# Hake cannibalism and inter-species predation model: A summary of a PhD thesis and the development of the model since IWS 2015

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This document reports on the progress of the Cape hake cannibalism and inter-species predation model (referred to henceforth as the hake predation model) between what was presented at the 2015 International Stock Assessment Workshop (IWS 2015) and what was submitted for a PhD thesis earlier this year (Ross-Gillespie 2016).

## 1    Key features of the model

The hake predation model uses as its base a modified version of the Rademeyer and Butterworth (2014) assessment model and adds a time-varying predation component to the natural mortality rates to account for hake-on-hake predation. Most of the modifications to the Rademeyer and Butterworth (2014) model were necessary in order to more easily incorporate the predation component. The details of the modifications can be viewed in the Introduction of Chapter 4 of Ross-Gillespie (2016), but a summary of differences is provided below:

| Rademeyer and Butterworth (2014) model | Predation "off" model |
|---|---|
| Sex-disaggregated | Sex-aggregated |
| Estimates growth curves by fitting to age-length keys | Does not fit to age length keys, and growth curves are fixed at the Rademeyer and Butterworth (2014) estimates |
| Modified Ricker stock-recruitment relationship | Beverton-Holt stock-recruitment relationship |
| Pope's approximation for the catch equation | Baranov formulation of the catch equation |
| Annual time-step (recruitment assumed to take place at the beginning of the year, and catches are assumed to be taken mid-year) | Monthly-time step (recruitment and catches are assumed to occur monthly throughout the year) |

The key features of the hake predation model are as follows.

1.1  The predator-prey interaction is modelled with a Holling Type II functional form.

1.2  The model considers hake as predators, hake as prey and a component labelled "other prey", accounting for non-hake prey in the diet of hake as predators. The model does not consider other predators of hake directly, but instead includes a fixed basal mortality rate to account for all other sources of mortality.

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1.3 The predation-related parameters in the model are estimated by fitting to the proportions of hake in the diet of hake predators derived from the DAFF 1999-2013 stomach content dataset, as well as to information on the predator-prey preference from this dataset.

1.4 Since estimates of daily rations have not been established for hake, the model is allowed to estimate these without much restriction. There is however, a lower bound of 0.1% of body mass enforced, as well as a penalty on the slope of log of the daily ration with the log of predator mass.

1.5 Estimates of the proportion of hake in the diet of hake predators, daily ration and predator-prey preference are time-varying model outputs.

1.6 The model uses a gamma function to model the preference exhibited by hake predators of a given age for hake prey of a given age.

1.7 The model incorporates a function that allows the extent to which hake prey on other hake to change with predator age.

1.8 The model incorporates a "depth-availability" vector that allows *M. capensis* preference to shift from *M. capensis* prey to *M. paradoxus* prey as the *M. capensis* predators grow larger and move into deeper waters.

1.9 A predator competition effect is mimicked by enforcing an upper bound on the predation mortality rates.

1.10 Calculations are implemented using a monthly time-step, rather than the annual one used in the standard assessment model, in order to account for the fact that the predation dynamics are likely to be much faster than the hake dynamics, so that the predation effect would likely be poorly approximated with a coarser time-step.

The equations for the predation components of the model are provided in Appendix A. The equations for the modified Rademeyer and Butterworth (2014) model on which the predation model is built can be viewed in Chapter 4 of Ross-Gillespie (2016).

## 2  Summary of recommendations from IWS 2015

Key recommendations from the 2015 International Stock Assessment Workshop, and responses to these recommendations, are listed below. Recommendations are shown in italics, with responses in normal font.

2.1 *The proportion of hake in the diet of hake predators should be based on estimated mass-at-ingestion, rather than on counts of prey items.* This was implemented, and the details are reported in Appendix 5.B of Ross-Gillespie (2016).

2.2 *The diet data should be developed based on predator age rather than predator length, since most hake for which stomach content data are analysed are ages. The use of such data in the predation model*

*would simplify the fitting process since the model is age-based.* This recommendation has been noted by the Fisheries Branch of the Department of Agriculture, Forestry and Fisheries (DAFF).

2.3 *The preference function should be normalised to sum to one across all hake prey species and ages.* This has been implemented.

2.4 *Allowance should be made for predation to differ between prey species and ages in the predation function.* An attempt has been made to address this with the depth availability vector (see point 3.3 in the next section for more details).

2.5 *The age plus-group should be extended from 10+ to 15+.* This change has been made.

2.6 *When conflict is experienced between the model fitting to the historical ICSEAF CPUE trend versus the diet data, priority should be given to the fit to the CPUE data since major reductions in catch rates are an important characteristic of southern African hake fisheries between the early- to mid-1960s and mid-1970s.* This priority has been taken into account in the model development process presented in Ross-Gillespie (2016).

2.7 *Likelihood components for the proportions of hake prey in the diets of hake predators of various lengths should be weighted appropriately if there is evidence of overdispersion.* Following the revised calculations for the proportion of hake in the diet of hake (Appendix 5.D of Ross-Gillespie 2016), the likelihood contributions for these proportions have become much more comparable with other likelihood components in the model, so that no adjustment was made. This should, however, be considered further in the future.

Table 5.A.1 of Appendix 5.A of the thesis provides a list of all the recommendations (with responses) for the hake predation model that have in the past been made by the IWS panel.

# 3 Summary of changes that have been made to the model since it was presented at IWS 2015

3.1 The model fits to revised estimates of the proportion of hake in the diet of hake predators. These proportions are based on estimates of mass-at-ingestion of the prey items to obtain a proportion by mass, rather than a proportion by number derived from counts of prey items as was done previously. The details of the methods used to estimate this mass-at-ingestion are given in Appendix 5.D of Ross-Gillespie (2016).

3.2 A lower bound of 0.1% and upper bound of 4% are enforced on daily ration as a percentage of body mass. This lower bound of 0.1% is based on a combination of (i) literature review, (ii) consideration of the von Bertalanffy growth curves as per the arguments of Essington *et al.* (2001), and (iii) consideration of the size-at-age data used to estimate the hake growth curve parameters in the Rademeyer and Butterworth (2014) model. Furthermore a penalty is added to force the slope of the log of the daily

ration against the log of the body mass to lie close to -1/3, a value also arising from consideration of the Essington *et al.* (2001) work. Appendix 5.E of Ross-Gillespie (2016) provides the details of the work underlying these assumptions.

3.3 The model now includes a depth-availability vector that allows the preference of *M. capensis* predators to shift from predominantly *M. capensis* prey to predominantly *M. paradoxus* prey as the *M. capensis* predators get larger (see equation 43 of Appendix A). This vector was introduced under the assumption that as *M. capensis* predators grow larger and move into deeper water, they will become more likely to encounter *M. paradoxus* prey of preferable size than *M. capensis* prey. Appendix 5.D of Ross-Gillespie (2016) provides some further justification for this assumption based on the depth distributions of the two species.

3.4 The $\theta$ function, which allows the rate at which hake prey on other hake to change with predator age, has been modified since IWS 2015. See the updated equation 23 of Appendix A.

3.5 The equation for the negative log-likelihood component for fitting to the proportion of hake in the diet of hake predators has been changed in order to incorporate the new proportions by length rather than the old counts by length; see equation 36 of Appendix A for details.

3.6 The model fits to preference data by age, rather than by length as was the case previously, as it was found that converting the model-predicted predator-prey preference counts (which are age-based) into length-based quantities added enormous variability. The length-based observed counts are converted to age-based counts externally to the model using the expected length-at-age values from the von Bertalanffy growth curves.

3.7 A predator competition term was introduced in order to prevent excessive predation when large predator cohorts moved through the model, thus damping the large predator-prey oscillations exhibited by the biomass trajectories and stabilising the estimation process. This competition term was implemented by enforcing an upper limit on the predation mortality. See Section A.4.4 of Appendix A for more details.

# 4 Base case development

A brief summary of the process followed in deciding the base case for the thesis is given here. In this process, a balance between the following factors was taken into account:

- The daily rations should not be too small, in particular those for *M. paradoxus*, which tended to become very low. Thus a lower bound on daily ration was introduced.

- The slope of the log of the daily ration with the log of predator mass should lie close to -1/3. A penalty was added to enforce this.

- The biomass trajectories should not exhibit unrealistic oscillations, which result from high predation mortality rate. To ensure this, the predator competition term was introduced to limit the predation mortality rate.

- The fit to the historical ICSEAF CPUE data should be adequate — many runs were rejected on this basis.

Several sensitivities were tested, but none provided a substantially better fit than the base case. Furthermore, there was not sufficient time when completing the thesis to test combinations of these sensitivities. In other words, assumptions made in the base case model (e.g. the value chosen for the competition term) would ideally need to be re-evaluated for each sensitivity run in order to fully evaluate the impact of that assumption to which sensitivity is being tested. The sensitivities tested were as follows.

1 Basal mortality: Age-independent basal mortality rates of 0.1 and 0.3 (instead of the 0.2 for the base case), as well as a basal mortality of 0.6 for zero year old hake decreasing linearly to 0.2 at age 2 were tested.

2 Stock recruitment: The Beverton-Holt relationship with the $h$ parameter estimated instead of fixed and the Rademeyer and Butterworth (2014) modified Ricker relationship were implemented.

3 Daily ration

  - Increase the lower limit on daily ration.

  - Force the daily ration of age 3 predators to be at 1.53% of body mass (a value taken from a combination of papers from the literature).

4 Reduce the proportion of hake that the model tries to fit (given the uncertainty in these estimates).

5 Force the *M. paradoxus* depletion level to various fixed levels.

# 5  Base case results and "switching"

The full set of results for the base case and the sensitivities can be viewed in Chapter 6 of Ross-Gillespie (2016). Figure 1 shows a selection of key results for the base case model. This Figure also shows results for the same base case model when run with different starting parameters, exhibiting a characteristic coined as "switching" in the thesis, which is explained on more detail in the following paragraph. Figure 2 shows the natural mortality rates estimated by the hake predation model, and compares them to those assumed on the Rademeyer and Butterworth (2014) model.

Through the countless model iterations and runs that were undertaken during the process of developing the predation model, it became clear that the model has a tendency to "switch" between fitting one group of data closely to fitting another. As can be seen in Figure 1, this can occur for a single model with different starting parameter vector values, suggesting a multi-modal negative log-likelihood surface whose global minimum

does not differ greatly in log-likelihood value from subsidiary minima. The second run achieved a better fit to the historical ICSEAF CPUE data, but a slightly lower daily ration for both *M. paradoxus* and *M. capensis* (although this latter feature does not impact the value of the negative log-likelihood as daily ration is still within the bounds imposed with a reasonable slope with age). However, the spawning biomass for *M. capensis* is substantially higher for this re-run in absolute terms and furthermore the extents of depletion for this species are much less severe than for the base case and the Rademeyer and Butterworth (2014) models. This last feature is perhaps the major unrealistic feature of this re-run, in that such a healthy *M. capensis* stock is hardly consistent with reports of severely low catch rates in the 1970s. In terms of the total negative log-likelihood, however, there is very little difference between these two runs (-118.38 for the base case and -118.80 for the re-run). This is because what the re-run gains in its fit to the historical CPUE data, it loses elsewhere, in this case in the fit to the catch-at-length data. This of course poses a challenge to the model development process, since these two runs, while qualitatively different, are equally "good" fits to the data from a penalised negative log-likelihood point of view.

# 6  Summary of findings

A brief summary of the main findings and conclusions of the thesis is provided here.

- The hake predation model is able to take hake-on-hake predation and cannibalism into account explicitly, while still providing a reasonable fit to the various sources of data available (related to abundance catch-at-size and feeding information). There are, however, some indications of data conflicts as well as of potential model over-parameterisation, which need to be addressed.

- When cannibalism and predation are taken into account, the *M. paradoxus* population exhibits a predation release in first half of the 20th century in response to a reduction of the *M. capensis* predator population by the early fishery. The *M. paradoxus* population peaks in 1956 at a spawning biomass that is some 30% larger than the pre-exploitation biomass. The *M. capensis* population shows an increase in the 1960s that is not evident to the same extent in the non-predation models, suggesting that the *M. capensis* population also experienced a predation release as a result of the exploitation of *M. capensis* predators by the fishery (and consequently reduced levels of *M. capensis* cannibalism).

- Despite these predation releases, the predation model estimates similar, even slightly higher, extents of depletion for *M. paradoxus*. The chief reason for this is the requirement to reflect the large drop in the ICSEAF CPUE data from the mid-1950s to mid-1970s. Higher predation levels give greater predation release, but show stronger oscillatory behaviour which is then unable to also fully reflect the ICSEAF CPUE decline. This finding is contrary to the hope expressed by some stakeholders in the fishery that taking account of this predation release would result in estimates of a substantially less depleted *M. paradoxus* resource.

- Direct estimates of the daily ration of Cape hake are not available since gastric evacuation studies have not been conducted for this species. Bounds for biologically realistic daily rations were obtained

from the literature and from theoretical considerations of fish bioenergetics. Without any constraints on the daily ration, the predation model does not provide biologically realistic estimates for these rations. With constraints on daily ration in place, the model remains able to provide a reasonable fit to feeding and other data sources, but also exhibits a tendency to "switch" between fitting one data source closely to fitting another. This is particularly the case for a higher *M. paradoxus* daily ration which results in a worse fit to the historical ICSEAF CPUE data.

- While the predation model still needs to be developed further, it shows good potential as a tool to improve the assessment and management of what is South Africa's most valuable fishery. An immediate and important spin-off from this work is the explicit provision of an indication of appropriate values to choose for hake mortality-at-age vectors (see Figure 2). Choices for these vectors constitute a major uncertainty in the current (non-predation) assessments of the hake resource, and these predation model results could provide a more justifiable basis for these vectors.

# 7 Future work

Table 1 lists outstanding panel recommendations as well as future work items arising from the thesis, along with rough priority ratings.

# References

Essington, T. E., Kitchell, J. F. and Walters, C. J. 2001. The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**(11), 2129–2138.

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Rademeyer, R. A. and Butterworth, D. S. 2014. Specifications of the South African hake 2014 Reference Case assessment. *Document MARAM/IWS/DEC14/Hake/P2 reviewed at the International Stock Assessment Workshop, Cape Town, December 2014.*

Ross-Gillespie, A. 2016. Modelling cannibalism and inter-species predation for the Cape hake species *Merluccius capensis* and *M. paradoxus*. *Ph.D. thesis, University of Cape Town, 1-203.*

**Table 1:** A summary of the recommendations of past International Stock Assessment Workshops that still need to be implemented, as well as additional future work items from the thesis. The recommendations have been sorted by category. Priorities have been allocated as high (H), medium (M) or low (L) by the author. A priority marked with an asterisk, however, indicates that this priority was allocated directly by the workshop panel.

| (A) Spatial structure | | |
|---|---|---|
| **Item** | **Source** | **Priority** |
| A1. Start with South Africa only, and perhaps incorporate Namibian data later if possible. | IWS 2011 | L |
| A2. Explicitly account for spatial structure, either using a movement model or by treating predation on the West and South coasts as separate fleets. | IWS 2014 | H* |
| A3. Depth segregation: Probably not feasible to take into account explicitly, but more sophisticated methods for modelling preference functions that change with predator age as a proxy for depth could be investigated. | Thesis | L |
| A4. Seasonal segregation: Segregation by season could be beneficial since the hake diet changes with prey availability, and given that the model incorporates a monthly time-step, it would be relatively straightforward to implement. However, whether the existing diet data could support further segregation by season (given the already sparse data for particularly the older hake) without compromising estimation variance would have to be investigated. | Thesis | L |
| (B) Population structure | | |
| B1. Disaggregate the model by sex to better fit, for example, the longline catch-at-age data. It should be possible to disaggregate the diet data by predator sex but not by prey sex. | IWS 2014 | H* |
| B2. Fit to age-length-key (ALK) data. | Thesis | M/L |
| B3. Implications of whether recruitment is taken to occur before or after predation should be explored. | IWS 2013 | M/H |
| B4. Implications of whether recruitment is taken to occur continually throughout the year or in peak periods should be explored. | Thesis | L/M |
| B5. Implement the modified Ricker stock-recruitment relationship for greater comparability with the current assessment model. | Thesis | M |
| B6. Consider alternate formulations of stock-recruit models for hake that incorporate cannibalism, both directly as a covariate and indirectly in how spawning stock biomass is defined (e.g. Link *et al.* 2012). | IWS 2014 | L |

**Table 1:** *...continued from the previous page*

| | | |
|---|---|---|
| B7. Test sensitivity to assumptions about the pre-1977 split of the catch between the two hake species. | Thesis | L |
| B8. Develop a model that tracks age and length cohorts, although this is likely to be computationally infeasible. | Thesis | L |
| B9. Explore alternatives to the assumption that the population is at equilibrium at the start of the model in 1916. | Thesis | L |
| B10. Develop methods for projecting under future catch scenarios. | Thesis | L |
| B11. Test alternative basal mortality rate assumptions. Each new basal mortality rate will have to be evaluated along with sensitivity to other assumptions such as the competition term. | Thesis | H |
| **(C) Diet data** | | |
| C1. Scale hake prey-by-species information upwards to account for unidentified hake prey. This applies to *M. capensis* predators only, since *M. paradoxus* are assumed to consume *M. paradoxus* only. Further investigation is required. | IWS 2013 | M |
| C2. Difference in feeding relationship between West and South Coast should be investigated. | IWS 2013 | H |
| C3. Plan, and then implement, a review of the sampling strategy for diet data given the results of the current model as well as other needs for diet data. This recommendation pertains to DAFF, and has been noted here for the record. | IWS 2014 | H* |
| C4. The diet data should be developed based on predator age rather than predator length, since most hake for which stomach content are analysed are aged. The use of such data in the predation model would simplify the fitting process since the model is age-based. This recommendation pertains to DAFF, and has been noted here for the record. | IWS 2015 | M* |
| C5. Develop methods to fit to preference data by length directly (although this may not be necessary if the diet data are developed based on predator age rather than length). | Thesis | L |
| **(D) Other Predators** | | |
| D1. Include other predators (seals) — if there is an increase/decrease in seal population try take this into account in the mortality rates. | IWS 2011 | H |
| D2. Include other predators (re-evaluate sources of hake mortality to identify which predators to add to the model). | IWS 2014 | H |

**Table 1:** *...continued from the previous page*

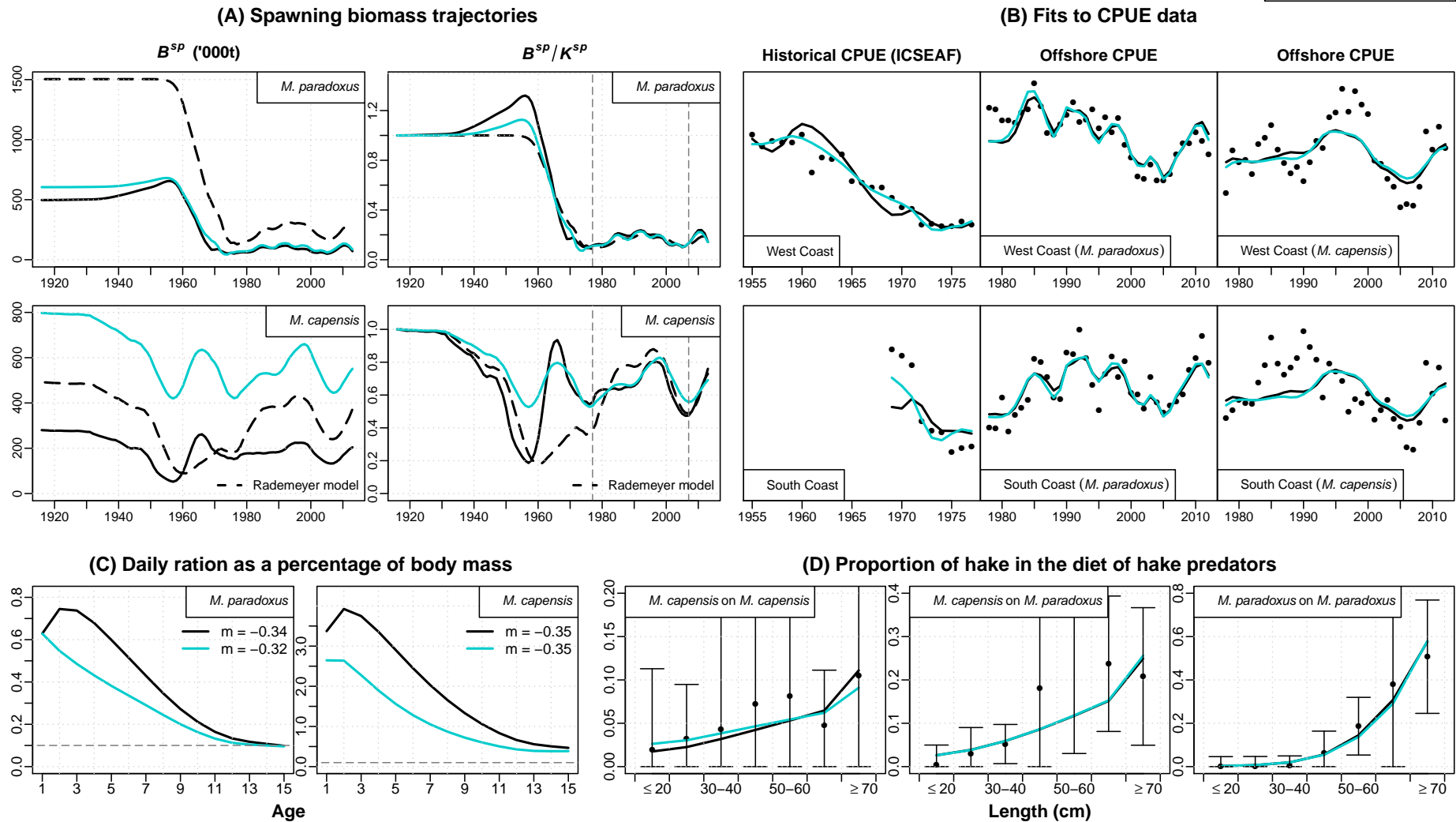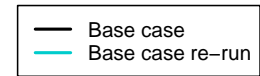| (E) Technical modelling aspects of the predation and cannibalism model | | |
|---|---|---|
| E1.Explore other functional forms (as in Kinzey and Punt 2009), including Holling Type III or Foraging Arena. | IWS 2011 | M |
| E2. Investigate alternative ways of implementing the competition term for model stability (currently an upper bound on the predation is enforced). | Thesis | M |
| E3. Run the model with coarser time steps. If satisfactory results can be obtained with fewer time-steps, this would greatly improve computational efficiency. | Thesis | M |
| (F) Data conflicts | | |
| F1. When conflict is experienced between the model fitting to the historical ICSEAF CPUE trend *versus* the diet data, priority should be given to the fit to the CPUE data since major reductions in catch rates are an important characteristic of southern African hake fisheries between the early- to mid-1960s and mid-1970s. | IWS 2015 | - |
| F2. Likelihood components for the proportions of hake prey in the diets of hake predators of various lengths should be weighted appropriately if there is evidence of overdispersion. Following the revised calculations for the proportion of hake in the diet of hake (Appendix 5.D of Ross-Gillespie 2016), the likelihood contributions for these proportions have become much more comparable with other likelihood components in the model. This should, however, be considered further in the future. | IWS 2015 | M* |

**Figure 1:** Summary plots of the results for the base case model and a re-run of the base case with different starting values for the estimable parameters, illustrating how the model can exhibit "switching". This Figure shows (A) the spawning biomass trajectories in absolute terms in thousand tons and relative to pre-exploitation biomass, (B) the fits to the commercial CPUE data, (C) the daily ration as a percentage of body mass, and (D) the fits to the proportions of hake in the diet of hake predators (with the 95% confidence intervals estimated from the diet data indicated by the error bars). The $m$ values under the legends of the daily ration plots are the slopes of the regressions of the log of daily ration against the log of body mass. In Block A, the vertical dashed lines in the $B^{sp}/K^{sp}$ plots mark 1977 and 2007, two years where the fishery experienced severely low catch rates. Note that "Rademeyer model" has been used to refer to the Rademeyer and Butterworth (2014) model (shown by dashed lines in Block (A)).
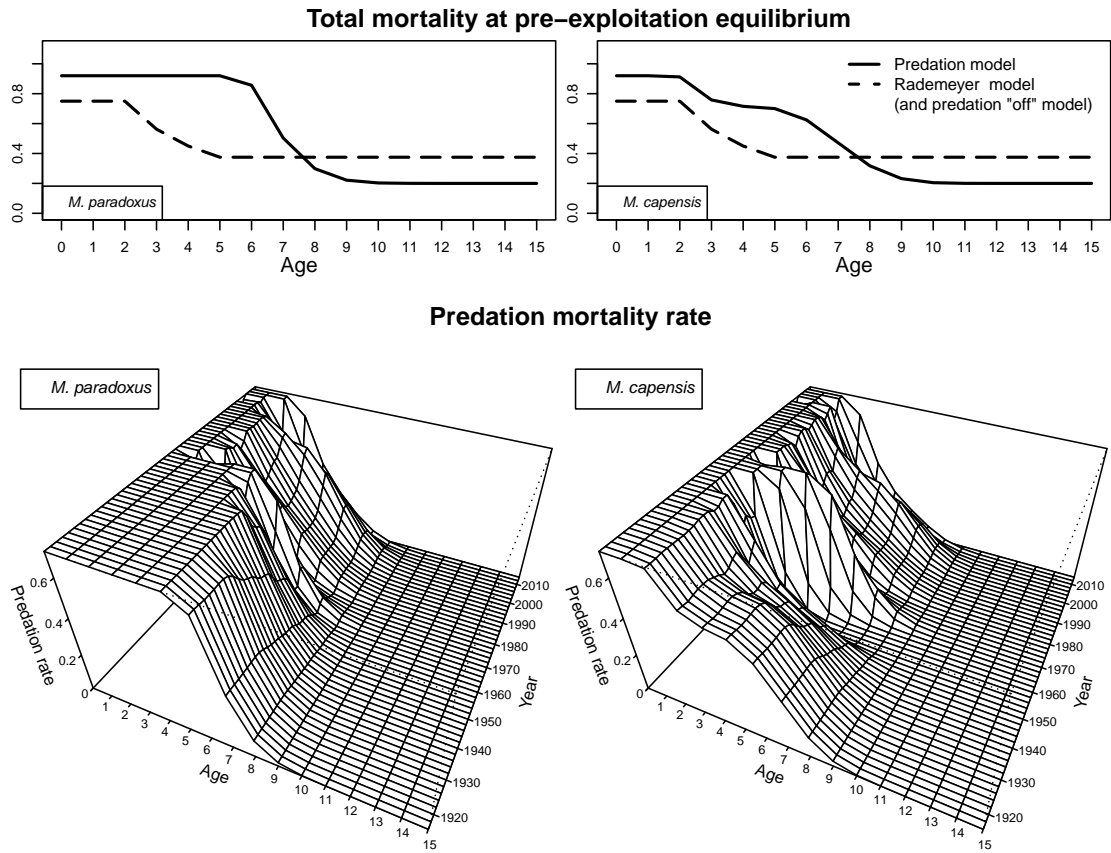
**Figure 2:** The top panel shows the total mortality as a function of age (in yr$^{-1}$) at pre-exploitation equilibrium for the base case predation model (solid black line) and for the Rademeyer and Butterworth (2014) model. The two plots on the bottom show a three-dimensional graphical representation of the predation mortality rates by age and year.

# Appendix A  Hake predation model equations

## A.1  Basic dynamics

Chapter 4 of Ross-Gillespie (2016) provides the details for the non-predation aspects of this model. The essential basic population dynamic equations have been repeated here.

The population numbers-at-age in year $y + 1$ are related to the numbers-at-age in year $y$ by:

$$N_{s,a,y+1} = \begin{cases} R_{s,y+1} & \text{for } a = 0 \\ N_{s,a-1,y}e^{-(Z_{s,a-1})} & \text{for } 0 < a \leq a_m - 1 \\ N_{s,a_m-1,y}e^{-(Z_{s,a_m-1})} + N_{s,a_m,y}e^{-(Z_{s,a_m})} & \text{for } a = a_m \end{cases} \tag{1}$$

where

$\quad N_{say}$     is the number of fish of species $s$ and age $a$ at the start of year $y$,

$\quad R_{sy}$     is the recruitment of fish (number of zero year old fish) of species $s$ at the start of year $y$,

$\quad a_m$     is the maximum age considered in the model (taken to be a plus-group),

$\quad Z_{sa}$     is the total mortality rate on fish of species $s$ and age $a$, and

$\quad C_{safy}$     is the number of hake of species $s$ and age $a$ caught in year $y$ by the fisheries fleet $f$.

**Adjustments for the monthly time-step**

Let the subscript $m$ denote month. The use of a monthly time step, as well as the fact that recruitment is assumed to occur each month (see Section A.1.1), means that the model needs to take the growth of individual fish into account throughout the year. A fish aged one month for example will not be the same size as a fish aged 11 months, even though both would be classed as 'zero 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 $\widetilde{N}_{s,\tilde{a},y,m}$ be the number of hake aged $\tilde{a}$ *months*. Then the number of hake aged $\tilde{a}+1$ months in the following month is given by:

$$\widetilde{N}_{s,\tilde{a}+1,y,m+1} = \widetilde{N}_{s,\tilde{a},y,m}e^{-Z_{saym}} \tag{2}$$

where $Z_{saym}$ is the total mortality for hake of species $s$ and age $a$ years in month $m$ of year $y$, and is given by:

$$Z_{saym} = M_s^{basal}/12 + P_{saym} + \sum_f S_{saf}F_{sfym} \tag{3}$$

where $M_s^{basal}$ is the basal natural mortality rate, $P_{saym}$ is the mortality due to hake-on-hake predation, $S_{saf}$ is the selectivity of fishing fleet $f$ on hake of species $s$ and age $a$, and $F_{sfym}$ is the fully selected instantaneous fishing mortality of fleet $f$ on hake of species $s$ in month $m$ of year $y$.

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

The number of hake aged $a$ years is then given by:

$$N_{saym} = \sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s,\tilde{a},y,m} \tag{4}$$

### A.1.1   Recruitment

Rademeyer and Butterworth (2014) assume the number of new recruits (i.e. zero-year old fish) at the start of each year is a function of the female spawning biomass. Since the predation model presented in Ross-Gillespie (2016) is sex-aggregated, total spawning biomass has been used instead. The relationship between recruitment and spawning biomass is characterised by a Beverton-Holt stock-recruitment relationship:

$$R_{sy} = \frac{\alpha_s B_{sy}^{sp}}{\beta_s + B_{sy}^{sp}} \; e^{(\zeta_{sy} - \sigma_R^2/2)} \tag{5}$$

where

$\quad R_{sy}$     is the recruitment in year $y$,

$\quad B_{sy}^{sp}$     is the spawning biomass of species $s$ in year $y$,

$\quad \zeta_{sy}$     reflects fluctuation about the expected recruitment for species $s$ in year $y$,

$\quad \sigma_R$     is the standard deviation of the log of the recruitment residuals, which is fixed on input, and

$\quad \alpha_s, \beta_s$     are parameters.

Let $h$ be the steepness of the stock-recruitment curve, corresponding to the fraction of the recruitment under pristine conditions, $R_{s0}$, that results when spawning biomass drops to 20% of its pristine level. The parameters $\alpha_s$ and $\beta_s$ can then be determined by:

$$\alpha = \frac{4hR_{sy_0}}{5h - 1} \tag{6}$$

and

$$\beta = \frac{K_s^{sp}(1 - h)}{5h - 1} \tag{7}$$

where

$\quad K_s^{sp}$     is the pre-exploitation equilibrium spawning biomass for species $s$,

$\quad R_{sy_0}$     is the recruitment for species $s$ at equilibrium, and

$\quad h$     is the steepness of the stock-recruitment curve.

**Adjustments for the monthly time-step**

In light of the monthly time-step of the predation model, recruitment is assumed to take place continually throughout the year[2], at the start of each month, i.e. a twelfth of the recruitment that would normally be determined by the Beverton-Holt relationship in a year is allocated to each month, but calculated from the spawning biomass in that month. Equation 5 becomes:

$$R_{sym} = \left(\frac{1}{12}\right) \frac{\alpha_s B_{sym}^{sp}}{\beta_s + B_{sym}^{sp}} \ e^{(\zeta_{sy} - \sigma_R^2/2)} \tag{8}$$

Here, $R_{sym}$ and $B_{sy}^{sp}$ are respectively the recruitment and spawning biomass in month $m$ of year $y$ (see Section A.1.2 for the definition of the monthly spawning biomass). Further, Equation 6 is adjusted to:

$$\alpha = \frac{4h(12R_{sy_0,m_0})}{5h-1} \tag{9}$$

where $R_{sy_0,m_0}$ is the recruitment of age zero (*in months*) hake in the first month considered in the model (see Section A.2.5 for details of the equilibrium set-up).

Rademeyer and Butterworth (2014) implement both the Beverton Holt and a modified Ricker stock-recruitment relationship, and in fact assume the modified Ricker relationship for their base case assessment. The predation model implements the Beverton-Holt stock-recruitment relationship in its base case model[3] (and fixes $h$ at 0.9 to aid stability, given that $h$ is poorly estimated, but likely high, in terms of the Rademeyer and Butterworth 2014 model), and the Ricker formulation is included only as a sensitivity test, along with a run that estimates the $h$ for the Beverton-Holt formulation. The modified Ricker was not implemented for the base case because of difficulties that arose early in the model development process when trying to estimate the $\gamma$ parameter, and as such the simpler Beverton-Holt relationship was preferred (although the modified Ricker relationship may well become the base case assumption in future developments of the model.)

### A.1.2 Spawning Biomass

The spawning biomass is calculated on a monthly basis and takes the weight of hake into account based on their age in months:

$$B_{sym}^{sp} = \sum_{a=1}^{a_m} f_{sa} \sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s\tilde{a}ym} w_{s\tilde{a}} \tag{10}$$

where

$f_{sa}$     is the proportion of fish of species $s$ and age $a$ that are mature,

$\widetilde{N}_{s\tilde{a}ym}$     is the number of hake of species $s$ and age $\tilde{a}$ months in month $m$ of year $y$, and

$w_{s\tilde{a}}$     is the mass of a hake of species $s$ and age $\tilde{a}$ months.

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[2]Although studies have shown hake to exhibit peak spawning periods, spawning does appear to occur throughout the year, so this assumption is unlikely to introduce any major bias. However, since combining seasonal recruitment with seasonal growth may well lead to more variation than assuming a constant rate of recruitment, sensitivity to this assumption of constant recruitment has been noted for future work.

[3]The modified Ricker is implemented in the Rademeyer and Butterworth (2014) base case model as there is evidence of decreasing recruitment at larger spawning biomass.

## A.2 Predation dynamics

This section describes how the predation mortality rate, $P_{saym}$, is developed. In order to distinguish between hake predator and prey species in the equations that follow, the superscripts $s_p$ and $a_p$ are used for the predators, while the subscripts $s$ and $a$ are used for the prey. Thus $N_{ym}^{s_p a_p}$ denotes the number of predators of species $s_p$ and age $a_p$, and $N_{saym}$ the number of prey of species $s$ and age $a$ in month $m$ of year $y$.

### A.2.1 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 hake predators of species $s_p$ and age $a_p$. Then the total predation rate on these particular prey is:

$$P_{saym} = \sum_{s_p, a_p} V_{saym}^{s_p a_p} \tag{11}$$

where $V_{saym}^{s_p a_p}$ is modelled here by a Holling Type II functional form[4]:

$$V_{saym}^{s_p a_p} = \breve{N}_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\nu_s^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\nu}_s^{s_p} \Phi_{sym}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{12}$$

Here

$\breve{N}_{ym}^{s_p a_p}$    is the number of hake predators of species $s_p$ and age $a_p$ in month $m$ of year $y$, relative to the equilibrium maximum age group (see Equation 28),

$\Phi_{sym}^{s_p a_p}$    is a relative measure of the abundance of hake prey of species $s$ available to hake predators of species $s_p$ and age $a_p$ in month $m$ of year $y$ (see Equation 29),

$\gamma_{sa}^{s_p a_p}$    is a preference function modelling the preference that a hake predator of species $s_p$ and age $a_p$ exhibits for hake prey of species $s$ and age $a$ (see Equation 21),

$\theta^{s_p a_p}$    is a function allowing for additional flexibility in the extent to which predation rates change with the age of the hake predator (see Equation 23),

$O_{other}^{s_p a_p}$    is the population size in numbers of other (non-hake) prey available to hake predators of species $s_p$ and age $a_p$, which is assumed to be time-invariant (see Section A.2.2), and

$\nu_s^{s_p}$, $\tilde{\nu}_s^{s_p}$ and $\tilde{\nu}_{other}^{s_p}$ 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:

$$E_{saym}^{s_p a_p} = V_{saym}^{s_p a_p} N_{saym} \frac{\left(1 - e^{-Z_{saym}}\right)}{Z_{saym}} \tag{13}$$

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[4]Equation 5.4 is in fact a re-parameterised version of the basic Holling Type II form. Further details of the relationship between the two are given in Section A.2.5.

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Finally, the mass of hake of species $s$ consumed in year $y$ by predators of species $s_p$ and age $a_p$ is given by:

$$Q_{sym}^{s_p a_p} = V_{saym}^{s_p a_p} \left( \sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s\tilde{a}ym} w_{s\tilde{a}} \right) \frac{\left(1 - e^{-Z_{saym}}\right)}{Z_{saym}} \tag{14}$$

The term $\sum_{\tilde{a}=12a}^{12a+11} \widetilde{N}_{s\tilde{a}ym} w_{s\tilde{a}}$ is the total weight of prey taking their individual weight by age in months into account.

### A.2.2  Other prey

The approach used for setting up the hake prey dynamics has been 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 available to hake predators of species $s_p$ and age $a_p$. Let the total mortality rate for other prey be given by:

$$Z_{other,ym}^{s_p a_p} = M_{other}^{basal}/12 + P_{other,ym} \tag{15}$$

where

$M_{other}^{basal}$ is the basal mortality rate for the other prey, fixed at 0.2 p.a., and

$P_{other,ym}$ is the predation mortality on other prey due to hake predators, given by:

$$P_{other,ym} = \sum_{s_p,a_p} V_{other,ym}^{s_p a_p} \tag{16}$$

$V_{other,ym}^{s_p a_p}$ is the mortality of other prey due to hake predators of species $s_p$ and age $a_p$ in month $m$ of year $y$, also modelled by a Holling Type II functional form[5]:

$$V_{other,ym}^{s_p a_p} = \breve{N}_{ym}^{s_p a_p} \frac{\nu_{other}^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\nu}_s^{s_p} \Phi_{sym}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{17}$$

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

$$Q_{other,ym}^{s_p a_p} = V_{other,ym}^{s_p a_p} \tilde{O}_{other}^{s_p,a_p} \frac{\left(1 - e^{-Z_{other,ym}}\right)}{Z_{other,ym}} \tag{18}$$

$\tilde{O}_{other}^{s_p,a_p}$ is a measure of the **mass** of the other prey available to a hake predator of species $s_p$.

*Other prey in numbers*

Since $O_{other}^{s_p,a_p}$ is multiplied by the estimable parameter $\tilde{\nu}_{other}^{s_p}$ in Equations 12 and 17, 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 consequently modelled by a simple exponential equation:

$$O_{other}^{s_p,a_p} = e^{-(o^{s_p})a_p} \tag{19}$$

where $o^{s_p}$ is an estimable parameter that can take on positive or negative values.

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[5]Similarly to Equation 12, Equation 17 is a re-parameterised version of the basic Holling Type II form. Further details are given in Section A.2.5

*Other prey by mass*

The mass of other prey available to a hake predator of species $s_p$ and age $a_p$ is taken to be a multiple of the other prey by numbers:

$$\tilde{O}_{other}^{s_p,a_p} = o_w^{s_p} O_{other}^{s_p a_p} \tag{20}$$

where $o_w^{s_p}$ is an estimable scaling parameter.

### A.2.3 Preference function

The preference function for hake predators on hake prey is modelled using a gamma function, as in Kinzey and Punt (2009):

$$\gamma_{sa}^{s_p a_p} = \left( G_{sa}^{s_p a_p} / \tilde{G}_s^{s_p} \right)^{\alpha^{s_p}-1} exp\left[ -\left( G_{sa}^{s_p a_p} - \tilde{G}_s^{s_p} \right)/\beta^{s_p} \right] \tag{21}$$

where

$\quad G_{sa}^{s_p a_p}$ is the logarithm of the ratio of the expected length of a hake predator of species $s_p$ and age $a_p$ to that of a hake prey of species $s$ and age $a$,

$\quad \tilde{G}_s^{s_p} = (\alpha^{s_p} - 1)\beta^{s_p}$ is the value of $G_{sa}^{s_p a_p}$ at which predator selectivity is at a maximum, and

$\quad \alpha^{s_p}$ and $\beta^{s_p}$ are estimable parameters.

In practice, $\tilde{G}_s^{s_p}$ is treated as the estimable parameter in the place of $\beta^{s_p}$, since $\tilde{G}_s^{s_p}$ (the peak of the preference function) is a more biologically meaningful quantity. Furthermore a prey-specific $\tilde{G}_s^{s_p}$ is estimated[6], since it is possible that the preference that *M. capensis* predators exhibit for *M. capensis* prey may peak at a different prey to predator size ratio than for *M. paradoxus* prey, given that the overlap between *M. capensis* predators and their prey differs between the two prey species. The preference function is normalised so that $\sum_{s,a} \gamma_{sa}^{s_p a_p} = 1$.

### A.2.4 Theta function

The $\theta^{s_p a_p}$ function provides additional flexibility for varying predation rates with predator age. Kinzey and Punt (2009) introduce $\theta^{s_p a_p}$ in order to *reduce* predation as predator age increases (for example to allow for the fact that larger fish may focus less on feeding and growth, and more on reproducing). They use the form:

$$\theta^{s_p a_p} = 1 + \omega^{s_p}\tilde{\omega}^{s_p}/\left(a_p + \tilde{\omega}^{s_p}\right) \tag{22}$$

where $\omega^{s_p}$ and $\tilde{\omega}^{s_p}$ are estimable parameters. When this form was implemented in the hake predation model, it resulted in older fish not eating enough, so that some changes were made to allow $\theta^{s_p a_p}$ to increase with predator age, with the following form:

$$\theta^{s_p,a_p} = w^{s_p,a_p} \left[ \frac{\omega^{s_p} + 5}{\omega^{s_p} + a_p} \right]^{\tilde{\omega}^{s_p}} \tag{23}$$

where $w^{s_p,a_p}$ is the weight of a hake predator of species $s_p$ and age $a_p$, and $\omega^{s_p}$ and $\tilde{\omega}^{s_p}$ are estimable parameters. The predator weight was included under the rationale that a predator is likely to eat more as

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[6]This prey-specificity applies only to *M. capensis* predators, since *M. paradoxis* is assumed not to eat *M. capensis*.

it gets bigger.

### A.2.5   Initial population setup

In order to obtain the pre-exploitation equilibrium structure, the total mortality values $Z_{say_0,m=1} = M_{sa}^{basal} + P_{s,a,y_0,m=1}$ are needed. However, to obtain $P_{s,a,y_0,m=1}$, the initial population structure is needed. To address this impasse, the formulation of Equations 12 and 17 was chosen so that the calculation of an initial structure was made possible using the methodology described below. 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 obtain an initial population structure 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 hake of age 15 and above (the age plus-group) are too large to be preyed upon by other hake, i.e $P_{s,a_m,y_0,m=1} = 0$ for $a_m = 15$. Thus the total mortality rate for this age group at pre-exploitation equilibrium (i.e. zero fishing mortality) is $Z_{s,a_m,y_0,m=1} = M_{sa_m}^{basal}$, where the basal mortality rate is fixed on input. The number of 14 year old hake can then be calculated from the number of 15 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 14 year old hake are 15 years and older, so that $P_{s,a_m-1,y_0,m=1}$ can then 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 on. By re-parameterising the predation equations as in Equations 12 and 17, 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.

*Derivation of Equations 12 and 17*

The formulation chosen for Equations 5.4 and 5.9 is to enable implementation of the approach above. To derive these equations, one starts from more fundamental Holling Type II parameterisations:

$$V_{saym}^{s_p a_p} = N_{ym}^{s_p a_p}\gamma_{sa}^{s_p a_p}\frac{\eta_s^{s_p}\theta^{s_p a_p}}{1 + \sum_s \tilde{\eta}_s^{s_p}\sum_a N_{saym}\gamma_{sa}^{s_p a_p} + \tilde{\eta}_{other}^{s_p}O_{other}^{s_p a_p}} \tag{24}$$

and

$$V_{other,ym}^{s_p a_p} = N_{ym}^{s_p a_p}\frac{\eta_{other}^{s_p}\theta^{s_p a_p}}{1 + \sum_s \tilde{\eta}_s^{s_p}\sum_a N_{saym}\gamma_{sa}^{s_p a_p} + \tilde{\eta}_{other}^{s_p}O_{other}^{s_p a_p}} \tag{25}$$

where

$N_{ym}^{s_p a_p}$ 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 $y$,

$\eta_s^{s_p}, \tilde{\eta}_s^{s_p}, \eta_{other}^{s_p}, \tilde{\eta}_{other}^{s_p}$ are estimable parameters, and

the other parameters are as for Equations 12 and 17.

Equations 24 and 25 are then re-written so that at unexploited equilibrium the $N_{say_0m}$ term is effectively removed from the denominator:

$$V_{saym}^{s_p a_p} = \frac{N_{ym}^{s_p a_p}}{N_{y_0,m=1}^{s_p a_p,max}} \gamma_{sa}^{s_p a_p} \frac{\left(\eta_s^{s_p} N_{y_0,m=1}^{s_p a_p,max}\right) \theta^{s_p a_p}}{1 + \sum_s \left(\tilde{\eta}_s^{s_p} \sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p} \frac{\sum_a N_{saym} \gamma_{sa}^{s_p a_p}}{\sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p}}\right) + \tilde{\eta}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{26}$$

and

$$V_{other,ym}^{s_p a_p} = \frac{N_{ym}^{s_p a_p}}{N_{y_0,m=1}^{s_p a_p,max}} \frac{\left(\eta_{other}^{s_p} N_{y_0,m=1}^{s_p a_p,max}\right) \theta^{s_p a_p}}{1 + \sum_s \left(\tilde{\eta}_s^{s_p} \sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p} \frac{\sum_a N_{saym} \gamma_{sa}^{s_p a_p}}{\sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p}}\right) + \tilde{\eta}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{27}$$

Defining

$$\breve{N}_{ym}^{s_p a_p} = \frac{N_{ym}^{s_p a_p}}{N_{y_0,m=1}^{s_p a_p,max}} \tag{28}$$

$$\Phi_{sym}^{s_p a_p} = \frac{\sum_a N_{saym} \gamma_{sa}^{s_p a_p}}{\sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p}} \tag{29}$$

$$\nu_s^{s_p} = \eta_s^{s_p} N_{y_0,m=1}^{s_p a_p,max} \tag{30}$$

$$\nu_{other}^{s_p} = \eta_{other}^{s_p} N_{y_0,m=1}^{s_p a_p,max} \tag{31}$$

$$\tilde{\nu}_s^{s_p a_p} = \tilde{\eta}_s^{s_p} \sum_a N_{say_0,m=1} \gamma_{sa}^{s_p a_p} \implies \tilde{\nu}_s^{s_p} \tag{32}$$

$$\tilde{\nu}_{other}^{s_p} = \tilde{\eta}_{other}^{s_p} \tag{33}$$

Equations 12 and 17 follow from Equations 26 and 27:

$$V_{saym}^{s_p a_p} = \breve{N}_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\nu_s^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\nu}_s^{s_p} \Phi_{sym}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}}$$

and

$$V_{other,ym}^{s_p a_p} = \breve{N}_{ym}^{s_p a_p} \frac{\nu_{other}^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\nu}_s^{s_p} \Phi_{sym}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}}$$

Strictly speaking, $\tilde{\nu}_s^{s_p}$ should be a function of predator age, but since it is not feasible to estimate this parameter for all ages, an age-independent $\tilde{\nu}_s^{s_p}$ is estimated instead.

At pre-exploitation equilibrium, Equation 12 simplifies to

$$V_{say_0,m=1}^{s_p a_p} = \breve{N}_{y_0,m=1}^{s_p a_p} \gamma_{sa}^{s_p a_p} \frac{\nu_s^{s_p} \theta^{s_p a_p}}{1 + \tilde{\nu}_s^{s_p} + \tilde{\nu} O_{other}^{s_p a_p}} \tag{34}$$

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

## A.3 Likelihood components

This section describes the additions that have been made to the (penalised) negative log-likelihood described in Chapter 4 of Ross-Gillespie (2016) in order to be able to estimate the predation model parameters. The 1999-2013 DAFF biological data set provides good information on two aspects of the hake diet: the proportion of hake in the diet of hake predators, and the preference that a hake predator of a given age exhibits for hake prey of different ages. The equations for how this information is incorporated into the likelihood are provided in this section. A further quantity of particular relevance to the predation model is the daily ration of hake. Since no direct estimates of this quantity are available for hake, daily ration has been handled in a slightly different manner, as explained in the model development section (see Section A.4.1).

Note that since there are no diet data available for hake predators of age $a_p = 0$ (and the model assumes that hake aged zero do not prey on hake), 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*).

### A.3.1 Proportion of hake in diet

The calculation of the observed proportion of hake in the diet of hake predators from the stomach content data is described in Appendix 5.D of Ross-Gillespie (2016). The model-predicted proportion of hake of species $s$ in the diet of predators of species $s_p$ and length class[7] $L_p$ in year $y$ is taken to be the total mass of hake of species $s$ consumed by these predators in year $y$, divided by the total mass of all prey consumed:

$$\hat{\rho}_{sy}^{s_p L_p} = \left( \sum_m \sum_{a_p \neq 0} \left( \sum_{l_p \in L_p} A^{s_p l_p a_p} \right) Q_{sym}^{s_p a_p} \right) \Big/ \left( \sum_m \sum_{a_p \neq 0} \left( \sum_{l_p \in L_p} A^{s_p l_p a_p} \right) \left( \sum_s Q_{sym}^{s_p a_p} + Q_{other,ym}^{s_p a_p} \right) \right) \quad (35)$$

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 14), $Q_{other,ym}^{s_p a_p}$ is the mass of other prey consumed by predators of species $s_p$ and age $a_p$ (Equation 18) and $A^{s_p l_p a_p}$ is the proportion of fish of species $s_p$ and age $a_p$ that are of length $l_p$. $\sum_{l_p \in L_p} A^{s_p l_p a_p}$ is the proportion of fish of species $s_p$ and age $a_p$ that fall into the 10cm length class $L_p$.

The contribution to the negative log-likelihood is given by:

$$-lnL+ = -\sum_y \sum_{s_p} \sum_{L_p} \sum_s \left( \rho_{s,obs}^{s_p L_p} - \hat{\rho}_y^{s_p L_p} \right)^2 \Big/ \left( 2 \left( \sigma_{\rho,s}^{s_p, L_p} \right)^2 \right) \quad (36)$$

where $\rho_{s,obs}^{s_p L_p}$ is the observed (year-averaged) proportion of hake in the diet of hake predators, adjusted to reflect prey mass at ingestion time and corrected for differential evacuation rates of different prey types (see Table 5.B.5 of Appendix 5.D of Ross-Gillespie 2016), and $\sigma_{\rho,s}^{s_p, L_p}$ its associated standard error (see Table 5.B.5 of Appendix 5.D of Ross-Gillespie 2016).

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[7]The length classes are $L_p \in \{\leq 20\text{cm}; \ 21 - 30\text{cm}; \ 31 - 40\text{cm}; \ \ldots; \ 61 - 70\text{cm}; \ > 70\text{cm}\}$, as defined in Appendix 5.D of Ross-Gillespie (2016). While data are available at 1 cm length intervals, this grouping was chosen to ensure reasonable sample sizes for each length class.

### A.3.2 Preference data

The 1999-2013 DAFF biological dataset provides counts of hake prey of species $s$ and length $l$ in the stomachs of predators of species $s_p$ and length $l_p$. The corresponding ages were calculated from the observed lengths using the pertinent von Bertalanffy growth curve[8] to obtain the counts by predator and prey ages (i.e. a form of cohort-splicing). These are provided in Table 3.9 of Chapter 3 in Ross-Gillespie (2016). Let these counts be denoted by $\zeta_{s,a,obs}^{s_p a_p}$, and let $\hat{\chi}_{s,a}^{s_p a_p}$ denote the model-predicted proportion of hake prey of species $s$ and age $a$ consumed by predators of species $s_p$ and age $a_p$ in year $y$, given by:

$$\hat{\chi}_{say}^{s_p a_p} = \frac{\sum_m E_{saym}^{s_p a_p}}{\sum_a \sum_m E_{saym}^{s_p a_p}} \tag{37}$$

where $E_{saym}^{s_p a_p}$ is 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 $a_p$ (Equation 13). The negative log-likelihood contribution is:

$$-lnL+ = -\sum_y \sum_{s_p, a_p \neq 0} \sum_{s,a} \zeta_{s,a,obs}^{s_p,a_p} \left( ln(\hat{\chi}_{say}^{s_p a_p}) - ln(\zeta_{s,a,obs}^{s_p a_p} / \sum_l \zeta_{s,a,obs}^{s_p a_p}) \right)$$

There is some discussion in Chapter 7 of Ross-Gillespie (2016) on the possibility of modeling preference directly as a function of length rather than of age.

## A.4 Further model development

The methods and equations presented thus far constitute what could be considered the rudimentary foundation of the predation model. This section describes the further model developments that were found necessary in order to find a reasonable fit to the data.

### A.4.1 Daily ration

The model was originally fit without any constraints on daily ration, to see if it was able to produce biologically realistic estimates for this quantity. It was, however, unable to do this and produced very low levels for the *M. paradoxus* daily ration (full results are provided in Chapter 6 of Ross-Gillespie 2016). Hence a penalty was added to the negative-log likelihood to prevent estimates of daily ration that are outside biologically realistic bounds. The full details of how estimates of these bounds were obtained are provided in Appendix 5.C of Ross-Gillespie (2016), but to summarise a lower bound of 0.1% of body mass and an upper bound of 4% of body mass were taken to be the limits of biological realism. The details of the model-predicted daily ration and likelihood contributions are provided below.

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 $y$, expressed as a percentage of predator body mass, defined by:

$$\hat{\delta}_{ym}^{s_p a_p} = \frac{\sum_s Q_{sym}^{s_p a_p} + Q_{other,ym}^{s_p a_p}}{\sum_{\tilde{a}_p = 12a_p}^{12a_p + 11} \widetilde{N}_{y,m}^{s_p, \tilde{a}_p} w^{s_p \tilde{a}_p}} \left( \frac{12}{365} \right) (100) \tag{38}$$

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[8]The sex-averaged growth curves (Table 4.2 of Chapter 4 of Ross-Gillespie 2016) were used to calculate the ages from the recorded lengths. Strictly speaking it would be better to use the sex-specific growth curves for the stomach samples where the gender of the predator has been recorded, but given the natural variance in length in a given age class, ignoring the gender in the age-length conversion seems unlikely to introduce any major bias.

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

$$\bar{\delta}^{s_p a_p} = \frac{1}{12 n_{diet}} \sum_{y_{diet}} \sum_{m=1}^{12} \hat{\delta}_{ym}^{s_p a_p} \tag{39}$$

where $n_{diet}$ is the number of years ($y_{diet}$) for which diet data are available to the model, namely 1999-2013.

The penalty added to the negative log-likelihood is of the following form:

$$-lnL+ = \sum_{s_p, a_p \neq 0} \begin{cases} \left( \bar{\delta}^{s_p a_p} - 0.1 \right)^2 / (2(0.01)^2) & \text{if } \bar{\delta}^{s_p a_p} < 0.1 \\ \left( \bar{\delta}^{s_p a_p} - 4.0 \right)^2 / (2(0.1)^2) & \text{if } \bar{\delta}^{s_p a_p} > 4.0 \\ 0 & \text{otherwise} \end{cases} \tag{40}$$

The different values for the standard error in the numerator of each of the above equations were chosen so that the likelihood receives a much higher penalty when the daily ration drops below 0.1 by a small amount than it would when it goes above 4.0 by that same amount.

### A.4.2  *M. capensis* preference for *M. capensis* compared *M. paradoxus* prey

Appendix 5.D of Chapter 5 of the thesis shows that as a *M. capensis* predator grows larger and moves into deeper water, it will be more likely to encounter *M. paradoxus* than *M. capensis* prey of a preferred size. Having no depth structure, the predation model has no direct way of taking account of this shift. A depth-availability vector, $D_s^{s_p a_p}$, was thus introduced to allow the *M. capensis* preference for *M. capensis* prey to decrease with predator age, and correspondingly increase with predator age for *M. paradoxus* prey. Equation 12 is consequently modified to:

$$V_{saym}^{s_p a_p} = \breve{N}_{ym}^{s_p a_p} \gamma_{sa}^{s_p a_p} D_s^{s_p a_p} \frac{\nu_s^{s_p} \theta^{s_p a_p}}{1 + \sum_s \tilde{\nu}_s^{s_p} \Phi_{sym}^{s_p a_p} + \tilde{\nu}_{other}^{s_p} O_{other}^{s_p a_p}} \tag{41}$$

and $\Phi_{sym}^{s_p a_p}$ from Equation 29 is redefined as:

$$\Phi_{sym}^{s_p a_p} = \frac{\sum_a N_{saym} \gamma_{sa}^{s_p a_p} D_s^{s_p a_p}}{\sum_a N_{say0, m=1} \gamma_{sa}^{s_p a_p} D_s^{s_p a_p}} \tag{42}$$

The depth-availability vector is defined as

$$D_s^{s_p a_p} = \begin{cases} e^{-s_D(a_p)} & \text{for } \textit{M. capensis} \text{ predators and } \textit{M. capensis} \text{ prey} \\ e^{-s_D(a_m)} e^{s_D(a_p)} & \text{for } \textit{M. capensis} \text{ predators and } \textit{M. paradoxus} \text{ prey} \\ 1 & \text{for } \textit{M. paradoxus} \text{ predators} \end{cases} \tag{43}$$

where $a_p$ is the predator age, $s_D$ is an estimable parameter and $a_m = 15$ is the maximum age considered in the model.

### A.4.3  Daily ration with predator age

At this stage of the development, the predation model still had very little informative data to estimate daily ration. The upper and lower bounds on daily ration introduced above provide no guidelines regarding what the daily ration should be between these bounds. However, the equations of Essington *et al.* (2001),

which were used to obtain the upper and lower bounds for the daily ration, also provide a further guideline that a regression of the log of daily ration against the log of the body weight should yield a slope of -1/3 (Appendix 5.C of Ross-Gillespie 2016). This relationship was incorporated into the negative log-likelihood to provide additional information for estimating the dependence of the daily rations on predator age. If $\delta_{slope}^{sp}$ is the slope of the regression of the log of the model-estimated daily ration ($ln\bar{\delta}^{s_p a_p}$) against the log of the expected weight ($lnw^{s_p a_p}$) for a predator of species $s_p$, then the following penalty is added to the negative log-likelihood:

$$-lnL+ = \sum_{s_p} \left( \delta_{slope}^{sp} - \left(-\frac{1}{3}\right) \right)^2 / \left(2(\sigma_{slope})^2\right) \tag{44}$$

A value of $\sigma_{slope} = 0.04$ was found to be sufficiently small to stabilise the estimation without giving undue weight to this penalty.

### A.4.4  Limiting the predation mortality rate: Introducing competition

Punt (1994) introduced a competition term into his hake predation model to prevent excessive predation when large predator cohorts moved through the model, thus damping the large predator-prey oscillations exhibited by his biomass trajectories and stabilising the estimation process. Similar issues with instability were experienced in the predation model presented in this thesis when high mortality rates led to unrealistic population oscillations once the *M. paradoxus* daily ration became large enough. A competition effect has thus similarly been introduced to this predation model, which has been implemented using the relatively simple approach of constraining the predation mortality rate, $P_{saym}$, to be less than a set limit $P_{lim}$ through the use of an ADMB posfun[9] penalty. Several values for $P_{lim}$ were tested, with a value of 0.06 found to be the most suitable for the base case model.

## A.5  Sensitivities

Greater details of the various sensitivity runs are provided in Chapter 6 of the thesis, since the rationales for some of these runs rely on the results of the base case model. In summary, however, sensitivity is explored to assumptions associated with the basal mortality rate, stock-recruitment relationship, daily ration (in terms of changing the lower limit as well as attempting to fix the daily ration of predators aged 3), the proportion of hake in the diet of hake predators and the *M. paradoxus* depletion level.

The estimable parameters for the predation component of the model are listed along with their bounds in Table A1 below.

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[9]Posfun is an ADMB function which prevents the quantity referenced from becoming negative.

**Table A1:** Predation-related parameters estimated in the model fitting procedure, in addition to those of the standard Rademeyer and Butterworth (2014) model presented in Table 4.7 of Ross-Gillespie (2016). The references to the equations where the parameters first appear are also listed.

| | Number of parameters | Parameters estimated | Bounds enforced | Equation |
|---|---|---|---|---|
| $\nu_s^{s_p}$ | 3 | $\nu_{cap}^{cap}$, $\nu_{par}^{cap}$ and $\nu_{par}^{par}$ | (0; 20) | Equation 12, 17 |
| $\nu_{other}^{s_p}$ | 2 | $ln\nu_{other}^{cap}$ and $ln\nu_{other}^{par}$ | (-40; 10) | Equation 17 |
| $\tilde{\nu}_s^{s_p}$ | 3 | $\tilde{\nu}_{cap}^{cap}$, $\tilde{\nu}_{par}^{cap}$ and $\tilde{\nu}_{par}^{par}$ | (0; 100) | Equation 12, 17 |
| $\tilde{\nu}_{other}^{s_p}$ | 2 | $ln\tilde{\nu}_{other}^{cap}$ and $ln\tilde{\nu}_{other}^{par}$ | (0; 30) | Equation 17 |
| $\alpha^{s_p}$ | 2 | $\alpha^{cap}$, $\alpha^{par}$ | (1; 150) | Equation 21 |
| $\tilde{G}_s^{s_p}$ | 3 | $\tilde{G}_{cap}^{cap}$, $\tilde{G}_{par}^{cap}$ and $\tilde{G}_{par}^{par}$ | (0.1; 2) | Equation 21 |
| $o^{s_p}$ | 2 | $o^{cap}$ and $o^{par}$ | (-20; 30) | Equation 20 |
| $\tilde{o}^{s_p}$ | 2 | $ln\tilde{o}^{cap}$ and $ln\tilde{o}^{par}$ | (-20; 50) | Equation 20 |
| $\omega^{s_p}$ | 2 | $\omega^{cap}$ and $\omega^{par}$ | (0; 20) | Equation 23 |
| $\tilde{\omega}^{s_p}$ | 2 | $\tilde{\omega}^{cap}$ and $\tilde{\omega}^{par}$ | (0; 20) | Equation 23 |
| $s_D$ | 1 | $s_D$ | (0; 1) | Equation 43 |
| **Total** | **24** | | | |