Current wintering habitat of an endemic seabird of Réunion Island, Barau's petrel *Pterodroma baraui*, and predicted changes induced by global warming

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ABSTRACT: The impacts of global climate change on marine ecosystems are of increasing concern. Because of their restricted distribution, endemic organisms are especially sensitive. In this context, we investigated the impact of climate change on the wintering habitats of Barau's petrel *Pterodroma baraui*, an Endangered endemic species of Réunion Island (western Indian Ocean). Birds were tracked with Global Location Sensing loggers, over 3 different years. We built suitability models to determine the environmental drivers that influence habitat selection. These models were then used to predict changes in the location and size of the wintering habitats in 2100. After breeding, Barau's petrels consistently migrate eastward to a large oceanic area in the central and eastern Indian Ocean (centred on the Ninety East Ridge). Three main factors best predicted the presence of wintering Barau's petrels: surface wind speed, sea surface temperature and chlorophyll *a* concentration. Adult Barau's petrels tended to select cool, oligotrophic areas with stronger than average winds. Based on these variables, we identified 3 distinct areas of high suitability. This suitable habitat is predicted to shift westward and southward in the future, as a consequence of global warming, and the surface of total suitable habitat for wintering Barau's petrels may be reduced by an average of 11% by the year 2100. These predictions are discussed in terms of biological conservation and adaptation to climate change. Our study is among the first to demonstrate the utility of using current tracking data and habitat modelling to predict the long-term effects of climate change on marine birds.

KEY WORDS: Barau's petrel · Indian Ocean · Global Location Sensing · GLS · Habitat suitability model · HSM · Ensemble model

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INTRODUCTION

Global warming, due to anthropogenic emissions of greenhouse gases, is now unequivocal, and the various scenarios of the Intergovernmental Panel on Climate Change (IPCC) all predict significant increases in atmospheric and oceanic temperatures during the course of the next century (IPCC 2014). Many environmental parameters such as precipitation, wind, ice extent and sea level are affected, which, in turn, impact all levels of marine and terrestrial biodiversity (e.g. Botkin et al. 2007, Cheung et al. 2009, La Sorte & Jetz 2010). In this context, there is an urgent need to identify the consequences of climate change on ecosystems, particularly how alterations in environmental drivers may lead to changes in the movements, distribution and habitat selection of animals. Such findings are crucial to understand species' exposure, sensitivity and adaptability to climate change (Nathan et al. 2008, Foden et al. 2013).

Rising air and sea surface temperatures affect phenology (Walther et al. 2002, Parmesan 2006, Rosenzweig et al. 2008), migration patterns (Cotton 2003) and food web structure (Alheit et al. 2009). The geographical distribution of a species is determined by optimal biotic and abiotic characteristics, which may be altered in response to climate change. As a consequence, range shifts, both in latitude and altitude, have been recorded for many terrestrial (Parmesan & Yohe 2003, Parmesan 2006, Chen et al. 2011) and marine organisms (Perry et al. 2005, Beaugrand et al. 2009, Weimerskirch et al. 2012).

Although distributional change is a key topic in studies of climate change effects on plankton and fish (Hays et al. 2005, Perry et al. 2005), it has received much less attention in seabirds (Sydeman et al. 2012). Few attempts have been made to predict the evolution of oceanic habitats of seabirds in response to global warming (but see Peron et al. 2012, Grémillet et al. 2015, Russell et al. 2015). However, the life history characteristics of seabirds make them particularly vulnerable to such environmental changes. All are central-place foragers when breeding (Weimerskirch et al. 1994), many perform long-range seasonal migrations (Robinson et al. 2007), and most are highly K-selected with typically a long life span, long generation time and low reproductive output (Durner et al. 2009). One of the only studies predicting the evolution of a seabird habitat modelled the effects of different climate warming scenarios, as defined by the IPCC, on the position of suitable foraging areas of king penguins *Aptenodytes patagonicus* from Crozet Island (Southern Indian Ocean; Peron et. al 2012). To our knowledge, no such studies are available for tropical seabirds, presumably as a consequence of the natural complexity of tropical systems.

Seabird distribution is influenced by different factors such as physical features (bathymetry, sea surface temperature, sea height anomalies, wind speed), prey availability and intrinsic behaviour (Grecian et al. 2012, Thaxter et al. 2012). After breeding, most seabird species perform long-distance migrations (Guilford et al. 2009, Egevang et al. 2010, Pinet et al. 2011). As the non-breeding period is of major importance for the population dynamics of seabirds (Chastel et al. 1995, Barbraud & Chastel 1999), identifying non-breeding foraging areas is a key priority for seabird conservation (Piatt et al. 2007, Le Corre et al. 2012, Oppel et al. 2012). It is therefore essential to improve our knowledge of seabird habitat use during the inter-breeding period, and to understand the role of environmental conditions in determining seabird movements and distribution.

Here, we studied the non-breeding, at-sea distribution of a tropical seabird species, Barau's petrel *Pterodroma baraui*, and its evolution under different climate warming scenarios as defined by the IPCC. Barau's petrel is an Endangered endemic seabird of Réunion Island (55.33° E, 21.07° S), with an estimated population of about 8000 breeding pairs (Le Corre et al. 2002). The species forages in the southwest Indian Ocean during the breeding season (Pinet et al. 2012) and migrates eastward to the central and eastern Indian Ocean during the non-breeding season (Pinet et al. 2011). The goals of this study were to (1) investigate inter-annual changes in the species' wintering habitats, (2) develop species distribution models (SDMs) in order to define the oceanographic features that characterize its winter habitats and (3) predict the future distribution of suitable habitats during the wintering period under the various scenarios of the IPCC.

MATERIALS AND METHODS

Tracking data

Both published and unpublished tracking data were used to describe the current wintering distribution and to model future habitats of adult Barau's petrels during the austral winter. Barau's petrels breed annually between September and April and perform long-distance migration to overwinter in the central and eastern Indian Ocean during the non-breeding period (Pinet et al. 2011, 2012). The pre-breeding phase (display, mating and pre-laying exodus) typically takes place in September to October, followed by incubation, and most chicks hatch between mid-December and mid-January. Chick-rearing ends in April, and all birds leave the colony and the entire western Indian Ocean until early September (Pinet et al. 2011, 2012). Global Location Sensing (GLS) loggers were deployed and recovered during 3 years on distinct birds at La Vallee des deux miches, a study colony of Barau's petrels located on Grand Bénare mountain, Réunion Island (altitude 2500 m). Between February and April 2008, 12 GLS loggers (Mk14; developed by the British Antarctic Survey [BAS], Cambridge) were deployed on breeding adult Barau's petrels, all of which were recovered between September and December 2008. Nine additional GLS loggers were deployed on breeding adults between November 2008 and March 2009, and recovered between September and December 2009. These data were previously published by Pinet et al. (2011). An

additional 12 GLS loggers (Mk15; developed by the BAS) were deployed in December 2011, and recovered in November 2012 to investigate inter-annual variability. For a more detailed description of the study area and the methods used to deploy and recover the GLS, and to calculate geolocation of birds, see Pinet et al. (2011).

SDM process

Data preparation

The number of tracked bird locations was broadly balanced within each study year. The number of locations varied by 14, 15 and 11% (for 2008, 2009 and 2012, respectively). For each study year, we performed kernel analysis on the wintering area of all individuals using the *adehabitat* package (Calenge 2006) within the R environment (R Development Core Team 2015), with a smoothing parameter (*h*) of 2° to match geolocator accuracy (BirdLife International 2004). We considered the 50% kernel density contours (k50) to represent the core areas of activity (Catry et al. 2009).

Environmental data were selected according to their biological relevance and availability. Both static (bathymetry, BATHY, m) and dynamic data were downloaded from NOAA Coastwatch (http://coast watch.pfel.noaa.gov/coastwatch/CWBrowserWW180. jsp). Dynamic data include chlorophyll *a* concentration (CHLA, mg m^{-3}), sea surface temperature (SST, °C), primary productivity (PP, mg C m^{-2} d^{-1}), sea surface height deviation (SSH, cm), wind speed (WIND, m s^{-1}), geostrophic zonal currents (CZ, cm s^{-1}) and geostrophic meridional currents (CM, cm s^{-1}). We used weekly data for CHLA, SST and PP and daily data for SSH, WIND, CZ and CM. Daily data were then averaged on a weekly basis. For each dynamic variable, weekly data corresponding to the dates of a given trip were averaged. Environmental maps were re-interpolated on a grid of 2 × 2° to match the GLS data resolution. We subsequently calculated the spatial gradients of BATHY, SST, CHLA, WIND, PP and SSH (BATHYG, SSTG, CHLAG, WINDG, PPG, SSHG, respectively) using the *slope* function from the *SDMTools* package (VanDerWal et al. 2014).

Prior to modelling, strongly correlated (coefficient of correlation > 0.8) predictors were identified by estimating all pairwise Spearman rank correlation coefficients. High correlation was found between CHLA and PP, and between CHLAG and PPG. Thus, we excluded PP and PPG from further analyses. We decided to use CHLA rather than PP because CHLA is a direct measure obtained from satellite imagery, whereas productivity is a calculated product (Behrenfeld & Falkowski 1997).

Ensemble modelling and evaluation

We used an ensemble model based on the aggregation of several models. This method improves the fit and robustness of the final model, limiting bias for each model while also avoiding overfitting of the final model (Araújo & New 2007, Marmion et al. 2009, Thuiller et al. 2009). For each year, an ensemble model was created with bird presences inside the core area and pseudo-absences, defined as localisations where absence is probable but uncertain. Pseudo-absences were randomly selected outside the core area within the maximum range achieved by the population each year, in the tropical Indian Ocean (limits: 40 to 120° E, 60° S to 20° N). This random selection was repeated 20 times so as not to affect the model results. Thus 20 datasets, combining a selection of pseudo-absence and presence data in the core area, constitute a set of initial data for the model. These datasets were then divided randomly into 2 parts; one was used to build the model (80% of the dataset) and the other to evaluate the model (20% of the dataset). This was repeated 10 times so that the random selection did not affect the results (Thuiller et al. 2009). Each of these datasets was then added to the environmental variables to build an ensemble model. True skill statistics (TSS), sensitivity and specificity were then calculated to evaluate the quality of the models. Sensitivity is the proportion of observed presences that were correctly predicted as presence and specificity is the proportion of observed pseudo-absences that were correctly predicted as absences. The TSS is a composite index, specially designed for ecological studies, that takes into account sensitivity and specificity. TSS is not sensitive to prevalence, contrary to the kappa index (Allouche et al. 2006). To our knowledge, TSS has never been used on ensemble modelling of suitable habitat distribution of seabirds. Oppel et al. (2012) are among the few who have modelled seabird distribution with an ensemble model, but they used the area under the receiver operating characteristic curve (AUC) to assess model accuracy. Here we selected TSS because both TSS and AUC provide highly correlated results and TSS is a simple and intuitive measure (Allouche et al. 2006).

TSS has been used to assess the accuracy of ensemble models on other species and, in particular, on landbirds (Coetzee et al. 2009, Barbet-Massin & Jiguet 2011). According to Coetzee et al. (2009), TSS > 0.8 is good to excellent and Thuiller (2013) considered TSS > 0.87 to be very high to excellent.

To build our ensemble models, we chose 9 methods derived from statistics and artificial intelligence. These methods (see Elith et al. 2006, Prasad et al. 2006, Hegel et al. 2010) were generalised linear models (GLMs; McCullagh & Nelder 1989), generalised additive models (Wood & Augustin 2002), multiple adaptive regression splines (Friedman 1991), random forest (Breiman 2001, Cutler et al. 2007), generalised boosting model, artificial neural network, classification tree analysis (Breiman et al. 1984), flexible discriminant analysis and maximum entropy (Phillips & Dudik 2008, Elith et al. 2011).

Then the 9 models were assembled with a weighted average. The weight assigned to each model was proportional to the quality of the model as measured by the TSS. Only models with a TSS > 0.80 were selected.

All non-significantly correlated environmental variables were first included into the models so as to determine which variables were related to bird distribution. Then, we selected only the most important variables (see next section) to model bird distribution in order to provide the most parsimonious models. A global ensemble model, including the 3 years of tracking data and only the most important variables, was then built. All models were built with the *biomod2* package (Thuiller et al. 2009) in R software.

Importance of variables and characteristics of suitable habitat

Variable importance was estimated with the *variables_importance* function in the *biomod2* package. This procedure uses Pearson correlation between the standard predictions and predictions where the variable of interest has been randomly permutated. This was realized 5 times. The score was calculated as 1 minus the correlation. Median scores of the 5 runs were then calculated (Thuiller et al. 2009). Higher values indicate a greater influence of the variable on the model, and values of 0 assumed no influence of that variable on the model. This process was realized with all variables.

For each year, values of the most important variables were plotted against the probability of presence, which

defined a habitat suitability index in the tropical Indian Ocean (limits: 30° to 120° E, 30° S to 20° N).

Prediction of future distribution of suitable habitat

Available data

Since 2013, climate change models have been classified according to 4 scenarios called representative concentration pathways (RCPs) and developed under the Coupled Model Inter-comparison Project 5 (CMIP5). Each scenario defines a specific trajectory of greenhouse gas emission and subsequent radiative forcing. RCPs are named according to their radiative forcing predicted for 2100 (in W m^{-2}). Higher radiative forcing indicates higher global warming. RCP 2.6 is a 'peak-and-decline' scenario; its radiative forcing level first reaches a value of around 3.1 W m^{-2} by mid-century, and returns to 2.6 W m^{-2} by 2100. This is the only scenario to produce an increase in temperatures of <2°C. RCP 4.5 and RCP 6.0 are 'stabilization' scenarios in which total radiative forcing is stabilized shortly after 2100, without overshoot, respectively at 4.5 and 6 W m^{-2}. RCP 8.5 is the most extreme scenario, displaying a continuous rise in radiative forcing, at the current pace, and leading to a value of about 8.5 W m^{-2} in 2100 (IPCC 2014).

Any scenario necessarily includes subjective elements and is open to various interpretations. CMIP5 combined all climate projections developed by the different modelling groups. We decided to use a mean of all these projections (available at http://climexp.knmi.nl/) because ensemble predictions are often closer to observed data than any individual model. Among the variables of interest for our seabird habitat models, only SST was predicted by the ensemble climate change model. SST data were available on a grid of 1.25 × 1.25°. We re-interpolated them on a grid of 2 × 2° with the 'lowres' function (*adehabitatMA* package; Calenge 2006) to match our tracking resolution data. Monthly SST predictions were available, and the median of the 6 wintering months for each year was calculated. Bathymetry, which is a static variable, was also available. SST and bathymetric gradients were calculated with the slope function from the *SDMTools* package (VanDerWal et al. 2014). WIND is predicted by some agencies, but these predictions show very important year-to-year variations (see 'Discussion' and Figs. S1–S4 in the Supplement, available at www.int-res.com/articles/suppl/m550p235_supp.pdf). Because of this lack of consistency, we decided not to include WIND in our predictive global model.

Ensemble modelling and forecasting

An ensemble model with the most important variables (see 'Results') was built first (hereafter named 'reference global model'). We then built an ensemble model with only the variables available for prediction (SST, BATHY, SSTG and BATHYG; named 'predictive global model'). The reference model provided a reference quality score to evaluate the loss of information when using only available variables for prediction.

Ensemble models were built with 2008, 2009 and 2012 tracking data. For each of the environmental variables, and for all pixels of the study area, we calculated the median of the values of the 3 studied years. Pseudo-absences were selected as explained previously. All steps to build ensemble models were conducted similarly for each year. To provide future distributions, for each scenario, multi-model mean SST predictions, bathymetry, gradients of SST predictions and gradients of bathymetry predictions were used. Future distributions were predicted for the short (year 2020), medium (year 2050) and long term (year 2100), allowing us to investigate long-term trends in response to marine habitat changes.

All statistical analyses were performed within the R environment (R Development Core Team 2015).

RESULTS

Characterization of wintering areas and wintering phenology

The overall wintering distribution of tracked birds in the core area (50% contour) was around the Ninety East Ridge between 78–97° E and 11–21° S in 2008, 75–91° E and 12–19° S in 2009 and 79–97° E and 14–22° S in 2012 (Fig. 1). The spatial overlap of wintering core areas varied from 25 to 89% between years, with a maximal overlap for 2008 and 2009, and a minimal overlap for 2009 and 2012. No significant inter-annual differences were observed in the mean date of arrival and departure from the wintering area (Table 1).

Suitable habitat modelling of the wintering areas

Model performance and explicative variables

Suitable habitat models for Barau's petrel yielded very good performance (TSS > 0.97). The models of the 3 years predicted the presence of petrels perfectly (sensitivity = 100%) and their absence correctly (specificity > 97%).

The variables which best explained the probability of petrel presence in 2008 were WIND (0.29) and SST (0.25), followed by CHLA (0.19) (Table 2). In 2009, SST (0.33) and CHLA (0.28) were the 2 main contributing factors (Table 2). WIND (0.77) and SST (0.44), had the greatest influence on the model in 2012, as in 2008 (Table 2). Finally, the 3 variables selected in our annual model were those that had the
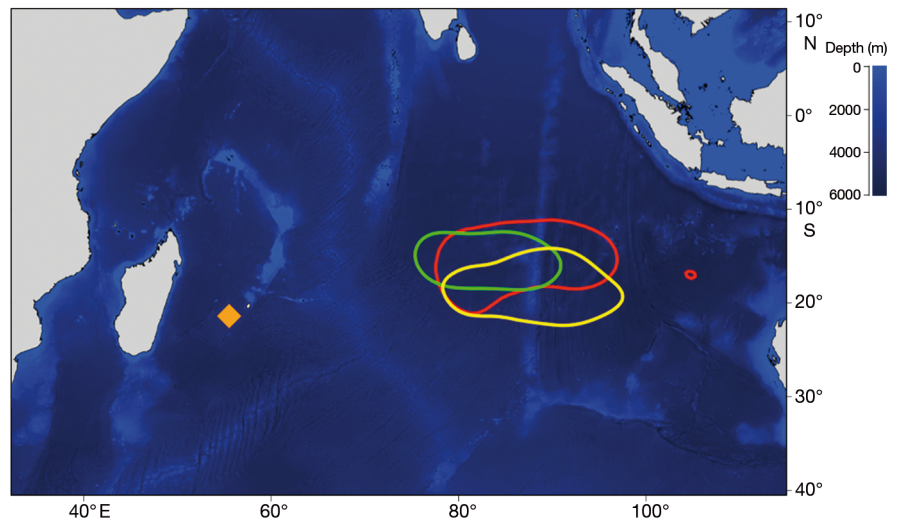

Fig. 1. Wintering core areas (50% kernel density) of Barau's petrels *Pterodroma baraui* tracked in 2008 (n = 12; red polygons), 2009 (n = 9; green polygon) and 2012 (n = 13; yellow polygon) in the Indian Ocean (limits: 30 to 120° E, 40° S to 10° N). The orange diamond indicates the Barau's petrel breeding colony at Réunion Island (55.33° E, 21.07° S). Background map represents bathymetry (m)

Table 1. Timing of the wintering period of Barau's petrels *Pterodroma baraui* tracked in 2008 (n = 12), 2009 (n = 9) and 2012 (n = 13). Mean ± SD of dates and residence times for the 3 years are given and compared using 1-way ANOVA. Dates are given as dd/mm/yy

Year	Arrival date (date ± days)	Departure date (date ± days)	Residence time (d)
2008	16/04/08 ± 12	26/08/08 ± 11	133 ± 20
2009	13/04/09 ± 12	21/08/09 ± 14	132 ± 15
2012	10/04/12 ± 5	15/08/12 ± 15	128 ± 14
Mean	13/04 ± 10	21/08 ± 13	131 ± 16
$F_{2,31}$	1.1638	2.3889	0.3359
p	0.3256	0.1084	0.7173

Table 2. Importance of each environmental variable in the prediction of ensemble models during wintering of Barau's petrels *Pterodroma baraui* tracked in 2008, 2009 and 2012. Indexes of variables range in importance from 0 (no influence of that variable on the model) to 1 (a large influence of that variable on the model)

	2008	2009	2012
Bathymetry, BATHY	0.02	0.07	0.05
Sea surface height, SSH	0.01	0	0
Wind speed, WIND	0.29	0.02	0.77
Chlorophyll *a* concentration, CHLA	0.19	0.28	0.04
Sea surface temperature, SST	0.25	0.33	0.44
Zonal currents, CZ	0.01	0	0.01
Meridional currents, CM	0	0	0
Gradients of bathymetry, BATHYG	0	0.01	0.01
Gradients of sea surface height, SSHG	0	0	0.01
Gradients of wind speed, WINDG	0	0	0
Gradients of chl *a* concentration, CHLAG	0.02	0.05	0.01
Gradients of sea surface temperature, SSTG	0.08	0.05	0.15

higher influence on the probability of presence over the 3 years; all other variables showed almost no contribution.

For each year, a parsimonious ensemble model with only 3 variables (WIND, SST, CHLA) correctly predicted the habitats suitable for Barau's petrels. Indeed, the TSS and specificity of these models were reduced by <4%, compared to complete models, and the sensitivity was not reduced.

Characteristics of suitable habitats

Suitable habitats in 2008, 2009 and 2012 were characterized by specific values of CHLA, SST and WIND (Figs. 2–4, respectively). Adult Barau's petrels tended to select cool (SST range: 24–27.5°C), oligotrophic areas (CHLA range:

Fig. 2. Chl *a* concentration (CHLA) according to the predicted probability of Barau's petrel *Pterodroma baraui* presence for (a) 2008, (b) 2009 and (c) 2012. Probabilities of presence are predicted by ensemble models with only the most important variables (WIND, CHLA and sea surface temperature, SST) for each year. Boxplots represent the distribution of CHLA values in the tropical Indian Ocean (limits: 30 to 120°E, 30°S to 20°N). Red dashed lines and green dot-dashed lines represent median CHLA in the tropical Indian Ocean and in suitable areas, respectively. Boxplots: midpoint: median; box limit: 1st and 3rd quartiles; whiskers: min. and max.; circles: outliers
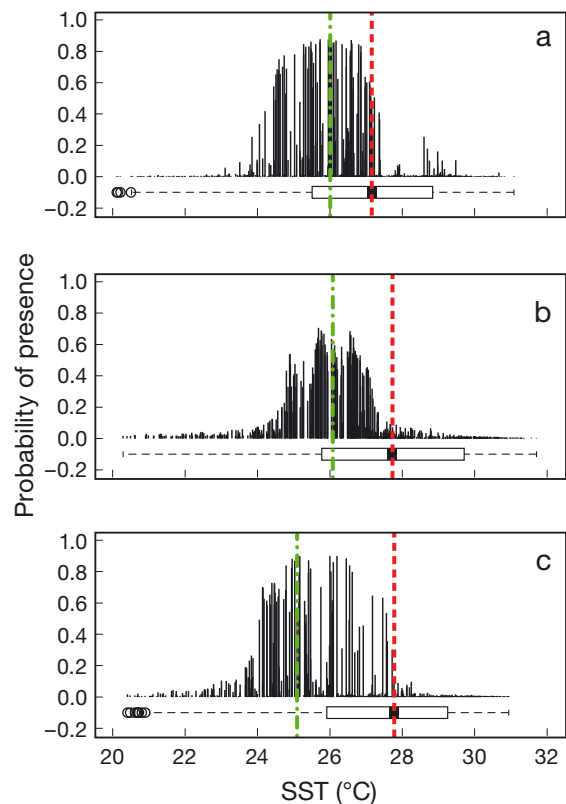

Fig. 3. Sea surface temperature (SST) values according to the predicted probability of Barau's petrel *Pterodroma baraui* presence for (a) 2008, (b) 2009 and (c) 2012. Probabilities of presence are predicted by ensemble models with only the most important variables (WIND, chl *a* [CHLA] and SST) for each year. Boxplots represent the distribution of values of SST in the tropical Indian Ocean (limits: 30 to 120°E, 30°S to 20°N). Red dashed lines and green dot-dashed lines represent median SST in the tropical Indian Ocean and in suitable areas, respectively. Boxplots: see Fig. 2
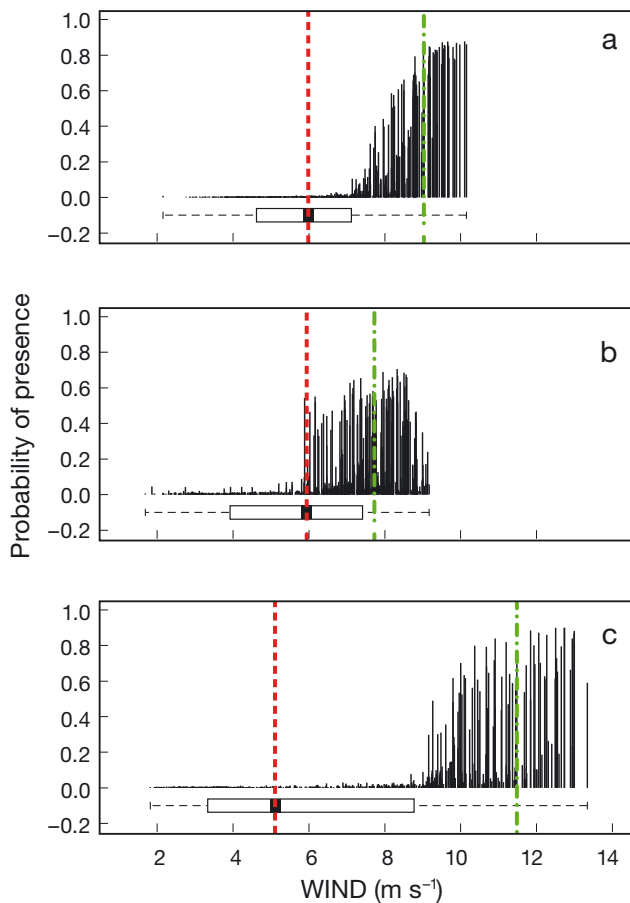
Fig. 4. Wind speed (WIND) values according to the predicted probability of Barau's petrel *Pterodroma baraui* presence for (a) 2008, (b) 2009 and (c) 2012. Probabilities of presence are predicted by ensemble models with only the most important variables (WIND, chl *a* [CHLA] and sea surface temperature, SST) for each year. Boxplots represent the distribution of values of WIND in the tropical Indian Ocean (limits: 30 to 120° E, 30° S to 20° N). Red dashed lines and green dot-dashed lines represent median WIND in the tropical Indian Ocean and in suitable areas, respectively. Boxplots: see Fig. 2

0.05–0.14 mg m^{-3}) with stronger than average winds (Figs. 2, 3 & 4).

CHLA in the tropical Indian Ocean has a very clear seasonal cycle every year with a peak in austral winter and the lowest values in austral summer (Fig. 5). Although CHLA in the core area of suitable wintering habitats of Barau's petrels was lower than in other regions of the Indian Ocean over the same period, it is of interest to note that it was at its maximum when the petrels were present. SST also showed a seasonal cycle every year, with lower values in austral winter and higher values in austral summer (Fig. 6).

Future suitable wintering habitat

Loss of information by using available variables

As already explained, TSS, sensitivity and specificity of the reference global model were equal to 0.98, 100% and 97.6%, respectively, and TSS, sensitivity and specificity of the predictive global model were equal to 0.95, 100% and 94.7%, respectively. This indicates that our models are powerful with a loss of less than 3% of TSS, sensitivity and specificity.

Predicted wintering areas

Our predictive global model produced 3 spatially distinct regions of suitable habitat for wintering Barau's petrels (Fig. 7). The western most area (between 50 and 75° E) corresponds partially to the current at-sea distribution of adult Barau's petrels when breeding, whereas the central area is situated around the Ninety East Ridge where adults currently migrate after breeding. The third, and eastern-most area, is situated between 100 and 115° E and is also sometimes used during winter (Pinet et al. 2011). In the future, these suitable areas are predicted to shift in position and to be reduced in size, according to the 4 scenarios of climate change (Figs. 8 & 9, see below).

Changes in suitable habitat

The climate change scenarios RCP 2.6, RCP 4.5 and RCP 8.5 predicted a decrease in the size of the suitable habitat, by about 33, 19 and 5%, respectively (Fig. 9a). All identified a westward shift of the suitable habitat (Fig. 9b). RCP 4.5, RCP 6.0 and RCP 8.5 also predicted a southward shift, of about 3°, 5° and 7°, respectively (Fig. 9c). The most optimistic climatic scenario (RCP 2.6) predicted a northward shift of 2° until 2020 and stagnation until 2100 (Fig. 9c). Overall, at the end of the 21st century, the suitable habitat is predicted to decrease in size, and to shift westward and southward.

DISCUSSION

This study is one of the first to model and predict the future oceanic habitat suitability for a seabird species, using current distribution assessed by light-level geolocation. The ensemble modelling approach developed in this study has seldom been
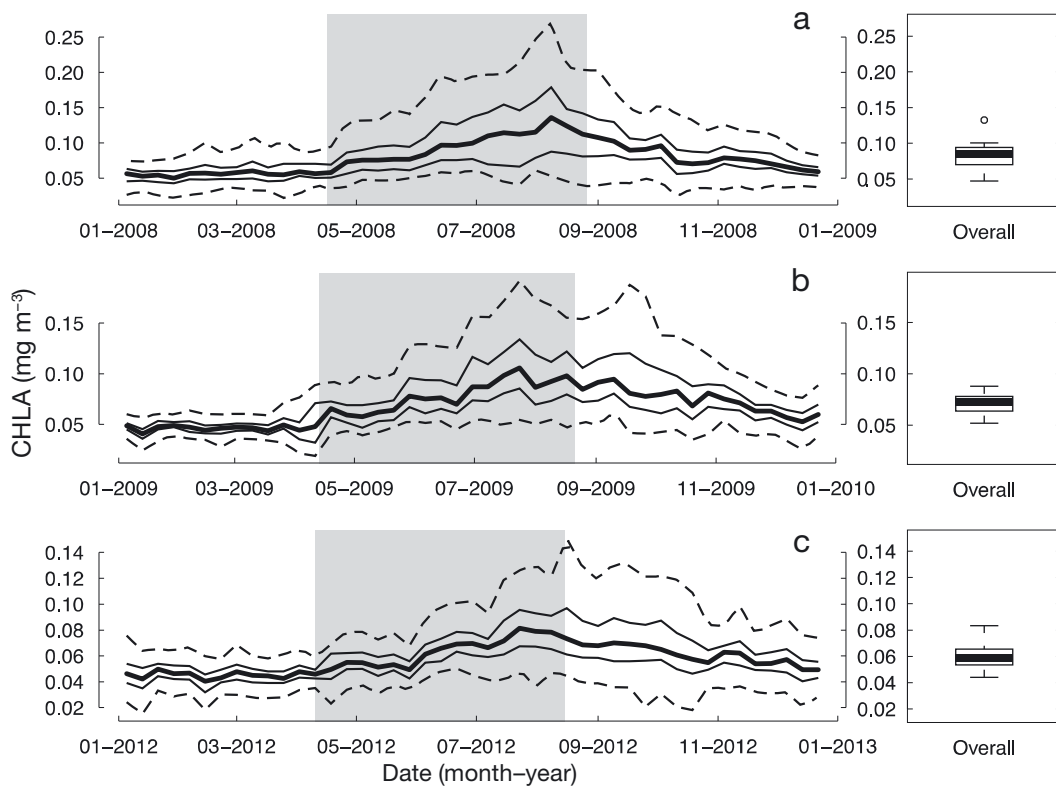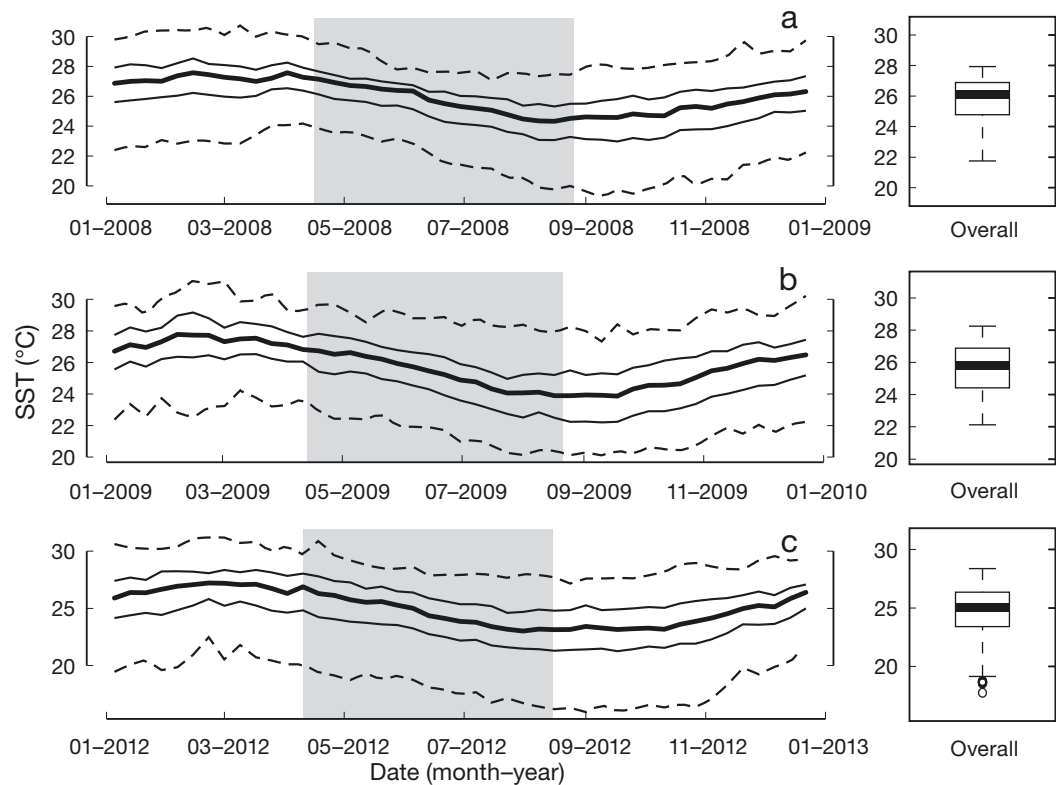
Fig. 5. Temporal variations of chl *a* concentration (CHLA) values in (a) 2008, (b) 2009 and (c) 2012 in the core area of suitable wintering habitats of Barau's petrels *Pterodroma baraui*. Solid bold lines represent median values, thin solid lines represent first and third quartiles, and dashed lines represent the extreme values. Boxplots represent overall CHLA distribution in the core area during wintering periods, and the shaded area represents the wintering period for each year. Boxplots: see Fig. 2

Fig. 6. Temporal variations of sea surface temperatures (SST) values in (a) 2008, (b) 2009 and (c) 2012 in the core area of suitable wintering habitats of Barau's petrels *Pterodroma baraui*. Solid bold lines represent median values, thin solid lines represent first and third quartiles and dashed lines represent the extreme values. Boxplots represent overall SST distribution in the core area during wintering periods, and the shaded area represents the wintering period for each year. Boxplots: see Fig. 2
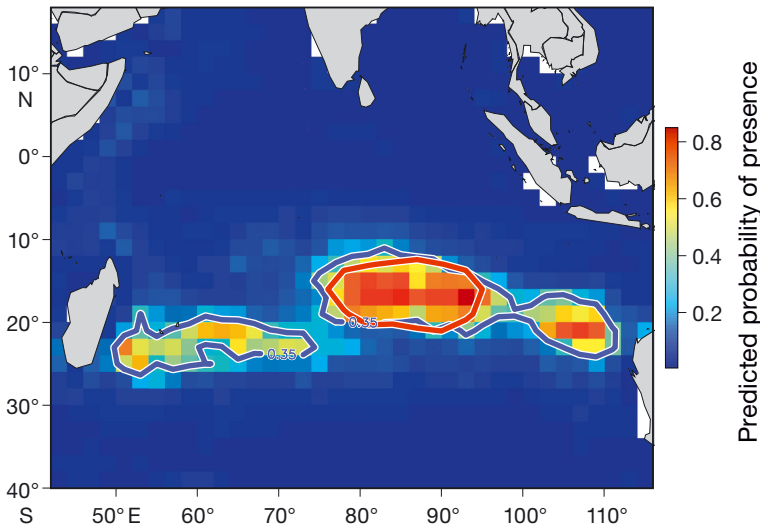
Fig. 7. Projections of suitable habitat for Barau's petrels *Pterodroma baraui* based on a predictive global model built with the means of the 3 study years (2008, 2009, 2012). Blue contours indicate the most suitable wintering areas (with a predicted probability of presence superior to the optimal threshold [0.35] maximizing sensitivity and specificity), and red contours indicate the current core area of the wintering habitat (mean of the 3 study years)

used for seabirds (but see Oppel et al. 2012), although it has proved its worth for plants and terrestrial animals (Araújo et al. 2006, Thuiller et al. 2009). Our ensemble models performed well to reproduce the current distribution of our study species. When selecting only the 3 most important variables (WIND, SST and CHLA) to build the most parsimonious ensemble models, the quality of models remained excellent in all cases. Thus, these 3 variables appear to be accurate predictors of Barau's petrel presence/absence. Unfortunately, only SST was predicted by the ensemble climate change model. WIND is predicted by some agencies (Institut Pierre-Simon Laplace; Atmosphere and Ocean Research Institute [The University of Tokyo], National Institute for Environmental Studies and Japan Agency for Marine-Earth Science and Technology;
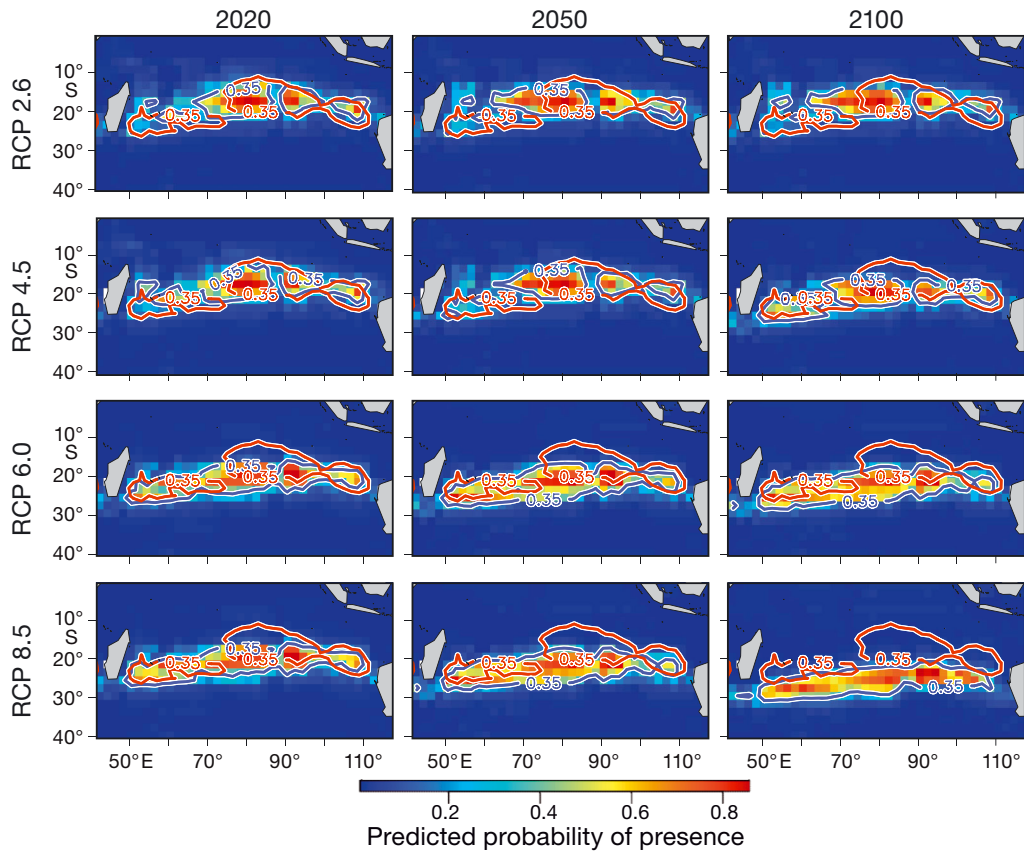

Fig. 8. Predicted future distribution of Barau's petrels *Pterodroma baraui* in 2020, 2050 and 2100 according to the 4 climate change scenarios (RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5, where RCP: representative concentration pathway). Blue contours indicate the most suitable wintering areas (with a predicted probability of presence superior to the optimal threshold [0.35] maximizing sensitivity and specificity) and red contours indicate the current most suitable wintering area (based on current data)
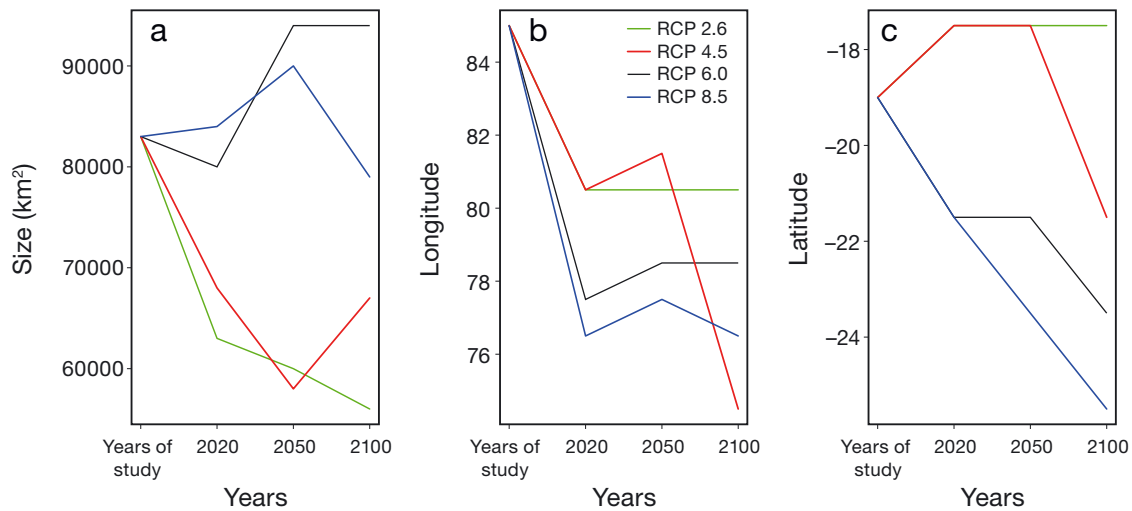
Fig. 9. Evolution over time of the (a) area, (b) longitude and (c) latitude (barycenter of each polygon) of the suitable wintering areas of Barau's petrels *Pterodroma baraui* in the future, according to the 4 climate change scenarios (RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5, where RCP: representative concentration pathway). Years of study were 2008, 2009 and 2012

Met Office Hadley Centre) but these predictions show very important year-to-year variations. Indeed, WIND is known to be highly variable between years, and future predictions mirrored this variability (see Figs. S2 & S3 in the Supplement). Predictions of WIND values were also highly variable depending on the scenario (Figs. S2 & S3). Central moving averages over 10 yr of WIND fluctuated over time but still showed important inter-annual variations. These inter-annual variations are more important than the general long-term trends. Central moving averages over 30 yr showed a slightly continuous increase of WIND in the core area with scenario RCP 2.6, stagnation with scenario RCP 4.5 and decrease with scenarios RCP 6.0 and RCP 8.5. Furthermore, the first (in 2029) and the last values (in 2085) of the time series of WIND were not significantly different from each other (Figs. S2 & S3). Because of this lack of consistency, we decided not to include WIND in our predictive global model. We added BATHY and BATHYG to our predictive model because bathymetry is known to interact with local productivity (Manghnani et al. 1998). We also added SSTG because gradients of SST are good indicators of frontal oceanographic zones (Chen et al. 2003). These 3 variables (BATHY, BATHYG and SSTG) are reported to be good predictors of seabird presence and are often used in seabird habitat modelling (Louzao et al. 2011). Indeed, they increased the performance (TSS) of our model by about 6%. Finally, the predictive global model was powerful, with a good TSS (0.95).

The 2 main biases of this study are related to the nature of the data. Positions inferred from light signals have an average (±SD) accuracy of 186 ± 114 km (Phillips et al. 2004). This low precision has little impact on our predictions, because our predictions on latitudinal and longitudinal shifts of the wintering areas of Barau's petrels are by far much larger than the resolution of the GLS. The other bias is inherent to the concept of pseudo-absences. Tracking data do not provide information on true absences of individuals. We have partially overcome this presence–absence bias through the use of randomly generated pseudo-absences, which make the model more powerful (Elith et al. 2006). The powerfulness of the different modelling techniques varied widely depending on how, where, and how many pseudo-absences were used (Barbet-Massin et al. 2012).

Current wintering habitats of Barau's petrels

Barau's petrels consistently used the same wintering area during the 3 years of the study. This high inter-annual consistency in wintering habitat selection has already been shown in various seabird species such as Arctic terns *Sterna paradisaea* (Egevang et al. 2010), Manx shearwaters *Puffinus puffinus* (Guilford et al. 2009) and white-chinned petrels *Procellaria aequinoctialis* (Péron et al. 2010), among others. This suggests that birds learn their migration strategy during their first years of life, and then reproduce this pattern annually (see for instance

Phillips et al. 2005, Yamamoto et al. 2014). The plasticity of such learned behaviour in the face of climate change is currently very poorly known. Further investigations involving tracking of young animals during their first years and repeated tracking (over multiple years) should be conducted to know how Barau's petrels learn their migration pathways and how adaptable they are to climate changes.

Habitat modelling and characteristics of current suitable habitat

The most influential variables for the at-sea distribution of Barau's petrels were, by order of importance, WIND, SST and CHLA. This was consistent over the duration of our study, although in 2009, WIND had a lower influence than SST and CHLA. This probably explains the lower performance of the model for that particular year.

Four major phenomena influence the interannual variability of the Indian Ocean: the Indian monsoons, the Indonesian through flow, the Indian Ocean Dipole (IOD) and the El-Niño-Southern Oscillation (ENSO) (Saji et al. 1999, Schott et al. 2009, Izumo et al. 2010). Complex interactions of these 4 phenomena regulate climate and oceanographic features of the oceanic region used by wintering Barau's petrels (e.g. Meyers et al. 2007, Luo et al. 2010). Positive IOD events cause a warming of the western Indian Ocean, while cooling the eastern part. Westward winds also blow stronger than average during positive IOD events, reversing surface currents. The Dipole Mode Index (DMI), which expresses the intensity of the IOD, was positive for the 3 years of the study but exhibited distinct levels. Interestingly, DMI was lowest during winter of 2009 (DMI in the winter of 2008, 2009 and 2012: 0.37, 0.06 and 0.39, respectively), implying weaker winds in the southeastern Indian Ocean, compared to 2008 and 2012. This could explain the lower contribution of the wind in the habitat suitability model of 2009. However, the inter-annual variation that we found in the habitat suitability models should be interpreted with caution, as our sample sizes were limited for any given year and were variable between years. Moreover, our sample sizes were quite low, probably making the detection of less used wintering areas difficult.

A recent study has demonstrated that winds optimize the movement of wandering albatross *Diomedea exulans* (Weimerskirch et al. 2012), which enables individuals to limit the loss of energy during the flight and may improve foraging success with positive demographic consequences. Barau's petrel

likely use wind to move between patches of food in the wintering area. Therefore, well-oriented wind may minimize the loss of energy during flight, as for most albatrosses and petrels.

SST has often been identified as the most influential environmental feature influencing habitat suitability for numerous species of seabirds (Tremblay et al. 2009). Seamounts, such as the Ninety East Ridge where Barau's petrels currently winter, induce upwellings, which may explain the lower SST observed in this region. Upwellings bring nutrient-rich waters towards the ocean surface, stimulating primary production and promoting the aggregation of micronekton. Furthermore, as surface-feeding predators, Barau's petrels frequently sit on the water when foraging (Pinet et al. 2012). We hypothesize that birds develop knowledge of their environment (via sensing or smelling), as previously suggested (Weirmerskirch et al. 2007, Kappes et al. 2010).

CHLA is an indicator of standing stock of phytoplankton, which is a good proxy of marine productivity. We expected that birds would select areas with high CHLA concentrations, as has already been shown in several other studies (e.g. Péron et al. 2010, Louzao et al. 2011). Local enrichments due to upwellings induced by seamounts, such as the Ninety East Ridge, create favourable conditions for food web development (Genin & Dower 2007). In agreement with Lévy et al. (2007), our study has shown that a pronounced seasonal phytoplankton bloom appears in the central Indian Ocean during austral winter (Fig. 5). Interestingly, the wintering of Barau's petrels coincides with these winter blooms, suggesting that individuals could benefit from seasonal enrichments, which may induce higher prey concentration.

However, other regions of the tropical Indian Ocean show much higher productivity (particularly the Somalia and Oman upwellings), yet for unknown reasons, none of these areas is targeted by adult Barau's petrels. Interestingly, a multispecies tracking study involving 11 tropical seabird species of the western Indian Ocean (Le Corre et al. 2012, M. Le Corre unpubl. data) also shows similar patterns: tropical seabirds, contrary to their temperate and polar counterparts, do not select rich upwelling areas during their non-breeding period. Further investigations on the foraging ecology, prey availability and energy needs of tropical seabirds during their non-breeding period would be necessary to better understand this paradox.

Barau's petrels are known to forage predominantly on surface-dwelling squids during the breeding season (Danckwerts et al. 2016), and indirect measure-

ments using stable isotopes and fatty acids suggest that it may be the same during the non-breeding season (Danckwerts et al. 2016). However, the links between the availability and abundance of these prey and the tropical marine environment is still poorly known.

Consequences of future changes in suitable habitat distribution

All scenarios predicted a shift of suitable habitat by 2100. Thus, the current wintering area of Barau's petrels may be less suitable in the future. Barau's petrels are endemic and highly philopatric (Pinet et al. 2011). Endemic species have adapted, on evolutionary scales, to specific conditions making them extremely sensitive to environmental changes, such as those brought by climate change (Grémillet & Boulinier 2009). Thus, we hypothesize that Barau's petrels may have difficulties changing their migration routes and strategies in a rapidly changing world. Furthermore, according to most IPCC scenarios, the size of the suitable habitat may decrease by the end of the 21st century. If this happens, the carrying capacity of wintering areas may be reduced, which may lead to greater intra- and inter-specific competition for prey. The long-term effects of these changes on the population dynamics of the species are currently unknown.

Future research considerations

As long-lived animals, seabirds may experience various wintering conditions during their lifetime. In the context of rapid climate change, it would be very interesting to investigate individual inter-annual fidelity to wintering areas, to know whether birds can adapt to a changing environment from one year to the next (see Yamamoto et al. 2014).

It would be also very interesting to investigate marine habitat selection and to predict climate-driven changes in habitat suitability when seabirds are central-place foragers, i.e. during the breeding season. Indeed, this period is crucial for the population dynamics but is also the most demanding in terms of individual energy expenditure. Thus climate change may have a greater impact on seabirds during this part of their life cycle.

The Indian Ocean is a marine hotspot of biodiversity, with major concentrations of emblematic or economically important species such as cetaceans, tur-

tles, sharks, tunas, billfish and seabirds (Le Corre et al. 2012, Mannocci et al. 2014). Our modelling approaches could be applied to this set of species to provide multi-specific predictions of habitat suitability and their changes in relation to global warming. This would be of great help to adapt conservation plans for the Indian Ocean in response to climate change.

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