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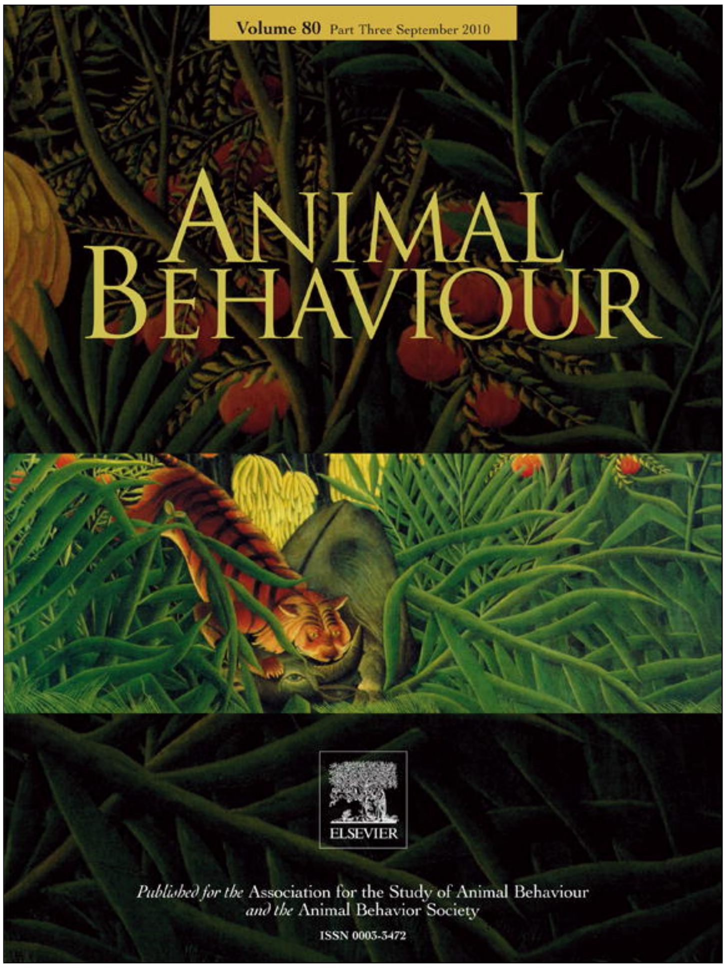

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Commentaries

Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS

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Since the 1980s, the Argos System operated by CLS Argos (http://www.argos-system.org) has become a dominant system for following large-scale movements of vertebrate species in marine and terrestrial ecosystems (Priede 1984; Duron-Dufreene 1987; Jouventin & Wiemerskirch 1990; Mate et al. 1997; Schwartz & Arthur 1999; Cushman et al. 2005; Laing et al. 2005), particularly for species that move considerable distances, or through inaccessible habitats, which limits the utility of more traditional Very High Frequency (VHF) radiotracking methods. Utilizing the physical principles of Doppler shift and a combination of animal-borne radiotransmitters (Platform Transmitter Terminal; PTTs) and satellite-borne receivers, the Argos system is able to geolocate equipped animals with global coverage (CLS 2008). The Argos System additionally provides a data-relay capability in that information gathered by Argos PTTs, such as device status, environmental temperature etc., can be encoded within the signals (messages) transmitted to satellites passing overhead.

The spatial quality of the Argos-derived locations is, however, of limited accuracy (Keating et al. 1991; Hays et al. 2001; Vincent et al. 2002), both for air-breathing marine vertebrates that spend much of their time submerged and therefore often obscured from overhead satellites (Ryan et al. 2004) and for terrestrial species occupying dense-canopied regions such as forests. Concern regarding spatial accuracy and the low number of high-quality locations, that is, those with low spatial error, are, however, compensated for by the overriding benefits of global coverage and the fact that study animals do not need to be recaptured.

Extensive movements of a range of vertebrate species have also been followed using the global positioning system (GPS), which provides increased location accuracy (Moen et al. 1996; Girard et al. 2002; Soutullo et al. 2007). This system utilizes a constellation of earth-orbiting satellites that continuously transmit information about their location and time (ephemeris and almanac data) to the earth's surface. GPS receivers collecting this information can calculate their location and elevation in real-time typically on the

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order of 100 m or less (Moen et al. 1997), or can archive information on detected GPS signals, which are subject to later processing into estimates of location. Despite this advantage, archival tracking units utilizing GPS geolocation need to be retrieved either by removal at recapture of the animal or by recovery of a self-release collar/harness bearing the tag (Moen et al. 1996; Haines et al. 2006; Steinfurth et al. 2008). The issue of recapture has been remedied by combining technologies, resulting in the development of Argos PTTs carrying GPS receivers (Schwartz & Arthur 1999; Soutullo et al. 2007). This hardware interfaces GPS quality estimates of location and the data-relay capabilities of the Argos System.

GPS and Argos-based geolocation methods are, however, not without shortcomings, for example, vegetation cover, weather, antenna position and altitude can all impact the transmission and/or receipt of signals from GPS satellites (Rempel et al. 1995) and subsequent transmission and/or receipt of messages at satellites hosting Argos receivers (Moen et al. 1997); yet there is an even more profound problem with marine vertebrates, particularly for traditional GPS units as they typically require from 30 s to several minutes to obtain a 'satellite lock' and location (Ryan et al. 2004). Often surfacing events are too short and wave wash, submersion and improper antenna orientation all prevent a traditional GPS receiver from maintaining signal lock, so that ephemeris data cannot be downloaded and thus collection of location information is impeded.

A recent development in obtaining accurate and precise geolocation information has been seen with Fastloc (Bryant 2007; Wildtrack Telemetry Systems Ltd, Leeds, U.K.) and TrackTag (NAVSYS Ltd, Edinburgh, U.K.), which are GPS receiver peripherals for integration into telemetry or archival wildlife-tracking hardware. This equipment has been designed specifically to address the problems facing traditional GPS receivers, that is, the need to download almanac and ephemeris data to determine position accurately when an unimpeded view of the sky is infrequent and ephemeral. These GPS receivers are able to record the presence of signals transmitted by GPS satellites, within milliseconds, and do not need to download ephemeris information carried in the GPS signal. Data regarding received GPS signals are stored onboard the device and are either transmitted utilizing the data-relay capabilities of the Argos system (Fastloc; Hazel 2009; Sims et al. 2009) or archived onboard the device (TrackTag; Schofield et al. 2007; Tobler 2009) for later recapture. These GPS data are then retrospectively analysed to derive likely locations. Fastloc-GPS technology provides the most appropriate method for following the movements of individuals from populations where site fidelity to attachment regions is not well understood and hence the chance of recapture and retrieval of equipment is low. The spatial accuracy of Fastloc-GPS-derived locations increases with the number of detected GPS satellite signals. The greater the number of satellites detected the more constrained the estimate of true location and therefore the greater the accuracy is. In stationary validation tests, mean Fastloc-GPS spatial accuracy (error) varied depending on the number of available satellites (eight satellites: 26 ± 19.2 m; four satellites: 172 ± 372.5 m; Hazel 2009).

GPS transmitters and Argos System receivers are supported on different satellite platforms and as such they provide independent estimates of animal location. The development of Fastloc-GPS technology and its integration into standard Argos PTT hardware now allows for in situ assessment of Argos-derived location data, facilitating a greater understanding of spatial error structure underlying Argos-derived locations in the field. Other authors have attempted to assess Argos location accuracy through analysis of data from static platforms (e.g. Hays et al. 2001; Vincent et al. 2002; Dubinin et al. 2010) or transmitters on rookery-based animals (e.g. Le Boeuf et al. 2000); however, these efforts generally have not been able to integrate the further complications associated with tracking animals in the marine environment, for example short surface intervals, sea surface conditions and biofouling. Recent attempts to assess Argos and Fastloc-GPS location accuracy have been made utilizing Argos–Fastloc PTTs (Hazel 2009; Sims et al. 2009); but with tracking durations that have been relatively short (range 4.5–92 days) and movements that have been spatially constrained, particularly with respect to the large-scale movements (greater than hundreds of kilometres) made by many migratory marine vertebrate species. Here we build upon these initial efforts and quantify the accuracy of Argos-derived locations using Argos–Fastloc PTTs directly fixed to animals at liberty over protracted periods of time while they undertake a range of movements.

Access to Argos–Fastloc PTTs allowed us to undertake quality assurance tests of Argos-derived location data for reconstructing migratory routes of adult female green sea turtles, *Chelonia mydas*, and adult female leatherback sea turtles, *Dermochelys coriacea*, and also during periods of internesting and foraging in neritic habitats. Using these data we seek to highlight the relative utility of Argos-derived locations of different reported accuracies and to inform data-filtering protocols to help utilize more of the relatively expensive data received from standard Argos PTTs. Finally, we seek to highlight the continued role for Argos-derived geolocation into the future.

METHODS

Equipment Deployments and Duty Cycles

Argos–Fastloc PTTs were fitted to green ($N = 5$) and leatherback ($N = 4$) turtles at nesting rookeries in the Atlantic Ocean. On Ascension Island (7.9°S, 14.4°W) green turtles were fitted with Argos–Fastloc PTTs manufactured by Sirtrack Tracking Solutions (Havelock, New Zealand; 0.5 W Argos transmitter, 2 × D lithium thionyl chloride cells; 675 g in air and approximately 0.4% of bodyweight; based on a mean + 1SD green turtle mass of 170 ± 17 kg estimated from morphometrics and Hays et al. 2002) using an epoxy-based attachment method (Godley et al. 2003) when females emerged on to nesting beaches to deposit eggs. Leatherback turtles were fitted with Argos–Fastloc PTTs manufactured by Wildlife Computers (Redmond, WA, U.S.A.; 0.5 W Argos transmitter, 4 × AA lithium cells; 250 g in air and therefore <0.1% bodyweight; based on a mean + 1SD leatherback turtle mass of 327 ± 25 kg estimated from morphometrics and Boulon et al. 1996) during periods of nesting at Pongara National Park, Gabon (0.2°N, 9.7°E). Argos–Fastloc PTTs were attached to leatherback turtles using a direct carapacial attachment method analogous to those used by Doyle et al. (2008) and Fossette et al. (2007). Ethical review of leatherback turtle Argos–Fastloc PTT attachment procedures was undertaken by the University of New Hampshire (U.S.A.) IACUC 060501.

Sirtrack and Wildlife Computer Argos–Fastloc PTTs differed in the degree of user-definable parameters for the number of Argos transmissions and the number and/or frequency of Fastloc-GPS locations to achieve in any 24 h period. Sirtrack Argos–Fastloc PTTs were programmed to achieve one successful GPS location every hour from a maximum of four attempts. Wildlife Computer Argos–Fastloc PTTs were permitted up to three Fastloc-GPS acquisition attempts every 6 h. Argos–Fastloc PTTs were fitted with salt water switches, which measure local conductivity. During periods of submersion in sea water, when conductivity is greatest, Argos transmissions and Fastloc-GPS capabilities were deactivated. Argos–Fastloc PTTs were not subject to duty cycling, that is, user-defined periods of time when transmission and reception

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capabilities can be switched on or off, and as such Argos–Fastloc PTTs were permitted to transmit signals during any surfacing event where salt water switch deactivation allowed.

Argos Data Preparation

Argos-derived locations and Fastloc-GPS data contained within signals (messages) received from Argos–Fastloc PTTs were automatically downloaded from CLS Argos using the Satellite Tracking and Analysis Tool (STAT; Coyne & Godley 2005). We used the following filtering and data manipulation techniques with custom-written Matlab routines to remove implausible Argos locations (The MathWorks, Natick, MA, U.S.A.).

(1) 'Swapping' is the technique used by CLS Argos to identify which of the potential mirror-image solutions for an animal's location, created on either side of the satellite path as it passes over an Argos PTT, is most plausible. On infrequent occasions CLS Argos selects the incorrect solution, so we applied a simple test to all Argos-derived location data to detect and swap these incorrectly identified locations. This test iteratively calculated the distance between the previous accepted location and the current primary and mirror locations. The primary location was swapped for the mirror location when the mirror location was closer in distance (minimum great-circle distance) to the previous accepted location.

(2) By far the most common filter used in the vertebrate-tracking literature is to exclude Argos-derived location data by location class (LC). LC is an estimate of spatial accuracy, that is, radial distance from the estimated position, associated with each location provided by CLS Argos (CLS 2008). In general, location accuracy is best when more transmissions (messages) are received from the PTT during a single overpass and when transmissions (messages) are received across the widest temporal range within the satellite overpass; a satellite overpass is typically on the order of 15 min at the equator. This provides the best possible geometry for estimating the Doppler shift and subsequently the location from the known PTT transmission frequency (wavelength). 'Standard' locations (LC 3–LC 0) are those derived from four or more messages; the estimated errors (1 standard deviation from the true location, assuming bivariate normal distributions of errors) are: LC 3: $<$250 m; LC 2: 250–500 m; LC 1: 500–1500 m; LC 0: $>$ 1500 m (CLS 2008). When fewer than four messages are received it is not possible to calculate an estimated accuracy; for these, CLS Argos provides 'auxiliary' or 'service plus' locations, termed LC A and LC B, but with no estimate of spatial accuracy. Locations are classified as invalid, or LC Z, if they do not pass at least two of Argos's plausibility tests (minimum residual error, transmission frequency continuity, minimum displacement and plausibility of velocity between locations; CLS 2008). For this analysis we excluded Argos-derived locations with LC Z and included all others, that is, LC 0–3, LC A and LC B.

(3) Using simple calculations it is possible to estimate the approximate 'speed over ground' of an animal from a previously obtained location. If the speed exceeds a user-defined threshold, representing maximum expected speed of travel, the location is excluded. A speed threshold of 5 km/h is often used for hard-shelled marine turtles (Luschi et al. 1998); we adopted this filter threshold and eliminated Argos locations, irrespective of their location class, if they indicated estimated movement speeds greater than this threshold.

(4) The azimuth filter evaluates three locations at a time and excludes the middle location if the inside angle is smaller than a user-defined threshold, under the premise that significant location errors are commonly associated with anomalous acute angles (Keating 1994). In this study we removed locations leading to an angle of 20 degrees or less.

Fastloc-GPS Data Preparation

Fastloc-GPS data, received within transmissions (messages) from Argos–Fastloc PTTs, were decoded and processed into GPS locations using manufacturer-specific software (Sirtrack Fastloc Admin Tool Version 1.1.4.7 and Wildlife Computers Fast-GPS Solver Version 2-Build 29). Fastloc-GPS locations can be estimated using signals from as few as four GPS satellites; however, the fewer the satellites the lower the confidence in the accuracy of any resulting location. Each Fastloc-GPS location is accompanied by an estimate of error, that is, residual, indicating the relative spatial accuracy of each location; however, this metric has little indicative power when the number of satellites used to determine a location is low. Fastloc-GPS locations derived using five or fewer GPS constellation satellites were discarded as were locations with residual errors greater than 30 (E. Bryant, personal communication).

Reconstructing Movement Paths

Movements of turtles were reconstructed from Argos-derived location data with LC 0–3, and LC A and LC B, which were subject to speed and azimuth filtering. The resulting time series of Argos-derived locations, for each turtle, were then subject to cubic interpolation (Tremblay et al. 2006) to a 6 h frequency. Movements of turtles were also reconstructed from filtered Fastloc-GPS data by connecting subsequent locations in time. To ensure comparability in data treatment between the two geolocation methods, Argos-derived and Fastloc-GPS, we further applied a speed and azimuth filter to each Fastloc-GPS time series data set but no locations were filtered.

Home Range Analysis

To investigate differences in the estimates of habitat utilization for green turtles from the differing geolocation methods, speed- and azimuth-filtered Argos-derived locations (excluding any LC Z, data subject to 'swapping'), and Fastloc-GPS locations (locations derived from six or more satellites and where residual error was 30 or less), were each resolved to single daily best (highest) quality locations. For Argos-derived location data, this represented the location with the highest location class occurring in each day. For Fastloc-GPS data, this represented the location with the lowest residual error in each 24 h period. This data reduction technique was adopted to manage autocorrelation that inherently exists within animal movement-tracking data sets (DeSolla et al. 1999). The resulting location data sets for each turtle, that is, Argos-derived and Fastloc-GPS, were then subjected to two-dimensional kernelling to estimate utilization distributions, a typical approach used to assess home range size (Worton 1989). Kernels (quartic) of turtle locations were produced using a gridding interval of 50 m and a smoothing factor of 750 m. Volume contour polygons describing 50% of most densely aggregated data were derived from the kernelled data; areas of these polygons that did not intersect land, which can occur for individuals that occupy neritic habitats very close to shore, were calculated using area integration.

Estimating Argos Location Error

Argos-derived locations for each turtle, irrespective of their location class, were matched to Fastloc-GPS locations only when these two independent estimates of position occurred within 1 h. For each of these Argos–Fastloc 'matched' locations we then determined the position closest in time to a 1 min-interpolated Fastloc-GPS data set; this interpolated position was then taken to be the reference location from which Argos-derived location class accuracy was estimated.

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Minimum straight-line scalar distance between these two geolocation events was then determined using great-circle principles. Absolute longitudinal and latitudinal errors were calculated. This procedure was undertaken twice, first using unfiltered Argos-derived locations and subsequently using speed- and azimuth-filtered Argos-derived locations; both Argos-derived location data sets excluded LC Z locations and were subject to ‘swapping’.

RESULTS

Argos-derived and Fastloc-GPS Location Data Sets

A total of 27 863 Argos transmissions (messages) were received from Argos–Fastloc PTTs ($N = 9$), resulting in 7926 Argos-derived locations. Argos-derived locations assigned location class LC Z were eliminated ($N = 196$, 2.5% of data set) and 0.5% of locations ($N = 36$; LC 2: $N = 8$; LC 1: $N = 6$; LC 0: $N = 9$; LC A: $N = 7$; LC B: $N = 6$) were subject to ‘swapping’, where the primary and mirror locations were exchanged. The number of remaining Argos-derived locations assigned to LC 3–LC 0 ($N = 2745$) represented 35.5% of the Argos data set ($N = 7730$); auxiliary locations LC A and LC B represented 27.3% ($N = 2116$) and 37.1% ($N = 2869$), respectively, of the data set.

A total of 5058 Fastloc-GPS locations were obtained from data received from the Argos–Fastloc PTTs ($N = 9$). Locations derived using five or fewer signals from GPS satellites ($N = 1653$; 32.7%) were eliminated, as were remaining locations with estimated residual errors greater than 30 ($N = 19$; 0.6%). Filtered Fastloc-GPS locations ($N = 3385$) were derived from (mean ± 1SD) 7.1 ± 0.9 satellites (range 6–10).

The mean at-liberty period for instrumented turtles (Appendix Fig. A1), derived from the day of PTT deployment to either the final Argos-derived location or final Fastloc-GPS location was 137 ± 43 days (range 68–191 days). In all instances, the duration of Argos-derived location data was equivalent to ($N = 4$) or longer than ($N = 5$) that of Fastloc-GPS location data. The mean duration of Fastloc-GPS location data was 117 ± 37 days (range 68–183 days).

Accuracy of Argos Locations

A total of 2126 estimates of Argos-derived location accuracy were possible (LC3: $N = 73$; LC 2: $N = 134$; LC 1: $N = 222$; LC 0: $N = 163$; LC A: $N = 666$; LC B: $N = 868$) when using Fastloc-GPS locations occurring within 1 h as spatial reference locations. Speed filtering of Argos-derived location data led to the removal of 610 estimates of Argos-derived location accuracy (LC3: $N = 8$; LC 2: $N = 27$; LC 1: $N = 67$; LC 0: $N = 76$; LC A: $N = 184$; LC B: $N = 248$), and azimuth filtering led to the removal of an additional 158 estimates (LC3: $N = 8$; LC 2: $N = 7$; LC 1: $N = 3$; LC 0: $N = 6$; LC A: $N = 35$; LC B; $N = 99$). Although we corrected for temporal differences between geolocation estimates, by interpolating the Fastloc-GPS location data, increases in the time threshold led to decreasing estimated accuracy for Argos-derived locations assigned to classes LC 1 and LC 0 in both the unfiltered and speed- and azimuth-filtered data sets (Fig. 1). We therefore report accuracy for Argos-derived locations where Argos-derived and Fastloc-GPS locations occurred within 30 min.

The relative accuracy of unfiltered Argos-derived locations (i.e. the mean and standard deviation of all scalar distances between the reference Fastloc-GPS location and associated Argos location; $N = 1320$; LC 3: 0.4 ± 0.3 km; LC 2: 0.8 ± 0.9 km; LC 1: 1.0 ± 1.3 km; LC 0: 5.6 ± 16.7 km; LC A: 3.5 ± 9.2 km; LC B: 14.3 ± 135.6 km) was broadly as expected according to previous tests of the system (Hays et al. 2001; Vincent et al. 2002; CLS 2008), with LC3 > LC 2 > LC 1 and LC A > LC 0 and LC B (Fig. 2). Errors in LC 3, LC 2 and LC 1 were, in some cases, substantial, with outliers being as much as 2.0, 5.2 and 8.8 km away from their paired interpolated Fastloc-GPS position (Fig. 2). In general, we found mean errors for locations assigned to LC 3 and LC 2 to be approximately twice as large as those published by CLS Argos (CLS 2008). Speed- and azimuth-filtering of Argos-derived location data (Fig. 2) resulted in increased accuracy for all location classes ($N = 848$; LC 3: 0.4 ± 0.2 km; LC 2: 0.7 ± 0.7 km; LC 1: 0.8 ± 0.7 km; LC 0: 2.3 ± 2.7 km; LC A: 1.4 ± 2.5 km; LC B: 1.8 ± 3.9 km). There were, however, still a small number of LC 3, LC 2 and LC 1 locations that were up to 1.0, 4.6 and 3.9 km, respectively, away from their estimated position (Table 1). In general, errors for all location classes were elliptical with greater longitudinal error (Fig. 3a–f, Table 1).

Animals on the Move

As examples, movement trajectories for single green and leatherback turtles were reconstructed using location data available from both geolocation methods. During directed movements over large spatial scales (many hundreds of kilometres), Argos-derived location data once filtered can provide a faithful representation of these wide-ranging directed movements (Fig. 4a, c). For more tortuous movements the higher proportion of ‘lower’ accuracy Argos-derived locations seen with the tracking of marine species become more problematic for reconstruction movements. For both individuals, the tortuous movements in neritic environments (Fig. 4b, d), as reconstructed from Argos-derived locations and Fastloc-GPS locations, appear to diverge, yet Argos-derived locations still appropriately geolocate individuals at order of tens of kilometres.

Home Range Assessment

Describing patterns of habitat use by diving animals, such as marine turtles, when they are resident in neritic habitats is particularly challenging as they spend much of their time submerged. We compared the two geolocation methods, Argos-derived and Fastloc-GPS, for green turtles whose behaviour facilitated home range assessment in neritic foraging ($N = 4$, Fig. 5a–d) and internesting ($N = 1$, Fig. 5e) habitats. Point-pattern kernelling of these Argos and Fastloc time series indicated that Argos-derived geolocation located individuals to approximate areas of habitation as described by Fastloc-GPS. Home range estimates from the two geolocation methods were broadly similar although Fastloc-GPS data tended to identify two centres of activity at neritic foraging sites, whereas Argos-derived positions resulted in more diffuse single habitat use areas.

For green turtles in neritic foraging habitats on the coast of Brazil, 50% home ranges were estimated to be 4.3 km^2, 3.8 km^2, 3.2 km^2 and 2.4 km^2 using Argos-derived location data and, for the respective turtles, 2.2 km^2, 1.1 km^2, 2.6 km^2 and 1.4 km^2 using Fastloc-GPS location data. For a single green turtle that remained near the island of Ascension for 37 days following Argos-Fastloc-GPS PTT attachment, the internesting habitat range was estimated to be 2.4 km^2 using Argos-derived location data and 0.7 km^2 using Fastloc-GPS location data. If Fastloc-GPS location is taken to be the more accurate of the geolocation methods, with errors one or two orders of magnitude less than Argos-derived location data, then we see Argos-derived location data can lead to home range estimates that are twice as large as with Fastloc-GPS.

DISCUSSION

Given the intense fundamental and applied interest in generating high-precision routes of vertebrates it is likely that the use of standard Argos PTTs and Argos–Fastloc PTTs will continue to increase; especially with the arrival of Fastloc-GPS PTTs opening up

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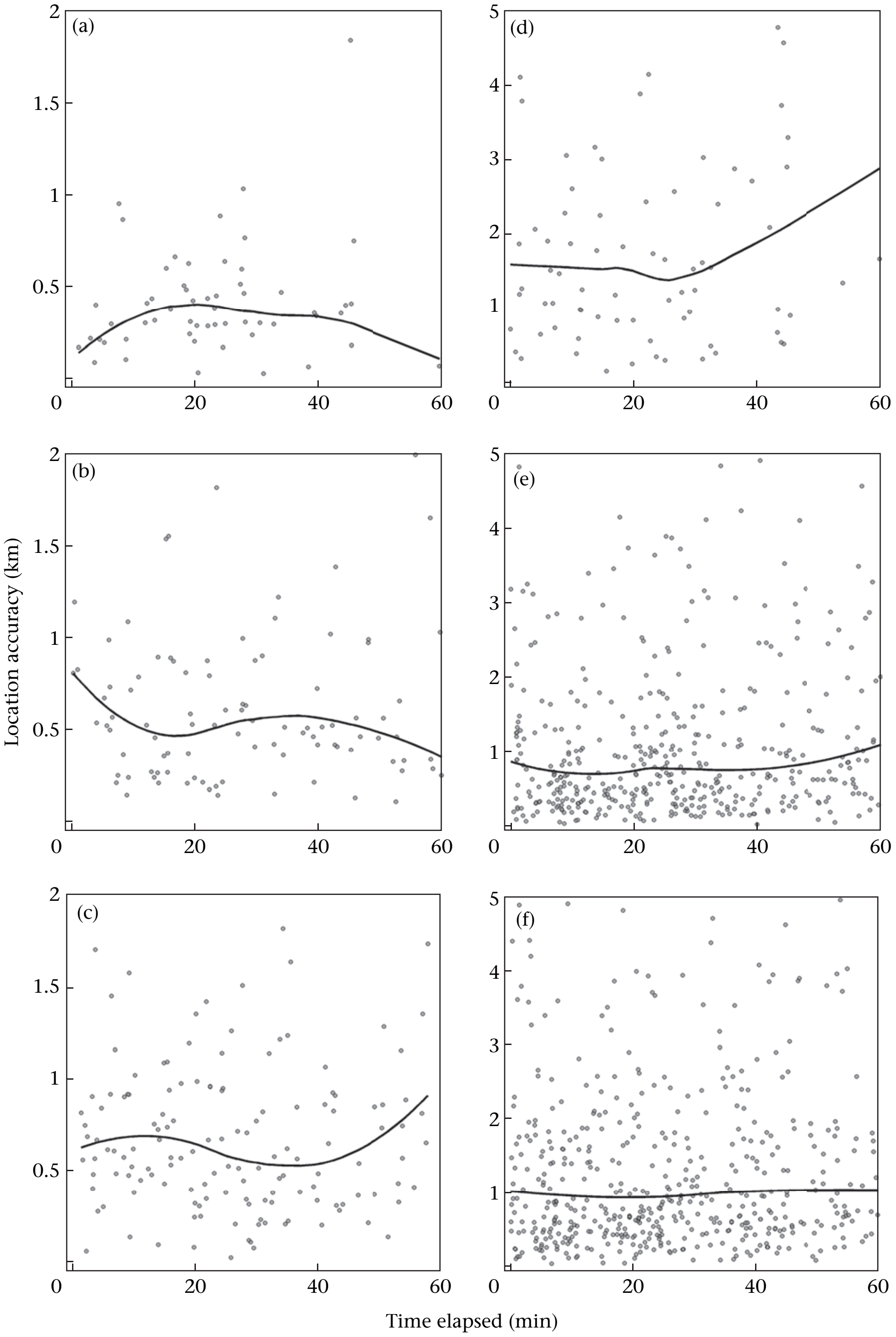

Figure 1. Relationship (solid line: locally weighted scatter plot smoothing; Cleveland 1979) of time elapsed between speed- and azimuth-filtered Argos-derived locations and estimated location accuracy for LC classes 3, 2, 1, 0, A and B (a–f, respectively) using 1 min-interpolated Fastloc-GPS reference locations. Argos-derived locations of standard (LC 3, LC 2 and LC 1) and auxiliary (LC 0, LC A and LC B) locations use differing *Y* axis limits. Number of locations (number of outliers, not shown): 57(0), 95(5), 141(11), 73(8), 424(23), 484(37) for LC classes 3, 2, 1, 0, A and B, respectively.

this latter technique for marine vertebrates (Schofield et al. 2007; Kuhn et al. 2009; Sims et al. 2009). It is, therefore, of great utility at this early stage to explore critically both methods including analysis of Argos-derived location accuracy, longevity and relative merits for reconstructing and analysing animal movements at different scales. We discuss each of these in turn.

Argos-derived Locations

The use of Argos–Fastloc PTT technology has allowed in situ testing of Argos-derived location accuracy at oceanic scales. Two major lessons emerge. First, Argos-derived location classes (LC) 3, 2 and 1 are likely to be almost as reliable as CLS Argos reports (CLS

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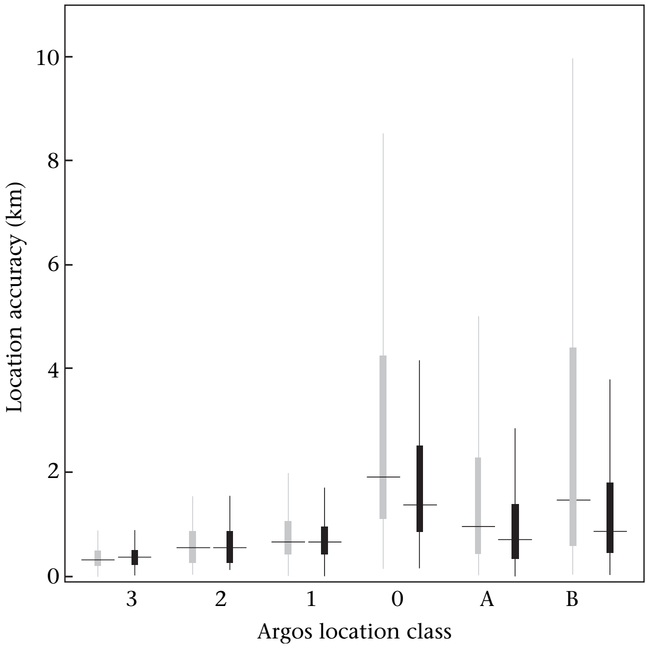

Figure 2. Distribution of estimated accuracy of Argos-derived location classes using unfiltered location data (grey bars) and speed- and azimuth-filtered location data (black bars). Horizontal line on each box indicates median value, edges of boxes are the 25th and 75th percentiles, Whiskers extend to mean of the distribution ± 2.7 standard deviations.

2008). However, it should be stressed that this does not mean that all locations assigned LC 3, LC 2 and LC 1 can be assumed to be highly accurate. Our data showed that a small proportion of these locations are unreliable and even after filtering some may be as much as several kilometres outside their reported error margins; this concords with the Argos definition of location accuracy estimates, which equates to 1 standard deviation from the true location. Second, in general we confirm the typical accuracy of LC A > LC B > LC 0 as has been described previously (Hays et al. 2001). After filtering, however, the accuracy of LC A was not a great deal better than that of LC B. Hays et al. (2001) presented a mean error of 0.99 km for LC A locations ($N = 18$) which was substantially lower than any published before (Boyd et al. 1998; Britten et al. 1999) or since (Robson et al. 2004; Troëng et al. 2005; Soutullo et al. 2007; this study).

To date, a number of publications from several research groups, including our own, have cited Hays et al. (2001) to justify the inclusion of LC A Argos-derived locations and the discarding of locations assigned LC 0 and LC B (e.g. sea turtles: Cardona et al. 2005; James et al. 2005; Shaver et al. 2005; Blumenthal et al. 2006; McMahon & Hays 2006; Cuevas et al. 2008; birds: Miller et al. 2005; Pinaud & Weimerskirch 2005; Soutullo et al. 2007; sharks: Rowat & Gore 2007). Given our findings, we would strongly caution against this approach in future studies and we would recommend the inclusion, when needed, of LC A and LC B Argos-derived locations in route reconstruction and the judicious use of speed and azimuth filtering to retain plausible locations assigned LC 0.

Our accuracy estimates for Argos-derived location classes, LC 3 to LC 1, broadly concord with Hazel (2009); for example: LC 3: this study: 0.4 ± 0.2 km ($N = 54$); Hazel (2009): 0.5 ± 0.2 ($N = 3$); LC 2: this study: 0.7 ± 0.7 km ($N = 81$); Hazel (2009): 0.8 ± 0.6 ($N = 5$). Yet our accuracy estimates for LC A and LC B are considerably smaller; for example: LC A: this study: 1.4 ± 2.5 km ($N = 398$); Hazel (2009): 8.0 ± 15.4 km ($N = 38$); LC B: this study: 1.8 ± 3.9 km ($N = 546$); Hazel (2009): 11.5 ± 19.7 km ($N = 95$). We note, however, that our data volumes are between 6 (LC B) and 10 (LC A) times greater for these classes, and in Hazel (2009) individuals were tracked in different habitat types with Argos–Fastloc PTTs attached to study animals using tethered systems. This attachment method is likely to promote better reception of GPS signals and transmission of Argos PTT messages, but probably increases entanglement risk and earlier cessation of PTT function.

Longevity of Tracking

Although our tags had a relatively short life span, this was to be expected considering the increased power demands for Fastloc-GPS data acquisition. The Argos–Fastloc PTTs used on leatherback turtles were considerably smaller, in mass, forward-facing cross-sectional profile and attachment technique, than those previously deployed on this species (leatherback sea turtles: Ferraroli et al. 2004; Hays et al. 2004; Shillinger et al. 2008). For green turtles, Argos–Fastloc PTTs generally lasted longer than traditional Argos PTTs on the same population (Luschi et al. 1998; Hays et al. 2001). Argos and Fastloc-GPS functions of the Argos–Fastloc PTTs appear generally to fail together, which is likely to result from tag detachment, antenna damage, biofouling, battery exhaustion or study animal mortality (Hays et al. 2007), but in some cases Fastloc-GPS did fail earlier. In principle, Argos transmissions (messages) can continue to be received with Fastloc-GPS locations encoded within them, without it being possible to determine Argos-derived locations; however, this was not observed in this study.

It is difficult to make meaningful like-for-like comparisons on the volume of locations produced by the two geolocation methods as pseudo duty cycling introduced by surfacing behaviour, Argos receiver availability and the programmed duty cycling of Fastloc-GPS acquisition, necessary to extend the operational life of PTTs, are all confounding. In principle, a Fastloc-GPS location can be gathered on almost all surfacing events, thereby providing a greater number

Table 1
Estimated accuracies of unfiltered and speed- and azimuth-filtered Argos-derived location classes

Location class	Unfiltered Argos locations				Speed & azimuth-filtered Argos locations			
	Locations	Accuracy (km)	Longitudinal error (degrees)	Latitudinal error (degrees)	Locations	Accuracy (km)	Longitudinal error (degrees)	Latitudinal error (degrees)
3	54	0.4±0.3 (0.00–2.0)	0.003±0.003	0.002±0.002	43	0.4±0.2 (0.03–1.0)	0.003±0.002	0.002±0.002
2	81	0.8±0.9 (0.04–5.2)	0.006±0.007	0.003±0.005	60	0.7±0.7 (0.14–4.6)	0.005±0.006	0.003±0.004
1	133	1.0±1.3 (0.03–8.9)	0.007±0.011	0.004±0.006	92	0.8±0.7 (0.03–3.9)	0.006±0.006	0.003±0.003
0	108	5.6±16.7 (0.16–167.2)	0.042±0.144	0.020±0.048	56	2.3±2.7 (0.16–15.2)	0.017±0.244	0.008±0.008
A	398	3.5±9.2 (0.03–107.5)	0.023±0.065	0.018±0.053	278	1.4±2.5 (0.03–29.4)	0.009±0.016	0.007±0.017
B	546	14.3±135.6 (0.04–223.3)	0.045±0.179	0.097±1.209	319	1.8±3.9 (0.04–61.4)	0.013±0.034	0.007±0.012

Means are given ±1SD and range is given in parentheses. Accuracy is the mean of the scalar distances between each Argos-derived location, with its assigned location class, and the identified reference Fast-GPS location.

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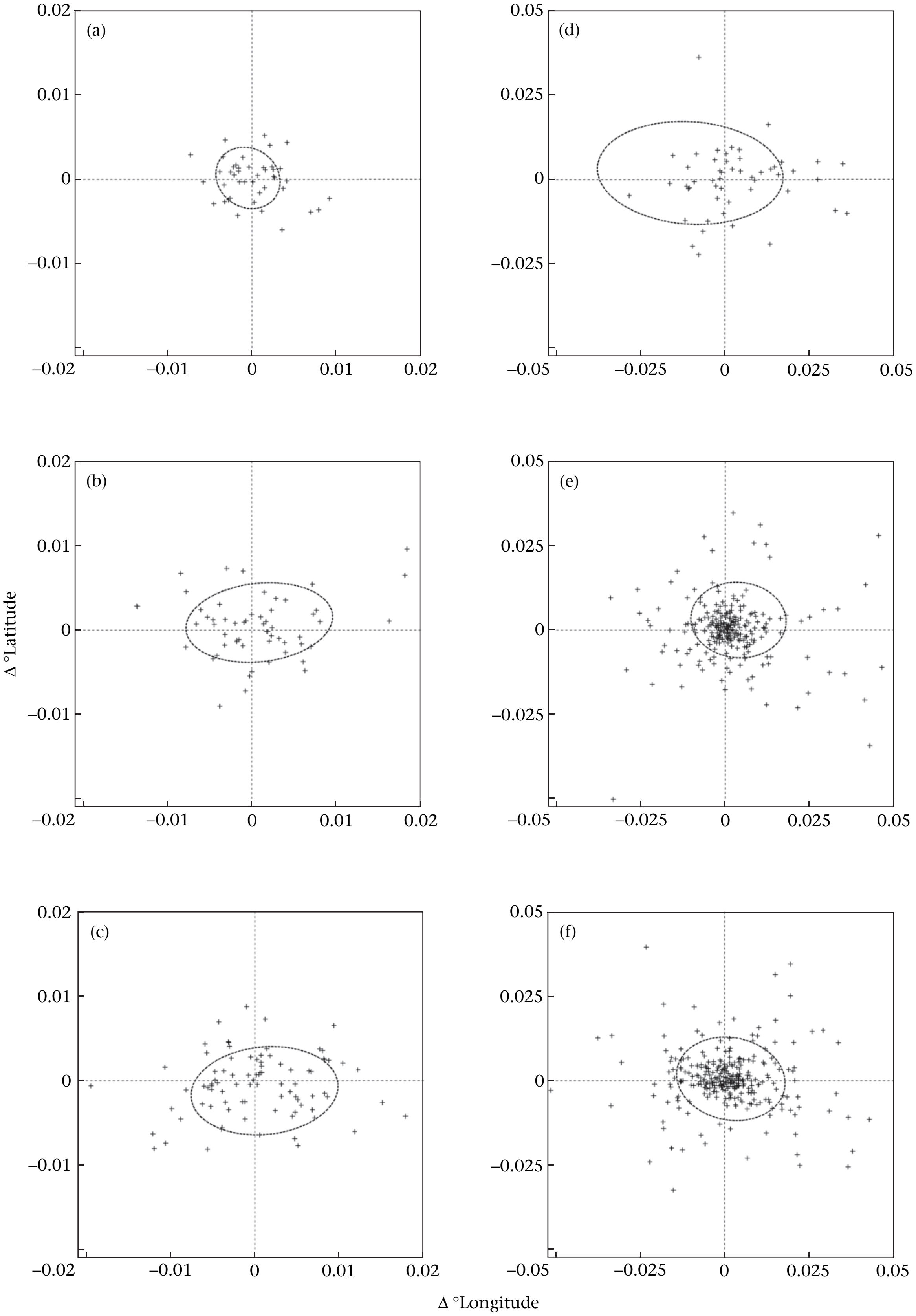

Figure 3. Estimated location accuracy of Argos-derived location classes 3, 2, 1, 0, A and B (a–f, respectively). Standard ellipses (polygon) fitted to 95% of data centred to origin using direct least-squares regression fitting. Number of locations (number of outliers, not shown): 43(0), 60(2), 92(4), 56(5), 278(10), 319(17) for LC classes 3, 2, 1, 0, A and B, respectively.

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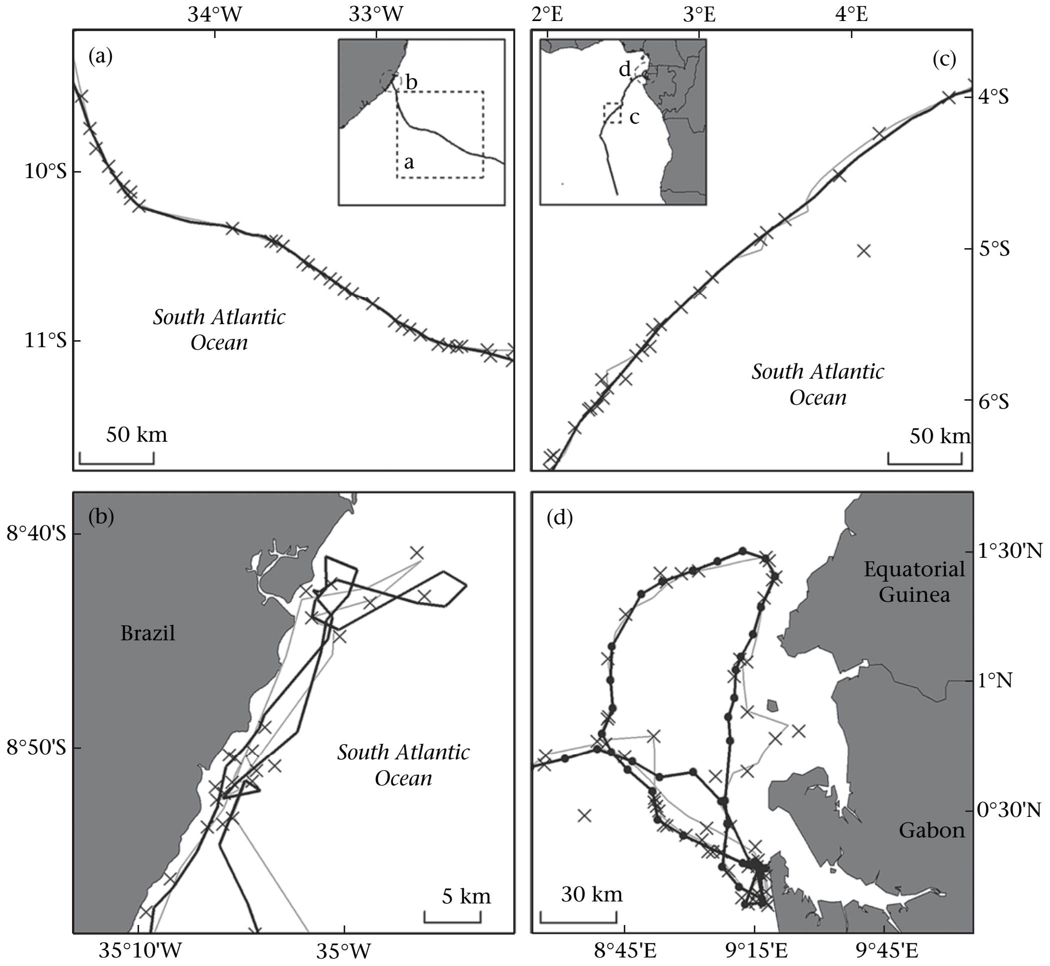

Figure 4. Movements of (a, b) a green and (c, d) a leatherback turtle recorded by Argos–Fastloc PTTs during (a, c) periods of directed movement and (b, d) periods of increased path tortuosity in neritic habitats. Fastloc-GPS reconstructed routes are indicated by a bold solid line, Argos-derived speed-filtered locations by crosses and reconstructed routes by a grey solid line.

of locations than available from typical Argos-derived geolocation, particularly as many surfacing events are likely to be inadequate for successful derivation of an Argos-derived location. In general we see that Fastloc-GPS can provide more locations than the standard Argos approach to geolocation, which are of greater spatial accuracy, but achieving this leads to reduced PTT longevity, owing to increased power demands.

Animals on the Move

The relative strengths and weaknesses of Argos-derived geolocation versus Fastloc-GPS geolocation are dependent upon the research objectives. It is clear, however, that Argos-derived geolocation is sufficient for tracking animals undertaking movements on the order of several hundred kilometres or more, but given the advent of Fastloc-GPS we see that Argos-derived geolocation data are not best suited for studies seeking to investigate at-sea decision making processed with oceanographic parameters or well-defined spatially explicit human impacts (Halpern et al. 2008; Seminoff et al. 2008; McClellan & Read 2009) or to feed into state-space-based modelling approaches (Jonsen et al. 2006; Sumner et al. 2009). In the future, Fastloc-GPS geolocation is likely to be the method of choice for undertaking home range assessment or investigating foraging behaviour in neritic or pelagic habitats; however, Argos-derived geolocation will be adequate if users seek to identify apparent areas of activity or overall patterns of fidelity (e.g. Broderick et al. 2007).

Caveats

There are two caveats to our analysis. First, there is some error with Fastloc-GPS (Hazel 2009), although it is likely to be at least one order of magnitude less than the in situ Argos errors we sought to parameterize. Second, Argos-derived and Fastloc-GPS locations were not simultaneous, and as such we had to interpolate a temporally coincident location along the Fastloc-GPS-derived track to evaluate the location class of individual Argos-derived locations. These may have introduced some error into our calculations.

As previously highlighted (Frazier 2000), we suggest that it is important for workers to continue to refine location class accuracy estimates because the parameters offered by CLS Argos more closely represent those experienced under ideal scenarios, yet field-quality assurance data rarely, if ever, match the CLS Argos criteria and regional differences appear to exist in LC accuracy (Dubinin et al. 2010). It is often left to Argos users to define both the error associated with 'auxiliary' location classes, which represent the main proportion of many tracking data sets (for which CLS Argos provides no reference), and what level of error they consider acceptable for their study. Additionally, we need constantly to

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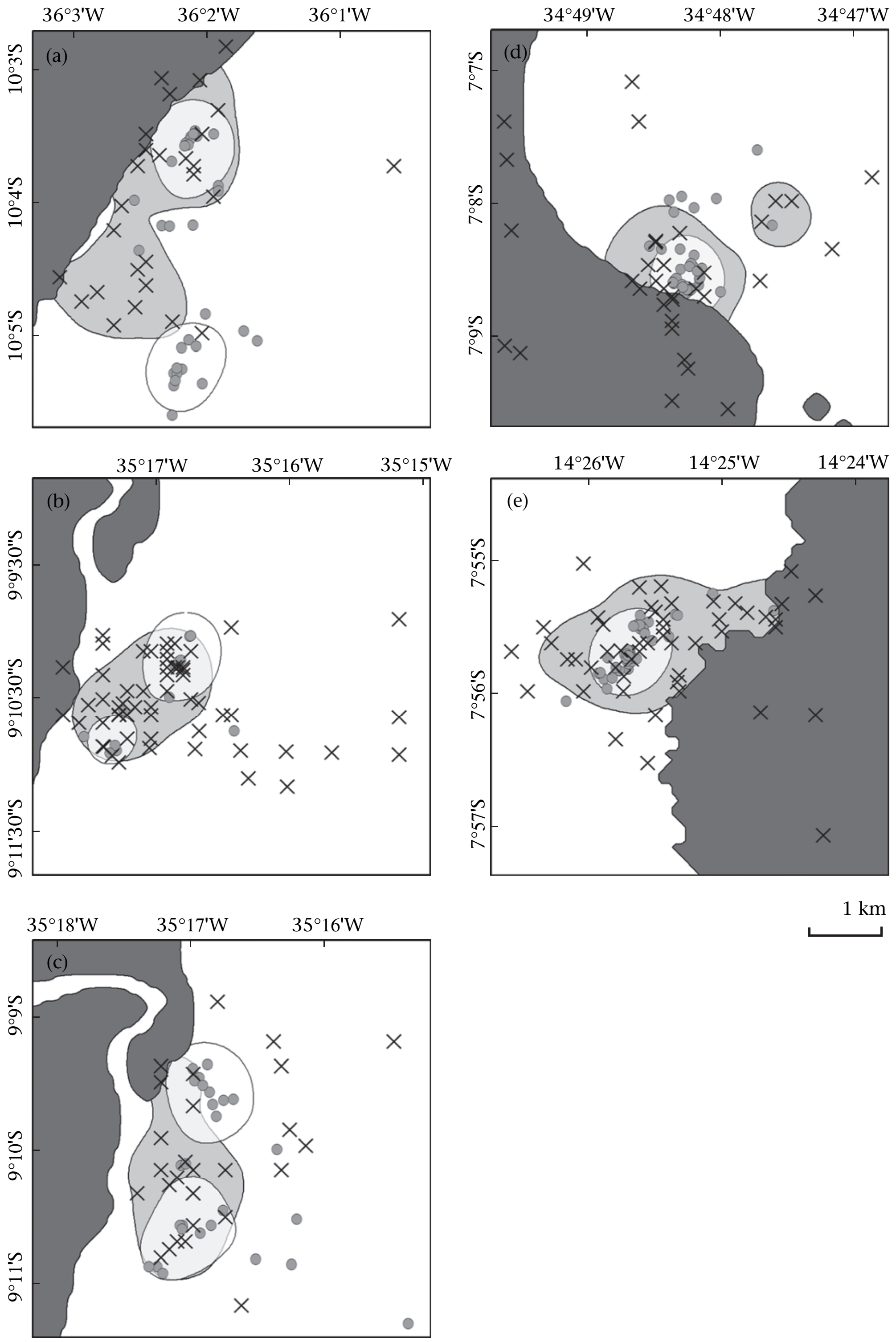

Figure 5. Home range estimates for green turtles in (a–d) neritic foraging habitats and (e) internesting habitat derived from Argos-derived (dark grey polygons) and Fastloc-GPS (light grey polygons) kernelled location data. Filled contours are 50% volume density estimates from quartic kernelling. Data shown are single daily estimates of position. Argos locations are indicated by crosses and Fastloc locations by filled circles.

reassess the parameters used for filtering data. Greater transparency in published satellite-tracking data will greatly inform the development of analytical techniques (Royer & Lutcavage 2008; Tougaard et al. 2008) accessible to the majority of wildlife biologists, without the need for expensive software or advanced statistical knowledge. Utilization of Fastloc-GPS has the potential to help us extract maximum information from archived Argos-derived location data sets as researchers combine data towards meaningful meta-analysis (Godley et al. 2008).

In closing, the use of Argos–Fastloc PTT technology is in its early stages and shows great promise but we suggest that given the increased cost (thus lowered sample size) and increased power

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demand (thus lowered tracking duration), that the technique is not a panacea to vertebrate tracking. Provided sufficient data volumes are obtained, there is clearly still a role for Argos-derived geolocation for large-scale movements, especially as filtering becomes more effective. The true power in Argos–Fastloc PTT tracking will be when high-resolution movements are needed for studies of navigation and home range in species that cannot be easily recaptured, for example sharks and rays (Gore et al. 2008; Pade et al. 2009; Skomal et al. 2009) and whales (Mate et al. 1997), particularly for species that spend short periods of time at, or near, the surface and where Fastloc-GPS can greatly improve upon light-based geolocation (Hill 1994) or Argos.

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APPENDIX

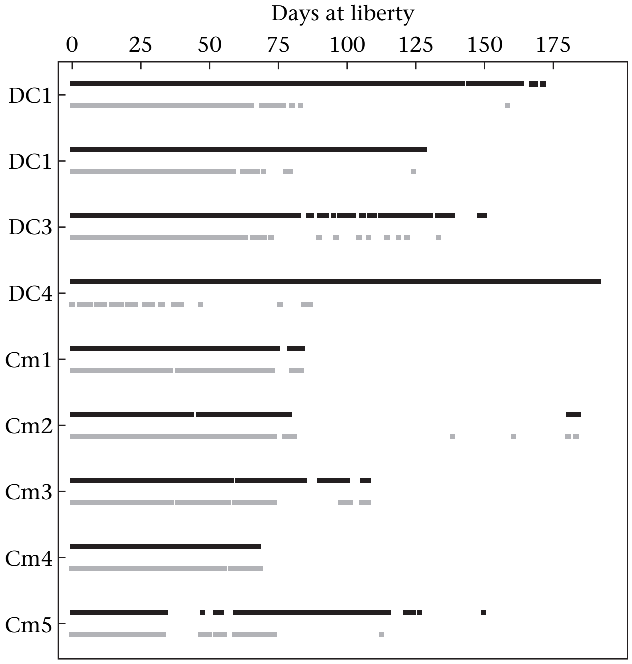

Figure A1. Temporal occurrence of unfiltered Argos-derived locations (black bars; location classes 3, 2, 1, 0, A and B) and Fastloc-GPS locations (grey bars), derived from six or more satellites with residual error of 30 or less. Green turtles: Cm 1–5; Leatherback turtles: Dc 1–4; green turtles: Cm 1–5.