Population abundance and seasonal migration patterns indicated by commercial catch-per-unit-effort of hakes (*Merluccius capensis and M. paradoxus*) in the northern Benguela Current Large Marine Ecosystem

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Abstract

We developed generalized additive models (GAM) to estimate standardized time series of population abundances for assessment purposes and to infer ecological and behavioural information of northern Benguela hakes (*Merluccius capensis* and *M. paradoxus*) using haul-by-haul commercial trawl catch rates data as proxies for hake densities. The spatial density patterns were validated using geostatistical modelling results of fisheries independent trawl survey data. The modelling indicated that abundance estimation and biological studies based on commercial catch per unit effort should be based on individual vessel id's rather than general vessel characteristics such as vessel size. The final models explained 79% and 68 % of the variability in commercial catch rates of *M. capensis* and *M. paradoxus*, respectively. The spatial density patterns were consistent and confirmed existing knowledge about these species in the northern Benguela. Furthermore, seasonal migration patterns were described for the first time and were found to correspond to the spawning areas and seasons. *M. capensis* migration patterns appear during August and September, while *M. paradoxus* shows substantially during the month of May to August. We recommend that assessment scientists take consideration of the present model of catch rates, the spatial and seasonal distribution maps constructed in this study to better understand the relationship between fleet dynamics and fish movement drivers to fishery catchability of the hake population in the northern Benguela. This would support an implementation of a species specific assessment and management.

Introduction

Commercial catch rates or *catch-per-unit-effort* (CPUE) calculated from mandatory daily logbooks reflects the behaviour of the fisheries, as well as fish behaviour and abundance (Maunder and Punt 2004; Jansen et al, 2013). Detailed process knowledge and auxiliary data from the fisheries are therefore imperative for extraction of unbiased abundance time series for fish stock assessments or to infer biological information about the fish. This can be done using statistical modelling, such as General Additive modelling (GAM) (Maunder and Punt 2004; Jansen et al, 2013). It has long been recognized that catchability may vary as function of changes in stock abundance and distribution (Gulland 1956), differences among vessels, dependent on biological characteristics such as the fish size (Beverton and Holt 1957), technological development (Marchal et al., 2007), diel effect (Kainge et al, 2015; Johnsen and Iilende, 2007) and environmental effects (Kainge et al., submitted).

Demersal trawl fishery in the northern Benguela is well-developed, exploiting shallow-water hake (*Merluccius capensis*) and deep-water hake (*M. paradoxus*) (Gordoa et al 1995; Wilhelm et al., 2015). The two hake species are morphologically very similar in appearance e.g. shape, colour and structure (Gordoa and Duarte, 1991, Lloris et al., 2005) but differing in number of vertebrae (von der Heyden et al., 2007), pigmentation of the gill rakers and colour of anal fin (Gordoa et al 1995). The morphological similarity and overlapping distribution between 250-400 m bottom depths (Both, 1985, Boyer and Hampton 2001; Burmeister 2001) have made it difficult to register the two species separately in the commercial catches. The two species are furthermore characterized by different ontogenetic vertical and horizontal migration patterns (size related distributions) (Jansen et al, 2016; submitted). *M. capensis* prefers 50-400 m bottom depth, while *M. paradoxus* inhabit deeper waters between 250 and 800 m (Gordoa and Duarte, 1991; Burmeister 2001). Both species appears to move away from their nursery areas as they grow larger and then return to the spawning areas as they mature (Jansen et al, 2016; submitted). The nursery areas for *M. capensis* in Namibia are found off Walvis Bay and the Orange River, while the South African west coast is the likely origin of *M paradoxus* (Jansen et al, 2016; submitted). No direct indication of seasonal alongshore movement in concentrations of *M. capensis* or *M. paradoxus* have been reported for Namibian waters (Gordoa et al., 2006).

Commercial fishing target hakes along the entire Namibian coastline. Fishing is mainly conducted by trawlers composed of wet fish and freezer factory trawlers. The wetfish trawlers (19 – 111 m in length, 224 - 7200 horse power) have a loading capacity of 100-200 tonnes of fresh fish packed on ice (Paterson et al 2013). Fish trips takes up to 12 days (Kirchner 2014). The freezer factory trawlers (19 -92 m in length and 415-4800 horse power), has larger holding capacity of 450 – 1000 tonnes. Catches are processed, packed and frozen on board. Fishing trips last for about 30 – 90 days (Kirchner 2014). The duration of a trawl varies between approximately 0.5 and 10 hours. Trawling is longer and in slightly deeper waters during night time (Johnsen and Iilende, 2007). The proportion of *M. capensis* is higher during the shorter hauls in shallower waters during the day (Johnsen and Iilende, 2007).

M. capensis and *M. paradoxus* are monitored through annual trawl surveys, on-board sampling of commercial catches and landing statistics. The data are synthesized in annual stock assessments using statistical catch-at-age modelling (Kirchner et al., 2012; Kathena et al., 2016). The two species are treated as one combined hake stock restricted to Namibia (Butterworth and Geromont, 2001; Johnsen and Kathena, 2012, Kirchner et al 2012; Kathena et al., 2016), despite strong indications of transboundary migrations between Namibia and South Africa of both species (Jansen et al 2016, Jansen et al., 2017, Strømme et al., 2016) and multiple stocks of *M. capensis* (Jansen et al.,2016, Jansen et al., 2015, Henriques et al., 2016). Species and stock specific transboundary assessments are imperative for provision of optimal and sustainable fisheries management advice. However, international coordination of transboundary assessments has not yet been achieved. Species specific data has been prepared by splitting of commercial hake catches from Namibia using a linear model fitted to daily samples by on-board fisheries observers (Johnsen and Kathena, 2012). However, this dataset has not yet been included in assessments or other analyses.

In this study, we conduct the first analysis of this unique dataset of haul-by-haul species specific catch and effort data. Statistical modelling of the catch rates are done with the aim of inferring ecological and behavioural information such as seasonal migrations, and to provide standardized time series of population abundance of *M. capensis* and *M. paradoxus* for future species specific assessments.

Materials and methods

The pre-processing of the data, visualization and the analysis are done using R statistical language (R Core Team, 2016). In the following, we present the input data and statistical modelling methods.

Commercial catch data

Logbook and observers data were extracted from the Fisheries Information and Management Systems (FIMS) database administered by NatMIRC (version July 17 2015). The haul-by-haul commercial trawl catch of hakes (in kg) were obtained from logbooks by vessel id (anonymized), vessel type (wet trawler or freezer trawler), Gross Register Tonnage (GRT), position, date, time, depth. The system also provided length distributions and a species specific ratio of *M.capensis* / *M.paradoxus* by year, month, and 0.5 ° latitude in 50 m depth intervals that was used to split the haul-by-haul catch data into catch by species (Johnsen and Kathena, 2012). This was based on observers that sampled minimum one haul per day. Only records from the period 1998-2014 are used in this study, data for the earlier years 1964-1997 were excluded due to incomparability in the data collection procedures.

Catch rates of hakes in non-hake targeted fisheries (such as trawling for monk (*Lophius sp.*)) are lower than in the fisheries that target hake. It would therefore bias the results if the non-hake targeted fisheries were primarily conducted in certain seasons or areas. The data set was therefore restricted to include only fishing trips that targeted hake. This information was available because it is mandatory by law to report the target species of each landing.

The dataset consisted of 764 633 individual trawl hauls. The hauls covered the entire latitudinal range of Namibia (17ºS - 30ºS) between approximately 200 m and 800 m depth (Figure 1) with between 22 845 and 60 897 hauls per year equally spread over the months (Figure 2a and b). Trawling duration ranged from 15 min to approximately 10 hours, with most hauls between 2 and 5 hours (96 %) (Figure 2c). The GRT of the 184 individual vessels ranged from 100 to 5 638 tonnes (Figure 2d). Freezer trawlers were generally larger than the wet trawlers (Figure 2d). The fishery has a minimum mesh size of 110 mm aimed to protect <36 cm hakes.

All commercial hake fishing in Namibia was prohibited in waters shallower than 200 m. Since 2006 wet and freezer trawlers in the area south of 25°S were furthermore prohibited to fish shallower than 300 and 350 m, respectively, and not allowed to target hake anywhere during the month of October.

The theoretical subsurface light intensity (*SS-PAR*) was calculated from position, date and time. The estimation assumed average oceanic atmospheric conditions, no clouds, no waves. The calculation was done in two steps: (1) calculating photosynthetically active radiation (PAR) i.e. wavelengths between 400-700 nanometers and solar angle using the astrocalc4r method in the fishmethods package (Jacobson et al., 2011). (2) Calculating the fraction of the light that was not reflected by the surface using the Snel's and Fresnel's laws of refraction and transmission (Weinberg, 1976).

Statistical Analysis

Statistical modelling was applied to derive the spatio-temporal pattern in the catch rates of hake using temporal (*Year, Month, Hour*), spatial (*Latitude, Longitude, Depth*) and fisheries parameters (*Vessel Id, GRT, Vessel type*). General Additive Models (GAM) was applied. GAM modelling was selected because it provides a simple, yet effective, way of accounting for nonlinear effects. Briefly, GAM is an extension of general linear models with the possibility to fit smoothing functions to some of the predictor variables as an integrated part of the model fitting.

Modelling of the *catch rate* (kg * hour of trawling $^{-1}$) of species *sp* (either *M. capensis* or *M. paradoxus*) was implemented with $Catch_{sp}$ (kg) as the response variable and the effort (*Duration* in hours) as an offset variable as recommended by Maunder and Punt (2004). The residuals from the fitted models were assumed to be normal distributed, independent and identically distributed (IID) after log-transformation of *Catch* and *Duration*.

The issue of strong multicollinearity is an issue in all regression type models (with multiple predictors), as the inclusion of strongly correlated variables in a model leads to model identifiability issue (affecting parameter estimation). Thus it is generally recommended to check for this and when found to either exclude one or more of those variable that share information (strongly correlated) or convert them into a single derived variable (e.g. using Principal Component Analysis PCA). The simplest way to check for this issue is pair-wise correlation among predictors to be used in the model. In addition one could also apply Variance Inflation Factor (VIF) to test for the existence of strong multi-collinearity (Zuur 2010). VIF was calculated using the car package (Fox and Weisberg 2011) in R, here we used the threshold value below 3.0 suggested in (Zuur et.al., 2009) as our criteria. The spatial predictor variables latitude and longitude were strongly correlated (spearman correlation coefficient r = 0.97 exceeding the limit of 0.6 (Zuur *et al.*, 2009)). Longitude was therefore excluded from the analysis because the spatial patterns of hake off Namibia can be well represented by latitude as a proxy for alongshore patterns and depth for the cross-shelf patterns (Jansen et al. 2016). The gear parameters were also correlated. Each starting model was therefore fitted with either *Vessel Id*, *GRT* or *Vessel Type* as the proxy for the effect of the vessel.

Consequently, the staring models consisted of the following predictor variables *Year*, *Month*, *Depth, Latitude* and one of the parameters representing the fishing operation (either *Vessel Id*, *Vessel type* or *GRT*). All starting model for *M. capensis* are listed in Table 1 and in Table 2 for *M. paradoxus*. Model 9 is given as equation 1 as an example:

$$\log(Catch_{sp}) = \beta_0 + \beta_1 * Year + \beta_2 * Month + \beta_3 VesselId + S_1(SS\_PAR) + S_2(Lat, Depth, by \cdot Month) + S_3(Lat, Depth, by \cdot Year) + \varepsilon \qquad (1)$$

s() was the penalized cubic regression spline 2D-smoothing function implemented in the “mgcv”-R-package as cardinal spline (Wood, 2011). It was applied to *Depth* and *Latitude* in order to allow for a non-linear smoothed spatial surface. Models were constructed with a general surface for all years and months, as well as models with year and/or month-specific surfaces (using the by-clause in the *s*()-function). Furthermore, *s()* was applied to *SS-PAR* in order to allow for a non-linear functional link. The smoothing parameter k (number of ‘‘knots’’) was set to 3 in order to allow for non-linearity whilst avoiding overfitting ecologically unrealistic functional forms (Jansen et al., 2012).

Model fitting was done in R (R Core Team 2016) using the “mgcv”-package (Wood, 2011). Model selection was done as “backwards modelling” based on, Akaike, r^2, p-values and ANOVA tests. Insignificant terms ($p > 0.05$) were sequentially removed. After each removal of the parameter with the highest p-value an ANOVA was used to test if reintroduction of the parameter improved the model significantly ($p > 0.05$). This procedure was continued until all remaining terms in the model contributed significantly to the model fit. The preferred model was selected as the fit with the lowest Akaike Information Criterion (AIC) value (Akaike, 1974). Finally, model assumptions were verified by plotting the residuals. The modelling assumed that the errors were normal distributed around the mean, residuals were therefore plotted against the fitted values. The modelling furthermore assumed that there were no residual patterns related to the predictor variables (covariate). These diagnostic plots include: plots of residuals versus each predictor variable (covariate) which is generally expected to show a rather random distribution of residuals over the range of each of the predictor variables; plots of residuals vs fitted values with the expectation that there are no major patterns and residuals are randomly distributed over the range of the fitted values; and quantile-quantile plots of the residuals which is expected to be roughly linear with no major curvatures in either ends.

Finally the predicted catch (standardized catches) was then plotted with the nominal catches. The model output was compared with information from fisheries independent surveys (the annual Namibian hake trawl survey in January - February, see survey details in e.g. Jansen et. al, 2016). This was done using an existing time series of yearly abundance indices (depth stratified average catch rates) from Kainge et al (2015) and distribution maps based on geostatistical model output from Jansen et al. (2016).

Results

Model validation indicated no violations of the model assumptions (supplementary information 3, 4 and 5). Model performance measures (AIC – Akaike Information Criterion and R^2) for the 9 catch model for *M. capensis* and *M. paradoxus*, were reported in Table 1 and Table 2, respectively. The best model fits (lowest Akiake values) were model number 9, explaining 78% and 68% of *M. capensis* and *M. paradoxus*, respectively. Parameter estimates, standard errors, t-values and p-statistics were reported for the best model fits in Table 3 and Table 4, respectively.

Catch rates of *M. paradoxus* were significantly higher than catch rates of *M. capensis*. The time series of the species were similar indicating a series of low values between 2002 and 2007, and a peak value in 2011 (Figure 3a). Lowest catch rates were seen during austral spring (October-November for *M. Capensis,* August-December for *M. Paradoxus*) (Figure 3b). The effect of *SS-PAR* was nearly identical for the two species and indicated that the hakes were more difficult to catch during dark conditions than during daylight conditions (Figure 3c).

The spatial patterns (latitude-depth surfaces) differed between the two species (Figure 4a and Figure 5a).

Catch rates of *M. capensis* consistently increased towards the north and the shallow (Figure 4a-b). The monthly distributions of catch rates of *M. capensis* appeared to shift to a slightly shallower and more southern distribution around August and September (Figure 4a-b). This coincided with an increase in fish size in the south (Figure 4c). Yearly distribution maps of catch rates also indicated some interannual variation. The two most extreme cases are mapped in Figure 6a-b.

Catch rates of *M. paradoxus* were consistently low in the north at bottom depths less than 400 m and in the south at less than 300 m. At greater depths, three patches of increased catch rates were indicated, namely at 300-450 m in the south, 500-600 m in the north and deeper than 750 m. Furthermore, there was a patch of low catch rates between 500 and 700 m in the south (
Figure 5a). Catch rates increased substantially around the patch at 300-450 m in the south during May to August (
Figure 5b). The size distributions of the three patches indicated increasing size with depth (
Figure 5c).

Spatial patterns of hake densities obtained from geostatistical modelling of fisheries independent trawl survey data indicated patterns similar to the patterns found in the present study. That was found for both *M. capensis* (Figure 7a and Figure 8a) and *M. paradoxus* (Figure 7b and Figure 8b) when comparing the same months (January-February) as the surveys were conducted.

Discussion

This study has demonstrated the necessity to consider *Vessel ID* and theoretical subsurface light intensity (*SS-PAR*) when performing a standardization of *M. capensis* and *M. paradoxus* commercial catch-per-unit-effort in the northern Benguela. The model developed in this study described 78% and 68% of the variability in the data for *M. capensis* and *M. pardoxus* respectively.

Statistical modelling exposed annual patterns of *M. capensis* and *M. paradoxus* commercial catch rates largely in line with Kainge et al., (2015) that were based on independent trawl surveys.

The *Vessel ID* model provided the best fit (Table 1 and 3). Implying that, the contribution of the individual *Vessel ID* was important, suggesting that the skill of the individual fishermen or other factors not captured by the technical characteristics such as investment in technology are important in this fishery. The theoretical subsurface light intensity (*SS-PAR*), revealed that both hake species are difficult to catch at night. This make sense because *M. capensis* are known to undertake diel vertical migration (Johnsen and Iilende 2007; Kainge et al 2015) maybe in search for food (Johnsen and Iilende 2007) or for spawning purpose (Sundby et al 2001; Gordoa et al 2006). The vertical migrations behaviour makes the hake inaccessible to the demersal trawl. Our results support previous findings by Johnsen and Iilende (2007), that observed that on averaged the commercial catch rates are about 3.6 times higher during the day than during the night.

Year effect showed a remarkably similarity between the two species. *M. paradoxus* catch rates are of relative higher magnitude than *M. capensis* (Fig 3 a). Both species catch rates were lower during 2002-2007, similar trends were observed in the trawl survey estimates (Kainge et al., 2015; Kathena et al., 2016). Kainge et al., (2017), examined effects of environment variables on survey catch rates and distribution, found that in 2011 the large *M. capensis* occurred predominantly in increasingly deeper water than in other years. This finding is supported by our study, where the catch rates of *M. capensis* was observed to be higher in 2011. Seasonal, once of, or gradual long-term shift towards deeper water, outside the restricted depth zone makes *M. capensis* more available to commercial fishing, which would lead to an increase in catch rates. The catch rates of *M. paradoxus* was also higher in 2011. The reason for this is unknown, but could be related to the same environmental abnormality that changes the distribution of *M. capensis*.

The seasonality in catch rates was evident from the monthly effect. The study observed lower catches of *M. capensis* during austral spring (October – November), while *M. paradoxus* it was mainly observed during (August – December). Several authors have documented spawning activities of the two species coinciding with those periods (Sundby et al., 2001; Kainge et al., 2007; Jansen et al., 2015, Wilhelm et al., 2015). The present study support previous findings by Gordoa et al., (2000) examining monthly variability in the catchability of hakes and related the unavailability of *M. capensis* to the commercial trawl to spawning activities. Kainge et al., 2007, found peaks in gonadosomatic indices from July to October. Similarly, Jansen et al., (2015) using gonad and body weight to infer peak spawning period found the peak spawning of *M. capensis* to be around September/ August. The drop in *M. paradoxus* catch rates also coincide with the peak spawning period around August in the northern Benguela and August to October in southern Benguela (Grote et al., 2012; Jansen et al., 2015).

Catch rates from commercial fisheries as a proxy for fish density

The relation between catch rates and fish density is complex. In this study we included light and vessel-specific characteristics, but the catch rates may have been affected by other factors that are important during the fishing processes, some of which are discussed here:

- Price of fish

Hake fishery is mainly exported and in 2007, an estimated 97% was exported, mostly as frozen, chilled or frozen raw material (Paterson et al., 2013). The world markets dictate the price of the Namibian hake. Historically, Spain has been the main market of these products. The Namibian hake industry does not have control over the selling transaction hence; revenue in this fishery is mainly influenced by the exchange rate and oil price. The weakening of the Euro lead to fall in hake fishery revenues

- Oil prices vs. distance to harbour

The spatial density of fish is not evenly distributed, where a skipper decides to fish largely determines the size and value of his catch. The skipper must consider not only the catch he is likely to make at different location but also the cost incurred in fishing at those location. As a consequence the catch rates and the catch per unit effort observed in a fishery depend not just on fish stock abundance but also on economic factors such as wage rates, fish and fuel prices. Kirchner (2014) found a change in oil price to have a negative effect on the hake fishing operations. For example in 2000 the total operational budget, oil price constitutes about 20% for wetfish trawlers and about 35-40% for freezer trawlers. Skipper can maximize his share of the fishing profit by operating his vessel at a particular distance from port. Poos et al., (2013), examining the rising fuel cost in beam trawl found that fishers already fishing close to port were not affected, but those that fish at larger distances were increasingly affected. This prediction is supported by Kirchner (2014) findings of hake fishery, were wetfish trawlers were limited to stay out at sea for a maximum of 7 days instead of the usual 12 days to reduce costs.

- Technological creeping

Due to technological advances the results should be interpreted with caution, because there are several possible underlying effects. In general technological improvements in fishing gear and electronics increase fishing power (Marchal et al., 2007). The improvements can influence both catch and effort and the overall profitability of the operation, i.e reducing the cost of the operation, which may not be reflected in the catch rates. Another important consideration concerning gear modification/ improvements is that changes are normally implemented rapidly by entire fleets in a relative short time (2-3 years) leading to very or no contrast between annual trends in catch and effort data (Marchal et al., 2007). As shown by Robin et al., (1998) technological innovation can spread quickly in a fleet of vessels competing for a common resource.

- Spatial closure

Close areas, potentially changes the relationship between catch rates and fish density as it eliminate valuable fishing ground and displace fishing effort.

The models with *Vessel Id* led to better fits than *GRT* and *Vessel Type*. The *Vessel Id* represents both the vessel characteristics such as type, size, engine power, acoustic properties. In addition, it is a fuzzy proxy for features that are not easily quantified, such as the captain and the crew's ability for efficient finding and catching of the fish as well as quality and maintenance level of the gear and instrumentation. The results thus indicate that abundance estimation and biological studies based on commercial CPUEs should be based on individual id's rather than general vessel characteristics such as vessel size.

Migration and distribution patterns

For the first time, maps and plots of species specific seasonal migration patterns of hake is provided for the northern Benguela. The spatial patterns in catch rates in fisheries independent trawl surveys were similar to the catch rates from the fisheries for the same months when the surveys were conducted supporting the findings by Jansen et al., (2015); Jansen et al., (2016) and Strømme et al., (2016). The scientific trawl surveys have been standardized with regards to gear and trawling operation, and the catchability is therefore assumed to be constant. Consequently, the relation between catch rates of the survey and fish density are affected by less factors (noise/bias). This validates, to some extent, the usage of the present model of catch rates from the fisheries as an

indicator of hake density and abundance. It is therefore possible, for the first time, to infer information about seasonal density distributions, and migration of *M. capensis* and *paradoxus*.
The study found differences between the spatial patterns of the two species. These findings support existing knowledge about the spatial distribution of *M. capensis* and *M. paradoxus* in the northern Benguela (Botha 1985; Jansen et al., 2015; Wilhelm et al., 2015). It is evident from supplementary information 3 and 4 that *M. capensis* inhabits shallower water at 200 – 350 m bottom depth and more northerly waters (17o S to 25o S) whereas *M. paradoxus* occupy the deeper water (Botha 1985), except in southern boarder were this species is found between 250-300 m supporting the findings by Johnsen and Kathena (2012). Our study found an increase in *M. capensis* catch rates towards the north and in shallow water.

Migration and distribution patterns - seasonal

The monthly distributions of *M. capensis* indicated a shift in distribution during austral winter, to a more southern and shallow distribution which matched the spawning area and season of the Walvis spawning component (stock) (Jansen et. al, 2015). The fish that endeavoured on this seasonal spawning migration was large and likely mature (larger than 25 cm, the size where 50 % of the M. capensis are mature (Wilhelm et al., 2015).

A high density patch of small *M. paradoxus* was found between 300 and 450 m. This matched the inflow of small fish from the nursery areas off the South African west coast (Strømme et. al, 2016; Jansen et al, submitted). The density of this patch increased substantially during the months May to August which indicated a seasonal peak in the northern transboundary feeding migration.

Summary

Our study provides useful information on the difference in spatial and seasonal patterns of the *M. capensis* and *M. paradoxus* in the northern Benguela. The final models explained most of the variability in the catch data. A multitude of factors affected the catch of both species including those that varied interannualy and seasonaly (for which the year and month variables acted as a surrogate), depth, latitude (SS-PAR) and individual *Vessle ID's* (as a proxy for vessel characteristics). For future studies it would be desirable to incorporate environmental and economic factors in the model fitting as these might improve the model performance. The spatiotemporal patterns found in this study, confirmed information from other sources such as scientific surveys, suggesting that the modelled spatio-temporal patterns were closely related to density. For the first time, we described the seasonal migration patterns of both species. The lack of coverage of *M. capensis* in shallow distribution areas is a problem for using this as a density time series as it was observed in year 2011 and also illustrated in figure 6. For *M. capensis* the density index covers more than one stock i.e. the Walvis Bay and the Orange river component (Jansen et al 2015). For *M. paradoxus* the density index only covers parts of the stock the rest is in South Africa (Jansen et al 2017).

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Legends for Figures

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

Figure 2. Commercial trawl hauls from the logbook dataset by year (a), month (b), haul duration(c) and GRT/vessel type (d).

Figure 3. Catch rates of *M. capensis* and *M. paradoxus* in the northern Benguela predicted by generalized additive model: yearly effect (a), monthly effect (b) and the light intensity (c). The thin dashed lines represent the 95% confidence interval from the GAM and central line is the mean prediction.

Figure 4. Catch rates distribution corresponding to depth distribution of *M. capensis* by latitude: (a) during spawning peak (August – September), (b) during (October- July), (c) Length frequency in the south during summer between 200-300 m (summer (S 200-300)) solid line, during winter between 200-300 m (winter (S 200-300)) solid line, while the dashed lines represent the north during summer between 200-300 m (summer(N 200-300)) and during winter between 200-300 m (winter(N 200-300)). An area with the color corresponding to 16% consists 16% of the population.

Figure 5. Catch rates distribution corresponding to depth distribution of *M. paradoxus* by latitude in the northern Benguela (a), patchness as a function of latitude, depth by month (S 375 (south at 375

m bottom depth)), N 550 (north at 550 m bottom depth) and 775 (at 775 m bottom depth for the entire coast line) (b), Length frequency sampled from the catches in the respective areas described above in (b) (c). An area with the color corresponding to 16% consists 16% of the population.

Figure 6. Year differences in catch rates distribution of *M. capensis* and *M. paradoxus* in the northern Benguela. Panel (a) and (b) catch rates distribution corresponding to the depth and latitude in year 2010 and year 2011 for *M. capensis*. Panel (c) and (d) are catch rates distribution for *M. paradoxus* for year 2013 and 2014. An area with the color corresponding to 16% consists 16% of the population.

Figure 7. Distribution maps by depth and latitude of *M. paradoxus* and *M. capensis* larger than the size selected in the hake fisheries (35 cm). Data from geostatistical modelling of trawl survey data in January-February 1998 to 2012 (Jansen et al., 2016, submitted). The distributions are illustrated as cumulative fractions, e.g. the sum of all areas with the color corresponding to 40 % represents 40 % of the total.

Figure 8. Distribution maps by depth and latitude of *M. capensis* and *M. paradoxus* taken during the period that coincide with the survey period January-February 1998 to 2014. An area with the color corresponding to 16% consists 16% of the population.

Tables

#	Species	Predictors	Akaike	Rsqr
1	Capensis	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + s(*GRT*, k = 3) + s(*Lat*, *Depth*, by = factor(*Year*)	2007142	0.76
2	Capensis	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + s(*GRT*, k = 3) + s(*Lat*, *Depth*, by = factor(*Month*)	2022716	0.76
3	Capensis	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + s(*GRT*, k = 3) + s(*Lat*, *Depth*, by = factor(*Year*)) + s(*Lat*, *Depth*, by = factor(*Month*)	2001005	0.77
4	Capensis	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + factor(*VesselType*) + s(*Lat*, *Depth*, by = factor(*Year*)	2046164	0.75
5	Capensis	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + factor(*VesselType*) + s(*Lat*, *Depth*, by = factor(*Month*)	2065297	0.74
6	Capensis	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) +	2039758	0.75

		factor(*VesselType*) + s(*Lat*, *Depth*, by = factor(*Year*)) + s(*Lat*, *Depth*, by = factor(*Month*)		
7	Capensis	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + factor(*VesselId*) + s(*Lat*, *Depth*, by = factor(*Year*)	1932356	0.79
8	Capensis	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + factor(*VesselId*) + s(*Lat*, *Depth*, by = factor(*Month*)	1943625	0.78
9	Capensis	offset(log(*Duration*)) + factor(*Year*) + factor*(Month*) + s(*SS-PAR*, k = 3) + factor(*VesselId*) + s(*Lat*, *Depth*, by = factor(*Year*)) + s(*Lat*, *Depth*, by = factor(*Month*)	1926369	0.79

Table 1. Model specifications for *M. capensis*. # indicate model number.

#	**Species**	**Predictors**	**Akaike**	**Rsqr**
1	Paradoxus	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + s(*GRT*, k = 3) + s(*Lat*, *Depth*, by = factor(*Year*)	2006809	0.64
2	Paradoxus	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + s(*GRT*, k = 3)	2022365	0.63

		+ s(*Lat*, *Depth*, by = factor(*Month*)		
3	Paradoxus	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + s(*GRT*, k = 3) + s(*Lat*, *Depth*, by = factor(*Year*)) + s(*Lat*, *Depth*, by = factor(*Month*)	2000695	0.64
4	Paradoxus	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + factor(*VesselType*) + s(*Lat*, *Depth*, by = factor(*Year*)	2046204	0.62
5	Paradoxus	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + factor(*VesselType*) + s(*Lat*, *Depth*, by = factor(*Month*)	2065278	0.61
6	Paradoxus	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + factor(*VesselType*) + s(*Lat*, *Depth*, by = factor(*Year*)) + s(*Lat*, *Depth*, by = factor(*Month*)	2039777	0.63
7	Paradoxus	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + factor(*VesselId*) + s(*Lat*, *Depth*, by = factor(*Year*)	1932205	0.68
8	Paradoxus	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + factor(*VesselId*) + s(*Lat*, *Depth*, by = factor(*Month*)	1943509	0.67

9	Paradoxus	offset(log(*Duration*)) + factor(*Year*) + factor(*Month*) + s(*SS-PAR*, k = 3) + factor(*VesselId*) + s(*Lat*, *Depth*, by = factor(*Year*)) + s(*Lat*, *Depth*, by = factor(*Month*)	1926258	0.68

Table 2. Model specifications for *M. paradoxus*. # indicate model number.

Parameter	**Estimated value**	**Standard error**	**t.value**	**p**
(Intercept)	5.65	0.033	171.886	<0.001
factor(Year)1999	-0.19	0.033	-5.707	<0.001
factor(Year)2000	-0.39	0.030	-12.815	<0.001
factor(Year)2001	-0.58	0.030	-19.135	<0.001
factor(Year)2002	-0.78	0.030	-26.017	<0.001
factor(Year)2003	-0.57	0.030	-18.977	<0.001
factor(Year)2004	-0.53	0.030	-17.421	<0.001
factor(Year)2005	-0.72	0.030	-23.907	<0.001
factor(Year)2006	-0.73	0.030	-24.101	<0.001
factor(Year)2007	-0.64	0.030	-21.039	<0.001
factor(Year)2008	-0.52	0.030	-17.321	<0.001
factor(Year)2009	-0.33	0.030	-10.776	<0.001
factor(Year)2010	-0.07	0.030	-2.188	0.029

factor(Year)2011	0.28	0.032	8.831	<0.001
factor(Year)2012	-0.15	0.030	-5.050	<0.001
factor(Year)2013	-0.11	0.030	-3.690	0.000
factor(Year)2014	-0.08	0.031	-2.682	0.007
factor(Month)2	-0.02	0.005	-4.141	<0.001
factor(Month)3	-0.02	0.005	-4.656	<0.001
factor(Month)4	-0.05	0.005	-9.494	<0.001
factor(Month)5	0.00	0.005	-0.369	0.712
factor(Month)6	0.03	0.005	5.783	<0.001
factor(Month)7	-0.01	0.005	-1.977	0.048
factor(Month)8	-0.10	0.005	-18.157	<0.001
factor(Month)9	-0.25	0.005	-46.446	<0.001
factor(Month)10	-0.45	0.007	-65.299	<0.001
factor(Month)11	-0.27	0.005	-48.877	<0.001
factor(Month)12	-0.15	0.006	-26.816	<0.001
factor(VesselId)7	-0.53	0.017	-31.716	<0.001
factor(VesselId)9	-0.82	0.040	-20.292	<0.001
factor(VesselId)11	-1.54	0.020	-77.632	<0.001
factor(VesselId)14	-0.53	0.017	-30.876	<0.001
factor(VesselId)20	-1.20	0.088	-13.546	<0.001
factor(VesselId)31	-1.34	0.021	-62.930	<0.001
factor(VesselId)36	-0.75	0.025	-30.185	<0.001
factor(VesselId)50	-1.35	0.030	-44.816	<0.001

factor(VesselId)60	-0.63	0.017	-37.109	<0.001
factor(VesselId)61	-1.07	0.031	-34.378	<0.001

Table 3. *M. Capensis* catch model # 9 parameter estimates, standard errors and *p*-vales. The last 138 *vessel Id*'s were omitted from this table was presented in supplementary information 1.

Parameter	**Estimated value**	**Standard error**	**t.value**	**p**
(Intercept)	6.23	0.022	278.813	<0.001
factor(Year)1999	-0.16	0.019	-8.147	<0.001
factor(Year)2000	-0.37	0.018	-20.528	<0.001
factor(Year)2001	-0.56	0.018	-31.087	<0.001
factor(Year)2002	-0.77	0.018	-42.588	<0.001
factor(Year)2003	-0.56	0.018	-30.896	<0.001
factor(Year)2004	-0.51	0.018	-28.26	<0.001
factor(Year)2005	-0.71	0.018	-39.064	<0.001
factor(Year)2006	-0.72	0.018	-39.087	<0.001
factor(Year)2007	-0.62	0.018	-34.026	<0.001
factor(Year)2008	-0.51	0.018	-27.893	<0.001
factor(Year)2009	-0.31	0.018	-16.966	<0.001
factor(Year)2010	-0.05	0.019	-2.675	0.007
factor(Year)2011	0.31	0.021	14.451	<0.001
factor(Year)2012	-0.14	0.018	-7.505	<0.001

factor(Year)2013	-0.1	0.019	-5.279	<0.001
factor(Year)2014	-0.07	0.019	-3.537	<0.001
factor(Month)2	-0.02	0.005	-4.163	<0.001
factor(Month)3	-0.02	0.005	-4.465	<0.001
factor(Month)4	-0.05	0.005	-9.297	<0.001
factor(Month)5	0	0.005	-0.101	0.92
factor(Month)6	0.03	0.005	6.206	<0.001
factor(Month)7	-0.01	0.005	-1.605	0.108
factor(Month)8	-0.1	0.005	-17.829	<0.001
factor(Month)9	-0.25	0.005	-46.096	<0.001
factor(Month)10	-0.44	0.007	-65.178	<0.001
factor(Month)11	-0.27	0.005	-48.626	<0.001
factor(Month)12	-0.15	0.006	-26.593	<0.001
factor(VesselId)7	-0.53	0.017	-31.644	<0.001
factor(VesselId)9	-0.82	0.04	-20.227	<0.001
factor(VesselId)11	-1.54	0.02	-77.491	<0.001
factor(VesselId)14	-0.53	0.017	-30.862	<0.001
factor(VesselId)20	-1.19	0.088	-13.447	<0.001
factor(VesselId)31	-1.34	0.021	-62.838	<0.001
factor(VesselId)36	-0.75	0.025	-30.008	<0.001
factor(VesselId)50	-1.35	0.03	-44.724	<0.001
factor(VesselId)60	-0.63	0.017	-37.069	<0.001
factor(VesselId)61	-1.07	0.031	-34.352	<0.001

Table 4. *M. paradoxus* catch model # 9 parameter estimates, standard errors and *p*-vales. The last 138 *vessel Id*'s were omitted from this table was presented in supplementary information 2.

Supplementary information

[In pdf]

Supplementary information 1. *M. capensis* catch model parameter estimates, standard errors, t-value and p-values for the final models.

Supplementary information 2. *M. paradoxus* catch model parameter estimates, standard errors, t-value and p-values for the final models.

Supplementary information 3. *M. capensis* and *M. paradoxus* catch model QQ plots and residual values

Supplementary information 4. *M. capensis* catch model validation plots and diagnostics.

Supplementary information 5. *M. paradoxus* catch model validation plots and diagnostics.