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# Application of an Age-Structured Production Model to Assess the Rock Lobster Populations at the Tristan group of islands 

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#### Abstract

Recent scientific recommendations for TACs for the rock lobster populations at the Tristan group of islands have been based on a replacement yield approach, which relies particularly on measures of recent increases in abundance provided by GLMstandardised CPUE data. These increases are compatible with the perception that these resources were overfished in the past, but then that subsequent reduced TACs applied over recent years have been less than sustainable yields and hence allowed for resource recovery. This recovery cannot continue indefinitely, however, as the resource would be expected to equilibrate (at probably a relatively high level) in the short- to medium-term, requiring a different method to determine appropriate TAC levels, as replacement yields would underestimate the production of which the resource was capable if equilibration occurred (possibly well) above the MSY level.


Developing such a different method is not straightforward, as existing information on these resources is limited, and does not admit precise estimation of the parameters that determine sustainable yields. Hence the approach planned is to develop, for each of the islands, a set of operating models that reasonably span the current range of uncertainties about resource dynamics. These will then be used to develop Management Procedures (decision rules), which will input future data forthcoming from these resources, to recommend TACs that will ensure sound sustainable management into the future despite these uncertainties.

Towards this end, the Tristan rock lobster resource at each of the four islands (Inaccessible, Nightingale, Gough and Tristan) is to be modeled using an age-structured-production-model (ASPM) which is fitted to the available CPUE and catch-at-length data for each. The model is sex-disaggregated ( $\mathrm{m} / \mathrm{f}$ ). Population dynamics equations have been modified from Baranov equations to Pope's approximation to speed the runtime of the program. A similar ASPM approach has been used to assess the South African south coast rock lobster fishery (Johnston and Butterworth 2008). A variety of applications of this approach for each island will provide the operating models to be used for Management Procedure testing.

This document first sets out the details of this assessment methodology, and then reports the results of its initial application to the lobster population at Nightingale Island.

## 1. The population model

The resource dynamics are modeled by the equations:

$$
\begin{align*}
& N_{y+1,0}^{m}=R_{y+1}  \tag{1}\\
& N_{y+1,0}^{f}=R_{y+1}  \tag{2}\\
& N_{y+1, a+1}^{m}=\sum_{l}\left[\vec{N}_{y, a, l}^{m} e^{-M^{n+12}}-\vec{C}_{y, a, l}^{m}-D_{j, a, l}^{m}\right] e^{-\mu^{* / 2}}  \tag{3}\\
& N_{y+1, a+1}^{f}=\sum_{l}\left[\vec{N}_{y, a, l}^{f} e^{-M^{\prime} / 2}-\vec{C}_{y, a, l}^{f}-D_{y, a, l}^{f}\right] e^{-\mu^{\prime} / 2} \tag{4}
\end{align*}
$$

where
$N_{y, a}^{m / f} \quad$ is the number of male or female ( $\mathrm{m} / \mathrm{f}$ ) lobsters of age $a$ at the start of year $y$,
$\vec{N}_{y, a, a}^{m / f} \quad$ is the number of male or female ( $m / f$ ) lobsters of age $a$ of length $l$ at the start of year $y$ (see equation 15 ),
$M^{m / f} \quad$ denotes the natural mortality rate for male or female ( $m / f$ ) lobsters which is constant for all $a$ (and here identical for male and female lobsters). Note that this value is fixed at 0.10 in this model.
$\vec{C}_{y, a, l}^{m / f} \quad$ is the catch of male or female ( $m / f$ ) lobsters of age $a$ of length $l$ in year $y$,
$D_{y, a, l}^{m / f} \quad$ is the number of male or female $(m / f)$ lobsters of age $a$ of length $l$ in year $y$ that die due to discard mortality, and
$p \quad$ is the maximum age considered (taken to be a plus-group).

The number of recruits of age 0 , of each sex, at the start of year $y$ is related to the spawner stock size by a stock-recruitment relationship:

$$
\begin{equation*}
R_{y}=\frac{\alpha B_{y}^{s p}}{\beta+\left(B_{y}^{s p}\right)^{\gamma}} e^{\varsigma_{y}} \tag{7}
\end{equation*}
$$

where
$\alpha, \beta$ and $\gamma$ are spawner biomass-recruitment parameters $(\gamma=1$ for a Beverton-Holt relationship),
$\varsigma_{y}$ reflects fluctuation about the expected (median) recruitment for year $y$, and $B_{y}^{s p}$ is the spawner biomass at the start of year $y$, given by:

$$
\begin{equation*}
B_{y}^{s p}=\sum_{a=0}^{p} f_{a} w_{a}^{f} N_{y, a}^{f} \tag{8}
\end{equation*}
$$

where $w_{a}^{f}$ is the begin-year mass of female lobsters at age $a$, and $f_{a}$ is the proportion of lobster of age $a$ that are mature.

In order to work with estimable parameters that are more meaningful biologically, the stock-recruit relationship is re-parameterised in terms of the pre-exploitation equilibrium female spawning biomass, $K^{s p}$, and the "steepness" of the stock-recruit relationship (recruitment at $B^{s p}=0.2 K^{s p}$ as a fraction of recruitment at $B^{s p}=K^{s p}$ ):

$$
\begin{equation*}
\alpha=\frac{4 h R_{1}}{5 h-1} \tag{9}
\end{equation*}
$$

and

$$
\begin{equation*}
\beta=\frac{\left(K^{s p}(1-h)\right)}{5 h-1} \tag{10}
\end{equation*}
$$

where

$$
\begin{equation*}
R_{1}=K^{s p} /\left[\sum_{a=1}^{p-1} f_{a} w_{a}^{f} e^{-\sum_{m b}^{m} w_{t}}+f_{p} w_{p}^{f} \frac{e^{-\sum_{p}^{-w_{t}}}}{1-e^{-w_{s}^{\prime}}}\right] \tag{11}
\end{equation*}
$$

The total catch by mass in year $y$ is given by:

$$
\begin{equation*}
C_{y}=\sum_{m / f} \sum_{a} \sum_{\mid \text {minin }} w_{a+\frac{1}{2}}^{m i f} \vec{C}_{\text {y,al }}^{m / f} \tag{12}
\end{equation*}
$$

where

$$
\begin{align*}
& \vec{C}_{y, a, l}^{m}=\vec{N}_{y, a, l}^{m} S_{l}^{m} F_{y}^{A}  \tag{13}\\
& \vec{C}_{y, a, l}^{f}=\vec{N}_{y, a, t, l}^{f} S_{l}^{f} F_{y}^{A} \tag{14}
\end{align*}
$$

where $w_{a+1 / 2}^{m / f}$ denotes the mid-year mass of a $m / f$ lobster of age $a$, and where
$S_{l}^{m / f} \quad$ is the length-specific selectivity for male/female lobsters,
$F_{y} \quad$ is the fully selected fishing mortality in year $y$ for lobsters, and which is constrained to be $\leq 1.0$,
$\min \quad$ is the minimum legal carapace length in mm , and

$$
\begin{equation*}
\vec{N}_{y, a, l}^{m / f}=N_{y, a}^{m / f} Q_{a, l}^{m / f} \tag{15}
\end{equation*}
$$

where $Q_{a, t}^{m / f}$ is the proportion of fish of age $a$ that fall in the length group $l$ for the sex and area concerned (thus $\sum_{l} Q_{a, l}^{m / f}=1$ for all ages $a$ ).
The matrix $Q$ is calculated under the assumption that length-at-age is normally distributed about a mean given by the von Bertalanffy equation (Brandão et al., 2002), i.e.:

$$
\begin{equation*}
l_{a} \sim N^{*}\left[l_{\infty}^{m / f}\left(1-e^{-\kappa\left(a-a_{0}\right)}\right) ; \theta_{a}^{2}\right] \tag{16}
\end{equation*}
$$

where
$N^{*} \quad$ is the normal distribution truncated at $\pm 3$ standard deviations, and
$\theta_{a}$ is the standard deviation of length-at-age $a$, which is modeled to be proportional to the expected length-at-age $a$, i.e.:

$$
\begin{equation*}
\theta_{a}=\beta^{*} l_{\infty}^{m / f}\left(1-e^{-K\left(a-a_{0}\right)}\right) \tag{17}
\end{equation*}
$$

with $\beta^{*}$ a parameter estimated in the model fitting process.
The number of lobsters that die due to discard mortality is calculated as follows:

$$
\begin{align*}
& D_{y, a, l}^{m}=d\left(\vec{N}_{y, a, l}^{m} S_{l}^{m} F_{y}^{A}\right)  \tag{18}\\
& D_{y, a, l}^{s}=d\left(\vec{N}_{y, a, l}^{\prime} S_{l}^{f} F_{y}^{A}\right) \tag{19}
\end{align*}
$$

where $D_{y, a, l}^{m / f}$ is calculated for $l<\min$, and $d$ is the value of discard mortality which is set equal to 0.1 here.

The model estimate of mid-year exploitable biomass is given by:

$$
\begin{equation*}
B_{y}=B_{y}^{m}+B_{y}^{f} \tag{20}
\end{equation*}
$$

where

$$
\begin{align*}
& B_{y}^{f}=\sum_{a} \sum_{l \geq \min } S_{l}^{f}\left[w_{a+\frac{1}{2}}^{f} \vec{N}_{y, a, l}^{f} e^{-w^{\prime} / 2}\right]  \tag{21}\\
& B_{y}^{m}=\sum_{a} \sum_{l \geq \min } S_{l}^{m}\left[w_{a+\frac{1}{2}}^{m} \vec{N}_{y, a, l}^{m} e^{-w^{\prime \prime / 2}}\right] \tag{22}
\end{align*}
$$

and where
$B_{y}$ is the total (male plus female) model estimate of mid-year exploitable biomass for year $y$.

Fishing proportion:

$$
\begin{equation*}
F_{y}=\frac{C_{y}^{\text {obs }}}{B_{y}} \tag{23}
\end{equation*}
$$

### 1.1 Catch-at-length proportions

$$
\begin{align*}
& \hat{p}_{y, l}^{m}=\frac{\sum_{a} \vec{C}_{y, a, l}^{m}}{\sum_{l} \sum_{m} \sum_{a} \vec{C}_{y, a, l}^{m}}  \tag{24}\\
& \hat{p}_{y, l}^{f}=\frac{\sum_{a} \vec{C}_{y, a, l}^{f}}{\sum_{l} \sum_{f} \sum_{a} \vec{C}_{y, a, l}^{f}} \tag{25}
\end{align*}
$$

where $\hat{p}_{y, f}^{m / f}$ is the estimated proportion of catch of $m / f$ lobsters in length class $l$ in year $y$.

### 1.2 Selectivity-at-length function

The selectivity function (which depends on length) is assumed constant over time. Male and female selectivity is estimated separately as follows:

$$
\begin{equation*}
S_{l}^{m / f}=\frac{e^{-\mu^{m / / t}}}{1+e^{-\sigma^{m /(t}\left(-l^{m *}\right)}} \tag{26}
\end{equation*}
$$

The estimable parameters are thus:

- $l_{*}^{m / f}$,
- $\mu^{m / f}$ and
- $\delta^{m / f}$

The selectivity functions for both males and females are re-scaled so that the maximum selectivity value is 1.0 .

### 1.3. Initial conditions

For the first year $\left(y_{0}\right)$ considered in the model, the stock is assumed to be at a fraction $(\theta)$ of its pre-exploitation spawning biomass, i.e.:

$$
\begin{equation*}
B_{y_{0}}^{s p}=\theta \cdot K^{s p} \tag{27}
\end{equation*}
$$

with the starting age structure:

$$
\begin{equation*}
N_{y_{0}, a}^{m / f}=R_{\text {start }} N_{\text {start }, a}^{m / f} \quad \text { for } 1 \leq a \leq m \tag{28}
\end{equation*}
$$

where
$N_{\text {start }, 1}^{m / f}=1$
$N_{\text {start }, a}^{m / f}=N_{\text {start, },-1}^{m / f} e^{-M_{a-1}^{m / f}}(1-\varphi) \quad$ for $2 \leq a \leq m-1$
$N_{\text {start }, m}^{m / f}=N_{\text {start }, m-1}^{m / f} e^{-M_{m-1}^{m / f}}(1-\varphi) /\left(1-e^{-M_{m}^{m / f}}(1-\varphi)\right)$
where $\varphi$ is the average fishing proportion over the years immediately preceding $y_{o}$.

## 2. The likelihood function

The model is fitted to CPUE and catch-at-length (male and female separately) data, to estimate model parameters. Contributions by each of these to the negative loglikelihood $(-\ln L)$, and the various additional penalties added are as follows.

### 2.1 Relative abundance data (CPUE)

The likelihood is calculated assuming that the observed abundance index is lognormally distributed about its expected (median) value:

$$
\begin{equation*}
C P U E_{y}=q B_{y} e^{\varepsilon_{y}} \text { or } \varepsilon_{y}=\ln \left(C P U E_{y}\right)-\ln \left(q B_{y}\right) \tag{32}
\end{equation*}
$$

where
$C P U E_{y}$ is the CPUE abundance index for year $y$,
$B_{y}$ is the model estimate of mid-year exploitable biomass for year $y$ in given by equation 20 ,
$q$ is the constant of proportionality (catchability coefficient), and
$\varepsilon_{y}$ from $N\left(0,(\sigma)^{2}\right)$.

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

$$
\begin{equation*}
-\ln L=\sum_{y}\left[\left(\varepsilon_{y}\right)^{2} / 2(\sigma)^{2}+\ln (\sigma)\right] \tag{33}
\end{equation*}
$$

where
$\sigma$ is the residual standard deviation estimated in the fitting procedure by its maximum likelihood value:

$$
\begin{equation*}
\hat{\sigma}=\sqrt{1 / n \sum_{y}\left(\ln C P U E_{y}-\ln \hat{q} \hat{B}_{y}\right)^{2}} \tag{34}
\end{equation*}
$$

where
$n$ is the number of data points in the CPUE series, and
$q$ is the catchability coefficient, estimated by its maximum likelihood value:

$$
\begin{equation*}
\ln \hat{q}=1 / n \sum_{y}\left(\ln C P U E_{y}-\ln \hat{B}_{y}\right) \tag{35}
\end{equation*}
$$

### 2.2 Catches-at-length (from Rademeyer 2003)

The following term is added to the negative log-likelihood:

$$
\begin{equation*}
-\ell \mathrm{n} L^{\operatorname{logst}}=w_{l e n} \sum_{y} \sum_{l} \sum_{m / f}\left\lfloor\ln \left(\sigma_{l e n} / \sqrt{p_{y, l}^{m / f}}\right)+p_{y, l}^{m / f}\left(\ln p_{y, l}^{m / f}-\ln \hat{p}_{y, l}^{m / f}\right)^{2} / 2\left(\sigma_{l n}\right)^{2}\right] \tag{36}
\end{equation*}
$$

where
$p_{y, l}^{m / f} \quad$ is the observed proportion of $m / f$ lobsters (by number) in length group $l$ in the catch in year $y$, and
$\sigma_{\text {len }}$ is the standard deviation associated with the length-at-age data, which is estimated in the fitting procedure by:

$$
\begin{equation*}
\hat{\sigma}_{l n}=\sqrt{\sum_{m / f} \sum_{y} \sum_{l} p_{y, l}^{m / f}\left(\ln p_{y, t}^{m / f}-\ln \hat{p}_{y, l}^{m / f}\right)^{2} / \sum_{m / f} \sum_{y} \sum_{l} 1} \tag{37}
\end{equation*}
$$

Equation (31) makes the assumption that proportion-at-length data are log-normally distributed about their model-predicted values. The associated variance is taken to be inversely proportional to $p_{y, f}^{m / f}$ to downweight contributions from observed small proportions which will correspond to small predicted sample sizes.

## 3. Further Model parameters

Natural mortality: Natural mortality $M^{m / f}$ for male and female lobsters is assumed to be the same ( $M$ ) for all age classes and both sexes, and is fixed here at 0.10 .

Age-at-maturity: The proportion of lobsters of age $a$ that are mature is approximated by $f_{a}=1$ for $a>5$ years (i.e. $f_{a}=0$ for $a=0, \ldots, 5$ ).

Minimum age: Age 0.
Maximum age: $p=20$, and is taken as a plus-group.
Minimum length: length 1 mm .
Maximum length: 180 mm , what is taken as a plus-group.
Mass-at-age: The mass $w_{a}^{m / f}$ of a $m / f$ lobster at age $a$ is given by:
where the values assumed for the observed growth parameters and length-weight are reported in Johnston (2010).

Stock-recruitment relationship: The shape parameter, $\gamma$, is fixed to 1 , corresponding to a Beverton-Holt form.

## 4. The Bayesian approach

The Bayesian method entails updating prior distributions for model parameters according to the respective likelihoods of the associated population model fits to the

CPUE and catch-at-length, to provide posterior distribution for these parameters and other model quantities.

The catchability coefficients ( $q$ ) and the standard deviations associated with the CPUE and catch-at-length data ( $\sigma$ and $\sigma_{l n}$ ) are estimated in the fitting procedure by their maximum likelihood values, rather than integrating over these three parameters as well. This is adequately accurate given reasonably large sample sizes (Walters and Ludwig 1994, Geromont and Butterworth 1995).

Modes of posteriors, obtained by finding the maximum of the product of the likelihood and the priors, are then estimated rather than performing a full Bayesian integration, due to the time intensiveness of the latter.

### 4.1 Priors

The following prior distributions are assumed:
$h \quad \mathrm{~N}\left(0.90, \mathrm{SD}^{2}\right)$ with $\mathrm{SD}=0.2$, where the normal distribution is truncated at $h=1$.
$l_{*}^{m / f}: \quad \mathrm{U}[1,170] \mathrm{mm}$
$\mu^{m / f} \quad \mathrm{U}[0,1]$
$\delta^{m / f} \quad \mathrm{U}[0,1]$
$\beta^{*} \mathrm{U}[0,1]$ (from equation 17)

### 4.2 Estimable parameters

| Parameter | What is it | Which equation | Number of <br> parameters |
| :--- | :--- | :---: | :---: |
| $K^{s p}$ | Pristine female spawning <br> biomass | 11 | 1 |
| $H$ | Steepness parameter of SR <br> function | 9,10 | 1 |
| $l_{*}^{m / f}$ | Selectivity function parameter | 26 | 2 |
| $\mu^{m / f}$ | Selectivity function parameter | 26 | 2 |
| $\delta^{m / f}$ | Selectivity function parameter | 26 | 2 |
| $\beta^{*}$ | Parameter of length-at-age <br> distribution | 17 | 1 |
| TOTAL |  |  | $\mathbf{9}$ |

## 5. Preliminary Results

For the purposes of these analyses the full Bayesian posteriors have not been evaluated. Instead estimates are reported for the joint posterior mode (corresponding the maximum penalized likelihood estimation), which is adequate for the purposes required here.

### 5.1 Nightingale

Model 1 fits to the full catch series, from 1949, assuming that the resource is at unexploited equilibrium at that time, i.e. $\theta=1$ and $\varphi=0$. The model is fit to CPUE data only. For the initial results shown, plausible selectivity vectors were input and $h$ fixed at 0.95 given indications that the data preferred a high value. However these initial results (see Figs 1-4) immediately indicated an inability to match the generally increasing CPUE trend from 1995 to 2008 given the historic catch series input (Fig. 1), which is why this fit has not immediately been refined.

Given the need for models that do fit the general trend in the CPUE data, an alternative approach was pursued of focusing only on more recent information, but consequently no longer assuming the resource to be at pre-exploitation equilibrium at the start of the period considered. Thus Models 2 -4 fit to the 1990+ catch series only, estimating the value of the parameter $\theta$ (see equation 27) in the model fit, but at this stage fixing $\varphi$ on input to be 0.01 as there is inadequate information content in the data to estimate this parameter as well in the fit. These models fit to CPUE and catch-at-length (CAL) data, with the latter allowing for the parameters of the selectivity function to be estimated. The CAL data are downweighted by 0.1 in the $-\ln \mathrm{L}$ to offset non-independence effects. Even so, the data are unable to yield precise estimates of key parameters, so that the fishing proportion in 2009 was forced (by way of adding a penalty function to the likelihood) to equal either:

Model 2: $\mathrm{F}(2009)=0.05$,
Model 3: $\mathrm{F}(2009)=0.1$, or
Model 4: $F(2009)=0.2$.
Estimates of parameter values and management related quantities for these four models are shown in Table 1, while Figs 1-4 show biomass and fishing mortality trajectories, and Figs 5 and 6 show the fits to the catch-at-length data and estimated selectivity-at-length functions respectively.

### 5.2 Inaccessible, Gough and Tristan

Due to time constraints, only limited work has been possible on fitting the model to data for the lobster populations at these islands. That work has nevertheless indicated there are problems for those populations also in reconciling the impacts of the historic catch series and recent increases in CPUE on the estimated resource trends.

## 6. Discussion and Further Work

The reason for developing these assessments is to provide operating models for testing candidate Management Procedures so as to provide the basis for recommending future TACs for each island. These models must span a reasonable range to reflect uncertainties concerning the resource dynamics. Model 1 does not fit
the Nightingale CPUE data adequately. This can be interpreted in two ways. The first is that the assessment results are nevertheless reliable and the recent upward trend in CPUE reflects either an unusual period of increasing catchability or an upward recruitment fluctuation. The other is that the data for the historic catch series are unreliable and so better ignored, which requires the Models 2-4 approach, with the span of these models (which the likelihood is unable to discriminate - see Table 1) hopefully covering a plausible range for the dynamics and current status of this population.

Models 1-4 are proposed to form the basis for testing candidate Management Procedures for this resource, being seen to reasonably reflect the range of uncertainty about its dynamics. They will nevertheless be refined somewhat before use in this manner, with Model 1 to be fit also to the CAL information, and Models 2-4 checked for the implications of using a larger (and likely more realistic) value for the initialization parameter $\varphi$.

A similar approach will then be applied to develop ranges of operating models for the resources at the other three islands.

## 7. References

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## MARAM/Tristan/2010/Mar/03

Table 1: Comparative model results for Nightingale. All biomass units in MT.

|  | Model 1 <br> Fit to 1949+ | Model 2 <br> $\mathrm{F}(2009)=0.05$ | Model 3 <br> $\mathrm{F}(2009)=0.1$ | Model 4 <br> $\mathrm{F}(2009)=0.2$ |
| :--- | :---: | :---: | :---: | :---: |
| $-\operatorname{lnL}(\mathrm{CPUE})$ | -4.506 | -10.02 | -9.98 | -9.99 |
| $-\operatorname{lnL}$ (CAL) | $(81.22)$ | -35.34 | -35.47 | -34.03 |
| $-\ln \mathrm{C}$ (Total) |  | -20.43 | -20.41 | -20.09 |
| $h$ | 0.95 | 0.91 | 0.91 | 0.91 |
| $\theta$ | 1 | 0.166 | 0.187 | 0.208 |
| $K^{s p}$ | 1034 | 5188 | 2857 | 1819 |
| $B_{\mathrm{i}}$ (growth variance) | Fixed $=0.1$ | 0.424 | 0.422 | 0.456 |
| $\mu^{m i}$ | Fixed $=0.074$ | 0.047 | 0.045 | 0.045 |
| $\mu^{f}$ | Fixed $=0.165$ | 0.144 | 0.143 | 0.142 |
| $\boldsymbol{l}^{m}$ | Fixed $=71.02$ | 73.38 | 73.39 | 74.12 |
| $\boldsymbol{Z}_{*}^{f}$ | Fixed $=69.53$ | 69.20 | 69.19 | 69.16 |
| $\delta^{m i}$ | Fixed=0.3 | 0.296 | 0.296 | 0.279 |
| $\delta^{f}$ | Fixed $=0.3$ | 0.464 | 0.463 | 0.464 |
| $B^{s p}(1990) / K^{s p}$ | 0.368 | 0.140 | 0.156 | 0.174 |
| $B^{s p}(2010) / K^{s p}$ | 0.610 | 0.160 | 0.574 | 0.512 |
| $B^{s p}(2010)$ | 631 | 3165 | 1641 | 932 |
| $B^{e x p}(2010)$ | 404 | 1507 | 745 | 364 |
| $F(1993)$ | 0.178 | 0.153 | 0.262 | 0.422 |
| $F(2009)$ | 0.171 | 0.05 | 0.100 | 0.200 |

Figure 1: Fits to Nightingale CPUE.


Figure 2: Nightingale model 1-4 F trends.


Figure 3: Nightingale Model 1-4 $B^{\text {sp }}$ trajectories.


Figure 4: Nightingale Model 1-4 $B^{s p} / K^{s p}$ trajectories.


Figure 5a: Nightingale CAL predicted vs observed for Model 1. Averaged values over all years are reported.



Figure 5b: Nightingale CAL predicted vs observed for Model 2. Averaged values over all years are reported.


Figure 5c: Nightingale CAL predicted vs observed for Model 3. Averaged values over all years are reported.


Figure 5d: Nightingale CAL predicted vs observed for Model 4. Averaged values over all years are reported.


Figure 6: Nightingale Model 3 selectivity functions.


