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Modelling species response to climate change in sub-Antarctic islands: echinoids as a case study for the Kerguelen Plateau

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Abstract

In the Kerguelen Islands, the multiple effects of climate change are expected to impact coastal marine habitats. Species distribution models (SDM) can represent a convenient tool to predict the biogeographic response of species to climate change but biotic interactions are not considered in these models. Nevertheless, new species interactions can emerge in communities exposed to environmental changes and the structure of biotic interactions is directly related to the potential resilience of ecosystems. Trophic interaction studies can help predict species vulnerability to environmental changes using carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios to generate trophic models. Using new available data inputs, we generated robust SDM and trophic interaction models to assess the potential response and sensitivity of three echinoid species to future worst-case scenarios of environmental change in the Kerguelen Plateau region. The two modelling approaches provide contrasting insights into the potential responses of each species to future environmental changes with both approaches identifying *Abatus cordatus* to be particularly vulnerable due to its narrow ecological niche and endemism to near-shore areas. Coupling insights gained from trophic niche ecology with species distribution modelling represents a promising approach that can improve our understanding and ability to predict the potential responses of species to future habitat changes.

Modéliser la réponse des espèces au changement climatique dans les îles subantarctiques : étude de cas chez les oursins du Plateau des Kerguelen

Résumé

Les multiples effets du changement climatique impactent d'ores et déjà les habitats marins côtiers des îles Kerguelen. Les modèles de distribution d'espèces (SDM) peuvent permettre de prédire la réponse des espèces au changement climatique mais ces modèles n'intègrent pas le rôle joué par les interactions entre espèces. La structure de ces interactions est pourtant déterminante dans le potentiel de résilience des écosystèmes. Elle peut être modifiée et de nouvelles interactions peuvent émerger dans les communautés exposées aux changements environnementaux. L'étude des interactions trophiques permet d'évaluer en partie la vulnérabilité des espèces aux changements environnementaux, l'analyse de bio-marqueurs tels que les rapports isotopiques du carbone ($\delta^{13}\text{C}$) et de l'azote ($\delta^{15}\text{N}$) permettant en particulier de produire des modèles d'interactions trophiques. Afin d'évaluer la réponse potentielle et la sensibilité d'espèces des Kerguelen aux changements environnementaux, nous avons produit des modèles de distribution d'espèces et de niche trophique grâce à de nouvelles données de terrain. Trois études de cas ont été choisies parmi les oursins, éléments communs et abondants des communautés benthiques côtières des Kerguelen. Les deux approches de modélisation prédisent des réponses contrastées des espèces aux changements environnementaux futurs selon le scénario le plus pessimiste du GIEC. D'autre part, les deux modèles identifient la même espèce, *Abatus cordatus*, comme étant particulièrement menacée en raison d'une niche écologique étroite et de son fort endémisme. L'utilisation conjointe de modèles de distribution et de modèles trophiques représente une réelle perspective d'amélioration des prédictions de réponse des espèces aux changements environnementaux.

Keywords: species distribution model, trophic niche, isotopic niche, biotic interaction, distribution dynamics

Introduction

In the Southern Ocean, and in the sub-Antarctic islands in particular, the multiple effects of climate change are already perceptible and include, among other factors, an increase in sea-surface temperature (Mélise et al., 2003; Ansorge et al., 2009, 2014), a decrease in rains, an increase in wind speed, and a rise of sunshine hours (Smith, 2002; Mélise et al., 2003; Rouault et al., 2005; Le Roux et al., 2008). Future scenarios predict warmer, fresher, and more acidic waters, in addition to more extreme climatic events and a more intense seasonality (Allan et al., 2013; Turner et al., 2014; Gutt et al., 2015). Such changes are expected to alter the structure and functioning of marine ecosystems (Allan et al., 2013; Gutt et al., 2015; Féral et al., 2016) and may lead to shifts in species distributions and in extreme cases, local extinctions (Walther et al., 2002; Doney et al., 2011). Coastal marine habitats of the sub-Antarctic islands are particularly at risk because shallow-water species do not necessarily have the opportunity to migrate to more favourable areas. Moreover, new conditions such as warmer waters, may favour the expansion of exotic and

invasive species (Smith, 2002; Allan et al., 2013; Kargel et al., 2014; Molinos et al., 2015; Byrne et al., 2016). Although no exotic species has been reported in coastal marine habitats of the Kerguelen Islands yet, this eventuality is not to be excluded (CCAMLR, 2008, 2013; Hureau, 2011; Féral et al., 2019).

Species distribution modelling (SDM) has long retained the attention of ecologists as a useful tool to predict species distribution range shifts in response to climate change (Tingley et al., 2014; Guillera-Arroita et al., 2015) and to address conservation issues (Ross and Howell, 2013; Marshall et al., 2014; Reiss et al., 2015; Zucchetto et al., 2016; Hill et al., 2017). SDM relates species occurrence records with environmental predictors (Elith et al., 2006; Elith and Leathwick, 2009) to estimate a species' ecological niche and predict the potential extent of suitable areas (Phillips et al., 2017). Distribution range shifts under climate change can be predicted by modelling species' suitable areas according to diverse ecological scenarios (Guisan and Thuiller, 2005; Reiss et al., 2015). High-risk areas for species viability can be depicted

on so-called risk maps, which can prove useful for conservation purposes (Elith and Leathwick, 2009; Václavík and Meentemeyer, 2012; Sánchez-Carnero et al., 2016), to define reference sites for environmental monitoring (Constable et al., 2014; Gutt et al., 2015, 2018), and for the establishment and management of marine protected areas (Chown et al., 2017; Coetzee et al., 2017; Gutt et al., 2018).

Running species distribution models to predict the geographic response of species to climate change requires extensive and reliable information systems. Initiatives such as the Census of Antarctic Marine Life (CAML) and the International Polar Year (2007–2008) have recently contributed to improving knowledge of species distribution patterns in the Southern Ocean, by initiating and implementing strong data policies at SCAR (the Scientific Committee on Antarctic research) level. Data policies include the use of globally recognised data management facilities such as the biodiversity.aq initiative (Van de Putte et al., 2018), which ensures free and open access to raw biodiversity data as well as a series of processing/analytical services and data products. An example product of such data is the Biogeographic Atlas of the Southern Ocean (De Broyer et al., 2014) that provides a detailed compilation of our current knowledge of the biogeography of the Southern Ocean. However, gaps still persist in our knowledge of species distribution due to sampling biases and the permanence of unexplored areas (Figure 1). SDM is a valuable alternative to predict species distribution over their entire range (Pierrat et al., 2012; Guillaumot et al., 2018a, 2018b).

SDM can predict the distribution of individual species, or species assemblages, as a function of abiotic predictors. One limitation of SDM is that they do not explicitly consider biotic interactions which are an important factor in determining a species' realised niche and community evolution (Van der Putten et al., 2010; Wisz et al., 2013). New species interactions can emerge in communities exposed to environmental changes (Albouy et al., 2014) and the structure of biotic interactions, and of trophic networks in particular, is directly related to the potential resilience of ecosystems (Loreau and Behera, 1999; Walther, 2010; Hattab et al., 2016). At species level, trophic studies can help predict species vulnerability to changes in the nature of trophic interactions and in food-source availability. Species with specialised feeding strategies

are only able to feed on a limited number of food sources (i.e. species with small trophic niches) and typically exhibit low trophic plasticity. This makes them more vulnerable to qualitative and quantitative changes in food availability.

Knowledge about trophic ecology of investigated species is highly needed to improve the reliability of model predictions. Over the last decades, stable isotopes have proven to be one of the most reliable integrative trophic markers, and have become a near-universal tool in ecology (Boecklen et al., 2011). The concept underlying this technique can be summarised by the idiom 'you are what you eat', whereby the isotopic composition of a consumer is a proportional mixture of the isotopic compositions of its food sources, with a slight enrichment towards the heaviest isotope (Boecklen et al., 2011; Layman et al., 2012). Moreover, stable isotope ratios of each element have specific properties, making the different tracers complementary. Carbon stable isotope ratios, hereafter noted $\delta^{13}\text{C}$, are mostly influenced by processes occurring at the base of food webs, and $\delta^{13}\text{C}$ variations throughout the subsequent trophic steps are typically low. This makes $\delta^{13}\text{C}$ a useful tracer of the food items directly, or indirectly supporting a consumer population (DeNiro and Epstein, 1978; Layman et al., 2012). Conversely, nitrogen stable isotope ratios ($\delta^{15}\text{N}$) exhibit a marked stepwise increase with increasing trophic levels, making $\delta^{15}\text{N}$ a useful indicator of both the food sources and the trophic position of consumers (DeNiro and Epstein, 1981; Layman et al., 2012). Recently, it has been proposed that stable isotope ratios of consumers can be used to build an isotopic niche, which can be considered as a proxy of the realised ecological niche (Newsome et al., 2007; Jackson et al., 2011). This isotopic niche is influenced by both habitat and trophic sources use (Newsome et al., 2007; Flaherty and Ben-David, 2010). Therefore, it can be used as a descriptor of consumer trophic ecology (Layman and Allgeier, 2012), although caution must be exercised, as temporal and spatial variation of isotopic composition of food items (baseline shifts; Boecklen et al., 2011) can act as a confounding factor.

Using new available data inputs on benthic species distribution and trophic ecology for the Kerguelen Plateau, we generated robust SDM and trophic niche models to assess the response and sensitivity of three benthic invertebrate species common to the Kerguelen Plateau to future worst-case

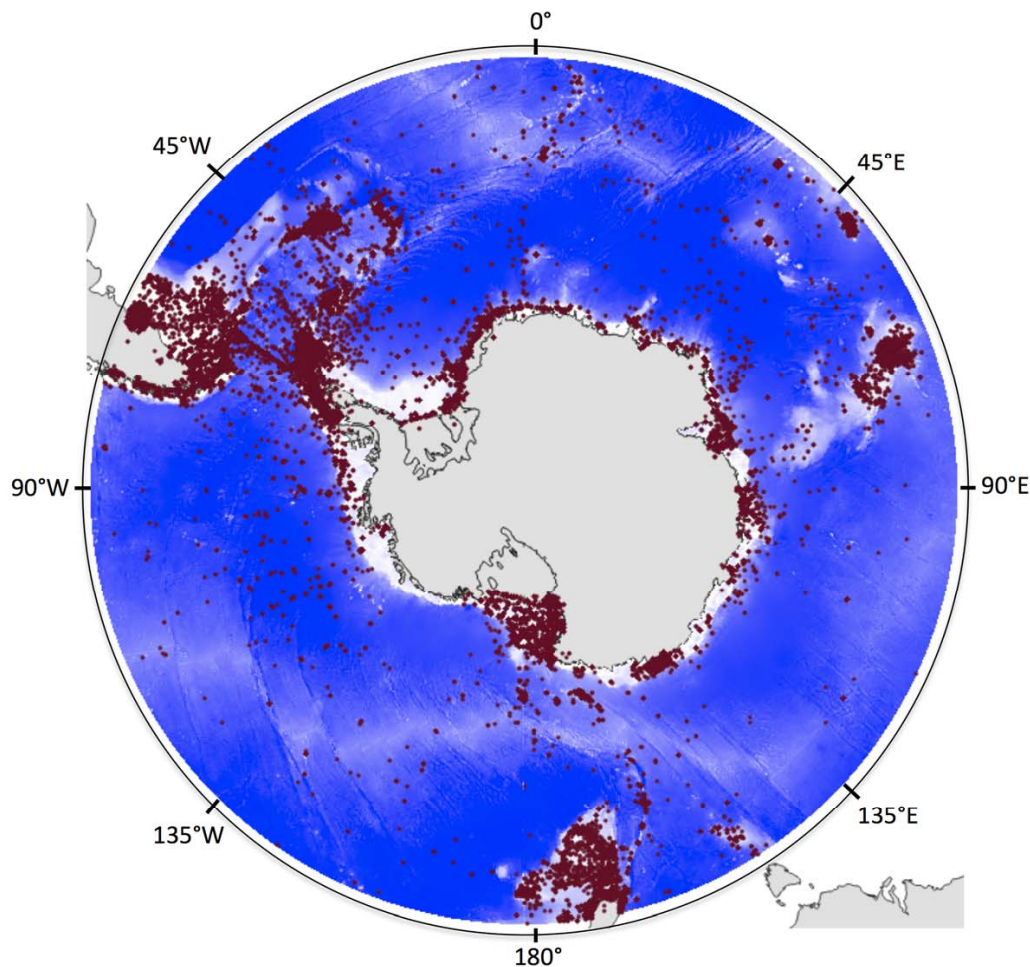


Figure 1: Benthic invertebrates sampling sites (indicated by red dots) across the Southern Ocean showing the existence of vast under-sampled areas (updated from De Broyer et al., 2014).

scenarios of environmental change. Three echinoid species that are common to sub-Antarctic benthic communities were selected. They occur in different habitats, from coastal areas to the deep-sea, and display various ecological traits including different nutrition strategies (David et al., 2005; Saucède et al., 2014; Michel et al., 2016).

Material and methods

Species Distribution Modelling (SDM)

SDM were generated using all species presence-only data extracted from the extensive echinoid database recently published by Fabri-Ruiz et al. (2017). This database compiles echinoid occurrences recorded in the Southern Ocean, south of 45°S, between 1872 and 2015. In the present work, three common species of the Kerguelen Plateau with contrasting ecological niches were selected, *Abatus cordatus* (Verrill, 1876), *Ctenocidaris nutrix*

(Thomson, 1876) and *Sterechinus diadema* (Studer, 1876). *Abatus cordatus* is a shallow deposit feeder that is endemic to the Kerguelen Plateau (Dell, 1972; Arnaud, 1974; Schatt and Féral, 1991; De Ridder et al., 1992; Poulin and Féral, 1996, 2001; Poulin et al., 2002; Saucède et al., 2014). *Ctenocidaris nutrix* is a carnivore that occasionally feeds on detritus, it has a wide distribution range, extending from the Kerguelen Plateau to the Antarctic coasts (Poulin and Féral 1996, 2001). *Sterechinus diadema* is an omnivore, feeding on a large array of food sources and widely distributed throughout the Southern Ocean (De Ridder et al., 1992; Poulin and Féral, 1995, 1996, 2001; Linse et al., 2008; Moya et al., 2012; Michel et al., 2016). A total of $n = 93$, $n = 160$ and $n = 528$ occurrences were used for modelling the distribution of the three species *A. cordatus*, *C. nutrix* and *S. diadema* respectively (Figure 2).

Environmental data was obtained from Fabri-Ruiz et al. (2017). Fifteen raster layers with a

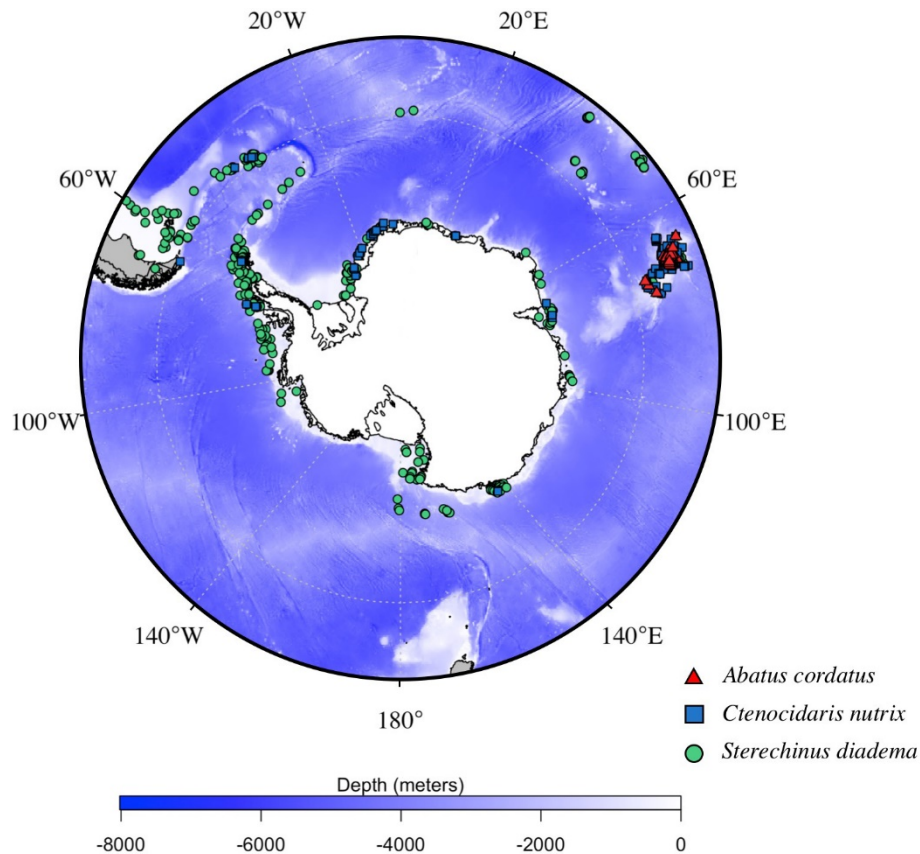


Figure 2: Species occurrence data used to run SDM of the three echinoid species (red triangles for *Abatus cordatus*, blue squares for *Ctenocidaris nutrix* and green circles for *Sterechinus diadema*).

grid-cell resolution of 0.1 degree were selected for three time periods: 1955–1974, 2005–2012 and 2050–2099 according to IPCC scenario RCP 8.5, the predicted worst-case scenario of environmental change (Table 1). The selected environmental descriptors are all relevant to echinoid ecology, cover the entire Southern Ocean (south of 45°S) and were tested as non-collinear between each other for improved modelling performance (Dormann et al., 2013). Collinearity was tested between all descriptors and the least ecologically relevant descriptors were removed for Variance Inflation Factor (VIF) > 5 following the stepwise procedure used in the usdm R package (Naimi et al., 2014) and Spearman correlation >0.85.

SDM were generated using the boosted regression trees (BRT) method, which is commonly used in ecology because it performs well with small datasets and has a good transferability in space and time (Elith et al., 2008; Heikkinen et al., 2012). Because species presence-only data were aggregated due to sampling bias, background data were selected using a target-background sampling method (Phillips

et al., 2009; Guillaumot et al., 2018b). A Kernel Density Estimation (KDE) of sampling effort was calculated on the extent of the Southern Ocean based on benthic sampling sites (Figure 1). It was used to weight the random sampling of background data used for modelling. SDM were first generated using environmental descriptors available for 2005–2012. Then models were projected for past conditions (1955–1974) and for the future climatic scenario RCP 8.5 (2055–2099). Prediction maps were binarised using the maximum specificity plus sensitivity (MaxSSS) threshold, commonly used in SDM based on presence-only data (Liu et al., 2013). Model accuracy was evaluated using the area under the receiver operated curve (AUC) (Fielding and Bell, 1997). All models were performed using the gbm R package (Ridgeway, 2015).

Trophic ecology

The trophic ecology of the three species (*A. cordatus*, *C. nutrix* and *S. diadema*) was investigated through the analysis of stable isotope compositions

Table 1: Environmental descriptors selected for species distribution models (after Fabri-Ruiz et al., 2017).

Environmental descriptors	Description
Depth	Bathymetric grid
Sea-surface temperature amplitude	Difference between austral summer (mean January–March) and winter (mean July–September) in sea-surface temperature
Mean seafloor temperature	Mean seafloor temperature
Seafloor temperature amplitude	Difference between austral summer (mean January–March) and winter (mean July–September) in seafloor temperature
Mean sea-surface salinity	Mean sea-surface salinity
Sea-surface salinity amplitude	Difference between austral summer (mean January–March) and winter (mean July–September) in sea-surface salinity
Mean seafloor salinity	Mean seafloor salinity
Seafloor salinity amplitude	Difference between austral summer (mean January–March) and winter (mean July–September) in seafloor salinity
Mean surface chlorophyll <i>a</i>	Mean surface chlorophyll <i>a</i> concentration in summer
Sediment	Sediment categories (see De Broyer et al., 2014)
Geomorphology	Geomorphologic features
Slope	Bathymetric slope
Mean seafloor oxygen concentration	Mean seafloor oxygen concentration
Sea-ice cover	Proportion of time the ocean is covered with sea-ice concentration over 85%
POC export	Average particulate organic carbon

of carbon (C) and nitrogen (N). Specimens were collected in November and December during three summer campaigns of the IPEV program PROTEKER, from 2012 to 2015, along the shorelines of the Kerguelen Islands, both in the north, the south and in the Morbihan Bay, at nine locations and 17 sampling sites ranging from 2 to 100 m depth (Figure 3; Table 2). Samples include 45 specimens of *A. cordatus* collected at five sites ranging between 2 and 90 m depth, 125 specimens of *C. nutrix* at seven sites between 20 and 100 m depth, and 139 specimens of *S. diadema* at nine sites between 5 and 100 m depth. All specimens were frozen at -20°C immediately after sampling. Individual measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were used to build the isotopic niche of each species. After dissection, the muscles of the Aristotle's lantern for *S. diadema* and *C. nutrix*, and the wall of the digestive tract for *A. cordatus* (the Aristotle's lantern is lacking in this taxon) were sampled for analysis following recommendations of Mateo et al. (2008). Tissue samples were washed with distilled water, frozen at -80°C for a few hours, and freeze-dried. Then they were cryo-crushed with liquid nitrogen and decarbonated under HCl (37% v/v) vapours for 24 hours. Isotopic ratios were determined by dry combustion using an elemental analyser (Vario micro, Elementar) coupled to an isotopic mass spectrometer (Isoprime, Elementar). Analytical reproducibility is 0.15‰ for carbon and 0.2‰ for

nitrogen. Isotopic compositions are expressed relative to the conventional standards, Vienna Pee Dee Belemnite (VPDB) for carbon (Craig, 1953) and atmospheric N_2 for nitrogen (Mariotti, 1983).

The R package Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson et al., 2011) was used to generate bivariate standard ellipses (SEs). SEs are bivariate equivalents of standard deviation. They contain only the 'typical' members of a population (but may not encompass outlier individuals in isotopic space). For this reason, they have been termed 'core isotopic niches', as their area (standard ellipse area, SEA) can be used as a proxy of resources most commonly used by the population (Layman and Allgeier, 2012). Besides SEA, other ecologically meaningful standard ellipse parameters were investigated such as eccentricity (ϵ) and the angle between the ellipse major axis and the biplot horizontal axis (θ) (Reid et al., 2016). Low ϵ (close to 0) indicates that ellipse shape is close to a circle, suggesting that isotopic variability is driven by both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Conversely, high ϵ (close to 1) suggests that the ellipse is elongated in shape, and that patterns of isotopic variation are predominantly driven by one of the two elements. Values of θ are useful to identify the most important drivers of isotopic variation. Values close to 0° suggest a higher contribution of $\delta^{13}\text{C}$ (multiple food items),

Table 2: Specimens sampled for isotope analyses.

Species	Location	Depth (m)	Number of specimens
<i>Abatus cordatus</i>	Baie du Hopeful	10	10
	Baie du Hopeful	50	10
	Port Matha	2	10
	Ile Suhm	90	5
	Port Couvreur	10	10
<i>Ctenocidaris nutrix</i>	Baie de l'Oiseau	100	10
	Baie Philippe	100	5
	Ile Haute	20	36
	Ile Suhm	20	37
	Ile Suhm	50	10
	Ile Suhm	90	2
	Port Couvreur	20	25
<i>Sterechinus diadema</i>	Baie de l'Oiseau	100	4
	Baie du Hopeful	90	8
	Fjord des Portes Noires	20	35
	Fjord des Portes Noires	75	10
	Iles du Prince de Monaco	15	30
	Iles du Prince de Monaco	100	10
	Port Couvreur	100	10
	Port Couvreur	20	22
	Port Matha	5	10

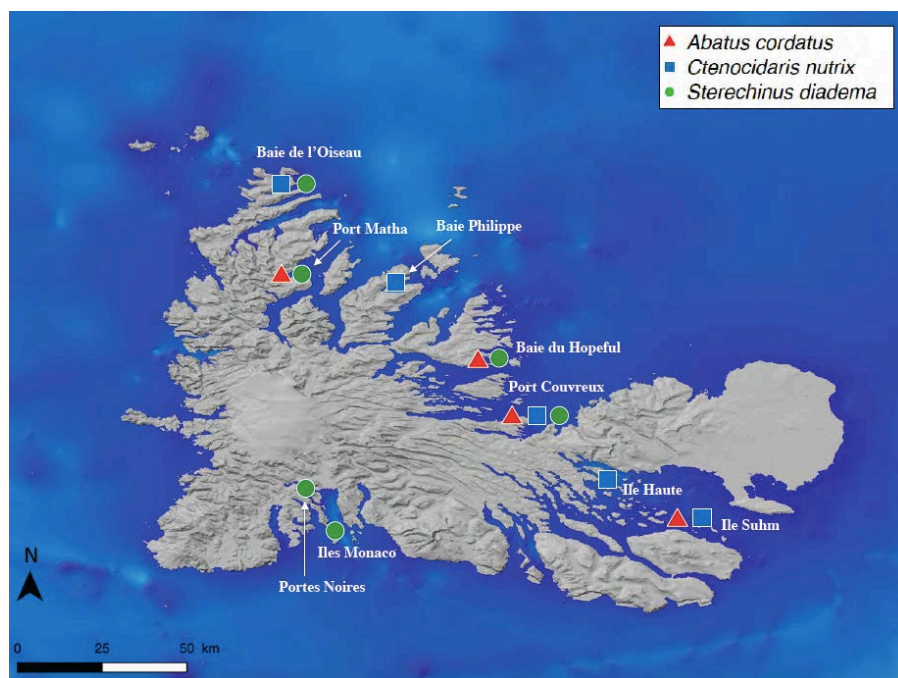


Figure 3: Sampling sites for isotopic analyses of the three echinoid species (red triangles for *Abatus cordatus*, blue squares for *Ctenocidaris nutrix* and green circles for *Sterechinus diadema*).

and values close to 90° , regardless of the direction, indicate a higher contribution of $\delta^{15}\text{N}$ (intraspecific variation in trophic position) (Reid et al., 2016).

Results

Species distribution range shift

All SDM generated for the present period (2005–2012) show high AUC values ($\text{AUC} > 0.879$) indicating good modelling performance. The predicted suitable areas differ between species (Figure 4) and the respective contributions of environmental descriptors vary between models (Figure 5a). The distribution of *A. cordatus* is exclusively predicted in shallow coastal areas of the Kerguelen Islands (Figure 4a). In contrast, distributions of *C. nutrix* and *S. diadema* are modelled from the sub-Antarctic Islands to the Antarctic coasts (Figures 4b, 4c).

For all three species, distribution range shifts are relatively weak between 1955–1974 and 2005–2012, the predicted suitable areas remain almost unchanged between the two time periods on the Kerguelen Plateau and in the entire Southern Ocean. The predicted distribution shifts are much more marked between 2005–2012 and 2050–2099 highlighting the sensitivity of species to future environmental changes. *Abatus cordatus* is endemic to coastal areas of the Kerguelen Plateau and is predicted to be more vulnerable to future environmental changes than the two other echinoids, *C. nutrix* and *S. diadema*, which are more widely distributed. Future distribution ranges are predicted to shift southward for *S. diadema* and *C. nutrix*, including local species loss, but no suitable area was predicted for *A. cordatus* under future conditions, highlighting its potential vulnerability (Figure 4).

Environmental descriptors that contribute the most to SDM vary between species according to their respective ecological niches. The distribution of the near-shore species *A. cordatus* is strongly controlled by seafloor temperature amplitudes (i.e. temperature range between summer maximums and winter minimums), particularly strong in shallow waters of the Kerguelen Islands (Figure 5a). The distribution of *C. nutrix* is controlled by environmental descriptors that vary at a broader spatial scale such as geomorphology, mean sea-surface salinity and temperature (Figure 5a). The same holds true for the widely distributed

S. diadema that is under the control of mean seafloor temperature which contributes the most to the model (Figure 5a).

Isotopic niche modelling and species vulnerability

Patterns of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic ratio variation are markedly different between the three species (Figure 6). Overall, *A. cordatus* displays the lowest $\delta^{15}\text{N}$ (mean \pm SD: $8.9 \pm 1.0\text{‰}$; full range: 6.9–10.1‰), whereas $\delta^{15}\text{N}$ values of *C. nutrix* are the highest (mean \pm SD: $12.3 \pm 1.1\text{‰}$) and are highly variable (full range: 8.4–15.8‰). $\delta^{15}\text{N}$ of *S. diadema* shows intermediary values (mean \pm SD: $10.6 \pm 0.7\text{‰}$; full range: 9.2–12.2‰). Mean $\delta^{13}\text{C}$ are comparable between all three species (*A. cordatus*: $-16.2 \pm 1.1\text{‰}$; *C. nutrix*: $-16.1 \pm 0.9\text{‰}$; *S. diadema*: $-15.4 \pm 3.0\text{‰}$; mean \pm SD in each case) (Figure 5), but dispersion of values is much larger for *S. diadema* than for the two other species (full ranges: -14.2 to -18.2‰ for *A. cordatus*; -13.7 to -18.4‰ for *C. nutrix* and -11.1 to -22.6‰ for *S. diadema*).

There is no overlap between the SEs associated with each species (Figure 6). The SE of *S. diadema* is markedly larger than both other species (SE are 5.7‰^2 for *S. diadema*, 3.1‰^2 for *A. cordatus* and 2.0‰^2 for *C. nutrix* respectively), and is almost horizontal ($\theta = 6.3^\circ$). Inclination is higher for *A. cordatus* ($\theta = -34.9^\circ$) and *C. nutrix* ($\theta = 52.1^\circ$). The measured incline of the standard ellipse for *A. cordatus* is close to a circle ($\epsilon = 0.81$) compared to the more elongated shape generated for both other species ($\epsilon = 0.93$ for *C. nutrix* and $\epsilon = 0.98$ for *S. diadema*).

Many ecological, physiological and environmental factors can influence the stable isotopic composition of consumers (Boecklen et al., 2011). While it is generally assumed that the stable isotope composition of a consumer's tissue can be influenced by a range of ecological, physiological and environmental factors, it is important to keep in mind that baseline shifts in isotopic composition of organic matter pools supporting consumers can also have a considerable influence (i.e. consumption of the same food item in spatially or temporally variable environments can also lead to differences in stable isotope composition (Flaherty and Ben-David, 2010; Woodland et al., 2012). In the present study, sampling occurred across a span of three years, which might account for part of the

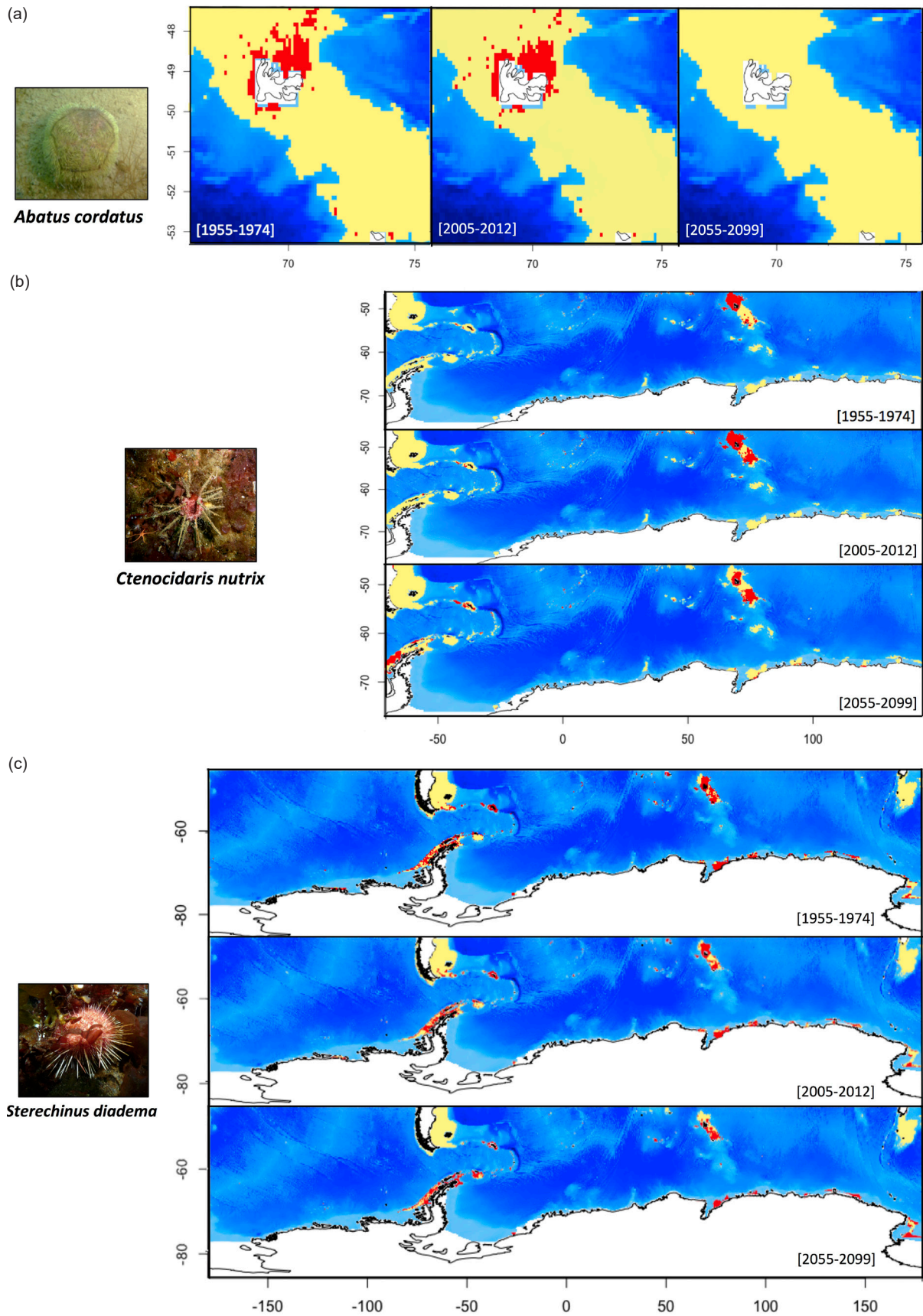


Figure 4: SDM of the three echinoid species (a) *Abatus cordatus*, (b) *Ctenocidaris nutrix*, and (c) *Sterechinus diadema* for past (1955–1974), present (2005–2012) and future (2055–2099) (IPCC RCP 8.5 scenario) periods. Species’ unsuitable (in yellow) and suitable (in red) areas are defined using the MaxSSS threshold.

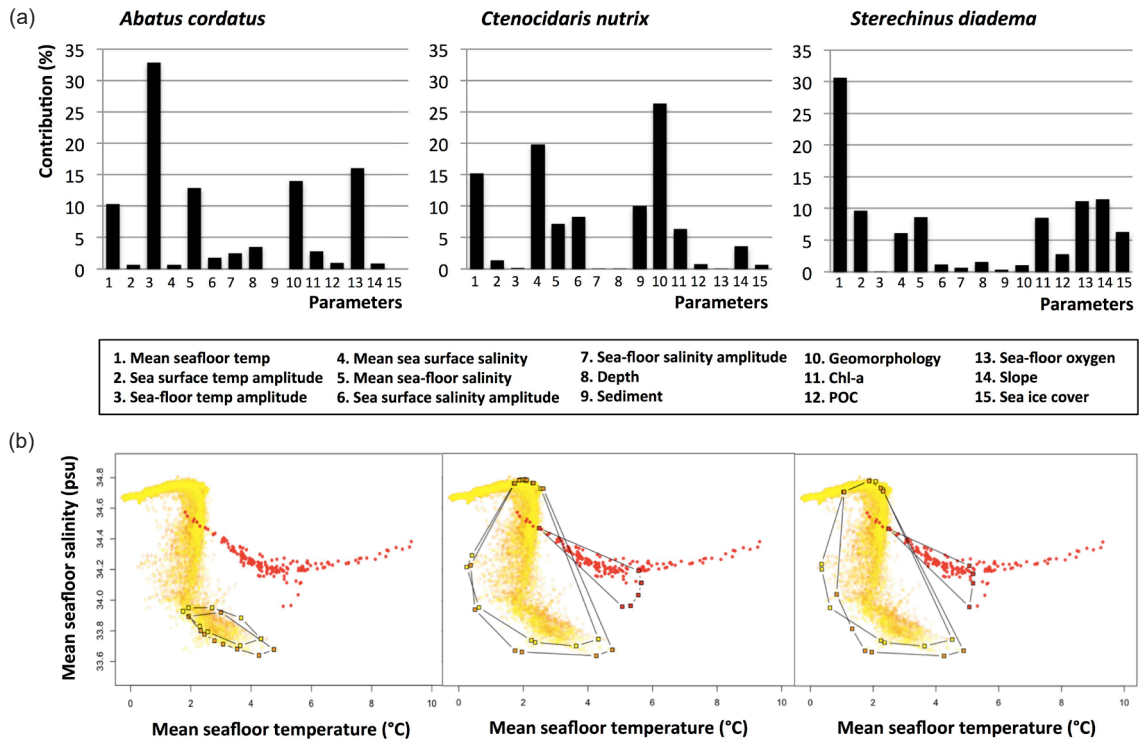


Figure 5: (a) Contribution (%) of each environmental descriptor to the SDM performed for *Abatus cordatus*, *Ctenocidaris nutrix* and *Sterechinus diadema*. (b) Display of environmental conditions present on the Kerguelen Plateau according to mean seafloor temperature and salinity. Values are shown for the three different periods using the following colour code: yellow for past (1955–1974), orange for present (2005–2012) and red for future (2055–2099) (IPCC RCP 8.5 scenario) conditions. Convex hulls (colour squares) delineate the portion of the environment space preferentially occupied by species (environmental values above the MaxSSS threshold) for each period. While the realised niches of *C. nutrix* and *S. diadema* are predicted to shift in the future (environmental range shift of convex hulls), the conditions are predicted to become unsuitable to the survival of *A. cordatus* (absence of convex hull).

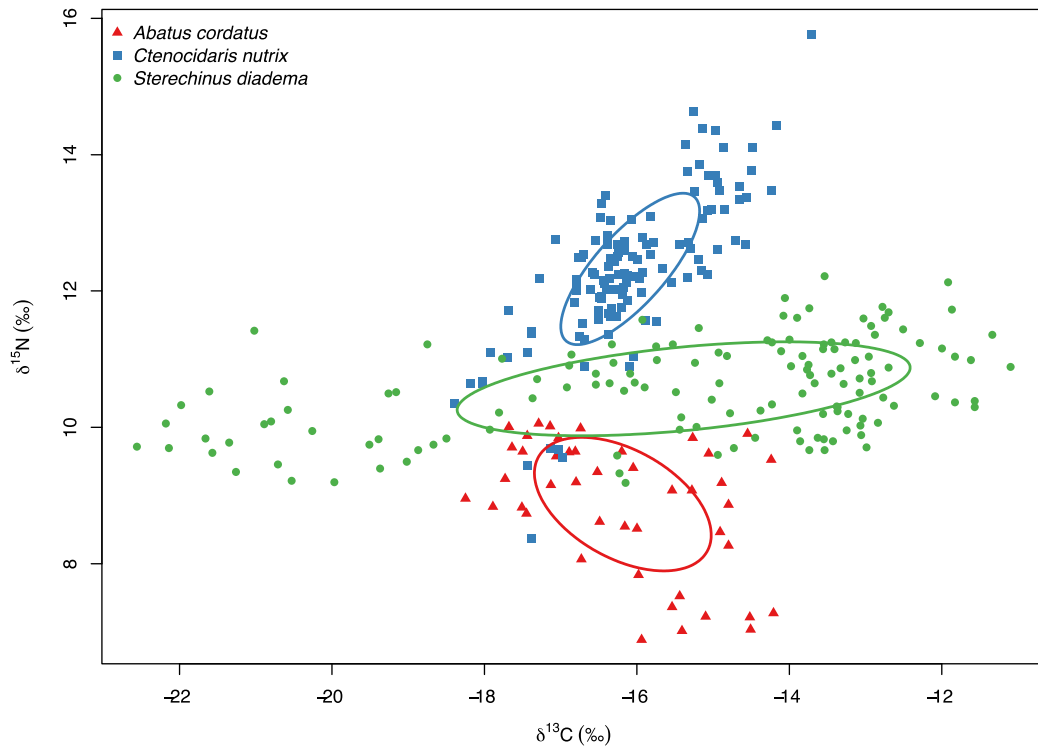


Figure 6: Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios (points, individual measurements) and isotopic niches (solid lines, standard ellipses) for the three echinoids.

observed isotopic variability (Figure 6). However, sampling was realised during the same season and tissue turnover is presumed to be slow, limiting the effect of temporal variations and suggesting that the different patterns of isotopic variability can still be of use to delineate the feeding strategies of the three studied species. Hence, isotopic niches of the three species seem to be distinct, suggesting different feeding habits that partly mirror family-specific observations made in the Antarctic Peninsula (Michel et al., 2016).

Since $\delta^{15}\text{N}$ values are known to show a stepwise increase with trophic levels (DeNiro and Epstein, 1981), the high $\delta^{15}\text{N}$ values of *C. nutrix* suggest that the species occupies the highest trophic position among the three studied echinoids, which is consistent with previous works (Jacob et al., 2003). Moreover, while the range of $\delta^{13}\text{C}$ covered by this species is narrow, dispersion of $\delta^{15}\text{N}$ values is very high. The isotopic niche of *C. nutrix* accordingly has a high eccentricity and higher θ values than the two other species (i.e. mostly vertical ellipse). All these results point out that isotopic variability in *C. nutrix* from the Kerguelen Plateau is driven by nitrogen-stable isotope ratios. The important spread in $\delta^{15}\text{N}$ values suggests a high inter-individual variability in the importance of animal-derived material for nutrition of *C. nutrix*, which is congruent with the various animal remains observed in the gut contents (sponges, bryozoans and crustaceans). This is also in line with previous observations from the Antarctic Peninsula, in which Cidaridae seem to be able to shift between detritus feeding, carnivory and scavenging in relation to prey availability (Michel et al., 2016). This also indicates a high feeding plasticity of the species and, potentially, its trophic resilience to potential trophic modification driven by global change.

Sterechinus diadema has the largest isotopic niche, suggesting this species feeds on a wider variety of resources than the two other species. The high eccentricity and the almost horizontal orientation of the ellipse clearly shows that the high isotopic variability in this species is mainly driven by $\delta^{13}\text{C}$. $\delta^{13}\text{C}$ of consumer's tissue is mostly influenced by producers directly or indirectly supporting their populations (DeNiro and Epstein, 1978). While identification of the baseline items is beyond the scope of this study, the wide range of $\delta^{13}\text{C}$ values covered by *S. diadema* suggests that the species feeds on various items originating from

pelagic and benthic sub-Antarctic environments (Jacob et al., 2006). This is supported by the predominant food items observed in the gut content of *S. diadema* in Kerguelen: macroalgae fragments, abundant epiphytic filamentous algae and diatoms, and animal remains (ascidians and molluscs). On the other hand, this species occupied a relatively narrow $\delta^{15}\text{N}$ range between the two other taxa. This could indicate an intermediary trophic position, and the potential ability to feed on both animal-derived matter as well as primary producers and/or organic matter pools (omnivorous). Overall, isotopic niche analysis points out that on the Kerguelen Plateau, *S. diadema* seems to be an omnivore with high trophic plasticity, able to thrive on a large number of different food items.

Abatus cordatus shows the lowest $\delta^{15}\text{N}$ of the three species, suggesting it also occupies the lowest trophic position. This is compatible with the deposit-feeding behaviour of the genus that ingests sediment to feed on the associated organic matter (David et al., 2005; Michel et al., 2016). The round shape of the isotopic niche of *A. cordatus* is due to variations in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. In the Antarctic Peninsula, it was suggested that the Schizasteridae exhibit low trophic plasticity, and that their isotopic ratios are more influenced by baseline shifts in isotopic composition of sediment-associated organic matter than by actual variation in their feeding habits (Michel et al., 2016). Our results could hint to a similar situation on the Kerguelen Plateau.

Discussion

Enhanced biodiversity data

The first scientific surveys of the Kerguelen Plateau date back to the oceanographic campaign of HMS *Challenger* in 1872. One and a half centuries later, our knowledge of benthic species distribution on the Kerguelen Plateau has significantly increased (Figure 7) but remains quite patchy (Améziane et al., 2011; Guillaumot et al., 2018b). Since the Biogeographic Atlas of the Southern Ocean (De Broyer et al., 2014) was published, results of recent field campaigns of the POKER and PROTEKER programs have significantly improved our knowledge of echinoid distribution on the Kerguelen Plateau. New data were compiled to append existing datasets and are now available through the biodiversity.aq data portal (Saucède et al., 2015b; Guillaumot et al., 2016; Fabri-Ruiz et al., 2017).

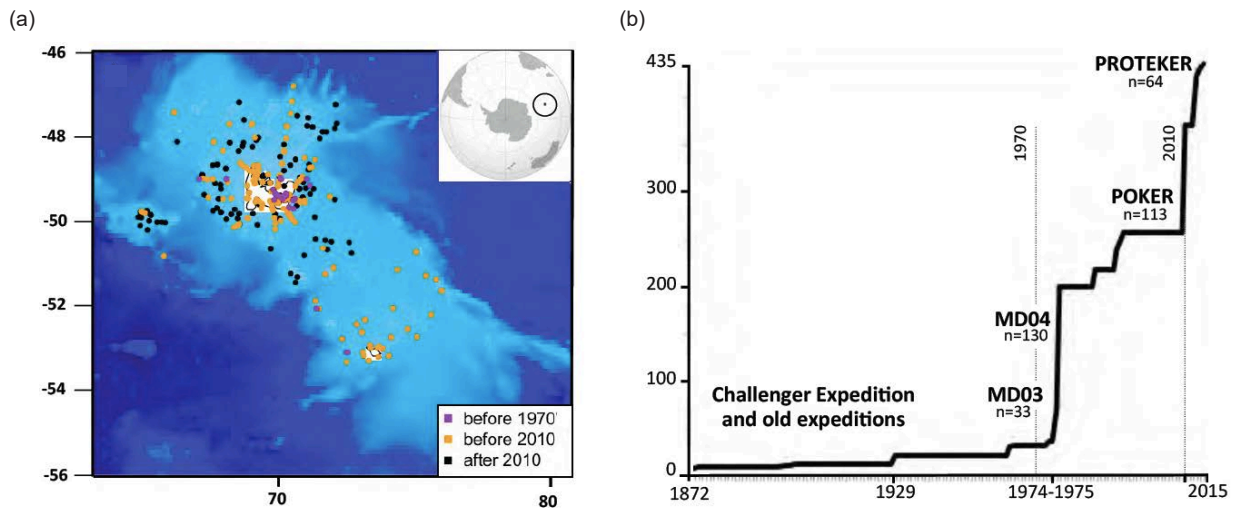


Figure 7: (a) All available echinoid occurrence records on the Kerguelen Plateau with chronological partition of data. (b) Chronological evolution of echinoid sampling effort (436 records in 2015) on the Kerguelen Plateau. Key sampling campaigns with number of records are mentioned (MD03 and MD04: oceanographic campaigns of the RV *Marion Dufresne I*, POKER: campaign of the FV *Austral*, and PROTEKER: three first summer campaigns of the IPEV program No. 1044).

In addition to new occurrence data, echinoid systematics is currently being revised using both molecular and morphological approaches (Díaz et al., 2011; Saucède et al., 2014, 2015a; David et al., 2016). Recent results have highlighted the urgent need for revision of echinoid systematics considering the significant discrepancy observed between nominal species delimitation and molecular evidence. For instance, six nominal species were initially attributed to the genus *Sterechinus*, which were restricted to distinct geographic areas and depth range. Molecular and morphological analyses have revealed that three distinct entities only could be identified in the genus (Díaz et al., 2011; Saucède et al., 2015a): the three nominal species *S. antarcticus*, *S. diadema* and *S. agassizii* cluster together and cannot be distinguished from each other, and *S. bernasconiae* is a subjective junior synonym of *Gracilechinus multidentatus*. Such a revision of echinoid systematics is a prerequisite for relevant ecological and biogeographic studies (Díaz et al., 2011; Saucède et al., 2015a).

Limitations to the SDM approach

The SDM approach has recently received growing interest from Southern Ocean marine biologists in regards to modelling the distribution of a large variety of organisms including plankton (Pinkerton et al., 2010), fish (Loots et al., 2007; Koubbi et al., 2011; Hill et al., 2017), cephalopods (Xavier et al., 2016), crustaceans (Basher and Costello, 2016;

Gallego et al., 2017), echinoids (Pierrat et al., 2012; Guillaumot et al., 2018a, 2018b) and top predators such as crabeater seals, fur seals, killer whales and minke whales (Nachtsheim et al., 2017; Thiers et al., 2017). Species occurrence datasets consist of compilations of often heterogeneous, temporally and spatially biased data that need to be corrected before modelling (Newbold, 2010; Tessarolo et al., 2014; Guillaumot et al., 2018b). Moreover, species absence data is usually not available and SDM must be generated using presence-only records, considered as less relevant and powerful in comparison with presence-absence SDM (Brotons et al., 2004). However, protocols were recently developed to partly compensate for these limitations and perform reliable SDM (Guillaumot et al., 2018b).

The relevance of models is also dependent on the availability and quality of environmental descriptors but few of them are available for coastal areas. The accuracy of model projections is also limited by the coarse resolution of environmental data. SDM could gain in relevance if complementary and high-resolution descriptors were made available to better model species fundamental niches (Austin and Van Niel, 2011; Bradie and Leung, 2017). In addition, few predictions are available for future abiotic factors. For the Kerguelen Plateau in particular, latitudinal heat flux and marine front positions are still debated, questioning the relevance of future climatic scenarios (Park et al., 2014; Vivier et al., 2015) and potentially impacting species model predictions for the region.

Modelling distribution dynamics

SDM require that species–environment relationships are considered at the equilibrium, an assumption that is particularly questionable in the context of environmental changes. Changing relationships between species and the environment call for more dynamic and process-based approaches. More reliable projections can be produced if physiological mechanisms that constrain species distributions are included in models (Kearney and Porter, 2009; Morin and Thuiller, 2009; Buckley et al., 2010; Kearney et al., 2010; Gutt et al., 2012; Briscoe et al., 2016). Mechanistic approaches are one possible avenue for achieving such models as they incorporate species functional traits in models using dynamic methods such as the dynamic energy budget (DEB) theory (Kooijman, 2010). DEB models describe how organisms use energy throughout their entire life cycle (embryo, juvenile, adult) according to the surrounding environment (temperature and food availability). Applied DEB studies are currently developing fast, with models already developed for several case studies (van der Meer, 2006, van des Meer et al., 2014; Thomas et al., 2016; Le Goff et al., 2017; see Jusup et al., 2017 for a review). Studies of Southern Ocean taxa are, however, only in their infancy, with only two benthic species modeled: *Odontaster validus* (Agüera et al., 2015) and *Laternula elliptica* (Agüera et al., 2017), and one pelagic, *Euphausia superba* (Jager and Ravagnan, 2015). Building physiological models requires a thorough understanding of a species' physiology across all development stages (Kearney and Porter, 2009). Data from the literature are often missing because of substantial technical and practical issues. This is particularly the case for Southern Ocean species, for which field campaigns and laboratory experiments imply significant logistic and financial constraints. Nevertheless, recent studies on the potential physiological responses of Antarctic marine species to environmental changes such as rising seawater temperatures, changes to salinity and alterations to pH conditions have begun to emerge (e.g. Kawaguchi et al., 2013; Peck et al., 2013; Collard et al., 2014; Suckling et al., 2015; Karelitz et al., 2017; Morley et al., 2016). Such studies will provide the required parameters to build physiological models with similar experiments currently underway in the Kerguelen Islands. In particular, the physiological response of the possibly endangered *A. cordatus* to multistress factors (temperature and pH) is studied during the summer

campaigns of the IPEV program PROTEKER. The expected results should refine model predictions of species sensitivity to environmental changes.

Once DEB models are produced, species' physiological range can be defined as a functional response to environmental parameters such as seawater temperature and food availability. Such models give fundamental information on thermal requirements and fitness components like survival, growth and reproduction. Species physiological traits can be spatially projected considering selected environmental features, which is referred to as trait distribution models (TDM). The combination of correlative (SDM) and mechanistic (TDM) spatial projections should contribute to better characterise distribution dynamics of marine species in response to environmental changes.

Conclusions

In the present study, SDM suggest contrasting responses of the investigated species under future environmental conditions (Figure 5b). Suitable areas of the shallow-water species *A. cordatus* are characterised by low salinity and moderate temperature conditions (33.6–33.9 and 3–4°C respectively). The species' niche is narrow and its suitable habitat is restricted to a small part of the Kerguelen Plateau. Projections for 2050–2099 indicate unsuitable conditions for the species on the Kerguelen Plateau (Figure 4a), with values of mean seafloor temperature and salinity predicted to shift beyond the limits of the species' niche (Figure 5b) potentially leading to the species' extinction. The two other species have wider ecological niches and show important temperature tolerance (0°C to +6°C). Therefore, the occupied niches of *C. nutrix* and *S. diadema* are predicted to shift in response to future changes (Figure 5b) and the species are predicted to adapt to future environmental conditions.

Overall, differences in trophic positions and feeding strategies of the three studied species are likely to modulate the ability of each species to cope with environmental changes. *Sterechinus diadema* seems to be an omnivorous species able to consume a large array of food items. Therefore, it seems likely that when facing changes in availability of specific food sources, this trophic plasticity could allow it to shift its diet towards other items, allowing this species a certain degree of resilience. *Ctenocidaris nutrix* exhibits clear preferences

towards consumption of animal-derived matter. Changes in benthic fauna abundance and/or identity could therefore interfere with its feeding. Nevertheless, this species also seems to display multiple feeding behaviours that could favour its resilience to changing environments. Finally, *A. cordatus* seems to have a low trophic plasticity, and to be restricted to deposit feeding. In this context, suitability of a given habitat for this species is likely to be conditioned by the quantity and quality of sediment-associated organic matter (Jansen et al., 2018). Moreover, changes in benthic–pelagic coupling and fluxes of organic matter to the benthos could put this species at risk of food shortage.

A serious limitation of SDM is the inability to explicitly incorporate biotic interactions. Integrating biotic interactions to SDM should improve model reliability (Van der Putten et al., 2010; Wisz et al., 2013; Leach et al., 2016), an interesting prospect for studies focusing on communities and ecosystems exposed to environmental changes (Loreau and Behera, 1999; Walther, 2010; Albouy et al., 2014; Hattab et al., 2016). In the present work, the two modelling approaches independently identified the same species, *A. cordatus* as being particularly at risk due to its narrow ecological niche and endemism to near-shore areas of the Kerguelen Plateau. Distribution range shifts induce changes in trophic interactions, suggesting that coupling trophic ecology with SDM will improve our understanding of species' responses to changing environments (Walther, 2010; Pellissier et al., 2013; Albouy et al., 2014; Hattab et al., 2016; Leach et al., 2016; Staniczenko et al., 2017). The most efficient way to couple trophic ecology and SDM approaches likely involves the use of numerical tools to generate meaningful ecological data from trophic markers such as stable isotopes. Unlike the isotopic niche models presented here, stable isotope mixing models allow for diet reconstruction and the quantification of a given consumer's reliance on a particular food item (Parnell et al., 2010; Layman et al., 2012; Phillips et al., 2014). Stable isotopes can also be used to provide continuous estimates of trophic position, which are simple ways to picture energy flow through complex communities and assess functional roles of organisms in natural ecosystems (Post, 2002; Layman et al., 2012; Quezada-Romegialli et al., 2018). Modern developments of these tools would provide robust numerical estimates of ecological parameters that could be used in spatially explicit models such as SDM and TDM.

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