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Oxygen and temperature influence the distribution of deepwater Cape hake *Merluccius paradoxus* in the southern Benguela: a GAM analysis of a 10-year time-series

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Generalised additive models (GAMs) were applied to survey data to assess the influence of dissolved oxygen, water temperature and year of sampling upon the presence/absence of small (≤ 15 cm TL), medium (16–34 cm TL) and large (≥ 35 cm TL) size classes of deepwater Cape hake *Merluccius paradoxus* captured off the west coast of South Africa. Data were obtained from surveys using the RV *Dr Fridtjof Nansen* conducted in 2003 and from 2005 to 2013 during summer (January–February). Among the variables investigated, oxygen was the most important for the small size class (juveniles), with both low and high constraints (two-sided, ‘just right’ option), whereas for the medium and large size classes the oxygen effects were one-sided (avoiding lows). This finding, in combination with other published information, suggests that the Orange Banks is a nursery ground for juvenile *M. paradoxus* and that the area covered by this nursery ground can vary with the optimal oxygen concentration. The temperature constraint was generally wider and weaker than that for oxygen, being two-sided for the small and medium hake and one-sided (avoiding highs) for the large hake. The medium hake displayed the greatest tolerance to the investigated variables, which resulted in the widest distribution for this size class. Temperature, oxygen and sampling year play an important role in determining the distribution of *M. paradoxus*, but details of the biology (life cycle) of the species, such as its pelagic–demersal transition and associated movements, are no less important.

Keywords: environmental constraints, generalised additive models, juvenile fish, nursery area, physicochemical characteristics, southeastern Atlantic

Online supplementary material: Additional information pertaining to the generalised additive models (GAMs) and related data is available at <https://doi.org/10.2989/1814232X.2019.1688681>. The list of models considered and the performance measures of each of the models, considered for the three size classes of *Merluccius paradoxus*, are presented in Tables S1 and S2. The climatologies of bottom temperature and dissolved oxygen are shown in Figure S1. Additional model diagnostics (e.g. calibration plots and residual variograms) are shown in Figures S2 and S3.

Introduction

Globally, hake species are commercially valuable fishes targeted by demersal fisheries and are important components of ecosystems (Arancibia 2015). Two hake species inhabit the southern Benguela upwelling ecosystem: deepwater Cape hake *Merluccius paradoxus* Franca, 1960 and shallow-water Cape hake *Merluccius capensis* Castelnau, 1861. This study considered the habitat of different life-history stages of *M. paradoxus* in the southern Benguela, which extends south of 27° S on the west coast of South Africa to 36° S (near Cape Agulhas) and eastwards to Port Alfred (Hutchings et al. 2009). Our study focused on the region from Cape Agulhas to the northern tip of the Orange Banks (Figure 1), where key life events are located for *M. paradoxus* (Grote et al. 2007, 2012; Stenevik et al. 2008; Garavelli et al. 2012; Strømme et al. 2015). Physical features that characterise this region are wind-driven coastal upwelling concentrated in upwelling cells, a shelf-edge Benguela

jet current flowing northwards and a subsurface poleward countercurrent (Kirkman et al. 2016).

Merluccius paradoxus occurs off Namibia and South Africa but mainly spawns in South African waters (Crawford et al. 1987; Grote et al. 2007; Strømme et al. 2015), between the western Agulhas Bank and St Helena Bay (Jansen et al. 2016) (Figure 1). It spawns all year round, with most spawning activity from August to October on the western Agulhas Bank (Durholtz et al. 2015; Jansen et al. 2015, 2016; Strømme et al. 2015), although individuals of *M. paradoxus* with mature gonads have been found as far north as 25° S (Jansen et al. 2015). During summer, when much larval transport of Cape hakes occurs, alongshore southeasterly winds on the west coast are important for transport success (Stenevik et al. 2008; Garavelli et al. 2012; Grote et al. 2012). Wind strength influences the vertical movement of larvae as they passively disperse to surface

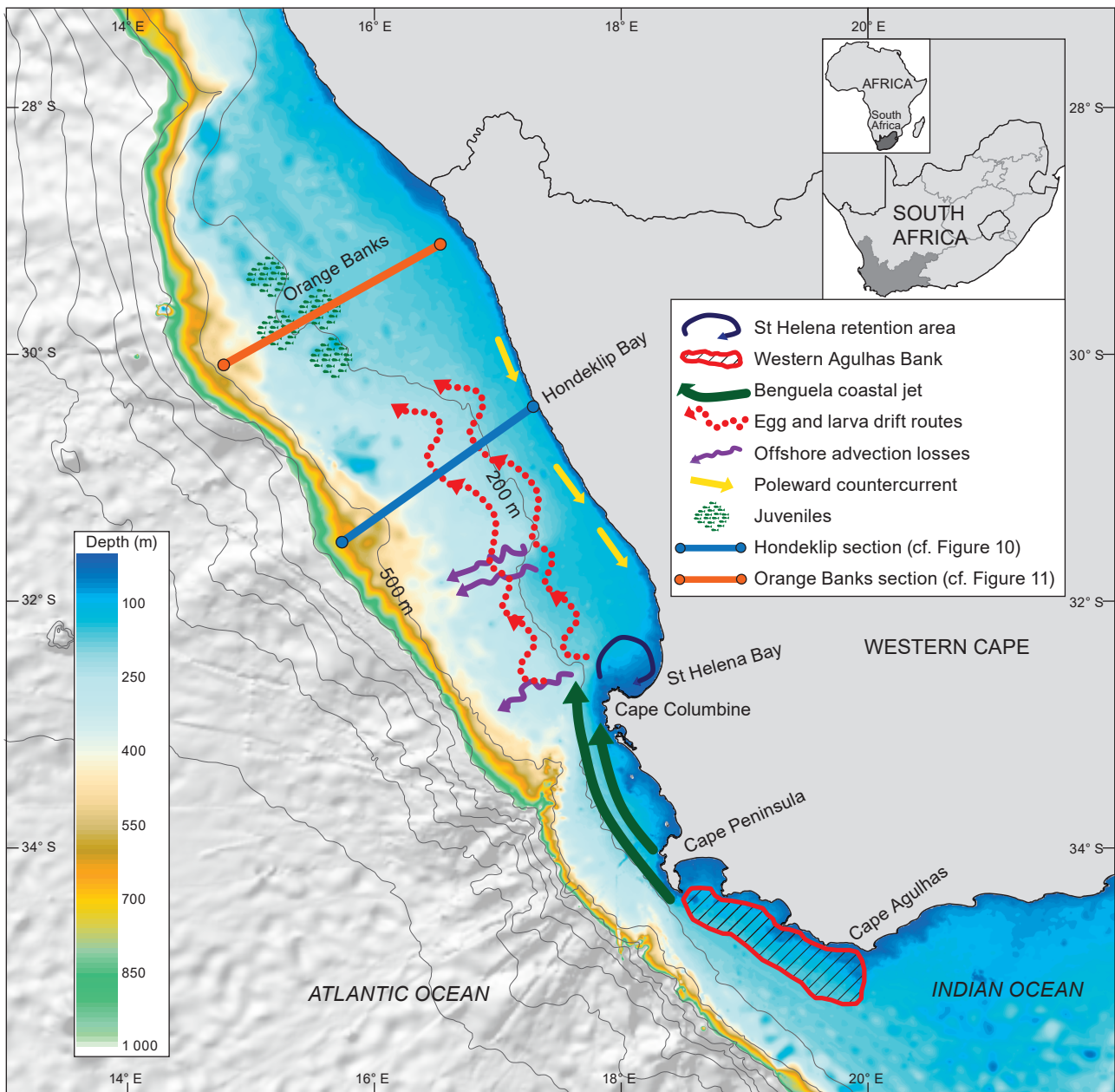


Figure 1: Schematic map of the west coast subsystem of the southern Benguela, showing the locations of key events in the life cycle of deepwater Cape hake *Merluccius paradoxus*, modified from the findings of Grote et al. (2007), Stenevik et al. (2008), Garavelli et al. (2012), Grote et al. (2012), Strømme et al. (2015), and Kirkman et al. (2016)

layers (Shannon et al. 1988), and large variability in wind forcing can have an effect on larval loss (Sundby 2016).

Local currents associated with upwelling favour retention of *M. paradoxus* juveniles in the lee of the Cape Columbine headland, within the shallow St Helena Bay (31–33° S, Figure 1). This area is a major nursery ground for many ecologically and commercially important fish species (Hutchings et al. 2002). However, most *M. paradoxus* eggs and larvae drift northwards towards the Orange Banks (Figure 1), growing into juveniles along the way (Stenevik et al. 2008; Grote et al. 2012; Jansen et al. 2015; Strømme et al. 2015). The Orange Banks are located between the Hondeklip Bay/Namaqualand

upwelling cell and the large, permanent Lüderitz upwelling cell. Moreover, the upwelling plumes in the southern Benguela also have a major effect on food availability for juvenile hakes since they control the cross-shore exchanges and spatial distribution of plankton (Barange et al. 1992). Upwelled water from Hondeklip Bay (Ostrowski et al. 2011) can enhance successful feeding of the juvenile hake on these nursery grounds. However, in contrast to the well-studied St Helena Bay nursery area (Hutchings et al. 2002), the Orange Banks area has not been intensively studied, and there are limited data on environmental variables influencing the distribution and abundance of *M. paradoxus* on these nursery grounds.

Hake juveniles and adults often have different temperature tolerances and preferences (Olivar et al. 1988). This might also apply to salinity and oxygen (e.g. Singh and Lamont 2016). In the west-coast region of the southern Benguela, particularly in St Helena Bay, low levels of dissolved oxygen can induce stress in Cape hakes (Roel and Bailey 1987). Unlike adult *M. capensis*, which can survive in low oxygen concentrations, *M. paradoxus* adults have not been found in oxygen-deficient waters (Millar 2000; Sundby et al. 2001). Hake catches have been found to depend on bottom temperature, oxygen and salinity (Botha 1986), but temperature and oxygen are believed to have stronger influences than salinity on hake distribution and abundance (Olivar et al. 1988). Singh and Lamont (2016) mostly found *M. paradoxus* juveniles in moderately oxygenated waters ($2\text{--}3.5\text{ ml O}_2\text{ l}^{-1}$) and it appeared that temperature was more important than oxygen in determining the distributions of *M. paradoxus* juveniles. Kainge et al. (2017) found that juveniles of *M. capensis* were more sensitive than juveniles of *M. paradoxus* to dissolved oxygen concentrations.

This study aims to link the occurrence of different size classes of *M. paradoxus* to two important environmental variables that influence them: near-bottom dissolved oxygen and water temperature. More specifically, the study aims to identify the ranges of these environmental variables within which *M. paradoxus* is found and to assess temporal stability of this environmental window by investigating interannual variability. Finally, we assess the importance of the Orange Banks as a nursery habitat for this species, taking into consideration all available evidence.

Materials and methods

Data sources

Data were obtained from demersal surveys by the RV *Dr Fridtjof Nansen*, conducted from 2003 to 2013 (Strømme et al. 2015) under the Ecosystem Approach to Fisheries (EAF)-Nansen Programme, through the NANSIS database at the Institute of Marine Research in Bergen, Norway. Technical details of the trawls used, methods of surveying, processing of the catch and processing of the data of these surveys are summarised in Axelsen and Johnsen (2015). Surveys were all geo-referenced and fish data and physical data were collected at each sampled station. Demersal surveys were mostly conducted in summer (January–February), but a few were carried out in May and October. The demersal trawling surveys followed a systematic transect design, with emphasis on estimating the distribution, abundance and biological condition of *M. paradoxus*, although the surveys also monitored *M. capensis* and other demersal fishes and invertebrates. Strømme et al. (2015) provided a framework to explain abundances, catch rates, distributions, size classes and the life cycle of *M. paradoxus*, including for the length class $<15\text{ cm TL}$. In this study we analyse the presence and absence in trawls of *M. paradoxus*, in terms of water temperature and dissolved oxygen concentrations, for each of three size classes defined by Strømme et al. (2015): small (juveniles, $\leq 15\text{ cm TL}$), medium (recruits, $16\text{--}34\text{ cm TL}$) and large (adults, $\geq 35\text{ cm TL}$).

Hydrographical data on water temperature and dissolved oxygen were collected with a Seabird 9plus

CTD (conductivity–temperature–depth) probe between the surface and 10 m off the bottom. CTD casts were made prior to each trawl station. The CTD dataset comprised 1 666 stations sampled over 11 years. Of these, CTD data for 2004 and 2007 were excluded from further analysis because of, respectively, incomplete coverage of the spatial domain of the study and the absence of nearshore CTD stations in important nursery areas. The statistical analyses were based on 1 412 trawl stations with data on presence and absence of the three size classes of *M. paradoxus*.

All samples of small-sized hake were checked for species identity using counts of vertebrae (usually 3–7 fish were examined in each sample, following the rule: ‘larger sample – more fish checked’; samples larger than this were impractical, for logistical reasons). Trawls in which a mix of juveniles of both hake species was theoretically possible (in the depth range 151–190 m: Strømme et al. 2015) and trawls where large numbers of juveniles (>100) were encountered were relatively rare (about 14% of all trawls with juveniles; the mean number of juveniles in other trawls was 29). Therefore, the probability of misidentification was relatively small in the total sample of trawls used for this study. Details about the separation of juvenile hake species using combinations of depth, vertebral count and distribution had been further investigated during dedicated cruises of the RV *Dr Fridtjof Nansen* (Stenevik et al. 2009; Strømme et al. 2012). During these cruises covering the Orange Banks, clear depth stratification was found between *M. capensis* and *M. paradoxus*, with no overlaps between species in single trawls. With the vast majority of trawls in the present study having only a few juveniles in the catch, it is unlikely there was serious misrepresentation of the area in which *M. paradoxus* was present. Overall, catches of juveniles of *M. capensis* constituted 6% of all juvenile individuals of hake caught. Validity of the vertebral count method was verified by Matthee and Gopal (2004), who performed blind genetic identification of 41 individuals of both species.

Data analysis

The analysis of the demersal survey data involved the following steps: (i) interpolation of the environmental data; (ii) matching biological stations to the interpolated environmental data and extracting values of environmental variables at each station; (iii) modelling the influence of the environmental variables on hake presence and absence using eight different generalised additive models (GAMs); (iv) assessing model performance; (v) selecting the best-performing model; and (vi) generating a map of habitat suitability based on the best model. These steps are described below in more detail.

Spatial interpolation

The fisheries surveys of the RV *Dr Fridtjof Nansen* covered the west coast with a dense grid (15×15 nautical miles) of CTD stations at fixed locations, revisited each year. The oceanographic data were used to produce maps describing interannual variability of near-bottom temperature and dissolved oxygen using an objective interpolation method, applicable to regularly sampled oceanographic fields (Bretherton et al. 1976). For each survey, we derived such a map using a method equivalent to optimal interpolation: kriging with moving neighbourhood (Chilès and Delfiner 1999). The

experimental variograms used a combination of spherical and linear models. The interpolation was carried out on a grid with the nominal 4 x 4 km pixel resolution, a subset of the global area coverage (GAC) grid used in the 4-km MODIS Aqua satellite products (<https://oceancolor.gsfc.nasa.gov/>). Supplementary Figure S1 presents the composite maps over the studied domain, which represent the climatologies characterising the mean bottom temperature and dissolved-oxygen conditions during the austral summers of 2003–2013.

Generalised additive modelling

To allow for non-linearity between the occurrence of hake and the environmental variables, GAMs were applied to the data. The form of the GAM, assuming the data y_i were generated by a Bernoulli process, is $y_i \sim \text{Bernoulli}(p_i)$, where p_i is the probability of occurrence and has a mean $\mu_i = p_i$ and variance $\sigma^2 = p_i(1 - p_i)$. Thus:

$$E(y_i) = \eta(p_i) = \text{logit}\left(\frac{p_i}{1-p_i}\right) = \alpha + \sum_{n=1}^N f(X_{i,n}) + \varepsilon_i$$

where $E(y_i)$ is the expected value of y_i ; $\eta(p_i)$ is the link function, which in this case is a logit link function; α is the intercept term; $f(X_{i,n})$ indicates the smoothing spline for each variable (n) at observation i , for $n = 1$ to N (number of variables); and ε_i is the residual.

Eight different GAMs were fitted to the data (Supplementary Table S1), using the 'mgcv' package (Wood 2011, 2017) in R (R Core Team 2019). In each case the occurrence of each *M. paradoxus* size class was linked to the sets of environmental variables (temperature and oxygen) from 2003 to 2013, but excluding 2004 and 2007. Variance-inflation factors for the environmental variables were less than three, indicating that collinearity of these variables was not an issue. A number of other R packages were used for data processing and visualisation (Bivand et al. 2013; Bache and Wickham 2014; Hijmans 2017; Wickham 2017; Bivand and Rundel 2018; Henry and Wickham 2018; Pebesma 2018).

Assessing model performance

The ability of the eight different GAMs to correctly classify presence for each of the three size classes of hake was assessed using the area under the curve (AUC) of the receiver operating characteristics curves. AUCs measure how often a randomly chosen true presence will have a higher probability of being predicted as presence than a randomly chosen absence. AUC values close to 0.5 indicate the model is no better than a random classifier, whereas values close to 1 indicate a good classifier (Kleinbaum and Klein 2010). Model performance was measured using k -fold cross-validation ($k = 5$) with 10 repetitions. The predictor variables were repeatedly re-shuffled and their relative importance was calculated by comparing the model prediction from the best model to that obtained after re-shuffling. An index of relative importance (IRI) was calculated for each repetition as:

$$\text{IRI} = 1 - \text{correlation}(\text{Pred}_{\text{ref}}, \text{Pred}_{\text{reshuf}})$$

Predictors with IRI values close to 1 are considered important and the converse is true for those with values close to 0 (Thuiller et al. 2016).

The numerical accuracy of model predictions was assessed visually using calibration plots, where the observed prevalence of occurrence was binned and plotted against the corresponding model-predicted probability of occurrence (Supplementary Figure S2). A close fit to the 1:1 line indicates good predictive abilities of the model. As an additional model diagnostic, spatial independence was also checked. This was done by calculating a sample variogram from the residuals and computing a variogram envelope with just the nugget effect included. A flat sample variogram enclosed in the nugget-effect-only variogram model indicates the absence of spatial structure; the resulting variogram of the residuals (Supplementary Figure S3) indicates no violation of assumptions of spatial independence.

Results

Response curves illustrating the partial effects of water temperature, dissolved oxygen and year from the best models for the three size classes indicate size-dependent associations of *M. paradoxus* with the environmental variables (Figure 2). The response curves indicate the ranges across which the variables exert an influence, and the flatness or steepness of the dome shapes indicate the rapidity of the responses as the variables change. The small *M. paradoxus* were associated with narrow ranges of oxygen concentrations and temperature. The medium *M. paradoxus* occurred in water with a narrow temperature range, having reduced occurrence at both the cool and warm ends of the measured range; they were also associated with moderate to high oxygen concentrations. The large hake occurred in water masses that were relatively cool and had elevated dissolved oxygen concentrations.

The interannual patterns were largely flat for the period 2003–2010, with some variability; the patterns for the last three years of the time-series were similar for the three size classes (Figure 2). The temporal patterns in the temperature and oxygen response curves for all three size classes were consistent over time; results are shown only for the small size class (Figures 3 and 4). The range and median of temperature and oxygen with which the three size classes were associated indicated a degree of overlap between the medium and large size classes (Figure 2). There was a general indication, in terms of the median, that temperature associations decreased with size: small > medium > large, and the opposite occurred for oxygen: small < medium < large (Figure 2).

The ability of the GAMs to discriminate between presence and absence of *M. paradoxus* was reasonably good for all selected size classes (Supplementary Table S2; Supplementary Figure S2). For the smallest size class, oxygen was the most important variable, followed by temperature. For the medium and large size classes temperature was the most important variable, followed by oxygen. Sampling year was least important in influencing the occurrence of the three size classes (Figure 5). These results are interpreted here as environmental regulation of presence/absence of the different size classes, and environmental determination (*inter alia*, see Discussion) of their nursery ground, the extent of which will change among years (Figures 6–8).

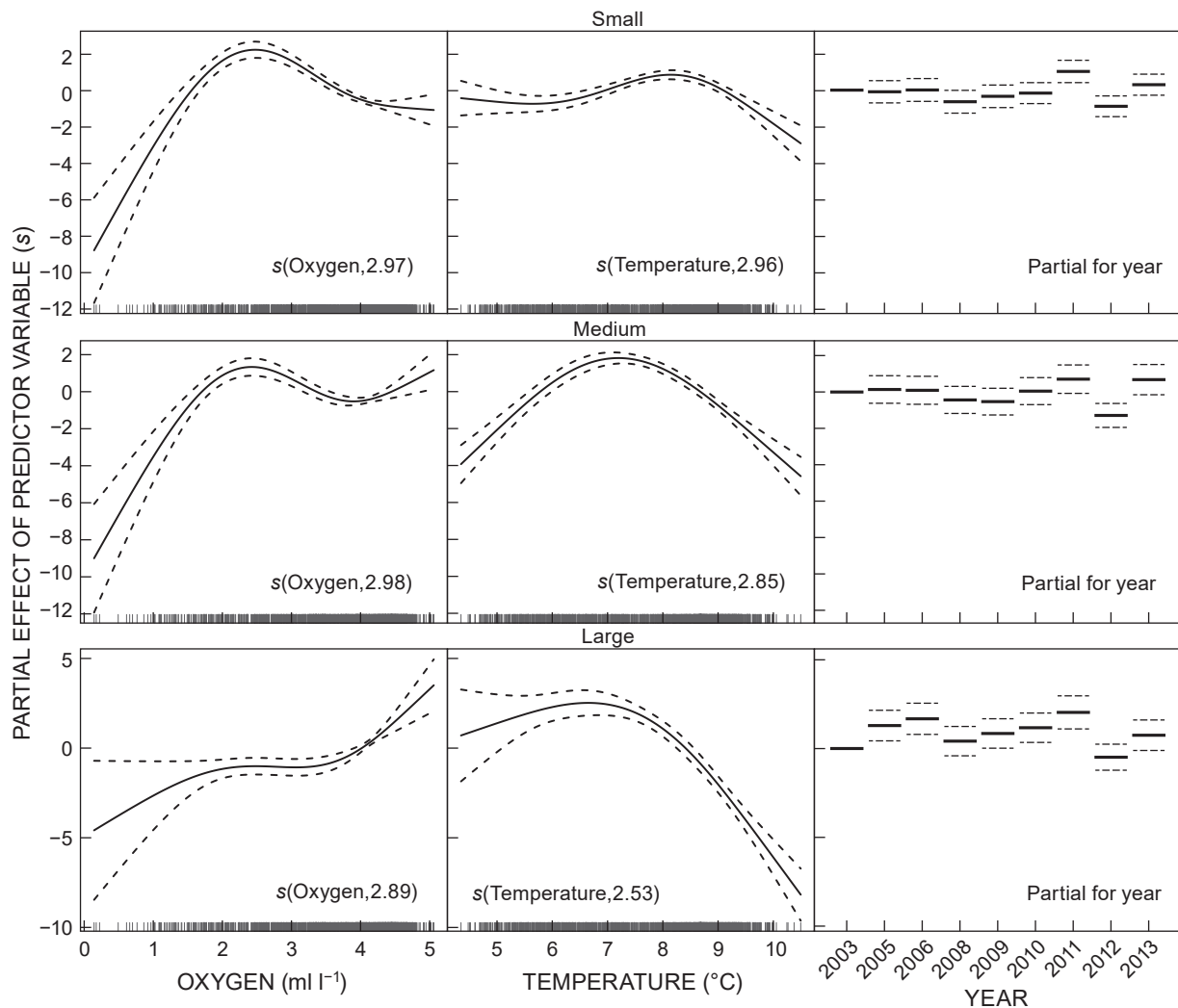


Figure 2: Results of the generalised additive models showing best model fits of associations of each of the three size classes of *Merluccius paradoxus* with dissolved oxygen concentration, bottom temperature, and year. Vertical axes show scaled partial effects of the predictor variable on a logit scale. Dashed lines indicate 95% confidence intervals. Rug plots represent the observations

The predicted probabilities of occurrence of *M. paradoxus* off the west coast indicated that small individuals were mostly associated with the shelf region (Figure 6), medium individuals with the shelf and shelf edge (Figure 7), and large individuals mainly with the shelf edge (Figure 8). Temporal patterns in the probability of occurrence varied among years. For small individuals, the greatest probabilities of occurrence generally extended in a band along the shelf from Cape Point to the Orange River (being widest in the north) (Figure 6). Medium individuals displayed the widest distribution, reflecting their tolerance of a wider range of values of investigated variables (Figures 7 and 9). Such patterns of distribution can be linked to the biological mechanisms of the *M. paradoxus* life cycle. These fish cannot survive in the deep when young because there are too many efficient predators; they gradually move into the deep as they approach adulthood because they became efficient predators themselves (Figure 8). Predicted probabilities of occurrence were converted into three classes

of habitat suitability: least suitable (0–0.4), moderately suitable (0.4–0.7), and optimal (0.7–1) (Figure 9). Temporal patterns in the areas of optimal habitat were generally flat but there also was substantial interannual variability (Figure 9).

On the basis of the above, two regions of the continental shelf were compared: the Hondeklip (Namaqua) region (Figure 10) and the Orange Banks (Figure 11). The entire vertical and horizontal habitats (defined in terms of the chosen variables) differed for these regions. The potential influence of differences in bottom environmental conditions and topography can be clearly seen from cross-shelf patterns in the probabilities of occurrence of small and large *M. paradoxus*. For the Hondeklip region, there was overlap in the predicted distributions of small and large individuals at about 25 nautical miles from the coast. Both size classes had similar and low predicted probabilities of occurrence at 60–70 nautical miles from the coast. Farther offshore the probability of occurrence of large individuals increased whereas that for small individuals

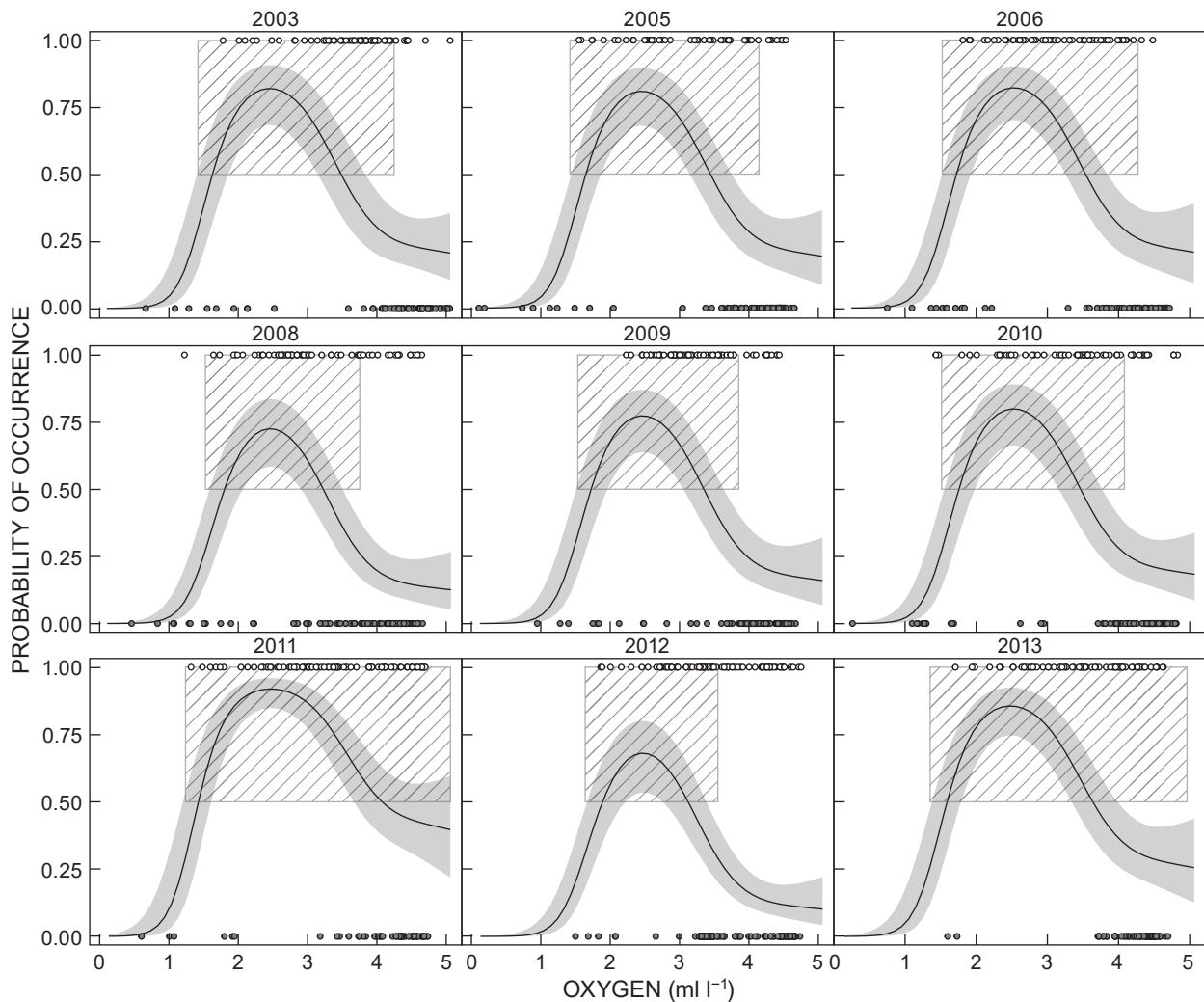


Figure 3: Results of the generalised additive models showing the probabilities of occurrence of small *Merluccius paradoxus* for different dissolved oxygen concentrations in each of nine years, between 2003 and 2013 (2004 and 2007 excluded). Hatched rectangles indicate ranges of most-probable occurrence. Lines represent medians, and shading represents 95% confidence intervals. Circles represent observations of hake presence (open circles) and absence (grey circles)

decreased. The overlap in the distribution of large with small *M. paradoxus* in the shallow water is likely related to the presence of relatively cool water (<9 °C) on the shelf. The predicted probabilities of occurrence of small and large individuals on the Orange Banks were different to those in the Hondeklip region, though differences appear also to be driven by environmental conditions over the shelf and shelf-edge regions. The predicted probability of occurrence for large *M. paradoxus* was low in the shelf region, whereas juveniles were found on the shelf, with a peak in probability of occurrence around 30 nautical miles from the coast and another peak farther offshore, at around 100–110 nautical miles from the coast. The probability of occurrence of large individuals increased beyond 70 nautical miles from the coast (shelf edge to slope region). This contrasting pattern of occurrence of small and large *M. paradoxus* is likely the result of prevailing relatively warm water (>9 °C) on the shelf, limiting the distribution of large individuals, and moderate to low dissolved oxygen (<4 ml O₂ l⁻¹) on the

shelf and in the shelf-edge region, potentially allowing small individuals to venture farther offshore.

Discussion

Distribution of Merluccius paradoxus

Current knowledge about *M. paradoxus* distributions is summarised below from four publications devoted specifically to this topic. The present study builds on the background provided by these publications.

Study of Le Clus et al. (2005)

This unpublished working-group document contains important, pioneering conclusions, but it is not easily accessed; hence, some of its key points are summarised here. The document compared the distribution and abundance of various size classes of *M. paradoxus* between the west and south coasts of South Africa. The work showed that the spatial dynamics changed with life-history stages, with old individuals

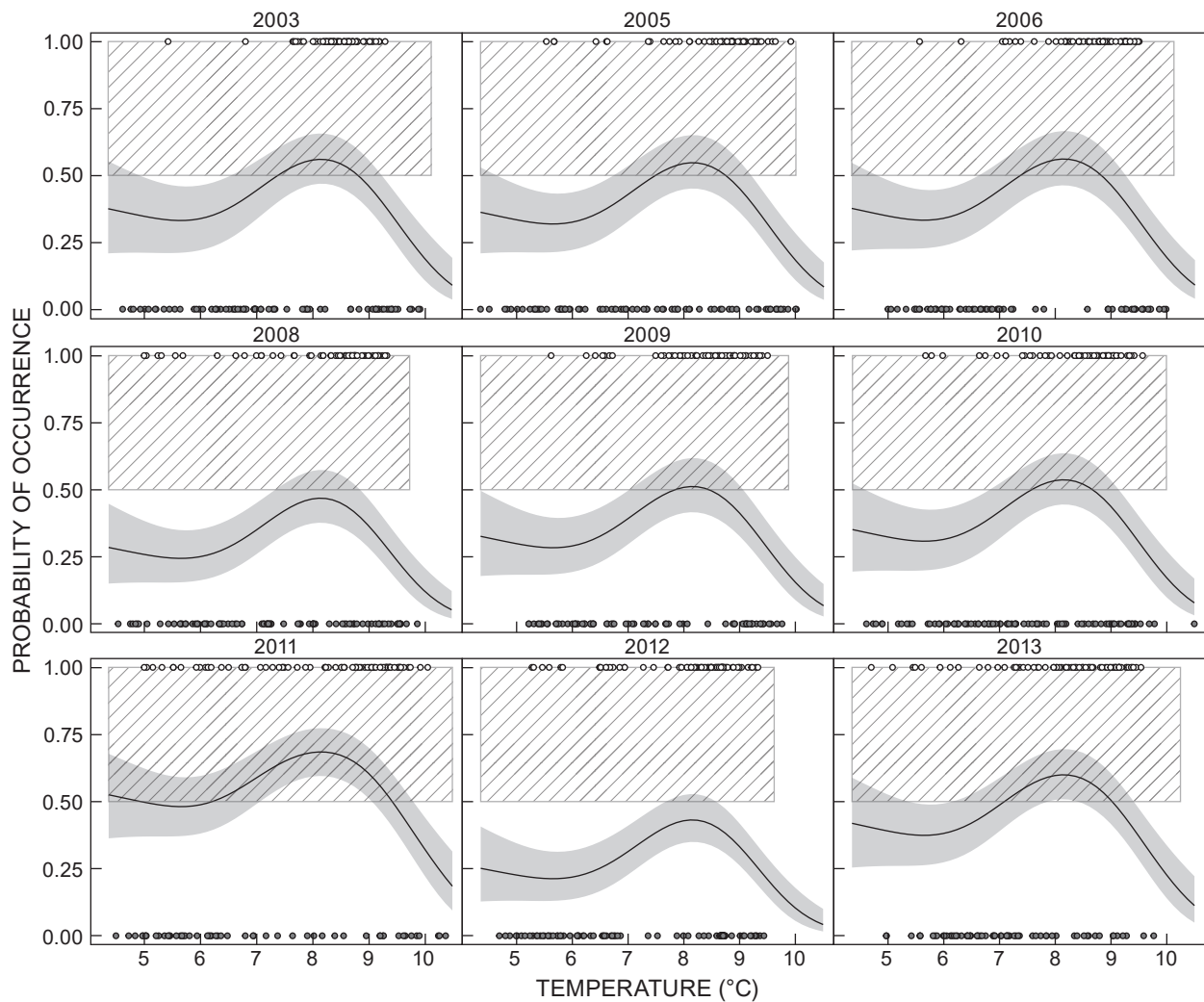


Figure 4: Results of the generalised additive models showing the probabilities of occurrence of small *Merluccius paradoxus* at different bottom temperatures, for each of nine years between 2003 and 2013 (2004 and 2007 excluded). Hatched rectangles indicate range of most-probable occurrence. Lines represent medians, and shading represents 95% confidence intervals. Circles represent observations of hake presence (open circles) and absence (grey circles)

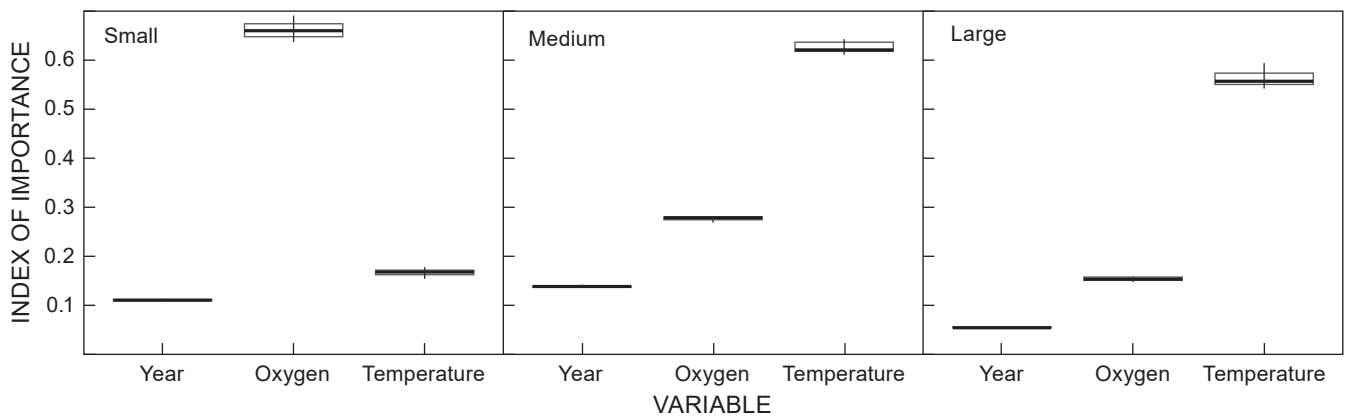


Figure 5: Results of the generalised additive models showing the relative importance of year, dissolved oxygen concentration, and bottom temperature in determining occurrences of the three size classes of *Merluccius paradoxus*

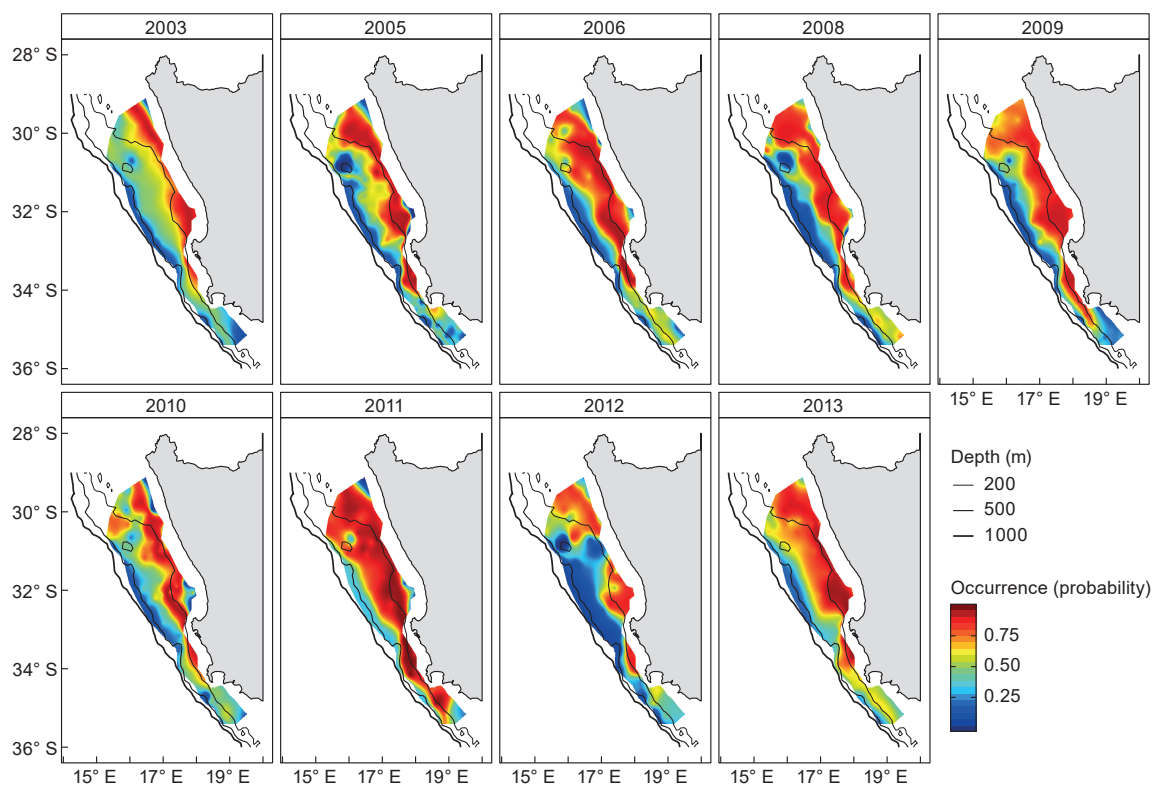


Figure 6: Habitat suitability maps off the west coast of South Africa for the small size class of *Merluccius paradoxus*, for each of nine years between 2003 and 2013 (excluding 2004 and 2007)

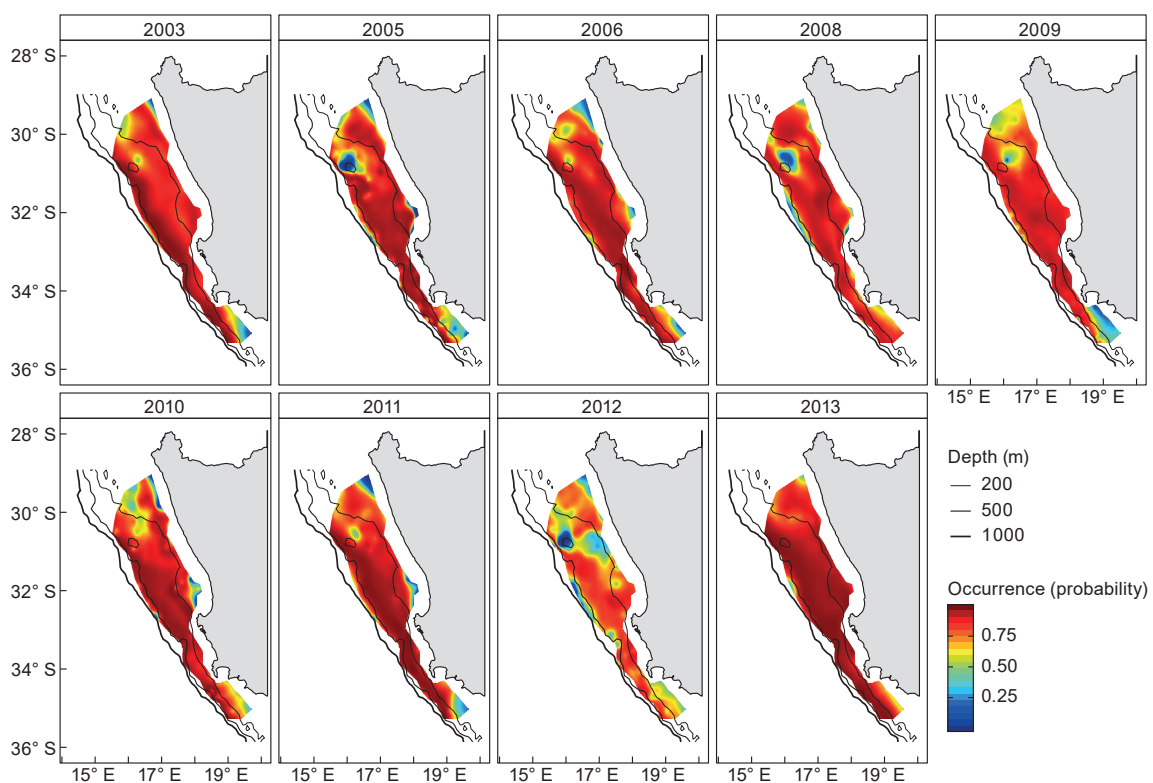


Figure 7: Habitat suitability maps off the west coast of South Africa for the medium size class of *Merluccius paradoxus*, for each of nine years between 2003 and 2013 (excluding 2004 and 2007)

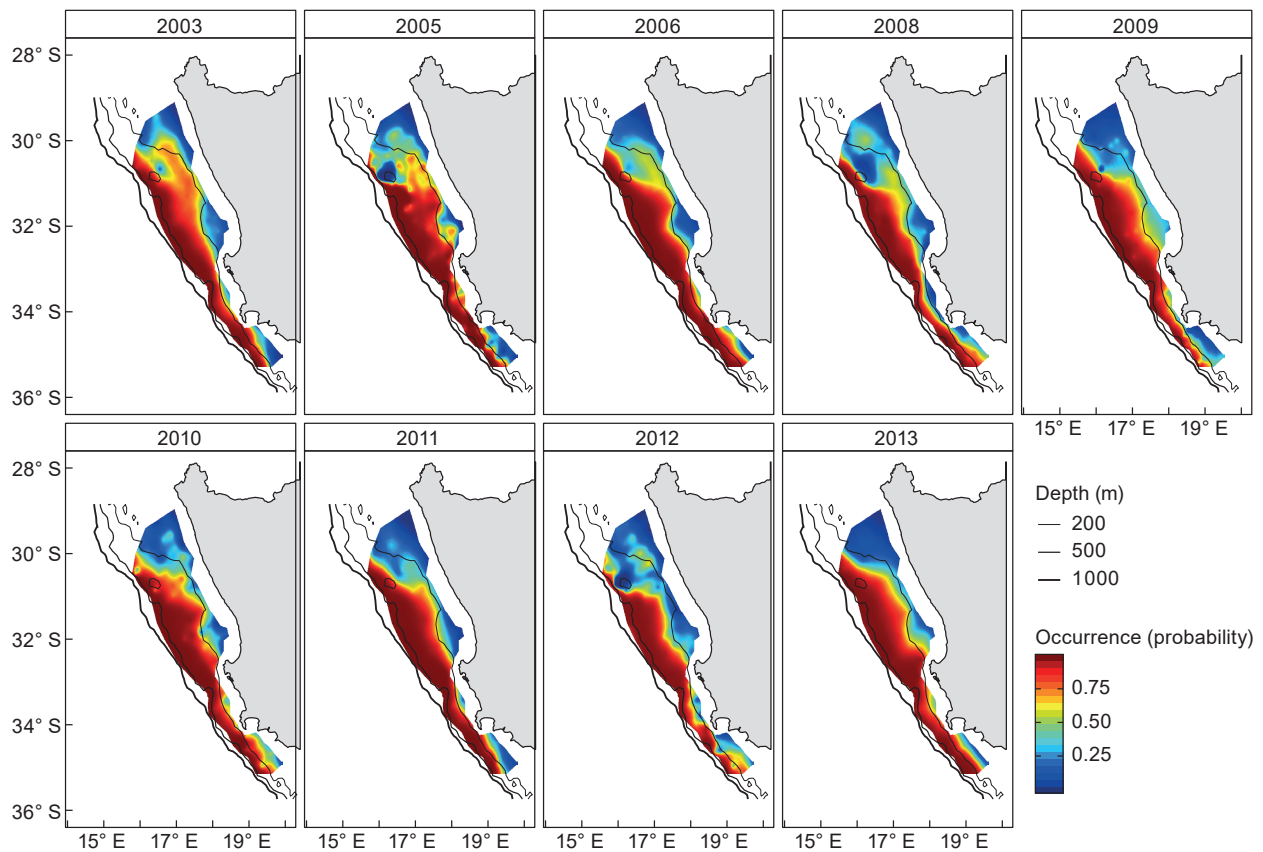


Figure 8: Habitat suitability maps off the west coast of South Africa for the large size class of *Merluccius paradoxus*, for each of nine years between 2003 and 2013 (excluding 2004 and 2007)

moving into deeper water, as well as moving southwards with increasing depth. For young individuals (<20 cm TL), the main densities were between the 100 and 300 m depth contours on the west coast north of St Helena Bay. Small *M. paradoxus* (16–34 cm TL) moved offshore, but also southwards to Cape Agulhas, mostly at depths >200 m. Fish of size classes >35 cm TL had similar spatial distributions, with densities increasing with depth to 400 m for medium-small individuals (35–45 cm TL) and to 600 m for medium-large and large individuals. High densities of medium-small *M. paradoxus* were found south of St Helena Bay and on the south coast. These observations were supported by polynomial models of alongshore distribution. Cannibalism and the distribution of prey species could influence the alongshore trends in density of *M. paradoxus*. Details of prey versus latitude were provided.

Based on these observations, Le Clus et al. (2005) concluded that densities of adult *M. paradoxus* were similar on the south and west coasts, after taking into account the larger surface area of the west coast continental shelf deeper than 200 m. The densities of juveniles and small-sized *M. paradoxus* on the south coast were lower than expected, indicating that the adult stock on the south coast might be supplemented from the west coast. The authors suggested that the two coasts might be equally suitable for adult fish but, as is the case for many other fish stocks, the west coast appears to be the preferred nursery locality.

Le Clus et al. (2005) hypothesised that *M. paradoxus* forms one stock in South African waters, and that the south coast component originates on the west coast, which implies longshore migration of young adults from the west coast to the south coast. The one-stock hypothesis was subsequently confirmed by Henriques et al. (2016), and the postulated longshore migration was confirmed and extended by Strømme et al. (2015).

Study of Strømme et al. (2015)

Strømme et al. (2015) analysed length frequencies along the main distribution range of *M. paradoxus* (from Port Alfred on South Africa's southeast coast to the Kunene River on the Namibia/Angola border), collected during one synoptic survey. They found that following size classes of *M. paradoxus* expanded from the area on and around the Orange Banks in northwesterly and southeasterly directions. The distributions of large fish, however, contracted to the slope area, roughly between Cape Point and Doring Bay (South Africa) on the west coast. The starting point of the expansion was interpreted as the main nursery ground of the species, and the end point of the contraction as the main spawning area. This interpretation implied at least two long-range migration routes (assuming one main spawning season), namely when expanding and then contracting north and south from various points of the range. Thus, the hypothesis of Le Clus et al. (2005),

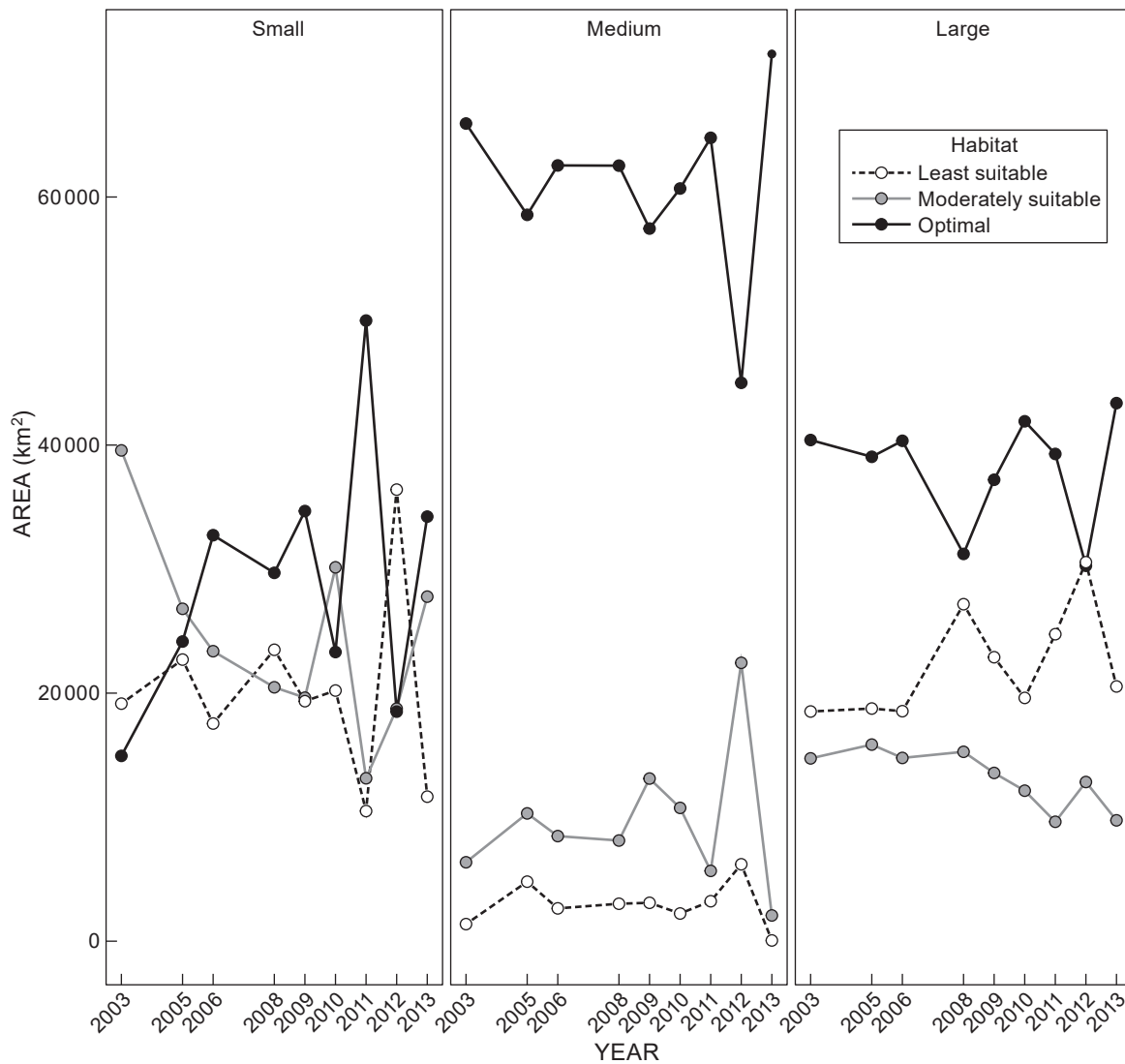


Figure 9: Temporal trends between 2003 and 2013 in areas of the three categories of habitat suitability (least suitable, moderately suitable, and optimal) for the three size classes of *Merluccius paradoxus*

linking *M. paradoxus* on both coasts of South Africa, was developed into a life-cycle scheme on a geographic scale. In addition, an argument was made for only two crucial and geographically restricted areas underpinning the scheme: a spawning area and a nursery area. The South African origin of *M. paradoxus* occurring (and being fished) in Namibia was established, and synchronous changes in abundance were shown for the populations in the two countries. The abundance of *M. paradoxus* juveniles varied among years and their distribution was variable but limited geographically, whereas adult populations were less variable in abundance and more widely distributed.

Study of Grüss et al. (2016)

The study by Grüss et al. (2016) had similar aims to those of the present study, using a similar principal method of analysis (i.e. GAMs), but it differed on a number of points. It was based on a stratified semi-random survey

design and, as a consequence, it was difficult to process the oceanographic data. Also, it was complicated in its structure, dealing with two southern African species of hake, using more variables for the analysis and dealing with more size categories. Spatial considerations were also treated differently. The results of the study identified geographic position and temperature as the main predictors of *M. paradoxus* presence/absence in both binomial GAMs and quasi-Poisson GAMs; bottom dissolved oxygen was important only in the quasi-Poisson GAM, and depth only for juveniles, which was surprising. The study identified three ontogenetic migrations of *M. paradoxus*.

Grüss et al. (2016) concluded that the probability of occurrence of large *M. paradoxus* was reduced by low bottom oxygen concentrations, but that of juveniles was not. We have modified, extended and developed this conclusion further in our study; juveniles of *M. paradoxus* occur most frequently in a relatively narrow range of dissolved oxygen (a two-sided

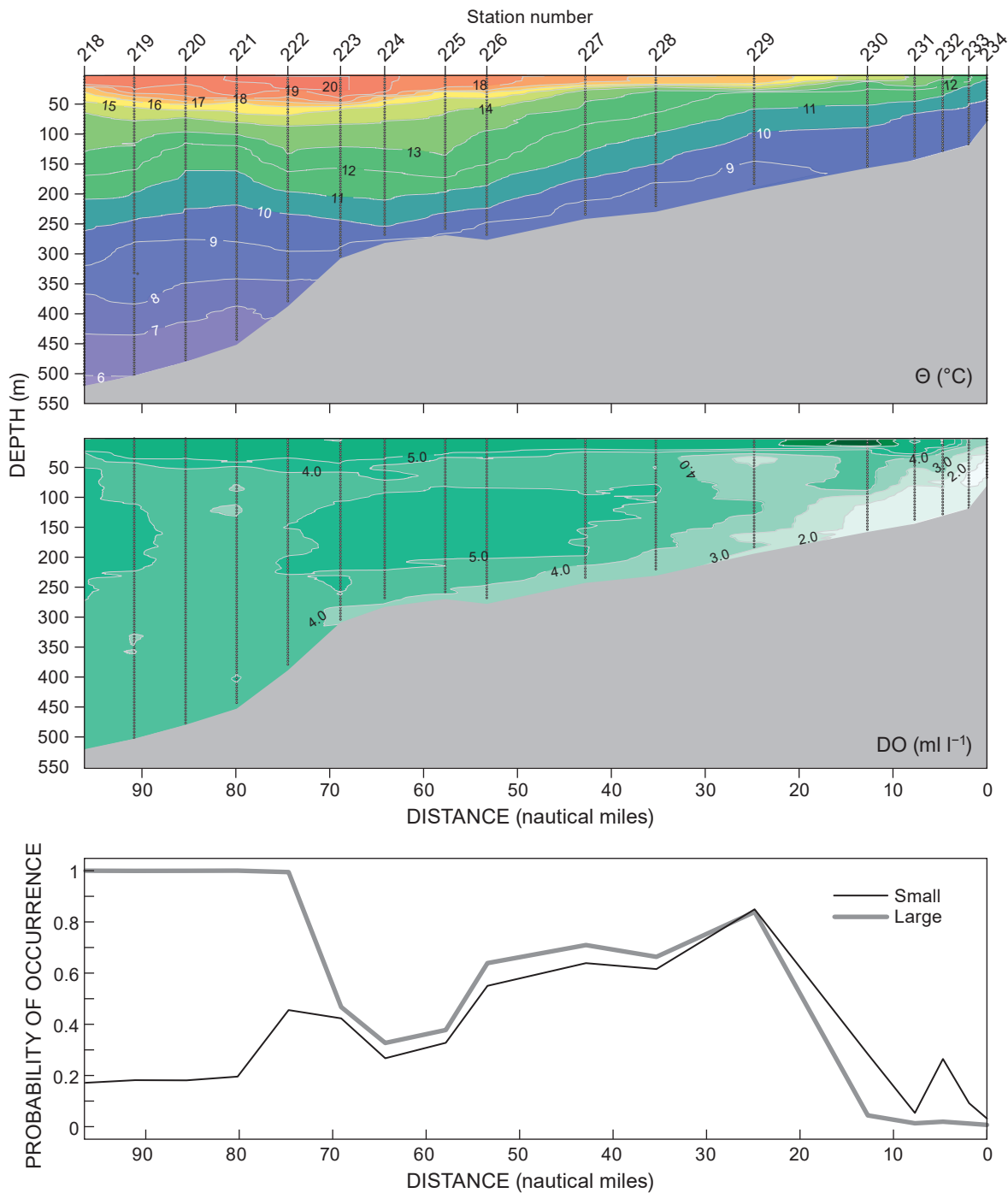


Figure 10: The water temperature (Θ , top panel) and dissolved oxygen (DO, middle panel) conditions in February 2005, observed along a section crossing the Hondeklip (Namaqua) region of the continental shelf, with the associated probabilities of occurrence (bottom panel) of juveniles (small) and adults (large) of *Merluccius paradoxus* predicted for that section. Predictions were generated using the best-performing generalised additive model (see Data analysis) with the temperature and oxygen nearest to the bottom at the position of each oceanographic station. Data were collected using the RV *Dr Fridtjof Nansen* on 17–18 February 2005

constraint), whereas large *M. paradoxus* are associated with higher concentrations of dissolved oxygen, having a one-sided constraint. The difference in the findings of the two studies might be because of the more complex nature of the analysis of Grüss et al. (2016) as compared with our analysis, which considered only two environmental variables.

Study of Jansen et al. (2017)

The study of Jansen et al. (2017) provided no substantially new interpretations of existing data. However, the analyses tried to incorporate all results of demersal surveys made in South Africa and Namibia. Thus, on the basis of a much larger dataset than previously analysed,

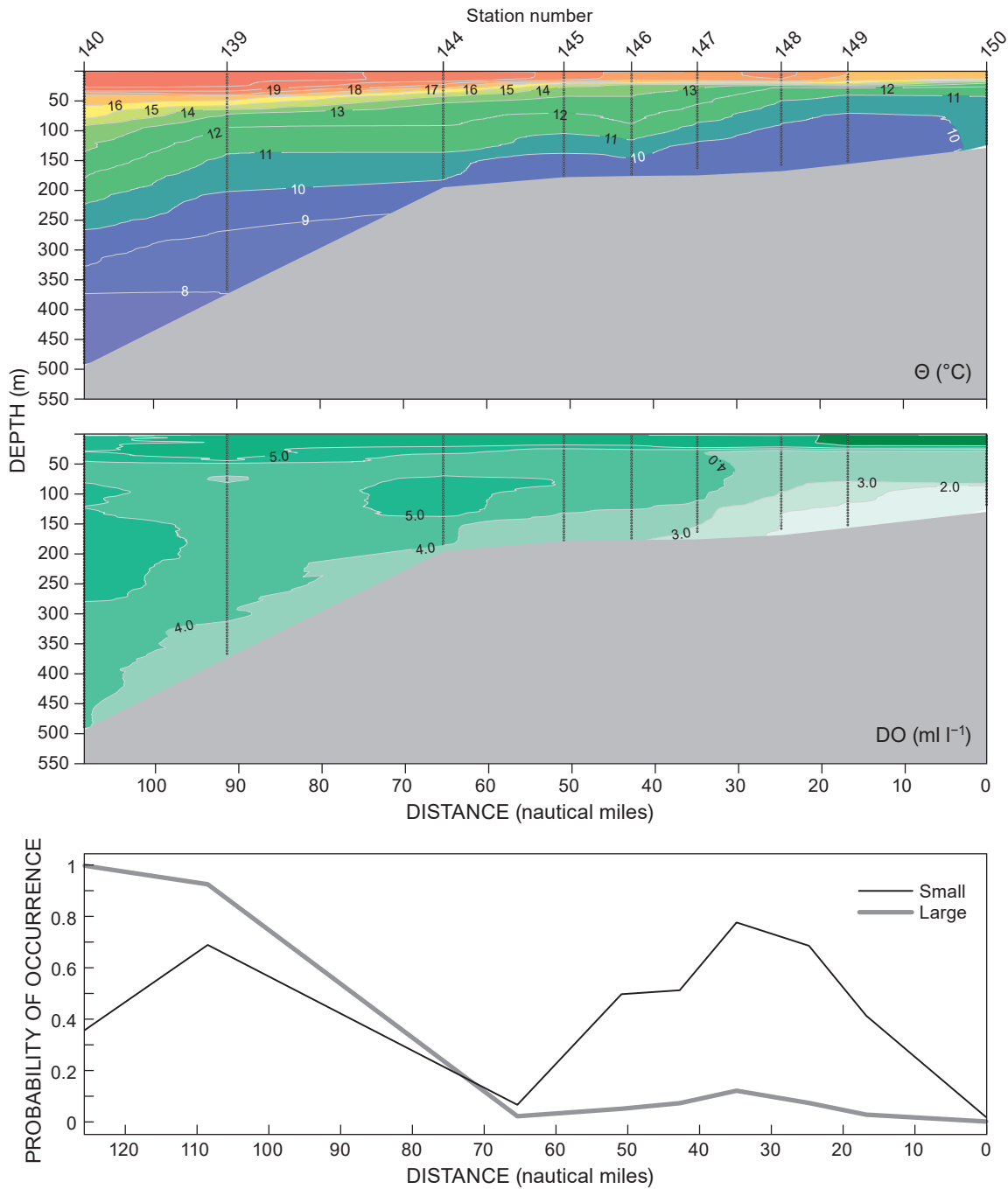


Figure 11: The water temperature (Θ , top panel) and dissolved oxygen (DO, middle panel) conditions in February 2005, observed along a section crossing the Orange Banks, compared with the probabilities of occurrence (bottom panel) of juveniles (small) and adults (large) of *Merluccius paradoxus* predicted for that section. Predictions were generated using the best-performing generalised additive model (see Data analysis) with the temperature and oxygen nearest to the bottom at the position of each oceanographic station. Data were collected using the RV *Dr Fridtjof Nansen* on 12 February 2005

as well as more sophisticated methods (geostatistical modelling), the results of Strømme et al. (2015) were fully confirmed. The study also prepared the way for further developments—exploring the reasons for correlations between locations, and untangling migration, mortality and growth modelled on a spatio-temporal scale. Biological issues were also mentioned, such as the possibility of

identifying different cohorts through the timing and location of their spawning events.

Environmental niche of *Merluccius paradoxus*

Our study has shown the importance of habitat, as determined by dissolved oxygen and water temperature, to the distribution of different size classes of *M. paradoxus*.

Previously, drift pathways were singled out as the most important determinants of nursery habitats for this species (Stenevik et al. 2008; Garavelli et al. 2012), supplemented by bathymetry (Ostrowski et al. 2011). Here, we add physicochemical characteristics of the environment. Together, these three aspects comprise important components considered in habitat-suitability modelling throughout the ontogeny of a species (Guisan et al. 2017). Our study addresses these basic requirements, setting the stage for detailed niche quantification and the modelling of habitat suitability in future studies.

The results of the GAM response curves for oxygen indicate that oxygen might have influenced the presence/absence of small *M. paradoxus* (<15 cm TL) more than that of the other two size classes. Small *M. paradoxus* were associated with environmental oxygen ranges that are restricted, indicating that their presence was likely associated with hypoxic conditions (<2 ml O₂ l⁻¹) (Monteiro and van der Plas 2006), although the small fish mostly inhabited oxygen-depleted water (2–3 ml O₂ l⁻¹) and appeared to occur less often in waters with high oxygen concentrations (>3 ml O₂ l⁻¹). In an analysis of the catch rates of both hake species, Kainge et al. (2017) found that oxygen was not an important covariate. Singh and Lamont (2016) found that *M. paradoxus* juveniles mostly occurred in moderately oxygenated water (2–3.5 ml O₂ l⁻¹). Millar (2000) explained that large individuals are not able to take up oxygen as efficiently as small individuals, because fish gills do not grow as fast as the body (Pauly 1998). This supports the findings of Wieland et al. (2012) that adult *M. capensis* use oxygen-depleted bottom water as a refuge, and hence the adults tend to overlap with juvenile *M. paradoxus* in terms of depth and spatial distribution. The strong association with oxygen-depleted water found in the present study of small *M. paradoxus* is in contrast to Roel and Bailey's (1987) speculation that *M. paradoxus* juveniles are intolerant of oxygen-depleted conditions.

Jarre et al. (2015) noted a restricted spatial extent of low-oxygen water off Hondeklip Bay, which appeared to merge with oxygen-depleted water near the Orange River mouth. The extension of oxygen-depleted water from these areas (Hondeklip Bay and the Orange River mouth) towards the Cape of Good Hope could occur if the coastal countercurrent were to carry water with low concentrations of oxygen as far as that (Jarre et al. 2015). Olivar et al. (1988) indicated that temperature and oxygen have strong influences on hake distribution and abundance. In a specific finding of Kainge et al. (2017), it was assumed that, based on the model they used, *M. paradoxus* are mainly influenced by temperature and geographical position.

Biological interpretation of the environmental relationships

The present study outlines some complexities determining the distribution of three size classes of an ecologically successful species (*M. paradoxus*); however, these forcing factors require consideration of the whole life cycle. Eggs and larvae are numerous but follow relatively limited pathways and exhibit patchy distributions (Stenevik et al. 2008; Grote et al. 2012) because of a combination of two factors: the environmental milieu and mortality. Juveniles must survive and grow in order to extend their range and increase their biomass (Grote et al. 2011, 2012). We have shown that the

environmental pathway of *M. paradoxus* juveniles is relatively narrow and they are probably most vulnerable, biologically, at that life stage, as informed by their distribution. For example, their oxygen-response curve is unimodal and double-constrained (Figures 2 and 3). There is a definite optimum at 2–3 ml O₂ l⁻¹. This optimum (as shown on the climatology map, Supplementary Figure S1) occurs along the outer boundary of the near-shore oxygen-depletion zone (see also Jarre et al. 2015), whereas the main oxygen-depletion region is geographically located nearshore. This mean pattern, based on 10 years of observations, coincides with the known egg and larval pathways of *M. paradoxus*, which are transported by the fast outer branch of the jet current (Stenevik et al. 2008; Garavelli et al. 2012; Grote et al. 2012; Jansen et al. 2015) and retained by the relatively stable system of the Orange Banks (Ostrowski et al. 2011), mostly along the mean depth contour of 200–212 m (Stenevik et al. 2009; Grüss et al. 2016). There, juveniles of *M. paradoxus* find optimal foraging conditions with an abundance of suitable prey (Stenevik et al. 2009; MRL unpublished data). Their other constraint (high oxygen, >3 ml O₂ l⁻¹, in the offshore direction) may be linked to predation (by *M. capensis*) and cannibalism by adult *M. paradoxus*, because adult abundance increases in the offshore direction. Adults of both these hake species are relatively scarce on the Orange Banks (Jansen et al. 2016, 2017), probably as a result of the lack of suitable prey and the abundance of such prey in the deeper waters nearby. This renders the Orange Banks suitable as a central nursery area for *M. paradoxus* (Strømme et al. 2015) (Figures 10 and 11).

Therefore, the oxygen-depletion threshold is the main environmental determinant of juvenile *M. paradoxus* distribution and, importantly, temporal and spatial (geographic) mechanisms underpin its influence, causing interannual variability in the extent of the main nursery area. The fact that areas of the highest probabilities of occurrence (Figure 6) do not completely agree with actual occurrence (Strømme et al. 2015) indicates there must be other controlling factors, most probably arising from the biology of the species. In the case of adult *M. paradoxus*, response curves and graphs depicting the relative importance of various factors in defining the sizes of distribution areas (Figures 2, 5 and 9) do not indicate any particular temperature or oxygen niche, except that temperature is important in defining large areas of adult distribution (Figure 8), which is already well known (e.g. Durholtz et al. 2015). Such broad ranges of occurrence justify consideration of other sources of variability as potentially being more critical than temperature and oxygen in determining where adult *M. paradoxus* occur. As already suggested by Grüss et al. (2016), trophic relations are likely to play an important role and should be investigated in detail from the perspective of how they might influence hake distributions.

Patterns of habitat suitability for small *M. paradoxus* over the mid-shelf waters off the Orange Banks along the 200-m contour were relatively stable. The stability of near-bottom conditions is likely to play a role in creating favourable environments for fishes, including *M. paradoxus* juveniles (Ostrowski et al. 2011; Wieland et al. 2012). This is similar to the preferred distribution of juveniles of European hake *Merluccius merluccius* in nursery areas with stable hydrographic conditions (Sánchez and Gil 2000).

A broad perspective on the importance of oxygen dynamics for the survival, presence, distribution and abundance of marine fishes was provided by Bertrand et al. (2011). They emphasise that the spatial and temporal dynamics of oxygen distributions can explain much more about the life cycle of many species than a one-dimensional perspective (such as that in this study). Oxygen concentrations differ across the vertical water column and change both during the course of the year and between years. Unfortunately, typical accounts of the importance of oxygen have been based on unidimensional perspectives (in this study: near-bottom) of this multidimensional environment, and on only a narrow period during the year, which changes from year to year (albeit only a little). However, most fish species migrate in the water column and across many gradients and boundaries; this ultimately means the difference between success and failure for individuals and, ultimately, for populations. This is a fascinating but challenging topic for future research, especially concerning juveniles of *M. paradoxus*.

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