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Can we generate robust species distribution models at the scale of the Southern Ocean?

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Abstract

Aim: Species distribution modelling (SDM) represents a valuable alternative to predict species distribution over vast and remote areas of the ocean. We tested whether reliable SDMs can be generated for benthic marine organisms at the scale of the Southern Ocean. We aimed at identifying the main large-scale factors that determine the distribution of the selected species. The robustness of SDMs was tested with regards to sampling effort, species niche width and biogeography.

Location: Southern Ocean.

Methods: The impact of sampling effort was tested using two sets of data: one set with all presence-only data available until 2005, and a second set using all data available until 2015 including recent records from campaigns carried out during the Census of Antarctic Marine Life (CAML) and the International Polar Year (IPY) period (2005–2010). The accuracy of SDMs was tested using a ground-truthing approach by comparing recent presence/absence data collected during the CAML and IPY period to pre-CAML model predictions.

Results: Our results show the significance of the SDM approach and the role of abiotic factors as important drivers of species distribution at broad spatial scale. The addition of recent data to the models significantly improved the prediction of SDM and changed the respective contributions of environmental predictors. However, the intensity of change varied between models depending on sampling tools, species ecological niche width and biogeographic barriers to dispersal.

Main conclusions: We highlight the need for new data and the significance of the ground-truthing approach to test the accuracy of SDMs. We show the importance of data collected through international initiatives, such as the CAML and IPY to the improvement of species distribution modelling at broad spatial scales. Finally, we discussed the relevance of SDM as a relevant marine conservation tool particularly in the context of climate change and the definition of Marine Protected Areas.

KEYWORDS

Antarctic, biogeography, conservation, Echinoidea, ecological niche, random forest, sampling effort, sub-Antarctic

1 | INTRODUCTION

Species distribution patterns in the Southern Ocean (SO) are the result of a complex interplay between geological, oceanographic, and ecological factors. During the Cenozoic, Australia separated from Antarctica and drifted northward, which opened the Tasmanian gateway and allowed the Antarctic Circumpolar Current (ACC) to develop. Subsequent ocean cooling led to a partial isolation of Antarctic biota from the rest of the world's oceans (Brandt, 2005; Clarke, Aronson, Crame, Gili, & Blake, 2004; Eastman, 2000). Climatic oscillations associated with glacial/interglacial cycles also strongly influenced the evolution of marine life (Allcock & Strugnell, 2012). As a consequence, modern Antarctic biodiversity displays unique biogeographic features and life history traits including high levels of endemism (Brandt et al., 2007; Griffiths, Barnes, & Linse, 2009; Kaiser et al., 2013; Saucède, Pierrat, Bruno, & Bruno, 2014), adaptations to freezing water temperatures (Cheng & William, 2007; Eastman, 2000; Portner, Peck, & Somero, 2007), and brooding (David & Mooi, 1990; Hunter & Halanych, 2008; Sewell & Hofmann, 2011). These unique features make the SO a fascinating, natural laboratory for eco-evolutionary and biogeographic studies (David & Saucède, 2015).

However, remoteness and extreme environmental conditions also make the SO a challenging region to carry out field work because of limited access and strong logistical and financial constraints (Gutt et al., 2017; Kaiser et al., 2013; Kennicutt et al., 2014). Over the last 10 years, significant efforts have been devoted to improve our knowledge of the SO biodiversity (Gutt et al., 2017; Kaiser et al., 2013; Schiaparelli, Danis, Wadley, & Michael Stoddart, 2013). Hence, in the framework of the Census of Antarctic Marine Life (CAML) and of the International Polar Year (IPY), 18 concurrent oceanographic campaigns were led to the Antarctic and new biodiversity data were aggregated (Schiaparelli et al., 2013). During the same time period, several oceanographic campaigns were also undertaken in the sub-Antarctic Crozet and Kerguelen archipelagos (Améziane et al., 2011; Féral et al., 2016). New marine biodiversity data were compiled and datasets made openly available through the SCAR Marine Biodiversity Information Network (De Broyer et al., 2017; Griffiths, Danis, & Clarke, 2011) and the Biogeographic Atlas of the SO (De Broyer et al., 2014). Nevertheless, major Linnean and Wallacean gaps still persist in our knowledge of Antarctic marine life. Under-sampled areas such as the deep sea (Brandt, Van de Putte, & Griffiths, 2014; Fabri-Ruiz, Saucède, Danis, & David, 2017), remote parts of the ocean such as the Amundsen Sea, and isolated islands such as Bouvet island (De Broyer et al., 2014; Griffiths et al., 2011) remain underinvestigated.

Species distribution modelling (SDM) represents a valuable tool to fill in these gaps. Offering a baseline for detecting, monitoring and predicting the impact of climate change on species and biota distribution (Gutt et al., 2015, 2017; Kennicutt et al., 2015). SDM are often applied to conservation issues and in Marine Protected Area designation processes (Franklin, 2013; Guisan et al., 2013; Rodríguez, Brotons, Bustamante, & Seoane, 2007). A growing number of large-scale SDM-based studies have recently been published for the SO (plankton, top predators, fish, and cephalopods) (Duhamel et al., 2014; Loots, Koubbi, & Duhamel, 2007; Nachtsheim, Jerosch, Hagen, Plötz, & Bornemann, 2017; Pinkerton et al., 2010; Thiers, Delord, Bost, Guinet, & Weimerskirch, 2017; Xavier, Raymond, Jones, & Griffiths, 2016). SDM developed for Antarctic benthic organisms are restricted to few case studies including deep-sea shrimps (Basher & Costello, 2016), cirripeds (Gallego, Dennis, Basher, Lavery, & Sewell, 2017) and echinoids (Pierrat et al., 2012).

A wide variety of SDM methods have been proposed (Elith & Graham, 2009; Elith et al., 2006), but several of their limitations have also been identified (Beale & Lennon, 2012) for which relevant techniques have been developed (Barry & Elith, 2006; Dormann, Purschke, Márquez, Lautenbach, & Schröder, 2008; Dormann et al., 2007; van Proosdij, Sosef, Wieringa, & Raes, 2016). Examples of such limitations are the effect of sampling effort (Clarke, Griffiths, Linse, Barnes, & Crame, 2007; Griffiths et al., 2009), sample size, and the addition of new records on model accuracy with the potential to impact model predictions and performance (Aguiar, da Rosa, Jones, & Machado, 2015; Wisz et al., 2008). Bias in spatial datasets also remains a critical issue for SDM predictions. Spatial bias in sampling records can translate into a bias in the environmental space and lead to inaccurate inferences and predicted distributions (Bystriakova, Peregrym, Erkens, Bezsmertna, & Schneider, 2012; Fourcade, Engler, Rödder, & Secondi, 2014; Loiselle et al., 2007; Stolar & Nielsen, 2015).

Recent studies (Qiao, Soberón, & Peterson, 2015; Saupe et al., 2012) have highlighted the effect of species niche width and biogeography on the performance levels of SDMs. SDMs carried out on broad-niche species with wide distribution range tend to be more sensitive to the quantity of data available than for narrow niche species with restricted distribution range (Hernandez, Graham, Master, & Albert, 2006; Tessarolo, Rangel, Araújo, & Hortal, 2014). Saupe et al. (2012) have also explored different configuration of major factors that constrain species distributions (abiotic factor and dispersal limitation). This study gives a framework to test whether SDM provide unrealistic modelled distribution and whether species distributions are more driven by the environment or by constraints to their dispersal. We can assume species with high dispersal capacity should be more constrained by the environment as in Hutchinson's Dream distribution pattern (Saupe et al., 2012), while endemic species should be more constrained by dispersal limitation as in the Wallace's Dream distribution model.

Can reliable and meaningful SDMs be generated for marine organisms at the scale of the SO? What is the effect of sampling effort, of species ecology and biogeography on model robustness? In the present work, we assessed the reliability and robustness of large-scale SDMs in the SO and tested the impact of sampling effort, species niche and biogeography on model outputs. Echinoids are common organisms in Antarctic benthic communities and occur in a large range of habitats. The impact of sampling effort was tested using presence/absence data from recent campaigns performed during the CAML and IPY period. To test for

the relevance of SDMs, five echinoid species were selected with different ecological niches (coastal or deep sea) and with contrasting life traits (brooders or broadcasters). Species biogeography has been taken into account, endemism and dispersal limitations by the Polar Front in particular. Considering species presence data and abiotic environmental descriptors together, we aimed at identifying the main large-scale factors that explain the distribution of the selected species taking into account potential bias that might impact model outputs.

2 | METHODS

2.1 | Study area

The study area extends from 45°S latitude to the Antarctic coastline and includes the entire SO (SO) from south of the Subtropical front to the Antarctic continent to the south. The northern part of the SO is limited by the ACC which is the strongest marine current on Earth (Barker & Thomas, 2004). It flows eastwards and is associated to several marine fronts that form narrow boundaries and partly isolate warmer Subtropical waters in the north from colder Subantarctic and Antarctic waters in the south (Roquet, Park, Guinet, Bailleul, & Charrassin, 2009; Sokolov & Rintoul, 2002). These marine fronts are distributed along a latitudinal gradient, including (from North to South): the Subtropical front (STF), the Subantarctic Front (SAF), the Polar Front (PF), the Southern ACC Front (SSACF) and the Southern Boundary (SACCB) (Figure 1). The PF plays an important role as a biogeographic barrier to species latitudinal dispersal.

2.2 | Occurrence records and studied species

Biological data used in our study are species occurrence records taken from an extensive echinoid database (Fabri-Ruiz et al., 2017) that includes field collections ranging from 1874 to recent oceanographic campaigns undertaken until 2015. Only occurrence records associated to sampling dates were considered in the study. Flow chart showing the protocol followed to assess the effect of sampling effort on SDM outputs (Supporting Information Figure S1.2).

For each species, occurrence records were subdivided into two datasets: a first dataset with records sampled prior to 2005 that is, with data available before the CAML period, then, a second dataset with all occurrences sampled until 2015. Five echinoid species were selected based on their contrasting auto-ecological traits, dispersal capabilities and biogeographic patterns (Table 1). They belong to two families: the Echinidae (*Dermechinus horridus* (Agassiz, 1878), *Sterechinus diadema* (Studer, 1876), and *Sterechinus neumayeri* (Meissner, 1900)), and the Cidaridae (*Ctenocidaris nutrix* (Thomson, 1876) and *Rhynchocidaris triplopora* (Mortensen, 1909). *S. neumayeri* and *R. triplopora* are exclusively distributed in Antarctic waters, south of the PF, whereas *C. nutrix* and *S. diadema* occur on both sides of the PF. *D. horridus* is a Subantarctic species distributed in the north of the PF. The selected species of Cidaridae are brooders and the Echinidae are broadcasters. Most of the Antarctic Cidaridae brood their young and have no planktonic stage in their life cycle. Conversely, Echinidae release planktotrophic larvae. These contrasting life traits suggest different dispersal capabilities and contrasting spatial distributions between species of the two families. The taxonomy of the five studied species is supported by molecular data.

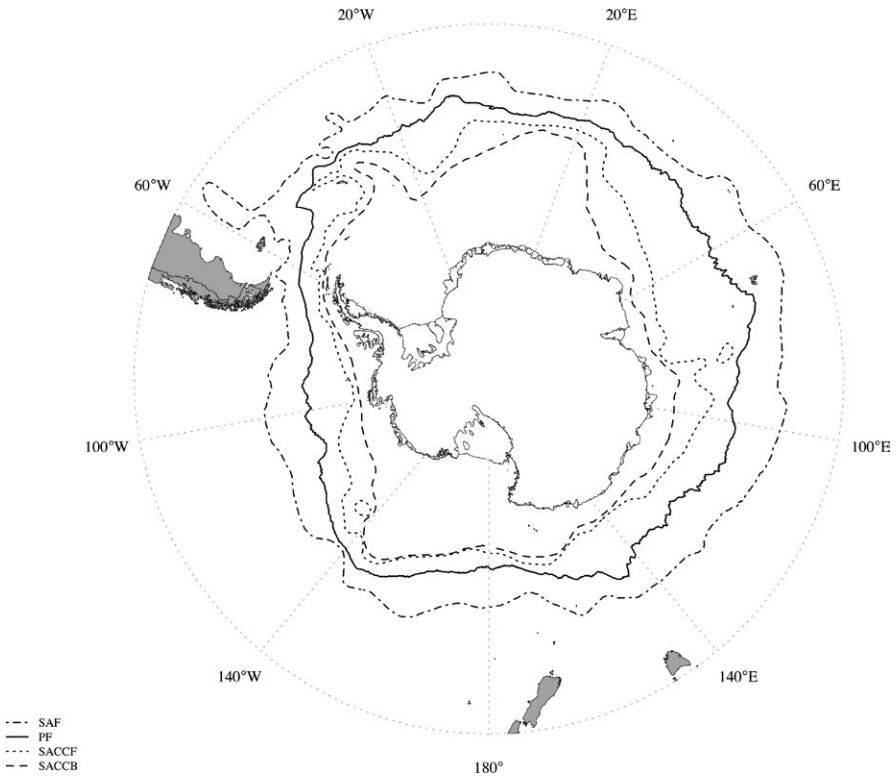

FIGURE 1 Map of the Southern Ocean with major oceanic fronts. Subtropical front (STF), the Subantarctic Front (SAF), the Polar Front (PF), the Southern ACC Front (SSACF) and the Southern Boundary (SACCB)

TABLE 1 Studied species dispersal mode and distribution

	Cidaridae		Echinidae		
	Ctenocidaris nutrix	*Rhynchocidaris triplopora*	*Dermechinus horridus*	*Sterechinus diadema*	*Sterechinus neumayeri*
Dispersal mode	Brooder	Brooder	Broadcaster	Broadcaster	Broadcaster
Distribution	Antarctic/Subantarctic	Antarctic	Subantarctic	Antarctic/Subantarctic	Antarctic

Sterechinus neumayeri and *Sterechinus diadema* have been recently identified as distinct genetic units (Díaz, Féral, David, Saucède, & Poulin, 2011); *Ctenocidaris nutrix*, *Rhynchocidaris triplopora* (Lockhart, 2006) and *Dermechinus horridus* (Saucède pers. comm.) have been confirmed by ongoing molecular works.

2.3 | Environmental descriptors

Environmental descriptors averaged over (1955–2012) were selected based on their ecological relevance for echinoids as established in previous studies works (David, Choné, Mooi, & De Ridder, 2005). These descriptors were compiled from different sources (Fabri-Ruiz et al., 2017) and adjusted to the same grid cell size (0.1°) using R 3.4 (R Core Team, 2017) and the *raster* package (Hijmans & van Etten, 2012). Prior to modelling, colinearity between variables was checked for and removed based on pairwise Pearson's correlation coefficient values computed between variables ($r > 0.7$) (Supporting Information Figure S1.2). Either thirteen (Antarctic species) or twelve (Subantarctic species), environmental predictors were selected (sea ice concentration was kept for Antarctic species): Seafloor salinity amplitude, Sea surface salinity amplitude, Seafloor temperature amplitude, Sea surface temperature amplitude, Chlorophyll a summer, Geomorphology, Depth, Seafloor oxygen mean, Seafloor salinity mean, Sea surface salinity mean, Slope, Seafloor temperature mean, Sea ice concentration (for Antarctic species only). Amplitude data correspond to winter minus summer averages.

2.4 | Modelling procedure

Several modelling procedures were carried out prior to selecting the most stable approach and showing the highest predictive performance (Supporting Information Figures S1.1 and S1.2). The Random Forest (RF) proved to be the most appropriate machine-learning method in our case study (Breiman, 2001). Models were performed using the *biomod2* package (Thuiller, Lafourcade, Engler, & Araújo, 2009) with R 3.4 (R Core Team, 2017). The parameter used to compute RF are: mtry = the square root of the number of variables, ntree = 500, nodesize = 5. For each species, distinct models were generated based on the pre and post – CAML datasets.

Because true absence data were not available, pseudo-absences were generated to build the models. Different strategies for selecting pseudo-absences are available in the literature based on the number of pseudo-absences, number of replicates and sampling design. The selection strategy can impact the predictive accuracy depending on models and occurrence data (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012). Considering our model choice (RF), Barbet-Massin et al. (2012) recommend to select pseudo-absences (for both periods) 2° apart from occurrence records. 1,000 pseudo-absences were generated for both periods. Each dataset was subdivided in two subsets: a first data subset including 70% of data was used as training data to calibrate the models, and a second subset (30% of data) was used to test the models.

Models were finally projected on the defined study area. The extent of the study area can be considered a critical factor for SDM (Anderson & Raza, 2010; Barve et al., 2011; Giovanelli, de Siqueira, Haddad, & Alexandrino, 2010). To limit extrapolation, occurrence records deeper than 2,500 me were removed from our analysis.

Since the first expedition in 1874, a variety of sampling gear has been used to collect specimens (Fabri-Ruiz et al., 2017). Using different sampling methods can generate sampling bias and particularly false absences because all gear types were not designed for the selected species (Ghiglione et al., 2017). However, samples obtained by catch can be included in presence-only SDM. It was not possible to test the effect of the sampling gear used on models because it would have restricted the dataset too much for building robust SDM.

A common issue in SDM is to predict as unsuitable parts of the environmental space that are undersampled and may correspond to specific and restricted geographic areas. To correct for sampling biases, occurrence records were weighted based on a map of Kernel Density Estimation (Elith, Kearney, & Phillips, 2010). The weighting layer was built based on all echinoid records and generated using Spatial Analyst in ArcGIS v10.2 (ESRI 2011).

Spatial autocorrelation (SAC) constitutes a critical issue of spatial analyses in ecology when variable values sampled at close locations are not independent (Legendre, 1993). SAC in SDM residuals infringes the «independent errors» assumption and can artificially inflate type I errors in models. To correct for SAC in our models, several replicates of pseudo absence selection were generated for calibration. Then SAC was quantified on residuals with the Moran I index using the Spatial Statistic Tools in ArcGIS. Replicates with significant SAC were removed. Model projection was done with 11 replicates without SAC for all species, which corresponds to the minimum number of replicates without SAC obtained for all species.

2.5 | Assessment of model performance

The quantitative evaluation of model performance helps determine the adequacy between SDM and occurrence data. In SDM studies, models are rarely tested a posteriori by carrying out field-based ground truthing (Costa, Nogueira, Machado, & Colli, 2010), as it involves major logistic and financial issues. Former studies highlighted how sample size can affect distribution models (Hernandez et al., 2006; Wisz et al.,

2008). A solution to this issue lies in the degradation of the initial dataset by randomly removing occurrences and testing the impact on model performance and spatial projections. Model validation is usually based on metrics like the TSS (True Skill Statistic) (Allouche, Tsoar, & Kadmon, 2006). The TSS is based on a confusion matrix that highlights the good match and mismatch between observed and predicted occurrences. However, one limit to the method is that location of the modelling error cannot be specified in the environmental space nor in geography (Barry & Elith, 2006). In addition, metrics like the TSS can assess the predictive ability of models based on presence-data only, but they do not take into account all sampled sites (including absence data) over the entire study area. Here, the TSS was calculated using the training (70% of data) and the validation data set (30% of data).

We assessed the predictive performance of models using TSS, but we also followed a ground-truthing approach to test for the accuracy of models (Supporting Information Figure S1.2) using a Chi-square test of the difference between the predicted occurrences based on models performed with the 2005 dataset and occurrence records collected after 2005 (including presence and absence data). The analysis aims to evaluate how well SDM generated with the 2005 dataset predict new occurrences collected after 2005. New observations were classified according to the predictions computed based on the 2005 dataset. True positives (TP) and True negatives (TN) observations correspond to a good match of presence (TP) and absence (TN) observations with predictions respectively. On the contrary, False positives (FP) and False negatives (FN) correspond to a mismatch between new records and predictions: absence predicted as presence is a False positive and a presence predicted as an absence is a False negative. The respective proportion of each class was summarized (Supporting Information Table S1.1) and mapped (Supporting Information Figure S1.3).

To better assess model improvement with increased sampling effort and disentangle the possible confounding factors, we compared the environments explored between the two periods (Pre and Post CAML) using the environmental hypervolume approach (Blonder, Lamanna, Violle, & Enquist, 2014; Blonder et al., 2018). This method is based on a multidimensional kernel density estimation procedure and allows delineating the boarders and probability density within n-dimensional hypervolumes. We determined the unique fraction of post-CAML hypervolume compared to pre-CAML hypervolume. This unique fraction is the environment not sampled during the pre-CAML period. We also provide the number of records of the post-CAML dataset not included in the hypervolume as based on the pre-CAML period.

3 | RESULTS

3.1 | Evolution of sampling effort through time

The sampling effort (in terms of occurrence records) has markedly changed over one and a half centuries (Figure 2). There were two significant events associated with a sharp increase in the number of occurrence records. In the 1970s, oceanographic campaigns of the

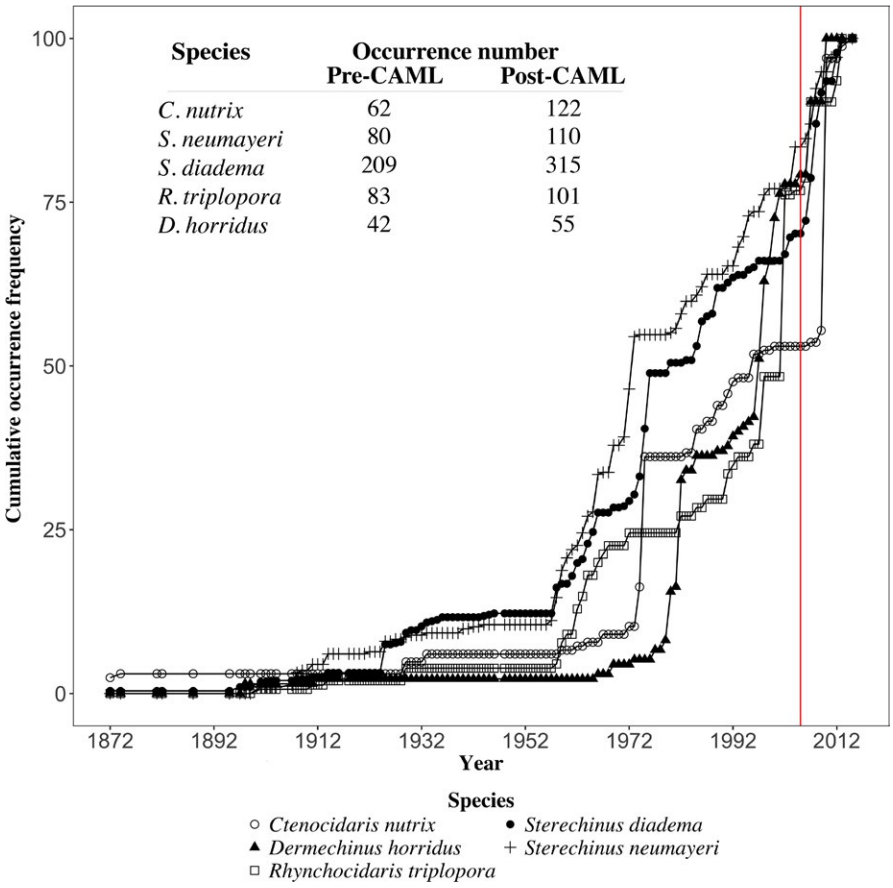

FIGURE 2 Evolution of sampling effort (occurrence number) over time for the five echinoid species considered in our study (the red line shows the start of the CAML period). The table shows the number of occurrence records before and after CAML and IPY-related campaigns [Colour figure can be viewed at wileyonlinelibrary.com]

RV *Marion Dufresne* on the Kerguelen Plateau and of the RV *Hero* along the Antarctic Peninsula strongly contributed to increasing the overall number of occurrence records after the campaigns, especially for two species, *S. diadema* and *S. neumayeri*. A second phase of important increase was reached in years 2000, mainly triggered by the campaigns carried out under the umbrella of CAML and the IPY along with some former (*R. triplopora* and *D. horridus*) and side campaigns (*C. nutrix* on the Kerguelen Plateau) during the same period. For *C. nutrix* and *S. diadema* in particular, 60 and 106 new occurrences were reported respectively during the period. In contrast, *S. neumayeri* occurrence records have regularly increased since 1970. *S. neumayeri* is a relative shallow-water echinoid with new samples being mainly reported during research programs carried out along the Antarctic shoreline, many specimens being sampled by scuba diving. Despite specific patterns of the evolution of sampling effort, the overall number of occurrence records has markedly increased following expeditions undertaken in years 2000 under the impulse of CAML and the IPY.

3.2 | Compared SDM performances

Overall, for each species, SDMs run both with all data available until 2005 (before CAML) and all data until 2015 (including CAML data) show high predictive performances with TSS values >0.8 (Figure 3), which indicate a relatively good match between observed and predicted occurrences. This is particularly the case for *D. horridus*, with TSS values above 0.90, while for the other four species TSS values are between 0.8 and 0.90. There are significant differences in TSS values between the two SDMs with the addition of new data in all species, and for *D. horridus* and *C. nutrix* in particular, with no overlap between TSS range values. TSS range values of models run with new data are smaller than those of models run without CAML data.

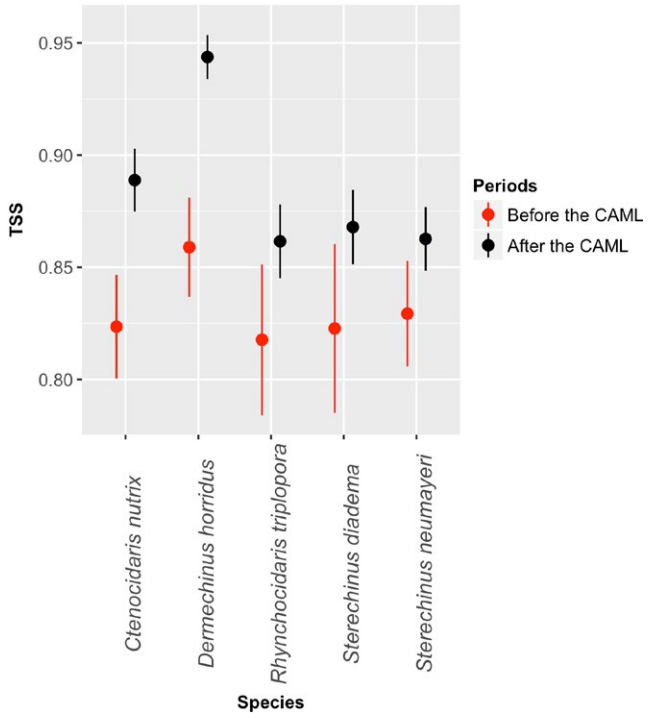

FIGURE 3 Compared predictive performance (mean and standard deviation) using the True Skill Statistics (TSS) for SDMs performed with and without (until 2005) recent data for the five echinoid species [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | SDM ground-truthing using new field data

SDM ground-truthing was carried out using new field records collected during the CAML period. Overall, the Chi-square tests reveal a significant mismatch between observed and modelled data ($p < 0.05$) for all species. However, results are divergent between species (Table 2). In all species but *S. diadema*, the mismatch between observed and modelled data is mainly due to the proportion of FP, which is not counterbalanced by TP and TN. FP were mainly identified on the Kerguelen Plateau for *C. nutrix* and *D. horridus* (Supporting Information Figure S1.3a,c), along the Antarctic Peninsula and in Adelie Land for *R. triplopora and S. neumayeri* (Supporting Information Figure S1.3b,e). TN proportions are high compared to TP, meaning that SDMs are mainly supported by absence records collected outside of the species areas. TN were mostly identified on the Antarctic continental shelf for *D. horridus* and *C. nutrix*, and north of the polar front for *S. neumayeri* and *R. triplopora*, where the species are respectively absent or present in low numbers. In *S. diadema*, the mismatch between observed and modelled data is mainly due to false predictions (FP and FN). True predictions (TP and TN) are present in equal proportion but are limited compared to false predictions. The proportion of FP is particularly high on the Kerguelen Plateau where most FP were found. The proportion of FN is also high in *S. diadema* compared to other species meaning that in certain areas the modelled distribution was underestimated compared to new records. This is particularly true in Adélie Land, and in the Ross and Weddell seas were many new records were reported (Supporting Information Figure S1.3d).

Overall, false predictions were not aggregated in the same area but scattered in different sectors depending on species. They are mainly due to the high proportion of FP identified on the Kerguelen Plateau, along the Antarctic Peninsula, in Adelie Land or in the Ross and Weddell seas where most campaigns were carried out during the CAML period. Therefore, modelled distributions were all overpredicted in the areas where campaigns were undertaken during the CAML period, which allows refining the extent of modelled areas. A high proportion of FP was identified during the POKER II campaign on the Kerguelen archipelago for Subantarctic species (Supporting Information Table S1.1). For Antarctic species, FP are mainly associated with campaigns Antarktis XXIII, Antarktis XXIX-3, and JR144 along the Antarctic Peninsula and the campaign CEAMARC in East Antarctica. The overall proportion of FN is low (Supporting Information Table S1.1) and associated to campaigns undertaken in the Ross and Weddell seas.

TABLE 2 Chi-square test assessing the good match between records obtained during the CAML period and SDM performed with pre-CAML data only

	p-Value	True negative (TN)	True positive (TP)	True prediction	False positive (FP)	False negative (FN)	False prediction
C. nutrix	<0.05*	64.81	18.89	83.7	12.96	3.33	16.29
D. horridus	<0.05*	85.93	4.07	90	9.26	0.74	10
R. triplopora	<0.05*	75.19	7.41	82.6	16.30	1.11	17.4
S. neumayeri	<0.05*	57.04	10.74	67.78	31.48	0.74	32.22
S. diadema	<0.05*	17.41	17.78	35.19	42.96	21.85	64.81

Notes. Match (TN and TP) and mismatch (FP and FN) proportions are given in percentage of the total number of records for new data.
*Significant values ($p < 0.05$) indicate a mismatch between the predicted distribution and new observed occurrences.

3.4 | SDM projection shifts

The addition of the records obtained during the CAML period causes projection shifts compared to SDM carried out using pre-CAML data only (Figure 4). This holds true for all species with a general expansion of suitable areas to different sectors of the Kerguelen Plateau and Antarctic continental shelf. Projection shifts are species dependent. The suitable areas of *C. nutrix* and *D. horridus* extend to the Kerguelen Plateau when new data are taken into account in the models (Figure 4a,c). The distribution of *C. nutrix* is modelled over the entire Kerguelen Plateau and along the Antarctic Peninsula following a patchy pattern. *D. horridus* is mainly modelled around the sub-Antarctic islands. For *R. triplopora* and *S. neumayeri*, SDM outputs did not vary much with the addition of new records (Figure 4b,e). New projections confirm the Antarctic affinity of the two species and show an extension of the species suitable areas along the Antarctic Peninsula and in the Ross Sea. *S. diadema* is the echinoid with the widest circumpolar distribution (Figure 4d). The new SDM projection shows an extension of suitable areas in the Ross and Weddell seas and

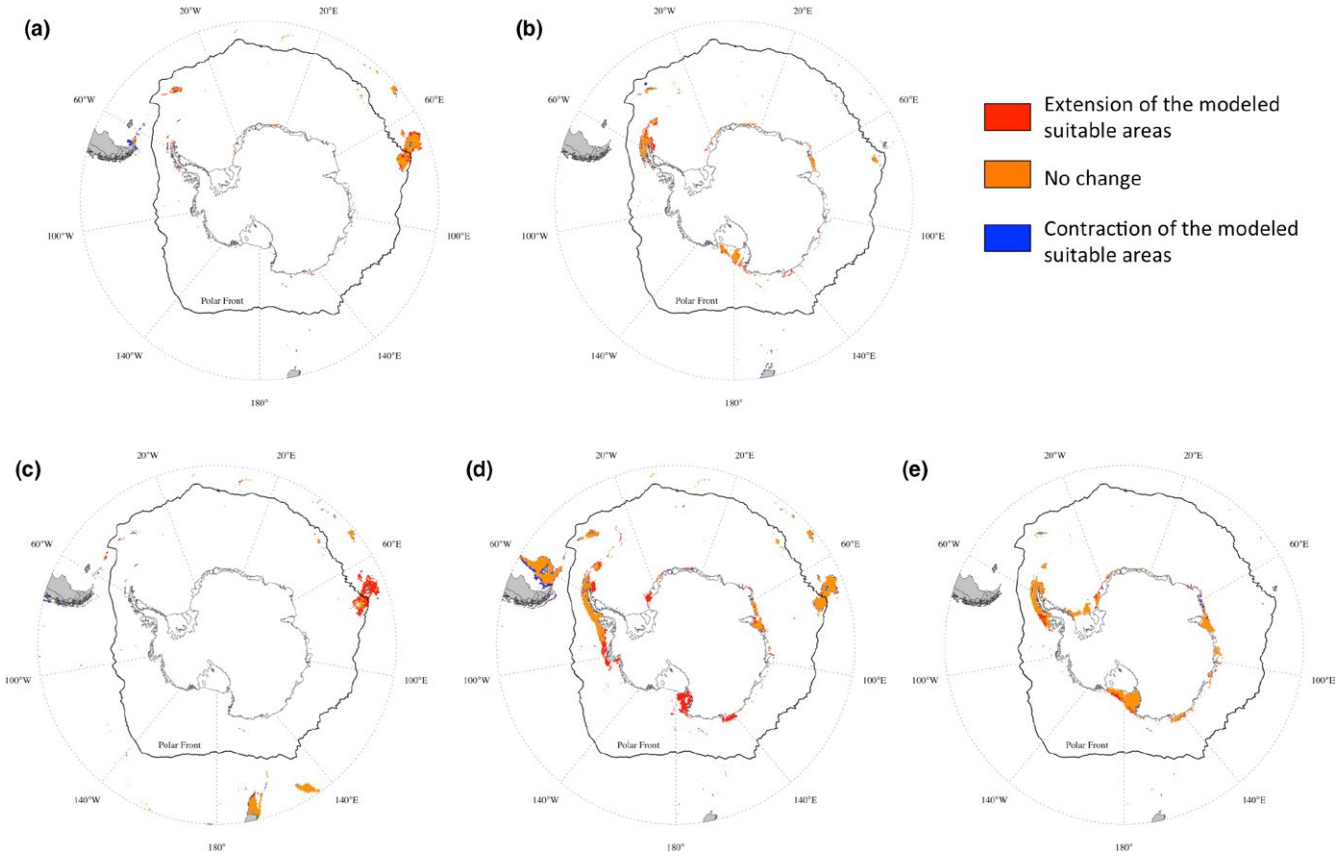

FIGURE 4 Projection shifts between SDMs carried out using recent CAML data or not for (a) *Ctenocidaris nutrix*, (b) *Rhynchocidaris triplopora*, (c) *Dermechinus horridus*, (d) *Sterechinus diadema* and (e) *Sterechinus neumayeri*. Orange areas indicate modelled suitable areas that remain unchanged between the two SDMs; in red the extension of suitable areas in the new projection; in blue the contraction of suitable areas [Colour figure can be viewed at wileyonlinelibrary.com]

along the Antarctic Peninsula, while the species was not predicted in these areas before new records were added to the model. Concomitantly, the new projection presents a substantial contraction of the species potential distribution in the Magellanic region, over the Argentinian continental shelf.

3.5 | Contribution of environmental predictors

The relative contribution of environmental predictors to SDM indicates the environmental parameters that best explain the species niche (Figure 5) and determine the extent of suitable areas.

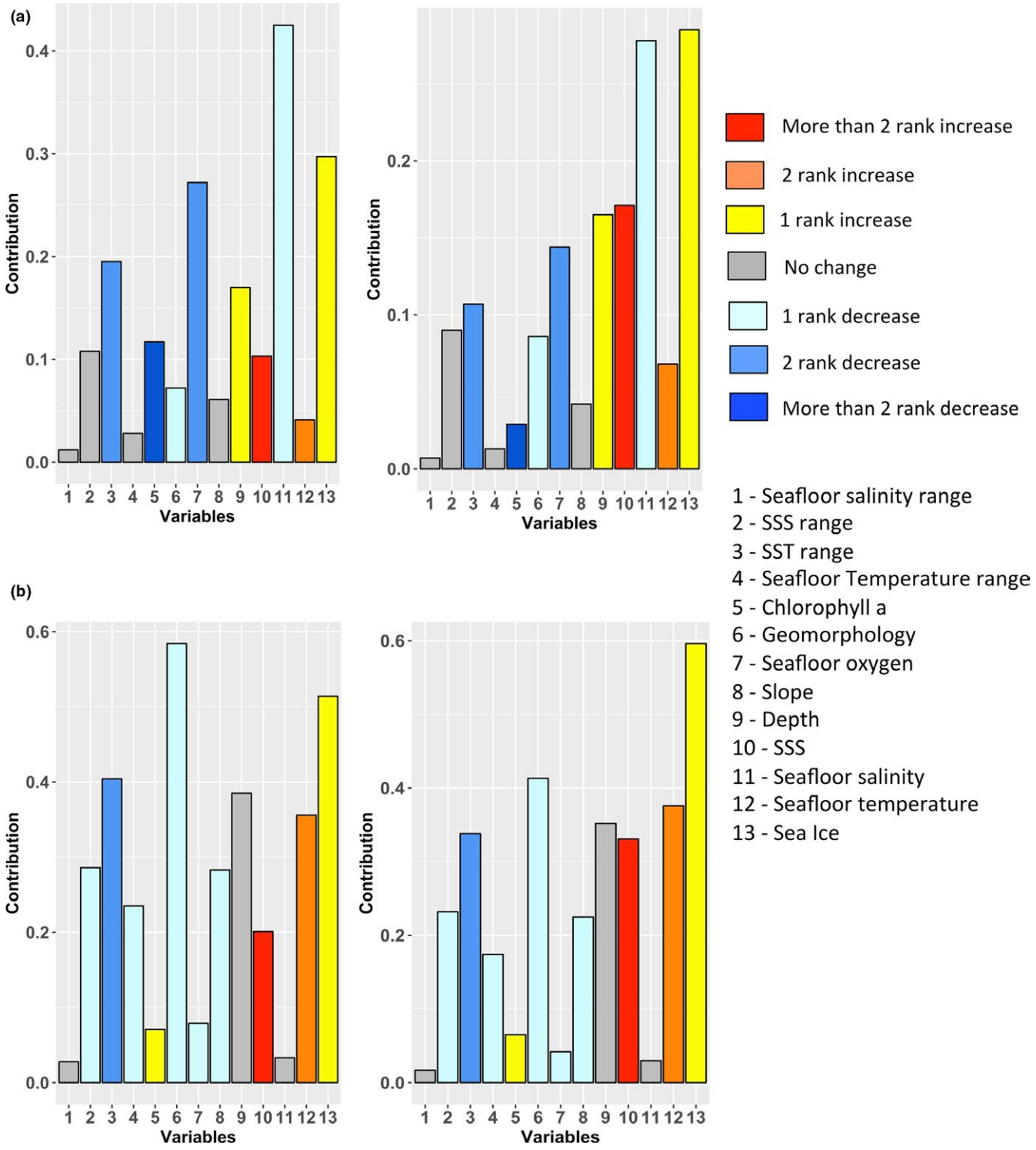

FIGURE 5 Relative contributions of environmental predictors to the models performed without (left barplots) and with CAML data (right barplots). Colours indicate the increase or decrease in the ranked order of each predictor between the two SDMs performed with and without new records for (a) *Ctenocidaris nutrix*, (b) *Rhynchocidaris triplopora*, (c) *Dermechinus horridus*, (d) *Sterechinus diadema*, (e) *Sterechinus neumayeri* [Colour figure can be viewed at wileyonlinelibrary.com]

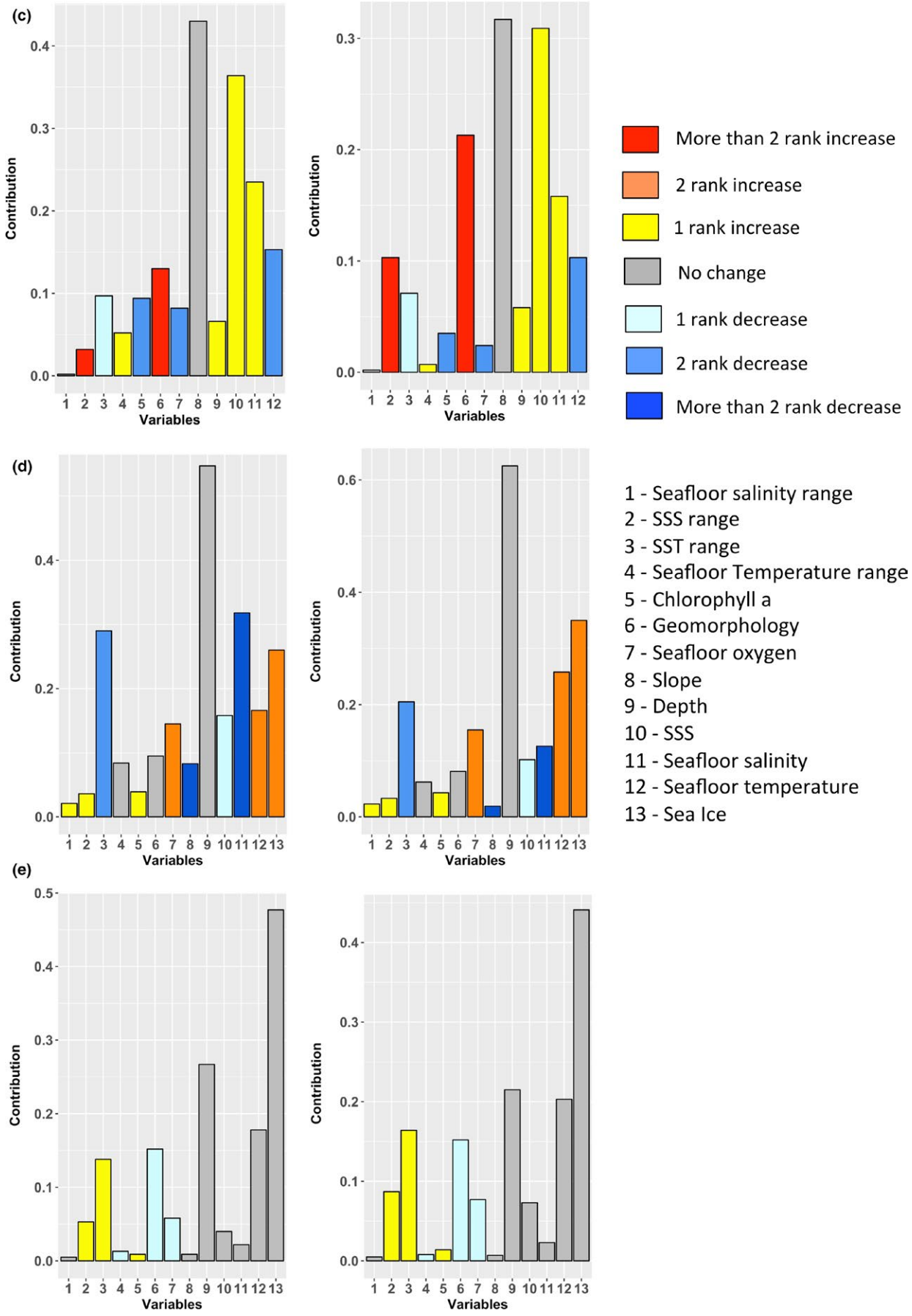

FIGURE 5B Continued

Sea ice is an important parameter for the four species present on the Antarctic shelf (*R. triplopora*, *S. diadema*, *S. neumayeri* and *C. nutrix*). For *D. horridus*, the fully Subantarctic species, slope and SSS play a preponderant role in species distribution (Figure 5c). Depth mainly contributes to explaining the distributions of *S. diadema* and *S. neumayeri* only (Figure 5d,e). In *R. triplopora*, many parameters contribute to the models: geomorphology, SST range, depth, SSS range and seafloor temperature (Figure 5b). In contrast, in *C. nutrix*, seafloor salinity and sea ice are the main contributors (Figure 5a).

The addition of data collected during the CAML period affected the respective contribution or the rank order of environmental parameters (Supporting Information Table S1.2, Figure 5). For all variables, any change in the ranking of the variable is not necessarily associated to a change in contribution value of the variable to the model but could be due to a variation of the contribution of another variable. Most changes occur for *C. nutrix*, *S. diadema* and *D. horridus*, while parameter contributions to SDMs performed for *R. triplopora* and *S. neumayeri* almost did not vary. Overall, for the five species, the rank order of the most contributing parameters remain stable (1 rank change or no change) between the two SDMs, except for seafloor oxygen, SST range and seafloor salinity. Depth, sea ice and seafloor temperature are three parameters that are among the most common descriptors to both SDMs performed for all species.

3.6 | Compared sampled areas and environments

For each species, we mapped occurrence records available for the two periods to identify new sampled areas during the post-CAML period (Supporting Information Figure S1.4). For *C. nutrix*, new occurrence data are located in the Antarctic Peninsula, while for *R. triplopora* and *S. neumayeri*, they were collected in areas already sampled along the Antarctic Peninsula and in the Ross sea. New records of *D. horridus* are located in the northern Kerguelen Plateau. *S. diadema* was sampled all around the SO during the CAML period and new records were collected in Adélie Land and in sectors of the Ross sea. *C. nutrix* and *S. diadema* shows a large number of new records not included in the pre-CAML hypervolume (49 and 26 points respectively) (Table 3). These species show the highest number of new records collected during the CAML period. Conversely, *D. horridus*, *R. triplopora* and *S. neumayeri* have a low number of new records (<10).

4 | DISCUSSION

4.1 | Model accuracy

Overall, the addition of new data significantly changed model outputs (Table 1) and led to better capture the environmental space occupied by the five species (Table 3). These changes lead to increase model performance and affect the patterns and extensions of species potential distributions as well as the contribution of environmental predictors. The predictive performance of models was assessed using two methods, the TSS metric and the ground-truthing analysis. The TSS value increased with the addition of new data, but differences are significant for two species only (*C. nutrix* and *D. horridus*) and values are usually high (>0.9) for all models (Figure 3). *C. nutrix* is the species with the highest number of new records that fall of the environmental hypervolume defined by pre-CAML data (Table 3). In contrast, *D. horridus* shows the lowest number of new records but considering the low number of records in total, this also leads to increase the TSS value. These results are in line with previous studies that showed that SDM accuracy tend to increase with the size of datasets (Hernandez et al., 2006; Wisz et al., 2008). In contrast, TSS values are not significantly different between the two periods for *S. neumayeri* and *R. triplopora* because most new records fall into the environmental hypervolume defined by pre-CAML data. Regarding *S. diadema*, new records are not included in the pre-CAML hypervolume but considering the species wide distribution, geographic and environmental spaces are not significantly modified (Wisz et al., 2008).

TABLE 3 Ratio of post-CAML records not included in the pre-CAML based environmental hypervolume over the total number of occurrence records

Species	Ratio of new points not included in pre CAML hypervolume
Ctenocidaris nutrix	49/60
Dermechinus horridus	3/13
Rhynchocidaris triplopora	8/18
Sterechinus diadema	26/106
Sterechinus neumayeri	9/30

The ground-truthing approach is a field-based method that compares model predictions with independent field data. In our study, an independent dataset was obtained from cruises carried out during the CAML period. The approach generated new results as well as more detailed information than the one obtained using the TSS approach. In addition, the ground-truthing approach allows to identify little sampled areas that are in need of new investigations. Therefore, the two approaches generate complementary information to evaluate the predictive performance of models.

4.2 | Sampling tools

The SDM ground-truthing highlights key differences between model projections and presence/absence data subsequently collected in the field. However, most model false predictions are due to FP that are mainly due to the low number of campaigns. For instance, in the Kerguelen Plateau area, FP of models generated for the three species *C. nutrix*, *S. diadema* and *D. horridus* are associated to the POKER II campaign. This campaign was a fish biomass survey in the northern Kerguelen Plateau (Duhamel & Hautecoeur, 2009). The high proportion of FP obtained during the campaign can be explained by the type of sampling gear deployed, a demersal otter trawl, which is designed to catch fish but is not well suited to sampling benthic species such as echinoids.

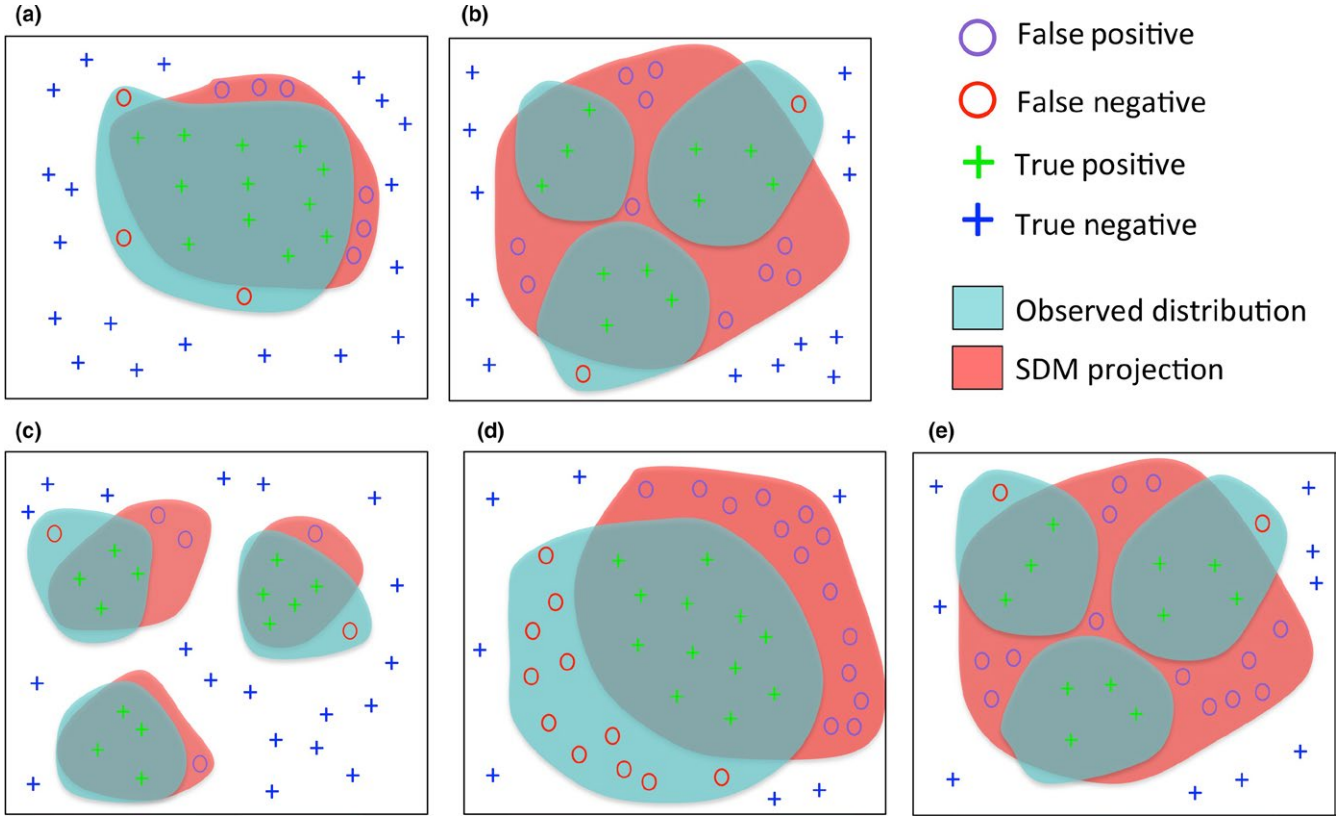

FIGURE 6 Theoretical representation of matching patterns between SDM and observed distribution data for the different species under study. (a) *C. nutrix*, (b) *R. triplopora*, (c) *D. horridus*, (d) *S. diadema*, (e) *S. neumayeri* [Colour figure can be viewed at wileyonlinelibrary.com]

Sampling gear selection is determined by the extent of the area to be investigated during campaigns and by the target organisms to be caught. However, each type of sampling gear presents specific benefits and limitations. Several studies have emphasized the relevance of using different, complementary gears at a same location to obtain a more comprehensive assessment of biodiversity distribution (Bouchet, Lozouet, Maestrati, & Heros, 2002; Flannery & Przeslawski, 2015; Ghiglione et al., 2017). This sampling strategy was adopted in several campaigns such as the CEAMARC campaign led in East Antarctica (Dettai et al., 2011; Hosie et al., 2011), campaigns ANT XXIX and ANT XXIII and campaign JR 144 along the Antarctic Peninsula (Gutt, 2008, 2013; Linse, 2006).

4.3 | SDM robustness and the ecological niche

The addition of new data to SDMs significantly changed the prediction of species distributions but the intensity of these changes vary between species as a function of ecological niche width (Figure 6). SDMs generated for broad-niche species with high tolerance to environmental variations are less robust than those produced for narrow niche species with low tolerance to environmental variations (Hernandez et al., 2006; Lobo & Tognelli, 2011; Mateo, Felicísimo, & Muñoz, 2010; Tessarolo et al., 2014) because modelling all abiotic conditions suitable to wide niche species is more challenging and leads to underestimating species potential distribution. Consequently, the addition of new data tends to refine model projections. Here, this is exemplified for *S. diadema* that is the studied species with the most extensive distribution and the widest ecological niche (Figure 6d). Formerly, the species distribution was underestimated but the species environmental space was better captured during the CAML sampling period, which is reflected in model outputs. In contrast, in narrow niche species, species tolerance to the abiotic environment is low and modelling species ecological niches is less difficult. In our study, *R. triplopora* and *S. neumayeri* are two species with relative narrow niches. Accordingly, the addition of new data induced few changes in the predicted distributions as well as in the contribution of environmental predictors.

4.4 | The significance of biogeographic barriers

Abiotic factors and dispersal capacity are the two main factors constraining species distribution. Understanding the relative importance of both factors is a necessary condition to carry out relevant SDMs and interpret distribution projections (Saupe et al., 2012). In the SO the major biogeographic barrier to species dispersal is represented by the Polar Front (PF). However, this barrier can be permeable to many organisms (Clarke, Barnes, & Hodgson, 2005) depending on their ecology and dispersal capabilities. In marine organisms, dispersal capabilities are closely, although not exclusively linked to the existence and duration of a larval stage in the development. In the

SO, planktonic larvae can be transported over long distances by the ACC and the Antarctic Costal Current, which are two important dispersal vectors and connectivity mechanisms between populations (Díaz et al., 2011; González-Wevar et al., 2017; Moreau et al., 2017).

Among the five studied species, *D. horridus*, *S. neumayeri* and *S. diadema* are three broadcast spawners with planktonic larvae of long duration (115 days) and have relative high dispersal capabilities (Bosch, Beauchamp, Steele, & Pearse, 1987). *S. diadema* is the studied species with the widest distribution range that was modelled on both sides of the PF. Biogeographic barriers and the associated environmental gradients do not impact the species distribution that corresponds to the Hutchinson's Dream-style configuration of Saupe et al. (2012). This means that abiotic factors (i.e., depth, sea ice and sea floor temperature) are the main drivers of species distribution over the study area.

C. nutrix is a brooding species with a much more limited distribution range than *S. diadema*. Mainly limited to the sub-Antarctic waters and the PF zone, it is almost not predicted on the continental shelf. Despite a limited distribution range and low dispersal capabilities, the PF does not seem to act as a biogeographic barrier as the species is found on both sides of this marine barrier. Therefore, a priori poor dispersal capabilities do not necessarily imply dispersal—limitation by biogeographic barriers and make SDM over the entire species distribution range relevant (Figure 6a).

The two species *S. neumayeri* and *R. triplopora* have a discontinuous distribution range around the Antarctic continent and consequently, results of the ground-truthing analysis showed a large proportion of FP (Figure 6b,e) observed on the Antarctic shelf. However, both species are Antarctic echinoids limited by the PF to the Antarctic continental shelf and southern part of the Kerguelen Plateau. The two species illustrate the Full Overlap-style configuration (Saupe et al., 2012) with a good match between the PF acting as a barrier to dispersal and the limiting environmental factors (i.e., sea ice, depth, seafloor temperature and geomorphology). Interestingly, SDMs of the two species remained almost unchanged when new presence data were added to the models, stressing model robustness and accuracy, as environmental descriptors can fully explain the species distribution.

D. horridus is exclusively present around sub-Antarctic islands and is characterized by a fragmented distribution (Figure 6c) on deep-sea slopes of oceanic plateaus. It is a broadcaster, which suggests good dispersal capabilities, but the PF acts as a total biogeographic barrier to the species distribution that is also limited by abiotic factors to the slopes of the sub-Antarctic plateaus and to the PF zone and sub-Antarctic waters. The species distribution is determined both by abiotic factors and a biogeographic barrier, which corresponds to the classic BAM-style configuration (Saupe et al., 2012), in which both the environment and dispersal–limitations determine species distribution. The presence of a biogeographic barrier (PF) to the species dispersal can alter SDM relevance and robustness (Saupe et al., 2012). This could account for the relative SDM instability when new data are included in the model (Figure 3).

4.5 | The relevance of the SDM approach to SO biological studies

4.5.1 | The relevance of the SDM approach

According to the ecological niche theory, abiotic factors determine the species fundamental niche (no biotic interactions), which is used as an approximation of the realized niche (both abiotic and biotic factors taken into account) to predict the species potential distribution (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Peterson, 2011). The approach is particularly relevant at broad spatial scale, when species distribution is strongly controlled by several, major abiotic factors with limited impact of biotic interactions and biogeographic barriers (Peterson, 2011; Saupe et al., 2012; Soberón, 2007; Soberón & Nakamura, 2009). In marine biomes, water temperature, salinity and depth are three abiotic factors that often determine the main patterns of species distribution (Gogina, Glockzin, & Zettler, 2010; Pierrat et al., 2012; Reiss, Cunze, König, Neumann, & Kröncke, 2011). In the present study, a restricted set of abiotic factors repeatedly represents the main contributors to SDMs. This set includes sea ice concentration, seafloor and sea surface salinity, depth, and seafloor temperature. These factors seem to be important drivers of species distribution at broad spatial scale, thereby supporting the use of SDMs to predict marine species distribution at the scale of the SO.

4.5.2 | SDM and climate change

Identifying the main parameters that control species distribution is central in the current context of climate change. The SO and the polar regions are facing some of the fastest rates of environmental change on the planet (Gutt et al., 2015; Helm, Bindoff, & Church, 2010; Jacobs, 2002; Meredith & King, 2005; Turner et al., 2014). Such changes will affect benthic communities among which echinoid fauna (Brown, Fraser, Barnes, & Peck, 2004; Gutt, 2001; Gutt & Piepenburg, 2003; Gutt & Starmans, 2001; Smale, Brown, Barnes, Fraser, & Clarke, 2008).

Numerous studies have shown the sensitivity of Antarctic species to temperature change (Barnes & Peck, 2008; Ingels et al., 2012; Peck, 2005; Peck, Morley, & Clark, 2010; Peck, Webb, & Bailey, 2004). Typically, the high Antarctic species *S. neumayeri*, the most studied echinoid in the SO, shows a high sensitivity of its planktonic larvae to water warming and freshening, which could lead to a decrease in the reproductive and development success of the species (Cowart, Ulrich, Miller, & Marsh, 2009; Ericson et al., 2012). Sub-Antarctic echinoids such as *D. horridus* could be expected to migrate southward if environmental conditions became warmer to the south. On the contrary, narrow niche species that are endemic to the Antarctic shelf and strictly adapted to freezing conditions such as *S. neumayeri* and *R. triplopora* might be more impacted, especially along the Antarctic Peninsula that is subject to fast warming (Meredith & King, 2005; Turner et al., 2014).

If species distribution partly reflects abiotic environmental constraints, species life history traits and plasticity will also condition dispersal limitations and the capacity of organisms to survive. In our study, the two brooding species *R. triplopora* and *C. nutrix* have smaller distribution areas than the three broadcasting species. Our results show that the distribution of the Antarctic species *R. triplopora* is restricted to the Antarctic shelf like *S. neumayeri* but has a less extensive distribution. Similarly, *C. nutrix* is mainly located on the northern Kerguelen Plateau and is rare on the Antarctic shelf. Conversely, *S. diadema* and *S. neumayeri* are broadcasters that are not limited by biogeographic barriers but are mainly constrained by abiotic conditions.

4.5.3 | SDM, marine protected areas and conservation issues

Since 2004, the CCAMLR (Commission of the Conservation of Antarctic Marine Living Resources) has worked on the establishment of an extended network of marine protected areas (MPAs) for the SO. MPAs have been established in the Ross Sea (CCAMLR, 2016) and the South Orkney Islands southern shelf (CCAMLR, 2009). National initiatives also led to the creation of MPAs around the Kerguelen and Crozet Islands (Koubbi, Guinet, et al., 2016; Koubbi, Mignard, et al., 2016), Heard and McDonald Islands (Commonwealth of Australia, 2014), the South Georgia and the South Sandwich Islands (Trathan et al., 2014), and the Prince Edward Islands (Lombard et al., 2007). Moreover, MPA proposals were submitted for the East Antarctic (CCAMLR, 2013) and the Weddell Sea (Teschke et al., 2013). In this context, SDMs have proved their value in improving our understanding of species distribution patterns and in designating potential MPAs (Hibberd, 2016; Koubbi, Guinet, et al., 2016).

However, our results show the importance of data quantity and quality control to ensure the relevance and reliability of the SDM approach. Presence-only datasets have to be used with caution. Sampling bias can affect the environmental space (Bystriakova et al., 2012; Loiselle et al., 2007) and impact SDM predictions and robustness. During the last 10 years, new methods have been developed to take into account sampling bias (Fithian, Elith, Hastie, & Keith, 2015; Phillips et al., 2009; Saucède, Pierrat, & David, 2014; Stolar & Nielsen, 2015). SDMs can provide a prediction of species potential distribution but need fieldwork studies to collect complementary data, identify potential gaps and test for SDM accuracy. In the SO, relevant sampling methods remain an important issue to limit biases related to False Positive predictions. We recommend to follow the framework provided by the CAML (Schiaparelli et al., 2013). Several gear types should be deployed with different mesh sizes at the same location for a good biodiversity assessment. The present results also show the need to better prospect certain areas of the SO that remain under-sampled. For example, the southern part of the Kerguelen Plateau has been poorly investigated (De Broyer et al., 2014) while it is a significant area for the connectivity between the sub-Antarctic islands (Kerguelen, Crozet, Heard Islands) and the Antarctic shelf.

Most of the biological sampling effort in the SO has been concentrated to the first 400 m in depth (Fabri-Ruiz et al., 2017). Exploring deeper areas remain a priority as many Antarctic shelf species extend their distribution range to 1,000 m depth and below such as the studied species *D. horridus* or *S. diadema* (Saucède, Pierrat, & David, 2014). Such an endeavour is only feasible in the framework of concerted efforts through international programs such as the CAML and IPY initiatives. In the present work, we wish to encourage conservationists and environmental managers to consider using species distribution modelling as a supplementary tool for conservation issues in the SO. We also think that SDM can conveniently assist scientists for planning future fieldwork programs and complement our knowledge of the SO marine life in little explored areas of this vast region.

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BIOSKETCH

Salomé Fabri-Ruiz is a PhD student. She is interested in species distribution modelling and spatial ecology applied to large scale area. Her current research focus on quantifying and mapping benthic marine biodiversity in the Southern Ocean using several statistical and mathematical methods.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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