



Foraging in a changing environment: habitat shifts of an oceanic predator over the last half century

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Spatial modelling studies stress the importance of predicting future species distribution in changing environments, but it is also important to establish historical distribution ranges of species to provide baseline conditions for understanding distribution shifts. We focused on pelagic ecosystems, the largest ecosystem on Earth. Based on boosting algorithms, we reconstructed the foraging patterns of an oceanic predator, wandering albatross *Diomedea exulans*, in the highly dynamic Southern Ocean over the last half century. To access the unobserved past oceanographic conditions, we used simulations of the OPA-PISCES oceanic model for the 1958–2001 period. Firstly, we validated the simulated oceanographic variables (sea surface temperature and height, wind speed and chlorophyll *a*) for the 1998–2001 period with remotely sensed oceanographic data, which were highly correlated, except chlorophyll *a*. Secondly, we developed two habitat models (based on simulated and observed oceanographic variables) describing the foraging probability of albatrosses. We detected no statistically significant differences between the two models and predictions of both models matched the observed distribution patterns reasonably. Finally, we projected the most likely historical key pelagic habitats of albatross for the 1958 to 2001 period and characterised recurrent, occasional and unfavourable foraging areas in a decadal basis based on average predictions and their standard deviations. Our findings 1) provided a historical baseline (1958–1968) of recurrent, occasional and unfavourable foraging habitats, 2) evidenced a progressive habitat shift the following decades driven by a propagation of sea surface height from SE South Africa towards Antarctica from 1958 to 2001 and 3) measured habitat change rates of wandering albatross over the last half century. To our knowledge, our study provides the first quantitative long-term assessment of the spatial response of a marine top predator to changing pelagic habitats of the Southern Ocean and highlighted the oceanographic mechanisms involved, offering new insights on future effects of climate change on the pelagic realm.

There is increasing evidence for ecological impacts of global change (i.e. the component of climate variability induced by anthropogenic activities), from polar to tropical environments, in a wide range of ecosystems and from species to communities (Parmesan 2006). Climate change affects the biota at different organization hierarchies and it can affect the 1) physiology of organisms and phenology, 2) community composition and interaction among organisms, 3) structure and dynamics of ecosystems, and specially 4) shifts in the distribution range of species (Walther et al. 2002). Most studies have focussed on the question of how species might respond to future environmental changes, but to correctly interpret current and future species distributions it is important to establish historical distribution ranges that would provide baseline conditions (e.g. low human impact) (Lotze and Worm 2009). Historical distribution ranges can help us to understand distribution shifts

that can result from natural variability and/or anthropogenic sources (Walther et al. 2005). For instance, the pelagic ecosystem in the Southern Ocean has been warming since the mid 1970s and extensive ice shelves have melted over the last 50 yr (Levitus et al. 2000, Vaughan et al. 2001). Different studies have already outlined a biological response to a probable ecosystem shift after the end of the 1970s when analysing long-term demographic data of top predators (Barbraud and Weimerskirch 2001, Croxall et al. 2002, Jenouvrier et al. 2003, 2005, Weimerskirch et al. 2003, Trathan et al. 2007). This ecosystem shift could be related to a change in the meridional atmospheric circulation during the 1970s, bringing more moisture from warm subtropical moisture sources to the Antarctic coast (Masson-Delmotte et al. 2003). This hypothesis agreed with observations of winter sea ice extension, sea surface temperature and Southern Oscillation Index trends at the end of the

1970s (Weimerskirch et al. 2003, Jenouvrier et al. 2005). However, more research is needed to investigate the drivers of this ecosystem shift, which could be indirectly assessed by studying the long-term dynamic of oceanic predator's habitats (Jenouvrier et al. 2005) and understand the overall response of pelagic communities to the changing environment (Richardson and Schoeman 2004).

Within this context, we studied the distribution patterns of the most wide-ranging pelagic seabird, wandering albatross *Diomedea exulans* in the highly dynamic Southern Ocean over the last half century. Conducting such analyses is often difficult due to the lack of historical data on the distribution of species and historical environmental data (Walther et al. 2005). Most studies on the past distribution of species have been conducted in terrestrial ecosystems (Elith and Leathwick 2009), but due to logistic constraints and data limitation (Parmesan 2006) only fewer examples exist in marine environments (Beaugrand et al. 2002, Beaugrand and Reid 2003, Bellier et al. 2007, Gigliotti et al. 2010). Satellite (observed) data provide important environmental information that help to better understand oceanographic processes and their influence on marine top predator distribution patterns (Louzao et al. 2009). However, they have been available only since the 1980s. An attractive alternative is to use oceanic models that provide valuable simulated oceanographic data prior to the 1980s. They are particularly valuable to better understand the ecological implications of changing environment. For example, OPA-PISCES oceanic models have produced reliable wind-forced oceanographic information from 1958 until 2001 (Aumont and Bopp 2006). The availability of both simulated and observed oceanographic data allows the application of predictive habitat models (Elith and Leathwick 2009) as a promising approach to reconstruct the most likely historical distribution ranges of pelagic species.

A considerable challenge in species distribution modelling is to disentangle the effects of non-stationary (i.e. variation of species-habitat relationships in space and/or time) and both spatial and temporal autocorrelation in the observations (that can bias estimates of model parameters) from the stationary effect of the environment. Recently in an attempt to refine existing statistical models, Hothorn et al. (2011) have developed such an approach based on boosting algorithms. This approach provides a universally applicable species distribution model since it is able to deal simultaneously with non-linearity, interactions between predictors, spatial autocorrelation and non-stationarity (Hothorn et al. 2011).

Here, we used boosting algorithms and both OPA-PISCES- and satellite-derived oceanographic variables to study the historical foraging patterns of the wandering albatross in the Southern Indian Ocean. Our ultimate aim was to assess how the quality of foraging habitat (i.e. the geographical distribution range where the species searches for food) of this species changed over the last half century (1958–2001). We characterised recurrent, occasional and unfavourable foraging areas by defining those marine areas where foraging is observed annually, varies greatly inter-annually and no foraging occurs, respectively, following Bellier et al. (2007). To accomplish this, it was firstly necessary to validate simulated oceanographic variables with

remotely sensed oceanographic variables for the 1998–2001 time window (where both datasets overlap). Secondly, we applied boosting algorithms to both data sets to assess whether they produced consistent results for the overlap time window. Finally, we applied species distribution models to the full historical OPA-PISCES time series to project the most likely historical key pelagic habitats of wandering albatrosses from 1958 to 2001. Foraging predictions were split in a decadal basis to further explore whether ecosystem shift of the late 1970s could promote spatial distribution shifts of wandering albatrosses. We believe that our approach could strengthen the scientific basis of conservation planning by providing biological distribution models based on environmental surrogates and a meaningful interpretation of habitat shifts, in addition to provide tools to set priorities in marine conservation (Lourie and Vincent 2004).

Material and methods

Tracking device deployment and analysis

Breeding wandering albatrosses of known age and sex were tracked from Crozet Island during the incubation period (December–March) of the 'validation period' (1998–2001). The incubation period is especially illustrative of environmental changes experienced by wandering albatrosses since they travel during this period routinely thousands of kilometres from their colony (mean: 1176 km, range: 61–3381), compared to shorter foraging trips performed during brooding (mean 450 km, range: 88–1800) (Louzao et al. 2011). During the chick-rearing period, wandering albatrosses alternate short and long foraging trips. Thus, foraging trips during the incubation period integrate larger environmental variability and can be considered more consistent in terms of foraging behaviour. Finally, long-term tracking data for this period demonstrated indirect consequence of climate change on the distribution of wandering albatrosses (Weimerskirch et al. 2012).

Sixty-eight albatrosses were equipped with 30–40 g Argos PTT Satellite Transmitters powered with battery and working in continuous mode, and used the same attachment procedure that has been used during the last 20 yr (Weimerskirch et al. 2007). Manipulation time was reduced to a minimum and the total mass of devices was far below the recommended 3% threshold (Phillips et al. 2003). For analysis, all Argos locations (classes A, B, 0, 1 to 3) were used after filtering unrealistic positions using a threshold of 90 km h⁻¹ (McConnell et al. 1992). We built a standard spatial grid (geographic coordinate system, WGS 1984) based on the geographic limits of the tracking data (from 6°E to 90°E and from 32°S to 65°S) with a spatial resolution of 1° (given the spatial resolution of OPA-PISCES data), where tracking locations and environmental data were overlaid.

To assess the foraging habitat, the albatross tracking data were analysed by means of the First Passage Time (FPT; more details in Supplementary material Appendix 1) (Fauchald and Tveraa 2003). This approach is based on identifying area restricted search behaviour along the foraging trips which is indicative of foraging. In this case birds alter their movement rates and/or frequencies of turns in response

to heterogeneously distributed resources. We detected the maximum scale at which albatrosses concentrated their foraging effort, as well as nested spatial scales following Fauchald and Tveraa (2003), Pinaud and Weimerskirch (2005) and Weimerskirch et al. (2007). Then, searching zones were identified along the foraging trips and a categorical binomial variable was assigned to each position, indicating whether at least one ‘foraging’ event occurred within a given cell or not (e.g. ‘not foraging’) (see more details in Louzao et al. 2011). Note that the entire foraging trip was analysed following Fauchald and Tveraa (2003) and Pinaud and Weimerskirch (2005) and consequently we did not remove locations with high FPT values occurring at night (Pinaud and Weimerskirch 2007). Overall, the total number of visited cells per trip ranged between 6 and 198, and ‘foraging’ records between 4 and 174 representing between the 3.13 and 75% of the total locations per foraging trip (Supplementary material Appendix 1, Table A1).

Foraging distribution modelling framework

Our distribution models were based on boosting algorithms developed in Hothorn et al. (2011). We assumed that the probability of albatross foraging at a given location s and time t under environmental conditions characterized by oceanographic variables $x = (x_1, \dots, x_p)$ is given by the inverse logistic transformation of the regression function f , considering individual id and sex effects:

$$P(\text{foraging of albatrosses} | x, s, t, id, sex) = \text{logit}^{-1}(f(x, s, t, id, sex)) \quad (1)$$

The model is a logistic regression model which relaxes the assumption of linearity of the effects of the explanatory variables and can be fitted by maximizing the binomial log-likelihood (or minimizing the negative likelihood). In order to set-up an appropriate regression model for describing foraging patterns, the regression function f was divided into global and local model components (Eq. 2). The global model component considered only oceanographic variables x and included non-linear terms and describes the conditional probability of foraging as a function of the oceanographic variables x that is stationary in space and time. We assume that the contribution by the oceanographic variables are additive but allowed for smooth non-linear effects of each variable (i.e. the oceanographic variables were modelled according to a generalized additive model). Because the correlation between observations will be additionally affected by unobserved variables varying in space and time, we explicitly included a local model component for dealing with spatio-temporal trends and individual effects in our model. The local model component captured unobserved heterogeneity caused by spatial autocorrelation and random terms. It is important to note that fitting the global model component, i.e. a traditional generalized logistic regression model, without taking the local model component into account may lead to biased effects due to spatio-temporal autocorrelation or effects induced by individual variability. We refrained from including interaction terms in the global component given data complexity. The model does also not

allow for interactions between space and time. We furthermore assume that the effects of the oceanographic variables in the global model component are stationary, i.e. are constant over the whole study area and constant over time. More formally, the model components of the foraging probability regression f were decomposed additively:

$$f(x, s, t) = \underbrace{f_{env}(x)}_{\text{global}} + \underbrace{f_s(s) + f_s(s, sex) + f_r(id) + f_r(t)}_{\text{local}} \quad (2)$$

where f_{env} , f_s and f_r represents the variation explained by the environment, spatial autocorrelation and random effects, respectively. Specifically, two spatial components were included: one general and a second one related to sex segregation in foraging grounds experienced by wandering albatrosses (i.e. which indicated the deviation for females; Weimerskirch and Jouventin 1987). The two functions $f_s(s)$ and $f_s(s, sex)$ describe the increase or decrease in the foraging probabilities at location s that cannot be attributed to any oceanographic variable (spatial trend). Furthermore, since the data consists of longitudinal observations of individuals, two random intercepts $f_r(id)$ and $f_r(t)$ were introduced to consider the effect of individual id at time t . Regarding the temporal random effect, we introduced the factor month plus year as random to quantify the effect of month and year on foraging probabilities (temporal trend). Once all components were fitted, the global model component $f_{env}(x)$ represented the albatross distribution model that described the constant (in space and time) regression effects of the oceanographic variables. We used this model component to predict the past foraging of wandering albatrosses. The advantage of this approach is that this model was unaffected from potential biases resulting from spatial or temporal autocorrelation in the observations (Hothorn et al. 2011).

Regarding model inference, the distributional properties of boosting models are hard to track analytically because the distribution of the estimated effects is not known. Therefore, model inference is performed by applying re-sampling procedures (Hothorn et al. 2011) which is similar to a multi-model inference approach. The model is fitted by minimizing the negative binomial log-likelihood with respect to the structured predictor term by means of an iterative algorithm. In this study, the algorithm starts with the null model predicting the mean foraging probability at all locations. In each iteration only the most informative model component is chosen, and therefore non-informative variables are not selected during this process. The method is prone to overfitting since too many iterations lead to a model that is not generalizable. In order to avoid this problem, the model is fitted on a (possibly weighted) subset of the observations only and the negative log-likelihood as a function of the number of boosting iterations is evaluated on the remaining observations. Here, we used a bootstrap resampling approach (with 50 bootstrap samples) for choosing the respective subsets of observations. The number of iterations with the smallest negative log-likelihood then defines the final model (i.e. the process stops when the out-of-bootstrap empirical risk starts to increase). Since only one model component is updated in each iteration, a small number of iterations lead to a parsimonious model in which

only a few components (or oceanographic variables in the case of an additive f_{env}) actually enter the model. This property of the algorithm is the key to efficient variable and component selection. In summary, the algorithm automatically selects an ‘optimal’ model out of a series of possible models (model selection). For the technical details and statistical properties of boosting-based model selection we refer readers to Hofner et al. (2011) and Hothorn et al. (2011).

Model predictive performance was evaluated by means of the out-of-bootstrap prediction error assessed by the empirical risk on the out-of-bootstrap observations. For the final model, the distribution of this measure indicates how well the model predicts foraging probabilities at locations that were not used for fitting the model. The risk function was defined in terms of the negative binomial log-likelihood, i.e. model fitting and model evaluation was performed using the same risk function. Whether the out-of-bootstrap empirical risk of the final model is stochastically smaller than the risk of the null model, we can conclude that the final model performs significantly better than random guessing by means of the null model.

Data analysis

We developed a four-step approach to predict retrospectively the foraging habitat of wandering albatrosses over the dynamic seascape of the Southern Ocean from 1958 to 2001.

Step 1: correlation between OPA-PISCES and satellite-based oceanographic variables

We validated the simulated (OPA-PISCES) oceanographic information by estimating the correlation between remotely sensed and simulated data for the 1998–2001 period (where both data sets overlap). Monthly dynamic oceanographic conditions (sea surface temperature – SST, chlorophyll *a* – CHL, sea surface height – SSH, and wind speed – WIND) were contrasted at a 1° spatial resolution for the four-year validation period (comprising a total of 48 months) by computing the Spearman rank correlation coefficients, r_s , between the two data sets. We expected to find high correlation between oceanographic variables of the two data sets. We also mapped the dynamic variables averaged across the 4 yr for each month to explore potential spatiotemporal trends (Supplementary material Appendix 2, Fig. A2.1). Similarly, the standard deviation (SD) of the 4-yr period was used as a measure of conditions stability (low and high SD representing stable and unstable oceanographic conditions, respectively).

Step 2: comparing species distribution models

To validate the OPA-PISCES oceanographic variables, we also used the distribution modelling approach described above. We compared the out-of-bootstrap negative log likelihood of two different models based on 1) satellite-based oceanographic variables plus static variables (bathymetry – BAT, gradient of bathymetry – BATG and distance to the colony – COLONY) and 2) OPA-PISCES derived oceanographic variables plus static variables. If the out-of-bootstrap negative log likelihood of the two models

would not differ significantly and the fitted values were similar both data sets would explain albatross foraging patterns to a similar extent and would yield basically the same foraging predictions. This would support the use of the simulated OPA-PISCES data to project albatross foraging habitat from 1958 to 2001. In addition, for model evaluation we compared the out-of-bootstrap likelihood for the constant null model (all effects restricted to zero) with that of the final model.

Step 3: retrospective habitat modelling

We mapped the most likely historical foraging habitats of wandering albatrosses breeding in Crozet to the spatial extent of the analysed tracking data (from 6°E to 90°E and from 32°S to 65°S). Whereas static variables were extracted once, dynamic variables were extracted monthly. Then, we applied our fitted distribution models with simulated oceanographic variables from January to March over the 1958–2001 period to obtain retrospective predictions of historical foraging habitats.

Step 4: historical spatial shifts

We split the time series in four decades (1958–1968, 1969–1979, 1980–1990 and 1991–2001) and the 11-yr predictions were averaged for each month and each grid cell and the standard deviation (SD) was used as a measure of stability in predicted habitat suitability in that grid cell during incubation (Louzao et al. 2011). Then, we characterised foraging areas by adapting the method proposed by Bellier et al. (2007) to our study. To that end we defined recurrent foraging areas, where foraging is observed annually, as grid cells with high mean (higher than the overall mean across all grid cells and 44 yr) and low SD (lower than the overall SD across all grid cells and 44 yr). Occasional foraging areas, where foraging varies greatly inter-annually were defined as grid cells with high SD (higher than the overall SD across all grid cells and 44 yr). Unfavourable foraging areas, where foraging is very infrequent, were defined as grid cells with low mean (lower than the overall mean across all grid cells and 44 yr) and low SD (lower than the overall SD across all grid cells and 44 yr).

Finally, to assess temporal changes in foraging probabilities we averaged the model predictions over 40–60°E at three latitudinal bands (30–40°S, 40–50°S, and 50–60°S) for the whole incubation period (January–March), as well as for Crozet. We applied sequential *t* tests to the complete four times series of foraging probability to detect whether regime shift occurred in the mean signal from 1958 to 2001 (Rodionov 2004).

Results

Correlation between observed and simulated oceanographic variables

By comparing observed and simulated data, we found that SST, SSH and WIND were highly correlated (Spearman-rank correlation coefficient for SST: $r_s = 0.989$, $p < 0.001$; for SSH: $r_s = 0.973$, $p < 0.001$; for WIND: $r_s = 0.886$, $p < 0.001$; Supplementary material Appendix 2, Fig. A2.2).

Spatially, simulations reasonably reproduced observed latitudinal gradients of SST, SSH and WIND (Supplementary material Appendix 2, Fig. A2.1). When exploring the average annual cycle, OPA-PISCES-based SST values reasonably reproduced remotely measured values, whereas WIND and SSH values were slightly and highly overestimated, respectively (Supplementary material Appendix 2, Fig. A2.3). However, OPA-PISCES data reasonably reproduced annual patterns of both SST, SSH and WIND. Regarding chlorophyll *a* (CHL), both datasets were only weakly correlated ($r_s = 0.315$, $p < 0.001$) and the OPA-PISCES model predicted less accurately primary productivity patterns from July to November (Supplementary material Appendix 2, Fig. A2.3b). A more detailed exploration showed that OPA-PISCES predictions reasonably matched CHL values for the incubation period of wandering albatrosses (January–March) both spatially and temporally (Supplementary material Appendix 2, Fig. A2.1b and A2.4, respectively). However, we decided to discard this predictor from the habitat modelling process due to the overall weak correlation with the observed values for the whole validation period.

Comparing foraging distribution models

A total of 68 independent albatrosses (30 females, 38 males) were tracked and provided foraging information on 3146 1°-sized cells. Despite high inter-individual variability in foraging areas, both latitudinal and longitudinal cross sections showed that some marine areas west of Crozet were more specifically targeted by more than 8 albatrosses (between 38–54°E and 36–50°S, Fig. 1). Within this broad area, two key areas were highlighted: the marine areas surrounding their breeding site (Crozet) and seamounts

such as Del Cano Rise (between Crozet and Prince Edward Islands).

We applied the two albatross distribution models to the observed data and the appropriate number of boosting iterations was determined by bootstrap. For the final number of iterations, the bootstrap distribution of the negative log-likelihood was smaller for the model based on remotely sensed oceanographic variables, but it was not statistically different from that of the model based on OPA-PISCES oceanographic variables ($t = -0.437$, $DF = 49$, $p = 0.663$; Supplementary material Appendix 3, Fig. A3.1a). Both data sets yielded very similar foraging probabilities and both models lead essentially to the same fitted values and patterns in the 1998–2001 time period (Supplementary material Appendix 3, Fig. A3.1b and Fig. A3.5, respectively). Finally, we compared the out-of-bootstrap distribution of the negative log-likelihood of the constant null model and final model for OPA-PISCES based modelling. The final model performs significantly better than the constant null model ($t = 27.79$, $DF = 24$, $p < 0.001$; Supplementary material Appendix 3, Fig. A3.1c). Therefore, we concluded that the model based on OPA-PISCES could be safely used to predict foraging patterns in the past.

Supplementary material Appendix 3, Fig. A3.2 shows the fitted regression relationships and the partial effects of the environmental variables for the remotely sensed oceanographic variables. The foraging probability mainly increased with sea surface height (SSH) and the spatial gradient in bathymetry. To a lesser extent, the foraging probability increased with the sea surface temperature (SST) and distance to the colony, whereas it decreased with wind speed (WIND). Variables such as bathymetry had no effect on foraging probability. Regarding the random components, there was not much variation over time but a remarkably large individual variation: some animals seem to forage

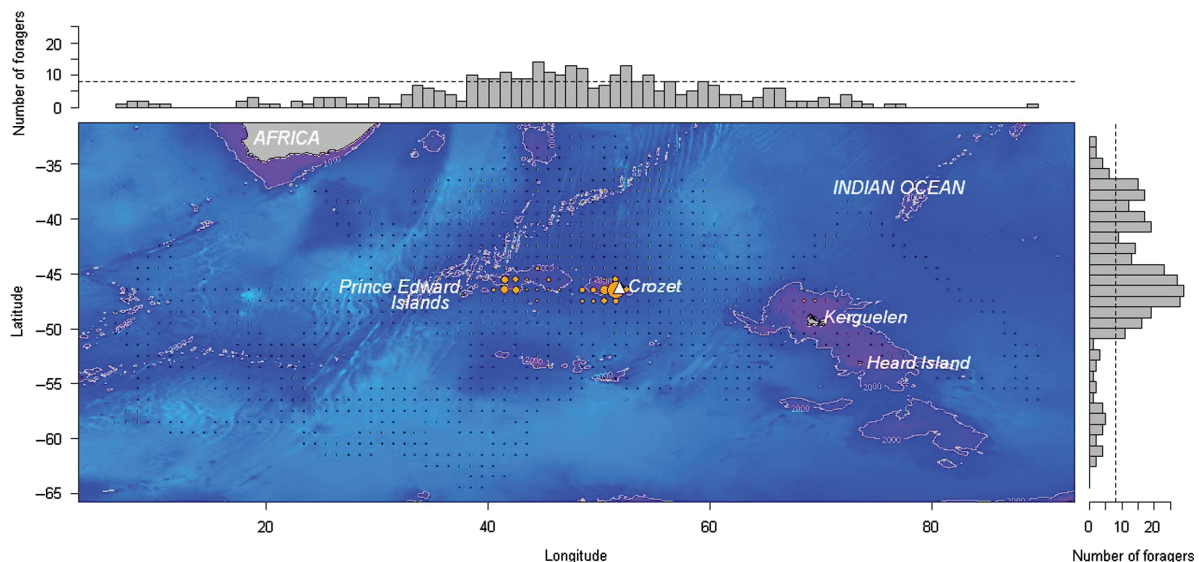


Figure 1. Number of foraging wandering albatrosses breeding in Crozet in each 1° cell over the southern Indian Ocean (1998–2001; central map). Orange dots are proportional to number of foragers (range: 1–23), whereas black dots indicate ‘not foraging’. Background blue scale represents regional bathymetry (range: 0–7303 m) and grey contours indicate the isobath of 200 m-depth limiting the continental shelf. Top and right-side histograms represent the number of foragers along the longitudinal and latitudinal axis with both dashed line indicating the threshold of 8 foragers.

more often compared to others. In addition, a considerable amount of unexplained variability was captured by the spatial component: foraging probabilities were higher in the north-east and south-west compared to the other areas. Female albatrosses avoided the south-eastern part of the Indian Ocean, where the foraging probability was smaller than in other areas (Supplementary material Appendix 3, Fig. A3.3a). Similar results were obtained with the OPA-PISCES distribution model (Supplementary material Appendix 3, Fig. A3.3b and A3.4).

Retrospective habitat modelling

For retrospective habitat modelling we applied the non-linear species–habitat relationships of the species distribution model that was fitted with OPA-PISCES data for the full 1958–2001 OPA-PISCES data set. We observed spatial differences in the foraging probability of wandering albatrosses during incubation after 1980. While the areas with high mean foraging probability conformed a longitudinal band south of 40°S between 1958 and 1968, this zonal band shifted southwards by 5° on latitude each decade (south of 45°, 50° and 55° between 1969–1979, 1980–1990 and 1991–2001; redder areas in Fig. 2a). A band (5° of latitude width) of foraging instability (i.e. high SD of predictions) was always placed north of the high mean foraging probability area, which also showed each decade a progressive poleward shift (Fig. 2b). As a consequence, different types of foraging habitats were arranged in zonal bands following a latitudinal gradient from unfavourable to recurrent habitats, which shifted southwards progressively decade by decade (Fig. 2c). In fact, recurrent foraging habitats decreased by 15.94% (SE: ± 1.48) ($t = -10.76$, $p = 0.008$) each decade, while unfavourable habitats increased by 14.28% (SE: ± 2.64) ($t = 5.40$, $p = 0.032$) (Fig. 3). Specific marine areas such as oceanic sub-Antarctic waters surrounding breeding colonies, the Southwest Indian Ridge (N–NW sector of Crozet), and seamounts such as Del Cano Rise (E of Prince Edwards Islands) and the seamount complex of Ob and Llena south of Crozet and Kerguelen Plateau remained as recurrent foraging areas for the species (high probability and low SD, Fig. 2).

Regarding the temporal changes in the foraging probability, predictions averaged over 40–60°E at three latitudinal bands (30–40°S, 40–50°S, and 50–60°S, see Fig. 2 for the spatial extend) showed different trends for the whole incubation period (January–March) from 1958 to 2001 (Fig. 4). Overall, averaged trends revealed two different latitudinal patterns before and after mid 1980s (Fig. 4a): the foraging probability increased from north to south before mid 1980s, whereas this trend was inverted after mid 1980s (Fig. 4b). However, the inversion of latitudinal foraging patterns did not occur at the same time since latitudinal foraging patterns propagated gradually in time from north to south (Fig. 4). In fact, we detected a shift from 1989 to 1995 in the northern band, from 1967 to 1986 in the central band and from 1991 to 2002 in the southern band (Fig. 4b).

Regarding the temporal changes in foraging probability at Crozet, we observed a similar trend to that of the central

latitudinal band (see black and red lines in Fig. 4a), with a marked regime shift from 1979 to 1985. The foraging probability at Crozet remained stable until 1979, after which there was a sharp decline of the foraging probability until 1985 and after it remained stable to date (see foraging probability change along the black line in Fig. 4b).

The main physical process driving the propagation of the foraging probability was the sea surface height (Supplementary material Appendix 4, Fig. A4.2 and A4.3), since foraging probability increased with SSH values of OPA-PISCES lower and higher than 1.0 and 2.5 cm, respectively (Supplementary material Appendix 4, Fig. A4.4). Other dynamic variables such as sea surface temperature and wind speed also partially contributed to these changes (Supplementary material Appendix 4, Fig. A4.2, A4.3 and A4.4).

Discussion

Historical foraging habitats of wandering albatrosses

Here, we presented a comprehensive modelling framework to make retrospective predictions of the historical distribution patterns of an oceanic predator during the last half century over the Southern Indian Ocean. To our best knowledge, our study provides the first quantitative assessment of the long-term spatial response of a marine top predator to changing pelagic habitats. We observed a progressive southward shift of areas with high foraging probability of wandering albatrosses from 1958 to 2001 in agreement with spatio-temporal (Péron et al. 2010, Weimerskirch et al. 2012) and demographic (Weimerskirch et al. 2003) studies. Our findings are important because they 1) provide a historical baseline (1958–1968) of recurrent, occasional and unfavourable foraging habitats, 2) evidence a progressive habitat shift the following decades and 3) measure habitat change rates over the last half century. While recurrent key areas formed a longitudinal band south of 40°S between 1958 and 1968, this zonal band shifted southwards by 5° on latitude each decade (south of 45°, 50° and 55° between 1969–1979, 1980–1990 and 1991–2001). In fact, recurrent foraging habitats decreased by 16% each decade, while unfavourable habitats increased by 14%.

Thus, our foraging models predicted progressive poleward shifts of the foraging habitats of wandering albatrosses which are well supported by Péron et al. (2010). These authors found a contemporary poleward shift in distribution of wandering albatrosses at subtropical latitudes by comparing vessel-based counts between 1980s and 2000s. Péron et al. (2010) suggested that both, a redistribution of the abundance of wandering albatrosses towards southern latitudes and a global decline might explain the observed southward shift. Recent evidence points to the redistribution hypothesis. Weimerskirch et al. (2012) found that the northern range of albatrosses tracked during the last 20 yr has shifted southward and that this was accompanied by an increase in flight speed influenced by changes in oceanic wind fields over the last 50 yr (Thompson and Wallace 2000, Gillett and Thompson 2003).

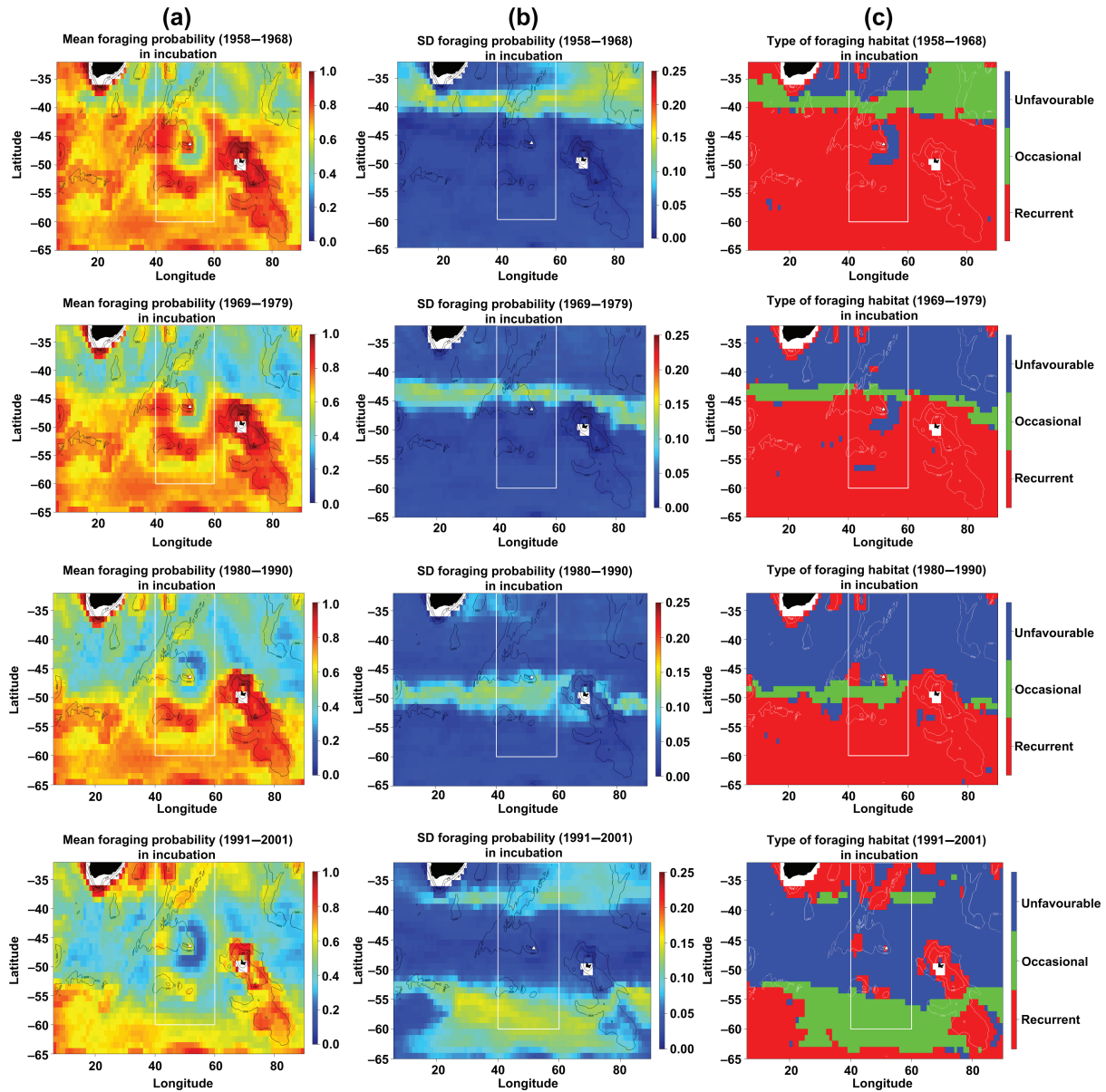


Figure 2. (a) Mean and (b) SD predictions of the foraging probability during incubation over the 44-yr study period (1958–2001). The right scale bar indicates mean foraging probability (from 0 to 1) or SD (from 0 to 0.25). Black contour lines represent the isobaths of 200, 1000 and 3000 m. (c) Types of foraging habitat for the four 11-yr periods (1958–1968, 1969–1979, 1980–1990 and 1991–2001). Recurrent foraging areas with high mean (higher than the overall mean across 44 yr) and low SD (lower than the overall SD across 44 yr) where foraging is observed annually; occasional foraging areas with high SD (higher than the overall SD across 44 yr) where foraging varies greatly inter-annually; unfavourable foraging areas with low mean (lower than the overall mean across 44 yr) and low SD (lower than the overall SD across 44 yr) where no foraging occurs. The right scale bar indicates the type of foraging area. The white square encompasses most of the foraging range of wandering albatrosses and matches the marine area analysed in Weimerskirch et al. (2012). Foraging predictions were extracted for further interpretation of their temporal evolution.

Disentangling how the effects of climate change are related with the physical and biological ecosystem components is a difficult task, but we were able to identify the sea surface height as main physical process driving the propagation of the foraging probability in our model. OPA-PISCES models predicted a progressive increase of SSH from SE South Africa towards Antarctica in a predominant SE direction from 1958 to 2001. Sea surface height measurements provide insights into ocean circulation, and

OPA-PISCES models captured the oceanic dynamic of the northern part of this biogeographic area, the Agulhas system. The Agulhas current is retroflected back to the Indian Ocean and oceanic eddies transport warm and salty Indian Ocean waters to the South Atlantic (Blastoch et al. 2009). Based on this evidence, the increase of sea surface height simulated by OPA-PISCES could indicate an intensification of the Agulhas Current System (Rouault et al. 2009). For example, Blastoch et al. (2009) found an increase of the

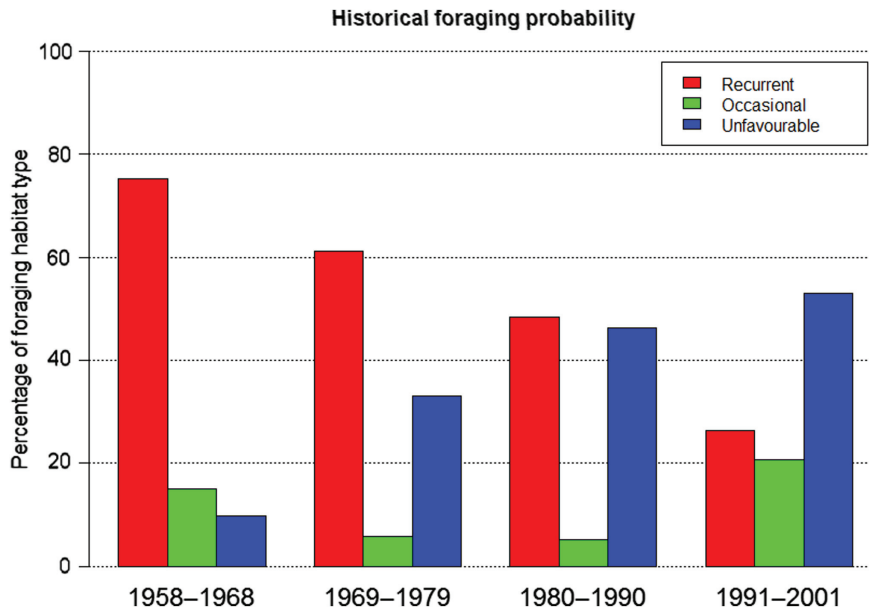


Figure 3. Percentage of pixels with recurrent, occasional and unfavourable habitats by decade (1958–1968, 1969–1979, 1980–1990 and 1991–2001).

transfer of Indian Ocean waters into the South Atlantic over the last decades related to changes in atmospheric circulation over the Southern Ocean (Thompson and Wallace 2000). These atmospheric changes also have promoted a poleward shift of oceanic wind fields (Thompson and Wallace 2000, Gillett and Thompson 2003), have greatly affected oceanographic processes such as the intensification of mesoscale eddy fields (Fyfe et al. 2007), and an increasing pattern of sea surface temperature and salinity in the southwest Indian Ocean (Biaostoch et al. 2009, Rouault et al. 2009).

While foraging habitats were dynamic, specific marine areas remained recurrent foraging areas. They included oceanic sub-Antarctic waters surrounding breeding colonies, the Southwest Indian Ridge (N–NW sector of Crozet), the seamount Del Cano Rise (E of Prince Edwards Islands), and the seamount complex of Ob and Llena south of Crozet and Kerguelen Plateau. The protection of these key areas is of paramount importance for the conservation of the species since they have not been only identified as (recurrent) key areas during the last half of the 20th century (1958–2001), but also during the beginning of the 21st century (1998–2008, Louzao et al. 2011). Pelagic protected areas are likely to be particularly effective where species occur predictably at some point in time and management can reflect this predictability (Grantham et al. 2011). We were able to demonstrate how the foraging importance (probability) of specific marine areas decreased progressively due to oceanographic processes. Thus, further research is needed to identify predictable multi-species hotspots in the pelagic realm, as well as key oceanographic processes driving their distribution (Grantham et al. 2011).

Future challenges in species distribution modelling

Species distribution models provide in absence of observed data the only applicable approach to reconstruct the baseline

biological conditions of pelagic key habitats for marine top predators. These organisms are necessary to monitor changes of marine ecosystems under reference (e.g. pristine) conditions and put recent changes into a meaningful context (Lotze and Worm 2009). Clearly, species distribution models are only as good as the underlying data (Hothorn et al. 2011) and we have demonstrated that wind-forced OPA-PISCES oceanic models successfully reproduced observed oceanographic information. Most of the spatial modelling studies forecasting potential range shifts beyond observed temporal windows, however, do not validate the reliability of simulated environmental data. Because the output of species distribution models has important implications for the selection of protected areas and their evolution in the future (Seo et al. 2009), we emphasize the importance of integrating validation procedures in habitat modelling exercises. For instance, chlorophyll *a* values poorly matched within the whole study area, even though OPA-PISCES data has been validated in the tropical Indian Ocean (Kone et al. 2009), probably related to the harsh weather conditions of sub-Antarctic and Antarctic waters (Gille 2002). While a previous study showed that wandering albatrosses did not directly respond to chlorophyll *a* values (Louzao et al. 2011), further research is needed to improve surrogates for primary productivity patterns in order to understand overall response of pelagic communities.

Improved predictions on future species distribution under climate change are needed for conservation planning (Seo et al. 2009) and modelling approaches accommodating non-linearity, interactions between predictors, spatial autocorrelation and non-stationarity such as boosting algorithms can help us improving future species predictions (Hothorn et al. 2011). The importance of local components such as spatial autocorrelation and individual variability showed that our data contained considerable heterogeneity that was not captured by the available environmental variables (Hothorn et al. 2011). Such heterogeneity is (in part) due to

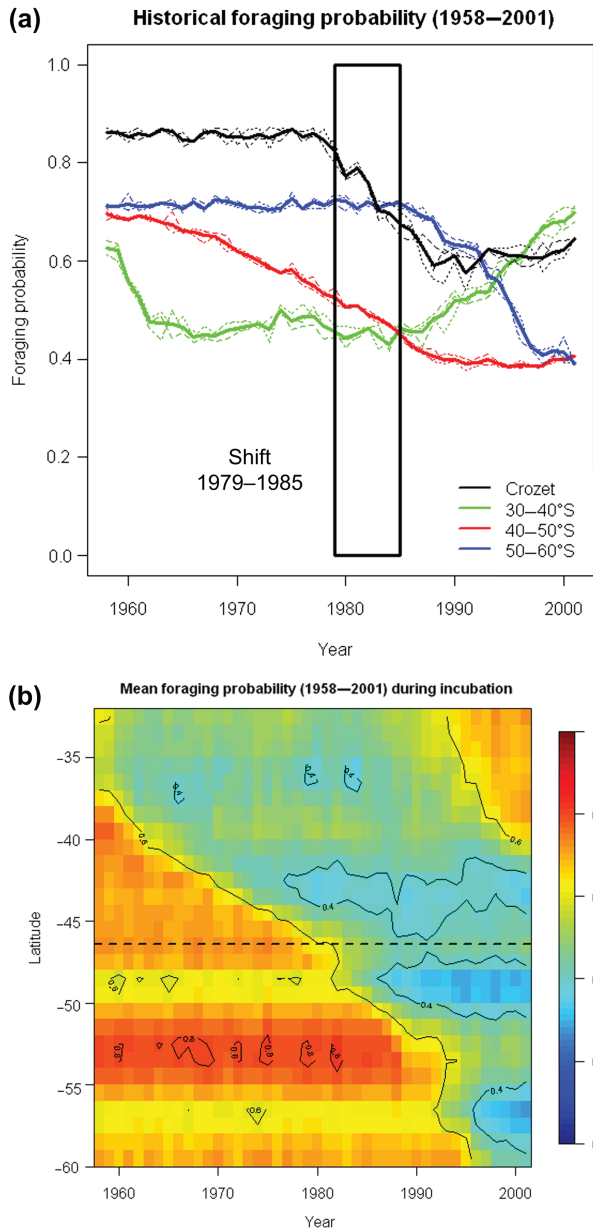


Figure 4. (a) Trajectory of foraging probabilities from 1958 to 2001 at Crozet (black line) and northern, central and southern band of latitudes (30–40°, 40–50° and 50–60°S represented by green, red and blue lines, respectively). Solid lines indicate average values for the incubation period, whereas the three dotted lines represent average values for January, February and March. Results of the sequential t tests are plotted (vertical black lines) indicating shifts in the temporal trend of foraging probability at Crozet. (b) Temporal change of average foraging probabilities over 40–60°E from latitude 32°S to 60°S between 1958 and 2001. The solid black line indicates the latitude of Crozet, whereas contour lines guide the temporal evolution of different values of the foraging probability.

individual variability in foraging patterns and sexual foraging segregation, as well as for the non-inclusion of important explanatory variables such as prey availability. Therefore, future development in species distribution models should try to project uncertainties related to the observation process, conceptual and numerical model formulations among others (Planque et al. 2011).

The obvious question if shifts of historical foraging probabilities of wandering albatrosses would also be related to changes in the distribution of their preys (primarily squids) is difficult to answer. This is because no long-term data exist on the distribution of these organisms since they are not the target of commercial fisheries (Weimerskirch et al. 2005). Wandering albatrosses are well known ship-followers and their distribution could be affected by the presence of fishing activity. However, different studies showed that the interaction of wandering albatrosses with fishing vessels may be the result of an overlap between the natural range of the species and fishing areas (Weimerskirch 1998, Cotté et al. pers. comm.) since both concentrate over strong bathymetric slope such as the shelf break (Cherel et al. 1996). Thus, wandering albatrosses could change their foraging behaviour next to fishing vessels (Bartumeus et al. 2010), but without influencing their overall foraging range. In a recent study of the white-chinned petrel *Procellaria aequinoctialis*, a seabird species which follows ships, it was suggested that birds and fishing vessels occupy the same overall zone with infrequent co-occurrence (19% of birds in the vicinity of vessels) (Delord et al. 2010). This result was confirmed by the relatively low occurrence of fishery-related items (4–22%) in chick food samples. Thus, our model predictions should be considered as the potential distribution of the overall foraging range of wandering albatrosses over the last half century. What is certain is that wandering albatross have adapted to fly optimally in their environment by adopting an optimal flight strategy by using the wind to reduce energy costs of flying (Weimerskirch et al. 2000). Thus, the foraging range of the species might shift in response to an adaptation to changes in oceanic wind fields, as has been already proved (Weimerskirch et al. 2012). Finally, our analyses were based on the assumption that wandering albatrosses did not change their behaviour and keep foraging in the same habitat. But we cannot dismiss the possibility that 1) individuals change habitat over time or 2) there is a selection of individuals foraging in different habitats over time.

In summary, our modelling procedure can be applied to predict key pelagic areas in the next decades within the current global change scenario in order to identify important marine areas for the conservation of top predators in the pelagic realm (Planque et al. 2011). In the case of wandering albatross, the predicted further intensification and poleward shift of westerlies under climate change scenarios should be less favourable, especially if the present trend in the use of wind continues to shift from tail to head winds (Weimerskirch et al. 2012). Climate change and its effects on the ecosystem are ongoing and accelerating, but poorly understood at regional scales. In addition, not all species, populations, sex, demographic categories and even individuals (present study) respond in similar manners to current environmental changes (Stenseth et al. 2002) and it also depends on dispersal capacity (Trathan et al. 2007). Thus, more comparative studies within and across species ranges are necessary to understand distribution shifts of upper-trophic level species and the overall response of pelagic communities to climatic change. Long-term demographic studies of marine species should be explored together with combined accurate distribution data on predator-prey systems, both during breeding and non-breeding seasons. Our study fills

this gap for wandering albatross and offers new insights on the potential link between ocean dynamics and pelagic habitats in the changing Southern Ocean.

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Supplementary material (Appendix E7587 at <www.oikosoffice.lu.se/appendix>). Appendix 1–4.