ISSN 1062-3590, Biology Bulletin, 2020, Vol. 47, No. 6, pp. 683–698. © Pleiades Publishing, Inc., 2020.

ECOLOGY

Diversity of Antarctic Echinoids and Ecoregions of the Southern Ocean

S. Fabri-Ruiz[a, b, *], N. Navarro[a, c, **], R. Laffont[a, *], B. Danis[b, ****], and T. Saucède[a, *****]**

[a]*UMR 6282 Biogéosciences, CNRS, EPHE, Université Bourgogne Franche-Comté, Dijon, 21000 France*

[b]*Marine Biology Lab, Université Libre de Bruxelle, Brussels, 1050 Belgium*

[c]*EPHE, PSL University, Paris, 75014 France*

**e-mail: salome.fabriruiz@gmail.com*

***e-mail: nicolas.navarro@u-bourgogne.fr*

****e-mail: remi.laffont@u-bourgogne.fr*

*****e-mail: bdanis@ulb.ac.be*

******e-mail: thomas.saucede@u-bourgogne.fr*

Received February 26, 2020; revised May 5, 2020; accepted May 5, 2020

Abstract—Significant environmental changes have already been documented in the Southern Ocean (e.g. sea water temperature increase and salinity drop) but its marine life is still incompletely known given the heterogeneous nature of biogeographic data. However, to establish sustainable conservation areas, understanding species and communities distribution patterns is critical. For this purpose, the ecoregionalization approach can prove useful by identifying spatially explicit and well-delimited regions of common species composition and environmental settings. Such regions are expected to have similar biotic responses to environmental changes and can be used to define priorities for the designation of Marine Protected Areas. In the present work, a benthic ecoregionalization of the Southern Ocean is proposed based on echinoids distribution data and abiotic environmental parameters. Echinoids are widely distributed in the Southern Ocean, they are taxonomically and ecologically well diversified and documented. Given the heterogeneity of the sampling effort, predictive spatial models were produced to fill the gaps in between species distribution data. A first procedure was developed using Gaussian Mixture Models (GMM) to combine individual species models into ecoregions. A second, integrative procedure was implemented using the Generalized Dissimilarity Models (GDM) to model and assemble species distributions. Both procedures were compared to propose benthic ecoregions at the scale of the entire Southern Ocean.

DOI: 10.1134/S1062359020060047

INTRODUCTION

Polar seas are among the regions on Earth that are undergoing climate change at a fast pace (Convey et al., 2009; Turner et al., 2014; Gutt et al., 2015). In the Southern Ocean, herein defined as water masses extending from the Antarctic continent to about 45° S latitude, increase in sea water temperature, water acidification, salinity decrease, and changes in sea ice regimes have already impacted the structure and functioning of marine ecosystems (Smith, 2002; Mélice et al., 2003; Rouault et al., 2005; Le Roux and McGeoch, 2008; Reygondeau and Huettmann 2014; Gutt et al., 2015). Southern Ocean marine life is particularly vulnerable to such environmental changes (Guillaumot et al., 2018; Ingels et al., 2012; Lohrer et al., 2013; Peck et al., 2004, 2010; Peck, 2005) due to unique physiologic and ecological traits including adaptations to subzero temperatures (Eastman, 2000; Cheng and William, 2007; Portner et al., 2007), high levels of endemism (Brandt et al., 2007; Griffiths et al., 2009; Kaiser et al., 2013; Saucède et al., 2014), and brooding behaviors (David and Mooi, 1990; Hunter and Halanych, 2008; Sewell and Hofmann, 2011). Further, ecosystems are also under the impact of direct anthropogenic pressures induced by fisheries, tourism and cruise ships (Lenihan et al., 1995; Aronseon et al., 2011). In this context, mapping the distribution of marine species is a prerequisite to good conservation practices.

Echinoids are well-diversified in the Southern Ocean with 10% of species worldwide and most species (68%) are endemic to the Southern Ocean (David et al., 2005). They are widely distributed in all marine habitats, from shallow areas of the continental shelf to deep abyssal plains and down to 6200 m depth (Mironov, 1995; Arnaud et al., 1998; Barnes and Brockington 2003; David et al., 2005; Brandt et al., 2007; Linse et al., 2008). They belong to various ecological guilds and count epifaunal and endofaunal spe-

cies that display various feeding behaviors (omnivorous, deposit-feeders, carnivorous, phytophagous/algivorous, scavengers), spawning modes (broadcasting or brooding), and developmental strategies (direct developers or indirect development including a planktonic larval stage) (see, e.g., Poulin and Féral, 1996; David et al., 2005; Saucède et al., 2014 for a synthesis). In addition, ctenocidarid echinoids include a large number of species in which primary spines provide suitable microhabitats to a wide variety of sessile organisms (Hétérier et al., 2004; Linse et al., 2008; Hardy et al., 2011).

Our knowledge of echinoid species distribution in the Southern Ocean is still fractional and biased by uneven sampling efforts and the spatio-temporal aggregation of data collection (Gutt et al., 2012; Guillaumot et al., 2018, 2019). Statistical tools and modeling approaches however have been developed to address this issue and determine the genuine factors that determine species distribution (Newbold, 2010; Barbet-Massin et al., 2012; Hijmans, 2012; Tessarolo et al., 2014; Guillaumot et al., 2018, 2019; Valavi et al., 2018). Ecological Niche Models (ENM), also known as Species Distribution Models offer a baseline for detecting, monitoring and predicting the impact of climate change on species and biota (Gutt et al., 2015; Kennicutt et al., 2015). An increasing number of studies have used ENM to predict the distribution of pelagic species in the Southern Ocean (Duhamel et al., 2014; Loots et al., 2007; Nachtsheim et al., 2017; Pinkerton et al., 2010; Thiers et al., 2017; Xavier et al., 2016) but few were developed for benthic organisms (see however: Basher and Costello, 2016; Gallego et al., 2017; Pierrat et al., 2012; Guillaumot et al., 2019; Fabri-Ruiz et al., 2019).

The ecoregionalization approach combines the analysis of environmental data and species distribution (Koubbi et al., 2011; Douglass et al., 2014) to identify spatially explicit, highly cohesive, and well-delimited regions of common species composition and environmental settings. They are delimited from adjacent areas by distinct but dynamic boundaries and constitute operational areas to address conservation issues (Grant, 2006; Koubbi et al., 2011; Gutt et al., 2018). Applied to the marine realm, ecoregions can be used to define priority areas for the designation of Marine Protected Areas (MPAs) and support management plans. In the Southern Ocean, ecoregions have been delineated for conservation purposes (Koubbi et al., 2016a, 2016b) based on fish assemblages (Koubbi et al., 2010, 2011; Hill et al., 2017).

In the present work, we analyze the main distribution patterns of echinoid species diversity in the Southern Ocean. Then we propose a benthic ecoregionalization of the Southern Ocean based on ENM generated with species distribution records and environmental descriptors, using an integrative approach that combines two complementary procedures. The first procedure was developed to model individual species distributions as a function of environmental descriptors and then combine all ENMs into ecoregions (Dubuis et al., 2011; Calabrese et al., 2014). Following a "predict then assemble" strategy (Ferrier and Guisan, 2006), we used a novel approach combining ENM using Random Forests (Breiman, 2001) and model-based clustering with Gaussian Mixture Models (Fraley and Raftery, 2006) following the procedure recently developed by Fabri-Ruiz et al. (2020). This procedure can provide the composition of species assemblages for each ecoregion but most common species only can be used as representative of the total fauna. A second, integrative procedure was implemented using the Generalized Dissimilarity Models (GDM) to model and assemble species distributions at the same time (Ferrier et al., 2007). All species occurrences are considered, including rare species, but the composition of species assemblages within ecoregions cannot be detailed. Both procedures are complementary and were compared to propose common benthic ecoregions at the scale of the entire Southern Ocean. These general ecoregions based on echinoid fauna can proove useful to address conservation issues.

MATERIALS AND METHODS

Study Area

The study area covers the Southern Ocean, herein defined as water masses extending from the Antarctic continent to 45° S latitude (Fig. 1a), at depths ranging from the surface to 2500 m, a depth range for which most species occurrence data were available. The area includes the Antarctic continental shelf and slope, Subantarctic islands and plateaus, and the continental shelf and slope of southern South America. The Southern Ocean is bordered to the north by the uninterrupted eastward drift of the Antarctic Circumpolar Current (ACC) that continuously circles around the Antarctic continent due to the absence of landmass and physical barriers. Associated to the ACC, there are several oceanographic fronts that isolate warmer Subtropical waters in the north from colder Subantarctic and Antarctic waters in the south and locally generates very steep latitudinal gradients in sea water temperatures and related abiotic and biotic factors of the environment (Sokolov and Rintoul, 2002; Roquet et al., 2009).

Occurrence Records and Studied Species

Species occurrence data were retrieved from an extensive and checked database that includes over 7100 georeferenced records from field samples collected between 1872 and 2015 (Fabri-Ruiz et al., 2017). Taxonomy and georeferenced positions were updated and checked for accuracy. Data are available at http://ipt.biodiversity.aq/resource?r=echinoids_occurrences_southern_ocean and includes occurrence records of all echinoid species reported in the South-

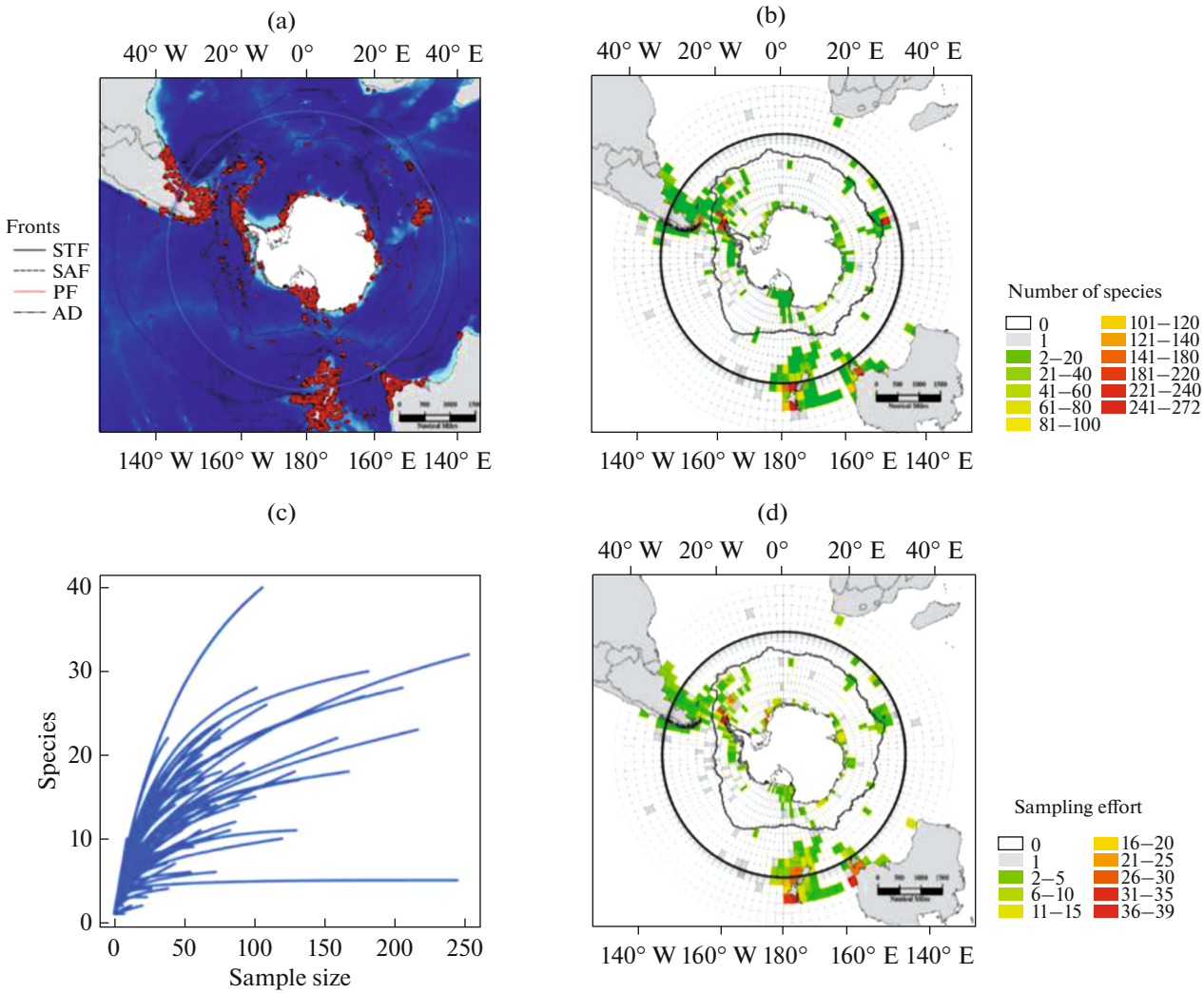


Fig. 1. Map showing all echinoid species occurrence records (red dots) of the database published by Fabri-Ruiz et al. 2017 (a), species richness values for 3 × 3 degree quadrats (b), with species accumulation curves per quadrat (c) and sampling effort for 3 × 3 degree quadrats (d). The position of 45° S latitude is displayed with the blue (a) and black circles (b, d). STF: Subtropical Front, SAF: Subantarctic Front, PF: Polar Front, AD: Antarctic Divergence.

ern Ocean from the Antarctic continent to 35° S latitude. In total, 201 species belonging to 31 families are reported in the database, many of them are endemic to the Southern Ocean (Saucède et al., 2014). Only species occurence data recorded south of 45° S were considered in the present analysis (Fig. 1a). Species records were aggregated to a pixel size of 0.1° × 0.1°, a scale determined by the resolution of environmental data available. Duplicates of species occurrence were removed from each pixel as occurrence duplication may bias model outputs (Guillaumot et al., 2019). Species richness and sampling effort were then computed for each 3 × 3 degree quadrat and geographic patterns displayed on maps (Figs. 1b, 1d). Patterns of species richness and sampling effort were also computed according to latitude (total number of species recorded for each 5 degree latitudinal band) and depth (total number of species recorded for each 200 m interval) from raw data extracted and checked from Fabri-Ruiz et al.'s occurrence database (Figs. 2b–2e).

Environmental Descriptors

Environmental descriptors were selected based on data availability and ecological relevance for explaining the distribution of echinoids as recommended in former studies on the subject (Pierrat et al., 2012; Saucède et al., 2014; Fabri-Ruiz et al., 2018, 2020) and more widely, for species distribution modelling (Anderson, 2013; Franklin, 2010). They were extracted from the database compiled by Fabri-Ruiz et al. (2017) and averaged for the (2005–2012) period. Prior to modeling, collinearity between descriptors was checked to limit possible biases in estimates of predictor contribution and in model predictive perfor-

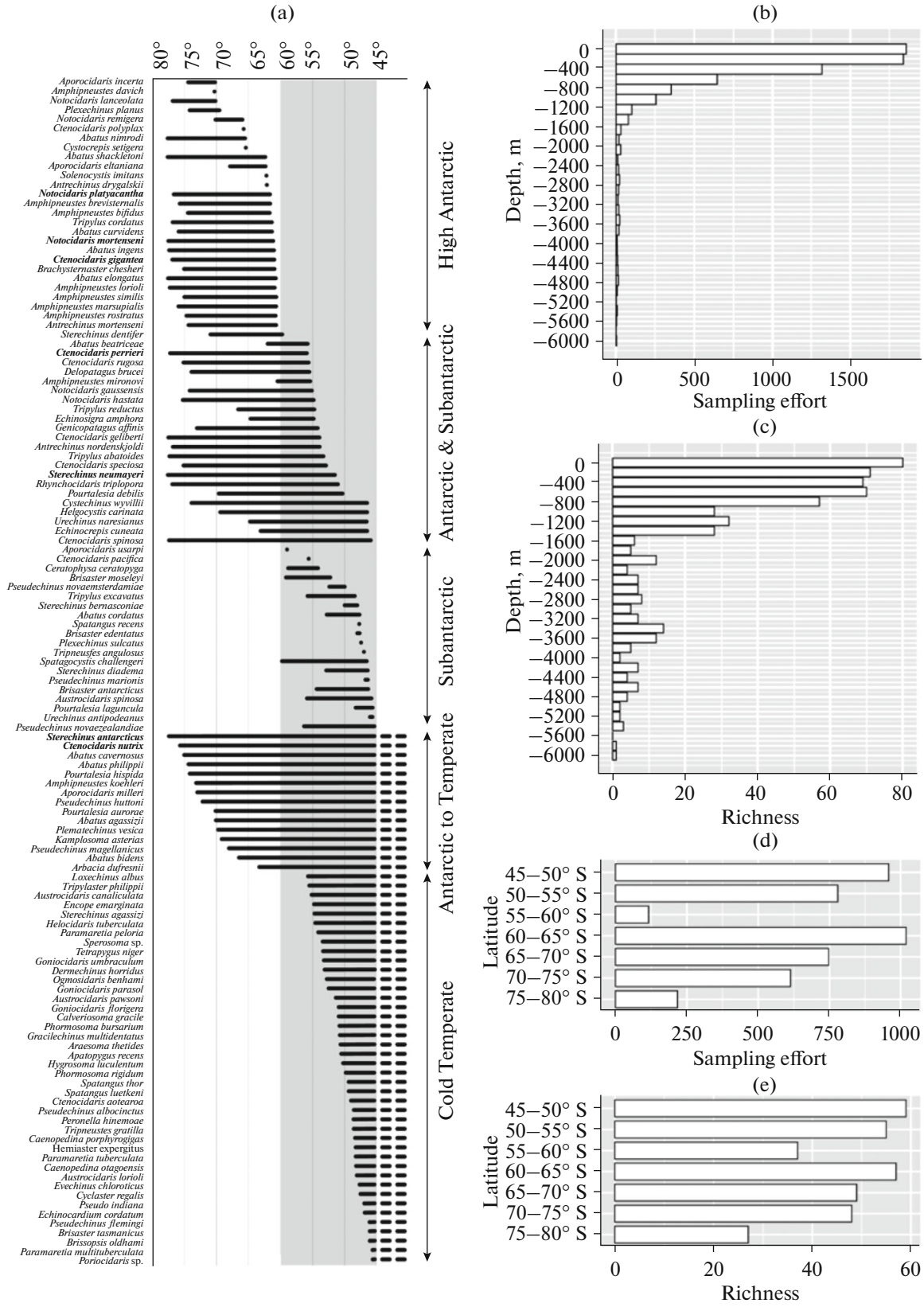


Fig. 2. Latitudinal distribution range of the 127 echinoid species recorded south of 45° S latitude. Species rank ordered from top to bottom by decreasing latitude. Dotted lines indicate distribution ranges that extend northward beyond 45° S latitude. Shaded grey corresponds to the Subantarctic area as delimited to the south by the Polar Front and to the north by the Subtropical Front (a). Overall sampling effort (b) and depth gradient of echinoid species richness (c). Sampling effort (d) and latitudinal gradient (e) of echinoid species richness in the Southern Ocean.

Table 1. Environmental descriptors used for RF and GDM models

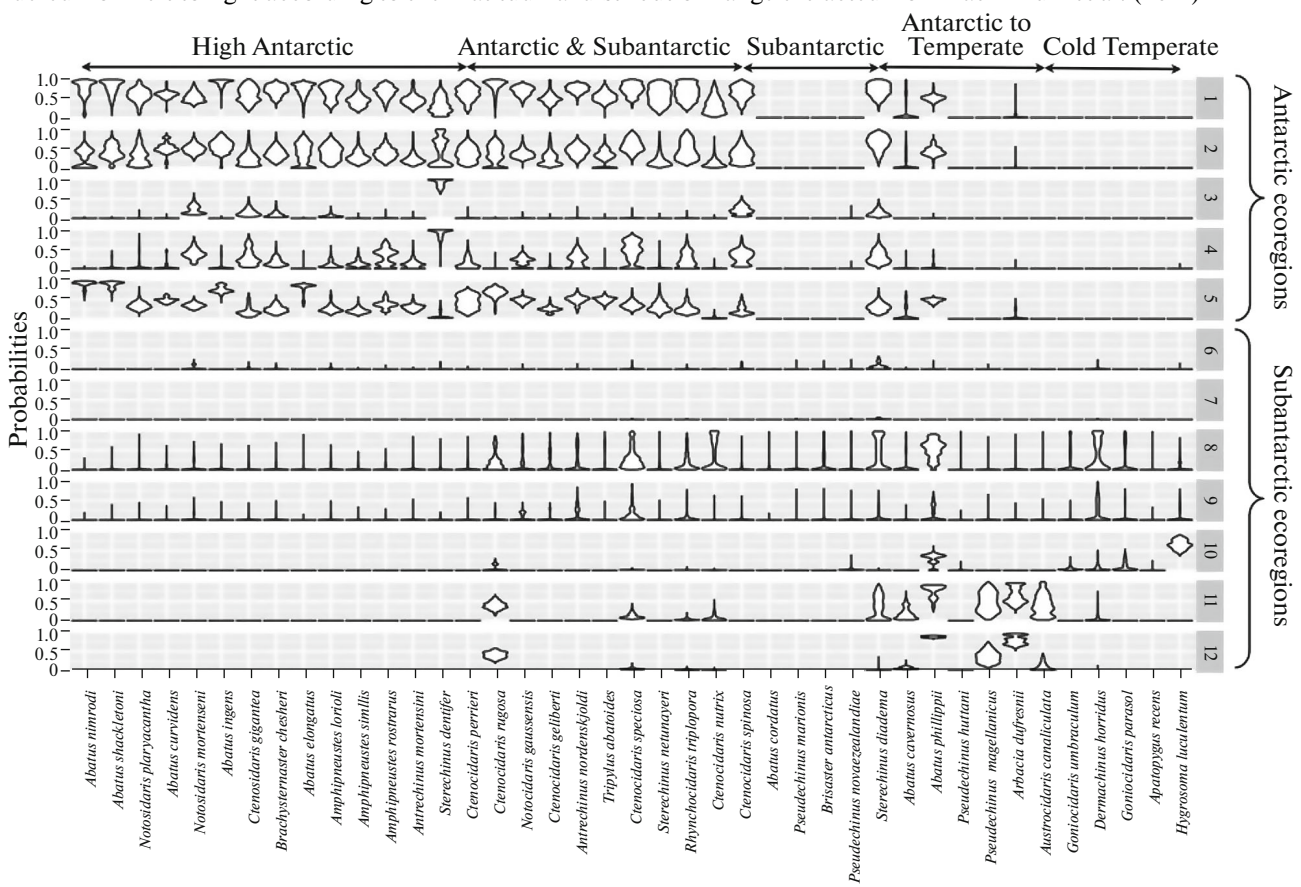
Environmental data	Years	Units	Sources
Depth		Meter	http://topex.ucsd.edu/WWW_html/mar_topo.html
Geomorphologic features		Categorial	ATLAS ETOPO2 2014 (Douglass et al., 2014)
Sea surface salinity range	2005–2012	PSS	https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Sea ice concentration			(Mormède et al., 2014)
Sea surface salinity	2005–2012	PSS	https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Sea surface temperature range	2005–2012	Celsius degrees	https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Seafloor oxygen concentration	1955–2012	mL/L	https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Seafloor salinity	2005–2012	PSS	https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Seafloor salinity range	2005–2012	PSS	https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Seafloor temperature	2005–2012	Celsius degrees	https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Seafloor temperature range	2005–2012	Celsius degrees	https://www.nodc.noaa.gov/OC5/woa13/woa13data.html
Slope		Unitless	(Mormède et al., 2014)
Summer chlorophyll concentration	2002–2009	mg/m^3	(Mormède et al., 2014)

mance using the Pairwise Pearson's correlation computed with the *virtual species* R package (Leroy et al., 2016). For correlation values exceeding 0.7, one predictor of a pair was removed based on ecological arguments that is, the most relevant predictor for modeling and interpreting echinoid distribution (Saucède et al., 2014; Fabri-Ruiz et al., 2018, 2020). Finally, 13 descriptors were used to run Random Forest models (RF) and 10 for the Generalized Dissimilarity Model (GDM) approach as categorical variables cannot be run in GDM. The selected environmental descriptors reflect the main settings of echinoid physical habitats (depth, geomorphology, slope, sea surface temperature range, seafloor temperature range, mean seafloor temperature, sea ice cover for Antarctic species), food resources (chlorophyll a concentration) and habitat chemistry (seafloor oxygen, seafloor salinity range, mean seafloor salinity, sea surface salinity range, mean sea surface salinity) (Table 1).

Species Distribution Modeling

Random forest and gaussian mixture models (RF-GMM). Species recorded with less than 15 pixels after pixel aggregation were not included in the analysis to ensure statistical robustness of models. Individual species distribution models were produced for 41 echinoid species using the Random Forest algorithm (RF, Breiman, 2001) (Table 2). The selected species are distributed over the entire study area, from Subantarctic islands and continental shelves to the deep Antarctic slope. They belong to nine families and are representative of the diversity of Antarctic echinoid taxa and show various dispersal modes and feeding strategies. The RF was proved relevant for modeling Antarctic echinoid distribution (Fabri-Ruiz et al., 2018, 2020) and models were performed using the *biomod 2* package (Thuiller et al., 2009) under R.3.4 (R Core Team, 2017). The number of classification trees was set to 500 and the node size to 5. The Mtry parameter (the number of candidate variables to include at each split) was tuned using tune RF function from the *caret* package (Kuhn, 2012). For each species, occurrence datasets were divided into two subsets: the first one (gathering 70% of occurrences) was used as training data and the second one (with the remaining 30% of occurrences) as test data. As presence-only data are available, pseudo-absences were generated following Barbet-Massin et al. (2012), with a number of pseudo-absences equal to the number of presences. To limit the effect of the uneven sampling efforts, the selection of pseudo-absences was weighted based on a Kernel Density Estimation (KDE) map used as a proxy of the sampling effort. The KDE map was established from all echinoid records of the database using Spatial Analyst in ArcGIS v10.2 (ESRI 2011) and following Guillaumot et al. (2019). This method can also limit the effect of spatial autocorrelation and the risk of unreliable model evaluation. Spatial autocorrelation can occur in model residuals and several replicates of pseudo-absences were generated to mitigate it during model calibration (Legendre 1993). The Moran's I index, which varies between -1 (negative spatial autocorrelation) and $+1$ (positive spatial autocorrelation) was computed as a measure of spatial autocorrelation using the *ape* R package (Paradis et al., 2008). Thirty

Table 2. Presence probability of the 41 echinoid species used for the RF-GMM model within each ecoregion. Species are ordered from left to right according to their latitudinal distribution range extracted from Fabri-Ruiz et al. (2017)



replicates of pseudo-absences were then selected with $p > 0.5$ (with p, the probability of null Moran's I).

From calibrated models, spatial projections of presence probability were generated using the selected set of environmental predictors. Individual species projections were then combined to delineate benthic ecoregions using Gaussian Mixture Models (GMM). GMM assumes that data are from a *finite* set of classes and data within each class can be modeled using a Gaussian distribution, the population being considered as a mixture. GMM were run with the *mclust* R package (Fraley and Raftery, 2006) and model VII that performed best to fit the data based on the BIC index (Bayesian Information Criterion) (Scrucca et al., 2016). The optimal number of clusters was estimated by successively combining mixture components to minimize the entropy level.

Generalized dissimilarity models. The Generalized Dissimilarity Model (GDM) is a nonlinear regression method used to reveal patterns of beta diversity and predict faunal dissimilarity between sites as a function of environmental differences (Ferrier et al., 2007). GDM has the advantage to consider all species occurrence data including rare species in contrast to the RF-GMM approach. However, only sites (=pixels) with more than four species records were selected for modeling given the low deviance values. Finally, 85 species were retained (Table 3). Environmental predictors used for GDM are chlorophyll-a concentration, depth, seafloor oxygen concentration, seafloor salinity range, seafloor salinity, seafloor temperature range, surface salinity range, sea surface salinity, slope and sea ice concentration.

To fit the model, a species dissimilarity matrix between all station pairs based on the Jaccard index is required. A set of I-spline functions is fitted for each predictor with the dissimilarity matrix as a response variable. The I-spline associated to each variable describes the relationship between beta diversity and the environmental gradient. Environmental descriptors are then transformed using this combination of I-spline functions and a PCA is performed to reduce dimensionality. Based on the correlation between the 10 environmental descriptors and beta diversity between stations, the algorithm predicts the ecological distance between all pixels of the map. Predictor contribution to the model is quantified by removing one variable at a time. The explained variance of the model without the considered variable is then compared to the variance of the complete model. All these analyses were performed using the *gdm* R package (Manion et al., 2016). Finally, ecoregions were determined by clustering pixel PCA score values using the Clara algo-

Table 3. List of the 85 echinoid species with enough records to be used in the Generalized Dissimilarity Model (GDM) method

Species	Family	Species	Family	Species	Family
Abatus agassizii	Schizasteridae	*Caenopedina otagoensis*	Pedinidae	*Notocidaris platyacantha*	Cidaridae
Abatus beatriceae	Schizasteridae	*Caenopedina porphyrogigas*	Pedinidae	*Paramaretia peloria*	Spatangidae
Abatus bidens	Schizasteridae	*Ceratophysa ceratopyga*	Pourtalesiidae	*Paramaretia tuberculata*	Spatangidae
Abatus cavernosus	Schizasteridae	*Ctenocidaris geliberti*	Cidaridae	*Phormosoma bursarium*	Phormosomatidae
Abatus cordatus	Schizasteridae	*Ctenocidaris gigantea*	Cidaridae	*Plexechinus planus*	Plexechinidae
Abatus elongatus	Schizasteridae	*Ctenocidaris nutrix*	Cidaridae	*Pourtalesia aurorae*	Pourtalesiidae
Abatus ingens	Schizasteridae	*Ctenocidaris perrieri*	Cidaridae	*Pourtalesia debilis*	Pourtalesiidae
Abatus nimrodi	Schizasteridae	*Ctenocidaris rugosa*	Cidaridae	*Pourtalesia hispida*	Pourtalesiidae
Abatus philippii	Schizasteridae	*Ctenocidaris speciosa*	Cidaridae	*Pourtalesia laguncula*	Pourtalesiidae
Abatus shackletoni	Schizasteridae	*Ctenocidaris spinosa*	Cidaridae	*Pseudechinus albocinctus*	Temnopleuridae
Amphipneustes brevisternalis	Schizasteridae	*Cystechinus wyvillii*	Urechinidae	*Pseudechinus flemingi*	Temnopleuridae
Amphipneustes koehleri	Schizasteridae	*Delopatagus brucei*	Schizasteridae	*Pseudechinus huttoni*	Temnopleuridae
Amphipneustes lorioli	Schizasteridae	*Dermechinus horridus*	Echinidae	*Pseudechinus magellanicus*	Temnopleuridae
Amphipneustes marsupialis	Schizasteridae	*Echinocardium cordatum*	Loveniidae	*Pseudechinus marionis*	Temnopleuridae
Amphipneustes mironovi	Schizasteridae	*Echinocrepis cuneata*	Pourtalesiidae	*Pseudechinus novaezealandiae*	Temnopleuridae
Amphipneustes rostratus	Schizasteridae	*Echinosigra amphora*	Pourtalesiidae	*Rhynchocidaris triplopora*	Cidaridae
Antrechinus mortenseni	Plexechinidae	*Evechinus chloroticus*	Echinometridae	*Solenocystis imitans*	Pourtalesiidae
Antrechinus nordenskjoldi	Plexechinidae	*Genicopatagus affinis*	Brissidae	*Spatagocystis challengeri*	Spatangidae
Apatopygus recens	Apatopygidae	*Goniocidaris parasol*	Cidaridae	*Spatangus luetkeni*	Spatangidae
Aporocidaris eltaniana	Cidaridae	*Goniocidaris umbraculum*	Cidaridae	*Spatangus thor*	Spatangidae
Aporocidaris incerta	Cidaridae	*Gracilechinus multidentatus*	Echinidae	*Sterechinus dentifer*	Echinidae
Aporocidaris milleri	Cidaridae	*Helgocystis carinata*	Pourtalesiidae	*Sterechinus diadema*	Echinidae
Arbacia dufresnii	Arbaciidae	*Hygrosoma luculentum*	Echinothuriidae	*Sterechinus neumayeri*	Echinidae
Austrocidaris canaliculata	Cidaridae	*Loxechinus albus*	Echinidae	*Tripylaster philippii*	Schizasteridae
Brachysternaster chesheri	Schizasteridae	*Notocidaris gaussensis*	Cidaridae	*Tripylus abatoides*	Schizasteridae
Brisaster antarcticus	Schizasteridae	*Notocidaris hastata*	Cidaridae	*Tripylus cordatus*	Schizasteridae
Brisaster moseleyi	Schizasteridae	*Notocidaris lanceolata*	Cidaridae	*Tripylus reductus*	Schizasteridae
Brisaster tasmanicus	Schizasteridae	*Notocidaris mortenseni*	Cidaridae	*Urechinus antipodeanus*	Urechinidae
				Urechinus naresianus	Urechinidae

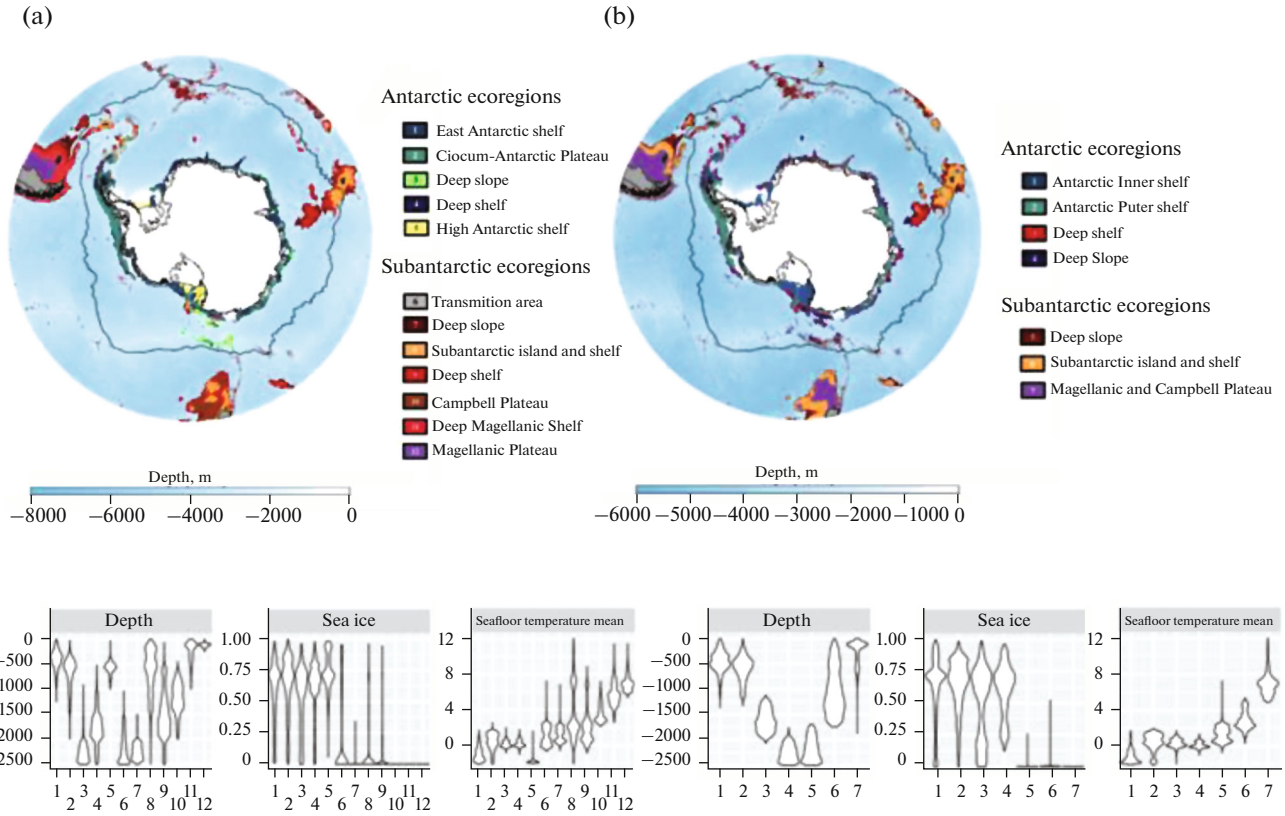


Fig. 3. Map of ecoregions with main contributing variables computed using the RF-GMM (a) and GDM (b) approaches.

rithm (Kaufmann and Rousseeuw, 1990). The number of clusters was defined using the *factoextra* (Kassambara and Mundt, 2016) and *cluster* (Maechler et al., 2012) R packages.

Model comparison. To compare the two ecoregionalization approaches, we performed an overall percentage of agreement between all ecoregions of the two models to propose a common regionalization (Fig. 4a). We first computed the percentage of common pixels between GDM and RF-GMM ecoregions (Fig. 4b). Then, based on this cross-table, we mapped areas of agreement between common ecoregions (Fig. 4a). Because the percentage of agreement between pixels may occur by chance, we computed a Kappa Cohen coefficient between ecoregions corresponding to a perfect matching map (Cohen, 1960). The range of possible values for the Kappa coefficient varies between −1 (worse match than expected by chance) to 1 (perfect match), and usually falls in between 0 (no better agreement than expected by chance) and 1. The Kappa coefficient analysis was performed using *vcd* R package (Meyer et al., 2020).

RESULTS

Species Distribution Range

127 echinoid species are recorded south of 45° S latitude (Fig. 2a). Species latitudinal distribution ranges show the key role played by the Antarctic Polar Front in echinoid distribution. Fifteen species (i.e. 12%) have a wide latitudinal distribution that covers temperate to Antarctic waters and on both sides of the Subantarctic area between 45° and 60° S wherein the position of the Polar Front fluctuates. Accordingly, 88% of species display more restricted distribution patterns attesting the structuring of echinoid diversity patterns with latitude. Five assemblages can be identified. First, 27 species are distributed south of 60° S latitude and never cross the Polar Front. These can be regarded as "high Antarctic." A second set encompasses 23 species that extend south of the Polar Front (60° S) and extend northward as far as 45° S latitude. These can be defined as "Antarctic and Subantarctic." A third pattern corresponds to 20 species distributed between the northernmost and southernmost limits of the Subantarctic area (from 45° S to 60° S) and can be characterized as "true Subantarctic." A fourth pattern is represented by the 15 "widespread" species with extended latitudinal ranges from high Antarctic to cold temperate regions. Finally, a fifth pattern is represented by 42 species that never extend south of 60° S, but extend farther north of 45° S and can be referred to as "cold temperate."

Richness Patterns

Because sampling effort has been uneven in the Southern Ocean (Griffiths et al., 2011) richness pat-

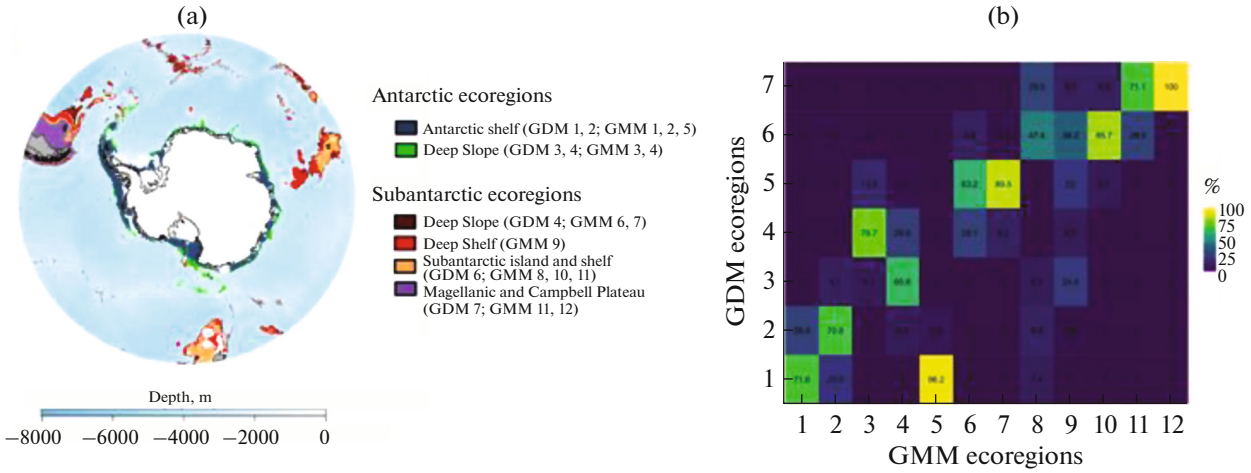


Fig. 4. General echinoid ecoregions of the Southern Ocean after merging the respective ecoregions modeled by the RF-GMM and GDM approaches: map showing the general biogeographic pattern structured into two Antarctic and four Subantarctic ecoregions (a), and the percentage of agreement between the respective ecoregions modeled by the two approaches (b).

terns should be considered with caution (Figs. 1b–1d, 2b–2e). Based on available data, species richness appears the highest along the Antarctic Peninsula and southern Scotia Arc, in the eastern Weddell side and in sectors of East Antarctica (Enderby and Adélie Lands) (Fig. 1b). In latitude, echinoid species richness decreases from 35° S to 60° S, increases from 60° S to 65° S, then decreases again southward until 70° S (Fig. 2e) (Saucède et al., 2014; Fabri-Ruiz et al., 2017). The high number of species recorded between 60° S and 65° S could reflect the high sampling effort devoted to the region of the Antarctic Peninsula (Figs. 1d, 2d) while conversely, sampling effort decreases southward until 70° S. This latitudinal gradient does not match with the global gradient in taxonomic marine diversity that decreases continuously from the tropics to the poles (Crame, 2004). This apparent mismatch between the two gradients could be due to the different scales at which gradients are considered. Hence, the reversal of the richness trend south of 60° S latitude matches both the southern boundary of Subantarctic waters and the southernmost position of the Polar Front that constitutes an oceanographic barrier to marine species dispersal. The Southern Ocean appears particularly enriched in echinoid species. However, this gradient in echinoid richness results from the averaging of longitudinal inequalities and regional peculiarities (Crame, 2004). There is a strong longitudinal inequality between the continental shelf of southern South America, where only 36 echinoid species are recorded and waters south of New Zealand and Australia in which 113 echinoid species and 62 genera were registered. If Antarctica appears as an enriched 'spot' in echinoid diversity, Australasia is definitely a hotspot (Barnes and Griffiths, 2007). Finally, the decrease of echinoid richness south of 65° S latitude can be linked to the narrowing of ocean surfaces at such high latitudes, all the more as most of these areas are under-sampled (Fig. 1d).

The highest number of species occurs between 100 m and 1000 m depth (Fig. 2c). Then species richness sharply decreases below 1500 m depth to reach the lowest values at 5000 m depth and below. Depth gradient clearly shows that the Antarctic continental shelf, which represents about 11% of continental shelf areas worldwide, encompasses the main part of echinoid richness, with that richness decreasing from the shelf break to the slope and deep-sea basins. Echinoid richness on the Antarctic shelf contrasts markedly with that of deep-sea areas in having a much higher number of species, the Antarctic shelf being inhabited by endemic and diversified echinoid taxa, mainly Ctenocidarinae and Schizasteridae. A weak increase in richness at approximately 3000 m depth can be explained by the wide ocean surfaces covered by deep-sea basins, in which a higher number of taxa might occur as compared to the relatively smaller surface of slope areas. However, deep-sea echinoids are still insufficiently known and exploration of deepest areas is still too cursory to assert that richness values might also reflect a true deep-sea diversity as suggested for other taxa (Brandt et al., 2007; Linse et al., 2007).

Echinoid Ecoregions

Twelve benthic ecoregions were identified using the RF-GMM approach (Fig. 3a). Five Antarctic ecoregions are characterized by high sea ice concentration and low sea water temperature values (Fig. 3a). South America (#11–12), the Campbell Plateau (#10) and the northern Kerguelen Plateau (#8) are well individualized. Seven ecoregions only were defined using the GDM procedure (Fig. 3b) with four Antarctic ecoregions with high sea ice concentration that differ

in depth range. The Argentinian and Campbell plateaus are merged into one single ecoregion (#7). Subantarctic Islands and shelf, and deep slopes are grouped into ecoregions #6 and #5 respectively.

Echinoid Assemblages

Echinoid assemblages can be examined for the 41 species used in the RF-GMM procedure (Table 2). According to the RF-GMM approach, 15 species are restricted to the Antarctic, 4 species restricted to the Subantarctic, the remaining species being distributed in both latitudes and in cold temperate areas. In terms of species richness, Antarctic ecoregions are richer with a total of 27 species over 16 species in the Subantarctic, including 9 species in the Magellanic areas and the Campbell plateau. Most Antarctic species are circum-polar in distribution and occur in the five Antarctic ecoregions, some species being widely distributed, such as *Sterechinus diadema*, *Abatus philippii*, and species of the genus *Ctenocidaris* found in ecoregions #1, #2, #5, #8, #9, #11, and #12. High Antarctic species of ecoregion #5 (*Abatus ingens*, *Abatus nimrodi*, *Abatus shackeltoni*, *Abatus elongatus* and *Ctenocidaris rugosa*) are particularly tolerant to very low seafloor temperature. In contrast, endemic species are restricted to Subantarctic ecoregions, such as *Hygrosoma luculentum* (#10), *Abatus cordatus* (#8), *Arbacia dufresni* (#11 and #12), *Austrocidaris canaliculata* (#11 and #12) and species of the genus *Pseudechinus* (#8, #9 or #11, #12) and *Goniocidaris* (#10). These species are either deep-sea (*Hygrosoma luculentum*) or shallow-water species (*Abatus cordatus*). In contrast, Subantarctic ecoregion #8 is characterized by the predominance of cold temperate (i.e. *Dermechinus horridus*) and widely distributed species (i.e. *Ctenocidaris nutrix* and *Ctenocidaris speciosa*). Deep-sea Antarctic and Subantarctic species (*Sterechinus dentifer*, *Sterechinus diadema*, *Ctenocidaris speciosa*, and *Ctenocidaris gigantea*) are widely distributed and not restricted to deep ecoregions (#3, 4, 8, 9) only.

Interestingly, despite contrasting species richness and endemicity levels between Antarctic and Subantarctic ecoregions, the three main echinoid families of the Southern Ocean (Echinidae, Cidaridae, and Schizasteridae) are represented and ecologically diversified in the different ecoregions. Deep-sea ecoregions #6 and #7 show very low suitability values for all species, because the studied species are at the limit of their distribution range. However, it can be assumed that these ecoregions are suitable to deeper species that could not be included in the present analysis due to the limited number of occurrence records.

Merged Ecoregions

A Kappa Cohen coefficient of 0.42 ($p < 0.001$) was computed between the respective ecoregions of the two models, which means that the overall match between ecoregions is significantly better than what can be expected by chance. This coefficient reaches a value of 0.7 ($p < 0.001$) when Antarctic ecoregions only are compared, which indicates a very good match between methods in the Antarctic area. Despite a different number of ecoregions modeled with the two approaches, a relative good match was independently obtained with the RF-GMM and GDM.

Further, the distinct ecoregions defined by the two approaches can be merged together into wider, general ecoregions, which in turn, can be subdivided into smaller/detailed areas depending on the modeling procedure (Fig. 4a). The computed percentage of common pixels between ecoregions (Fig. 4b) indicates that the Antarctic is mainly structured into two main ecoregions: the Antarctic shelf (GDM1, 2; GMM 1, 2, 5) and the deep slope (GDM 3, 4; GMM 3, 4). The Subantarctic area comprises four main ecoregions: the deep slope (GDM 4; GMM 6, 7), the deep shelf (GMM 9), the Subantarctic islands and shelves (GDM 6; GMM 8, 10, 11) and the Magellanic and Campbell plateaus (GDM 7; GMM 11, 12). The deep shelf (GMM 9) is here retained as a distinct ecoregion as it is also present at the limit of the Antarctic zone, south of the Polar Front (southern Kerguelen Plateau), and corresponds to species assemblages associated to particular geomorphologic features (i.e. deep shelf areas).

DISCUSSION

Sampling Effort and Taxonomic Biases

Sampling effort has long been heterogeneous in the Southern Ocean. It has been the highest along the Antarctic Peninsula and off New Zealand (>200 samples), two areas characterized by a high species number (25–30) (Fig. 1b). In contrast, the number of species remains low (2–5 species) in the region of the Kerguelen Plateau while it has been intensively sampled as well (POKER 2 and PROTEKER cruises). Our knowledge of genus and species distributions is strongly biased by the quality of sampling effort. This is evidenced by the comparison between the number of collected samples and the recorded number of species (Fig. 1d).

Several areas have been little sampled including Antarctic waters close to the sea ice margin and deep ocean basins, most records being concentrated in the first 400 meters (Fig. 2b) and in the vicinity of scientific stations like in the north of the Kerguelen Plateau, in Adélie Land or along the Antarctic Peninsula. Conversely, the southern Kerguelen Plateau and eastern sector of the Ross Sea have been little explored (Fig. 1d). Overall, this holds true for latitudes comprised between 55° and 60° S, and south of 70° S (Fig. 2d). These under-sampled parts of the Southern Ocean constitute challenging areas for future scientific cruises. However, new sampling technics and standardizations

over the last few years improved our knowledge of the Southern Ocean biodiversity (Kaiser et al., 2013). Common tools have been developed like ecological niche modeling in order to interpolate occurrence records to under-sampled areas and allow improving our knowledge of species potential distribution areas.

Echinoid Biogeography

Former biogeographic studies (Hedgpeth, 1969, David et al., 2005, Pierrat et al., 2013, Saucède et al., 2014) suggest that echinoid faunas of the Southern Ocean, south of 45° S and less than 1000 m depth, are structured into three main faunal provinces: (1) southern New Zealand, (2) southern South America and the Subantarctic islands and (3) the high Antarctic. Faunal affinities between Subantarctic and South American regions had already been reported for a wide range of taxonomic groups (Barnes and De Grave, 2001; Montiel et al., 2005; Linse et al., 2006; Rodriguez et al., 2007; Griffiths et al., 2009) and have been interpreted as the result of larval dispersal through the Antarctic Circumpolar Current. This hypothesis is also supported by molecular analyses for echinoids with planktonic larvae (Díaz et al., 2011, 2018), although long-distance and either passive drafting (Leese et al., 2010) or active motion of echinoids without planktonic larvae cannot be excluded.

In the present work, a benthic ecoregionalization is modeled based on a large dataset of echinoid species albeit belonging to one single taxonomic class. These ecoregions are also in good agreement with biogeographic patterns described in former studies on other benthic taxa. Specifically, this is the case in sponges (Downey et al., 2012), mollusks (Linse et al., 2006; Pierrat et al., 2013), bryozoans (Barnes and Griffiths, 2007; Griffiths et al., 2009), and starfish (Moreau et al., 2017). For instance, the main distinction between Antarctic and Subantarctic ecoregions (Linse et al., 2006; Barnes and Griffiths, 2007; Griffiths et al., 2009; Downey et al., 2012; Pierrat et al., 2013), as well as faunal affinities between Subantarctic islands (Kerguelen, Crozet, Marion Prince Edward) and southern South America were all emphasized in previous biogeographic works on bivalves (Pierrat et al., 2013), cheilostome bryozoans (Griffiths et al., 2009) and starfish (Moreau et al., 2017). This can be explained by the role of the Antarctic Circumpolar Current, the main dispersal vector and biogeographic barrier for benthic organisms of the Southern Ocean, which alternatively isolate Antarctic and Subantarctic fauna and connect distant regions inside the Antarctic and Subantarctic provinces (Pearse et al., 2009; Moon et al., 2017; González-Wevar et al., 2018).

The good congruence between present, echinoid ecoregions and biogeographic patterns observed in other benthic organisms can also be explained by other abiotic factors. Typically, depth, seafloor temperature and sea ice concentration are important contributors to ecoregions delineation; they are also important drivers of the distribution of the benthos at large spatial scale (Gutt, 2001; David et al., 2005; Pierrat et al., 2012; Guillaumot et al., 2019). Interestingly, in the present work, the Campbell and Magellanic plateaus are grouped together into one single "Magellanic and Campbell Plateau" ecoregion in the GDM approach (ecoregion #7) while echinoid assemblages differ as shown in the RF-GMM approach (Fig. 3, Table 2). Overall, biogeographic studies also agree on that these two regions clearly stand apart. The modeled GDM ecoregion #7 results from the similarity of abiotic conditions prevailing over the Magellanic and Campbell plateaus, including similar depth, sea ice and sea surface temperature ranges (Fig. 3). In contrast, the RF-GMM approach is more sensible to faunal assemblages and biogeographic patterns, and the two regions were included into distinct ecoregions (Fig. 3, Table 2). Finally, general biogeographic patterns are not just the result of present conditions but are also the legacy of common evolutionary events triggered by climate history and the paleogeography of the Southern Ocean (Saucède et al., 2013; Saucède et al., 2014; Crame, 2018).

The Relevance of Marine Protected Areas (MPAs)

Fabri-Ruiz et al. (2020) recently reviewed that Acted Marine Protected Areas (MPAs) of the Southern Ocean and current proposals brought by the Commission for the Conservation of Marine Living Resources (CCAMLR) for East Antarctica, the Antarctic Peninsula and the Weddell, are representative of benthic ecoregions. This is particularly true for Subantarctic islands, which are of high conservation value given the extreme isolation of small oceanic islands and archipelagoes where unique habitats and endemic species may be particularly at risk. This is exemplified by the echinoid *Abatus cordatus* and its emblematic populations that thrive in shallow coastal areas of the Kerguelen Islands (Guillaumot et al., 2018; Saucède et al., 2019). The associated MPAs preserve faunal connectivity between populations and species of Subantarctic islands and shelves. Connectivity is key in conservation biology as it conditions the resilience of populations under critical conditions or after local disturbances (Carr et al., 2017).

In contrast, important gaps prevail in the current network of existing MPAs as Antarctic ecoregions are under-represented (Fabri-Ruiz et al., 2020). These results highlight the need to improve the representativity of Antarctic MPAs as recently proposed by CCAMLR in East Antarctica, the Weddell Sea and the Antarctic Peninsula. East Antarctica (Drygalsky, d'Urville-Sea Mertz, MacRobertson) remains unprotected whereas a first plan was proposed to CCAMLR in 2012 by the European Union and Australia. Tourism is increasing (Lenihan et al., 1995; Aronson et al., 2011) in Antarctica particularly in the Antarctic Penin-

sula and the Weddell Sea due to the proximity of these regions with South America. New MPA proposals were also made for these two regions in 2013 and 2017 (Teschke et al., 2013; Capurro, 2017).

The present benthic ecoregionalization of the Southern Ocean based on echinoid biogeography can therefore constitute a useful and promising approach to examine the ecological and biogeographic relevance of existing and proposed Antarctic MPAs. Beyond the echinoid case-study, the present approach can be applied to other marine fauna and used to address general conservation issues at large biogeographic scales.

ACKNOWLEDGMENTS

This research was supported by the French Polar Institute (program no. 1044—Proteker). It is respectively contribution no. 41 and no. 17 to the vERSO and RECTO projects (http://www.rectoversoprojects.be), funded by the Belgian Science Policy Office (BELSPO).

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

REFERENCES

Anderson, R.P., A framework for using niche models to estimate impacts of climate change on species distributions, *Ann. N.Y. Acad. Sci.*, 2013, vol. 1297, no. 1, pp. 8–28.

Arnaud, P.M., López, C.M., Olaso, I., Ramil, F., Ramos-Esplá, A.A., and Ramos, A., Semi-quantitative study of macrobenthic fauna in the region of the South Shetland Islands and the Antarctic Peninsula, *Polar Biol.*, 1998, vol. 19, no. 3, pp. 160–166.

Aronson, R.B., Thatje, S., McClintock, J.B., and Hughes, K.A., Anthropogenic impacts on marine ecosystems in Antarctica, *Ann. N.Y. Acad. Sci.*, 2011, vol. 1223, no. 1, pp. 82–107.

Barbet-Massin, M., Jiguet, F., Albert, C.H., and Thuiller, W., Selecting pseudo-absences for species distribution models: how, where and how many?: how to use pseudo-absences in niche modelling?, *Methods Ecol. Evol.*, 2012, vol. 3, no. 2, pp. 327–338.

Barnes, D.K.A. and Brockington, S., Zoobenthic biodiversity, biomass and abundance at Adelaide Island, Antarctica, *Mar. Ecol. Progr. Ser.*, 2003, vol. 249, pp. 145–155.

Barnes, D.K.A. and De Grave, S., Ecological biogeography of southern polar encrusting faunas, *J. Biogeogr.*, 2001, vol. 28, no. 3, pp. 359–365.

Barnes, D.K.A. and Griffiths, H.J., Biodiversity and biogeography of southern temperate and polar bryozoans, *Global Ecol. Biogeogr.*, 2007, vol. 17, no. 1, pp. 84–99.

Basher, Z. and Costello, M.J., The past, present and future distribution of a deep-sea shrimp in the Southern Ocean, *PeerJ.*, 2016, vol. 4, e1713.

Brandt, A., Gooday, A.J., Brandão, S.N., Brix, S., Brökeland, W., Cedhagen, T., Choudhury, M., Cornelius, N., Danis, B., De Mesel, I., Diaz, R.J., Gillan, D.C., Ebbe, B., Howe, J.A., Janussen, D., Kaiser, S., Linse, K., Malyutina, M., Pawlowski, J., Raupach, M., and Vanreusel, A., First insights into the biodiversity and biogeography of the Southern Ocean deep sea, *Nature.*, 2007, vol. 447, no. 7142, pp. 307–311.

Breiman, L., *Random Forests*, UC Berkeley TR567, 1999.

Breiman, L., Random forests, *Machine Learning*, 2001, vol. 45, pp. 5–32.
https://doi.org/10.1023/A:1010933404324

Calabrese, J.M., Certain, G., Kraan, C., and Dormann, C.F., Stacking species distribution models and adjusting bias by linking them to macroecological models, *Global Ecol. Biogeogr.*, 2014, vol. 23, no. 1, pp. 99–112.

Capurro, A., Domain 1 Marine Protected Area Preliminary Proposal PART A-1: Priority Areas for Conservation, *SC-CAMLR-XXXVI*/17, 2017.

Carr, M.H., Robinson, S.P., Wahle, C., Davis, G., Kroll, S., Murray, S., Schumacker, E.J., and Williams, M., The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment, *Aquat. Conserv.: Mar. Freshwater Ecosyst.*, 2017, vol. 27, no. S1, pp. 6–29.

Cheng, C.H. and William, H.W., Molecular ecophysiology of Antarctic notothenioid fishes, *Philos. Trans. R. Soc., B*, 2007, vol. 362, no. 1488, pp. 2215–2232.

Cohen, J., Kappa: coefficient of concordance, *Educ. Psych. Meas.*, 1960, vol. 20, no. 37.

Convey, P., Bindschadler, R., Di Prisco, G., Fahrbach, E., Gutt, J., Hodgson, D.A., Mayewski, P.A., Summerhayes, C.P., Turner, J., and Consortium, A., Antarctic climate change and the environment, *Antarct. Sci.*, 2009, vol. 21, no. 6, pp. 541–563.

Crame, J.A., Pattern and process in marine biogeography: a view from the poles, in *Frontiers of Biogeography: New Directions in the Geography of Nature,* Lomolino, M.V. and Heaney, L.R., Eds., Oxford Univ. Press, 2004, pp. 271–291.

Crame, J.A., Key stages in the evolution of the Antarctic marine fauna, *J. Biogeogr.*, 2018, vol. 45, no. 5, pp. 986–994.

David, B. and Mooi, R., An echinoid that "gives birth": morphology and systematics of a new Antarctic species, *Urechinus mortenseni* (Echinodermata, Holasteroida), *Zoomorphology.*, 1990, vol. 110, no. 2, pp. 75–89.

David, B., Choné, T., Mooi, R., and de Ridder, C., *Antarctic Echinoidea*, Liechtenstein: ARG Gantner, 2005.

Díaz, A., Féral, J.-P., David, B., Saucède, T., and Poulin, E., Evolutionary pathways among shallow and deep-sea echinoids of the genus *Sterechinus* in the Southern Ocean, *Deep Sea Res., Part II*, 2011, vol. 58, nos. 1–2, pp. 205–211.

Díaz, A., Féral, J.-P., David, B., Saucède, T., and Poulin, E., Genetic structure and demographic inference of the regular sea urchin *Sterechinus neumayeri* (Meissner, 1900) in the Southern Ocean: the role of the last glaciation, *PLoS One*, 2018, vol. 13, no. 6, e0197611.

Douglass, L.L., Turner, J., Grantham, H.S., Kaiser, S., Constable, A., Nicoll, R., Raymond, B., Post, A., Brandt, A., and Beaver, D., A hierarchical classification of benthic biodiversity and assessment of protected areas in the southern ocean, *PLoS One*, 2014, vol. 9, no. 7, e100551.

Downey, R.V., Griffiths, H.J., Linse, K., and Janussen, D., Diversity and distribution patterns in high southern latitude sponges, *PLoS One*, 2012, vol. 7, no. 7, e41672.

Dubuis, A., Pottier, J., Rion, V., Pellissier, L., Theurillat, J.-P., and Guisan, A., Predicting spatial patterns of plant species richness: a comparison of direct macroecological and species stacking modelling approaches, *Diversity Distrib.*, 2011, vol. 17, no. 6, pp. 1122–1131.

Duhamel, G., Hulley, P.-A., Causse, R., Koubbi, P., Vacchi, M., Pruvost, P., Vigetta, S., Irisson, J.-O., Mormède, S.A.-B., M., Dettai, A.A.-D., H.W. AU-Gutt, J. AU-Jones, C.D., Kock, K.-H., Lopez Abellan, L.J., and Van de Putte, A.P., Biogeographic patterns of fish, in *Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research*, De Broyer, C., Koubbi, P., Griffiths, H.J., Raymond, B., d'Udekem d'Acoz, C., Van de Putte, A.P., Danis, B., David, B., Grant, S., Gutt, J., Held, C., Hosie, G., Huettmann, F., Post, A., and Ropert-Coudert, Y., Eds., Cambridge UK: Scientific Committee on Antarctic Research, 2014, pp. 328–362.

Eastman, J., Fishes on the Antarctic continental shelf: evolution of a marine species flock?, *J. Fish Biol.*, 2000, vol. 57, pp. 84–102.

ESRI, ArcGIS Desktop, *Environmental Systems Research Institute*, Redlands, CA, 2011.

Fabri-Ruiz, S., Saucède, T., Danis, B., and David, B., Southern Ocean Echinoids database—an updated version of Antarctic, Subantarctic and cold temperate echinoid database, *Zookeys.*, 2017, no. 204, pp. 1–20.

Fabri-Ruiz, S., Danis, B., David, B., and Saucède, T., Can we generate robust species distribution models at the scale of the Southern Ocean?, *Diversity Distrib.*, 2018, vol. 25, no. 1, pp. 1–17.

Fabri-Ruiz, S., Danis, B., David, B., and Saucède, T., Can we generate robust Species Distribution Models at the scale of the Southern Ocean, *Diversity Distrib.*, 2019, vol. 25, pp. 21–37,
https://doi.org/10.1111/ddi.12835

Fabri-Ruiz, S., Danis, B., Navarro, N., Koubbi, P., Laffont, R., and Saucède, T., Benthic ecoregionalization based on echinoid fauna of the Southern Ocean supports current proposals of Antarctic Marine Protected Areas under IPCC scenarios of climate change, *Global Change Biol.*, 2020 (in press).

Ferrier, S. and Guisan, A., Spatial modelling of biodiversity at the community level, *J. Appl. Ecol.*, 2006, vol. 43, no. 3, pp. 393–404.

Ferrier, S., Manion, G., Elith, E., and Richardson, K., Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment, *Diversity Distrib.*, 2007, vol. 13, pp. 252–264.

Fraley, C. and Raftery, A.E., *MCLUST Version 3 for R: Normal Mixture Modeling and Model-Based Clustering*, 2006.

Franklin, J., *Mapping Species Distributions: Spatial Inference and Prediction*, Cambridge Univ. Press, 2010.

Gallego, R., Dennis, T.E., Basher, Z., Lavery, S., and Sewell, M.A., On the need to consider multiphasic sensitivity of marine organisms to climate change: a case study of the Antarctic acorn barnacle, *J. Biogeogr.*, 2017, vol. 44, no. 10, pp. 2165–2175.

González-Wevar, C.A., Segovia, N.I., Rosenfeld, S., Ojeda, J., Hüne, M., Naretto, J., Saucède, T., Brickle, P., Morley, S., Féral, J.-P., Spencer, H.G., and Poulin, E., Unexpected absence of island endemics: long-distance dispersal in higher latitude sub-Antarctic *Siphonaria* (Gastropoda: Euthyneura) species, *J. Biogeogr.*, 2018, vol. 45, no. 4, pp. 874–884.

Grant, S., *Bioregionalisation of the Southern Ocean: Report of the Experts Workshop (Hobart, September 2006)*, WWF—Australia Head Office, Sydney, 2006.

Griffiths, H.J., Barnes, D.K.A., and Linse, K., Towards a generalized biogeography of the Southern Ocean benthos, *J. Biogeogr.*, 2009, vol. 36, no. 1, pp. 162–177.

Griffiths, H.J., Danis, B., and Clarke, A., Quantifying Antarctic marine biodiversity: the SCAR-MarBIN data portal, *Deep Sea Res., Part II*, 2011, vol. 58, nos. 1–2, pp. 18–29.

Guillaumot, C., Fabri-Ruiz, S., Martin, A., Eléaume, M., Danis, B., Féral, J.-P., and Saucède, T., Benthic species of the Kerguelen Plateau show contrasting distribution shifts in response to environmental changes, *Ecol. Evol.*, 2018, vol. 8, no. 12, pp. 6210–6225.

Guillaumot, C., Artois, J., and Saucède, T., et al., Broad-scale species distribution models applied to data-poor areas, *Progr. Oceanogr.*, 2019, vol. 175, pp. 198–207.

Gutt, J. On the direct impact of ice on marine benthic communities, a review, *Polar Biol.*, 2001, vol. 24, pp. 553–564.

Gutt, J., Zurell, D., Bracegridle, T., Cheung, W., Clark, M., Convey, P., Danis, B., David, B., Broyer, C., and Prisco, G., Correlative and dynamic species distribution modelling for ecological predictions in the Antarctic: a cross-disciplinary concept, *Polar Res.*, 2012, vol. 31, no. 1, p. 11091.

Gutt, J., Bertler, N., Bracegirdle, T.J., Buschmann, A., Comiso, J., Hosie, G., Isla, E., Schloss, I.R., Smith, C.R., and Tournadre, J., The Southern Ocean ecosystem under multiple climate change stresses, an integrated circumpolar assessment, *Global Change Biol.*, 2015, vol. 21, no. 8, pp. 1434–1453.

Gutt, J., Isla, E., Bertler, A.N., Bodeker, G.E., Bracegirdle, T.J., Cavanagh, R.D., Comiso, J.C., Convey, P., Cummings, V., De Conto, R., De Master, D., di Prisco, G., d'Ovidio, F., Griffiths, H.J., Khan, A.L., López-Martínez, J., Murray, A.E., Nielsen, U.N., Ott, S., Post, A., Ropert-Coudert, Y., Saucède, T., Scherer, R., Schiaparelli, S., Schloss, I.R., Smith, C.R., Stefels, J., Stevens, C., Strugnell, J.M., Trimborn, S., Verde, C., Verleyen, E., Wall, D.H., Wilson, N.G., and Xavier, J.C., Cross-disciplinarity in the advance of Antarctic ecosystem research, *Mar. Genomics*, 2018, vol. 37, pp. 1–17.

Hardy, C., David, B., Rigaud, T., De Ridder, C., and Saucède, T., Ectosymbiosis associated with cidaroids (Echinodermata: Echinoidea) promotes benthic colonization of the seafloor in the Larsen Embayments, Western Antarctica, *Deep Sea Res., Part II*, 2011, vol. 58, nos. 1–2, pp. 84–90.

Hedgpeth, J.W., Introduction to Antarctic zoogeography, in *Distribution of Selected Groups of Marine Invertebrates in Waters South of 35° S Latitude. Antarctic Map Folio Series 11,* Bushnell, V.C. and Hedgpeth, J.W., Eds., New York: Am. Geogr. Soc., 1969 pp. 1–9.

Heterier, V., De Ridder, C., David, B., and Rigaud, T., Comparative biodiversity of ectosymbionts in two Antarctic cidarid echinoids, *Ctenocidaris spinosa* and *Rhynchocidaris triplopora, Echinoderms*, 2004, pp. 201–205.

Hijmans, R.J., Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model, *Ecology*, 2012, vol. 93, no. 3, pp. 679–688.

Hill, N.A., Foster, S.D., Duhamel, G., Welsford, D., Koubbi, P., and Johnson, C.R., Model-based mapping of assemblages for ecology and conservation management: a case study of demersal fish on the Kerguelen Plateau, *Diversity Distrib.*, 2017, vol. 23, no. 10, pp. 1216–1230. https://doi.org/10.1111/ddi.12613

Hunter, R.L. and Halanych, K.M., Evaluating connectivity in the brooding brittle star *Astrotoma agassizii* across the Drake Passage in the Southern Ocean, *J. Hered.,* 2008, vol. 99, pp. 137–148.

Ingels, J., Vanreusel, A., Brandt, A., Catarino, A.I., David, B., De Ridder, C., Dubois, P., Gooday, A.J., Martin, P., Pasotti, F., and Robert, H., Possible effects of global environmental changes on Antarctic benthos: a synthesis across five major taxa: possible effects of global environmental changes on Antarctic benthos, *Ecol. Evol.*, 2012, vol. 2, no. 2, pp. 453–485.

Kaiser, S., Brandão, S.N., Brix, S., Barnes, D.K.A., Bowden, D.A., Ingels, J., Leese, F., Schiaparelli, S., Arango, C.P., and Badhe, R., Patterns, processes and vulnerability of Southern Ocean benthos: a decadal leap in knowledge and understanding, *Mar. Biol.*, 2013, vol. 160, no. 9, pp. 2295–2317.

Kassambara, A. and Mundt, F., Factoextra: extract and visualize the results of multivariate data analyses, R package version 2016.

Kaufmann, L. and Rousseeuw, P.J., *Finding Groups in Data: An Introduction to Cluster Analysis*, New York: Wiley, 1990.

Kennicutt, M.C., Chown, S.L., Cassano, J.J., Liggett, D., Peck, L.S., Massom, R., Rintoul, S.R., Storey, J., Vaughan, D.G., and Wilson, T.J., A roadmap for Antarctic and Southern Ocean science for the next two decades and beyond, *Antarct. Sci.*, 2015, vol. 27, no. 1, pp. 3–18.

Koubbi, P., Ozouf-Costaz, C., Goarant, A., Moteki, M., Hulley, P.-A., Causse, R., Dettai, A., Duhamel, G., Pruvost, P., Tavernier, E., Post, A.L., Beaman, R.J., Rintoul, S.R., Hirawake, T., Hirano, D., Ishimaru, T., Riddle, M., and Hosie, G., Estimating the biodiversity of the East Antarctic shelf and oceanic zone for ecoregionalisation: example of the ichthyofauna of the CEAMARC (Collaborative East Antarctic Marine Census) CAML surveys, *Polar Sci.,* 2010, vol. 4, no. 2, pp. 115–133.

Koubbi, P., Moteki, M., Duhamel, G., Goarant, A., Hulley, P.-A., O'Driscoll, R., Ishimaru, T., Pruvost, P., Tavernier, E., and Hosie, G., Ecoregionalization of myctophid fish in the Indian sector of the Southern Ocean: results from generalized dissimilarity models, *Deep Sea Res., Part II*, 2011, vol. 58, nos. 1–2, pp. 170–180.

Koubbi, P., Causse, R., Chazeau, C., Coste, G., Cotté, C., D'Ovidio, F., Delord, K., Duhamel, G., Forget, A., and Gasco, N., *Ecoregionalisation of the Kerguelen and Crozet Islands Oceanic Zone*, part I: *Introduction and Kerguelen Oceanic Zone*, Paris, 2016a.

Koubbi, P., Mignard, C., Causse, R., Da Silva, O., Baudena, A., Bost, C., Cotte, C., d'Ovidio, F., Della Penna, A., and Delord, K., *Ecoregionalisation of the Kerguelen and Crozet Islands Oceanic Zone*, part II: *The Crozet Oceanic Zone*, 2016b.

Kuhn, M., *The Caret Package*, R package version 2012.

Leese, F., Agrawal, S., and Held, C., Long-distance island hopping without dispersal stages: transportation across major zoographic barriers in a Southern Ocean isopod, *Naturwissenschaften*, 2010, vol. 97, pp. 583–594.

Le Roux, P.C. and McGeoch, M.A., Rapid range expansion and community reorganization in response to warming, *Global Change Biol.*, 2008, vol. 14, no. 12, pp. 2950–2962.

Legendre, P., Spatial autocorrelation: trouble or new paradigm?, *Ecology*, 1993, vol. 74, no. 6, pp. 1659–1673.

Lenihan, H.S., Kiest, K.A., Conlan, K.E., Slattery, P.N., Konar, B.H., and Oliver, J.S., Patterns of survival and behavior in Antarctic benthic invertebrates exposed to contaminated sediments: field and laboratory bioassay experiments, *J. Exp. Mar. Biol. Ecol.*, 1995, vol. 192, no. 2, pp. 233–255.

Leroy, B., Meynard, C.N., Bellard, C., and Courchamp, F., Virtualspecies, an R package to generate virtual species distributions, *Ecography*, 2016, vol. 39, no. 6, pp. 599–607.

Linse, K., Griffiths, H.J., Barnes, D.K.A., and Clarke, A., Biodiversity and biogeography of Antarctic and sub-Antarctic Mollusca, *Deep Sea Res., Part II*, 2006, vol. 53, nos. 8–10, pp. 985–1008.

Linse, K., Cope, T., Lörz, A.-N., and Sands, C., Is the Scotia Sea a centre of Antarctic marine diversification? Some evidence of cryptic speciation in the circum-Antarctic bivalve *Lissarca notorcadensis* (Arcoidea: Philobryidae), *Polar Biol.*, 2007, vol. 30, no. 8, pp. 1059–1068.

Linse, K., Walker, L.J., and Barnes, D.K.A., Biodiversity of echinoids and their epibionts around the Scotia Arc, Antarctica, *Antarct. Sci.*, 2008, vol. 20, no. 3, pp. 227–244.

Lohrer, A.M., Cummings, V.J., and Thrush, S.F., Altered sea ice thickness and permanence affects benthic ecosystem functioning in Coastal Antarctica, *Ecosystems*, 2013, vol. 16, no. 2, pp. 224–236. https://doi.org/10.1007/s10021-012-9610-7

Loots, C., Koubbi, P., and Duhamel, G., Habitat modelling of *Electrona antarctica* (Myctophidae, Pisces) in Kerguelen by generalized additive models and geographic information systems, *Polar Biol.*, 2007, vol. 30, no. 8, pp. 951–959.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., and Hornik, K., *Cluster: Cluster Analysis Basics and Extensions*, R package version 2012.

Manion, G., Lisk, M., Ferrier, S., Nieto-Lugilde, D., and Fitzpatrick, M.C., *GDM: Functions for Generalized Dissimilarity Modeling*, R package version 2016.

Mélice, J.L., Lutjeharms, J.R.E., Rouault, M., and Ansorge, I.J., Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years, *S. Afr. J. Sci.*, 2003, vol. 99, nos. 7–8, pp. 363–366.

Meyer, D., Zeileis, A., Hornik, K., Gerber, F., Friendly, M., and Meyer, M.D., *VCD*, R package version 2020.

Mironov, A.N., Holasteroid echinoids, 2. *Pourtalesia, Zool. Zh.*, 1995, vol. 74, no. 12, pp. 59–75.

Montiel, A., Gerdes, D., Hilbig, B., and Arntz, W.E., Polychaete assemblages on the Magellan and Weddell Sea shelves: comparative ecological evaluation, *Mar. Ecol. Prog. Ser.*, 2005, 297, pp. 189–202.

Moon, K.L., Chown, S.L., and Fraser, C.I., Reconsidering connectivity in the sub-Antarctic, *Biol. Rev.*, 2017, vol. 92, no. 4, pp. 2164–2181.

Moreau, C., Saucède, T., Jossart, Q., Agüera, A., Brayard, A., and Danis, B., Reproductive strategy as a piece of the biogeographic puzzle: a case study using Antarctic sea stars (Echinodermata, Asteroidea), *J. Biogeogr.*, 2017, vol. 44, no. 4, pp. 848–860.

Mormède, S., Irisson, J.-O., and Raymond, B., Distribution modelling, in *Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research*, De Broyer, C., Koubbi, P., Griffiths, H.J., Raymond, B., d'Udekem d'Acoz, C., Van de Putte, A.P., Danis, B., David, B., Grant, S., Gutt, J., Held, C., Hosie, G., Huettmann, F., Post, A., and Ropert-Coudert, Y., Eds., Cambridge UK: Scientific Committee on Antarctic Research, 2014, pp. 27–29.

Nachtsheim, D.A., Jerosch, K., Hagen, W., Plötz, J., and Bornemann, H., Habitat modelling of crabeater seals (*Lobodon carcinophaga*) in the Weddell Sea using the multivariate approach Maxent, *Polar Biol.*, 2017, vol. 40, no. 5, pp. 961–976.

Newbold, T., Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models, *Progr. Phys. Geogr.*, 2010, vol. 34, pp. 3–22.

Paradis, E., Strimmer, K., Claude, J., Jobb, G., Opgen-Rhein, R., Dutheil, J., Noel, Y., Bolker, B., and Lemon, J., *The APE Package, Analyses of Phylogenetics and Evolution*, R package version 2008.

Pearse, J.S., Mooi, R., Lockhart, S.J., and Brandt, A., Brooding and species diversity in the Southern Ocean: selection for brooders or speciation within brooding clades?, in *Smithsonian at the Poles: Contributions to International Polar Year Science*, Krupnik, I., Lang, M.A., and Miller, S.E., Eds., Washington DC: Smithsonian Institution Scholarly Press, 2009, pp. 181–196.

Peck, L., Prospects for surviving climate change in Antarctic aquatic species, *Front. Zool.*, 2005, vol. 2, no. 1, pp. 2–9.

Peck, L., Webb, K.E., and Bailey, D.M., Extreme sensitivity of biological function to temperature in Antarctic marine species, *Funct. Ecol.*, 2004, vol. 18, no. 5, pp. 625–630.

Peck, L., Morley, S.A., and Clark, M.S., Poor acclimation capacities in Antarctic marine ectotherms, *Mar. Biol.*, 2010, vol. 157, no. 9, pp. 2051–2059.

Pierrat, B., Saucède, T., Laffont, R., De Ridder, C., Festeau, A., and David, B., Large-scale distribution analysis of Antarctic echinoids using ecological niche modelling, *Mar. Ecol. Progr. Ser.*, 2012, vol. 463, pp. 215–230.

Pierrat, B., Saucède, T., Brayard, A., and David, B., Comparative biogeography of echinoids, bivalves and gastropods from the Southern Ocean, *J. Biogeogr.*, 2013, vol. 40, no. 7, pp. 1374–1385.

Pinkerton, M.H., Smith, A.N.H., Raymond, B., Hosie, G.W., Sharp, B., Leathwick, J.R., and Bradford-Grieve, J.M., Spatial and seasonal distribution of adult *Oithona similis* in the Southern Ocean: predictions using boosted regression trees, *Deep Sea Res., Part I*, 2010, vol. 57, no. 4, pp. 469–485.

Portner, H.O., Peck, L., and Somero, G., Thermal limits and adaptation in marine Antarctic ectotherms: an integrative view, *Philos. Trans. R. Soc., B*, 2007, vol. 362, no. 1488, pp. 2233–2258.

Poulin, E. and Féral, J.-P., Why are there so many species of brooding Antarctic echinoids?, *Evolution*, 1996, vol. 50, no. 2, pp. 820–830.

R Core Team, *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria, 2017.

Reygondeau, G. and Huettmann, F., Past, present and future state of pelagic habitats in the Antarctic Ocean, in *Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research*, De Broyer, C., Koubbi, P., Griffiths, H.J., Raymond, B., d'Udekem d'Acoz, C., Van de Putte, A.P., Danis, B., David, B., Grant, S., Gutt, J., Held, C., Hosie, G., Huettmann, F., Post, A., and Ropert-Coudert, Y., Eds., Cambridge UK: Scientific Committee on Antarctic Research, 2014, pp. 397–403.

Rodríguez, E., López-González, P.J., and Gili, J.M., Biogeography of Antarctic sea anemones (Anthozoa, Actiniaria): what do they tell us about the origin of the Antarctic benthic fauna?, *Deep Sea Res., Part II*, 2007, vol. 54, no. 16, pp. 1876–1904.

Roquet, F., Park, Y.-H., Guinet, C., Bailleul, F., and Charrassin, J.-B., Observations of the Fawn Trough Current over the Kerguelen Plateau from instrumented elephant seals, *J. Mar. Syst.*, 2009, vol. 78, no. 3, pp. 377–393.

Rouault, M., Mélice, J.-L., Reason, C.J., and Lutjeharms, J.R., Climate variability at Marion Island, Southern Ocean, since 1960, *J. Geophys. Res.: Oceans*, 2005, vol. 110, no. C05007.

Saucède, T., Pierrat, B., Brayard, A., and David, B., Palaeobiogeography of Austral echinoid faunas: a first quantitative approach, *Geol. Soc., Spec. Publ.*, London, 2013, vol. 381, no. 1, pp. 117–127.

Saucède, T., Pierrat, B., and David, B. Echinoids, in *Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research*, De Broyer, C., Koubbi, P., Griffiths, H.J., Raymond, B., d'Udekem d'Acoz, C., Van de Putte, A.P., Danis, B., David, B., Grant, S., Gutt, J., Held, C., Hosie, G., Huettmann, F., Post, A., and Ropert-Coudert, Y., Eds., Cambridge, UK: Scientific Committee on Antarctic Research, 2014, pp. 213–220.

Saucède, T., Guillaumot, C., Michel, L., Fabri-Ruiz, S., Bazin, A., Cabessut, M., García-Berro, A., Mateos, A., Mathieu, O., De Ridder, C., Dubois, P., Danis, B., David, B., Díaz, A., Lepoint, G., Motreuil, S., Poulin, E., and Féral, J.-P., Modelling species response to climate change in sub-Antarctic islands: echinoids as a case study for the Kerguelen Plateau, in *The Kerguelen Plateau: Marine Ecosystems and Fisheries*, Welsford, D.C., Dell, J., and Duhamel, G., Eds., Australian Government–Department of the Environment–Australian Antarctic Division, 2019, pp. 95–116.

Scrucca, L., Fop, M., Murphy, T.B., and Raftery, A.E., mclust 5: Clustering, Classification and Density Estimation Using Gaussian Finite Mixture Models, *The R Journal*, 2016, vol. 8, no. 1, p. 289.

Sewell, M.A. and Hofmann, G.E. Antarctic echinoids and climate change: a major impact on the brooding forms, *Global Change Biol.*, 2011, vol. 17, no. 2, pp. 734–744.

Smith, S.D., Kelp rafts in the Southern Ocean, *Global Ecol. Biogeogr.*, 2002, vol. 11, pp. 67–69.

Sokolov, S. and Rintoul, S.R., Structure of Southern Ocean fronts at 140° E, *J. Mar. Syst.*, 2002, vol. 37, no. 2, pp. 151–184.

Teschke, K., Bornemann, H., Bombosch, A., Brey, T., Brtnik, P., Burkhardt, E., Dorschel, B., Feindt-Herr, H., Gerdes, D., and Gutt, J., Progress report on the scientific data compilation and analyses in support of the development of a CCAMLR MPA in the Weddell Sea (Antarctica), *SC-CAMLR-XXXII*, 2013, pp. 1–29.

Tessarolo, G., Rangel, T.F., Araújo, M.B., and Hortal, J., Uncertainty associated with survey design in species distribution models, *Diversity Distrib.*, 2014, vol. 20, pp. 1258–1269.

Thiers, L., Delord, K., Bost, C.-A., Guinet, C., and Weimerskirch, H., Important marine sectors for the top predator community around Kerguelen Archipelago, *Polar Biol.*, 2017, vol. 40, no. 2, pp. 365–378.

Thuiller, W., Lafourcade, B., Engler, R., and Araújo, M.B., BIOMOD—a platform for ensemble forecasting of species distributions, *Ecography*, 2009, vol. 32, no. 3, pp. 369–373.

Turner, J., Barrand, N.E., Bracegirdle, T.J., Convey, P., Hodgson, D.A., Jarvis, M., Jenkins, A., Marshall, G., Meredith, M.P., Roscoe, H., Shanklin, J., French, J., Goosse, H., Guglielmin, M., Gutt, J., Jacobs, S., Kennicutt, M.C., Masson-Delmotte, V., Mayewski, P., Navarro, F., Robinson, S., Scambos, T., Sparrow, M., Summerhayes, C., Speer, K., and Klepikov, A., Antarctic climate change and the environment: an update, *Polar Record.*, 2014, vol. 50, no. 3, pp. 237–259.

Valavi, R., Elith, J., Lahoz-Monfort, J.J., and Guillera-Arroita, G., blockCV: an R package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models, *bioRxiv*, 2018, p. 357798.

Xavier, J.C., Raymond, B., Jones, D.C., and Griffiths, H., Biogeography of cephalopods in the Southern Ocean using habitat suitability prediction models, *Ecosystems*, 2016, vol. 19, no. 2, pp. 220–247.