Geostatistical modelling of the spatial life history of post-larval deepwater hake Merluccius paradoxus in the Benguela Current Large Marine Ecosystem

T Jansen, K Kristensen, TP Fairweather, P Kainge, JN Kathena, MD Durholtz, JE Beyer & UH Thygesen


To link to this article: https://doi.org/10.2989/1814232X.2017.1379437

Published online: 15 Nov 2017.

Submit your article to this journal

Article views: 3

View related articles

View Crossmark data
Geostatistical modelling of the spatial life history of post-larval deepwater hake Merluccius paradoxus in the Benguela Current Large Marine Ecosystem

T Jansen¹²*, K Kristensen², TP Fairweather³, P Kainge⁴, JN Kathena⁴, MD Durholtz³, JE Beyer² and UH Thygesen²

¹ Benguela Current Commission, Swakopmund, Namibia
² Technical University of Denmark – National Institute of Aquatic Resources (DTU Aqua), Charlottenlund, Denmark
³ Branch: Fisheries Management, Department of Agriculture, Forestry and Fisheries (DAFF), Cape Town, South Africa
⁴ Ministry of Fisheries and Marine Resources (MFMR), Swakopmund, Namibia

Optimal and sustainable management of fish resources cannot be ensured without a thorough understanding of the migration patterns and population (demographic stock) structure. Recent studies suggest that these aspects of the economically and ecologically important deepwater hake Merluccius paradoxus are not reflected in the current assessment and management practices for the Benguela Current Large Marine Ecosystem. In this study, we compiled data from multiple demersal trawl surveys from the entire distribution area and applied state-of-the-art geostatistical population modelling (GeoPop) to estimate growth rate, mortality, and spatial and temporal distribution patterns of M. paradoxus. The data and the model enabled us to follow temporal and spatial changes in the distribution and infer movements from the recruitment/nursery areas, through the juvenile phase and the adults’ migration to the spawning areas outside/upstream of the nursery areas. The results indicated one primary recruitment/nursery area on the west coast of South Africa and a secondary less-productive recruitment/nursery area on the south coast near Port Elizabeth. Juveniles initially migrated away from the main recruitment area, followed by natal homing by larger individuals. This pattern was highly consistent through the time-series of the study. This perception of a, primarily, panmictic population that performs transboundary migrations between Namibia and South Africa corresponds largely to the hypothesis and data plots given in recent studies. We recommend that fisheries assessment, advice and management take into consideration these aspects of the distribution and population (stock) structure of M. paradoxus.

Keywords: demersal trawl survey, GeoPop model, mortality, Namibia, natal homing, population structure, South Africa, Template Model Builder, transboundary migration

Online supplementary material: Supplementary Information for this article is available at http://dx.doi.org/10.2989/1814232X.2017.1379437. The materials detail the method used to account for the gear effect on catch rates of Merluccius paradoxus.

Introduction

Deepwater hake Merluccius paradoxus is a key demersal fish species in the Benguela Current Large Marine Ecosystem (BCLME), a productive upwelling system off the west coast of southern Africa (5–37° S, 0–26° E). Merluccius paradoxus inhabit the continental-shelf slope from around 17° S in Angola/Namibia to about 27° E in South Africa (Figure 1) (Durholtz et al. 2015).

Merluccius paradoxus spawn mainly in areas of 200–650 m bottom depths between 34.5° S and 36.5° S on the South African west coast. Spawning individuals have been found as far as 25° S in Namibia, and 27° E off the South African south coast, at depths ranging from 170 to 837 m (Jansen et al. 2015a). Spawning off the coast of South Africa takes place throughout the year, with increased intensity around March and August–October (Jansen et al. 2015a). Merluccius paradoxus are considered juvenile until they reach the ‘immature’ stage at approximately 20 cm (16.8 cm [SE 3.1]) at which point they have developed macroscopically visible ovaries and testes. The majority of M. paradoxus mature between 35 and 48 cm (L₉₀ = 42 cm) (Singh et al. 2011).

Onshore, offshore and alongshore ontogenetic migration has been indicated for M. paradoxus (Le Clus et al. 2005; Grüss et al. 2016; Strømme et al. 2016). Based on catch rates by length class from South African surveys between 1990 and 2003, Le Clus et al. (2005) concluded that M. paradoxus on the South African west and south coasts were connected and likely belonged to the same ‘stock.’ Gruss et al. (2016) confirmed this view, with survey data between 2003 and 2011, using the same size-class distinctions as Le Clus et al. (2005). Stremme et al. (2016) extended this view to include Namibia, where they found a large proportion of M. paradoxus in the size range of approximately 25–55 cm, indicating a southern origin and a subsequent migration
back to South Africa as the hakes grew larger. Juvenile *M. paradoxus* occupy 'shallower' waters (180 m) followed by lifelong movements towards even deeper waters, as their common name implies (Botha 1980; Gordoa and Duarte 1991; Payne and Punt 1995; Burmeister 2001; Grüss et al. 2016; Strømme et al. 2016). Catches of large *M. paradoxus* are made to 1 000 m deep (Mas-Riera 1991; Burmeister 2001).

The spatio-temporal spawning and migration patterns described above are in accordance with the most recent and comprehensive genetic study of *M. paradoxus*, by Henriques et al. (2016), which found no significant spatial differences and concluded, in accordance with Bloomer et al. (2009), that the population structure is panmictic. However, Henriques et al. (2016) found significant temporal differences and suggested that this was from chaotic genetic patchiness rather than indicative of multiple stocks, as had been suggested in a study by von der Heyden et al. (2010).

The area around the Lüderitz Upwelling Cell and the Orange River Cone (LUCORC) region (25°–29° S) forms a natural barrier between the northern and southern Benguela (Agenbag and Shannon 1988; Rae 2005; Lett et al. 2007). Therefore, and for practical/political simplicity, the national border between Namibia and South Africa (the Orange River at 29° S) is still regarded as the boundary dividing *M. paradoxus* into two nationally managed stocks (Grant et al. 1988, 1987; Burmeister 2005; Figure 1). Thus, stock assessment and fisheries management advice has not yet adapted to growing evidence of *M. paradoxus* as a single panmictic demographic stock, displaying transboundary movements between Namibia and South Africa. As a result, it is unknown if the current fisheries practice for *M. paradoxus* in the BCLME is sustainable and optimal as it is based on stock assessments that used incorrect assumptions about the species' demographics.

The above-mentioned important migration issues call for a thorough examination of all available survey data for this species. Until now, the limitation of physical processing power has prevented a comprehensive, statistically valid modelling analysis of big data challenges. However, recent developments in geostatistics and model-fitting have facilitated analyses of large datasets from trawl surveys, leading to new biological insights (Kristensen et al. 2014; Jansen et al. 2016, 2015b).

In this study we apply these methods to a large set of demersal-trawl survey data, from Namibia and South Africa, to demonstrate the spatial life history of post-larval *M. paradoxus*. This is the first analysis of *M. paradoxus* to integrate information contained in the South African, Namibian and Norwegian surveys that have been conducted so far in the BCLME.

We aimed to test whether the trawl data support the hypothesis of one panmictic population with transboundary migration. Furthermore, we studied the species'
size-specific movements for future application to improved regional stock assessments.

**Materials and methods**

The analytical approach and statistical modelling applied to the data in this study were the same as used and described in detail by Jansen et al. (2016). Likewise, the description of methods regarding the GeoPop model summarises that of Jansen et al. (2016).

**Scientific trawl survey data**

The data used in this study were collected during demersal-trawl research surveys conducted over the period 1998–2011 in the Benguela–Agulhas ecosystem, between 17° S (northern border of Namibia) and 27° E on the South African south coast (Figure 1).

Surveys conducted in Namibian waters used a Gisund Super demersal trawl towed by chartered commercial trawlers, all of which had been intercalibrated using the Norwegian research vessel Dr Fridtjof Nansen. The Namibian surveys used a systematic transect survey design that semi-randomly sampled stations along a series of fixed transects. The South African surveys were conducted on board the research ship Africana using two different configurations ('old' or 'new') of a German four-panel demersal trawl and followed a pseudo-random stratified sampling design. Data collected during surveys by the RV Dr Fridtjof Nansen using the Gisund Super gear and transect survey design in both Namibian and South African waters were also included in the study. The various gear types, their operation and rigging are described by Axelsen and Johnsen (2015). Trawling duration was typically 30 minutes during all surveys, and data from hauls shorter than 25 minutes or longer than 35 minutes were excluded from the analyses. No trawl data were available from Angolan waters. *Merluccius paradoxus* has been reported from Angolan waters in some years, most recently from a demersal survey in 2015, where the species was found south of Baia dos Tigres (around 18°30’ S) in southern Angola (Staby et al. 2015). The reason why this species has not been reported on a regular basis from surveys off Angola has been attributed to identification problems, bearing in mind that different scientific personnel participate in these surveys (pers. comm.: Kumbi Kilongo, Benguela Current Commission; and Oddgeir Alvheim, Institute for Marine Resources, Norway); consequently, this was deemed a good reason not to include the fragmented data in the present analysis. The biomass of *M. paradoxus* in Angolan waters, however, is considered negligible (in 2015 only 680 tonnes of hake was recorded, which was dominated by *M. paradoxus* [Staby et al. 2015]) as compared with that in Namibian and South African waters.

Where feasible, the total catch made during each trawl was sorted to the lowest taxonomic level possible, the catch of each species was weighed, and individual fish were measured. Large catches were subsampled and the relevant raising factors applied to estimate the length composition of the total catch. Catches from the ‘old’ and ‘new’ South African gears were deterministically converted to a Gisund equivalent catch using an estimated length-specific gear effect (see Supplementary Information, available online). For computational reasons, inclusion of gear-effect estimation as an integral part of the main GeoPop model was not possible.

The observation that sea winds in excess of 25 knots may have compromised the performance of the gear, and hence the associated data (Wieland et al. 2013), was used as a basis to exclude data from nine of the hauls in South African waters.

The final survey dataset used in this study encompassed 6 343 trawl hauls, 57% of which contained *M. paradoxus*. Catches of *M. paradoxus* ranged from 0 to 28 844 individuals per haul, with a mean catch of 867 fish in the non-zero hauls. Thus, the dataset comprised a total of 3.1 million records of *M. paradoxus*. The data generally represented the entire region, with the exception of the shallow area (20–100-m depths) in central Namibia which is characterised by extensive untrawlable grounds (Figure 1).

The samples were relatively evenly distributed over the time-series (Figure 2a). Most samples off Namibia and the South African west coast were taken in January–February, while the south coast of South Africa was generally sampled in April–May (Figure 2b). Trawling was predominately done during the day (Figure 2c) at depths of 20–960 m (Figure 2d).

As described by Jansen et al. (2016), the difference in the timing of the various surveys, coupled with the spawning phenology of deepwater hake, made it impossible to estimate the exact age of the fish in the samples. *Merluccius paradoxus* spawn throughout the year, but with increased intensity around March and August–October; consequently, the recruits in Namibia and on the South African west coast were primarily surveyed approximately 4.5 and 10.5 months after spawning (Jansen et al. 2015a) in January–February. However, surveys off the South African south coast took place in April–May, approximately 7 and 13 months after the major spawning events. The young hake therefore entered the survey catches at various sizes and ages. For illustration purposes, mean age of the young-of-the-year hakes that entered the catches was set to 6 months.

**The GeoPop model**

GeoPop was used to estimate abundance indices of each size class of deepwater hake at each point in space and in time. The basis of the dynamics was a non-spatial size-spectrum model of *M. paradoxus*. A stochastic spatio-temporal model was then used to distribute each size class over the study area, taking small-scale patchiness and selectivities of the gears into account. The combination model is known as a log Gaussian Cox process model. Similar models have previously proved their value for assessing populations of Atlantic cod Gadus morhua (Lewy and Kristensen 2009; Kristensen et al. 2013), whiting *Merlangius merlangus* (Nielsen et al. 2014), Atlantic mackerel Scomber scombrus larvae and juveniles (Jansen et al. 2012, 2015b), and shallow-water hake *Merluccius capensis* (Jansen et al. 2016).

Initial attempts to fit this type of model to the hake data from demersal surveys in the Benguela–Agulhas system were unsuccessful because estimating such a large number
of latent variables exceeded the limits of the physical processing power (Jansen et al. 2013). As described by Jansen et al. (2016), this problem was solved by using the R package Template Model Builder (TMB) (Kristensen et al. 2015) as an alternative to AD Model Builder (ADMB), and running the software on a r3.8xlarge platform under Amazon Elastic Compute Cloud (https://aws.amazon.com/ec2/instance-types/).

The model formulation and notation used in this study were identical to the novel model in Kristensen et al. (2013). Stochastic population dynamics was governed by a McKendrick–von Foerster equation (Kot 2001) in log-densities \( \phi(s,t) \) by adding white noise \( \varepsilon(s,t) \) with intensity \( \sigma^2 \) to account for unpredictable rapid fluctuation in recruitment, growth \( g \) and mortality \( z \) \( \frac{\partial \phi}{\partial t} - g \frac{\partial \phi}{\partial s} - z + \varepsilon \lambda(s_i,x_j,t_j) = \exp[\phi(s_i,t_j) + \eta(s_i,x_j,t_j) + \eta_0(s_i,j) + \log \text{sel}(s_i)] \)

Here \( \phi(s,t) = \log n(s,t) \), where \( n(s,t) \) is the number of \( M. \text{paradoxus} \) with a body length between \( s \) and \( s + ds \) caught in a typical haul with unselective reference sampling gear at time \( t \) (Kristensen et al. 2013). The population dynamics were discretised into 47 size classes and 32 time-steps.

Figure 2: Demersal trawl survey samples (hauls) in the Benguela–Agulhas ecosystem by (a) year, (b) ordinal day, (c) hour of the day, and (d) depth.
per year, and the noise term was implemented by adding independent random Gaussian variables to every size class at every time-step. Consequently, the field \( \varphi(s,t) \) was represented by 21,056 random effects in the period 1998–2011 (47 size class × 14 years × 32 time-steps per year). The growth rate \( g \) and the total mortality rate \( z \) were assumed constant and should consequently be interpreted as rates averaged over time.

The size-spectrum \( \varphi \) was then distributed over the Benguela–Agulhas system by adding a spatial component \( \eta(s) \) to the log-densities of hake \( \varphi(s,t) + \eta(s,x,t) \) where \( x \) is a position in two-dimensional space. The latent variables in the statistical process are values of this field on a discrete grid (278 cells, each measuring 50 × 50 km) and the parameters (listed in Table 1) govern their distribution. The field \( \eta \) was modeled as a Gaussian-distributed mean-zero term of variance \( \sigma^2 \) that is correlated with space, time and size. All correlations were assumed to decay exponentially with spatial distance, time lag and size difference, and were also assumed to be multiplicative. Spatial correlation was assumed to be isotropic (direction independent), and to avoid correlation over land (e.g. the Cape region in South Africa) the spatial correlation effect was modelled as a Gaussian Markov random field (cell-to-cell chains). The parameter estimates for these correlations were expressed as a correlation distance \( H \), decorrelation time \( T \) and decorrelation size \( L \), which were the distances in space, time or size where the correlations had decayed to \( e^{-1} \) (≈ 0.14). The temporal resolution was represented by annual time-steps, resulting in the spatio-temporal element of the model comprising a total of 182,924 random variables (47 size classes × 14 years × 278 grid cells).

To estimate the large-scale abundance field from the survey hauls, noise from local patchiness must be removed. The reasoning is that fish, on the scale of the single haul \( (s,j) \), are not Poisson-distributed, but aggregate in patches produced by the Department of Agriculture, Forestry and Fisheries (DAFF) from macrostructural analyses of sagittal otoliths (DD, DAFF, unpublished data), as described by Jansen et al. (2016). The length-based model outputs were presented by both Rademeyer (2012) and Fisheries (DAFF) from macrostructural analyses of sagittal otoliths (DD, DAFF, unpublished data), as described by Jansen et al. (2016).

The estimated mortality was compared visually with the length-to-age conversions, the abundance estimates were also projected onto a straight-line axis that represented the coastline from the Namibia–Angola border (11° E, 17° S) in the north, via Cape Point (18.5° E, 34° S) to east of Port Elizabeth on the South African south coast (27.5° E, 34° S) (see Figure 1). Multiannual average distributions were calculated as the unweighted average distribution of multiple years.

The length-based model outputs were presented by both length and absolute age. The length-to-age conversions were implemented using deepwater hake age–length keys produced by the Department of Agriculture, Forestry and Fisheries (DAFF) from macrostructural analyses of sagittal otoliths (DD, DAFF, unpublished data), as described by Jansen et al. (2016).

The estimated mortality was compared visually with the results from Rademeyer (2012) by plotting the abundance index from GeoPop by length and age, overlaid by the abundance index at age 1.3 decaying by the growth rate \( g \), with a particular gear was considered compound Poisson-distributed with the stochastic intensity:

\[
\lambda(s_j,t_j) = \exp[\varphi(s_j,t_j) + \eta(s_j,x_j,t_j) + \eta_0(s_j,t_j) + \log \text{Sel}(s_j)]
\]

The Poisson distribution allows for zero catches, while the log Gaussian randomness of \( \lambda \) implies over-dispersed catches (relative to Poisson), both allowing for very high counts and for many more zero catches than would be found in a pure Poisson model.

The parameters in the model were estimated using the maximum likelihood principle based on the Laplace approximation, following the principles of Kristensen et al. (2013).

The fitted model was then used to calculate annual estimates of the abundance index of hake in each size class in each 50 × 50 km cell. To evaluate possible alongshore movement patterns, the abundance estimates were also projected onto a straight-line axis that represented the coastline from the Namibia–Angola border (11° E, 17° S) in the north, via Cape Point (18.5° E, 34° S) to east of Port Elizabeth on the South African south coast (27.5° E, 34° S) (see Figure 1). Multiannual average distributions were calculated as the unweighted average distribution of multiple years.

Table 1: Model parameter estimates and standard errors; units denoted by ‘——’ are dimensionless. CV = coefficient of variation

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
<th>Estimate</th>
<th>Standard error</th>
<th>CV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \sigma^2 )</td>
<td>Variance of the space–time–size correlations</td>
<td>–</td>
<td>20.934</td>
<td>1.265</td>
<td>6</td>
</tr>
<tr>
<td>( \sigma^2 )</td>
<td>Variance of population dynamics</td>
<td>–</td>
<td>0.033</td>
<td>0.006</td>
<td>18</td>
</tr>
<tr>
<td>( T )</td>
<td>Decorrelation time</td>
<td>year</td>
<td>30.088</td>
<td>2.220</td>
<td>7</td>
</tr>
<tr>
<td>( L )</td>
<td>Decorrelation size</td>
<td>cm</td>
<td>79.069</td>
<td>1.894</td>
<td>2</td>
</tr>
<tr>
<td>( H )</td>
<td>Spatial decorrelation distance</td>
<td>km</td>
<td>480.606</td>
<td>31.087</td>
<td>6</td>
</tr>
<tr>
<td>( \sigma_0^2 )</td>
<td>Variance of the nugget effect</td>
<td>–</td>
<td>12.350</td>
<td>0.283</td>
<td>2</td>
</tr>
<tr>
<td>( g )</td>
<td>Growth rate</td>
<td>cm/year</td>
<td>8.320</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>( z )</td>
<td>Total mortality</td>
<td>1/year</td>
<td>0.325</td>
<td>0.218</td>
<td>67</td>
</tr>
<tr>
<td>( g_{\text{Gisund}} )</td>
<td>Fish size at half-selection (Gisund)</td>
<td>cm</td>
<td>8.372</td>
<td>0.882</td>
<td>11</td>
</tr>
<tr>
<td>( SR_{\text{Gisund}} )</td>
<td>Selection range (Gisund)</td>
<td>cm</td>
<td>1.414</td>
<td>0.308</td>
<td>22</td>
</tr>
</tbody>
</table>
database (Amante and Eakins 2009) using the ‘marmap’ package (Pante et al. 2015). Mean depth was calculated for each cell and isobaths were produced for the maps. Finally, hake abundance in cells with a mean depth exceeding the deepest trawl haul (960 m) was set to 0 (the deepest observed *M. paradoxus* catch was at 934 m).

**Results**

The parameter estimates (and associated standard errors) of the model fitted to the catch data are given in Table 1. Hake densities were found to be correlated in space and size with a spatial decorrelation distance (*H*) of 481 km and a length de-correlation range (*L*) of 79 cm. These patterns were found to be very stable from year to year, with a temporal decorrelation (*T*) spanning 30.1 years (CV = 7%), and could therefore be examined as averages over the entire time-series.

Estimated variance parameters revealed a roughly equal contribution from spatial patterns (*σ² = 20.9*) and the nugget effect (*σ² = 12.4*). In comparison, the contribution from population dynamics was much smaller (*σ² = 0.03*). The variance in abundance of a given size class at a single point in time and space was therefore completely dominated by large-scale spatial effects and local effects rather than by demographic effects.

*Merluccius paradoxus* were not fully recruited to the trawl survey in their first year. This was evident from the estimated selection of the reference gear ‘Gisund’ (*Gisund = 8.4 cm, SR Gisund = 1.4 cm*). Furthermore, the increase in estimated population abundance (catch rates) up to 1.3 years (22 cm) suggests that the selection ogive did not capture the entire span of the ‘recruitment’ to the survey.

The total mortality rate of *M. paradoxus* was estimated as 0.33 year⁻¹ (CV = 67%). The abundance at size decreased faster when the fish exceeded approximately 55 cm (Figure 3). It is therefore plausible that the mortality varied through life and between areas. The growth rate was estimated to be 8.3 cm year⁻¹ (CV = 00.01%). Despite the very weak population effect (*σ² << σ²* and *σ² << σ²*), these estimates (mortality and growth) resembled previously reported rates (Figure 3 and 4). The total mortality rate was lower than the mortality estimated in the South African stock assessment (mean *z* from 2–10 years = 0.57; Rademeyer [2012]) (Figure 3), but was similar for hakes that were fully recruited to the survey (older than 1.3 years). However, the cohort signals were too weak to be used for tracking of single cohorts and their effects on spatio-temporal distribution fields were negligible.

**Spatial patterns (distribution, migration, population structure)**

The spatial distribution of the catch rate of *M. paradoxus* was estimated and used to infer age- and size-related migration patterns. This was done for length groups corresponding to ages from 0.3 years, the approximate age when a new cohort first appears in the surveys, to 9.3 years.

To examine the alongshore migration patterns, we projected the length–age-specific spatial distributions onto an axis consisting of two straight lines, one from the Namibia–Angola border (Kunene River mouth) in the
The alongshore projections (Figures 5 and 6) and distribution maps (Figures 7 and 8) indicated horizontal movements throughout the lifespan of *M. paradoxus*. The initial distributions of the approximately 0.3-year-olds (recruits) and the 1.3-year-olds (juveniles) indicated one main nursery area (Figures 6 and 7). During the species’ first 7 years of the life, the distribution shifted gradually from year to year, indicating considerable alongshore movements. In the north, considerable quantities of *M. paradoxus* appeared to move northwards from the area around the Orange River—their most likely origin. In lesser numbers, *M. paradoxus* moved eastwards along the south coast of South Africa.

*M. paradoxus* were most widespread at the age of approximately 4.3 years (51 cm) when almost 100% were mature (50% mature at 42 cm [Singh et al. 2011]). Later, the distributions progressively contracted in the vicinity of the nursery area (Figures 5, 6 and 8). The species’ movements north of the Orange River (the border between Namibia and South Africa) and east of Cape Agulhas thus indicated natal homing as the most parsimonious explanation. Consequently, transboundary movements likely occurred between the exclusive economic zones (EEZs) of Namibia and South Africa.

*Merluccius paradoxus* initially appeared to move to shallower waters, about 180 m depth, after which, at approximately 0.5–5 years of age, they gradually moved deeper. From age 5 years they were mainly found between 350 and 650 m, possibly moving into slightly shallower waters to spawn (Figure 9).
Discussion

The present analysis was based on the largest database of *Merluccius paradoxus* trawl survey data available to date, combining for the first time surveys by Namibian, Norwegian and South African fisheries research institutes. The quantitative geostatistical modelling exposed spatial migration patterns largely in line with patterns evident from the visual inspection of presence/absence outline maps (Strømme et al. 2016). Comparable to Strømme et al. (2016) and Le Clus et al. (2005), we assumed that the spatial shifts in distribution over the lifespan of post-larval *M. paradoxus* were primarily reflective of migration and to a lesser extent mortality; however, as mentioned by Grüss et al. (2016), the effects of spatial variation in mortality of Cape hakes remains to be studied.

**Spatial patterns (distribution, migration, population structure)**

The results indicated one primary recruitment/nursery area on the west coast of South Africa and a secondary less productive recruitment/nursery area around Port Elizabeth on the south coast. After the juvenile stage, *M. paradoxus* expand their distribution, followed by natal homing by larger mature individuals. This pattern was highly consistent through the study’s time-series data as indicated by the very long decorrelation time.
The return migration from Namibia appeared to take place when the *M. paradoxus* surpass 50 cm. Assuming a similar maturation rate as in South Africa (Singh et al. 2011), almost 100% of these fish would be mature. However, very few appear to spawn in Namibian waters (Jansen et al. 2015a). Deepwater hake on the south coast of South Africa appeared to move slightly westwards and then halt this geographical movement after reaching maturation sizes. This corresponds to the reports of spawning in this area by Jansen et al. (2015a). However, few recruits were observed, indicating that they were either outside the survey area, transported by currents to the west coast before they could be caught in the trawls, underestimated (unaccounted gear avoidance, related to factors such as vertical distribution), or that their reproduction in this area is less successful than on the west coast.

The spatial life-history patterns are consistent with a single population unit (stock) hypothesis, yet indicate an additional, much smaller component on the eastern part of South Africa’s south coast. The level of interconnection (mixing/straying) between these components (stocks) appears to exceed the minimum threshold for genetic differentiation (Carvalho and Hauser 1994) and likely explains the absence of genetic divergence observed by Henriques et al. (2016), both with mtDNA and nuclear microsatellite markers. *Merluccius paradoxus* reached their deepest distribution

---

**Figure 8:** Distribution maps for deepwater hake *Merluccius paradoxus* at the ages of approximately (a) 4.3 years, (b) 5.3 years, (c) 6.3 years, and (d) 7.3 years. The distributions are illustrated as cumulative fractions (for example, the sum of all areas, with the colours corresponding to up to 40%, represents 40% of the total). Solid line represents the exclusive economic zones.
at a size of approximately 50–55 cm (Figure 9), when it was abundant at depths below 600 m; however, only 4.4% and 0.1% of the hauls were taken at depths greater than 600 and 800 m, respectively (Figure 2). The perceived increase in mortality at sizes greater than approximately 50 cm (Figure 3) may therefore be explained by fish moving out of the surveys’ coverage.

**Population dynamics**

The effect of the population dynamics in the model was minuscule ($\sigma^2_\epsilon << \sigma^2$ and $\sigma^2_\epsilon << \sigma^2_\eta$), which could be a consequence of the year-round spawning and recruitment of *M. paradoxus* combined with the difference in the timing of the South African south-coast and west-coast surveys. Despite this, the growth and mortality rates appeared to be relatively well estimated, as indicated by the low standard deviations of the estimates and the comparison with values reported from age readings and stock assessments. A plausible explanation for this result, which is consistent with what was found for shallow-water hake *M. capensis* (Jansen et al. 2016), is that the variability in the size-structured spatial patterns is so relatively large that the contribution from the population dynamics is not required to explain patterns in data.

**Model performance**

Modelling the time-varying heterogeneous spatial distribution of *M. paradoxus* by correlations (between cells, between years and between size-specific catches) produced a clearer picture of the trends in alongshore distribution of *M. paradoxus* by size or age (Figure 10b) than the simple average of catches (Figure 10a). The fact that this picture, and hence the conclusions, become clearer after removal of local noise (nugget effect) in post-processing of the GeoPop results (Figure 10c), adds confidence to the application of that model.

The data and model fit for *M. paradoxus* did not indicate any large spatial differences in small-scale variability (nugget effect), unlike that presented for *M. capensis* by Jansen et al. (2016). This is evident by comparing Figure 10 in this study with Figures 5 and 6 in Jansen et al. (2016). A possible explanation for the abovementioned unexpected pattern for *M. capensis* could be data-quality issues associated with subsampling of the catches.

**Model validation**

Whereas a previous study (Kristensen et al. 2013) supported the GeoPop approach as an appropriate description of a different dataset, we did not pursue rigorous model validation in the present study. Noting that model validation cannot be based on naive residuals (observed values minus predicted values), validation of these types of models can follow one of two paths (Thygesen et al. 2017). On the first path, one computes one-step prediction residuals and inspects for patterns; however, the computational complexity of the current model rendered this approach unfeasible. Alternatively, one can generate a single sample of the latent variables from their posterior distribution, and inspect for patterns that are implausible under the model assumptions. This approach, which was followed by Kristensen et al. (2013), is computationally feasible, even for models as complex as the present one, provided that we accept the Gaussian approximation of the posterior distribution. Kristensen et al. (2013) next performed goodness-of-fit tests, based on qq-plots and confidence bands, and found that the model passed these validation steps. However, these are generic tests that may have limited strength towards specific model fallacies, and it is conceivable that more-targeted tests may falsify the model.

For example, the model is based on fairly coarse simplifications, such as constant growth and constant mortality, as well as a spatio-temporal autocovariance structure, and each of these assumptions could in principle be scrutinised. Indeed, we applied the model exactly to identify patterns in the data that were not present in the model equations (e.g. the presence of specific recruitment areas). We conclude that a fully satisfying validation of models of this type is a task with both technical and conceptual challenges, which should be addressed in future works.

**Future model developments**

The GeoPop model has been made possible by Template Model Builder’s computational approach to general statistical problems with many unobserved random variables, as well as the availability of memory and processing power through cloud computing. GeoPop represents a major improvement to earlier approaches, specifically by including population dynamics, spatial patterns and small-scale size-structured clustering. Since GeoPop lies at the boundary of what is currently computationally feasible, a number of compromises had to be made with respect to the ecological fidelity of the model—and it is foreseeable that future developments in algorithms and computational resources will allow further refinement of the model assumptions. Here, we list three candidates for such refinements:

1. Currently, the correlation structure in the spatial fields is assumed to be isotropic (i.e. independent of direction). It

![Figure 9: Depth distribution of deepwater hake Merluccius paradoxus by length and approximate age. Dashed line indicates the weighted mean depth](image-url)
Figure 10: Alongshore distributions of deepwater hake *Merluccius paradoxus* by size and approximate age: (a) simple average of catches, (b) GeoPop model fit, and (c) GeoPop model after removal of local noise (nugget effect). The spatial distributions were projected onto a curvilinear axis following the coastline from the Namibia–Angola border (Kunene River) in the north to Port Elizabeth, South Africa, in the southeast. For purposes of comparison, this figure is similar in format to Figure 5 in Jansen et al. (2016). WB = Walvis Bay, OR = Orange River, SHB = St Helena Bay, CA = Cape Agulhas, PE = Port Elizabeth.
is plausible that correlations between different locations depend not only on distance, but also on differences in depth or other key habitat parameters. Some extensions are relatively straightforward and could, for example, be achieved by changing coordinates from latitude and longitude to alongshore distance and depth. However, this solution would have other flaws, since for instance it would regard an off-shore bank as an extension of the near-coast space. A more general and robust structure could be obtained by modelling the fluxes in space that drive the redistribution of the fish between time-points; this could include diffusive fluxes, which would be anisotropic, as well as advective fluxes, which indicate preferred migrations. While such an extension is appealing from the point of view of first principles in spatial ecology, by explicitly modelling migrations, it would lead to correlation structures that make computations much more demanding. In general, inference in spatio-temporal dynamics, including model selection, is a computationally intensive task wherein the trade-off between fidelity and feasibility must be constantly reassessed as computational abilities expand.

2. The growth dynamics and the mortality patterns are grossly simplified, in that both are assumed constant. A major effort would be required to allow for changes in growth rates, explained by current sizes and possibly also environmental covariates, as well as varying mortality, most importantly described by spatio-temporal patterns and sizes of catches in the fisheries (available from log-book and landings data). Ultimately, the inclusion of such patterns could lead to a spatio-temporal size-based assessment model. The effort required for this development would be very substantial, but single steps in this direction are currently being prepared.

3. It could be envisioned to include different population components, differing in timing and location of spawning. This would facilitate the tracking of individual cohorts.

Conclusions

The perception of the migration and population patterns of *Merluccius paradoxus*, as derived from the first geostatistical modelling of data from the main survey countries in the region (Namibia, South Africa and Norway), largely corresponds to the hypothesis and data plots presented by Le Clus et al. (2005) and Strømme et al. (2016), yet differs from current management-assessment practices in Namibia, and South Africa, where *M. paradoxus* continue to be separately managed as two stocks.

Acknowledgements — We wish to thank the lab and field assistants from the Ministry of Fisheries and Marine Resources (MFMNR, Namibia), the Department of Agriculture, Forestry and Fisheries (DAFF, South Africa), the Institute for Marine Research (Norway), as well as Dr Tore Strømme (FAO/Norway) and the captains and crews of the RS *Africana* and RV *Dr Fridtjof Nansen* which sampled and measured the deepwater hake analysed in the present study. The sampling effort was funded by the MFMNR (Namibia), DAFF (South Africa) and EAF-Nansen Project (FAO/Norway). Data analysis and publishing was funded by EuropeAid through the EcoFish project (CRIS Number C-222387).

References


