Evaluating distribution modelling using kernel functions for northern royal albatrosses (*Diomedea sanfordi*) at sea off South America

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Abstract Satellite telemetry can provide unique information on the biology and behaviour of mobile animals such as albatrosses. Determining areas of concentrated activity, essential resources and time-related changes in range use is of great importance for theoretical biology, practical conservation, and fisheries management. Utilisation Distributions (UDs), from a probabilistic model of the relative time spent by an animal in an area, were prepared using a kernel function in a Geographical Information System. Properties of the model were investigated, using satellite-tracking data from six northern royal albatrosses (*Diomedea sanfordi*) during eight over-wintering visits to seas off South America. We analysed UD areas and shape for different settings of the kernel smoothing parameter, a variety of location subsets associated with different sample sizes, sampling time periods and telemetry regimes. Small samples and intermittent transmission regimes reduced the UD range area. Individual bird data sets were combined to give comparable UDs. The UD model may help comparison of range areas and the identification of resource use, but they cannot identify an activity without additional information. For pelagic seabirds, UD preparation and interpretation require judgement and care.

INTRODUCTION
The oceanic distributions of seabirds are imperfectly known, but their areas of concentrated activity may be of special interest. Information from specimens, beach patrols, at-sea sightings, banding programmes and more recently, satellite telemetry, GPS and geo-location studies each produce different insights into these distributions. Telemetry studies provide unique new information on some of the areas used and may indicate concentrations of populations and species with important consequences for theoretical biology, practical conservation, and fisheries management (Salamolard & Weimerskirch 1993; Weimerskirch *et al*. 1993; Nicholls *et al*. 2002; Prince *et al*. 1998; Robertson *et al*. 2003a; Robertson *et al*. 2003b; BirdLife International 2004). Such seabird tracking studies have produced large datasets, typically from a limited number of individuals, which in some cases have been tracked intermittently for up to two years.

Raw tracking data sets consist of a time series of geographic locations (fixes). In one type of quantitative analysis this series of locations can be transformed into an estimate of the 'probability of occurrence' being the utilisation distribution (UD). Seaman & Powell (1996) define UD as "a probabilistic model of home range that describes the relative amount of time that an animal spends in any place" (see also Worton 1989, 1995). Such UD models use contours to map areas of equal probability of an animal's occurrence (Anderson 1982; Naef-Daenzer 1993; Seaman & Powell 1996). It is a quantitative and objective approach, designed to model an animal's use of space, changes in time, and the animal's response to spatial patterns of environmental variables (Naef-Daenzer 2000). The technique has been used to analyse and display the distribution and the presumed use of resources by albatrosses, including their implied relationship with fisheries (Weimerskirch 1998; Brothers *et al*. 1998; Wood *et al*. 2000).

Kernels and UDs are a powerful modelling tool, but their flexibility makes it necessary to adjust the analysis to the hypothesis being tested. The kernel is the shape placed over each location. The

process of summing the kernels creates a measure of abundance, either as a density, or the probability of occurrence across the range (BirdLife International 2004). A utilisation distribution (UD) map is produced by drawing contours around calculated areas of equal density where the contours include the area of a given probability of finding the animal. We investigated some of the complexity and power of kernels and UDs using a set of satellite telemetry locations from six non-breeding northern royal albatrosses (*Diomedea sanfordi)* off South America and far from their breeding colony in New Zealand. Examples are provided to illustrate the flexibility of the method, along with some suggestions for optimal applications when using satellite telemetry data.

METHODS
Kernel analysis
Non-parametric methods that make no assumptions about an underlying stochastic process are an improvement on parametric methods for mapping and analysing an animal's range (Worton 1989, 1995). One such method is a kernel function producing a utilisation distribution (UD) as the grid or contour map of calculated areas of equal density showing a given probability of finding the animal. The process does not require that the data be serially independent (also called time-dependent or auto correlated). These data are typically obtained from satellite and radio tracking experiments (DeSolla *et al.* 1999).

The model UD is constructed by placing a kernel over each location, replacing each location point with a probability distribution (e.g. a bivariate Gaussian distribution of a volume of 1). Subsequently, the kernel probabilities are summed for the total UD. For technical reasons, these sums are calculated only at the intersections of a grid laid over the study area. The matrix of densities is then used to interpolate contours of equal density. The grid layout has no effect on the outcome of the model, provided that the size of the grid cells is smaller than the area covered by the kernel. It is possible to use a kernel function matching the precision of the location where that is known (as is the case for this set of Argos satellite locations; Nicholls *et al.* 2003). Alternatively, different shaped kernels e.g. bivariate normal Gaussian, adaptive or truncated Gaussian, or cylindrical kernels may be used and the x-y components of the variance can be made equal (Worton 1989; Naef-Daenzer 1993).

The most important parameter is the smoothing (or bandwidth) set by the user. The smoothing effect of kernel estimations is adjusted for the purpose of each analysis (e.g. finding the range extent requires smoothing, while the identification of core areas requires little smoothing), and there is no simple objective criterion. Smoothing depends on the bandwidth or '**h**' parameter. A smoothed version at the 'ad hoc' level (which is a quickly-calculated approximation according to kernel theory to estimate the least-squares cross-validation level (LSCV) of smoothing) can provide a measure of the extent of the UD for an animal's home range (Burt 1943), but conceals many details in range use. A lightly smoothed version (at ~0.1 of LSCV) identifies concentrations within the home range, and so may potentially identify the locations or resources intensively favoured by the animal. These kernel details should be reported to facilitate comparison between studies and allow quantitative comparison between an animal's centres of activity and environmental factors.

Study species and data sets
Northern royal albatrosses are a biennial breeder nesting mainly at the Chatham Islands and with a small mainland colony at Taiaroa Head, near Dunedin, New Zealand. Initially, one northern royal albatross was investigated off South America during the non-breeding part of its biennial cycle. For the main part of this study, we used a dataset of 548 locations obtained in 1996. The bird (failed breeder 21316) was tagged with a CLS : Argos system satellite transmitter (PTT) at its breeding colony on Middle Sister Island, Chatham Islands, and was tracked over a four-month period from New Zealand to the Patagonian shelf, east of South America (Nicholls *et al.* 2002). The PTT was programmed to transmit every 84 seconds for 25 hours (on), followed by 23 hours with no transmissions (off). From day one approximately 10 locations were received on odd-numbered days, followed by 0-2 locations on the next day. This cycle was available for 110 days, beginning 21 March 1996. Smaller data sets were obtained for seven other visits off South America by immature pre-breeders (2) and failed breeders (3) (Table 1).

The local time was calculated from Coordinated Universal Time (UTC) by correcting for longitude. The 'day-night' portions of the day (examples arbitrarily selected with the day period equalling 0700 h to 1800 h) were calculated using this local time. The travel speed to each location was calculated using the great circle distance and time between two locations. As speeds measured over too-short or too-long a period are subject to large errors, so only records where the time interval between successive locations was >1 h and <4 h were selected.

A Lambert equal-area azimuthal projection, centred on the South Pole with 60°W as the standard meridian, was used for mapping. After experimenting with a range of smoothing between two times and 0.1 of the LSCV value of **h** = 78 293 m; a rounded LSCV value, **h** = 80 000 m, was used

Table 1 Yearly datasets of Argos locations of northern royal albatross (*Diomedea sanfordi*) and kernel areas for the range ($p = 95\%$) and core ($p = 50\%$) areas using a single smoothing value, $h = 40$ km, for all samples. To allow comparison with the different transmitter regimes, four datasets (*) were reduced to simulate a portion-of-one-day on every six days to match the sampling regime for the other data sets. RR = PTT transmission repetition rate.

Bird			Transmitter					Full datasets								Every 6th day set or subset (*)			
ID #	Sex	Status	Location	Type	RR	On	Off	Period		Dur-ation	No. Locs. $n =$	Locs. / day	h	Kernel Area (1000 km²)		No. Locs. $n =$	h	Kernel Area (1000 km²)	
					sec	hrs	hrs			days			km	95%	50%		km	95%	50%
21316	F	Failed breeder	Sisters I	ST10	84	25	23	21-Mar-96	30-Jun-96	101	548	5.4	40	364	16	155 *	40	300	26
23738	M	Failed breeder	Sisters I	ST10	90	9	135	15-Feb-97	3-Aug-97	169	119	0.7	40	179	18	119	40	179	18
26590	F	Failed breeder	Sisters I	ST10	90	9	135	21-Feb-97	2-Sep-97	193	155	0.8	40	294	28	155	40	294	28
23738	M	Failed breeder	Sisters I	ST10	90	9	135	14-Jan-98	23-Jul-98	190	207	1.1	40	278	38	207	40	278	38
26593	M	Failed breeder	Taiaroa Head	ST10	77	6	66	24-Feb-98	10-Sep-98	198	618	3.1	40	123	20	113 *	40	140	19
26590	F	Failed breeder	Sisters I	ST10	90	9	135	25-Feb-98	5-Jul-98	130	113	0.9	40	222	26	113	40	222	26
21805	M	Pre-breeder	Taiaroa Head	MT pico	80	8	140	9-Apr-98	21-Aug-98	134	114	0.9	40	339	31	59 *	40	246	27
6750	F	Pre-breeder	Taiaroa Head	ST10	88	6	33	18-Apr-98	24-Oct-98	189	495	2.6	40	107	6	154 *	40	155	6
Mean											296			238	23	134		227	23
sd														96	10			63	9

for comparisons. The standard 95% (range) and 50% (core) probabilities were prepared with additional probabilities calculated for selected figures. The model UDs were calculated by using Animal Movement Extension (AME) v2 (Hooge *et al.* 2002), a software tool from the Geographical Information System Arc View 3.2.

The **h** parameter is expressed as length and its unit in AME is set with the Distance Unit of the View Properties. Random samples of locations were generated with AME using Random Selection (without replacement), and the various location subsets using its Query capability. For the smaller random samples, we made 5-10 repeats. The relationship between sample size and 95% areas was quantified using a hyperbolic function, $y = a-b/x$, where a estimates the asymptote for 'infinite' sample size.

If the locations are presented on a mapped projection then an equal area projection is appropriate. For small geographic areas (mammalian home ranges) a Mercator projection suffices, however the enormous area used by an albatross requires an equal-area projection; this meets the requirements of most kernel software for Euclidean coordinates, and was used here.

A random sample of the animal's range use and activity was not obtained from Argos with transmitters operating on an intermittent-transmitting regime. The actual data received depends on the transmitting times of the satellite tag (PTT), the available reception by the satellite, the quality of the record received, and the time since the previous location. Simulations by leaving out days from this original data set provide such a reduced data set, and the user can be assured that the data received after more than a day's gap in transmissions are the same as that obtained after just one day without reception (CLS : Argos FAQ). This technique was used to reduce the best transmitting regimes to a lowest common regime for three birds (21805, 6750 & 26593) as it was for the simulations for the subsets of bird 21316. The same smoothing **h** = 40 km (Table 1) was applied to all the data sets comparing UDs between birds, being our assessment of ranges which did not encompass land areas.

RESULTS
Effect of smoothing on range area or shape
The effect of the smoothing bandwidth **h** was investigated using the best location dataset (from bird 21316). Using the LSCV value as a starting point, utilisation distributions were derived for that value, and for multiples and fractions of it. The modelled representations produced by different amounts of smoothing are different, with the 95% range areas covering from 81 000 to 1 157 000 km^2 (Appendix) and between one and multiple of fragments within the range (Fig. 1A-D, Appendix). Over-smoothing (**h** > 0.5*LSCV; Fig. 1A) resulted in a poor representation of the range by including areas beyond those recorded for the bird. With under-smoothing (**h** < 0.1*LSCV; Fig. 1D) the result differs little from the point pattern and may emphasise areas where there was a higher-than-average number of observations (i.e. sampling artefacts). Between these modelled extremes lies an appropriate choice for a given hypothesis (e.g. Fig. 1B & Fig. 1C).

Effect of sample size on UD range area for different probabilities
There is a relationship between the sample size and range areas measured for a given UD level. It is a cumulative probability function, with an asymptote at the real area (for a given kernel function and set of biological and telemetry conditions). The area associated with the asymptote decreases with decreasing probability, so there is a family of curves relating range area to sample size for each probability. We quantified these relationships for the 95% and 50% probability ranges for a series of random samples drawn from the original data set of 548 locations of bird 21316 on the Patagonian shelf (Fig. 2).

The non-linear regression explains a very high proportion of the variance in the sample-area relationship (range-area in 1000 km^2 = 360.050-(4103.4/sample size); $R^2 = 0.77$, $n = 59$, $p < 0.001$; Fig. 2A). Smaller samples, particularly those less than 20% of the data set, progressively under-estimated the area for the 95% probability range. The core area (probability of 50%) achieved an asymptote at quite small random samples. Variance increased as the sample size decreased. Random samples of 100 or more locations were sufficient to estimate the total area at ~360 050 ± *se* 4370 km^2 for 95% probability range (Fig. 2A).

Random samples vs. intermittent sets of locations
To test for regime-dependent deviations from the range-area relationship, we used the residual of the estimated 95% ranges to the expected area as calculated from the range-area regression on random samples. We did not detect significant deviations from the general range-area relationships for subsets that had been generated using time of day, amount of light or Argos location class (ANOVA, main effects $F_{7;168} = 9.86$, $p < 0.0001$, Pairwise Tukey HSD test for unequal *n*: Even/Odd days, Day/Night, Location Class, Time of Day vs. Random : all n.s.; Fig. 2B).

Subsets of locations obtained in one day, on every four, six and eight days (and all the different replicates available by starting the subsets on successive days - see Methods), were extracted and

random samples were derived from these subsets. They appear not to asymptote to the same value of ~360 050 km² as with the full data set.

There were highly significant differences in relation to PTT duty cycle (ANOVA, main effects as given above, Pairwise Tukey HSD test for unequal n: one day in every four days vs. random $p = 0.04$; one day in every six days vs. random: $p < 0.001$; one day in every eight days vs. random: $p < 0.001$). Fig. 2C shows the range-area regressions for the three PTT duty cycles tested. With increasing 'off' periods, the area estimates decreased markedly. The range asymptote for the one-day in every eight days duty cycle was $247\,600 \pm se\ 13\,963$ km², which is approximately 70% of the asymptote obtained with the random samples. The shape of the UD obtained from one day in every eight day subsets (Fig. 3B & C) also differed from those obtained when using the full dataset (Fig. 3A) or a smaller, but random sample (Fig. 3D).

Effect of location accuracy

Argos classifies the quality of locations into seven location classes (LC). For the type of PTT fitted to the birds in our experiment the accuracy of these classes has been measured in the field and the precision ranged from <2.5 km (1SD) for LC = 3, 2, 1; 25 km (1 sd) for LC = A & 0, and was ~100 km (1 sd) for LC = B & Z (Nicholls $et\ al.$ 2003; Nicholls & Robertson unpubl. data).

Range areas ($p = 0.95$) were calculated for four sets of location precision, namely LC = 2 & 1, A, 0 and B & Z. The areas are comparable to those obtained from similarly sized random samples (Fig. 2B, Appendix). The range areas obtained with the more precise locations (LC = 2, 1 & A) were within or below the variance obtained with random samples; values obtained with the less precise (LC = 0, B & Z) locations were slightly larger than those derived from similarly sized random samples. This is to be expected, but the effect is small and all the selected locations for these LCs were considered to be equivalent when preparing the modelled UDs.

Seasonal and day-night differences

Bird 21316, used most of the Patagonian shelf during the 110-day tracking period, but used different sectors of it in different time phases. After an initial flight over the shelf between 56°S and 42°S in late March, the bird mostly used this southern portion (46° - 53°S) until mid-April. It subsequently moved to middle latitudes (40°- 45°S), where it stayed until mid-June and in the last days (before the battery was exhausted), moving to the sector north of 40°S in late June (Fig. 4, Appendix). The range in any one of these time-periods was a fraction of the overall range, and much of the ranges occupied in these three periods were mutually exclusive. Reduced range area in all

three periods was a biological phenomenon and not a consequence of the sample size or sampling regime associated with each subset.

Many birds have a nocturnal roost when they are stationary, while during daytime they forage in a different area. To assess whether time of day or activity affect range-area derivation we compared the ranges obtained by using subsets of locations obtained at different times and at two different travel speeds ($\leq$ 5 km/h, > 5 km/h) by day and night-time. Range areas for samples from various times of the day were within the confidence limits; that is the range was similarly estimated from observations collected at different times of the day (Fig. 2B, Fig. 5). The bird remained in the same region by night as it occupied by day.

Results for subsets with slow and fast travel speed during day- and night-time are shown in Figs. 2B & 6A-D). Data points for the day- and night-time subsets with fast travel speed were very close to the range-area regression line; values obtained for the slow travel speed subsets tended to be lower than those of random samples, but not significantly so (pairwise Tukey HSD test for unequal n: Fast $p =$ 1.00, Slow $p = 0.13$; Fig. 2B).

The range is consistently smaller for locations with slow speeds than locations with fast speeds, whether by day (Fig. 6A, C) or by night (Fig. 6B, D). The difference is likely to be due to behaviour, and not a result of the tracking procedures. The amount of time spent on the water and the number of times a bird takes-off and lands on the sea at this part of the northern royal albatross over-wintering period, does differ for night and day (CJRR unpubl. data).

Individual influences in range utilisation off South America

Results obtained for bird 21316 indicate that even a few locations obtained at regular short periods produce similar UDs to large samples; however interrupted sampling reduced the estimates of the UD area even when there were a relatively large number of records. It is instructive to examine the variation in UD area between individual birds, provided the samples are comparable. We tracked eight visits to the seas off South America by six birds; two birds visited the Patagonian shelf in successive years, 1997 and 1998. The transmitter sampling regimes were different (Table 1). To compare these 'over-wintering' areas, we reduced the better-sampled birds to an equivalent sampling as the least-sampled birds, namely, to a portion of one day on every six (see Methods).

The estimated area of the range ($p = 0.95$) per individual visit to South America varied between 140 000 and 300 000 km² with a mean of 227 000 $\pm sd$ 63 000 km² (Table 1, Fig. 7). The birds on the Patagonian shelf were located between 55ºS and

35ºS over periods of 101-193 days between 14 January and 24 October of the respective years. All these birds used the mid shelf (from 25 km offshore to the shelf break at 200 m isobath) extensively and all used the shelf break and slope (200-3000 m isobath) with all but one using the latter habitat intensively. The Falkland Rise was used by four of the birds, but elsewhere the mid-shelf region was more variably used. Three birds spent considerable time inshore with some instances near fishing ports, while another bird only occurred inshore as it flew past the Falkland Islands before reaching the main shelf, and one bird did not occur inshore. Thus three distinct habitats of the Patagonian region were used. All birds had a patchy occupancy. All had a small core area, typically about a tenth of the area of their range (Table 1). The two birds tracked in different years showed a similar distribution on successive annual visits.

The bird that over-wintered for 1998 off Chile generally remained on the shelf and shelf slope with flights out into the Pacific Ocean until it departed this over-wintering area (Fig. 7D, Table 1). The Chilean shelf is narrow and the distinction between the offshore, shelf and shelf-break habitats is close to the resolution of the locations, but all three habitats were occupied.

To obtain a summary of the distribution on the Patagonian shelf, the six-day subsets of the seven bird-year visits ($n = 962$) were combined into a single UD where the combined range ($p = 0.95$) and the core ($p = 0.50$) areas are illustrated (Fig. 8A). A comparison, not illustrated here, was made of the UD for the entire data set ($n = 1751$) on the Patagonian shelf. The best-sampled bird 21316 ($n = 548$) noticeably biased this UD. There was overlap of the (colour coded) individual bird core ($p = 0.50$) areas (Fig. 8B), although not all visits occurred in the same years. The Falkland Rise was occupied by overlapping core areas from four visits (two core areas are hidden in Fig. 8B). Several overlapping core areas from visits in different years occupied the narrow shelf break of the Patagonian shelf, between 37ºS and 45ºS. Two birds had overlapping core areas in the same year (birds 23738 & 26590 in 1998; Fig. 7F, G). All birds used the shelf. Within that area, they appeared to be selecting the same geographic areas within and between years.

Seasonal changes in UD for all datasets (at equivalent sampling regimes) combined are shown in Fig. 9, where locations from the bird over-wintering off Chile were treated separately in the preparation of the UDs. Overall, birds located on the Patagonian shelf followed the trend for bird 21316 (Fig. 4), namely locations on the shelf at mid latitudes, then an occurrence west of Falkland Islands before extending northwards over the shelf and the shelf break. The bird over-wintering off Chile remained within a more restricted range (Fig. 9).

DISCUSSION

Calculating utilisation distributions requires that a wide (if not full) representation of the animal's movements and activities is included, and that the telemetry data be collected at time intervals that appropriately represent the animal's trajectory (Naef-Daenzer 1994; Wood *et al.* 2000; Selkirk & Bishop 2002). As with all data, the result of the analysis cannot be better than the underlying dataset. Argos satellite tracking locations only approximate this state for, although there is worldwide daily coverage, within a day the coverage is unequal (e.g. fewer location fixes at low latitudes). Further, if the transmissions are intermittent, then the data may not be representative, a key finding of this study.

Where appropriate time intervals are met or closely approximated (Naef-Daenzer 1993, 2000), there are advantages in using the kernel function to model UDs. They can give much better estimates of the range (e.g. minimum convex polygons), a quantitatively-modelled estimate of the density of locations and potential resource use within the home range. They require no assumption about the shape of the range and do not require serial independence. Scale or the grid density used in the analysis has minimal effect. The animal's UD makes it possible to broadly quantify the allocation of activity time amongst different sites, and so to model its potential response to changes in resource quality and distribution (Naef-Daenzer 1993, 2000; Wood *et al.* 2000).

Practical considerations for UD modelling

Major differences in samples size and transmission regimes make comparisons difficult. This study indicates that samples sizes of 150+ locations, consistently measured the 95% probability range. Much smaller samples seemed to be reliable for estimating the more intensely used ranges at a 50% probability. The smallest samples, as expected, fragment the ranges. For this extremely mobile animal, days when no location fixes were obtained resulted in reduced range estimations being calculated for which increased numbers of locations did not compensate. Reducing the datasets to the lowest common denominator (sampling regime) minimised the bias associated with unequal sampling. There was a clear difference in the UDs produced with the combined full (but unequally-sampled) datasets and the combined reduced (but similarly-sampled) data sets and subsets. An alternative approach is to use the best available data for each bird (or visit) and combine equally weighted individual UDs. This approach was not investigated in this study.

Interpretation of the modelled UDs

The use of UDs can measure an animal's range and positions of high occurrence. For any given

hypothesis (e.g. Fig 1 examples), the kernel mapping function can be adjusted by altering its parameters. In pelagic animals, bathymetry, currents, ocean fronts, upwellings, high productivity areas and, where available, fishing effort locations can require a fine scale definition, while 10 - 300 km (we used 40 km) is useful for the core and range estimations. Importantly in a pelagic environment, a concentration of locations does not in itself indicate a foraging activity. Thus commuting to or from breeding grounds, coastlines, wind patterns, sleeping, roosting at night or when becalmed, may create local or ephemeral concentrations of occurrence unrelated to foraging.

Proving the identification of important food sources or regions where birds are at risk from fishing activity is impossible from location data alone. Distinguishing commuting from exploratory foraging flights and, separating these from feeding is impossible without additional instrumentation (Wilson *et al.* 1995). Wood *et al.* (2000) assumed that the areas of concentration were foraging activity (following Weimerskirch 1998), as distinct from the transit flights undertaken by breeding adults to and from the nest. It would be a mistake to make the same assumption and apply the same procedures to a UD prepared for immatures, adults that failed, or successful breeding adults during their entirely pelagic phases (i.e. when not constrained to return to land). Presumably, 'over-wintering' birds organise their activity and energy budgets differently for the purposes of restoring condition and fat reserves and moulting. Evidence from archival tags shows that for the northern royal albatrosses on the Patagonian shelf spend 60-80% of their time sitting on the water (CJRR unpubl. data). Thus, relating the UDs based on locations alone to specific bird activities remains speculative.

For wandering albatrosses (*Diomedea exulans*) breeding in the Indian Ocean, activity and distribution patterns showed marked differences between the incubation, brooding and post-guard periods (Weimerskirch *et al.* 1993). Adults from the Crozet population had localised mid-ocean distributions during the non-breeding sabbatical year (Weimerskirch & Wilson 2000), but there are also migration flights and localised distributions near Australia for individuals of this species (Nicholls *et al.* 1995). It is likely that there will be similar changes during other periods of the year for that species, as has been documented for other species (Stahl & Sagar 2000; Robertson & Nicholls 2000; Hyrenbach *et al.* 2002; Hyrenbach & Dotson 2003), including the northern royal albatross (this paper).

The oceanographic regions used here follow those defined by Piola (2003) for albatross habitat use on the Patagonian shelf. The two areas identified as most important from the combined UDs for over-wintering northern royal albatrosses are known to be highly productive areas, namely the 'open shelf' (especially the Falkland rise) and the 'shelf-break front'. UDs of three of the birds were also consistent with a use of 'tidal fronts' (notably off the Valdéz Peninsula) although an alternate explanation is an association with vessels based in the fishing ports of the Gulfs of San Matias and San Jorge. At different times during the over-wintering the birds persistently occupied two widely separated habitats as though one habitat alone was insufficient for their needs. It is not clear why the birds did not use the 'Magellanic' region or shelf areas east of the Falkland Islands. Significantly both these areas are recognised as being associated with distinct oceanographic regimes (Piola 2003).

The UDs have proved useful at summarising use of oceanic habitats and seasonal changes in distribution for the northern royal albatross. The UDs have indicated substantial overlap in the much-occupied core areas, both between individuals during the same period, and any individuals between successive years. The analysis has emphasised the probabilistic nature of the UDs so that different samples of the population will produce different UDs. There will not be an exact one-to-one match with the modelled UD and the environmental indices. Challenges remain on how best to quantify range overlaps and to relate the birds' UDs to their environment.

Kernels are a useful tool for generalising the point location data into range maps and indicating areas of unequal occupancy. For this species, sampling at any time of day, and only a few observations per day were representative, but absence of sampling for periods of ≥ 4 d resulted in missed areas that were never sampled no matter how many other observation are available. The significance of high occupancy of marine areas by seabirds is not indicated by satellite telemetry locations or kernel modelling alone, without independent measures of the activities of the birds in such areas. Using this analysis and the kernelling we were able to show aspects of the seasonal distribution of the northern royal albatrosses during their 'over-wintering' period off South America.

The combination of biological (especially for these non-breeding albatrosses) and telemetry considerations, promote the need for caution when making the generalisations inherent with the kernelling process. They indicate the difficulties of using these location data without sufficient supporting analysis and interpretation. While possibly clear amongst the scientific community, will these distinctions be equally clear to conservation organisations, and be accepted by the fishing industry if such distributional analyses are used as a basis for exclusion zones? The application of such model UD

maps for identifying possible marine protection or exclusion zones needs considerable care.

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APPENDIX

The range and core areas (p = 95% and p = 50% respectively) for bird 21316 in March–June 1996, using the entire dataset, or various subsets. Areas were calculated with a kernel function using different smoothing values of **h** for the entire dataset and **h** = 40 000 m for all subsets and samples.

| $P =$	Dataset		No. loc.	Utilisation Distribution Area (1000 km^2)		
	Type	Description		Mean ±	*sd*	*n =*
95	All @ h=10 000m	0.125 * LSCV	548	81		1
95	All @ h=20 000m	0.25 * LSCV	548	159		1
95	All @ h=40 000m	0.5 * LSCV	548	364		1
95	All @ h=81 032m	1.0 * LSCV	548	656		1
95	All @ h=162 064m	2 * LSCV	548	1157		1
50	All @ h=40 000m	0.5 * LSCV	548	16		1
95	Transmission Regime	1 day-on every 4 days	250	312	51	2
95	Transmission Regime	1 day-on every 6 days	164	257	48	3
95	Transmission Regime	1 day-on every 8 days	124	231	54	4
95	Even # day	even day - mostly off	57	276		1
95	Odd # day	1 day-on (~10 loc/day)	491	362		1
95	Season Phase	early	205	220		1
95	Season Phase	middle	314	208		1
95	Season Phase	late	29	50		1
95	Day-Night	Day 0700-1800 h	299	320		1
95	Day-Night	Night 1800-0700 h	249	371		1
95	Day-night Speed	Day-Fast	131	321		1
95	Day-night Speed	Night-Fast	189	339		1
95	Day-night Speed	Night-Slow	77	205		1
95	Day-night Speed	Day-Slow	27	124		1
95	ARGOS Location Class	1, 2	48	218		1
95	ARGOS Location Class	A	34	218		1
95	ARGOS Location Class	0	438	370		1
95	ARGOS Location Class	B, Z	28	263		1
95	Random Samples	5% sample	27	217	30	6
95		10% sample	54	272	25	10
95		20% sample	109	332	33	5
95		30% sample	164	336	30	5
95		40% sample	219	336	45	5
95		50% sample	274	329	11	5
95		60% sample	328	344	21	5
95		70% sample	383	359	11	6
95		80% sample	438	361	4	5
95		90% sample	493	361	11	5
95		95% sample	520	358		1
50	Random Samples	5% sample	27	18	11	6
50		10% sample	54	14	5	10
50		20% sample	109	16	5	5
50		30% sample	164	14	3	5
50		40% sample	219	15	2	5
50		50% sample	274	14	1	5
50		60% sample	328	14	2	5
50		70% sample	383	17	2	6
50		80% sample	438	16	2	5
50		90% sample	493	16	2	5
50		95% sample	520	15		1
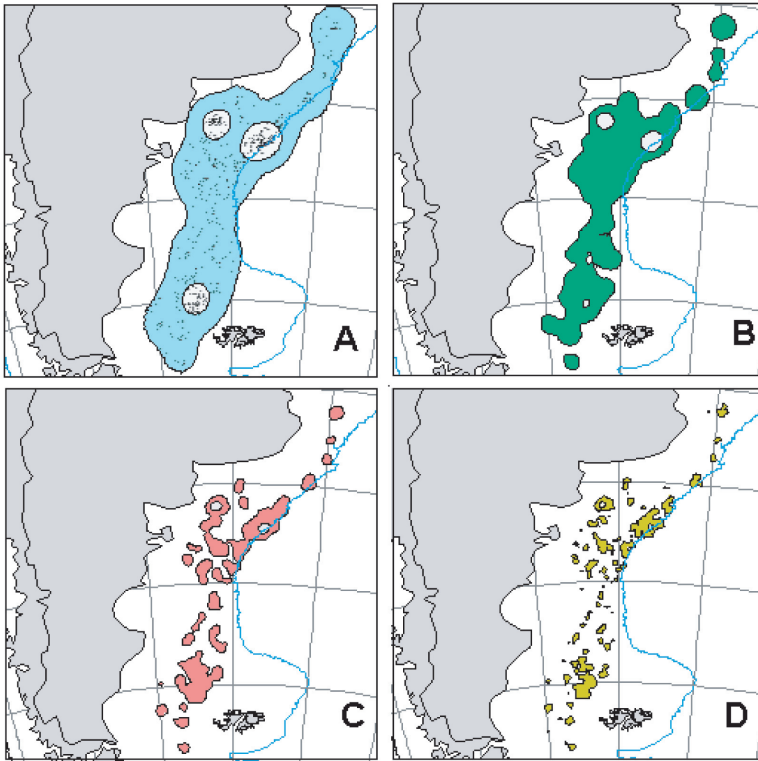
Figure 1 The effect of different smoothing regimes on utilisation density (UD) was modelled from 548 locations for the northern royal albatross (*Diomedea sanfordi*) 21316 on the Patagonian shelf. The 95% and 50% probability contours are shown, overlaid on bathymetry (1000 m isobath). Positions of the actual Argos locations are shown as • in Fig. 1A. Smoothing bandwidth **h =** LSCV (1A); 0.5 (1B); 0.25 (1C); 0.125 (1D).
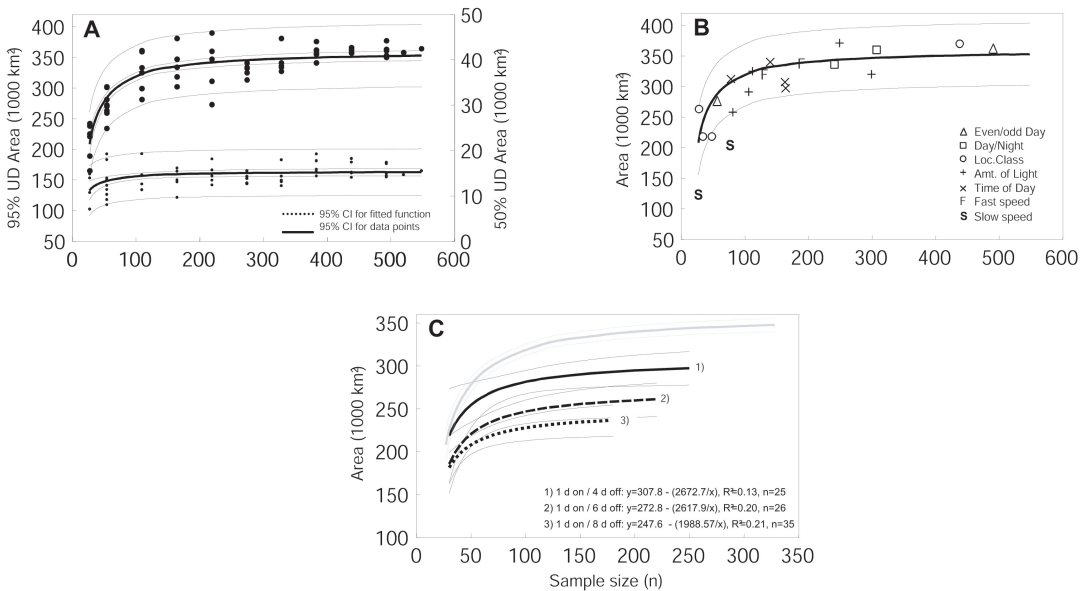

Figure 2 Range-area relationships for various subsets of the 548 locations (bird 21316). 2A: Random sub-samples (5-100% of locations), 95% (top) and the 50% (bottom) probability ranges; regression line for the 95% probability range: y = 360.05-(4103.4/x) (R^2 = 0.78, *n* = 59, *p* < 0.001); 2B: Selected subsets of locations, 95% probability range; regression line and 95% CI for data points from Fig. 2A; 2C: Subsets of locations simulating increasing PTT duty cycles, 95% probability range; regression lines and 95% CI for predictions (black), regression from Fig. 2A **(**grey).

Figure 3 Utilisation density for bird 21316 using different samples from two transmitting regimes. The probability contours are 95, 90, 75, 50, 25 and 10%. The 1000 m isobath is shown and the smoothing is set at **h** = 40 km (~0.5*LSCV). 3A: All locations (*n* = 548); 3B, C: Representative subsets of locations obtained during transmitting regimes of one day in every eight days, with two different start days (*n* = 143 and *n* = 135 respectively); 3D: Random sample of 20% of locations (*n* = 109). Note: Fig. 3A has more probability contours, but is otherwise the same UD shown in Fig. 1B.
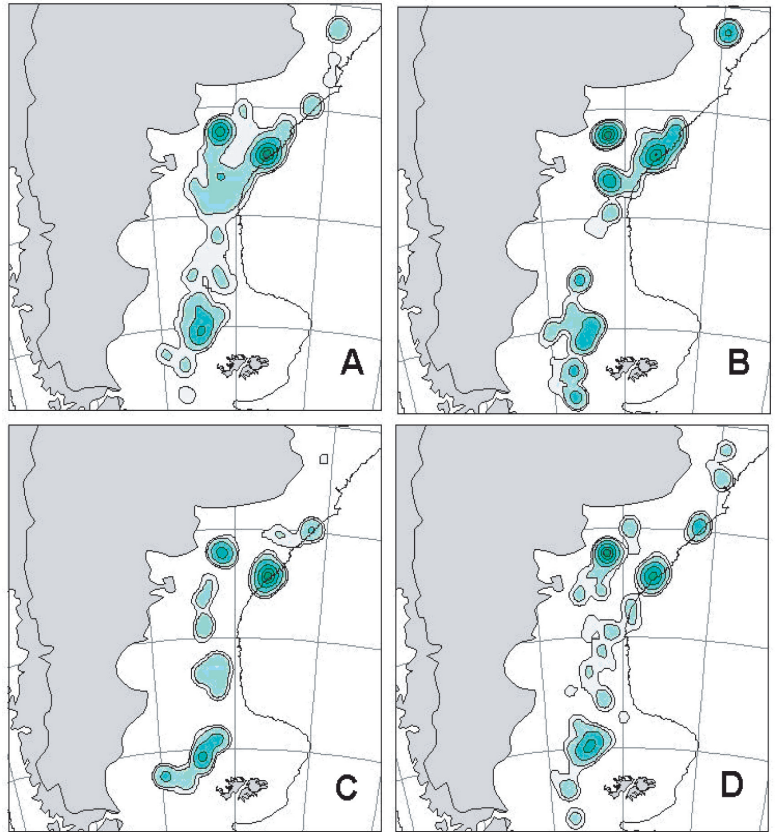
Figure 4 Seasonal differences in range use by bird 21316. Periods: 21 March–22 April (*n* = 205; blue), 23 April–21 June (*n* = 314; green), 22 June–30 June (*n* = 29; red). Smoothing set at **h** = 40 km; probability contours and bathymetry as in Fig. 3.
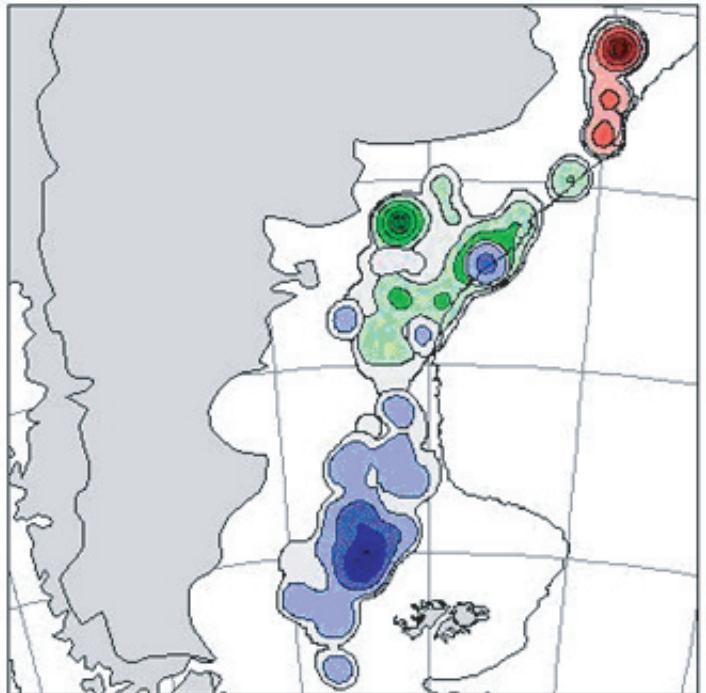
Figure 5   Range use by bird 21316; during day-time (0700–1800h, *n* = 218; red, 5A) and night-time 1800–0700h, (*n* = 330; blue, 5B). Smoothing set at **h** = 40 km, probability contours and bathymetry as in Fig. 3.
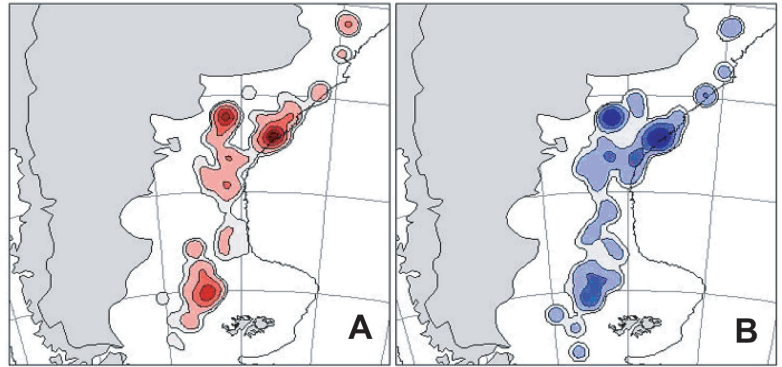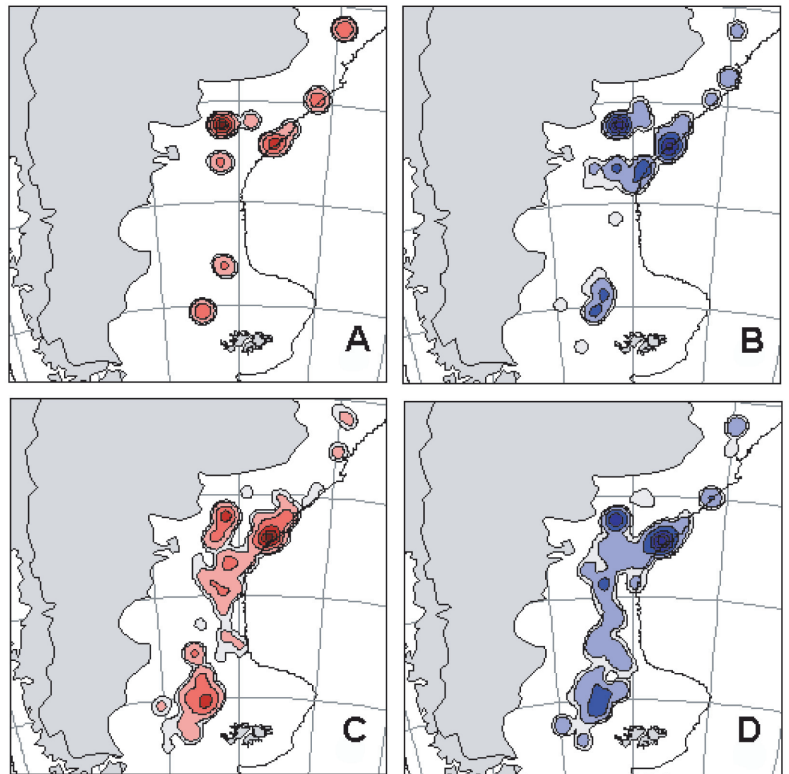

Figure 6 Modelled distribution for bird 21316 when travelling at speeds ≤ 5 km/h during day-time (*n* = 27, red 6A); and night-time (*n* = 77, blue 6B), when travelling at speeds > 5 km/h during day-time (*n* = 131, red 6C) and night-time (*n* = 189, blue 6D). See Methods for measuring speeds. Smoothing set at **h** = 40 km; probability contours and bathymetry as in Fig. 3.
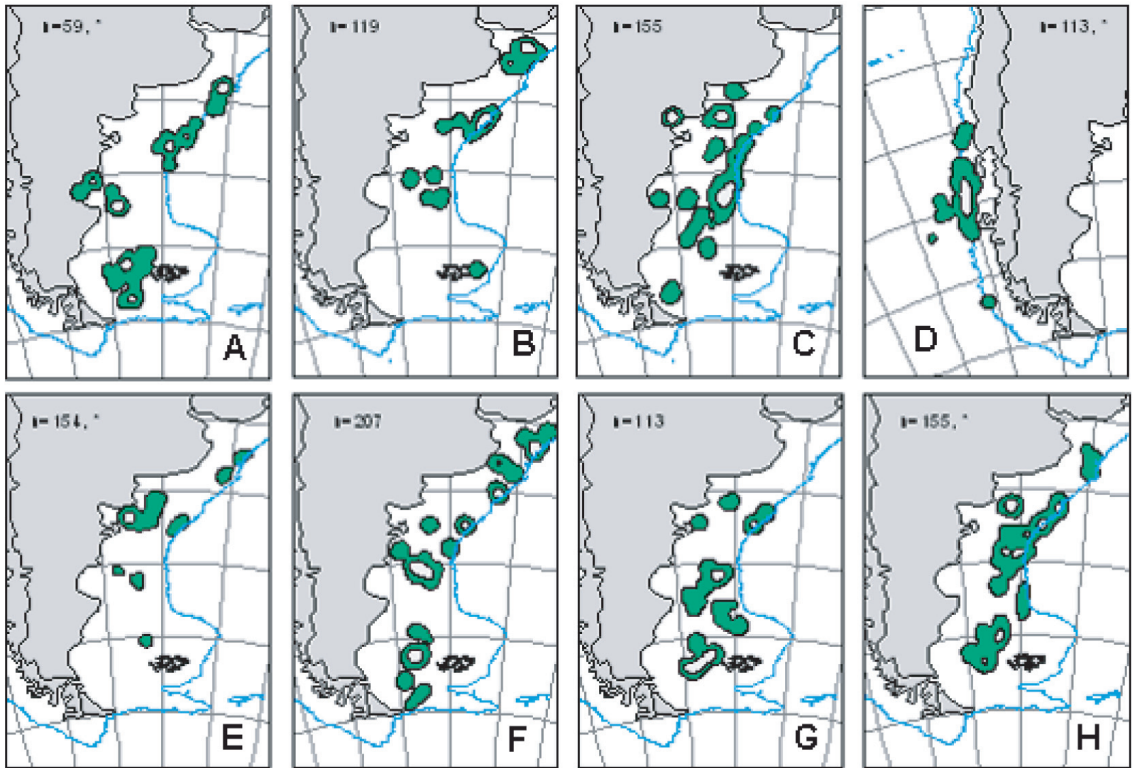
Figure 7   Yearly Utilisation Densities for six birds, two of which over-wintered in consecutive years. The sampling regimes were either a six-day duty cycle or a subset from a better sampling regime (marked *). Maps show the 95% and 50% probability contours, sample size, 1000m isobath, and Kernel smoothing set at **h** = 40 km. 7A: Bird 21805 in 1998 (subset); 7B: Bird 23738 in 1997; 7C: Bird 26590 in 1997; 7D: Bird 26593 in 1998 (subset); 7E: Bird 06750 in 1998 (subset); 7F: Bird 23738 in 1998; 7G: Bird 26590 in 1998; 7H: Bird 21316 in 1996 (subset).
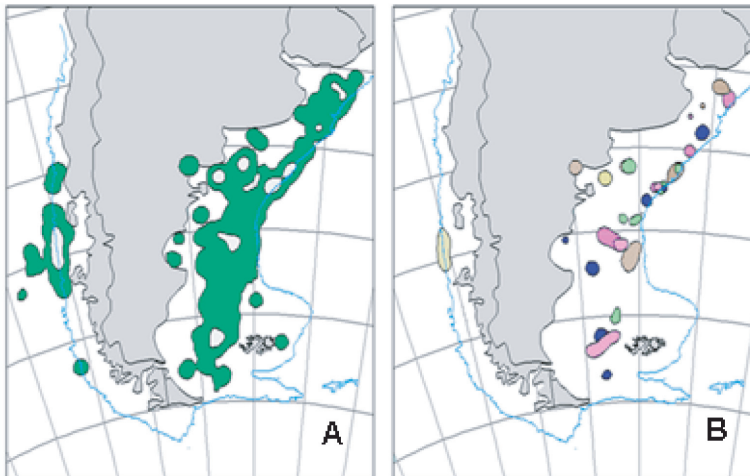

Figure 8   Overall utilisation density. 8A: Range (p = 95%) and core areas (p = 50%) for all birds and years combined; 8B: Core areas (p = 50%) for each birds' visits showing the extent of geographical overlap by the individuals' visits. Note: two additional core areas over the Falkland Rise concealed. Kernel smoothing set at **h** = 40 km. The 1000 m isobath is shown.