Distribution and migration of deep-water hake (*Merluccius paradoxus*) in the Benguela Current Large Marine Ecosystem examined with a geostatistical population model – a preview *

Teunis Jansen[1,5], Kasper Kristensen[5], Uffe Høgsbro Thygesen[5] and Jan E. Beyer[5]

1) BCC – Benguela Current Commission, Private Bag 5031, Swakopmund, Namibia.
2) MFMR – Ministry of Fisheries and Marine Resources, PO Box 912, Swakopmund, Namibia.
3) DAFF – Department for Agriculture, Forestry & Fisheries, Cape Town, South Africa.
4) Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway.
5) DTU AQUA – National Institute of Aquatic Resources, Charlottenlund, Denmark
6) Rhodes University, Department of Ichthyology and Fisheries Science, P.O. Box 94, Grahamstown 6140, South Africa

Corresponding author: Teunis Jansen; DTU AQUA - *National Institute of Aquatic Resources, Technical University of Denmark; Charlottenlund castle, 2920 Charlottenlund, Denmark; Tel.: +4530667840; Fax: +4533963333; E-mail address:* Tej@aqua.dtu.dk.

*** Disclaimer #1:** This study is *in progress.* The results are not final, so they should not be used outside the EcoFish phase II workshop.

*** Disclaimer #2:** Following scientists are contributing to this study: Paul Kainge[2], Deon Durholtz[3], Tore Strömme[4], Marek Lipinski[6], John Kathena[2], Margit Wilhelm[1,5], Tracey Fairweather[3], Sarah Paulus[2], Henrik Degel[5], Hashali Hamukuaya[1]

Abstract

Deep-water cape hake (*Merluccius paradoxus*) is of primary ecological and economic importance in the Benguela Current Large Marine Ecosystem in South Africa and Namibia. The assessment and management is done for two separate stocks, assuming no transboundary movements and no spatial population patterns within each stock area (country). Results from single transboundary surveys have indicated that this is not likely to be true. In the present study, we combine data from multiple demersal trawl surveys from the entire Benguela large marine ecosystem to estimate spatial and temporal distribution patterns of *M. paradoxus*. We follow the natal homing hakes from 0.5 to 7.5 years of age as they form three main spatial trends. From the centrally located nursery area on the African south-west coast, they initiate their migration in their second year. The resident hakes stay or move up to 3-400 km south or north, only to return in their third or fourth year. The migratory hakes migrate up to 1200 km either north or south-east and return at the age of 6+ years. The alongshore migrations are combined with migrations towards deeper waters. From the nursery area at 150-250 m depth they move deeper and at the age of 4 most of the hakes are in 350+ m of depth.

Our results indicate a transboundary nursery hotspot, as well as transboundary migration of several cohorts. Consequently, assessment and fisheries management could be improved by shifting to an internationally scope.

We also suggest that the southern migratory part of the population migrate out of the area covered by the surveys. Incomplete coverage of the stock appears to be a problem for stock assessment; an extension of the survey should therefore be considered.

Our analyses were done with a new Latent Cohort GeoPop model – a geostatistical model (aggregated log Gaussian cox process model with correlations). The purpose of this version is to track the cohorts in time and space.

Keywords: *Hake, northern Benguela, southern Benguela, Merluccius, paradoxus, transboundary, migration, geostatistics, LGC, growth, gear selectivity, South Africa, Namibia, demersal trawl*

Introduction

Deep-water cape hake (*Merluccius paradoxus*) is among the most dominant demersal fish species in the South East Atlantic. The species is ecologically important in the Benguela Current Large Marine Ecosystem as an opportunistic predator (mainly fish, including hake) (Botha, 1980; Payne et al., 1987), and as prey for the top predators such as fur seals, cephalopods, sea birds and many demersal and pelagic fish species (Pillar & Wilkinson, 1995). *M. paradoxus* (together with the sympatric shallow water hake *M. capensis*) is also targeted by fisheries throughout its distribution (BCC, 2012). Annual hake landings in Namibia, South Africa and Angola averaged 300,000 tonnes per year in 2000-2010, with nearly 30% being *M. paradoxus* (BCC, 2012). Hakes are the economically most important fish stocks in both Namibia and South Africa, worth about 5 % of the GDP in Namibia (MFMR & NPC, 2013).

M. paradoxus inhabit the continental shelf slope from around 17°S in Angola/Namibia to about 27°E in South Africa (Payne, 1989). Spawning takes place between 200 and 600 meter depth South and West of South Africa (Jansen & et al., in prep)+other refs. Established views suggest a largely stationary population with some local inshore-offshore movement and weak patterns of geographical hot-spots (Payne & Punt, 1995). However, it has been suggested earlier (Le Clus et al., 2005) that this picture may be inadequate, largely due to sampling limitations. An analysis of DNA microsatellites indicated one panmictic stock (Bloomer et al., 2009). This was confirmed when examining in mtDNA from less than three years old hakes (von der Heyden et al., 2010). However, the mtDNA revealed significant differences between hakes from each side of the Orange River mouth (i.e. national border between Namibia and South Africa) (von der Heyden et al., 2010). The spatial population structure (stock structure) thus remains uncertain and several hypotheses have been proposed. Most recently, an analysis of length distributions from survey catches supported the panmictic view and described alongshore and offshore migrations patterns (Strømme et al., In prep.). Today, the species is assessed and managed separately in Namibia and South Africa (Figure 1).

Nearly all studies of the biology and ecology of *M. paradoxus* have been on a local or national scale, even though several decades of high quality research survey data have been collected from demersal bottom trawl surveys throughout its entire distribution area. Regional transboundary analyses on the combined survey data sets (which only recently became available) have not been performed because the data are not directly comparable. The various surveys conducted by the three vessels have used different trawl gear with different catch efficiency. In the present study, we quantify this effect, so we can address the spatial population dynamics with a state-of-the-art integrated geostatistical population model. We develop a new version of the “GeoPop” model, which combines a novel geostatistical approach with a simple population model. The central aim of the study is to analyse the spatial population dynamics. We do this by estimating time series of cohort-specific distributions and map them for examination of putative migration patterns.

Materials and methods

Scientific trawl survey data

M. paradoxus were caught during demersal trawl surveys on the continental shelf and slope in the Benguela-Agulhas ecosystem from 17°S in the North, round Cape of Good Hope to 27°E in the west (Fig. 1). The surveys are conducted each year in January-May for routine biomass calculations by the Ministry of Fisheries and Marine Resources (MFMR) in Namibia and the Department of Agriculture Forestry and Fisheries (DAFF) in South Africa. No trawl samples were available from Angolan waters due to species identification problems between *M. capensis* and *M. paradoxus* and *M. polli* (Benguela hake, which is largely caught in Angola). Three different trawl gear types were used, each fishing at a different trawl speed or with different size spread or ropes (Table 1). Total catch was weighed and sorted by species. Large catches were subsampled. The weight of the hake catch (separated by species) was recorded and total lengths of individual hake were measured in cm (rounded down). Subsamples were subsequently raised to the total catch.

The standardized efficiency of the trawl was compromised by very strong winds in 2002 and 2011off the South African west coast (Wieland et al, in prep). These stations were therefore removed from the dataset.

Catch Per Unit Effort (CPUE) of each length group in each haul was calculated as number per hour trawled. This measure was used as a relative index of hake density.

The survey dataset consisted of 7.1 million measures *M. paradoxus* in 7,000 trawl hauls from 1998 to 2011. 324 of the hauls were especially informative in relation to gear inter-calibration, because they were taken with different gears, less than 3 hours apart and at a maximum distance of 18 nautical miles (nm). The samples were from the entire region (Figure 1), and they were fairly equally distributed among the years (Figure 2a). Most samples were taken in January-February, while the South African South coast was covered in April-May (Figure 2b). Trawling was predominantly done during the day (Figure 2c). The Gisund trawl was used most frequently (Figure 2d).

The Latent Cohort GeoPop model

A geostatistical model (aggregated log Gaussian Cox process model with correlations) was used to describe the density index of *M. paradoxus* cohorts through space and time, along environmental gradients, observed using various gear types, as the hake recruited, grew and died.

Related models have previously proved their value for cod (Kristensen et al., 2013; Lewy & Kristensen, 2009) and mackerel larvae (Jansen et al., 2012). However, this new “Latent Cohort GeoPop model” tracks the cohorts. This is not only biologically meaningful, it is also advantageous for the complex and time consuming model fitting algorithm to reduce the number of parameters from 100 length classes to eight year classes. To obtain growth rates independent of otoliths-based age data, we integrated a length-frequency analysis (LFA) in the model complex. The LFA estimates the age distribution of a given length class by following the cohort-peaks in the length frequencies as they grow (Equation 2).

We modelled the density index (CPUE) for eight age classes in the period 1998 to 2012. The cohorts were followed in time steps of one year and in a spatial resolution of 25x25 km. These 135,120 (8 age classes x 15 years x 1126 grid-cells) random variables were assumed to follow a log Gaussian distribution, and determine the mean of catch (in numbers), which are assumed to follow a Poisson distribution, conditional on densities. This model structure is referred to as a log-Gaussian Cox process model, and has been shown as a good representation of count data from catches that are correlated, over-dispersed and with many zero-values (Kristensen et al., 2013). The Poisson distribution allows for zero catches, while the randomness of the density fields imply over-dispersed catches (relative to Poisson) and in particular many more zero catches than would be found in a pure Poisson model. Finally, the catches inherit the correlation structure of the density field.

A key feature of the model was the utilization of the information that resides in the patchy distribution of fish. This behavioural element was modelled in three parts: First and second, patchiness in space and in time on a large scale (correlations between cells) and, third, the tendency of fish to aggregate with fish in similar sizes on a local scale (within age groups, within trawl hauls, "nugget effect").

The spatial large-scale correlation was assumed to decay with distance and the stability over time of these patterns was estimated as the correlation from year to year of the density in a given cell. Temporal correlation decayed exponentially with distance in time (years) and spatial correlation did approximately the same. However, in order to avoid correlation over land (e.g. the Cape point), we implemented the spatial correlation effect as a Gaussian Markov random field. To present the parameter estimates of these correlations in a meaningful way, we expressed the distance (*H*) and de-correlation time (*T*), as the distance in space and in time where the correlations have decayed to e^{-1} (explaining approx. 14% of the variance). Documentation of these correlation structures were published in Kristensen et al. (2013).

The third relation in the model that should reflect fish behaviour was the "nugget effect". Catches of certain fish sizes tend to be over-represented in trawl hauls compared to the size distribution in the sampled population. This may be due to size structured aggregations (schools) or because the local habitat favours fish of a certain size e.g. through the available type of food. This local effect was accounted for by estimating the age-class specific variation in the hauls (σ_N^2).

A simple population model related the cohort abundance index from one year to the next, by estimating the mean recruitment (N_0) and mean total mortality (*Z*). These processes were assumed to be independent of space and time. The mean total mortality was modelled as a constant corresponding to the exponential decay model:

$$N_t = N_0 e^{-\overline{Z}\Delta t} ,$$

where N_t was the abundance after the mortality $\overline{Z}$ (year^{-1}) in Δt time steps (in years)

We linked the observations by length to cohorts, by a size spectrum analysis. This part of the model followed the cohort signals as abundance peaks that grew up through the size spectrum. For simplicity, we assumed that the size distribution the individual fish in a cohort is given by a Gaussian density with a mean determined by a von Bertalanffy growth model:

$$L = L_{inf}(1 - e^{-K(a-t_0)}),$$

where L is the mean length in cm at age class *a* (years), $L_{\inf}$ (cm) the mean length of infinitely old fish, i.e. the asymptotic length at which growth is theoretically zero, K (Year^{-1}) is the rate at which L approaches $L_{\inf}$ and t_0 (years) is the x-axis interception, i.e. a theoretical age at length 0 cm.

The standard deviation of the Gaussian distributed individual lengths around the mean length at age was assumed to increase linearly with age with $\sqrt{\sigma^2_{rate}}$ from the initial standard deviation $\sqrt{\sigma^2_{init}}$.

The first cohort peak was assigned an age of 0.5 years, …

Finally, the catch is affected by the catchability of the gear and this effect was implemented as

$$SF_G = \gamma(1 + 3^{-(2/SR_G)(l - L50_G)})^{-1},$$

where *SF* is the selection factor, γ is the efficiency factor, *SR* is the selection range and L50 is the fish length (cm) at half selection for three different gear types *G*.

The parameters in the model were estimated using the maximum likelihood principle based on the Laplace approximation and thus the estimation follows the principles of Kristensen et al. (2013). However, the present model was more challenging due to non-convexity issues of the aggregated log Gaussian Cox process and the much larger area and amount of data - see details in Supplementary information 2. When possible, we followed the parameter notation of Kristensen et al. (2013). A more concise documentation of the present model was furthermore given in Supplementary information 1.

The fitted model was finally used to calculate annual estimates of the relative index of hake density (CPUE) for each cohort in each age class (0.5-7.5) in each 25 x 25 km cell. These spatiotemporal distribution patterns were also transformed into a more meaningful coastline-oriented coordinate system. This was done by projecting the estimated abundances in the Cartesian coordinate system onto a curvilinear axis following the coastline from Port Elizabeth on the South-African south coast to the Namibia-Angola border (Kunene River) in the North (see Fig. 1). The shortest distance to any point on the coastline, as defined in the R package “mapdata” (Becker et al. 2013), was used. The same coastline definition was used for all maps (Figure 1).

Results

The model was fitted to the catch data and the parameter estimates are given in Table 2. The fitted model explained 67% of the variation in the data. However, it was not possible to estimate the uncertainties of the parameters using the standard approach, because of an irregularity in the likelihood surface. [***Disclaimer #3: This is the challenge we are addressing at the moment. The estimation problem mainly affects the gear selectivity. The distribution-maps are to a large extent OK, however, the overall density estimates, especially Namibia vs. South African south coast are not scaled correctly yet. We have therefore removed text and figures about the gear effect and growth. The rest is given for the user to understand the approach and get an understanding of the information that will be provided in the final peer reviewed paper***].

The resulting standard errors of the parameter are given in Table 2.

Spatial patterns (distribution, migration and population structure)

The relative index of hake density (CPUE) was estimated by year and age class in each of the grid-cells throughout the study area. The hake densities were found to be spatially correlated with a spatial de-correlation distance (*H*) of 268 km. [spatial variance]. The local abundance varied substantially from haul to haul, with a CV of 70% (nugget effect). The spatial patterns of the cohorts were found to be fairly stable with a temporal de-correlation period (*T*) spanning 2.4 years. We illustrated the main trends in age specific distributions by mapping the average spatial distributions of the six cohorts that the model could follow from the ages of 0.5 to 7.5 years (Figure 3-7). These average distributions were then used to infer putative migrations through their life. We analysed the alongshore and the off-shore (depth) migration separately.

For scrutiny of alongshore migration patterns, we projected the distributions onto a curvilinear axis following the coastline from Port Elizabeth in the south-east to the Namibia-Angola border (Kunene River) in the North. The resulting alongshore distributions were then plotted by age for each cohort (Figure 5-9) and for the average of all cohorts (Figure 7-11). The 0.5 year old recruits were concentrated in an elongate retention area from Cape point to 50 km north of the Orange River mouth. Highest densities were found north of the Olifants River mouth (Figure 3 and Figure 7). This initial pattern was preserved well into the second year, after which, *M. paradoxus* began an alongshore redistribution (Figure 7-11). From the age of 2.5 years, the distribution was clearly different than the recruit distribution, showing that the recruits had spread out. This developed into a broad resident patch at the nursery area, divided from a northern and an eastern migrating patch. They reached their outermost positions at the age of 4.5, after which they slowly returned. However, the southern migrating patch on the South African south coast disappears between the age of 4 and 6, close to the edge of the surveyed area (around 27°E). These patterns were illustrated by adding the movements of the centre of gravity (CoG) on each side of Orange River mouth and Cape good hope onto Figure 8 (grey dashed lines). We estimated the south-eastern CoG between the age of 4 and 6 by assuming an annual alongshore movement at the same distance as observed in the northern migration. At the age of 5, the northernmost observed hakes had migrated at least 1200 km and the CoG had reached a distance of 750

km to the Orange River. In total, the hakes have moved up to 2400 km alongshore in 7.5 years, assuming a complete return migration. The alongshore migration was combined with migration towards deeper waters (Figure 9). At the age of 6.5, where 99 % of *M. paradoxus* are mature (Singh et al., 2011), the migrating components of the population seemed to have returned to the spawning area (Jansen & et al., in prep). The depth distribution was narrower towards the south (Figure 9). We could thus confirm the well-known offshore migration to deeper waters with age (Figure 10) and expand the understanding of the depth migration by showing systematic spatial differences.

The distribution maps and plots showed that the border between Namibia and South Africa, presently used to separate *M. paradoxus* stocks, is in a high density nursery area. The national border did not coincide with any discontinuity of the recruit distribution (Figure 7). Examination of the distribution changes through the first 4 years of life of each year class indicated transboundary movements of the year classes 1998, 1999 and 2000. Transboundary migration may very well have taken place every year since then, but this is not clearly reflected in the distribution sequences.

The double-sided return migration clearly demonstrates natal homing, but with an unknown precision. Furthermore, a large part of the population seemed to be more resident "resident" with none or short migrations in relation to the nursery and spawning area.

Abundance time series

CPUE time series of the recruits were calculated for each area (Figure 11a). The overall annual recruitment increased substantially from a relatively low level in 1998-2002, to a higher level in 2003-2011. The recruitment was relatively stable in each of these periods. The increase in recruitment was followed by an increase in larger *M. paradoxus* (Figure 11c).

Discussion

The GeoPop Model and its fit to the observations

The finding of a ridge in the likelihood surface lead to some concern whether the fitting procedure had found the global optimum. The reliability of the estimates was therefore tested by selecting "true" parameters for a virtual population example. The population was then sampled and the parameters were estimated from the samples. This demonstrated that the original parameters could be re-estimated despite of the irregularity of the likelihood surface. This test was documented in Supplementary information 2.

[ToDo: temporal variance age vs. cohorts in space]

Spatial patterns (distribution, migration and population structure)

Maps and plots of the distribution of *M. paradoxus* were created as age explicit overviews for the entire Benguela large marine ecosystem. The most parsimonious change from one age distribution to the next clearly indicated ontogenic migration patterns of the juvenile and adult hake.

The migration patterns are generally in agreement with the results presented in Strömme et al. (in prep), but with some differences:

1. We find the 0.5 years old recruits in an elongate retention area from Cape point to 50 km north of the Orange River mouth, while Strömme et al. (in prep) found one central nursery area between Hondeklip Bay and Orange Banks.
2. Strömme et al. (in prep) found an initial coastward migration of 10-15 cm fish, which did not appear in our results. This coastward migration could have been missed due to our annual time steps. This was similarly missed in a GeoPop analysis of migration of *M. capensis* (Jansen & et al., In prep.).
3. [Tore/Marek, could you please add other differences, if any, to this list]

Furthermore, our findings suggest that the Southern migrating subpopulation moves, either vertically or horizontally, out of the area covered by the South African south coast survey. The subpopulation disappeared close the eastern edge of the survey area only to reappear two years later. The disappearance coincides with the age where the northern migrating hakes are at the greatest distance from the nursery/spawning, thus strongly suggesting that the disappearance is due to eastern migration out of the survey area. Therefore, we recommend that the South Africa south coast survey be extended at least 600 km to the east in order to cover the main distribution of the 4-6 year old eastern migrating hakes. This corresponds approximately to 30°E outside Durban. The disappearance of the 4-6 year old eastern migrating hakes corresponds to an unexplained drop in south coast survey selectivity in the assessment of *M. paradoxus* (Rademeyer & Butterworth, 2013). If this hypothesis is verified, then the assessment model should feature an estimation of the missing hake.

A similar problem with insufficient depth coverage of the surveys has been raised in the literature. While the Namibian survey has covered the area down to 6-700 m, the South African west coast survey has missed substantial parts of the population of larger fish because the survey only fished down to 500 m before 2011 (Wieland et al. in prep).

In our treatment of the spatial patterns, we presented annual snapshots of austral summer distributions. Seasonal migration patterns were not included. Such seasonal movements have been suggested as annually repeated inshore-offshore movement of hake in South African waters (Millar, 2001), with the offshore movement happening in winter where the *M. paradoxus* is known to spawn (Jansen & et al., in prep)+other refs.

The indication of transboundary migrations between South Africa and Namibia, suggests that assessment and management can be done more optimal internationally than nationally. A new assessment approach could also consider explicit modelling of the large scale pattern of resident versus migratory parts of the population. These three temporary subpopulation units could be growing at different rates. Most likely also experience different natural and fisheries mortality rates in the years when they are semi-separated. Accounting for these dynamics in a transboundary integrated stock

assessment model that includes hake size-species interactions, may provide management advice closer to the maximum the sustainable yield (MSY).

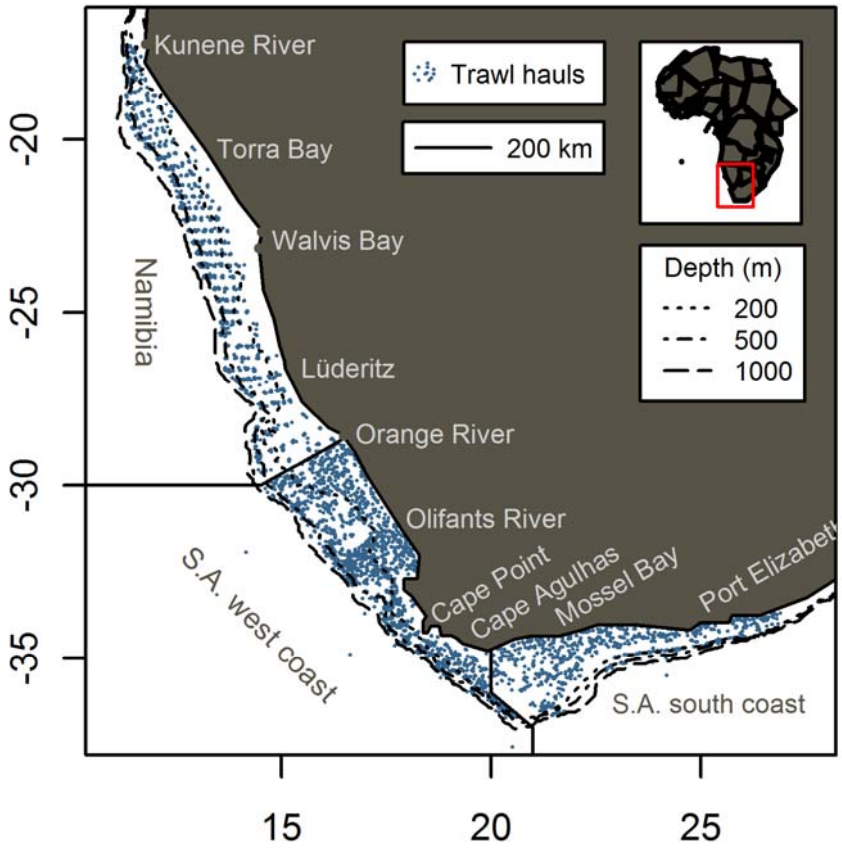
Conclusion

[See abstract]

Acknowledgements

We wish to thank the lab and field assistants from NatMirc (Namibia), DAFF (South Africa) and Norway that sampled and measures the many hakes analyzed in the present study. The sampling was funded by MFMR (Namibia), DAFF (South Africa) and Norway. Data analysis and publishing was funded by EuropeAid through the EcoFish project (CRIS Number C-222387).

Figure legends



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317 Figure 1. Map of study area with sample locations (dots), isobaths and place names referred in the text.

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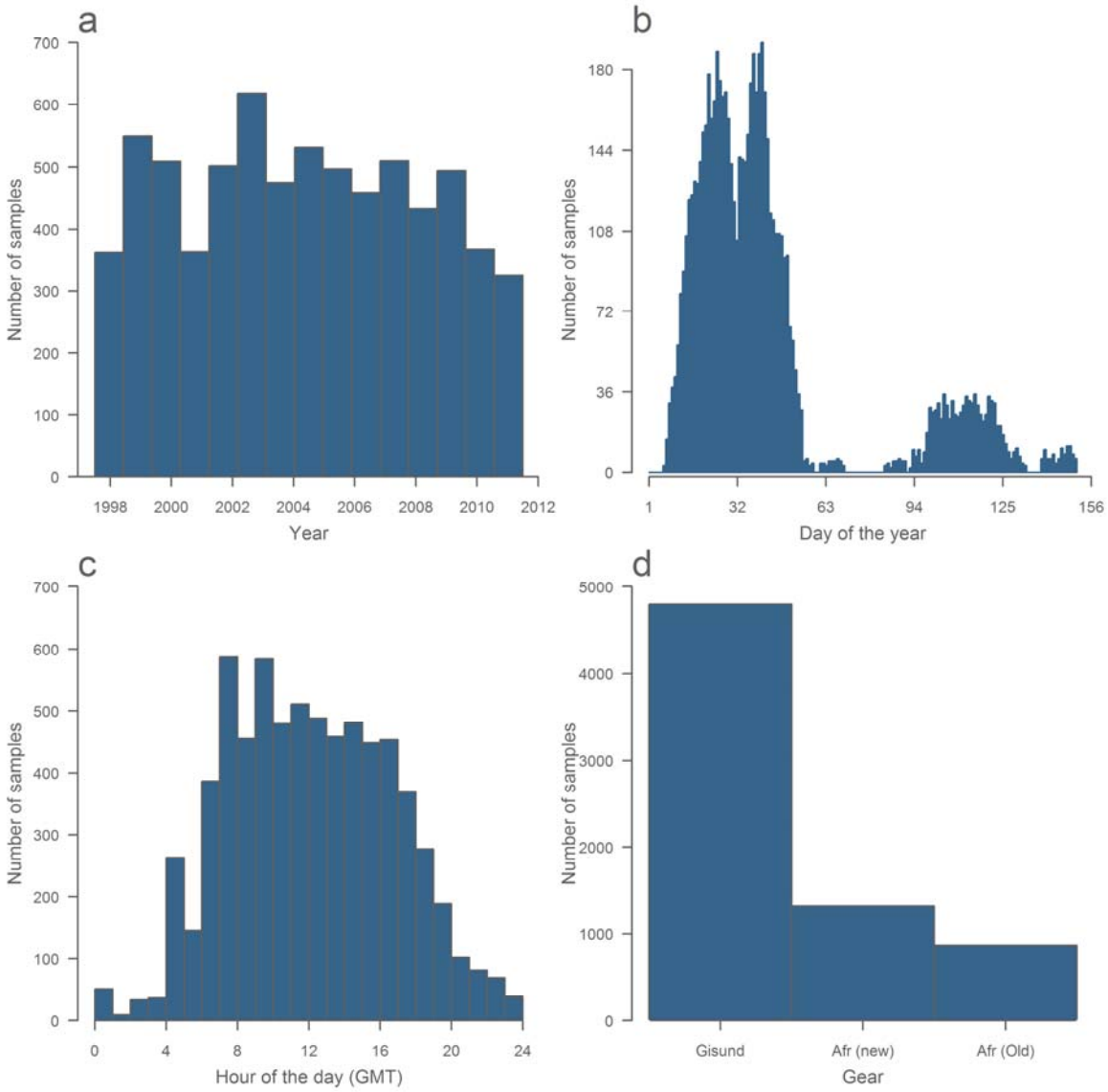

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320 Figure 2. Bottom trawl survey samples (trawl hauls) from 1998-2011 in the studied area. Number of
321 samples by a) year. b) ordinal day. c) hour of the day. d) gear type.

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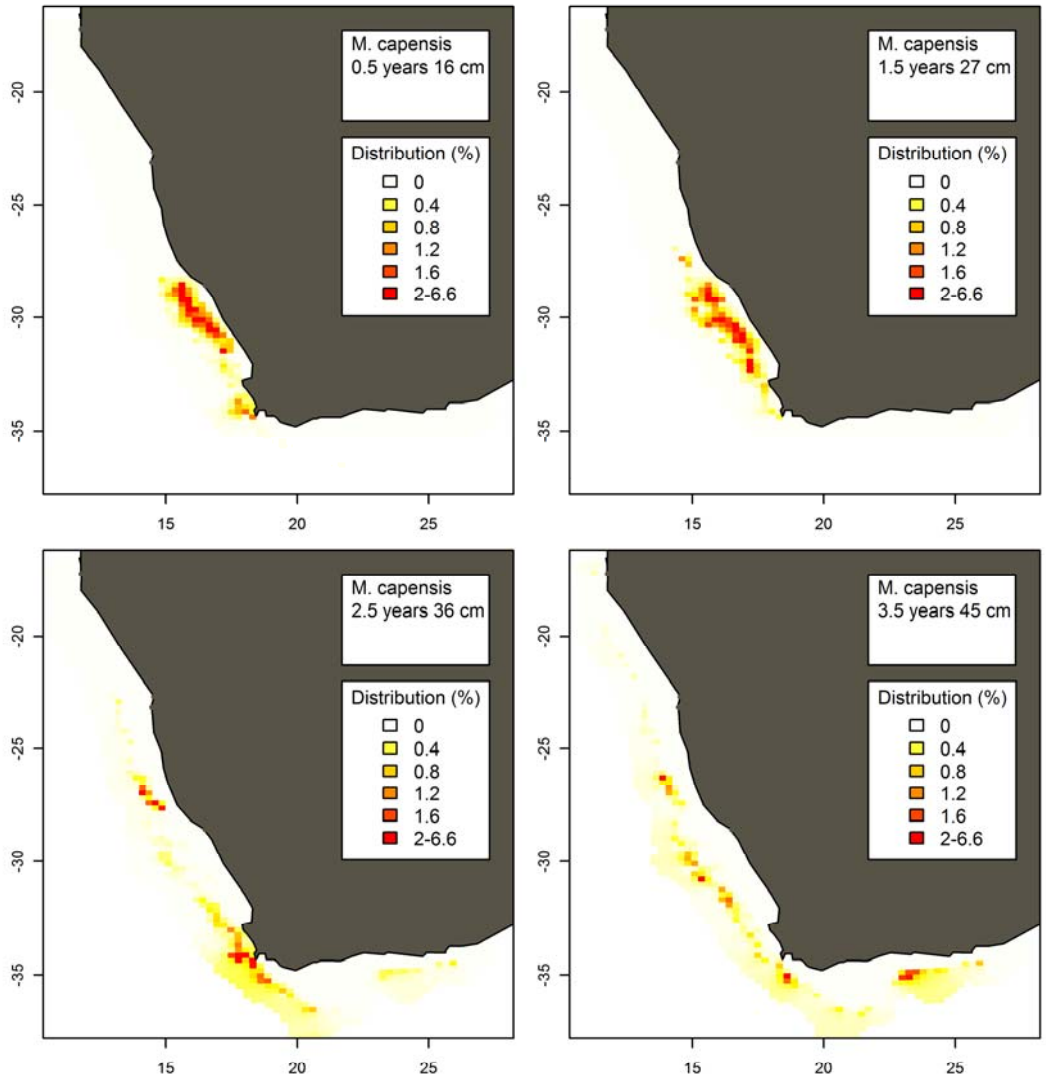

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324 Figure 3. Distribution maps of deep water cape hake (*M. paradoxus*) by age. a) 0.5 years. b) 1.5 years. c)
325 2.5 years. d) 3.5 years.

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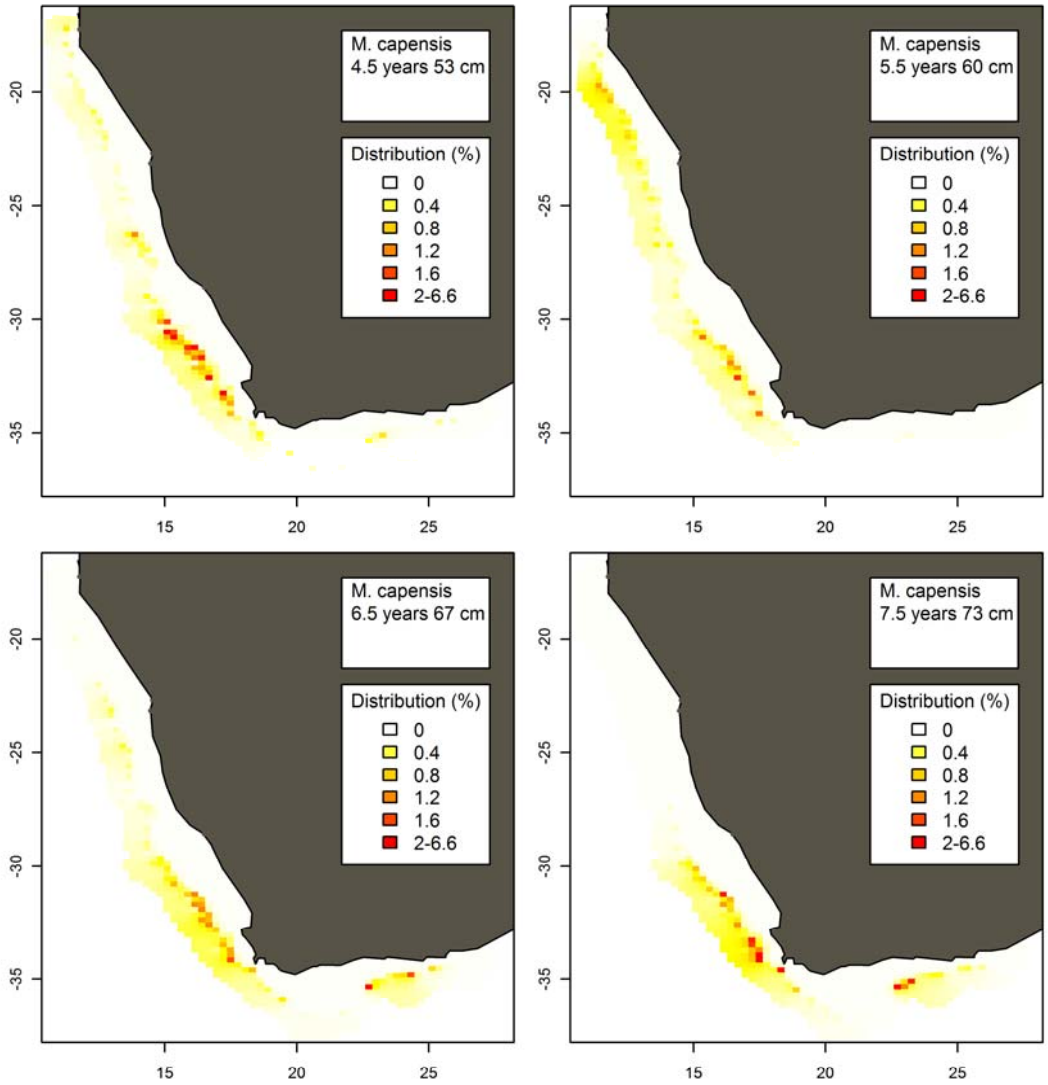

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328 Figure 4. Distribution maps of deep water cape hake (*M. paradoxus*) by age. a) 4.5 years. b) 5.5 years. c)
329 6.5 years. d) 7.5 years.

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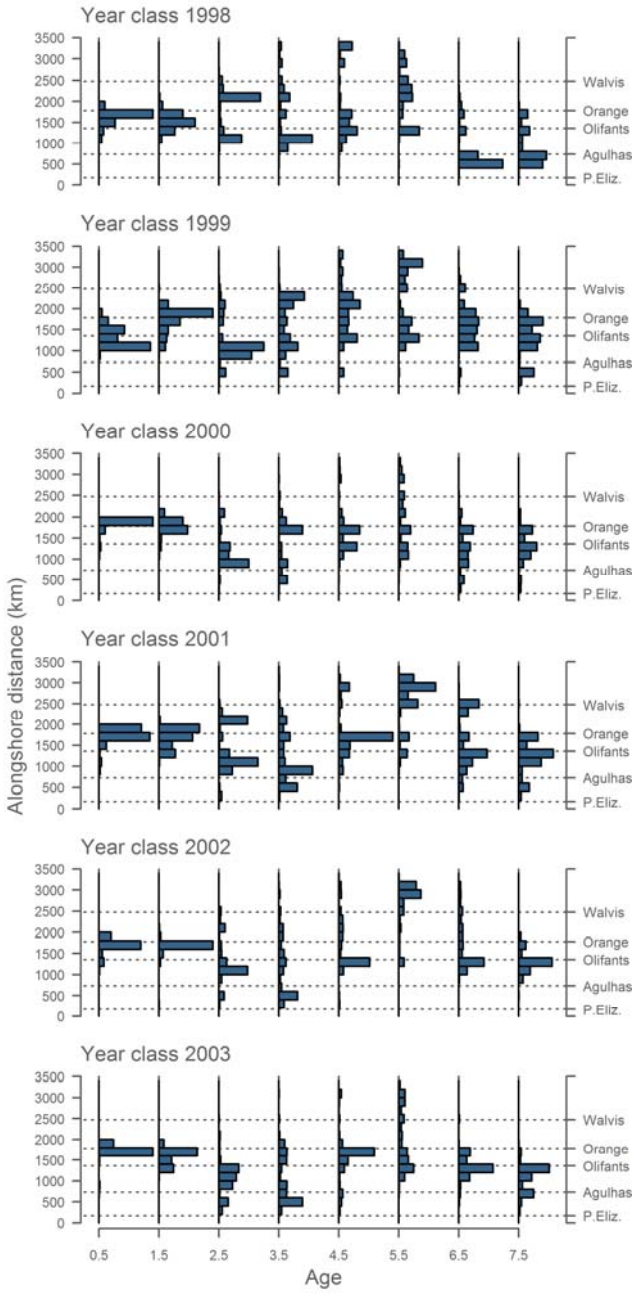


Figure 5. Alongshore distribution in number of fish by age for cohorts 1998-2002 of deep water cape hake (*M. paradoxus*). The spatial distribution has been projected onto a curvilinear axis following the coastline from Port Elizabeth in the south-east to the Namibia-Angola border (Kunene River) in the North.

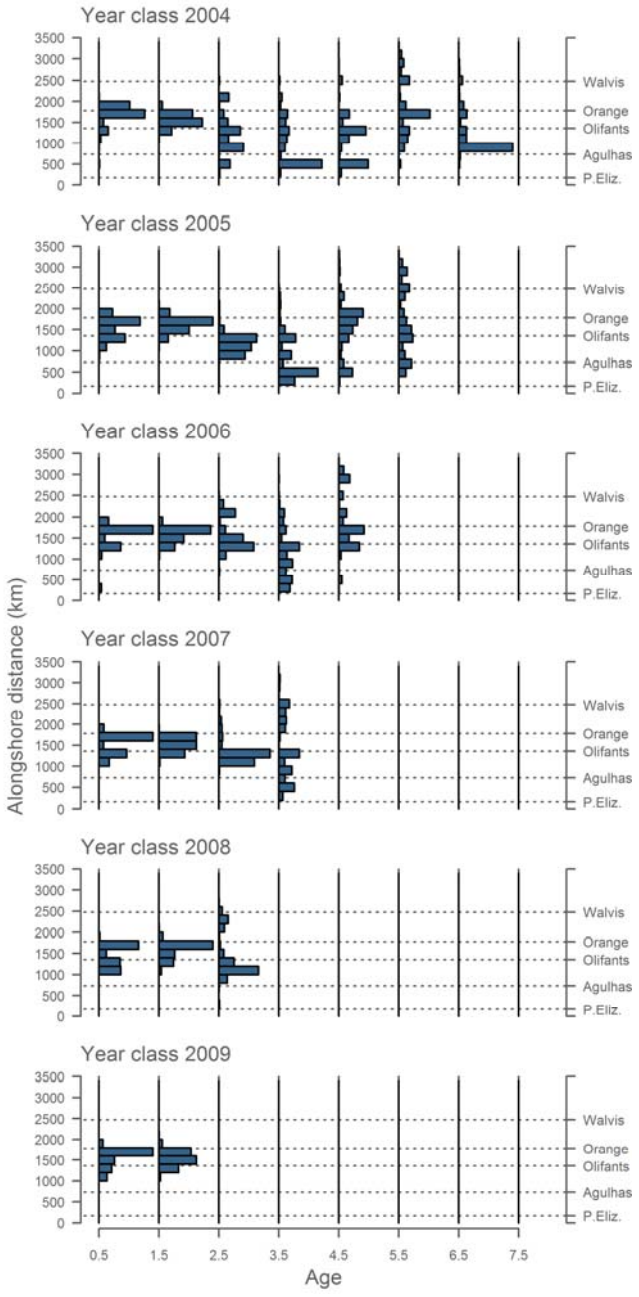
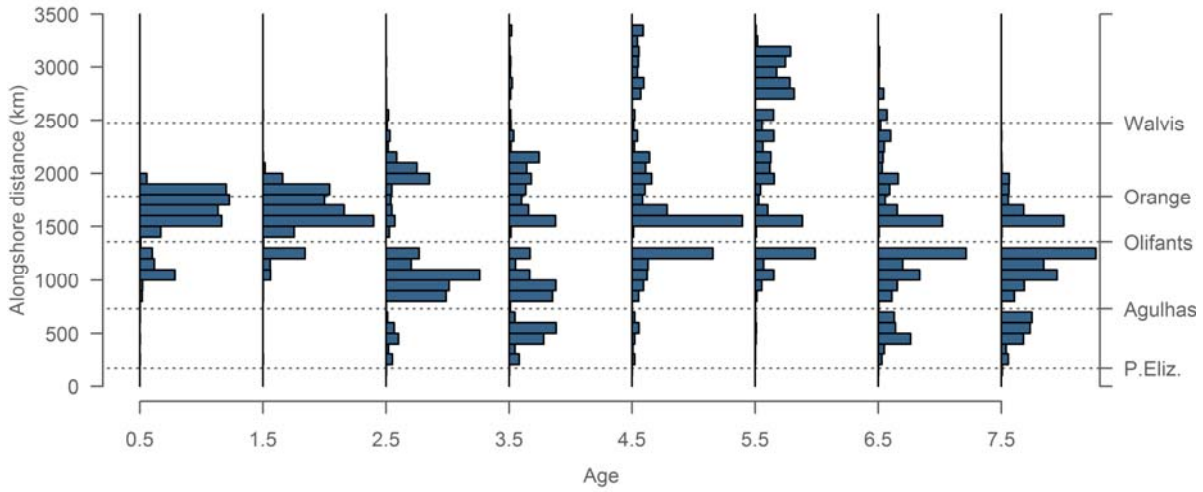


Figure 6. Alongshore distribution in number of fish by age for cohorts 2004-2008 of deep water cape hake (*M. paradoxus*). The spatial distribution has been projected onto a curvilinear axis following the coastline from Port Elizabeth in the south-east to the Namibia-Angola border (Kunene River) in the North.



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344 Figure 7. Alongshore distribution by age of deep water cape hake (*M. paradoxus*). Average of all year
345 classes. The spatial distribution has been projected onto a curvilinear axis following the coastline from
346 Port Elizabeth in the south-east to the Namibia-Angola border (Kunene River) in the North.

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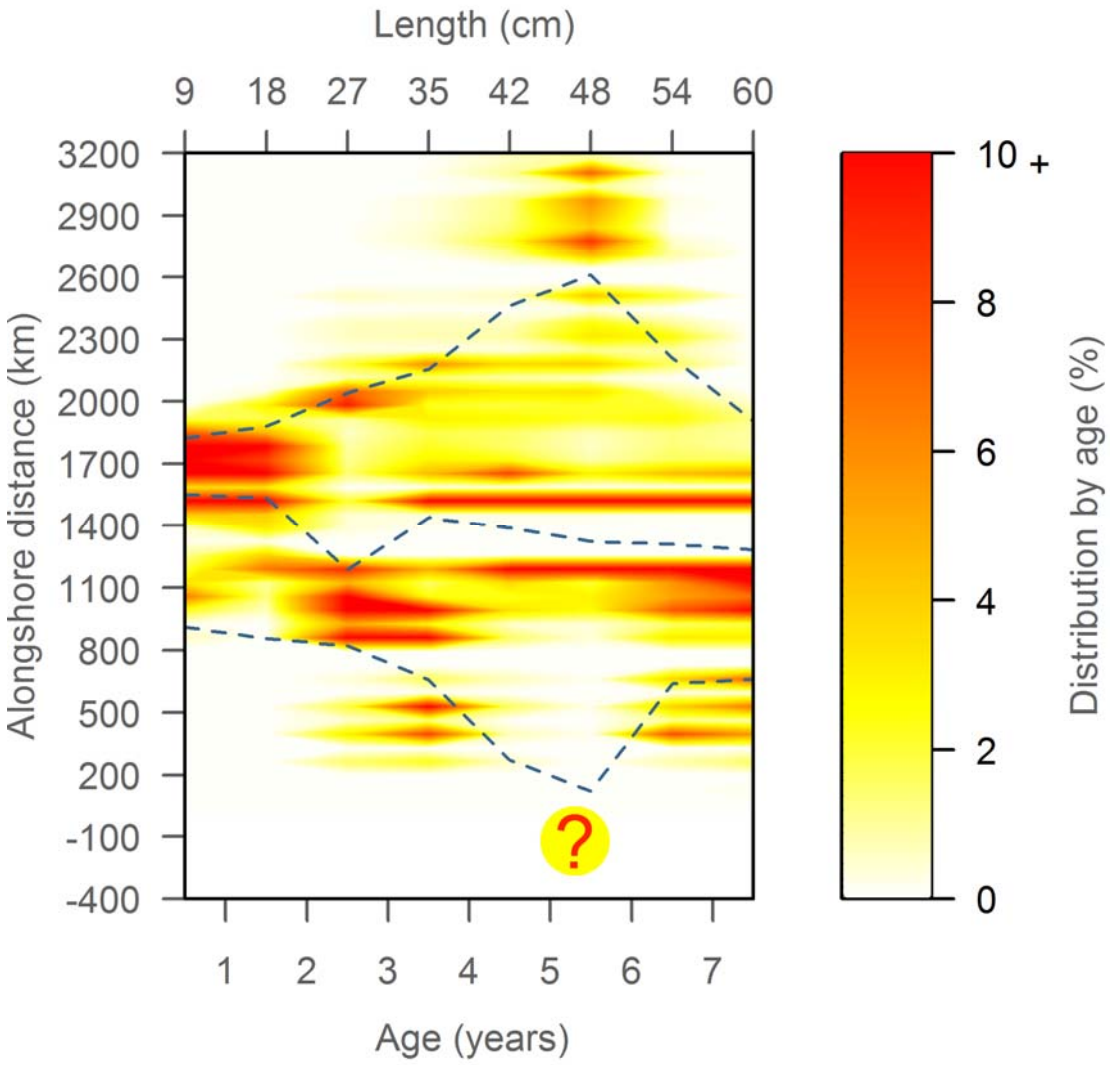

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349 Figure 8. Alongshore distribution of deep water cape hake (*M. paradoxus*) by age and mean length. The
350 Centre of Gravity is indicated by grey dashed lines for hakes north of 2150 km and south of 1550 km.
351 The spatial distribution has been projected onto a curvilinear axis following the coastline from Port
352 Elizabeth in the south-east to the Namibia-Angola border (Kunene River) in the North.

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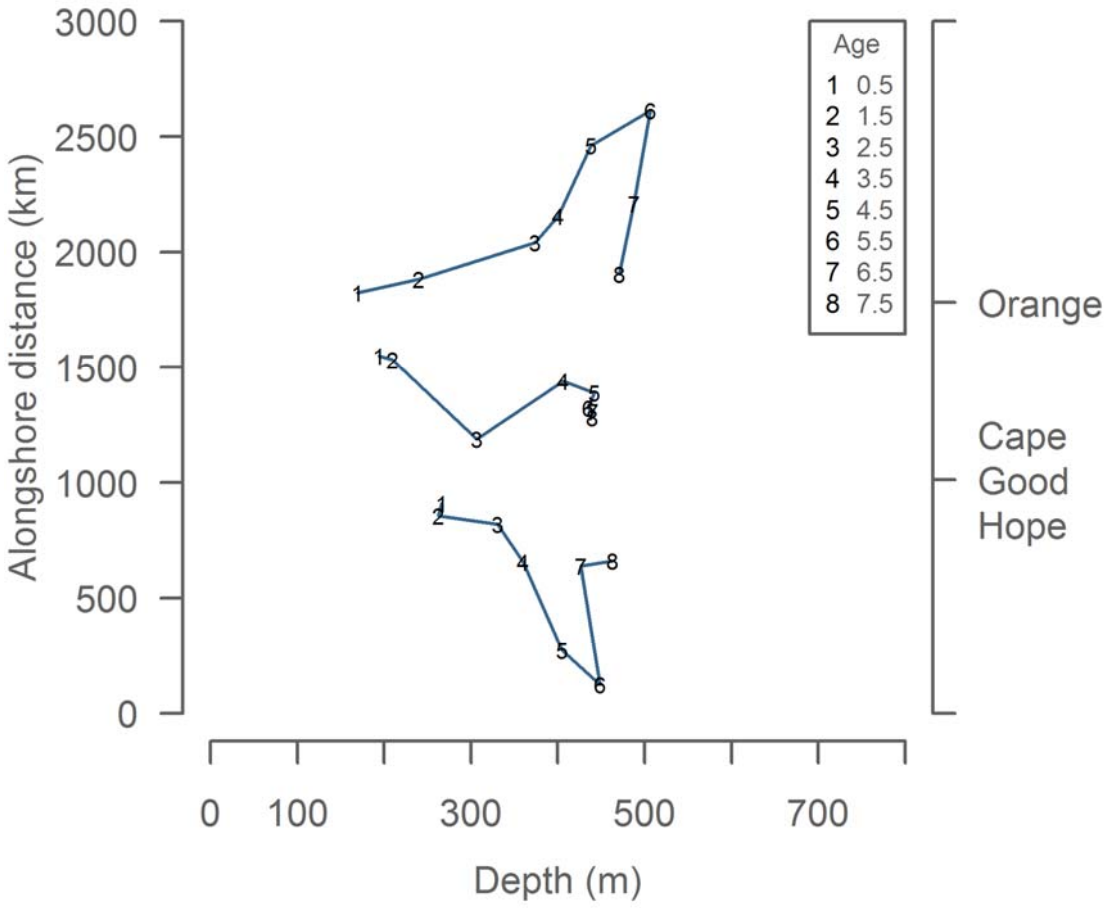

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355 Figure 9. Centre of Gravity by age of deep water cape hake (*M. paradoxus*) on each side of the Orange
356 River mouth (national border between South Africa and Namibia).

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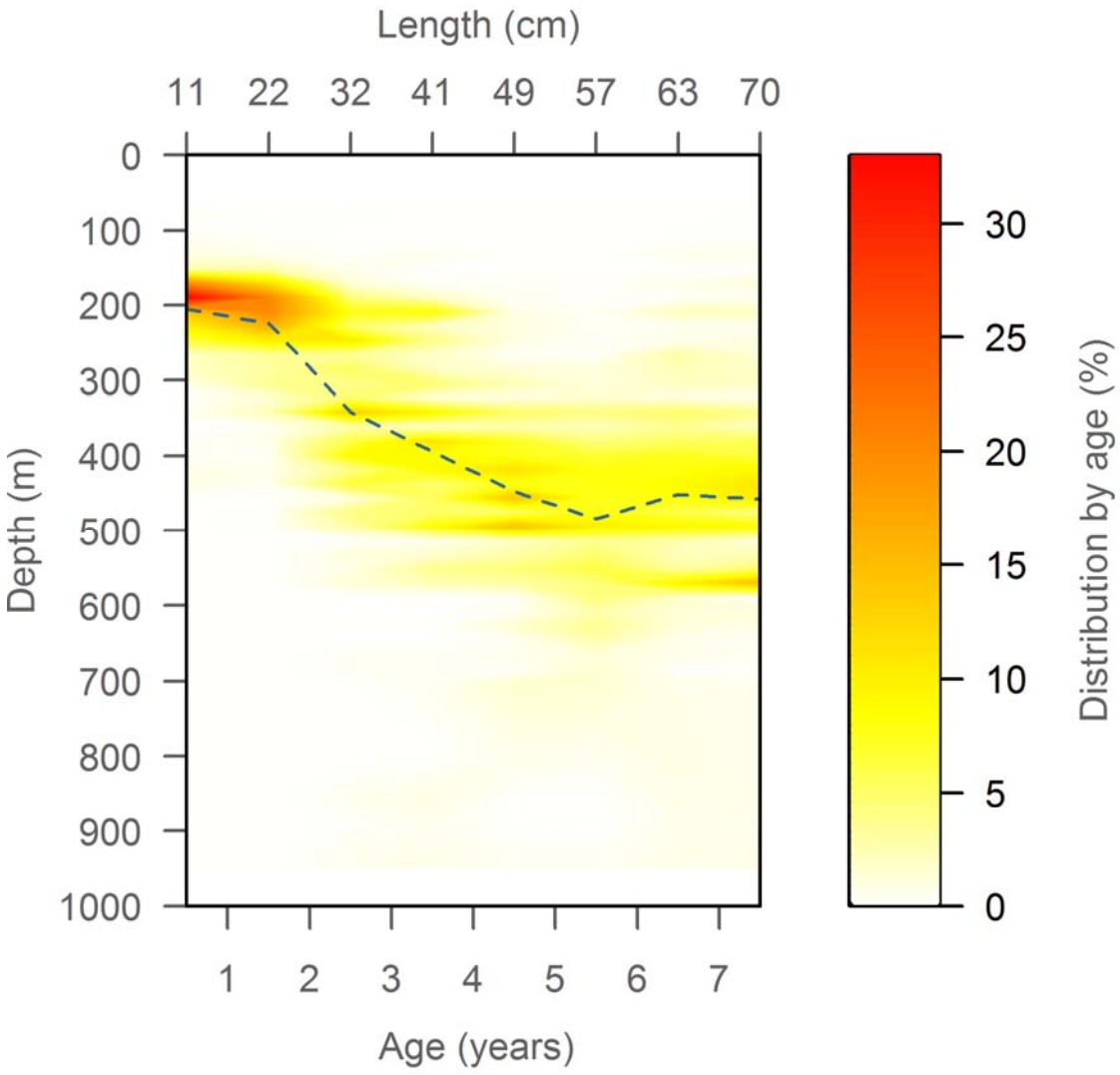

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359 Figure 10. Depth distribution of deep water cape hake (*M. paradoxus*) by age and mean length. Grey
360 dashed line indicates the mean depth.

361

362 [Excluded]

363 Figure 11. Abundance index time series of deep water cape hake (*M. paradoxus*). a) 0.5 year old
364 (recruits). b) 1.5-2.5 year old (juveniles). c) 3.5-7.5 year old (large juveniles and adults).

365

366 Supplementary information 1. Description of the “Latent Cohort GeoPop model”.

GeoPop: The latent cohort model

1 Description of the Latent Cohort GeoPop model

The model is a modification of the length-based GeoPop. The model contains two major components:

1. A model of the space-time distribution of cohorts and
2. A simple size spectrum model for each cohort.

In the following we describe the model components. Model parameters are listed in table 2.

2 Component 1 – cohort correlation

A Gaussian Markov random field was used to model log-abundance $\eta(x,t,c)$ of hake as function of space, time and cohort identifier (year class). Here we describe how the correlation structure was defined and why. Since a cohort defines a fixed group of individuals it is natural to expect that the distribution pattern of a cohort changes continuously in space and time. A simple choice of correlation structure for a given cohort c is the space time separable correlation of the form

$$\rho(\Delta x, \Delta t) = \rho(x, \Delta x)\rho(\Delta t)$$

Here Δx denotes spatial distance while Δt denotes time distance. The correlation structure states that the similarity of abundance at two space time locations (x_0, t_0) and (x_1, t_1) decays with both spatial distance $|x_0 - x_1|$ and time distance $|t_1 - t_0|$. The rates of decay are unknown and must be estimated. The decay rates describe how fast the distributional patterns change over time and how spatially aggregated the species is. In particular we use the same correlation structures as used in Kristensen et al. (2013): $\rho(x, \Delta x)$ is defined as the correlation induced by a Gaussian Markov random field, and $\rho(\Delta t)$ is an exponential decaying correlation function. (These principles are also similar to Jansen et al. (2012)). This correlation structure describes the space time dynamics of a given cohort. The model is formulated for multiple cohorts by assuming independence between cohorts. The independence assumption allows cohort c to follow a completely different spatio-temporal life history than any of the other cohorts. The overall correlation structure becomes

$$\rho(\Delta x, \Delta t, \Delta c) = \rho(x, \Delta x)\rho(\Delta t)1_{(\Delta c=0)}$$

where Δc denotes the integer distance between two year classes.

3 Component 2 – link to trawl observations

The available data are length frequencies from trawl hauls without any age measurements. Such data obviously only hold indirect information about the individual cohorts. In order to link our spatio-temporal cohort model with the observations we must formulate a model of the size distribution of cohorts. For simplicity

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it is assumed that the size distribution of cohort c at time t of age $a = t - c$ is given by a Gaussian density with a mean determined by a von bertalanffy growth curve and a standard deviation that increase linearly with time:

$$f_c(s,t) = \frac{1}{\sqrt{2\pi\sigma_a^2}} \exp\left(-\frac{1}{2}\frac{(s-\mu_a)^2}{\sigma_a}\right)$$

where $\mu_a = L_\infty(1 - \exp(-k \cdot a))$ and $\sigma_a = \alpha + \beta \cdot a$. We define the haul specific cohort strength $w_c(x,t)$ as affected by the following contributions:

1. Cohort recruitment strength $\log r(c)$ which is assumed to be a normal random effect.
2. Cohort age a and mortality z.
3. The spatial distribution $\eta(x,t,c)$ of the cohort, and
4. Small scale space-time variations in cohort strength $\eta_0(x,t,c)$ - the nugget effect:

$$\log w_c(x,t) = \log r(c) - z \cdot t + \eta(x,t,c) + \eta_0(x,t,c)$$

The observed size distribution in a spatial point x at time t is an aggregation of all cohort size distributions in the particular spatial point:

$$\lambda(s,x,t) = \sum_c w_c(x,t) f_c(s,t)$$

Finally our measurements are assumed Poisson distributed conditionally on the intensity $sel(s)\lambda(s,x,t)$ where $sel(s)$ denotes a two-parameter gear selectivity function. In case of multiple different gears, sel is extended with an overall efficiency parameter γ for each gear. The γ for the Gisund trawl was fixed to one since only relative selectivity can be estimated.

Supplementary information 2. Documentation of parameter estimation test.

Supplementary information 3. Distribution maps of deep water cape hake (*M. paradoxus*) by cohort and age.

Tables

Gear name	Standard trawl speed (knots)	Constraining rope	Door spread (m)	Sweep lengths (m)	Wing spread (m)	Headline height (m)	Mesh size in codend (mm)
Gisund	3.0	Yes	50	40	21	?	10
Old Africana	3.5	No	?	50	26	1.7 – 4.4	35
New Africana	3.5	No	?	9	24.1 – 29.2	2.8 – 4.8	35

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377 Table 1. Specifications of the bottom trawl gears.

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Symbol	Description	Unit	Estimate	Mean of estimates from bootstrap	Standard error
ℓ_{50}^{Gisund}	Fish size at half selection (Gisund)	cm	...	...	...
$\ell_{50}^{SA\_New}$	Fish size at half selection (SA_New)	cm	...	...	...
$\ell_{50}^{SA\_Old}$	Fish size at half selection (SA_Old)	cm	...	...	...
SR^{Gisund}	Selection range (Gisund)	cm	...	...	...
SR^{SA_New}	Selection range (SA_New)	cm	...	...	...
SR^{SA_Old}	Selection range (SA_Old)	cm	...	...	...
γ_{SA_New}	Gear efficiency factor (SA_New vs. Gisund)	1	...	...	...
γ_{SA_Old}	Gear efficiency factor (SA_Old vs. Gisund)	1	...	...	...
N_0	Mean recruitment	#/year	...	...	...
$\sigma_{N_0}^2$	Recruitment variance	1	...	...	...
K	Growth rate (Von Bertalanffy)	$year^{-1}$	...	...	...
t_0	Theoretical age at length 0 cm (Von Bertalanffy)	year	...	...	...
$\overline{Z}$	Total mortality	$year^{-1}$	...	...	...
H	Spatial decorrelation distance	km	...	...	...
σ^2	Spatial variance parameter	1	...	...	...
σ_N^2	Variance of the nugget effect	1	...	...	...

T	Decorrelation time	year^{-1}	...	...	...
σ^2_{init}	Initial length variance of cohorts	1	...	...	...
σ^2_{rate}	Rate of increase in length variance of cohorts	year^{-1}	...	...	...

Table 2. Model parameter estimates and standard errors.

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