

Modelling cannibalism and inter-species predation for Cape hake *Merluccius capensis* and *M. paradoxus*: Model specifications and preliminary results

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1 Introduction

In summary, this work aims to build on that done by Punt and Leslie (1995) and Punt and Butterworth (1995) in the development of a multispecies model for the two Cape hake species, *Merluccius capensis* and *M. paradoxus*. There, the authors aimed to construct a model which included hake, seals and other predatory fish 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 of the hake cannibalism and inter-species predation model presented in this document is to update the work done by Punt and Leslie (1995) with new data, and to extend the model to the level of the current hake assessment model.

The hake cannibalism and inter-species predation model was first presented to the International Stock Assessment Workshop (IWS) in 2011 and was reviewed again in 2013 and 2014. A list of past panel recommendations for the cannibalism model is provided in Table 1 of MARAM/IWS/DEC15/Hake/BG3.

At the time of IWS 2013, the most notable problems surrounding the cannibalism model were extremely slow model runs as well as instability arising from the manner in which the initial population equilibrium setup was structured in the model. Suggestions made by the panel as well as interim modifications to the model have helped to resolve these issues. At IWS 2014, the greatest area of concern was that the model battled to fit all of the proportion of hake in diet, daily ration and trend data simultaneously, although the methodology and preliminary results showed promise for a reasonable base case model that takes hake predation and cannibalism into account.

Alongside more subtle model improvements and development, there are three main aspects in which the model has changed from last year.

1. The model now fits directly to catch-at-length data rather than catch-at-age data as before.
2. In 2014, the model fit to diet data by age, and diet data were converted from counts-at-length to counts-at-age using von Bertalanffy growth curve parameters. The model now fits to diet data by length directly.
3. Diet data informing proportion of hake in the diet of hake predators have been weighted by the survey estimate of the population density for the stratum in which samples were collected (see

MARAM/IWS/DEC15/Hake/BG1 and MARAM/IWS/DEC15/Hake/BG3 for more detail). Weighting the diet data by stratum density substantially lowers the estimates of proportion of hake in the diet of *M. paradoxus* predators, which is more consistent with the cannibalism and predation model.

4. The manner in which the preference function is evaluated at the discrete ages utilised in the model has been modified. Details are given in Appendix A.
5. Yellow highlights have been used to indicate where changes have been made to equations from the 2014 model.

Preliminary results have been presented for the predation and cannibalism model with predation levels at 100% (predation ‘on’) and at 0% (predation ‘off’). Comparisons are shown to the results of the Rademeyer and Butterworth (2014) model. At this point in time, the model fits to the CPUE data are not entirely satisfactory and further models runs are currently in progress to try to improve the fits. An addendum to this document will be provided at IWS 2015 should sufficient improvements be achieved.

2 Data

The data used are the same as those presented in Rademeyer and Butterworth (2014). 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 database 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. Following a recommendation from the panel at the 2014 International Stock Assessment Workshop, only diet data from the West Coast have been used.

2.1 Daily ration

Punt and Leslie (1995) present estimates of daily ration for hake, but since no direct experiments have been conducted for hake to determine gastric evacuation rates there is considerable uncertainty around these estimates. As such the model presented in this paper fits to a rough estimate of daily ration as a percentage of body mass, which Punt and Leslie (1995) estimate to lie somewhere between 1.1 and 4.4% for *M. capensis* and somewhere between 0.7 and 4.1% for *M. paradoxus*.

2.2 Proportion of hake in diet

The 1999-2013 DAFF data set consists of a total of 7692 non-empty stomachs, of which 10% contain only hake prey, 88% contain non-hake prey, while the remaining 2% contain a mixture of hake and other prey. For simplicity, these mixed samples were apportioned to either 100% hake prey or 0% hake prey through rounding (the percentage hake is calculated by the weight of the prey samples in the stomachs). Tables 1-4 shows the resulting numbers that are input into the model to inform proportion of hake in diet.

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 length in the stomachs of predators by species and length. The data are given in Tables 5-8. Currently hake that have not been identified has *M. capensis* or *M. paradoxus* are not included in the preference counts.

3 Basic dynamics

This model uses a monthly time step, and the subscript m denotes month. The use of a monthly time step means that the model needs to take into account the growth of individual fish throughout the year. A fish aged 1 month for example will not be the same size as a fish aged 11 months, even though both would be classed as '0 year old' hake. As such, the model keeps track of the number of hake in each age-class by *month* and uses these for the basic calculations. Let $\tilde{N}_{s,\tilde{a},y,m}$ be the number of hake aged \tilde{a} months. Then, assuming a Baranov approximation for the catches, the number of hake aged $\tilde{a} + 1$ months in the following month is given by

$$\tilde{N}_{s,\tilde{a}+1,y,m+1} = \tilde{N}_{s,\tilde{a},y,m} e^{-Z_{saym}} \quad (3.1)$$

where the a suffix in the total (monthly) mortality rate Z_{saym} is the age in years. In other words, the mortality rate is taken to be the same for all fish that have the same age in years, and is given by

$$Z_{saym} = M_{sa}^{basal}/12 + P_{saym} + \sum_f S_{saf} F_{symf} \quad (3.2)$$

M_{sa}^{basal} is the basal natural mortality rate, which has been set at 0.3 for the results presented in this document. P_{saym} is the mortality due to predation, and $\sum_f S_{saf} F_{symf}$ the fishing mortality in month m .

Note that for the month of January (i.e. $m = 1$), $\tilde{N}_{s,a+1,y,1} = \tilde{N}_{s,a,y-1,12} e^{-Z_{s,a,y-1,12}}$.

The number of hake age a years is then given by

$$N_{saym} = \sum_{\tilde{a}=12a}^{12a+11} \tilde{N}_{s,\tilde{a},y,m} \quad (3.3)$$

The spawning biomass calculations take into account the weight of hake based on their age in months:

$$B_{sym}^{sp} = \sum_{\tilde{a}=12a_{mat}}^{12a_{mat}+11} \tilde{N}_{s,\tilde{a},y,m} w_{s\tilde{a}} \quad (3.4)$$

where a_{mat} is the age at maturity, taken to be four years, and $w_{s\tilde{a}}$ is the weight of a hake of species s and age \tilde{a} months.

Note that in the equations that follow, subscripts s and a are used for the prey species (e.g. N_{saym}) and superscripts s_p and a_p are used for predator species (e.g. $N_{ym}^{s_p a_p}$).

4 Predation dynamics

4.1 Hake prey

The following equations are based in part on those given in Kinzey and Punt (2009), with several adjustments. Let $V_{saym}^{s_p a_p}$ be the mortality rate of hake prey of species s and age a due to predators of species s_p and age a_p . Then

$$P_{saym} = \sum_{s_p, a_p} V_{saym}^{s_p a_p} \quad (4.1)$$

where

$$V_{saym}^{s_p a_p} = N_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\nu_s^{s_p} \theta^{s_p a_p}}{1 + \sum_{s,a} \tilde{\nu}_s^{s_p} N_{saym} \gamma_{sa}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \quad (4.2)$$

Here

$N_{ym}^{s_p a_p}$ is the number of hake predator fish of species s_p and age a_p in month m of year y ,

N_{saym} is the number of hake prey fish of species s and age a in month m of year y ,

$\gamma_{sa}^{s_p a_p}$ is a preference function modelling the preference that a predator of species s_p and age a_p exhibits for prey of species s and age a ,

$\theta^{s_p a_p}$ is a function allowing for additional flexibility in the extent to which predation rates change with predator age, and

$O_{other}^{s_p a_p}$ is the population size in numbers of other (non-hake) prey available to hake predators of species s_p and age a_p , assumed to be time-invariant.

$\nu_s^{s_p}$, $\tilde{\nu}_s^{s_p}$ and $\tilde{\nu}_{other}^{s_p}$ are estimable parameters.

Since $O_{other}^{s_p a_p}$ is multiplied by the estimable parameter $\tilde{\nu}_{other}^{s_p}$, the magnitude of $O_{other}^{s_p a_p}$ does not matter, only how it varies relative to predator age a_p . $O_{other}^{s_p a_p}$ is modelled by a simple exponential equation:

$$O_{other}^{s_p a_p} = e^{-(o^{s_p})a_p} \quad (4.3)$$

where o^{s_p} is an estimable parameter that can be positive or negative.

The number of hake prey of species s and age a consumed in month m of year y by predators of species s_p and age a_p is given by

$$E_{saym}^{s_p a_p} = \frac{V_{saym}^{s_p a_p}}{Z_{saym}} N_{saym} (1 - e^{-Z_{saym}}) \quad (4.4)$$

The mass of hake of species s consumed in year y by predators of species s_p and age a_p is given by

$$Q_{sym}^{s_p a_p} = \frac{V_{saym}^{s_p a_p}}{Z_{saym}} N_{saym} w_{sa} (1 - e^{-Z_{saym}}) \quad (4.5)$$

4.2 Other prey

The approach used for setting up the hake prey dynamics was mirrored in setting up the equations for the amount of other prey consumed.

Recall that $O_{other}^{s_p a_p}$ is the number of non-hake prey fish available to hake predators of species s_p and age a_p . This quantity is assumed to be time-invariant. Let the total mortality rate for other prey fish be given by

$$Z_{other,ym}^{s_p a_p} = M_{other}^{basal} / 12 + P_{other,ym} \quad (4.6)$$

where

M_{other}^{basal} is the basal mortality rate for the other prey fish, fixed at 0.2, and
 $P_{other,ym}$ is the predation mortality on other prey fish due to hake predators, given by

$$P_{saym} = \sum_{s_p, a_p} V_{other,ym}^{s_p a_p} \quad (4.7)$$

$V_{other,ym}^{s_p a_p}$ is the mortality of other prey fish due to hake predators of species s_p and age a_p in month m of year y , given by

$$V_{other,ym}^{s_p a_p} = N_{ym}^{s_p a_p} \frac{\nu_{other}^{s_p} \theta^{s_p a_p}}{1 + \sum_{s,a} \tilde{\nu}_s^{s_p} N_{saym} \gamma_{sa}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \quad (4.8)$$

The mass of other prey consumed in year y by predators of species s_p and age a_p is then given by

$$Q_{other,ym}^{s_p a_p} = \frac{V_{other,ym}^{s_p a_p}}{Z_{other,ym}} \tilde{O}_{other}^{s_p, a_p} (1 - e^{-Z_{other,ym}}) \quad (4.9)$$

Here $\tilde{O}_{other}^{s_p, a_p}$ is a measure of the **mass** of the other prey fish available to a hake predator of species s_p (as opposed to $O_{other}^{s_p, a_p}$, which represents the population size in numbers). $\tilde{O}_{other}^{s_p, a_p}$ is approximated by an exponential equation:

$$\tilde{O}_{other}^{s_p, a_p} = \tilde{\delta}_a^{s_p} \exp(\tilde{\delta}_b^{s_p}) \quad (4.10)$$

where $\tilde{\delta}_a^{s_p}$ and $\tilde{\delta}_b^{s_p}$ are estimable parameters.

4.3 Parameter simplification

In order to reduce the number of estimable parameters in an already complex model, each of $\nu_s^{s_p}$ and $\tilde{\nu}_s^{s_p}$ are taken to be independent of (hake) prey species, i.e.

$$V_{saym}^{s_p a_p} = N_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\nu^{s_p} \theta^{s_p a_p}}{1 + \tilde{\nu}^{s_p} \sum_{s,a} N_{saym} \gamma_{sa}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \quad (4.11)$$

and

$$V_{other,ym}^{s_p a_p} = N_{ym}^{s_p a_p} \frac{\nu_{other}^{s_p} \theta^{s_p a_p}}{1 + \tilde{\nu}^{s_p} \sum_{s,a} N_{saym} \gamma_{sa}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \quad (4.12)$$

4.4 Preference function

The preference function is modelled using a gamma function, as in Kinzey and Punt (2009):

$$\gamma_{sa}^{s_p a_p} = \left(G_{sa}^{s_p a_p} / \tilde{G}^{s_p} \right)^{\alpha^{s_p} - 1} \exp \left[- \left(G_{sa}^{s_p a_p} - \tilde{G}^{s_p} \right) / \beta^{s_p} \right] \quad (4.13)$$

where

$G_{sa}^{s_p a_p}$ is the logarithm of the ratio of the expected length of a fish of species s_p and age a_p to that of a fish of species s and age a , and

$\tilde{G}^{s_p} = (\alpha^{s_p} - 1) \beta^{s_p}$ is the value of $G_{sa}^{s_p a_p}$ at which predator selectivity is 1.

Some additional details as to the method used to extract discrete values from a continuous gamma function are given in the Appendix.

4.5 Theta function

Kinzey and Punt (2009) introduce $\theta^{s_p a_p}$ in order to *reduce* predation as predator age increases, i.e. to allow for the fact that larger fish may focus less on feeding and growth, and more on reproducing. They use the form

$$\theta^{s_p a_p} = 1 + \omega^{s_p} \tilde{\omega}^{s_p} / (a_p + \tilde{\omega}^{s_p}) \quad (4.14)$$

When this form was implemented in the model presented here, it resulted in older fish not eating enough. In Ross-Gillespie and Butterworth (2014), a different function was explored, which mimicked the weight-at-age function used for hake, under the logic that a predator is likely to eat more in proportion to its own weight increasing. **Currently, $\theta^{s_p a_p}$ is set equal to 1** as the introduction of $\tilde{O}_{other}^{s_p a_p}$ in Equation 4.9 seems to allow for sufficient daily ration for older fish.

4.6 Initial population setup

Obtaining an initial population setup provides a challenge when modelling predation and cannibalism. In order to obtain the equilibrium structure, the total mortality values $Z_{s a y_0, m=1} = M_{s a}^{basal} + P_{s, a, y_0, m=1}$ are needed. However, in order to obtain $P_{s, a, y_0, m=1}$, the initial population structure is needed. Note that y_0 is the first year considered in the model, namely 1916, and $m = 1$ is the first month, January.

The approach used to resolve this issue starts with the oldest hake predators and systematically moves to zero year old hake, computing predation rates along the way. The basic assumption is that a hake fish of age 10 and above (the plus age group) is too large to be preyed on by other hake, i.e. $P_{s, a_m, y_0, m=1} = 0$, where $a_m = 10$ is the maximum age considered in the model. Thus the total mortality rate is $Z_{s, a_m, y_0, m=1} = M_{s a_m}^{basal}$, where the basal mortality rate is fixed on input. The number of 9 year old hake can then be calculated from the number of 10 year old hake: $N_{s, a_m-1, y_0, m=1} = N_{s, a_m, y_0, m=1} e^{Z_{s, a_m, y_0, m=1}}$. It is then assumed that the only hake predators for 9 year old hake are 10 years and older, and $P_{s, a_m-1, y_0, m=1}$ can be calculated from $N_{s, a_m, y_0, m=1}$, allowing $N_{s, a_m-2, y_0, m=1} = N_{s, a_m-1, y_0, m=1} e^{Z_{s, a_m-1, y_0, m=1}}$ to be determined and so forth. By re-parameterising the predation equations (see Equation 4.22), one can set $N_{s, a_m, y_0, m=1} = 1$ initially, and once $N_{s, a, y_0, m=1}$ has been obtained for all a , the numbers can be scaled so that the spawning biomass equals the model-estimated parameter value. One problem with this approach is that if $P_{s, a, y_0, m=1}$ gets too big (which can happen during the minimisation process), then $e^{Z_{s, a y_0, m=1}}$ can “explode”. An upper bound of 0.5 has thus been enforced on the $P_{s, a, y_0, m=1}$ values.

In order to implement this approach, adjustments need to be made to Equations (4.11) and (4.12), so that the $N_{s a y_0 m}$ term is effectively removed from the denominator at unexploited equilibrium.

Rewrite Equation 4.11 and 4.12 as

$$V_{s a y m}^{s_p a_p} = \frac{N_{y m}^{s_p a_p} \gamma_{s a}^{s_p a_p}}{N_{y_0, m=1}^{s_p a_p, max}} \frac{(\nu^{s_p} N_{y_0, m=1}^{s_p a_p, max}) \theta^{s_p a_p}}{1 + \left(\tilde{\nu}^{s_p} \sum_{s, a} N_{s a y_0, m=1} \gamma_{s a}^{s_p a_p} \right) \frac{\sum_{s, a} N_{s a y m} \gamma_{s a}^{s_p a_p}}{\sum_{s, a} N_{s a y_0, m=1} \gamma_{s a}^{s_p a_p}} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \quad (4.15)$$

and

$$V_{other, y m}^{s_p a_p} = \frac{N_{y m}^{s_p a_p}}{N_{y_0, m=1}^{s_p a_p, max}} \frac{(\nu_{other}^{s_p} N_{y_0, m=1}^{s_p a_p, max}) \theta^{s_p a_p}}{1 + \left(\tilde{\nu}^{s_p} \sum_{s, a} N_{s a y_0, m=1} \gamma_{s a}^{s_p a_p} \right) \frac{\sum_{s, a} N_{s a y m} \gamma_{s a}^{s_p a_p}}{\sum_{s, a} N_{s a y_0, m=1} \gamma_{s a}^{s_p a_p}} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \quad (4.16)$$

Define

$$\tilde{N}_{ym}^{s_p a_p} = \frac{N_{ym}^{s_p a_p}}{N_{y_0, m=1}^{s_p a_p, max}} \quad (4.17)$$

$$\Phi_{hake, ym}^{s_p a_p} = \frac{\sum_{s,a} N_{saym} \gamma_{sa}^{s_p a_p}}{\sum_{s,a} N_{say_0, m=1} \gamma_{sa}^{s_p a_p}} \quad (4.18)$$

$$\eta^{s_p} = \nu^{s_p} N_{y_0, m=1}^{s_p a_p, max} \quad (4.19)$$

$$\eta_{other}^{s_p} = \nu_{other}^{s_p} N_{y_0, m=1}^{s_p a_p, max} \quad (4.20)$$

$$\tilde{\eta}^{s_p a_p} = \tilde{\nu}^{s_p} \sum_{s,a} N_{say_0, m=1} \gamma_{sa}^{s_p a_p} \implies \tilde{\eta}^{s_p} \quad (4.21)$$

Then

$$V_{saym}^{s_p a_p} = \tilde{N}_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\eta^{s_p} \theta^{s_p a_p}}{1 + \tilde{\eta}^{s_p} \Phi_{hake, ym}^{s_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \quad (4.22)$$

and

$$V_{other, ym}^{s_p a_p} = \tilde{N}_{ym}^{s_p a_p} \frac{\eta_{other}^{s_p} \theta^{s_p a_p}}{1 + \tilde{\eta}^{s_p} \Phi_{hake, ym}^{s_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \quad (4.23)$$

Since it is not feasible to estimate an age-dependent $\tilde{\eta}^{s_p a_p}$, an age-independent $\tilde{\eta}^{s_p}$ is estimated instead, and the following penalty is added to the negative log-likelihood:

$$-lnL+ = \sum_{a_p} \left(\tilde{\eta}^{s_p} - \tilde{\nu}^{s_p} \sum_{s,a} N_{say_0, m=1} \gamma_{sa}^{s_p a_p} \right)^2 \quad (4.24)$$

However, implementing Equation 4.24 is problematic since $\tilde{\eta}^{s_p}$ is now estimated instead of $\tilde{\nu}^{s_p}$. Rearranging Equation 4.21 it can be seen that ideally $\tilde{\eta}^{s_p} / \sum_{s,a} N_{say_0, m=1} \gamma_{sa}^{s_p a_p}$ should be equal to a constant for all predator ages a_p . The following penalty is thus added to the negative log-likelihood:

$$-lnL+ = \sum_{s_p} \sum_{a_p \neq 0} \left(\frac{\tilde{\eta}^{s_p}}{\sum_{s,a} N_{say_0, m=1} \gamma_{sa}^{s_p a_p}} - \frac{\tilde{\eta}^{s_p}}{mean_{a_p} \left(\sum_{s,a} N_{say_0, m=1} \gamma_{sa}^{s_p a_p} \right)} \right)^2 \quad (4.25)$$

At equilibrium, Equation 4.22 simplifies to

$$V_{say_0, m=1}^{s_p a_p} = \tilde{N}_{y_0, m=1}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\eta^{s_p} \theta^{s_p a_p}}{1 + \tilde{\eta}^{s_p} + \tilde{\nu} O_{other}^{s_p a_p}} \quad (4.26)$$

Further, $V_{say_0, m=1}^{s_p a_p, max} = \gamma_{sa}^{s_p a_p} \frac{\eta^{s_p} \theta^{s_p a_p}}{1 + \tilde{\eta}^{s_p} + \tilde{\nu} O_{other}^{s_p a_p}}$, i.e. this is now independent of the (unknown) initial population size.

5 Estimation process

In order to obtain reasonable starting positions for the parameters to be estimated, an approach was taken whereby the parameters are estimated initially with predation ‘‘off’’, and thereafter the predation level is

gradually increased. For this “scaling-up” approach, the majority of the predation-related parameters are taken to be independent of predator species, i.e. Equations 4.22 and 4.23 become

$$V_{saym}^{s_p a_p} = \tilde{N}_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\eta \theta^{s_p a_p}}{1 + \tilde{\eta} \Phi_{hake,ym}^{s_p a_p} + \tilde{\nu}_{other} O_{other}^{s_p a_p}} \quad (5.1)$$

and

$$V_{other,ym}^{s_p a_p} = \tilde{N}_{ym}^{s_p a_p} \frac{\eta_{other} \theta^{s_p a_p}}{1 + \tilde{\eta} \Phi_{hake,ym}^{s_p a_p} + \tilde{\nu}_{other} O_{other}^{s_p a_p}} \quad (5.2)$$

The level of predation is varied by introducing a parameter λ to Equation 3.2:

$$Z_{saym} = (M_{sa}^{basal} + (1 - \lambda) (M_{sa} - M_{sa}^{basal})) / 12 + \lambda P_{saym} + \sum_f S_{saf} F_{symf} \quad (5.3)$$

M_{sa} is the total natural mortality when predation is “off” and is defined in the same manner as in Rademeyer and Butterworth (2014), with $M_{2-} = 0.75$ and $M_{5+} = 0.3$. When $\lambda = 0$, predation is “off” and

$$Z_{saym} = (M_{sa}) / 12 + \sum_f S_{saf} F_{symf} \quad (5.4)$$

When $\lambda = 1$, Equation 5.3 reduces back to Equation 3.2 and predation is “on”. By fixing the value of λ iteratively at values between 0 and 1, the predation level can be stepped up gradually.

6 Likelihood components

Note that since there are no diet data available for hake predators of age $a_p = 0$, this age group is not included in any of the likelihood contributions from the diet data. The minimum predator length considered in the model is 19cm, which corresponds roughly to one year old hake (1.1 years for *M. capensis* and 0.93 years for *M. paradoxus*).

6.1 Daily ration

Let $\hat{\delta}_{ym}^{s_p a_p}$ be the model estimate of the total daily ration of a predator of species s_p and age a_p in month m of year y , as a percentage of predator body mass, defined by

$$\hat{\delta}_{ym}^{s_p a_p} = \frac{\sum_s Q_{sym}^{s_p a_p} + Q_{other,ym}^{s_p a_p}}{\sum_{\tilde{a}_p=12a_p}^{12a_p+11} \tilde{N}_{y,m}^{s_p, \tilde{a}_p} w^{s_p \tilde{a}_p}} * 12/365 * 100 \quad (6.1)$$

Bearing in mind that the model tracks hake cohorts by month and sums them to obtain the yearly numbers, the denominator of Equation 6.1 takes weight by month into account, since for example a fish of age 1 month will not have the same weight as a fish of age 11 months (similar to Equation 3.4). $\sum_{\tilde{a}_p=12a_p}^{12a_p+11} \tilde{N}_{y,m}^{s_p, \tilde{a}_p} w^{s_p \tilde{a}_p}$ is thus the combined mass of the predators that consumed the combined mass of hake calculated in the numerator.

The average daily ration as a percentage of body weight, $\bar{\delta}^{s_p a_p}$, is given by

$$\bar{\delta}^{s_p a_p} = \frac{1}{12 n_{diet}} \sum_{y_{diet}} \sum_{m=1}^{12} \hat{\delta}_{ym}^{s_p a_p} \quad (6.2)$$

where n_{diet} is the number of years (y_{diet}) for which diet data are available to the model. For the results presented here that corresponds to 1999-2013.

Punt and Leslie (1995) estimate daily ration as a percentage of body weight to lie somewhere between 1.1 and 4.4% for *M. capensis* and somewhere between 0.7 and 4.1% for *M. paradoxus*. For the results presented here, a penalty has been added to the negative log likelihood when the model-estimated $\delta^{s_p a_p}$ is outside the range of [0.5%,7%].

$$-lnL+ = \sum_{s_p a_p \neq 0} \begin{cases} (0.5 - \bar{\delta}^{s_p a_p})/0.5/(2 * 0.5^2) & \text{if } \bar{\delta}^{s_p a_p} < 0.5 \\ (\bar{\delta}^{s_p a_p} - 7)/7/(2 * 0.5^2) & \text{if } \bar{\delta}^{s_p a_p} > 7 \\ 0 & \text{otherwise} \end{cases} \quad (6.3)$$

6.2 Proportion of hake in diet

Diet composition data are available for the years 1999-2013, where

$n_{y,obs}^{s_p l_p}$ is the observed number of hake predators of species s_p and length l_p with non-empty stomachs in year y , and

$p_{y,obs}^{s_p l_p}$ is the observed number of hake predators of species s_p and age l_p with hake prey in the stomach content in year y .

The model-predicted proportion of hake in diet in year y is taken to be an average for that year:

$$\hat{\rho}_y^{s_p l_p} = \left(\sum_m \sum_{a_p \neq 0} A^{s_p l_p a_p} \sum_s Q_{sym}^{s_p a_p} \right) / \left(\sum_m \sum_{a_p \neq 0} A^{s_p l_p a_p} \left(\sum_s Q_{sym}^{s_p a_p} + Q_{other,y,m}^{s_p a_p} \right) \right) \quad (6.4)$$

where $Q_{sym}^{s_p a_p}$ is the mass of hake of species s consumed by predators of species s_p and age a_p (Equation 4.5), and $A^{s_p l_p a_p}$ is the proportion of fish of species s_p and age a_p that fall into length group l_p .

The likelihood contribution is given by:

$$-lnL+ = - \sum_y \sum_{s_p l_p} \left(p_{y,obs}^{s_p l_p} \ln \hat{\rho}_y^{s_p l_p} + (n_{y,obs}^{s_p l_p} - p_{y,obs}^{s_p l_p}) \ln(1 - \hat{\rho}_y^{s_p l_p}) \right) \quad (6.5)$$

6.3 Preference data

Let $\zeta_{s,l,obs}^{s_p l_p}$ be the number stomach contents of hake predators of species s_p and length l_p observed to contain hake prey of species s and length l , summed over the years 1999-2013. Remembering that $p_{y,obs}^{s_p l_p}$ is the total observed number of hake predators of species s_p and length l_p with hake prey in the stomach content in year y , the model-predicted proportion of hake prey of species s and length l in the stomachs of predators of species s_p and length l_p , $\hat{\chi}_{s,l}^{s_p l_p}$, is calculated as follows

$$\hat{\chi}_{s,l}^{s_p l_p} = \frac{\sum_y p_{y,obs}^{s_p l_p} E_{s,l,y,m}^{s_p l_p}}{\sum_y p_{y,obs}^{s_p l_p} \sum_l E_{s,l,y,m}^{s_p l_p}} \quad (6.6)$$

$E_{s,l,y,m}^{s_p l_p}$ is the number of hake prey of species s and length l consumed in month m of year y by predators of species s_p and length l_p and is derived from $E_{s,l,y,m}^{s_p l_p}$ (Equation 4.4) as follows:

$$E_{s,l,y,m}^{s_p l_p} = \sum_{a_p \neq 0} \sum_a A^{s_p l_p a_p} A_{sla} E_{s,a,y,m}^{s_p a_p} \quad (6.7)$$

The approach in Equation 6.6 is taken from Kinzey and Punt (2009) and gives more weight to years in which there are more data available in calculating average model-predicted preference for the years in which diet data are available.

The negative log-likelihood contribution is

$$-lnL+ = - \sum_{s_p, l_p} \sum_{s, l} \left(\zeta_{s, l, obs}^{s_p l_p} \ln(\hat{\chi}_{s, l}^{s_p l_p}) - \zeta_{s, l, obs}^{s_p l_p} \ln(\zeta_{s, l, obs}^{s_p l_p} / \sum_a \zeta_{s, l, obs}^{s_p l_p}) \right) \quad (6.8)$$

7 Results

Results are shown for three cases:

- Predation ‘on’ - the predation model with predation levels at 100 %
- Predation ‘off’, - the predation model with predation levels at 0%, which is essentially a sex-aggregated version of the Rademeyer and Butterworth (2014) model with a monthly time step
- Rademeyer RC - the reference case of the Rademeyer and Butterworth (2014) model

Figure 1 shows the spawning biomass trajectories in terms of absolute values (Figure 1a), relative to pre-exploitation spawning biomass K^{s_p} (Figure 1b) and relative to the mid-century spawning biomass estimates (Figure 1c). Figure 1c has been included out of interest, since the only available observed trend data are for the second half of the century, and as such there is no way of knowing whether population was increasing or decreasing before then. Figure 1c thus compares the trajectories relative to the mid-century estimates.

Figure 2 shows the fits to the CPUE data for the three cases. Figure 3 shows the model estimates of daily ration and proportion of hake in the diet of hake predators for the Predation ‘on’ case, while Figure 4 shows the pre-exploitation mortality (i.e. excluding fishing mortality) for all three cases.

Note that Appendix B contains some figures from the hake cannibalism document presented at IWS 2014, for comparison purposes.

8 Discussion

There is good agreement between the Rademeyer RC and the Predation ‘off’ model results, both in terms of population trajectory (Figure 1) and fits to the CPUE data (Figure 2). While there are some difference between the absolute estimate of pre-exploitation biomass¹ (Figure 1a), the relative trends (Figures 1b and c) are reasonably consistent especially considering that the Rademeyer RC model is sex-disaggregated and that the Predation‘off’ model utilises a monthly time step — the two models are as such not entirely comparable.

The Predation ‘on’ model fits well to the diet data (Figure 3), but what is of concern is the poor fit to the CPUE data, especially the historical ICSEAF data (Figure 2a), which clearly indicates some misspecification between the model and trend data. This is currently being looked into further, including up-weighting the

¹Note that the absolute estimate of pre-exploitation biomass for these hake models is generally relatively variable across different sensitivities of the same model, and differences such as those observed in Figure 1a are not uncommon.

ICSEAF likelihood component and implementing different values of the basal mortality. The fact that the older ICSEAF data are not well documented and possibly not that reliable should, however, be kept in mind.

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Table 1: Number of non-empty stomachs of *M. capensis* predators are provided per 2cm length class (DAFF data set, T. Fairweather, *pers. comm.*).

a_p	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	
1999	8	4	4	2	4	9	4	5	4	3	8	6	5	5	7		2	5	4	3	4	4	6	3	4	7	2	1	3	4	2		
2000	8	3	5	7	5	4	2	2	5	6	1	2	3	3	2	5	3	2	3	3	3	4	5	2	6	2	2	6	4		1		
2001	4	3		1	1	3	2	3	2	3	3	1	2			2	2	1	1			1	2	2	2	1	3	4	1	1	3	3	
2002																																	
2003	6	9	4	5	5	9	5	3	8	5	4	4	5	4	6	5	5	2	4	7	6	4	5	9	5	4	2	3	3				
2004	8	8	13	4	7	9	13	8	10	14	8	7	9	7	6	10	6	6	5	4	8	2	5	4	7	9	5	2	3	2			
2005	7	12	8	5	5	7	8	6	6	4	3	6	2	5	3	6	8	4	4	5	3	5	4	6	1	2	4	2	4	1	1	1	
2006	14	16	8	8	4	7	3	4	5	3	4	4	1	3	2	4	10	3	6	2	3	7	8	8	3	2	1	4		1			
2007	2	1	2	10	10	12	6	7	3	5	1	1			3		1	2		2	2		1	1				1					
2008	6	7	5	7	4	3	6	4	3		5	2	6	5	4	6	4	3					1	1	3	1		1	1			1	
2009	2		4	1	7	3	1	5	5	3	6	5	3	1	6	5	7	5	4	10	7	6	8	2	5	2	1		1				
2010	6	1	5	4	4	2	4	1	5	3	3	5	3	1		3	6	2	7	3	5	4	5	8	4	10	12	7	3	1	1		
2011	1	5	6	9	7	10	12	15	12	16	10	11	10	3	6	8	13	6	10	14	8	3	8	4	6	5	4	8	5	4	1	1	1
2012	1	2	5	6	4	2	6	3	5	3	1	5	4	3	8	7	8	11	6	4	1	3	4	7	6	9	4	6	2	3		2	
2013		1		2	3	6	3	3	2		3	9	1		2	3	1	2	5	3	6	5	6	7	5	3	3	2	3	4	1		

Table 2: Number of non-empty stomachs of *M. paradoxus* predators are provided per 2cm length class (DAFF data set, T. Fairweather, *pers. comm.*).

a_p	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	
1999	6	4	4	3	4	4	4	2	3	6	2	2	1	3	3	1	2	1		1		1		1								1	
2000	4	6	7	5	6	3	3	2	2	5	4	2	2		3	2	2		1	3	2		1	1	1		2	1					
2001	2	2	1	1	3	3			1	2	1	3	2	1	2		1	1															1
2002																																	
2003	12	7	6	2	4	5	3	5	8	6	3	5	4	3	1	3	2	2	2	2	1		4	1	2	2	1					2	
2004	5	10	15	11	4	6	13	5	7	4	2	1	2	4	3	3	2	2	2	3	2	2		3			1	3					
2005	7	5	7	10	6	6	4	5	4	4	3	1	3			1	1	1	2			2		2			3				1		
2006	7	6	10	16	15	10	8	6	4	5	2	4	4	3	1	6	5	2	5	1	1	1	1			1							
2007	17	7	2	2	5	1					3	2	2	1		6	2	2	2	3	1	2	1	1			1				2		
2008	8	4	8	7	3	1	1	2	3	3		1	1	2	1	2		1	1	1		3	1	2	1		1	1		1		1	
2009	10	4	4	4	3	1	3	6	2	3	2	2	4	3	4	1	2		3			1	3	1	1	1							
2010	2			1			2		1	2	1	1	3	1	1	1		3		4		1		1	1		1						
2011	4	4	3	3	3	2	5	3	4	5	1	4	1		3	1	3	2	3	2	3	2	1	3		1	2	3	1	1	4		
2012				2	3	1			2	1	1	2	1	1	2		1	2	1	2	1		3			2		2	1	1			
2013	2		1	3		1	2		2	1		2		4	1		1	1		1			1	1				1					

Table 3: Number of *M. capensis* stomachs containing more than 50 % (by prey weight) hake are given per 2cm length class. The original data are from the DAFF data set (T. Fairweather, *pers. comm.*) and these data have been weighted by stratum-density (see Case B of MARAM/IWS/DEC15/Hake/BG1) to obtain the estimates provided here.

a_p	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81
1999										1		2	1	1	4.7			2	1		1.3	1	3.9	1.9		2.8					2	
2000				1	4				1				0.6	0.6	1	4	1.5	2	2	0.2	2	3	1.2		0.9	1	1	2.4				
2001																	1						1.6	2			1			1	1.6	2
2002																																
2003				0.9		0.3			1.2	0.3	1		2.1	2.7	3.6	2.7			3	5	2.3	3	3	4.1	5	2	2	2				
2004					3.9	0.3	4.6	2.3		4.4	4	1	4	1	3.5	4.8	1.7	1.7	1.9	2	6	2	4.2	4	3.4	2.1	1	2			2	
2005	1.3	1.2					1	1						0.7	1	1.8	5.8	4	3	2	1	3.2	3	1.9		1		1	2			1
2006								1	0							3.1	5.6	1	0.3	1		2.3	1.4	1		1.7						
2007										0.8		1					1			2								1				
2008					1							1				1.3	1.4	1.9							0.5							
2009			1.7					1	1.6	2		2.1		1	1	2.5	2.9	2	3.7	7.4	1.2	1	1.4	2	2.3	1				1		
2010					2	1	2	1	2	2	2.3	2.9	2			2	2.4	1	5.4	1	0.3	1	2	2.4	0.2	4.7	2.6	7	2			
2011		0.1		1.1		0	0	1.3	0.1	1	1.1	2.9			1.5	4.7	9.3	2.6	5	10.1	7.7	2			2.5	2.6	2.1	2.7	2.8	0.9		
2012					1	2			1.2	1.2		2.7		1	2.2	4.2	5.3	5.4	3.3	2	1	1.8	1.8	2.9	4.4	4.5	3	4.7	1			1.7
2013		1		1.1	2	2.1	1.6				1.4		1		1			2	1.6	3	2.5	0.2	1.4		2	1.9		1.5			2.7	

Table 5: *M. capensis* preference for *M. capensis* prey by predator and prey length. The breakdown of number of fish of each prey length found in the stomachs of predator fish is given for each predator length (DAFF data set, T. Fairweather, *pers. comm.*). Note that these data are for the West Coast only and have been aggregated over the years 1999-2013. These data have not been weighted by depth stratum.

	Prey length (<i>M. capensis</i>)																				
	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	
19	1																				
21		1																			
23	1																				
25																					
27	2	1		1																	
29	1	2																			
31		1	1																		
33			2	2	2																
35																					
37					1	1	1														
39			1	1			1														
41						2															
43								1	1												
45																					
47							1														
49								1													
51																					
53				1					1												
55		1						1													
57						1	1						1								
59						1	1														
61																					
63						1															
65																					
67															1						
69		1							1												
71																					
73										1		1					1				
75																					
77							1														
79																					
81																					
83																					
85																					
87																					
89																					
91																					1

Table 6: *M. capensis* preference for *M. paradoxus* prey by predator and prey length. The breakdown of number of fish of each prey length found in the stomachs of predator fish is given for each predator length (DAFF data set, T. Fairweather, *pers. comm.*). Note that these data are for the West Coast only and have been aggregated over the years 1999-2013. These data have not been weighted by depth stratum.

	Prey length (<i>M. paradoxus</i>)																				
	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	
19																					
21																					
23																					
25	1	1																			
27	1	2	1																		
29		1																			
31		1	2	1	1																
33																					
35		1						1													
37		1		1	1	1															
39			1		2																
41				1		2	1														
43	1			1		3															
45								1	1												
47	1	1				1	1	2													
49				1	3		2	1	3												
51		1		1	2	3	6	1						1							
53					1		1		4	2		1									
55					1		2	2	2	2	1										
57		1		2	1	2	6	4	1	2	2										
59		1			1	2	5	2	1	1	1										
61					1	2			1		1										
63						2	1			3		1									
65		1							4		3	2		2		1					
67							2	3	3	1	5			1		1					
69							1	5	3	2	1										
71							1	1	1	1											
73					1		1	2	1	2	1	1		1	1			2			
75								1		1	1		2	2							
77							1				1	1									
79									1											1	
81							1			1		1			1	1					1
83								1													
85							1		1												1
87																					
89																					
91							1														

Table 7: *M. paradoxus* preference for *M. paradoxus* prey by predator and prey length. The breakdown of number of fish of each prey length found in the stomachs of predator fish is given for each predator length (DAFF data set, T. Fairweather, *pers. comm.*). Note that these data are for the West Coast only and have been aggregated over the years 1999-2013. These data have not been weighted by depth stratum.

	Prey length (<i>M. paradoxus</i>)																				
	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	
19																					
21																					
23																					
25																					
27																					
29																					
31																					
33																					
35	1																				
37																					
39																					
41						1	1														
43								1													
45					1																
47					1																
49																					
51					1						1										
53							2	1													
55							1														
57							1			2											
59				1			1			1											
61										1											
63				1	1	1											1				
65									1		1	2									
67					1																
69																	1				
71										1					1		1				
73							1			1	1										
75								1													
77																				1	
79						1	1			1										3	
81																				1	
83									1		1	1									
85																					
87																					
89																					
91													1								

Table 8: *M. capensis* predator preference for *M. capensis* vs *M. paradoxus* prey.

<i>M. capensis</i> predator length	Number of <i>M. capensis</i> prey in samples	Number of <i>M. paradoxus</i> prey in samples
19	1	
21	1	
23	1	
25		2
27	4	4
29	3	1
31	2	5
33	6	
35		2
37	3	4
39	3	3
41	2	4
43	2	5
45		2
47	1	6
49	1	1
51		15
53	2	9
55	2	1
57	3	21
59	2	14
61		5
63	1	7
65		13
67	1	16
69	2	12
71		4
73	3	13
75		7
77	1	3
79		2
81		6
83		1
85		3
87		
89		
91	1	1

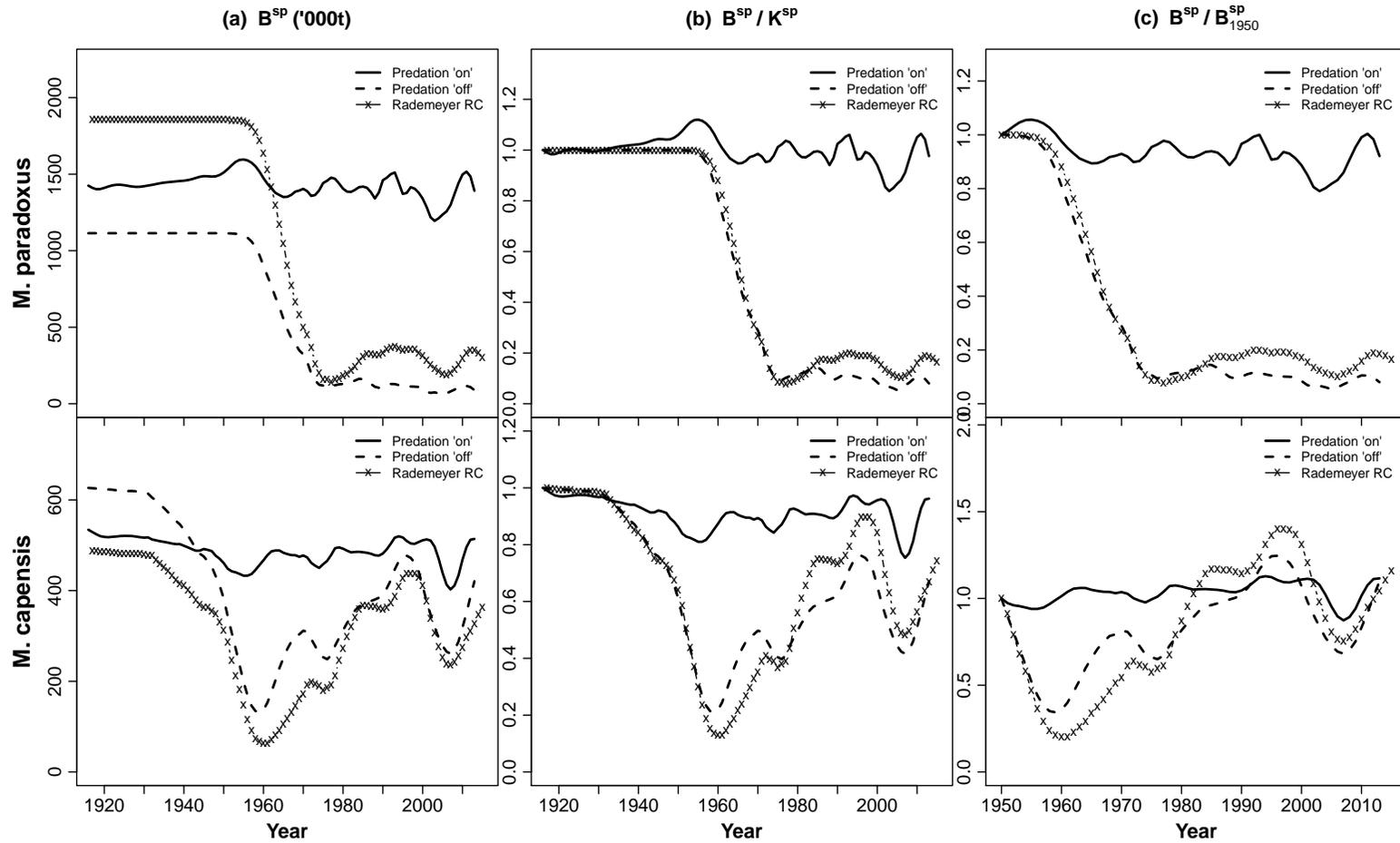


Figure 1: Spawning biomass trajectories are shown for the predation and cannibalism model (solid black line), the predation and cannibalism model with predation 'off' (dashed line) and for the Rademeyer and Butterworth (2014) reference case model (crosses). Figure (a) shows the spawning biomass trajectories in terms of absolute values, figure (b) shows the trajectories relative to the pre-exploitation spawning biomass, and figure (c) shows the trajectories relative to the maximum population size.

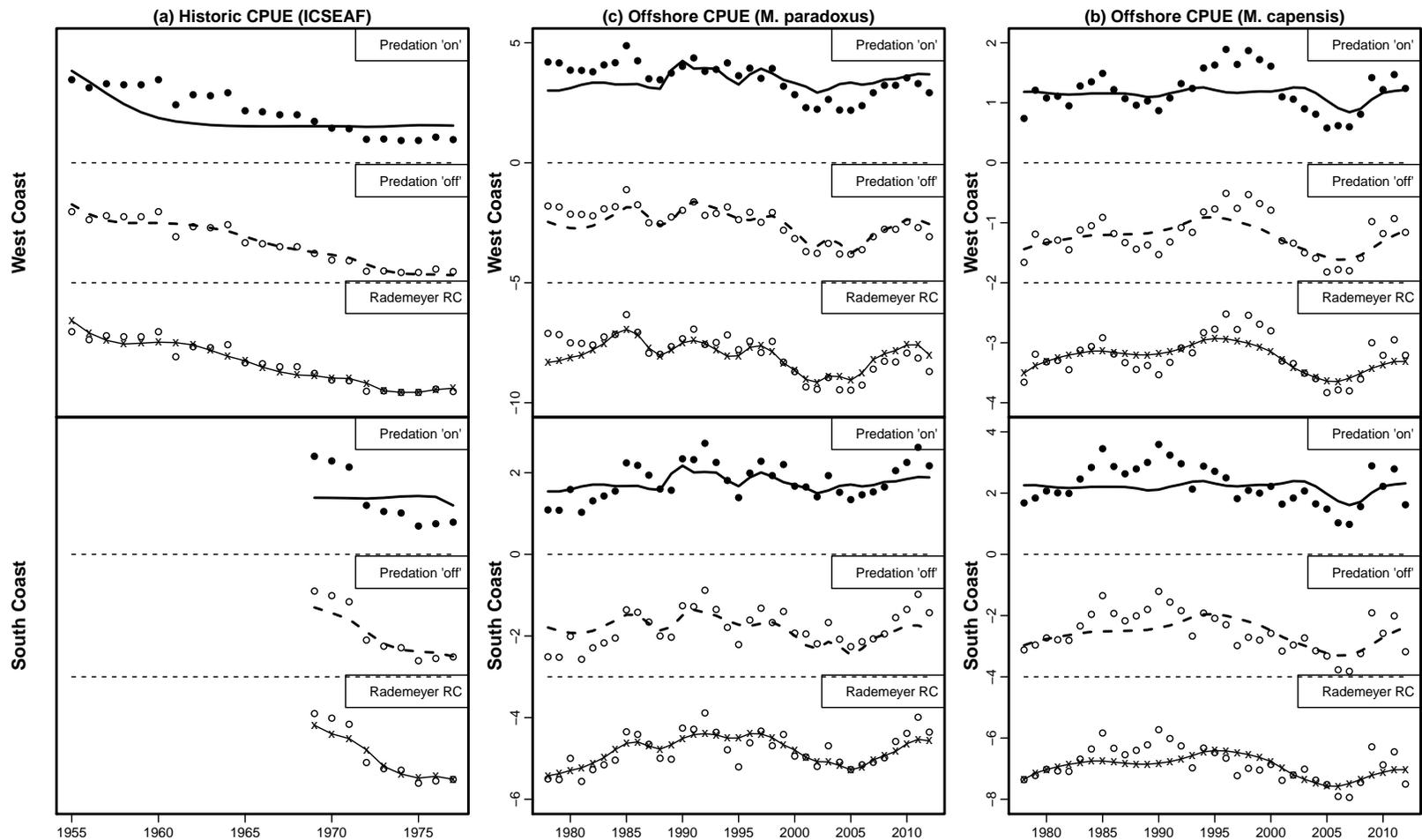


Figure 2: Spawning biomass trajectories are shown for the predation and cannibalism model (solid black line), the predation and cannibalism model with predation 'off' (dashed line) and for the Rademeyer and Butterworth (2014) reference case model (crosses). Figure (a) shows the spawning biomass trajectories in terms of absolute values, figure (b) shows the trajectories relative to the pre-exploitation spawning biomass, and figure (c) shows the trajectories relative to the maximum population size.

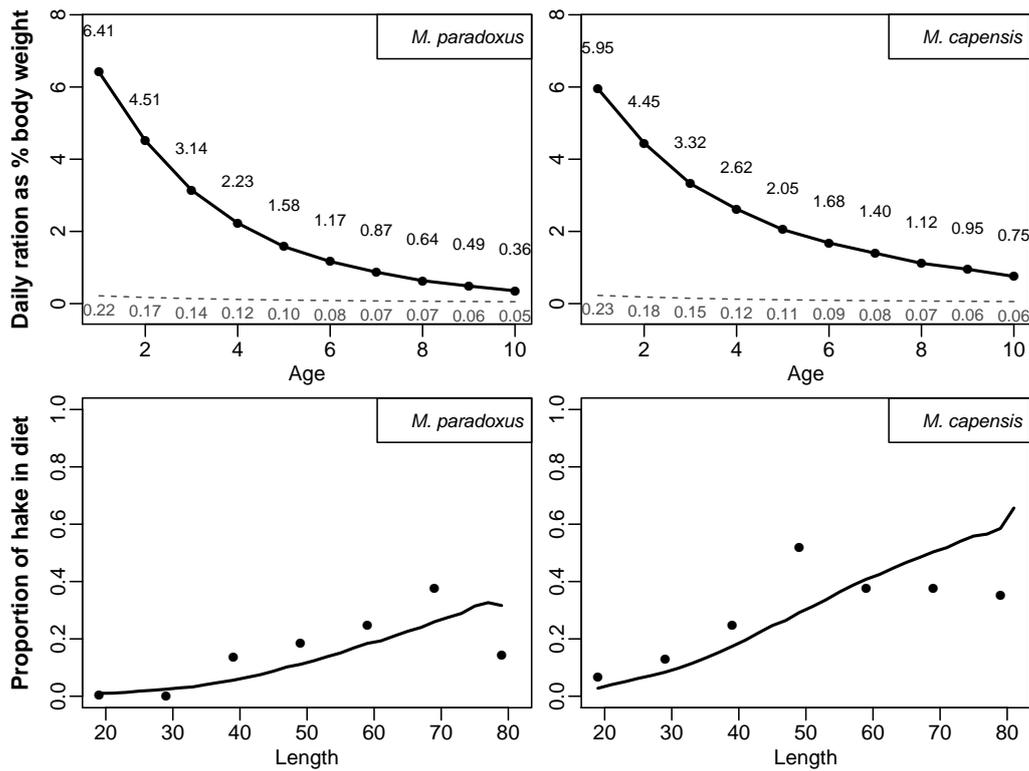


Figure 3: Fits to the diet data for the predation and cannibalism model (predation on). The top two panels show the model-estimated total daily ration in terms of a percentage of body mass. The grey numbers and dashed lines indicate the theoretical absolute minimum daily ration derived from the von Bertalanffy equation for growth. The bottom two panels show the model estimated proportions of hake in the diet of hake predators, along with the observed data. Note that the observed data have been weighted by stratum density and aggregated over the years 1999-2013 (Case B of MARAM/IWS/DEC15/Hake/BG1).

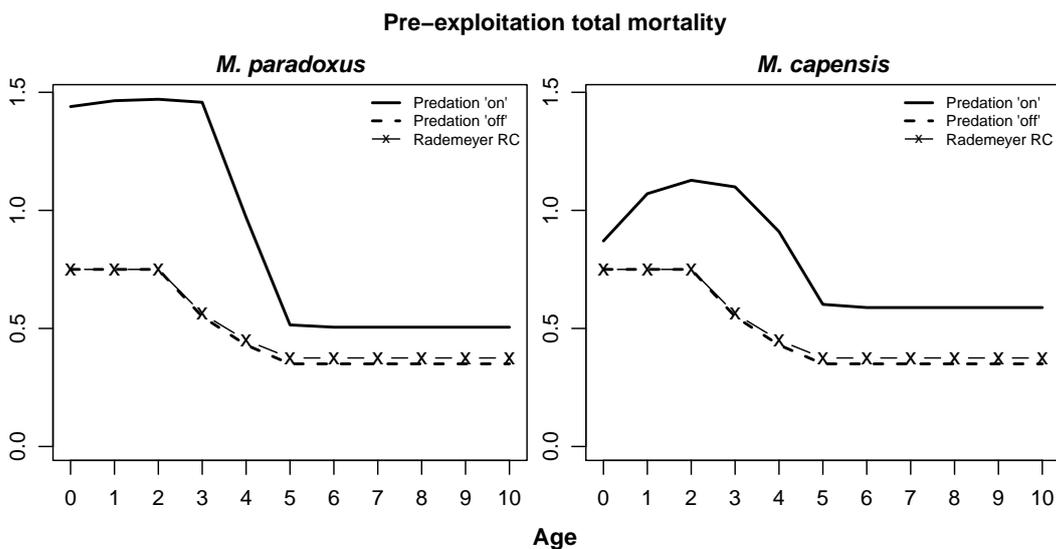


Figure 4: This figure shows the pre-exploitation total natural mortality values for the predation and cannibalism model (solid black line), the predation and cannibalism model with predation 'off' (dashed line) and for the Rademeyer and Butterworth (2014) reference case model (crosses).

Appendix A Evaluating the preference function

The preference that a predator of species s_p and age a_p exhibits for a prey fish of species s and age a is modelled by the continuous gamma function of Equation 4.13, repeated here:

$$\gamma_{sa}^{s_p a_p} = \left(G_{sa}^{s_p a_p} / \tilde{G}^{s_p} \right)^{\alpha^{s_p}-1} \exp \left[- \left(G_{sa}^{s_p a_p} - \tilde{G}^{s_p} \right) / \beta^{s_p} \right] \quad (\text{A.1})$$

The preference $\gamma_{sa}^{s_p a_p}$ is thus evaluated at each discrete age $a, a_p = 0, 1, \dots, a_m$. This can, however, lead to some irregular behaviour during the minimisation process. If, for example, α^{s_p} is sufficiently large (resulting in a narrow gamma distribution), it is possible that for a given predator age, virtually the entire gamma distribution will lie between two discrete prey age groups, resulting in zero preference exhibited for hake by that predator age group. This is illustrated in Figure A.1. Here, for example, in the second column ($\alpha^{s_p} = 100$) and for predator age 2, the narrow gamma distribution lies almost entirely between prey age 0 and age 1. Thus simply evaluating Equation A.1 at age 0 and 1 will result in almost zero preference shown by predators of age 2 for hake prey.

One way of dealing with this is to evaluate Equation A.1 prey ages $a; a + \frac{1}{12}; a + \frac{2}{12}; \dots; a + \frac{11}{12}$. The value of the preference function is then taken to be the average of the function evaluated at these 12 increments. This approach has been taken for the results presented in this document. Note that the predator age $a_p + \frac{1}{2}$ is used to evaluate $\gamma_{sa}^{s_p a_p}$.

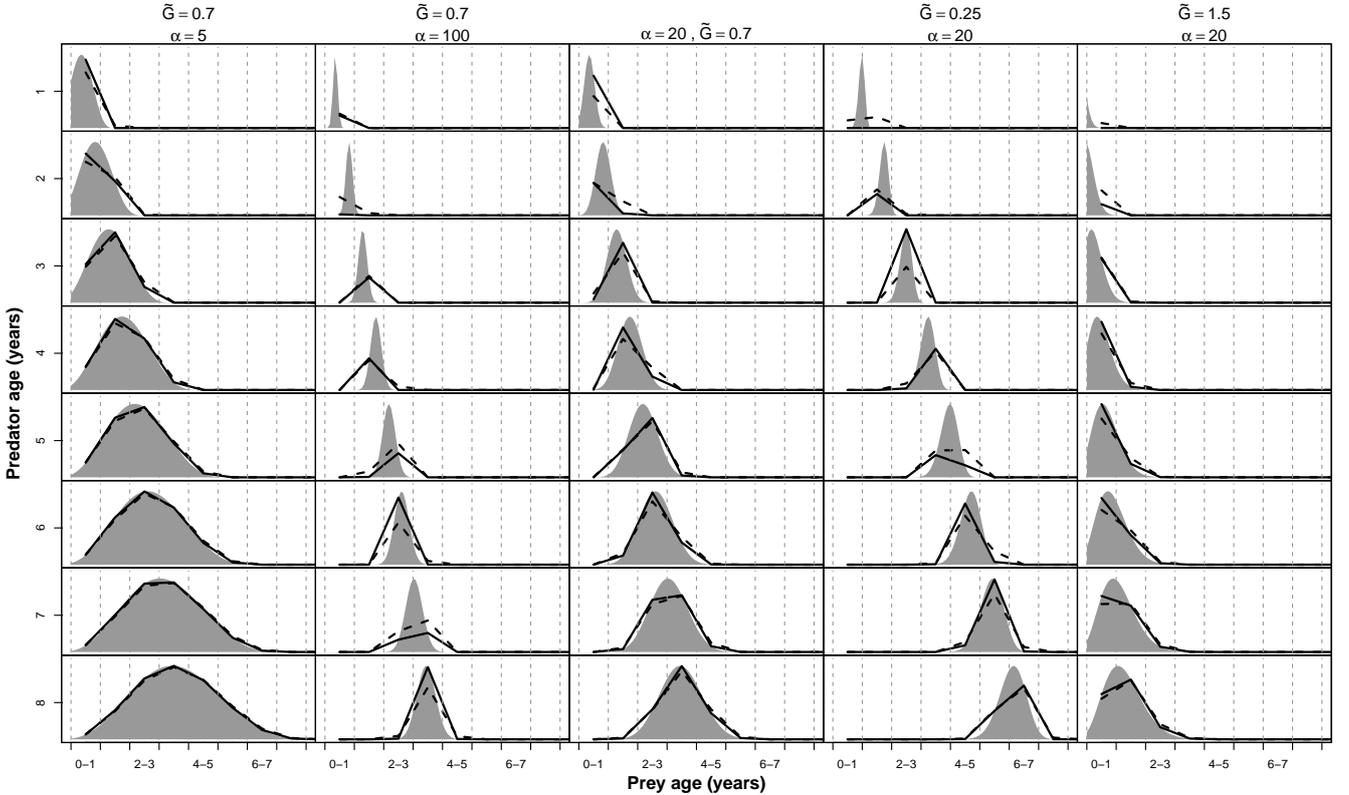


Figure A.1: The grey shaded areas indicate the underlying gamma distribution from Equation A.1 for different values of α^{s_p} and \tilde{G}^{s_p} . The solid black lines show the values that would be input into the model if $\gamma_{sa}^{s_p a_p}$ were simply taken to be the value of the gamma distribution at the discrete predator and prey ages a_p and a . The dashed lines shows the values of $\gamma_{sa}^{s_p a_p}$ that arise when the preference function is averaged over 12 increments for each prey age group.

Appendix B Some figures from MARAM/IWS/DEC14/Hake/P8rev

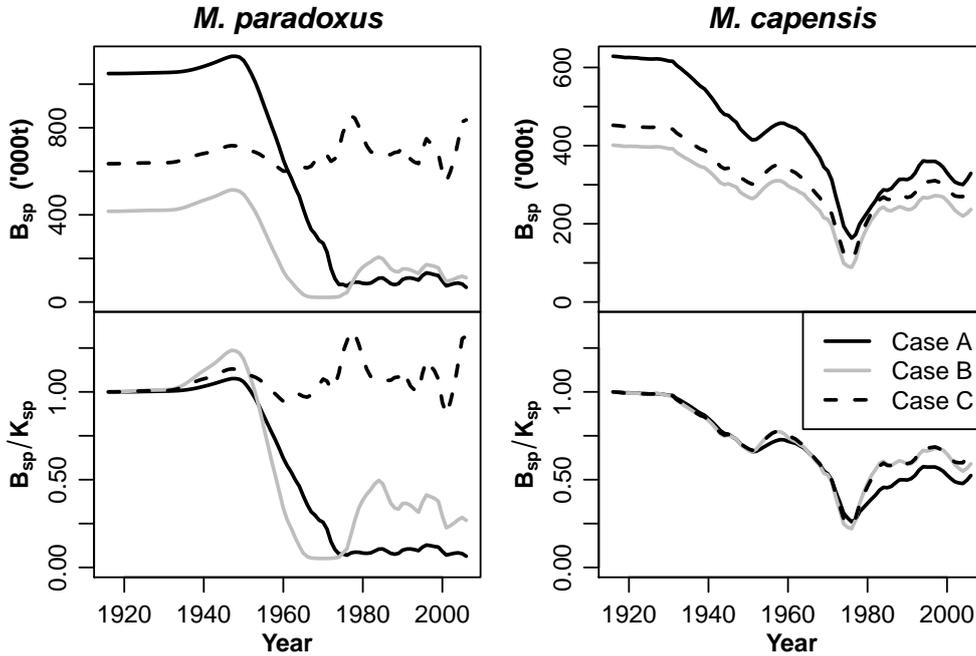


Figure B.1: Model-estimated spawning biomass for the two species, shown both in absolute terms and as a proportion of the unexploited equilibrium value. The solid black line is used for Case A (no up-weighting of diet data); the grey solid line is used for Case B (up-weighting of the daily ration data only); the black dashed line is used for Case C (up-weighting of both daily ration and proportion of hake in diet data).

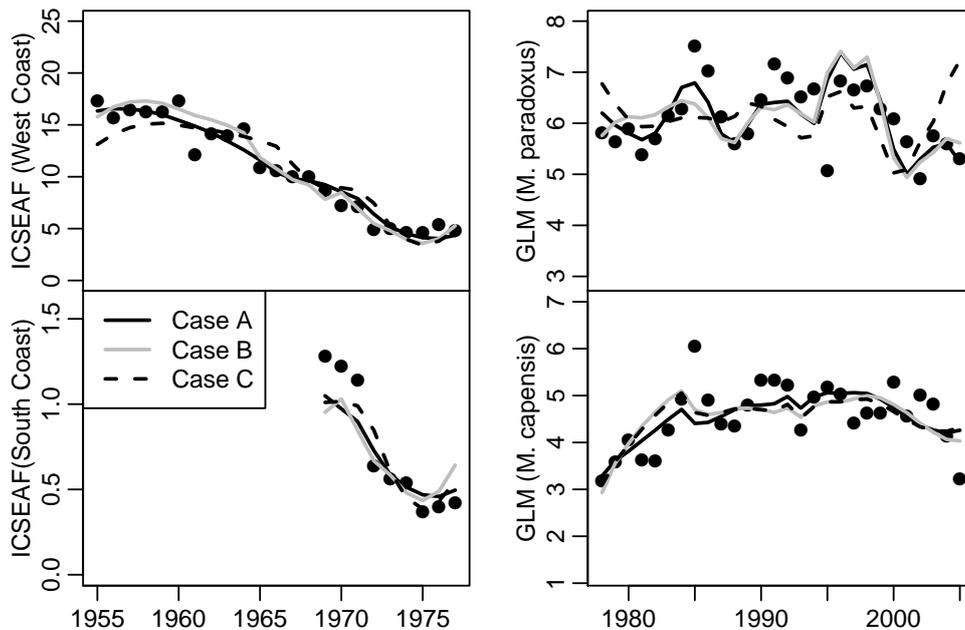


Figure B.2: Fits to the four CPUE abundance indices. The historical ICSEAF CPUE data apply to both species combined, while the GLM-standardised CPUE data are species-disaggregated.

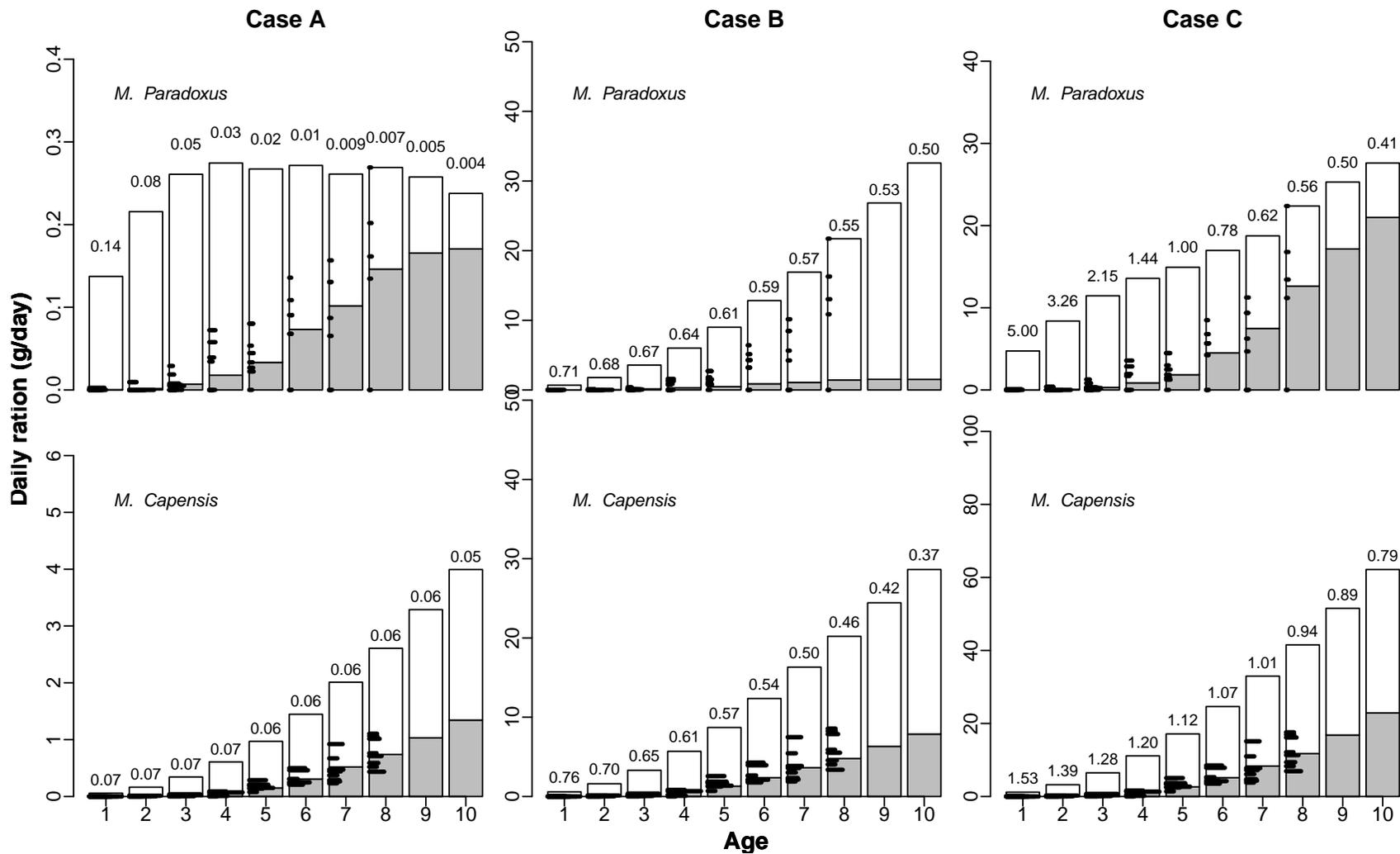


Figure B.3: Plot showing model-estimated total daily ration, as well as proportion of hake in diet – the grey component of each bar is the component of the diet comprising hake. The black horizontal lines mark the expected hake components in the diet given the yearly observations (cross-reference Figure ??). The length of the lines is indicative of the number of samples available in a particular year to compute an average proportion of hake in diet. The numbers above each bar give the daily ration as a percentage of predator body weight.

