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An age-structured assessment model for red snapper that allows for multiple stocks, fleets and habitats.

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Introduction

The most recent assessments of red snapper in the Gulf of Mexico have been based on a two step approach where the length composition data are aged using the probabilistic method of Goodyear (1997) and then the resulting age composition matrices used along with indices of abundance in an age-structured statistical model (ASAP, Legault and Restrepo 1998). Ideally, these two steps should not be independent because the indices of abundance contain information on relative cohort strength that is pertinent to the interpretation of the length composition data. Moreover, as currently formulated, neither step admits the possibility of having multiple stocks with ranges that overlap. 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). There is also some indication that populations in the northwest and southwest potions of the Gulf of Mexico may be different (Wilson et al., 2001). Thus, 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 present an alternative age-structured statistical algorithm that accommodates several intermixing stocks being fished by multiple fleets in multiple habitats. It is hoped that the proposed models will facilitate further discussion at the upcoming SEDAR data workshop for red snapper, particularly as regards integrating new types of information (e.g., otolith-based information on age composition by stock), modeling the relationship between stock and recruitment, and defining meaningful reference points.

Methods

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 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, so there can be multiple cohorts per year to mimic the effect of temporally protracted spawning and to accommodate seasonal movement and fishing patterns. 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

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

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

Population dynamics model

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

$$(2)\qquad N_{cah} = \begin{cases} R_c T_h & a = 1 \\ \sum_k T_{ashk} \tilde{N}_{c,a-1,k} & 1 < a \le A \end{cases}$$

$$(3)\qquad \tilde{N}_{cah} = N_{cah} e^{-Z_{ash}}$$

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 variable R_c denotes the initial recruitment to age class 1 of cohort c, T_h is the probability that a new recruit will start out in habitat h, T_{ashk} is the probability that a fish from age-class a will move to habitat j if it is in habitat k at the beginning of season s, N_{cah} is the number of fish in habitat h at the beginning of the season after movement has taken place and $\tilde{N}_{cah}$ is number remaining in habitat h at the end of the season after mortality (Z) has taken place.

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 an 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 probability distribution corresponding to (4) may be written

$$(5) \quad T_{ashk} = \tau_{ash} \frac{e^{-d_{hk}/u_a}}{\sum_i e^{-d_{hk}/u_a}}$$

$$\sum_h \tau_{ash} = 1$$

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:

$$(6) \quad Z_{ash} = M_a + \sum_i F_{iash}$$

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:

$$(7) \quad F_{iasyh} = q_{iy} v_{ia} \delta_{ih} \, {}^{f_{iy}}\!\big/_{n\{s\}}$$

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, 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 for a given year 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, size limit regulations, 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 $\sigma\{f_{iy}\}$. Note that for σ sufficiently large the f_{iy} essentially become free parameters and for $\sigma = 0$, $f_{iy} = \mu\{f_{iy}\}$. Inter-annual variations may also be introduced by expressing the median as polynomial function of *y* or power function of abundance *N*.

The absence of data during the ‘prehistoric period’ generally precludes the estimation of unconstrained changes in the fishing mortality rate. Accordingly, the prehistoric fishing mortality rates for each fleet are computed as

$$(7) \quad F_{iasyh} = q_{i\psi} v_{ia} \delta_{ih} \, f_{iy}^{obs} \big/ n_{s(i)} \qquad y < \psi$$

where ψ is the first year in the ‘data’ period and f_{iy}^{obs} is an input effort series.

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,

$$(9) \quad \begin{aligned} R_{xc} &= \mu\{R_{xc}\} e^{\varepsilon_y} \\ \varepsilon_y &= \rho\{R_{xc}\}\varepsilon_{y-1} + \delta_{xy} \end{aligned} \quad ,$$

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):

$$(10) \quad \mu\{R_{xc}\} = \begin{cases} R_{0,x}\phi_{xc}\alpha^{\,1-\phi_{xc}} & \text{Ricker} \\ R_{0,x}\dfrac{\alpha\phi_{xc}}{1+(\alpha-1)\phi_{xc}} & \text{Beverton and Holt} \end{cases}$$

(see appendix 1 and Figure 1).

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

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

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

$$(12)\qquad S_{xc} = \sum_a E_{xas} \sum_h N_{x\hat{c}ah}$$

$$S_{0,xc} = R_{0,xc} \sum_a E_{xas} \exp\left(- \sum_{j=1}^{a-1} M_{xj} \right)$$

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:

$$(13)\qquad S_{xc} = \sum_a \sum_j E_{jas} N_{j\hat{c}ah'}$$

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 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

$$(14) \qquad C_{i,s\{c,a\},y\{c,a\}} = \sum_h \frac{F_{iash}}{Z_{ash}} \tilde{N}_{cah} (1 - e^{-Z_{ash}})$$

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.

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.

One issue of concern is how best to deal with the situation where some fraction of the catch is discarded and subsequently dies. For the commercial fishery, estimates of the number landed (harvest *H*) are available, but not the number discarded for most years. One possibility is to infer the number of discarded fish that died (*D*) from the age composition of the total kill (*K*) under the presumptions that selectivity is fundamentally age-based and discarded fish were below the size limit. In that case, the number of discarded fish from each age class that dies *D* is

$$(19) \quad D_{iasy} = d_{ias} K_{iasy} \frac{1 - G_{L|a}}{G + d_{ias}(1 - G_{L|a})}$$

$$G_{L|a} = \sum_{l=L}^{n\{l\}} g\{l|a\}_{isy}$$

where *d* is the release mortality fraction and $G_{L|a}$ is the cumulative probability of a fish being as large or larger than the size limit *L*. In this context the catch equation (14) would refer to the total kill *K* and equations 15 to 17 would refer to the harvest *H*,

$$(20) \quad H_{iasy} = K_{iasy} - D_{iasy}$$

In the case of the recreational fishery, estimates are provided by MRFSS for both the number harvested (observed or unobserved) and the number released alive. However, MRFSS does not provide information on the size or age composition of the released fish. A similar approach could be taken to that above, but it is possible that a large fraction of the releases occur for reasons other than the minimum size limit (bag limits or the catch-and-release ethic). It would be helpful to the modeling effort if some guidance could be provided on this aspect of recreational discards (the proportion of releases which might be above the minimum size) during the SEDAR data workshop.

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. One possibility is to assume the current relative allocation of effort is constant and then maximize the yield per recruit or yield statistics over all stocks and habitats by varying the overall scale of effort. A difficulty with this 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 ξ (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

$$(14) \qquad \xi = \frac{\sum_{a=1}^{A} E_a e^{-\sum_{i=0}^{a-1} F v_i + M_i}}{\sum_{a=1}^{A} E_a e^{-\sum_{i=0}^{a-1} M_i}}$$

More generally, ξ 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 $\mathcal{D}$, $P(\Theta \mid \mathcal{D})$. By application of Bayes rule it is easy to show that

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

where $P(\mathcal{D} \mid \Theta)$ 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)

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

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

$$(14) \qquad \min_{\Theta} \left\{ -\log_{\mathrm{e}} \mathrm{P}(\mathscr{D} \,|\, \Theta) - \log_{\mathrm{e}} \mathrm{P}(\Theta) \right\} \qquad .$$

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.,

$$-\log_e \mathrm{P}(\boldsymbol{C}|\Theta) = \begin{cases} 0.5\sum\limits_i \sum\limits_y \sum\limits_s \left(\dfrac{C_{isy}^{obs} - C_{isy}}{\sigma\{C_{isy}\}} \right)^2 - \log_{\mathrm{e}} \left[\sigma^2 \{C_{isy}\} \right] & \textit{normal} \\ 0.5\sum\limits_i \sum\limits_y \sum\limits_s \left(\dfrac{\log_{\mathrm{e}}(C_{isy}^{obs} / C_{isy})}{\sigma\{\log_{\mathrm{e}} C_{isy}\}} \right)^2 - \log_{\mathrm{e}} \left[\sigma^2 \{\log_{\mathrm{e}} C_{isy}\} \right] & \textit{lognormal} \end{cases}$$

where the superscript *obs* distinguishes the observed data from the value predicted by the model. The variable σ{} 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

$$-\log_e \mathrm{P}(\boldsymbol{p}_a|\Theta) = \sum_i \sum_y \sum_s n_{isy} \sum_a p_{iasy}^{obs} \log_{\mathrm{e}} p_{iasy}$$

$$-\log_e \mathrm{P}(\boldsymbol{p}_l|\Theta) = \sum_i \sum_y \sum_s n_{isy} \sum_l p_{ilsy}^{obs} \log_{\mathrm{e}} p_{ilsy}$$

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), indices of abundance (I) and effort (f) of each fleet are modeled as

$$\sigma^2\{C_{iy}\} = \chi^2\{C_{iy}\} + \lambda\{C_i\}\boldsymbol{\sigma}^{\mathbf{2}}$$

$$\sigma^2\{I_{iy}\} = \chi^2\{I_{iy}\} + \lambda\{I_i\}\boldsymbol{\sigma}^{\mathbf{2}} \tag{19}$$

$$\sigma^2\{f_{iy}\} = \chi^2\{f_{iy}\} + \lambda\{f_i\}\boldsymbol{\sigma}^{\mathbf{2}}$$

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 will be implemented using the nonlinear optimization package AD Model Builder (Otter Research Ltd.[1]), which provides facilities for estimating the mode and shape of the posterior distribution.

Summary

This exercise has revealed several important issues that need to be addressed from a stock assessment modeling perspective:

1. The ability to discriminate between stocks. Is it sufficient to justify conducting a multi-stock, multi-area assessment?
2. The use of available stock-specific age-composition data to estimate potential mixing between stocks.
3. The most appropriate spawner-recruit relationship. Is steepness really 0.95? Do members from one stock contribute substantially to the recruitment of other stocks?
4. Appropriate reference points for a multi-stock analysis.
5. Modeling the discards of the various fleets.

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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 $\alpha = aS_0/R_0$ 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

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

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

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

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

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

Defining $\phi = S/S_0$ gives equation (10).

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)

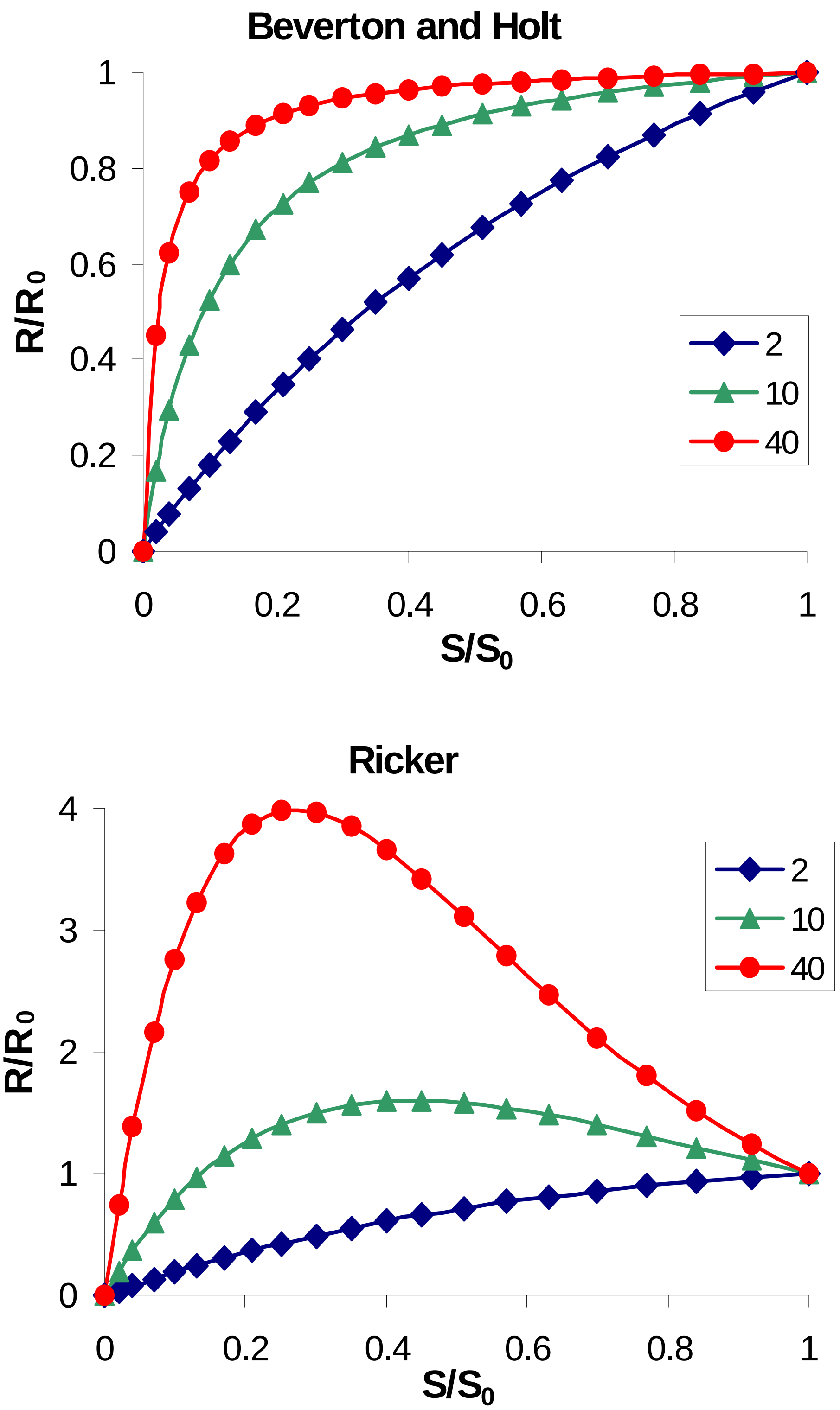

Figure 1. Examples of scaled Beverton-Holt and Ricker spawner-recruit relationships for various values of α.

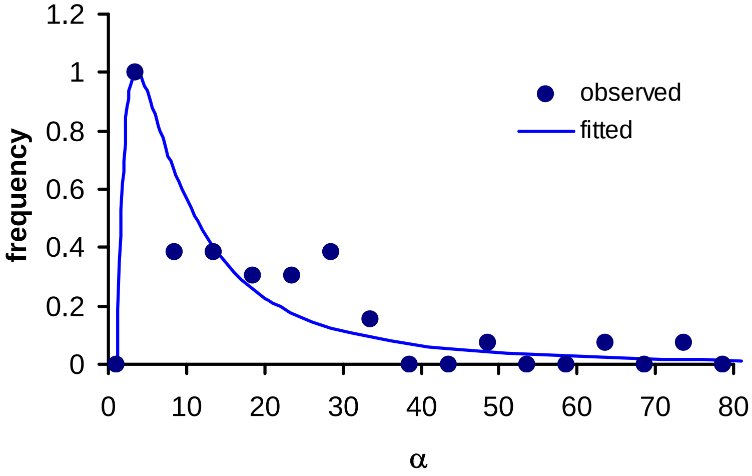

Figure 2. Lognormal prior for the maximum lifetime fecundity parameter (α) derived from the values in Myers et al. (1999) that correspond to species categorized as periodic strategists by Rose et al. (2001). The lognormal density was fitted to the values of α-1 (with median 9.8 and log-scale variance 1.31) and then shifted 1 unit to provide a prior for α.