An Application of Statistical Catch-at-Age Assessment Methodology to Assess US South Atlantic Wreckfish

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Summary

The available information on past catches, CPUE and catch-at-length distributions is sufficient to allow the application of Statistical Catch-at-Age methodology to assess the US South Atlantic wreckfish resource. The assessment is carried out for all combinations of four natural mortality (M) and three steepness values. A poor log-likelihood plus an inability to reflect a recent upward trend in CPUE rules out the lowest value of M = 0.025 yr^{-1} considered. Although the fit to the length distribution data improves steadily as M is increased, estimated abundances become realistically large as M approaches 0.1. For the range of M (0.05 to 0.075) over which reasonable and realistic fits to the data are obtained, the resource is not overfished and overfishing is not occurring. The corresponding estimates of *MSY* range from 278 to 1293 thousand lbs, and suggest that a yet more optimistic conclusion about the resource can be reached than that drawn from a recent DCAC based analysis, with an appreciable increase in the ABC above its current level of 250 thousand lbs being defensible.

Introduction

The most recent analysis of the South Atlantic wreckfish (*Polyprion americanus*) resource to provide advice on appropriate catch levels (Anon. 2011a) has been carried out using the Depletion Corrected Average Catch (DCAC) formula developed by MacCall (2009). This is a method developed to estimate sustainable yield in data poor situations. It requires relatively few inputs, including the sum of past catches, the number of years over which they have been taken, an estimate of the extent (in relative terms) to which these catches have reduced the biomass, the natural mortality M, and a relationship between F_{MSY} and M.

However there are more data than those listed amongst the inputs required for DCAC that are available for this wreckfish resource. These include time series of CPUE values and of the distribution of catch-at-length in the fishery. This allows for the application of Statistical Catch at Age (SCAA) methodology to assess the resource. By making use of more of the data available, and also avoiding some of the assumptions needed to derive the DCAC formula, it should be possible to achieve improved (more reliable) estimates of sustainable yield for the resource. This paper pursues initial analyses using the SCAA methodology towards that end.

Data and Methodology

The catch, CPUE and commercial catch-at-length (CAL) data used in the analyses of this paper are listed in Tables in Appendix A. Note the explanation accompanying Table A1 detailing the assumptions made for landings over the 2001-2008 period for which these data are not publically available.

The details of the SCAA assessment methodology are provided in Appendix B.

Because in particular of uncertainty about the most appropriate choice of a value for natural mortality *M* (see Anon. 2011a), assessments have been run across a grid of four values for *M* (0.025, 0.05, 0.075 and 0.1 yr^{-1}), and three values for the steepness *h* (see Appendix B for details) of the Beverton-Holt stock recruitment relationship assumed (0.6, 0.75 and 0.9), which would seem to cover the plausible range for this parameter. Steepness is frequently utilised as a parameter which characterises stock productivity relative to *M* in meta-analyses of comparative population dynamics across different resources. These two parameters were selected for the grid used as they are not well known *a priori* for this stock, and both are highly influential in determining sustainable yield levels with higher values of either reflecting a more productive resource.

Results

The results of applications of the model across the grid of four values of *M* and three of *h* considered are shown in Table 1. Quantities of management importance, such as the value of *MSY*, show greater sensitivity to the value of *M* than to that of *h*. The fit to the CPUE data is optimal for *M* = 0.05, whereas for the CAL data the fit improves monotonically as the value of *M* is increased. These fits are contrasted in Fig. 1: the lowest value of *M* is unable to reflect the recent CPUE increase, whereas higher values manifest an increasing inability to fit to the CPUE decline in the earlier years. For the lower *M* values, the model predicts a much greater proportion of larger fish in the catch than are observed.

Clearly there is some tension between the CPUE and CAL data in the context of fitting the model. However, taking an overview of the results, these would clearly seem to exclude both the lowest and the highest values of *M* considered. The overall fit is considerably worse in log-likelihood terms for *M* = 0.025, whereas for *M*=0.1 the biomass estimates become unrealistically large in absolute terms. Results for *M*=0.05 to 0.075 would seem to span the plausible range, with whichever end of this range is to be favoured depending on the reliability/weight to be accorded to the CPUE relative to the CAL data. More details of the model fits for these two values of *M* and the central choice of 0.75 for steepness *h* are shown in Fig. 2 for *M* = 0.05 and Fig. 3 for *M* = 0.075.

Discussion

Anon. (2011a, Table 2) reports estimates of sustainable yield from 18 different DCAC model parametrizations (including values of *M* ranging from 0.025 to 0.075) which range from 175 to 449 thousand lbs.

For the ranges of natural mortality *M* (0.05 to 0.075) and steepness *h* (0.6 to 0.9) considered plausible for the SCAA model evaluated here, the estimates of *MSY* range from 278 to 1293 thousand lbs. The spawning biomass at *MSY* is estimated to range from 33% to 21% of the corresponding pre-exploitation value K^{sp}, with the current spawning current from some 40% to 300% above this level. Current fishing mortality (*F*) values are below F_{MSY} throughout this range, so that the resource is neither overfished, nor is overfishing occurring.

The Anon. (2011a) concluded that "the level of current take appears sustainable and could potentially be increased (note that the ABC at present is 250 thousand lbs). The results from the arguably more extensive and rigorous approach of this paper suggest that a yet more optimistic conclusion can be drawn, with an appreciable increase in the ABC above its current level being defensible.

The greater flexibility of the SCAA approach compared to DCAC would allow for yet further analyses to be conducted, for example the computation of confidence intervals, or the impact of different functional forms from that assumed for the commercial selectivity-at-length. Before going further, however, it would seem best to first await a wider discussion of these initial results for a form of "first review".

References

Anon. 2011a. Draft for SSC review: Depletion-corrected Average Catch Estimates for U.S. South Atlantic Wreckfish. NOAA Fisheries Service.

Anon. 2011b. Amendment 20A to the Fishery Management Plan for the Snapper Grouper Fishery of the South Atlantic Region.

MacCall AD. 2009. Depletion corrected average catch: a simple formula for estimating sustainable yields in data poor situations. ICES Journal of Marine Science, 66: 2267-2271.

Peres MB and Haimovici M. 2004. Age and growth of southwestern Atlantic wreckfish Polyprion americanus. Fisheries Research 66: 157-169.

Vaughan DS, Manooch CS and Potts JC. 2005. Assessment of the Wreckfish Fishery on the Blake Plateau. American Fisheries Society Symposium 25: 195-120.

Table 1: Results for the 12 runs presented of this paper, with different *M* and *h* values. Values fixed on **input are bolded**.

Run	1	2	3	4	5	6	7	8	9	10	11	12
h	**0.6**	**0.75**	**0.9**	**0.6**	**0.75**	**0.9**	**0.6**	**0.75**	**0.9**	**0.6**	**0.75**	**0.9**
M	**0.025**	**0.025**	**0.025**	**0.05**	**0.05**	**0.05**	**0.075**	**0.075**	**0.075**	**0.1**	**0.1**	**0.1**
'-lnL:overall	-30.0	-30.8	-31.5	-50.8	-50.3	-49.9	-51.7	-51.6	-51.5	-51.9	-51.9	-51.9
'-lnL:CPUE	-28.7	-29.1	-29.4	-30.1	-29.7	-29.3	-23.6	-23.6	-23.5	-22.1	-22.1	-22.1
'-lnL:CAL	-1.3	-1.8	-2.1	-20.7	-20.7	-20.6	-28.1	-28.0	-28.0	-29.8	-29.8	-29.8
'-lnL:RecRes	-	-	-	-	-	-	-	-	-	-	-	-
γ	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
θ	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
ζ	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
K^{sp} (tons)	7852	7745	7670	7842	7957	8062	16632	16823	17046	3268830*	3268850*	3268890*
B^{sp}_{2010} (tons)	2556	2545	2549	3694	3976	4208	13550	13907	14243	3266560	3266730	3266870
B^{sp}_{2010}/K^{sp}	0.33	0.33	0.33	0.47	0.50	0.52	0.81	0.83	0.84	1.00	1.00	1.00
$MSYL^{sp}$	0.32	0.28	0.22	0.33	0.28	0.23	0.33	0.28	0.21	0.32	0.26	0.23
B^{sp}_{MSY} (tons)	2550	2143	1725	2597	2258	1846	5493	4667	3567	1055890	860563	764284
$B^{sp}_{2010}/B^{sp}_{MSY}$	1.00	1.19	1.48	1.42	1.76	2.28	2.47	2.98	3.99	3.09	3.80	4.27
MSY ('000 lb and tons)	151 (68)	186 (84)	220 (100)	278 (126)	350 (159)	419 (190)	846 (384)	1,065 (483)	1,293 (587)	225,066 (102088)	282,456 (128120)	340,745 (154560)
F_{MSY}	0.03	0.04	0.07	0.06	0.10	0.17	0.11	0.20	0.44	0.22	0.46	0.92
F_{2010}	0.05	0.05	0.05	0.04	0.04	0.03	0.01	0.01	0.01	0.00	0.00	0.00
σ_{com}	0.14	0.14	0.14	0.13	0.14	0.14	0.19	0.19	0.19	0.20	0.20	0.20
σ_{len}	0.15	0.15	0.15	0.11	0.11	0.11	0.10	0.10	0.10	0.10	0.10	0.10

* The actual estimate is infinity; the value given is simply where the numerical procedure ceases iterating further; this applies also to other biomass-related estimates.

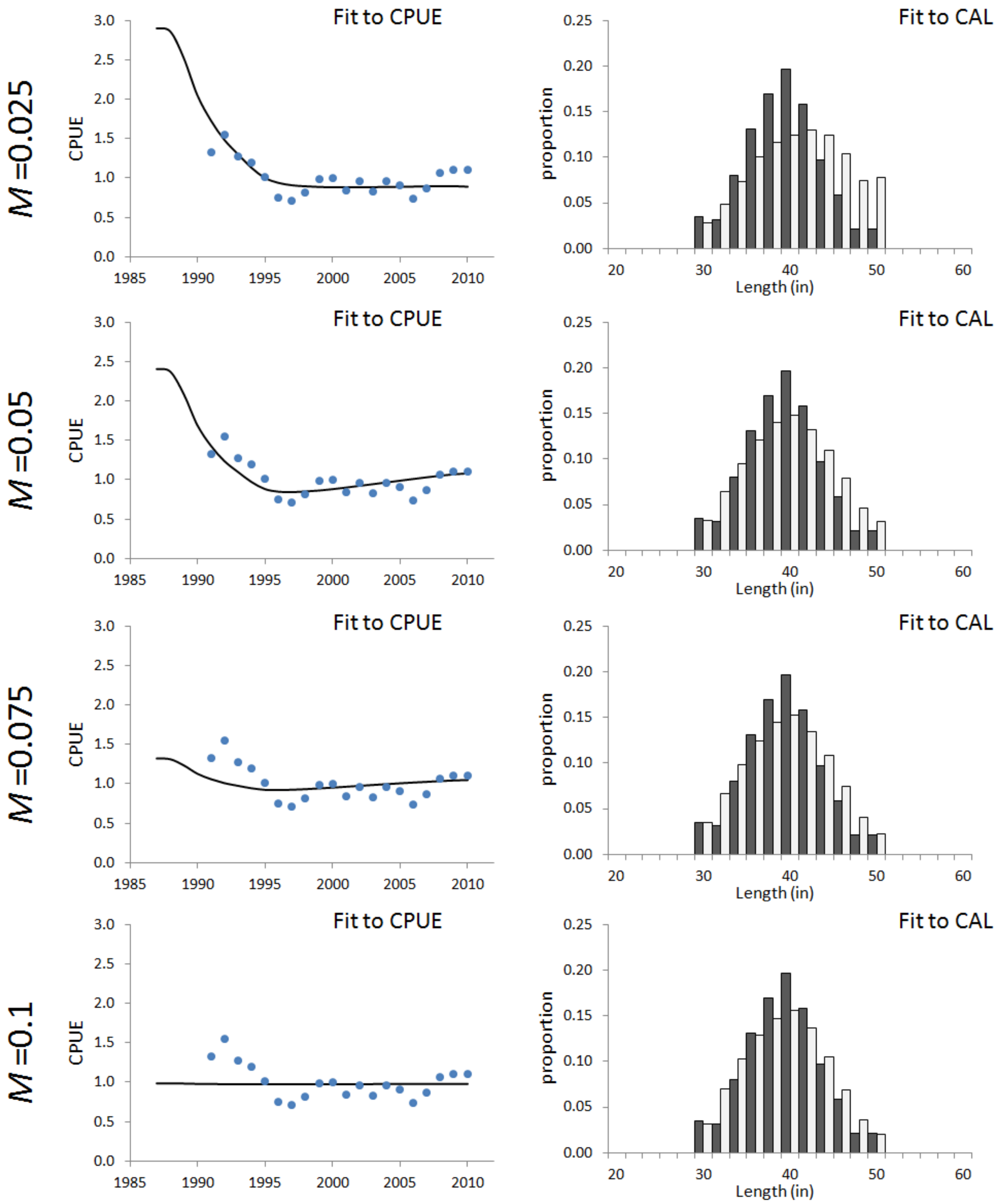

Fig. 1: Fit to the CPUE and CAL data (as averaged over all the years with data available; for the CAL, the filled bars reflect the data) for the four runs with *h*=0.75.

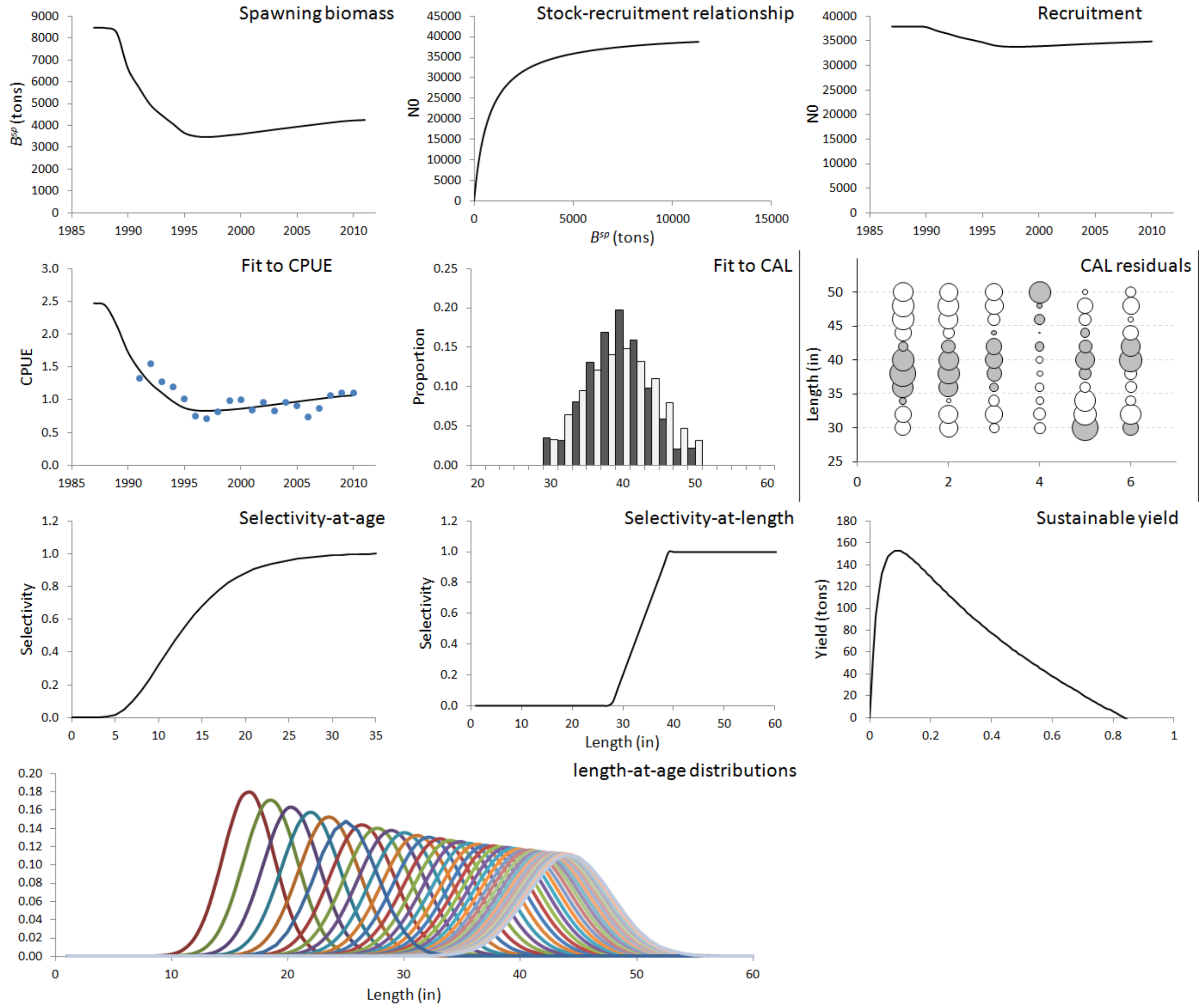

Fig. 2: Results for run 5 (h=0.75, M=0.05). The Fit to CAL is averaged over years for which data are available; for the CAL residuals, the size (area) of the bubble is proportional to the magnitude of the corresponding standardised residual (for positive residuals the bubbles are grey, whereas for negative residuals they are white); for the length-at-age distributions, the distributions, starting from the left, correspond to ages 0, 1, 2, ... , 35.

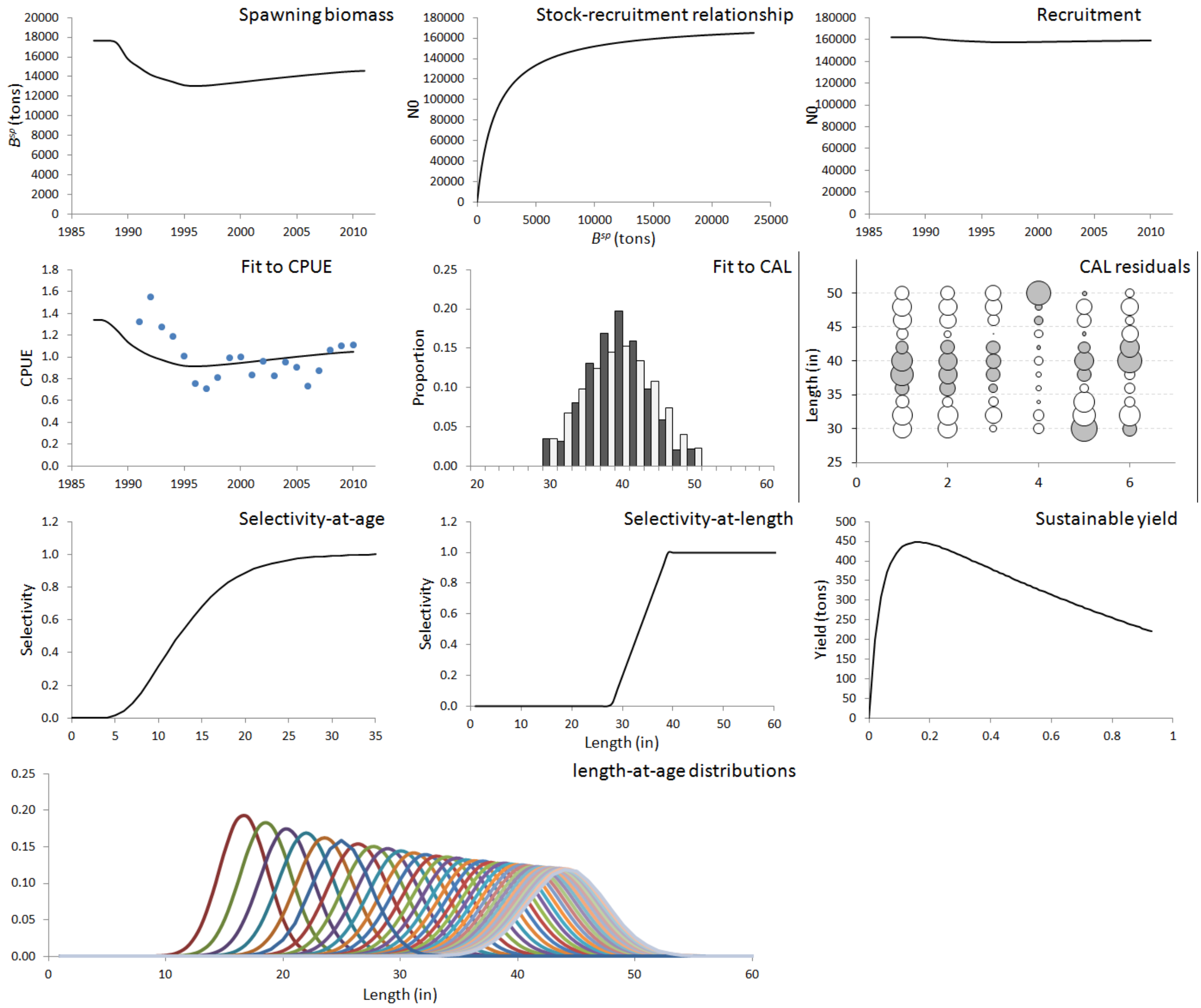

Fig. 3: Results for run 8 (h=0.75, M=0.075). The notations and conventions are as for Fig. 2.

APPENDIX A – Data

Table A1: Annual landings (thousand metric tons) of US south Atlantic wreckfish, 1967-2010 (Anon. 2011b,, Table 3-2).

Year	Landing (tons)	Year	Landing (tons)
1987	12.701	1999	95.481
1988	206.824	2000	76.246
1989	1680.54	2001	76.879*
1990	957.885	2002	76.879*
1991	873.658	2003	76.879*
1992	576.315	2004	76.879*
1993	519.243	2005	76.879*
1994	545.793	2006	76.879*
1995	292.562	2007	76.879*
1996	180.017	2008	76.879*
1997	113.268	2009	98.179
1998	95.618	2010	116.718

*Landings for 2001/2002 through 2008/2009 are confidential because there were fewer than three vessels that fished wreckfish during those years and/or fewer than three dealers purchased wreckfish in those years. Anon. (2011a) gives the sum of landings for 1989-2010 as 15.220 million pounds, so the remainder of the catch was attributed equally to the years 2001-2008. Results in this paper will not be very sensitive to this assumption.

Table A2: Wreckfish standardized catch-per-unit-effort data (summarized in Figure 1 of Anon. 2011a).

Year	Standardized CPUE	Year	Standardized CPUE
1991	1.325	2001	0.837
1992	1.552	2002	0.965
1993	1.272	2003	0.827
1994	1.190	2004	0.957
1995	1.009	2005	0.908
1996	0.755	2006	0.737
1997	0.712	2007	0.872
1998	0.810	2008	1.066
1999	0.991	2009	1.101
2000	1.003	2010	1.110

Table A3: Wreckfish size frequency data (summarized in Figure 3 of Anon. 2011a).

Total Length (in)	Frequency of Measured Lengths by Fishing Year					
	88-91	92-95	96-99	00-03	04-07	08-10
20	0	0	0	0	0	0
22	0	0	0	1	0	0
24	0	0	1	1	22	0
26	3	5	5	3	14	0
28	7	18	35	9	8	3
30	22	37	59	17	15	6
32	93	205	130	64	10	4
34	316	635	276	110	34	16
36	626	1125	406	137	85	21
38	937	1388	501	157	126	25
40	979	1456	526	152	149	46
42	745	1196	455	142	108	36
44	469	785	308	101	75	14
46	226	381	175	82	36	12
48	76	126	55	43	13	3
50	36	54	13	21	8	3
52	14	12	8	18	2	0
54	10	15	4	11	3	0
56	8	10	1	5	1	0
58	1	7	1	4	0	0
60	1	0	0	0	1	0
>60	1	0	0	0	0	0

Appendix B - The Statistical Catch-at-Age Model

The text following sets out the equations and other general specifications of the SCAA followed by details of the contributions to the (penalised) log-likelihood function from the different sources of data available and assumptions concerning the stock-recruitment relationship. Quasi-Newton minimization is then applied to minimize the total negative log-likelihood function to estimate parameter values (the package AD Model Builder™, Otter Research, Ltd is used for this purpose).

B.1. Population dynamics

B.1.1 Numbers-at-age

The resource dynamics are modelled by the following set of population dynamics equations:

$$N_{y+1,0} = R_{y+1} \qquad \text{(B1)}$$

$$N_{y+1,a+1} = \left(N_{y,a}\, e^{-M_a/2} - C_{y,a}\right) e^{-M_a/2} \qquad \text{for } 0 \le a \le m-2 \qquad \text{(B2)}$$

$$N_{y+1,m} = \left(N_{y,m-1}\, e^{-M_{m-1}/2} - C_{y,m-1}\right) e^{-M_{m-1}/2} + \left(N_{y,m}\, e^{-M_m/2} - C_{y,m}\right) e^{-M_m/2} \qquad \text{(B3)}$$

where

$N_{y,a}$ is the number of fish of age *a* at the start of year *y* (which refers to a calendar year),

R_y is the recruitment (number of 0-year-old fish) at the start of year *y*,

M_a denotes the natural mortality rate for fish of age *a*,

$C_{y,a}$ is the predicted number of fish of age *a* caught in year *y*, and

m is the maximum age considered (taken to be a plus-group).

B.1.2. Recruitment

The number of recruits (i.e. new 0-year old) at the start of year *y* is assumed to be related to the spawning stock size (i.e. the biomass of mature fish) by a deterministic Beverton-Holt stock-recruitment relationship:

$$R_y = \frac{\alpha B_y^{\text{sp}}}{\beta + B_y^{\text{sp}}} \qquad \text{(B4)}$$

where

α and β are spawning biomass-recruitment relationship parameters,

B_y^{sp} is the spawning biomass at the start of year *y*, computed as:

$$B_y^{\text{sp}} = \sum_{a=0}^{m} f_a w_a^{\text{strt}} N_{y,a} \qquad \text{(B5)}$$

where

w_a^{strt} is the mass of fish of age *a* at the beginning of the year, and

f_a is the proportion of fish of age *a* that are mature.

In order to work with estimable parameters that are more meaningful biologically, the stock-recruitment relationship is re-parameterised in terms of the pre-exploitation equilibrium spawning biomass, K^{sp}, and the "steepness", *h*, of the stock-recruitment relationship, which is the proportion of the virgin recruitment that is realized at a spawning biomass level of 20% of the virgin spawning biomass. In the fitting procedure applied in this paper, K^{sp} is estimated, while *h* is fixed at either 0.6, 0.75 or 0.9.

B.1.3. Catches-at-age

The catches at age in number in year *y* are given by:

$$C_{y,a} = N_{y,a}\, e^{-M_a/2}\, S_{y,a}\, F_y^* \qquad \text{(B6)}$$

where

$C_{y,a}$ is the catch-at-age, i.e. the number of fish of age *a*, caught in year *y*,

F_y^* is the proportion of a fully selected age class that is fished, and

$S_{y,a}$ is the commercial selectivity (i.e. combination of availability and vulnerability to fishing gear) at age *a* for year *y*; when $S_{y,a} = 1$, the age-class *a* is said to be fully selected.

Selectivity is estimated as a function of length (see section B3.1) and then converted to selectivity-at-age:

$$S_{y,a} = \sum_l S_{y,l} A_{a,l} \qquad \text{(B7)}$$

where $A_{a,l}$ is the proportion of fish of age *a* that fall in the length group *l* (i.e., $\sum_l A_{a,l} = 1$ for all ages).

The matrix $A_{a,l}$ is calculated under the assumption that length-at-age is normally distributed about a mean given by the von Bertalanffy equation, i.e.:

$$L_a \sim N\left[L_\infty\left(1 - e^{-\kappa(a-t_o)}\right); \theta_a^2\right] \qquad \text{(B8)}$$

where

θ_a is the standard deviation of length-at-age a, which is modelled to be proportional to the expected length-at-age *a*, i.e.:

$$\theta_a = \beta L_\infty\left(1 - e^{-\kappa(a-t_o)}\right)^\gamma \qquad \text{(B9)}$$

with β an estimable parameter and $\gamma = 0.5$ (a value which was found to lead to reasonable fits to the data).

The model estimate of the mid-year exploitable ("available") component of biomass is calculated by converting the numbers-at-age into mid-year mass-at-age (using the individual weights of the landed fish) and applying natural and fishing mortality for half the year:

$$B_y^{\text{ex}} = \sum_{a=0}^{m} \tilde{w}_{y,a}^{\text{mid}} S_{y,a} N_{y,a} e^{-M_a/2}(1 - S_{y,a} F_y^* / 2) \tag{B10}$$

where

$\tilde{w}_{y,a}^{\text{mid}}$ is the selectivity-weighted mid-year weight-at-age *a* landed in year y, and

$$\tilde{w}_{y,a}^{\text{mid}} = \sum_l S_{y,l} w_l A_{a,l} \Big/ \sum_l S_{y,l} A_{a,l}$$

with

w_l is the weight of fish of length *l*.

B.1.4. Initial conditions

In general, the first year for which annual catch data are available may not correspond to the first year of (appreciable) exploitation, so that one cannot necessarily make the assumption in the application of this SCAA model that this initial year reflects a population (and its age-structure) at pre-exploitation equilibrium. For the first year (y_0) considered in the model therefore, the stock is assumed to be at a fraction (θ) of its pre-exploitation biomass, i.e.:

$$B_{y_0}^{\text{sp}} = \theta \cdot K^{\text{sp}} \tag{B11}$$

with the starting age structure:

$$N_{y_0,a} = R_{\text{start}} N_{\text{start},a} \qquad \text{for } 1 \le a \le m \tag{B12}$$

where

$$N_{\text{start},0} = 1 \tag{B13}$$

$$N_{\text{start},a} = N_{\text{start},a-1} e^{-M_{a-1}} (1 - \phi S_{a-1}) \qquad \text{for } 1 \le a \le m-1 \tag{B14}$$

$$N_{\text{start},m} = N_{\text{start},m-1} e^{-M_{m-1}} (1 - \phi S_{m-1}) \Big/ (1 - e^{-M_m} (1 - \phi S_m)) \tag{B15}$$

where ϕ characterises the average fishing proportion over the years immediately preceding y_0.

For the applications considered here however, the population starts at its pre-exploitation equilibrium level (*K*) with an equilibrium age-structure, where

$$R_0 = K^{sp} \Bigg/ \left[\sum_{a=1}^{m-1} f_a w_a^{\text{strt}} e^{-\sum_{a'=0}^{a-1} M_{a'}} + f_m w_m^{\text{strt}} e^{\sum_{a'=0}^{m-1} M_{a'}} \right] \tag{B16}$$

In all the applications considered in this paper, however, the stock has been assumed to be at its pre-exploitation equilibrium level with the associated age structure at the start of 1987.

B.2. The likelihood function

The model is fit to a CPUE index and commercial catch-at-length data to estimate model parameters. Contributions by each of these to the negative of the (penalised) log-likelihood (- $\ell\text{n}L$) are as follows.

B.2.1 CPUE relative abundance data

The likelihood is calculated assuming that the observed CPUE abundance is log-normally distributed about its expected value:

$$I_y = \hat{I}_y \exp(\varepsilon_y) \quad \text{or} \quad \varepsilon_y = \ell n(I_y) - \ell n(\hat{I}_y) \tag{B17}$$

where

I_y is the CPUE abundance index for year *y*,

$\hat{I}_y = \hat{q}\ \hat{B}_y^{\text{ex}}$ is the corresponding model estimate, where $\hat{B}_y^{\text{ex}}$ is the model estimate of exploitable resource biomass as described in equation B10,

$\hat{q}$ is the constant of proportionality (catchability) for the CPUE abundance series, and

ε_y from $N\left(0,(\sigma_y)^2\right)$.

The contribution of the CPUE data to the negative of the log-likelihood function (after removal of constants) is then given by:

$$-\ell n L^{\text{CPUE}} = \sum_y \left\{ \ell n(\sigma_{com}) + (\varepsilon_y)^2 / (2\sigma_{com}^2) \right\} \tag{B18}$$

where

σ_{com} is the standard deviation of the residuals for the logarithm of the CPUE index, which is estimated in the fitting procedure by its maximum likelihood value:

$$\sigma_{com} = \sqrt{\frac{1}{n}\sum_y \left[\ell n(I_y) - \ell n(\hat{I}_y)\right]^2} \tag{B19}$$

where *n* is the number of data points for the CPUE index.

The catchability coefficient q for the CPUE abundance index is estimated by its maximum likelihood value:

$$\ell n\,\hat{q} = 1/n \sum_y \left(\ln I_y - \ln \hat{B}_y^{\text{ex}}\right) \tag{B20}$$

B.2.2. Commercial catches-at-length

The contribution of the catch-at-length data to the negative of the log-likelihood function under the assumption of an "adjusted" lognormal error distribution is given by:

$$-\ell n L^{\text{CAL}} = w_{len} \sum_{y*} \sum_l \left[\ell n\left(\sigma_{\text{len}} / \sqrt{p_{y*,l}}\right) + p_{y*,l}\left(\ell n\, p_{y*,l} - \ell n\, \hat{p}_{y*,l}\right)^2 / 2(\sigma_{\text{len}})^2 \right] \tag{B21}$$

$p_{y*,l} = C_{y*,l} \Big/ \sum_{l'} C_{y*,l'}$ is the average observed proportion of fish caught between years y_1 and y_2 that are of length *l*,

$\hat{p}_{y*,l} = \sum_{y=y_1}^{y_2} \hat{C}_{y,l} \Big/ \sum_{y=y_1}^{y_2} \sum_{l'} \hat{C}_{y,l'}$ is the model-predicted average proportion of fish caught between years y_1 and y_2 that are of length l,

where

$$\hat{C}_{y,l} = N_{y,a} \, A_{a,l} \, S_{y,l} e^{-M_a/2} F_y \tag{B22}$$

and

σ_{len} is the standard deviation associated with the catch-at-age data, which is estimated in the fitting procedure by:

$$\hat{\sigma}_{\text{len}} = \sqrt{\sum_{y*} \sum_{l} p_{y*,l} \left(\ell n \, p_{y*,l} - \ell n \, \hat{p}_{y*,l} \right)^2 / \sum_{y*} \sum_{a} 1} \tag{B23}$$

The log-normal error distribution underlying equation (B21) is chosen on the grounds that (assuming no ageing error) variability is likely dominated by a combination of interannual variation in the distribution of fishing effort, and fluctuations (partly as a consequence of such variations) in selectivity-at-length, which suggests that the assumption of a constant coefficient of variation is appropriate. However, for lengths poorly represented in the sample, sampling variability considerations must at some stage start to dominate the variance. To take this into account in a simple manner, motivated by binomial distribution properties, the observed proportions are used for weighting so that undue importance is not attached to data based upon a few samples only.

Commercial catches-at-length are incorporated in the likelihood function using equation (B21), for which the summation over length l is taken from age l_{minus}= 30 in (considered as a minus group) to l_{plus}=50 in (a plus group).

The w_{len} weighting factor may be set to a value less than 1 to downweight the contribution of the catch-at-length data (which tend to be positively correlated between adjacent length groups) to the overall negative log-likelihood compared to that of the CPUE data. The calculations reported in this paper have, however, all been carried out with $w_{len} = 1$.

B.3. Model parameters

B.3.1. Fishing selectivity-at-length:

The commercial fishing selectivity, S_l , takes on the following form:

$$S_l = \begin{cases} 0 & \text{if } l < l_1 \\ (l - l_1)/(l_2 - l_1) & \text{if } l_1 \le l \le l_2 \\ 1 & \text{if } l > l_1 \end{cases} \tag{24}$$

with l_1 and l_2 estimated in the fitting procedure.

The selectivity is assume to stay constant over time.

B.3.2. Biological parameters

Growth curve:

$$l_a = l_\infty\left(1 - e^{-\kappa(a-t_o)}\right) \tag{25}$$

where

l_∞=121 cm, κ=0.063 yr^{-1} and t_0=-6.3 yr^{-1} (from Peres and Haimovici, 2004).

Weight-at-age:

Begin-year:

$$w_a^{\text{strt}} = \alpha\left(l_a\right)^\beta \tag{26}$$

and mid-year:

$$w_a^{\text{mid}} = \alpha\left(l_{a+1/2}\right)^\beta$$

where α=6.20572x10^{-6} and β=3.21 (from Peres and Haimovici, 2004, with α taken as the average of the male and female values), and units in terms of gm and cm.

Percentage maturity-at-age:

Maturity-at-age is assumed to be 0 below 5, and 100% at age 8 with a linear relationship between these two ages (from Vaughan *et al*. 2001)

Natural mortality M:

Taken to be either 0.025, 0.05, 0.075 or 0.1 yr^{-1} (age-independent).