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Using correlative and mechanistic niche models to assess the sensitivity of the Antarctic echinoid *Sterechinus neumayeri* to climate change

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Abstract

The Southern Ocean is undergoing rapid environmental changes that are likely to have a profound impact on marine life, as organisms are adapted to sub-zero temperatures and display specific adaptations to polar conditions. However, species ecological and physiological responses to environmental changes remain poorly understood at large spatial scale owing to sparse observation data. In this context, correlative ecological niche modeling (ENMc) can prove useful. This approach is based on the correlation between species occurrences and environmental parameters to predict the potential species occupied space. However, this approach suffers from a series of limitations amongst which extrapolation and poor transferability performances in space and time. Mechanistic ecological niche modeling (ENMm) is a process-based approach that describes species functional traits in a dynamic environmental context and can therefore represent a complementary tool to understand processes that shape species distribution in a changing environment. In this study, we used both ENMc and ENMm projections to model the distribution of the Antarctic echinoid *Sterechinus neumayeri*. Both models were projected according to present (2005–2012) and future IPCC scenarios RCP 4.5 and 8.5 for (2050–2099). ENMc and ENMm projections are congruent and predict suitable current conditions for the species on the Antarctic shelf, in the Ross Sea and Prydz Bay areas. Unsuitable conditions are predicted in the northern Kerguelen Plateau and South Campbell Plateau due to observed lower food availability and higher sea water temperatures compared to other areas. In contrast, the two models diverge under future RCP 4.5 and 8.5 scenarios. According to ENMm projections, the species would not be able to grow nor reach sexual maturity over the entire ocean, whereas the Antarctic shelf is still projected as suitable by the ENMc. This study highlights the complementarity and relevance of EMN approaches to model large scale distribution patterns and assess species sensitivity and potential response to future environmental conditions.

Keywords Ecological niche model · Dynamic energy budget · Species distribution model

Introduction

Polar regions—and the Southern Ocean in particular—are increasingly affected by climate changes (Stammerjohn et al. 2008, 2012; Schofield et al. 2010; Turner et al. 2014).

Temperature records over the previous decades unambiguously show an overall warming of water masses within the Antarctic Circumpolar Current area, from the surface down to 2000-m depth, at a more rapid pace than average shifts measured in the global ocean (Gille 2002; Böning et al. 2008; Giglio and Johnson 2017). Contrasts, however, exist between regions of the Southern Ocean. For instance, a 1 °C rise in sea water temperature has been recorded down to 25 m in the water column at Potter Cove (King George Island, Antarctic Peninsula) over 19 years, with a decrease in sea ice extent (Meredith and King 2005). At the same time, sea ice has significantly been increasing in the Ross Sea both in concentration, extent (Comiso and Nishio 2008) and duration (Stammerjohn et al. 2012).

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In the last report (IPCC 2015) of the Intergovernmental Panel on Climate Change (IPCC) CMIP5 (Coupled Model Intercomparison Project), climate models predict a global warming of the entire water column south of the Polar Front by the end of the century under either moderate (RCP 4.5) or business-as-usual Representative Concentration Pathway scenarios (RCP 8.5) (Turner et al. 2009, 2014; Liu and Curry 2010). Associated to this overall warming, changes in the extent and duration of the Antarctic seasonal sea ice and water freshening close to glacier melting sources are also expected (Meredith and King 2005; Bracegirdle et al. 2008; Stammerjohn et al. 2012). The Antarctic sea ice plays a crucial role in ecosystem functioning and regulates the timing of primary production (Petrou et al. 2016). Changes in sea ice regimes will impact the dynamics of phytoplankton blooms. Primary production constitutes an essential food intake for the benthos (Smith et al. 2006; Lohrer et al. 2013; Petrou et al. 2016; Schofield et al. 2017). Therefore, changes in phytoplankton dynamics could have a profound effect on the structure and functioning of benthic ecosystems.

The tectonic, climate and glacial history of the Southern Ocean (waters below 60°S in latitude) have conditioned the evolution of the Antarctic marine biota through various adaptive radiations, speciation, dispersal and extinction events. Associated to the isolation of the Antarctic continent, this led to the evolution of an original benthic fauna unparalleled in other parts of the world's ocean (Arntz et al. 1997; Clarke et al. 2005; Linse et al. 2006; Barnes and Griffiths 2007; Griffiths et al. 2009; Pearse et al. 2009; Rogers et al. 2012; David and Saucède 2015). High Antarctic marine benthic invertebrates have adapted to sub-zero temperatures and their feeding strategies have been conditioned by the seasonality in food availability due to the variation of sea ice dynamics (Knox 2006). Antarctic species commonly exhibit low metabolic and growth rates associated with a high longevity compared to temperate and tropical species (Pearse and Giese 1966; Brey 1991; Nolan and Clarke 1993; Peck and Bullough 1993; Brey et al. 1995; Peck et al. 2016). Most of the marine species present on the Antarctic shelf are consequently stenothermic (Peck 2002, 2005) and very sensitive to seawater warming and temperature variations (Peck et al. 2009). Temperature changes can affect their physiological performance, phenology and distribution (Morley et al. 2009, 2010, 2011; Peck et al. 2009).

Along Antarctic coasts, marine benthic communities are at the southernmost boundary of the temperature latitudinal gradient of the marine biome (Peck et al. 2005). Consequently, in a context of warming temperatures, species are spatially limited and cannot easily migrate or find refuges to survive (Peck and Conway 2000).

Monitoring and predicting the response of Antarctic species to environmental change is challenging as gaps still persist in our knowledge of Antarctic marine species distribution (Kaiser et al. 2013; Kennicutt et al. 2014, 2019; Gutt et al. 2018), despite the significant efforts led during the International Polar Year and the Census of Antarctic Marine Life (Schiaparelli et al. 2013; Fabri-Ruiz et al. 2019). Data collection and experimental setups are strongly conditioned by financial and technological limitations in such a remote and hardworking region (extreme climate conditions, difficult to access) (Gutt et al. 2012). Ecological niche modeling (ENM) can represent an alternative to overcome this issue.

Correlative ecological niche models (ENMc) can be used to predict species distribution based on the statistical relationship between species occurrence records and abiotic conditions (Guisan and Thuiller 2005; Pearson 2007; Elith and Leathwick 2009). ENMc provides a spatial representation of the species' realized niche under the assumption of equilibrium between species' distribution and the abiotic environment (Guisan and Zimmermann 2000; Pearson and Dawson 2003). In contrast, mechanistic ecological niche model (ENMm) uses eco-physiological data and life history traits to describe organisms' physiology. They can predict species capabilities to survive, grow and reproduce under changing environmental conditions and describe a part of the species fundamental niche (Brown et al. 2004; Kearney et al. 2008, 2009; Sousa et al. 2008; Cabral and Kreft 2012).

ENMc has been widely developed for the study of Antarctic marine organisms such as pelagic plankton and fish (Pinkerton et al. 2010; Duhamel et al. 2014), deep-water shrimps (Basher and Costello 2016), cirripeds (Gallego et al. 2017), molluscs (Xavier et al. 2016), echinoids (Pierrat et al. 2012; Fabri-Ruiz et al. 2019, 2020), or sea stars (Guillaumot et al. 2019). In contrast, ENMm (such as the projection of Dynamic Energy Budget models, DEB, Kooijman 2010) has never been developed for Antarctic species case studies so far, due to the more important amount of data required to implement the DEB model (eco-physiological data on the different species life stages; van der Meer 2006; Kearney and Porter 2009), and the novelty of the DEB projection method (Thomas and Bacher 2018).

Once created, DEB models are published in the Add-my-Pet collection (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/about.html), that already provides a list of 37 Antarctic marine and terrestrial species. Among them, the most commonly found in communities and well-studied Southern Ocean benthic invertebrates are the sea star *Odontaster validus* (Agüera et al. 2015), the bivalve *Laternula elliptica* (Agüera et al. 2017), the echinoid *Abatus cordatus* (Guillaumot 2019a, Arnould-Pétré et al. 2021), the gastropod *Nacella concinna* (Guillaumot et al. 2020a) and the bivalve *Adamussium colbecki* (Guillaumot 2019b). DEB models have also been developed for pelagic species such as the Antarctic krill *Euphausia superba*, the salp *Salpa thompsoni* (Jager and Ravagnan 2015; Henschke et al. 2018) and also

for marine mammals such as the elephant seal *Mirounga leonina* (Goedegebuure et al. 2018).

Providing relevant projections of the impact of climate change on biodiversity is crucial to conservation biology (McMahon et al. 2004; Gotelli et al. 2009; Gutt et al. 2012; Evans et al. 2015; Pertierra et al. 2020). Usually, ENMc and ENMm are independently used to study the relationship of a species with its environment (Dormann et al. 2012). Combining both approaches has only recently emerged in link with computing advances (Kearney et al. 2010; Buckley et al. 2011; Dormann et al. 2012; Meineri et al. 2015; Briscoe et al. 2016; Enriquez-Urzelai et al. 2019; Pertierra et al. 2020). This combination was proved efficient to improve predictions compared to simple models, as ENMm can address the deficits of ENMc by explicitly including processes, offering the opportunity to describe, within and without the predicted suitable boundaries of the ENMc predictions, the process-based causes of the species distribution (Kearney and Porter 2009; Dormann et al. 2012). It can also provide more insight into drivers that shape species current distribution and potential distribution shifts under changing environmental conditions (Kearney and Porter 2009; Buckley et al. 2011; Ceia-Hasse et al. 2014; Meineri et al. 2015).

The echinoid *Sterechinus neumayeri* (Meissner 1900) is abundant, common and endemic to the Antarctic continental shelf. It has widely been studied in various fields such as reproductive biology, embryology, toxicology, ecology and physiology (Bosch et al. 1987- McMurdo; Stanwell-Smith and Peck 1998- Signy Island; Marsh et al. 1999, 2001- McMurdo; Tyler et al. 2000—Rothera; Brockington and Peck 2001—Rothera; Pace and Manahan 2007—McMurdo; Moya et al. 2012- Bellingshausen Sea; Yu et al. 2013—McMurdo; Lister et al. 2015- McMurdo; Alexander et al. 2017—Peterson Channel).

Widely distributed all around Antarctica (Fig. 1), its distribution ranges from the subtidal zone to 800-m depth with most records found in shallow waters of the continental shelf above 400-m depth (David et al. 2005). Recent molecular studies showed that the species combines a unique genetic entity all around the Antarctic continent (Díaz et al. 2011, 2018). It plays an important ecological role in structuring benthic communities. The "grazing" pressure exerted by *S. neumayeri* is believed to control the local distribution of bryozoans and spirorbid annelids and could therefore have a negative feedback on the recruitment of some sessile species (McClintock 1994; Bowden 2005; Figuerola et al. 2013). Adult specimens are omnivorous and mainly feed on bryozoans, foraminifera, polychaetes, diatoms and macro-algae (McClintock 1994; Amsler et al. 1999; Jacob et al. 2003; Michel et al. 2016). As in many other Antarctic species, the development rate of *S. neumayeri* is low (Bosch et al. 1987), longevity can exceed 40 years (Brey 1991; Brey et al. 1995) and the feeding period is seasonal (Brockington and

Peck 2001). *S. neumayeri* is a broadcast spawner, planktonic larvae can drift in the water column for more than 8 months before metamorphosis takes place on the seabed (Pearse and Giese 1966) (see details in Online resource 1 and Online resource 2). The test of adult specimens can reach a final size of seven centimeters in diameter (Brey et al. 1995).

In the present work, we used both ENMc and ENMm approaches to project the distribution response of *S. neumayeri* to present-day conditions and to future IPCC scenarios of climate change RCP 4.5 and RCP 8.5. ENMc was generated to predict species distribution in these environmental conditions using the Random Forest (Breiman 2001) algorithm. The DEB model created for *S. neumayeri* was spatially projected (i.e., ENMm model) in these three environmental scenarios. The results of both ENMc and ENMm were compared to get more insight into the physiological processes and mechanisms that constrain the species distribution and assess model performances and ecological significance under present-day conditions and future scenarios of climate change.

Material and methods

Correlative ecological niche model (ENMc)

Occurrence data and environmental predictors

An ENMc was generated using georeferenced presence-only data of *S. neumayeri* extracted from an extensive Southern Ocean echinoid distribution database (Fabri-Ruiz et al. 2017) that includes field samples collected between 1901 and 2015 (Fig. 1). Considering the broad spatial scale of the analysis and the congruence between historical and present-day presence records (David et al. 2005; Fabri-Ruiz et al. 2019), it is here assumed that the species distribution did not significantly change over the last century at the scale of the entire Southern Ocean.

Environmental predictors used in the study were extracted from Fabri-Ruiz et al. (2017) (Online resource 3). Predictors were selected based on their ecological relevance for explaining the distribution of *S. neumayeri* (Pierrat et al. 2012; Saucède et al. 2014; Fabri-Ruiz et al. 2019). Collinearity between descriptors was tested to limit possible biases in predictor contributions and model predictive performances and the presence of spatial autocorrelation (Dormann et al. 2012). For this purpose, we performed a Spearman pairwise correlation test between descriptors that were iteratively removed for correlation values of $r_S > 0.8$ (Dormann et al. 2012). Over 26 possible descriptors, 13 were used to run the models. The physical habitat was described using the following descriptors: depth, geomorphology, slope, sea surface temperature range, seafloor temperature range, mean
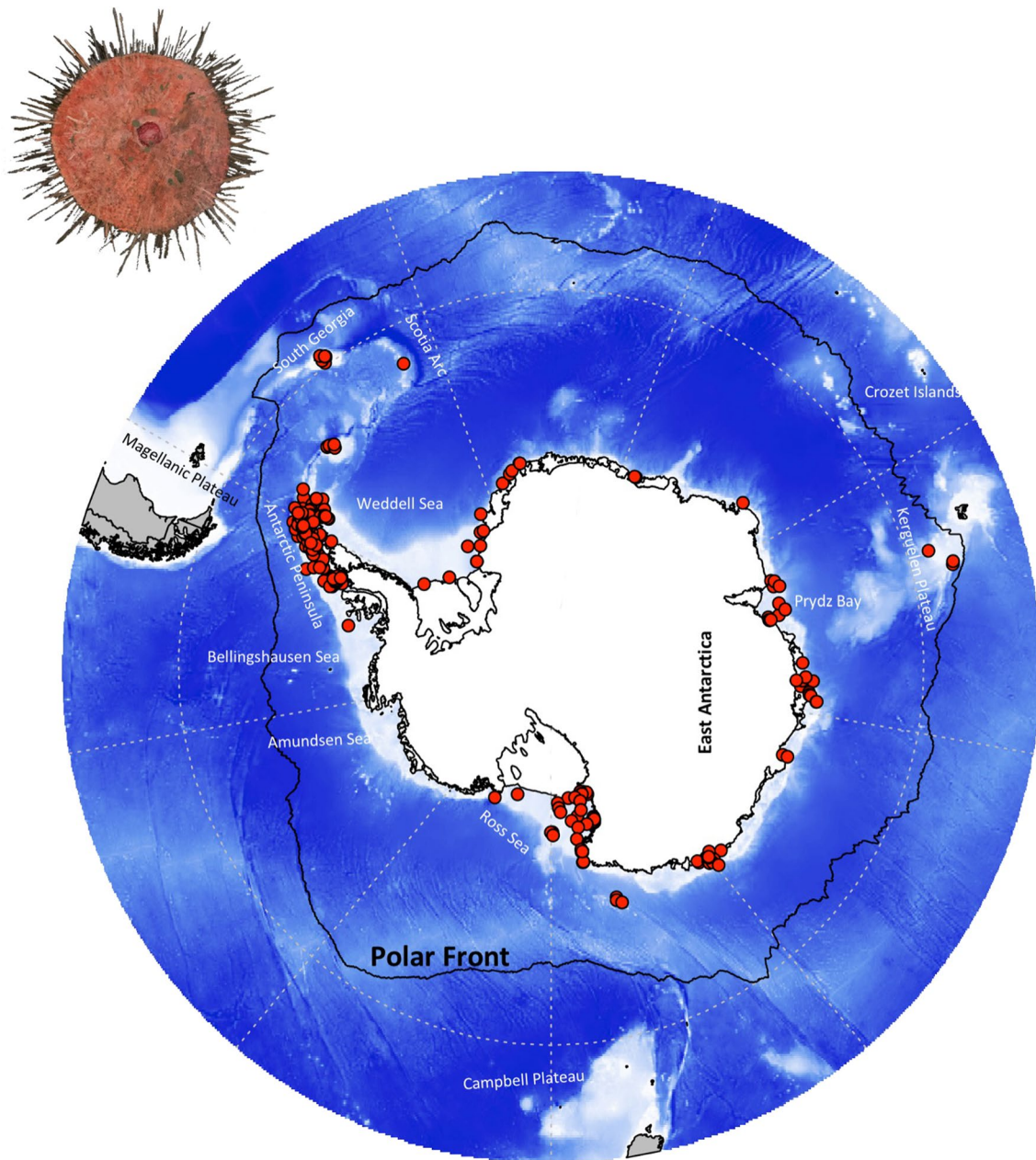
Fig. 1 *Sterechinus neumayeri* occurrence data extracted from Fabri-Ruiz et al. (2017). (red dot) Illustration of *Sterechinus neumayeri* © J-G. Fabri

seafloor temperature and sea ice cover. Summer chlorophyll-a concentration was used as a proxy of food resources and habitat chemistry was described based on seafloor salinity, seafloor salinity range, sea surface salinity range, sea surface salinity and seafloor oxygen (Online resource 3). Predictor 'range' is here defined as the difference between winter and summer mean values.

Future projections were based on IPCC scenarios RCP 4.5 and RCP 8.5 (IPCC 2015, Online resource 4) extracted from the NOAA database (https://www.esrl.noaa.gov/psd/ipcc/ocn/ (accessed on 2019-12-19)). Future projections were not available for seafloor oxygen conditions under IPCC scenarios. The descriptor was therefore considered unchanged (present conditions) in future models.

ENMc calibration

The distribution of *S. neumayeri* was modeled using Random Forests (RF) (Breiman 2001) computed with the *biomod2* package (Thuiller et al. 2009) under R.3.4 (R Core

Team 2017). In a former study, RF were proved relevant to model the distribution of *S. neumayeri*, models showing high and stable predictive performances and appropriately captured the species environmental envelope (Fabri-Ruiz et al. 2019). Here, the ENMc was parameterized with 500 classification trees, a tree number that minimizes the difference in predictive performance between models. This number was selected by testing different values of tree number (50, 100, 500 and 1000). Five node size (minimum size of the final node of any tree) and mtry = 13 (the number of candidate variables to include at each split) was tuned using the 'tuneRF' function from the *caret* package (Kuhn 2012). The occurrence dataset was randomly split into a 70% subset used to train the model and a 30% subset to test model predictions. As only presence data were available, pseudo-absences were randomly generated following Barbet-Massin et al. (2012) with a number of pseudo-absences equal to the number of presences. Fifty pseudo-absence replicates were generated and for each, ten evaluation runs were computed.

Spatial sampling bias is generally pervasive in species occurrence data, which were typically not evenly sampled across the ocean (Broyer and Koubbi 2014). This may generate strong spatial autocorrelation in model residuals, that is, the fact that close observations in geography will be more similar than random (Legendre 1993). The presence of spatial autocorrelation breaks the assumption of "independent errors" when significant (Dormann et al. 2007) and lead to unreliable model evaluation (Phillips et al. 2009; Kramer-Schadt et al. 2013; Warren et al. 2014).

To limit this bias, pseudo-absence data were sampled following the same sampling pattern as all Antarctic echinoid records available in the Southern Ocean. A Kernel Density Estimation map established from all Antarctic echinoid records using Spatial Analyst in ArcGIS v10.2 (ESRI 2011) was used to target the pseudo-absence sampling accordingly (Phillips et al. 2009; Guillaumot et al. 2018). In total, 50 pseudo-absence replicates were generated and spatial autocorrelation was quantified for each pseudo-absence replicates using the Moran I index computed with the *ape* R package (Paradis et al. 2008). Moran I measures the average correlation value of a variable between values taken at close localities. It is an easy correlation index to interpret, that varies between − 1 (negative spatial autocorrelation: values at close localities are opposite compared to the mean value) and + 1 (positive spatial autocorrelation: values at close localities are similar), with 0 for an absence of spatial autocorrelation. The significant values of spatial autocorrelation statistic are indicated by a *p* value. Over the 50 replicates of pseudo-absences, we selected thirty replicates showing $p > 0.5$ (with *p,* the *p* value of the significance of Moran's I), other pseudo-absences replicates have depicted a *p* value less than 0.5.

The wide extent of the study area implies that a wide range of environmental conditions may be used to fit the models and lead to overestimate and extrapolate the species modeled niche (Giovanelli et al. 2010; Barve et al. 2011; Anderson 2013; Guillaumot et al. 2020b). To limit extrapolation, the modeling area was limited to the maximum species registered depth (800 m, David et al. 2005) for model calibration and projection.

Model predictive performances were assessed with the TSS metric (True Skill Statistics) (Allouche et al. 2006) that is the sum of the sensitivity (proportion of correctly predicted presences) and the specificity (proportion of correctly predicted absences) minus one (*sens* + *spec* − 1). The contribution of environmental predictors to the models was provided as "contribution permutation" available under the *biomod2* R package (Thuiller et al. 2009). For each predictor, contribution permutation was calculated as the Pearson correlation coefficient between model predictions by randomly permuting the predictors. For this purpose, we performed ten permutation runs. The higher the value, the more the predictor contributes to the model. Response plots were provided to show the relationship between habitat suitability for *S. neumayeri* and environmental predictors.

ENMc projections

ENMc projections were generated using three sets of environmental predictors: for the present time (2005–2012), for scenario RCP 4.5 (2050–2099) and scenario RCP 8.5 (2050–2099). Presence probability maps of *S. neumayeri* were produced with values close to zero indicating low presence probabilities, and values close to one indicating high presence probabilities.

Mechanistic ecological niche model ENMm (spatial projection of Dynamic Energy Budget models)

Model description

DEB models provide a mechanistic and quantitative description of the energy fluxes in an organism that assimilates and uses energy for its maintenance, growth and reproduction throughout its entire life cycle (Kooijman 2010). DEB theory aims at describing how species energy fluxes change according to environmental conditions (i.e., food and temperature) and can help estimate the species fundamental niche (Kearney and Porter 2004). DEB models rely on physiological and experimental data/traits (Kearney and Porter 2004; van der Meer 2006). This approach models a part of the species fundamental niche.

In DEB models, energy flows between four state variables: reserve (E), structure (V), maturation (E_{H}) and

reproductive buffer (E_R) (Fig. 2). Energy enters into the body by food (X) ingestion at a rate $\dot{p}_X$.

$$\dot{p}_X = \{\dot{p}_{Xm}\}fL^2 \tag{1}$$

with

$$f = \frac{X}{X + X_K} \tag{2}$$

corresponding to the food functional response (Eq. 2). X is the amount of available resources (mg m^{-3}) and X_k the half-saturation parameter (mg m^{-3}).

$\{\dot{p}_{Xm}\}$ = max. surface area-specific ingestion rate (J cm^{-2}. d^{-1}).

L = individual's length (in cm).

DEB models use a version of a Hollings' type II functional response. The functional response f changes when the resource (X) is different and varies between 0 and 1 (Meer 2006).

Chlorophyll-a concentration was considered as a relevant proxy of food resources for *S. neumayeri* (McClintock 1994; Jacob et al. 2003; Michel et al. 2016). In Cape Evans (McMurdo), Pearse and Gierse (1966), based on gut content, have emphasized that food of *S. neumayeri* could be mainly

constituted of diatoms which is also emphasized by Brockington et al. (2001).

Sea surface chlorophyll-a concentration data (X in Eq. 2) and gut content (f in Eq. 2) were obtained from a long-term experiment conducted at Rothera Station (Western Antarctic Peninsula) in 1997–1998 (Brockington and Peck 2001). A nonlinear least squares regression was performed to adjust the functional response (Eq. 2) using chlorophyll-a concentration and gut content (Online resource 5 for more details). The estimation gives a value of 2.95 mg m^{-3} for the half-saturation coefficient (X_k).

After food ingestion, the energy is assimilated and stored into the reserve compartment at a given rate expressed in Joules per time ($\dot{p}_A$). The energy leaving the reserve ($\dot{p}_C$) is subdivided according to the "kappa-rule" (κ-rule) in between somatic maintenance ($\dot{p}_M$), growth (proportion κ of energy contained into the reserve compartment), maturity maintenance ($\dot{p}_J$), maturation and reproduction ($\dot{p}_R$, proportion 1 − κ) (Meer 2006; Kooijman 2010). Maturity does not contribute to the total body mass. The amount of energy contained in the maturity compartment thresholds the different life stages of the species during its life cycle (birth: ability to feed, puberty: ability to reproduce) (Jusup et al. 2017; Online resource 2). Once puberty is reached, the
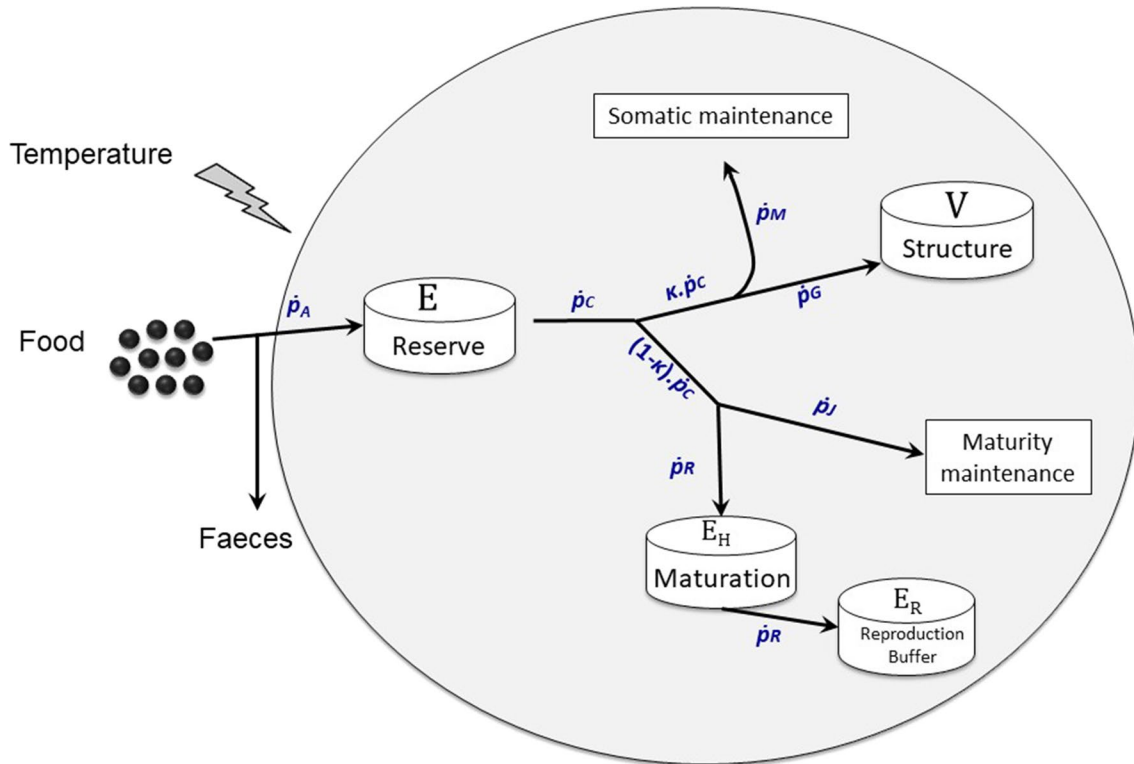

Fig. 2 Conceptual representation of the standard Dynamic Energy Budget model. Arrows show energy flows (J d^{-1}) involved in the dynamics of the four state variables (represented by boxes: reserve (E), structure (V), maturation (E_H) and reproductive buffer (E_r). $\dot{p}_A$ is the assimilation rate into the reserve, $\dot{p}_C$ is the energy rate leaving the reserve which is divided in two branches: $\kappa\dot{p}_C$ allocated to the somatic maintenance ($\dot{p}_M$) and growth ($\dot{p}_G$) and $(1-\kappa)\dot{p}_C$ allocated to maturity maintenance ($\dot{p}_J$), maturation and reproduction ($\dot{p}_R$)

species is considered to be a fully developed adult, and the energy initially allocated to maturation begins to be used for reproduction.

There is no competition between the two branches of the κ-rule, which means that an organism can continue to grow and reproduce at the same time. However, energy is still primarily allocated to maintenance to prioritize body functions essential to the organism survival (i.e., maintenance of cell concentration gradients, protein turnover, enzymes, mucus production, osmoregulation) and the maintenance of maturity (maintenance of the structure complexity).

Reserve compounds do not need maintenance as energy is continuously used. Growth corresponds to the increase of the body structure, and maturation is the energy dissipated or expended by the body in the increase of maturity.

Estimation of DEB model parameters

The DEB model was parameterized using literature data from field and experimental works mainly led at McMurdo and Rothera stations, Antarctica (Table 1, Online resource 6, 7).

Zero-variate data correspond to single measurements at a given time (characterized by specific food and temperature conditions) and uni-variate data are relationships between two variables (e.g., mass, oxygen consumption etc. against duration, temperature, etc.). From these data, DEB parameters were estimated using the covariation method (Lika et al. 2011a, b; Marques et al. 2018), that aims at looking for the combination of parameters (Table 1) that minimizes the

difference between observations and predictions (i.e., minimizing the loss function). The evaluation of the parameter estimation is assessed by calculating the Symmetric Mean Squared Error (SMSE) varying between 0 and 1 and the Mean Relative Error (MRE) which can vary between 0 and ∞. For each univariate and zero-variate data the relative error was computed as the ratio of the absolute error value to the variate value.

Description of temperature sensitivity using Arrhenius temperature and changes in body shape using post-metamorphic shape coefficient are detailed in Online resource 8. All analyses were conducted under MATLAB 2016 using the *DEBtools* repository (https://github.com/add-my-pet/DEBtool_M/).

Rothera data were used to perform sensitivity analysis of DEB model estimation (Online resource 9). For this purpose, marginal confidence intervals of the estimated parameters were computed to provide the uncertainty related to the parameter estimations using the covariation method (Stavrakidis-Zachou et al. 2019). The profile method (Marques et al. 2019) was used to build the profile of the loss function of each parameter and estimate the level of the loss function that corresponds to the uncertainty. A total of 1000 Monte-Carlo datasets was generated by adding a constant centered log-normal scatter to the predictions of each zero and uni-variate data. The threshold value of the loss function Fc that is used to assess the uncertainty level was obtained from $P(X < Fc) = 0.9$, with 0.9 being the confidence level initially chosen in the procedure. The marginal confidence interval of each parameter is the interval of values for which the loss function is below the threshold value Fc.

Spatial projection of the DEB model

For each pixel of the study area, food (i.e., summer chlorophyll-a concentration converted into f (0–1) according to the procedure explained above) and temperature were both used as input into the DEB model, that consequently calculated how energy is used and allocated to the different compartments, given these environmental conditions. Projections of the DEB model were performed according to present-day conditions (2005–2012) and future RCP 4.5 and RCP 8.5 scenarios (2050–2099) (Online resource 10). Different simulations were carried out for temperature or food changes only.

A first projection provides the maximum size reached by individuals, which gives information on species ability to survive and invest energy into growth. It also provides a quantitative estimate of the stress experienced by *S. neumayeri* at large spatial scale, the smaller individuals, the less suitable the environment. According to DEB theory, the somatic maintenance has priority over reproduction and growth to ensure survival. In order to identify regions

Table 1 DEB parameter values estimated by the covariation method (Lika et al. 2011a, b; Marques et al. 2018)

DEB parameters	Unit	Value
z, zoom factor	–	1.364
$\delta_{M.emb}$, shape coefficient embryos	–	0.487
$\delta_{M.lrv}$, shape coefficient larvae	–	0.505
δ_M, shape coefficient	–	0.612
$\{\dot{F}_m\}$, maximum specific searching rate	L d^{-1} cm^{-2}	6.5
κ_X, digestion efficiency of food to reserve	–	0.83
$\dot{v}$, energy conductance	cm d^{-1}	0.033
κ, allocation fraction to soma	–	0.722
κ_R, reproduction efficiency	–	0.95
$[\dot{p}_m]$, volume-specific somatic maintenance	J cm^{-3}d^{-1}	24.42
$\dot{k}_J$, maturity maint rate coefficient	d^{-1}	$2.5 \cdot 10^{-3}$
$[E_G]$, specific cost for structure	J cm^{-3}	2350
E_H^b, energy maturity at birth	J	$4.5 \cdot 10^{-3}$
E_H^j, energy maturity at metamorphosis	J	0.3
E_H^p, energy maturity at puberty	J	2266
$\dot{h}_a$, Weibull aging acceleration	d^{-2}	$2 \cdot 10^{-8}$
S_G, Gompertz stress coefficient	–	$1 \cdot 10^{-4}$

where individuals are able to survive from an energetic point of view, the somatic maintenance flow $\dot{p}_M$ was calculated according to the given food and temperature conditions and compared to the values of the total energy available from the reserve $\dot{p}_C$. When somatic maintenance values are higher than the energy available in the reserve compartment ($\dot{p}_M > \dot{p}_C$), it suggests that individuals do not have enough energy to maintain their soma and should die (Fig. 2). $\dot{p}_M$ values were also compared to the flow $\kappa.\dot{p}_C$, that corresponds to the proportion of the mobilized energy from the reserve that is invested into growth and the somatic maintenance. The organism survives if $\dot{p}_M < \kappa.\dot{p}_C$. On the other hand, if $\dot{p}_M < \dot{p}_C$ but $\dot{p}_M > \kappa.\dot{p}_C$ the organism will have difficulties to maintain its soma and a part of the energy allocated to maturation, reproduction and growth will be redirected to somatic maintenance.

A second projection provides suitable areas for reproduction that is, areas in which environmental conditions allow the species to invest energy into growth and reproduction. In DEB theory, the organism can reproduce when enough energy has been invested into maturity ($E_H > E_H^p$), passing from the juvenile to the adult life stage ('puberty' threshold). To assess whether individuals can invest energy into reproduction, we first calculated the size (L_p) at which individuals reach puberty (Eq. 3) for each pixel of the projection map. The DEB parameter shape coefficient δ_M estimated by the model is used to translate physical measurements taken from experimental data to the structural length used by the model (Online resource 8).

$$L_p = \frac{L_m.l_p}{\delta_M} \tag{3}$$

L_m: Maximum structural size (cm).
l_p: Standardized size at sexual maturity (= puberty) (unitless).
δ_M: Shape coefficient of post-metamorphic individuals (unitless).

Considering the body length at puberty (L_p), we then identified if somatic maintenance could be ensured at puberty ($\dot{p}_c > \dot{p}_M$ and $\kappa.\dot{p}_C > \dot{p}_M$). The total cost of maintenance ($\dot{p}_M + \dot{p}_J$) was also compared to the outflow from the reserve $\dot{p}_C$, with $\dot{p}_C > \dot{p}_M + \dot{p}_J$ meaning that individuals can invest energy into reproduction. All DEB models were computed from R functions available at https://github.com/Echinophoria/DEB/

Results

Species distribution models under present-day conditions

Correlative ecological niche model (ENMc)

For the ENMc generated under present-day environmental conditions, the average predictive accuracy of model replicates is good (TSS = 0.64 ± 0.078), which indicates a relatively good match between observed and predicted occurrences. High species presence probabilities ($p > 0.8$) are predicted south of the Polar Front: over the Antarctic shelf, along the Western Antarctic Peninsula and the Scotia Arc region (Fig. 3a). The highest values are in the northern tip of the Western Antarctic Peninsula, in East Antarctica and in the Ross Sea. Medium values ($p \sim 0.5$) are mainly located in the Amundsen and Bellingshausen seas, the Weddell Sea and in South Georgia. Regions located north of 55°S latitude such as the Kerguelen, Magellanic and Campbell plateaus are mostly predicted as unsuitable areas ($p < 0.2$). Environmental predictors that most contribute to the model are seafloor temperature, geomorphology, slope, sea ice cover and depth, in decreasing order of importance (Fig. 3b). Chlorophyll-a concentration was used as an indirect proxy of food supply but it does not contribute much to the model (ranked seventh most contributing predictor). Parameters such as seafloor oxygen concentration, seafloor temperature range, seafloor salinity, seafloor salinity range and sea surface salinity do not contribute much to the model.

Curves of the species response to main environmental predictors allow visualizing conditions that are the most suitable for species distribution (Fig. 3c). These are shallow areas (< 400-m depth) represented in geomorphology as banks, coastal terranes, seamounts and volcanoes (Online resource 12) with positive slope values ($> 0.05°$), cold water sea floor temperatures ($< 1\,°C$) and weak sea ice coverage ($< 60\%$) (Fig. 3c and Online resource 11). The response curve to chlorophyll-a concentration values shows little variation, the highest probability values corresponding to low chlorophyll-a concentrations (< 2 mg m^{-3}, Fig. 3c).

Projection of the dynamic energy budget model (ENMm)

Experimental data available for the different life stages of *S. neumayeri* allow a robust prediction of DEB parameters (Online resource 6, Online resource 7) with a total
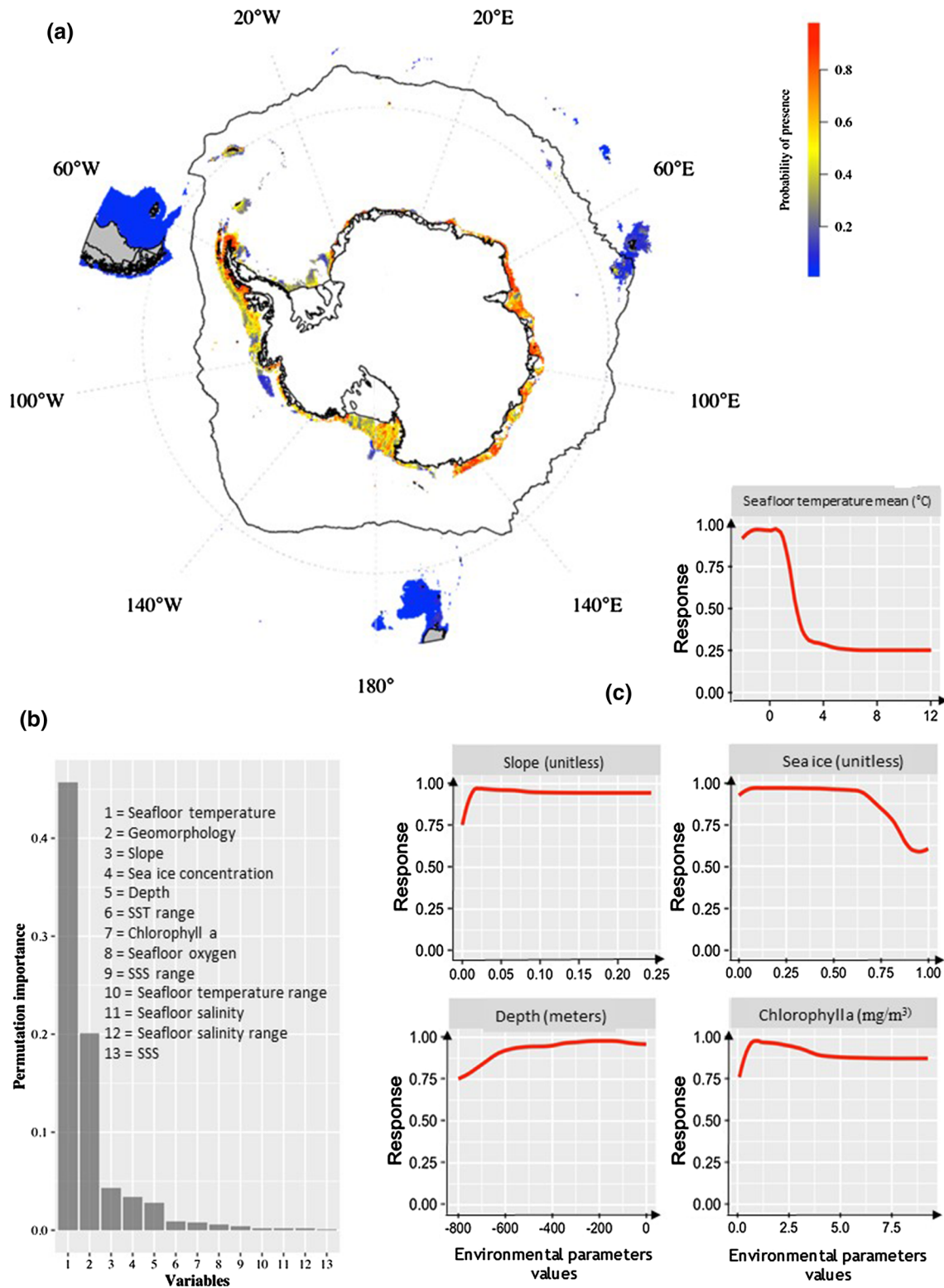
Fig. 3 **a** Spatial projection of the ENMc under present-day conditions in the Southern Ocean with **b** the respective contributions of environmental descriptors to the model and **c** the species response (presence probability) to the main contributing predictors (mean seafloor temperature, slope, sea ice coverage and depth) and for chlorophyll-a concentration (as a proxy of food supply). No response curve can be displayed for geomorphology, which is a categorical variable (see Online resource 12)

goodness of fit resulting in relative low error values (MRE = 0.095 and SMSE = 0.119). For comparison, the values fall within the range of median values usually obtained for DEB models (median MRE < 0.1; Marques et al. 2018). Most zero-variate and uni-variate data are accurately described by the estimated model parameters with low error values. For uni-variate data, the highest relative error values are obtained for the C/N mass of fertilized egg (RE = 0.29) and the uni-variate data Ash Free Dry Mass (AFDM, g) vs. O_2 consumption in µmol/h in summer (RE = 0.27) (Online resource 6, Online resource 7). The pre-metamorphic larval size is slightly underestimated in the model but the error is low (RE = 0.093) (Online resource 6a). The prediction of the adult size-age relationship also shows a low error value (RE = 0.13) (Online resource 6b) as for the weight-size data (RE = 0.05) (Online resource 6c). Models of winter and summer oxygen consumption ~ weight data have similar patterns (Online resource 6d, e) with a shift in oxygen consumption values for individuals of 0.2 g (AFDM), which corresponds to a transition stage between the embryo and the pre-metamorphic larvae.

Model validation gives low marginal confidence intervals for each parameter (Online resource 9), which means that the DEB model is stable.

The predicted suitable areas were projected for the different size classes (Fig. 4a). Overall, the Antarctic shelf is suitable to the largest individuals (> 5 cm), while the Magellanic Plateau is predicted as suitable for individuals < 4 cm. Suitable areas for individuals of the maximum size class are restricted to regions of East Antarctica (Prydz Bay, the Amundsen-Bellingshausen and the Ross seas) and in the Western Antarctic Peninsula. Areas predicted as unsuitable to the species survival are the South Campbell and northern Kerguelen plateaus. Small individuals (< 2 cm) are predicted to survive at all latitudes south of 45° south, from the Magellanic Plateau to the Antarctic shoreline but individuals of 1–2 cm are restricted to the Kerguelen Plateau, the Western Antarctic Peninsula and some regions in East Antarctica.

Reproduction is possible when individuals grow over 3 cm in diameter, that are individuals able to invest energy into reproduction (Fig. 4b). Suitable areas for the species to reproduce are mainly located on the Magellanic Plateau and East Antarctica, in Prydz Bay and the Amundsen-Bellingshausen and the Ross seas. The Kerguelen and Campbell plateaus are predicted as unsuitable to the species reproduction as hypothetical individuals present in these areas would never reach sexual maturity.

Projections under IPCC scenarios of climate change

Correlative ecological niche model (ENMc)

Projections of ENMc of *S. neumayeri* according to IPCC scenarios RCP 4.5 and RCP 8.5 (Fig. 5) display few changes compared to present-day maps (Fig. 3a), and both scenarios give very similar results. Areas predicted as suitable under future conditions are mainly predicted in the Ross Sea and in East Antarctica. In contrast, the species presence probabilities are low in the Bellingshausen and Amundsen seas compared to present-day projections. All areas located north of the Polar Front are predicted as unsuitable with very low presence probabilities ($p < 0.2$).

Projection of the mechanistic ecological niche model (ENMm)

Three projections were performed for each IPCC scenario according to (1) both food availability and temperature (Fig. 4c–f), (2) temperature only (Figs. 6a, b, 7a, b) and (3) food availability only (Figs. 6c, d, 7c, d). "Food and temperature" and "food only" projections give similar model outputs under both IPCC scenarios for maximum size and reproduction areas (Figs. 4c–f, 6c, d, 7c, d). The main differences with present-day models are located on the Antarctic shelf and Magellanic Plateau, which are mostly predicted as unsuitable to the species. In contrast "temperature only" projections (Figs. 6a, b, 7a, b) show no noticeable change with present-day models, and model outputs are identical under both IPCC scenarios of climate change.

Projections of "food and temperature" (Fig. 4c, e) and "food only" (Fig. 7c, d) models predict that individuals may reach very small sizes over the entire species distribution range, with a maximum size predicted to reach 1 cm only in the Weddell and Ross seas, in East Antarctica and on the Kerguelen and Campbell plateaus. Size is also predicted to be small (< 2 cm) along the Antarctic Peninsula and on the Magellanic Plateau. As a consequence, reproduction is predicted as impossible over the entire species distribution range under future IPCC scenarios, the model predicting that no energy would be available for maturity, maintenance and reproduction (Figs. 4d, f, 6c, d).

The "temperature only" model (Fig. 7a, b) predicts unsuitable areas for growth over the Kerguelen Plateau and some areas in East Antarctica (Prydz Bay excepted). In contrast, large individuals (> 4 cm) are predicted in the Bellingshausen-Amundsen seas, the Ross Sea and on the Magellanic Plateau. Suitable areas for the species reproduction match with areas where individuals can reach up to 2 cm in size that is, in the Bellingshausen-Amundsen seas, the Ross Sea and Prydz Bay areas (Fig. 6a, b).
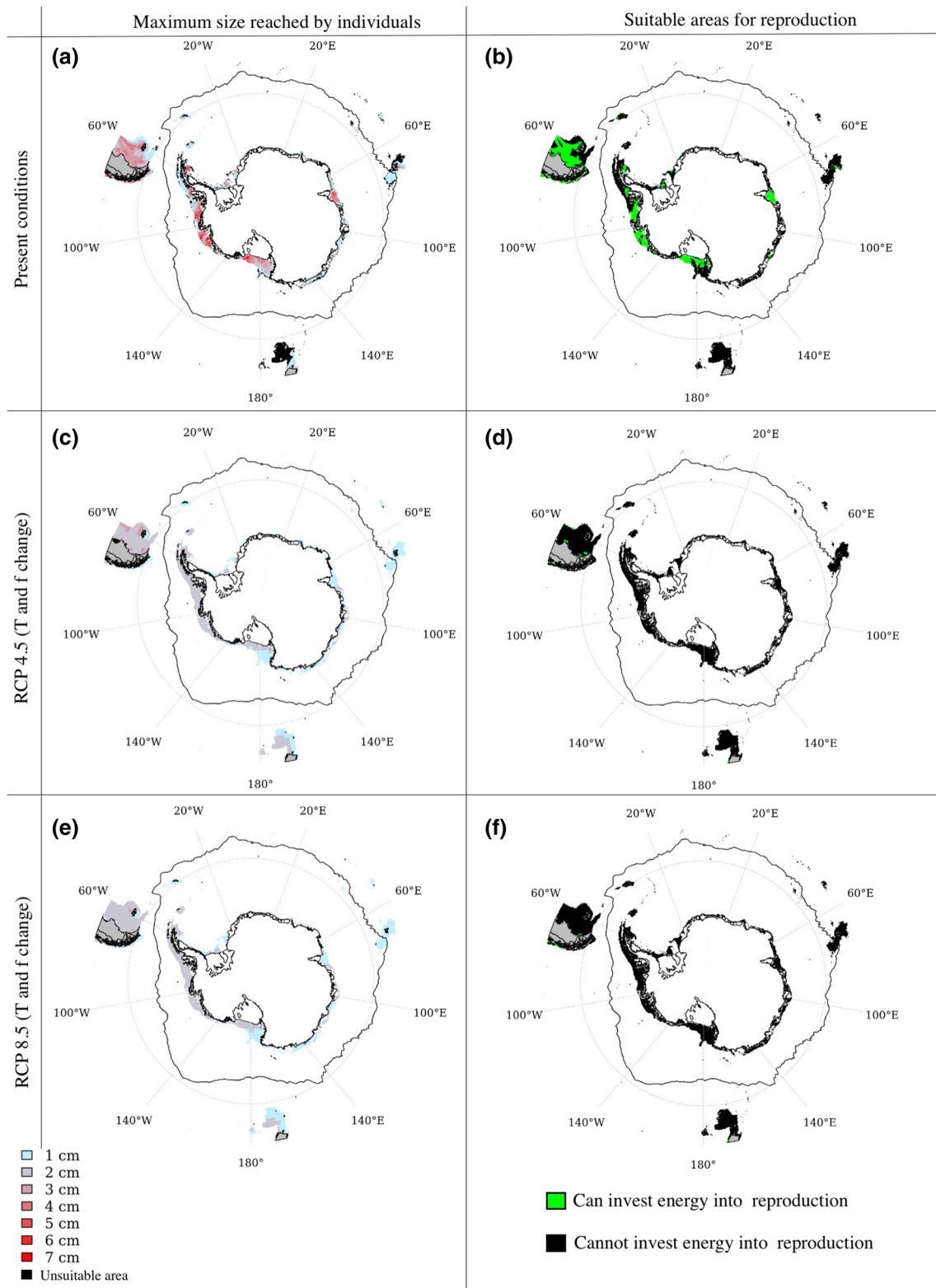
Fig. 4 Projection maps of the mechanistic ecological niche model (DEB). **a**, **c**, **e** classes of maximum size reached by individuals and **b**, **d**, **f** suitable areas for reproduction under present-day conditions (**a**, **b**), RCP 4.5 (**c**, **d**) and RCP 8.5 (**e**, **f**) scenarios. Future projections were modeled for both food and temperature changes

RCP 4.5   RCP 8.5
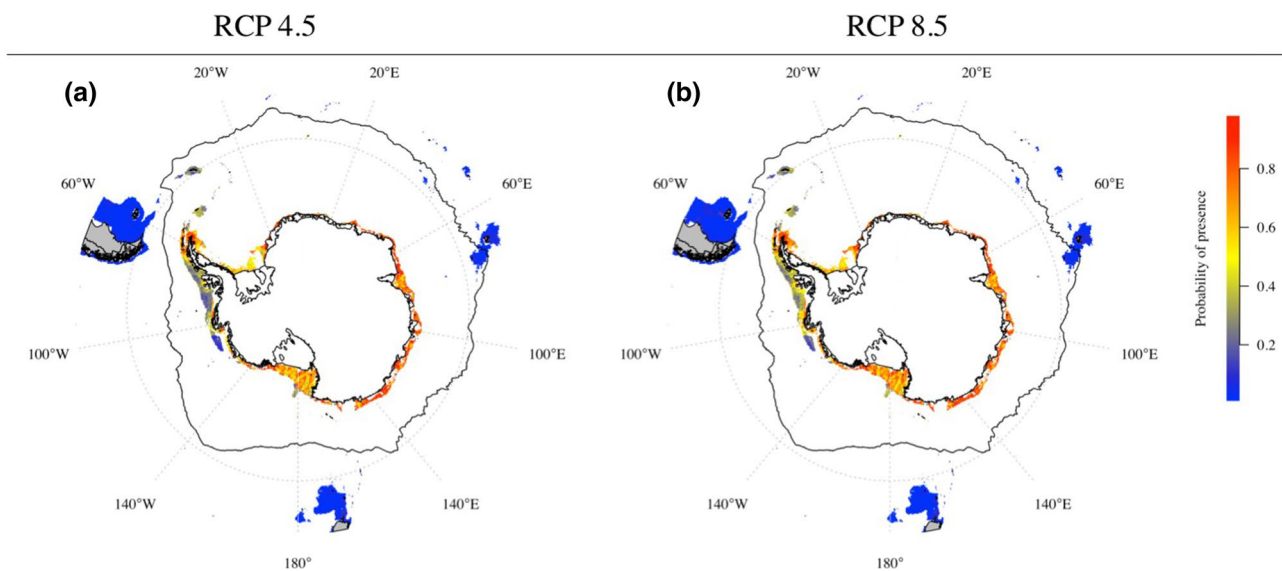
Fig. 5 Projection of the correlative model under **a** RCP 4.5 (left panel) and **b** RCP 8.5 (right panel) scenarios (2050–2099)

Discussion

Model projections and their ecological significance

Present-day projections

The ENMc predicts suitable conditions to *S. neumayeri* in Antarctic cold waters south of the Polar Front for the present time period (temperature $< +2$ °C, Fig. 2 and Online resource 11). This is in line with our knowledge of the species biogeography, which is endemic to the Antarctic continental shelf (Pierrat et al. 2012; Fabri-Ruiz et al. 2019, 2020). Temperature is usually a major driver of species distribution as already shown in former studies on Antarctic echinoid species (Saucède et al. 2014, 2017; Guillaumot et al. 2018; Fabri-Ruiz et al. 2019). Along with geomorphology, slope and depth, these variables are related to main habitat characteristics (Online resource 12) and are considered to have a dominant role in the structure and composition of benthic communities (O'Brien et al. 2009; Kaiser et al. 2013; Post et al. 2014).

In addition to the importance of the environment, the endemicity of Antarctic benthic fauna is also believed to be favored by the presence of the Antarctic Circumpolar Current acting as a biogeographic barrier to dispersal towards the north (Arntz et al. 1997; Linse et al. 2006; Barnes and Griffiths 2007; Griffiths et al. 2009). For instance, 68% of Antarctic echinoids species (Saucède et al. 2014), 74% of gastropods (Schiaparelli and Linse 2014) and 57% of bivalves (Linse 2014) were reported to be endemic to the Antarctic continental shelf.

Highly stable DEB models were produced (Online resource 9) and projections also show that under present conditions, Antarctic regions such as the western part of the Ross Sea, Prydz Bay area, the East Antarctic Peninsula and the Bellingshausen-Amundsen seas are predicted to be suitable for the species growth and reproduction (Fig. 4). This is line with observed data in these regions where *S. neumayeri* is adapted to low temperatures with display of low aerobic scopes (Peck and Conway 2000; Peck 2002; Pörtner and Knust 2007). Previous works focused on the development rate of embryos and data were provided on the range of suitable temperatures for planktonic larvae to grow. Stanwell-Smith and Peck (1998) showed an increase in development rates between -2 °C and $+2$ °C, with low and stable rates between $+0.2$ °C and $+1.7$ °C. Development rates do not increase for temperatures above $+2$ °C. Bosch et al. (1987) and Pauline et al. (2013) reported the onset of larval development between -0.8 °C and $+0.5$ °C, and between -1.8 °C and -0.9 °C, respectively. Kapsenberg and Hofmann (2014) reported a larval upset at -0.7 °C. Finally, food supply is also reported as sufficient for individuals to survive and allocate energy to reproduction (Online resource 10).

In contrast, the Kerguelen Plateau, the Western Antarctic Peninsula, East Antarctica (except Prydz Bay) and eastern part of the Ross Sea were modeled as suitable areas but for small individuals only (< 2 cm). In these regions, the energy available and stored in the reserve compartment ($\dot{p}_c$) is only sufficient to ensure somatic maintenance ($\dot{p}_M$) but cannot cover energy costs related to growth and/or reproduction ($\dot{p}_M > \kappa \dot{p}_c$) as the somatic maintenance has priority over processes in the model. In these regions, the maintenance
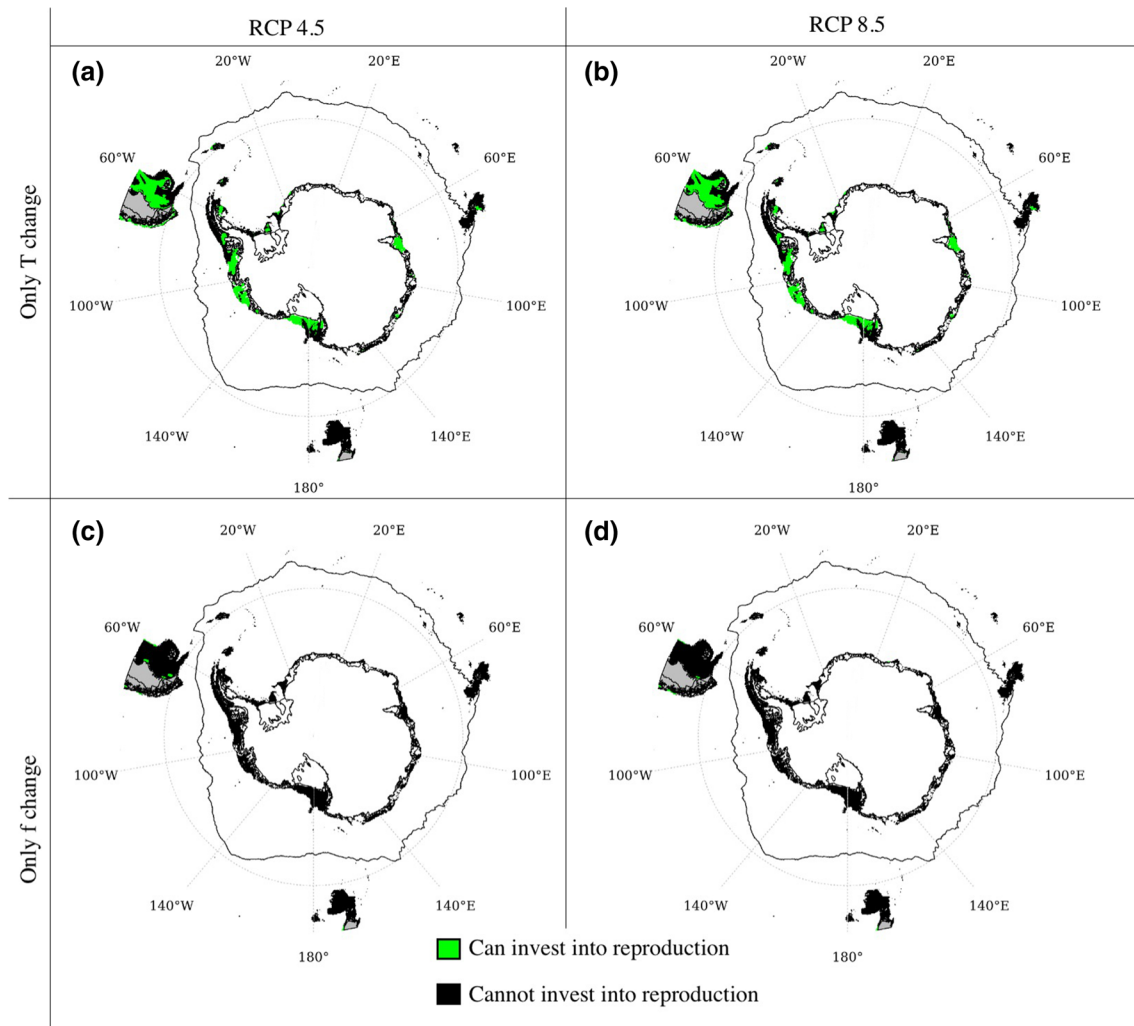
Fig. 6 Projections of the DEB ENMm under future conditions: predicted suitable areas to the species reproduction under IPCC scenarios RCP 4.5 (left panel) and RCP 8.5 (right panel). Predictions were modeled temperature change only (top panels) and food availability change only (bottom panels), respectively

of species populations would exclusively depend on larval supply from other areas. This could be possible via the Antarctic Circumpolar Current that is a major vector of larval dispersal in the Southern Ocean (Pearse et al. 2009; Moon et al. 2017; González-Wevar et al. 2018), but this hypothesis remains to be tested and supported by field data.

Projections under future scenarios of climate change

Future projections of ENMc showed few changes in the species potential distribution over the Antarctic shelf. This can be explained by the important contribution of physical descriptors, geomorphology, slope and depth to the model, three variables that were considered unchanged in a near future in the model, being here considered that predictions of sea level rise should have little effect on model outputs

at large, ocean-wide scale (Conto and Pollard 2016). Local shifts in the species distribution probabilities are, however, predicted, compared to the present-day model. They are mainly localized in the Bellingshausen-Amundsen seas and are triggered by future predictions of temperature rise and reduction in sea ice coverage (Online resource 10). A reduction in sea ice coverage will have serious impacts on the seasonal production of food supply and will also result in a reduction of the protection of shallow benthic organisms from UV-B induced damages (Lister et al. 2010). Changes in ice regime is also expected to have multiple impacts in the region due to ice shelf melting and collapses. This will result in the freshening of Antarctic waters and associated changes in water biogeochemistry, and to an increase in the intensity of iceberg scouring on seabeds in shallow water, coastal areas (Meredith and King 2005; Bracegirdle et al. 2008; Stammerjohn et al. 2012). This phenomenon was
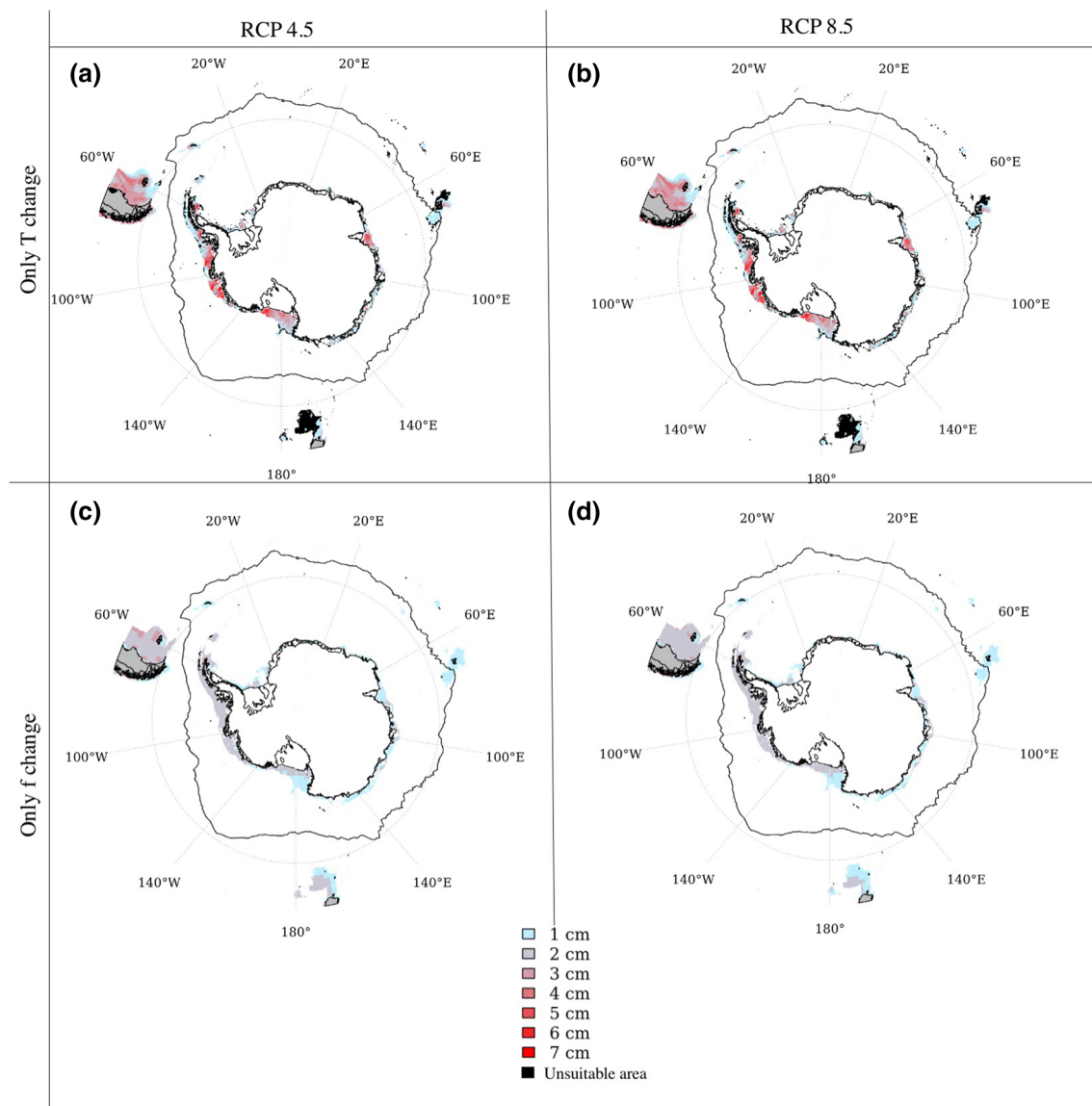
RCP 4.5   RCP 8.5

Fig. 7 Projections of the DEB ENMm under future conditions: maximum size reached by individuals under IPCC scenarios RCP 4.5 (left panel) and RCP 8.5 (right panel). Predictions were modeled for temperature change only (top panels) and food availability change only (bottom panels), respectively

shown to have serious effects on the structure of benthic communities, (Gutt 2001; Gutt and Starmans 2001; Gutt and Piepenburg 2003), resulting in a decrease in habitat heterogeneity and local (alpha) diversity (Brown et al. 2004; Barnes and Souster 2011).

In projections of the ENMm performed for future conditions, the combined effect of "temperature and food change" on individual physiology is predicted to induce important shifts in energy availability (Fig. 4c–f). The allocation of energy into reproduction is predicted to become impossible anymore and growth rates are predicted to strongly decrease in the entire Southern Ocean. These results suggest a high sensitivity of *S. neumayeri* to environmental changes under

RCP 4.5 and 8.5 scenarios. Overall, this also stresses the important impact of food availability for benthic species. The seasonal phytoplankton bloom is known to constitute an important source of food for many species (Brockington and Peck 2001; Ahn et al. 2003; Jacob et al. 2003; Michel et al. 2016; Agüera et al. 2017), and predicted shifts and decrease in this resource might have important consequences for marine communities.

In the ENMm, the future "only temperature change" projection (Figs. 6a, b, 7a, b) is identical to the present-day projection. Medium size (~4 cm) to large (>5 cm) individuals as well as suitable areas for reproduction are predicted north of the Polar Front for both periods. We could expect a

synergetic and cumulative effect on growth and reproduction under "temperature and food change" (Fig. 4) than under "only food change" (Figs. 6c, d, 7c, d) or "only temperature change" (Figs. 6a, b, 7a, b). On the contrary, our results suggest similarities between "only food change" and "temperature and food change" projections are similar. Metabolic rates of Antarctic species increase with temperature, as does the oxygen consumption. If temperature rises and oxygen supply are insufficient to meet the organism metabolic needs, the organism switches to an anaerobic metabolism (Peck and Conway 2000; Peck 2002; Pörtner and Knust 2007). The ability of individuals to survive depends on their ability to maintain an anaerobic metabolism over time. As a result, rising temperatures should lead to changes in the survival and resilience of Antarctic marine invertebrates.

S. neumayeri occurs in shallow waters compared to other *Sterechinus* species (David et al. 2005; Díaz et al. 2011). The hypothesis of a possible in-depth migration to colder waters and less UV exposed areas may be considered. In the future, warmer temperatures could occur in deeper areas corresponding to optimal temperature window of the species and decrease in sea-ice cover could also lead to higher exposure to UV-B in shallow waters. However, studies suggest that it may compete in these environments with *Sterechinus diadema*, its sister species living in deeper habitats (Jacob et al. 2003; Díaz et al. 2011). Moreover, pressure increase with depth reduces the thermal optimal window for the development of eggs and embryos, generating a new physiological stress and reducing the species fitness and survival (Tyler et al. 2000). It can therefore be assumed that current environmental changes are expected to lead to a potential reduction in the distribution of *S. neumayeri*.

Model comparison and complementarity

Model comparison

Overall, ENMc and ENMm run for present-day conditions provide congruent projections (Figs. 3, 4a, b). For the Antarctic shelf, in regions such as the Ross Sea and the Prydz Bay area in particular, the ENMm predicts the prevalence of large (> 4 cm) and sexually mature individuals and the ENMc shows high presence probabilities. These regions are characterized by cold temperatures and high food availability (f > 0.5), which are favorable conditions for the species development and survival. In contrast, in the northern Kerguelen Plateau and the Campbell Plateau, low presence probabilities are modeled by the ENMc due to warm water temperatures (> 4 °C) (Fig. 2 and Online resource 10), and small (< 1 cm) and sexually immature individuals are predicted by the ENMm due to low food availability limiting growth and reproduction (Online resource 10). Model projections, however, do not match for certain areas. For instance, small and sexually immature individuals are predicted along the Antarctic Peninsula in the ENMm, whereas the ENMc predicts high presence probabilities. In the sub-Antarctic, the ENMm predicts suitable conditions for the species growth (> 3 cm) and reproduction on the Magellanic Plateau, whereas this area is predicted unsuitable in the ENMc. *S. neumayeri* is known to be endemic to the Antarctic Peninsula and East Antarctic shelf (David et al. 2005; Saucède et al. 2014), which suggests that the ENMm projection may not predict the species current distribution properly. This can be explained by the lack of eco-physiological data documenting the species response to variations in food resources and temperature (Bosch et al. 1987; Stanwell-Smith and Peck 1998; Marsh et al. 1999, 2001; Tyler et al. 2000; Brockington and Peck 2001; Alexander et al. 2017). On the other hand, temporal scales of physiological experiments are over a limited time frame and different from the temporal scale of the used environmental layers, which characterize overall climate conditions.

In ENMm, the Arrhenius temperature is the parameter that determines the metabolic rate as a function of temperature variation (Online resource 8). In the present model, the Arrhenius temperature was estimated based on three measurement points only (Bosch et al. 1987), which may induce a lack of precision in the simulation of the species metabolic rate. In addition, lower and upper lethal temperatures could not be entered in the model due to the absence of relevant physiological data (Online resource 6) and the species optimal temperature range could not be determined precisely. As a consequence, the modeled physiological performance of the species tends to increase constantly with temperature and partly outreaches the biological optimum.

Only data on chlorophyll-a concentration and on the gut content were available to model the functional response of *S. neumayeri* to food resources (McClintock 1994; Jacob et al. 2003; Michel et al. 2016). Therefore, in the model, sea surface chlorophyll-a concentration in summer was used as a proxy of food resources for *S. neumayeri* (Online resource 5), which is an opportunistic, omnivorous feeder. The species does not feed directly on chlorophyll-a but is indirectly dependent on this food supply as it feeds on various sources of particulate organic matter deposited on the sea floor as well as some suspension feeders (Smith et al. 2006; Lohrer et al. 2013; Petrou et al. 2016; Schofield et al. 2017). In addition, winter conditions are known as periods of low chlorophyll-a concentrations in Antarctic surface waters (Thomalla et al. 2011; Deppeler and Davidson 2017), which could not be used as input in the model projection due to the lack of satellite data for this season. In a DEB model developed for the Antarctic bivalve *Laternula elliptica* (King and Broderip 1832), Agüera et al. (2017) showed that reserve is seasonal and that low food availability generated a 25% loss in the species body mass, also delaying gonadal development. In

S. neumayeri, post-metamorphic individuals do not feed in winter (Brockington and Peck 2001) but no quantitative data on energy allocation are available for this season. Additional works would be useful to refine the present DEB model. Complementary data based on new eco-physiological experiments describing the effect of different levels of food supplies, abundant, limited, or starvation, on the metabolic rate should contribute to improving model accuracy (Sarà et al. 2013; Augustine et al. 2014; Hamda et al. 2019).

Complementarity between modeling approaches

The two modeling approaches mainly differ in their scientific objectives. To run the ENMc, 13 abiotic parameters were used to describe part of the species realized niche, the effect of biotic interactions and biogeographic constraints also indirectly acting on model outputs through the position of observed occurrences and the spatial correlation between abiotic descriptors, biotic factors and biogeographic barriers. Projections therefore partly fit to the species realized distribution because they partly take into account the multi-dimensions of the species realized niche. Parameters of the physical habitat such as geomorphology were shown to have an important role in the structuring and composition of Antarctic benthic communities (O'Brien et al. 2009; Kaiser et al. 2013; Post et al. 2014); such parameters were not considered to run the ENMm. In contrast, the ENMm integrates the effect of temperature and food resources on the species physiology, focusing on two dimensions of the species fundamental niche, whatever its distribution and realized niche. The ENMm provides biological insights to comprehending the physiological processes that underpin the observed species distribution.

Major differences between models show up when it comes to run future projections under IPCC RCP scenarios. ENMm predicts unsuitable conditions for the species growth and reproduction over the entire ocean. In contrast, ENMc models predict the species persistence on the Antarctic shelf, the Bellingshausen and Amundsen seas excepted. The ENMc uncertainties increase when species' responses to environmental conditions are extrapolated out of the range of values for which the model was trained (Guillaumot et al. 2020b). This holds particularly true for future conditions that do not prevail in present-day environments yet (Fitzpatrick and Hargrove 2009; Elith et al. 2010; Jiménez-Valverde et al. 2011; Dormann et al. 2012) so that the ENMc may fail to predict as unsuitable environmental conditions that would exceed the species physiological tolerance (Anderson 2013). Moreover, without presence–absence nor abundance data, habitat suitability is partly biased because all presences are treated equally. With presence–absence and if possible, abundance data, more discrimination of suitable habitat is gained, which is beneficial when ENMc is used to project

species distribution across space and time. Adding absence data is known to provide greater ability to delineate species' range boundaries and produce more accurate models (Howard et al. 2014; Yates et al. 2018).

Such discrepancies between the two modeling approaches in a context of climate change were already highlighted in previous studies. For instance, Buckley et al. (2011) showed that ENMm predicted much greater migrations with climate change than ENMc in a study on Lepidotera. Further, Kearney et al. (2008) modeled that toad species survival in southern Australia would no longer be possible due to global warming according to ENMm, while the ENMc still predicted the region as suitable.

In the present study, while suggesting unrealistic projections on the Magellanic Plateau under present-day conditions, future projections of the ENMm are more in line with a majority of works suggesting that climate change would induce unsuitable conditions to the survival of Antarctic benthic marine ectotherms (Peck et al. 2014; Hawkins et al. 2018). All these results highlight the necessary complementarity of ENMc and ENMm approaches for providing independent and relevant projections, relying either on biogeographic (ENMc) or physiological (ENMm) data (Kearney et al. 2009; Morin and Thuiller 2009). Comparing and combining projections from different modeling approaches provide more insight on both species present-day distributions and sensitivity to future projections (Guisan and Zimmermann 2000; Elith and Graham 2009; Elith et al. 2010).

Future prospects

The present work underlines ENMc as a useful and powerful approach to predict current species distribution. ENMc is relatively simple to implement and do not require a deep knowledge of population dynamics nor of ecological processes linking organisms to their abiotic environment. They can be applied to a large number of taxa (Guisan and Zimmermann 2000; Elith and Graham 2009; Elith et al. 2010) and are often used upstream to address conservation issues (Evans et al. 2015). However, ENMc does not imply any inference on causal relationships between species distribution and environmental descriptors, and such relationships may also imply indirect responses to colinear variables that are not entered in the model (Guisan and Thuiller 2005).

In a context of environmental changes, extrapolation represents a serious limitation to ENMc that have limited capacities to transfer model outputs both in space and time (Yates et al. 2018; Guillaumot et al. 2020b). In the present study, such a limitation is highlighted by the mismatch between ENMm and ENMc future projections of *S. neumayeri*. ENMm appears to be more informative than the ENMc when it comes to describe species distribution under changing environmental conditions. However, few Antarctic

species have been the focus of detailed eco-physiological studies and few mechanistic models were developed, considering the important amount of physiological data required. Mechanistic models are therefore generally used when species physiology has been relatively well studied (Kearney et al. 2008; Buckley et al. 2011; Evans et al. 2015; Thomas and Bacher 2018) and our knowledge of marine species physiology is usually biased toward 'model' species that most interest the public and researchers (Clark and May 2002; Sousa-Silva et al. 2014; Feng and Papeş 2017). Many authors have stressed the importance and benefits of considering mechanistic approaches for conservation purposes and the implementation of management plans (Cooke and O'Connor 2010; Cooke et al. 2012, 2014; Evans et al. 2015). If the integration of biological data into open-access databases has significantly increased with multiple initiatives such as TRY, Globtherm, FSRD, Anage, GenBank, add-my-pet (De Magalhaes and Costa 2009; Kattge et al. 2011; Karányi et al. 2013; Bennett et al. 2018; Marques et al. 2018), there is still no data portal devoted to describing species physiological traits. Mining such data through experiments and the literature to perform mechanistic models remains a complex, time-consuming task, limiting the integration of ENMm into conservation strategies (Evans et al. 2015). In contrast, ENMc is mainly based on occurrence or abundance data that are made available through international databases allowing open-access data sharing (Pearse et al. 2018; Wüest et al. 2020). Common databases would be particularly valuable to address ecological issues linking patterns to processes across spatial and temporal scales, and improving our knowledge of ecosystem functioning in a context of climate change (Sutter et al. 2015).

Conclusion

The present study highlights the complementarity of correlative and mechanistic ENM to predict species present distributions and sensitivity to changing environmental conditions. Overall, congruent projections were obtained with the two modeling approaches for present-day conditions. In contrast, different models were generated under future scenarios. Both models agree on the fact that *S. neumayeri* is circum-polar in distribution with suitable areas restricted to the Antarctic continental shelf area (< 400 m), with low temperatures ($< 2\ °C$), limited sea ice concentrations ($< 50\%$) and high food availability ($f > 0.7$). The ENMm approach provided an additional understanding of physiological processes determining the species distribution with regards to growth and sexual maturity as a function of temperature and food availability.

The combination of ecological modeling, ENMm and ENMc, with satellite remote sensing and climate models provides a valuable approach to study large-scale responses of marine species to climate change (Guisan and Thuiller 2005; Pearson 2007; Elith and Leathwick 2009; Kearney and Porter 2009; Buckley et al. 2011; Thomas and Bacher 2018; Rodríguez et al. 2019). Multiple challenges, however, remain to be overcome. Eco-physiological data are still needed to produce reliable mechanistic DEB models, including data on Arrhenius temperatures. In addition, ENMm does not take into account extrinsic factors that shape species distribution such as biogeographic barriers, physical habitats and biotic interactions (predation/competition/facilitation). Combining correlative and mechanistic models in an integrative approach therefore constitutes a promising perspective, which has already been developed for certain terrestrial and marine organisms (Elith et al. 2010; Dormann et al. 2012; Roos et al. 2015; Mathewson et al. 2017; Rodríguez et al. 2019), and could prove particularly relevant to predict the sensitivity of Antarctic organisms to a fast changing environment.

Authors contributions SFR, CG, TS and BD conceived the idea and designed the manuscript. SFR, CG and AA provided data and validated the methodology. SFR and CG compiled and analyzed the data. All authors equally contributed to the interpretation of analyses. SFR, CG and TS wrote the manuscript with contributions and inputs from all authors.

Declarations

Conflict of interest The authors declare no conflict of interest.

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