Modelling cannibalism and inter-species predation for Cape hake *Merluccius capensis* and *M. paradoxus*: an update to MARAM IWS/DEC13/Ecofish/P10.

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Summary

An update is given to the hake predation model presented in MARAM IWS/DEC13/Ecofish/P10. Several modifications have been made to the earlier model, following recommendations by the panel at IWS DEC13 and interim model development. The current model, while still troubled with some conflicts, shows promise as a reasonable base case model that takes predation and cannibalism into account. Results are given for three cases that give increasing weight to various diet data likelihood components. It was found that if the model fits well to the trend data and proportion of hake in diet, the fit to daily ration is poor. On the other hand, if the model fits well to the daily ration and proportion of hake in diet data, the consequential loss is a worse fit to the trend data. This document presents some of the diet data that are available, the methodology for the current model, and a selection of results for the three cases, as well as a list of suggested discussion points.

1 Introduction

The model presented in this document is an update to the one presented in MARAM IWS/DEC13/Ecofish/P10. The model has been modified substantially following recommendations made by the panel at the International Stock Assessment Workshop in December 2013, and also as a result of model exploration and development undertaken since then. Table 1 summarizes the panel recommendations made in 2011 and 2013.

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 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.

Some of the problems with the model presented in MARAM IWS/DEC13/Ecofish/P10 included 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 at IWS DEC 2013 as well as interim modifications to the model have helped to resolve these issues. While there are still some conflicts that need to be addressed (for example the model battles to all of the fit proportion of hake in diet, daily ration and trend data simultaneously), the methodology and preliminary results presented here show promise for a reasonable base case model that takes hake predation and cannibalism into account.

Table 1: Recommendations made by the panel of the International Stock Assessment workshops in 2011 and 2013

Recommendation	**Date**	**Status**
Start with South Africa only, and perhaps incorporate Namibian data later if possible.	IWS DEC 2011	The model considers South Africa only.
Exclude South Coast initially, but implement coastal segregation later if possible since feeding will likely differ on the two coasts.	IWS DEC 2011	The current model has no coastal segregation.
No depth segregation.	IWS DEC 2011	The model does not have formal depth segregation, although it does try to take depth structure into account to some degree (see Appendix A).
Ignore sex structure initially, and only later extend model to something similar to the current hake assessment model.	IWS DEC 2011	The model is sex-aggregated.
Do not include other predators (seals) initially, but if there is an increase/decrease in seal population try take this into account in the mortality rates.	IWS DEC 2011	The model does not include predators other than hake.
Do not fit to catch-at-length (CAL) and age-length-key (ALK) data initially	IWS DEC 2011	The model does not fit to CAL or ALK data.
A Holling Type II functional form should be implemented initially, but other forms (as in Kinzey and Punt 2009) could be explored, including Holling Type III or Foraging Arena.	IWS DEC 2011	The model uses a Holling Type II functional form.

Scale hake prey-by-species information upwards to account for unidentified hake prey.	IWS DEC 2013	This has not been done yet, but will be done soon along with some general data checking and verification.
Implications of whether recruitment is taken to occur before or after predation should be explored.	IWS DEC 2013	This has not been explored yet.
Daily ration should not be prespecified but rather included as a likelihood component.	IWS DEC 2013	This has been implemented, and daily ration is no longer a fixed quantity in the model.
Difference in feeding relationship between West and South Coast should be investigated.	IWS DEC 2013	This has not yet been undertaken.
The feeding functional response should be parameterised to simplify the equilibrium setup.	IWS DEC 2013	This has been implemented.
Include an "other food" component as in Kinzey and Punt (2009).	IWS DEC 2013	This has been implemented.
Use the "Hybrid" method with a Baranov catch formulation for catches.	IWS DEC 2013	This has been implemented.

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 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. Note that the original data are given in terms of predator and prey lengths and have been converted to ages using the von Bertalanffy growth curve parameters given in Rademeyer *et al.* (2008).

2.1 Daily ration

The model presented in MARAM IWS/DEC13/Ecofish/P10 utilised estimates of daily ration from Punt and Leslie (1995), since no direct experiments have been conducted for hake to determine gastric evacuation rates. There is however considerable uncertainty around these estimates of daily ration, and 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. Table 2 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 age in the stomachs of predators by species and age. The data have been combined for coasts and over all the years and are given in Table 3 and Table 4.

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 $\tilde{\tilde{N}}_{s,\tilde{a},y,m}$ 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

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

where the a suffix in the total 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

$$Z_{saym} = M_{sa}^{basal} + P_{saym} + \sum_f S_{saf} F_{symf} \tag{3.2}$$

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} the mortality due to predation, and $\sum_f S_{saf} F_{symf}$ the fishing mortality.

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

The number of hake age a years is then given by

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

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

$$B^{sp}_{sym} = \sum_{\tilde{a}=12a_{mat}}^{12a_{mat}+11} \tilde{\tilde{N}}_{s\tilde{a}ym} w_{s\tilde{a}} \tag{3.4}$$

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. $N^{s_pa_p}_{ym}$).

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 $V^{s_pa_p}_{saym}$ 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

$$P_{saym} = \sum_{s_p,a_p} V^{s_pa_p}_{saym} \tag{4.1}$$

where

$$V^{s_pa_p}_{saym} = N^{s_pa_p}_{ym} \gamma^{s_pa_p}_{sa} A^{s_pa_p}_{sa} \frac{\nu^{s_p}_s \theta^{s_pa_p}}{1 + \sum_{s,a} \tilde{\nu}^{s_p}_s N_{saym} \gamma^{s_pa_p}_{sa} A^{s_pa_p}_{sa} + \tilde{\nu}^{s_p}_{other} O^{s_pa_p}_{other}} \tag{4.2}$$

Here

- $N^{s_pa_p}_{ym}$ 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,
- $\gamma^{s_pa_p}_{sa}$ 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,
- $A^{s_pa_p}_{sa}$ is an availability matrix that models the geographic availability of prey of species s and age a to predators of species s_p and age a_p based on depth distributions (Appendix A),
- $\theta^{s_pa_p}$ is a function allowing for additional flexibility in the extent to which predation rates change with predator age, and
- $O^{s_pa_p}_{other}$ is the population size of other (non-hake) prey available to hake predators of species s_p and age a_p, assumed to be time-invariant.

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

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

$$E^{s_pa_p}_{saym} = \frac{V^{s_pa_p}_{saym}}{Z_{saym}} N_{saym} \left(1 - e^{-Z_{saym}}\right) \tag{4.3}$$

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

$$Q^{s_pa_p}_{sym} = \frac{V^{s_pa_p}_{saym}}{Z_{saym}} N_{saym} w_{sa} \left(1 - e^{-Z_{saym}}\right) \tag{4.4}$$

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. Note that the inclusion of an other prey component, as well as the inclusion of the $\tilde{\nu}^{s_p}_{other}O^{s_p a_p}_{other}$ term in the denominator of Equation 4.2, are two significant changes to the earlier model.

Let $O^{s_p a_p}_{other}$ be 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. Further, let the total mortality rate for other prey fish be given by

$$Z^{s_p a_p}_{other,ym} = M^{basal}_{other} + P_{other,ym} \tag{4.5}$$

where

M^{basal}_{other}	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

$$P_{saym} = \sum_{s_p,a_p} V^{s_p a_p}_{other,ym} \tag{4.6}$$

$V^{s_p a_p}_{other,ym}$ 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

$$V^{s_p a_p}_{other,ym} = N^{s_p a_p}_{ym} \frac{\nu^{s_p}_{other}\theta^{s_p a_p}}{1 + \sum_{s,a} \tilde{\nu}^{s_p}_{s} N_{saym}\gamma^{s_p a_p}_{sa} A^{s_p a_p}_{sa} + \tilde{\nu}^{s_p}_{other}O^{s_p a_p}_{other}} \tag{4.7}$$

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

$$Q^{s_p a_p}_{other,ym} = \frac{V^{s_p a_p}_{other,ym}}{Z_{other,ym}} O^{s_p,a_p}_{other} w_{other}\left(1 - e^{-Z_{other,ym}}\right) \tag{4.8}$$

where w_{other} is a measure of the mass of the other prey fish.

4.3 Parameter simplification

In order to reduce the number of estimable parameters in an already complex model, each of ν and $\tilde{\nu}$ are taken to be species independent, i.e.

$$V^{s_p a_p}_{saym} = N^{s_p a_p}_{ym}\gamma^{s_p a_p}_{sa} A^{s_p a_p}_{sa} \frac{\nu\theta^{s_p a_p}}{1 + \sum_{s,a} \tilde{\nu} N_{saym}\gamma^{s_p a_p}_{sa} A^{s_p a_p}_{sa} + \tilde{\nu}O^{s_p a_p}_{other}} \tag{4.9}$$

and

$$V^{s_p a_p}_{other,ym} = N^{s_p a_p}_{ym} \frac{\nu\theta^{s_p a_p}}{1 + \sum_{s,a} \tilde{\nu} N_{saym}\gamma^{s_p a_p}_{sa} A^{s_p a_p}_{sa} + \tilde{\nu}O^{s_p a_p}_{other}} \tag{4.10}$$

Note that there is confounding between the $\nu^{s_p}_{other}$ and $O^{s_p a_p}_{other}w_{other}$ parameters, as well as the $\tilde{\nu}^{s_p}_{other}$ and $O^{s_p a_p}_{other}$ parameters in Equations 4.7 and 4.8 above. As such the ν and $\tilde{\nu}$ parameters for other prey can be equated to the ν and $\tilde{\nu}$ parameter for hake prey, since the $O^{s_p a_p}_{other}w_{other}$ and $O^{s_p a_p}_{other}$ terms give the necessary freedom in the estimation process.

4.4 Preference function

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

$$\gamma_{sa}^{s_p a_p} = \left(G_{sa}^{s_p a_p}/\tilde{G}^{s_p}\right)^{a^{s_p}-1} exp\left[-\left(G_{sa}^{s_p a_p} - \tilde{G}^{s_p}\right)/\beta^{s_p}\right] \tag{4.11}$$

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.

4.5 Theta function

$\theta^{s_p a_p}$ is the only function in the predation equations (apart from the preference and availability matrices) that allows the predation to vary directly with predator age. 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

$$\theta^{s_p a_p} = 1 + \omega^{s_p}\tilde{\omega}^{s_p}/\left(a_p + \tilde{\omega}^{s_p}\right) \tag{4.12}$$

When this form was implemented in the model presented here, it resulted in older fish not eating enough. A different function was thus explored, which mimics 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.

$$\theta^{s_p a_p} = w^{s_p a_p} \tag{4.13}$$

In other words $\theta^{s_p a_p}$ is simply the estimated mass (in kg) of a hake fish of species s_p and age a_p.

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 $Z_{say_0 1} = M_{sa}^{basal} + P_{say_0 1}$ are needed. However, in order to obtain $P_{s,a,y_0 1}$, the initial population structure is needed. Three main approaches to obtaining an initial population setup have been explored. Note that y_0 is the first year considered in the model, namely 1916, and 1 is the first month, January.

1. Assume $P_{say_0 1} = 0$ initially. Calculate population setup. Compute a new $P_{say_0 1}$ based on this population structure. Recalculate population structure based on new $P_{say_0 1}$ values. Repeat until an equilibrium as been reached.

   Problem: This approach was used in MARAM IWS/DEC13/Ecofish/P10 and can sometimes lead to non-damped oscillations for certain parameter combinations in the minimisation process.

2. Use an approach similar to that given in OLRAC (2008), where the equilibrium total mortality values are estimated in the same from as the Rademeyer model. These values can then be used to obtain an initial population structure, which in turn can be used to calculate the predation rates. The basal mortality rate, M_{sa}^{basal}, is then just the total mortality less the predation rate at equilibrium, and is

assumed to be time-invariant.

Problem: Once the initial population structure is obtained and used to calculate P_{say_01}, it can happen that the predation rates P_{say_01} *exceed* the estimated total mortality (i.e. M_{sa}^{basal} has to be negative if $Z_{say_01} = M_{sa}^{basal} + P_{say_01}$) and the population will in fact not be at equilibrium. A somewhat complicated method of scaling down the $\nu_s^{s_p}$ (from Equation 4.17) values if $Z_{say_01} < P_{say_01}$ so that $Z_{say_01} = P_{say_01}$ was implemented. However this seemed to have a similar effect to putting an upper bound on $\nu_s^{s_p}$. As $\nu_s^{s_p}$ was increased in the estimation process to reach the target proportion of hake in the diet, the model would scale $\nu_s^{s_p}$ down to keep it within the bounds of the estimated Z_{say_01} values.

3. The third approach is the one currently being used. It 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 $P_{s,a_m,y_01} = 0$, where $a_m = 10$ is the maximum age considered in the model. Thus the total mortality rate is $Z_{s,a_m,y_01} = M_{sa_m}^{basal}$, 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: $N_{s,a_m-1,y_01} = N_{s,a_m,y_01}e^{Z_{s,a_m,y_01}}$. 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_01} can be calculated from N_{s,a_m,y_01}, allowing $N_{s,a_m-2,y_01} = N_{s,a_m-1,y_01}e^{Z_{s,a_m-1,y_01}}$ to be determined and so forth. By re-parameterising the predation equations (see Equation 4.17), one can set $N_{s,a_m,y_01} = 1$ initially, and once N_{s,a,y_01} has been obtained for all a, the numbers can be scaled so that the spawning biomass equals the model-estimated parameter value.

   Problem: If P_{say_01} gets too big (which can happen during the minimisation process), then $e^{Z_say_01}$ can "explode". An upper bound of 0.5 has thus been enforced on the P_{say_01} values.

In order to implement this third approach, adjustments need to be made to Equations (4.9) and (4.10), so that the N_{say_0m} term is effectively removed from the denominator at unexploited equilibrium. Define

$$\tilde{N}_{ym}^{s_pa_p} = \frac{N_{ym}^{s_pa_p}}{N_{y_01}^{s_pa_{p,max}}} \tag{4.14}$$

$$\Phi_{hake,ym}^{s_pa_p} = \frac{\sum_{s,a} N_{saym}\gamma_{sa}^{s_pa_p}A_{sa}^{s_pa_p}}{\sum_{s,a} N_{say_01}\gamma_{sa}^{s_pa_p}A_{sa}^{s_pa_p}} \tag{4.15}$$

and

$$\Phi_{other,ym}^{s_pa_p} = O_{other}^{s_pa_p}/O_{other}^{s_pa_p} = 1 \tag{4.16}$$

Equation 4.9 and 4.10 then become respectively

$$V_{saym}^{s_pa_p} = \tilde{N}_{ym}^{s_pa_p}\gamma_{sa}^{s_pa_p}A_{sa}^{s_pa_p}\frac{\eta\theta^{s_pa_p}}{1+\tilde{\eta}_{hake}^{s_p}\Phi_{hake,ym}^{s_pa_p}+\tilde{\eta}_{other}^{s_p}\Phi_{other,ym}^{s_pa_p}} \tag{4.17}$$

$$V_{other,ym}^{s_pa_p} = \tilde{N}_{ym}^{s_pa_p}\frac{\eta\theta^{s_pa_p}}{1+\tilde{\eta}_{hake}^{s_p}\Phi_{hake,ym}^{s_pa_p}+\tilde{\eta}_{other}^{s_p}\Phi_{other,ym}^{s_pa_p}} \tag{4.18}$$

Strictly speaking, $\tilde{\eta}_{hake}^{s_p}$ and $\tilde{\eta}_{other}^{s_p}$ are functions of a_p ($\tilde{\eta}_{hake}^{s_pa_p} = \tilde{\nu}\sum_{s,a} N_{say_01}\gamma_{sa}^{s_pa_p}A_{sa}^{s_pa_p}$ and $\tilde{\eta}_{other}^{s_pa_p} = \tilde{\nu}O_{other}^{s_pa_p}$). For the results presented in this document, however, they are treated as age-independent, with the following penalty added to the likelihood to ensure that the effective $\tilde{\nu}$ parameter is as consistent as possible, i.e. $\tilde{\eta}^{s_p a_p}_{hake} / \sum_{s,a} N_{say_0 1} \gamma^{s_p a_p}_{sa} A^{s_p a_p}_{sa} \approx \tilde{\eta}^{s_p a_p}_{other} / O^{s_p a_p}_{other}$.

$$-lnL+ = weight * \sum_{s_p} \left(\tilde{\eta}_{hake} \sum_{s,a} N_{say_0 1} \gamma^{s_p a_p}_{sa} A^{s_p,5}_{sa} - \tilde{\eta}_{other} O^{s_p,5}_{other} \right)^2 \tag{4.19}$$

Further, η should be a function of s_p ($\eta^{s_p} = \nu N^{s_p,a_p,max}_{y_o,1}$), with the following addition to the likelihood

$$-lnL+ = weight * \left(\eta^{cap} / N^{cap,a_{p,max}}_{y_o,1} - \eta^{par} / N^{par,a_{p,max}}_{y_o,1} \right)^2$$

However for results presented in this document, this has been treated as species-independent, and a case where η^{s_p} is estimated instead of η will need to be tested.

At equilibrium, Equation 4.17 simplifies to

$$V^{s_p a_p}_{say_0 1} = \tilde{N}^{s_p a_p}_{y_0 1} \gamma^{s_p a_p}_{sa} A^{s_p a_p}_{sa} \frac{\eta \theta^{s_p a_p}}{1 + \tilde{\eta}^{s_p}_{hake} + \tilde{\eta}^{s_p}_{other}} \tag{4.20}$$

Further, $V^{s_p a_{p,max}}_{say_0 1} = \gamma^{s_p a_p}_{sa} A^{s_p a_p}_{sa} \frac{\eta \theta^{s_p a_p}}{1 + \tilde{\eta}^{s_p}_{hake} + \tilde{\eta}^{s_p}_{other}}$.

5 Likelihood components

5.1 Daily ration

Let $\rho^{s_p a_p}_{ym}$ be 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

$$\rho^{s_p a_p}_{ym} = \frac{\sum_s Q^{s_p a_p}_{sym} + Q^{s_p a_p}_{other,ym}}{N^{s_p a_p}_{ym} w^{s_p a_p}} * 12/365 * 100 \tag{5.1}$$

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

$$\bar{\rho}^{s_p a_p} = \frac{1}{12 n_{diet}} \sum_{y_{diet}} \sum_{m=1}^{12} \rho^{s_p a_p}_{ym} \tag{5.2}$$

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 1999-2006, although once the model has been updated to make use of the most recent data, it will run to 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 $\rho^{s_p a_p}$ is outside the range of [0.5%,5%].

$$-lnL+ = \sum_{s_p a_p} \begin{cases} (0.5 - \bar{\rho}^{s_p a_p})/0.5/(2 * 0.5^2) & \text{if } \bar{\rho}^{s_p a_p} < 0.5 \\ (\bar{\rho}^{s_p a_p} - 5)/5/(2 * 0.5^2) & \text{if } \bar{\rho}^{s_p a_p} > 5 \\ 0 & \text{otherwise} \end{cases} \tag{5.3}$$

5.2 Proportion of hake in diet

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

$n^{s_pa_p}_{y,obs}$ is the observed number of hake predators of species s_p and age a_p with non-empty stomachs in year y, and

$p^{s_pa_p}_{y,obs}$ is the observed number of hake predators of species s_p and age a_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:

$$Prop^{s_pa_p}_y = \left(\sum_m \sum_s Q^{s_pa_p}_{sym}\right) / \left(\sum_m \left(\sum_s Q^{s_pa_p}_{sym} + Q^{s_pa_p}_{other,ym}\right)\right) \tag{5.4}$$

The likelihood contribution is given by

$$-lnL+ = -\sum_y \left(p^{s_pa_p}_{y,obs} lnProp^{s_pa_p}_y + (n^{s_pa_p}_{y,obs} - p^{s_pa_p}_{y,obs}) ln(1 - Prop^{s_pa_p}_y)\right) \tag{5.5}$$

5.3 Preference data

Let $\zeta^{s_pa_p}_{s,a,obs}$ be the number stomach contents of hake predators of species s_p and age a_p observed to contain hake prey of species s and age a, summed over the years 1999-2013. Remembering that $p^{s_pa_p}_{y,obs}$ is the total observed number of hake predators of species s_p and age a_p with hake prey in the stomach content in year y, the model-predicted proportion of hake prey of species s and age a in the stomachs of predators of species s_p and age a_p, $Pref^{s_pa_p}_{s,a,mod}$, is calculated as follows

$$Pref^{s_pa_p}_{s,a,mod} = \frac{\sum_y p^{s_pa_p}_{y,obs} E^{s_pa_p}_{s,a,ym}}{\sum_y p^{s_pa_p}_{y,obs} \sum_a E^{s_pa_p}_{s,a,ym}} \tag{5.6}$$

The above approach from Kinzey and Punt (2009) 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

$$-lnL+ = -\sum_{s_p,a_p} \sum_{s,a} \left(\zeta^{s_pa_p}_{s,a,obs} ln(Pref^{s_pa_p}_{s,a,mod}) - \zeta^{s_pa_p}_{s,a,obs} ln(\zeta^{s_pa_p}_{s,a,obs} / \sum_a \zeta^{s_pa_p}_{s,a,obs})\right) \tag{5.7}$$

6 Results

Results are given for three cases:

Case A is a straight-forward minimisation using the methodology described in this document. For this approach, the model was able to fit to the trend data and proportion of hake in diet information, but battled to produce reasonable estimates of daily ration as a percentage of body weight.

Case B aims to improve the unrealistically low daily ration as a percentage of body weight values from Case A, by up-weighting the likelihood contribution for daily ration (Equation 5.3) by a factor of 10. This approach leads to a more reasonable fit to daily ration as a percentage of body weight, but a worse fit to trend data, and a poor fit to proportion of hake in diet.

Case C simultaneously up-weights the daily ration likelihood by a factor of 10 and the proportion of hake in diet likelihood component (Equation 5.5) by a factor of 5. For this case both the fit to the daily ration and the proportion of hake in diet are reasonable, but the consequential loss is a substantially worse fit to the trend data.

These three cases are intended to highlight some areas of conflict between the model, the diet data and the trend information, and to illustrate some scenarios where different data components are given more weight.

Table 5 gives the negative log-likelihood values for the various data sources that are input into the model, for all three cases. The differences in likelihood between Cases B and C compared to Case A are also given.

Figure 1 shows the model-predicted population trajectories, both in terms of spawning biomass in absolute terms, and spawning biomass relative to equilibrium values. Figure 2 shows the fits to the commercial CPUE data.

Figure 3 shows the model-estimated daily ration, daily ration as a percentage of body mass, as well as model-estimated and observed proportions of hake in diet for all three cases. Figure 4 shows the fit to proportion of hake in diet as a separate plot. Figure 5 gives the diet break-down of *M. capensis* predators in terms of *M. capensis* and *M. paradoxus* prey. This plot shows both the observed and model-predicted proportion of total hake consumed by *M. capensis* predators that consists of *M. capensis* prey. Figure 6 gives the breakdown of predator preference for both species, by predator and prey species, and by age.

7 Discussion

The model presented here is a substantial improvement on that in MARAM IWS/DEC13/Ecofish/P10, in terms of model stability, computing time taken for model runs and the model's ability to fit, if forced, various data components. There are however still some issues and conflicts that need to be addressed. During discussions at this International Stock Assessment Workshop, input on the following would be appreciated.

1. General thoughts on and suggestions for the current set of model equations.

2. Suggestions for resolving the apparent conflicts between the model, trend information, daily ration and proportion of hake in diet.

3. Figure 5 shows an interesting trend in that as the daily ration and proportion of hake in diet likelihood components are up-weighted, the *M. capensis* component in the diet of *M. capensis* predators gets smaller. This likely contributes to the somewhat bizarre population trajectory for *M. paradoxus* spawning biomass in Figure 1 - since *M. capensis* are eating more *M. paradoxus*, the *M. paradoxus* population will be much more affected by fluctuations in the *M. capensis* population. Insights on this observation would be valued.

4. Suggestions for the form of the $\theta^{s_p a_p}$ function (Equation 4.13), a function which relates predator consumption rate to predator age.

5. Given the panel recommendations in 2011 and 2013 (Table 1) and limited time available, what further model developments should be prioritised?

Note that further variations on the model are currently being explored, and results will be presented as an addendum (time permitting) if they provide useful further insights. These variations include (a) variations of the form of $\theta^{s_p a_p}$, in particular exploring powers of $w^{s_p a_p}$ (Equation 4.13) greater and smaller than one, (b) up-weighting the preference data alongside the daily ration and proportion of hake in diet, in particular the component relating to the proportion of *M. capensis* prey in the diet of *M. capensis* predators, and (c) testing different values for the fixed basal mortality rates.

8 References

Kinzey, D. and Punt, A.E. 2009. Multispecies and single-species models of fish population dynamics: comparing parameter estimates.

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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 hake *Merluccius capensis* and M. paradoxus. *South African Journal of Marine Science, 16:1, 37-55.*

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.

Table 2: Hake diet composition given in terms of numbers of non-empty stomachs and number of stomachs containing hake prey (DAFF data set, T. Fairweather, *pers. comm.*). Note that the model in its current form utitlizes these data only to the year 2006.

		Predator age															
		Total no. of non-empty stomachs								No. of stomachs containing hake prey							
	Year	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
M. capensis	1999	67	54	58	47	49	49	38	54	0	0	3	6	7	7	5	9
	2000	58	72	53	40	37	28	35	25	1	5	1	5	8	6	5	5
	2001	66	43	40	26	25	24	27	31	0	0	0	0	2	5	5	7
	2002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2003	109	102	90	62	72	58	48	44	0	3	3	9	14	20	22	12
	2004	85	118	118	127	90	69	51	36	1	9	13	15	14	22	12	14
	2005	67	82	63	62	61	46	26	27	3	1	1	2	18	8	3	11
	2006	124	96	95	67	70	76	41	24	0	1	2	1	15	13	9	7
	2007	82	73	47	56	67	51	27	26	0	4	2	2	13	8	9	11
	2008	108	72	58	77	73	62	38	14	1	1	0	4	3	13	14	3
	2009	7	16	20	17	25	22	8	2	1	1	5	6	12	4	3	1
	2010	12	105	115	88	142	88	60	23	1	11	17	14	35	13	22	8
	2011	15	72	91	73	81	57	55	38	1	4	6	4	25	13	18	11
	2012	3	23	14	16	29	14	24	13	0	3	4	4	14	8	16	5
	2013	9	14	12	9	13	23	13	13	1	7	1	2	7	4	4	4

		Predator age															
		Total no. of non-empty stomachs								No. of stomachs containing hake prey							
	Year	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
M. paradoxus	1999	25	23	22	10	6	2	2	2	0	1	0	0	0	0	0	2
	2000	21	29	14	8	10	4	4	0	0	0	1	1	3	1	2	0
	2001	12	9	9	6	5	2	1	1	0	0	1	0	1	1	0	0
	2002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2003	42	51	45	14	12	6	6	4	0	0	1	2	2	2	0	3
	2004	55	59	46	19	10	6	5	1	1	0	0	5	3	2	3	0
	2005	31	39	34	10	8	5	3	2	0	0	1	0	1	0	1	1
	2006	61	93	54	18	12	4	4	0	0	0	1	0	1	1	1	0
	2007	49	23	18	19	10	5	2	5	0	1	0	4	1	2	1	3
	2008	41	21	21	8	3	6	3	1	0	0	0	0	1	4	3	1
	2009	30	15	12	13	4	5	2	0	0	0	1	0	1	2	2	0
	2010	5	7	26	16	12	4	2	0	0	0	0	0	2	2	1	0
	2011	12	16	19	21	19	14	12	13	0	0	1	2	3	3	3	8
	2012	1	6	6	12	10	5	5	5	0	0	1	0	2	3	4	3
	2013	5	6	6	9	4	5	3	1	0	0	0	0	0	3	2	0

Table 3: Predator preference by predator and prey age. The breakdown of number of fish of each prey age found in the stomachs of predator fish is given for each predator age (DAFF data set, T. Fairweather, *pers. comm.*). Note that these data are coast-aggregated and have been aggregated over the years 1999-2013.

	M. cap. pred., *M. cap.* prey								*M. cap.* pred., *M. par.* prey								*M. par.* pred., *M. par.* prey							
	Prey age																							
Predator age	0	1	2	3	4	5	6	7	0	1	2	3	4	5	6	7	0	1	2	3	4	5	6	7
1	4								2								0							
2	22	0							10	1							1	0						
3	8	7	0						12	3	0						0	4	0					
4	9	5	0	0					6	33	3	0					2	4	0	0				
5	5	7	4	0	0				13	38	5	0	0				1	8	2	0	0			
6	3	2	1	3	0	0			1	37	17	2	0	0			1	3	4	0	0	0		
7	0	3	3	3	1	0	0		0	16	15	3	0	0	0		0	4	3	0	0	0	0	
8	0	0	0	4	7	0	0	0	0	4	3	3	4	0	0	0	0	3	5	1	0	0	0	0

Table 4: *M. capensis* predator preference for *M. capensis* vs *M. paradoxus* prey. Note that the numbers here are the sums of the rows of the *M. capensis* predator sections in Table 3 above.

M. capensis predator age	0	1	2	3	4	5	6	7	8
Number of *M. capensis* prey in samples	0	4	22	15	14	16	9	10	11
Number of *M. paradoxus* prey in samples	0	2	11	15	42	56	57	34	14

Table 5: Negative log likelihood values for the three cases. The changes in likelihood values between Case A and Case B, as well as between Case A and Case C have also been given. Changes in the likelihood of greater than 5 have been highlighted in grey.

	-lnL			ΔlnL	
Likelihood component	Case 1	Case 2	Case 3	Case 2	Case 3
Catch penalty	0.00	0.62	0.00	0.62	0.00
CPUE GLM capensis	-46.66	-46.25	-45.55	0.41	1.11
CPUE GLM paradoxus	-54.18	-50.00	-42.17	4.17	02.01
CPUE ICSEAF SC	-10.61	-7.39	-10.77	3.21	-0.16
CPUE ICSEAF WC	-37.30	-35.03	-27.35	2.27	9.95
CPUE survey capensis	-16.31	-17.71	-16.38	-1.41	-0.07
CPUE survey paradoxus	-13.29	-12.75	-6.93	0.54	6.35
CAA offshore	-40.85	-22.83	-33.75	18.02	7.11
CAA inshore	-22.70	-25.34	-24.39	-2.65	-1.70
CAA longline	-12.60	-13.34	-13.22	-0.74	-0.62
CAA survey capensis	62.83	68.76	65.13	5.93	2.30
CAA survey paradoxus	-27.38	-24.44	-17.76	2.95	9.62
New gear penalty	0.61	0.63	0.58	0.02	-0.03
Recruitment penalty	10.75	9.75	15.52	-1.00	4.77
Daily ration capensis	17.47	1.01	0.00	-16.46	-17.47
Daily ration paradoxus	18.59	0.00	0.35	-18.59	-18.25
Prey preference	375.44	385.17	405.86	9.73	30.43
Prop hake in diet capensis	1009.78	1014.00	999.30	4.22	-10.48
Prop hake in diet paradoxus	133.07	163.99	132.65	30.92	-0.42

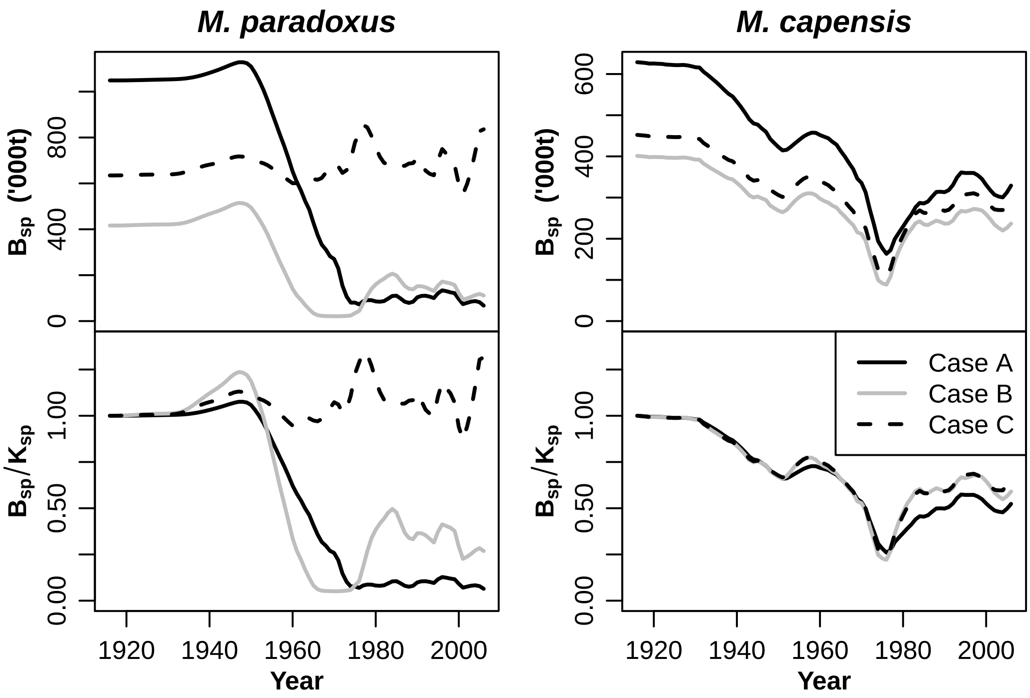

Figure 1: Model-estimated spawning biomass for the two species, shown both in absolute terms and as a proportion of the unexploited equilibrium value. The solid black line is used for Case A (no up-weighting of diet data); the grey solid line is used for Case B (up-weighting of the daily ration data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

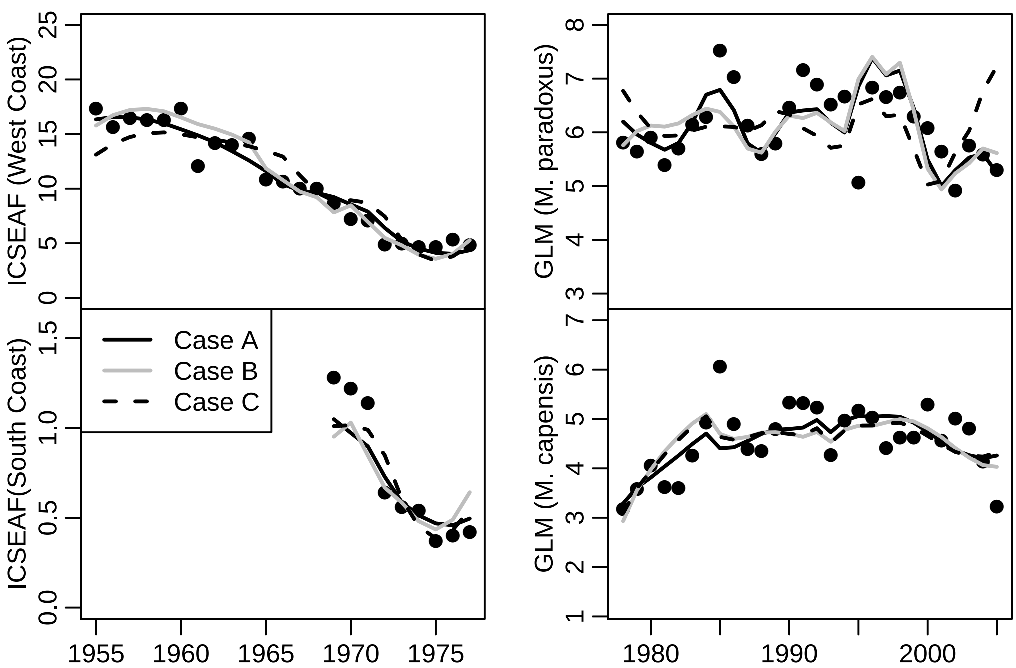

Figure 2: Fits to the four CPUE abundance indices. The historic ICSEAF CPUE data apply to both species combined, while the GLM-standardised CPUE data are species-disaggregated.

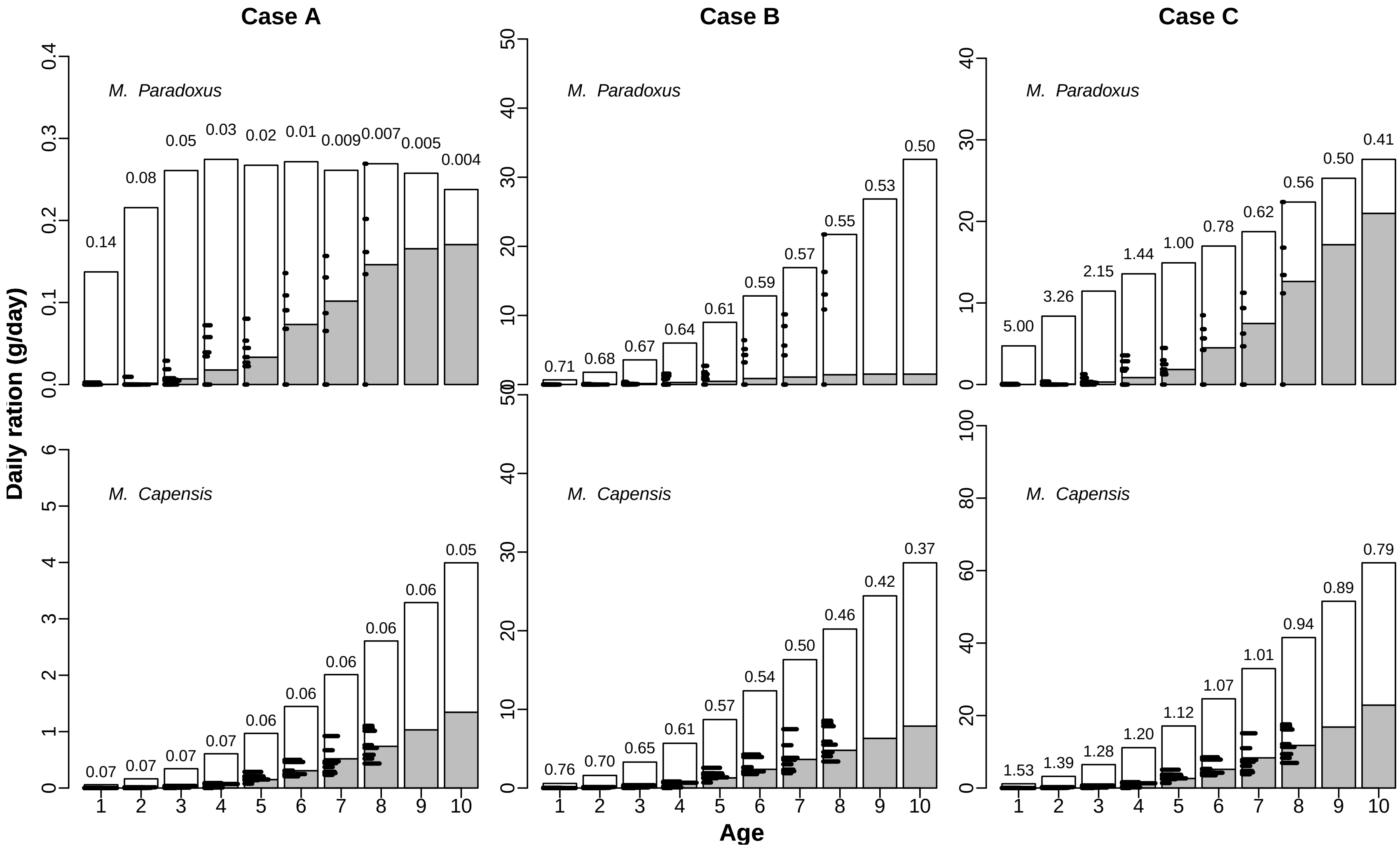

Figure 3: Plot showing model-estimated total daily ration, as well as proportion of hake in diet – the grey component of each bar is the component of the diet comprising hake. The black horizontal lines mark the expected hake components in the diet given the yearly observations (cross-reference Figure 4). 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.

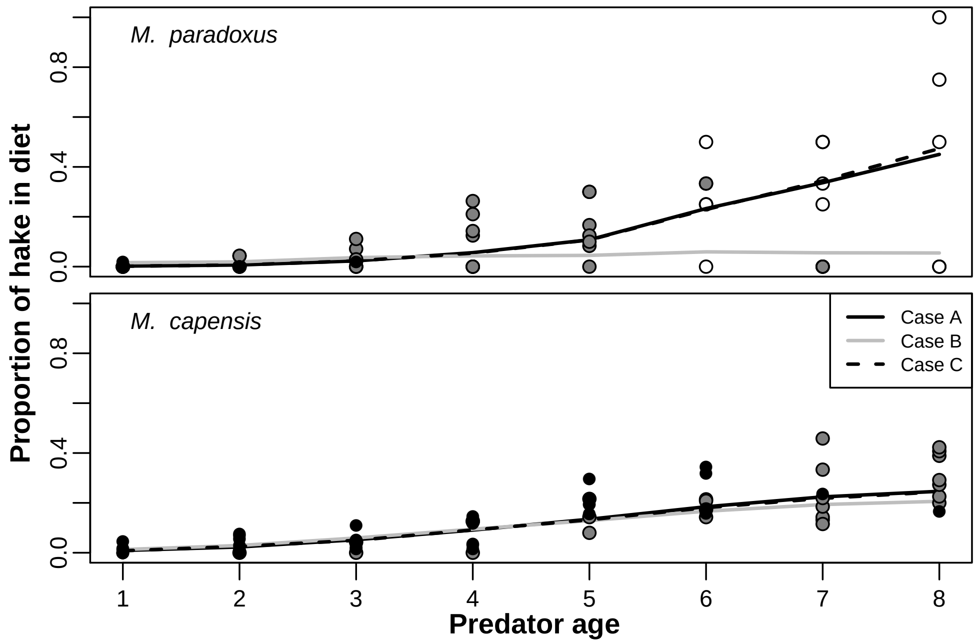

Figure 4: Proportion of hake in diet. The points show the observed average yearly proportion of predators that have hake prey in their stomach contents (inferred from Table 2). The shading of the points is indicative of the number of samples that gave rise to the averages: black-filled circles for more than 50 sample points in a particular year, grey-filled circles for less than or equal to 50 but more than 5, while the empty circles are used for less than or equal to 5 samples. The lines show the model-estimated proportions for the three cases, taken to be the average proportion of hake over the years 1999-2006 (which are the years in the model corresponding to the years in which diet data are available).

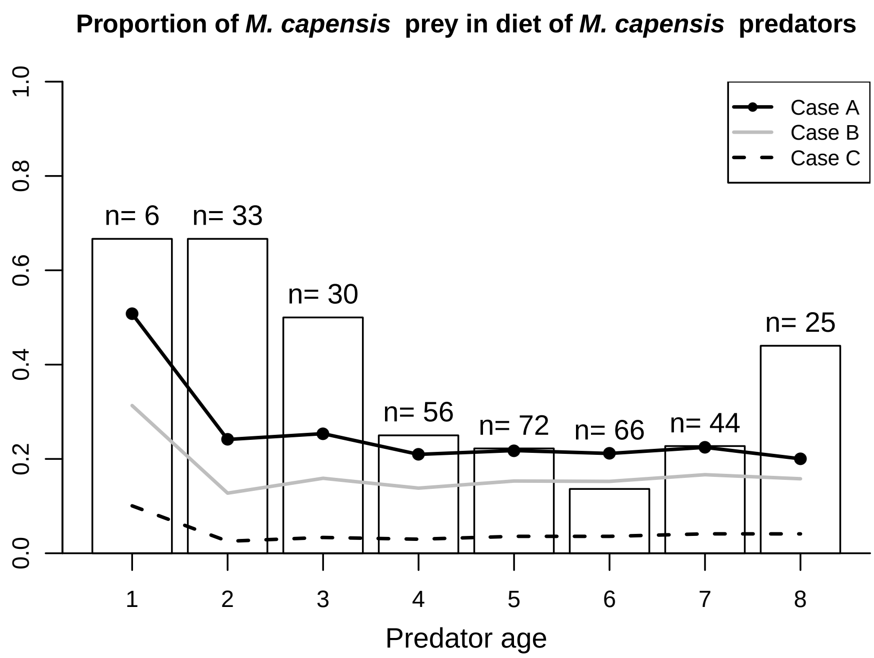

Figure 5: Proportion of total hake consumed by *M. capensis* predators that consists of *M. capensis* prey. The white bars show the observed values (from Table 4), while the solid lines show the model estimated values for the three cases.

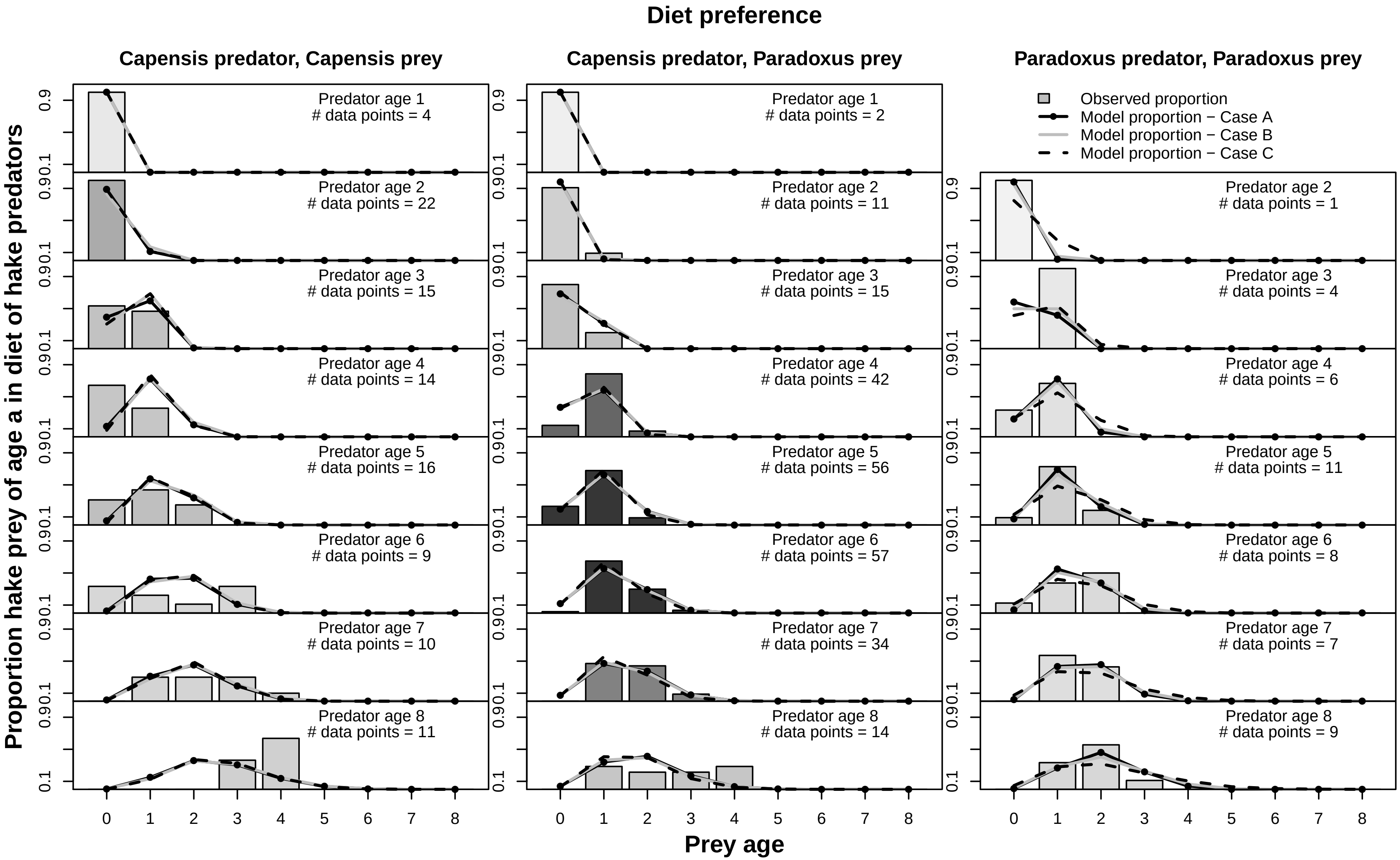

Figure 6: Predator preference given by predator and prey species and age.

A Appendix: Taking account of geographic segregation

The preference function from Equation 4.11 models the preference that a predator of age a_p will have for a prey of age a, and the parameters of the preference function are informed by stomach content data. One problematic area is that while, for example, a *M. capensis* predator of age 1 would happily eat a *M. paradoxus* fish of age 0, in reality their geographic distributions do not overlap 100%. This led to the introduction of an "availability" matrix, A, that tries to take this into account. The first step was to plot the depth distributions by age. These were obtained from the stomach content data, which gave the depth at which hake were caught. The distributions are shown in Figure A.1 to Figure A.3.

The proportion of overlap was then computed for each predator and prey age groups, i.e. the proportion of hake of age a that were caught at a depth at which a predator of age a_p has at some stage been caught. These proportions are shown by the shaded regions in Figure A.4. Normal curves were fit to each predator and prey age combination, and fits are shown by the solid black line in Figure A.4. The values from the fitted curves where then used to populate the availability matrix $A_{sa}^{s_p a_p}$, and are given in the tables below. Note that the normal curves were fit so that when predator and prey were of the same species and age, the proportion of overlap is one.

Table A.1: Proportion geographic overlap of *M. capensis* predators with *M. capensis* prey. The predator ages are given down the first column and the prey ages along the first row.

	0	1	2	3	4	5	6	7	8	9	10
1	0.97	1.00									
2	0.94	0.99	1.00								
3	0.87	0.94	0.99	1.00							
4	0.52	0.69	0.85	0.96	1.00						
5	0.45	0.60	0.75	0.88	0.97	1.00					
6	0.41	0.54	0.67	0.80	0.91	0.98	1.00				
7	0.42	0.53	0.64	0.75	0.85	0.93	0.98	1.00			
8	0.32	0.42	0.53	0.64	0.75	0.85	0.93	0.98	1.00		
9	0.24	0.32	0.42	0.53	0.64	0.75	0.85	0.93	0.98	1.00	
10	0.17	0.24	0.32	0.42	0.53	0.64	0.75	0.85	0.93	0.98	1.00

Table A.2: Proportion geographic overlap of *M. capensis* predators with *M. paradoxus* prey. The predator ages are given down the first column and the prey ages along the first row.

	0	1	2	3	4	5	6	7	8	9	10
1	0.76	0.55									
2	0.99	0.85	0.62								
3	0.99	0.96	0.80	0.56							
4	1.00	0.97	0.86	0.71	0.54						
5	0.99	0.93	0.85	0.74	0.63	0.51					
6	0.99	0.95	0.89	0.81	0.72	0.62	0.52				
7	0.95	0.91	0.84	0.77	0.68	0.60	0.51	0.43			
8	0.90	0.84	0.77	0.69	0.61	0.53	0.46	0.38	0.32		
9	0.90	0.84	0.77	0.69	0.61	0.53	0.46	0.38	0.32	0.26	
10	0.90	0.84	0.77	0.69	0.61	0.53	0.46	0.38	0.32	0.26	0.21

Table A.3: Proportion geographic overlap of *M. paradoxus* predators with *M. paradoxus* prey. The predator ages are given down the first column and the prey ages along the first row.

	0	1	2	3	4	5	6	7	8	9	10
1	0.97	1.00									
2	0.89	0.97	1.00								
3	0.83	0.92	0.98	1.00							
4	0.50	0.68	0.84	0.96	1.00						
5	0.30	0.46	0.65	0.83	0.95	1.00					
6	0.37	0.50	0.64	0.78	0.90	0.97	1.00				
7	0.25	0.36	0.49	0.63	0.77	0.89	0.97	1.00			
8	0.22	0.31	0.43	0.55	0.69	0.81	0.91	0.98	1.00		
9	0.15	0.22	0.31	0.43	0.55	0.69	0.81	0.91	0.98	1.00	
10	0.09	0.15	0.22	0.31	0.43	0.55	0.69	0.81	0.91	0.98	1.00

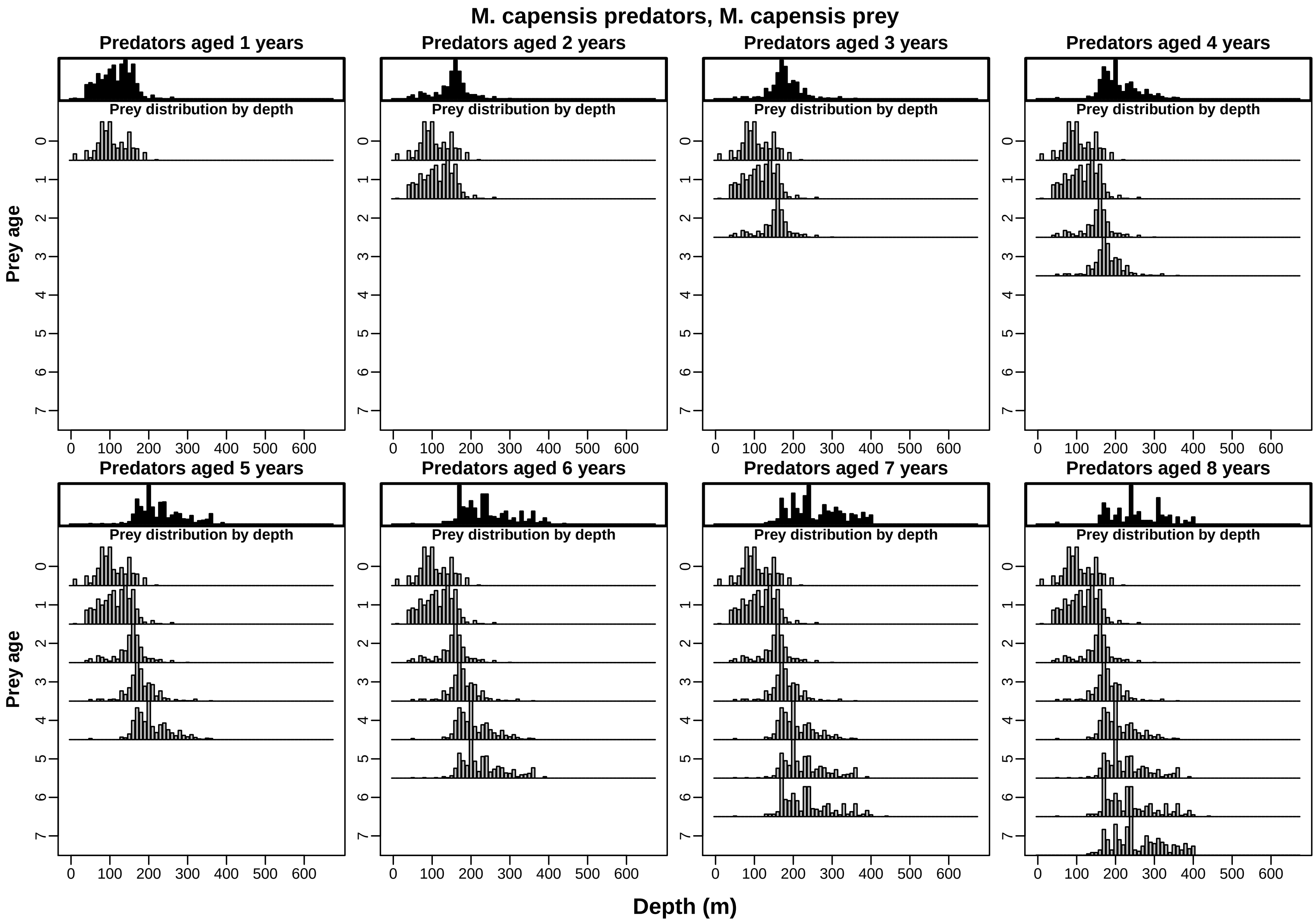

Figure A.1: Depth distribution for *M. capensis* predators by age, given alongside the depth distributions by age for *M. capensis* prey

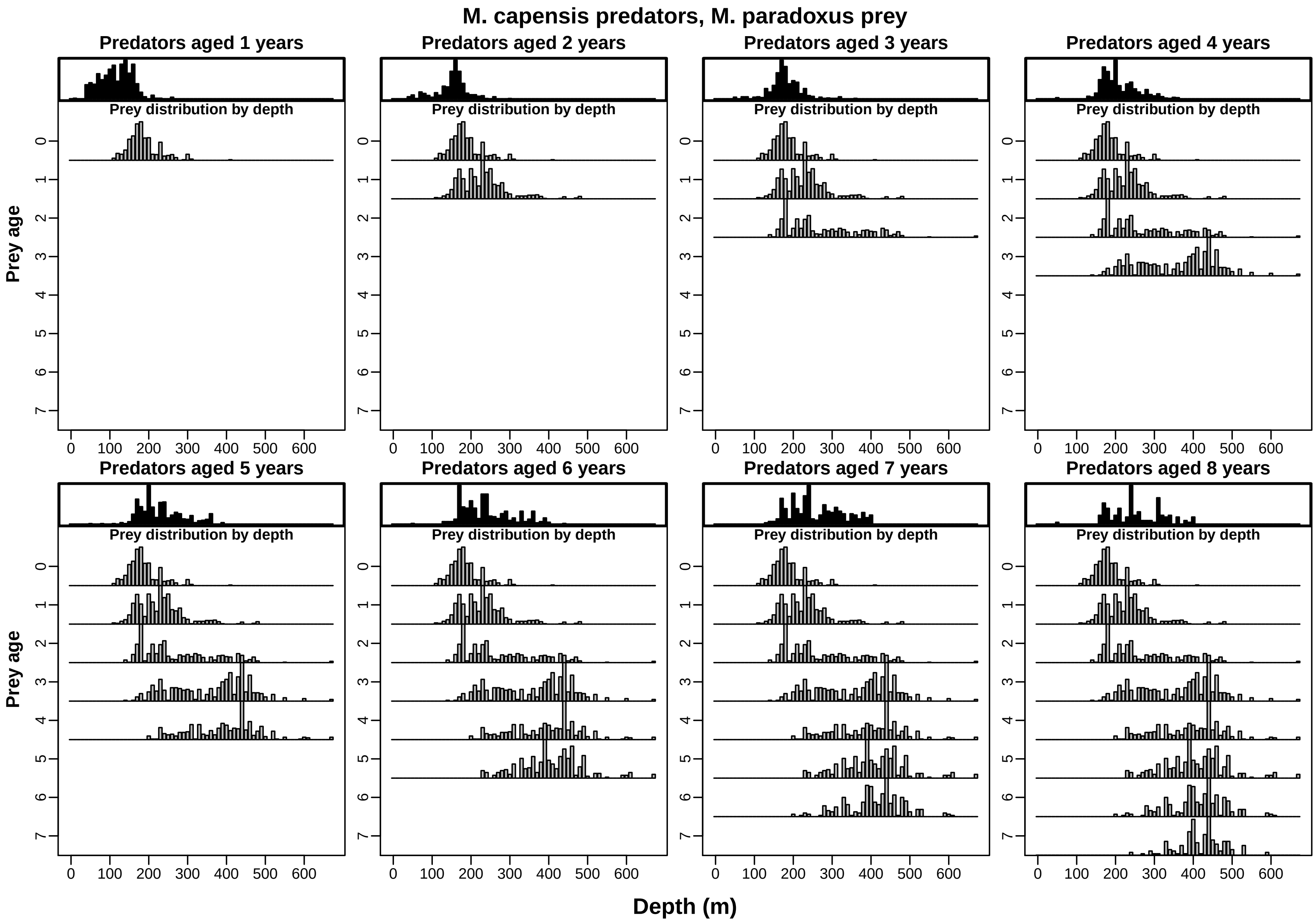

Figure A.2: Depth distribution for *M. capensis* predators by age, given alongside the depth distributions by age for *M. paradoxus* prey

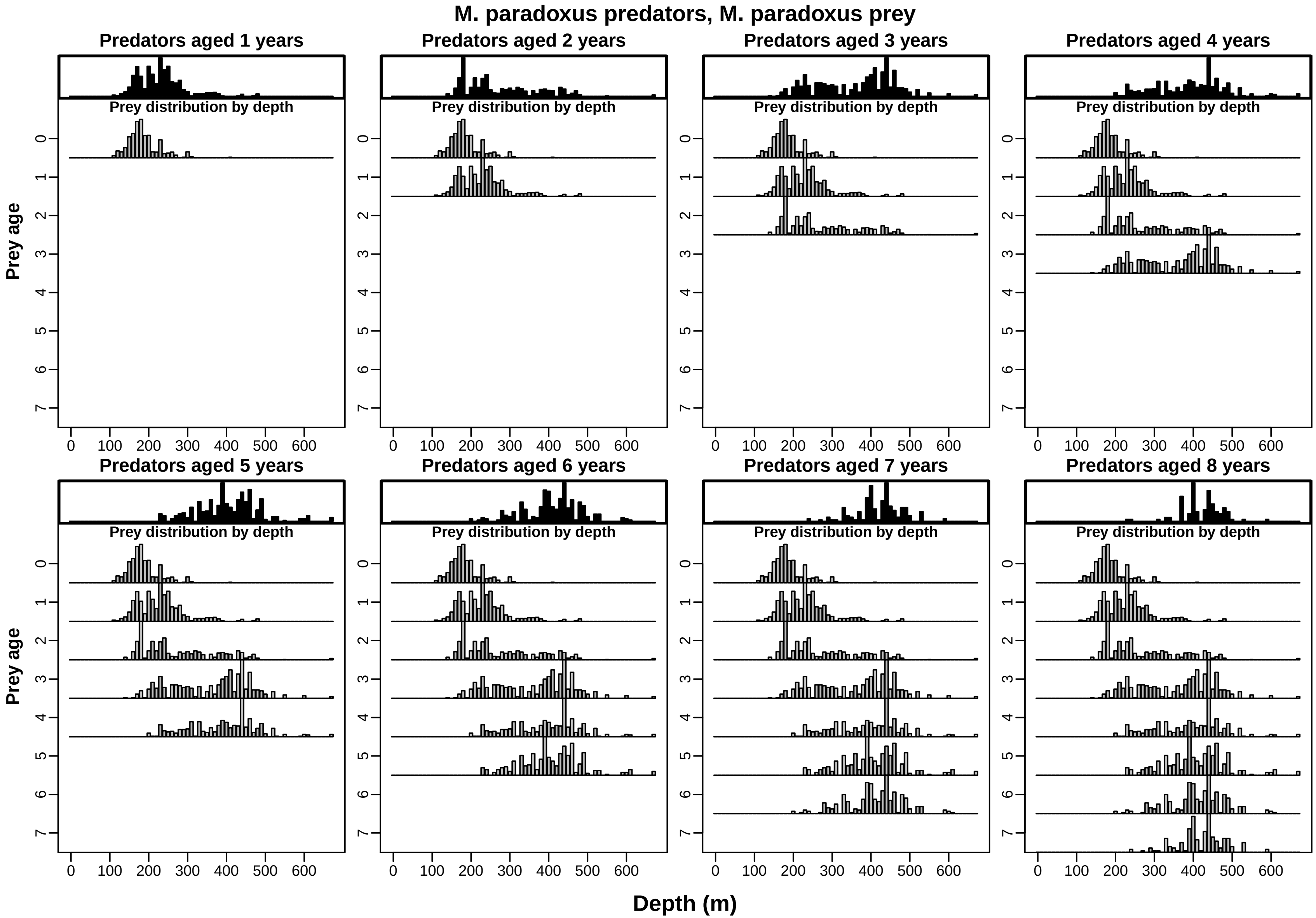

Figure A.3: Depth distribution for *M. paradoxus* predators by age, given alongside the depth distributions by age for *M. paradoxus* prey

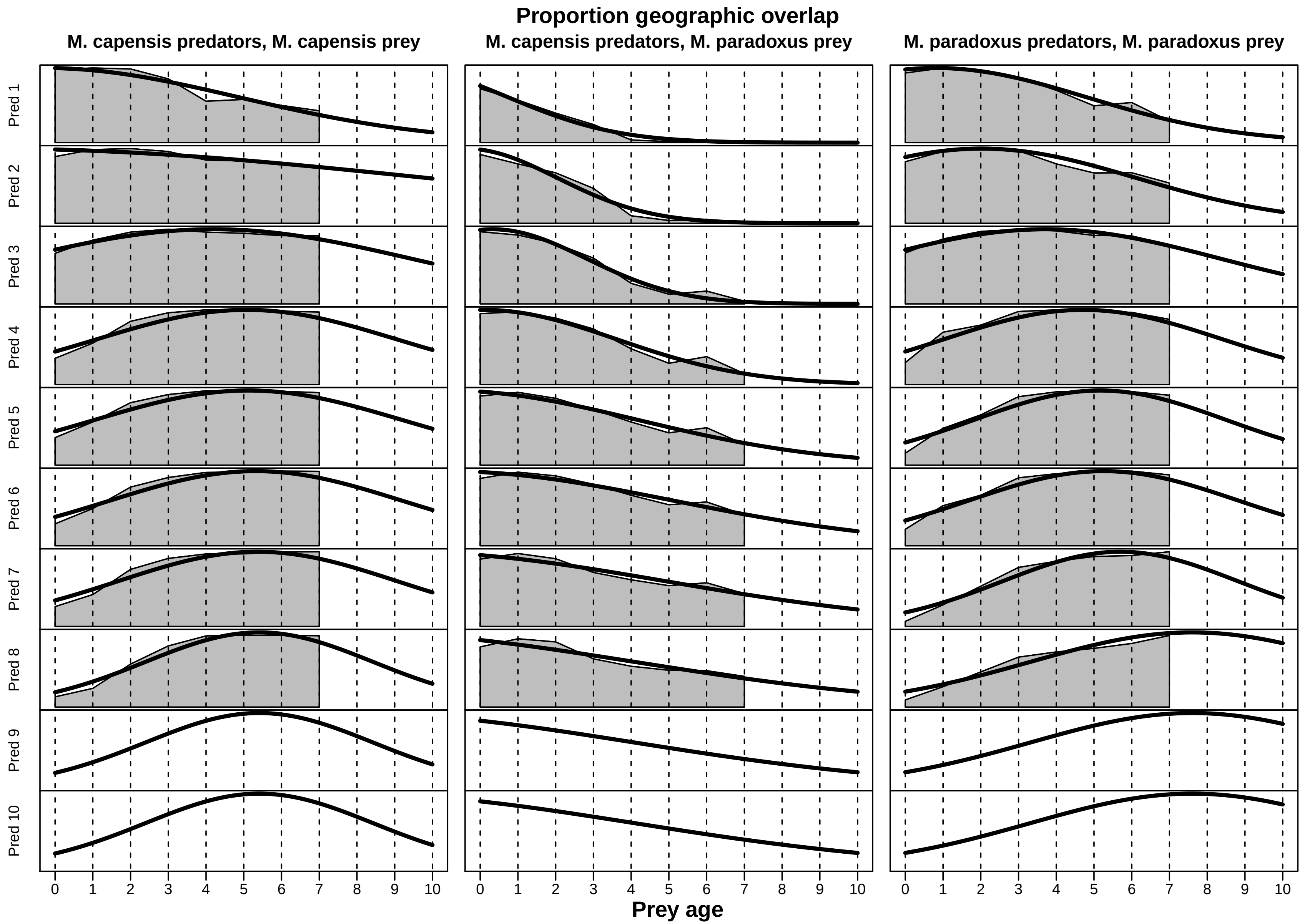

Figure A.4: Plots showing the proportion of geographic overlap found for predator and prey age groups. The grey shaded area indicates the observed proportions, while the solid black line shows the fit to a normal curve. Since no data are available for hake of ages greater than 8 years, the curves have been extrapolated for these ages. For prey ages greater than 8, the curve has simply been extended. For predator ages 9-10, the curve for predator age 8 has been duplicated.