

A brief summary of past analyses taking hake cannibalism and inter-species predation into account in assessments

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1. Introduction

It is almost two decades since the first attempt was made by Andre Punt at taking account of cannibalism and inter-species predation when modelling the dynamics of the two hake species. That work was initiated not with hake assessments *per se* in mind, but rather to address the issue of the potential impact on the hake fishery of consumption of hake by a then expanding seal population. It addressed the situation on the SA west coast only, as data on consumption was better for that region.

Little more has been done on this issue in the intervening years, except for some work by OLRAC (see below). Over this time considerable further data have become available, and the situation of low computing power which limited Punt's earlier work has now changed for the better by more than an order of magnitude. Thus it seems appropriate to revisit this issue now, in the first instance in the context of the assessment of the hake populations.

This document first summarises the earlier work mentioned above, and the proceeds to offer some suggestions and questions concerning initial further directions.

2. Punt (1995) work

Note that unless stated otherwise, information presented here is taken from Punt (1995).

What issue did the model address?

Cape hake were estimated to constitute some 14-15% of the diet of the Cape fur seal. The seal population had been on the increase since the early 1970s and concern was expressed about the impact that the consumption of hake by seals has on hake catches.

The Benguela Ecology Programme workshop on seal-fishery biology interactions (Anon. 1991) was convened to discuss the biological interaction between seals and fisheries. The primary purpose of workshop was to provide advice on how to quantify any effect of consumption of fish by seals on catch rates and catch levels for fisheries, and to develop a general protocol using South African / Namibian situation as a specific example.

Punt (1995) 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 level of hake *TACs* and catch rates. He also aimed to investigate the effect of seal culling on the fishery.

Anon. (1991) recommended that existing hake management procedure (production model estimation-procedure and the $f_{0.2}$ harvesting strategy, as described in Appendix 1.2 of Punt, 1995) should be used to calculate future *TACs*, which would then be assumed to be taken exactly. Monte Carlo simulation was used to calculate the consequences of different levels of hake consumption by seals, and involved three steps:

1. A number of operating models (OMs) of the system were constructed. These are mathematical / statistical models of the fishery and the component species of the system. Each alternative model represents an alternative yet plausible representation of the system. Each OM reflects a different level of future consumption of hake by seals, a different level of predation / cannibalism for hake, or different values for some of the population dynamics model parameters which are poorly known. The OM is used to generate artificial data sets and to determine the effects of a series of management decisions over time.
2. A number of simulations (100) were carried out. Each simulation involved applying the then current management procedure for hake over a 20-year period to an artificial data set generated by the operating

model. These (100) different sets corresponded to the statistical distributions associated with model parameters and future observations for each alternative overall model considered.

3. The results of the simulations were summarized by means of a small number of performance indices. These indices were chosen so that it would be straightforward for decision-makers to assess whether different levels of consumption of hake by seals were likely to have a substantial impact on the future prospects for the hake fishery.

What data were used?

Hake stomach content data:

Payne *et al.* (1987) detailed that stomach content data were collected during research cruises carried out by the Sea Fisheries Research Institute (SFRI). Each trawl was designed to last some 30 minutes, but because of the irregular topography of the sea bed, some trawls were shorter. The total catch from each trawl was sorted into species and weighed. Where possible, all hake caught were measured; otherwise stratified random subsamples of the hake catch were taken to estimate the length composition and the number of hake per species in the trawl.

A small subsample (usually 10 fish) was selected for biological analysis. These hake were selected so that at least three fish per species per 1-cm size-class were analysed during each half cruise. The purpose of this sampling scheme was to construct a representative age-length key for that component of the population vulnerable to the gear (Payne *et al.* 1987). Since distribution of predators and prey is not uniform across the survey area, this was likely to lead to some biases.

Age, length and mass were determined, maturation state was recorded and stomach contents were analysed. The stomach content analysis first involved visual classification of stomach by degree of fullness (Payne *et al.* 1987). Non-everted stomachs were removed whole and contents examined: Digestion state, mass and, where possible, length of each prey item were noted and the prey item was classified to the lowest possible taxon. Everted stomachs could not be analysed. Any items deemed to have been swallowed in the net were discounted.

Data from only the July 1988, January 1989, July 1989, January 1990, June 1990, January 1991, February 1992 and January 1993 cruises were considered, because the data for the surveys prior to July 1988 were not recorded in a consistent machine-readable manner. Analyses of the stomach content data collected during the cruises carried out between 1983 and 1986 may be found in Payne *et al.* (1987).

A sample of 2646 hake stomachs was considered in the study (this number was deduced by summing the sample sizes given in Table 2.4 in Punt, 1995, which classifies the hake stomachs considered in the study into empty, containing food and everted by length class). As well as summarising the classification of hake stomachs into empty, full and everted, by length-class, food items found in the stomachs of the hake were listed, and a breakdown of stomach contents of the two Cape hake species by mass, prey species group and predator length-class and age class was given. Further, the fraction of each hake age-class in the diet of hake age-classes by prey and predator species were calculated from the observed length distributions of hake in the stomachs of other hake by applying an age-length key.

Other hake data used in the study presented in Punt (1995)

- Hake catches by mass for every year from 1917 to 1992
- CPUE data (1955-1992), which were calculated from the directed effort of only part of the fleets involved in the fishery and are given in tons per standard day (Punt, 1994).
- Biomass survey data (1983-1993)

Seal data

Owing to time constraints the seal data has not been summarized here, but can be found in detail in Punt (1995).

What was the basic model structure?

The model considered hake, seals and “other predatory fish” but off the South African west coast only. In addition to feeding information considerations, this was because the catch of hake off the south coast was only about half of that off the west coast, and because there were more seals off the west coast. The base case model considered a single hake

species only (by pooling the two hake species), while two-hake species operating models were considered as sensitivity tests.

Age structure

The “other predatory fish” were modelled using a two-component (adult/juvenile) model since the age-structure of this element of the system was not considered qualitatively important. Both hake and seal populations however were modelled using fully age-structured models, since the diets of hake and seals change with age and were assumed to change over time because of changes in prey abundance.

Hake component of the operating model

Some important aspects of the model are highlighted below:

- The model was discrete with a six month time step, rather than continuous which would greatly increase computer-time requirements. This was argued as unlikely to affect the qualitative conclusions of the study.
- Sex structure was ignored, and therefore the number of recruits was a function of total mature biomass rather than its female component only.
- The model allowed for cannibalism/predation by hake, predation by seals and predation by “other predatory fish”.
- Recruitment was related to spawner-biomass by the Beverton-Holt stock-recruitment relationship.
- Took into account that most large *M. paradoxus* will have migrated out of the fishing grounds by the time they enter the plus-group.
- Hake fishery was approximated by a pulse fishery at midyear.
- Predation

The number of hake of eaten by “other predatory fish” was assumed to be related to the abundance of hake of species i and age a by a Holling Type II feeding relationship. Consumption of one age-class of hake by “other predatory fish” was assumed to be independent of the consumption of any other age-class. The number of hake of species i and age a which are eaten by "other predatory fish" was given by the equation:

$$D_{y,a}^{i,predfish} = u_a^i B_y^{opf} \left[1 - \exp\left(-v_a^i w_{a+1/4}^i N_{y,a}^i e^{\eta_{y,a}^{i,predfish} - \sigma_\eta^2/2}\right) \right]$$

where

u_a^i is the maximum number of hake of species i and age a which "other predatory fish" could plausibly eat during the first half of the year, if the system was at its average unexploited equilibrium level,

B_y^{opf} is the biomass of adult "other predatory fish", expressed as a fraction of its unexploited equilibrium level,

v_a^i is a parameter which determines the extent of saturation in the feeding functional relationship,

σ_η reflects variation in the diet, and

$\eta_{y,a}^{i,predfish}$ is from $N(0; \sigma_\eta^2)$

The number of hake dying as a result of predation by hake is more complex than predation by “other predatory fish” since size- and age-structure of these components change over time. It was assumed that the number of hake lost to predation by hake is affected by the number of predators, the number of prey, the “desirability” of different species / age-classes to a particular predator.

- It was assumed that that the daily hake ration of a predator of species j (either seals, *M. capensis* or *M. paradoxus*) is given by a Holling Type II feeding functional relationship, and also that the total daily ration remains constant throughout the year.

- The model allowed for competition between hake in a cohort when the biomass of that cohort was large. This was done to reduce unstable behaviour on occasions as a result of enormous cohorts moving through the population, thereby removing almost all of the juveniles by predation/cannibalism.

“Other predatory fish” component of the operating model

The “other predatory fish” model divided the population into adults (mature/recruited) and juvenile (immature/unrecruited) animals. The adults were subject to natural and fishing mortality, while the juveniles were subject to mortality due to hake and seal predation, cannibalism, as well as other factors. Stomach content data suggested that “other predatory fish” formed only a small component of diet of hake, and as such the impact of hake on “other predatory fish” was taken to be much smaller than that of seals.

Analysis of stomach content data

Cape hake are opportunistic feeders and therefore the relative importance of the various food items in their diet was considered likely to differ from area to area because of variation in the local abundance of the different prey species. This source of bias was ignored in the analysis because the variance which resulted from disaggregating the data by area (and season) tended to dominate the bias resulting from pooling.

The daily ration in grams of prey species s by predators in length class l was assumed to depend on average ingested mass of prey species s , as well as total evacuation time in days of prey species s .

The consumption model was based on the assumption that hake do not feed regularly, but instead ingest a meal (which may consist of several prey species) and digest it until the stomach is empty, after which they feed again. This assumption seemed justified, as fully digested and fresh prey items had been observed together only rarely in hake stomachs (Payne *et al.* 1987).

The model used for estimating time to 90% evacuation depended on the mass of the stomach contents, gastric evacuation rate, time since ingestion and a parameter which determines the shape of the relationship between stomach mass and time.

No experiments had been conducted to determine the gastric evacuation rate of hake. Therefore data from experiments conducted for other gadoids were used. Quantities needed to estimated parameters of the model for estimating gastric evacuation rate were meal size, time between ingestion and collection of stomach, mass in the stomach at sampling, temperature and predator mass. Model parameter estimates were very imprecise, so additional constraints were introduced from results from other studies in literature.

Estimation of free parameters

There were four estimable parameters for the single-hake-species model, and six estimable parameters for the two-hake-species model:

- K (carrying capacity) for hake (K^c and K^p for the two-hake-species model)
- h (steepness of the stock-recruitment relationship) for hake, and
- κ (parameter that determines the extent of saturation in the feeding functional relationship) for hake and seals (one for hake – or two for the two-hake-species model - and one or two for seals)

Three sources of information were used to estimate the parameters:

- For the one-hake-species model, the fraction of hake in the seal diet in 1991 is constrained to a specific value.
- The model should mimic the trends in the hake *CPUE* and biomass survey data. This is achieved by maximising a likelihood function.
- The fraction of hake in the diet of seven-year-old hake in 1991 should be as close to 35% as possible, which was the average of the fractions estimated for the respective diets of seven-year-old *M. capensis* and *M. paradoxus* hake.

When extending to a two-hake-species model there are two further sources of data:

- The split in 1991 of the hake component of the seal diet into *M. capensis* and *M. paradoxus* should satisfy the specifications in this regard as closely as possible.
- The ratio of *M. capensis* to *M. paradoxus* in recent years should mimic the species split indicated by the biomass survey estimates.

Sensitivity tests and performance indices

The effects of future consumption of hake by seals were examined using a hierarchy of operating models. A number of sensitivity tests were conducted, which, for the one-hake-species model, varied the extent of hake competition, the gear fishing selectivity on hake, the seal carrying capacity, the natural mortality rate, the fraction of hake in “other predatory fish” and seal diets, quantity of hake discards, the extent of variability in catchability, the extent of predation of seals on “other predatory fish” and hake on “other predatory fish”, the extent of cannibalism in “other predatory fish”, and MSYR, fishing mortality and exploitation rate of “other predatory fish”.

Sensitivity tests for the two-hake mode varied the fraction of *M. paradoxus* in the seal diet, the seal carrying capacity, and the fraction of hake in the seal diet.

Five measures of performance indices were chosen to quantify the behaviour of alternative management procedures over a projection period to year n :

- i. Average annual catch of hake over projection period
- ii. Depletion of the exploitable component of the hake biomass at the end of the projection period
- iii. Lowest (hake) depletion during the projection period
- iv. Interannual variability of hake catches
- v. Net present value (monetary terms)

What were the conclusions?

The following conclusions are taken directly from Punt (1995):

- 1) Knowledge of the fraction of hake in the diet of seals of hake is poor. Estimates obtained have high variance and could be substantially biased for a number of reasons. Information on the hake proportion of the hake diet is rather better, though there are some uncertain factors in this regard as well.
- 2) Anon. (1991) cautioned against regarding the quantitative results of this modelling exercise as reliable, but stated that (when culling options are compared to an absence of culling): “consistent increases or decreases in a summary statistic under a variety of assumptions about parameters would be noteworthy”. There are consistent indications for the one-hake-species models that as the size of a possible future seal cull is increased from zero, the catch rate and hence profitability of the hake fishery increase, while the average annual consumption of hake by seals decreases, under an $f_{0.2}$ harvesting strategy.
- 3) For the one-species-hake models, it seems that benefits to the hake fishery from a seal cull are larger for higher values of seal carrying capacity and the current fraction of hake in the seal diet. Conversely, for smaller values of these parameters (e.g. seals very close to their carrying capacity, or a 10% rather than 15% hake component of the seal diet), particularly large culls are needed for noticeable benefits to the hake fishery.
- 4) When observation and process error are introduced into the calculations, the medians of the distributions of the performance indices are hardly different from the deterministic results. Increased levels of observation and process error lead to wider distributions; process error is the main contributor to the variability, with future observation error having relatively little effect.
- 5) Results are qualitatively different for the two-hake-species operating model. In the case where the seals consume *M. capensis* only, a seal cull is counter-beneficial to the fishery because the consequent greater numbers of large *M. capensis* result in increased predation on *M. paradoxus*, whose abundance then declines to a greater extent than that of *M. capensis* increases. This result is less marked if seals predate on *M. paradoxus* as well (an aspect concerning which existing data provide little discriminating power given the difficulties of interpretation of seal stomach data).

3. Intermediate done by OLRAC

2008 work

OLRAC (2008) gave an overview of a method for incorporating hake predation and cannibalism into hake stock assessment calculations. The methods used the existing stock assessment methodology as a basis and developed this further only insofar as was required to capture the essential features of predation within the hake complex. The aim of the work was to calculate the basal mortality rate (a constant determining the proportion of deaths due to all causes

other than hake predation), but also the number of hake for each age class, gender and species consumed by hake, so that these could be included in the hake dynamics calculations.

The stock assessment methodology was as described in Rademeyer and Butterworth (2006), except that inter-species predation was incorporated, Pope's approximation was used for the catch equations instead of the Baranov equations, the model was sex-disaggregated and different individual weights were used for males and females.

The model made use of preference functions, which incorporated the assumption that predators of a particular size or age and sex have 'preferences' for prey of different sizes or age or sex. This function was used to split the amount of prey of a given species consumed by a predator into amounts per prey age class and prey gender. The preference functions were assumed to have the following features:

- A predator's preference function becomes zero when prey reach 45% of the length of the predator.
- No hake with a body length greater than 45cm total length is ever preyed upon by other hake.
- A predator's preference for prey peaks when prey lengths are 50% of their maximum possible prey length.
- Predator preferences drop to zero again when hake prey lengths decrease to 15% of the maximum possible prey length.

A beta function was used to interpolate across the full range of the preference function.

Dietary information was taken from Punt and Leslie (1995) and quartic or cubic relationships were fit to the daily ration percentages. The total daily and annual hake consumption rates were expressed initially in terms of daily ration as a percentage of body mass. These values were fitted to the age class information using an exponential curve, which was then used to obtain interpolated values for all age classes 0-15. Dietary percentages were assumed to fluctuate according to changes in the 'Prey preference weighted biomass' (the preference function weighted sum of the biomass at age and gender values across all age classes and genders for the prey species under consideration), via a relationship which is similar to the Holling Type II equation.

Three variants of the model were explored: a base case cannibalism model, a model that reduced all consumption rates by a factor of three (since it was thought that consumption amounts may have been overstated), and a model that excluded all predation of the 0 age group fish. (It was argued that in fisheries science it is generally accepted that considerable non-linear complexity occurs prior to the commercial recruitment of fish, and as such it might seem unreasonable to isolate and explicitly model just the hake predation related aspects of this, especially in the younger age classes.)

OLRAC (2008) presented the results of the work without further discussion. The results included a predator ranking for the two hake species in terms of age and sex, a comparison between the OLRAC assessment results to those obtained in Rademeyer and Butterworth (2007), as well as the parameter estimates, biomass trajectories and likelihood profiles for the variants and sensitivities. Plots of the preference functions used were also shown.

The main finding of this study was that across a wide range of assumptions about hake diet, predatory and cannibalistic processes led to estimates of *M. paradoxus* depletion levels that were more optimistic than had been estimated by assessments in which natural mortalities were year invariant (OLRAC, 2011).

2011 work

A DWG meeting in 2008 suggested modifying the OLRAC work as outlined above by including specific information (submitted to the workshop on seal-fishery biological interactions held in 1991 at UCT, Anon., 1991) about the preference of different sizes of hake (as predator) for different sizes of hake (as prey). The aim of the incorporation of these data was to address the criticism made at the DWG meeting that the set of prey-preference functions used in OLRAC (2008) were not necessarily consistent with the available data.

The 2011 work therefore focussed on the modification of the prey preference functions to achieve better agreement between model quantities and the available data. Modifications included estimating (with an upper bound of one) the maximum size of prey that can be consumed by a hake predator, which before had been fixed at 0.45 of the predator size; estimating the minimum size of prey that can be consumed by a hake predator, which before had been fixed at 50% of the maximum prey size; and estimating the proportion of the maximum size of prey at which the preference of a predator for prey reaches a maximum.

Further, OLRAC (2011) noted that the Holling Type II equation used for estimating the percentage of hake in the diet of hake dictates that the percentage of hake in the diet of other hake has to decrease as the hake resource is depleted. Modifications were made to allow the reverse to occur as well.

Finally, a penalty was added to the log-likelihood function to incorporate observed stomach content information in the overall model fitting process. While the 2008 work produced a likelihood profile for the *M. paradoxus* depletion levels, the updated work used the maximum likelihood approach.

4. Work planned

What issues are to be addressed?

It is proposed to initially model only hake to keep early work as simple as possible, but perhaps include the seal and other predatory fish components at a later stage. The primary question to be answered is whether taking interspecies predation and cannibalism into account will impact the key assessment results and thus potentially future management objectives

What further data are now available?

Assessment related

The following list has been provided by Rademeyer (pers. commn):

- Offshore trawl catches by species (1978-2010)
- Inshore trawl catches, assumed to be *M. capensis* only (1960-2010)
- Longline catches by species (1983-2010)
- Handline trawl catches, assumed to be *M. capensis* only (1985-2010)
- CPUE data
 - South and West coast historic (ICSEAF) CPUE (1969-1977 for the SC, 1955-1977 for the WC)
 - GLM standardized CPUE data separated by species (Glazer, 2006) (1978-2010)
- Survey abundance estimates and associated standard errors for both species (1985-2011)
- Catches-at-age (catches-at-length for years in which no ALK are available)
 - Summer survey for both species (1986-2011)
 - Winter survey for both species (1986-1990)
 - *Nansen* summer survey for both species (2000-2001)
 - Spring survey for both species (2001-20011)
 - Autumn survey for both species (1991-2011)
 - Offshore trawl fleet for both species combined (1975-1996, 2005-2007)
 - Inshore fleet for *M. capensis* only (1989-2000)
 - Longline fleet for *M. capensis* only (1994-2000)

Feeding data

The stomach content database is currently being validated by DAFF and as such a detailed summary of the number of records will not be given here. A rough estimate based on the current invalidated dataset is that there are likely to be around five times as many samples available for this study as were available in 1995, although this figure will be revised once the validated dataset is available.

Each hake record gives:

- Biological information, including fish number, total length in cm, wet weight of whole fish, sex, maturity, weight of fish gonad in grams, stomach state (empty, 25% full, 50% full, 75% full, 100% full, everted and regurgitated), weight of fish stomach contents in grams, total number of items in stomach (different species or same species in diff stages of digestion) and otolith number.
- Stomach content information, including regurgitated state (no sign of food, food in mouth - none lost, food in mouth - some lost, and stomach flaccid end – possibly some lost), species code for prey item, wet weight of prey item, min and max prey length in cm (for recent years), number of individuals the prey item was composed of, digested state (caught, very fresh, partially digested, well digested, only traces).

What model structure should first be attempted?

Spatial structure

The proposal is to start with South Africa only, and perhaps incorporate Namibian data at a later stage if possible. A matter for discussion is whether to look at the west coast only or the whole of South Africa. The latter seems preferable as today South African hake stocks are assumed to be common across both west and south coasts, which were treated separately in the early 1990s.

A further question is what spatial structure is needed. Punt (1995) looked at three longshore sections: North of 32°S, 32-34°S, South of 34°S on only the west coast. An initial suggestion is to look at two longshore (west and south) and two offshore (depth) strata.

Population dynamics

It is proposed to ignore sex structure initially for simplicity, and only much later extend the model to something similar to Rademeyer's current hake assessment. A more pertinent question is if there is a need to immediately include other predators, such as seals and Punt (1995)'s "other predatory fish", or if it would suffice to initially restrict the model to hake alone,

Fitting to data

Rademeyer's current hake assessments fit to catch-at-length and age-length-key data. Would it be best to do this also, or rather to restrict for simplicity to years for which ageing has been conducted, and age-distributions can be calculated by combining ALKs and CAL distributions external to the model fitting process?

Feeding aspects

The Holling Type II form for feeding relationships as given in Punt (1995) will definitely be implemented, but the question is if others should be tried also (for example foraging arena model as in EwE). Further, given more and a longer time series of feeding data, should any attempt be made to allow relationships to have an estimable temporal component?

Punt (1995) gives estimates of daily rations. Since there is now substantially more data available, these would need to be updated. In 1995, there were no data for hake to estimate the evacuation rate directly, so instead information derived from other gadoid species had to be used. Is there any such hake-specific data available now?

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