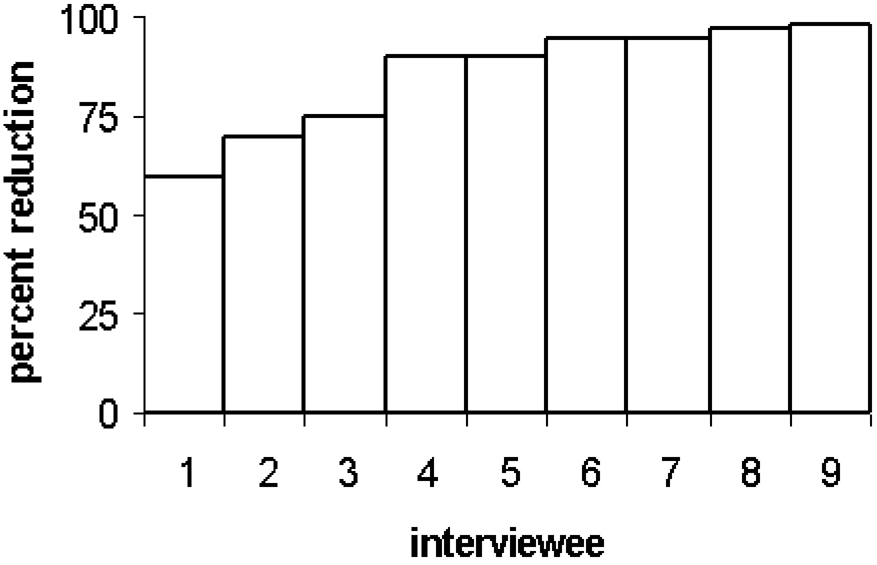


Figure 2. Summary of anecdotal reports from 9 individuals concerning the abundance of adult-sized goliath grouper in 1990 relative to their abundance during the 1950's and 60's. To qualify, interviewees must have been actively diving or fishing in southern Florida prior to the early 1960's as well as near the time of the moratoriums (1990).

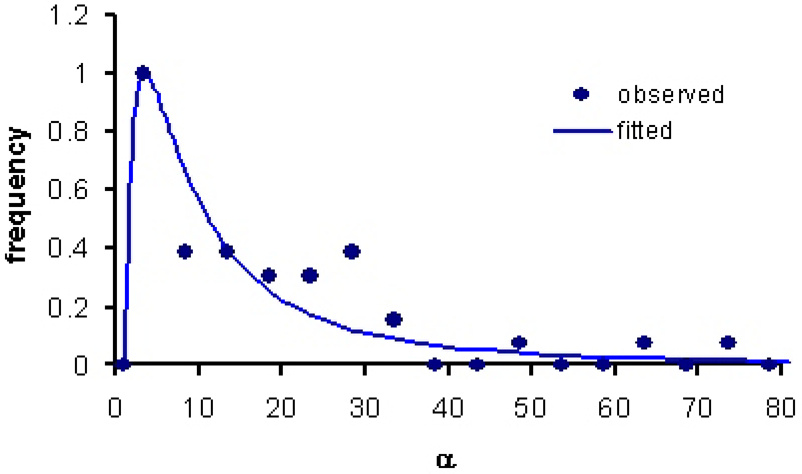


Figure 3. Lognormal prior for the maximum lifetime fecundity parameter (*a*) derived from the values in Myers et al. (1999) that correspond to species categorized as periodic strategists by Rose et al. (2001). The lognormal density was fitted to the values of *a*-1 (with median 9.8 and log-scale variance 1.31) and then shifted 1 unit to provide a prior for *a*.

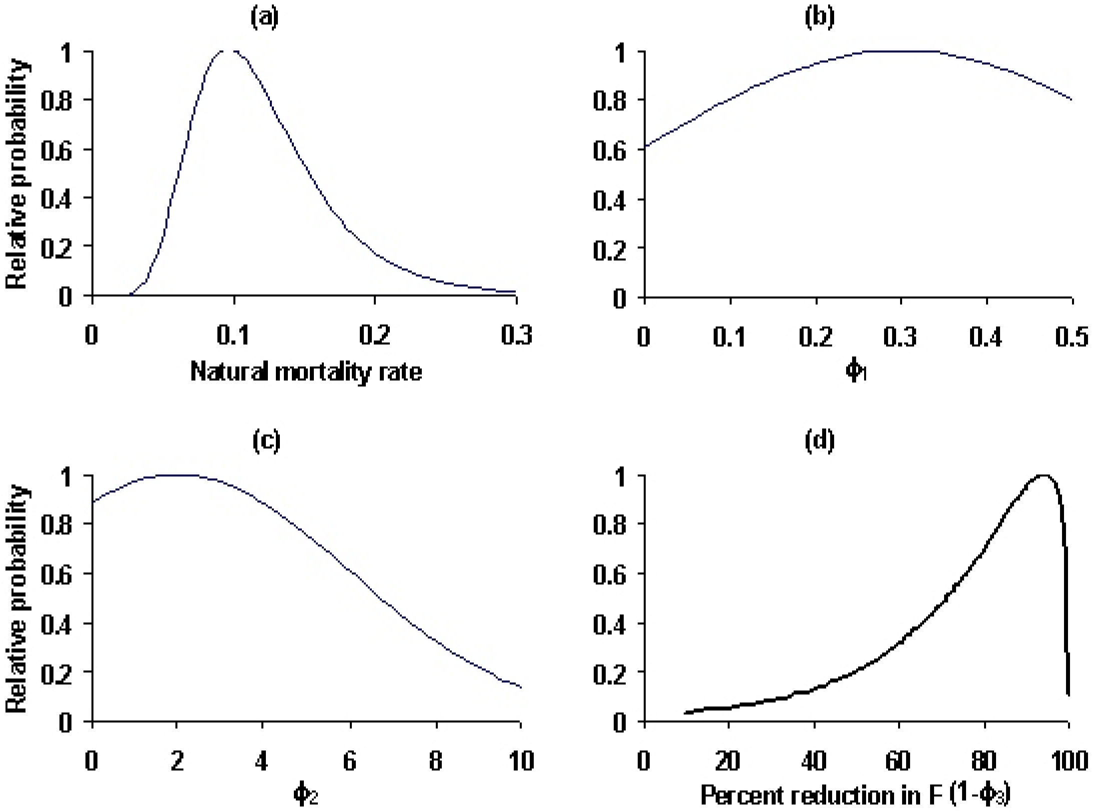


Figure 4. Priors for the mortality rate parameters: (a) lognormal prior for natural mortality rate, (b) truncated normal prior for ϕ_1, (c) truncated normal prior for ϕ_2 (d) gamma prior for ϕ_3. The upper and lower boundaries for each parameter are as given on the horizontal axes.

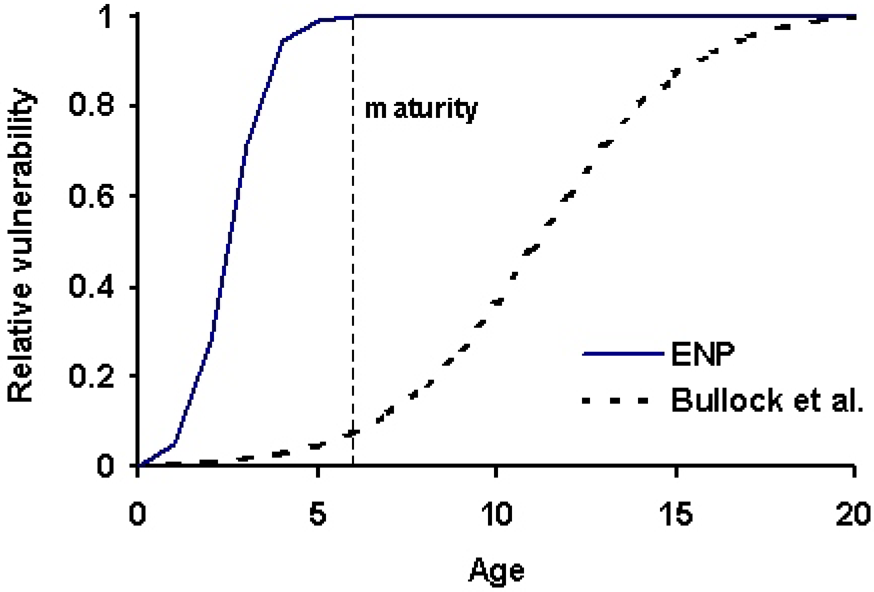


Figure 5. Selection curves fitted to age composition data derived from the Everglades National Park creel census (ENP) and opportunistic sampling from offshore fishing trips (Bullock et al.).

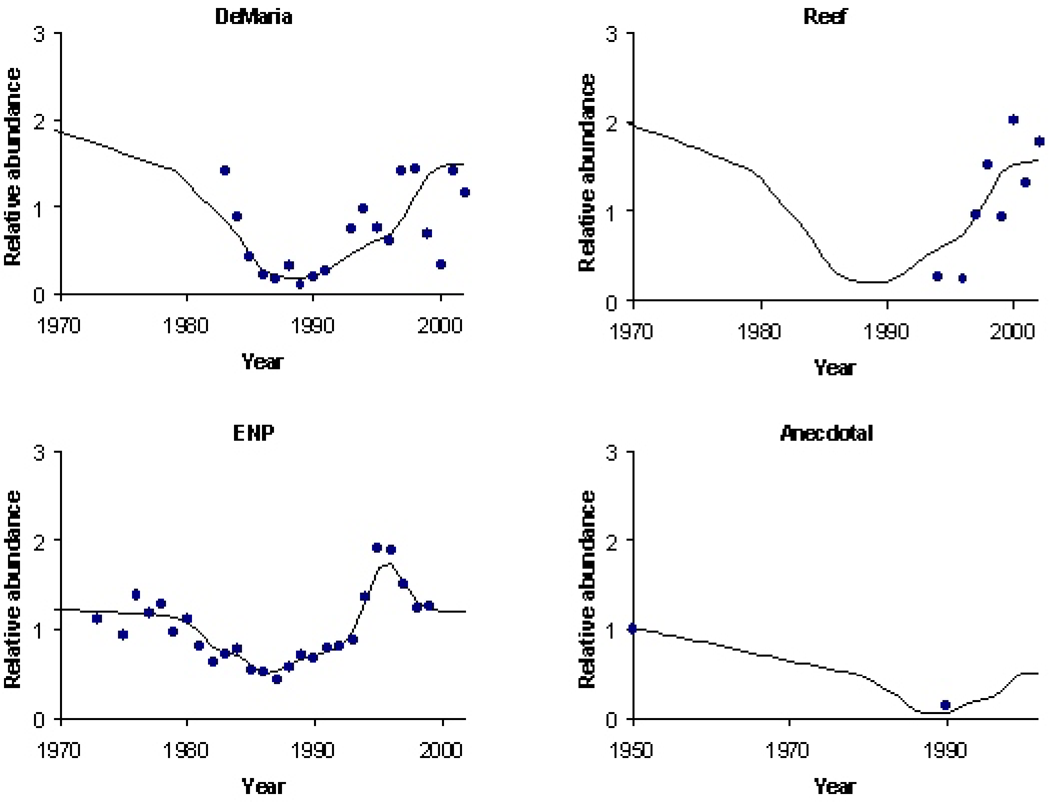


Figure 6. Base model fit to the four indices of abundance.

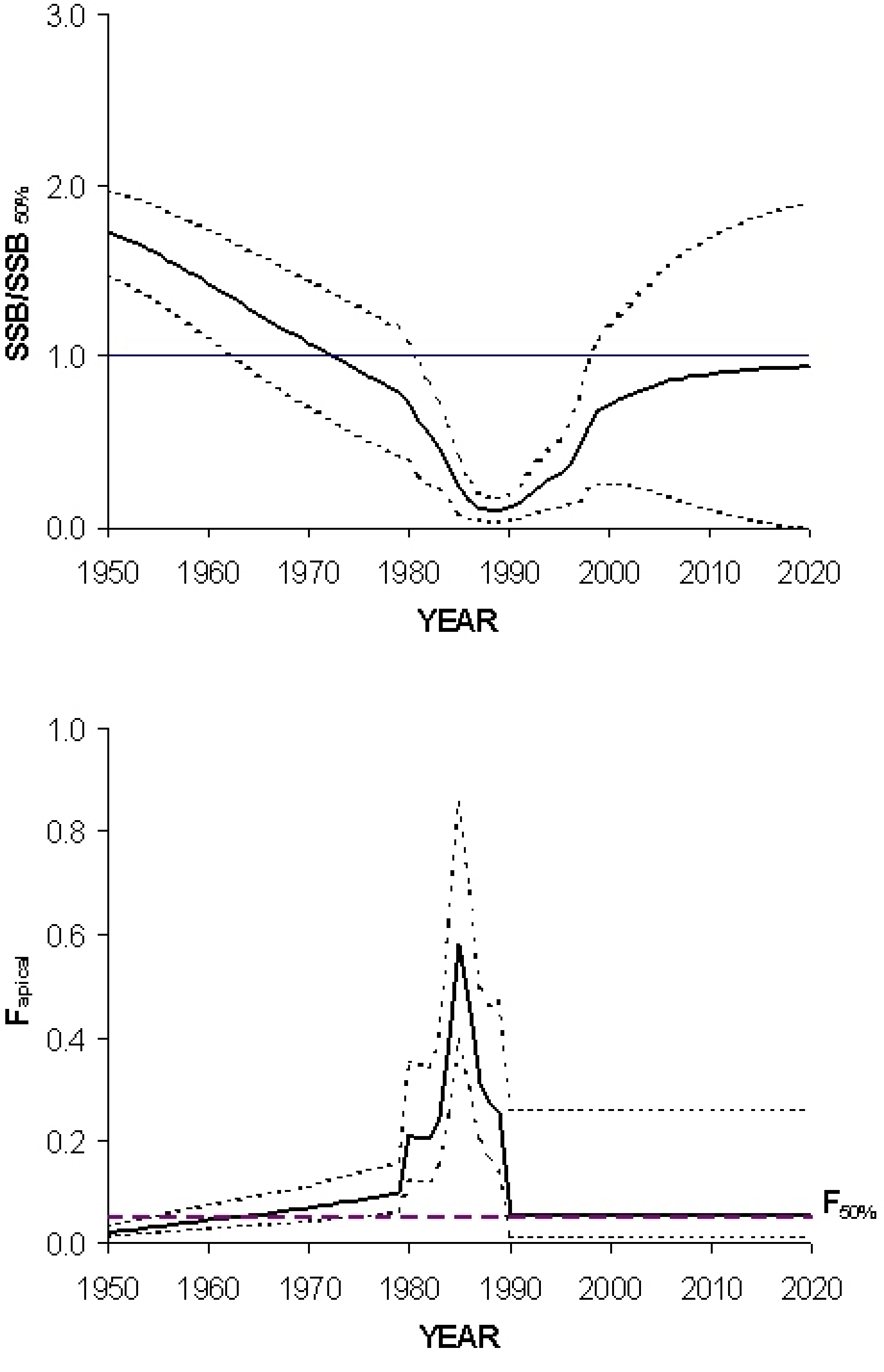


Figure 7. Base model predictions of relative spawning biomass and fishing mortality rate with approximate 80% confidence limits.

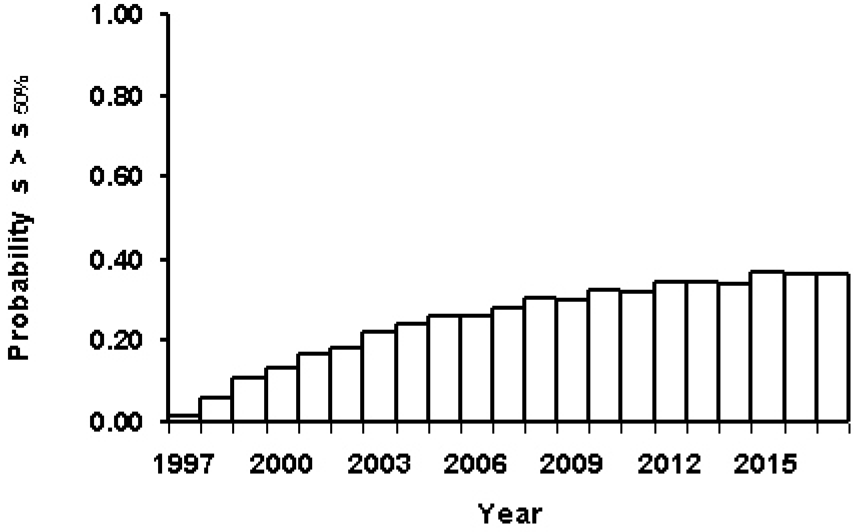
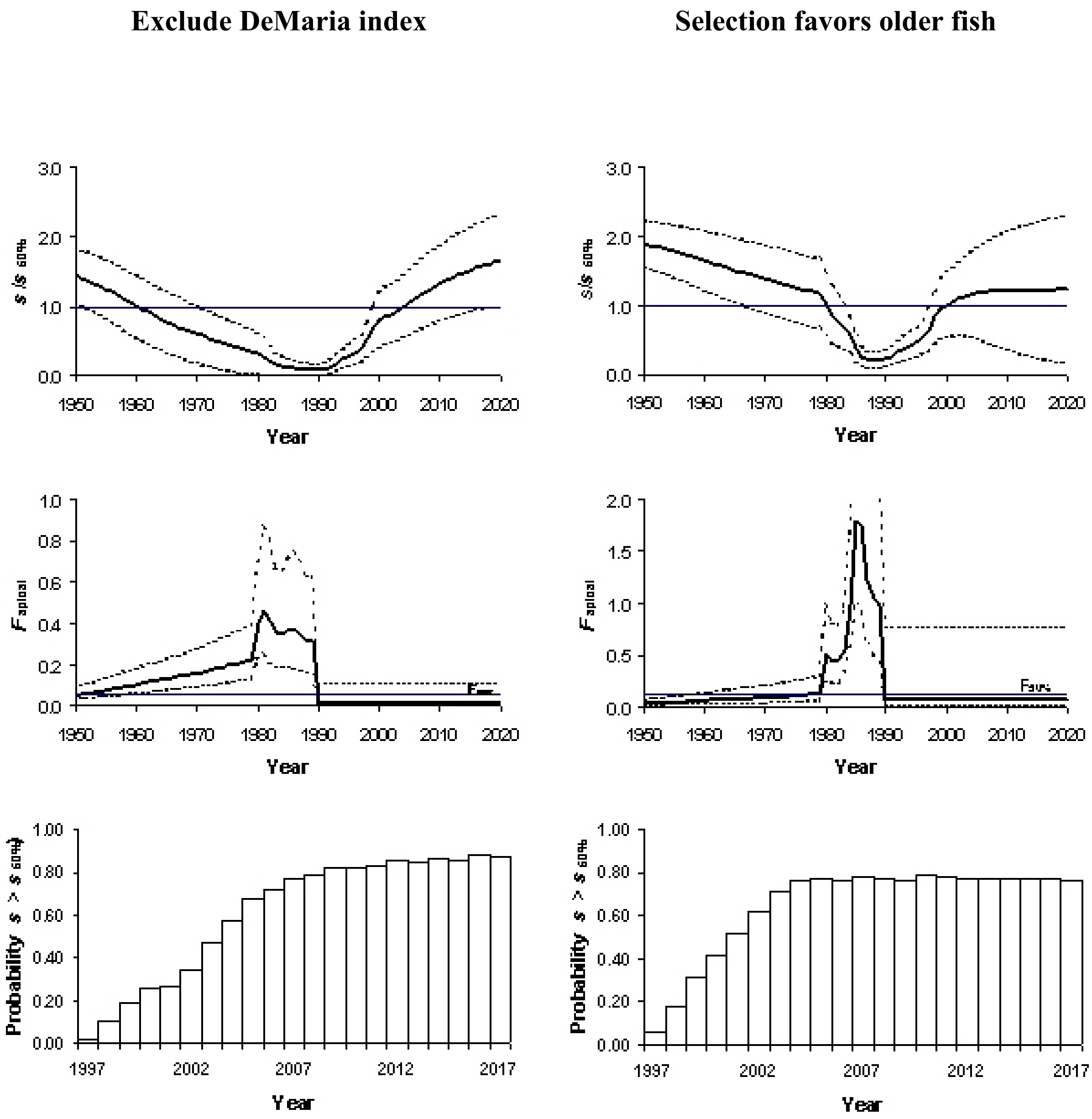


Figure 8. Predicted probability that the stock will have recovered to levels exceeding the equilibrium spawning biomass associated with a spawning potential ratio of 50%.


Exclude DeMaria index

Selection favors older fish

Figure 9. Spawning biomass, fishing mortality and the probability of recovery by year for the sensitivity runs excluding the DeMaria index (left) and using the selection curve favoring older fish (right).

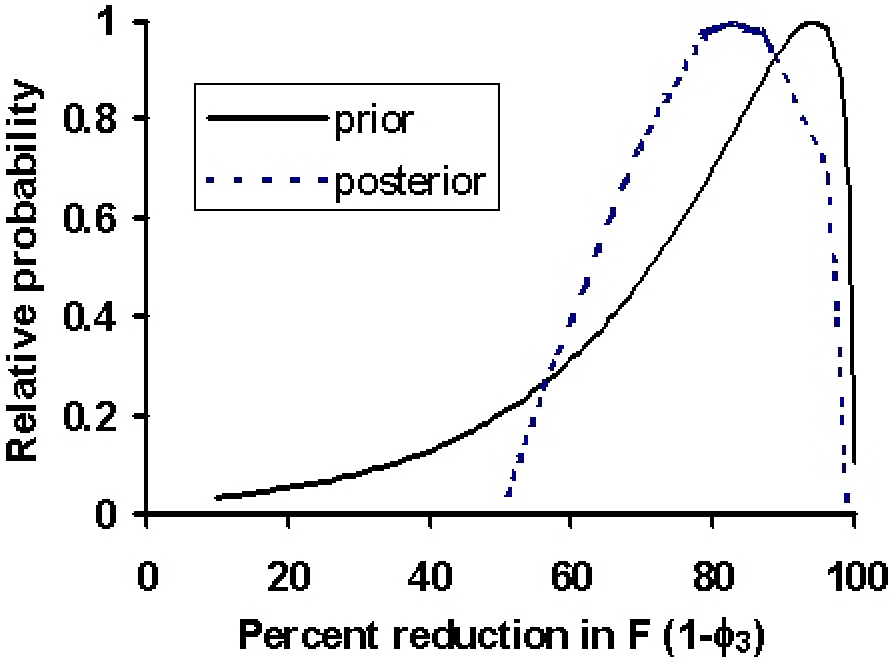


Figure 10. Posterior and prior distributions for the effectiveness of the harvest ban in reducing *F* from the levels observed during the 1980's.

Appendix to SCRS/04/110 -- Application of Catch-free model to Mako Shark

Elizabeth N. Brooks

The catch-free model was applied to short fin mako as an illustration of the method. Simplifying assumptions were made with respect to biological input. Ages 1-6 were assumed to be immature, 50% of age 7 was assumed to be mature, and 100% of ages 8 and older were mature. Due to the protracted gestation period, the age of a pregnant shark is greater than the age when fertilization occurred by up to 18 months. To incorporate this, the maturity ogive was shifted by an increment of 1 year. The littersize was assumed to be a constant 12.75 for all mature ages (E. Cortes, pers. comm..). Assuming a 1:1 sex ratio, littersize was halved to account for reproduction by female adults only. It is believed that a resting period occurs after parturition, so that reproduction may be triennial. Thus, littersize was multiplied by 0.33 to account for the fact that, on average, only 1/3 of the population produces pups in a given year. Annual pup survival and a natural mortality rate for all sharks older than 1 year were estimated. A lognormal prior was placed on pup survival with a mode of 0.76 and a log-scale CV of 0.15; the estimate was constrained to lie in the interval [0.70, 0.81] (E. Cortes, pers. comm..). Beyond age 1, annual survival is believed to range from 0.84 to 0.93. This corresponds to an instantaneous natural mortality rate, M, of 0.17 to 0.07. A lognormal prior was specified for M, with a mode of 0.13 and a log-scale CV of 0.3; the estimate was constrained to lie in the interval [0.05,0.2]. Parameters for a von Bertalanffy growth model were taken from Cailliet et al. (1983): $L\infty = 321$ cm, $k = 0.072$, $t0 = -3.75$; parameters for converting length to weight ($weight = aL^b$) were taken from (Kohler et al. 1995): $a = 5.24E-06$, and $b = 3.141$.

Fishery input to the model was limited to one CPUE index, an average of the Japanese Longline logbook series (1971-2000) as given in the Final Report from the Atlantic Shark Stock Assessment meeting (Halifax, Canada, 11-14 September 2001) and the US longline logbook series (1986-2003) as reported in SCRS/2004/111. This combined index is given in Table 1 and Figure 1. A logistic selectivity function was estimated from length frequency data given in SCRS/2004/106. For females in the NED, the estimated age at 50% selectivity is 5 years, and the slope of the selectivity curve was 2 (P. Apostolaki, pers. comm..). An additional index of abundance was created to extend the time series of information back to 1950, when the population was assumed to be at virgin levels. This abundance index assumed various levels of depletion from 1950 to 1971, and the annual values represented a linear decrease from a virgin level to the estimated 1971 depletion. An example of this series is given in Table 1 for an assumed depletion of 25% in 1971. Two additional levels of depletion were investigated, 50% and 10%. Initial model runs did not include effort, rather a constant F was estimated for the historic period, and an average F with annual deviations was estimated for the modern period. Nominal effort measured in number of hooks could potentially be used to estimate a trend in F during the historic period where no CPUE observations are available. Two additional model runs were performed where a linear trend in F was estimated for the historic and modern period using the longline effort for the North Atlantic (see Appendix Figure 2). Appendix Figure 3 shows two potential trend fits to a plot of relative abundance (the combined index) to relative effort, which may provide guidance for hypothesizing depletion levels in the period before relative abundance information is available.

For the model with no effort and an assumption of 25% depletion by 1971, the estimate of current spawning stock biomass (SSB) is 43.2% of virgin level, which is greater than the estimated SSBmsy (Table 2). The current fishing mortality rate (Fcurr) is estimated to be 0.0682, which is just slightly over Fmsy (Table 2). The estimates of pup survival and natural mortality are very close to the mode of their priors, suggesting that there is very little information from which to estimate these parameters. The parameter $\hat{\alpha}$, maximum lifetime reproduction from Myers et al. (1999), can be derived from equation (A.1) in SCRS/2004/110. Defining pup survival as survival at low density, it is equivalent to the slope at the origin of the spawner-recruit curve. Thus, from (A.1), $\hat{\alpha}$ = (pup survival)X(virgin level spawners per recruit). Virgin level spawners per recruit (spr0) and the estimate for $\hat{\alpha}$ are given in Table 2. In the 25% depletion example, the estimate for $\hat{\alpha}$ is 4.47. This is reasonably close to the distribution of possible $\hat{\alpha}$ values from life table analyses, which yielded an estimated mean of 3.62 and standard deviation of 0.74 when a lognormal distribution was fit (E. Cortes, pers. comm..).

The fit to the indices (the combined US/Japan longline and the abundance index that mimics an assumed depletion) for all three depletion scenarios are given in Appendix Figure 4. Both the diagnostics (AIC, AICc, and objective function value) and the plots suggest that the model fits the 10% historic depletion assumption best, although the difference between the model fits is fairly small. The relative trend in SSB for all three scenarios is given in Appendix Figure 5.

The model estimates of Fcurr, Fmsy, and SSBmsy are fairly stable, and the assumption of historic depletion in 1971primarily affects the model estimate of historic fishing mortality rate (Fhist). Given that the model estimates of pup survival and M are so close to the prior specifications, sensitivity runs to alternate prior formulations are recommended.

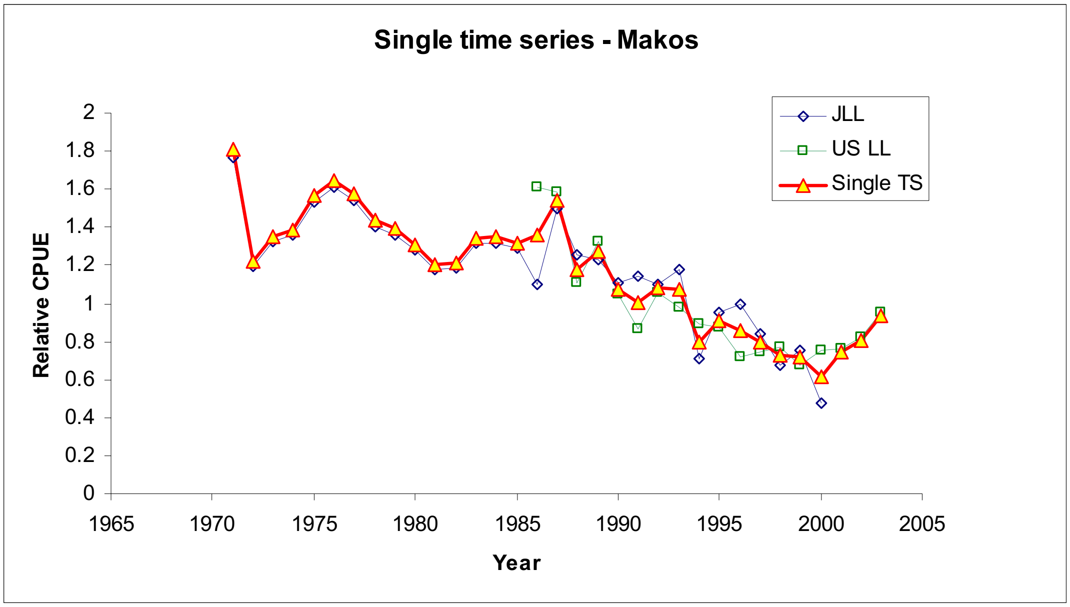
Results from a model run where the nominal effort was included and a linear trend in F was estimated are given in the last column of Table 2. A depletion of 25% in 1971 was assumed. The historic F ranges from near 0 in 1956 to about 0.2 in 1971. The current level of fishing mortality (in year 2003) is 0.258, which would imply a very gradual increase in F from 1971-2003 (Appendix Figure 6). These estimates are very different from the models that did not include effort, however, the estimate of Fmsy and SSBmsy are quite similar. Consequently, the reference points indicate overfishing (F/Fmsy = 3.63) and an overfished stock (SSB/SSBmsy=0.183). The fits to the indices and the trend in SSB are shown in the middle and bottom panels of Appendix Figure 6. Alternative assumptions about the trend of historic fishing and the level of depletion could be explored.

Appendix Table 1. Indices for the catch-free application to mako shark. Table entries of (–1) indicate missing values.

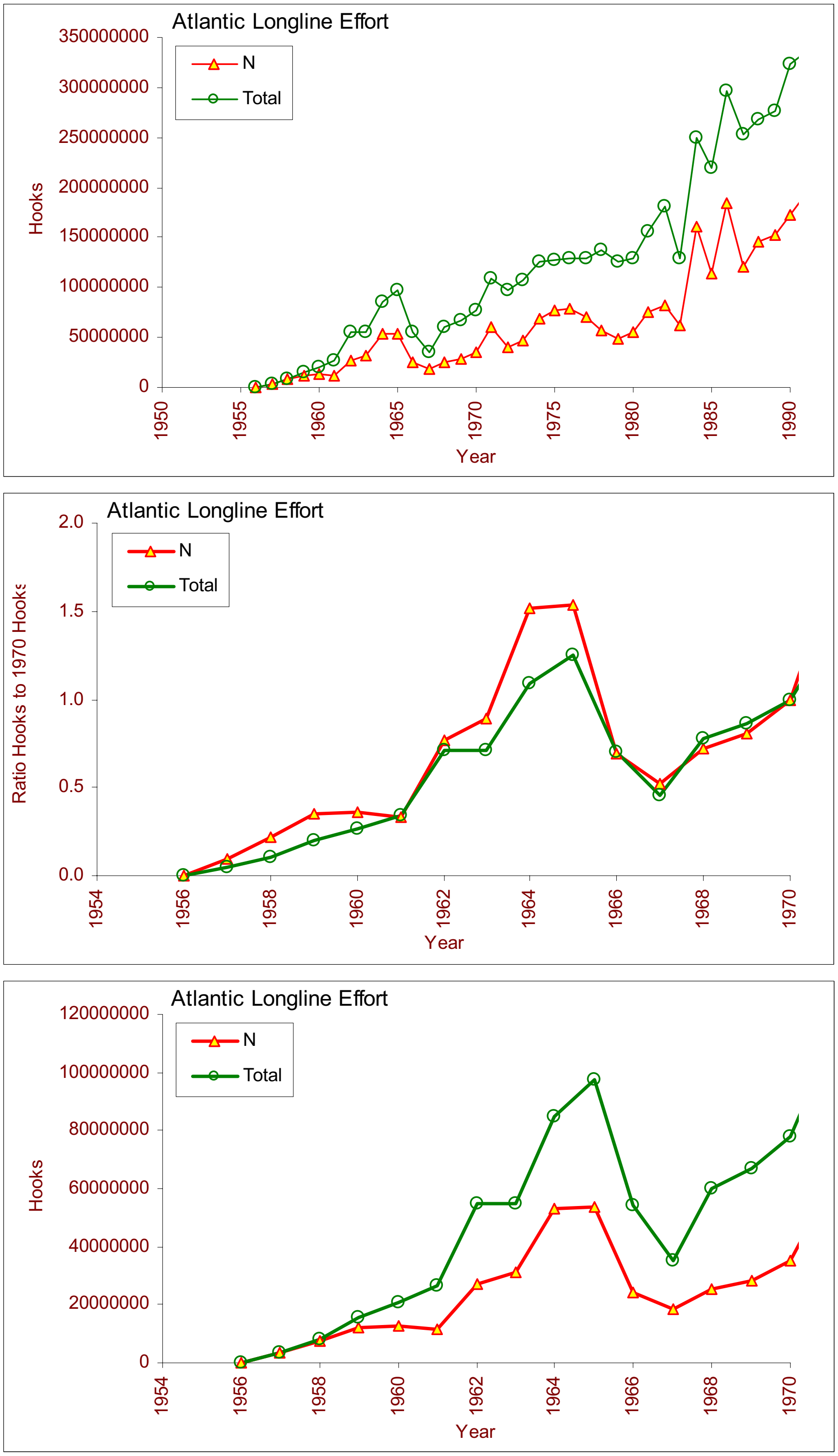
US/Japan LL	Historic Depletion	Year
-1	1	1950
-1	0.988	1951
-1	0.976	1952
-1	0.964	1953
-1	0.952	1954
-1	0.94	1955
-1	0.929	1956
-1	0.917	1957
-1	0.905	1958
-1	0.893	1959
-1	0.881	1960
-1	0.869	1961
-1	0.857	1962
-1	0.845	1963
-1	0.833	1964
-1	0.821	1965
-1	0.81	1966
-1	0.798	1967
-1	0.786	1968
-1	0.774	1969
-1	0.762	1970
1.805	0.75	1971
1.224	-1	1972
1.354	-1	1973
1.385	-1	1974
1.564	-1	1975
1.644	-1	1976
1.576	-1	1977
1.434	-1	1978
1.391	-1	1979
1.311	-1	1980
1.199	-1	1981
1.212	-1	1982
1.342	-1	1983
1.348	-1	1984
1.317	-1	1985
1.356	-1	1986
1.538	-1	1987
1.181	-1	1988
1.277	-1	1989
1.076	-1	1990
1.003	-1	1991
1.079	-1	1992
1.077	-1	1993
0.799	-1	1994
0.913	-1	1995
0.857	-1	1996
0.792	-1	1997
0.723	-1	1998
0.715	-1	1999
0.614	-1	2000
0.744	-1	2001
0.807	-1	2002
0.934	-1	2003

Appendix Table 2. Catch-free model estimates for three assumed levels of historic depletion for mako shark, with no effort series, and one result for 25% assumed depletion using nominal hook effort.

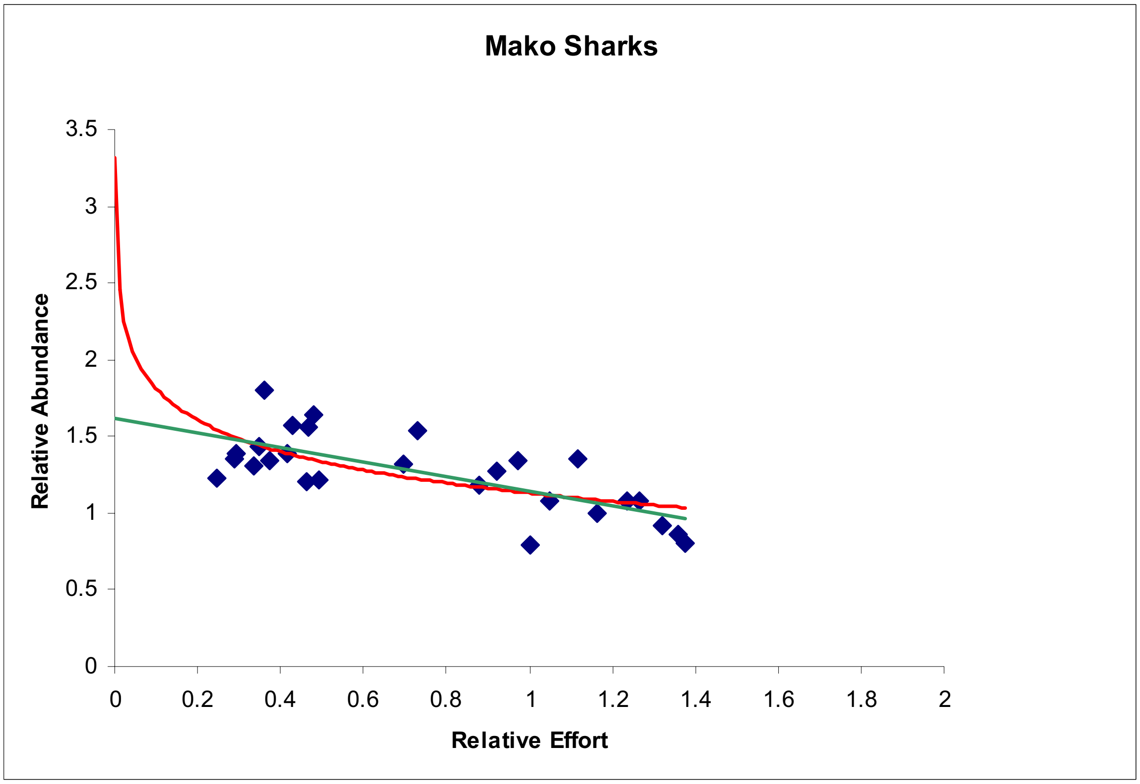
	Percent depletion assumed in 1971			
Model Result	**10%**	**25%**	**50%**	**25%, effort**
Fhist (1950-1971)	0.00511	0.00511	0.0568	linear trend, from ~ 0 to 0.2
Fcurr	0.0632	0.0682	0.0787	0.258
Fmsy (fleet)	0.0613	0.0610	0.0595	0.071
Fcurr/Fmsy(fleet)	1.032	1.118	1.323	3.63
SSBcurr/SSB0	0.467	0.432	0.363	0.069
SSBmsy(fleet)/SSB0	0.399	0.399	0.402	0.376
SSBcurr/SSBmsy(fleet)	1.1511	1.082	0.903	0.183
pup survival	0.756	0.755	0.751	0.786
M	0.132	0.132	0.134	0.12
spr0	5.96	5.93	5.75	7.17
$\hat{\alpha}$	4.50	4.47	4.32	5.64
AIC	13.4266	13.6092	14.2345	15.4194
AICc	357.427	357.609	358.235	577.819
objective function	-36.2867	-36.1954	-35.8827	-29.203



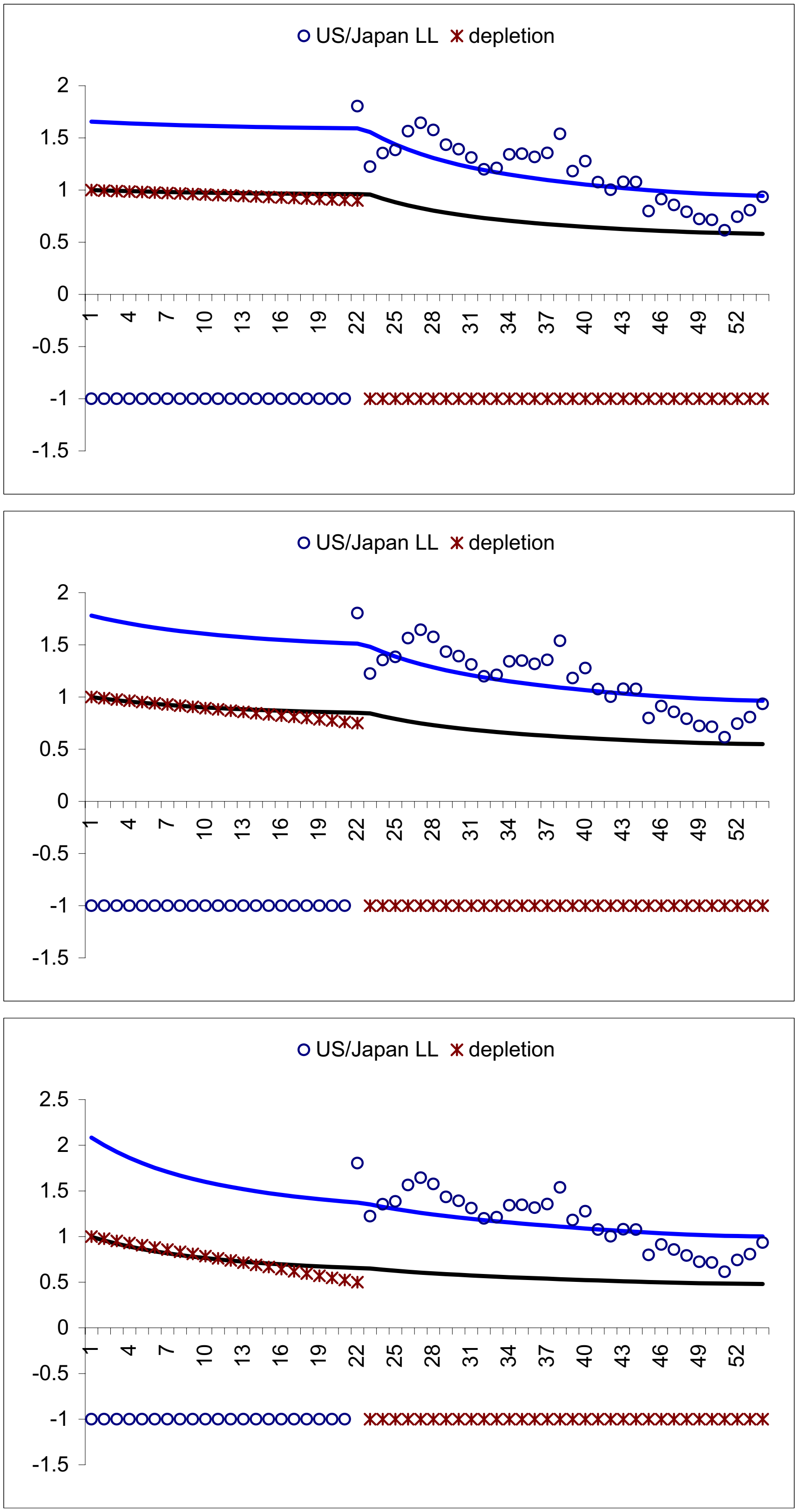
Appendix Figure 1. Single time-series of mako shark relative abundance based on US and Japanese Longline standardized CPUE.



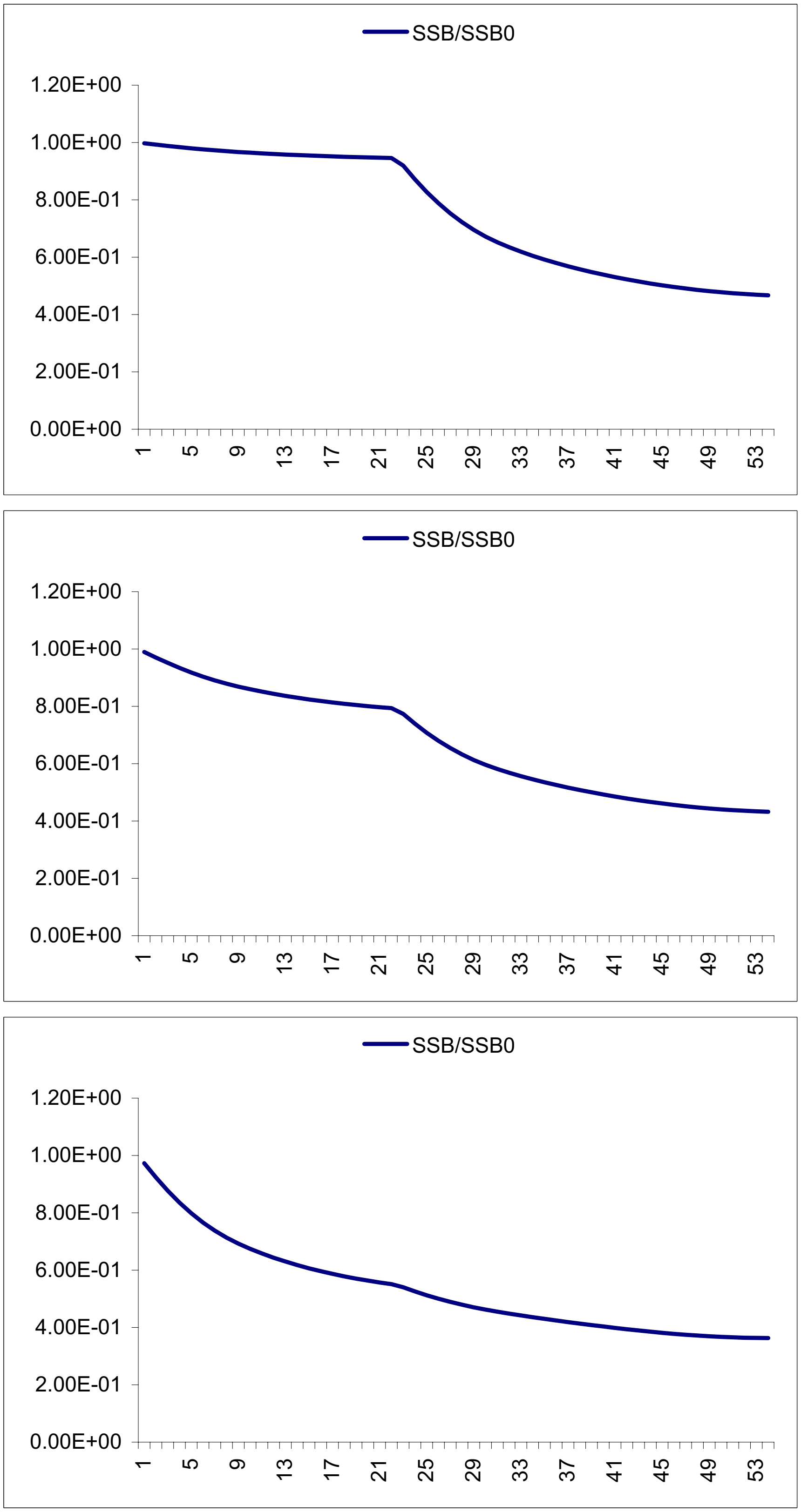
Appendix Figure 2. Nominal reported longline fishing effort in the Atlantic from ICCAT Task II data base, potentially useful for guiding hypotheses about change in F prior to the period for which relative abundance data are available.



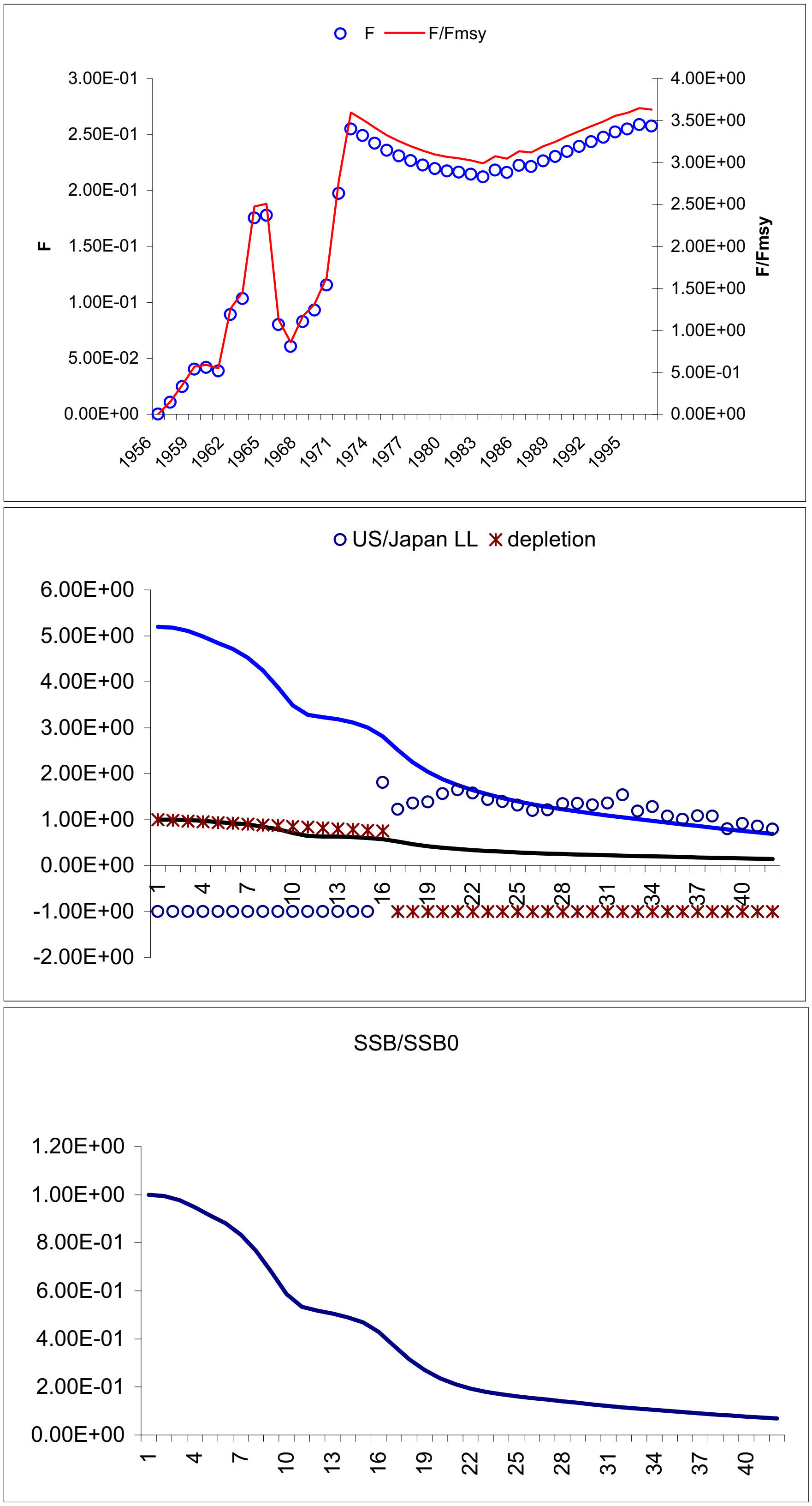
Appendix Figure 3. Relationship between nominal longline fishing effort reported to ICCAT for the north Atlantic and relative abundance of mako sharks based upon the single time series in Appendix Figure 1 with a linear and exponential trend fit to the time-series.



Appendix Figure 4. Catch-free model fit to the combined US/Japan longline index and the abundanceindex relating the assumed depletion level in 1971 for mako shark. Top: 10% depletion; Middle: 25% depletion; Bottom: 50% depletion.



Appendix Figure 5. Catch-free model fit to the combined US/Japan longline index and the abundance index relating the assumed depletion level in 1971. Top: 10% depletion; Middle: 25% depletion; Bottom: 50% depletion.



Appendix Figure 6. Trend in fishing mortality, F, estimated from the inclusion of nominal effort; fit to combined index and assumed depletion index of 25% by 1971; trend in SSB.