Incorporating cannibalism and inter-species predation effects into the hake assessment model: Methods and some preliminary results

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Summary

Hake cannibalism and inter-species predation is modelled explicitly using a Type II functional response. Because of the fast dynamics of predation compared to other processes, the standard hake assessment model is converted from a yearly to a monthly time-step. Convergence of model fits is difficult to achieve both because of providing good estimates for starting values and of the tendency of the model towards oscillating behaviour. Thus far satisfactory fits have been obtained only from a somewhat reduced level of predation compared to that thought to occur. These results suggest that both hake species are at higher levels relative to pristine than for the standard assessment.

1 Introduction

This work aims to build on that done in the early 1990s on the development of a multispecies model for the two Cape hake species, *M. capensis* and *M. paraodoxus* (Punt and Butterworth 1995, Punt *et al.* 1995, Punt and Leslie 1995 and Butterworth *et al.* 1995). There, the authors aimed first to construct a model which included hake, seals and other predatory fish with their feeding interactions, and then to use this model to assess the consequences of different levels of consumption of hake by seals on the hake fishery in the context of the change in the size of sustainable hake TACs and catch rates. They also aimed to investigate the effect of seal culling on the fishery.

In the years that have passed since, more data have become available, and the hake assessment models have been continuously developed. The aim is to update the work done by Punt and Butterworth (1995) with new data, and to extend the model to the level of the current hake assessment model (Rademeyer 2013).

In order to get the model working, a simplified approach has been taken, based in part on recommendations made at the annual International Stock Assessment Workshop held at the University of Cape Town in December 2011:

1. The model considers South Africa only and has no coastal segregation.
2. There is no sex-structure or offshore (depth) structure.
3. No other predatory fish or seal predators have been considered at this stage.
4. The model has not been fit to catch-at-length data or age-length keys.

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5. A Holling Type II feeding relationship has been used.

6. The feeding relationship parameters are assumed to be time-independent.

The base model is based on the sex-aggregated Rademeyer *et al.* (2008) model. Two major changes have been made prior to incorporating predation effects:

1. A Pope approximation has been used for the catch equation, instead of the Baranov formulation. This was done to reduce the number of estimable parameters in the model.

2. A monthly time-step was introduced instead of the usual annual time-step. This was done to take into account the fact that the predation dynamics are assumed to be much faster than the hake dynamics, so that the predation effect would be poorly approximated with a coarser time-step. A further benefit of a monthly time-step is to improve the accuracy of the Pope approximation for the effect of the catches taken by the fishery.

This document details the nomenclature used and adjustments made to the population dynamics in order to introduce a monthly time-step. It also gives the details of how predation and cannibalism effects have been incorporated, along with some initial results.

2 Data

The data used are the same as those presented in Rademeyer *et al.* (2008). In addition, stomach content data have been made available by the Fisheries Branch of the Department of Agriculture, Forestry and Fisheries (T. Fairweather, *pers. comm.*):

1. Fully validated biological and stomach data for 1999-2009 for the West Coast

2. Fully validated biological and stomach data for 2010-2013 for the West Coast

3. Mostly validated biological and stomach data for 1999-2009 for the South Coast

4. Access version of biological and stomach data for 2010-2013 for South Coast (with only two surveys completed in 2010 and 2011)

Three diet-related quantities are of particular interest for the modelling work presented in this paper. Note that the data are given in terms of predator and prey lengths, which have been converted to ages using the von Bertalanffy growth curve parameters given in Rademeyer *et al.* (2008).

2.1 Daily ration

Since no direct experiments have been conducted for hake to determine gastric evacuation rates, estimates of daily ration data have been taken from Punt and Leslie (1995), where data for haddock, cod and whiting predators were used to estimate the parameters of the evacuation model. The data are shown in Fig 1. A logistic function was fit to these data to estimate daily rations for older fish.

2.2 Proportion of hake in diet

The 1999-2013 DAFF data set was used to obtain estimates of proportion of hake in the diet of hake. A GLM was used to standardise for predator species, predator age, year and coast. A binomial distribution was assumed, where the presence of hake prey in a stomach sample was seen as a 'success'. Of a total of 7692 non-empty stomachs, 10% contained only hake prey, 88% contained no hake prey, while the remaining 2% contained a mixture of hake and other prey. These mixed samples were apportioned to either 100% hake prey or 0% hake prey through rounding. Fig 2 shows the resulting proportion of hake in the diet of hake, along with the proportion of hake in diet given in Punt and Leslie (1995).

2.3 Predator preference

Data informing the predator preference function were also obtained from the 1999-2013 DAFF data set, in the form of counts of prey items by species and age in the stomachs of predators by species and age. The data have been combined for coast and over all the years and are shown in Fig 3.

3 Nomenclature

In the equations that follow,

$N_{y,s,a}$	is the number of hake in year y of species s and age a (in years),
$\eta_{y,m,s,a}$	is the number of hake in month m of year y of species s and age a (in years), and
$\tilde{\eta}_{y,m,s,\tilde{a}}$	is the number of hake in month m of year y of species s and age $\tilde{a}$ (in months).

In other words, the symbol 'η' is used to denote a monthly population size (as opposed to an annual population size N), and '$\tilde{\ }$' is used to indicate that age $\tilde{a}$ is given in months, rather than years.

When considering predator-prey interactions, s and a will be used for prey species, while s_p and a_p will be used for predator species. Further, s, a will be used as subscripts, while s_p, a_p will be used as superscripts. For example:

$N_{y,s,a}$	and	$\eta_{y,m,s,a}$	refer to prey numbers, and
$N_y^{s_p,a_p}$	and	$\eta_{y,m}^{s_p,a_p}$	refer to predator numbers.

4 Population dynamics

4.1 Basic population dynamics

Population dynamics are calculated on a monthly basis in terms of age in months:

$$\begin{aligned}
\tilde{\eta}_{y,m+1,s,0} &= R_{y,m+1,s} \\
\tilde{\eta}_{y,m+1,s,\tilde{a}+1} &= \left(\tilde{\eta}_{y,m,s,\tilde{a}} e^{-Z_{y,m,s,\tilde{a}}/2} - \tilde{C}_{y,m,s,\tilde{a}}\right) e^{-Z_{y,m,s,\tilde{a}}/2} \quad \text{for } 0 \leq \tilde{a} \leq a_{\max} - 2 \\
\tilde{\eta}_{y,m+1,s,\tilde{a}_{\max}} &= \left(\tilde{\eta}_{y,m,s,\tilde{a}_{\max}-1} e^{-Z_{y,m,s,\tilde{a}_{\max}-1}/2} - \tilde{C}_{y,m,s,\tilde{a}_{\max}-1}\right) e^{-Z_{y,m,s,\tilde{a}_{\max}-1}/2} + \\
&\quad \left(\tilde{\eta}_{y,m,s,\tilde{a}_{\max}} e^{-Z_{y,m,s,\tilde{a}_{\max}}/2} - \tilde{C}_{y,m,s,\tilde{a}_{\max}}\right) e^{-Z_{y,m,s,\tilde{a}_{\max}}/2}
\end{aligned} \tag{4.1}$$

where

$R_{y,m,s}$	is the recruitment of hake of species s in month m of year y (Section 4.2),
$\tilde{C}_{y,m,s,\tilde{a}}$	is the total number of fish of species s and age $\tilde{a}$ months that were caught in month m of year y (Section 4.3), and
$\tilde{a}_{\max}$	is the maximum age considered in the model, taken to be 180 months (i.e. $a_{\max} = 15$ years).
$Z_{y,m,s,\tilde{a}} = M_{m,s,\tilde{a}} + P_{y,m,s,\tilde{a}}$	is the natural mortality rate (months^{-1}) for hake of species s and age $\tilde{a}$ months in year y and month m,
$M_{m,s,\tilde{a}}$	is the basal mortality rate (months^{-1})[2] for hake of species s and age $\tilde{a}$ months in month m, and
$P_{y,s,m,\tilde{a}}$	is the mortality rate in year y of hake of species s and age $\tilde{a}$ months owing to predation and cannibalism (Section 4.5).

The above hold for $1 \leq m \leq 11$ (i.e. months Febuary to December). The January dynamics depend on the numbers in December of the previous year:

$$\begin{aligned}
\tilde{\eta}_{y,1,s,0} &= R_{y,1,s} \\
\tilde{\eta}_{y,1,s,a+1} &= \left(\tilde{\eta}_{y-1,12,s,\tilde{a}} e^{-Z_{y-1,12,s,\tilde{a}}/2} - \tilde{C}_{y-1,12,s,\tilde{a}}\right) e^{-Z_{y-1,12,s,\tilde{a}}/2} \quad \text{for } 0 \leq \tilde{a} \leq a_{\max} - 2 \\
\tilde{\eta}_{y,1,s,a_{\max}} &= \left(\tilde{\eta}_{y-1,12,s,\tilde{a}_{\max}-1} e^{-Z_{y-1,12,s,\tilde{a}_{\max}-1}/2} - \tilde{C}_{y-1,12,s,\tilde{a}_{\max}-1}\right) e^{-Z_{y-1,12,s,\tilde{a}_{\max}-1}/2} + \\
&\quad \left(\tilde{\eta}_{y-1,12,s,\tilde{a}_{\max}} e^{-Z_{y-1,12,s,\tilde{a}_{\max}}/2} - \tilde{C}_{y-1,12,s,\tilde{a}_{\max}}\right) e^{-Z_{y-1,12,s,\tilde{a}_{\max}}/2}
\end{aligned} \tag{4.2}$$

The monthly and annual numbers by age-in-years are calculated from the age-in-months numbers, $\tilde{\eta}_{y,m,s,\tilde{a}}$, as follows:

$$\eta_{y,m,s,a} = \sum_{\tilde{a}=12a}^{12a+11} \tilde{\eta}_{y,m,s,\tilde{a}} \tag{4.3}$$

$$N_{y,s,a} = \eta_{y,1,s,a} \quad \text{(i.e. the January numbers)} \tag{4.4}$$

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[2] The basal mortality rate, $M_{s,a}$, is assumed to be constant with time. Therefore the monthly basal mortality rate is simply $M_{m,s,a} = M_{s,a}/12$. Also it is assumed that all cohorts within a particular year class experience the same basal mortality, i.e. $M_{m,s,\tilde{a}} = M_{m,s,a}$ for $12a \leq \tilde{a} \leq 12a + 11$ (i.e. $\tilde{a}$ is the age in months of a fish aged a years).

When calculating the monthly and annual spawning biomasses, one cannot assume that all fish of a certain age a (in years) will have the identical mass as derived from the weight-at-age relationship. Each year-group will have 12 cohorts (e.g. fish aged 1 in years will range from 12 to 23 months, etc), along with an associated range of masses. Therefore monthly and annual biomass values by age, $B_{y,m,s,a}$ and $B_{y,s,a}$, are defined as follows:

$$B_{y,m,s,a} = \sum_{\tilde{a}=12a}^{12a+11} \tilde{w}_{s,\tilde{a}}\, \tilde{\eta}_{y,m,s,\tilde{a}} \tag{4.5}$$

$$B_{y,s,a} = B_{y,1,s,a} \text{ (i.e. the January mass)} \tag{4.6}$$

where $\tilde{w}_{s,\tilde{a}}$ is the weight of a fish of species s and age $\tilde{a}$ in months.
The monthly and annual spawning biomasses are then given by:

$$B^{sp}_{y,m,s} = \sum_{a=1}^{a_{\max}} f^{\text{mat}}_{s,a} B_{y,m,s,a} \tag{4.7}$$

$$B^{sp}_{y,s} = \sum_{a=1}^{a_{\max}} f^{\text{mat}}_{s,a} B_{y,s,a} \tag{4.8}$$

where $f^{\text{mat}}_{s,a}$ is the maturity-at-age vector, taken to be zero for ages less than 4 years and 1 for ages greater than 4 for both hake species, as for the Rademeyer *et al.* (2008) model.

4.2 Recruitment

Recruitment is assumed to take place throughout the year and is calculated each month from the estimated spawning biomass for that month. A Beverton-Holt stock recruitment relationship is assumed.

$$R_{y,m,s} = \frac{\alpha B^{sp}_{y,m,s}}{12\,(\beta + B^{sp}_{y,m,s})} \tag{4.9}$$

where α and β are stock recruitment parameters. Note that the division by 12 allows the α parameter value to be comparable to what would follow for a model with a annual time-step.
Recruitment for year y is defined as the sum of the recruitment from July in the previous year to June in the current year, i.e.

$$R_{y,s} = \sum_{m=7}^{12} R_{y-1,m,s} + \sum_{m=1}^{m=6} R_{y,m,s} \tag{4.10}$$

Note that the quantity $R_{y,s}$ itself is not used anywhere in the model. It is purely an output for comparison purposes, and above definition was chosen in order to be consistent with the Rademeyer *et al.* (2008) model, where recruitment takes place in January.

4.3 Catches

Catches are assumed to be equally distributed throughout the year, i.e. for each month m, $C^{obs}_{y,m,f,s} = C^{obs}_{y,f,s}/12$. The model estimated monthly catch is given by:

$$C_{y,m,f,s} = \sum_{\tilde{a}} S_{y,f,s,\tilde{a}} F_{y,m,f,s} \tilde{w}_{s,\tilde{a}} \tilde{\eta}_{y,m,s,\tilde{a}} e^{-(M_{m,s,\tilde{a}}+P_{y,m,s,\tilde{a}})/2} \tag{4.11}$$

Note that age in months is used here. For each month, the fishing mortality can then be calculated using a closed form equation:

$$F_{y,m,f,s} = C^{obs}_{y,m,f,s} \Big/ \left(\sum_{\tilde{a}} S_{y,f,s,\tilde{a}} \tilde{w}_{s,\tilde{a}} \tilde{\eta}_{y,m,s,\tilde{a}} e^{-(M_{m,s,\tilde{a}}+P_{y,m,s,\tilde{a}})/2} \right) \tag{4.12}$$

Note that a Pope approximation has been used for this initial model, in order to reduce the number of estimable parameters in the minimisation (the non-linear Baranov equations would be "solved" by treating F as an estimable paramter).

$\tilde{C}_{y,m,s,\tilde{a}}$ is then given by

$$\tilde{C}_{y,m,s,\tilde{a}} = \sum_{f} S_{y,f,s,\tilde{a}} F_{y,m,f,s} \tilde{\eta}_{y,m,s,\tilde{a}} e^{-(M_{m,s,\tilde{a}}+P_{y,m,s,\tilde{a}})/2} \tag{4.13}$$

4.4 Initial population setup

The initial population vector under equilibrium conditions is computed for age in months, i.e. $\tilde{\eta}_{y_0,m,s,\tilde{a}}$. Since the predation rates $P_{y,m,s,\tilde{a}}$ are needed to calculate $\tilde{\eta}_{y_0,m,s,\tilde{a}}$, but conversely $\tilde{\eta}_{y_0,m,s,\tilde{a}}$ is needed to calculate $P_{y,m,s,\tilde{a}}$, this leads to some complications in obtaining an initial population vector.

The following approach was therefore taken. Predation values are set to zero initially, allowing an initial population structure to be calculated based solely on the basal mortality rate. This population structure is then used to calculate non-zero predation rates, which are in turn used to recalculate the population structure. This iterative process is repeated until an equilibrium is reached, at which point the resulting population structure is used to start the model calculations.

4.5 Predation

Note that barring the preference function (Equation 4.18), the predation equations are based on, or very similar to, those given in Punt and Butterworth (1995).

The predation rate (months^{-1}) is taken to be the total mass of hake of species s and age a consumed by other hake, divided by the total biomass of hake of species s and age a available. In other words:

$$1 - e^{-P_{y,m,s,a}} = \frac{\sum_{s_p} \sum_{a_p} \eta^{s_p,a_p}_{y,m} R^{s_p,a_p}_{y,s,a} (365/12)}{w_{s,a} \eta_{y,m,s,a}} \tag{4.14}$$

where $R^{s_p,a_p}_{y,s,a}$ is the portion of the daily ration of a predator of species s_p and age a_p which is composed of prey of species s and age a. This quantity is given by:

$$R^{s_p,a_p}_{y,s,a} = R^{s_p}_{y,a} \frac{\gamma^{s_p,a_p}_{s,a} N_{y,s,a}}{\sum\limits_{s'} \sum\limits_{a'} \gamma^{s_p,a_p}_{s',a'} N_{y,s',a'}} \tag{4.15}$$

where

$R^{s_p}_{y,a}$	is the total mass of hake consumed daily by a predator of species s_p and age a_p years, and
$\gamma^{s_p,a_p}_{s,a}$	is the preference function, i.e. a measure of the desirability that a predator of species s_p and age a_p will exhibit for a prey fish of species s and age a (see Equation 4.18).

The total daily mass of hake consumed by a predator fish in year y is given by:

$$R_y^{s_p,a_p} = \widetilde{R}^{s_p,a_p}\left(1 - exp\left\{-\kappa^{s_p,a_p} V_y^{s_p,a_p} / \left(\omega\sqrt{N_{y_0}^{s_p,a_p}} + \sqrt{N_y^{s_p,a_p}}\right)\right\}\right) \tag{4.16}$$

where

$\widetilde{R}^{s_p,a_p}$	is the total daily ration consumed by a predator of species s_p and age a_p and is input from data,
κ^{s_p,a_p}	is the parameter determining the extent of saturation in the feeding functional form, and
$V_y^{s_p,a_p}$	is the total biomass of hake (adjusted by the preference function) which is available for consumption, given by:

$$V_y^{s_p,a_p} = \sum_s \sum_a w_{s,a} \gamma_{s,a}^{s_p,a_p} N_{y,s,a} \tag{4.17}$$

The $\left(\omega\sqrt{N_{y_0}^{s_p,a_p}} + \sqrt{N_y^{s_p,a_p}}\right)$ term allows for competition between hake in a cohort to avoid unstable model behaviour resulting from enormous cohorts of hake moving through the population. ω is a factor which determines the extent of competition and is set to 0.01 for the base case (Punt, 1994).

A gamma function from Kinzey and Punt (2008) is used for the preference function.

$$\gamma_{s,a}^{s_p,a_p} = \left[G_{s,a}^{s_p,a_p} / \widetilde{G}^{s_p}\right]^{\alpha^{s_p}-1} e^{-(G_{s,a}^{s_p,a_p} - \widetilde{G}^{s_p})/\beta^{s_p}} \tag{4.18}$$

where

$G_{s,a}^{s_p,a_p}$	is the log of the predator size (species s_p, age a_p) as a fraction of prey size (species s, age a),
$\widetilde{G}^{s_p} = (\alpha^{s_p} - 1)\beta^{s_p}$	is the value of $G_{s,a}^{s_p,a_p}$ when $\gamma_{s,a}^{s_p,a_p} = 1$ (i.e. for maximum preference), and
α^{s_p}, β^{s_p}	are parameters that are estimated in the model by fitting to feeding data available.

Note that the daily ration, $R_{y,s,a}^{s_p,a_p}$, is assumed to remain constant throughout the months of any particular year.

4.6 Likelihood adjustments

Most likelihood components are the same as those used in the Rademeyer *et al.* (2008) model. However two additional sources of data are available to estimate the predation parameters: fraction of hake in diet, as well as prey age- and species-composition by predator age and species.

4.6.1 Fraction of hake in diet

For years in which hake diet data are available, information on the fraction of hake in hake diet of a predator of species s_p and age a_p can be extracted, i.e. information on the value of $R_y^{s_p,a_p}/\widetilde{R}^{s_p,a_p}$ (see Equation 4.16). Values of κ^{s_p,a_p} are needed such that the model estimated fractions roughly match those observed. A likelihood contribution is therefore added as follows:

$$-lnL+ = \sum_{s_p}\sum_{a_p}(ln\sigma^{s_p}) + \left(\sqrt{H_{y_t}^{s_p,a_p}} - \sqrt{H_{y_t,obs}^{s_p,a_p}}\right)^2 / (2(\sigma^{s_p})^2) \tag{4.19}$$

where

$H_{y_t}^{s_p,a_p} = R_{y_t}^{s_p,a_p}/\widetilde{R}^{s_p,a_p}$ is the model-estimated fraction of hake (species combined) in the diet of a predator fish of species s_p and age a_p in a target year y_t where data are available,

$H_{y_t,obs}^{s_p,a_p}$ is the corresponding observed fraction of hake in diet, and

$(\sigma^{s_p})^2$ is the variance estimated by:

$$\sigma^{s_p} = \sqrt{\sum_{a_p} \left(\sqrt{H_{y_t}^{s_p,a_p}} - \sqrt{H_{y_t,obs}^{s_p,a_p}} \right)^2 / \sum_{a_p} 1} \tag{4.20}$$

4.6.2 Predator preference

Break-down of predator diets in terms of prey age and species informs predator preference. These data are shown in Fig 3 and are incorporated into the likelihood through a binomial approach:

$$-lnL+ = -\sum_{s_p}\sum_{a_p}\sum_{a} r_{s,a}^{s_p,a_p} lnp_{y_t,s,a}^{s_p,a_p} - r_{s,a}^{s_p,a_p} ln(r_{s,a}^{s_p,a_p}/n_s^{s_p,a_p}) \tag{4.21}$$

where

$r_{s,a}^{s_p,a_p}$ is the number of hake prey items of species s and age a that were found in the stomachs of predators of species s_p and age a_p,

$n_s^{s_p,a_p}$ is the total number of stomach samples of predator fish of species s_p and age a_p that contained prey items of species s, and

$p_{y_t,s,a}^{s_p,a_p}$ is the model-estimated proportion of hake of species s and age a in the diet of predators of species s_p and age a_p, given by:

$$p_{y_t s,a}^{s_p,a_p} = R_{y_t,s,a}^{s_p,a_p} / \sum_{a} R_{y_t,s,a}^{s_p,a_p} \tag{4.22}$$

Note that the prey break-down given in Fig 3 has been obtained from diet data from both coasts and over all the years (1999-2013). The year 2006 has been used for y_t in the results reported here. Allowing for changes with year could be incorporated at a later stage.

4.7 Estimation process

4.7.1 Feeding functional form (κ^{s_p,a_p})

κ^{s_p,a_p} could either be estimated separately for each s_p and each $a_p \geq 1$, or an approach similar to that of Punt and Butterworth (1995) could be taken, where it is assumed that the current fraction of hake in the diet of the predators is a constant multiple of what the values were under pristine conditions. In other words, given a predator species s_p, the way in which the individual $H_y^{s_p,a_p}$ values relate to one another across the ages a_p should remain constant over time.

Here the latter approach has been used for simplicity, so that only one constant, λ^{s_p}, needs to be estimated for each species. Given λ^{s_p}, κ^{s_p,a_p} can be calculated from:

$$H_{y_t,obs}^{s_p,a_p} = \lambda^{s_p} H_{y_0}^{s_p,a_p} = \lambda^{s_p} \left(1 - e^{-\kappa^{s_p,a_p} V_{y_0}^{s_p,a_p}}\right) \tag{4.23}$$

where $H_{y_0}^{s_p,a_p}$ is the model-estimated fraction of hake in the diet of a predator of species s_p and age a_p under pristine conditions.

4.7.2 Preference function

Two parameters need to be estimated per species for the preference function, α^{s_p} and β^{s_p}. As an initial approach, α^{s_p} has been estimated in the model (informed by the preference data), and β^{s_p} has been set so that predator preference peaks when prey length is 41% of predator length (see Fig 4).

4.7.3 Model instability

The estimation process was somewhat hampered by instabilities that arose from the predator-prey dynamics, including oscillations (both damped and undamped) for certain parameter combinations in the minimisation process, as well as populations going extinct. The use of Pope's approximation most likely contributes to the latter problem as catches can easily exceed the available population size after mortality owing to predation has been taken into account.

In order to at least get a qualitative feel for what effect predation and cannibalism are having on the population dynamics, the natural mortality was defined in the following way to try to address the model's sensitivity to starting positions:

$$Z_{y,m,s,\tilde{a}} = M_{s,\tilde{a}}^{\text{basal}} + (1-\mu)M_{s,\tilde{a}}^{\text{no pred}} + \mu P_{y,m,s,\tilde{a}} \tag{4.24}$$

where

$M_{s,\tilde{a}}^{\text{basal}}$ is the basal mortality, set to 0.35 (corresponding roughly to the natural mortality estimated for hake of age 5 years and older in Rademeyer *et al.* 2008),

$M_{s,\tilde{a}}^{\text{no pred}}$ is calculated such that $M_{s,\tilde{a}}^{\text{basal}} + M_{s,\tilde{a}}^{\text{no pred}}$ matches the mortality rates estimated in Rademeyer *et al.* (2008), and

μ is a scaling parameter.

When $\mu = 0$, the mortality rates match those from Rademeyer *et al.* (2008). When $\mu = 1$, predation is fully incorporated. In principle, by slowly scaling μ from 0 to 1, suitable starting estimates for the parameters can be found, as we start from the well-behaved Rademeyer *et al.* (2008) fit and slowly move towards the predation model formulation. However, problems of instability (in particular oscillations and populations going extinct) still occur. Therefore, an additional adjustment was introduced, limiting the total mass of hake consumed. This was done by multiplying the numerator in Equation 4.14 by a fraction θ. This somewhat artificial approach was used to obtain the initial results presented in this paper. Note further that only K^{s_p}, λ^{s_p} and α^{s_p} have been estimated here - the remaining parameters have been fixed at the $\lambda^{s_p} = 0$ (i.e. zero predation) values.

5 Initial Results and Discussion

Results obtained to date are shown in Fig 5. Ideally we seek results for $\mu = 1$ and $\theta = 0$, but thus far reasonable convergence has only be obtained as far as $\mu = 0.7$ and $\theta = 0.7$. The main feature of this last result is that modelling predation explicitly suggests that both species are less depleted relative to their initial sizes than when no predation effects are considered (Fig 6).

Further work will aim towards solutions with $\mu = 1$ and θ as high as possible. If fits cannot be obtained with $\theta = 1$, an alternative functional response involving more damping, such as the foraging arena model used in Ecosim, will be considered. The use of the Baranov instead of Pope formulation for the catch equations, implemented with the "Hybrid method" (A.E. Punt, *pers. comm.*), may also go a long way in helping the estimation process.

6 References

Butterworth, D.S., Punt, A.E., Oosthuizen, W.H. and Wickens, P.A. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 3. Modelling the dynamics of the Cape fur seal *Arctocephalus pusillus pusillus. South African Journal of Marine Science, 16:1,161-183.*

Punt, A.E. 1994. Data analysis and modelling of the seal-hake biological interaction off the South African West Coast.

Punt, A.E. and Leslie, R.W. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 1. Feeding and diet of the Cape hakes *Merluccius capensis* and *M. paradoxus. South African Journal of Marine Science, 16(1): 37-55.*

Punt, A.E., David, J.H.M and Leslie, R.W. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 2. Feeding and diet of the Cape fur seal *Arctocephalus pusillus pusillus. South African Journal of Marine Science, 16(1):, 85-99.*

Punt, A.E and Butterworth, D.S. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals *Arctocephalus pusillus pusillus* and the Cape hakes *Merluccius capensis* and *M. paradoxus. South African Journal of Marine Science, 16(1): 255-285.*

Rademeyer, R.A. and Butterworth, D.S. 2013. 2013 update of the South African Hake reference case assessment. Paper FISHERIES/2013/NOV/SWG-DEM67, also paper MARAM IWS/DEC13/Hake/P2.

Rademeyer, R.A. and Butterworth, D.S. and Plagányi, É.E. 2008. Assessment of the South African hake resource taking its two-species nature into account. *African Journal of Marine Science, 30(2): 263-290.*

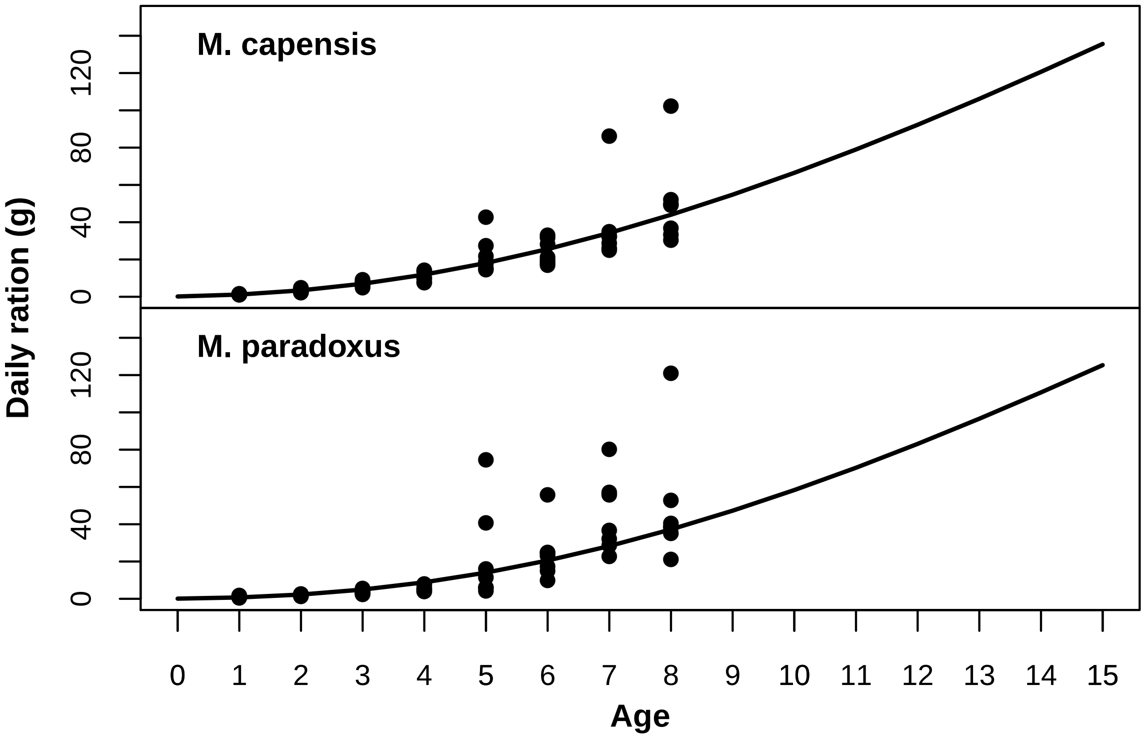

Figure 1: Estimates of daily ration from Punt and Leslie (1995), for the years 1988-1992. The solid black lines show the values that were used in the model, based on a logistic fit to the data.

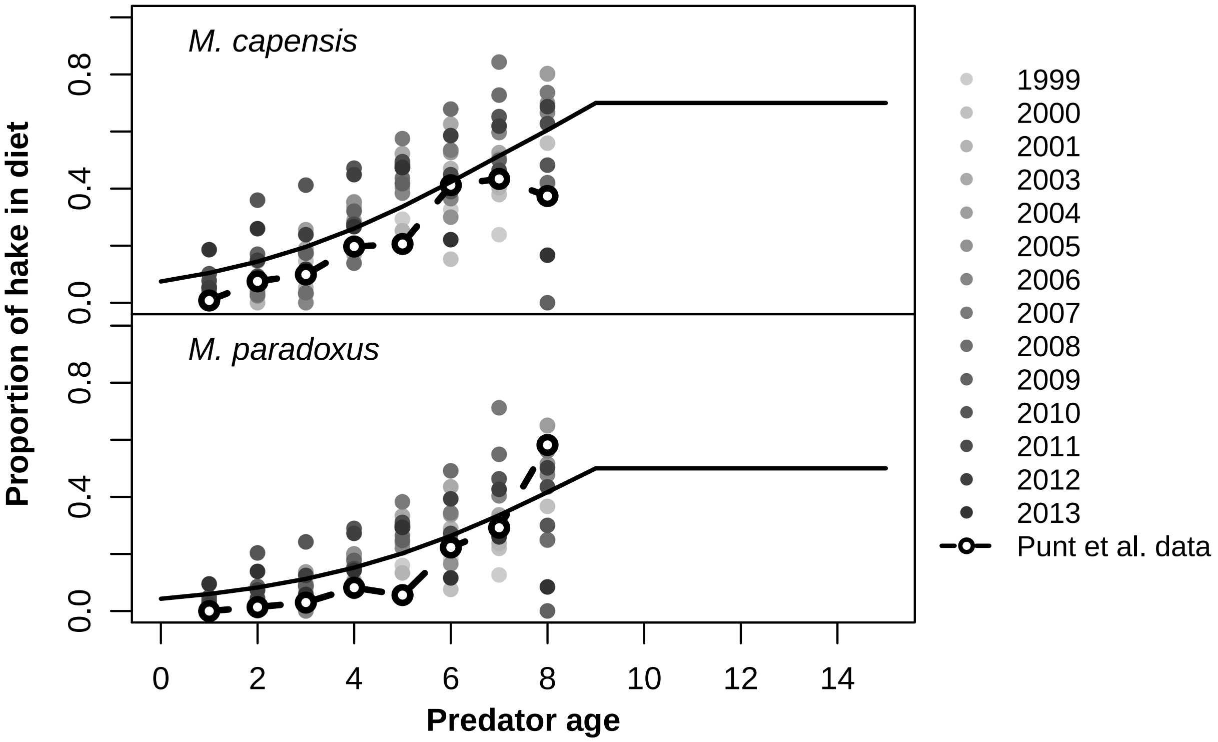

Figure 2: GLM estimated proportion of hake in diet for 1999-2013 on the West Coast. The points show estimates from individual years, with the darkest points corresponding the most recent years. The solid black line shows a the values that were used in the model (a logistic fit for ages 0-8 and constant for ages >8). The dashed line shows the estimates given in Punt and Leslie (1995).

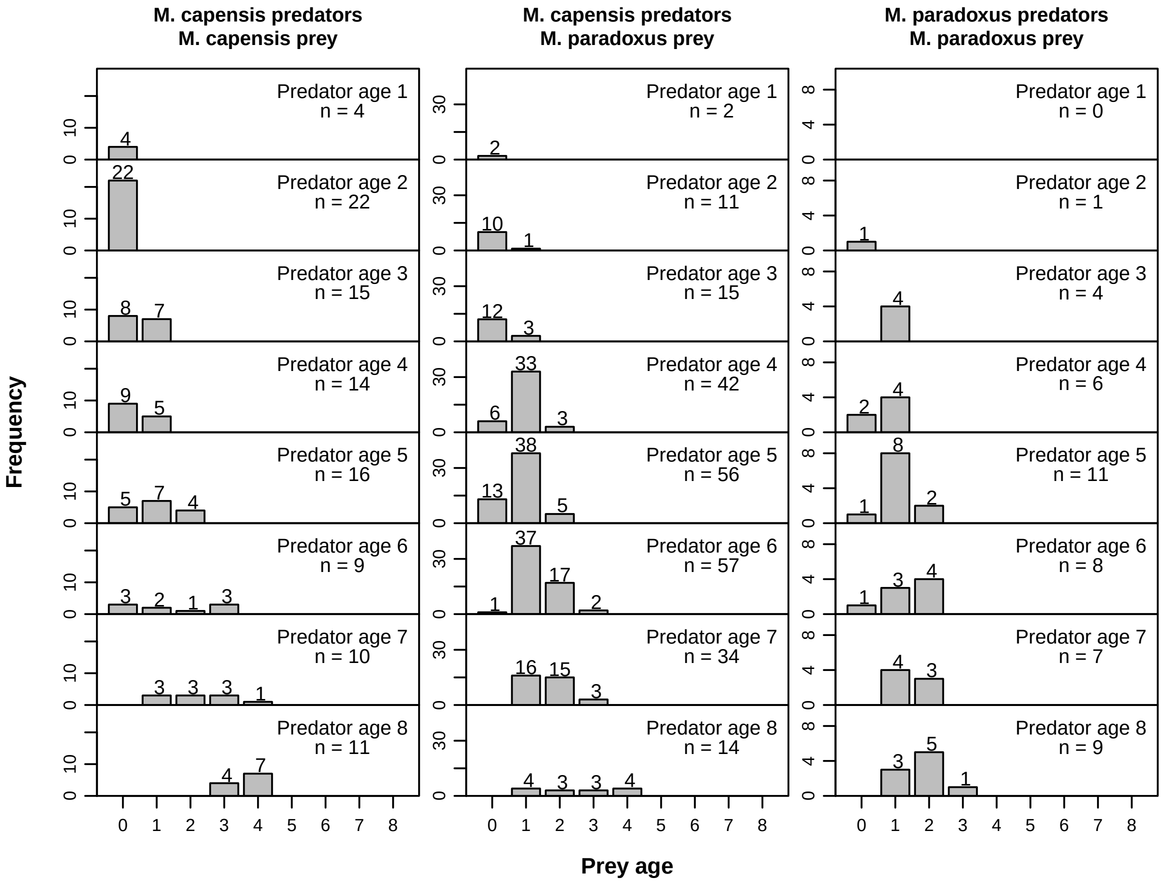

Figure 3: Break down of prey items by age and species for both predator and prey.

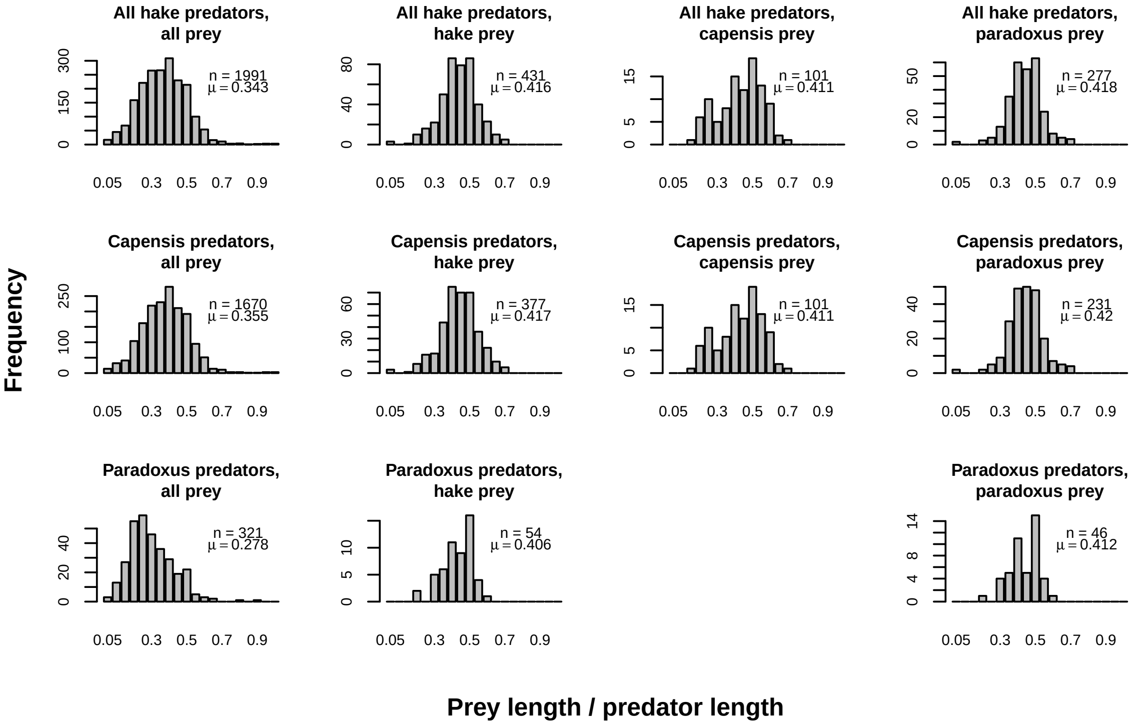

Figure 4: Histograms showing frequency of prey items in the stomachs of predators, giving an indication of peak preference.

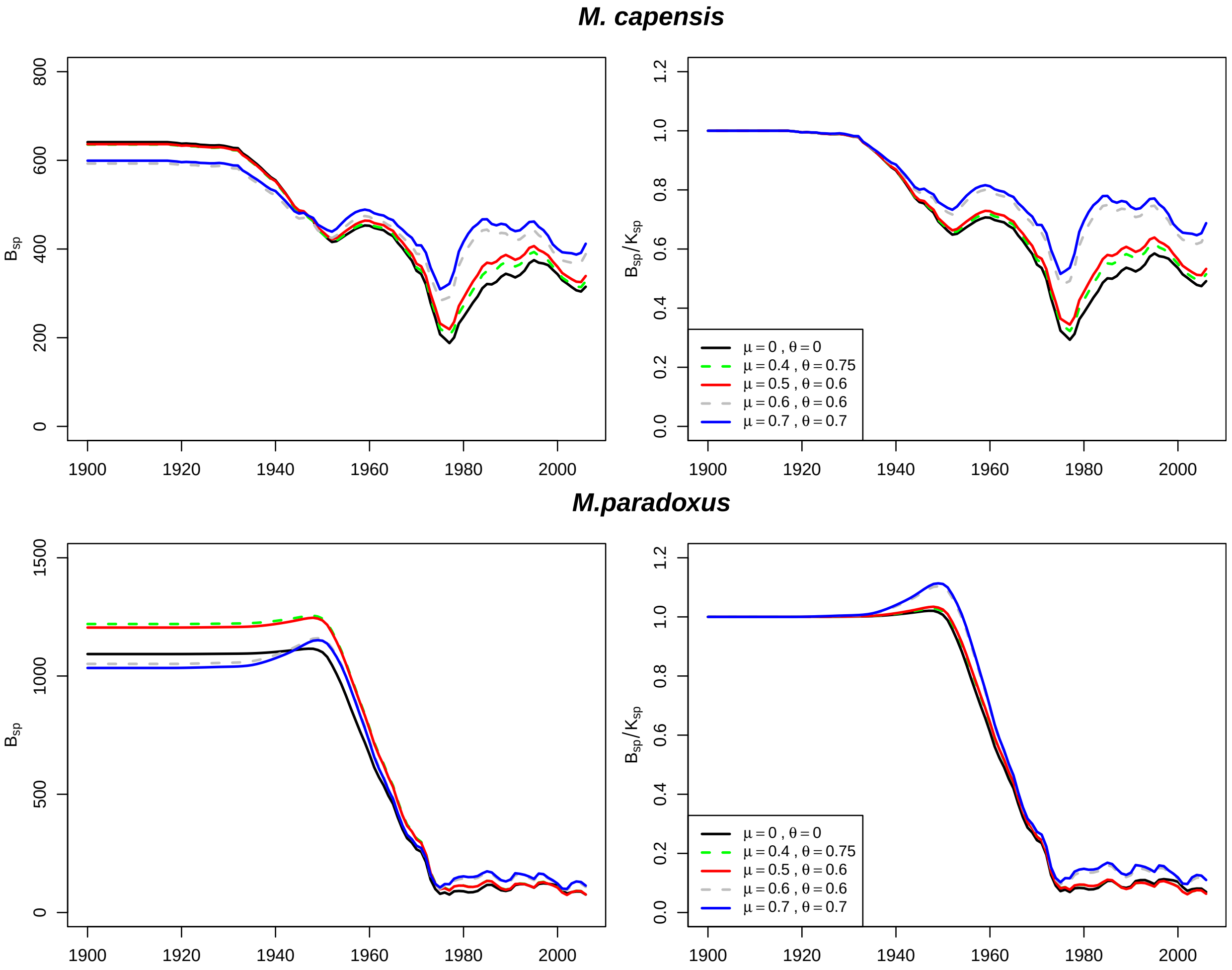

Figure 5: Model-estimated spawning biomass for gradually increasing predation rates. Please note that these results are of a preliminary nature and intend only to illustrate the effect of adding predation and cannibalism.

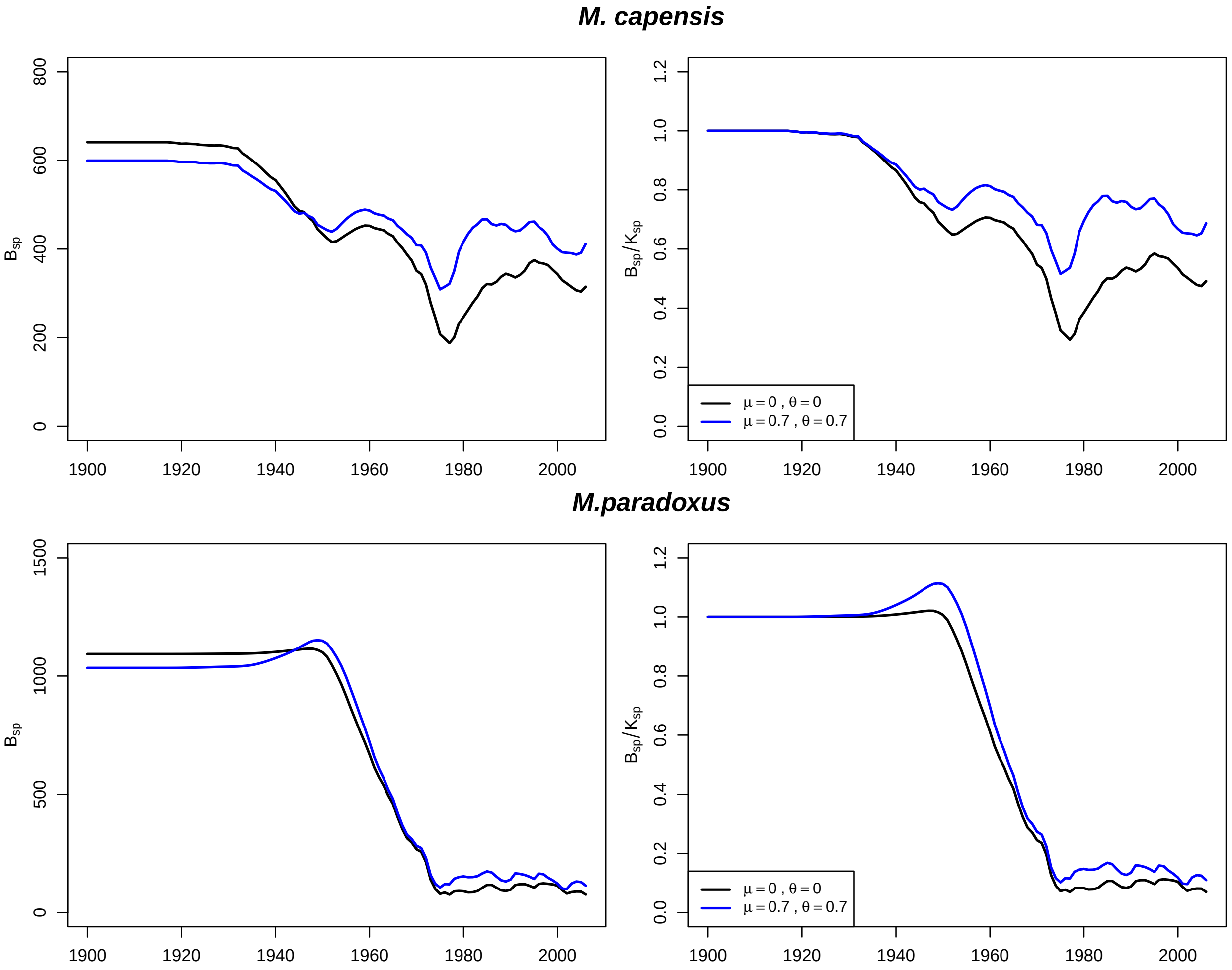

Figure 6: Repeat of Fig 5, except that population trajectories are shown only for the no-predation case and the $\mu = 0.7$, $\theta = 0.7$ case. Please note that these results are of a preliminary nature and intend only to illustrate the effect of adding predation and cannibalism.