

Conserving pelagic habitats: seascape modelling of an oceanic top predator

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Summary

1. Currently pelagic ecosystems are changing significantly due to multiple threats. An important management policy is to establish marine protected areas, until now overlooked due to the difficulty of declaring 'high seas' protected areas, obtaining long-term distribution data on indicator species and the dynamic nature of these ecosystems.

2. Within this framework, we developed predictive habitat suitability models of an oceanic predator, the vulnerable wandering albatross *Diomedea exulans*, in the highly dynamic Southern Ocean. Based on a long-term tracking database (1998–2008), we estimated three quantitative ecological indices that complementarily describe the hierarchical habitat use of the species at multiple spatial scales: where the species (i) spent more time (the seascape, based on the time spent per area), (ii) searched for prey (the foraging habitat, based on zones of increased foraging intensity using first passage time), and (iii) fed (the feeding habitat, based on prey capture data).

3. Predictive habitat models reasonably matched the observed distribution patterns and described albatross multi-scale habitat use as a hierarchical arrangement: albatrosses foraged over topographic features in subtropical waters, nested within the wider seascape due to the constraint imposed by the colony effect, whereas feeding occurred nested over the continental shelf and seamounts in areas of low oceanographic variability within the Polar Frontal Zone.

4. Within the current oceanographic conditions, the location of key pelagic habitats for albatrosses breeding in the southern Indian Ocean encompassed certain topographic features such as pelagic areas surrounding main breeding sites, seamounts and submarine mountain ranges. The placement of these pelagic hotspots depends on the current sea surface temperature conditions.

5. *Synthesis and applications.* The present study provides two key conservation and management tools. First, we provide the first map to support the development of a prospective network of priority conservation zones across the southern Indian Ocean based on habitat predictions of an oceanic indicator species. This could be used not only to support conservation of top predators but also the underlying biodiversity associated with pelagic key habitats. Secondly, the developed habitat modelling procedure is widely applicable and could be used to track changes in species distribution in both marine and terrestrial environments within the current global change scenario.

Key-words: first passage time, habitat modelling, indicator species, network of marine protected areas, prey capture data, Southern Ocean, time spent per unit area, wide-ranging predators, wandering albatross

Introduction

The structure and functioning of pelagic ecosystems are changing significantly due to multiple threats (e.g. climate change, overfishing and pollution; Game *et al.* 2009). It is increasingly

reported that overexploitation of natural resources following new technological development has caused adverse impacts on the oceanic environment (Game *et al.* 2009). For instance, deep ocean habitats in remote areas are being exploited as traditional fishing grounds have been depleted. The need for an ecosystem-based approach for marine conservation applies to the protection of all trophic levels, including top predators

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(Hooker & Gerber 2004). Species belonging to the higher trophic levels play a key role in ecosystem functioning (Heithaus *et al.* 2008), but they are declining worldwide at a rapid rate (Myers & Worm 2003), driven to severely low levels, and consequently affecting other species and habitats (Norse & Crowder 2005). Similarly, the loss of these taxa will have important effects in pelagic ecosystems, but being difficult to detect, further research is needed in order to elucidate their ecological effects (Heithaus *et al.* 2008).

A major conservation initiative for the protection of marine ecosystems is the establishment of marine protected areas (MPAs), specially focused on coastal areas for protecting sessile and sedentary taxa (Hooker & Gerber 2004; Game *et al.* 2009). The protection of pelagic ecosystems has been largely overlooked until now due to the difficulty of (i) declaring 'high seas' protected areas, (ii) obtaining long-term distribution data on pelagic species and (iii) the dynamic character of pelagic habitats (Game *et al.* 2009). Some of the challenges of identifying key pelagic habitats could be overcome by using ecological indicator species characteristic of a particular habitat or biological community. These species could be used to assess biodiversity hotspots for candidate protected areas (Zacharias & Roff 2001).

In the case of marine conservation and management, indicator species should be distributed over wide distribution ranges, easy to observe and not be continuously harvested (Zacharias & Roff 2001). Although selecting indicator species is controversial, seabirds have been identified as potentially good indicators (Zacharias & Roff 2001). They are easy to monitor thanks to their land-based breeding which facilitates the study of their at-sea distribution via tracking devices. Albatrosses and petrels are the most pelagic of seabirds, occurring in all oceans and are therefore especially suited as indicator species (Furness & Camphuysen 1997). Moreover, they are highly sensitive components of the marine ecosystem since major system shifts will be reflected in their population sizes (Weimerskirch *et al.* 2003). Within this framework, we studied the distribution patterns of the wandering albatross *Diomedea exulans* (Linnaeus, 1758) in a highly dynamic pelagic ecosystem: the Southern Ocean, where the species breeds in several sub-Antarctic islands. The need for urgent conservation measures is highlighted by analysis of long-term demographic data that has revealed a rapid population decline over three generations and has classified the wandering albatross as Vulnerable (BirdLife International 2009). Fishing bycatch is suspected to be the main factor affecting this decline, through a reduction in adult survival and juvenile recruitment (Weimerskirch, Brothers & Jouventin 1997).

Understanding the features that determine the distribution of oceanic predators is a prerequisite for identifying key areas for their conservation, and hence guides the establishment of MPAs. We developed habitat suitability models to define the pelagic habitats of this threatened albatross breeding in French Southern Territories, which comprises 40% of the global breeding population (Delord *et al.* 2008). Our study is based on a long-term tracking database (1998–2008). This provides a unique opportunity for considering different oceanographic scenarios, which allows us to consider the dynamic character

of pelagic ecosystems when delineating MPAs. Based on an integrative habitat modelling approach, we estimated three different quantitative ecological indices that complementarily describe the hierarchical habitat use of the species at multiple spatial scales: where the species (i) spent more time (the seascape, based on the time spent per area), (ii) searched for prey (the foraging habitat, based on zones of increased foraging intensity using first passage time, FPT) and (iii) fed (the feeding habitat, based on prey capture data). Within the distribution range of the species, the identification of the seascape provides a global and wider perspective of the pelagic habitat use, integrating information on different behaviours such as foraging and resting. The delineation of the foraging habitat gives insights into a more specific behaviour: prey searching. Ultimately, the definition of the feeding habitat affords the most specific activity: feeding, without consideration of other habitat uses. Since albatrosses are central place foragers and could change their foraging strategies and habitats depending on the breeding stage (Weimerskirch *et al.* 1993), we studied in more detail habitat use during the incubation and brooding periods. Finally, we interpreted the complementarity of all three habitat modelling outputs in relation to the ecology of the species, within the oceanographic context of the southern Indian Ocean. We discuss the implication of our results in the current conservation scenario, which involves different Regional Fisheries Management Organisations (RFMOs). To our knowledge, this is the first time that different ecological indices quantifying habitat use at different spatial scales have been applied to characterize the pelagic habitat of a wide-ranging top predator.

Materials and methods

BIRD TRACKING

Birds of known age and sex were tracked at Crozet and Kerguelen Islands (southern Indian Ocean), during both incubation (December–March) and brooding (April) periods over 8 years from 1998 to 2008 (Table S1, Supporting information). Albatrosses were equipped with three different tracking devices: Argos PTT Satellite Transmitters powered with battery and working in continuous mode (134 birds; 1998–2003), global positioning system (GPS; 18 birds during the 2002–2005 period) and duty-cycle GPS/Argos satellite transmitters solar panel (22 birds; 2008). Proportionally, 13% of the equipped birds were from Kerguelen. Additionally, some of the birds tracked with Argos PTT (1998–2001) and GPS (2002–2005) were also equipped with stomach temperature transmitters (STT; Weimerskirch, Gault & Chérel 2005; Weimerskirch *et al.* 2007). Since some of the tracked individuals performed more than one foraging trip, we randomly selected one per bird (to avoid pseudo-replication) totalling 149 foraging trips from Crozet and 18 from Kerguelen. The total mass of devices was below the recommended 3% threshold (Phillips, Xavier & Croxall 2003) and the same procedure has been used over the last 20 years (Weimerskirch *et al.* 2007).

Analyses were performed on complete foraging trips (93% of trips); although incomplete trips were also included when prey capture data were available (STT were regurgitated before birds returned to the colony). We used all Argos locations (classes A, B, 0, 1–3),

after filtering positions above 90 km h^{-1} (McConnell, Chambers & Fedak 1992). Speed filtering led to the removal (in average) of the 5.1% of the positions of one foraging trip (range: 0–37.1, Table S1, Supporting information).

HABITAT USE ECOLOGICAL INDICES: A THREE-LEVEL HIERARCHICAL APPROACH

We applied different methodological approaches to identify different marine habitat use of the wandering albatross at multiple spatial scales, within the R environment (R Development Core Team 2008). We built a standard spatial grid based on the geographic limits of the tracking data (from 1°W to 124°E and from 30°S to 68°S) where tracking locations and environmental data were overlaid. The 0.25° cell size (152×500 cells) was chosen according to the available oceanographic data (Table 1) and the accuracy of the tracking devices.

Time spent per unit area

We used the *tripGrid* function (*trip* package) which resamples each individual track at a higher temporal resolution by linear interpolation (every 60 s) in order to approximate the time spent in each 0.25° -size cell (more details in <http://staff.acecrc.org.au/~mdsummer/Rutas/trip-demo.pdf>). Then, we estimated the percentage of time spent in each cell relative to the total duration of the trip.

First passage time

Within the marine environment, resources are distributed heterogeneously, thus animals often alter their movement rates and/or frequencies of turns in response to local resource abundance by adopting an area-restricted search behaviour, resulting in slow speed and sinuous trajectories (Benhamou 1992). We detected the scale at

which animals alter their movements (i.e. concentrates its foraging effort) in response to landscape heterogeneity based on FPT analysis (Pinaud & Weimerskirch 2005). Also, we identified nested spatial scales which might have an important biological meaning (Fauchald & Tveraa 2003; Pinaud & Weimerskirch 2005). Then, we identified zones of high FPT values (i.e. higher foraging effort) along the tracks for both maximum and nested spatial scales above a FPT threshold value determined from its multimodal distribution (see Fig. S1, Supporting information; Pinaud & Weimerskirch 2007). Finally, we assigned a categorical binomial variable to each position of the interpolated track, indicating whether the albatross was 'foraging' or 'not foraging' within a given cell. Note that the entire foraging trip was analysed following Fauchald & Tveraa (2003) and Pinaud & Weimerskirch (2005) and consequently we did not remove locations with high FPT values occurring at night (Pinaud & Weimerskirch 2007).

Prey capture

A total of 34 breeders were tracked and equipped with STT to locate prey capture events (Weimerskirch, Gault and Chérel 2005, 2007). Stomach temperature data were analysed in order to determine positions of feeding events along each track, and then re-coded into a binary 'feeding'/'not feeding' variable, indicative of whether at least one feeding event occurred within a given cell.

HABITAT MODELLING PROCEDURE: IDENTIFYING PELAGIC HABITATS

We used a hierarchical modelling approach to identify those environmental variables (see details in Table 1) that most accurately reflected the seascape and both foraging and feeding habitats of wandering albatross within the information theoretic approach (Fig. S1, Supporting information; Louzao *et al.* 2009).

Table 1. Biologically relevant explanatory variables used for habitat modelling and associated oceanographic processes. Dynamic variables were downloaded on a monthly basis. Since they differed in spatial resolutions, they were aggregated to match the standard grid of 0.25° cell size. Static variables were extracted once and aggregated. BAT, SST, CHL, SLA, and WIND were not normally distributed and we used the median as it is less strongly influenced by outliers (Zuur, Ieno & Smith 2007)

| Explanatory variables ¹ | Satellite | Spatial resolution | Range ² (min–max) | Oceanographic process |
|--|------------|--------------------|------------------------------|--|
| <i>Dynamic</i> | | | | |
| Chlorophyll <i>a</i> (CHL, mg m^{-3}) | SEAWIFS | 0.1° | 0.051–1.657 | Ocean productivity domains |
| CHL gradient (CHLG) ³ | SEAWIFS | 0.1° | 0.000–99.487 | Frontal systems |
| Sea surface temperature (SST, $^\circ\text{C}$) | PATHFINDER | 0.04° | 0.45–24.60 | Water mass distribution |
| SST gradient (SSTG) ³ | PATHFINDER | 0.04° | 2.00–82.33 | Frontal systems |
| Sea level anomaly (SLA, cm) | AVISO | 0.25° | –0.619–1.052 | Presence of eddies |
| SLA gradient (SLAG) ³ | AVISO | 0.25° | 0.214–58.912 | Frontal systems |
| Wind speed (WIND, m s^{-1}) | BLENDED | 0.25° | 5.822–12.746 | Wind speed |
| <i>Static</i> | | | | |
| Bathymetry (BAT, m) | ETOPO | 0.03° | 80.735–5847.816 | Coastal vs. pelagic domains |
| BAT gradient (BATG) ³ | ETOPO | 0.03° | 0.187–96.522 | Presence of topographic features (shelf-break, seamount) |
| Distance to colony (COLONY, km) | – | – | 12.256–3354.582 | Breeding colony influence on central-place-foragers |

¹Extracted from the Environmental Research Division, Southwest Fisheries Science Center and US National Marine Fisheries Service (<http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowerWW360.jsp>).

²Oceanographic data ranges are based on the time spent data, the most extensive training dataset ($n = 23\,021$ observations).

³Spatial gradients were estimated as their proportional change (PC) within a surrounding 3×3 cell ($0.75^\circ \times 0.75^\circ$) grid using a moving window as follows: $\text{PC} = [(\text{maximum value} - \text{minimum value}) \times 100] / (\text{maximum value})$.

Selecting predictors

Prior to modelling, all environmental variables were standardized (Zuur, Ieno & Smith 2007). Strongly 'correlated' ($|r_s| > 0.5$) predictors were identified by estimating all pair-wise Spearman rank correlation coefficients (Table S2, Supporting information). Then, we removed those explaining less deviance by comparing Akaike Information Criteria values (AICs) of generalized linear mixed models (GLMMs) with only one predictor to avoid collinearity and related problems with parameter estimations (Zuur *et al.* 2007). This approach led to the removal of different predictors depending on the habitat index and breeding stage considered (indicated in Table 2).

Habitat models

Once 'non-correlated' environmental variables were identified, GLMMs were fitted for all possible linear combinations of predictors based on the *lmer* function (*lme4* package; Pinheiro & Bates 2000). For each breeding stage, the (log-transformed) percentage of time-spent per unit area was fitted with a Gaussian error distribution (identity link), whereas the two binomial dependent variables ('foraging/not foraging' and 'feeding/not feeding') were fitted with a binomial error distribution (logit link). We only included the 'individual identity' as a random term in order to account for individual effects, although 'year' and/or 'sex' effects were also tested (to account for inter-annual variability in sampling effort and sex-related foraging ground location) but AIC values did not improve (decrease).

Model selection and inference

Within the Information Theoretic Approach, we evaluated competing models by assessing their relative support (based on AIC and Akaike weight) in relation to observed data, rather than using the best single model approach (Burnham & Anderson 2002). When the model with lowest AIC value has an Akaike weight value lower than 0.9, a model averaging procedure might be more appropriate to account for parameter uncertainty (Burnham & Anderson 2002). Therefore, we constructed a 95% confidence set of models where the sum of Akaike weights was > 0.95 (Louzao *et al.* 2009). Accordingly, averaged coefficients were estimated from the 95% confidence set of models containing that variable, as well as variance estimator in order to assess the precision of the estimates (Burnham & Anderson 2002).

Model checking

In parallel, we checked the distribution and spatial autocorrelation of the residuals, but no significant evidence was found (results not presented) and we did not consider any spatial autocorrelation structure in GLMMs.

Model evaluation

To assess the predictive performance of habitat models, we estimated the concordance index (*C-index*) of the averaged models estimated with the *Hmisc* package (Harrell 2001). This index is equivalent to the area under the Receiver Operating Characteristics curve (AUC) and probably the most useful measurement for distribution modelling (Vaughan & Ormerod 2005), since it allowed the comparison of the predictive performance of all three models (time spent: continuous, foraging and feeding: binomial; Harrell 2001). The *C-index* varies from 0.5 to 1 with the following model predictive performance classifi-

cation: > 0.9 excellent, 0.9–0.8 good, 0.8–0.7 reasonable, 0.7–0.6 poor and 0.6–0.5 unsuccessful (Swets 1988).

We applied a cross-validation procedure using two different approaches: (1) an independent dataset for time spent and foraging patterns in order to assess the predictive performance of averaged models (built with data from Crozet) in predicting distribution patterns of birds from Kerguelen and (2) bootstrapping the original data for feeding patterns (no independent dataset) which provides an alternative approach for evaluating the model with the original data (Guisan & Zimmermann 2000; McAlpine *et al.* 2008). Working on two spatially distinct groups (Crozet and Kerguelen) allowed us to assess the model performance to predict in different conditions/areas. Although both populations differed slightly in their habitat availability, a previous study showed no evidence of difference in habitat selection (Pinaud & Weimerskirch 2007).

During 1000 simulations, models within the 95% confidence set were fitted to 70% of the test dataset and the modelling output was then used to predict distribution patterns of the remaining 30%. Then, the *C-index* was estimated for each simulation (up to 1000) and the mean, upper and lower 95% confidence interval (CI) of the *C-index* were used as a cross-validation measure of the predictive performance of the models (McAlpine *et al.* 2008). If the lower 95% CI limit did not include the 0.5 value, there was evidence that averaged habitat models were able to accurately predict beyond training dataset.

Mapping predictions

We mapped the predicted spatial distribution of the three habitat use ecological indices. Predictors were extracted yearly for each month (January–March: incubation and April: brooding) from 1998 to 2008 and we applied the 95% confidence set of models to predict the seascape and both foraging and feeding habitats. The 11-years predictions were averaged for each month and the standard deviation (SD) was used as a measure of predicted habitat stability (low and high SD representing stable and unstable habitats, respectively). Habitat predictions for albatrosses were represented as continuous surface probabilities.

Once time spent, foraging, and feeding predictions were mapped, we further analysed their relationship with water mass distribution. We first extracted the mean predictions of habitat models for January and April (as representative of the incubation and brooding, respectively) over the 11-years study period (1998–2008) around the mean distribution ranges of both breeding periods (see Results). Secondly, mean sea surface temperature (SST) values averaged over the 11-years study period corresponding to January and April were extracted as previously and matched to habitat predictions cell by cell. Finally, SST values were aggregated in relation to main water masses described in the southern Indian Ocean (Park *et al.* 2002): Subtropical Zone ($SST > 13$ °C), sub-Antarctic zone ($9^{\circ} < SST < 13$ °C), Polar Frontal Zone ($4^{\circ} < SST < 9$ °C) and Antarctic zone ($SST < 4$ °C).

Results

Wandering albatrosses travelled up to thousands of kilometres from the colony during incubation (mean: 1176 km, range: 61–3381) and brooding (mean 450 km, range: 88–1800) (Fig. 1). During the brooding period, adults made shorter trips (mean: 72 h, range: 5–286) compared to the incubation period

Table 2. Averaged (\pm SE) coefficients of habitat models (seascape, foraging and feeding habitats) developed for the incubation and brooding stages for wandering albatross. Also, the Concordance index (C -index) is shown for averaged models and cross-validation, as well as the number of models within the 95% confidence set. The most important predictors for each habitat model are denoted in bold. NI: indicate non included predictors (i.e. 'Correlated' environmental variables). Dynamic variables are marked with an asterisk

| | Seascape | | | Foraging Habitat | | | Feeding Habitat | | |
|----------------------------------|-------------------------------------|-------------------------------------|--|-------------------------------------|-------------------------------------|--|--------------------------------------|--------------------------------------|--|
| | Incubation | Brooding | | Incubation | Brooding | | Incubation | Brooding | |
| | | | | | | | | | |
| Averaged model | | | | | | | | | |
| Intercept | -1.209 \pm 0.078 | 0.201 \pm 0.104 | | 0.013 \pm 0.043 | 0.011 \pm 0.063 | | -0.777 \pm 0.143 | -1.112 \pm 0.165 | |
| Chlorophyll a (CHL)* | -0.037 \pm 0.009 | NI | | -0.197 \pm 0.043 | -0.201 \pm 0.065 | | 0.207 \pm 0.051 | -0.004 \pm 0.01 | |
| CHL gradient (CHLG)* | 0.042 \pm 0.009 | 0.023 \pm 0.006 | | 0.051 \pm 0.009 | NI | | NI | 0.039 \pm 0.011 | |
| Sea Surface Temperature (SST)* | 0.156 \pm 0.031 | 0.155 \pm 0.027 | | 0.292 \pm 0.087 | 0.545 \pm 0.296 | | -0.161 \pm 0.051 | 0.033 \pm 0.014 | |
| SST gradient (SSTG)* | NI | -0.01 \pm 0.007 | | -0.061 \pm 0.012 | 0.131 \pm 0.043 | | -0.282 \pm 0.101 | -0.324 \pm 0.118 | |
| Sea Level Anomaly (SLA)* | -0.048 \pm 0.009 | -0.009 \pm 0.006 | | -0.026 \pm 0.007 | -0.131 \pm 0.064 | | 0.071 \pm 0.017 | -0.051 \pm 0.018 | |
| SLA gradient (SLAG)* | -0.028 \pm 0.01 | -0.01 \pm 0.006 | | -0.017 \pm 0.008 | -0.217 \pm 0.088 | | NI | -0.407 \pm 0.187 | |
| Wind Speed (WIND)* | NI | NI | | NI | NI | | NI | NI | |
| Bathymetry (BAT) | NI | NI | | NI | NI | | NI | NI | |
| BAT gradient (BATG) | 0.166 \pm 0.032 | 0.181 \pm 0.035 | | 0.599 \pm 0.358 | 0.225 \pm 0.061 | | 0.21 \pm 0.052 | 0.269 \pm 0.076 | |
| Distance to colony (COLONY) | 0.029 \pm 0.01 | NI | | 0.485 \pm 0.235 | NI | | NI | NI | |
| C-index averaged model | 0.680 \pm 0.004 | 0.701 \pm 0.01 | | 0.693 \pm 0.015 | 0.601 \pm 0.034 | | 0.600 \pm 0.077 | 0.731 \pm 0.049 | |
| Mean (\pm SD) | | | | | | | | | |
| Cross-validation | | | | | | | | | |
| Mean C -index (CI 95%) | | | | | | | | | |
| 70% test dataset | 0.651 (0.644–0.657) | 0.638 (0.621–0.654) | | 0.590 (0.565–0.614) | 0.777 (0.717–0.852) | | 0.620 (0.563–0.710) | 0.736 (0.682–0.783) | |
| 30% test dataset | 0.647 (0.632–0.662) | 0.618 (0.580–0.658) | | 0.554 (0.503–0.605) | 0.717 (0.600–0.828) | | 0.559 (0.453–0.656) | 0.656 (0.590–0.725) | |
| Models within 95% confidence set | 3 | 13 | | 14 | 10 | | 27 | 59 | |

(mean: 251 h, range: 63–559). The tracking data revealed that a core marine area surrounding Crozet that extended to the west (~1400 km from west to east and ~300 km from north to south) was exploited by 6–113 wandering albatrosses between the South Subtropical Front and the Subantarctic Front (green area surrounding Crozet, Fig. S2, Supporting information). In addition, at least two birds visited a large buffer area surrounding Crozet and Kerguelen (yellow area, Fig. S2, Supporting information).

MODELLING THE SEASCAPE–TIME SPENT PER AREA

A total of 149 foraging trips from Crozet were analysed corresponding to 23 021 observations (86% to incubation, Fig. 1a). For incubation, the model with the lowest AIC included all ‘non-correlated’ environmental variables, whereas during brooding only SST and bathymetric gradient (BATG) were included. Since these two models yielded an Akaike weight of 0.85 and 0.240, respectively, and some model uncertainty was present (3 and 13 models in the 95% confidence set for incubation and brooding, respectively), a model averaging approach was applied. For both breeding stages, averaged models showed a reasonable model performance (*C-index* values) and SST and BATG had the strongest positive effect on time spent (based on the sign of averaged coefficients, Table 2). These results indicated that wandering albatrosses from Crozet spent more time in areas of high bathymetric variability such as shelf-breaks and seamounts during both breeding stages, which corresponded to subtropical waters during incubation and to sub-Antarctic waters during brooding (Kruskall–Wallis test for incubation $H_{3,8227} = 2408.36$, $P < 0.001$; Kruskall–Wallis test for brooding $H_{2,1216} = 192.08$, $P < 0.001$, Fig. 2). Overall, our model predictions showed an increasing trend of time spent from Antarctic to subtropical waters.

Model predictions matched observed patterns within the range of wandering albatrosses and identified pelagic areas beyond the training dataset where albatrosses might spend more time in the southern Indian Ocean: areas surrounding sub-Antarctic oceanic breeding colonies, the Southwest Indian Ridge (N-NW sector of Crozet), and seamounts such as Del Cano Rise (E of Prince Edward Islands) and the seamount complex of Ob and Llena south of Crozet and Kerguelen (bluer areas, Figs 1a and 3a). Those areas were consistently identified as important during incubation (low SD in predictions), whereas the marine area associated with the retroflexion of the Agulhas Current was especially variable, in response to the highly dynamic nature of this frontal system (which was not detected during brooding; Fig. 3a). The *C-index* values of the cross-validation indicated that averaged habitat models from Crozet had the ability to predict time spent patterns from Kerguelen (Table 2).

MODELLING THE FORAGING HABITAT–ZONES OF INCREASED FORAGING INTENSITY

Foraging behaviour was recorded for 122 birds from Crozet totalling 5716 observations (82% corresponding to incuba-

tion; Fig. 1b). Chlorophylla (CHL), SST and BATG were common to both models with the lowest AIC, in addition to distance to the colony (COLONY) during incubation and SSTG, sea level anomaly (SLA) and SLA gradient (SLAG) during brooding. Since these two models yielded an Akaike weight of 0.136 and 0.395 and model uncertainty was present (14 and 10 models in the 95% confidence set for incubation and brooding, respectively; Table 2), models were averaged. During incubation, averaged models showed a reasonable model performance (but poorer predictions for brooding) and BATG and SST (in addition to COLONY during incubation) had the stronger positive effect on albatrosses foraging probability (Table 2). Thus, foraging might occur within the same oceanographic context where albatrosses spent more time, but was more constrained by the distance to the colony (compared Fig. 1a,b). Also, all wandering albatrosses searched for prey more intensively in subtropical waters during incubation, but with no preference between sub-Antarctic or Polar Frontal Zone waters (shorter trips) during brooding (Kruskall–Wallis test for incubation $H_{3,8227} = 1274.70$, $P < 0.001$; Kruskall–Wallis test for brooding $H_{2,1216} = 186.95$, $P < 0.001$, Fig. 2). Predicted foraging habitat not only matched the spatial location of predicted seascapes, but also the stability of pelagic habitats: stable around main breeding colonies, seamounts and mountain ranges, in contrast to the dynamic habitat related to the Agulhas retroflexion current (compared Fig. 3a,b). The cross-validation output indicated that foraging patterns from Kerguelen were better predicted during brooding than during the incubation period (Table 2).

MODELLING THE FEH–PREY CAPTURE

A total of 34 independent breeders were equipped with STT yielding 754 observations (31% during incubation; Table S1, Supporting information) within the shelf area of Crozet (green areas, Fig. 1c). Models with the lowest AIC values included SSTG for both breeding stages, in addition to SLAG and BATG during brooding. Since these models had an Akaike weight of only 0.068 and 0.148 for incubation and brooding, models were averaged and the 95% confidence set was comprised by 27 and 59 models, respectively (Table 2). Averaged feeding habitat models yielded poor predictions for incubation, independently of the very reasonable predictions for brooding. SSTG and BATG (in addition to SLAG during brooding) had the strongest negative and positive effect on albatross feeding probability during both breeding stages, respectively. Therefore, feeding occurred in areas of high bathymetric variability characterized by low SST variability within the Polar Frontal Zone during both breeding stages (Kruskall–Wallis test for incubation $H_{3,8227} = 462.10$, $P < 0.001$; Kruskall–Wallis test for brooding $H_{2,1216} = 336.37$, $P < 0.001$, Figs 2 and S3d, Supporting information). Again, averaged predictions highlighted similar key feeding areas of the wandering albatross for both breeding stages (Fig. 3c). Marine areas of high mesoscale activity yielded the strongest variability in predictions at 40°S related to the retroflexion of the Agulhas Front to the west

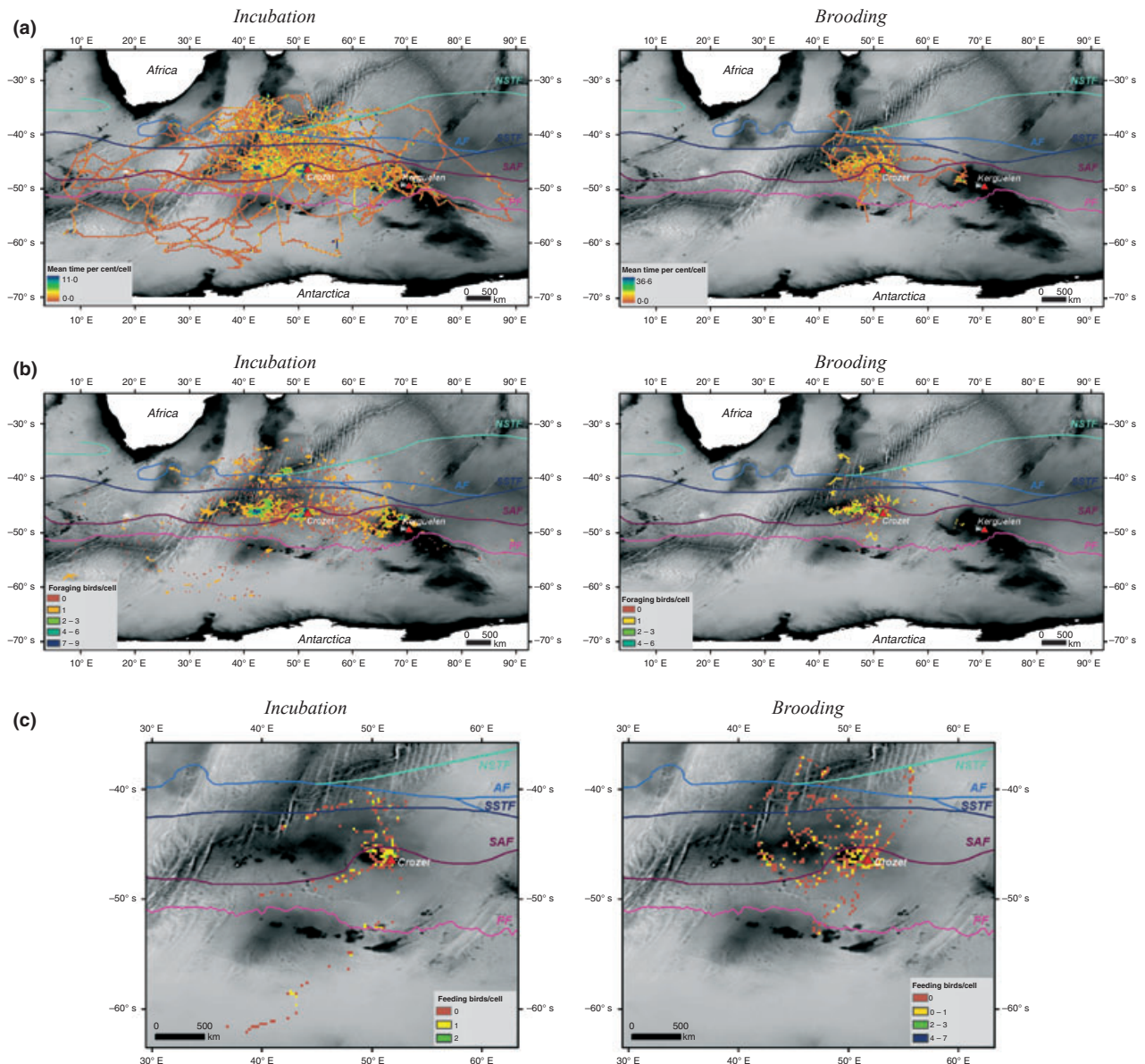


Fig. 1. Observed patterns of (a) time spent (mean percentage of time spent by all birds visiting each cell), (b) foraging (number of foraging birds in each cell) and (c) feeding patterns (number of feeding birds in each cell) of Crozet during incubation and brooding periods (1998–2008). Mean position of the main frontal systems (Agulhas Front: AF in blue; the North and South Subtropical fronts: NSTF in green and SSTF in dark blue, respectively; Subantarctic Polar front: SAF in fuchsia and Polar Front: PF in rose, respectively) are identified (Belkin & Gordon 1996). Studied breeding colonies are represented by red triangles.

and the South Subtropical Front to the east (see Figs 3c and S3). Predictions yielded poor values for incubation, but reasonable predictions for brooding (see cross-validation results in Table 2).

Discussion

Given their extraordinary movement capacities (Weimerskirch *et al.* 2000), the habitat modelling of this wide-ranging animal presents an exceptional and challenging opportunity to consider the dynamic nature of pelagic ecosystems. By combining three different quantitative ecological indices, this study offers a comprehensive ecological picture of marine habitat use of a

top predator and the first integrative spatially explicit ecological study of the wandering albatross with important conservation implications. Previous studies have focused on one of the applied methodologies (e.g. time spent—Hyrenbach, Fernández & Anderson 2002; FPT—Pinaud & Weimerskirch 2005), but none of them have developed an integrative modelling procedure.

LINKING ALBATROSS ECOLOGY AND AN INTEGRATIVE HABITAT MODELLING PROCEDURE

Wandering albatrosses have a distinct foraging strategy based on extensive movement at low cost, by travelling constantly

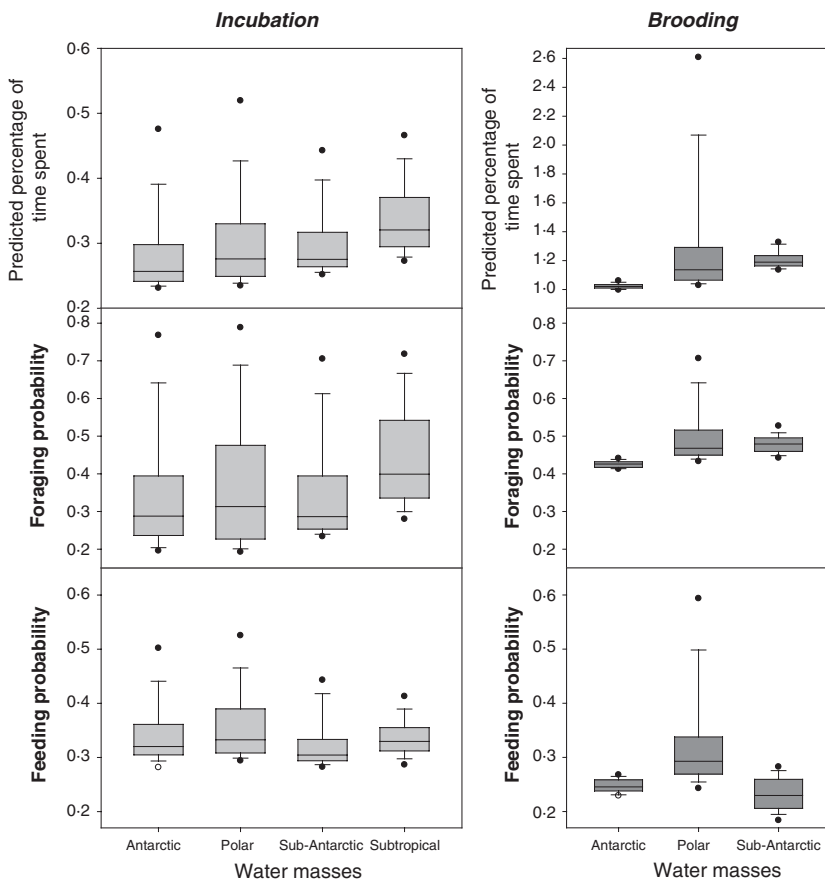


Fig. 2. Predictions (median, 25–75% interquartile range, non-outlier range, and outliers) of all three predicted habitats in relation to water masses during both breeding stages (subtropical: Subtropical Zone, sub-Antarctic: sub-Antarctic zone, polar: Polar Frontal Zone, and Antarctic: Antarctic zone; Park *et al.* 2002). Note the different y-axis scale of predicted percentage of time spent for both periods.

and quickly to maximize their probability of encountering isolated prey patches (Weimerskirch *et al.* 2000, 2005). Breeding albatrosses are typical central-place foragers that adjust their movements at various scales, from ocean basin (thousand of kilometres) to fine scales (100 m) in response to the oceanographic context (Fritz, Said & Weimerskirch 2003), i.e. the patchy and dispersed distribution of their main prey, squids (Weimerskirch, Gault and Chérel 2005, 2007). Moreover, the species uses two different foraging tactics: ‘foraging in flight’ and ‘sit and wait’, the former being the main and more efficient tactic (Weimerskirch *et al.* 2007). Taken together, this evidence underscores the fact that the species occupies a unique niche in the marine environment (Weimerskirch, Gault and Chérel 2005).

Our predictive habitat models reasonably matched the observed distribution patterns and described albatross multi-scale habitat use with the expected hierarchical arrangement of marine resource distribution: small scale feeding habitat nested within larger scale habitats (Fauchald & Tveraa 2003). Results for time spent and foraging patterns were similar, indicating that albatrosses foraged over topographic features in subtropical waters, and nested within the wider seascape due to the constraint imposed by the colony effect. Prey searching behaviour along the shelf-break (Weimerskirch *et al.* 2007) confirms the importance of this topographic feature as foraging ground of the species. Since foraging behaviour spatially overlaps with areas where albatrosses spent more time, one could hypothe-

size that they invest time in areas where they search for prey. The hierarchical system is usually used to describe prey patch arrangement, which supports the use of the wandering albatross as an ecological indicator species (Chérel & Weimerskirch 1999).

One of the main contributions of this study to the ecology and conservation of pelagic top predators is the capacity to predict key pelagic habitats in the near future or when data are not available for specific years (Guisan & Zimmermann 2000). Kernel analysis is the traditional method for the identification of key habitats, drawing probability contours of equal density from the tracking locations (Worton 1989), but it does not allow the prediction of potential habitats. Thus, developing habitat suitability models can overcome these limitations and improve our current knowledge on species distribution. However, this approach must be considered cautiously because it assumes that the habitat associations defined for specific conditions can be extrapolated to non-sampled areas. Our cross-validation exercise showed the general ability of averaged models to predict the distribution patterns of wandering albatrosses in two closely related populations, but also revealed the wide distribution range of the species and high inter-individual differences (i.e. relative low *C-index* in some cases). Species with less restricted ecological requirements and/or distribution ranges can be modelled less accurately than species with more restricted requirements/ranges (Segurado & Araújo 2004).

PELAGIC HABITATS OF WIDE-RANGING ANIMALS

Understanding the movement patterns and habitat associations of these highly mobile organisms is critical to the effective monitoring and implementation of conservation measures. Our tracking study highlighted that the core distribution area of breeding albatrosses was restricted on average to ca. 1200 and 450 km during incubation and brooding, respectively. This core area was limited by both the South Subtropical Front and the Sub-Antarctic Front in the north and south, respectively (Weimerskirch *et al.* 2005). Although the pelagic habitats of wandering albatrosses changed between incubation and brooding, the foraging strategies and total mass of prey captured did not, which indicated that birds used similar foraging strategies, and that prey availability was probably similar in both stages (Weimerskirch, Gault and Chérel 2005).

Overall, both static and dynamics variables were involved in explaining multi-scale habitat use of the species, with important implications for delineation of MPAs. Within the breeding range, three topographical features were identified as key pelagic habitats: marine areas surrounding sub-Antarctic oceanic breeding islands (Prince Edward Islands, Crozet, Kerguelen and Heard), seamounts (Ob and Llena south Crozet; Del Cano Rise between Crozet and Prince Edward) and submarine mountain ranges (Southwest Indian Ridge). Two oceanographic variables (SST and BATG) directly drive key habitats of wandering albatrosses, which were consistently identified across breeding stages and years. This could be explained by the fact that these topographical features promote the confluence of the main frontal systems not only in the Crozet and Kerguelen Basins, but also in the Southwest Indian Ridge (Park *et al.* 2002). These convergence zones are areas of strong mesoscale activity, where primary productivity is higher and intense upwelling/downwelling processes occur (Nel *et al.* 2001; Park *et al.* 2002). Within these convergence zones, high aggregations of prey occur, and they have been identified previously as high conservation areas for seabirds (Harris *et al.* 2007). In the Southern Ocean, the association of top predators with frontal systems influenced by bathymetric features has been well documented and seems to be a major feature driving top predator distribution within this biogeographic area (Nel *et al.* 2001). Finally, the position of the retroflexion of the Agulhas current showed the strongest variability in predictions, suggesting substantial inter-annual variability of the habitat preference in this area. All these results underline the importance of considering the dynamic nature of pelagic habitats when planning conservation initiatives to protect highly mobile animals.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

The identification of key marine areas (e.g. foraging areas and migration corridors) might be a priority action for the conservation of a given species or community (Hooker & Gerber 2004). However, a precondition for this is to establish standard guidelines in order to similarly collect and analyse distribution

data that allows comparison of key habitats of different oceanic species on a global scale. Based on our integrative habitat modelling procedure (especially model evaluation) and the ecological context of each habitat use, the wider time spent per unit area might be the most useful ecological index for conservation purposes, since it integrates different habitat uses.

Once the location and extent of key top predator habitat areas are identified, it is necessary to ensure their legal protection (Louzao *et al.* 2009). Currently, different international conservation agreements force governments to protect 20–30% of all marine habitats under their jurisdiction (i.e. Economic Exclusive Zones – EEZs) by 2012 (Lombard *et al.* 2007). However, seabirds are not subjected to any specific spatially explicit conservation initiative in the southern Indian Ocean and most of the current regulations are associated with the management of fisheries (Game *et al.* 2009). The distribution of wandering albatrosses breeding in Crozet and Kerguelen overlaps with three different RFMOs: the Indian Ocean Tuna Commission (IOTC), the Commission for the Conservation of Southern Bluefin Tuna and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), as well as the Illegal, Unregulated and Unreported fishing (IUU, Fig. 3). Wandering albatrosses spend most of their life travelling across the Southern Ocean encountering different RFMOs and IUU fleets (Weimerskirch *et al.* 1997), the latter representing the major portion of the annual seabird bycatch (BirdLife International 2009).

Our results provide two key conservation and management tools: (i) the first map to support development of a prospective network of priority conservation zones (marine Important Bird Areas) across the southern Indian Ocean; and (ii) habitat suitability models for tracking changes in the distribution of a given species. By plotting habitat predictions, a prospective network of pelagic sites can be planned that could encompass marine areas surrounding sub-Antarctic oceanic breeding islands (Prince Edward Islands, Crozet, Kerguelen and Heard), seamounts (Ob and Llena south Crozet; Del Cano Rise between Crozet and Prince Edward) and submarine mountain ranges (Southwest Indian Ridge). Our results match well with the recently created Prince Edward Islands MPA (the first MPA within the distribution of the species; Lombard *et al.* 2007). This protection could be expanded to other key pelagic habitats. A network of important protected sites could be used not only to support conservation of top predators (with important implications for fishery and ecosystem management), but also the underlying biodiversity associated with key habitats of top predators in the pelagic realm (e.g. Louzao *et al.* 2006, 2009). These pelagic habitats are important within certain sea surface temperature conditions and their boundaries might be tracked based on water mass distribution (i.e. SST), which is already an essential tool of the spatial management of certain fisheries (e.g. Hobday & Hartmann 2006). The association of wandering albatrosses with dynamic oceanographic variables reflects the importance of dynamic, spatially explicit conservation initiatives for oceanic top predators. Finally, present habitat

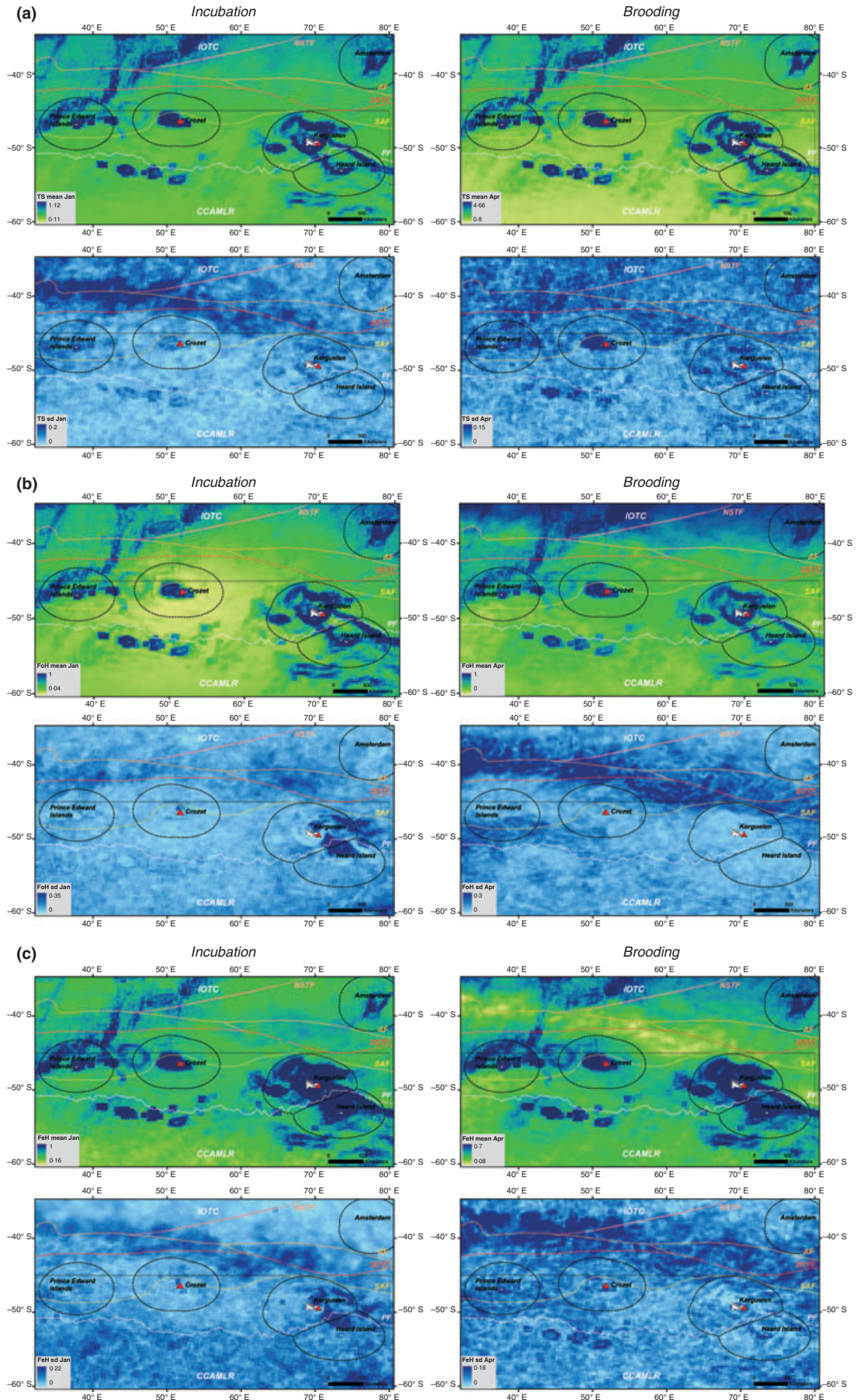


Fig. 3. Mean (\pm SD) predictions of habitat models (upper and lower panel, respectively) for (a) time spent (TS), (b) foraging habitat (FoH) and (c) feeding habitat (FeH) during incubation (January) and brooding (April) stages (left and right panel, respectively) over the 11-years study period (1998–2008). We also highlighted the main management units: EEZs (lines of black dots) are shown surrounding main oceanic islands (Prince Edward Islands, Crozet, Kerguelen, Heard Island and Amsterdam, from west to east) and Regional Fisheries Management Organizations (IOTC: Indian Ocean Tuna Commission, CCAMLR: Commission for the Conservation of Antarctic Marine Living Resources). Mean position of the main frontal systems (Agulhas Front: AF in orange; the North and South Subtropical fronts: NSTF in rose and SSTF in red, respectively; Subantarctic Polar front: SAF in yellow and Polar Front: PF in white, respectively) are identified (Belkin & Gordon 1996). Studied breeding colonies are represented by red triangles.

suitability models are useful to predict trends in key pelagic areas of wandering albatrosses during the next decades in a global change scenario. In a wider context, our integrative modelling approach is applicable to a wide range of species for habitat conservation in both marine and terrestrial environments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of the tracking procedures.

Table S2. Summary of pair-wise correlation analysis of environmental variables.

Figure S1. Workflow of the habitat modelling procedure.

Figure S2. Number of birds visiting each 0.25° cell from Crozet and Kerguelen Islands.

Figure S3. Mean (\pm SD) of different oceanographic variables averaged over the 11-year study period (1998–2008).

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