

Fine-scale environmental effects on Cape hake survey catch rates in the northern Benguela, using data from a trawl-mounted instrument package

Paulus Kainge^{1,2,*}, Kai Wieland²

¹National Marine Information and Research Centre (NatMIRC), Ministry of Fisheries and Marine Resources, Swakopmund, Namibia

²DTU Aqua – National Institute of Aquatic Resources, Technical University of Denmark, 9850 Hirtshals, Denmark

ABSTRACT: We investigated fine-scale effects of environmental variables associated with habitat distribution for 4 size groups of Cape hakes, *Merluccius capensis* and *M. paradoxus*, using generalized additive models (GAMs) with a negative binomial error distribution. This study took place during the Namibian hake trawl survey of 2016, and was made possible for the first time in Namibia by collecting oceanographic information with a trawl-mounted instrument package concurrently with the catch data. Depth, geographical position, bottom oxygen and bottom temperature had the most pronounced effect on the catch rates of both hake species, whereas solar zenith angle representing diel effects and surface layer chlorophyll appeared to be less important. The explained deviance for the best models ranged from 71.4 % for *M. capensis* to 92.7 % for *M. paradoxus* between 43 and 57 cm in length. Differences in catch rates between species and size groups were most pronounced for bottom depth and bottom oxygen. The results show the potential value of trawl-mounted instrumental packages for the collection of reliable environmental data important in the study of environmental influence on abundance, catch rates and distribution, and in turn in the assessment and management of a resource.

KEY WORDS: Survey catchability · Bottom trawl catch rates · Benguela current system · Green water effect · Negative binomial GAM ·

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

Useful environmental variables collected near the seabed during survey trawling are crucial for investigating environmental effects on catch rates. In the northern Benguela (off the coast of Namibia), the National Marine Information and Research Centre (NatMIRC) of the Ministry of Fisheries and Marine Resources (MFMR) conducts annual bottom trawl surveys to estimate the abundance and biomass distribution of hake populations in Namibian waters. Survey biomass, together with commercial catch per unit effort (CPUE), are part of the stock assessment model for determining management

measures such as total allowable catches (TAC). Survey biomass estimations show that shallow-water Cape hake *Merluccius capensis* is more abundant in Namibian waters than deep-water Cape hake *Merluccius paradoxus*, which is predominantly found in the southern part of the survey area (Burmeister 2005, Kainge et al. 2017). The 2 species have depth-related distributions; more than 75 % of *M. capensis* are found shallower than 300 m while the same proportion of *M. paradoxus* are found deeper than 300 m depth (Burmeister 2001, Kainge et al. 2015).

The northern Benguela ecosystem is very productive due to high upwelling intensity (Hutchings et al.

*Corresponding author: paulus.kainge@mfmr.gov.na

2009). It was overfished in the 1970s and 1980s, although reduced biomass of key ecological species has also been attributed to the Benguela Niño that occurred in 1995 (Heymans et al. 2004). Following these changes, the ecosystem moved into a new stable state (Heymans & Tomczak 2016), where population-level shifts in demersal fish communities were detected (Kirkman et al. 2015). One of the key features of this productive system are seasonal phytoplankton blooms, characterized by chlorophyll *a* (chl *a*) concentration as a measure of phytoplankton biomass (Bartholomae & van der Plas 2007, Louw et al. 2016). Surface chl *a* has a species-specific regional effect on body condition of gadoids (Rueda et al. 2015).

Several factors affect the reliability of bottom trawl surveys for the estimation of demersal fish abundance, and the efficiency of trawl surveys depends on the availability of target species (Godø 1994, Kotwicki et al. 2015). Time of day has an effect on the availability of the hakes captured in the bottom trawl, thereby affecting the survey catch rates. The most pronounced effect is for *M. capensis*, for which catch rates decline drastically after sunset (Kainge et al. 2015). Other environmental variables such as temperature and oxygen content (which both vary with depth), and in particular, latitude, have been found to affect hake catch rates and abundance distribution in Namibian waters (Hamukuaya et al. 1998, Gordoa et al. 2000, Monteiro et al. 2008, Kainge et al. 2017). Bottom water conditions in the area around the central Namibian shelf are hypoxic ($<0.5 \text{ ml l}^{-1}$) (Bailey 1991, Hamukuaya et al. 1998). The extent of bottom hypoxia varies temporally and spatially and is believed to play a very important role in the dynamics of hake, especially *M. capensis*, which occupies this habitat (Hamukuaya et al. 1998, Bartholomae & van der Plas 2007, Monteiro et al. 2008).

The distribution of nutrients and surface chlorophyll concentrations have been used as a proxy for food availability, as well as successful recruitment for hake (Hutchings et al. 2009, Druon et al. 2015). In the southern Benguela, high catch rates of shallow- and deep-water hake were recorded outside the surface layer chlorophyll concentrations while very low catch rates were observed at all levels of surface layer chlorophyll (Wieland et al. 2013), which could be evidence that the catches are not affected by dense chlorophyll concentrations ('green water'). Kainge et al. (2017) observed that depth, bottom layer temperature or bottom layer dissolved oxygen affect the distribution of hakes, but found no effect of time of day on catch rates. However, anecdotal information from

fishermen suggests that hakes stay on the bottom if the sun shines brightly but lift off the bottom if the sky is cloud covered (Paterson & Kainge 2014), and green water may have the same effect on hake behavior as cloud cover. Furthermore, the study by Kainge et al. (2017) was limited, because in the majority of the years very few CTD data were collected at trawl stations and chlorophyll was not measured at all.

This paper therefore aims at testing some of the hypotheses resulting from Kainge et al. (2015, 2017), now using *in situ* data collected by a trawl-mounted instrument package (memory CTD with additional sensors) which allows data collection simultaneously with the catches (Wieland et al. 2014a). The trawl-mounted instrument package was equipped with a sensor for fluorescence, and hence surface chlorophyll concentration was added as an additional covariate in the analysis.

MATERIALS AND METHODS

Fish data, gear and methodology

Data from the annual Namibian demersal survey of January and February 2016 were used in this study. The survey was, for the first time, carried out with the new Namibian research vessel RV 'Mirabilis' but otherwise followed the same design, methodology and gear as previous years, as described in Axelsen & Johnsen (2015) and Kainge et al. (2015, 2017). Trawl stations were selected along fixed transects perpendicular to the coast (Fig. 1) with at least 1 station in each depth zone (<100, 101–200, 201–300, 301–400, 401–500, 501–600 and 601–700 m). In general, fishing usually started in the coast part of a transect in the morning and progressed into deeper water during the day. Fishing at depths <400 m is usually restricted to daylight hours, as hake (especially shallow-water Cape hake *Merluccius capensis*) are known to rise off the bottom at night (Huse et al. 1998, Gordoa et al. 2006, Johnsen & Iilende 2007). During the 2016 survey, a total of 188 valid trawl stations were carried out, of which 39 stations were outside the 07:00 to 19:00 h local time period (Fig. 1), and 7 of these 'night' hauls were shallower than 400 m. The survey lasted from 12 January to 20 February 2016 and extended over 12° in latitude and 12° in longitude. Hence, sunrise and sunset at the sampling stations ranged from 06:15 to 07:10 h and 19:44 to 20:05 h local time, respectively.

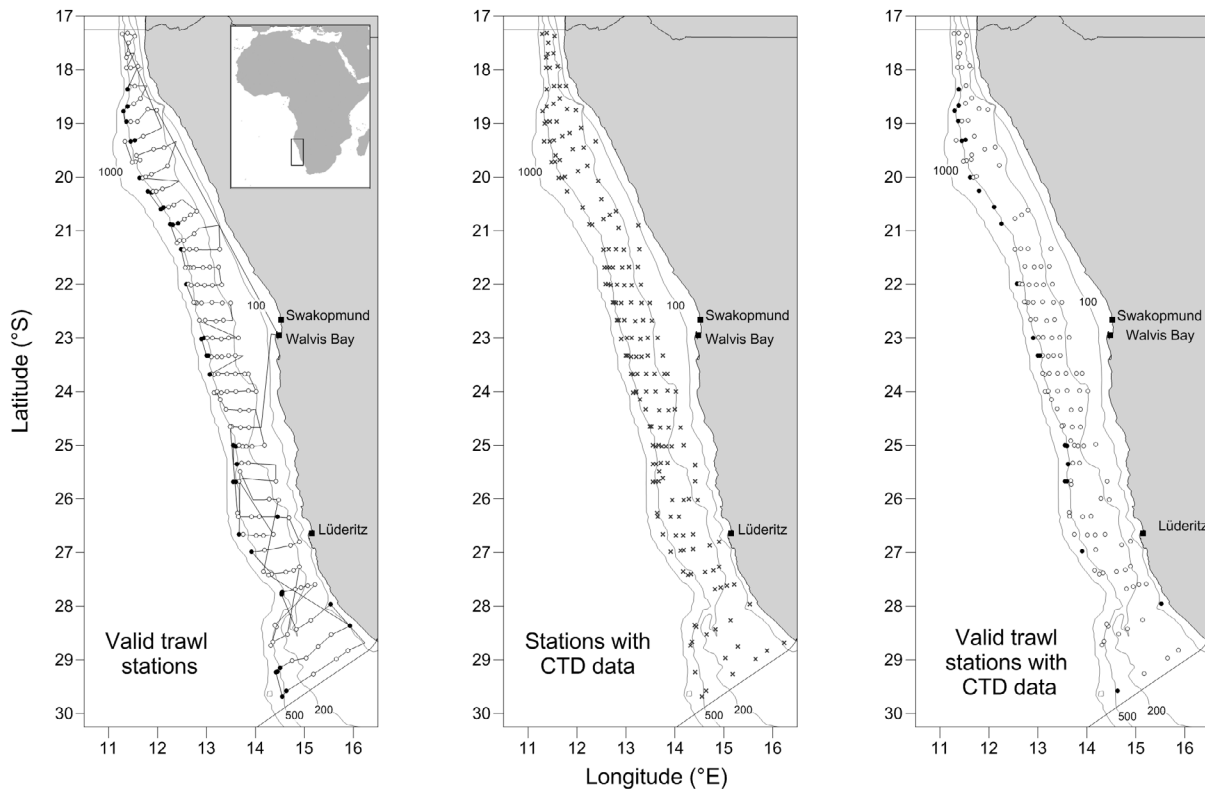


Fig. 1. Study area along the coast of Namibia showing location of trawl stations (open circles: day; solid circles: night) with cruise track, CTD stations and aligned trawl/CTD stations conducted during 2016

Light level data

Solar zenith angles that are computed based on local time, date and location (latitude, longitude) are useful for interpreting survey catch rates for species that have diel vertical migration patterns when nei-

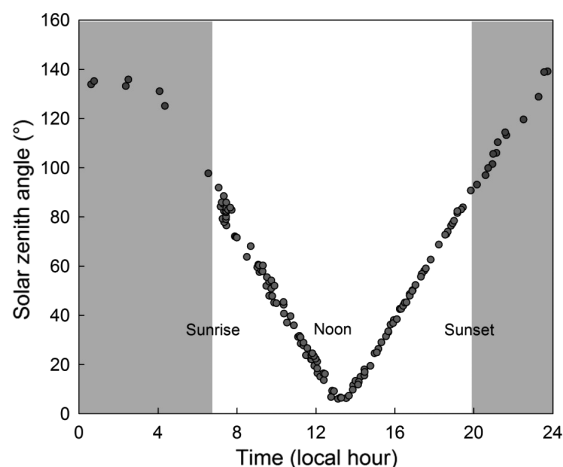


Fig. 2. Solar zenith angle and time of day for the Namibian Cape hake survey in 2016 (values for valid trawl stations with instrument package data only; grey shaded area indicates night time)

ther the position of the sun nor the actual light level are measured in the field (Jacobson et al. 2015). The solar zenith angle lies between a line drawn straight up from the center of the earth through the observer's position and a line drawn from the observer to the center of the sun, providing a proxy for illumination under average atmospheric and clear sky conditions (Frouin et al. 1989). Solar zenith angles are preferable to time of day because they account for difference in irradiance due to latitude and longitude as well as day of the year. Calculations of solar zenith angles were done using AstroCalc4R (Jacobson et al. 2011); the relationship with local time of day for the Namibian hake survey data used in the present dataset is illustrated in Fig. 2.

Trawl-mounted instrument package data

The trawl-mounted instrument package (Seabird Seacat SBE-19plusV2 CTD with SBE 43 oxygen and WetLabs fluorescence and turbidity sensors) was deployed for the first time during the hake biomass survey in 2016. Water samples were taken and Winkler titration was used to correct the oxygen

measurements, but no *in situ* calibration of the fluorescence sensor was carried out. Bottom layer values (deepest 1 m bins) were used for temperature, salinity and dissolved oxygen, and chlorophyll concentration for the surface layer down to 50 m depth was calculated from the fluorescence measurements based on factory calibration and summing the recordings from 1 m depth bins. Battery problems were encountered at several stations, and in total 151 profiles with complete instrument package data which matched valid trawl stations (Fig. 1) were available for analysis.

Initial variable selection for model fitting

Correlations between covariates (zenith, temperature, oxygen, chlorophyll, depth, year and geographical position) were examined and variance inflation factors (VIFs) were calculated to detect collinearity. Environmental covariates for which Pearson's correlation coefficient (r) was greater or equal to 0.7 in absolute value (Dormann et al. 2013) and a VIF value greater than 3 were considered strongly correlated and were treated in different competitive models to minimize collinearity (Guisan et al. 2002, Wintle et al. 2005, Zuur et al. 2009, Dormann et al. 2013, Sagarese et al. 2014).

Model selection, evaluation and statistical analysis

Generalized additive models (GAMs) (Hastie & Tibshirani 1990, Zuur et al. 2009) were used to study the relationships between total numbers of hake estimated and environmental variables prevalent at those specific stations. GAMs are nonparametric or semi-parametric generalizations of multiple linear regressions. GAMs have the advantage of being able to model non-linearity in the relationship between the response and predictor(s) by using non-parametric smoothing functions. The general form of a GAM is based on the assumption that the mean response (μ) is related to the predictor variables (X_1, \dots, X_P) by the following relationship:

$$g(\mu) = \alpha + \sum_{j=1}^P f_j(X_j) + \epsilon \quad (1)$$

where $g(\mu)$ is the link function defining the relationship between the response and the additive predictor, α the intercept term of the response when the predictors are zero (no categorical variables used), f is the smoothing function for variable j and P is the

maximum number of variables listed below. The f_j values are estimated in a flexible manner and each of them is a regression spline in the component X_j (Hastie et al. 2001). ϵ is the error term representing measurement error or any variation unexplained by the model. Full models were:

- (1) $g(\mu_{il}) \sim s(\text{zenith}_{il}) + s(\text{lon}_{il}, \text{lat}_{il}) + s(B_{\text{tem}_{il}}) + s(\text{Chl}_{50il}) + \text{offset}[\log(\text{SweptArea}_{il})]$
- (2) $g(\mu_{il}) \sim s(\text{zenith}_{il}) + s(\text{lon}_{il}, \text{lat}_{il}) + s(B_{\text{oxy}_{il}}) + s(\text{Chl}_{50il}) + s(\text{Depth}_{il}) + \text{offset}[\log(\text{SweptArea}_{il})]$

where i denotes station, l denotes size group and the expected response μ is the number of fish per haul for the different size groups. B_{tem} is bottom temperature, Chl_{50} is chlorophyll in the upper 50 m and B_{oxy} is bottom oxygen. A negative binomial (NB) distribution was used with a log link and $\log(\text{swept area})$ as offset assuming proportionality between catch in numbers and effort. The interaction term $s(\text{lon}, \text{lat})$ was included in order to account for possible spatial autocorrelation (Wood 2006, Grüss et al. 2016), and longitude and latitude were transformed to Universal Transverse Mercator (UTM) coordinates to represent real distances.

We used the NB distribution considering that the data are counts which include a large number of zero observations (zero-inflation) and that the variance exceeds the mean (over-dispersion) (Wood 2006, Zuur et al. 2009). Cubic regression splines were used and we applied a maximum of 5 and 25 degrees of freedom restrictions on the number of knots, k (i.e. $k = 5$ for the 1D smoothers and $k = 25$ for the 2D smoother) and a gamma of 1.4 to heavily penalize each degree of freedom in order to avoid overfitting (Zuur et al. 2009, Sagarese et al. 2014). The number of knots determines the 'wiggleness' or smoothness of the curve (Wood 2006, Zuur et al. 2009). A typical full model was then formulated in R (R Core Team 2016) as follows (example of model type 2):

$$N_{h,l} \sim s(\text{zenith}_i, k = 5) + s(\text{lon}_i, \text{lat}_i, k = 25) + s(B_{\text{oxy}_i}, k = 5) + s(\text{Chl}_{50i}, k = 5) + s(\text{Depth}_i, k = 5) + \text{offset}[\log(\text{SweptArea}_i)], \text{family} = \text{NB}(\text{link} = 'log'), \text{gamma} = 1.4 \quad (2)$$

where h denotes the hake species (either *M. capensis* or *M. paradoxus*) and l is the length group (all, <21 cm [juveniles], 21–42 cm [small], 42–57 cm [medium] and >57 cm [large], based on commercial sorting grades), i denotes station, and s are smoothing splines.

From the summaries of the candidate models, the deviance explained (R^2) and Akaike's informa-

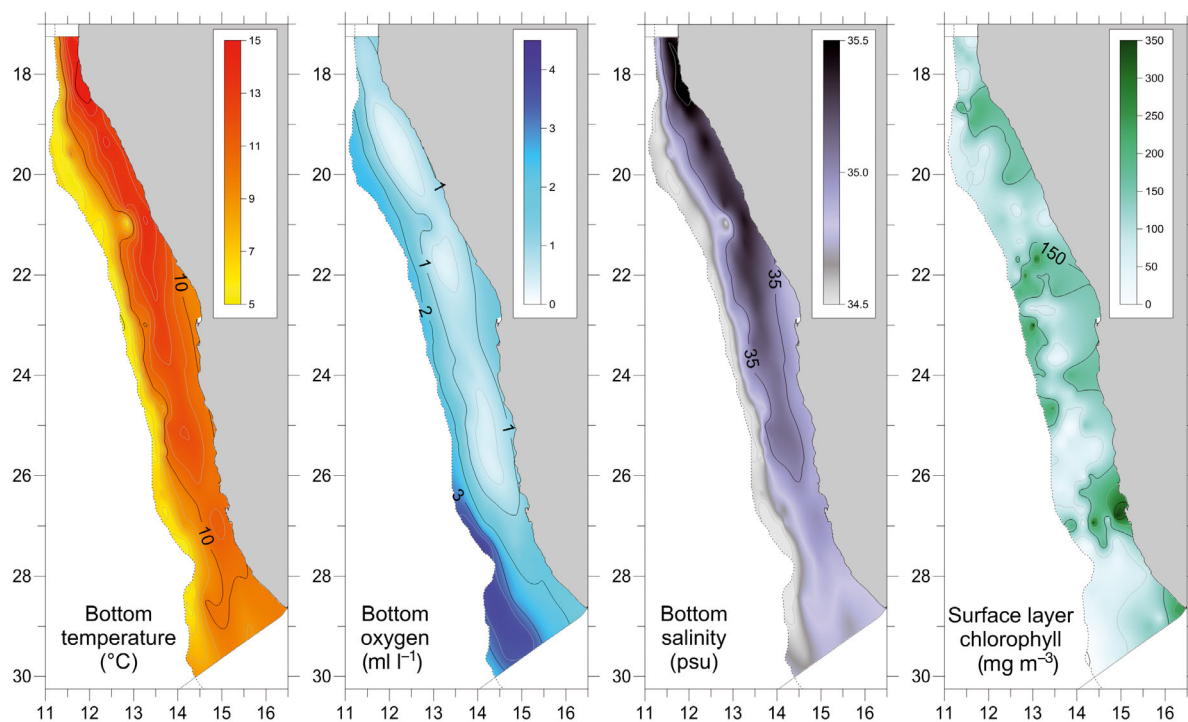


Fig. 3. Spatial distributions of bottom temperature, bottom oxygen, bottom salinity and surface chlorophyll along the Namibian coast during the 2016 demersal survey

tion criterion corrected for low number of observations (AIC_c ; Hurvich & Tsai 1989) were used to measure and compare the goodness of fit and complexity of the candidate models; the model with the lowest AIC_c was chosen as having the best variable combinations (Zuur et al. 2009, Sagarese et al. 2014). This model selection was performed independently for each of the 2 species and length groups. To verify homogeneity and normality, residuals of the best models were explored visually (residuals vs. fitted, histograms and quantile–quantile [QQ] plots), and plotted versus each covariate in the candidate models, including those not significant and those that were correlated with each other to detect non-linearity, unequal error variances and outliers (Zuur et al. 2009, Zuur & Ieno 2016). Furthermore, Pearson residuals were also plotted against spatial coordinates (variograms) in order to assess any spatial auto-correlation or evidence of non-independence of model residuals.

The GAM model was fitted using the ‘mgcv’ package (Wood 2011) while VIFs were calculated with library files from the Highland Statistics LTD (Zuur et al. 2009) of the programming and software development environment R v.3.3.2 (R Core Team 2016). In addition, Surfer® 13.0 was used for mapping.

RESULTS

Hydrographic conditions

Spatial distributions of bottom temperature, bottom oxygen, bottom salinity and chlorophyll in the upper 50 m surface layer along the Namibian coast during the 2016 demersal survey are shown in Fig. 3. Bottom waters were warmer in the north (13 to 14°C), and that warm water extended to the central areas, although in a narrow band, up to 25°C (Fig. 3). The salinity concentration followed the same pattern as that of temperature. Inshore bottom waters contained oxygen concentrations lower than 1 ml l⁻¹, while high oxygen concentrations (>3 ml l⁻¹) were observed in the offshore area, in particular south of 26°S (Fig. 3). High chlorophyll concentrations (250 to 350 mg m⁻³) were observed off Lüderitz (between 26 and 28°S), as well as at 3 other areas at 24°S, off 22°S and off Cape Frio to the north (at 19°S) (Fig. 3).

Horizontal distribution of hake

The spatial distribution of the 2 hake species by length during the 2016 demersal survey in January and February is shown in Fig. 4. During the 2016 sur-

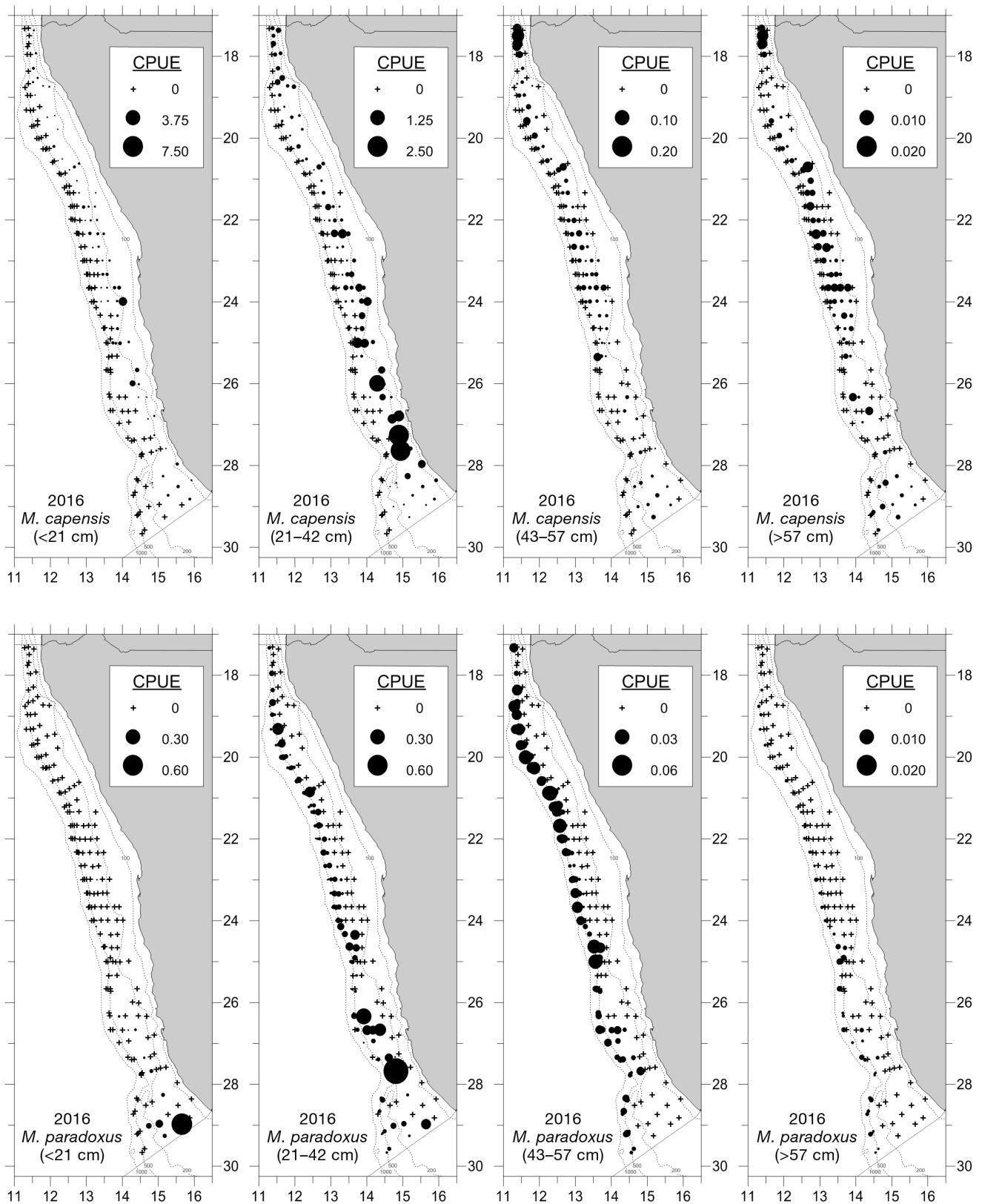


Fig. 4. Spatial distribution of survey catch rates of different size groups of shallow- and deep-water Cape hake *Merluccius* spp. during 2016 (CPUE: catch per unit effort, in number per square nautical mile $\times 10^6$)

vey, juvenile (<21 cm) *Merluccius capensis* were found closest to the coast in the central area (between 24 and 26°S), while small individuals (21–42 cm) were most abundant in the south and the 2 larger size groups (43–57 and >57 cm) were most dominant in the north close to the border with Angola (Fig. 4). Juvenile *Merluccius paradoxus* were restricted to the south-easternmost part of the survey area and appeared to move northwards with increasing sizes, and catch rates increased with depth towards the offshore limit of the survey mainly for the medium-size group (43–57 cm; Fig. 4). Large (>57 cm) individuals of *M. paradoxus* were rare and occurred only south of 24°S.

Correlation between variables

Strong and highly significant correlations were found between some of the environmental variables, e.g. bottom temperature and oxygen concentration, bottom depth and bottom salinity (Table 1), and the *r* and VIF analysis suggested that these variables be kept apart in the models. The VIFs for the initial full models were below the desired value of 3 in all cases, ranging from 1.05 to 2.88 (Table 1).

Model fitting, evaluation and selection

No spatial auto-correlation or independence of the model residuals was observed from the empirical variograms, except for the juvenile *M. paradoxus* (<21 cm) (Fig. 5). In general, the assessment of normality of the best model fits, the QQ plots, fitted values and frequency distributions of Pearson residuals for both species showed no violation of model assumptions, i.e. the covariates exhibited a linear relationship and no patterns were observed in the

residuals (Fig. 6). However, the QQ plot of the best model fit for juvenile *M. capensis* and the frequency distributions of Pearson residuals for the juvenile, small and largest size groups of *M. capensis*, as well as for juvenile *M. paradoxus* were not as good as for the other size groups of both species (Fig. 6). Nevertheless, there does not appear to be any remaining structure in the residuals, as can be seen in the plots of residuals versus all covariates (Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m584p185_supp.pdf), except for juvenile *M. paradoxus* (<21 cm), which is likely caused by the presence of very few positive hauls that were limited to the southernmost part of the survey area.

The best models based on AIC_c were model type 2 for *M. capensis* of all size groups, and *M. paradoxus* of small, medium and large size groups (Table 2). Model type 1 was only best for juvenile *M. paradoxus*. Based on the best models, depth and geographical position, oxygen and chlorophyll were the most important explanatory variables, explaining 82.9, 85.9, 71.4 and 85.8% of the variability in catches of *M. capensis* of all size groups, as well as 77.8, 92.7 and 82.6% in small, medium and large *M. paradoxus* respectively (Table 2). Catches of juvenile *M. paradoxus* were, however, influenced by geographical position and temperature, which explained 80.6% of the variability in catches (Table 2).

Effect of environmental variables on hake catches

The partial effects of the best model covariates on the catch rates of the 2 hake species of different size groups are shown in Fig. 7. In general, depth, geographical position, bottom oxygen and bottom temperature had the most pronounced effect on the catch rates of both hake species, whereas zenith and chlorophyll appeared to be less important.

Table 1. Correlation between covariates (Pearson's correlation coefficient, lower left) and significance level for correlation (upper right; ns: not significant). B_{tem}: bottom temperature; B_{sal}: bottom salinity; B_{oxy}: bottom oxygen; Chl₅₀: upper 50 m chlorophyll; VIF: variance inflation factor (subscript 1, 2 indicates model type)

	B _{tem}	B _{sal}	B _{oxy}	Depth	Zenith	Chl ₅₀	LonLat	VIF	VIF ₁	VIF ₂
B _{tem}	–	<0.001	<0.001	<0.001	<0.001	ns	ns	99.95	1.34	–
B _{sal}	0.98	–	<0.001	<0.001	<0.001	ns	0.006	66.28	–	–
B _{oxy}	–0.76	–0.80	–	<0.001	<0.001	0.008	<0.001	3.89	–	2.76
Depth	–0.92	–0.85	0.57	–	<0.001	ns	0.04	12.42	–	2.36
Zenith	–0.46	–0.42	0.30	0.46	–	ns	ns	1.37	1.35	1.32
Chl ₅₀	0.10	0.14	–0.22	0.04	0.13	–	ns	1.11	1.07	1.10
LonLat	0.08	0.22	–0.44	0.17	0.11	0.15	–	2.88	1.05	1.84

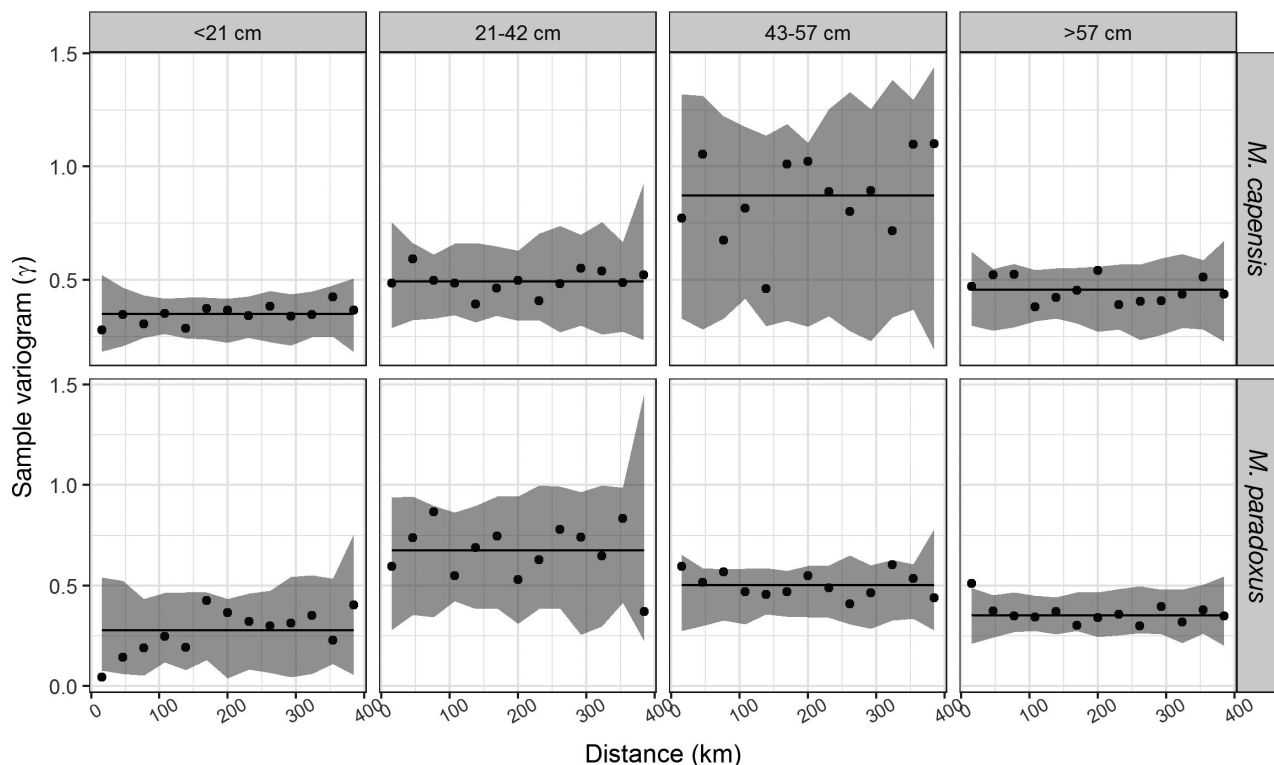


Fig. 5. Experimental variograms (points) of the residuals from the negative binomial generalized additive models (GAMs) fitted for different size groups of *Merluccius capensis* and *M. paradoxus*. Shaded areas: 95% envelope of the variograms simulated under the assumption of no spatial structure; solid line: fitted nugget variogram

The response of the catch rates of juvenile (<21 cm) and small (21–42 cm) *M. capensis* to bottom oxygen shows an almost linear negative decrease, whereas for medium (43–57 cm) and large (>57 cm) *M. capensis*, a positive effect on the catch rates was shown for bottom oxygen concentrations between 0 and 3 ml l⁻¹ (Fig. 7a). Depth appeared to be an important variable for all size groups of *M. capensis*, showing a dome-shaped response with a pronounced negative effect at depths below 300 m (Fig. 7a). The distribution of juvenile *M. capensis* was concentrated in the inshore depths from the south to about 20°S in the north, while smaller individuals were concentrated in the southern part between 28 and 30°S. The larger fish were more prevalent in the deeper areas, with the medium sizes highly concentrated in the south off Lüderitz and north (Fig. 7a), which closely resembles the observed horizontal distribution (Fig. 4). Zenith was only significant for small (21–42 cm)

M. capensis, indicating slightly higher catches with increasing zenith angles (Fig. 7a). Model type 1, which included bottom temperature, did not yield the best fit for any of the 4 size groups of *M. capensis* (Table 2), and thus the response of the catch rates to bottom temperature is not shown here. Chlorophyll was significant for all size groups but had little effect on the catch rates when compared to other covariates.

The catch rates of juvenile *M. paradoxus* responded negatively to bottom temperature when values dropped below 10°C, indicating that they avoid the deeper offshore areas (Fig. 7b). Catch rates of small (21–42 cm) and medium-sized (43–57 cm) individuals responded negatively to bottom oxygen concentrations below 1.5 ml l⁻¹ and to depths shallower than 300 m (Fig. 7b). Catch rates of large *M. paradoxus* showed a similar response to depth but with an even more pronounced preference for greater (>500 m) depths. Chlorophyll played a minor role, being sig-

Fig. 6. Quantile–quantile plots (deviance residuals vs. theoretical quantiles), Pearson residuals against fitted values and the respective frequency distribution of residuals for the final best models for different size groups of (a) *Merluccius capensis* and (b) *M. paradoxus*

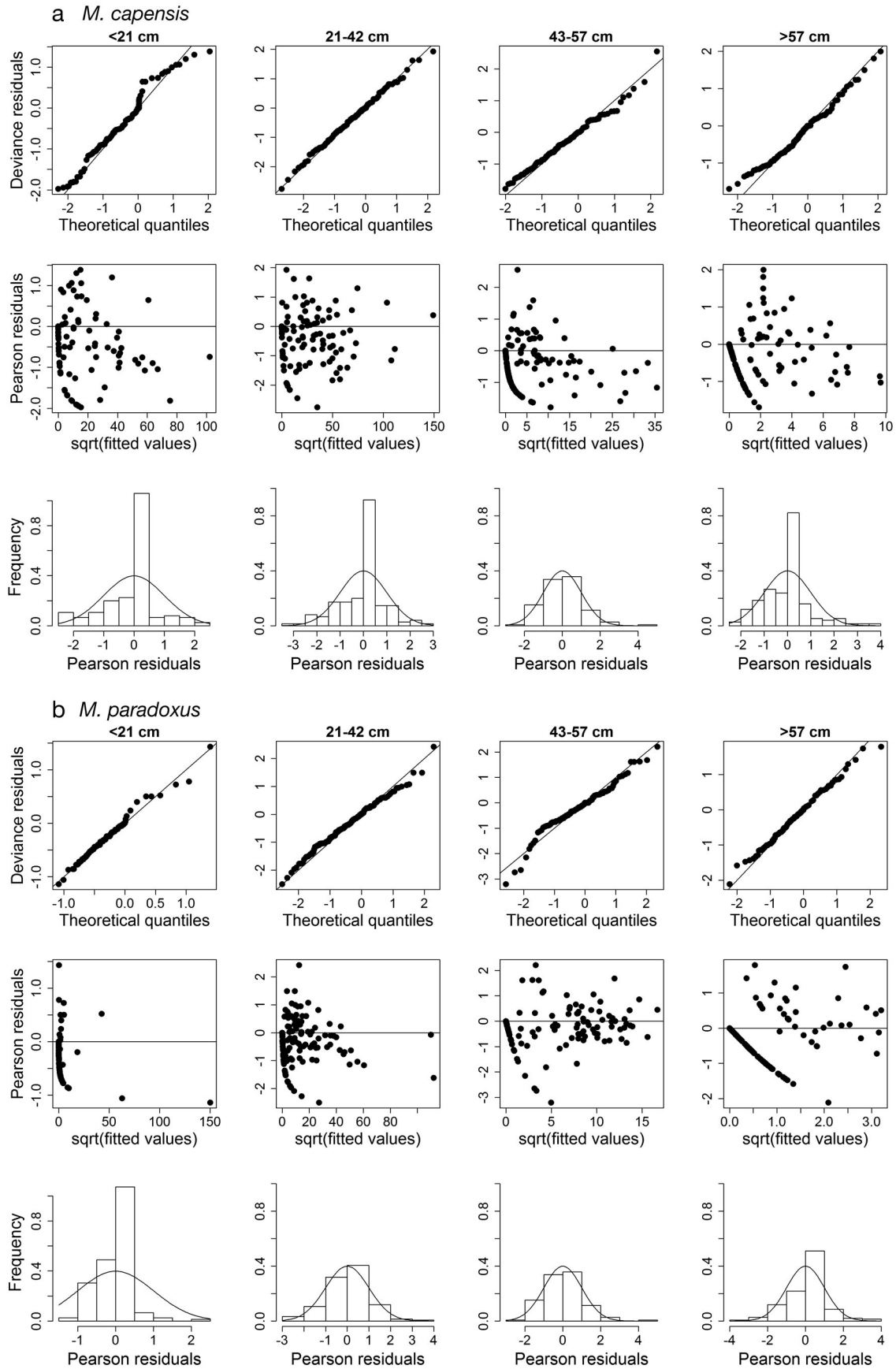


Table 2. Model performance with significance level (p) of each covariate, deviance explained and corrected Akaike's information criterion (AIC_c) for the candidate models. The best models (according to the AIC_c value) for each size group are highlighted in **bold**. Lon: longitude; Lat: latitude; B_{tem}: bottom temperature; B_{oxy}: bottom oxygen; Chl₅₀: upper 50 m chlorophyll; ns: not significant; (–) not included

Size group (cm)	Model type	Significance level of model terms (p)						Deviance explained (%)	AIC _c
		Zenith	LonLat	B _{tem}	B _{oxy}	Chl ₅₀	Depth		
<i>Merluccius capensis</i>									
<21	1	ns	<0.001	<0.001	–	0.05	–	76.7	892.91
	2	ns	<0.001	–	<0.001	0.001	<0.001	82.9	859.72
21–42	1	ns	<0.001	<0.001	–	0.05	–	85.2	1291.51
	2	0.01	0.01	–	<0.001	0.01	<0.001	85.9	1281.67
43–57	1	ns	0.001	<0.001	–	<0.001	–	56.9	821.50
	2	ns	<0.001	–	<0.001	0.001	<0.001	71.4	801.99
>57	1	ns	0.001	<0.001	–	0.01	–	55.9	539.49
	2	ns	<0.001	–	<0.001	0.01	<0.001	85.8	475.38
<i>Merluccius paradoxus</i>									
<21	1	ns	<0.001	0.001	–	ns	–	80.6	204.13
	2	ns	0.01	–	ns	ns	0.05	79.7	218.90
21–42	1	ns	<0.001	<0.001	–	ns	–	61.9	1322.14
	2	ns	<0.001	–	<0.001	0.05	<0.001	77.8	1262.66
43–57	1	ns	<0.001	<0.001	–	ns	–	86.7	889.34
	2	ns	<0.001	–	<0.001	ns	<0.001	92.7	826.75
>57	1	ns	<0.001	0.01	–	ns	–	77.3	264.13
	2	ns	<0.001	–	ns	ns	<0.001	82.6	248.05

nificant only for the small size group (Table 2), but with little effect on the catch rates at all (Fig. 7b). The modelled response to geographical distribution (Fig. 7b) closely reflected the observed horizontal distribution (Fig. 4) for all size groups.

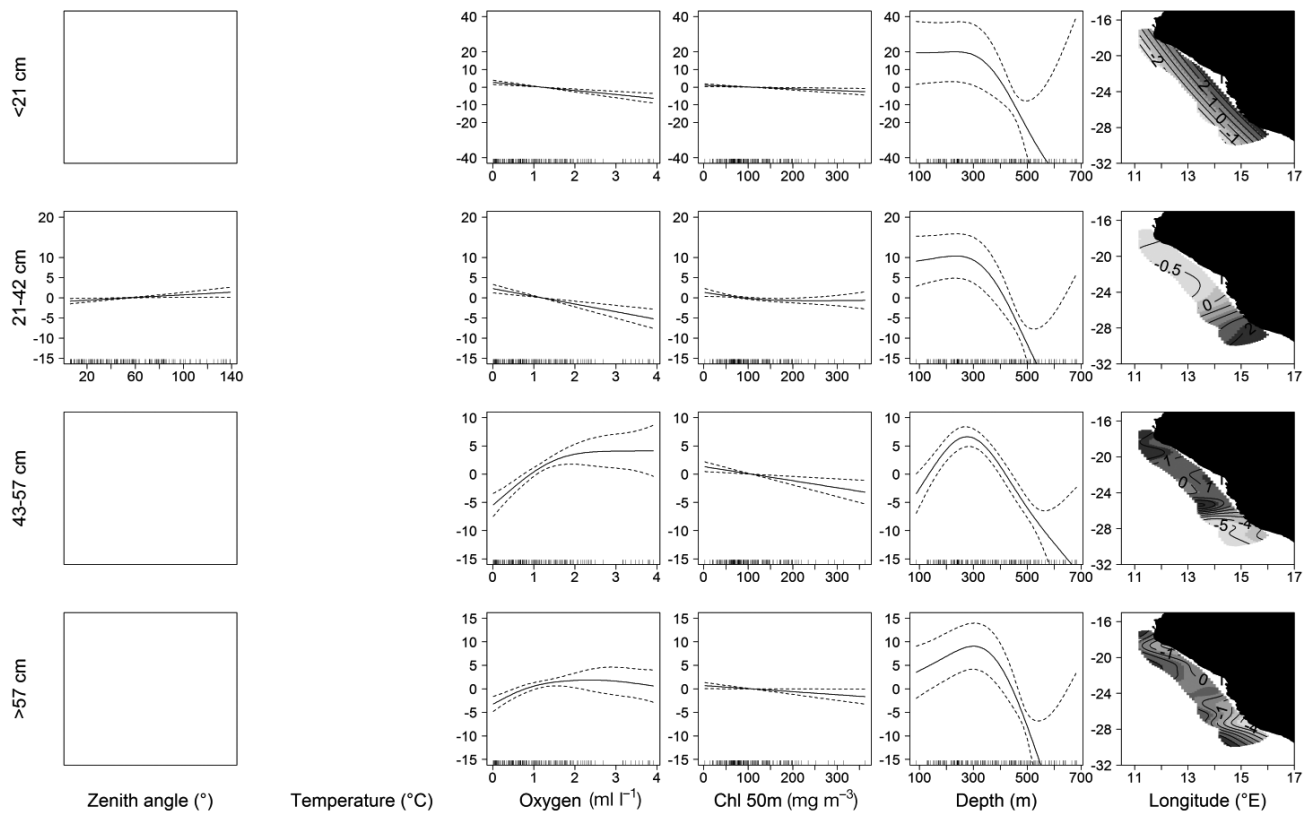
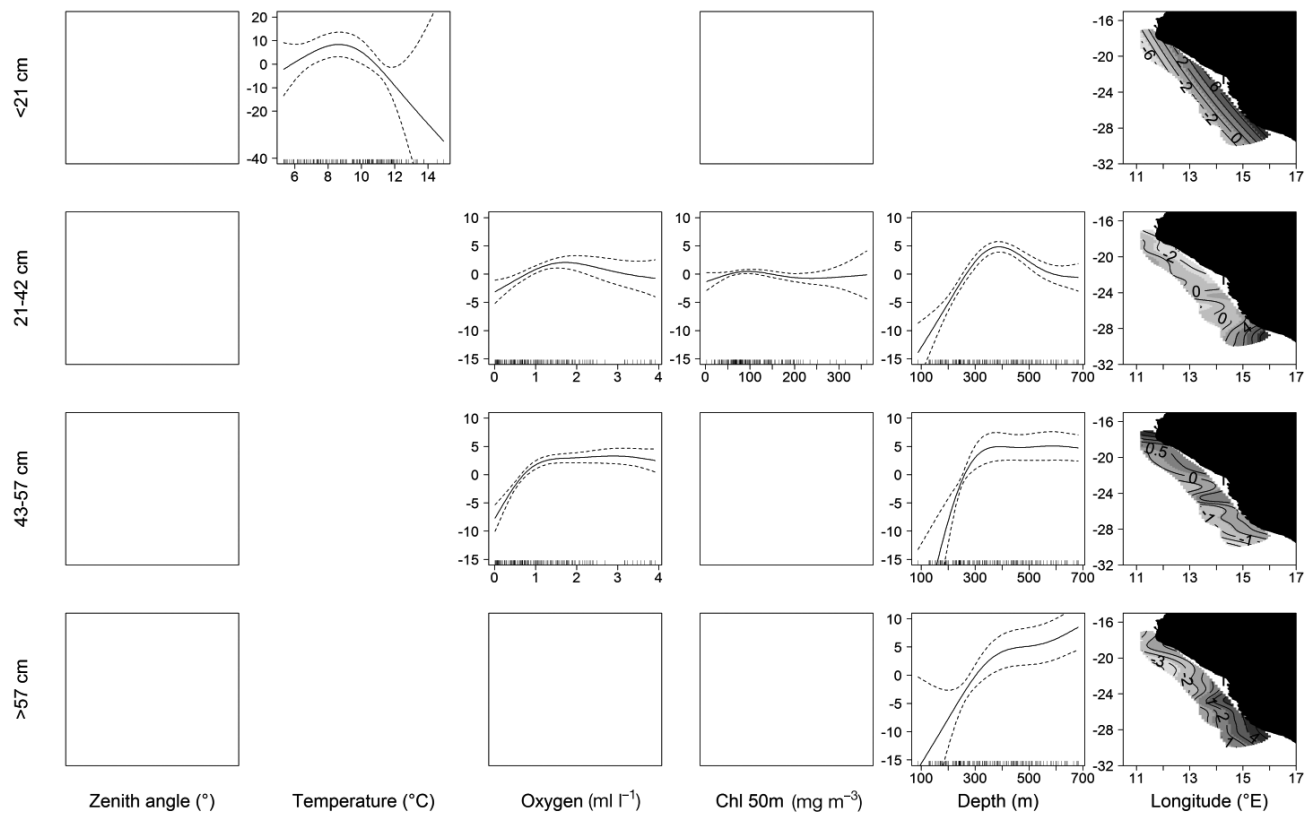
DISCUSSION

In this study, we investigated the fine-scale effect of environmental variables associated with hake habitat distribution, such as solar zenith angle, bottom depth, geographic position, bottom temperature, bottom oxygen, bottom salinity and surface layer chlorophyll, for 4 size groups of the 2 Cape hake species (*Merluccius capensis* and *M. paradoxus*) during the Namibian hake trawl survey of 2016. Oceanographic information was collected with a trawl-mounted instrument package at the same time as the

catch data. This was done for the first time in Namibian waters, and hence problems in matching catch rates with environmental information on the same spatial and temporal scale (which have been encountered in previous studies in the Benguela current region; Kirkman et al. 2013, Kainge et al. 2017) could be avoided.

We used GAMs, which have an advantage over linear models because they can accommodate non-linear relationships and have the ability to uncover hidden structures in the data through the use of smoothing functions (Wood 2006). Despite the relatively low number of observations and many zero catches, especially for the juveniles of both species and large *M. paradoxus*, the models' diagnostics were satisfactory and reasonable model fits were obtained. Results for juveniles (<21 cm) should be interpreted with caution due to apparent spatial correlation, which was likely caused by the presence of

Fig. 7. Response plots of the best models showing the partial effect of the significant smoothing functions on the catches of (a) *Merluccius capensis* and (b) *M. paradoxus* for different size groups (solid lines). The y-axis represents the contribution of the smoother to the fitted values, which is the effect of covariates on respective size group, except for the last panel where the y-axis represents latitude (°S). Dotted lines: 95 % confidence limits; the distribution of the raw observations is shown on the x-axis. Empty boxes represent covariates that were not significant while missing boxes represent covariates that were not included to avoid collinearity problems. In the sixth panel, the surface and contour lines describe the spatial effect of a 2-D smoothing function on the catches (with darker shading representing higher catches)

a) *M. capensis*b) *M. paradoxus*

very few positive hauls that were limited to the southernmost part of the survey area. However, this should be expected as juvenile *M. paradoxus* are only found in southern Namibia, because their nursery areas are located south of the Orange River (Strømme et al. 2016).

A caveat existed when temperature was highly correlated with oxygen and depth, and hence these covariates could not be included in the same model. In most cases the best models were not those which had bottom temperature as the primary covariate (model type 1) but that does not mean that temperature is irrelevant for the distribution of the 2 hake species. However, the models with bottom oxygen concentration and depth (model type 2) together with geographical position had a higher explanatory power. It is worth noting that a bivariate term (latitude–longitude interaction) was used in the model in order to account for possible spatial autocorrelation, but may be a confounding variable. However, when the model was run without it, the best models remained the same and the explained deviance was not reduced by much — apart from large *M. paradoxus*, for which the explained deviance reduced from 83 to 60%. Also worth mentioning is the use of *r* and VIF in order to assess correlation and detect collinearity. Although these statistics are normally used for linear models, they are also useful in GAMs (Guisan et al. 2002) because GAMs can be robust due to penalization of parameters (Dormann et al. 2013).

The within-species trends towards greater depth, lower bottom temperature and higher bottom oxygen concentration with increasing size as well as the between-species differences with respect to these covariates are in line with those of Kainge et al. (2017) for Namibian waters. They are also in accordance with findings for the South African west coast (Grüss et al. 2016), and reflect the general migration and distribution patterns of the 2 hake species in the Benguela upwelling system (Burmeister 2001, Gordoa et al. 2006, Wieland et al. 2014b, Jansen et al. 2016, Strømme et al. 2016).

Almost no diel effect on catch rate was found in the present study. This is in contrast to observations by Huse et al. (1998, 2001), Johnsen & Lilende (2007) and Kainge et al. (2015). But similar to Kainge et al. (2017), who found the same results, the dataset contained very few stations which were sampled outside the daylight period. Nonetheless, it appears advisable to restrict sampling, at least in the area shallower than 400 m, to the period between ca. 15 min past sunrise and 15 min before sunset for each location rather than a fixed local time period, considering

the change of the length of the daylight period during the course of the survey.

The area off Lüderitz is known for its low chlorophyll concentration due to its powerful upwelling cell and the high associated turbulence (Bartholomae & van der Plas 2007, Hutchings et al. 2009). The normal high chlorophyll area north of Lüderitz (Bartholomae & van der Plas 2007, Hutchings et al. 2009) was not visible here because our sampling was a snapshot (compared to e.g. weekly averages) and there were also no stations in the area north of Lüderitz. However, a dedicated environmental survey along 26°S has confirmed that extensive and dense phytoplankton blooms developed in the Lüderitz bay and lasted between the second half of January and mid-April 2016, after increased sea surface temperatures were observed (K. Grobler unpubl. data), and phytoplankton blooms are usually associated with warm water (Schulien et al. 2017).

Chlorophyll concentration had little effect on the catch rates, although it was significant for all *M. capensis* size groups, as well as in the small-sized group for *M. paradoxus*. Areas of high chlorophyll concentrations, which could be linked to high productive areas, were observed, and these are expected to result in hakes lifting off the bottom due to reduced light levels (Wieland et al. 2013). During the 2016 survey, high catch rates of especially small-sized fish (21 to 42 cm) of both species were, however, observed around the same areas of high chlorophyll concentration. This indicates that ‘green water’ has little or no effect on hake catch rates (Wieland et al. 2013). The current version of the instrument package is unfortunately not equipped with a low-level light sensor such as used by e.g. Kotwicki et al. (2009) and Huse et al. (1998). Solar zenith angle does not account for variability in cloud cover or foggy conditions. Although vertical migration may persist despite such variability (Neilson & Perry 1990), light attenuation in the water column may be affected by high chlorophyll concentrations in the surface layer but the effect of low levels on hake catch rates could not be demonstrated here.

Our results demonstrate that the use of a trawl-mounted instrument package can collect useful and reliable environmental data that can be used to improve the understanding of variability in hake catchability without requiring additional ship time. This will enable quantification of environmental effects on scientific CPUE data and thereby correction of survey time-series in order to produce reliable biomass estimates for stock assessment and advice on catch quota. We therefore encourage continuous use

of the trawl-mounted instrument package on a permanent basis during routine monitoring of demersal fish resources in Namibian waters.

Acknowledgements. The authors acknowledge contributions of the survey staff (scientists and vessel officers) of the National Marine Information and Research Centre (NatMIRC) in Swakopmund, who collected the data analyzed in this study, especially Vasana Tutjavi (NatMIRC) for his operation of the trawl-mounted instrument package. We also thank Anja van der Plas (NatMIRC) for preparing the data for temperature, salinity and corrected dissolved oxygen and Dawit Yemane (DAFF, Cape Town) for assistance on calculation and plotting of the variograms. The Ministry of Fisheries and Marine Resources in Namibia is thanked for funding the annual surveys. This study was co-funded by the European Union through the Ecofish project (EuropeAid grant 2010/222387) and administered by the Benguela Current Commission (BCC). Finally, we thank 2 anonymous reviewers for their quality comments and recommendations which improved the manuscript.

LITERATURE CITED

- ✦ Axelsen BE, Johnsen E (2015) An evaluation of the bottom trawl surveys in the Benguela Current Large Marine Ecosystem. *Fish Oceanogr* 24:74–87
- Bailey GW (1991) Organic carbon flux and development of oxygen deficiency on the modern Benguela continental shelf south of 22°S: spatial and temporal variability. In: Tyson RV, Pearson TH (eds) *Modern and ancient continental shelf anoxia*. Special Publication No. 58, The Geological Society, London, p 171–183
- ✦ Bartholomae CH, van der Plas AK (2007) Towards the development of environmental indices for the Namibian shelf, with particular reference to fisheries management. *Afr J Mar Sci* 29:25–35
- ✦ Burmeister LM (2001) Depth-stratified density estimates and distribution of the Cape hake *Merluccius capensis* and *M. paradoxus* off Namibia deduced from survey data, 1990–1999. *S Afr J Mar Sci* 23:347–356
- ✦ Burmeister L (2005) Is there a single stock of *Merluccius paradoxus* in the Benguela ecosystem? *Afr J Mar Sci* 27: 23–32
- ✦ Dormann CF, Elith J, Bacher S, Buchmann C and others (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:027–046
- ✦ Druon JN, Fiorentino F, Murenu M, Knittweis L and others (2015) Modelling of European hake nurseries in the Mediterranean Sea: an ecological niche approach. *Prog Oceanogr* 130:188–204
- ✦ Frouin R, Lingner DW, Gautier C (1989) A simple analytical formula to compute clear sky total and photosynthetically available solar irradiance at the ocean surface. *J Geophys Res* 94:9731–9742
- Godø OR (1994) Factors affecting reliability of groundfish abundance estimates from bottom trawl surveys. In: Ferno A, Olsen S (eds) *Marine fish behaviour in capture and abundance estimation*. Fishing News Books, Oxford, p 166–199
- ✦ Gordoa A, Maso M, Voges L (2000) Monthly variability in the catchability of Namibian hake and its relationship with environmental seasonality. *Fish Res* 48:185–195
- ✦ Gordoa A, Lesch H, Roderigas S (2006) Bycatch: complementary information for understanding fish behaviour. Namibian Cape hake (*M. capensis* and *M. paradoxus*) as a case study. *ICES J Mar Sci* 63:1513–1519
- ✦ Grüss A, Yemane D, Fairweather TP (2016) Exploring the spatial distribution patterns of South African hakes using generalized additive models. *Afr J Mar Sci* 38:395–409
- ✦ Guisan A, Edwards TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol Model* 157:89–100
- ✦ Hamukuaya H, O'Toole MJ, Woodhead PMJ (1998) Observations of severe hypoxia and offshore displacement of Cape hake over the Namibian shelf in 1994. *S Afr J Mar Sci* 19:57–61
- Hastie TJ, Tibshirani RJ (1990) Generalized additive models. Monographs on statistics and applied probability 43. Chapman & Hall, London
- Hastie T, Tibshirani R, Friedman J (2001) The elements of statistical learning: data mining, inference, and prediction. Springer, New York, NY
- ✦ Heymans JJ, Tomczak MT (2016) Regime shifts in the northern Benguela ecosystem: challenges for management. *Ecol Model* 331:151–159
- ✦ Heymans JJ, Shannon LJ, Jarre A (2004) Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s, and 1990s. *Ecol Model* 172:175–195
- ✦ Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. *Biometrika* 76:297–307
- ✦ Huse I, Hamukuaya H, Boyer DC, Malan PE, Strømme T (1998) The diurnal vertical dynamics of Cape hake and their potential prey. *S Afr J Mar Sci* 19:365–376
- ✦ Huse I, Iilende T, Strømme T (2001) Towards a catchability constant for trawl surveys of Namibian hake. *S Afr J Mar Sci* 23:375–383
- ✦ Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM and others (2009) The Benguela Current: an ecosystem of four components. *Prog Oceanogr* 83:15–32
- Jacobson L, Seaver A, Tang J (2011) AstroCalc4R: software to calculate solar zenith angle; time at sunrise, local noon and sunset; and photosynthetically available radiation based on date, time and location. www.nfsc.noaa.gov/publications/crd/crd1114/crd1114.pdf (accessed 13 June 2017)
- ✦ Jacobson LD, Hendrickson LC, Tang J (2015) Solar zenith angles for biological research and an expected catch model for diel vertical migration patterns that affect stock size estimates for longfin inshore squid, *Doryteuthis pealeii*. *Can J Fish Aquat Sci* 72:1329–1338
- ✦ Jansen T, Kristensen K, Kainge P, Durholtz D and others (2016) Migration, distribution and population (stock) structure of shallow-water hake (*Merluccius capensis*) in the Benguela Current Large Marine Ecosystem inferred using a geostatistical population model. *Fish Res* 179: 156–167
- ✦ Johnsen E, Iilende T (2007) Factors affecting the diel variation in commercial CPUE of Namibian hake—Can new information improve standard survey estimates? *Fish Res* 88:70–79
- ✦ Kainge P, Wieland K, Feekings J (2015) Diel effects on bottom-trawl survey catch rates of shallow- and deep-water Cape hakes *Merluccius capensis* and *M. paradoxus* off Namibia, using solar zenith angle. *Afr J Mar Sci* 37: 583–592

- ✦ Kainge P, Van der Plas AK, Bartholomae CH, Wieland K (2017) Effects of environmental variables on survey catch rates and distribution by size of shallow- and deep-water Cape hakes, *Merluccius capensis* and *Merluccius paradoxus* off Namibia. *Fish Oceanogr* 26:680–692
- ✦ Kirkman SP, Yemane D, Kathena J, Mafwila SK and others (2013) Identifying and characterizing demersal fish biodiversity hotspots in the Benguela Current Large Marine Ecosystem: relevance in the light of global changes. *ICES J Mar Sci* 70:943–954
- ✦ Kirkman SP, Yemane D, Atkinson LJ, Kathena J and others (2015) Regime shifts in demersal assemblages of the Benguela Current Large Marine Ecosystem: a comparative assessment. *Fish Oceanogr* 24:15–30
- ✦ Kotwicki S, De Robertis A, von Szalay P, Towler R (2009) The effect of light intensity on the availability of walleye pollock (*Theragra californica*) to bottom trawl and acoustic surveys. *Can J Fish Aquat Sci* 66:983–994
- ✦ Kotwicki S, Horne JK, Punt AE, Ianelli JN (2015) Factors affecting the availability of walleye pollock to acoustic and bottom trawl survey gear. *ICES J Mar Sci* 72:1425–1439
- ✦ Louw DC, van der Plas AK, Mohrholz V, Wasmund N, Junker T, Eggert A (2016) Seasonal and interannual phytoplankton dynamics and forcing mechanisms in the Northern Benguela upwelling system. *J Mar Syst* 157:124–134
- ✦ Monteiro PMS, van der Plas AK, Mélice JL, Florenchie P (2008) Dynamical characteristics of interannual hypoxia variability in a coastal upwelling system: climate and ecosystem state implications. *Deep Sea Res I* 55:435–450
- ✦ Neilson JD, Perry RI (1990) Diel vertical migrations of marine fishes: An obligate or facultative process? *Adv Mar Biol* 26:115–168
- ✦ Paterson B, Kainge P (2014) Rebuilding the Namibian hake fishery: a case for collaboration between scientists and fishermen. *Ecol Soc* 19:49
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Rueda L, Massuti E, Alvarez-Berastegui D, Hidalgo M (2015) Effect of intra-specific competition, surface chlorophyll and fishing on spatial variation of gadoid's body condition. *Ecosphere* 6:175
- ✦ Sagarese SR, Frisk MG, Cerrato RM, Sosebee KA, Musick JA, Rago PJ (2014) Application of generalized additive models to examine ontogenetic and seasonal distributions of spiny dogfish (*Squalus acanthias*) in the Northeast (US) shelf large marine ecosystem. *Can J Fish Aquat Sci* 71:847–877
- ✦ Schulien JA, Peacock MB, Hayashi K, Raimondi P, Kudela RM (2017) Phytoplankton and microbial abundance and bloom dynamics in the upwelling shadow of Monterey Bay, California, from 2006 to 2013. *Mar Ecol Prog Ser* 572:43–56
- ✦ Strømme T, Lipinski MR, Kainge P (2016) Life cycle of hake and likely management implications. *Rev Fish Biol Fish* 26:235–248
- Wieland K, Durholtz D, Fairweather T (2013) Environmental effects on hake catchability in the South African West Coast Survey. Paper IWS/DEC13/Ecofish/P3, presented at MARAM/DAFF International Fisheries Stock Assessment Review Workshop, 2–6 December 2013, Cape Town
- Wieland K, Hutchings L, Durholtz D (2014a) Application of a trawl mounted instrument package for studying environmental effects on hake catchability. Presented at Benguela Current Commission Annual Science Forum, 13–15 October 2014, Swakopmund. www.benguelacc.org/index.php/en/component/docman/doc_download/653-day-2-wieland (accessed 13 June 2017)
- Wieland K, Durholtz MD, Fairweather TP, Glazer J, Leslie RW (2014b) Presence-absence relationship with bottom temperature for deep water hake (*Merluccius paradoxus*) on the west coast of South Africa and its potential for adjusting survey indices. Paper MARAM IWS/DEC14/Hake/BG14, presented at International Fisheries Stock Assessment Review Workshop, 1–5 December 2014, Cape Town. www.dtu.dk/english/service/phonebook/person?id=41542&tab=2&qt=dtupublicationquery (accessed 28 June 2017)
- ✦ Wintle BA, Elith J, Potts JM (2005) Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of NSW. *Austral Ecol* 30:719–738
- Wood SN (2006) Generalized additive model: an introduction with R. Chapman & Hall, New York, NY
- ✦ Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc B* 73:3–36
- ✦ Zuur AF, Ieno EN (2016) A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol Evol* 7:636–645
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY