

Ecological niche modelling of cold-water corals in the Southern Ocean (N Antarctic), present distribution and future projections due to temperature changes

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ABSTRACT: An urgent necessity to understand the effect of climatic change on scleractinian cold-water coral (CWC) ecosystems has arisen due to increasing ocean warming and acidification over the last decades. Here, presence–absence records of 12 scleractinian CWC species from research expeditions and the literature were compiled and merged with model-generated pseudo-absence data and 14 environmental variables. The best-fitting results of 9 species distribution models (SDMs) were combined to an ensemble habitat suitability model for CWCs in the northern Southern Ocean (Weddell Sea and Antarctic Peninsula) by means of the open-source R package 'biomod2'. Furthermore, 2 future scenarios of increasing bottom sea temperature were used to investigate the spatial response of scleractinians to temperature change. The resulting (current scenario) potential ecological niches were evaluated with good to excellent statistical measures. The results predict that present areas of highest probability of CWC occurrence are around the Antarctic Peninsula, South Orkney Islands and Queen Maud Land, with preference to geomorphic features such as seamounts. The distribution of CWC habitats is mainly driven by distance to coast and ice shelves, bathymetry, benthic calcium carbonate, and temperature. Under warming conditions, CWCs are predicted to expand their distribution range by 6 and 10% in 2037 and 2150, respectively, compared to the present distribution. The future models using increased bottom temperature revealed a stable CWC distribution for most parts of the study area. However, habitat shifts are expected to the Filchner Trough region, the adjacent continental shelves, as well as to the eastern side of the Antarctic Peninsula.

KEY WORDS: Scleractinian coral · Ensemble models · Environmental change · Habitat suitability model · Spatial distribution · Weddell Sea · Antarctica

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1. INTRODUCTION

The Antarctic region is characterized by low and constant temperatures and generally by little fluctuation of the abiotic conditions, at least in marine environments. Antarctic organisms have experienced more than 20 million years of adaptation to a stable and predictable environment, resulting in a high number of endemic species, which are sensitive to

strong divergences and anomalies (O'Loughlin et al. 2011, Peck et al. 2014). Nevertheless, the marine diversity in this area is relatively high (Clarke & Johnston 2003). Within this polar region, benthic species are abundant and taxonomically diverse, especially in comparison with the Arctic (Orejas et al. 2000).

The Weddell Sea is regarded as one of the biodiversity hotspots of the Antarctic (Gili et al. 2006). The region plays an important role in driving global

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thermohaline circulation and ventilating the abyssal ocean as well as regulating the global sea level (Griffiths 2010, Deininger et al. 2016). It is also characterized by an extreme seasonal variability due to sea ice and comprises many types of geomorphic features of the Southern Ocean seafloor, such as canyons and seamounts, known to support vulnerable and transient marine ecosystems (Douglass et al. 2014). All these characteristics render the Weddell Sea a unique and diverse area that provides a refuge for different ecosystem components.

Large parts of Antarctic benthic communities consist of sessile suspension feeders such as sponges, anthozoans, bryozoans, and ascidians (Dayton et al. 1986, Brey & Gerdes 1997, Waller et al. 2011). Within the anthozoans, scleractinian cold-water corals (CWCs) are common on the Antarctic continental shelves and solitary rather than reef-building (Roberts et al. 2009). Scleractinian CWCs have a global distribution range from shallow tropical areas to the depths of the Antarctic region (Cairns 2007), which reflects their long evolutionary history and their capacity to spread and thrive under a high variety of environmental conditions. Their skeletons are mainly made of calcium carbonate in the form of aragonite, and these corals use their tentacles to capture food from ambient waters (Cairns 2007, Gofredo et al. 2011). Understanding their global distribution and the controlling environmental factors remain difficult because ecological studies regarding their habitat preferences in the Southern Ocean do not exist. Abiotic data and species distribution information from many deep-sea areas around the world are missing (Roberts & Cairns 2014).

Antarctic scleractinian CWCs comprise ~17 species distributed around continental Antarctica and the Antarctic archipelagos (Cairns 1982). The available studies on scleractinian species from the north Antarctic relate to taxonomic identifications and distribution (Cairns 1982, 1990, Schejter et al. 2016), reproductive biology (Waller et al. 2008), and metabolism (Henry & Torres 2013).

The difficulties in monitoring benthic components in remote and inaccessible ecosystems such as the Southern Ocean have frequently been addressed using predictive models (Gonzalez-Mirelis & Lindegarth 2012). Species distribution models (SDMs) are useful tools to improve the understanding of the distribution of marine organisms in response to the environmental conditions (Wiley et al. 2003, Robinson et al. 2011)

In this study, we apply species distribution algorithms to presence and pseudo-absence data of different scleractinian CWCs and environmental vari-

ables regulating their distribution to provide current and future geographical ranges of species distribution of the order Scleractinia in the Weddell Sea and the Antarctic Peninsula. The detailed statistical analysis and pre-selection of abiotic variables might provide new insights into their habitat suitability as well as their environmental tolerances and constraints.

The aims of this study are (1) to explore the environmental response of scleractinian CWCs over their entire geographical range in the Weddell Sea and the Antarctic Peninsula, (2) to predict potential suitable habitats for the presence of these species, and (3) to project their future distribution under temperature change scenarios.

These key aspects inform ecologists and political decision-makers about the evolutionary and dynamic response and the spatial distribution of these ecosystem-building organisms. This knowledge is crucial for the conservation of their polar habitats.

2. MATERIALS AND METHODS

2.1. Study area

The study area extends from ~80° W to 40° E and from the Antarctic coasts to 60° S offshore the ice shelves Larsen C, Ronne, Filchner, Brunt, Riiser-Larsen, Quarisen, Ekstrøm, Jelbart, and Fimbul (Fig. 1). The water depth is ~500 m on average and ranges from 100 m at some parts of the ice shelf edge to 800–4000 m on the continental shelf and the slope. The deepest and largest area in the abyssal plane reaches around 5300 m depth (Hillenbrand et al. 2014, Jerosch et al. 2016).

The area is geomorphologically characterized by a narrow shelf and steep continental slope in the east and a wide shelf (500 km from the coast) in the southern part (Jerosch et al. 2016). Three cross-shelf troughs (Filchner Trough, Hughes Trough and Ronne Trough) extend offshore the Filchner and Ronne Ice Shelves (Fig. 1) and exhibit an important dipping (depths ~1200, 500 and 650 m, respectively) towards the continent (Haid 2013).

2.2. Pre-modelling

2.2.1. Occurrence data

The specimens used in this study were mainly collected on 'RV Polarstern' expeditions between 1989 and 2014 with demersal gears (i.e. bottom and agas-

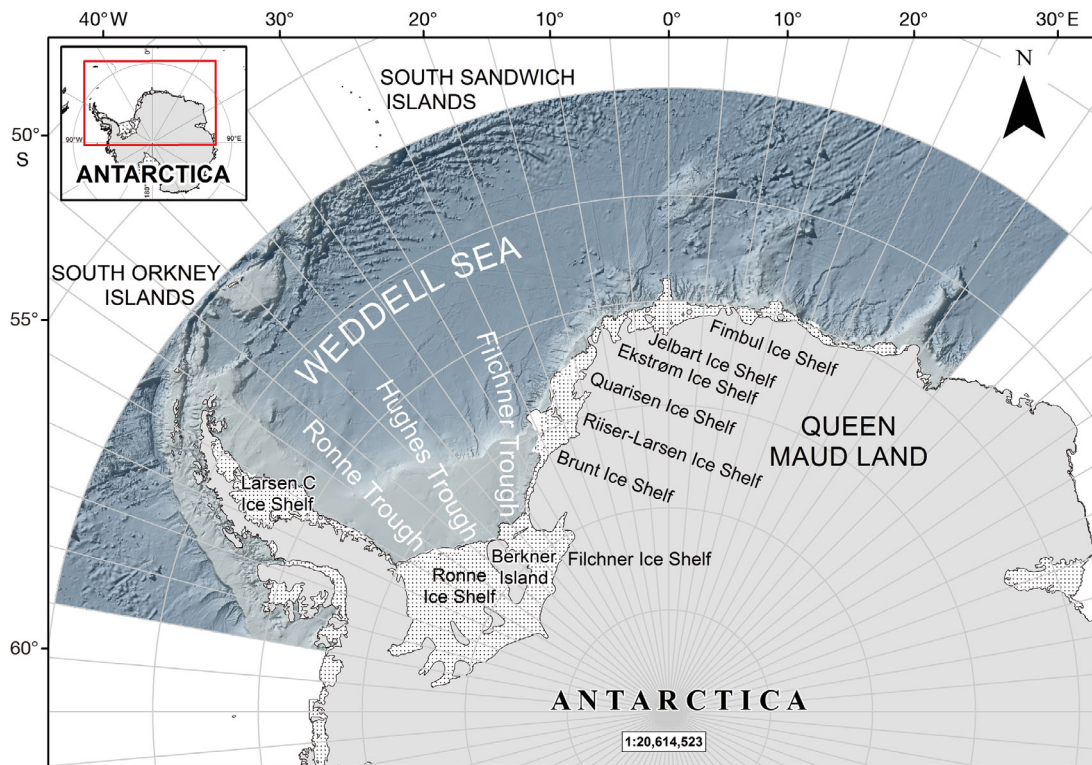


Fig. 1. Overview of the study area in the Weddell Sea and Antarctic Peninsula (map projection: South Pole Stereographic EPSG 102021). The blue color corresponds to the classification of the area's bathymetry (deep: dark blue; shallower: light blue/white)

siz trawl, dredges). Samples were either identified or fixed on board in ethanol 70% or alternatively in buffered formalin 10%, and then finally preserved in ethanol 70%. The specimens were identified at the Department of Zoology of the University of Sevilla, Spain.

The database was completed with data made available through the Antarctic Biodiversity Information Facility (AntaBif) (www.biodiversity.aq) considering just the records identified and described by Cairns (1982). A total of 242 presences and 69 absences were finally gathered (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m628p073_supp.pdf). Twelve different scleractinian species from 8 genera (*Flabellum*, *Javania*, *Paraconotrochus*, *Caryophyllia*, *Fungiacyathus*, *Leptopenus*, *Balanophyllia*, and *Desmophyllum*) were identified (Fig. S2).

The main issue that prevented models from being performed at the species level was the limited number of reliable identifications related to the study area. Relying completely on electronic databases would have led to a higher degree of uncertainty, as has been noted in other studies with Scleractinia (Guinotte & Davies 2014) and Octocorallia (Yesson et

al. 2012). For these reasons, only the reliable coral records were binned and modelled at the order level. Detailed information on specimens' distribution at the species level can be found in the supplementary material (Fig. S2).

2.2.2. Environmental variables selection

In total, 27 environmental variables of the seafloor were compiled from different sources (Table 1), first, according to data availability for the study area, and second, to their documented physiological relevance for CWCs. A stepwise selection method (Guyon & Elisseeff 2003) was applied to remove irrelevant and redundant input variables based on different types of statistical and variable selection algorithms (Fig. S3). This pre-processing achieved an improved model performance by only using effective parameters and produced a faster and more understandable and interpretable model.

We started with highly correlated (Pearson correlation coefficient $|r| \geq 0.9$), collinear and interdependent variables. Further, all variables with a variance inflation factor (VIF) >10 (Besley & Kuh 1980)

Table 1. Summary of the environmental variables used in the analysis. The variables highlighted in **bold** constitute the final pre-selected set used for model building. The BPI indicates whether a pixel is part of a convex (crest, ridge), concave (trough, valley), or flat (plains) feature in the terrain (Weiss 2001). The processed data compilation is available from PANGAEA (doi:10.1594/PANGAEA.895586). NetCDF: Network Common Data Form; wt%: percent weight; dpm: disintegrations min⁻¹

Parameter	Data source	Time period	Data type	Units	Source
Bathymetry (Bathy)	IBCSO	1986–2012	Raster	m	www.ibcso.org/
Distance to coast/ice shelf (Dist_coast)	IBCSO	1986–2012	Raster	m	This study
Slope (Slope)	IBCSO	1986–2012	Raster	degrees	Jerosch et al. (2016)
Broad benthic positioning index (Broad_BPI)	IBCSO	1986–2012	Raster	unitless	Jerosch et al. (2016)
Bottom total organic carbon (TOC)	PANGAEA	1983–1992	Polygon features	wt%	Seiter et al. (2004)
²³⁴ Thorium flux (Th234_flux)	PANGAEA	1978–2013	Data points	dpm m ⁻² d ⁻¹	www.pangaea.de/?q=param128822
Biogenic silica (BioSi)	PANGAEA	1978–2013	Data points	%	www.pangaea.de/?q=param71
Benthic Calcium carbonate (CaCO₃)	PANGAEA	1978–2013	Data points	%	www.pangaea.de/search?q=param70
Total organic carbon flux (TOC_flux)	PANGAEA	1978–2013	Data points	g m ⁻² yr ⁻¹	www.pangaea.de/?q=param7062
Silica (SiO ₂)	PANGAEA	1978–2013	Data points	µg l ⁻¹	www.pangaea.de/?q=param88096
Quartz (Quarz)	PANGAEA	1978–2013	Data points	wt%	Seiter et al. (2004)
Oxygen utilized (UO ₂)	WOA13	1982–2013	Raster	ml l ⁻¹	www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13oxnu.pl?parameter=A
Saturated oxygen (Sat_O ₂)	WOA13	1982–2013	Raster	%	www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13oxnu.pl?parameter=O
Dissolved oxygen (DO)	WOA13	1982–2013	Raster	ml l⁻¹	www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13oxnu.pl?parameter=o
Silicon (Si)	WOA13	1982–2013	Raster	µm l⁻¹	www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13oxnu.pl?parameter=i
Nitrate (Ni)	WOA13	1982–2013	Raster	µm l⁻¹	www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13oxnu.pl?parameter=n
Phosphorus (P)	WOA13	1982–2013	Raster	µm l⁻¹	www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13oxnu.pl?parameter=p
Bottom temperature (Temp)	FESOM	1990–2009	Raster	°C	Wang et al. (2014)
Bottom current speed (Speed)	FESOM	1990–2009	Raster	m s⁻¹	Wang et al. (2014)
Salinity (SAL)	FESOM	1990–2009	Raster	PSU	Wang et al. (2014)
Temperature seasonal difference (Temp_diff)	FESOM	2001–2009	Raster	°C	Wang et al. (2014)
Salinity seasonal difference (SAL_diff)	FESOM	2001–2009	Raster	PSU	Wang et al. (2014)
<i>Fragilariopsis kerguelensis</i> (Fra_k a, b, c)	SDM	2013	Raster	%	Pinkernell & Beszteri (2014)
Chlorophyll a (Chl a, mean and median)	OC-CCI v3.0	1997–2016	NetCDF	mg m ⁻³	www.esa-oceancolour-cci.org/

were considered to cause high collinearity (Akinwande et al. 2015) and hence were excluded. Interdependency among variables was tested via the Monte Carlo Feature Selection-Interdependency Discovery graph (MCFS-ID). For a detailed description of the graph principles and elaboration, refer to Dрамиński & Koronacki (2018). Multicollinearity and interdependency analyses are useful to identify the groups of predictors that are most likely to have the same effect on the response variable (Dormann et al. 2013). The top explanatory variables with the largest predictive power in describing the distribution of CWCs were kept; those contributing the weakest predictive power were excluded. This was achieved by comparing the ranks of variables, assigned by 5 machine-learning methods, chosen based on review studies of the most used and cited algorithms in ecology modelling (Aho et al. 2014, Tang et al. 2014, Jović et al. 2015, Degenhardt et al. 2019). The comparison included the classification tree method (Class_tree) (De'ath & Fabricius 2000), the random forest (RF) (Breiman 2001), the Boruta algorithm (Boruta) (Kursa & Rudnicki 2010), the recursive features elimination (rfe) (Kuhn 2012), and the Monte Carlo feature selection method (MCFS) (Dрамиński & Koronacki 2018).

In order to know to which extent a reduction of the predictors set is possible without compromising the accuracy of the model, a final step of variable selection was performed by using 3 optimal-subset selection methods: principal component regression (PCR) (Wehrens & Mevik 2007), regularized regression through Ridge and Lasso techniques (Hastie & Qian 2017), and stepwise Akaike's information criterion (AIC) (Akaike 1973).

2.2.3. Model parameters

Most of the SDMs require absence data, which are frequently unavailable and often not reliable. To overcome this limitation, the use of pseudo-absence datasets has become very common in ecological modelling (Wisž & Guisan 2009).

Based on the methodology used by Barbet-Massin et al. (2012), we compared the results of 3 different numbers of pseudo-absences (500, 1000, and 10000), 3 methods to generate them (Random, Disk and SRE) (Thuiller et al. 2016), and one weighting scheme for all the SDMs. For each combination of parameters, 10 replicates with different presence data selections were performed to account for the variability in model accuracy (Fig. S4).

We tested how the method of generating pseudo-absences affects model accuracy. For each number of pseudo-absences and each method, the mean true skill statistics (TSS) and the receiver operating characteristic (ROC) (Fielding & Bell 1997, Allouche et al. 2006) were compared. Finally, we compared the mean TSS scores across the number of replicates for each combination of pseudo-absence pools to determine the optimum number of replicates, beyond which the TSS decreases for most of the SDMs.

2.3. Modelling present and future CWC distribution

Ten of the most commonly used SDMs for habitat suitability were applied to model the distribution of scleractinians within the study area (Fig. 2). The SDMs are built under the biodiversity modelling package biomod2 v.3.1-64, described in detail by Thuiller et al. (2014), using the R statistics environment (R v.3.1.2, R Core Team 2014). The modelling techniques include regression, classification, and machine-learning methods, as explained by Elith & Graham (2009): multivariate adaptive regression splines (MARS); generalized linear models (GLMs); gradient boosting models (GBMs); generalized additive models (GAMs); flexible discriminant analysis (FDA); classification tree analysis (CTA); random forest (RF); artificial neural network (ANN); low-memory multinomial logistic regression (MAXENT); and surface range envelope, usually called BIOCLIM (SRE). The models were fitted by assigning an equal weight to each presence and absence point. The dataset was divided into 2 subsets: a random sample from 70% of the total database was used to calibrate (train) the models, whereas the remaining data (30%) were used to evaluate model predictions (Thuiller 2003). A total of 60 calibrated models (from 10 SDMs, 2 replicates of pseudo-absences and 3 evaluation runs) were used to project scleractinian distribution for the entire Weddell Sea and the Antarctic Peninsula under the environmental conditions selected in Section 2.2.2.

Each model was evaluated by using the mean TSS and the ROC (3 runs each) for a robust assessment of model performance (Fielding & Bell 1997, Allouche et al. 2006). The TSS is a prevalence independent metric which corresponds to the sum of sensitivity and specificity minus one—the sensitivity being the proportion of presences correctly predicted, and the specificity the proportion of absences correctly predicted (Barbet-Massin et al. 2012). TSS values range

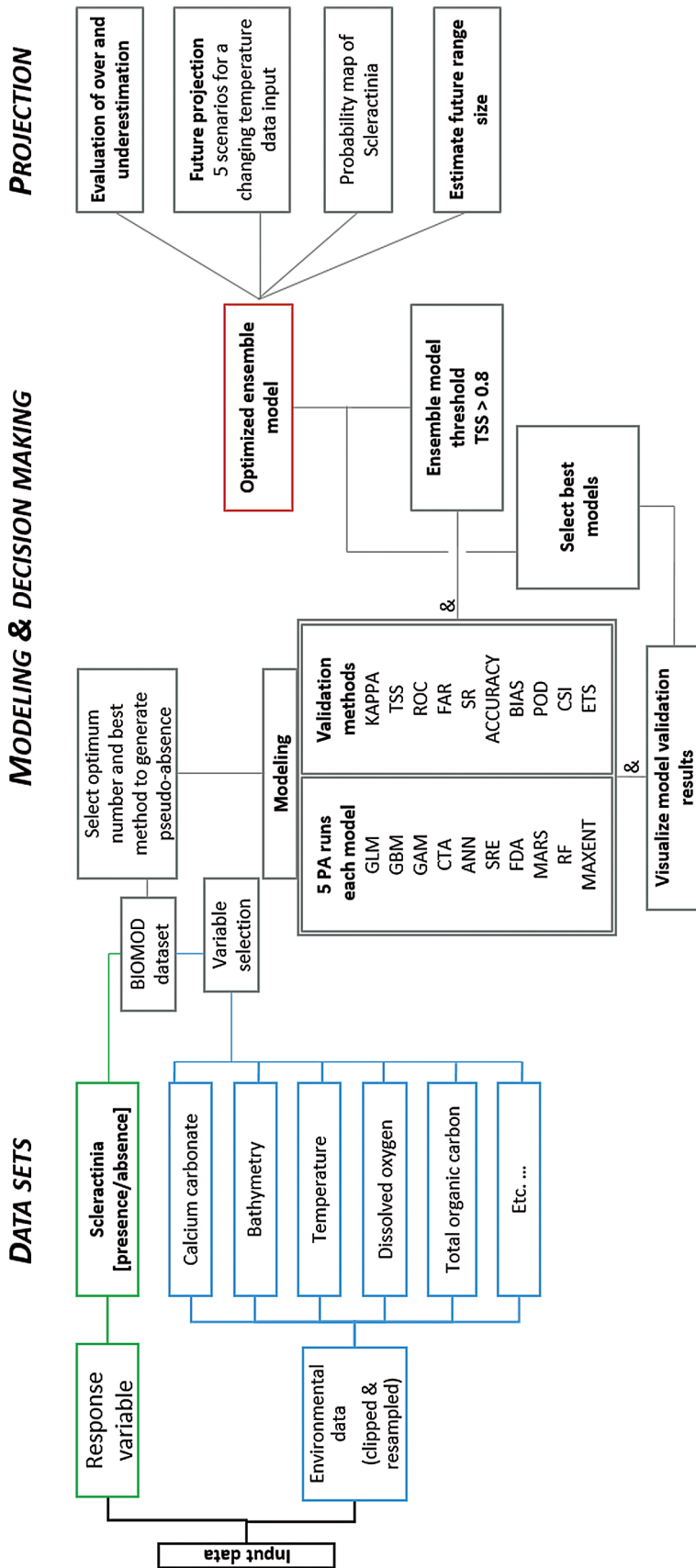


Fig. 2. Workflow diagram. The figure summarizes the steps used to prepare the input data, the species modelling procedure, and the generated outputs. Abbreviations of the model algorithms are explained in Section 2.3. Evaluation methods: ROC: relative operating characteristic, KAPPA: Cohen's Kappa (Heidke skill score), TSS: true skill statistic (Hanssen and Kuipers discriminant, Peirce's skill score), FAR: false alarm ratio, SR: success ratio, ACCURACY: accuracy (fraction correct), BIAS: bias score (frequency bias), POD: probability of detection (hit rate), CSI: critical success index (threat score), ETS: equitable threat score (Gilbert skill score)

from -1 (poor performance) to +1, indicating a perfect agreement between the observed and expected distributions. Generally, a TSS value of ≥ 0.7 corresponds to good or very good performance (Thuiller et al. 2009b). The area under the ROC curve (AUC) is a threshold-independent accuracy index that ranges from 0 to 1 (1: highly accurate prediction, 0.5: prediction no better than random). According to Pearce & Ferrier (2000), ROC rates > 0.9 indicate a very good performance because the sensitivity rate is high, relative to the false positive rate. Pooling the most accurate single models to a meta-model (ensemble model, EM) improves the reliability and accuracy of individual SDMs and overcomes some of their modelling limitations (Breiner et al. 2015). Therefore, only the individual models that complied an evaluation threshold of $TSS \geq 0.8$ (Thuiller et al. 2009a) were combined to a mean EM. The results of the EM were compared to the best models (highest TSS) projected by the MAXENT and RF methods, to discern the differences between the consensus model and a widely used SDMs to predict CWC distribution. The results of the worst-performing SDM (SRE) were also examined.

Simulations of the bottom temperature in the Weddell Sea and the Antarctic Peninsula, generated by the global multiresolution Finite Element Sea Ice–Ocean Model (FESOM) (Wang et al. 2014) were used for the approximation of future climate in the study area. These simulations cover the A1B scenario suggested in the IPCC Fourth Assessment Report (AR4) (Pachauri & Reisinger 2007) and are forced with the atmospheric output from the global climate projections by the Hadley Centre Climate Model (HadCM3). For more details, refer to Timmermann &

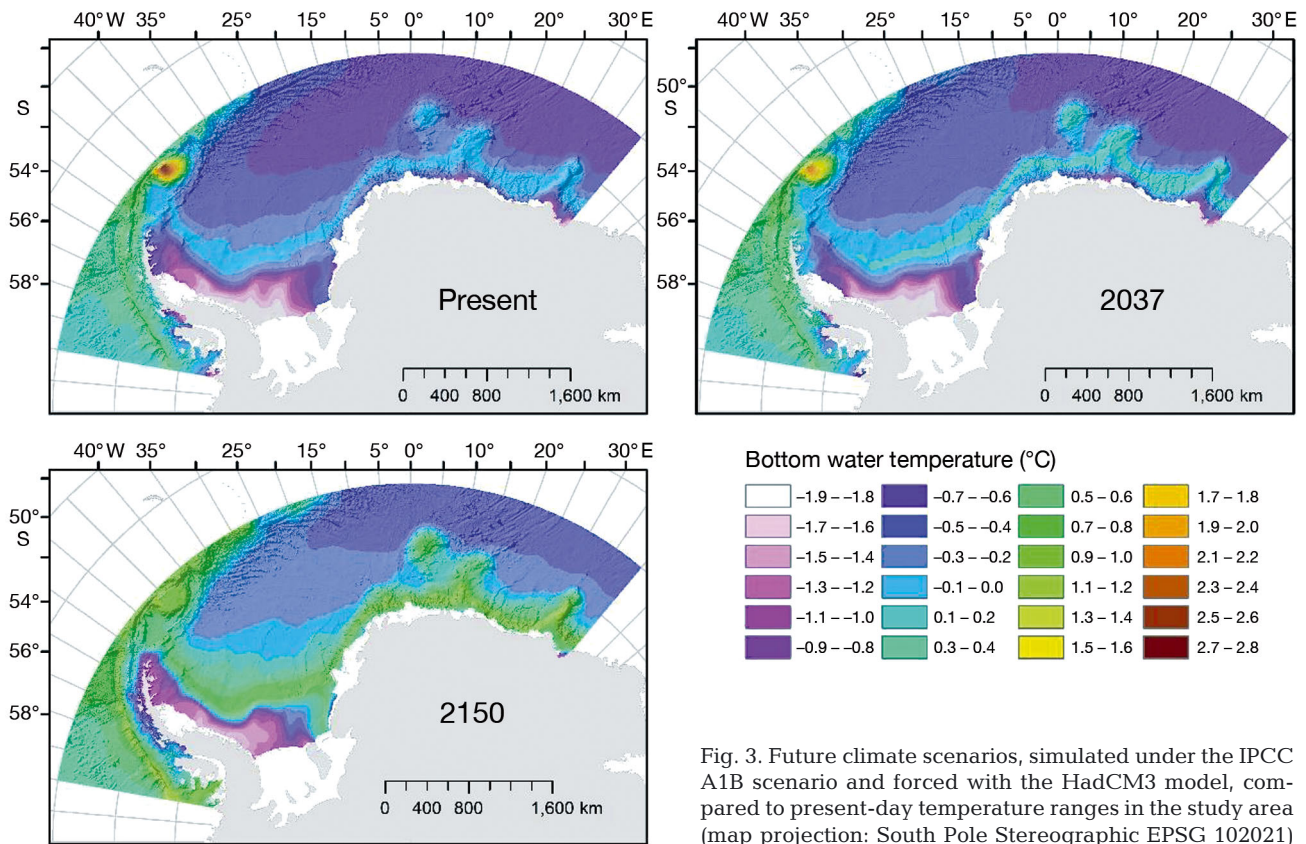


Fig. 3. Future climate scenarios, simulated under the IPCC A1B scenario and forced with the HadCM3 model, compared to present-day temperature ranges in the study area (map projection: South Pole Stereographic EPSG 102021)

Hellmer (2013). According to these scenarios, an overall warming is expected for the Weddell Sea that will become more important during the 22nd century (Fig. 3). This trend would especially affect the Filchner Trough and the area off Filchner and Ronne Ice Shelf. The warming in the bottom water would amount to 2.5°C by 2150, compared to the present conditions. Further trends projected by the model indicate the bottom water temperature around South Orkney Islands to decrease by 1 to 2°C or more by 2037 (Fig. 3). This cooling is predicted to persist, and a decrease from a maximum of ~4°C in the present scenario to a maximum of 1.4°C of bottom water is projected for 2150. Similarly, a cooling by ≤1°C is predicted to affect the coasts and the ice shelf areas off Coats Land and Queen Maud Land and around the Antarctic Peninsula. This does not apply to the Larsen C Ice Shelf in the east of the Peninsula, where a warming (from ca. -0.8 to 0.2°C) is projected for 2037. Interestingly, the north-eastern side of the Antarctic Peninsula is also predicted to cool down by 2150 after a minor warming phase around 2037 (Fig. 3).

Each model scoring the evaluation threshold (TSS ≥ 0.8) was projected applying the same model prop-

erties and the same predictor set of environmental variables as under current conditions, but with future regional FESOM temperature values predicted for the years 2037 and 2150, separately. These additional individual SDMs were averaged to 2 future scleractinian distribution EMs for the study area.

The relative size of scleractinian habitat loss, gain, and stability for the time slice considered in species-climate modelling under future scenarios was estimated using the range size function of the package biomod2 (Thuiller et al. 2016). Therein, net range size change is calculated as the difference between the percentage of pixels 'gain' (PercGain) and the percentage of pixels 'loss' (PercLoss). Consequently, a pixel could have 4 different values: -2 (lost area for the scleractinian species), -1 (no effect on the habitat, CWC occurrence predicted for the presence and the future), 0 (no CWC occurrence; neither predicted for the present nor for the future), and 1, habitat gain; the given location was not occupied in the present but is predicted to be CWC habitat in the future (Thuiller et al. 2016). The comparison was applied to the study area, pixel by pixel, on the EM's mean distribution under current conditions and the EM's mean distribution of each future scenario.

3. RESULTS

3.1. Environmental variables selection

Based on the stepwise selection process and expert recommendations, a final set of 14 candidate variables (Table 1) was kept for model-building. Further reduction of the number of variables might be possible, but we focused on eliminating those which are not relevant, are perfectly correlated, truly redundant or ranked as the least important (see Figs. S5–S7 and Tables S1–S5). We kept a variety of predictors that cover different aspects of the study area's environment to investigate their possible connection to the distribution of scleractinians.

3.2. Model parameters

With a number of pseudo-absences equal to 10 000, the models reach higher ROC and TSS for all the SDMs (Fig. S8) and thus a better quality. Using 10000 pseudo-absences per replicate, the number of replicates did not affect the model quality (Fig. S9). Pseudo-absences selected with a geographical distance exclusion (2 km minimum distance) yielded predictions with higher sensitivity and specificity (Fig. S10) for most of the SDMs. Therefore, 10 000 pseudo-absences generated with 2 km circular distance buffer and 2 replicates were considered to build the final model. The variables importance for the EM, estimated by 3 evaluation runs, determined the model input parameters.

3.3. Model evaluation

Most individual SDMs had high mean TSS values > 0.70 and ROC values > 0.90 (Fig. 4), indicating good to excellent model performance. While RF (TSS: 0.86–0.89 and ROC: 0.969–0.972) and GBM (TSS: 0.86–0.89 and ROC: 0.969–0.972) scored the best evaluation results, the SRE algorithm had the lowest mean predictive accuracy (Fig. 4) and the worst fit with the data (TSS: 0.51–0.58 and ROC: 0.76–0.79). Globally, the results of the EM are comparable to the current distribution projected by MAXENT and RF (Fig. 5). However, minor differences are observed. For instance, MAXENT projected a slightly lower probability of occurrence of CWC in the western side of the Antarctic Peninsula. Moreover, unlike the EM, which did not show any possible presences off Ronne Ice Shelf, MAXENT predicted a low probability of occurrence (~20%) in this area (Fig. 5). The RF method projected the same hotspots of CWC but lower probabilities of occurrence, compared to the EM. The SRE method, which performed the worst, showed relatively expanded areas of high probabilities of presence (100%), compared to the other SDMs, and assigned zero occurrence to the rest of the study area (Fig. 5).

From the 60 initial models, 29 scored higher TSS than the chosen threshold (TSS = 0.8) and were retained to build the EM (Fig. 4). Five of each 6 models of the algorithm RF and GBM were included. FDA and MAXENT were over the threshold with 4 runs each, while GAM and

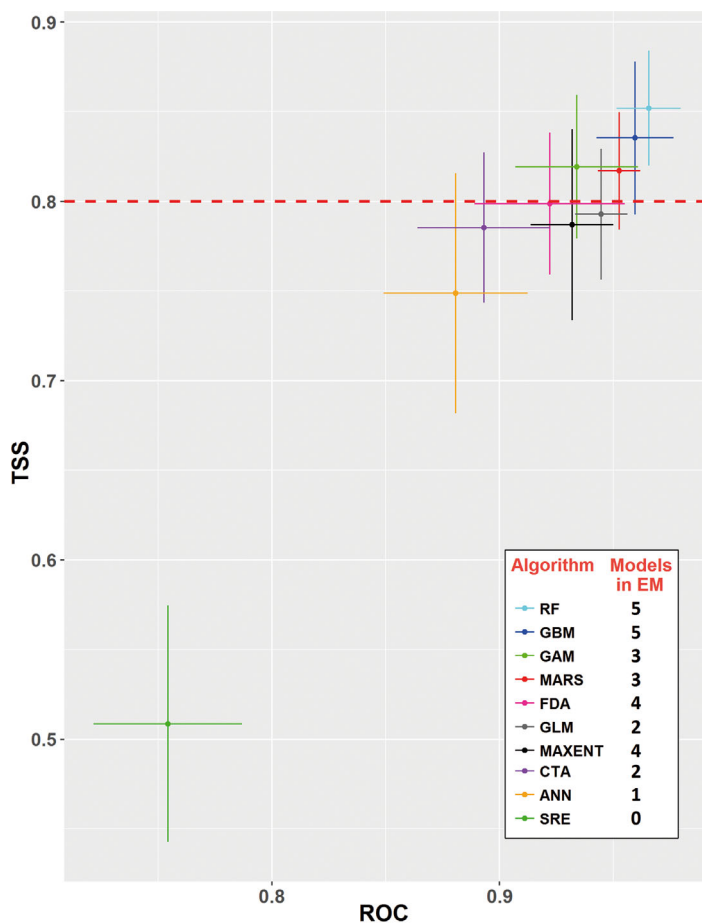


Fig. 4. Mean evaluation scores (receiver operation characteristic, ROC, and true skill statistic, TSS) of the different species distribution models (SDMs) ordered by algorithm. See Section 2.3 for model abbreviations. Points represent the average score and lines the standard deviation of the evaluation scores across each model's runs. The dashed red line represents the chosen TSS threshold to include models in the ensemble model (EM). The number of runs from each SDM that scored the threshold and have been included in the EM are indicated in the legend

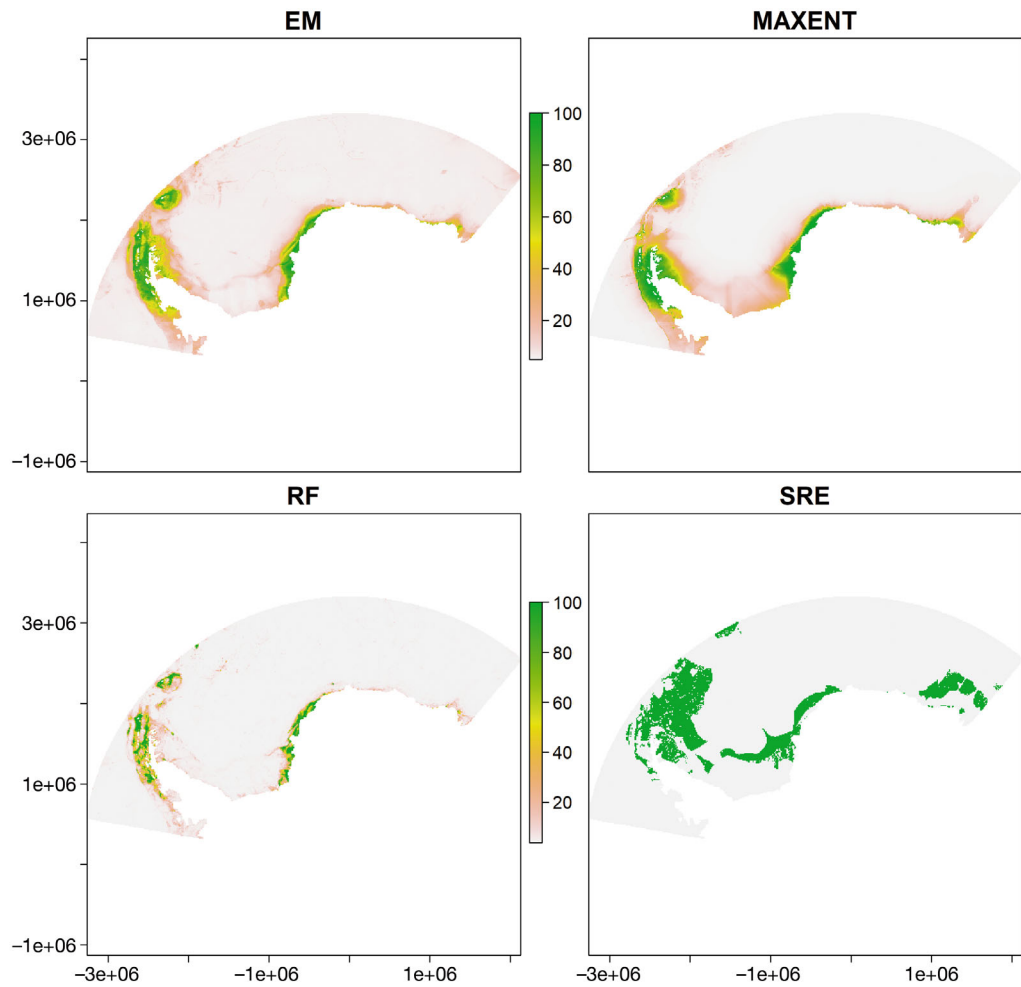


Fig. 5. Comparison of the ensemble model (EM) with the best run (10 runs in total) of each algorithm: MAXENT, random forest (RF) and surface range envelope (SRE). The maps represent the probability (in %) of occurrence of scleractinians projected for the study area by each algorithm under present environmental conditions

MARS participated with 3 models each. Two runs of CTA and GLM satisfied the chosen threshold and were added to the EM set. Furthermore, only 1 ANN model was kept, and no SRE runs were included (Fig. 4).

Overall, the mean EM scored better evaluation results than the median probabilities and was chosen for the analysis. For instance, TSS and ROC scores of the mean EM were slightly higher than those of the median EM (Table 2). While the sensitivity for the mean EM was more important, the median EM performed better when predicting absences (specificity).

3.4. Present distribution of CWC

The distribution map (Fig. 6) shows that the occurrence of CWC is largely limited to the areas around the continental margins and ice shelves. The most important aggregate of presence data is observed around the Antarctic Peninsula and Larsen C Ice Shelf between 70° and 60° S. Another potential hot-

spot for CWCs is the area around South Orkney Islands. In contrast to the Ronne Ice Shelf where very low occurrence probability was projected, scleractinians were present all along the Antarctic coasts between the Filchner and Jelbart Ice Shelves from west to east, respectively. Towards the east, the distribution range appears to shrink and becomes even more restricted, due to the continental margin (Fig. 6). Decreasing probability from the continental shelf to the offshore regions is projected, which

Table 2. Evaluation scores of the ensemble model; EM (TSS and ROC) and the corresponding sensitivity and specificity. The sensitivity is the proportion of presences correctly predicted, while the specificity is the proportion of absences correctly predicted

	TSS	ROC	Sensitivity	Specificity
EM_mean	0.91	0.99	97.934	93.087
EM_median	0.905	0.987	96.281	94.245

allows both a latitudinal and longitudinal distribution pattern to be distinguished. For instance, the highest probabilities of occurrence (>80%) are seen between the coast and 70°S around Coats Land and Queen Maud Land. Beyond 70°S (70° to 60°S), the presences of CWCs are limited to the Antarctic Peninsula and South Orkney Islands. The area between 35°W to 40°E and 70°S to 60°S is characterized by very scarce to zero presence of CWC species (Fig. 6).

3.5. Habitat suitability

The scleractinians' environment is mainly defined by the distance to coast or ice shelves (importance ≈ 0.33), the concentration of benthic calcium carbonate (importance ≈ 0.32) followed by the temperature (importance ≈ 0.16), and the bathymetry (importance ≈ 0.14) (Fig. 7). Temperature was ranked as the third

most important covariate, which makes it a good candidate to estimate potential changes in the distribution due to warmer future climate conditions. Interestingly, Thorium flux (importance ≈ 0.12) is 1 of the 5 most important habitat predictors for CWC presence (Fig. 7). In contrast, slope, current speed, quartz concentration, and total organic carbon (TOC) input were least relevant for CWC presence/absence (Fig. 7).

The ranges of variability of the different environmental parameters defining the occurrence of scleractinians are summarized in Table 3. By intersecting only the presences of CWCs and the environmental variables, the constructed Bean plots (Fig. 8) and the EM response curves (Fig. 9) revealed different species–environment relationships. The species were restricted to depths shallower than 1500 m (Table 3, Figs. 8 & 9). However, some records (17%), mainly associated with *Fungiacyathus marenzelleri* and *Leptopenus antarcticus*, were found much deeper

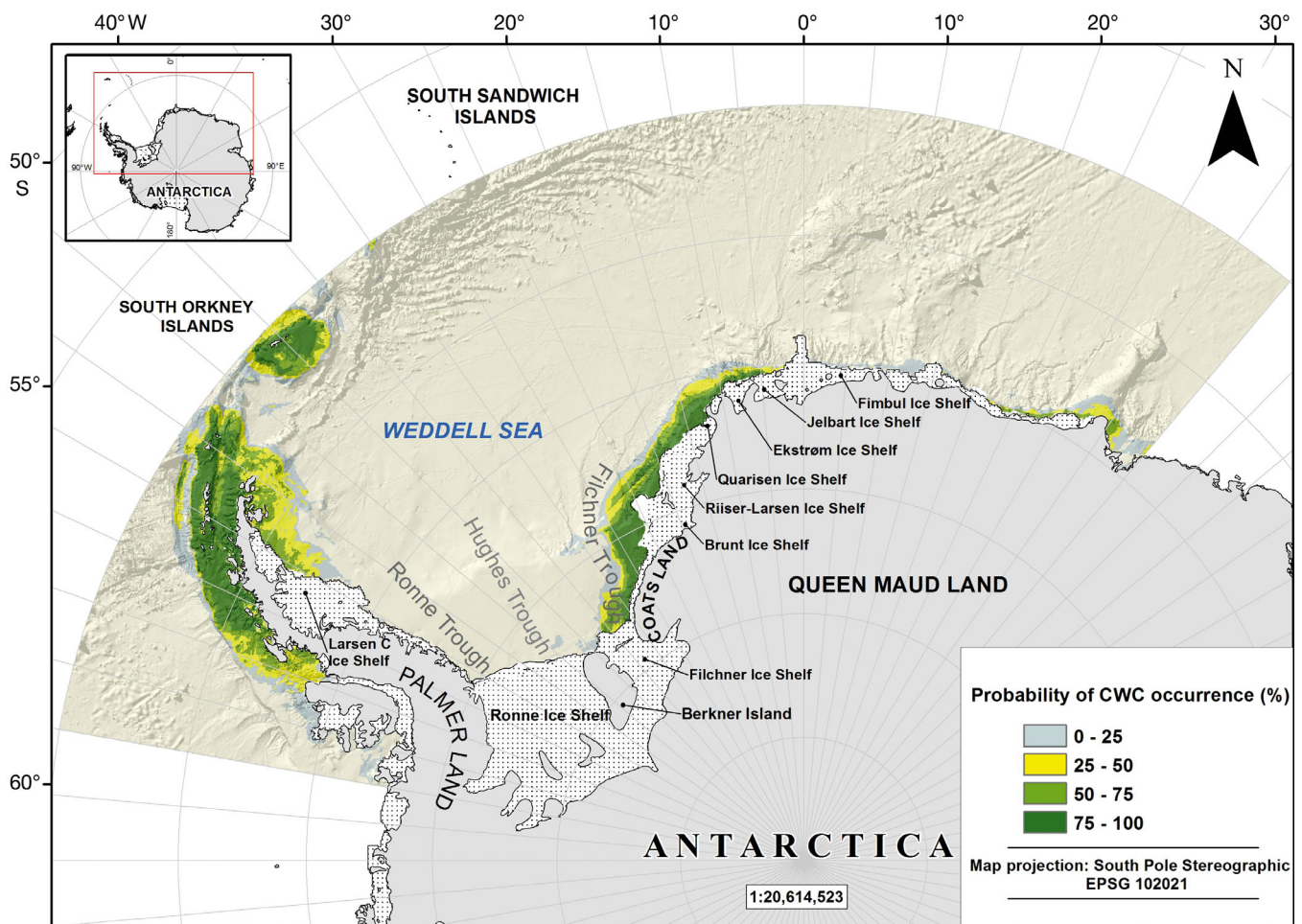


Fig. 6. Probability of occurrence (%) of cold-water corals (CWCs) under present conditions. The distribution map is derived from the ensemble model projection under current environmental conditions

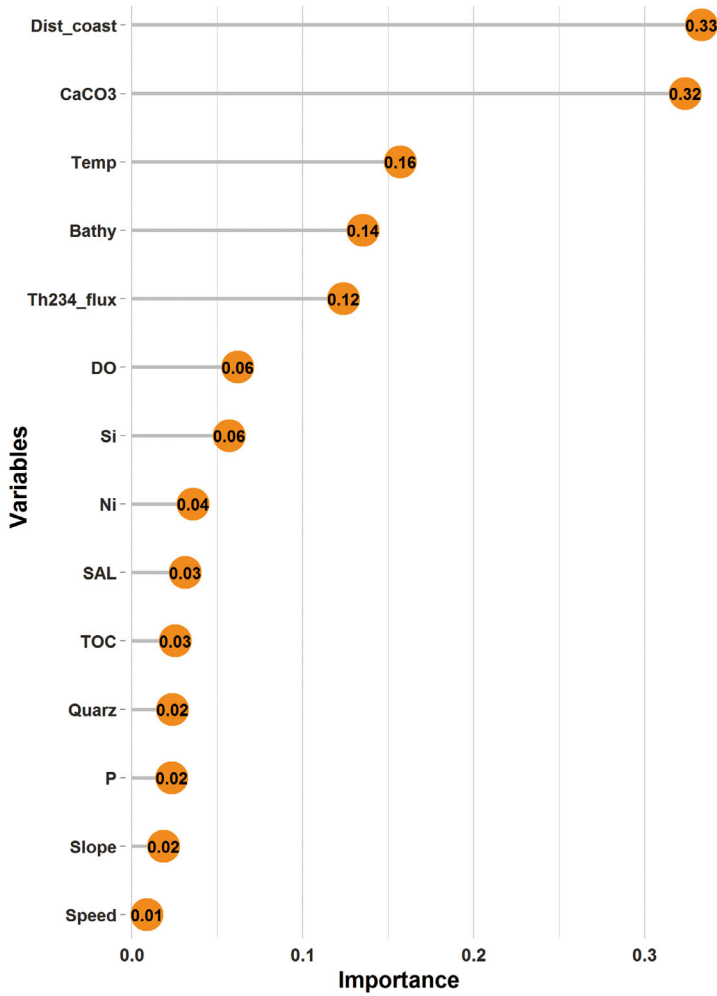


Fig. 7. Variable importance of the different environmental covariates derived from the ensemble model. Abbreviations are explained in Table 1

CaCO₃ content is associated with the presence of CWC in the Western Weddell Sea compared to the Western Antarctic Peninsula.

The species follow an optimum curve for the mean temperature with high probabilities in areas where values are between 0°C and 3.5 °C (Table 3, Figs. 8 & 9).

3.6. Future distribution of CWCs

Under the FESOM simulations (IPCC, A1B), the probability of distribution would remain close to the present-day conditions by 2037, with a slight decrease around South Orkney Islands and the east of Antarctica (Fig. 10). The geographical range of probabilities higher than 25 % is expected to expand off Ekstrom, Quarisen, Riiser-Larsen and Filchner Ice Shelves, from east to west. Even higher probabilities (50–75 %) were simulated for 2037 near Filchner Trough, potentially linked to the warming observed around Filchner Trough and Ronne-Filchner Ice Shelf. No important changes are predicted for the Antarctic Peninsula by 2037, except for an increase (from 50–75 % to 75–100 %) in the

(Fig. S11). The broad benthic positioning index (BPI_broad) corresponding to these deep records exhibited negative values, contrary to most of the other presences (Fig. S12).

As observed in the distribution map, high probability of presence is linked to continental areas and ice shelves where the distance to the coast is <100 km. A probability of occurrence higher than 50 % corresponds to a concentration of benthic CaCO₃ in the water lower than 10 % (Figs. 8 & 9). It is worth mentioning that this variable is correlated with the distance to coast and ice shelves (Fig. S5). Further investigation of the data allowed to distinguish between the Western Antarctic Peninsula and the Western Weddell Sea in terms of benthic CaCO₃ content. For instance, lower

Table 3. Summary of the descriptive statistics of the different variables corresponding to areas where cold-water corals were present and the relative optimal ranges of highest occurrence's probability projected by the ensemble model. For variable abbreviations, please refer to Table 1

Variable	Min.	Mean	Max.	Optimal range
Bathy (m)	101.4	619.9	5123.9	<1500
CaCO ₃ (%)	0.9604	5.2226	14.4613	1–2.5
DO (ml l ⁻¹)	4.508	5.308	7.092	5–5.5
Dist_coast (km)	0	65384	672512	<100
Ni (µmol l ⁻¹)	28.5	32.92	34.22	32–34
P (µmol l ⁻¹)	2.177	2.263	2.382	2.2–2.25
Quarz (wt %)	5.117	24.025	376.337	5–10
SAL (PSU)	34.12	34.6	34.71	34.4–34.7
Si (µmol l ⁻¹)	72.84	120.12	140.91	100–130
Slope (°)	0.06748	2.29645	12.32066	0–2
Speed (m s ⁻¹)	0	0.009477	0.110498	0.1
Temp (°C)	-1.754525	0.704228	3.564883	0–3.5
TOC (wt%)	0.2076	0.3415	0.574	0.2–0.3
Th234_flux (dpm m ⁻² d ⁻¹)	292.8	1083.1	1660.8	1200–1600

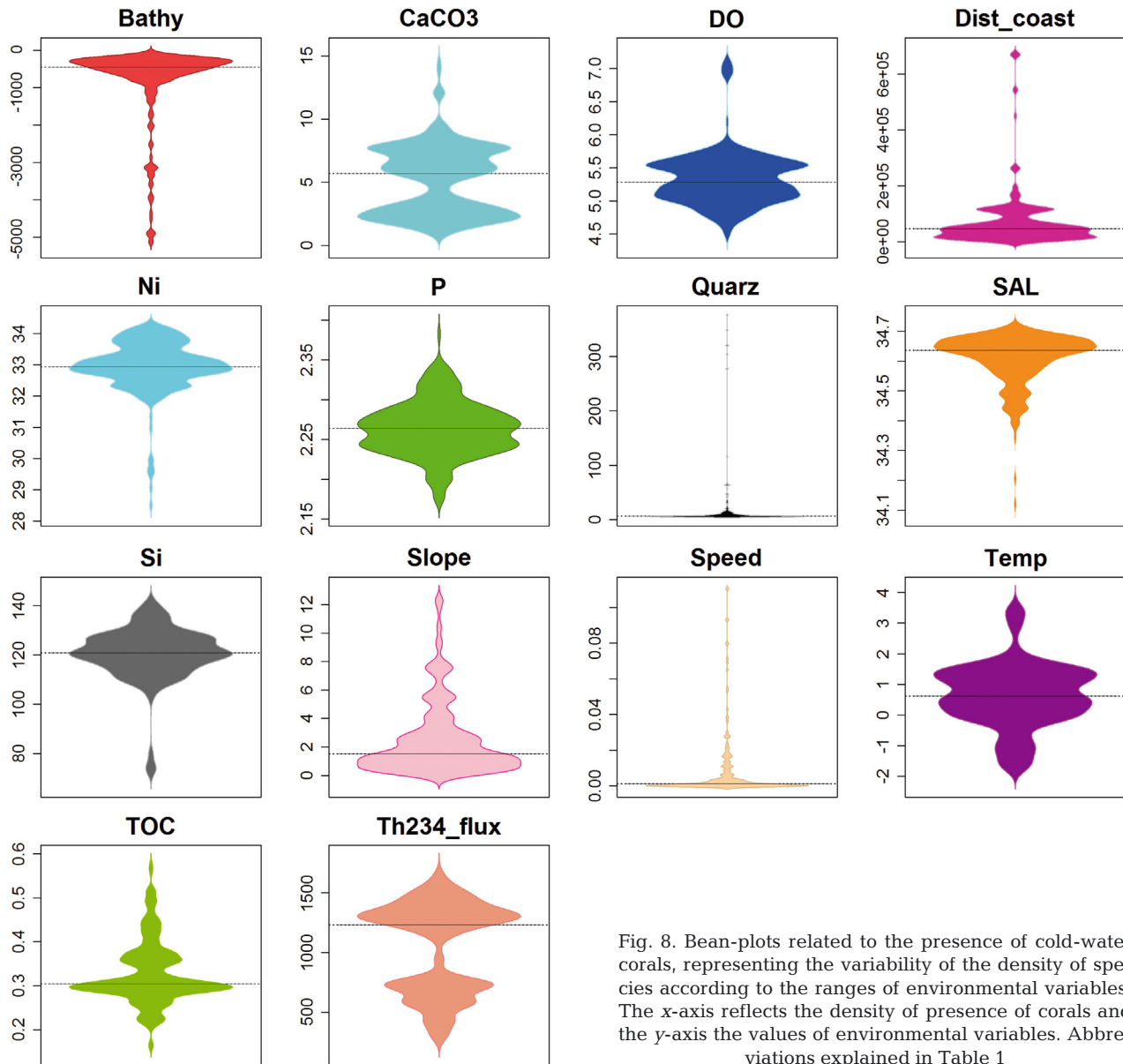


Fig. 8. Bean-plots related to the presence of cold-water corals, representing the variability of the density of species according to the ranges of environmental variables. The x-axis reflects the density of presence of corals and the y-axis the values of environmental variables. Abbreviations explained in Table 1

Table 4. Estimate of the proportion and relative number of pixels (or habitat) lost, gained, and stable for the time slice considered in species-climate modelling under future scenarios. The column 'Loss' refers to the number of lost pixels compared to the present conditions; 'Stable0' is the number of pixels in the study area which are not currently occupied by the given species and not predicted to be; 'Stable1' represents the number of pixels currently occupied by the given species and predicted to remain occupied into the future; 'Gain' is the number of gained pixels compared to the present distribution; 'PercLoss' and 'PercGain' correspond to the percentage of currently occupied sites to be lost and the new sites to be occupied, respectively; 'Current RangeSize' is the total number of occupied pixels in the present; and 'Species RangeChange' is equal to $\text{PercGain} - \text{PercLoss}$

Scenario	Loss	Stable0	Stable1	Gain	PercLoss	PercGain	Species RangeChange	Current RangeSize
2037	2848	497093	36274	2572	7.28	6.574	-0.705	39122
2150	3311	495576	35811	4089	8.463	10.452	1.989	39122

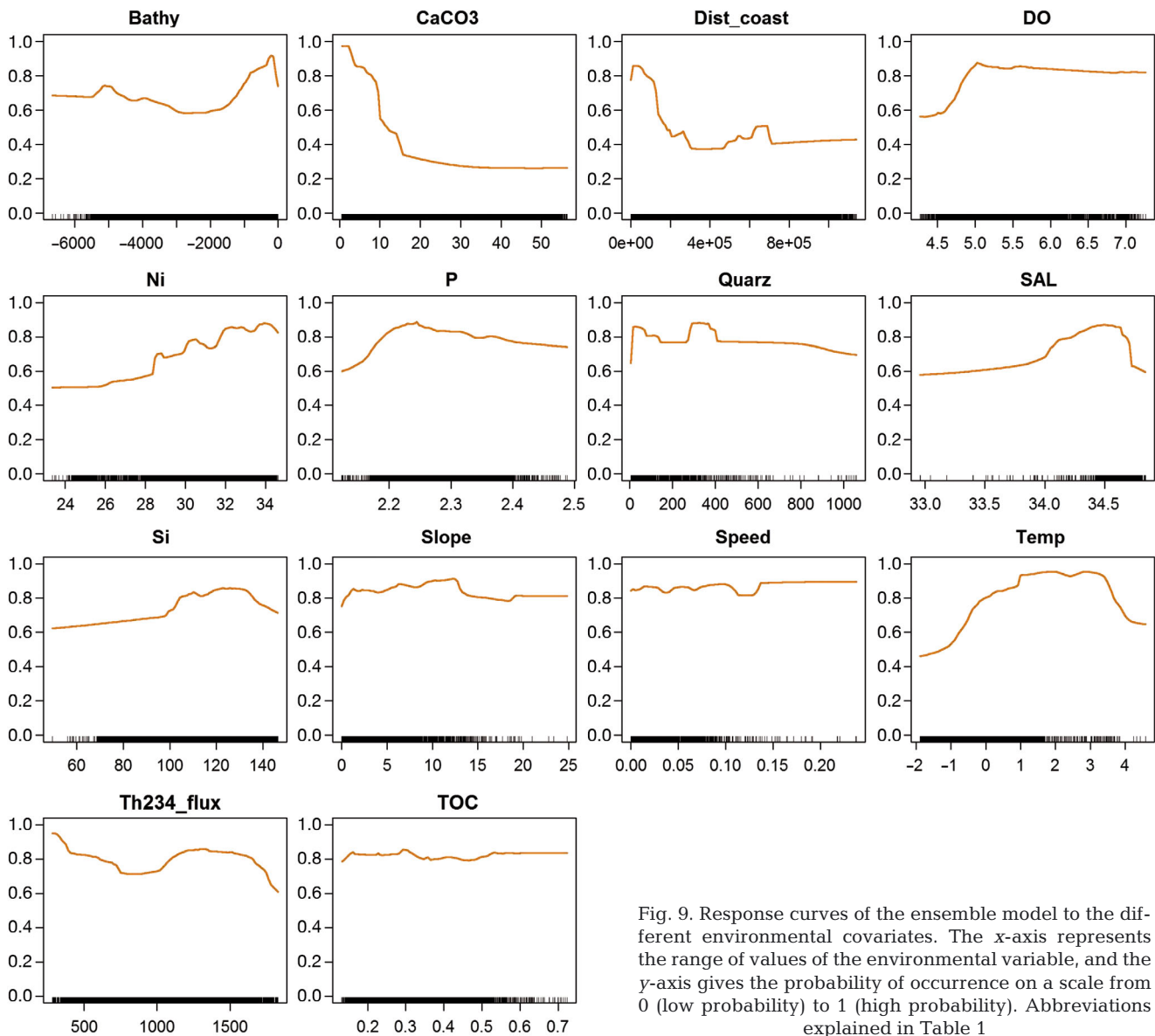


Fig. 9. Response curves of the ensemble model to the different environmental covariates. The x-axis represents the range of values of the environmental variable, and the y-axis gives the probability of occurrence on a scale from 0 (low probability) to 1 (high probability). Abbreviations explained in Table 1

probability of occurrence of the species near Larsen C Ice Shelf in the north-east. In contrast, under the 2150 scenario, most of the areas around the Peninsula are faced with declining occurrence probabilities (Fig. 10). In contrast, the geographical range of distribution will continue to grow off Coats Land and around the Filchner Trough in 2150. This predicted expansion is associated with an increase of the areas with probability between 50 and 75% (Fig. 10). Moreover, little extension of the locations characterized by a probability of presence between 25 and 50% is expected off Larsen C Ice Shelf.

As observed in the forecasted probability maps (Fig. 10), the changes of distribution under the 2037

scenario are minor (~0.7%). For instance, the lost space (7.28%) mainly around South Orkney Islands and east of Antarctica (Table 4, Fig. 11) would be compensated by the gained distribution (~6.6%) around Filchner Trough and the Larsen C Ice Shelf (Table 4, Fig. 11). However, under the 2150 scenario, the gain in area of distribution is predicted to be higher than the loss, and thus, an overall increase of the distribution range by ~2% is possible (Table 4). This expansion is predicted for the regions around Filchner Trough and Coats Land (Fig. 11).

The raster data compilation of input data and results are available in PANGAEA (doi:10.1594/PANGAEA.895586).

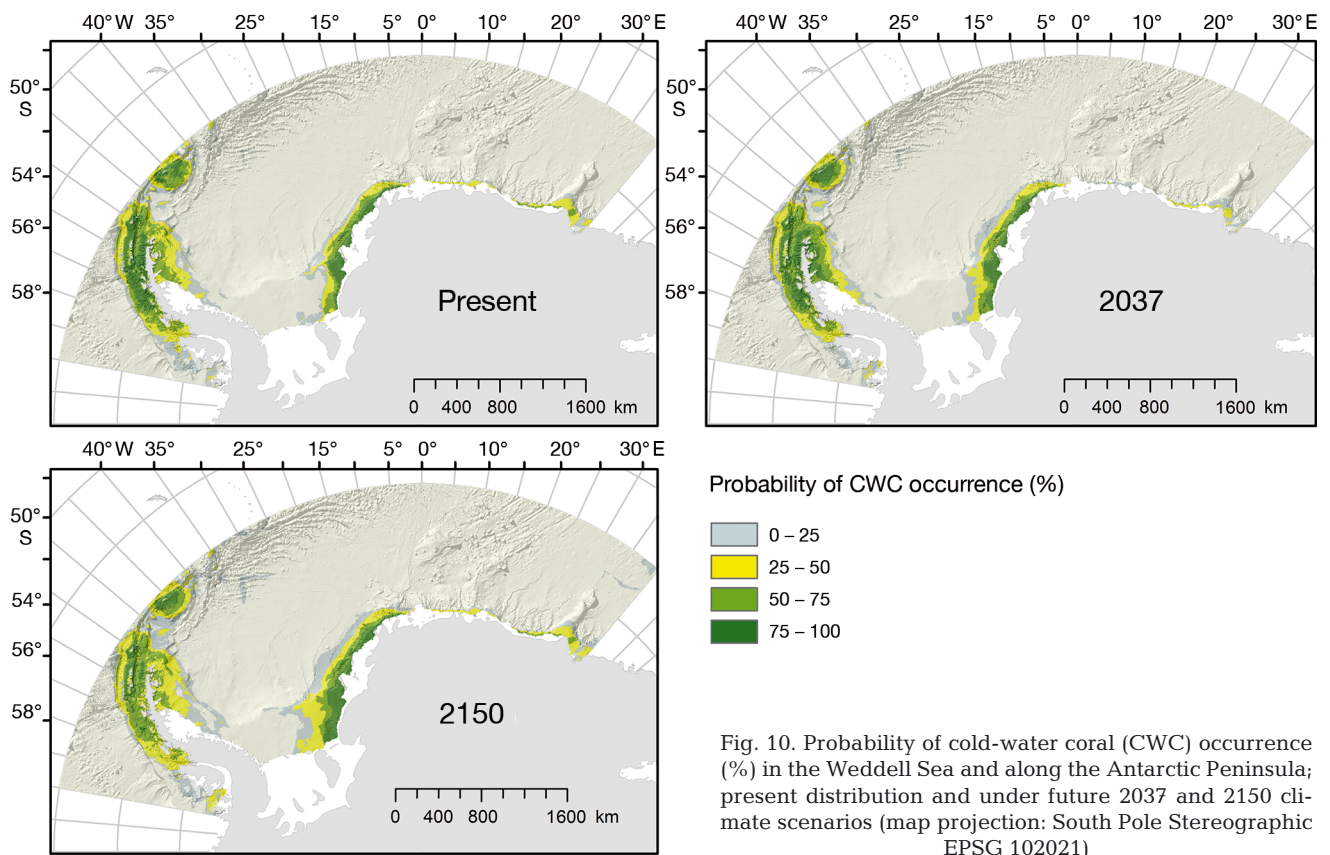


Fig. 10. Probability of cold-water coral (CWC) occurrence (%) in the Weddell Sea and along the Antarctic Peninsula; present distribution and under future 2037 and 2150 climate scenarios (map projection: South Pole Stereographic EPSG 102021)

4. DISCUSSION

This is the first study disentangling the environmental factors that determine the distribution of CWCs in the Antarctic region. SDMs were used to determine the habitat range of those species in the North Antarctic region (Weddell Sea and Antarctic Peninsula). A pre-selection of relevant environmental variables and modelling parameters was achieved, and the species tolerances regarding these variables were studied statistically. A potential future habitat shift due to climate change was projected and will be discussed.

An exhaustive search for an optimal variable subset based on a given machine-learning algorithm is

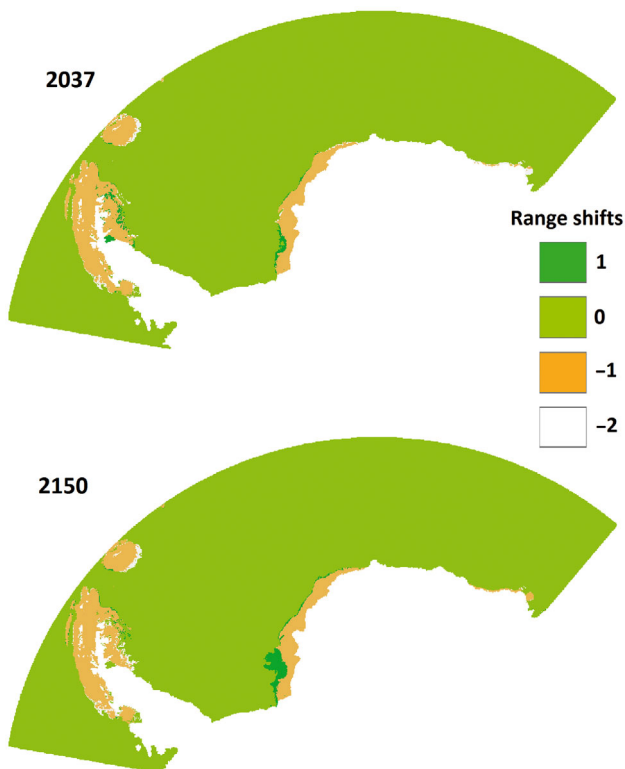


Fig. 11. Estimated changes in the range size of cold-water coral distribution under the future warm climate scenarios. For each scenario, a pixel could have 4 different values (color scale): -2 if the given pixel is predicted to be lost by the species, -1 if the given pixel is predicted to be available for the species both in the present and in the future, 0 if the given pixel was not occupied and will not be in the future, 1 if the given pixel was not occupied and is predicted to be into the future

impossible in most cases (Murray & Conner 2009, Aho et al. 2014, Jović et al. 2015). The applied step-wise strategy for variable selection showed a beneficial synergy between methods and was useful to reduce model complexity, even for this purely predictive study. The incorporation of false species absences and very low numbers of presence records may increase uncertainties (Guisan & Thuiller 2005). This highlights the importance of a good selection of the number of pseudo-absences and the method to generate them, before modelling.

The model evaluation results support the idea that there is no universal 'best' modelling technique that can be used in ecology. These results are in agreement with other studies on terrestrial and marine systems. For instance, the RF and GBM algorithms were used in several other studies because of their performance and good predictive accuracy relative to other model types (Cutler et al. 2007, Reiss et al. 2011, Vorsino et al. 2014, Mi et al. 2017). Moreover, GAM, GLM, MAXENT, FDA, and MARS also perform well (Araújo et al. 2005, Elith et al. 2006, Kharouba et al. 2009, Reiss et al. 2011). Similarly to this study, Elith et al. (2006) and Reiss et al. (2011) found that the SRE method performed poorly compared to the other SDM techniques.

Unlike other works, which focused on regression algorithms while modelling the marine environment (Venables & Dichmont 2004, Chatfield et al. 2010, Gogina et al. 2010), this study demonstrates that machine-learning and classification techniques are also successful in predicting species distribution.

The consensus methods or ensemble modelling were usually used (Marmion et al. 2009, Thuiller et al. 2009b, Vorsino et al. 2014) to reduce the inconsistencies between different SDMs. Likewise, in this study, the EM based on average function algorithms increased the accuracy, compared to the individual species distribution forecasts, to a TSS equal to 0.91. This recommended method (Buisson et al. 2010) has some advantages compared to single models. For instance, EMs can be more realistic, because choosing the model with the highest accuracy does not necessarily mean that it will provide the most realistic simulations of the species distribution in a new area or under future climate conditions (Thuiller et al. 2009b). Also, using an approach based on combined algorithms helps to summarize the agreements among projections generated by individual models (Marmion et al. 2009).

Common uncertainties associated with global models may affect the analysis. Although we tried to use the most relevant variables for the analysed taxa,

there are other factors such as large-scale historical constraints and biotic interactions that are known to affect species distributions (Beale & Lennon 2012, Chefaoui & Serrão 2017) and are difficult to take into account. Also, sampling difficulties in the Antarctic region due to ice conditions can prevent access to deeper regions (e.g. trawl hauls deeper than 1500 m accounted only for 3% of the total samplings). Thus, some locations may show low habitat suitability despite being able to host populations. This effect might be related to sampling, which may produce inaccurate estimations in the niche and derived distributions (Hortal et al. 2008).

The results predict that the present areas of highest probability of scleractinians occurrence are around the Antarctic Peninsula, South Orkney Islands and Queen Maud Land coast. Because the occurrence data were limited to these areas, an independent field survey is necessary to check the model beyond these locations.

The concentrations of Si in the areas occupied by CWCs (73 to 141 $\mu\text{mol l}^{-1}$) can be a proxy of food availability. Keller et al. (2007) examined the skeleton composition of scleractinians and explained the presence of Si by a possible food source based on radiolarians with siliceous skeletons.

Distance to coast and ice shelves, benthic CaCO_3 concentrations, temperature and bathymetry accounted for the highest contributions to scleractinian habitat predictions. Scleractinian CWC presence was linked to the continental shelf and slope, restricted to depths shallower than 1500 m. The BPI values suggest that CWCs most likely inhabit tall seamounts and peaks or ridges. However, some species (genus *Fungiacyathus* and *Leptopenus*) were also recorded in areas that are trenches or depressions. Both kinds of habitats were indicated as favourable by some authors (Genin et al. 1986, Dolan et al. 2008, Cordes et al. 2016, Keller et al. 2017). Keller et al. (2017) justified this variability in the terrain characteristics of the scleractinians' habitat by the food availability, which is controlled by lateral currents. They also demonstrated the presence of CWCs in trenches and topographic depressions serving as food traps.

Current speed and TOC were expected to be among the important variables as CWCs are filter feeders, dependent on organic matter falling from the surface or via advective currents (Kiriakoulakis et al. 2005, Cordes et al. 2016). However, the distribution of CWCs was only mildly affected by these 2 covariates. In general, polar marine species are stenothermal and, with some exceptions, adaptation to their environment includes lower growth rates and

metabolism compared to their non-polar relatives (Peck 2002). Experimental studies on solitary scleractinian CWCs have showed a low metabolic rate, and thus low nutritional requirements, of those species in comparison with tropical reef-building corals (Henry & Torres 2013). In this sense, we can relate the relatively low concentrations of P and nitrate encountered in the study to this hypothesis.

According to Keller et al. (2017), asymmetry and irregularities in the distribution of CWCs in the Weddell Sea are related to physical barriers or to food availability in response to current circulations. They further evidence that the distribution pattern of Scleractinia depends on larval dispersal and ocean productivity formed by the deep part of the conveyor belt. The Warm Deep Water (WDW) is the warmest water mass in the Weddell Sea, characterized by a temperature above 0°C and salinity between 34.64 and 34.72 PSU (Foster & Carmack 1976). Such properties are optimal for scleractinians, as inferred from this study. WDW is generally found at depths between 150 and 1500 m (Fahrbach et al. 2004). Hence, the distribution pattern of species might follow WDW circulation.

The majority of coral records were found in areas where the benthic CaCO₃ falls below 10%. Scleractinian coral skeletons are mainly made of calcium carbonate in the form of aragonite (Goffredo et al. 2011). Though calcification is a complex process, precipitation of aragonite in corals is mainly controlled by the intra-skeletal organic matrix rather than surface ocean pH or calcium carbonate in seawater (Falini et al. 2015). Moreover, it has been demonstrated that an excess of Ca decelerates the growth of CWCs (Keller et al. 2007), which can explain their preferences for an optimal range of CaCO₃ concentrations. The low optimal ranges of benthic CaCO₃ for scleractinians are, hence, mainly related to their distribution pattern. For instance, scleractinians are more abundant, in the western Weddell Sea, near the continental shelf. In this area, high CaCO₃ concentrations are only found on the outer shelf, due to the presence of calcareous foraminifera, and only low content of sedimentary CaCO₃ can be found near the continental shelf (Hauck et al. 2011, 2012). In the Western Antarctic Peninsula, the CaCO₃ can have both a sedimentary and macrozoobenthic origin in some places (Hauck et al. 2012), which may explain its slightly higher content. The low benthic CaCO₃ concentration maybe also a proxy of the type of substrate inhabited by CWC, which does not necessarily consist only of hard material. In the same time, it appears also that soft bottoms and high sediment

loads are not suitable for scleractinians. This is reflected by their preference for areas with quartz content between 5 and 10 wt%, as has been found in this study. To summarize, the results of the benthic CaCO₃ and quartz contents support the idea of the complexity of CWC substrates, which can be muddy/sandy with variable hard material proportions, as described by Cairns (2007) and Sentoku et al. (2018).

Thorium flux concentrations varied between 293 and 1661 dpm m⁻² d⁻¹. Thorium is highly reactive to organic and inorganic particles. Moreover, ²³²Th concentration can be used to quantitatively assess the fraction of lithogenic material in marine sediment (Martínez García et al. 2009). For instance, high concentrations of ²³²Th might imply that the supply of lithogenic material is dominated by changes in the eolian input of terrigenous material through time. However, the relative importance of the redistribution of lithogenic material of terrigenous origin, surface currents, and intermediate waters, which could eventually return to the surface by upwelling (Blain et al. 2007), is difficult to evaluate (Martínez-García et al. 2009). The ²³²Th depletion is also a result of export processes and phytoplankton development (van der Loeff et al. 2011). Thus, thorium could also reflect the high importance of abundance of plankton and food availability to scleractinians.

The results revealed the importance of temperature to define the geographical distribution of corals. This is consistent with previous studies that confirmed the positive influence of temperature on the calcification rate of CWCs (Gori et al. 2016 and references therein). However, long-term exposure to high temperatures may increase respiration of CWCs. This could lead to an increase of energy needs and, thus, food demand, to maintain cell homeostasis and optimal metabolism (Gori et al. 2016, Hanz et al. 2019). Consequently, shifts to a carbohydrate or lipid-based metabolism or a reduction of the calcification rate are possible, especially if the available food is not sufficient to compensate for the increase in energy demand (Gori et al. 2016).

Hellmer et al. (2012) forecast a high ice loss in the Filchner-Ronne Ice Shelf (80% of the present Antarctic surface mass balance), leading to a redirection of warmer coastal currents, previously separated by a slope front from the cold shelf water, southward towards the Filchner Ice Shelf front and the Filchner Trough, by the beginning of the 21st century. Under present climate, this area is the coldest in the Weddell Sea and corresponds to the lower limit of suitable bottom temperature for CWCs, as identified in this

study. Thus, predicted bottom water temperatures in this location would remain within the present optimum range of Weddell Sea scleractinians. This may explain the projected expansion of their geographical distribution by 6 to 10% near Filchner Trough and the adjacent continental shelves, despite the warming of water.

Nevertheless, CWC response to a further rise in bottom temperature can be different. By 2150, the fifth IPCC assessment report (AR5) projects the highest CO₂ partial pressures (pCO₂) under the Representative Concentration Pathways scenario RCP8.5 (pCO₂ between 1371 to 2900 μ atm). This rise of CO₂ concentrations in air would increase ocean acidification, which would probably lead to a 40% decrease of the known global distribution of CWCs. Several studies explained the possible effects of future climate variability on the metabolism and occurrences of CWCs, which are sensitive to warming waters because of their upper thermal limits (Cordes et al. 2016, Gori et al. 2016).

Carbonate saturation state in seawater is temperature-dependent and, hence, much lower in cold waters. CWCs are, therefore, known to occur close to the saturation horizon (Cordes et al. 2016). Evidence from Guinotte et al. (2006) indicates that the depth of the aragonite saturation horizon (ASH) may be a limiting factor in deep-water coral occurrence, because of the difficulty of extracting calcium carbonate to form skeletons, below the ASH. In the same context, Orr et al. (2005) simulated the effects of CO₂ release on the carbonate saturation state and showed that, under the IPCC 'business as usual' scenario (IS92a) where little is done to mitigate CO₂ emissions, the depth of the ASH would rapidly shoal in the 21st century. These findings were recently corroborated by Negrete-García et al. (2019), who projected a very fast decrease of the ASH in the Southern Ocean under the emission scenario RCP8.5. This means that CWCs would be exposed to under-saturated conditions and dead coral skeletons would start dissolving. However, Fautin et al. (2009) showed that some scleractinians can live below the ASH, and some occur exclusively in relatively deep water (e.g. *Fungiacyathus marenzelleri*, *Leptopenus antarcticus*, and many species of *Flabellum*). Hence, he suggested that some solitary scleractinian CWCs could be unaffected by the ASH shoaling and others may adapt by ceasing the production of skeleton, becoming morphologically like corallimorpharians. McCulloch et al. (2012) demonstrated that deep CWCs have a considerable resilience to lowered saturation states. Zheng & Cao (2014) projected that, in general, scler-

actinian corals were able to maintain both skeletal growth and density under such conditions by allocating increased energy to calcification, fuelled by higher food intake.

Oxygen was not encountered as one of the main variables establishing the current distribution of scleractinian corals, perhaps related to the general concept that polar taxa have lower aerobic scopes, in addition to lower metabolic rates and growth (Peck 2002, Henry & Torres 2013). However, since some CWCs live at oxygen-minimum zone depths (Georgian et al. 2014), small future changes in oxygen concentration, in response to warming, could be significant, and deoxygenation may lead to changes in sea-surface productivity and affect CWCs nutrition (Cordes et al. 2016).

This study shows that the spatial distribution of the CWC community will change in the future scenarios analysed. However, it is difficult to predict how the species composition of these communities could vary in the different niches, due to the lack of knowledge on the biology and environmental tolerance of these species, except for some reproductive trends (Waller et al. 2008, Waller & Feehan 2013), and the uncertainty of the current general systems (which provide food and other physicochemical parameters) that could be established in these future scenarios. If the upward migration of the ASH due to the uptake of anthropogenic CO₂ (Feely et al. 2012) and the intrusion of Circumpolar Deep Water (CDW) on the Antarctic continental shelves increases the water temperature (Sallé 2018) or limits food supply (or oxygen) to compensate for metabolic needs (e.g. Henry & Torres 2013, Gori et al. 2016), the vertical distribution of some species of CWCs could also be locally or regionally affected.

5. CONCLUSIONS

Polar scleractinians are a grossly understudied group. This study gives an insight into their habitat preferences in the North Antarctic region (Weddell Sea and Antarctic Peninsula) based on environmental variables. Increasing our understanding of the spatial organisation of CWC communities in relation to environmental variables will enable a more targeted sampling and surveying of the species. At the same time, the use of predictive modelling techniques that improve the robustness of extrapolated habitat distribution maps in areas where sampling opportunities are limited offers a cost-effective means of providing vital information to resource

managers and scientists. In this study, we demonstrate that the spatial distribution of CWCs depends on environmental and geomorphological requirements, as well as their nutritional needs. Distance to the coast and ice, benthic CaCO₃ concentration, temperature, and bathymetry were the variables that strongly predicted the habitat preferences of scleractinian CWCs.

Adding more environmental variables that are changing in the region, such as salinity, ice shelf extent, and aragonite saturation, would most likely strengthen the projections of future CWC distribution.

The model results in this study are assumed to provide accurate distribution scenarios because of the agreement between the identified presence records from expeditions and the documented records in the literature, the high-quality and high-resolution environmental data basis, and the good to excellent evaluation measures in terms of ROC and TSS. However, a field validation set from a systematic sampling effort for all species would ultimately improve the individual SDM predictions.

In addition to their role in promoting ecosystem functions like carbon cycling, the complexity of CWC habitat enhances the heterogeneity of the continental margin and thus contributes to the increase of biodiversity at the community level with the associated fauna (polychaetes, amphipods, etc.). Consequently, the effect of future climate on scleractinian habitat raises concerns about its potential impact on the global biogeochemical cycles and their biotic interspecific interactions.

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