

The seasonal distribution and habitat use of marine top predators in the southern Indian Ocean

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Introduction

The Southern Ocean, spanning around 10% of the world's ocean surface, includes some of the most productive marine regions of Earth and is a critical component of the global marine ecosystem (Grant *et al.* 2006). Despite its perceived isolation the region is coming under increased pressure from climate change (Chown & Froneman 2008, Walther *et al.* 2002), overexploitation (Constable *et al.* 2000) and pollution (Ryan & Moloney 1993). Protected areas are being used as a tool to safeguard terrestrial and coastal systems worldwide, but the pelagic realm is sorely underrepresented (Game *et al.* 2009). This has driven the global call for the identification of a representative network of high seas marine protected areas (MPAs) (Hislop 2007). However there are several barriers to overcome in designating and managing high seas MPAs, not least of which are accounting for often highly mobile pelagic species and the ephemeral features they target (Game *et al.* 2009). Surveying such a vast expanse of ocean to provide information for the placement of MPAs is logistically and financially difficult. However the suite of marine top predators which return to land in order to breed and moult (i.e. seabirds and seals) can provide an accessible window on the ecology of pelagic regions. Marine top predators are themselves in decline, producing cascades down the trophic levels (Heithaus *et al.* 2008), and are thus an appropriate keystone species to target for MPA designation.

The Prince Edward and Crozet island groups are home to globally important colonies of marine top predators (Condy 1981, Chown *et al.* 1998, Guinet *et al.* 1994, 1996, 1999, Crawford *et al.* 2003a, Ryan & Bester 2008), several of which are listed as threatened (IUCN 2008). These seabirds and seals utilise the surrounding oceans both inside and outside the EEZs of South Africa and France, bringing them into contact with legal fisheries and unlicensed vessels operating in the area. They can be affected either directly (through bycatch, entanglement, ingestion of debris and pollution) (Weimerskirch *et al.* 1997, Kock 2001, Nel *et al.* 2000, 2002, Barbraud *et al.* 2008) or indirectly (competition for resources) (Gremillet *et al.* 2000, Ainley & Blight 2009) by fishing activities.

Seabirds and seals tracked in the region have been shown to target oceanographic features such as sea mounts, frontal systems and eddies (e.g. Bost *et al.* 1997, Jonker & Bester 1998, Nel *et al.* 2001). These biological "hotspots" are expected to be areas of high productivity, indicative of ecosystem

linkages between trophic levels (Sydeman *et al.* 2006), and their identification is thus vital for the management of less easily surveyed ecosystem components. There is much evidence that the foraging areas of the colonies overlap, and that similar oceanographic features are being targeted. Weimerskirch *et al.* (2004) provided a brief characterisation of this overlap for wandering albatross *Diomedea exulans*, and in the same volume Weimerskirch & Nel (2004) discuss hotspots identified from breeding tracking data of seven species of procellariiform in the southern Indian Ocean. This latter analysis was limited by the skewed availability of tracking data from certain sites and species, and the lack of data from crucial stages of the life and annual cycles.

Changes to habitats brought on by fluctuating environmental conditions such as the El Niño Southern Oscillation (ENSO) and climate change have been shown to influence top predator populations in the Southern Ocean (Guinet *et al.* 1994, Crawford *et al.* 2003b, Weimerskirch *et al.* 2003, Inchausti *et al.* 2003, Barbraud *et al.* 2008, Ryan & Bester 2008). Grey-headed albatross *Thalassarche chrysostoma* in the region targeted ephemeral oceanographic features (Nel *et al.* 2001), and showed a considerable degree of inter-annual variability in their foraging site selection in the south Atlantic (Phillips & Croxall 2004). Similar changes in habitat selection and foraging location have been shown for Indian yellow-nosed albatross *T. chlororhynchos* (Pinaud *et al.* 2005) and Antarctic fur seal *Arctocephalus gazella* (Guinet *et al.* 1994, Lea *et al.* 2006). While tracking data can provide important insights into habitat selection and distribution during a particular season, the development of spatial habitat usage models allows the variability in habitat location together with changing climatic conditions to be examined.

The use of tracking data to reveal habitat preferences has increased with the availability of remote-sensed data, particularly in the marine environment where adequate surveying is expensive (Charrassin & Bost 2001, Guinet *et al.* 2001, Hyrenbach *et al.* 2002, Suryan *et al.* 2006, Bailleul *et al.* 2007). Tracking studies from the Prince Edward and Crozet Islands have been carried out since 1989, on at least 14 of the 22 species of penguin, albatross, petrel and pinniped breeding on the two island groups (Jouventin & Weimerskirch 1990, Bost *et al.* 1997, Jonker & Bester 1998, Catard *et al.* 2000, Nel *et al.* 2000, 2002, Bailleul *et al.* 2005, Pinaud & Weimerskirch 2007, R. Crawford unpubl data, M.N. Bester unpubl data). Here we attempt to answer some of the key questions concerning the at-sea distribution of top predators in the south-west Indian Ocean, specifically the identification of preferred habitats utilised by populations from the two island groups and the effects of seasonal and inter-annual climatic changes. By examining these using remote tracking data from a representative suite of top predators from both island groups, the study aims to provide recommendations for the better spatial protection of these species and the ecosystem as a whole.

Methods

Study Area

The region of the south-west Indian Ocean this study concentrates on includes two groups of Subantarctic islands - the Prince Edward Islands in the west and the Crozet Archipelago to the east (Fig. 1). The islands lie between the Subtropical Convergence to the north and the Antarctic Polar Front to the south with the Subantarctic Front meandering between the two, placing a considerable temperature gradient within range of seabirds and seals foraging from the islands. In addition several bathymetric features contribute to the oceanographic complexity of the region: the southern end of the Southwest Indian Ridge, known as the Andrew Bain Fracture Zone, forces the Antarctic

Circumpolar Current through a narrow gap, where it speeds up and produces mesoscale turbulence which traverses the islands (Lutjeharms & Ansorge 2008). Joining the two island groups is the Del Cano Rise, which serves to channel the Subantarctic Front north of the Crozet Plateau, weakening it and forming eddies which allow the development of phytoplankton blooms on the Crozet Plateau (Venables *et al.* 2007). These factors, and the development of warm eddies from north of the Subantarctic Front, and colder eddies from the Antarctic Polar Front, ensure that the range of oceanographic habitats available in the region is considerably higher than in other regions of the Southern Ocean (Nel *et al.* 2001, Lutjeharms & Ansorge 2008).

In terms of management much of the region (up to 30°S) falls within the convention area of CCAMLR, which has shown the most progress of all high-seas fishery management organisations in reducing incidental bycatch in its fisheries (Small 2005). The Exclusive Economic Zones (EEZs) of France and South Africa include potentially important habitats such as portions of the Subantarctic Front, Southwest Indian Ridge, Del Cano Rise and Crozet Plateau, and there have been efforts from France and South Africa to establish Marine Protected Areas within the EEZs of the Crozet and Prince Edward Islands (taaf.fr, Nel & Omardien 2008). However large areas of the Del Cano Rise and Southwest Indian Ridge fall outside both the EEZs and CCAMLR, and the waters of the Subtropical Convergence Zone are mostly unprotected, the only management coming from regional fisheries management organisations (RFMOs) primarily concerned with tuna fisheries.

Tracking data

For the Prince Edward Islands sufficient tracks were available for the development of habitat models for three species: wandering albatross *Diomedea exulans* (WA), subantarctic fur seal *Arctocephalus tropicalis* (SAFS) and sooty albatross *Phoebastria fusca* (SA). See Nel *et al.* (2002) for details on the deployment of PTTs on breeding wandering albatrosses at Marion Island. See de Bruyn *et al.* (2009) for details on the deployment of PTTs on lactating subantarctic fur seals at Marion Island. PTTs were deployed on adult sooty albatrosses on Marion Island during the final stages of breeding (April/May) in 2008 and 2009. The devices remained on the birds during the post-breeding migration and continued tracking until the batteries failed or they became detached.

The albatross tracking data were filtered as described in Taylor (2004). The filtering method used for the fur seals is described in de Bruyn *et al.* (2009). Tracks were split into foraging trips by identifying when the animal left and returned to the vicinity (< 100km) of the colony for more than 24 hours. For each foraging trip the time spent (in minutes) in each 0.25° grid cell was determined by assuming that the animal moved in a straight line at a constant speed between successive uplinks.

Environmental parameters

Satellite-derived response variables for the models were downloaded by month from BloomWatch (coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW360.jsp) (Table 1) and the gradients for bathymetry, chlorophyll-a (CHL-a), primary productivity (PP), sea surface height deviation (SSHD) and sea surface temperature (SST) were calculated using ArcGIS 9.2's Slope function. All grids were then standardised to a cell size of 0.25° using the Neighbourhood function in ArcGIS 9.2 and taking the median, as this is less likely to be influenced by outliers (Zar 1999). Distance to the colony was calculated as the great circle distance between the island and the centre of each 0.25° grid cell. The "wind_diff" variable, defined as the angular difference between the satellite-derived wind vector

and the average heading of all path sections of a trip for that period within each 0.25° grid cell, was calculated from each time spent grid. Appropriate environmental variables to include in each model were chosen based on probable biological relevance and availability concurrent with the tracking period. Although BRT models (see below) handle effects between predictors, a Spearman Rank cross-correlation analysis was performed for the environmental variables included in each model to aid interpretation of results.

Habitat models

The use of tracking data and satellite-derived environmental parameters to create models of habitat preference requires methods able to deal with presence-only data, non-linear relationships, missing environmental information and interactions between environmental parameters. Boosted regression trees (Elith *et al.* 2006, Leathwick *et al.* 2006) (BRT) are an ensemble method for fitting statistical models that have the advantages of using a tree-based method (accommodating different types of variables and missing data) while allowing them to model complex response surfaces by combining many simple models. They have recently been used to predict suitable habitat for a range of species from fish and corals (Pittman *et al.* 2009, Leathwick *et al.* 2006) to insects (Roura-Pascual *et al.* 2009, Duncan *et al.* 2009) and trees (Moisen *et al.* 2006), and perform well against more traditional methods such as GAM and GLM (Elith *et al.* 2006). The technique optimizes predictive performance by iteratively developing a large number of small regression trees from random subsets of the data. Each successive tree predicts the residuals from the previous tree to gradually boost the predictive performance of the overall model (Friedman 2002). Further advantages to the approach are that there is no need to pre-select or transform the predictor variables, and it is resistant to outliers.

Here boosted regression tree models were fitted in R (R Development Core Team 2009) using the *gbm* package (Ridgeway 1999) and *gbm.step* function written by Elith *et al.* (2008) to determine the optimal number of trees. A Poisson error distribution was assumed. Exploratory analyses comparing cross-validation deviance reduction were used to choose optimal settings for tree complexity, learning rate and bag fraction for each model, such that the optimal number of trees was over 1000 (Elith *et al.* 2008). Models were then simplified as described in Elith *et al.* (2008) in order to remove those terms with low predictive performance. Seasonal habitat suitability was predicted from monthly climatologies of the included environmental parameters obtained from BloomWatch. In the case of chlorophyll-a no climatology was available so the monthly means of the MODIS data from July 2002 to January 2010 (i.e. all available data) were substituted in the predictive maps. Where “wind_diff” was included as an explanatory variable four maps were created for each month, assuming the average heading in each cell to be 1) away from the colony, 2) towards the colony, 3) circling the colony in a clockwise direction and 4) circling the colony in an anti-clockwise direction. The final predictive map was calculated as the mean of these four grids.

Evaluating the models

Evaluation of presence-only models tends to be qualitative, as the statistics available are largely untested and not broadly accepted (Wintle *et al.* 2005). Models were examined for ecological realism of the fitted responses and variable selection and response were compared to similar habitat usage models where available.

Inter-annual variability

The models for each species were used to predict preferred habitat when the Southern Oscillation Index was particularly low (-2.7, February 1998) and high (+2.7, February 2008) (NOAA National Weather Service Climate Prediction Centre <http://www.cpc.ncep.noaa.gov/data/indices/soi>). The former period falls within the particularly strong 1997/98 El Nino event, the latter during the 2007/8 La Nina event.

Results

Tracking data

Breeding WA of both sexes were tracked during incubation (2 males and 2 females), brood/guard (4 males and 4 females) and late chick-rearing (5 males and 5 females). Two females' breeding attempts failed during chick-rearing and their tracks are not included in the model. Two successive years of tracking provided 13 tracks for lactating SAFS. Nine SA of unknown sex were tracked from late breeding through the post-breeding migration in two successive seasons. Totals of the resultant time spent grids are shown in Fig. 2, and Table 2 summarizes the total number of tracking hours for each species during each month.

Habitat models

The optimal settings used and results of the final models are presented in Table 3. Table 4 lists the environmental predictors for each species and their relative contributions to the initial (unsimplified) model.

Although distance to the colony explained more than 14% of the variance in each model, including this term in the predictive models tended to overshadow other seascape features (compare Figs 9 and 10). All animals tracked were breeders thus their choice of habitat was constrained by having to return to the colony. Large proportions of the populations of species breeding on Marion Island will be pre-breeders or non-breeders (up to 70% in the case of biennially breeding albatrosses such as WA and SA), and so the importance of this term to the species' as a whole, particularly during the non-breeding season for which no tracking data were obtained, was probably over-estimated. In addition, the aim of this study is to identify important foraging areas lying between the Prince Edward and Crozet Islands, a region which is within the breeding foraging distance of all the species examined. This term has thus been dropped from subsequent models.

Wandering albatross from Marion Island

Primary productivity and CHL-a were strongly correlated ($|r_s| > 0.5$) and so only CHL-a was included in the model. The only other strong correlation was found between wind speed and SST, but both variables were retained. After the removal of distance to the colony, bathymetry and the angle between the predominant wind direction and the average heading had the highest relative contributions to the model (Table 4). Variables indicating the presence of fronts or ocean productivity were the least important overall and were removed in model simplification. Partial responses of the variables included in the simplified model for WA show a preference for high speed tail or side winds, along plateaus or sea mounts and warmer waters with low oceanographic variability (indicated by SSHD gradient) (Fig. 3). However these graphs are not perfect

representations of the effects of each variable if there are strong correlations or interactions in the data (Elith *et al.* 2008). An examination of variable interactions showed two strong effects (residual variance > 10): those between SSHD and bathymetry, and SST and bathymetry, revealing a preference for neritic zones when oceanographic variability is high and when sea surface temperatures are high (> 15°C) (Fig. 4).

Plotting the predicted habitat averaged over all seasons highlights a strong preference for bathymetric features such as the Crozet and Kerguelen Plateaus and the Southwest Indian Ridge (Fig. 10). Although the Del Cano Rise is of similar depth, only the Africana II Bank in the south-west and a region along the central northern shelf-break are predicted to be highly favourable year-round. The few areas highlighted that are not tied directly to bathymetric features include regions to the north-east of the Crozets and west of Kerguelen. Areas avoided are mainly the southern abyssal plains and the Crozet Basin.

Although the preference for plateaus and rises remains strong throughout the year, in the winter months the region to the north-east of Crozet increases in importance, together with an increased avoidance of the southern abyssal plains (Fig. 11). During this period selection across the Del Cano Rise becomes wider, a preference which moves south of the Rise during the summer months. Selection for the Africana II Bank is unaffected by this shift and remains high year-round.

Subantarctic fur seal from Marion Island

Environmental variables for the period SAFS were tracked showed a correlation between primary productivity and SST, but both were retained in the model. Lactating fur seals showed a preference for sea mounts/plateaus, warmer, less productive waters and milder zonal currents (Fig. 5). The relationship with oceanographic variability is less easy to interpret, with trends being bi-modal with SST gradient, inverse with primary productivity gradients, and weakly positive for SSHD gradients. The simplification process indicated a reduction in predictive performance with the removal of even a single predictor, and so all 10 predictors (with the exception of distance to the colony) were retained. However bathymetry and SST gradient had by far the largest relative contributions (Table 4), with primary productivity gradient, currents and SST being of secondary importance. Examination of interaction effects revealed strong relationships between SST gradient and both bathymetry and SST. Lower gradients were preferred in waters above 3000m depth, and higher gradients were absent at lower SST (<10°C) (Fig. 6).

Predicted favourable habitat over all seasons is strongly tied to the Del Cano Rise (Fig. 12), excluding the western section and the Africana II Bank but extending further off the shelf-break to the north-east. The Crozet Plateau and Conrad Rise are also favoured, with selection for deeper sections of the Conrad Rise. Strong selection for non-topographical features occurs primarily north of the gap between the Del Cano Rise and Crozet Plateau. Basins and abyssal plains are generally avoided, although regions south of Crozet and in the Crozet Basin show some selection.

Selection for bathymetric features remains relatively constant throughout the year (Fig. 13). However the importance of the region north of the Del Cano-Crozet gap fluctuates greatly, almost disappearing from September to December. A smaller region to the north-west of the Del Cano Rise shows preference in January and February, shifting further north in May and June before disappearing.

Sooty albatross from Marion Island

Correlation analysis showed a strong relationship between wind speed and SST, but again both predictors were included. Only five variables were retained after model simplification, with SST, wind velocity and relative wind direction having the largest proportional contributions (Table 4). Predictors indicating the presence of fronts and ocean productivity were dropped from the model with no reduction in predictive performance. The partial dependence plots indicate a bi-modal relationship with wind speed, and a preference for warmer, deeper waters (Fig. 7). However, probably because of the high correlation of the two, wind speed and SST showed a strong interaction (Fig. 6). Fig. 6 also shows the next-strongest interaction, between SST and SSHD.

In contrast to the above two species, the predicted habitat for SA shows an avoidance of plateaus and a selection for shelf slopes between 2000 and 3000m, including the southern edge of the Del Cano Rise and the western portion of the Southwest Indian Ridge (Fig. 14). Preference is also shown for a wide arc to the east of the Crozets which is not linked to a bathymetric feature. Otherwise the Crozet Basin and the southern abyssal plain are avoided.

Seasonal predicted habitat shifts dramatically throughout the year, with selection for the Del Cano region strongest during the winter months (Fig. 15). During summer preferred habitat moves south of the Del Cano Rise and to the east of the Crozets, with a variable region to the north-west of the Crozet EEZ emerging as favourable.

Inter-annual variability

The predicted distribution of preferred habitat between ENSO events changes dramatically for all three species (Fig. 16). For WA during the El Nino event the Marion-Crozet latitudes show high selection, with distribution concentrated over the Andrew Bain Fracture Zone to the west, the southern portion of the Del Cano Rise and the Crozet Plateau extending south down to the 4000m isobath. The Southwest Indian Ridge, Mozambique and Madagascar Plateaus show less selection than during an average February (Fig. 11). In contrast the La Nina habitat resembles the average, with selection in the Del Cano region concentrating on the Africana II Bank.

The location of preferred SAFS habitat in shows variation particularly over deeper waters. However selection for the Del Cano Rise and Crozet Plateau remain high. This contrasts with the average distribution for this time of year which is concentrated over the Del Cano Rise only (Fig. 13).

Predicted SA habitat during February for El Nino, La Nina and average years all show a band of favourable habitat along the southern slope of the Prince Edward Crozet Ridge, from the Southwest Indian Ridge in the west to a high concentration south-east of Crozet in the east, which is not highlighted in the average annual habitat (Fig. 14). During an El Nino year this band is predicted to be wider, extending to the southern edges of the Del Cano Rise. It contracts in average and La Nina years, with a break developing south of the Crozet Plateau, but is similar in overall latitudinal extent.

Discussion

Model performance

The albatross models matched well to the known foraging behaviour of these species while breeding:

Wandering albatross from Crozet were shown to have a dual foraging strategy during breeding, interspersing long looping pelagic flights with shorter commutes to nearby shelves (Weimerskirch *et al.* 1993, 1994). The course of the longer oceanic flights was determined wind direction (Weimerskirch *et al.* 1993), the energy expenditure of flight with tail and side winds being much lower than with head winds (Weimerskirch *et al.* 2000). Similar habitat preferences were observed in the South Georgia population of WA, where chick-rearing adults made local trips to neritic and slope waters and more distant searches to oceanic and slope regions (Phillips *et al.* 2009). These findings concur with the large contributions of wind and bathymetry to the habitat model (Fig. 3). The interaction between bathymetry and SST (Fig. 4) is probably related to the preference shown for the Southwest Indian Ridge north of the Subtropical Front. The range of sea surface height anomalies over neritic waters (Fig. 4) could result from the upwellings and eddies created as the Antarctic Circumpolar Current encounters the Southwest Indian Ridge and moves across the Prince Edward Islands .

The sooty albatross is viewed as one of the most oceanic of the albatrosses (Weimerskirch 1997), a habitat preference reflected well in the model by the large contributions of wind speed and SST (Fig. 7). Breeding birds tracked from Crozet foraged mainly in subantarctic waters north of the Polar Front, and did not appear to be tied to specific oceanographic features (Weimerskirch 1997, Inchausti *et al.* 2003, Pinaud & Weimerskirch 2007). Wind speed and direction were shown to be important in determining flight routes of the light-mantled albatross *P. palpebrata* (Phillips *et al.* 2005). Although the sooty and light-mantled albatross forage over different thermal zones, they are morphologically similar and it is expected that wind would impose similar constraints on their flight (Shaffer *et al.* 2001). Surprisingly the model identified a preference for shelf-slopes between 2000 and 4000m (Fig. 7), a relationship which has not been reported for the sooty albatross, although it was identified in light-mantled albatrosses tracked from South Georgia (Phillips *et al.* 2005).

In contrast to the albatross models, the habitat usage model for subantarctic fur seals showed much higher CV deviance while retaining all 10 environmental predictors (Table 2), although the contributions of only two of these (bathymetry and SST gradient) accounted for 38% of the variance. Lactating SAFS tracked from Crozet showed a similar preference for waters around 2000m in depth (Fig. 5), none leaving the Crozet Plateau during the two months of the study (Bailleul *et al.* 2005). However they appeared to concentrate in areas of high primary productivity, in contrast to the current model which shows a very weak relationship with primary productivity (although de Bruyn *et al.* (2009) assert that higher chlorophyll-a concentrations influenced the distribution of tracks used in this study). Georges *et al.* (2000) found that the foraging habitat of lactating female SAFS tracked from Amsterdam Island was associated with the Subtropical Front, and that changes in SST and SST gradient around the island affected diving activity and time spent at sea. The relative importance of these variables in the model thus appears justified (Fig. 5). de Bruyn *et al.* (2009) also found a preference for positive and negative SSHD, a relationship not mirrored in the model which shows selection for positive anomalies only. The interaction between SST gradient and bathymetry is clearly due to SST variability being low over the preferred Del Cano Rise, and the range of SST gradients found in warmer waters is probably a result of forays to the Subtropical Front (Fig. 8).

Model bias

The models presented here predict the known habitat choices of breeding animals well as they were based on tracks obtained from breeding (or in the case of SA from June onwards, post-breeding) individuals. In WA habitat selection has been shown to change through the breeding season (Weimerskirch *et al.* 1993). Although birds were not tracked over the entire breeding season (which lasts from January to December) each of the breeding stages is represented (Table 2) and so this should not have biased the habitat predictions. The tracking data for SA are from the end of the breeding season following birds into the post-breeding migration. Weimerskirch *et al.* (1987) assert that their foraging habits are as pelagic during breeding as non-breeding, but it is possible that, especially during the demanding brood/guard period, preferred foraging locations may alter and shift closer to the islands.

Less is known about the distributions of non-breeding adults and pre-breeders, which may comprise a significant proportion of the population. Post-fledging WA have been tracked from Crozet and were found to use areas north of the adults' ranges, showing a preference for warmer waters and lower wind velocities (Weimerskirch *et al.* 2006). Although these birds showed some selection for the Southwest Indian Ridge, distribution in the south-west Indian Ocean was concentrated over the pelagic waters of the Crozet Basin, in direct contrast to the distribution of breeding adults and the predicted habitat. The small sample of failed breeders occurring in this dataset (but not included in the model) suggest that non-breeding adult WA prefer the warmer waters of the Subtropical Convergence Zone, possibly due to intense competition with breeding birds closer to the colony (Nel *et al.* 2002). Geolocator tags were deployed on adult WA on Marion Island at the end of breeding and retrieved following the sabbatical year (P.G. Ryan, unpubl. data). The locational error associated with these data is an order of magnitude higher than that of the PTT data used in this study (Taylor 2004), but there is some indication that birds in the southern Indian Ocean preferred warmer waters, with no particular preference for bathymetric features other than the Southwest Indian Ridge immediately north of Marion Island and the northern slope of the Kerguelen Plateau. However overall adults on sabbatical spent almost 70% of their time within the south-west Indian Ocean, highlighting its importance for non-breeders as well. Currently no studies have examined the habitat preferences of non-breeding adult and juvenile sooty albatrosses, although a tracking study on juveniles is underway at Crozet (H. Weimerskirch, pers. comm.). A similar situation exists for SAFS.

An additional source of bias could arise from sexual segregation in habitat preferences, usually attributed to sexual dimorphism resulting in competitive exclusion or differing constraints on flight or diving ability (Shaffer *et al.* 2001, González-Solís *et al.* 2000a, Phillips *et al.* 2004, Hofmeyr *et al.* 2010, Boyd *et al.* 1998). This has been shown for WA (Weimerskirch *et al.* 1993, Weimerskirch 1997, Nel *et al.* 2002) but is unlikely to have affected the model presented here as the sexes are fairly evenly represented in the tracking data. SA also exhibit sexual dimorphism (Marchant & Higgins 1990), but genders of the tracked birds were unknown and so the effect sample bias (if there is a difference in habitat selection between the sexes) cannot be determined. Only female SAFS were tracked and it is not known whether males follow similar distributions. Antarctic fur seal *A. gazella* males in the Scotia Sea were found to forage further from the colony, diving deeper than females (Boyd *et al.* 1998). Although Antarctic fur seals utilise different habitats from SAFS, they target the same prey (Klages & Bester 1998, Makhado 2002, Bailleul *et al.* 2005) and are morphometrically

similar, so it is possible that male SAFS breeding on Marion Island have a different preferred habitat from that presented here.

In this study all breeding stages (and in the case of the albatrosses, all sexes) were combined to create a single habitat usage model for the species. However as the preferred habitat of a species depends to some extent on the status and gender of the individuals, there is an argument for creating individual models for each age class, breeding stage and gender, and combining the resultant predicted habitat weighted by the proportion of the population falling into each class. The small samples of tracking data available, and the lack of data for sections of the population, preclude this approach at present.

Seasonal and inter-annual variation

Changes in preferred habitat between the seasons was most marked in the sooty albatross (Fig. 14), with areas like the Crozet Plateau going from avoided during the summer to preferred in the winter months. This variation is not unexpected in an oceanic forager, although no studies have been published concurring with this prediction. The main ephemeral feature targeted by all three species appears to be the region bordering the Crozet Basin, along the northern and north-eastern edge of the Crozet EEZ. However the times of year when this region is preferred differ, with WA selection highest in June/July, and that of SA from July through to January, moving further south with each month. SAFS show some selection of this region for most of the year except summer. The feature could be associated with the channelling of the Subantarctic Front north between the Del Cano Rise and the Crozet Plateau, where it eventually spills into the Crozet Basin.

Comparing the El Nino/La Nina years (Fig. 16) again shows the most marked difference in SA. Here the predicted habitat for SAFS also shows high variability, probably due to the changing positions of ephemeral eddies/fronts, but preference for the main bathymetric features of the Del Cano Rise and Crozet Plateau is retained. By comparison the shift in WA habitat is minor. Although no empirical study has been conducted, Weimerskirch (2004) hold that if inter-annual differences in foraging locations of WA do exist they will be slight as birds are primarily influenced by wind conditions. They do note, however, that the presence of fisheries could influence distributions and these change from year to year.

Comparison of habitat preferences between Prince Edwards and Crozet populations

The wandering albatross colony breeding at Crozet has been the subject of intensive tracking studies spanning several years (Weimerskirch *et al.* 1993, 1994, 2000, 2006). Currently a habitat usage model based on this tracking data is being developed (Louzao in prep). Although a different method (Generalized Linear Mixed Models) is being used, comparisons between predicted habitat and the environmental variables influencing these predictions are possible. Louzao *et al.* (in prep) have identified SST gradient, SSHD gradient, SST, CHL-a, SSHD and bathymetry gradients .

As yet no other species breeding on both island groups has had habitat usage models developed, although this is underway for the rockhopper and macaroni penguins (J-B. Thiebot & C. Bost pers comm.). However de Bruyn *et al.* (2009) has noted some important differences in the foraging behaviour of subantarctic fur seals from the two populations: lactating Crozet seals feed close by the colony in short overnight trips, whereas seals from Marion Island travel further and their trips last

several days. The authors attribute this difference to the fast, unimpeded flow of water past Marion Island, which prevents the build-up of chlorophyll near the island (Hunt *et al.* 2001). On the other hand the shape of the Crozet Plateau and location predominantly west of the archipelago allows high chlorophyll concentrations to accumulate, supporting the myctophid fish which are the primary prey of these seals (Bailleul *et al.* 2005). Many top predators depend on such aggregations and concentrate their foraging effort along features where these aggregations predictably occur. Local differences in bathymetry could thus have an influence on the distributions of several species breeding on the islands.

Preferred habitats across all models

The environmental parameters with the greatest predictive power for all three species were distance to the colony, bathymetry, SST and, for the albatrosses, wind speed and direction (Table 4). Even the distribution of a supposedly oceanic forager such as the sooty albatross showed some relationship with bathymetry. Topographical features were also the most prominent preferred habitat averaged across all seasons, as would be expected (Figs 10, 12 and 14). Comparing the predicted habitats over an average year with those at the height of the 1997/98 El Niño and the 2007/2008 La Niña events shows this selection for bathymetric features to be relatively stable: for WA the Africana II Bank remains highly preferred; SAFS habitat is predicted over most of the Del Cano Rise, excluding the extreme southern and western edges; and SA prefers the southern shelf-break of the Rise, between 2000 and 3000m. (During the La Niña event SA preference did shift further south, but remained above the 4000m isobath (Fig. 16)). This connection with fixed bathymetric features provides an opportunity for the spatial management of an important habitat for top predators breeding on the Prince Edward and Crozet archipelagos. An often-quoted drawback of declaring MPAs on the high seas is the variability of habitats and the difficulty of adequately delineating a management area (Game *et al.* 2009).

Implications for conservation and MPAs

As mentioned earlier, the region of the south-west Indian Ocean encompassing the Prince Edward Islands and Iles Crozet includes a great diversity of habitats. This is reflected in the numbers of marine top predators utilising the islands for breeding: the Prince Edwards and Crozets collectively are home to approximately 70% of the world population of wandering albatross, 54% of king penguin *Aptenodytes patagonicus*, 33% of Indian yellow-nosed albatross, 27% of sooty albatross and 21% of the southern rockhopper penguin *Eudyptes chrysocome* (Gales 1997, Crawford & Cooper 2003, Woehler & Croxall 1997, Woehler 1993). Other seabird colonies of importance are grey-headed (16%) and light-mantled (13%) albatross, southern *Macronectes giganteus* (12%) and northern *M. halli* (14%) giant-petrels, macaroni penguin *E. chrysolophus* (15%) and many species of burrow-nesting petrels, the populations of which are difficult to estimate (Gales 1997, Ryan & Bester 2008, Ellis *et al.* 1998). 33% of the world population of subantarctic fur seals also breed on the islands (Ryan & Bester 2008, Guinet *et al.* 1994). While the highest densities of these species will occur within the EEZs many will be commuting to foraging grounds in international waters (Ryan & Bester 2008, Nel *et al.* 2001, 2002, Pinaud & Weimerskirch 2007, de Bruyn *et al.* 2009, Bailleul *et al.* 2005).

The three models presented here show wide differences in habitat selection, from primary preference for permanent bathymetric features to dependence on predictors indicative of

ephemeral features such as fronts and eddies. There is much evidence for niche specialization in marine top predators in the Southern Ocean (Cherel *et al.* 2006, 2007, Phillips *et al.* 2008, Pinaud & Weimerskirch 2007, Weimerskirch 1997), and foraging partitioning occurs between species with similar foraging ecology (e.g. northern and southern giant-petrels (González-Solís *et al.* 2000b), light-mantled and sooty albatrosses (Inchausti *et al.* 2003, Phillips *et al.* 2005), Antarctic and subantarctic fur seals (Bailleul *et al.* 2005)). In some species, especially those exhibiting sexual dimorphism, foraging ranges may differ between the sexes (Shaffer *et al.* 2001, González-Solís *et al.* 2000a, Hofmeyr *et al.* 2010, Boyd *et al.* 1998), and even between individuals of the same species, particularly during the non-breeding season when individuals appear to frequent “favoured” foraging grounds (Cherel *et al.* 2006, Phillips *et al.* 2005, 2008). However there is also evidence that these species target predictable resources, or “hotspots”, which may be permanent features such as seamounts and shelf-breaks or seasonal in nature such as upwellings, fronts and eddies (Weimerskirch 2007, Phillips *et al.* 2008, Bost *et al.* 1997, Jonker & Bester 1998, Nel *et al.* 2001). Certainly the predicted habitat for the three species presented here have in common at least one permanent (the Del Cano Rise, including its southern shelf-break) and one ephemeral (the southwestern edge of the Crozet Basin, north of the Crozet EEZ) feature in the high seas in close proximity to both island groups. Thus while it is impractical to protect the entire range of these highly mobile pelagic species, foraging grounds which are important to several species, particularly during the vulnerable and demanding breeding period, can be identified for future management. This is easier for bathymetric features as they are easily definable and usually limited in size. However the protection of predictable ephemeral features should not be overlooked, as there are species, such as the grey-headed albatross (Nel *et al.* 2001) which feed exclusively in these zones.

Acknowledgements

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