



Swansea University
Prifysgol Abertawe



Cronfa - Swansea University Open Access Repository

This is an author produced version of a paper published in:

Marine Biology

Cronfa URL for this paper:

<http://cronfa.swan.ac.uk/Record/cronfa35936>

Paper:

Thomson, J., Börger, L., Christianen, M., Esteban, N., Laloë, J. & Hays, G. (2017). Implications of location accuracy and data volume for home range estimation and fine-scale movement analysis: comparing Argos and Fastloc-GPS tracking data. *Marine Biology*, 164(10)

<http://dx.doi.org/10.1007/s00227-017-3225-7>

This item is brought to you by Swansea University. Any person downloading material is agreeing to abide by the terms of the repository licence. Copies of full text items may be used or reproduced in any format or medium, without prior permission for personal research or study, educational or non-commercial purposes only. The copyright for any work remains with the original author unless otherwise specified. The full-text must not be sold in any format or medium without the formal permission of the copyright holder.

Permission for multiple reproductions should be obtained from the original author.

Authors are personally responsible for adhering to copyright and publisher restrictions when uploading content to the repository.

<http://www.swansea.ac.uk/library/researchsupport/ris-support/>

1 **Implications of location accuracy and data volume for home range estimation and fine-**
2 **scale movement analysis: comparing Argos and Fastloc-GPS tracking data**

3

4 J.A. Thomson^{1*}, L. Börger², M.J.A. Christianen^{3,4}, N. Esteban², J.-O. Laloë¹, G.C. Hays¹

5

6 ¹Deakin University, Geelong, Australia, School of Life and Environmental Sciences, Centre for
7 Integrative Ecology, Warrnambool, VIC 3280, Australia

8 ²Department of Biosciences, Swansea University, Swansea SA2 8PP, UK

9 ³Institute for Wetland and Water Research, Radboud University Nijmegen, Heyendaalseweg
10 135, 6525 AJ Nijmegen, The Netherlands

11 ⁴Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103,
12 9700 CC Groningen, The Netherlands

13

14 * corresponding author: jordy.thomson@deakin.edu.au; +61 3 556 33037

15

16

17

18

19

20

21

22 **Keywords:** habitat use; home range analysis; movement ecology; satellite telemetry; satellite
23 tracking; sea turtle

24

25 **Abstract**

26 The advent of Fastloc-GPS is helping to transform marine animal tracking by allowing the
27 collection of high-quality location data for species that surface only briefly. We show how the
28 improved location accuracy of Fastloc-GPS compared to Argos tracking is expected to lead to far
29 more accurate home range estimates, particularly for animals moving over the scale of a few km.
30 We reach this conclusion using simulated data and home range estimates derived from empirical
31 tracking data for green sea turtles (*Chelonia mydas*) equipped with Argos linked Fastloc-GPS
32 tags at three different foraging areas (western Indian Ocean, Western Australia and Caribbean).
33 Poor quality Argos locations (e.g., location classes A, B) produced home range estimates ranging
34 from 10 to 100 times larger than those derived from Fastloc-GPS data, whereas high-quality
35 Argos locations (location classes 1-3) produced home range estimates that were generally
36 comparable to those derived from Fastloc-GPS data. However, the limited number of Argos class
37 1-3 locations obtained for all three turtles – an average of 14.6 times more Fastloc-GPS locations
38 were obtained compared to Argos class 1-3 locations – resulted in blurred patterns of space use.
39 In contrast, the high volume of Fastloc-GPS locations revealed fine-scale movements in striking
40 detail (i.e., use of discrete patches separated by just a few hundred m). We recommend careful
41 consideration of the effects of location accuracy and data volume when developing sampling
42 regimes for marine tracking studies and make recommendations regarding how sampling can be
43 standardized to facilitate meaningful spatial and temporal comparisons of space use.

44 **Introduction**

45 Understanding patterns of space use by animals lies at the heart of many ecological studies and
46 also underpins many efforts to make evidenced-based management decisions, for example as
47 part of conservation planning (Cooke 2008). Thanks to increased accessibility of tracking
48 technology (Kays et al. 2015; Hays et al. 2016), both the number of taxa tracked and the number
49 of studies collecting movement data across different habitats are rapidly increasing. However,
50 the ability to reliably detect differences in space use among individuals, species and locations
51 crucially depends on the sampling regime used including the accuracy and amount of location
52 data obtained (Börger et al. 2006a, b; Frair et al. 2010; Hebblewhite and Haydon 2010;
53 Montgomery et al. 2011; McClintock et al. 2015). While the importance of the quality and
54 abundance of location data for studying animal movements has been well known for some time
55 in certain fields, particularly terrestrial ecology (e.g., Harris et al. 1995), in other fields with a
56 shorter tracking history the message is less well appreciated. As such, it is important to revisit
57 some of the key messages in home range estimation to avoid methodological artefacts obscuring
58 true differences in space use.

59

60 In the marine context, a major advance in recent years has been the advent of Fastloc-GPS
61 tracking (Kuhn et al. 2009; Hazen et al. 2012; Hoenner et al. 2012). Conventional GPS receivers
62 need several seconds to generate a location estimate, which has precluded their use on marine
63 species that only surface briefly. In contrast, Fastloc-GPS overcomes this problem with the rapid
64 (typically tens of milliseconds) acquisition of GPS data when an animal surfaces and subsequent
65 post-processing to derive position estimates. Fastloc-GPS has massively improved the accuracy
66 of location data compared to traditional Argos tracking and is now widely used to track diverse

67 marine taxa including sea turtles (Hazel et al. 2009; Schofield et al. 2010a, b), marine mammals
68 (Costa et al. 2010) and fish (Sims et al. 2009). Fastloc-GPS tags can be deployed as data-loggers,
69 which store data for subsequent download when the unit is retrieved, or can be interfaced with an
70 Argos tag (i.e. Argos linked Fastloc-GPS tags) so that data are received by the Fastloc-GPS
71 receiver and then relayed via the Argos system.

72

73 Here, we consider the implications of high resolution Fastloc-GPS tracking for home range
74 estimation and fine-scale movement analysis in sea turtles. First, we use simulations to show the
75 general importance of location accuracy for home range estimation. We then support these
76 simulations with empirical data collected for green turtles (*Chelonia mydas*) tracked using Argos
77 linked Fastloc-GPS tags, which allowed the utility of both the Argos and Fastloc-GPS data to be
78 compared for the same individuals. Finally, we provide recommendations for how future work
79 might proceed to identify fine-scale patterns of space use within and among individuals, species
80 and study systems in the marine environment.

81

82 **Materials and Methods**

83 *Simulations*

84 To evaluate the impact of location accuracy on home range estimation, we generated
85 distributions of the location of simulated animals whose available habitat size varied by three
86 orders of magnitude. For computational simplicity, we drew animal locations ($N = 1000$) from a
87 bivariate normal distribution within square-shaped habitats of 1, 10, 100 and 1000 km². We
88 considered these to be the ‘true’ animal locations. We then used the package *adehabitatHR*
89 (Calenge 2006) in R v. 3.3.2 (R Core Team 2016) to estimate the 95% home range of the animal

90 in each habitat size via the fixed kernel method (Worton 1989). We used the reference bandwidth
91 (h_{ref}) as a smoothing parameter, which is suitable for bivariate normal data (Calenge 2006) and
92 provides a conservative estimate thanks to oversmoothing (Bowman and Azzalini 1997).

93

94 We then introduced errors to the ‘true’ animal locations to obtain home range size estimates
95 under different levels of location accuracy. We did so by drawing random errors from a bivariate
96 normal distribution with a mean of 0 and a standard deviation (SD) ranging from 0 to 2 km in
97 increments of 0.01. This range was selected because it would encompass Fastloc-GPS errors
98 (Hazel et al. 2009, Dujon et al. 2014) and most Argos location class errors excluding those with
99 the highest uncertainty such as classes 0 and B (Costa et al. 2010). Our aim here was not to
100 evaluate specific location classes because reported errors vary considerably among studies
101 (Table 1). Rather, we sought to assess the impact of location accuracy along a gradient that
102 would include location qualities commonly encountered in sea turtle home range studies. For
103 simplicity, we assumed that latitudinal and longitudinal errors were equivalent. While we are
104 aware that Argos error distributions tend to be elliptical, with longitudinal exceeding latitudinal
105 errors (Hays et al. 2001; Costa et al. 2010; Boyd and Brightsmith 2013), this does not affect our
106 ability to illustrate the general impact of location quality on home range estimation across orders
107 of magnitude of animal movements.

108

109 The random errors ($N = 1000$ for each theoretical animal) were added to the ‘true’ simulated
110 animal locations to create error-added location data sets. We then used the kernel method, as
111 above, to estimate each animal’s 95% home range size using the error-added locations and
112 calculated the percent error between this value and the true home range size. This was repeated

113 10 times for each animal for a total of $4 \times 10 \times 201 = 8040$ iterations. We calculated the mean
114 percent error at each increment of SD (location error) and smoothed the resulting curve for each
115 simulated animal by calculating a running mean spanning three consecutive data points. For ease
116 of visualization, percent error data were $\log_{10}(x+1)$ -transformed.

117

118 *Empirical case study*

119 We equipped green turtles with Argos linked Fastloc-GPS tags (SPLASH10-BF tags, Wildlife
120 Computers, Seattle, Washington) at three sites around the world: the Chagos Archipelago (Indian
121 Ocean) in 2012, Shark Bay (Western Australia) in 2016 and Bonaire (Caribbean Netherlands) in
122 2016. These units collected and transmitted both Argos and Fastloc-GPS locations. To compare
123 home-range estimates from Argos versus Fastloc-GPS data, we selected one representative data
124 set from each site: a green turtle tracked for 14 months in the Chagos Archipelago, one tracked
125 for 3 months in Shark Bay and one tracked for 5 months in Bonaire. To compare the number of
126 Fastloc-GPS versus Argos locations obtained, we used data from all the turtles equipped in the
127 Chagos Archipelago and Shark Bay. Since the tags deployed in Bonaire were also programmed
128 to relay other data (e.g., depth) at the expense of sending Fastloc-GPS data, we did not include
129 these tags in the comparison of location data volume.

130

131 To remove locations that were likely erroneous, we filtered Argos and Fastloc-GPS data using
132 previously established methods. First, we examined each track and visually identified locations
133 that appeared inconsistent with adjacent points. We then applied a filter that excluded these
134 locations if they necessitated speeds-of-travel that were unrealistic based on known green turtle
135 swimming speeds during migration (i.e., $> 200 \text{ km d}^{-1}$) (Luschi et al. 1998; Dujon et al. 2014;

136 Hays et al. 2014; Christiansen et al., 2017). In addition, for Fastloc-GPS, we excluded locations
137 with a residual value ≥ 35 , which is standard for Fastloc-GPS data (Dujon et al. 2014). These
138 steps are representative of filtering applied in most Argos and Fastloc-GPS studies, and removed
139 a small ($< 1\%$) proportion of locations.

140
141 To remove the impact of fine-scale autocorrelation, we randomly selected a single location per
142 day from each location class (see below) for each turtle prior to estimating home range sizes. We
143 used the R package `adehabitatHR` to estimate home range size, as above. However, we used a
144 different smoothing approach since the ‘real-world’ latitude and longitude data were multi-modal
145 (i.e., not bivariate normal) and using the reference bandwidth can cause a large amount of over-
146 smoothing in such cases, leading to overestimation of home range size (Worton 1989; Kie 2013).
147 Instead, using a custom script in R, for each home range estimate we identified the minimum h-
148 value below which the continuous home range contour breaks up into two or more polygons (the
149 minimum-h rule, see Fieberg and Börger 2012 and references therein). Due to low sample size in
150 certain location classes, we pooled Argos classes 1, 2, and 3 together, lumped Fastloc-GPS
151 locations derived from 9 satellites with those derived from 8 satellites, and excluded Argos class
152 0 entirely.

153
154 Subsequently, in order to account for the possible impact of data volume on home range
155 estimation, we standardized the number of locations used to estimate home range size across
156 location classes. We did so for each individual by randomly selecting 75% of the smallest sample
157 size available in a location class for all location classes for that turtle 10 times. We then
158 estimated the 95% home range size at each iteration and calculated the mean and SE for each

159 location class. Since our aim here was to evaluate the trend in home range size across location
160 classes within each site/individual, as opposed to comparing turtle home range sizes among
161 sites/individuals, it was not necessary to use the same volume of data for each turtle. Therefore,
162 for our present purpose, we allowed the number of locations to vary from turtle-to-turtle based
163 on the amount of data obtained by each tag. For the Chagos turtle, many fewer locations were
164 available in Argos location classes 1-3 compared to other classes so we did not sub-sample this
165 location class, instead producing a single estimate of home range size.

166

167 **Results**

168 *Simulations*

169 The degree of error in home range size estimates in our simulations depended strongly on
170 location accuracy (SD) and habitat size (Fig. 1). Specifically, as habitat size increased, the
171 accuracy of locations needed to reliably estimate home range size decreased. For example, at a
172 habitat size of 1000 km², a location error distribution with an SD < 1.67 km was necessary to
173 produce < 10% error in home range size estimates. In contrast, at a habitat size of 1 km², a
174 location error distribution with an SD of < 0.06 km was necessary to achieve < 10% error (Fig.
175 1). The former case would likely include Argos location classes 1-3 and all Fastloc-GPS
176 locations, while the latter case would likely only include Fastloc-GPS locations derived from ≥ 5
177 satellites.

178

179 *Empirical case study*

180 For green turtles in the Chagos Archipelago, Western Australia and the Caribbean, home range
181 estimates declined by a factor of approximately 10, 12, and 100, respectively, when moving from

182 the poorest to the best location quality (Fig. 2). Argos location classes A and B dramatically
183 overestimated home range size whereas Argos location classes 1-3 provided generally
184 comparable estimates to Fastloc-GPS data, with the exception of the Caribbean turtle (Fig. 2).
185 However, Fastloc-GPS tracking revealed much more restricted movements and a much higher
186 degree of patchiness in space use compared to Argos tracking, which tended to blur the pattern
187 of space use (Fig. 3). This was true even when considering only the best-quality Argos data (i.e.,
188 location classes 1-3, Fig. 4). In this case the sparseness of class 1-3 Argos locations meant that
189 details of how multiple focal patches were used by each animal went unobserved. Compared to
190 location accuracy, standardizing data volume across location classes had a relatively minor
191 impact on the trend in home range size from the poorest to best location quality for both turtles
192 (Fig. 2).

193

194 On average there were 14.6 times (range 6.8 – 27.0) more Fastloc-GPS locations obtained
195 compared to high-quality (location class 1-3) Argos locations and this pattern for more Fastloc-
196 GPS data occurred across all individuals (Fig. 5). This increased volume of locations underlies
197 the much clearer pattern of space use that emerged when plotting the Fastloc-GPS data and the
198 tendency of these data to reveal how multiple small patches were used by each individual.

199

200 **Discussion**

201 In recent years, technological advances have led to rapid improvement in the quality of locations
202 obtainable for air-breathing marine vertebrates and some fish and, hence, increased variability in
203 track quality in the literature (e.g., Table 2 for sea turtles). As such, consideration of the impacts
204 of location accuracy and data volume for home range estimation and fine-scale movement

205 analysis for these species is timely. We have shown that location accuracy can profoundly
206 impact estimated home range size, with exceedingly large errors likely to occur under a
207 combination of low location accuracy and fine-scale animal movements. Furthermore, we have
208 shown that Fastloc-GPS tracking can reveal movement patterns in fine detail (i.e., patch use) in
209 situations where Argos data cannot. In studies looking at space use, we emphasize that it is
210 important to consider the level of location error inherent in the tracking system and how this
211 error interacts with the scale of movement to impact the picture of space use that emerges (see
212 also Montgomery et al. 2011 for terrestrial examples). Moreover, we urge caution when
213 comparing home range estimates obtained from different tracking systems or tag configurations
214 that provide locations of different levels of accuracy.

215

216 Recent movement analyses for sea turtles have been made using light-based geolocation, radio
217 telemetry, acoustic telemetry, Argos satellite tracking and Fastloc-GPS tracking, which have a
218 wide range of location accuracies (Table 2). These studies all provide important space use data
219 that are consistent within each study. For example, Schofield et al. (2010b) used Fastloc-GPS
220 data from loggerhead turtles in the Mediterranean to show that oceanic foragers had home ranges
221 > 50 times larger than neritic foragers, while Esteban et al. (2017) used Fastloc-GPS to quantify
222 the number of clutches individual green turtles laid in a single breeding season. However, while
223 Fastloc-GPS tracking has been available for several years, due to the lower cost of Argos tags,
224 many studies still rely on Argos locations (e.g., Hawkes et al. 2011; Fujisaki et al. 2016; Shaver
225 et al. 2016). Given the magnitude of error in home range estimates identified in our theoretical
226 and empirical examples (see also Witt et al. 2010), we argue that comparison of home range
227 estimates, in addition to other movement metrics (e.g., Bradshaw et al. 2007), should only be

228 made after carefully accounting for differences in location quality between tracks. For example,
229 it might be of interest to examine variation in home range size over space or time using a
230 combination of newer Fastloc-GPS and older Argos tracks. To do this reliably would require
231 decaying the GPS data by introducing random Argos-level errors to the GPS data (similar to the
232 approach taken in our theoretical home range analysis) and standardizing sample size among
233 tracks.

234
235 In addition to highlighting the relationship between location accuracy, the scale of animal
236 movements and home range estimation, we have demonstrated the potential for Fastloc-GPS data
237 to yield valuable new insights into the patterns, drivers and consequences of the movements of
238 sea turtles at very fine spatial scales (e.g., patch use dynamics). This utility of Fastloc-GPS for
239 examining fine-scale movements will likely apply to other marine taxa that only surface briefly
240 including some marine mammals, birds and fish. As in our study, an increased number of
241 Fastloc-GPS locations has been noted when Argos linked Fastloc-GPS tags have been attached
242 to fish (Sims et al. 2009; Evans et al. 2011). The increased number of Fastloc-GPS locations we
243 found is likely due to the fact that data for a Fastloc-GPS location can be encoded in a single
244 Argos uplink, while many uplinks in a single satellite overpass are required to generate an Argos
245 location of class 1-3. As such, the finding of a vastly greater volume of Fastloc-GPS locations
246 compared to Argos locations when using Argos linked Fastloc-GPS tags will likely be broadly
247 consistent across taxa. Furthermore, Fastloc-GPS tags can be used in data loggers, which can
248 increase data volume by a further order of magnitude compared to the data volumes recoverable
249 by satellite (Schofield et al. 2010b).

250

251 Future comparative studies that analyze GPS-based tracks of foraging turtles in a standardized
252 manner hold considerable potential to advance our understanding of turtle space use, trophic
253 relationships and functional roles in coastal ecosystems. It should be noted that, in addition to
254 location accuracy and data volume (e.g., Seaman et al. 1999; Börger et al. 2006a,b), other
255 components of home range analysis are also known to influence estimates of home range size
256 and should therefore be accounted for when designing comparative studies. For example, KDEs
257 can be strongly influenced by the smoothing parameter used (Worton 1989; Kie 2013), and the
258 choice of smoothing parameter will depend on the structure of the location data and the
259 particular question being asked (Fieberg and Börger 2012). Similarly, Service Argos have been
260 trying to improve the quality of their tracking data. Specifically, Service Argos introduced a new
261 method of estimating platform locations which combines their traditional approach – using the
262 Doppler shift in received uplink frequencies and a least-squares algorithm – with interpolation
263 between locations using Kalman filtering (Lopez et al. 2014). This new method of processing
264 tends to provide smoother tracks but the autocorrelation between locations introduced by Kalman
265 filtering will need to be considered if these data are used in home range estimation, especially
266 when compared with tracks without Kalman filtering. We hence urge researchersto retain both
267 the unfiltered locations as well as the Kalman-filtered locations and the estimated error ellipse.
268 Doing so will create the potential to implement more sophisticated analyses accounting for the
269 error of each single location. Refer to McClintock et al. (2015) for arguments regarding the
270 importance of using the error ellipse and not the error circle in movement analyses as well as the
271 importance of not discarding more ‘inaccurate’ locations (see Ironside et al. 2017 for a similar
272 remark for terrestrial GPS data).

273

274 Moreover, aspects of the movement pattern of animals may sometimes interact with methods of
275 data processing to influence the picture that emerges of space use. For example, visual
276 observations have shown that green turtles often rest in certain areas at night and then travel to
277 foraging locations during the day (Bjorndal 1980). The specifics of these movements have
278 recently been recorded in high resolution with Fastloc-GPS tracking (Christiansen et al. 2017),
279 with the finding that nighttime resting and daytime foraging areas may be several km apart. So,
280 in this case, only using daytime or nighttime locations, even if they are of high resolution, would
281 not capture the full extent of space use (see also general discussion in Fieberg and Börger 2012).
282 Likewise, locations around dawn and dusk are needed to identify migration corridors between
283 areas occupied during the night and day. Again, Fastloc-GPS opens up the potential of
284 addressing these questions but, at the same time, comparative studies of space use, across
285 individuals and across studies, will require careful consideration of these sources of variability.
286
287 In conclusion, our results highlight an important yet underappreciated aspect of movement
288 ecology study design for air-breathing marine vertebrates and some fish. Our understanding of
289 the fine-scale movements of these taxa lags well behind that of terrestrial vertebrates, which have
290 been tracked effectively using Argos and GPS systems for some time. For general considerations
291 on study design, we recommend consulting the framework that has grown out of that body of
292 work (e.g., Seaman et al. 1999; Börger et al. 2006a, b; Frair et al. 2010; Hebblewhite and
293 Haydon 2010; Montgomery et al. 2011; Fieberg and Börger 2012; McClintock et al. 2015;
294 Ironside et al. 2017). Here, we emphasize that location accuracy relative to the expected scale of
295 animal movements should be a key methodological consideration and we recommend caution

296 when comparing home range estimates and other movement metrics derived from tracking
297 systems with different location qualities and data volumes.

298

299 **Compliance with Ethical Standards**

300 All applicable international, national, and/or institutional guidelines for the care and use of
301 animals were followed. Fieldwork in Shark Bay was conducted under Department of Parks and
302 Wildlife (DPaW) Regulation 17 license #SF010887 and Florida International University IACUC
303 approval #IACUC-15-034-CR01. Fieldwork in Bonaire was conducted under a permit from the
304 “Openbaar Lichaam Bonaire” nr. 558/2015-2015007762 and was performed using appropriate
305 animal care protocols. In the Chagos Archipelago, fieldwork was approved by the Commissioner
306 for the British Indian Ocean Territory (BIOT) (research permit dated 2 October 2012) and
307 Swansea University Ethics Committee, and complied with all relevant local and national
308 legislation. The authors have no conflicts of interest.

309

310 **Acknowledgements**

311 We thank the Department of Parks and Wildlife, Western Australia for their assistance in
312 deploying satellite tags in Shark Bay. Fieldwork in Bonaire was funded by the Netherlands
313 Organization of Scientific Research (NWO-ALW 858.14.090). We thank Sea Turtle
314 Conservation Bonaire for their assistance in deploying satellite tags in Bonaire. Fieldwork in the
315 Chagos Archipelago was supported by a Darwin Initiative Challenge Fund grant (EIDCF008),
316 the Department of the Environment Food and Rural Affairs, the Foreign and Commonwealth
317 Office, College of Science of Swansea University, and the BIOT Scientific Advisory Group of
318 the FCO.

319

320

321 **References**

322 Bjørndal KA (1980) Nutrition and grazing behaviour of the green turtle *Chelonia mydas*. Mar
323 Biol 56:147–154. doi: 10.1007/BF00397131

324

325 Börger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T
326 (2006a) Effects of sampling regime on the mean and variance of home range estimates. J Anim
327 Ecol 75:1393–1405. doi: 10.1111/j.1365-2656.2006.01164.x

328

329 Börger L, Franconi N, Ferretti F, Meschi F, De Michele G, Gantz A, Coulson T (2006b) An
330 integrated approach to identify spatiotemporal and individual-level determinants of home range
331 size. Am Nat 168:471–485. doi: 10.1086/507883

332

333 Bowman AW, Azzalini A (1997) Applied smoothing techniques for data analysis. Clarendon,
334 Oxford.

335

336 Boyd JD, Brightsmith DJ (2013) Error properties of Argos satellite telemetry locations using
337 least squares and Kalman filtering. PLoS ONE:e.63051. doi: 10.1371/journal.pone.0063051

338

339 Bradshaw CJA, Sims DW, Hays GC (2007). Measurement error causes scale-dependent
340 threshold erosion of biological signals in animal movement data. Ecol Appl 17:628–638.

341

342 Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of space
343 and habitat use by animals. Ecol Model 197:516–519. doi: 10.1016/j.ecolmodel.2006.03.017

344

345 Christiansen F, Esteban N, Mortimer JA, Dujon AM, Hays GC (2017). Diel and seasonal
346 patterns in activity and home range size of green turtles on their foraging grounds revealed by
347 extended Fastloc-GPS tracking. *Mar Biol* 164: 10. doi: 10.1007/s00227-016-3048-y
348

349 Cooke SJ (2008) Biotelemetry and biologging in endangered species research and animal
350 conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endanger*
351 *Species Res* 4:165–185. doi: 10.3354/esr00063
352

353 Costa DP, Robinson PW, Arnould JPY, Harrison A-L, Simmons SE, Hassrick JL, Hoskins AJ,
354 Kirkman SP, Oosthuizen H, Villegas-Amtmann S, Crocker DE (2010) Accuracy of ARGOS
355 locations of pinnipeds at-sea estimated using Fastloc GPS. *PLoS ONE*: e8677. doi:
356 10.1371/journal.pone.0008677
357

358 Dujon AM, Lindstrom RT, Hays GC (2014) The accuracy of Fastloc-GPS locations and
359 implications for animal tracking. *Methods in Ecology and Evolution* 5, 1162–1169. doi:
360 10.1111/2041-210X.12286
361

362 Esteban N, Mortimer JA, Hays GC (2017). How numbers of nesting sea turtles can be over-
363 estimated by nearly a factor of two. *Proc R Soc Lond B* 284: 20162581. doi:
364 10.1098/rspb.2016.2581
365

366 Evans K, Baer H, Bryant E, Holland M, Rupley T, Wilcox C (2011) Resolving estimation of
367 movement in a vertically migrating pelagic fish: Does GPS provide a solution? *J Exp Mar Biol*
368 *Ecol* 398:9–17. doi: 10.1016/j.jembe.2010.11.006
369

370 Fieberg J, Börger L (2012) Could you please phrase “home range” as a question?
371 *J Mammal* 93:890–902. doi: 10.1644/11-MAMM-S-172.1
372

373 Frair JL, Fieberg J, Hebblewhite M, Cagnacci F, DeCesare NJ, Pedrotti L (2010) Resolving
374 issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data.
375 *Phil Trans R Soc B* 365:2187–2200. doi: 10.1098/rstb.2010.0084
376

377 Fujisaki I, Hart KM, Sartain-Iverson AR (2016) Habitat selection by green turtles in a spatially
378 heterogeneous benthic landscape in Dry Tortugas National Park, Florida. *Aquat Biol* 24:185–
379 199. doi: 10.3354/ab00647
380

381 Fuller WJ, Broderick AC, Phillips RA, Silk JRD, Godley BJ (2008) Utility of geolocating light
382 loggers for indicating at-sea movements in sea turtles. *Endang Species Res* 4:139–146. doi:
383 10.3354/esr00048
384

385 Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ
386 (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? *Endang*
387 *Species Res* 4:3–22. doi: 10.3354/esr00060
388

389 Harris S, Cresswell WJ, Forde PG, Trewehella WJ, Woollard T, Wray S (1995) Home-range
390 analysis using radio-tracking data – a review of problems and techniques particularly as applied
391 to the study of mammals. *Mammal Rev* 20:97–123. doi: 10.1111/j.1365-2907.1990.tb00106.x
392

393 Hawkes LA, Witt MJ, Broderick AC, Coker JW, Coyne MS, Dodd M, Frick MG, Godfrey MH,
394 Griffin DB, Murphy SR, Murphy TM, Williams KL, Godley BJ (2011) Home on the range:
395 spatial ecology of loggerhead turtles in Atlantic waters of the USA. *Diversity Distrib* 17:624–
396 640. doi: 10.1111/j.1472-4642.2011.00768.x
397

398 Hays GC, Åkesson S, Godley BJ, Luschi P, Santidrian P (2001) The implications of location
399 accuracy for the interpretation of satellite-tracking data. *Anim Behav* 61:1035–1040. doi:
400 10.1006/anbe.2001.1685
401

402 Hays GC, Mortimer JA, Ierodiaconou D, Esteban N (2014) Use of long-distance migration
403 patterns of an endangered species to inform conservation planning for the world’s largest marine
404 protected area. *Conserv Biol* 28:1636–1644. doi: 10.1111/cobi.12325
405

406 Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM, Bailey H, Bailleul F, Bowen
407 WD, Caley MJ, Costa DP, Eguíluz VM, Fossette S, Friedlaender AS, Gales N, Gleiss AC, Gunn
408 J, Harcourt R, Hazen EL, Heithaus MR, Heupel M, Holland K, Horning M, Jonsen I, Kooyman
409 GL, Lowe CG, Madsen PT, Marsh H, Phillips RA, Righton D, Ropert-Coudert Y, Sato K,
410 Shaffer SA, Simpfendorfer CA, Sims DW, Skomal G, Takahashi A, Trathan PN, Wikelski M,

411 Womble JN, Thums M. (2016). Key questions in marine megafauna movement ecology. Trends
412 Ecol Evol 6:463–475. doi: 10.1016/j.tree.2016.02.015
413
414 Hazel J (2009) Evaluation of fast-acquisition GPS in stationary tests and fine-scale tracking of
415 green turtles. J Exp Mar Biol Ecol 374:58–68. doi: 10.1016/j.jembe.2009.04.009
416
417 Hazen EL, Maxwell SM, Bailey H, Bograd SJ, Hamann M, Gaspar P, Godley BJ, Shillinger GL
418 (2012) Ontogeny in marine tagging and tracking science: technologies and data gaps. Mar Ecol
419 Prog Ser 457:221–240. doi: 10.3354/meps09857
420
421 Hebblewhite M, Haydon DT (2010) Distinguishing technology from biology: a critical review of
422 the use of GPS telemetry data in ecology. Phil Trans R Soc B 365:2303–2312. doi:
423 10.1098/rstb.2010.0087
424
425 Hoenner X, Whiting SD, Hindell MA, McMahon CR (2012) Enhancing the use of Argos satellite
426 data for home range and long distance migration studies of marine animals. PLoS One 7:e40713.
427 doi: 10.1371/journal.pone.0040713
428
429 Ironside KE, Mattson DJ, Arundel TR, Hansen JR (2017) Is GPS telemetry location error
430 screening beneficial? Wildl Biol 2017:wlb.00229
431
432 Kays R, Crofoot MC, Jetz W, Wikelski M (2015) Terrestrial animal tracking as an eye on life
433 and planet. Science 348:aaa2478. doi: 10.1126/science.aaa2478

434

435 Kie J (2013) A rule-based *ad hoc* method for selecting a bandwidth in kernel home-range
436 analyses. *Anim Biotelemetry* 1:13.

437

438 Kuhn CE, Johnson DS, Ream RR, Gelatt TS (2009) Advances in the tracking of marine species:
439 using GPS locations to evaluate satellite track data and a continuous-time movement model. *Mar*
440 *Ecol Prog Ser* 393:97–109. doi: 10.3354/meps08229

441

442 Lopez R, Malardé J-P, Royer F, Gaspar P (2014) Improving Argos Doppler location using
443 multiple-model Kalman filtering. *IEEE Trans Geosci Remote Sens* 52:4744–4755. doi:
444 10.1109/TGRS.2013.2284293

445

446 Luschi P, Hays GC, Del Seppia C, Marsh R, Papi F (1998) The navigational feats of green sea
447 turtles migrating from Ascension Island investigated by satellite telemetry. *Proc Roy Soc Lond B*
448 265:2279–2284. doi: 10.1098/rspb.1998.0571

449

450 McClintock BT, London JM, Cameron MF, Boveng PL (2015) Modelling animal movement
451 using the Argos satellite telemetry location error ellipse. *Methods Ecol Evol* 6:266–277. doi:
452 10.1111/2041-210X.12311

453

454 Montgomery RA, Roloff GJ, Ver Hoef JM (2011) Implications of ignoring telemetry error on
455 inference in wildlife resource use models. *J Wildl Manage* 75:702–708. doi: 10.1002/jwmg.96

456

457 Ogden JC, Robinson L, Whitlock K, Daganhardt H, Cebula R (1983) Diel foraging patterns in
458 juvenile green turtles (*Chelonia mydas* L.) in St. Croix United States Virgin Islands. J Exp Mar
459 Biol Ecol 66:199–205. doi: 10.1016/0022-0981(83)90160-0
460

461 Papi F, Liew HC, Luschi P, Chan EH (1995) Long-range migratory travel of a green turtle
462 tracked by satellite: evidence for navigational ability in the open sea. Mar Biol 122:171–175. doi:
463 10.1007/BF00348929
464

465 R Core Team (2016) R: A language and environment for statistical computing. R Foundation for
466 Statistical Computing, Vienna, Australia. URL <https://www.R-project.org/>.
467

468 Renaud ML, Carpenter JA, Williams JA (1995) Activities of juvenile green turtles, *Chelonia*
469 *mydas*, at a jettied pass in South Texas. Fish Bull 93:586–593.
470

471 Schofield G, Hobson VJ, Lilley MKS, Katselidis KA, Bishop CM, Brown P, Hays GC (2010a).
472 Inter-annual variability in the home range of breeding turtles: Implications for current and future
473 conservation management. Biol Conserv 143:722–730. doi: 10.1016/j.biocon.2009.12.011
474

475 Schofield G, Hobson VJ, Fossette S, Lilley MKS, Katselidis KA, Hays GC (2010b). Fidelity to
476 foraging sites, consistency of migration routes and habitat modulation of home range by sea
477 turtles. Diversity and Distributions 16:840–853. doi: 10.1111/j.1472-4642.2010.00694.x
478

479 Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects
480 of sample size on kernel home range estimates. *J Wildl Manage* 63:739–747. doi:
481 10.2307/3802664
482

483 Seminoff JA, Jones TT (2006) Diel movements and activity ranges of green turtles (*Chelonia*
484 *mydas*) at a temperate foraging area in the Gulf of California, Mexico. *Herpetol Conserv Biol*
485 1:81–86.
486

487 Shaver DJ, Hart KM, Fujisaki I, Rubio C, Sartain-Iverson AR, Peña J, Gamez DG, Miron RD,
488 Burchfield PM, Martinez HJ, Ortiz J (2016) Migratory corridors of adult female Kemp's ridley
489 turtles in the Gulf of Mexico. *Biol Conserv* 194:158–67. doi: 10.1016/j.biocon.2015.12.014
490

491 Sims DW, Queiroz N, Humphries NE, Lima FP, Hays GC (2009). Long-term GPS tracking of
492 ocean sunfish *Mola mola* offers a new direction in fish monitoring. *PLoS ONE* 4: e7351. doi:
493 10.1371/journal.pone.0007351
494

495 Swimmer Y, McNaughton L, Foley D, Moxey L, Nielsen A (2009) Movements of olive ridley
496 sea turtles *Lepidochelys olivacea* and associated oceanographic features as determined by
497 improved light-based geolocation. *Endang Species Res* 10:245–254. doi: 10.3354/esr00164
498

499 Taquet C, Taquet M, Dempster T, Soria M, Ciccione S, Roos D, Dagorn L (2006) Foraging of
500 the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean),
501 determined by acoustic transmitters. *Mar Ecol Prog Ser* 306:295–302. doi: 10.3354/meps306295

502

503 Thums M, Whiting SD, Reisser JW, Pendoley KL, Pattiaratchi CB, Harcourt RG, McMahon CR,
504 Meekan MG (2013) Tracking sea turtle hatchlings – A pilot study using acoustic telemetry. J
505 Exp Mar Biol Ecol 440:156–163. doi: 10.1016/j.jembe.2012.12.006

506

507 Vincent C, McConnell BJ, Ridoux V, Fedak MA (2002) Assessment of Argos location accuracy
508 from satellite tags deployed on captive gray seals. Mar Mamm Sci 18:156–166. doi:
509 10.1111/j.1748-7692.2002.tb01025.x

510

511 Whiting SD, Miller JD (1998) Short term foraging ranges of adult green turtles (*Chelonia*
512 *mydas*). J Herpetol 32:330–337. doi: 10.2307/1565446

513

514 Witt MJ, Åkesson S, Broderick AC, Coyne MS, Ellick J, Formia A, Hays GC, Luschi P, Stroud
515 S, Godley BJ (2010). Assessing accuracy and utility of satellite-tracking data using Argos-linked
516 Fastloc-GPS. Anim Behav 80:571–581. doi: 10.1016/j.anbehav.2010.05.022

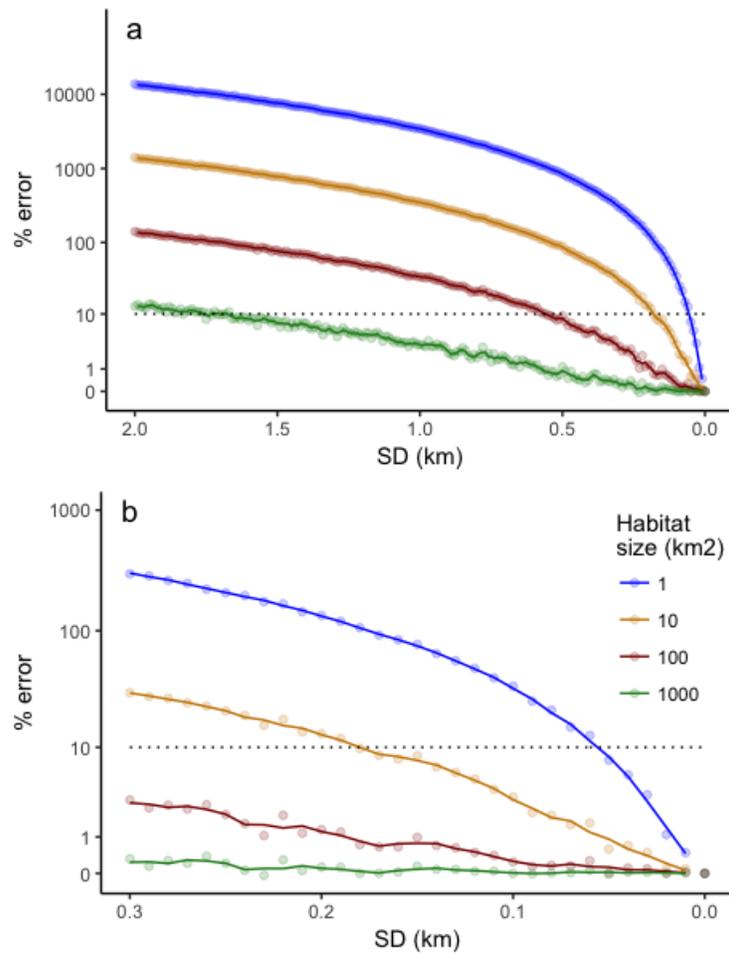
517

518 Worton BJ (1989). Kernel methods for estimating the utilization distribution in home-range
519 studies. Ecology 70:164–168. doi: 10.2307/1938423

520

521

522 **Figure captions**



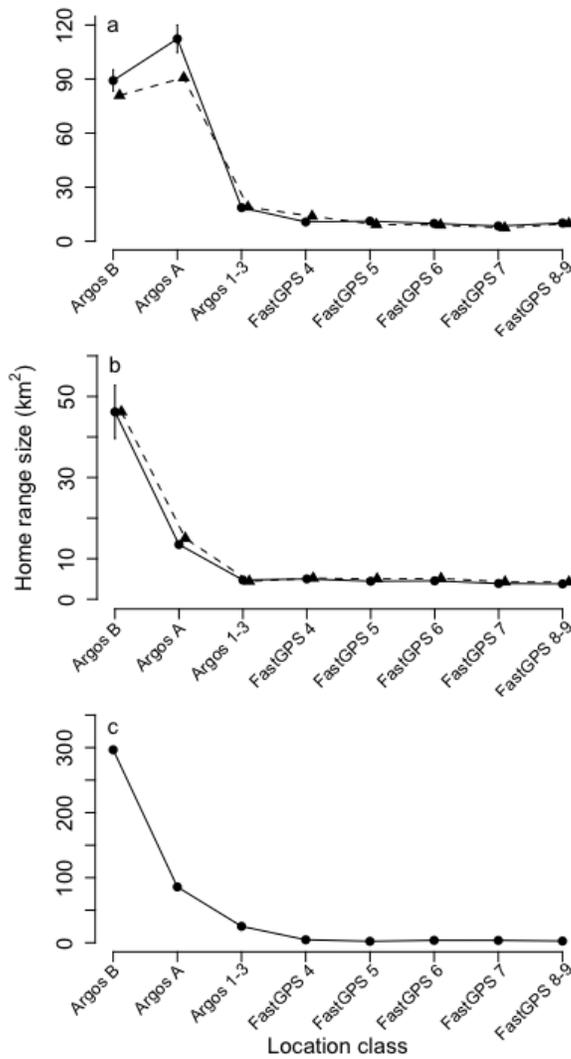
523

524 **Fig. 1:** Percent error between the true and error-added 95% home range estimates for simulated
525 animals within square-shaped habitats of 1, 10, 100 and 1000 km² across different location
526 qualities including all values of SD from 0-2 (A) and SD ≤ 0.3 (B). Percent error data are shown
527 on a log₁₀(x+1) scale due to large differences in these values at high SDs, although axis labels are
528 untransformed for ease of interpretation. Values below the horizontal dashed line represent <
529 10% error between the error-added and true home range size.

530

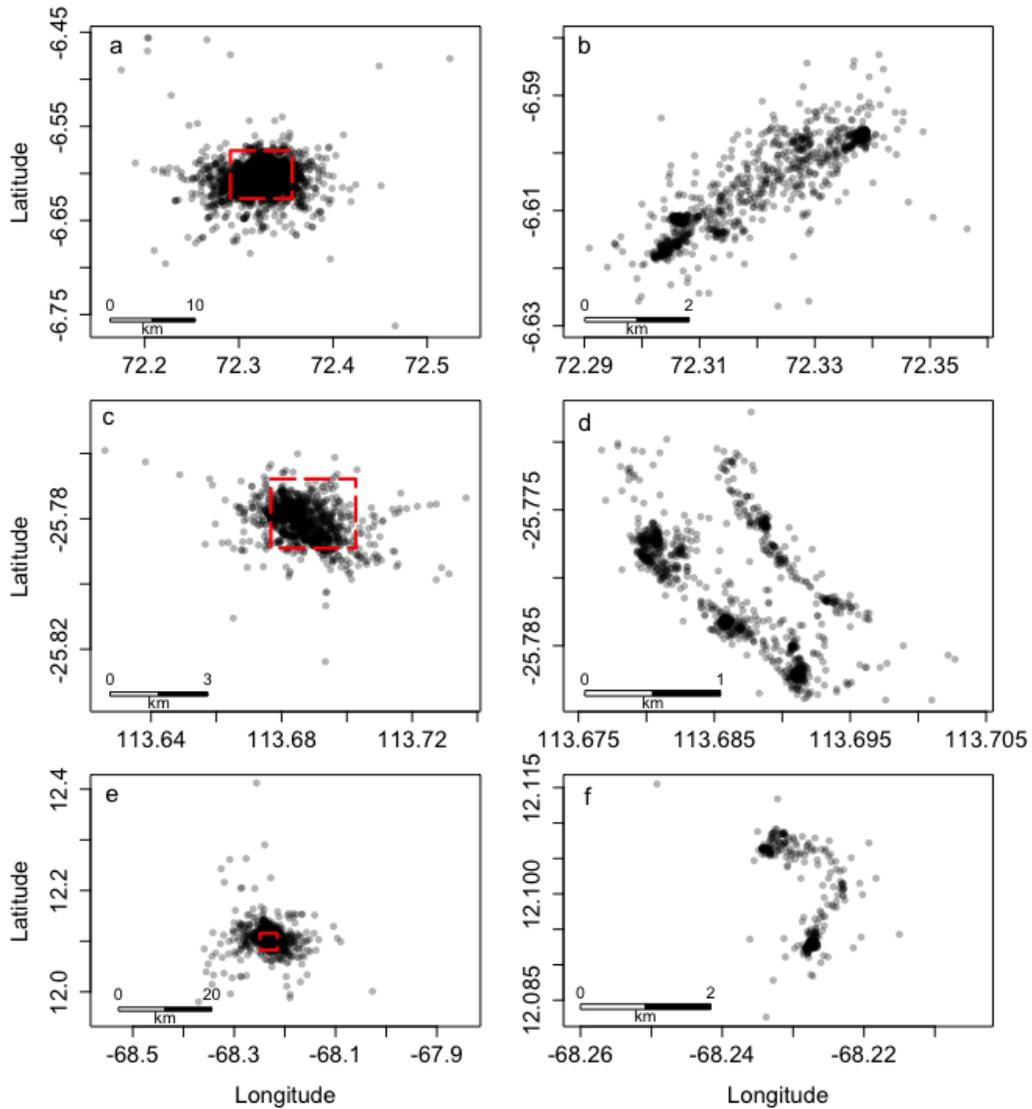
531

532

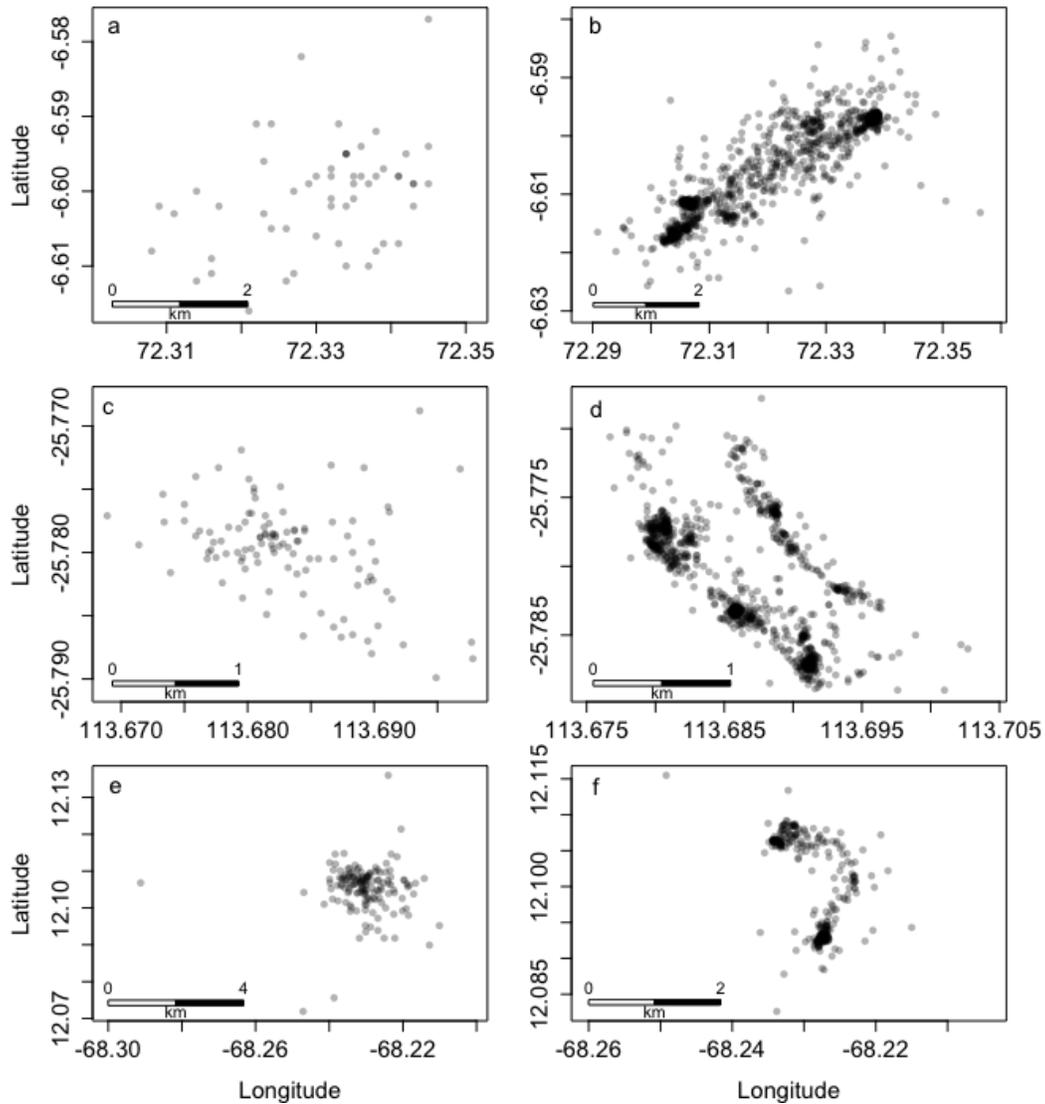


533

534 **Fig. 2:** Estimated 95% home range sizes derived from different location qualities for a green
 535 turtle tracked for 14 months in the Chagos Archipelago, western Indian Ocean (A), another
 536 tracked for 3 months in Shark Bay, Western Australia (B), and a third tracked for 5 months in
 537 Bonaire, Caribbean Netherlands. For (A) and (B), the dashed line with triangles represents home
 538 range estimates based on all available data (1 location per day) per location class while the solid
 539 line with circles represents the mean (\pm SE) estimate based on sub-sampled data to standardize
 540 data volume across location classes (see Materials and Methods). For the Chagos turtle, the
 541 estimate for Argos location classes 1-3 is a single value based on all available locations due to
 542 low sample size.



543
 544 **Fig. 3.** Argos (left panels) and Fastloc-GPS (right panels) location distributions for a green turtle
 545 tracked for 14 months in the Chagos Archipelago, western Indian Ocean (A, B), another tracked
 546 for 3 months in Shark Bay, Western Australia (C, D), and a third tracked for 5 months in
 547 Bonaire, Caribbean Netherlands (E, F). Argos plots include all location data (classes A, B, 0, 1, 2
 548 and 3) while Fastloc-GPS plots include locations derived from ≥ 4 satellites. Points have been
 549 made transparent to show location density. Note differences in scale among plots. To emphasize
 550 the differences in scale, red squares within Argos panels show the extent of the Fastloc-GPS data
 551 for that study site.



553

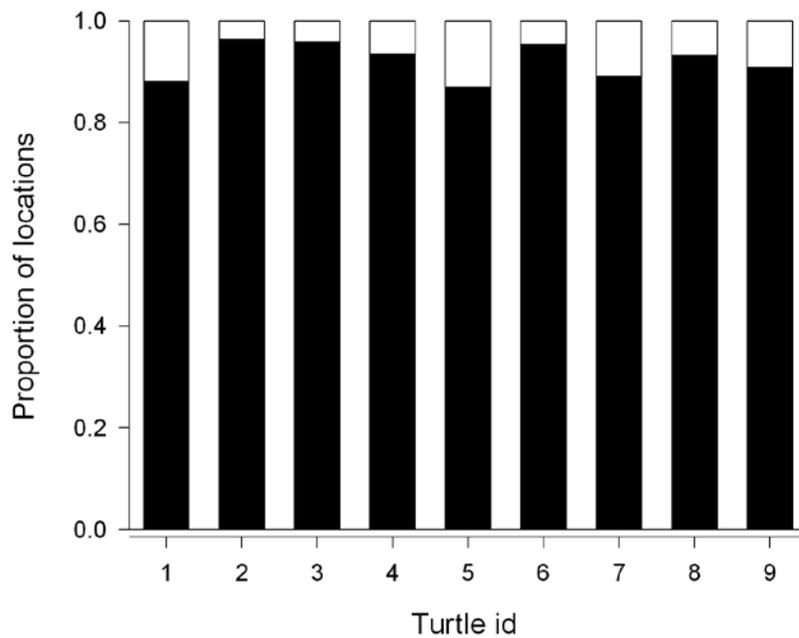
554 **Fig. 4.** Differences in movement detail provided by the most accurate Argos data (classes 1-3,
 555 left panels) and Fastloc-GPS data (locations derived from ≥ 4 satellites, right panels) for the three
 556 green turtles. Points have been made transparent to show location density. Note minor
 557 differences in scale among plots.

558

559

560

561



562

563 **Fig. 5.** For nine turtles tracked using Fastloc GPS Argos transmitters, the proportion of Fastloc
564 GPS locations (derived from ≥ 4 satellites and with residual values < 35 , filled bars) compared to
565 high-accuracy Argos locations (location class 1-3, open bars). Turtles 1-4 were equipped on
566 Diego Garcia, Chagos Archipelago while turtles 5-9 were tagged in Shark Bay, Western
567 Australia.

568 **Tables**

569 Table 1: Variation in Argos location class accuracies in three studies that reported the same statistics (68th percent
 570 normal distribution, in km) for latitudinal and longitudinal error separately.

Source	Method	Error (68th percentile, lat/long)				
		LC B	LC A	LC 0	LC 1	LC 2
Hays et al. 2001	stationary test on land	5.23 / 7.79	1.39 / 0.81	4.29 / 15.02	1.03 / 1.62	0.28 / 0.62
Vincent et al. 2002	on animals, study pool	4.596 / 7.214	0.762 / 1.244	2.271 / 3.308	0.494 / 1.021	0.259 / 0.485
Costa et al. 2010	on animals, at sea	4.642 / 8.253	2.788 / 4.373	1.795 / 2.855	0.574 / 0.879	0.468 / 0.729

571

572

573 Table 2: Summary of telemetry methods used to track sea turtle movements and their
 574 approximate location accuracy.

Method	Approximate location accuracy	Typical movements revealed	Examples
Light-based geolocation	Tens to hundreds of km	Long-term, coarse-scale movements (e.g., breeding migrations)	Fuller et al. 2008 Swimmer et al. 2009
Radio telemetry	Tens of m to > 1 km	Short-term, fine-scale movements in a spatially restricted area	Renaud et al. 1995 Whiting and Miller 1998
Active acoustic telemetry	< 10 to hundreds of m	Short-term, fine-scale movements in a spatially restricted area	Ogden et al. 1983 Seminoff and Jones 2006
Passive acoustic telemetry	< 10 to hundreds of m	Long-term, fine-scale movements in a spatially restricted area	Taquet et al. 2006 Thums et al. 2013
Argos satellite tracking	Hundreds of m to > 10 km	Long-term, coarse to medium-scale movements (e.g., breeding migrations, transits between foraging sites)	Luschi et al. 1998 Papi et al. 1995 Godley et al. 2008 (review)
Fastloc GPS tracking	Tens to hundreds of m	Long-term, fine-scale movements (e.g., foraging patch use, breeding migrations, inter-nesting movements)	Hazel et al. 2009 Schofield et al. 2010a, b Dujon et al. 2014 Christiansen et al. 2017

575