

# Method used to include cannibalism and inter-species predation in the species, sex, age and size disaggregated hake stock assessment model.

by

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## 1 Summary

The following is an overview of methods used for results presented elsewhere:

1. The starting model is the latest stock assessment model for hake - cannibalistic and predatory features were added to this model. None of the code or algebra for the pre-existing log-likelihood functions are impacted by these modifications. There are potential additional LLFs which use stomach content data but these have not yet been incorporated into this method.
2. The model used here is species, sex, age and size disaggregated. Most quantities are size dependent and age dependence is a calculated result. For example, fishing selectivities, hake ration and dietary quantities are size based. The age dependence of these quantities is a calculated result.
3. Hake ration is based on published work from the 1990s (Punt and Leslie, 1995), which was used in OLRAC (2008a) to develop age-based relationships for an age structured version of the cannibalistic assessment model. Here we have modified these age dependent relationships to reflect size dependence, using simple growth equations. The same applies to the dietary composition of hakes. At this stage neither the hake rations nor the dietary percentages are either year dependent or vary in relation to prey availability, or the density of the stock.
4. Idealized equations have been used to describe the size preference of hake predators for hake, prey based on the  $\beta$  function. In the implementation described here, initial values for these size preference functions were based on inspection of the data in Butterworth and Harwood (1991) and BEP (1991), also presented in Table 7-4. The parameters of interest are the  $\beta$  function parameters, as well as the minimum, maximum and optimum sizes for the preference functions, which are predator and prey species and size dependent. The intention is that ultimately the parameters governing these equations will become fitted parameters, but this has not yet been implemented.
5. The model is not coast disaggregated.
6. The propagation of the population vector presents some runtime challenges. For example, use of month as a timestep requires 12 different calls to the predatory calculations, which could push runtimes to unfeasible levels. A compromise approach is used here. Firstly, we express the predatory effect as a natural mortality coefficient using an argument based on the limit to zero of the time step length, and secondly we base the predation for year  $y$  on a population vector that is first reduced by  $\frac{1}{2}$

a year of natural mortality, where the predatory component of this natural mortality is the value from year  $y-1$ . Further work using the alternative multiple time step approach is envisaged for the future.

7. Natural mortality is viewed as the sum of a year independent base natural mortality coefficient (which is species, sex and age dependent), and another hake predatory natural mortality coefficient which is year dependent (as well as being dependent on species, sex and age). The latter is calculated from the hake predatory equations defined here. A pristine total natural mortality coefficient which is species and age dependent is defined and parameterised as a declining logistic function of age, and the pristine hake predatory natural mortality coefficient is constrained so that it cannot exceed the total natural mortality. This simplifies the calculation of the unexploited population vector. The base natural mortality is year invariant and is calculated as the difference between total natural mortality and hake predatory natural mortality under equilibrium unexploited conditions.
8. Use of information based on stomach content analyses potentially makes additional data available to the model fitting process. Typical data are the percentage by weight or by number of hake in hake stomachs, where this may be disaggregated by species. In the work reported here such data are not formally including in the overall stock assessment log-likelihood function, instead we show the comparison. Future work is intended to incorporate these data in a formal way.
9. The version of the model that is presented here is coded using both ADMB and TMB.

## 2 Methods in detail

### 2.1 Dynamic and Equilibrium Equations

There are two places where modifications to reflect cannibalism and inter species predation are required in the conventional stock assessment model:

1. **Dynamics:** Updating the population vector from one year to the next.
2. **Equilibrium:** Calculation of the population vector under unexploited equilibrium conditions.

### 2.2 Dynamics

Modifying the dynamic equations involves changes to the conventional updating equations, which are based on Pope's approximation in OLRAC SPS's present version of the hake stock assessment model, viz.:

$$N_{s,g,y+1,a+1} = \left( N_{s,g,y,a} e^{-\frac{M_{s,g,y,a}}{2}} - C_{s,g,y,a} \right) e^{-\frac{M_{s,g,y,a}}{2}} \quad (1)$$

In the non-cannibalism version of the stock assessment analysis,  $M_{s,g,y,a}$  is dependent only on age, but is year, species and gender invariant. However, when considering cannibalism and inter species predation, the total natural mortality becomes dependent on all four indices; year, species, gender and age. In the formulation proposed here, the total natural mortality,  $M_{s,g,y,a}$  is modelled as the sum of a cannibalistic / interspecies predation component of natural mortality  $M_{s,g,y,a}^c$  and a base natural mortality coefficient  $M_{s,g,a}^{base}$ .  $M_{s,g,y,a}^c$  is year, species, gender and age dependent, while the base natural mortality rate,  $M_{s,g,a}^{base}$ , is species, gender and age dependent but year invariant. This is reflected in the following equation for total natural mortality:

$$M_{s,g,y,a} = M_{s,g,y,a}^c + M_{s,g,a}^{base} \quad (2)$$

The relevance of this equation will become clear later on.

A particular indexing system is used here when necessary. That is to index species as a predator using  $s$ , and to index species as a prey using  $sp$ . A similar convention is used for gender,  $g$  and  $gp$ , age,  $a$  and  $ap$  and size,  $l$  and  $lp$ . This distinction is usually only necessary when both prey and predators are referred to by the same quantity or in the same equation. At other times this distinction may not be required and we then revert to the use of  $s, g, a, l$  for index designations.

The first step in the schema proposed here is to calculate the total amount **by number** of prey hake in the cohort  $sp, gp, y, ap$  which is consumed by predator hake of all species, genders and ages in the period  $y$  to  $y+\Delta t$ . This amount is denoted here as  $\Delta t PRED_{sp, gp, y, ap}$ , where  $PRED_{sp, gp, y, ap}$  would be the annual equivalent consumption were all population numbers invariant over that year. In order to calculate  $\Delta t PRED_{sp, gp, y, ap}$  a particular calculation sequence is followed, as is now described. Assuming a position in time at the beginning of year  $y$ , the calculation sequence is initiated by distributing numbers at age across the length dimension, as follows:

$$n_{s,g,y,a,l} = N_{s,g,y,a} P_{s,g,a,l} \quad (3)$$

- $n_{s,g,y,a,l}$  are the number of hake of species  $s$ , gender  $g$ , year  $y$ , age class  $a$  and length  $l$  at the beginning of the year.
- $N_{s,g,y,a}$  are the number of hake of species  $s$ , gender  $g$ , year  $y$  and age class  $a$  at the beginning of the year.
- $P_{s,g,a,l,q}$  are the proportion of hake at the beginning of the year of species  $s$ , gender  $g$ , age class  $a$  which are of length  $l$ .

The next step is to calculate the **quantity by mass** that the number of hake  $n_{s,g,y,a,l}$  consume of hake of difference species in the period between  $y$  and  $y+\Delta t$ . We denote this quantity by  $HAKewtEATEN_{s,g,y,a,l,q,sp}$ , where  $HAKewtEATEN_{s,g,y,a,l,q,sp}$  is the annual consumption were the population numbers invariant over the full year. It is expressed in terms of constituent amounts that are calculable based on certain published information (as is described later on and in Appendix A), i.e.

$$\Delta t HAKewtEATEN_{s,g,y,a,l,q,sp} = \Delta t HAKESPP\%_{s,y,l,sp} 365.25/100 Ration\%_{s,l} w_{sp, gp, lp} n_{s,g,y,a,l} \quad (4)$$

Where

1.  $s$  denotes species as a predator and  $sp$  denotes species as a prey - a similar convention is used for gender,  $g$  and  $gp$ , age,  $a$  and  $ap$  and size,  $l$  and  $lp$ , as described earlier.
2.  $w_{s,g,l}$  is the body weight of an individual hake  $s,g,y,l$ , while  $w_1 n_{s,g,y,a,l}$  is the weight of all hake in  $s,g,y,a,l$ .
3.  $Ration\%_{s,l}$  is the percentage of body weight that hake of a particular species and length consume daily.
4.  $HAKESPP\%_{s,y,l,sp}$  is the weight % of the diet of hake  $s,y,l$  consisting of hake species  $sp$ .
5.  $\Delta t HAKewtEATEN_{s,g,y,a,l,sp}$  is the mass of hake of  $sp$  eaten by hake  $s,g,y,a,l$  in the period between the beginning of year  $y$  and  $y+\Delta t$ , while  $HAKewtEATEN_{s,g,y,a,l,sp}$  is the full year equivalent amount for an invariant population vector during the year.

In order to determine how  $\Delta t HAKewtEATEN_{s,g,y,a,l,sp}$  is distributed across  $lp, gp$  and  $ap$ , the variable  $PREF_{s,l,sp,lp}$  is defined as the preference that hake  $s,l$  have for different sizes  $lp$  of hake of species  $sp$ . By preference is meant the relative proportions **by number** of prey of size  $lp$  that are eaten by a prey of size  $l$ , under conditions that equal numbers of all sizes of prey are available. If the numbers of prey are not equal,

then the relative proportions eaten by size are reduced in proportion to the available prey numbers by size. These preferences are assumed to be age, both  $a$  and  $ap$ , and gender, both  $g$  and  $gp$ , invariant (see Appendix A). Note that there is nothing special about how a particular preference function has been scaled. Thus the amount  $PREF_{s,l,sp,lp} n_{sp,gp,y,ap,lp}$  is a relative number of hake eaten by other hake. The subscripts on  $PREF_{s,l,sp,lp}$  indicate that there may be four different preference functions, i.e. for  $s = \textit{Merluccius paradoxus}$  or ***Merluccius capensis***, and for  $sp = \textit{Merluccius paradoxus}$  or ***Merluccius capensis***.

It is necessary for  $PREF_{s,l,sp,lp} n_{sp,gp,y,ap,lp}$  to be suitably scaled, and the scaling must be at the level of resolution of  $s, g, y, a, l, sp$ , since this is the scale of resolution at which the consumption by weight of hake  $sp$  by hake  $s, g, y, a, l$  can be calculated via the equation

$\Delta t HAKEwtEATEN_{s,g,y,a,l,sp} = \Delta t HAKESPP\%_{s,y,l,sp} 365.25/100 Ration\%_{0,s,l} W_{s,g,l} n_{s,g,y,a,l}$ . Using an appropriate scaling factor,  $K_{s,g,y,a,l,sp}$ , the preference functions just defined,  $PREF_{s,l,sp,lp}$ , and body weight and numbers at age in the population,  $w_{sp,gp,lp}$  and  $n_{sp,gp,y,ap,lp}$ , the following is an alternative expression for  $\Delta t HAKEwtEATEN_{s,g,y,a,l,sp}$ :

$$\Delta t HAKEwtEATEN_{s,g,y,a,l,sp} = \Delta t K_{s,g,y,a,l,sp} \sum_{lp} PREF_{s,l,sp,lp} \left[ \sum_{gp} \sum_{ap} w_{sp,gp,lp} n_{sp,gp,y,ap,lp} \right] \quad (5)$$

Which can be alternatively written as

$$\Delta t HAKEwtEATEN_{s,g,y,a,l,sp} = \Delta t K_{s,g,y,a,l,sp} \sum_{lp} PREF_{s,l,sp,lp} W_{sp,y,lp} \quad (6)$$

where  $W_{sp,y,lp}$  is the weight of hake of species  $sp$ , length  $lp$  at the beginning of year  $y$ , i.e.

$$W_{sp,y,lp} = \sum_{gp} \sum_{ap} w_{sp,gp,lp} n_{sp,gp,y,ap,lp} \quad (7)$$

The scaling factor  $K_{s,g,y,a,l,sp}$  can be solved as:

$$K_{s,g,y,a,l,sp} = \frac{HAKEwtEATEN_{s,g,y,a,l,sp}}{\sum_{lp} PREF_{s,l,sp,lp} W_{sp,y,lp}} \quad (8)$$

With the scaling factor  $K_{s,g,y,a,l,sp}$  one can calculate the number of species, gender, age and size of hake eaten by hake of a given species, gender, age and size,  $\Delta t v_{s,g,y,a,l,sp,gp,ap,lp}$

$$\Delta t v_{s,g,y,a,l,sp,gp,ap,lp} = \Delta t K_{s,g,y,a,l,sp} PREF_{s,l,sp,lp} n_{sp,gp,y,ap,lp} \quad (9)$$

Therefore the total number of  $sp, gp, y, ap$  hake which are consumed by other hake,  $\Delta t PRED_{sp,gp,y,ap}$ , can be obtained by summing up  $\Delta t v_{s,g,y,a,l,sp,gp,ap,lp}$  across all predator indices  $s, g, y, a, l$ , i.e.

$$\Delta t PRED_{sp,gp,y,ap} = \sum_s \sum_g \sum_a \sum_l \Delta t v_{s,g,y,a,l,sp,gp,ap,lp} \quad (10)$$

or by substitution from the above equations:

$$\Delta t PRED_{sp,gp,y,ap} = \Delta t \sum_s \sum_g \sum_a \sum_l \left[ \frac{HAKEwtEATEN_{s,g,y,a,l,sp}}{\sum_{lp} PREF_{s,l,sp,lp} W_{sp,y,lp}} PREF_{s,l,sp,lp} n_{sp,gp,y,ap,lp} \right] \quad (11)$$

Which can also be expressed in the following way:

$$\Delta t PRED_{sp,gp,y,ap} = \Delta t \sum_s \sum_g \sum_a \sum_l \left[ \frac{HAKEwtEATEN_{s,g,y,a,l,sp}}{\sum_{gp} \sum_{ap} \sum_{lp} PREF_{s,l,sp,lp} w_{sp,gp,lp} n_{sp,gp,y,ap,lp}} PREF_{s,l,sp,lp} n_{sp,gp,y,ap,lp} \right] \quad (12)$$

Updating the population numbers from  $y$  to  $y+\Delta t$  is now achievable using the following difference equation approximation which is valid for small  $\Delta t$ :

$$N_{s,g,y+\Delta t,a} = (N_{s,g,y,a} - \Delta t PRED_{sp,gp,y,ap}) e^{-\Delta t M_{s,g,a}^{base}}, \quad (13)$$

where, as defined previously,  $M_{s,g,a}^{base}$  is the year invariant base natural mortality coefficient. This equation could form the basis for a sequential updating process on, for example, a monthly basis. A significant limiting factor is however the runtime involved in these calculations. The following approximation is therefore an interim measure which has been put in place to limit the runtime. Note that, based on the earlier definitions of  $M_{s,g,a}^{base}$ , the year invariant base natural mortality coefficient, and  $M_{s,g,y,a}^c$ , the year dependent cannibalism and predation linked natural mortality coefficient, equation (12) can be written alternatively as:

$$N_{s,g,y+\Delta t,a} = N_{s,g,y,a} e^{-\Delta t (M_{s,g,y,a}^c + M_{s,g,a}^{base})} \quad (14)$$

and from this,

$$\Delta t PRED_{sp,gp,y,ap} = N_{s,g,y,a} \frac{M_{s,g,y,a}^c}{(M_{s,g,y,a}^c + M_{s,g,a}^{base})} \left(1 - e^{-\Delta t (M_{s,g,y,a}^c + M_{s,g,a}^{base})}\right) \quad (15)$$

In the limit for small  $\Delta t$ , equation (15) becomes

$$PRED_{sp,gp,y,ap} = N_{s,g,y,a} M_{s,g,a}^c$$

i.e.

$$M_{s,g,y,a}^c = \frac{PRED_{sp,gp,y,ap}}{N_{s,g,y,a}} \quad (16)$$

A possible interim approximation (interim until further improvement in runtime permits the monthly updating equation to be used instead) is therefore to assume that the natural mortality coefficient from equation (16) can be extrapolated to the full year in the following updating equation:

$$N_{s,g,y+1,a+1} = \left( N_{s,g,y,a} e^{-\frac{(M_{s,g,y,a}^c + M_{s,g,a}^{base})}{2}} - C_{s,g,y,a} \right) e^{-\frac{(M_{s,g,y,a}^c + M_{s,g,a}^{base})}{2}} \quad (17)$$

This approximation is considered too crude and an improvement which is considered to be better is to use

$$PRED_{sp,gp,y,ap} = \sum_s \sum_g \sum_a \sum_l \left[ \frac{HAKEwtEATEN_{s,g,y,a,l,sp}}{\sum_{lp} PREF_{s,l,sp,lp} W_{sp,y,lp}} PREF_{s,l,sp,lp} n_{sp,gp,y,ap,lp} e^{-\frac{(M_{s,g,y-1,a}^c + M_{s,g,a}^{base})}{2}} \right] \quad (18)$$

as the basis for the calculation of  $M_{s,g,y,a}^c = \frac{PRED_{sp,gp,y,ap}}{N_{s,g,y,a}}$ . This involves the use of the population numbers present in the middle of year but these are calculated based on the cannibalistic natural mortality coefficient component from the previous year (to avoid the obvious circularity that would arise from using the same year value). The same year mid-year population numbers are however recalculated using the value of  $M_{s,g,y,a}^c$  thus calculated, and not by use of  $M_{s,g,y-1,a}^c$ .

### 2.3 Equilibrium and parameterization of natural mortality

As a precursor to the description of the equilibrium calculations, the total natural mortality prevailing under pristine conditions,  $M_{s,g,y=p,a}$ , is parameterized using the following equation:

$$M_{s,g,y=p,a} = \frac{\phi_s}{(1 + e^{\kappa_s(a - \theta_s)})} + \rho_s \quad (19)$$

(where  $y=p$  is the first year in the stock assessment run sequence which is assumed to be under pristine equilibrium conditions). In equation (19) the natural mortality parameterisation is species specific. The calculation of the equilibrium population vector follows in the usual manner based on the pristine total natural mortality values  $M_{s,g,y=p,a}$ . The year invariant base natural mortality coefficient  $M_{s,g,a}^{base}$  is calculated as follows

$$M_{s,g,a}^{base} = M_{s,g,y=p,a} - M_{s,g,y=p,a}^c \quad (20)$$

Although there is a chance that equation (20) provides a negative value for one or more elements of the array  $M_{s,g,a}^{base}$ , this is excluded by the use of the “posfun” function in ADMB and TMB.

The modifications described above have no further implications for the mathematical logic of the latest sex, species, age and size structure hake stock assessment model.

## 2.4 Constraints on total natural mortality

The natural mortality penalty term is derived from the average natural mortality levels for *M. capensis* and *M. paradoxus* for a version of the “cannibalistic” stock assessment model, values that are taken to be the same for both species, based on Figure 1 of FISHERIES/2016/MAR/SWG-DEM/05:

| Age Class | Average M |
|-----------|-----------|
| 0         | 0.90      |
| 1         | 0.90      |
| 2         | 0.90      |
| 3         | 0.76      |
| 4         | 0.62      |
| 5         | 0.48      |
| 6         | 0.34      |
| 7         | 0.20      |
| 8         | 0.20      |
| 9         | 0.20      |
| 10        | 0.20      |
| 11        | 0.20      |
| 12        | 0.20      |
| 13        | 0.20      |
| 14        | 0.20      |
| 15        | 0.20      |

For average total natural mortality values over 1917 – 2016 from the model, deviations from the reference values above are calculated for each age class and species, squared and summed up over all ages and for both species. The final SS is then inflated by a factor of 5 to produce the penalty term used in the model fits.

## 2.5 Constraints on base natural mortality

A constraint is imposed which forces the base natural mortality value to be larger than 0.2 for both species and sexes and all ages.

### 3 Appendix A: Daily ration as % of body weight, hake in the diet of hake and hake preference functions

The modifications to the stock assessment calculations described here involve the following new quantities:

1. Daily ration as % of body weight.
2. Hake in diet of hake.
3. Preference functions.

The derivation of these quantities for the purpose of the results shown in this document are described below.

#### 3.1 Daily ration as % of body weight

The daily ration of hakes  $Ration\%_{0,s,l}$  is represented as a % of body weight and is modelled as a function of species  $s$  and size  $l$ . The dietary information for this study has been extracted from Punt and Leslie (1995), Table VIII. This table cites estimates of daily ration in grams for each prey item, as well as the total daily ration as a function of age class. Table 7-1 is a reproduction of this information from OLRAC (2008a) where the age dependence of the daily ration information from Punt and Leslie (1995) was fitted using a separate exponential function for each species. Figure 7-1 and Figure 7-2 represent these relationships graphically. Since the fundamental measure in the stock assessment model of this document is the size of hake, these relationships have been converted to relationships in terms of body size. This has been achieved by using the relationship in the age domain to calculate  $Ration\%_{0,s,l}$  values for each age from 0 to 15 in steps of 0.25, and then converting these ages to length using the average male / female growth rate for each species. The result is a table of values of  $Ration\%_{0,s,l}$  versus size  $l$ . This relationship was then refitted using polynomial equations, and the predicted values from this equation was used in the stock assessments. The polynomial fits referred to are shown in Figure 7-3.

Table 7-1. A table recording how daily ration (%) information from Punt et al (1992) is used to obtain annual consumption factors ("Annual factor") to estimate annual predator consumption as a function of annual predator biomass. The daily% fitted values are obtained from an exponential fit to the recorded daily% values

| Age class | M. paradoxus |               |               | M. capensis |               |               |
|-----------|--------------|---------------|---------------|-------------|---------------|---------------|
|           | Daily%       | Daily% fitted | Annual factor | Daily%      | Daily% fitted | Annual factor |
| 0         | 1.3          | 0.8578        | 3.13          | 2.7         | 2.2453        | 8.20          |
| 1         | 1            | 0.7521        | 2.75          |             | 2.1726        | 7.93          |
| 2         |              | 0.6594        | 2.41          |             | 2.1023        | 7.67          |
| 3         |              | 0.5782        | 2.11          | 1.5         | 2.0343        | 7.43          |
| 4         | 0.2          | 0.5069        | 1.85          |             | 1.9684        | 7.18          |
| 5         |              | 0.4445        | 1.62          |             | 1.9047        | 6.95          |
| 6         |              | 0.3897        | 1.42          |             | 1.8431        | 6.73          |
| 7         |              | 0.3417        | 1.25          |             | 1.7834        | 6.51          |
| 8         | 0.3          | 0.2996        | 1.09          |             | 1.7257        | 6.30          |
| 9         |              | 0.2627        | 0.96          |             | 1.6699        | 6.09          |
| 10        |              | 0.2303        | 0.84          |             | 1.6158        | 5.90          |
| 11        |              | 0.2019        | 0.74          |             | 1.5635        | 5.71          |
| 12        |              | 0.1770        | 0.65          |             | 1.5129        | 5.52          |
| 13        |              | 0.1552        | 0.57          |             | 1.4640        | 5.34          |
| 14        |              | 0.1361        | 0.50          |             | 1.4166        | 5.17          |
| 15        | 0.15         | 0.1193        | 0.44          | 1.4         | 1.3707        | 5.00          |

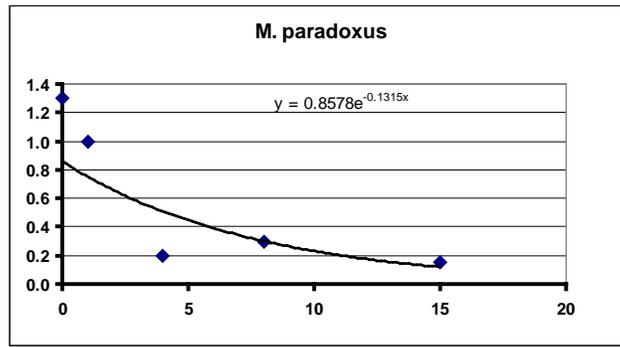


Figure 7-1. Recorded and fitted daily% consumption values for *M. paradoxus*. These values are daily rations expressed as a percentage of body weight. The y-axis values are thus percentages, and the x-axis values are age

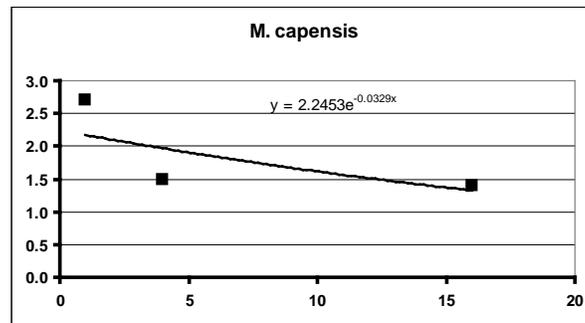


Figure 7-2. Recorded and fitted daily% consumption values for *M. capensis*. These values are daily rations expressed as a percentage of body weight. The y-axis values are thus percentages, and the x-axis values are age.

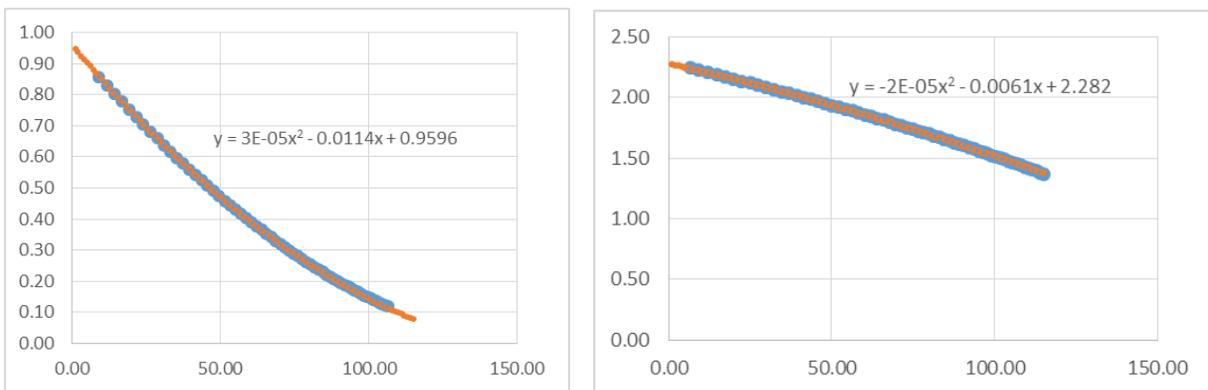


Figure 7-3. The relationship between daily ration as a % of body weight versus hake length for *M. paradoxus* (left panel) and *M. capensis* (right panel). The circles are the values derived from the exponential equation that was originally fitted against age, and the solid line is the polynomial equation value that was fitted to these values.

### 3.2 Hake in the diet of hake

The variable  $HAKESPP\%_{s,y,l,sp}$  is the % by mass of the species *sp* in the diet of species *s*, for different lengths *l* of the prey species. In this notation it is a function of year as well, since the intention is that this quantity will eventually be modelled as a function of the relative biomasses of prey and predator species via non-linear equations such as the Holling Type II equation (Holling, 1965). For the present implementation, this quantity has been fixed at a year invariant level. Table 7-2 reproduces the data from Punt and Leslie (1995) that forms

the basis of the values for  $HAKESPP\%_{s,y,l,sp}$  used here. In OLRAC (2008a) these values were fitted as a function of age in using polynomial relationships as shown in Figure 7-4 and Figure 7-5.

Since the fundamental measure in the stock assessment model of this document is the size of hake, these relationships have been converted to relationships in terms of body size. This has been achieved by using the relationship in the age domain to calculate  $HAKESPP\%_{s,y,l,sp}$  values for each age from 0 to 15 in steps of 0.25, and then converting these ages to length using the average male / female growth rate for each species. The result is a table of values of  $HAKESPP\%_{s,y,l,sp}$  versus size l. This relationship was then refitted using logistic equations, and the predicted values from these logistic equations were then used in the stock assessments. These logistic equation fits are shown in Figure 7-6.

Table 7-2. The dietary information for this study has been extracted from Punt and Leslie (1995), Table VIII. This table (i.e. VIII of Punt and Leslie, *ibid*) cites estimates of daily ration in grams for each prey item, as well as the total daily ration. This information is provided for each predator age class, and is reproduced in this table. The following table reproduces the information, where the bold normal type quantities refer to daily ration in grams and the italicized quantities are proportions of the daily amount, the quantities  $HAKESPP\%_{s,y,a,sp}$ .

|                            |              | <b>Predator</b>            |              |              |               |               |               |               |               |  |
|----------------------------|--------------|----------------------------|--------------|--------------|---------------|---------------|---------------|---------------|---------------|--|
|                            |              | <b><i>M. Capensis</i></b>  |              |              |               |               |               |               |               |  |
|                            |              | <b>Predator age class</b>  |              |              |               |               |               |               |               |  |
| <b>Prey</b>                | <b>0</b>     | <b>1</b>                   | <b>2</b>     | <b>3</b>     | <b>4</b>      | <b>5</b>      | <b>6</b>      | <b>7</b>      | <b>8+</b>     |  |
| <b><i>M. Paradoxus</i></b> | <b>0.000</b> | <b>0.010</b>               | <b>0.080</b> | <b>0.360</b> | <b>1.350</b>  | <b>2.860</b>  | <b>5.740</b>  | <b>8.820</b>  | <b>9.660</b>  |  |
| <b><i>M. Capensis</i></b>  | <b>0.000</b> | <b>0.000</b>               | <b>0.110</b> | <b>0.220</b> | <b>0.700</b>  | <b>1.050</b>  | <b>2.390</b>  | <b>4.020</b>  | <b>6.060</b>  |  |
| <b>Total</b>               | <b>0.670</b> | <b>1.320</b>               | <b>3.260</b> | <b>7.030</b> | <b>11.170</b> | <b>20.850</b> | <b>23.910</b> | <b>35.150</b> | <b>45.640</b> |  |
| <b><i>M.Paradoxus%</i></b> | <i>0.000</i> | <i>0.008</i>               | <i>0.025</i> | <i>0.051</i> | <i>0.121</i>  | <i>0.137</i>  | <i>0.240</i>  | <i>0.251</i>  | <i>0.212</i>  |  |
| <b><i>M.Capensis%</i></b>  | <i>0.000</i> | <i>0.000</i>               | <i>0.034</i> | <i>0.031</i> | <i>0.063</i>  | <i>0.050</i>  | <i>0.100</i>  | <i>0.114</i>  | <i>0.133</i>  |  |
| <b>Total hake%</b>         | <i>0.000</i> | <i>0.008</i>               | <i>0.058</i> | <i>0.083</i> | <i>0.184</i>  | <i>0.188</i>  | <i>0.340</i>  | <i>0.365</i>  | <i>0.344</i>  |  |
|                            |              | <b>Predator</b>            |              |              |               |               |               |               |               |  |
|                            |              | <b><i>M. Paradoxus</i></b> |              |              |               |               |               |               |               |  |
|                            |              | <b>Predator age class</b>  |              |              |               |               |               |               |               |  |
| <b>Prey</b>                | <b>0</b>     | <b>1</b>                   | <b>2</b>     | <b>3</b>     | <b>4</b>      | <b>5</b>      | <b>6</b>      | <b>7</b>      | <b>8+</b>     |  |
| <b><i>M.Paradoxus</i></b>  | <b>0.000</b> | <b>0.000</b>               | <b>0.020</b> | <b>0.100</b> | <b>0.570</b>  | <b>0.550</b>  | <b>4.870</b>  | <b>11.610</b> | <b>22.110</b> |  |
| <b><i>M.Capensis</i></b>   | <b>0.000</b> | <b>0.000</b>               | <b>0.000</b> | <b>0.000</b> | <b>0.000</b>  | <b>0.000</b>  | <b>0.000</b>  | <b>0.000</b>  | <b>0.000</b>  |  |
| <b>Total</b>               | <b>0.610</b> | <b>1.210</b>               | <b>2.150</b> | <b>3.420</b> | <b>5.430</b>  | <b>21.770</b> | <b>23.460</b> | <b>49.050</b> | <b>41.840</b> |  |
| <b><i>M.Paradoxus%</i></b> | <i>0.000</i> | <i>0.000</i>               | <i>0.009</i> | <i>0.029</i> | <i>0.105</i>  | <i>0.025</i>  | <i>0.208</i>  | <i>0.237</i>  | <i>0.528</i>  |  |
| <b><i>M.Capensis%</i></b>  | <i>0.000</i> | <i>0.000</i>               | <i>0.000</i> | <i>0.000</i> | <i>0.000</i>  | <i>0.000</i>  | <i>0.000</i>  | <i>0.000</i>  | <i>0.000</i>  |  |
| <b>Total hake%</b>         | <i>0.000</i> | <i>0.000</i>               | <i>0.009</i> | <i>0.029</i> | <i>0.105</i>  | <i>0.025</i>  | <i>0.208</i>  | <i>0.237</i>  | <i>0.528</i>  |  |

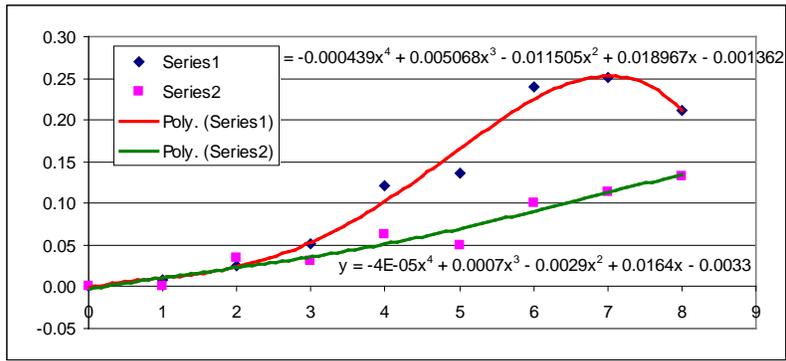


Figure 7-4. Recorded and fitted dietary consumption estimates of hake eating hake, expressed as a proportion of the total consumption, from Punt and Leslie (1995), Table VIII. The above is for *Merluccius capensis* as predator, and both *Merluccius capensis* and *M. paradoxus* as prey. The curves are fitted curves, being fourth order polynomials.

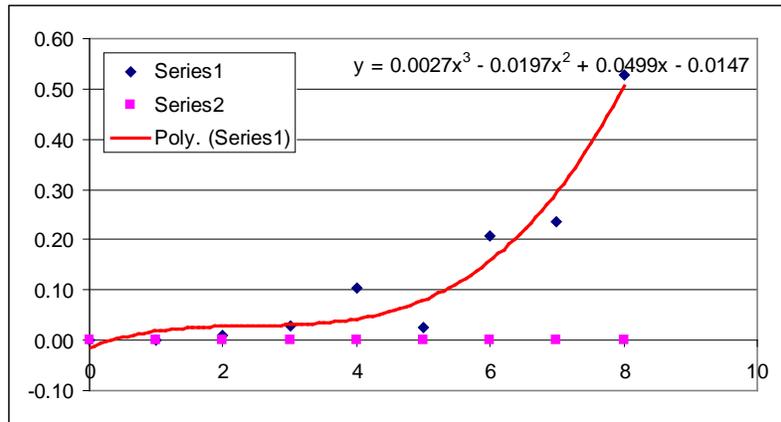


Figure 7-5. Recorded and fitted dietary consumption estimates of hake eating hake, expressed as a proportion of the total consumption, from Punt and Leslie (1995), Table VIII. The above is for *Merluccius paradoxus* as predator, and both *Merluccius capensis* and *M. paradoxus* as prey. The curves are fitted curves, being a third order polynomial.

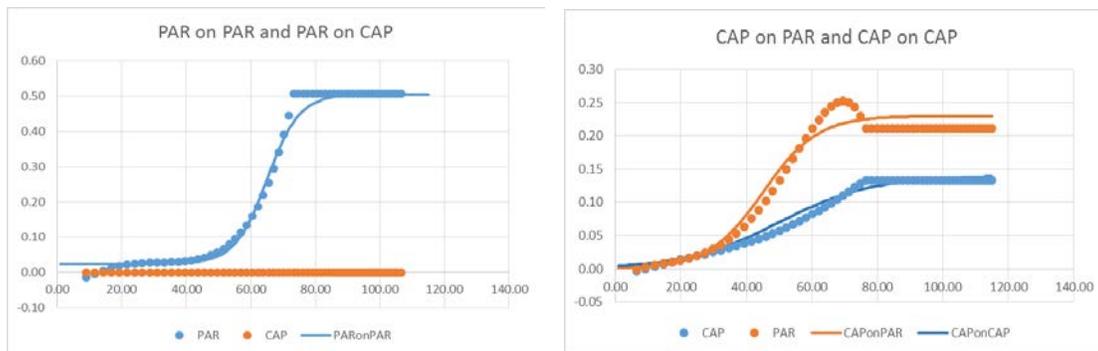


Figure 7-6. Fits of  $HAKESPP\%_{s,y,l,sp}$  as a function of length, where the solid lines are logistic equation approximations to the dotted relationships which are derived from the original equations expressed in terms of age. .

### 3.3 Preference functions

The preference functions  $PREF_{s,l,sp,lp}$  are prey and predator species and size dependent. Since **paradoxus** do not consume **capensis**, the following table describes the values relevant to the other three situations:

- $PREF_{s=Paradoxus,l,sp=Paradoxus,lp}$
- $PREF_{s=Capensis,l,sp=Paradoxus,lp}$
- $PREF_{s=Capensis,l,sp=Capensis,lp}$

Table 7-3. Quantities that are used to completely define the prey preference function for hakes. There are only three sets of values because **M. paradoxus** does not prey on **M. capensis**.

|   | PARADOXUS<br>eating<br>PARADOXUS | CAPENSIS<br>eating<br>PRADOXUS | CAPENSIS<br>eating<br>CAPENSIS |
|---|----------------------------------|--------------------------------|--------------------------------|
| <b>Opt/Max:</b> $\left(\frac{Opt}{Max}\right)_{s,sp}$ | 0.681                            | 0.694                          | 0.711                          |
| <b>Max/Pred:</b> $\left(\frac{Max}{l}\right)_{s,sp}$  | 0.756                            | 0.754                          | 0.803                          |
| <b>Min/Max:</b> $\left(\frac{Min}{Max}\right)_{s,sp}$ | 0.249                            | 0.244                          | 0.129                          |

The following calculation steps are involved:

- Maximum size consumed  $Max_{s,sp}(l) = l \times \left(\frac{Max}{l}\right)_{s,sp}$  (21)

- Optimum size consumed:  $Opt_{s,sp}(l) = Max_{s,sp}(l) \times \left(\frac{Opt}{Max}\right)_{s,sp}$  (22)

- Minimum size consumed:  $Min_{s,sp}(l) = Max_{s,sp}(l) \times \left(\frac{Min}{Max}\right)_{s,sp}$  (23)

- $x^* = \frac{Opt_{s,sp}(l) - Min_{s,sp}(l)}{Max_{s,sp}(l) - Min_{s,sp}(l)}$  (24)

- $p = 5$  (25)

- $q = \frac{p-1}{x^*} - (p-2)$  (26)

If the prey size  $lp$  lies between the minimum and maximum size consumed by a predator of size  $l$ , then

$$PREF_{s,l,sp,lp} = \left(\frac{lp - Min_{s,sp}(l)}{Max_{s,sp}(l) - Min_{s,sp}(l)}\right)^{p-1} \left(1 - \frac{(lp - Min_{s,sp}(l))}{Max_{s,sp}(l) - Min_{s,sp}(l)}\right)^{q-1} \quad \forall \quad Min_{s,sp}(l) \leq lp \leq Max_{s,sp}(l) \quad (27)$$

otherwise

$$PREF_{s,l,sp,lp} = 0.00 \quad (28)$$

Also, for the reasons given above:

$$PREF_{Paradoxus,1,Capensis,1p} = 0.00 \quad \forall \quad 1 \leq l \leq 105, \quad 1 \leq lp \leq 105. \quad (29)$$

Table 7-4. Size based prey preference information from seal workshop held 1991. (Source: Benguela Ecology Programme workshop on seal–fishery biological interactions; September 1991. University of Cape Town; 1991. Benguela Ecology Programme Working Paper, BEP/SW91/R2. 22 pp.)

| <i>Predator=M. capensis</i>  |          |      |      |      |      |     |   |   |    |
|------------------------------|----------|------|------|------|------|-----|---|---|----|
| PREDATOR AGE                 | PREY AGE |      |      |      |      |     |   |   |    |
|                              | 0        | 1    | 2    | 3    | 4    | 5   | 6 | 7 | 8+ |
| <i>M. capensis</i>           |          |      |      |      |      |     |   |   |    |
| 0                            |          |      |      |      |      |     |   |   |    |
| 1                            | 100      |      |      |      |      |     |   |   |    |
| 2                            | 46.1     | 53.9 |      |      |      |     |   |   |    |
| 3                            | 42       | 53.3 | 4.7  |      |      |     |   |   |    |
| 4                            | 14       | 48.8 | 36.2 | 0.9  |      |     |   |   |    |
| 5                            | 2.4      | 19.2 | 66.5 | 11.9 |      |     |   |   |    |
| 6                            | 6.4      | 23.3 | 43   | 24   | 3.3  |     |   |   |    |
| 7                            | 0        | 6.2  | 45.1 | 38.9 | 8.7  | 0.1 |   |   |    |
| 8+                           | 0        | 5    | 11.1 | 41.8 | 33.1 | 8.9 | 0 |   |    |
| <i>M. paradoxus</i>          |          |      |      |      |      |     |   |   |    |
| 0                            |          |      |      |      |      |     |   |   |    |
| 1                            | 100      |      |      |      |      |     |   |   |    |
| 2                            | 72.4     | 27.6 |      |      |      |     |   |   |    |
| 3                            | 15.7     | 80.3 | 4    |      |      |     |   |   |    |
| 4                            | 7.4      | 72.2 | 20.1 | 0    |      |     |   |   |    |
| 5                            | 2.7      | 45.3 | 45.3 | 6.5  | 0    |     |   |   |    |
| 6                            | 3.9      | 40.8 | 49.8 | 5.4  | 0    |     |   |   |    |
| 7                            | 0.1      | 31.1 | 54.9 | 10.9 | 2.4  | 0   |   |   |    |
| 8+                           | 0        | 9.4  | 68.5 | 12.6 | 7    | 2.5 |   |   |    |
| <i>Predator=M. paradoxus</i> |          |      |      |      |      |     |   |   |    |
| PREDATOR AGE                 | PREY AGE |      |      |      |      |     |   |   |    |
|                              | 0        | 1    | 2    | 3    | 4    | 5   | 6 | 7 | 8+ |
| <i>M. paradoxus</i>          |          |      |      |      |      |     |   |   |    |
| 0                            |          |      |      |      |      |     |   |   |    |
| 1                            |          |      |      |      |      |     |   |   |    |
| 2                            | 99.3     | 0.7  |      |      |      |     |   |   |    |
| 3                            | 32       | 67.5 | 0.5  |      |      |     |   |   |    |
| 4                            | 30.3     | 66.4 | 3.2  |      |      |     |   |   |    |
| 5                            | 2        | 49   | 47.7 | 0.7  | 0.7  |     |   |   |    |
| 6                            | 0        | 21.1 | 58.2 | 7.3  | 13.4 |     |   |   |    |
| 7                            | 0        | 10.3 | 72.4 | 7.4  | 10   |     |   |   |    |
| 8+                           | 0        | 4.1  | 71.9 | 15   | 9    |     |   |   |    |