

Accuracy of geolocation estimates for flying seabirds

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ABSTRACT: Geolocation (Global Location Sensing or GLS logging) using archival light-recording tags offers considerable potential for tracking animal movements, yet few studies of flying seabirds have exploited this technology. Our study evaluated its effectiveness for determining foraging ranges of black-browed albatrosses *Thalassarche melanophrys* fitted simultaneously with GLS loggers and satellite-transmitters (Platform Terminal Transmitters, PTTs). After some preliminary validation, the position of an albatross could be determined by geolocation with a mean error \pm SD of 186 ± 114 km (SDs of 1.66° and 1.82° of latitude and longitude, respectively). Errors from identical static loggers were lower (mean \pm SD of 85 ± 47 km, with overall SDs of 0.61° and 0.99° of latitude and longitude, respectively) and less variable, with the difference attributable to variation in sensor orientation, intermittent shading by plumage, and the difficulty of correcting for extensive, potentially non-linear movements of flying birds. Iterative smoothing reduced both the mean error and the inflation of kernel ranges derived from GLS data, but over-smoothing contracted the extremes of the range. This reduced the overlap with radial cores apparent in the control data, and should be avoided for multi-nuclear GLS fix distributions. The accuracy of GLS tags is more than adequate for tracking migration and breeding-season foraging ranges of pelagic species, and for identifying broad-scale habitat preferences, overlap and potential conflict with commercial fisheries.

KEY WORDS: Geolocation · Error estimation · Kernel analysis · Smoothing · Albatrosses

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INTRODUCTION

Recent refinements in solid-state electronics and the development of lightweight transmitters and loggers have transformed the investigation of temporal and spatial variation in habitat use of marine animals, and the relationships between at-sea distribution and environmental characteristics (Prince et al. 1998, Le Boeuf et al. 2000, Block et al. 2001, Wilson et al. 2002). Much of this information has been collected using satellite tags (Platform Terminal Transmitters, PTTs). These send a brief radio signal to polar-orbiting NOAA satellites, with the location calculated from the Doppler shift in transmission frequency as the satellite moves relative to the PTT. Although this technology has proved very effective for a diverse range of marine and terrestrial taxa, there are inherent limitations. One is the considerable expense involved in purchasing

devices and processed satellite data. Another is instrument size and shape, with even the smallest of the current generation presenting potential problems in terms of hydrodynamic drag for small penguins and increased wing-loading for flying seabirds (Wilson et al. 1986, Culik et al. 1994, Phillips et al. 2003). Long-term attachment can also prove difficult, particularly for seabirds, as devices taped or glued to feathers are lost during the winter moult, and the use of harnesses is not currently a satisfactory alternative (Phillips et al. 2003). Consequently, much more is known about breeding-season activities, when adults are central-place foragers constrained to return to land to incubate or feed offspring, than about foraging strategies and ranges during migration.

An alternative to satellite-telemetry for determining habitat use is geolocation (Global Location Sensing or GLS logging). To date, this has been applied to a small

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(but taxonomically diverse) range of species that include tuna, seals, penguins and albatrosses (DeLong et al. 1992, Wilson et al. 1995, Tuck et al. 1999, Weimerskirch & Wilson 2000, Block et al. 2001). GLS loggers record ambient light, from which sunset and sunrise times are estimated from thresholds in light curves; latitude is derived from day length, and longitude from the time of local midday with respect to Greenwich Mean Time and Julian day (DeLong et al. 1992, Wilson et al. 1992, Hill 1994). The advantages over PTTs are reduced costs (with no satellite requirements), small size, extended battery life, and if attached securely (for example, to a leg band on a flying seabird), indefinite device retention. Disadvantages are that recapture is necessary before data can be downloaded, only 2 locations (ca. local midday and midnight) are available per day, and it is impossible to estimate latitude for variable periods around the equinoxes (Wilson et al. 1992, Hill 1994). Accuracy is also much lower and more variable for several reasons (Hill 1994, Wilson et al. in press). Mean errors following filtering (to remove unrealistic fixes) or smoothing (to reduce variability in errors) range from 19 to 140 km for static devices and <40 to 380 km for free-ranging penguins and seals (see 'Discussion'), with one study concluding that performance was too low even to permit intra-seasonal or inter-specific comparisons in foraging areas (Hull 1999).

Despite its apparent potential to help identify key foraging areas and migration routes, information critical for understanding predator-prey interactions and for targeting conservation efforts, only a few studies of flying seabirds have exploited GLS technology (Tuck et al. 1999, Grémillet et al. 2000, Nel et al. 2000, 2002, Weimerskirch & Wilson 2000). This reflects partly the relatively recent introduction of miniaturized loggers, but also the paucity of information on accuracy for this type of application. Our study was designed to highlight the utility of the approach, as well as evaluate its effectiveness in delineating the foraging ranges of breeding black-browed albatrosses fitted simultaneously with both GLS loggers and satellite-transmitters. To do so, we compared accuracy of position estimates and overlaps in kernel estimates of home range sizes after data processing by several filtering and smoothing techniques. As far as we are aware, this is the first published study to assess rigorously the performance of GLS loggers on a flying seabird.

MATERIALS AND METHODS

Fieldwork was carried out at Bird Island, South Georgia (54°00' S, 38°03' W) on black-browed albatrosses *Thalassarche melanophrys*. Shortly after the end of brooding (late January 2002), 12 adults were

fitted with 30 g satellite-transmitters (PTT 100; Microwave Telemetry), a 9 g combined salt-water switch and GLS logger (British Antarctic Survey, for details see Afanasyev in press), and a 17 g radio-transmitter with an internal loop antenna (Sirtrack). The radio-transmitters allowed exact arrival and departure times to be recorded using an automatic radio-receiver logger system. Each PTT was attached to 6 to 8 mantle feathers using Tesa® tape, and the logger and radio-transmitter attached to 30 mm high plastic bands fitted to each tarsus. Total instrument mass corresponded to ca. 1.7% of the mean mass of adults at the end of the brood-guard period. Devices were left on adults for successive foraging trips until retrieval 50 to 60 d later, with the exception of 1 bird whose nest failed 52 d after deployment, and whose devices were retrieved the next year. PTT deployment had no significant effect on mean foraging trip duration, breeding success, or probability of returning in the following season (Phillips et al. 2003).

The GLS loggers measured intensity of visible light every 60 s, and recorded the maximum reading within each 10 min interval. Light data were analysed using MultiTrace software (Jensen Software Systems) with the correction factor for the relative distance travelled during the day compared with the night set to 0.7 (based on the PTT data). Given the inaccuracy of latitude estimation during equinoxes (Hill 1994), analysis was restricted to the period from device deployment to the point when location estimates were clearly affected (ca. 2 wk prior to the vernal equinox). Any locations derived from light curves with obvious interruptions or interference around the times of sunset or sunrise (probably a result of changes in orientation or intermittent shading of the sensor; see 'Discussion') were noted during processing and subsequently excluded if obviously anomalous (Hill 1994). Data were then processed in 1 of 2 ways: (1) an iterative forward/backward-averaging filter (McConnell et al. 1992) was run to remove any locations that required unrealistic flight speeds (>35 km h⁻¹ sustained over a 48 h period, based on the PTT data); or (2) iterative smoothing was applied, i.e. the interpolation of intermediate fixes between successive locations (Pütz 2002, Wilson et al. in press), with fixed start and end points around any periods of missing data. Data were smoothed 2, 4, 6 or 8 times, and the iterative speed filter then applied to remove the few unlikely locations remaining (0.7, 0.3, 0.1 and 0%, respectively). The great-circle distance between consecutive fixes was used in all velocity calculations.

A speed filter (McConnell et al. 1992) was also used to validate PTT data (Service ARGOS Location Classes 0–3, A and B), in this case allowing a maximum permissible velocity of 80 km h⁻¹ because of the much

shorter sampling intervals compared with GLS fixes. To estimate the errors in geolocation, we calculated the deviation in latitude, longitude and great-circle distance for each unsmoothed and smoothed GLS fix from the mean position of all valid PTT locations obtained during the corresponding day or night. In addition, for unsmoothed locations, potential consistency among birds and among days in great-circle, latitudinal and longitudinal errors were examined using ANOVA. For these analyses, midnight fixes only were used: (1) because the mean PTT fix is likely to better represent the actual position, as the albatrosses travelled less at night than during the day (based on PTT data); and (2) to reduce the problem of lack of serial independence of consecutive locations calculated from the same dawn or dusk event. The few nights when a GLS location was available from only 1 bird were excluded. As the distribution of errors in great-circle distance had a slight right skew, analyses were performed on square-root transformed data (which did conform to a normal distribution).

Fixed kernel home range analyses were performed separately for mean PTT, smoothed and unsmoothed GLS datasets, using the Animal Movement extension in Arcview GIS 3.2 (ESRI). The most appropriate smoothing parameter (h) was chosen via least squares cross-validation (Worton 1989) for the unsmoothed GLS data, and then applied as standard for the other datasets. Although locations were not serially independent, this is not a requirement for kernel analysis (De Solla et al. 1999). Density contours corresponding to 95, 90 and 50% kernels were calculated for locations in a Lambert Equal-Area Azimuthal (South Pole) projection, and overlaps in foraging ranges between GLS and mean PTT kernels calculated. An additional kernel analysis was run incorporating all valid PTT fixes

obtained throughout the study period to check if this would be a better representation of the maximum extent of foraging areas. In fact, these kernels were more or less indistinguishable from those estimated using mean PTT fixes, and are not considered further.

In addition, GLS data were available from 3 static devices deployed at Bird Island at a similar time in the previous year (5 December 2000–17 February 2001). These data were processed using MultiTrace, as above, and results compared with device locations determined using differential GPS. Potential consistency in errors (great-circle distances) among devices and among days was examined using ANOVAs, with midday fixes only used in the comparisons to reduce the problem of lack of serial independence.

RESULTS

Free-ranging albatrosses

Concurrent GLS and PTT data were obtained for the 12 black-browed albatrosses for a total of 138 complete, and 12 incomplete foraging trips. Filtering because of light-level interference and unrealistic flight speeds removed 12.2 and 2.0%, respectively, of the original GLS locations, with considerable variation among birds (Table 1). The distribution of all unsmoothed GLS, and the corresponding mean PTT locations are shown in Fig. 1. The overall mean distance between the valid GLS and mean PTT locations was 186 km, with overall SDs in latitudinal and longitudinal errors of $\pm 1.66^\circ$ and $\pm 1.82^\circ$, respectively (Table 1). There was consistent variation among birds in great-circle and latitudinal, but not longitudinal errors ($F_{11,329} = 3.61$, $p < 0.001$, $F_{11,329} = 1.92$, $p < 0.05$ and

Table 1. *Thalassarche melanophrys*. Summary of position estimates using geolocation for free-ranging black-browed albatrosses

Bird ID	No. of valid locations	No. of locations with light-level interference	No. of locations failing velocity filter	Mean great-circle error \pm SD (km)	SD of latitudinal error ($^\circ$)	SD of longitudinal error ($^\circ$)
B182	52	0	1	161 \pm 82	1.37	1.27
O071	49	29	0	201 \pm 105	1.64	2.03
O093	54	5	0	217 \pm 107	1.55	1.96
O094	51	12	2	251 \pm 132	2.06	2.71
O150	35	12	0	176 \pm 86	1.49	1.57
O205	66	0	5	143 \pm 131	1.49	1.45
O293	67	6	1	175 \pm 106	1.51	1.95
O296	56	0	1	198 \pm 139	1.93	1.69
O474	68	0	0	145 \pm 84	1.29	1.24
O626	53	12	0	233 \pm 125	1.93	2.05
W675	90	0	4	174 \pm 106	1.57	1.62
W685	43	21	2	187 \pm 91	1.51	1.93
All	684	97	16	186 \pm 114	1.66	1.82

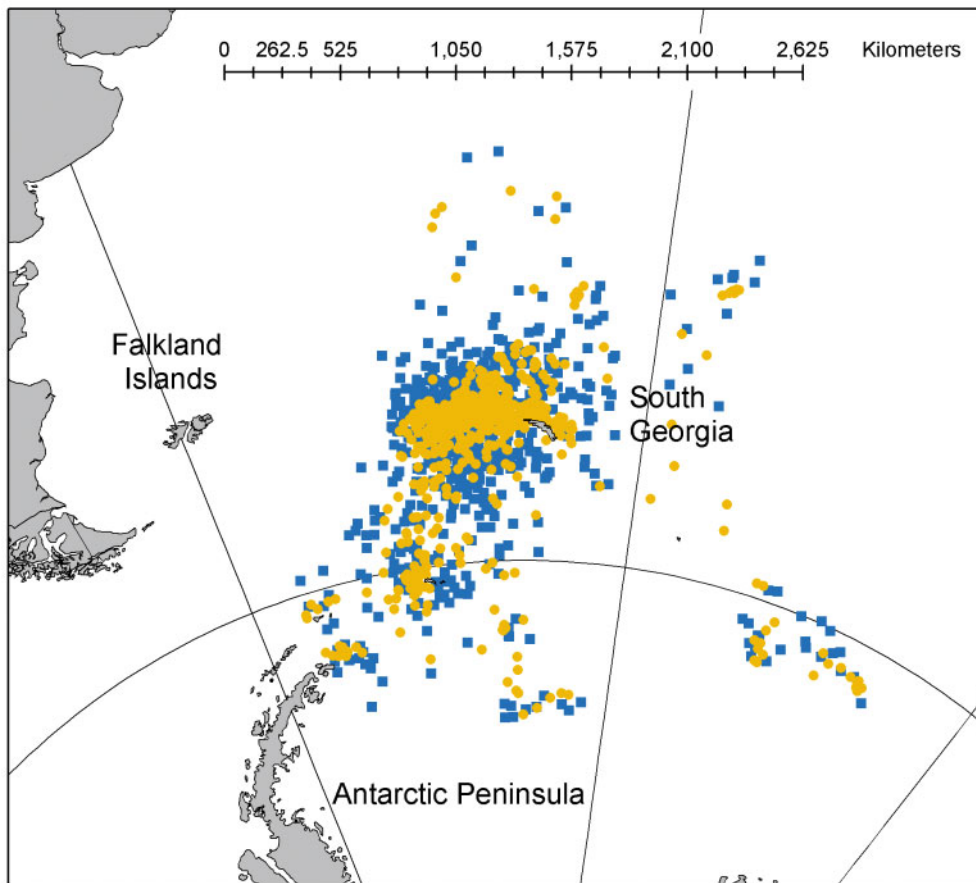


Fig. 1. *Thalassarche melanophrys*. Distribution of Global Location Sensing (GLS, blue), and corresponding mean Platform Terminal Transmitter (PTT, yellow) locations for 12 free-ranging black-browed albatrosses tracked from South Georgia during chick-rearing in 2002

$F_{11,329} = 1.19$, not significant [NS], respectively), and also among nights in great-circle, latitudinal and longitudinal errors ($F_{42,298} = 1.60$, $p < 0.05$, $F_{42,298} = 1.67$, $p < 0.01$ and $F_{42,298} = 1.86$, $p < 0.005$, respectively).

Errors (great-circle distances) were reduced by 9% from a mean of 186 km for the unsmoothed data, to 169 km after smoothing twice, then by a further 3% to 164 km after smoothing 4 times, but with little improvement thereafter (Table 2). There was considerable variation between individuals in the degree to which repeated smoothing influenced errors, with the greatest improvement apparent for birds that tended to travel less far from the colony.

Kernel density contours for valid unsmoothed and smoothed GLS locations, overlaid on kernels from the mean PTT locations are shown in Fig. 2. For each density contour (50, 90% and 95%), the GLS kernel based on the original valid locations (unsmoothed) encompassed a high proportion of the corresponding PTT kernel, but not vice versa. Each iteration of the smoothing procedure reduced the inflation of the GLS range, but gradually drew in the extremes of the distribution, resulting in increasing exclusion of parts of the PTT range.

Static data

No interference to dawn or dusk light curves was evident in data from the static GLS loggers. The overall mean distance from the GLS estimate to the known location of each device was 84.7 km, with overall SDs in latitudinal and longitudinal errors of 0.61° and 0.99° , respectively (Table 3). Considering midday fixes only, there were no consistent differences between devices in great-circle, latitudinal or longitudinal errors ($F_{2,219} = 0.02$, NS, $F_{2,219} = 0.07$, NS and $F_{2,219} = 0.06$, NS, respectively). In contrast, there were highly consistent differences between days in great-circle, latitudinal and longitudinal errors ($F_{73,148} = 62.5$, $p < 0.001$, $F_{73,148} = 156.1$, $p < 0.001$ and $F_{73,148} = 155.8$, $p < 0.001$, respectively).

DISCUSSION

The mean error in GLS locations from the static loggers was 85 km, and from those on the 12 free-ranging black-browed albatrosses was 186 km for unsmoothed data, reduced to 169 km after smoothing twice. These

Table 2. *Thalassarche melanophrys*. Effects of smoothing on great-circle errors from GLS loggers on free-ranging black-browed albatrosses

Bird ID	No. of valid locations	Unsmoothed	Mean great-circle error \pm SD (km)				Mean distance from colony (km)
			Number of times data were smoothed				
			2 \times	4 \times	6 \times	8 \times	
B182	52	161 \pm 82	141 \pm 72	132 \pm 66	127 \pm 63	123 \pm 62	300
O071	49	201 \pm 105	174 \pm 96	162 \pm 90	157 \pm 85	154 \pm 82	285
O093	54	217 \pm 107	194 \pm 96	185 \pm 94	182 \pm 91	181 \pm 88	442
O094	51	251 \pm 132	230 \pm 120	224 \pm 116	221 \pm 116	222 \pm 117	365
O150	35	176 \pm 86	162 \pm 86	155 \pm 87	150 \pm 89	148 \pm 89	427
O205	66	143 \pm 131	149 \pm 119	148 \pm 112	150 \pm 109	154 \pm 107	709
O293	67	175 \pm 106	159 \pm 101	156 \pm 101	158 \pm 100	162 \pm 99	754
O296	56	198 \pm 139	184 \pm 138	181 \pm 132	182 \pm 128	186 \pm 125	986
O474	68	145 \pm 84	126 \pm 72	119 \pm 65	117 \pm 59	115 \pm 54	345
O626	53	233 \pm 125	211 \pm 113	200 \pm 110	193 \pm 108	189 \pm 107	355
W675	90	174 \pm 106	157 \pm 95	154 \pm 87	157 \pm 87	159 \pm 87	629
W685	43	187 \pm 91	168 \pm 77	170 \pm 87	169 \pm 85	169 \pm 85	277
All	684	186 \pm 114	169 \pm 104	164 \pm 100	162 \pm 98	162 \pm 97	426

levels of accuracy are in the mid-range compared with previous studies, which in particular for free-ranging animals appear heavily dependent on the degree of post-processing (Table 4). Part of the variation originates from extrinsic and intrinsic factors including time of year and location (affecting latitude estimation in particular), weather conditions, and although unimportant in our short-term study, uncorrected clock-drift over long deployments (see Wilson et al. in press for a recent review). Of these, weather effects are probably the most important, almost certainly accounting for the consistency in errors among days apparent for both static devices and free-ranging birds in our study. There are also differences in logger design; some incorporate a blue filter to ensure the photoreceptor records the light least sensitive to cloud cover, improving performance at least in static trials (Wilson et al. in press). Recording resolution also varies, although because the software incorporates algorithms that interpolate between records to determine the time that designated dawn/dusk light thresholds were reached, intervals of up to 15 min are adequate for geolocation (Hill 1994, Le Boeuf et al. 2000), and compared with other factors, the influence of recording interval on relative accuracy appears to be slight (Wilson et al. in press).

Table 3. Summary of position estimates for static GLS loggers at Bird Island, South Georgia

Logger ID	No. of valid locations	Mean great-circle error \pm SD (km)	SD of latitudinal error ($^{\circ}$)	SD of longitudinal error ($^{\circ}$)
LM11	148	85.7 \pm 46.8	0.62	1.01
LM28	148	83.5 \pm 46.8	0.60	0.97
LM59	148	85.0 \pm 48.7	0.62	1.00
All	444	84.7 \pm 47.3	0.61	0.99

In studies of flying birds, GLS loggers are usually leg-mounted, with the sensor of variable orientation, and potentially shaded, obscured by feathers if the leg is tucked into plumage during flight, or with light levels attenuated by water if the bird sits on the sea around dawn and dusk. These intermittent events account for the varying degrees of interference detected in light curves from bird-mounted (but not static) loggers in our study, and given their unpredictability are probably impossible to correct even with some form of curve replacement (cf. Wilson et al. 1995, in press for diving species). For highly mobile animals, there is the additional difficulty of producing in effect an instantaneous estimate of location at local midday and midnight using GLS (or control PTT fixes), which in the case of an albatross might have travelled 400 km in 12 h. Although the relative time spent travelling during the day versus night can be incorporated in the algorithms, this assumes directed linear flight. This is an unlikely scenario for albatrosses foraging in a highly patchy and unpredictable marine environment, in which flight velocity and direction probably change continuously depending on encounter rate and profitability of prey patches.

Post-processing of data also affects both the real and the perceived accuracy of geolocation. Identification and subsequent removal of locations associated with obvious light level interference was critical in our study, and given the association with more or less random events (see above), the only drawback was a reduction in sample size (by 12%). Other approaches to processing, however, might produce systematic biases. For example, removal of spurious locations requiring

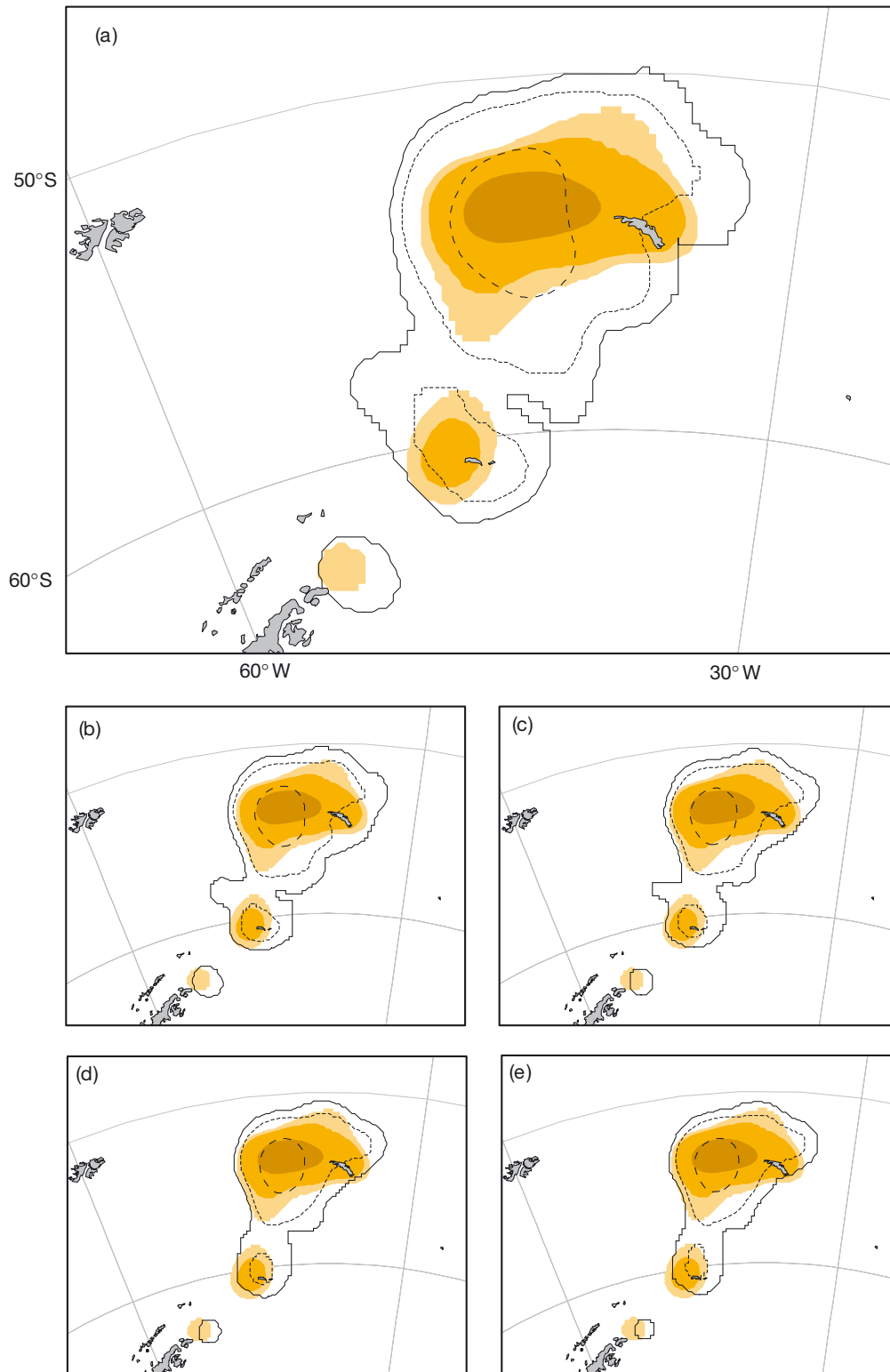


Fig. 2. *Thalassarche melanophrys*. Kernel density contours for GLS locations that were (a) unsmoothed, (b) smoothed 2 \times , (c) smoothed 4 \times , (d) smoothed 6 \times , and (e) smoothed 8 \times , overlaid on kernels from the mean PTT locations of 12 black-browed albatrosses tracked from South Georgia during chick-rearing in 2002. For GLS data, 95, 90 and 50% contours represented by solid, short dashed and long dashed lines, respectively. For PTT data, 95, 90 and 50% contours represented by increasing darkness of colour tone

Table 4. Review of geolocation errors in published studies. SST: sea surface temperature

Deployment	Mean error (km)	Details	Source
Static trials			
Stationary subsurface mooring	137	n = 137 locations, 4 accurate devices	Welch & Eveson (1999)
On land	120–130	n = 146 d	Wilson et al. (1992)
On land	110	n = 11 locations from 5 devices	Beck et al. (2002)
On land	37.5, 18.8 ^a	n = 14 d	Wilson et al. (in press)
On land	34	n = 52 locations	Wilson et al. (1995)
Free-ranging animals			
Elephant seals <i>Mirounga angustirostris</i>	148	Latitudinal ambiguities corrected by matching logged SST with remote SST data	Le Boeuf et al. (2000)
Grey seals <i>Halichoerus grypus</i>	1043, 94 ^b		Beck et al. (2002)
King penguins <i>Aptenodytes patagonicus</i>	352, 102 ^c , 70 ^d	n = 16 locations from 1 individual	Wilson et al. (in press)
Magellanic penguins <i>Spheniscus magellanicus</i>	Within 40–150 (no mean provided)	Depending on quality of light records	Wilson et al. (1995)
Rockhopper and Royal penguins <i>Eudyptes chrysocome</i> and <i>E. schlegelis</i>	383 (latitude) 189 (longitude)		Hull (1999)
Wandering albatrosses <i>Diomedea exulans</i>	As high as 200 (no mean provided)		Wilson et al. (2002)
^a After smoothing 10×; ^b locations corrected by comparison of dive/temperature data with bathymetry and remote SST data (assuming benthic foraging); ^c correcting for diving behaviour; ^d after smoothing 9×			

unrealistic travel speeds is common practise in both GLS and PTT studies (e.g. Prince et al. 1998, Hull 1999), and has been incorporated into more complex algorithms (Beck et al. 2002). In this last study (see Table 4), corrected locations were available for only 60% of the original dataset, based to a large extent (58% of cases) on the assumption that movements of >148 km from the previous approved point were implausible. Although a degree of filtering is probably appropriate for most, if not all, studies, this should be approached cautiously as over-conservatism undoubtedly reduces the likelihood of detecting short-term, long-distance, exploratory excursions.

Smoothing, which reduces the variability in latitude and longitude estimates, is very effective in reducing the mean error in position estimates (Wilson et al. in press, this study). This approach works best if errors are random and independent (Welch & Eveson 1999), which is not exactly true for GLS locations, as errors inevitably show some serial correlation because consecutive positions are derived from the same dawn and dusk events. Nonetheless, modelling of foraging ranges of black-browed albatrosses from smoothed datasets offered some advantages over unsmoothed locations, as errors in geolocation inevitably result in range inflation (Fig. 2). An unfortunate disadvantage of repeated smoothing, however, was the gradual contraction of the extremes of the range towards its centre, reducing the overlap with radial cores apparent in the control data. This was particularly obvious for indi-

viduals that travelled furthest from the colony often to several cores (Table 2 and authors' unpubl. data). In a recent study, GLS data collected near the equinox from king penguins *Aptenodytes patagonicus* had to be smoothed 7 times to gain a realistic picture of foraging patterns (Pütz 2002). Although this seems reasonable given the simple range structure at that particular colony, our study indicates that over-smoothing can sometimes be misleading and should be applied cautiously for multinuclear GLS fix distributions.

In conclusion, this validation study illustrates the scale at which GLS devices are useful for tracking the movements of flying birds. Clearly with mean errors post-processing of 169 to 186 km, GLS loggers have excellent potential for identifying foraging ranges of highly pelagic species during the breeding season, as well as tracking large-scale migration. Although range kernels estimated using GLS loggers are somewhat inflated, they nonetheless allow the clear demarcation of core feeding areas. The loggers used on black-browed albatrosses represented a compromise in terms of cost, battery longevity, memory capacity, recording resolution and sensor type (limited to a photoreceptor and a salt-water switch). Incorporation of a temperature probe to improve latitude estimation during the equinox (Delong et al. 1992), new approaches to data-processing (such as threshold-free methods using the shape of light curves; www.lotek.com/library.htm#adv), and further miniaturization are likely to increase the accuracy, as well as the

number of potential target species. For migratory species in particular, the data generated will provide the first comprehensive opportunities to examine within- and between-season variation in foraging site-fidelity, and determine the mesoscale environmental characteristics associated with apparent winter hotspots. In addition, they will allow the unambiguous identification of areas of interaction and potential conflict with commercial fisheries. This is essential for effective conservation management, particularly for those species in which fisheries-associated mortality has resulted in recent catastrophic population declines (Weimerskirch et al. 1997, 1999, Croxall et al. 1998).

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