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An alternative assessment of the red snapper (*Lutjanus campechanus*) fishery in the U.S. Gulf of Mexico using a spatially-explicit age-structured assessment model: Preliminary results

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Introduction

Red snapper (*Lutjanus campechanus*) have been fished in the Gulf of Mexico (Fig. 1) since at least 1850 (Camber, 1955). A few years after the Civil War a substantial fishery developed out of Pensacola, Florida (Jarvis 1935) and by the early 1900's most of the snapper grounds from the Campeche Banks to Florida had been fished (Carpenter 1965). As early as the 1880's there were indications that red snapper were becoming less abundant in some areas. Stearns (1883), for example, remarked that "most of the old fishing grounds are barren, and smacks have to go farther each year to find new ones." By the 1950's most of the snapper banks off Florida were considered impoverished and notable declines in catch per unit effort were evident on the Campeche Banks despite an increase in the efficiency of the fleet (Camber 1955). Nevertheless, catches generally have remained on the order of several million pounds throughout the time series with dips during the Great Depression and World War II. During the 1960's the size and efficiency of the commercial fleet increased greatly (Carpenter 1965), but without a corresponding increase in catch, suggesting that red snapper populations throughout the Gulf of Mexico were by that time already fully-exploited and perhaps even overfished.

Prior assessments of red snapper in the Gulf of Mexico (e.g., Schirripa and Legault 1999[1]) have been based on data beginning in the 1980's, when red snapper populations are likely to have already been depressed. The lack of contrast in such data makes it difficult to develop meaningful estimates of stock status, particularly in relation to abundance-based reference points such as the equilibrium spawning biomass at maximum sustainable yield. The restriction to data collected since the 1980's is a consequence of both gaps in the available historical record and limitations of the methodology employed. The former has partly been addressed by Porch et al. (2004), who have supplemented the extant electronic data bases with observations gleaned from historical documents. The latter is addressed by the age-structured statistical model described in this paper.

Recent studies of red snapper life history characteristics and otolith microchemistry suggest that there is a rather strong demarcation between the populations living east and west of the Mississippi river (Cowan et al., 2002). This demarcation seems to be corroborated by conflicting trends in the indices of abundance from the two regions (SEDAR AW...). Nevertheless, tag-recapture information suggests that red snapper occasionally move substantial distances (Patterson et al. 1999) and otolith microconstituent analyses suggest that some fish do move from one side of the river to the other (Cowan et al., 2002). Hence, it may be prudent to assess and manage these stocks as separate units, but perhaps allowing some degree of intermixing.

The purpose of this paper is to apply an alternative age-structured statistical algorithm that accommodates several intermixing stocks being fished by multiple fleets in multiple habitats and uses otolith-based information on age composition by stock in an attempt to estimate mixing rates. The approach also attempts, for the first time, to include information from the fishery since before the Civil War.

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[1] Schirripa, M. J. And Legault, C. M. 1999. Status of the red snapper in U.S. waters of the Gulf of Mexico updated through 1998. Sustainable Fisheries Division Contribution SFD-99/00-75. Southeast Fisheries Science Center. 75 Virginia Beach Dr. Miami, FL 33149-1099. 86 p.

Model Structure

The basic population structures in the model are "stock" and "habitat." A stock is defined here to be a group of animals with similar life-history characteristics, but not necessarily a unique genetic make up. For example, a stock may be identified with a growth-morph, sex, or species. The concept of a habitat is equally abstract, representing any form of spatial domain where the concentration of the stock or fleet may vary in important ways from the overall mean. The model also distinguishes three eras of exploitation: a 'prehistoric' period, during which no data are available; a 'data' period, when presumably there are data useful for estimating abundance and mortality; and a 'future' period, when mortality rates are assumed (input). The calculations are done on a seasonal basis to accommodate seasonal movement and fishing patterns and to mimic the effect of temporally protracted spawning by allowing for multiple cohorts per year. The model tracks the abundance of each cohort throughout its life span as shown in Table 1. The duration of the prehistoric period is set equal to the number of seasonal age-classes so as to generate a complete age-structure by the beginning of the first year of the data period.

The age-classes range from 1 to A, where r is the age (in seasons) associated with age-class 1 and subsequent age-classes are incremented forward by one season. The last age-class, A, is not cumulative, i.e., fish are assumed to have a maximum life span of $A+r-1$ seasons. The calendar year y and season s are inferred from the cohort c and age-class a as

$$(1)\qquad \begin{aligned} y\{c,a\} &= y_0 + \text{int}\left\{\frac{c+a-2}{n\{s\}}\right\} \\ s\{c,a\} &= c+a-1-\text{int}\left\{\frac{c+a-2}{n\{s\}}\right\} n\{s\} \end{aligned}$$

where y_0 is the first year of the prehistoric period, int$\{x\}$ is the integer portion of quantity x and $n\{s\}$ is the number of seasons in a year. Hereafter, the notation $\{c,a\}$ will be omitted for compactness, with the implicit understanding that s and y are derived quantities. Otherwise, curly braces are used throughout to distinguish function arguments from calculation precedence.

Population dynamics model

The progression from one age-class to the next is modeled as

$$(2)\qquad N_{cah} = \sum_k \tilde{N}_{cak}\, T(h|k,a,s)$$

$$(3)\qquad \tilde{N}_{c,a+1,h} = \begin{cases} R_c \tau_h & a = 0 \\ N_{cah} e^{-Z_{ash}} & 1 \le a < A \\ 0 & a \ge A \end{cases}$$

where the subscripts c, s, a and h (or k) index cohort, season, age-class and habitat, respectively. The subscript indexing stock has been omitted for convenience of notation, but the equations should be understood to depend on stock as well. The variables $\tilde{N}_{cah}$ and N_{cah} denote the number of survivors in habitat h before and after the movement event, which is assumed to occur instantaneously at the beginning of the season (T denotes the transfer probability described below). The variable R_c denotes the initial recruitment to age class 1 of cohort c and τ_h is the probability that a new recruit will start out in habitat h. The variable Z denotes the instantaneous total mortality rate.

Movement

Movement is modeled as a diffusive process where the net pull towards a given habitat is a function of the difference between the intrinsic attraction of a habitat (β_1) and the difficulty in getting to it (β_2):

$$(4) \quad T \propto e^{-(\beta_2 - \beta_1)}$$

Here β_2 is expressed as the effective distance between habitats d_{hk} divided by the diffusion velocity u_a of each age-class in distance units per season (which may or may not be proportional to swimming speed) and β_1 is a categorical variable that varies by habitat, age-class and season. Hence, the conditional probability that a fish will transfer to habitat h given its current location k may be written

$$(5) \quad T(h|k,a,s) = \frac{\tau_{ash} e^{-d_{hk}/u_a}}{\sum_i \tau_{asi} e^{-d_{ik}/u_a}}$$

Essentially, this is a discrete version of the Joseph and Sendner (1958) diffusion equation immersed in an inhomogeneous advection field. The τ parameters can be thought of as the relative distribution of the cohort among habitats that would be achieved with an infinite diffusion velocity u. Purely diffusive motion is achieved when the τ parameters are identical and the matrix of distance parameters d_{hk} is symmetric ($d_{hk} = d_{kh}$).

Mortality

The instantaneous mortality rate Z is modeled as the sum of coefficients reflecting natural (M) and fishing-related (F) causes:

$$(6) \quad Z_{asyh} = M_a + \sum_i F_{iasyh}$$

where i indexes a particular source of fishing mortality, hereafter referred to as a fleet. The fishing mortality rate parameters are further decomposed into separable age-dependent and time-dependent effects:

$$(7) \quad F_{iasyh} = q_{iy} v_{ia} f_{iy} \xi_{iay} \delta_{ih} / n\{s\}$$

where q represents the catchability of the most vulnerable age-class, v_a represents the relative vulnerability of the remaining age-classes, f is the total effort exerted by the fleet, ξ is the probability that a fish will die once it is caught (landed or released but died), and δ_{ih} equals 1 or 0 depending on whether the fleet does or does not operate in habitat *h*. Essentially, this model assumes fishing effort is spread evenly over the seasons and habitats the fleet is operating, but may vary from year to year. The vulnerability parameters implicitly include the effects of factors such as gear selectivity and the fraction of the stock exposed to the fishery.

Interannual variations in *f* and *q* are modeled as first-order, lognormal auto-regressive processes, e.g.,

$$(8)\quad \begin{aligned} f_{iy} &= \mu\{f_{iy}\}e^{\varepsilon_{iy}} \\ \varepsilon_{iy} &= \rho\{f_{iy}\}\varepsilon_{i,y-1} + \eta_{iy} \end{aligned}$$

where μ and ρ represent the median and correlation coefficient of the f_{iy}, respectively, and the η_{iy} are normal distributed random variables with mean zero and standard deviation $\sigma\{f_{iy}\}$. In the present application, the $\mu\{f_{iy}\}$ are model inputs, hopefully based on some index of the relative effort expended by each fishery. For σ sufficiently large, the f_{iy} essentially become free parameters and the values of $\mu\{f_{iy}\}$ become arbitrary. However, the absence of data during the 'prehistoric period' generally precludes the estimation of unconstrained changes in effort. Accordingly, for the prehistoric period σ is set to 0, such that $f_{iy} = \mu\{f_{iy}\}$.

Recruitment and the definition of spawning success

The recruitment to the first age-class of each cohort (*R*) is modeled as a first-order, lognormal auto-regressive process,

$$(8)\qquad \begin{aligned} R_{xc} &= \mu\{R_{xc}\}e^{\varepsilon_y} \\ \varepsilon_y &= \rho\{R_{xc}\}\varepsilon_{y-1} + \delta_{xy} \end{aligned} \qquad ,$$

where the subscript *x* indexes stock, μ is the median recruitment, ρ is the correlation coefficient and δ is a normal-distributed random variate having mean 0 and standard deviation $\sigma\{R_{xc}\}$ (ostensibly representing the effect on recruitment of fluctuations in the environment). The median can be a constant or specified as truncated Ricker (1954) or Beverton and Holt (1957) functions that have been recast in terms of the maximum lifetime reproductive rate (α), virgin recruitment during peak season (R_0) and spawning success relative to virgin levels during peak season (ϕ):

$$(9)\qquad \mu\{R_{xc}\} = \begin{cases} R_{0,x}\phi_{xc}\alpha^{1-\phi_{xc}} & \text{Ricker} \\ R_{0,x}\dfrac{\alpha\phi_{xc}}{1+(\alpha-1)\phi_{xc}} & \text{Beverton and Holt} \end{cases}$$

(see appendix 1 and Figure 1). These two formulations are essentially the same as those cast in terms of the "steepness" parameter *h* (recruitment relative to unfished level when spawning product is 20% of unfished level), where

$$(10)\ )\qquad h = \begin{cases} 0.2\alpha^{4/5} & \text{Ricker } (0.2 \le h) \\ \dfrac{\alpha}{\alpha+4} & \text{Beverton and Holt } (0.2 \le h < 1) \end{cases}$$

In the case of a single unit stock and a single habitat, the definition of relative spawning success is straightforward,

$$(11)\qquad \begin{aligned} &\phi_c = S_c / S_0 \\ &S_c - \sum_a E_{a\hat{s}} N_{\hat{c}a} \qquad (\hat{c} = c - r - a + 1) \\ &S_0 = R_0 \sum_a E_{a\hat{s}} \exp\left(-\sum_{j-1}^{a-1} M_j\right) \end{aligned}$$

where E_{as} represents a measure of the seasonal egg production of a given age class, the subscript $\hat{s}$ in the expression for S_0 represents the peak spawning season, and the subscript $\hat{c}$ in the expression for S_c indexes the cohort that was age *a* at the time of spawning (*r* seasons prior to the recruitment of cohort *c*). When there are multiple stocks and multiple habitats, a number of alternatives present themselves. One extreme is to assume that all members of a given stock contribute to the net spawning success of that stock such that

$$(12)\qquad \begin{aligned} &S_{xc} - \sum_a E_{xa\hat{s}} \sum_k N_{x\hat{c}ak} \\ &\quad S_{0,xc} = R_{0,xc} \sum_a E_{xa\hat{s}} \exp\left(-\sum_{j-1}^{a-1} M_{xj}\right) \end{aligned}$$

where *E* is an index of the per-capita number of eggs produced by each age class. The underlying assumption behind (12) is that all members of a given stock are equally likely to contribute to the spawning product of that stock regardless of their current location, as might occur if the adults generally migrate back to the spawning habitat or the larvae are spatially well-mixed. Alternatively, one could assign a habitat to each stock as a spawning habitat and assume all fish located in that habitat contribute to the spawning product regardless of their stock affiliation:

$$(13)\qquad S_{xc} - \sum_a \sum_j E_{ja\hat{s}} N_{j\hat{c}ak'}$$

where j is used to sum over stocks and h' denotes the spawning habitat (here the expression for S_0 is tedious to write, but can be obtained from equations 1 and 2 with recruitment fixed to the stock specific values of $R_{0,xc}$ and zero fishing mortality). In this case the members of the various stocks are assumed to spawn opportunistically, but the stock their progeny are affiliated with is the one associated with the particular spawning habitat. Various scenarios in between (12) and (13) may be admitted by choosing (13) and altering the movement coefficients such that some fraction of the stock migrates into the assigned spawning habitats.

It is not possible to compute the relative spawning success for times prior to the first r+1 seasons of the data period because not all of the contributing age-classes will have been accounted for (recall Table 1). Accordingly, the recruitment parameters for this time period are modeled as random deviations from a constant median value (which may be estimated).

Data models

The basic data structure in the model is the "fleet," which is defined here as an entity with relatively constant selection characteristics (i.e., vulnerability coefficients). In this sense a fleet can include a collection of individuals with different selection habits as long as the aggregate selection pattern does not vary much through time. Fishery-independent surveys may be regarded as fleets with negligible catch. Predators other than humans may also be treated as a "fleet" if there are some data relating to their consumption of the stocks in question.

The basic catch equation for each fleet is

$$(14) \qquad C_{i,s\{c,a\},y\{c,a\}} = \sum_{h} \frac{F_{iasyh}}{\xi_{ay} Z_{asyh}} \tilde{N}_{cah} (1 - e^{-Z_{asyh}})$$

where season s and year y are inferred from cohort c and age-class a via equation 1. In the present application there are four basic types of data associated with the seasonal catches of each fleet–total catch C_{isy}, an index of abundance I_{isy}, age composition p_{iasy} and length composition p_{ilsy}:

$$(15) \quad C_{isy} = \sum_{a} C_{iasy}$$

$$(16) \quad I_{isy} = C_{isy} \,/\, f_{isy}$$

$$(17) \quad p_{iasy} = C_{iasy} \,/\, C_{isy}$$

$$(18) \quad p_{ilsy} = \sum_{a} p_{iasy}\, g\{l|a\}_{isy}$$

where g is a function of the growth parameters that expresses the probability that a fish from age-class a is length l. Although the calculations are made over the entire life span of each cohort, provision is made for the last age category in the data to be cumulative for fish older than a certain age (a plus-group) or larger than a certain size.

One issue of concern is how best to deal with the situation where some fraction of the catch is discarded (released) and subsequently dies, i.e., how to parameterize ξ. Under the presumption that discarded fish are mostly below the size limit L ,

$$(19) \quad \xi_{iay} = 1 - (1 - d_{ias})G_{L|a}$$

where *d* is the fraction of released fish that die and $G_{L|a}$ is the probability that a captured fish will be smaller than the size limit given that it is age *a*. For the commercial fishery, estimates of the number landed (harvest *H*) are available, but seldom the number caught (*C*) or discarded (*D*). Again, assuming discarded fish are mostly below the size limit, one obtains

$$(20a) \quad H_{iasy} = G_{L|a}C_{iasy}$$

$$(20b) \quad D_{iasy} = (1 - G_{L|a})C_{iasy}$$

The corresponding number discarded dead (*DD*) and total number killed (*K*) are

$$(20c) \quad DD_{iasy} = d_{ias}D_{iasy}$$

$$(20d) \quad K_{iasy} = H_{iasy} + DD_{iasy}$$

In the case of the recreational fishery, estimates for both the number harvested (observed or unobserved) and the number discarded alive are provided by the Marine Recreational Fisheries Statistics Survey[2] (MRFSS). The MRFSS does not provide information on the size or age composition of the released fish, however most of these appear to be below the minimum size limit (K. Burns, pers. Comm.). Accordingly,

An important innovation proposed for this model is the incorporation of age-composition samples identified to stock (Cowan et al. 2002). This will potentially allow the movements of each stock to be quantified. In that case, equations (17) and (18) still apply, but a subscript is included to reference stock.

Reference points

The computation of yield per recruit and MSY based reference points is complicated by the existence of multiple fleets operating in multiple habitats on multiple stocks. For example, the maximum sustainable yield obtained by maximizing over all stocks and fleets simultaneously will generally be lower than the sum of values obtained when each stock is treated as though it were harvested independent of the other stocks. Moreover, maximizing over all fleets simultaneously can lead to a situation where fleets that are less efficient in terms of yield are allocated negligible effort. The approach taken here is to assume the relative allocation of effort among directed fleets and the

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[2] Marine Recreational Fisheries Statistics Survey. National Marine Fisheries Service. Fisheries Statistics and Economics Division, 1315 East-West Highway Silver Spring, MD 20910.

absolute effort of undirected fleets are constant at current levels (an average of recent years). The relative effort allocations may also be modified by a series of multipliers to anticipate the effect of future regulations. The maximum sustainable yield is then computed by varying the overall scale of the effort of the directed fleets so as to maximize their landings over select stocks and habitats. Essentially the method assumes that the effort of some fleets can be controlled directly, while others cannot.

A difficulty with the MSY approach is that it can lead to a situation where less productive stocks are extirpated as a consequence optimizing the exploitation of more productive stocks. A less risk-prone policy would be to adopt a strategy based on maintaining the equilibrium spawning potential ratio *SPR* (Goodyear, 1993) above some fixed value. The spawning potential ratio is defined as the expected lifetime fecundity per recruit at a given *F* divided by the expected lifetime fecundity in the absence of fishing. In the simplest case of one fishery, one stock, one season and one habitat it can be obtained as

(21) $$SPR = \frac{\sum_{a=1}^{A} E_a e^{-\sum_{i=0}^{a-1} Fv_i + M_i}}{\sum_{a=1}^{A} E_a e^{-\sum_{i=0}^{a-1} M_i}}$$

More generally, SPR is equivalent to ϕ when recruitment is constant. Thus, it may be calculated for various combinations of fishing effort by initializing the recursion implied by equation (13) with the same arbitrary recruitment values for all scenarios (including no fishing).

Parameter estimation

A Bayesian approach to estimation is adopted wherein one seeks to develop a 'posterior' probability density for the vector of parameters Θ that is conditioned on the data D, $P(\Theta \mid D)$. By application of Bayes rule it is easy to show that

(22) $$P(\Theta|D) \propto P(D|\Theta)\, P(\Theta) .$$

where $P(D \mid \Theta)$ is the sampling density (likelihood function) and $P(\Theta)$ is the prior density (in this case the analyst's best guess of the probability density for Θ). Estimates for Θ may be obtained by integrating the posterior (the classical Bayes moment estimator)

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

or by minimizing its negative logarithm (the highest posterior density estimator, Bard 1974)

(24) $$\min_{\Theta} \left\{ -\log_e P(D|\Theta) - \log_e P(\Theta) \right\} \qquad .$$

Sampling densities

Sampling densities, also known as likelihood functions, measure the disparity between the model predictions and observed data. Catch, index and effort data are assumed to be normal or lognormal distributed, e.g.,

$$(25)\qquad -\log_e \mathrm{P}(\boldsymbol{C}|\Theta) = \begin{cases} 0.5\sum_i \sum_y \sum_s \left(\dfrac{C_{isy}^{obs} - C_{isy}}{\sigma\{C_{isy}\}}\right)^2 - \log_e \left[\sigma^2\{C_{isy}\}\right] & normal \\ 0.5\sum_i \sum_y \sum_s \left(\dfrac{\log_e(C_{isy}^{obs} / C_{isy})}{\sigma\{\log_e C_{isy}\}}\right)^2 - \log_e \left[\sigma^2\{\log_e C_{isy}\}\right] & lognormal \end{cases}$$

where the superscript *obs* distinguishes the observed data from the value predicted by the model. The variable $\sigma\{\}$ is the standard deviation of the enclosed quantity. Note that a similar term would be implemented when data exist on the number of releases (as are provided by the MRFSS recreational survey).

Data describing the age and length composition of a sample ought to be multinomially distributed provided measurement error is low. In that case, the appropriate log-likelihood functions for the age and length composition of the catch are

$$(26)\qquad \begin{aligned} -\log_e \mathrm{P}(\boldsymbol{p}_a|\Theta) &= \sum_i \sum_y \sum_s n_{isy} \sum_a p_{iasy}^{obs} \log_e p_{iasy} \\ -\log_e \mathrm{P}(\boldsymbol{p}_l|\Theta) &= \sum_i \sum_y \sum_s n_{isy} \sum_l p_{ilsy}^{obs} \log_e p_{ilsy} \end{aligned}$$

where again the superscript *obs* distinguishes the observed data from the value predicted by the model and *n* indicates the effective sample size input by the analyst. An option is provided to use the ‘robust likelihood’ function of Fournier et al. (1998) instead of the multinomial distribution.

Prior densities

Prior densities are similar to sampling densities in that they measure the disparity between the model predictions of a parameter and other information known about it. The difference is that sampling densities express the probability of observing some information (data) given the model estimates, whereas prior densities express the probability of observing the model estimates given some information (prior knowledge). In cases where the prior and sampling densities are both normal, the solution will be the same no matter whether the information is treated as data or as prior knowledge. Otherwise, the solutions can be quite different.

Ideally, prior densities should be based on previous analyses of data sets that are no longer available (or otherwise intractable to use). Where data-based priors are unavailable, the analyst may choose to adopt functional forms that are relatively uninformative over the plausible range of parameter values. For example, the logarithm of the natural mortality rate might be treated as uniformly distributed between -5 and 2. The primary advantage of using uninformative priors is that the potential for introducing biases is minimized. On the other hand, if the data relating to a particular parameter are too sparse, the solution may be so uncertain as to be rendered meaningless. This observation has led some to develop prior densities based on expert opinion (e.g., Wolfson et al. 1996, Punt and Walker, 1998) or analyses of other species (e.g., Liermann and Hilborn 1997, Maunder and Deriso 2003).

One parameter of special concern in the analysis of Gulf of Mexico red snapper is the steepness of the stock recruitment relationship. Previous analyses have estimated this parameter to be implausibly close to the mathematical limit of 1.0 (Anon., 1999), suggesting it may not be well-determined. A possible alternative is to develop a prior based on 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). Porch et al. (2003) used this approach to construct a prior for the related parameter α (see Figure 2). 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. It might be best to incorporate this uncertainty in a more rigorous fashion.

Covariance parameters

It is not generally possible to obtain consistent estimates for all of the elements of the covariance matrix associated with (12), i.e., the correlation coefficients and variances. In the case of the fishery (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 habitat (IWC 1994). To accommodate such possibilities, the variance parameters for the catches (*C*) and indices of abundance (I) may be modeled as

$$\begin{aligned} \sigma^2\{C_{iy}\} &= \chi^2\{C_{iy}\} + \lambda\{C_i\}\sigma^2 \\ \sigma^2\{I_{iy}\} &= \chi^2\{I_{iy}\} + \lambda\{I_i\}\sigma^2 \end{aligned} \tag{27}$$

where the χ^2 are the annual observation variances associated with each type of data (estimated outside the model), σ^2 reflects some overall process variance (estimated within the model), and the λ 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 variances corresponding to the age and length composition data are implicit functions of sample size, which is controlled on input.

The model has been 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.

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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.

Application to red snapper

Model structure

The model described above was applied to information on red snapper populations in U.S. waters during the years from 1872 to 2003. Five fisheries were designated for each of two regions (east and west): handline, longline, recreational, closed season discards and shrimp bycatch. Three four-month seasons were modeled, starting in January. Spawning was assumed to occur during the second season. Mixing, when it occurs, was assumed to be diffusive in nature, i.e., fish move more or less independently of where they were spawned. Spawning was also assumed independent of natal origins, i.e., there is no site fidelity.

Thirty age classes were modeled starting with age 1, with the number of age 1 fish being computed as a Beverton and Holt function of the spawn produced during the preceding year. This approach essentially assumes that the bycatch rate is negligible compared to mortality rate owing to natural density-dependent processes (see discussion by Powers and Brooks, 2004)

Parameter specifications. The vulnerability and catchability coefficients for each specific fleet was assumed to be relatively unchanged through time, but allowed to vary with age and among fleets. The relative effort of each fleet was allowed to vary by year essentially as a free parameter (thus the effective selectivity of the fishery as a whole varied noticeably through the years). The vulnerability coefficients for the fishery independent surveys were fixed as described by (reference).

Natural mortality was fixed to 0.6 yr-1 for age 1 and 0.1 yr-1 thereafter (a second run was made using a value of 0.3 yr-1 for age 1 as a sensitivity analysis). The fecundity at age (including maturity) was set to the vector derived from the age-conditioned model described by Porch (), normalized to a maximum value of 1 (at age 30). Thus, the spawning stock estimates for any given year are *not* the actual number of eggs produced by the population, but should be interpreted as the number of 30 year-old spawners required to produce the same number of eggs (effective number of fully-productive spawners).

Likelihoods and priors. The catch, effort, and relative abundance indices were assumed to be approximately lognormal distributed. Age composition was assumed to be multinomial distributed. A lognormal prior (see Knowlis 2004a) was imposed on α with a median value of 13.3 and log-scale variance of 1.28 (equivalent to a mean steepness of about .86). The remaining parameters were treated as free parameters constrained to lie with bounds that encompassed the range of plausible values (essentially the same as specifying uninformative priors over the feasible range).

Data employed

Landings data. The commercial landings data used in this exercise are discussed by Turner et al. (2004) for the period from 1963 onwards and by Porch et al. (2004) for the period before that. The annual recreational harvest since 1981 is based on the NMFS Marine Recreational Fishery Statistical Survey (MRFSS), Texas Parks and Wildlife Survey and NMFS headboat survey as described by Turner et al (2004). The recreational harvest statistics used for earlier years (1946-1980) were reconstructions based on U.S. census data (Scott 2004). It is assumed that prior to 1946 the recreational take was negligible in comparison to the commercial take owing to the relative inaccessibility of the fishing grounds (powered vessels were few and expensive, making offshore trips mostly a past time for the wealthy). The bycatch of juveniles from the offshore shrimp fishery is based on the series produced by Nichols (2004) and discussed by Turner and Porch (2004), which extends back to 1972. A time series of offshore shrimping effort, which extends for the entire history of the fishery, was also used to tune the model (see Porch and Turner 2004). The catch during the closed season was derived by Turner et al. (2004).

The CV's used to weight each catch data point were fixed at 0.1 (arbitrary low value) for the commercial fleets inasmuch as they represent a census. The exceptions are for years when no census was taken, in which case the effective CV's were computed from the census estimates immediately before and after the year in question (absolute difference divided by the mean); the reasoning being that the true value likely lies somewhere between those values. The CV's for the recreational catches after 1981 came from the variance estimates produced by the MRFSS (Diaz, pers. comm.); the CV's for the catch inputs prior to 1982 were assigned arbitrary high CVs (1.0) inasmuch as they were not actually observed . The CV's for the shrimp bycatch are based on the CV's of the overall index (ages 0-2), but modified by the proportion that are not age zero (see Turner and Porch 2004). An additional process variance term is not included (cf. Equation 27); instead it is assumed that process variances effecting the catch are adequately modeled by inter-annual deviations in recruitment and fishing mortality rates.

Indices of abundance. Ten indices of abundance were used, 5 for each region (east or west). These include the handline CPUE series based on log books (McCarthy and Cass-Calay 2004), the MRFSS recreational indices (Cass-Calay 2004), SEAMAP larval indices (Lyczkowski-Shultz et al. 2004), SEAMAP trawl survey (Nichols et al. 2004) and video surveys (Gledhill and Ingram 2004). The handline logbook indices were modeled in this case as landings per unit effort rather than catch per unit effort, thereby taking into account the potential discards owing to the minimum size limit and removing the major objection to their use by the previous SEDAR panel.

The CV's for the indices of abundance are based on the year-specific estimates that come from the GLM-based procedures used to standardize them (see the references cited above). These are regarded as representing observation variance. To this the model adds an internally-estimated process variance term, which is intended to represent random discrepancies between the trends in the indices and the trends in the actual population it purports to track (see equation 27).

Index values were rescaled to approach the magnitude expected for the population to facilitate the estimation of the catchability scaling parameters (e.g., it allows the initial guesses to be set to 1 and makes setting the upper and lower limits more intuitive).

Age composition. The age composition (and effective sample sizes) used for the commercial and recreational fisheries is described by Knowlis (2004b). Inasmuch as the model makes seasonal calculations with spawning occurring during the second season (midyear), the data for each year were aggregated by the actual integer age in years (i.e., it is not necessary to shift the ages by 0.5 to track cohorts as VPA must do). The age composition for the shrimp by catch was based on model output from Nichols (2004). The age composition used for the closed season is described by Turner et al. (2004).

Length composition. Length composition (and effective sample sizes) data were available for the commercial and recreational fleets from 1981 to the present (see Brooks 2004). The data were fit on a seasonal rather than annual basis to better accommodate the rapid growth exhibited by younger red snapper. The population growth curve and coefficient of variation of length about age were fixed to the values estimated by Diaz at al. (2004).

Projection specifications

The future course of the red snapper fishery was modeled through 2032 using the population dynamics equations described earlier. Owing to time constraints, only deterministic projections were made, however it is possible in principle to conduct stochastic projections and estimate the uncertainty via the inverse-Hessian method.

Future recruitment is assumed to follow the pattern dictated by the estimated Beverton and Holt spawner-recruit relationship. The fleet-specific vulnerability patterns used in the projections were set equal to the estimated values and the minimum size limits for each fleet were assumed to remain unchanged. The fleet-specific apical fishing mortality rates for the first year of the projections (2004) were set equal to “current levels”, in this case the average of the estimates for the last three years (making the implicit assumption that the effort in 2004 was about the same as the 2001-2003 average). For subsequent years the apical fishing mortality rates were either fixed to various rates (including zero, “current”, and several different benchmarks relating to MSY and spawning potential ratio) or determined numerically by matching an imposed catch quota (TAC) on the directed component of the fishery. In case of the latter, it was not always possible to achieve the higher TACs for all of the projection years. In such cases the model selects a catch schedule as close to the TAC as possible without completely extirpating the stock before 2032. In deriving this schedule, the model assumed that the fishery is more likely to attempt to meet the quota during the earliest years of the projections than in subsequent years.

In some cases the shrimp effort (not bycatch) was assumed to be reduced by various percentages. Closed season discards were assumed to occur at the same rate regardless of the size of the quota.

Results

Model 1: no intermixing between east and west, $M_1 = 0.6$ yr^{-1}

Model fits to data. The model matched the total catch data quite well with the exception of certain unusually high values that happen to have high CV’s associated with them (Figure 3). These include the 1983 peak in the eastern recreational catch series and the high shrimp bycatch during some of the early years. The model fit most of the indices of abundance reasonably well (Figure 4), but could not reconcile the increasing trend in the western larval index (representing spawners) with the flat or declining trends indicated by the other western indices. The model fits to the SEAMAP trawl series show a strong residual pattern where the predictions for the early years are considerably lower than the trawl values, but the predictions for the later years are considerably higher. The mismatch for the early years can be attributed the very high CV's associated with those data. The mismatch in more recent years reflects the influence of the bycatch data, which, in the context of relatively constant effort, suggests recruitment generally has increased in recent years. The shrimp effort series were fit very well (Figure 5) owing to the rather low observation CV's assigned to those data (10%).

The fits to the age composition data, aggregated over all years, appear to be quite good (Figure 6). It should be kept in mind, however, that the fits to individual years are more noisy, particularly where the sample size was small.

Parameter estimates. The estimated vulnerability and apical fishing mortality rates (*F* on the most vulnerable age group) are shown in Figure 7. In general, the vulnerabilty of red snapper to the recreational and commercial hand line fleets follows a dome-shaped pattern with a peaks at age 1 or 2 for the former and at age 5 for the latter. (It should be reiterated that the vulnerability coefficients reflect the probability of being caught and includes undersized fish; the probability of being caught and landed is the vulnerability coefficient multplied by the probability that a fish is greater than the size limit.) The vulnerabilty of red snapper to the commercial long line fleet follows a logistic pattern with older animals (10+) being the most vulnerable. The vulnerability patterns for the closed season "fleets" were between the hand line and longline. As expected, age 1 fish were much more vulnerable to shrimp trawls than age 2 or older.

The estimated trends in apical fishing mortality (the *F* on the most vulnerable age class) indicate persistent increase for all fleets. Although recreational fishing in the east appears to have declined markedly in recent years, it remains at rather high levels. The highest mortality rates were exhibited by the western shrimp fishery followed by the eastern recreational and western commercial handline fisheries. Note, however, that the high shrimp bycatch *F* applies to a single age group, whereas the lower apical *F'*s estimated for the handline and recreational fleets apply to multiple age classes.

There does not appear to be a strong relationship between the number of recruits and the effective number of spawners during the previous years. Estimates of the maximum potential spawn per recruit (α) were near the limit of 151 imposed by the model, which translates to a steepness of 0.974.

Estimated population trends. The estimates of historical trends in the effective number of spawners and age 1 recruits are shown in Figure 8. Under pristine conditions, the western population of red snapper in U.S. waters is estimated to have been about three times as large and three times as productive as the eastern population. The eastern population, which was fished hard early in the 1900's, shows the first signs of decline. The western population is not estimated to have declined substantially until the 1950's. By the 1980's both populations had been seriously depleted and were below the level required to maintain MSY. The extent of the depletion depends on the way in which MSY is defined (see below).

Projections. Projected trends in the effective number of spawners and total landings are shown for various permutations of "current" conditions in Figure 9. The spawning stock reference points in this figure assume the effort of the directed fleets can be scaled down to maximize long-term landings while the shrimp bycatch and closed season discards continue at current levels (i.e., are not controlled). Hereafter the yield associated with this long-term strategy shall be referred to as MSY{directed, post-shrimp}, which is estimated to be about 3.1 million lbs for the east and 3.2 million lbs for the west (the value for the west is similar to the value for the east owing to the much larger western shrimp bycatch). The spawning potentials of the eastern and western populations are estimated to have been reduced to 35% and 49 %, respectively, of the level associated with SMSY{directed, post-shrimp}. The current fishing mortality rate exerted by the directed fleet is estimated to be about 2.6 times greater than FMSY{directed, post-shrimp}. Not surprisingly, the projections indicate that the current TAC of 9.12 million lbs (Figure 9a) is not sustainable. Current levels of effort (Figure 9b) may be sustainable, but the population will be driven to dangerously low levels. The 9.12 million lb TAC may be sustainable with a severe reduction in shrimp bycatch (Figure 9c), but the spawning stock would remain well below SMSY{directed, post-shrimp}. On the other hand, the spawning stock is projected to recover in less than ten years in the absence of any directed harvest (Figure 9d, assuming closed season discarding does not increase) or no fishing-related mortality (Figure 9e).

The projections where fishing is assumed to be reduced from current levels in 2004 to FMSY{directed, post-shrimp} suggest a full recovery to SMSY{directed, post-shrimp} is possible by 2032 (Figure 10), largely owing to a series of fortuitous recruitments estimated to have occurred over the last several years. Reductions in shrimp effort would of course hasten this recovery.

The potential for recovery also depends on the way the benchmark is defined. To this point only F and S levels associated with MSY{directed, post-shrimp} have been examined. An alternative is to define MSY as the maximum long-term landings that could have been achieved prior to the advent of offshore shrimp trawling, hereafter referred to as MSY{directed, pre-shrimp}. In that case the equilibrium landings amount to 3.8 million lbs for the east and 8.4 million lbs for the west (see Figure 11). The spawning potential of the east and west is estimated to be 35% and 22% of SMSY{directed, pre-shrimp}. Current levels of fishing mortality are estimated to be 2.3 times greater than FMSY{directed, pre-shrimp}. By definition, catches equal to MSY{directed, pre-shrimp} cannot be achieved, let alone sustained, with a nonzero shrimp bycatch (Figure 11b).

Another alternative is to define MSY in terms of the entire fishery, assuming the effort of all fleets can be scaled down by the same proportion, including shrimp bycatch and closed season discarding. This is the so-called "linked-selectivity" approach, sometimes referred to as "policy neutral" because all fleets endure the same proportional reduction in effort (technically this is policy-neutral only with respect to red snapper, other important concerns notwithstanding). Hereafter this definition shall be referred to as MSY{all}. The total equilibrium landings for the east and west are 3.9 and 8.7 million lbs, respectively. Note that these are slightly greater than the corresponding values for MSY{directed, pre-shrimp}, despite the fact that some shrimp bycatch is still allowed, because it is assumed in this case that the closed season discards would be reduced by the same proportion as the other fleets (i.e., the control is on effort). The spawning potential of the east and west is estimated to be 15% and 8% of SMSY{all}. Current levels of fishing mortality are estimated to be about 4 times greater than FMSY{directed, pre-shrimp}.

One disadvantage of MSY-based reference points, such as have been discussed so far, is that the corresponding biomass targets change with the vulnerability pattern. For example, (e.g., SMSY{directed, post-shrimp} is less than half of SMSY{directed, pre-shrimp}. Clearly policies based on the former are more risk-prone than policies based on the latter. Moreover, in cases where one stock is larger and more productive than another, MSY-based policies can sometimes lead to the extirpation of the less productive stock. A more stable and potentially less risky policy might be based on maintaining a particular spawning potential ratio (SPR). While the fishing mortality rate associated with a given SPR (F%SPR) depends on the current vulnerability pattern, the corresponding long-term spawning potential (S%SPR) does not. For this paper the value of F%SPR is chosen so that the SPR value of the most affected stock is equal to the desired level; the SPR level achieved by the remaining stock being greater than or equal to the desired level. In the present case (model 1), SPR levels greater than about 16% cannot be attained under current levels of offshore shrimp effort. Trajectories of yield and relative spawning potential for SPR levels of 5%, 10% and 15% are shown in Figure 12. The trends under the FMSY{directed, post-shrimp} policy closely match the trends under an F5%{directed, post-shrimp}, while the trends for the FMSY{directed, pre-shrimp} policy look much like the trends for the F10%{directed, post-shrimp} policy. Generally speaking, policies based on maintaining such low SPR values are regarded as extremely risk prone for most stocks.

Model 2: no intermixing between east and west, $M_1 = 0.3\ yr^{-1}$

Model 2 was identical to model 1 above except that the value of M for the first age group was reduced from 0.6 yr^{-1} to 0.3 yr^{-1}. The fits to the data were not quite as good as for model 1 (i.e., the objective function was slightly larger), but the corresponding graphs are essentially the same. The vulnerability and fishing mortality rate patterns are similar to model 6. The steepness estimates no longer approach the boundary constraints, but are still high (0.966 for the east and 0.973 for the west). The main effect is a substantial reduction in the estimates of the historical abundance and productivity of the western stock (Figure 13). The estimates for MSY{directed, post-shrimp} increased slightly for the east (to 3.4 million lbs compared with 3.1 for model 1), but decreased substantially for the west (to 2.3 million lbs compared with 3.2 for model 1). The relative condition of the stock appears to be similar to that estimated by model 1. For example, the current fishing mortality rate is estimated to be about 3.4 times FMSY{directed, post-shrimp} and the spawning potential for the east and west is estimated to be 30% and 57% of SMSY{directed, post-shrimp}, respectively. The implications of FMSY and FSPR policies will therefore be similar to those discussed earlier for model 1 (Figure 14), however constant catch policies will be less optimistic for any given level of TAC.

Model 3. no intermixing between east and west, $M_1 = 0.6\ yr^{-1}$, drop handline indices

Dropping the logbook-based handline indices, which indicate a substantial increase in the east and substantial decline in the west, had little impact on the assessment. The most obvious effect was a small increase in the estimated productivity of the western stock (Figure 14). The value of MSY{directed, post-shrimp} for the western fishery increased from 3.2 million pounds to 3.5 million while that for the eastern fishery remained at about 3.1 million lbs. Again, the relative condition of the stock appears to be similar to that estimated by model 1: the current fishing mortality rate is estimated to be about 2.6 times FMSY{directed, post-shrimp} and the spawning potential for the east and west is estimated to be 36% and 45% of SMSY{directed, post-shrimp}, respectively.

Model 4. no intermixing between east and west, $M_1 = 0.6$ yr^{-1} , length-based reproduction

Use of the length-based fecundity at age relationship rather than the age-based relationship (see Porch 2004 for details) also had a relatively minor impact on the outcome of assessment. The most obvious effect was a small increase in the estimated productivity of the western stock (Figure 14). The value of MSY{directed, post-shrimp} for the western fishery increased from 3.2 million pounds to 3.4 million while that for the eastern fishery remained at about 3.1 million lbs. Again, the relative condition of the stock appears to be similar to that estimated by model 1: the current fishing mortality rate is estimated to be about 2.6 times FMSY{directed, post-shrimp} and the spawning potential for the east and west is estimated to be 36% and 52% of SMSY{directed, post-shrimp}, respectively.

Model 5. no intermixing between east and west, $M_1 = 0.6$ yr^{-1} , incorporation of length data

Not finished

Model 6. With trans-regional mixing of adults, $M_1 = 0.6$ yr^{-1}.

Not run yet

Acknowledgments

none yet.

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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:

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

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

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

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 $\alpha = aS_0/R_0$ may be interpreted as maximum possible number of recruits produced by each spawner over its lifetime (Myers et al. 1998).

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

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

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

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

and, since $a = \alpha R_0/S_0$,

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

Defining $\phi = S/S_0$ gives equation (9).

Note that when spawning extends over multiple seasons in the model, but the same spawner-recruit function is used for each season, then R_0 and S_0 should be interpreted as the virgin levels associated with a particular reference season. In that case, R_0 and S_0 will not necessarily be greater that the virgin values associated with other seasons.

Table 1. Schematic representing the method of accounting used in the proposed stock assessment algorithm. The entries represent a cohort, with cohort 1 being born in season 1 of year 1, cohort 2 being born in season to of year 1, and so on. In this example there are four years of data, eight seasonal age-classes, and each year as two seasons. Thus, in order to have a complete age-structure by the first season of the data period (season 1 of year 5), it is necessary to track the first seven cohorts recruited immediately prior to the data period.

		Prehistoric period								Data period								Future period	
year		1	1	2	2	3	3	4	4	5	5	6	6	7	7	8	8	9	9...
season		1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2...
Age	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	2		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
	3			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	4				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	5					1	2	3	4	5	6	7	8	9	10	11	12	13	14
	6						1	2	3	4	5	6	7	8	9	10	11	12	13
	7							1	2	3	4	5	6	7	8	9	10	11	12
	8								1	2	3	4	5	6	7	8	9	10	11

|
First year complete age
structure
is available (ψ)

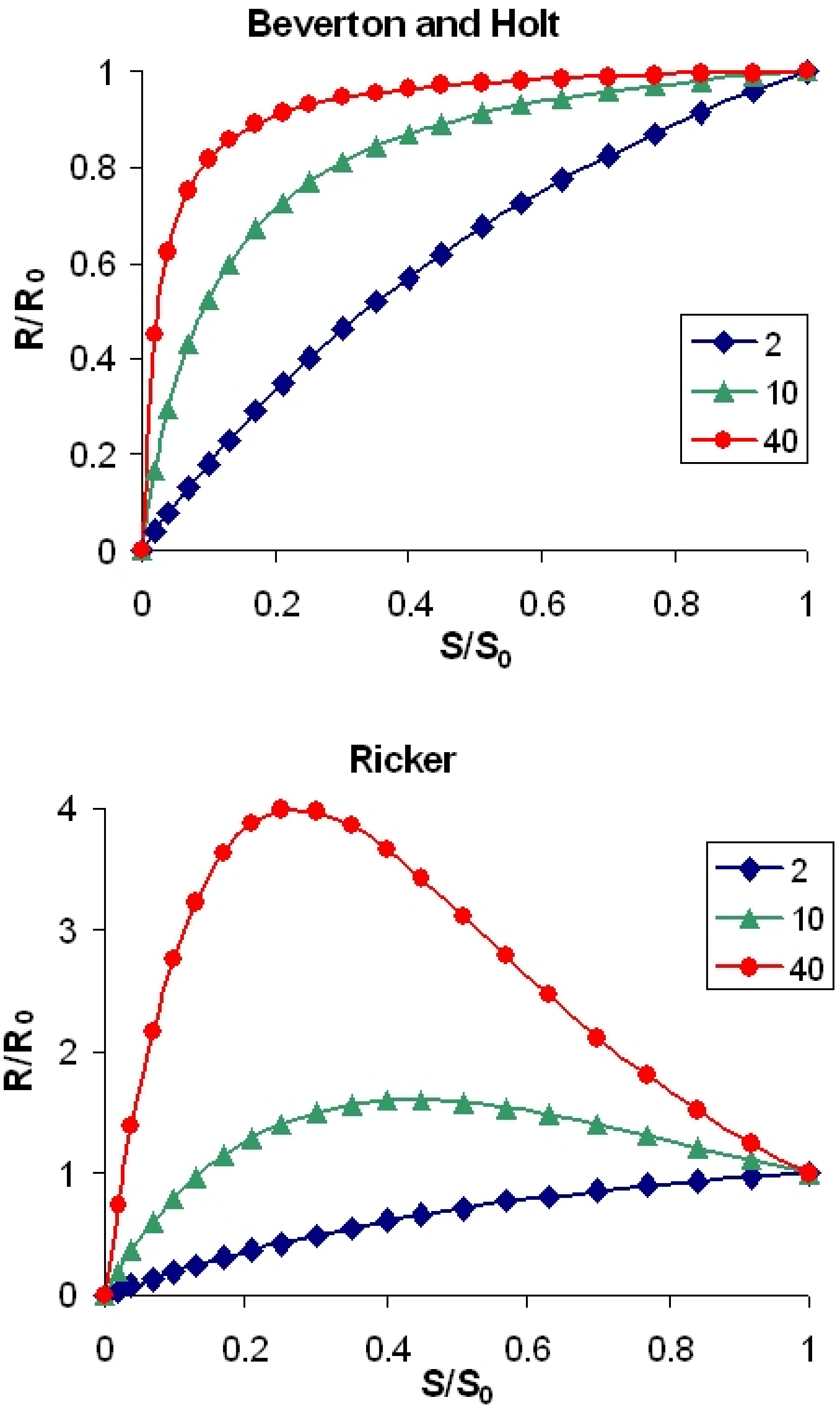

Figure 1. Examples of scaled Beverton-Holt and Ricker spawner-recruit relationships for various values of α.

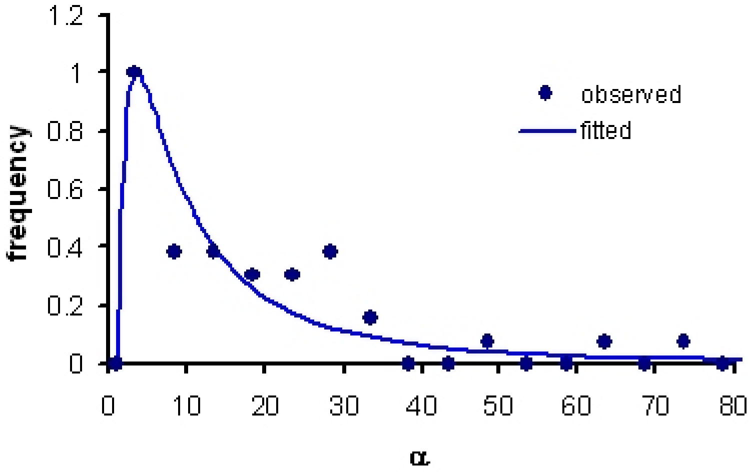

Figure 2. Lognormal prior for the maximum lifetime fecundity parameter (α) derived from the values in Myers et al. (1999) that correspond to species categorized as periodic strategists by Rose et al. (2001). The lognormal density was fitted to the values of α-1 (with median 13.3 and log-scale variance 1.28) and then shifted 1 unit to provide a prior for α.

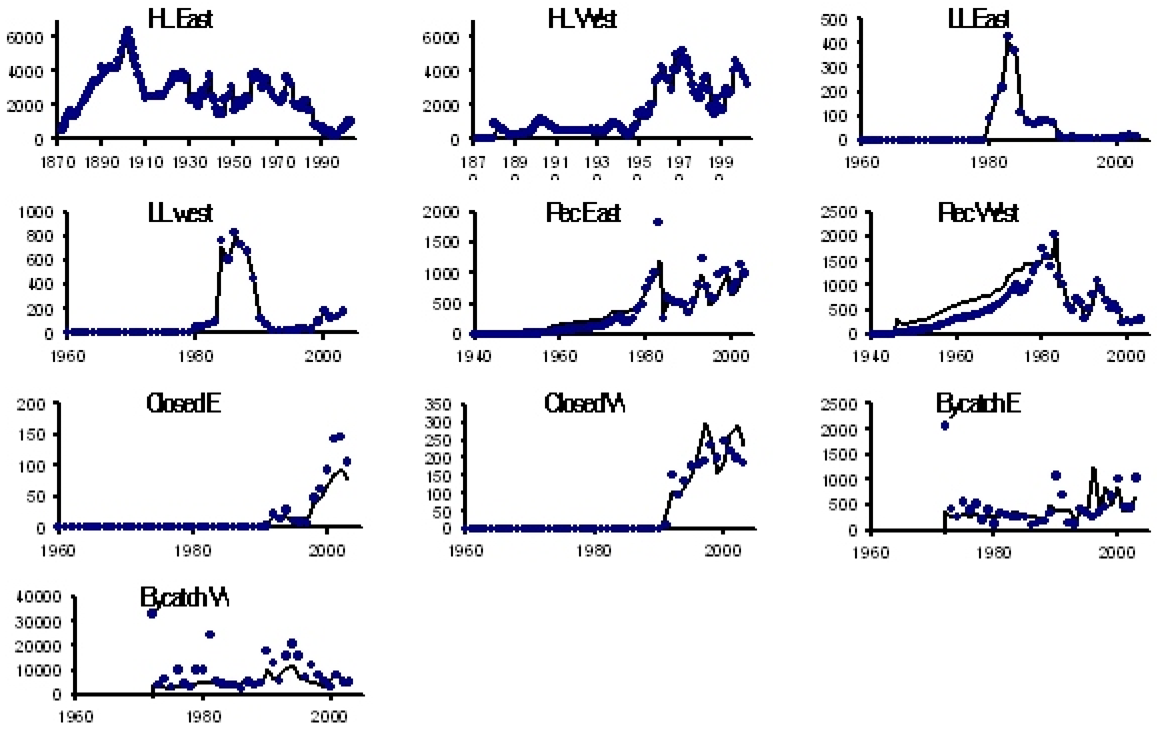

Figure 3. Model fits to the total landings in weight for the handline (HL) and longline (LL) fleets, total number landed for the recreational fleet (REC), and total number killed for the closed season (CS) and shrimp bycatch.

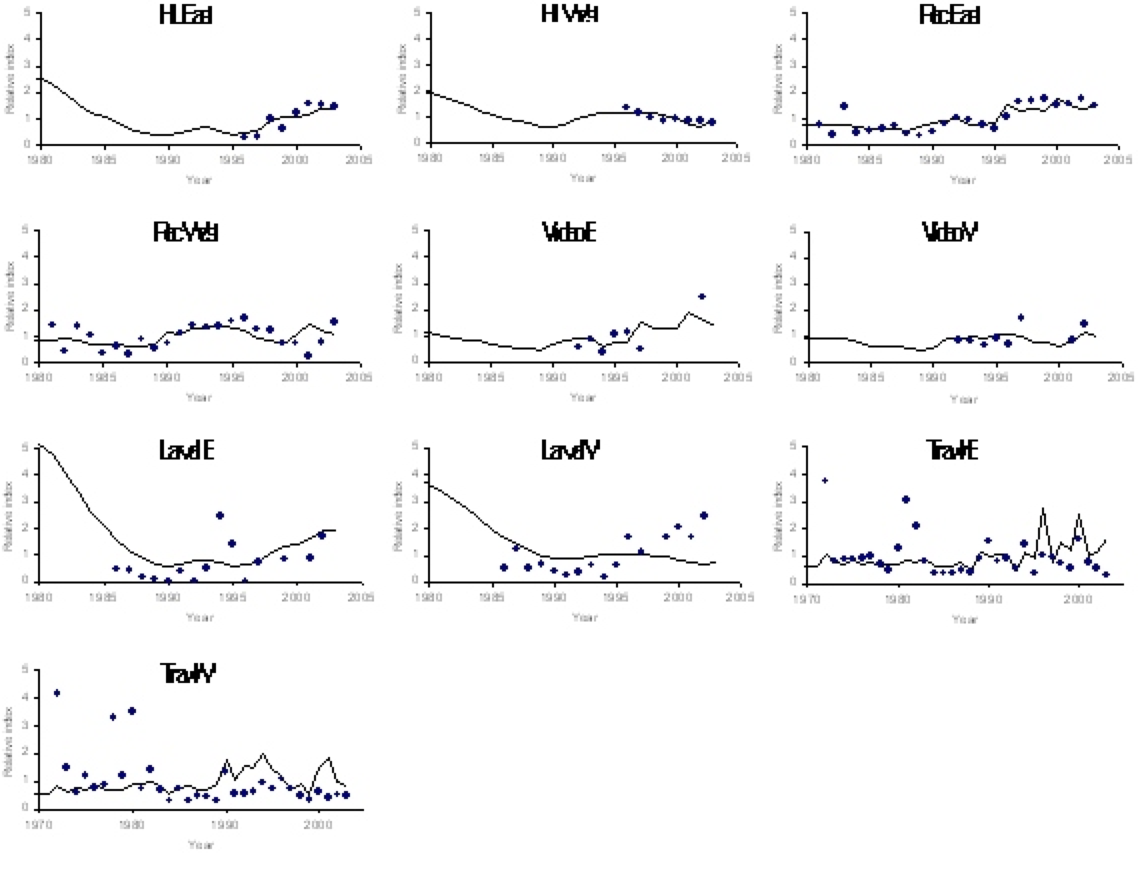

Figure 4. Model fits to indices of abundance (rescaled by their respective means).

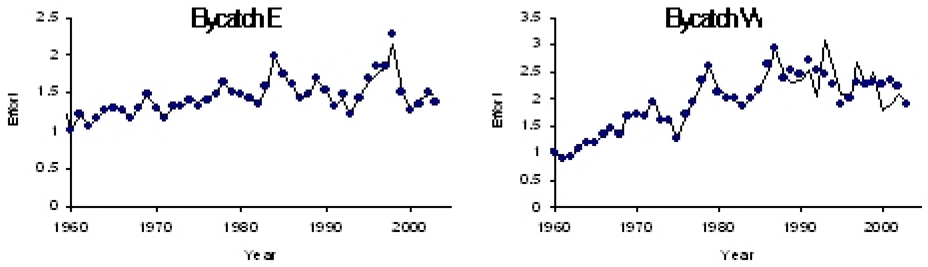

Figure 5. Model fits to the shrimp trawl effort series.

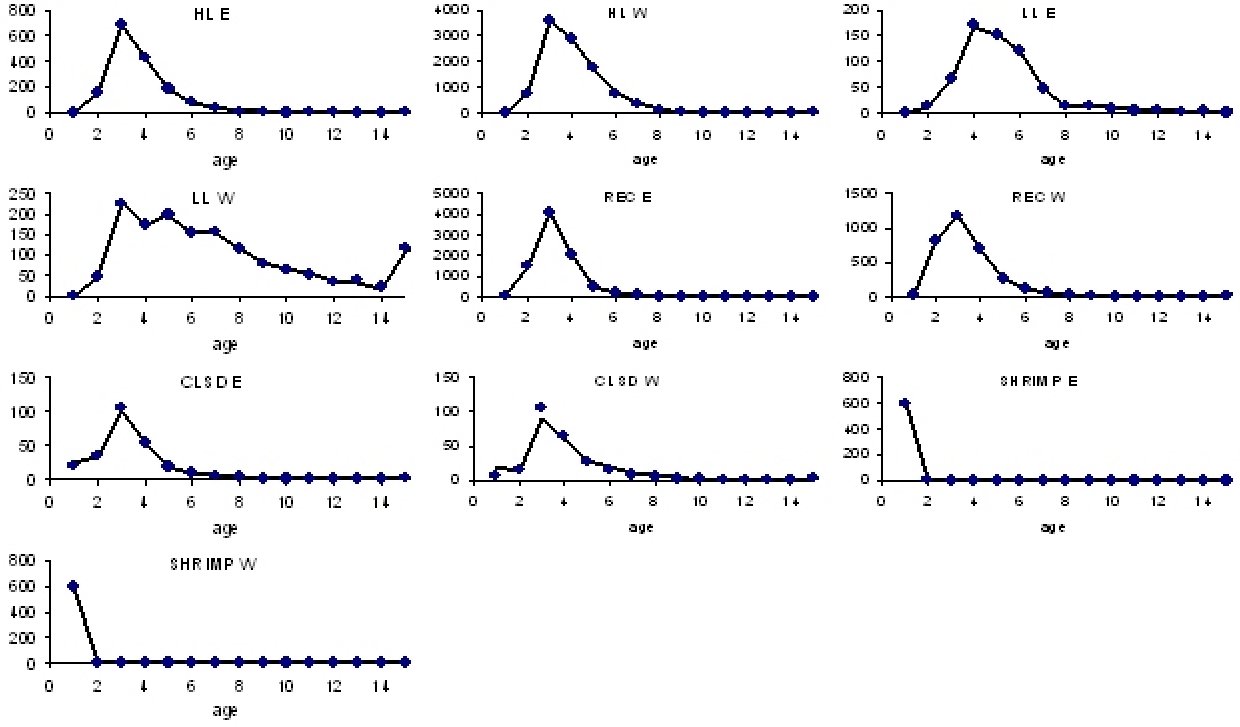

Figure 6. Model fits to the age composition data (aggregated across years).

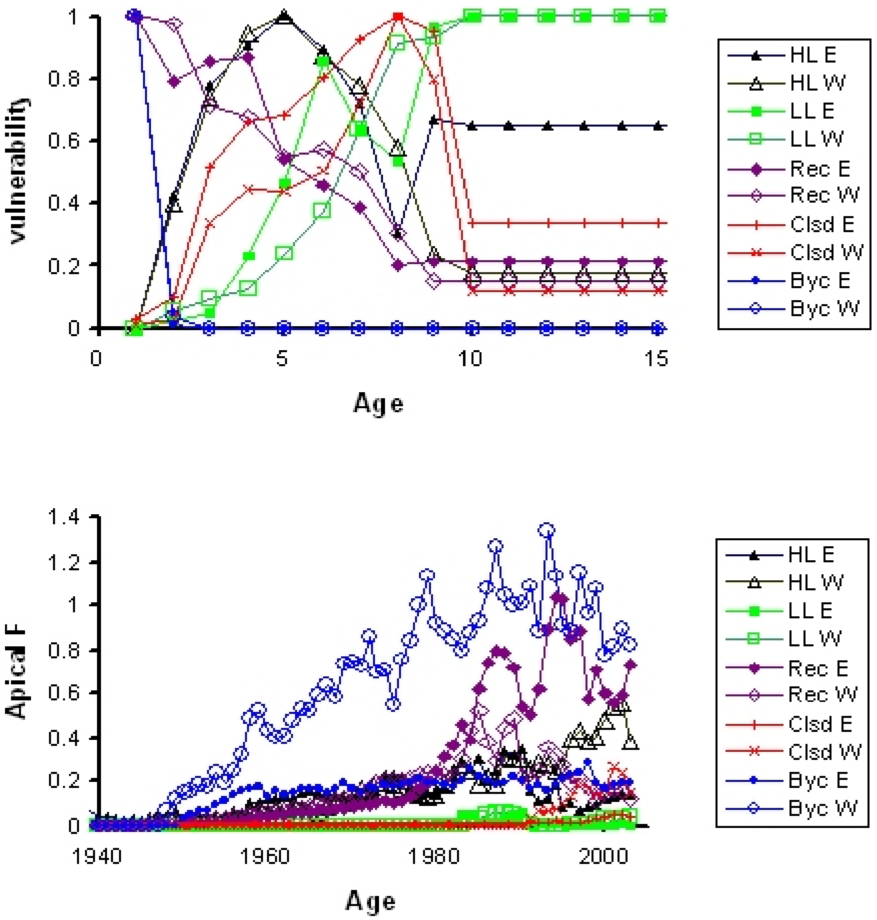

Figure 7. Model estimates of vulnerability and apical fishing mortality rate for each fleet.

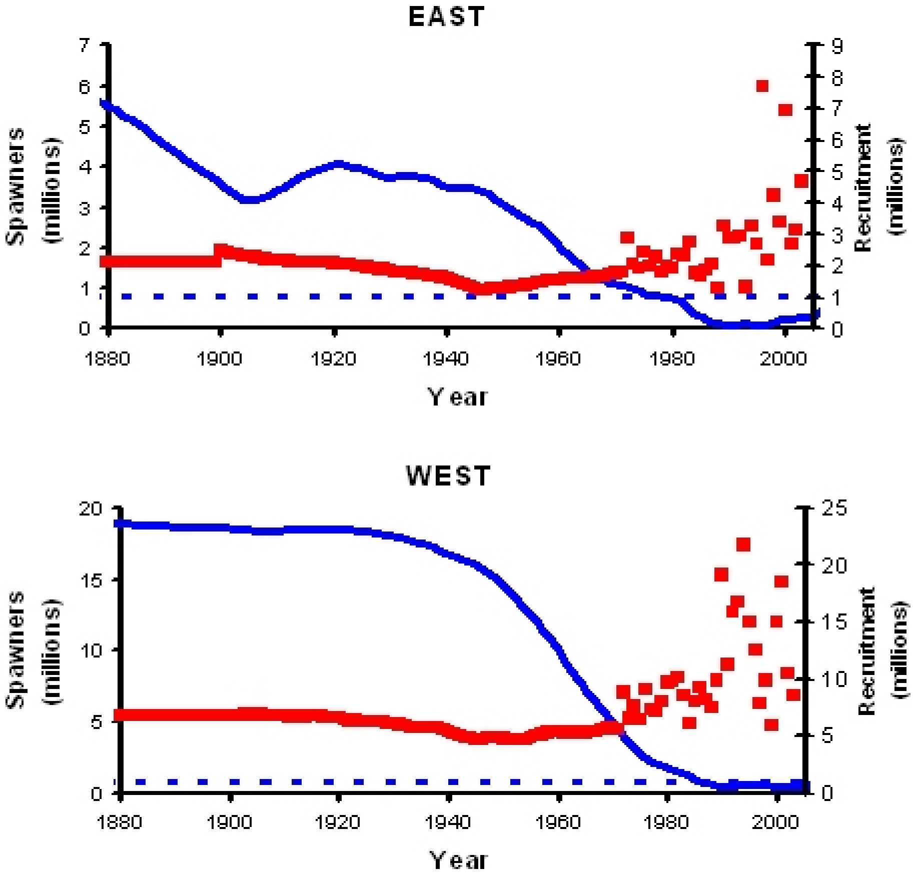

Figure 8. Model 1 estimates of the effective number of spawners (lines) and corresponding number of age 1 recruits (squares). The horizontal line gives the effective number of spawners associated with MSY{directed, post-shrimp}.

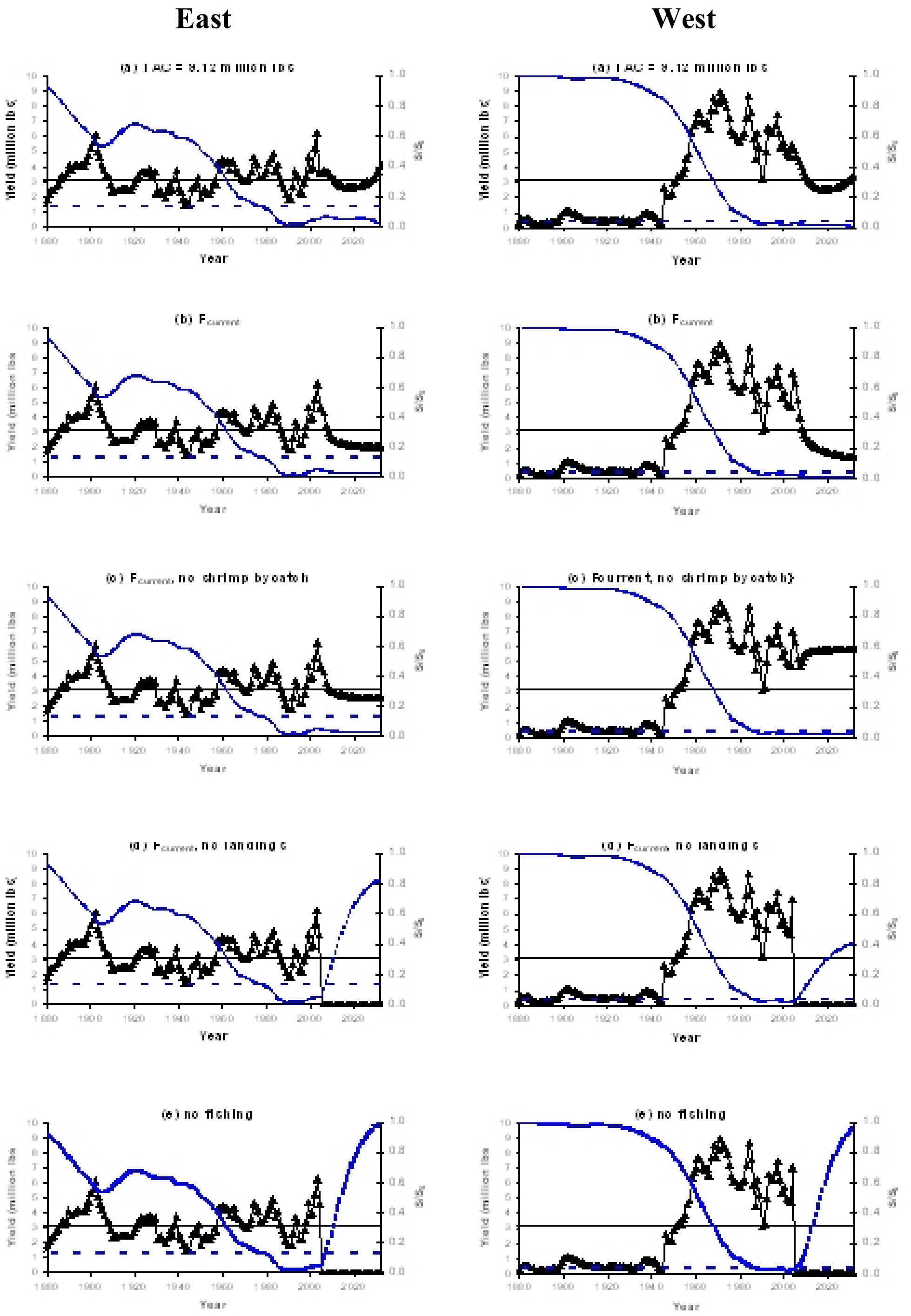

Figure 9. Projected trends in effective number spawners relative to virgin levels (S/S_0, lines lines) and landings (yield in weight, triangles) when (a) the current TAC is maintained (b) current *F* levels are maintained (c) current *F* levels are maintained, except no shrimp bycatch, (d) current *F* levels are maintained, except no landings and (e) no fishing. Horizontal lines represent MSY (solid) and SMSY (dashed).

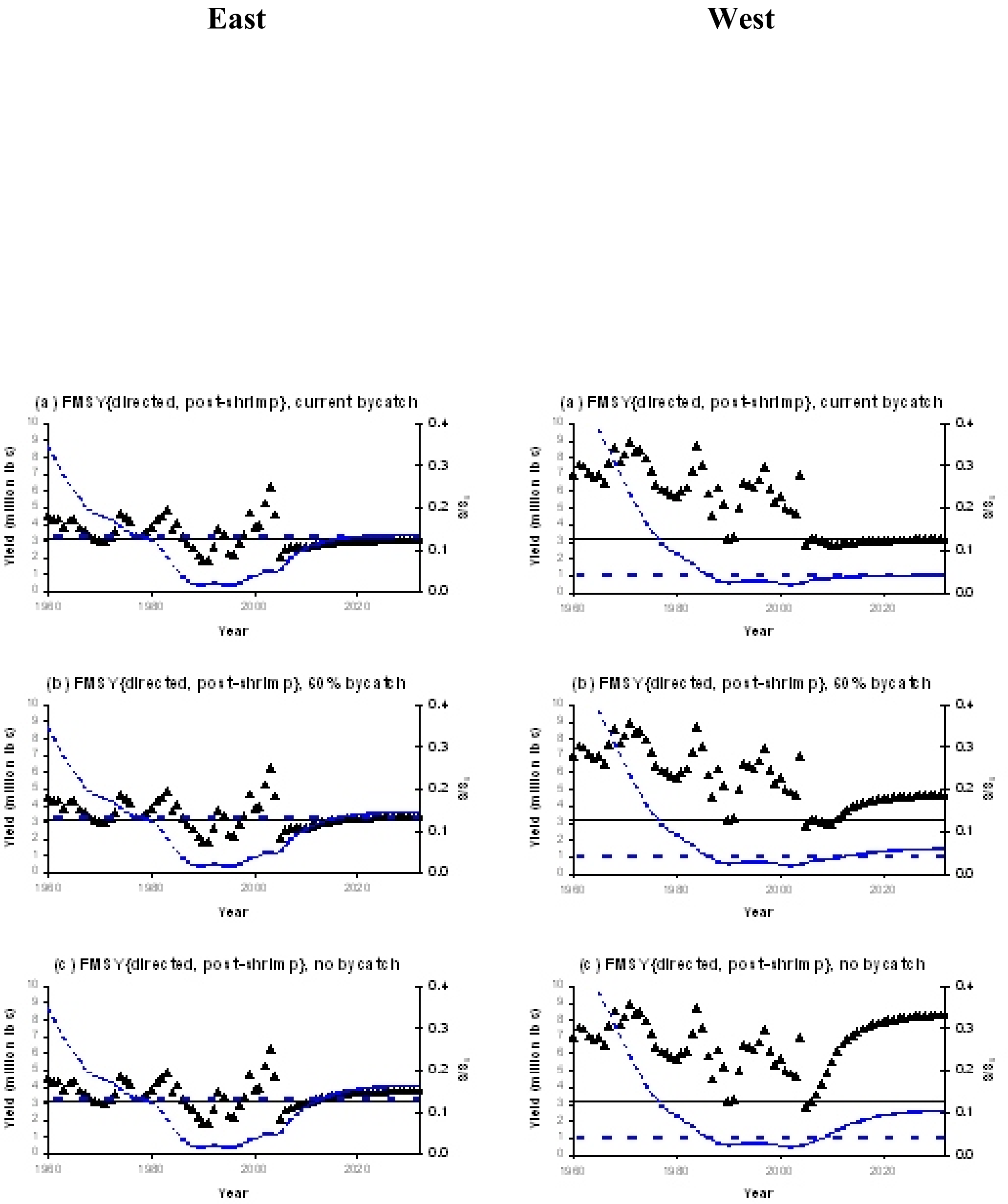

Figure 10. Projected trends in effective number spawners relative to virgin levels (S/S_0, dashed lines) and landings (yield in weight, triangles) when the directed fleet fishes at FMSY{directed, post-shrimp}, closed season discards continue at current rates and (a) shrimp effort continues at current rates; (b) shrimp effort is reduced by 40% after 2007; (c) shrimp effort is zero. Horizontal lines represent MSY (solid) and SMSY (dashed).

East **West**

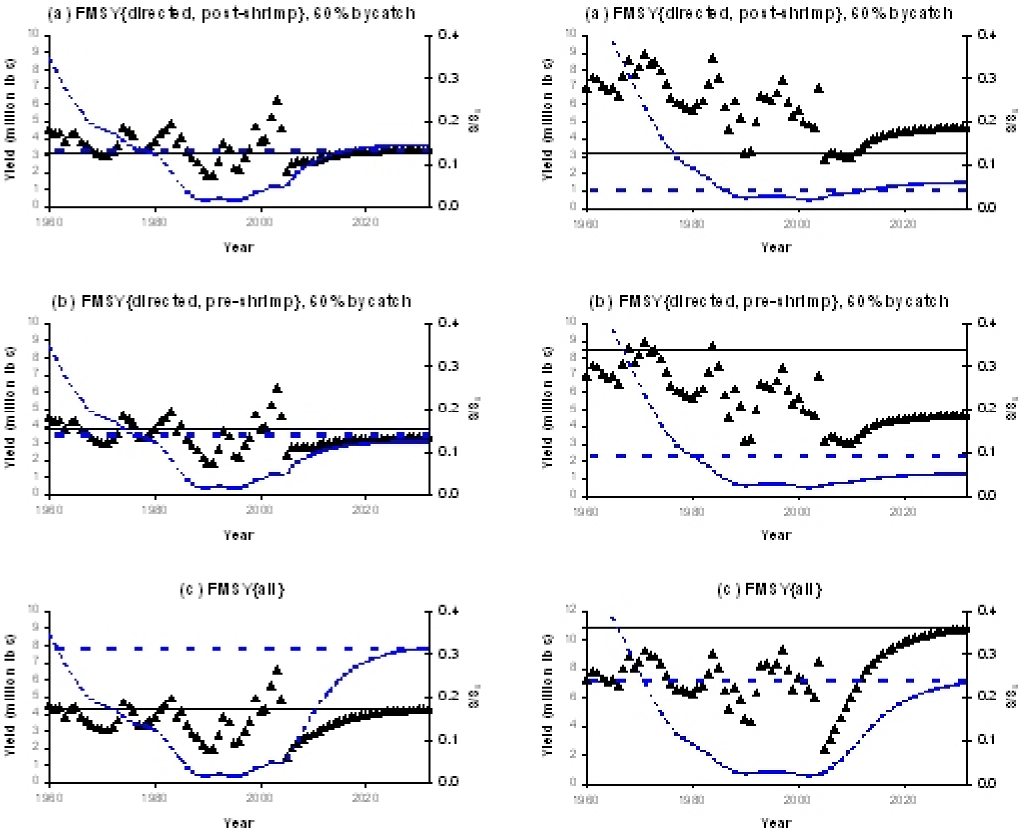

Figure 11. Projected trends in effective number spawners relative to virgin levels (S/S_0, dashed lines) and landings (yield in weight, solid lines) when closed season discards continue at current rates, shrimp effort is reduced by 40% after 2007 and (a) the directed fleet fishes at FMSY{directed, post-shrimp}; (b) the directed fleet fishes at FMSY{directed, pre-shrimp}; (c) all fleets (including shrimp bycatch and closed season discarding) are constrained to fish at FMSY{all}. Note that for case (c) the yield statistic includes the shrimp bycatch and closed season discards, not just the landings. Horizontal lines represent MSY (solid) and SMSY (dashed).

East **West**

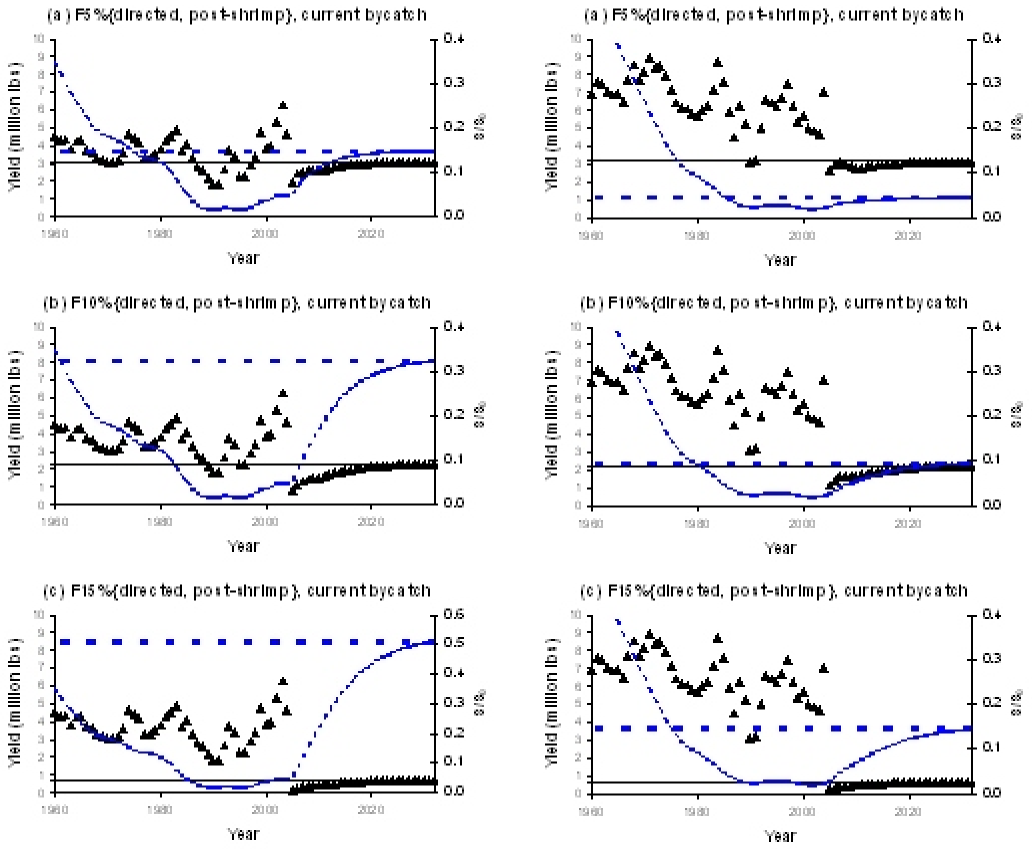

Figure 12. Projected trends in effective number spawners relative to virgin levels (S/S_0, solid lines) and landings (yield in weight, dashed lines) when closed season discards and shrimp effort continue at current rates and the directed fleet fishes at F15%{directed}, F10%{directed} and F5%{directed}. Horizontal lines represent the long-term yield (solid) and spawning potential (dashed) associated with the given SPR levels.

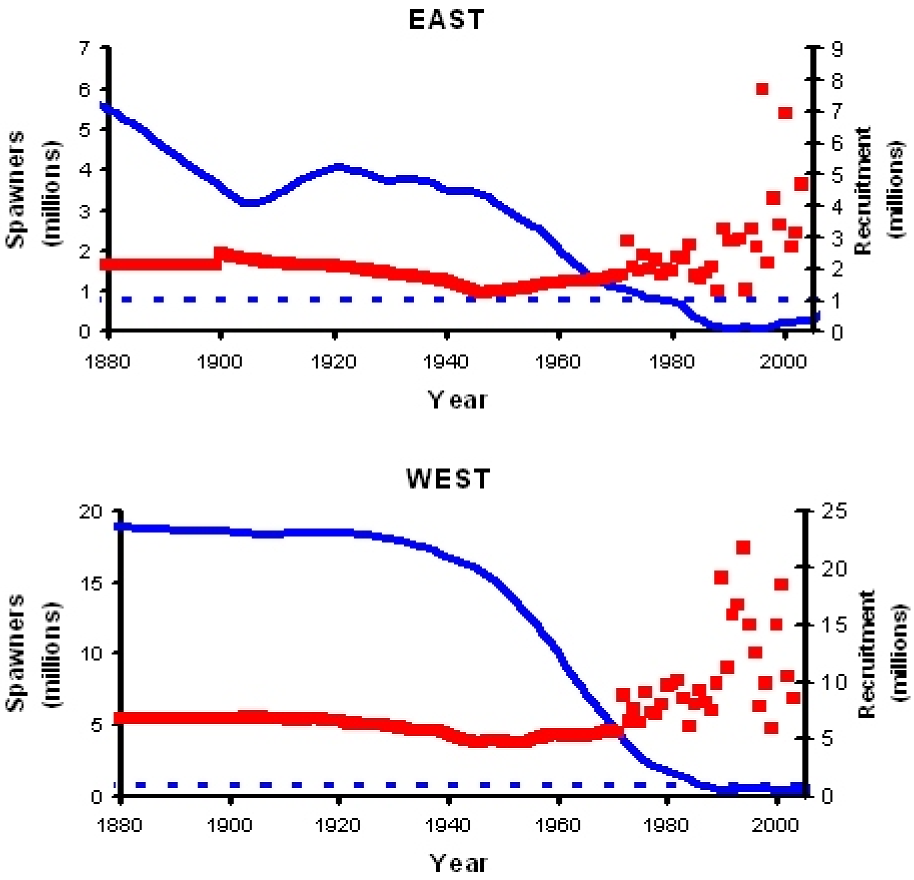

Figure 13. Model 2 (M_1=0.3) estimates of the effective number of spawners (lines) and corresponding number of age 1 recruits (squares). The horizontal line gives the effective number of spawners associated with MSY{directed, post-shrimp}.

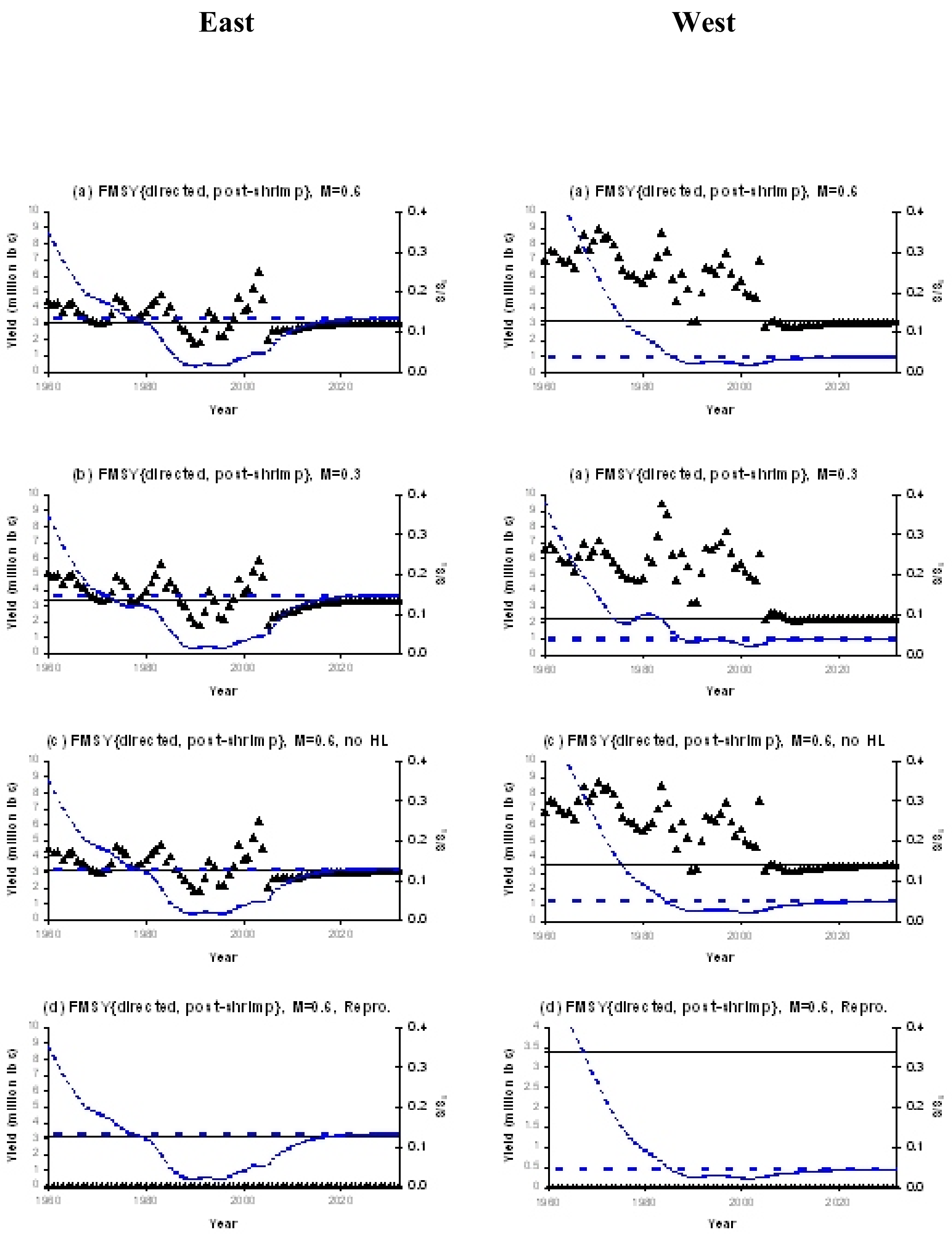

Figure 14. Projected trends in effective number spawners relative to virgin levels (S/S_0, solid lines) and landings (yield in weight, dashed lines) when closed season discards and shrimp effort continue at current rates and the directed fleet fishes at FMSY{directed, post-shrimp} assuming (a) M_1=0.6, (b) M_1=0.3, (c) M_1=0.6, but no handline indices and (d) M_1=0.6, but length-based reproductive potential curve.