This is the published version (version of record) of:


Available from Deakin Research Online:

http://hdl.handle.net/10536/DRO/DU:30031546

Reproduced with kind permission of the copyright owner. 2010, Costa et al This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Copyright** : 2010, Costa et al
Accuracy of ARGOS Locations of Pinnipeds at-Sea Estimated Using Fastloc GPS

Daniel P. Costa1, Patrick W. Robinson1, John P. Y. Arnould2, Autumn-Lynn Harrison1, Samantha E. Simmons1, Jason L. Hassrick1, Andrew J. Hoskins2, Stephen P. Kirkman4, Herman Oosthuizen3, Stella Villegas-Amtmann1, Daniel E. Crocker5

1 Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, California, United States of America, 2 School of Life and Environmental Sciences, Deakin University, Burwood, Victoria, Australia, 3 Marine and Coastal Management, Department of Environmental Affairs, Rogge Bay, South Africa, 4 Animals Demography Unit, Department of Zoology, University of Cape Town, Rondebosch, South Africa, 5 Department of Biology, Sonoma State University, Rohnert Park, California, United States of America

Abstract

Background: ARGOS satellite telemetry is one of the most widely used methods to track the movements of free-ranging marine and terrestrial animals and is fundamental to studies of foraging ecology, migratory behavior and habitat-use. ARGOS location estimates do not include complete error estimations, and for many marine organisms, the most commonly acquired locations (Location Class 0, A, B, or Z) are provided with no declared error estimate.

Methodology/Principal Findings: We compared the accuracy of ARGOS locations to those obtained using Fastloc GPS from the same electronic tags on five species of pinnipeds: 9 California sea lions (Zalophus californianus), 4 Galapagos sea lions (Zalophus wollebaeki), 6 Cape fur seals (Arctocephalus pusillus pusillus), 3 Australian fur seals (A. p. doriferus) and 5 northern elephant seals (Mirounga angustirostris). These species encompass a range of marine habitats (highly pelagic vs coastal), diving behaviors (mean dive durations 2–21 min) and range of latitudes (equator to temperate). A total of 7,318 ARGOS positions and 27,046 GPS positions were collected. Of these, 1,105 ARGOS positions were obtained within five minutes of a GPS position and were used for comparison. The 68th percentile ARGOS location errors as measured in this study were LC-3 0.49 km, LC-2 1.01 km, LC-1 1.20 km, LC-0 4.18 km, LC-A 6.19 km, LC-B 10.28 km.

Conclusions/Significance: The ARGOS errors measured here are greater than those provided by ARGOS, but within the range of other studies. The error was non-normally distributed with each LC highly right-skewed. Locations of species that make short duration dives and spend extended periods on the surface (sea lions and fur seals) had less error than species like elephant seals that spend more time underwater and have shorter surface intervals. Supplemental data (S1) are provided allowing the creation of density distributions that can be used in a variety of filtering algorithms to improve the quality of ARGOS tracking data.

Introduction

The ability to track the movements of animals is fundamental to understanding animal foraging ecology, migratory behavior, habitat use and general life history parameters [1,2,3]. Electronic tracking technology revolutionized the study of animal ecology and is now relied upon as the predominant means of estimating animal movement [4]. A number of electronic tracking methods are available including VHF telemetry, light-level geolocation, ARGOS satellite telemetry and, most recently, GPS tracking [5,6,7,8,9,10,11]. Of these, ARGOS telemetry is one of the most widely used in marine studies [12] and has the significant advantage that the data are acquired remotely in real time via satellite anywhere on the planet (www.ARGOS-system.org). ARGOS satellite telemetry has expanded our understanding of the fine scale movements of marine birds, [13,14,15], sea turtles [16,17], sharks [18,19] and marine mammals [7,11,12,20,21].

The ARGOS system consists of modules attached to low-orbiting weather satellites of the National Oceanic and Atmospheric Administration (NOAA). Modules record satellite tag transmissions and later download these data back to Earth for processing by Service ARGOS (Toulouse France, or Landover MD). Tag geoposition is calculated from the Doppler shift of the transmitted radio frequency and requires a minimum of three
successive transmissions during a single satellite pass. Locations are based on 7 levels of accuracy: location class (LC) LC-3 with a stated error of less than 150 m, LC-2 with error of 150–350 m, LC-1 with error of 350–1000 m, LC-0 with error greater than 1000 m, and LC-A, LC-B and LC-Z that do not include error estimates.

Unfortunately, the least accurate positions are the most common for many marine animal tracking studies [22]. For example, 89% of ARGOS location estimates from a recent northern elephant seal track (Costa et al. unpublished data) were of LC 0, A, B, or Z and, thus, had no declared error estimate. Furthermore, the errors for the remaining location classes, as provided by ARGOS-CLS, are 68th percentile predictions (separately for latitude and longitude) rather than full error distributions making it difficult to incorporate into animal movement models.

Spatial error is problematic for many applications, such as determination of area-restricted search, behavioral mode (i.e. foraging, searching, migrating, etc) of far-ranging species, or even simple home-range analyses for individuals exhibiting range-residency [23,24,25,26,27]. If unknown, spatial error can also mask accurate descriptions of true location as well as derived-behavioral states in a scale-dependent fashion. That is, smaller scale patterns will show increased degradation with the addition of ARGOS error. The temporal resolution of tracking data can have similarly detrimental effects on its behavioral interpretation. However, ARGOS transmitters are often set to a fixed transmission rate, so that the temporal resolution of the resulting track is solely dependent on animal behavior. Fortunately, a variety of interpolation techniques are available to mitigate variations in temporal resolution [7,24,27,28]. In contrast, spatial error is propagated both as a result of animal behavior (surfacing behavior, travel speed etc.) and technical limitations [26]. To date, spatial error of ARGOS positions has not been measured in an empirically robust manner for free-ranging marine animals. The first attempts to estimate ARGOS location error in marine animals were made by comparing the known position of an ARGOS tag prior to deployment or while the animal remained at a known location [29]. However, such estimates failed to account for animal behavior at sea. Factors contributing to location errors when animals are at sea include attenuated or missed transmissions due to rapid surfacing behavior, limited total time available for transmissions, and the commonly overlooked impact of temperature-induced frequency instability [30,31,32,33]. Vincent and others [34] attached ARGOS transmitters to captive gray seals, *Halichoerus grypus*, housed in outdoor tanks to simulate the natural environment and diving behavior of free-ranging seals. They compared the known position of the tank to the locations provided by the ARGOS transmitters and found a lower uplink rate and a shift toward poorer location qualities (0, A, and B) and discovered that ARGOS errors were non-normally distributed. Using acoustic telemetry, White and Sjoberg (2002) followed three free-ranging gray seals on which they had deployed ARGOS transmitters, and took comparative GPS positions from their vessel. They reported location accuracies for LC-0 LC-A, LC-B those not reported by Service ARGOS. Recently Hazel (2009) using a combination of Fastloc GPS and acoustic devices with three green sea turtles, *Chelonia midas*, found ARGOS errors greater than those reported by ARGOS [35]. However, the tracking devices were housed in a float tethered to the turtles making comparisons to studies where the tracking devices are directly attached to the animal (on the head or back) problematic. While these studies provide useful insights into ARGOS error, they do not provide a robust assessment of ARGOS location error for free ranging marine animals under the conditions most existing data have been collected.

Until recently GPS technology could not be used on diving animals because of the time required for the antenna to be at the surface and clear of wave splash to obtain a satellite fix and maintain the almanac. The recent development of Fastloc GPS technology has made it possible to simultaneously collect GPS and ARGOS locations from freely-ranging marine animals (Fastloc GPS hardware developed by Wildtrack Telemetry Systems Ltd, Leeds, United Kingdom). Standard navigational GPS units require many seconds or even minutes of exposure to GPS satellites to calculate positions and the onboard calculations consume considerable power. In contrast, Fastloc GPS can obtain GPS satellite information in less than 100 ms and can transmit the location information within the narrow bandwidth confines of the ARGOS system. The Fastloc uses a novel intermediate solution that couples brief satellite reception with limited onboard processing to reduce the memory required to store or transmit the location. This system captures the GPS satellite signals, identifies the observed satellites, calculates their pseudo-ranges without the ephemeris or satellite almanac and then transmits the pseudo-ranges via ARGOS. While only a portion of the locations can be transmitted via ARGOS, all of them are archived and therefore can be retrieved as long as the tag is recovered. Final locations are post-processed from the pseudo-ranges once the data are received using archived GPS constellation orbitography archives maintained by NASA (http://cddis.gsfc.nasa.gov).

Here, we assess the accuracy of ARGOS locations via comparisons to Fastloc GPS locations obtained from the same electronic tags on five species of pinnipeds. These species cover a range of marine habitats (highly pelagic vs coastal), diving behaviors (mean dive durations 2–21 min) and range of latitudes (equator to temperate) and a wide range of locations across the globe (South Africa, Eastern North Pacific Ocean, Southern California Bight, southeast Australia and the Galapagos Islands).

**Methods**

**Ethics Statement**

The animal use protocol for this research was reviewed and approved by the University of California at Santa Cruz Institutional Animal Care and Use Committee and followed the guidelines established by the Canadian Council on Animal Care and the ethics committee of the Society of Marine Mammalogy. Research was carried out under the following research permits: northern elephant seals and California sea lions, U.S.A. National Marine Fisheries Service permits #87-1743 and 87-1851; Galapagos sea lions, Parque Nacional Galapagos #084/06PNG; Australian fur seals, Department of Natural Resources and Environment research permits 978/003, RP-97-112 and 10000187; and Cape fur seals permit issued by the Ministry of Marine and Coastal Management to H. Oosthuizen.

**Data Collection**

To assess *in-situ* error of ARGOS positions, we attached ARGOS-linked Fastloc GPS tags (manufactured by Wildlife Computers, Sirtrack Ltd., or the Sea Mammal Research Unit, SMRU Ltd) to individuals representing five species of pinnipeds. Nine California sea lions (*Zalophus californianus*) were captured on San Nicolas Island, California, USA in November 2007 and recaptured in January 2008. Four Galapagos sea lions (*Zalophus wollebaeki*) were captured on Gaamaño Islet, Galapagos, Ecuador during August 2006 and recaptured two weeks later. Six Cape fur seals (*Arctocephalus pusillus pusillus*) were captured at Kleineee seal.
Three Australian fur seals (A. p. doriferus) were captured at Kanowna Island, northern Bass Strait, Australia in June 2006 and were recaptured two weeks later. Five northern elephant seals (Mirounga angustirostris) were captured at Ano Nuevo State Park, San Mateo County, California, USA in February 2008 and recaptured in May 2008. We used standard capture, sedation, and instrument attachment protocols [11,36,37]; all individuals were healthy adult females exhibiting normal foraging migrations.

In addition to animal deployments, we evaluated the accuracy of GPS positions on land in a stationary test of four Fastloc GPS tags. Tags were placed within a one-meter square with an open view of the sky at Long Marine Lab in Santa Cruz, California, USA to collect positions for 24 h.

Data Handling
Each deployment yielded an ARGOS track and an archived GPS track. All tracks were truncated to remove periods on land immediately after attaching the tags and immediately prior to removing the tags. ARGOS data were downloaded daily to a local database. ARGOS occasionally updated the location class of previously downloaded locations and these changes were automatically incorporated into our database. ARGOS tracks were filtered using a 100 km-hr\(^{-1}\) speed filter to remove extreme outliers as we were interested in the performance of the ARGOS system and not the performance of filtering algorithms. This outlier filter removes only the most obviously erroneous locations as a simple speed filter for pinnipeds typically assumes a maximum swim velocity of less than 10 km-hr\(^{-1}\). As the GPS tracks were our estimate of "true" position and since occasional errors are generated from the GPS tracks, we used a conservative filter for all GPS tracks: 10 km-hr\(^{-1}\) and 170-degree angle.

To determine the accuracy of ARGOS location estimates, we first identified all ARGOS locations obtained within five minutes of any GPS position. Next, the "true" position of the animal at the exact time of the ARGOS uplink was estimated via linear interpolation between the two neighboring GPS positions [38]. This procedure ensures every estimate of ARGOS error was based on a GPS position proximate in both space and time to the true position of the animal. We then calculated several error statistics from each ARGOS-GPS pair: great-circle distance, bearing, longitude component of error, and latitude component of error. The magnitudes of distance errors were fitted to a lognormal distribution for each ARGOS location class using a maximum likelihood approach.

### Table 1. The mean ARGOS error in kilometers along with the standard deviation and sample size for each of the 5 species of pinnipeds.

<table>
<thead>
<tr>
<th>Species</th>
<th>Error in km</th>
<th>LC-3</th>
<th>LC-2</th>
<th>LC-1</th>
<th>LC-0</th>
<th>LC-A</th>
<th>LC-B</th>
<th>LC-Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cape fur seal</td>
<td>1.38</td>
<td>1.08</td>
<td>1.13</td>
<td>3.03</td>
<td>6.58</td>
<td>6.98</td>
<td>1.50</td>
<td></td>
</tr>
<tr>
<td>std dev</td>
<td>±1.62</td>
<td>±0.92</td>
<td>±0.99</td>
<td>±2.52</td>
<td>±8.77</td>
<td>±9.30</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>2</td>
<td>5</td>
<td>19</td>
<td>21</td>
<td>38</td>
<td>27</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>California sea lion</td>
<td>0.60</td>
<td>0.95</td>
<td>1.05</td>
<td>3.87</td>
<td>4.41</td>
<td>7.67</td>
<td>89.70</td>
<td></td>
</tr>
<tr>
<td>std dev</td>
<td>±0.56</td>
<td>±1.00</td>
<td>±1.01</td>
<td>±5.59</td>
<td>±6.47</td>
<td>±10.80</td>
<td>±28.47</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>14</td>
<td>71</td>
<td>184</td>
<td>102</td>
<td>81</td>
<td>85</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Australian fur seal</td>
<td>0.34</td>
<td>0.75</td>
<td>2.18</td>
<td>10.41</td>
<td>19.76</td>
<td>97.71</td>
<td>9.71</td>
<td></td>
</tr>
<tr>
<td>std dev</td>
<td>±0.20</td>
<td>±0.512</td>
<td>±1.40</td>
<td>±13.12</td>
<td>±35.96</td>
<td>±115.81</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>5</td>
<td>9</td>
<td>11</td>
<td>13</td>
<td>5</td>
<td>10</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Galapagos sea lion</td>
<td>0.26</td>
<td>0.94</td>
<td>1.04</td>
<td>4.34</td>
<td>5.22</td>
<td>20.50</td>
<td>31.87</td>
<td></td>
</tr>
<tr>
<td>std dev</td>
<td>±0.18</td>
<td>±1.81</td>
<td>±1.09</td>
<td>±3.35</td>
<td>±4.63</td>
<td>±30.85</td>
<td>±20.36</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>12</td>
<td>19</td>
<td>36</td>
<td>23</td>
<td>16</td>
<td>8</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Northern eel</td>
<td>0.91</td>
<td>3.04</td>
<td>3.99</td>
<td>101.17</td>
<td>49.23</td>
<td>164.45</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>std dev</td>
<td>±0.50</td>
<td>0.00</td>
<td>±5.83</td>
<td>±341.94</td>
<td>±189.33</td>
<td>±236.35</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>3</td>
<td>1</td>
<td>8</td>
<td>52</td>
<td>206</td>
<td>11</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 1. A representative track of a female Cape fur seal off the western coast of South Africa obtained using ARGOS (black) or Fastloc GPS (yellow) tags. All filtered locations are presented in this figure, while the comparison between ARGOS and GPS used only locations that were obtained within 5 min of each other.
doi:10.1371/journal.pone.0008677.g001
Argos location quality proportions were compared between species using a G-test. Location errors were log transformed and modeled using a linear mixed effects model (SAS 9.1) with individual animal as a random effects subject term and species and location quality as fixed effects. Model residuals were assessed for approximate normality. The ARGOS-GPS data pairs used in this analysis are available as supplementary material to allow further analysis of these data (S1).

All analyses were performed using custom-written software in Matlab R2007a (The Mathworks Natick, MA) and Systat 12 (Chicago, IL).

**Results**

Matched ARGOS/GPS tracks were obtained from 28 individuals comprising five species of pinnipeds. A total of 7,318 ARGOS positions and 27,046 GPS positions were collected. Of these, 1,105 ARGOS positions were obtained within five minutes of a GPS position and were retained for further analysis. The mean time between ARGOS-GPS pairs was on average 1.16 days (median 0.58 days) with less than 1% (81) of these pairs occurring within an hour of each other. An example of the data used to compare ARGOS against GPS locations is provided for a Cape fur seal (Fig. 1). Error estimates (great-circle distance, bearing, longitude component of error, and latitude component of error) were calculated for each ARGOS position and are available as supplementary material. Mean ARGOS error for all LC combined was 19.44 km with a standard deviation of 116.89 km (median error 1.91 km). The mean ARGOS error, standard deviation and sample size for each of the ARGOS location classes are summarized for each species in Table 1. Location quality proportions varied significantly between species ($G^2 = 525.3$, df = 28, $p < 0.001$). When controlled for location quality, location error varied between species ($F_{4,1071} = 7.8$, $p < 0.001$). Post-hoc comparison of least square means revealed that irrespective of...
location quality, elephant seals had higher errors than all of the
otariid species and Australian fur seals had higher errors than the
other otariids. (Sidak adjustment, p<0.001).

The GPS positions obtained from the 4 tags used in the
stationary test had a mean error of 35.69 m with 95% of GPS
positions falling within 86 m of the mean geographic location of all
positions (Fig. 2).

ARGOS position errors from the animal borne tests were
centered on “true” locations but extreme outliers were numerous
and did not occur in a circular-uniform distribution (Fig. 3).
Similarly, for the direction frequency of ARGOS errors, the east/
west (longitudinal) error component was large relative to the
north/south component (latitudinal) (Fig. 4).

We found larger than expected errors for the three LCs (3, 2,
and 1) for which error estimates are provided by ARGOS (Fig. 5).
The remaining LCs exhibit a stepwise increase in error and a
substantial reduction in accuracy for LC-Z locations (Fig. 5). Two-
dimensional visualization of the ARGOS errors show increased
dispersion with lower quality locations but also a distinct
directional offset in the extreme outliers (Fig. 6). This was
particularly apparent in LC-A and LC-B locations. As the data
were clearly skewed we chose to fit the distance errors to
lognormal distributions for each LC (Table 2).

The species’ diving behavior was also an important factor in the
relative location error. Species with similar behaviors had similar
location errors (Fig. 7 Table 3), whereas species with dissimilar at-
sea behaviors had divergent location errors. For example, location
error was smaller for species that spend more time on the surface
and make shorter duration dives (sea lions and fur seals; 2.2–
4.0 min) than species that make long dives followed by short
surface intervals (elephant seals; 21.3 min) (Fig. 7). It is important
to note that behavior likely impacts both the relative proportion
of the LCs and the error within each LC.

Discussion

We assessed the accuracy of ARGOS locations for free-ranging
pinnipeds by comparing ARGOS locations to Fastloc GPS
locations (matched closely in time, but also interpolated for
improved accuracy), which we treated as true locations. Although
our on-land stationary test of Fastloc GPS showed greater location
error than that achieved with a commercial handheld GPS unit
(e.g. 3m Garmin Inc., Olathe, KS), the accuracy was still 4 times
greater than the best ARGOS position estimates (Fastloc GPS
36 m; ARGOS LC-3 = 150 m). We, therefore, conclude that

Figure 5. A box and whisker plot of the ARGOS error
associated with each location class is given in this figure. Red
bars represent the 68% error as estimated by ARGOS. Note the log-
scaling of the y-axis.
doi:10.1371/journal.pone.0008677.g005

Figure 6. This figure provides the ARGOS error as standardized to a fixed location (N = 1105). Data are log+1 transformed (negative
values were reflected before transformation).
doi:10.1371/journal.pone.0008677.g006
Table 2. Parameters describing lognormal probability distribution for the distance (km) of ARGOS error for each location class.

<table>
<thead>
<tr>
<th>ARGOS LC</th>
<th>Sample Size</th>
<th>μ</th>
<th>σ</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>33</td>
<td>-1.198</td>
<td>1.02</td>
</tr>
<tr>
<td>2</td>
<td>107</td>
<td>1.026</td>
<td>0.693</td>
</tr>
<tr>
<td>1</td>
<td>251</td>
<td>1.199</td>
<td>0.712</td>
</tr>
<tr>
<td>0</td>
<td>167</td>
<td>1.381</td>
<td>0.521</td>
</tr>
<tr>
<td>A</td>
<td>192</td>
<td>1.622</td>
<td>0.506</td>
</tr>
<tr>
<td>B</td>
<td>336</td>
<td>1.623</td>
<td>0.612</td>
</tr>
</tbody>
</table>

Fastloc GPS provides an appropriate method to assess ARGOS error on free-ranging marine animals.

Incorporating ARGOS error in track analysis is certainly not a novel idea. Attempts to measure this error empirically have ranged from simple stationary land tests to acoustic tracking of free-ranging satellite-tagged seals and turtles (Table 4). However, these studies are problematic for four reasons: (1) The methodology used in most of these studies failed to capture several sources of ARGOS location error; (2) the studies that properly account for these additional sources of ARGOS error suffer from very small sample sizes and thus cannot adequately describe the error for some ARGOS LCs; (3) many of the studies report either mean errors or 68th percentile errors in lieu of a full distribution (this is problematic for the implementation of results in modeling exercises and may result in the application of an inappropriate distribution); and (4) the extreme variability in estimates of ARGOS error within a particular LC between studies is problematic for proper implementation. For example, published values for LC-0 error span an entire order of magnitude (Table 4). The lack of congruence between previous studies may also be due to a combination of low sample sizes, variability in animal behavior, and study protocol. Nevertheless, it is re-assuring that the two studies that arguably employ the most realistic validation method (Fastloc GPS) obtained the most similar error estimates (Table 4; this study and [35]). This is somewhat unexpected as we might have expected better accuracy from ARGOS transmitters in a tethered float [35] compared to tags mounted on the head or mid back (this study). Regardless, our study is one of the first to empirically determine ARGOS location error from marine animal-borne satellite tracking units where the tag was directly attached to the animal, thereby appropriately accounting for the combined effects of factors known to influence the accuracy of position estimates.

There is no question that GPS tracks are superior to those obtained with ARGOS (Fig 1). We applied only a basic speed filter to create the tracks in Figure 1 and, with the more sophisticated filtering and smoothing algorithms now available, ARGOS tracks can be considerably improved [24,28,39]. However, our estimates of ARGOS error were significantly larger than those provided by ARGOS (approximately 300% greater for LC-3 and LC-2). Although published estimates of ARGOS error vary widely (Table 4), estimates from this study show larger than expected errors for the better location classes and smaller than expected errors for poor location classes.

Inspection of the ARGOS error distributions revealed two features of interest in the direction of the offset: 1) errors are heavily biased in the east/west axis (Fig. 3); and 2) the outliers do not occupy a circular uniform distribution around the true location but instead are preferentially found on the diagonals (Fig. 5 LC-A & LC-B). This pattern has been previously reported (22, 34) and is due to the polar orbit of the ARGOS satellite. The non-uniformity of ARGOS errors around the true location has direct impacts to existing modeling techniques [26,28,39]. Typically points are sampled in one of two ways: 1) an X-Y approach by sampling from a distribution of latitudinal error and separately from a distribution of longitudinal error; or 2) a polar approach by sampling from a distribution of straight-line distance and then from a uniform distribution for direction. Both methods do not adequately account for the observed distribution of outliers (exemplified in LC-A and LC-B). We recommend a polar approach where both distance and angle distributions are defined by empirical ARGOS error data to properly account for the unique two-dimensional shape of the error distributions. These can be created using the supplementary material provided (S1).

Species-specific differences in track quality are predominantly due to variation in surfacing intervals and dive durations shifting the frequency of LCs. Hays et al. (2001) suggest that ARGOS error, even within a particular LC, is highly variable and likely...
dependent upon animal diving behavior. Ideally, ARGOS error should be assessed independently for each tracking study. While this is rarely possible, we have provided data derived from different species with a range of surfacing behaviors (Table 1 & 3). Not surprisingly, location errors were similar for the two sea lion species that swim on the surface and have similar diving patterns (Table 1, Fig. 7B). In comparison, northern elephant seal ARGOS tracks were characterized by considerably greater location error (Table 1, Fig 7A). This result is not unexpected considering that the dive duration of elephant seals is about as long as the time an ARGOS satellite is overhead (20 min), meaning that all of the location information will most likely be transmitted during a single 2 to 3 minute surface interval. In contrast, fur seals and sea lions are likely to surface on multiple occasions while the ARGOS satellite is overhead, providing for more uplinks. In addition, an ARGOS tag attached to an elephant seal is likely to undergo a greater range of temperatures (4–15°C), and more frequent temperature changes, than a tag attached to either a fur seal or sea lion. This is because the deep diving nature of elephant seals will take the tag through a greater range of ambient temperatures and, once at the surface, the satellite tag is likely to warm rapidly after spending 21 min at depths between 400–600m. Other

Table 3. Summarizes the species, sample size, location and duration of deployment and the data obtained for that species, along with data on their diving behavior.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample size</th>
<th>Mean latitude</th>
<th>Mean longitude</th>
<th>Deployment duration (weeks)</th>
<th># ARGOS positions</th>
<th># GPS positions</th>
<th>Mean ARGOS LC</th>
<th>Mean error (km) light filter</th>
<th>Mean error (km) no filter</th>
<th>Mean dive duration (min)</th>
<th>reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>California sea lion</td>
<td>9</td>
<td>33.92</td>
<td>-119.970</td>
<td>8</td>
<td>4746</td>
<td>9219</td>
<td>540</td>
<td>1-0 (3.80)</td>
<td>3.59</td>
<td>9.49</td>
<td>2.2</td>
</tr>
<tr>
<td>Galapagos sea lion</td>
<td>4</td>
<td>0.764</td>
<td>-90.413</td>
<td>2</td>
<td>344</td>
<td>1705</td>
<td>117</td>
<td>1-0 (3.41)</td>
<td>4.29</td>
<td>88.56</td>
<td>4</td>
</tr>
<tr>
<td>Cape fur seal</td>
<td>6</td>
<td>29.802</td>
<td>16.267</td>
<td>4</td>
<td>917</td>
<td>1597</td>
<td>113</td>
<td>0-A (4.53)</td>
<td>4.72</td>
<td>18.67</td>
<td>2.5</td>
</tr>
<tr>
<td>Australian fur seal</td>
<td>3</td>
<td>39.357</td>
<td>146.304</td>
<td>2</td>
<td>165</td>
<td>919</td>
<td>54</td>
<td>1-0 (3.70)</td>
<td>23.21</td>
<td>92.74</td>
<td>2.9</td>
</tr>
<tr>
<td>Northern elephant seal</td>
<td>9</td>
<td>42.739</td>
<td>-135.902</td>
<td>12</td>
<td>1146</td>
<td>13606</td>
<td>301</td>
<td>A-B (5.74)</td>
<td>61.38</td>
<td>173.11</td>
<td>21.3</td>
</tr>
<tr>
<td>Stationary test of GPS</td>
<td>4</td>
<td>36.949</td>
<td>-122.066</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4. Comparison of ARGOS error from different studies. (If two values are present in a cell, this indicates ‘latitude/longitude’).

<table>
<thead>
<tr>
<th>Source</th>
<th>Method</th>
<th>Statistic</th>
<th>LC-3</th>
<th>LC-2</th>
<th>LC-1</th>
<th>LC-0</th>
<th>LC-A</th>
<th>LC-B</th>
</tr>
</thead>
<tbody>
<tr>
<td>ARGOS</td>
<td>Theoretical</td>
<td>68th percentile</td>
<td>0.15/0.15</td>
<td>0.35/0.35</td>
<td>1.00/1.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>This study on animals</td>
<td>on sea</td>
<td>Mean</td>
<td>0.487</td>
<td>0.939</td>
<td>1.110</td>
<td>4.342</td>
<td>31.512</td>
<td>36.077</td>
</tr>
<tr>
<td>This study on animals</td>
<td>on sea</td>
<td>68th percentile</td>
<td>0.486</td>
<td>1.011</td>
<td>1.201</td>
<td>4.182</td>
<td>6.185</td>
<td>10.276</td>
</tr>
<tr>
<td>This study on animals</td>
<td>on sea</td>
<td>68th percentile Lat/long</td>
<td>0.225/0.340</td>
<td>0.468/0.729</td>
<td>0.574/0.879</td>
<td>1.795/2.855</td>
<td>2.788/4.373</td>
<td>4.642/8.253</td>
</tr>
<tr>
<td>Hazel 2009</td>
<td>on animals, at sea</td>
<td>68th percentile</td>
<td>0.482</td>
<td>0.785</td>
<td>1.430</td>
<td>5.179</td>
<td>8.072</td>
<td>11.484</td>
</tr>
<tr>
<td>Goulet et al. 1999</td>
<td>stationary test on land</td>
<td>68th percentile</td>
<td>-</td>
<td>-</td>
<td>1.335</td>
<td>43.799</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Keating et al. 1991</td>
<td>stationary test on land</td>
<td>68th percentile</td>
<td>0.361</td>
<td>0.903</td>
<td>1.188</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mate et al. 1997</td>
<td>stationary test on land</td>
<td>68th percentile</td>
<td>0.3</td>
<td>0.9</td>
<td>2.3</td>
<td>7.5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>McConnell et al. 1992b</td>
<td>on animals, on land</td>
<td>68th percentile</td>
<td>-</td>
<td>1.022</td>
<td>2.238</td>
<td>3.792</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Britten et al. 1999</td>
<td>on animals, on land</td>
<td>68th percentile</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>11.5</td>
<td>6.8</td>
<td>98.5</td>
</tr>
<tr>
<td>Vincent et al. 2002</td>
<td>on animals, study pool</td>
<td>68th percentile Lat/long</td>
<td>0.157/0.295</td>
<td>0.259/0.485</td>
<td>0.494/1.021</td>
<td>2.271/3.308</td>
<td>0.762/1.244</td>
<td>4.596/7.214</td>
</tr>
<tr>
<td>Burns and Castellini 1998</td>
<td>on animals, on ice</td>
<td>Mean Lat/long</td>
<td>-</td>
<td>-</td>
<td>4.1/2.5</td>
<td>8.8/5.5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Boyd et al. 1998</td>
<td>Stationary test on land</td>
<td>Mean</td>
<td>1.228</td>
<td>1.115</td>
<td>1.566</td>
<td>3.779</td>
<td>18.843</td>
<td>22.841</td>
</tr>
<tr>
<td>Hays et al. 2001</td>
<td>stationary test on land</td>
<td>Mean Lat/long</td>
<td>0.12/0.32</td>
<td>0.28/0.62</td>
<td>1.03/1.62</td>
<td>4.29/15.02</td>
<td>1.39/0.81</td>
<td>5.23/7.79</td>
</tr>
<tr>
<td>Le Boeuf et al. 2000</td>
<td>on animals, on land</td>
<td>Mean</td>
<td>0.8</td>
<td>1.4</td>
<td>2.7</td>
<td>9.3</td>
<td>28.3</td>
<td>48.4</td>
</tr>
<tr>
<td>Nicholls et al. 2007</td>
<td>stationary test on land</td>
<td>Mean</td>
<td>0.5</td>
<td>0.7</td>
<td>1.7</td>
<td>16</td>
<td>5</td>
<td>38</td>
</tr>
<tr>
<td>White and Sjoberg 2002</td>
<td>on animals, at sea</td>
<td>Grand mean</td>
<td>-</td>
<td>-</td>
<td>4.434</td>
<td>5.349</td>
<td>6.477</td>
<td>45.345</td>
</tr>
</tbody>
</table>

Note: Percentile and mean values are presented.
doi:10.1371/journal.pone.0008677.t004
investigators may want to create their own error distributions using an appropriate subset of the ARGOS error data provided here as supplementary material (S1), considering species-specific diving behaviour (Table 3). Basic descriptions of movements over large spatial scales do not require a detailed understanding of ARGOS location error but the implementation of quantitative analytical tools that derive behavioral states requires accurate knowledge of the error structure [28,39,40]. This is particularly true for analyses at or near the spatio-temporal resolution of the tracking data itself, as these analyses will be particularly sensitive to estimates of error and may provide spurious interpretations if inaccurate estimates are used. Several studies highlight the utility of error distributions in both track “filtering” and behavioral interpretation [26,40,41,42,43]. New track improvement algorithms bypass traditional filtering techniques (i.e. simple removal of points) in favor of using all positions weighted by error estimates of the corresponding location class. Several studies use this approach in either a frequentist or Bayesian framework to re-create a more accurate track [28,39]. In addition, these methods are used to extrapolate the likely behavioral state of the tagged animal [39,44]. Although Fastloc GPS drastically improves the quality of tracking data of diving marine animals and will facilitate analyses at smaller spatio-temporal scales, the abundance of historic ARGOS tracking records and relative ease of ARGOS tracking (i.e. no recapture requirement) will ensure a continued demand for analytical approaches using these data. It is essential that these analyses use realistic error distributions to recreate a more accurate track and ensure estimates of behavioral states are not driven by noise in the position estimates. Future work should investigate the impact of track quality parameters, such as accuracy and frequency of positions, on biological interpretation of animal movement data.

Supporting Information

Data S1 The supplemental data consists of an error estimate for each ARGOS location within five minutes of any GPS position. The supplemental file is broken into separate files for each of the five species of pinnipeds. For each species file the individual animals are identified by “Animal ID” and the great-circle distance, bearing, longitude component of error, and latitude component of error that was calculated for each ARGOS location are provided along with the ARGOS location class (LC) given for that location and the associated GPS residual value. A digital copy of these data are available from the corresponding author. Found at: doi:10.1371/journal.pone.0008677.s001 (0.14 MB PDF)

Acknowledgments

We thank the following for help during various phases of the fieldwork: Robin Weber for the creation and maintenance of the ARGOS database; Grace Smith and many other Navy Personnel at the San Nicolas Island Outlying Landing Field; Luis Hueckstadt, and many volunteers for assistance with field work at Año Nuevo State Park; Carey Kuhn, Luis Hueckstadt, Mary Zavanelli, David Casper, Sandy Salazar, Matt Rutishauser, Veronica Michuy for field assistance in the Galapagos Islands; Don Kotze, Steven McCue, Helene de Nys, Darrel Anders and Mdu Seakamela for field assistance support in South Africa. This research was conducted as part of the Tagging of Pacific Predators (TOPP) program.

Author Contributions

Conceived and designed the experiments: DPC PWR JPYA. Performed the experiments: DPC PWR JPYA SS JHL AH SK HO SVA. Analyzed the data: PWR ALH DEC. Contributed reagents/materials/analysis tools: DPC JPYA HO. Wrote the paper: DPC PWR.

References