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Journal

Marine Biology, 147(4)

ISSN

0025-3162

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Publication Date

2005-08-01

Peer reviewed

**Comparison of light- and SST-based geolocation with satellite telemetry in
free-ranging albatrosses**

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Abstract Light-based archival tags are increasingly being used on free-ranging marine vertebrates to study their movements using geolocation estimates. These methods use algorithms that incorporate threshold light techniques to determine longitude and latitude. More recently, researchers have been using sea surface temperature (SST) to determine latitude in temperate regions. The accuracy and application of these algorithms have not been validated on free-ranging birds. Errors in both geolocation methods were quantified by double-tagging Laysan (*Phoebastria immutabilis* Rothschild) and black-footed (*P. nigripes* Audubon) albatrosses with both leg mounted archival tags that measured SST and ambient light, and satellite transmitters. Laysan albatrosses were captured and released from breeding colonies on Tern Island, northwestern Hawaiian Islands (23° 52'N, 166° 17'W) and Guadalupe Island, Mexico (28° 31'N, 118° 10'W) and black-footed albatrosses were from Tern Island. Studies were carried out between December 2002 and March 2003. For all birds combined, the mean \pm SD Great Circle (GC) distance between light-based locations and satellite derived locations was 400 ± 298 km ($n = 131$). Errors in geolocation positions were reduced to 202 ± 171 km ($n = 154$) when light-based longitude and SST-based latitude (i.e. SST/light) were used to establish locations. The SST/light method produced comparable results for two Laysan albatross populations that traveled within distinctly different oceanic regions (open ocean vs. more coastal) whereas light-based methods produced greater errors in the coastal population. Archival tags deployed on black-footed albatrosses returned a significantly higher proportion of lower quality locations, which was attributed to interference of the light sensor on the tag. Overall, the results demonstrate that combining measures of light-based longitude and SST-based latitude significantly reduces the error in location estimates for albatrosses, and can provide valid latitude estimates during the equinoxes, when light-based latitude measurements are indeterminate.

Key words: Argos, black-footed Albatross, foraging, geolocation, Laysan Albatross, *Phoebastria*, satellite tracking, sea surface temperature

Introduction

Understanding the spatial and temporal scales over which animals operate is a fundamental interest of ecologists because it provides significant insight into how they interact within their environment (Schneider 1994). Marine birds, turtles, mammals, and fish associate with oceanic processes at fine to ocean-basin scales (Hunt Jr. et al. 1999; Le Boeuf et al. 2000; Polovina et al. 2000; Bradshaw et al. 2002; Fritz et al. 2003) but their responses to specific oceanographic features are often difficult to ascertain because continuous observation of individuals at sea is often impractical. Development of microprocessor-based electronic archival tags and transmitters (i.e. tracking devices) has given researchers more remote tools to track free-ranging marine vertebrates at sea (Costa 1993; Gunn et al. 1994; Le Boeuf et al. 2000; Polovina et al. 2000; Boustany et al. 2002; Weimerskirch et al. 2002).

A variety of methods have been used to examine the distribution of seabirds in relation to spatial and temporal processes, including radio VHF tags (Anderson and Ricklefs 1987; Pennycuik et al. 1990), satellite telemetry (Jouventin and Weimerskirch 1990; Davis and Miller 1992; Prince et al. 1992; Catard et al. 2000), light-based geolocation (Grémillet et al. 2000; Hull 2000; Weimerskirch and Wilson 2000; Phillips et al. 2004), and GPS (Weimerskirch et al. 2002; Grémillet et al. 2004). Each method has inherent advantages and disadvantages but overall, satellite telemetry using Argos-based receivers has been most commonly employed because the accuracy of satellite-derived locations is generally within a few kilometers of the true location. Accuracy depends on the frequency of instrument transmission and the latitude of the bird being tracked, and multiple locations can be obtained per day (Fancy et al. 1988). Nonetheless, the use of satellite telemetry to study long-term movements (e.g. months to years) is problematic because satellite platform terminal transmitters (PTTs) can place unreasonable weight and drag

constraints on the bird. They are expensive if lost, power requirements limit the transmission rate, and tag loss can be high due to attachment failure (reviewed by Phillips et al. 2004).

Light-based geolocation archival tags offer a promising alternative for long-term tracking of free-ranging seabirds because the devices are small (< 10 g), are considerably cheaper than satellite PTTs, and can be fixed more securely to leg bands thus avoiding the problem of instrument loss during molt (Wilson et al. 2002; Phillips et al. 2004).

Despite the increasing use of light-based archival tags on seabirds (Grémillet et al. 2000; Hull 2000; Weimerskirch and Wilson 2000; Phillips et al. 2004), we lack studies validating the method's accuracy. To date, only one study (Phillips et al. 2004) has quantified the error of geolocation archival tags on a flying seabird. Stationary trials (Wilson et al. 1992; Welch and Eveson 1999) and experiments on non-flying seabirds (Hull 1999), marine mammals (DeLong et al. 1992; Le Boeuf et al. 2000; Beck et al. 2002), and free-swimming fishes (Teo et al. 2004) have produced a wide range of geolocation error estimates (34–1,043 km from known locations, reviewed by Phillips et al. 2004). In general, the greatest source of error in location estimates using the geolocation method is attributed to the calculation of latitude (see below). We therefore conducted additional tests on different species at different locations to characterize the performance of this methodology on free-ranging seabirds more accurately.

To calculate a location on the globe using light-based geolocation, accurate estimates of the times of sunrise and sunset are critical for determining longitude and latitude (DeLong et al. 1992; Gunn et al. 1994; Welch and Eveson 1999; Musyl et al. 2001). Small errors in the estimates of day length can generate significant errors in latitude estimates, and errors in latitude increase as day of the year approaches a solar equinox (DeLong et al. 1992; Hill 1994; Welch and Eveson 1999; Musyl et al. 2001). Variation in the accuracy of geolocation can also vary with

type of tag and algorithms used to determine the locations (Welch and Eveson 1999; Musyl et al. 2001). Lastly, large directional movements over short time intervals by a subject can also increase the errors in estimated day length thereby contributing to errors in location estimates based on light levels (Welch and Eveson 1999). This last concern applies to fast moving birds like albatrosses and petrels because they may travel hundreds of kilometers per day (Pennycuik 1982; Alerstam et al. 1993; Catard et al. 2000; Weimerskirch et al. 2002). In the North Pacific, three albatross species (Laysan, *Phoebastria immutabilis*; black-footed, *P. nigripes*; short-tailed, *P. albatrus*) breed in sub-tropical waters but range into sub-arctic waters to the north while foraging. These albatross species offer a good platform to test the accuracy of light-based geolocation because they travel over a wide range of latitudes, originating from low latitude breeding sites (e.g. 20–30°N).

Given the larger errors in latitude of light-based geolocation, especially around the solar equinoxes, measures of sea surface temperature (SST) have been suggested as a means of improving estimates of latitude (Smith and Goodman 1986; DeLong et al. 1992; Gunn et al. 1994; Hill 1994). Recently, two studies developed and tested algorithms to improve location estimates based on a combination of threshold light techniques for estimating longitude and SST to estimate latitude (Beck et al. 2002; Teo et al. 2004). Both studies showed that overall errors in location estimates were reduced by a factor of 4–10 when latitude was calculated from measures of SST collected by the archival tag and compared to SST obtained from orbiting satellites. This method can also estimate latitude during the equinoxes when calculations based on light levels are indeterminate (DeLong et al. 1992; Musyl et al. 2001).

The objective of the present study was to validate and compare the use of light-based and SST-based (i.e. SST/light) geolocation estimates of location with satellite telemetry on free-

ranging birds. These tests were performed on two albatross species at two breeding sites in the North Pacific Ocean. Each bird was equipped with a satellite transmitter and a geolocation archival tag that measured light and SST. Because both breeding colonies are at relatively low latitudes (23°N and 28°N) yet these albatrosses travel to high latitudes to feed, we were able to evaluate the performance of geolocation archival tags on fast moving birds that cover an expansive area of the North Pacific Ocean.

Methods and materials

The movement patterns of ten Laysan (*Phoebastria immutabilis* Rothschild) and seven black-footed (*P. nigripes* Audubon) albatrosses were studied during the incubation and chick-brooding periods from December 2002 to February 2003 on Tern Island, French Frigate Shoals, northwestern Hawaiian Islands (23° 52'N, 166° 17'W). Another 12 Laysan albatrosses were studied during the same reproductive periods from January to March 2003 on Guadalupe Island, Baja California, Mexico (28° 31'N, 118° 10'W).

Tracking devices: satellite transmitters and archival tags

To compare the accuracy of the tracking devices, each bird carried both a 30-g satellite PTT (Pico-100, Microwave Telemetry, Columbia, Maryland, USA) and a 6-g geolocation archival tag (hereafter called an archival tag or tag; Lotek LTD 2400, Lotek Wireless., St. John's, Newfoundland). The combined mass of these devices was approximately 1% of total bird body mass. Satellite PTTs were attached to feathers on their backs with Tesa® tape (Weimerskirch et al. 1994) and were programmed to transmit a radio signal every 90 s. PTT transmissions were localized by orbiting satellites of the Argos system (Fancy et al. 1988). Archival tags were attached to plastic identification bands placed around each bird's tarsus. The tags recorded light

intensity every 60 s (Fig. 1a), processed the light data onboard with proprietary algorithms from the manufacturer, and recorded the estimated daily longitude and latitude to a ‘day log’.

Longitude was determined from the difference between noon in UTC (Coordinated Universal Time) and the time of local solar noon or midnight, and latitude was estimated from the total length of each daytime or nighttime cycle (Ekstrom 2004). The clock on the tags recorded each parameter in relation to UTC, not local time.

Testing the effects of archival tag placement

Eight birds (three Laysan and two black-footed albatrosses from Tern Island and three Laysan albatrosses from Guadalupe Island) were equipped with a PTT and two archival tags (~42 g total which was 1.1–1.4% of body mass): one attached to the tarsus and the other mounted on the back next to the satellite PTT. This allowed us to test the effects of light interference from feather coverage and/or behavior because albatrosses often tuck their legs into body feathers during flight and extend them when they land or take off, which can affect the amount of light exposure to the sensor on the tag. We assumed that tags placed on the bird’s back would experience less light interference from feather coverage. These tests also allowed us to test tag orientation in relation to placement on the bird’s body.

Stationary trials

We conducted five trials with individual Lotek LTD 2400 archival tags fixed to a stationary object at two sites. One trial was conducted on Tern Island from 26–30 December 2002. Four other trials were conducted at Snares Island, New Zealand (48° 01’ S, 166° 36’ E) from 14–24 February 2003. Tags were placed either at the top of a small building (Tern Island) or on the branch of leafless tree (Snares Island) to maximize light exposure. In either case, the building or tree was < 20 m above sea level. Tags were left to collect data for 5–10 d and the true location of

each stationary object was established with a handheld GPS (eTrex Venture, Garmin®, Olathe, Kansas).

Potential errors in geolocation estimates

Latitude estimates are highly sensitive to errors in day length determined with light-based geolocation (Welch and Eveson 1999; Musyl et al. 2001; Teo et al. 2004). In order to improve accuracy in latitude estimates, the archival tags were also programmed to record environmental temperatures ($\pm 0.1^\circ\text{C}$) at 32-s intervals. The time taken for the temperature sensor to record a step change of 90% in temperature was approximately 60 s. Since the tags were placed on the bird's tarsus, abrupt changes in temperature were likely to represent a change in activity level such as landing or taking off from the sea surface (Weimerskirch et al. 1995; Wilson et al. 1995; Weimerskirch and Guionnet 2002; Wilson et al. 2002). Stable temperatures would indicate periods when the bird was sitting on the sea surface (Fig. 1b; Weimerskirch et al. 1995; Wilson et al. 1995). Tag temperatures would tend to be higher (i.e. closer to body temperature) and more variable when birds were off the water because albatrosses either tuck their legs under feathers (Weimerskirch and Guionnet 2002; Wilson et al. 2002) or extend them when landing and taking off. Thus, whenever the tag recorded a stable low temperature for >20 min, we assumed that the bird was on the water and the tag was measuring SSTs. Since the 20-min period was much longer than the lag time of the tag and the temperature was stable during this time period, the lag time of the tag did not affect the accuracy of the recorded SSTs.

The SST data and the light-based longitudes collected by each tag were then compared to remotely sensed SST data (see below) to estimate the daily latitudes using an algorithm described by Teo et al. (2004). Essentially, a pixel in the remotely sensed reference SST grid that intersects the light level longitude estimate and the northern latitudinal limit was identified.

Assuming the bird was in the northern hemisphere, latitudinal searches were limited to a range from 0 to 70° N. The search area within the reference SST grid was then established around the specified pixel. For this study, we assumed that albatrosses could randomly sample the ocean surface within a 500×300 km area for each day (longitude and latitude, respectively), although the search grid was centered on the light-based longitude of the specified day. The SSTs within this search area were compared to the SSTs measured by the tag to determine how well they matched. After this, the algorithm moved to the next pixel south of the original pixel and the process was repeated until the southern latitudinal limit was reached. Three indices were used in turn to match the SSTs, and the center of the best matching search area was considered the mean location of the albatross for the given day. The three indices were: 1) the weighted sum of the number of matching SSTs, 2) the sum of squares of the differences between the proportion of SSTs measured by the tag and the expected proportion of SSTs in the search area, assuming that the surface sampled was a bivariate Gaussian distribution, and 3) the weighted sum of the number of matching pixels within the search area. A complete description of the algorithm can be found in Teo et al. (2004).

An iterative simulation using data from four birds showed that a search area of 500×300 km within the SST grid consistently produced the lowest errors. This was also biologically reasonable because the Argos data demonstrated that the albatrosses traveled on average $528 \pm 166 \text{ km d}^{-1}$. The remotely sensed SST grids used in this study were equal angle, global, 8-day composites of nighttime SST grids from the moderate resolution imaging spectroradiometer (MODIS, <ftp://podaac.jpl.nasa.gov>, thermal IR SST, 0.1°C and 4 km resolution). Thus, we obtained two estimates of geolocation: one based purely on measurements of light (i.e. “light”) and the other based on light-based longitudes and SST-based latitudes (i.e. “SST/light”).

Evaluation of location quality

Location data obtained from the satellite PTTs were filtered using purpose-built routines from the IKNOS toolbox (Y. Tremblay, unpubl.) developed with MATLAB software (The MathWorks, Natick, Massachusetts). The filtering routine used five criteria to determine the validity of an Argos location: 1) realistic travel speeds ($< 90 \text{ km h}^{-1}$) of a bird between consecutive locations; 2) the change in azimuth of a bird between consecutive locations; 3) the Argos location class (i.e. 1–3 were “trusted” whereas 0, A, and B, were “checked”); 4) the time elapsed between consecutive locations ($>12 \text{ min}$); and 5) whether a location was on land or at sea.

To illustrate the variability in accuracy of geolocation positions, both raw (unfiltered) and post-processed (filtered) locations were presented. However, the range of errors for raw locations was large, so only the median, minimum, and maximum of errors were presented. All raw locations were then filtered in a sequence of steps to eliminate unrealistic positions. These data were then used in the remaining statistical analyses. The filtering process began with the removal of locations that were estimated with light level threshold curves that contained gross anomalies in light conditions around the time of sunset and sunrise (Gunn et al. 1994; Phillips et al. 2004; Teo et al. 2004). These anomalies greatly affect the accuracy of geolocation estimates and can result from interference of the light sensor on the archival tag due to feather coverage, bird activity around the time of sunset or sunrise, and or weather conditions (Phillips et al. 2004). SST/light-based geolocation positions were further inspected for anomalous latitude estimates that resulted from the comparison between tag-derived SSTs and remotely sensed SSTs in regions with substantial cloud cover. Locations involving comparison of SSTs within a search grid that contained $>80\%$ cloud cover had too few SST measurements for the algorithm to

reliably determine latitude (Teo et al. 2004). Therefore, these locations were removed from the analysis. Finally, all remaining geolocations were validated using the speed filter developed for the Argos data. However, locations were only checked for realistic travel speeds ($< 35 \text{ km h}^{-1}$ during a 48 hr period; this study; Phillips et al. 2004) between geographical positions.

In order to compare Argos and geolocation positions, we condensed the Argos fixes into a single daily longitude and latitude to match the time resolution output of the Lotek LTD 2400 archival tags, which was a single location d^{-1} . Geolocation estimates determined by Lotek LTD 2400 archival tags are based on a UTC day. Thus, in the North Pacific region, the tag estimated longitude based on the midpoint between sunset and sunrise (i.e. local midnight). Similarly, Argos receivers calculate geographical positions based on a UTC day. Therefore, single daily Argos locations were determined by interpolating the longitude and latitude of a bird's location between consecutive Argos fixes that matched the time (in UTC) equidistant between sunset and sunrise measured by the archival tag (i.e. local midnight; Fig. 1a). Assuming an albatross' trajectory between consecutive locations was straight, the interpolated position (hereafter called the Reference location or Ref) should be the most comparable location with that estimated by the archival tag. For comparison with other studies (e.g. Beck et al. 2002; Phillips et al. 2004 – nighttime locations only), we also averaged all valid Argos locations (hereafter called Avg. Argos) obtained in a 24-h period into a single longitude and latitude for that given day and compared this to the Reference location and the geolocation positions. Our analysis included only those days for which a valid location was obtained with each method: 1) Reference location, 2) Avg. Argos, 3) light-based geolocation, and 4) SST/light-based geolocation.

Statistical analyses

Since the Longitude-Latitude coordinate system is not isometric (i.e. one degree of longitude does not represent the same distance at all latitudes), we calculated the absolute error (Great Circle [GC] distance) between locations estimated with each method (i.e. Avg. Argos, light, and SST/light) and the corresponding Reference location established with Argos data. For comparison with other studies, we also present geolocation errors as the standard deviation (SD) of longitudinal and latitudinal differences (in °) with respect to Reference locations. Statistical analyses were performed using SYSTAT 10.2 (SPSS Inc, Chicago, Illinois) with a significance level of $P \leq 0.05$ for statistical tests. All data are presented as mean \pm 1 SD.

Results

A total of 304 at-sea tracking days (from Argos data) were available, with 13.2 ± 2.8 (range 7–20) Argos locations d⁻¹ for each bird. After filtering, 77.0% of Argos locations were accepted as valid. A total of 226 geolocation estimates was obtained from the archival tags for comparison with Argos Reference locations.

Albatross distribution at sea

The overall distribution of albatrosses at sea determined by Argos locations differed by species and breeding location. Laysan albatrosses from Tern Island frequented higher latitudes ($n = 123$ d, mode = 40°N, range = 24.7°) and traveled over a broader range of longitudes ($n = 123$ d, mode = 158°W range = 58.0°) than the other study groups. Black-footed albatrosses had the most restricted range of movement in both latitude ($n = 40$ d, mode = 36°N, range = 15.3°) and longitude ($n = 40$ d, mode = 167°W, range = 25.7°) compared to Laysan albatrosses from both breeding sites. Laysan albatrosses from Guadalupe Island frequently remained at lower latitudes

($n = 63$ d, mode = 30°N , range = 22.0°) and within the California coast region, as reflected by the modal longitude ($n = 63$ d, mode = 119°W , range = 34.7°).

Comparison of location errors

Avg. Argos positions differed from their corresponding Reference locations by an average GC distance of 41.4 ± 30.6 km (range = 155 km, $n = 226$). However, the absolute difference in GC distance (i.e. $|\text{Ref} - \text{Avg. Argos}|$) was on average, 26.9 ± 26.3 km (range = 135 km, $n = 226$).

The variability in geolocation error (i.e. GC distances) of unfiltered data was large. For example, geolocation estimates based solely on light levels for all birds combined ranged from as low as 5 km to as large as 17,516 km (Table 1). Similarly, errors from unfiltered SST/light-based measurements ranged over several orders of magnitude (Table 1). Overall, the majority of error in geolocation estimates was due to interference of the light sensor on archival tags because the removal of locations that failed this quality check (23%; Table 1) reduced the maximum geolocation error of both methods to 2,929 km for all birds combined. Further removal of SST/light-based locations that were affected by high cloud cover (5.2%), and other locations that failed the speed filter (24.7% for light-based locations and 11.5% for SST-based locations) resulted in 131 valid locations based on light levels and 154 valid locations based on SST/light (original for both was 226 locations). Interestingly, 75% of all unfiltered locations for black-footed albatrosses ($n = 40$) were removed due to interference of the light sensor on the tag, but none of the remaining locations failed either of the other filtering procedures (Table 1).

The mean error (i.e. GC distance) of all filtered light-based locations was 400 ± 298 km whereas the mean error of all filtered SST/light-based locations was 202 ± 171 km. There was no overlap in the 95% Confidence Intervals (CI) of the means between each geolocation method, suggesting that SST/light-based measurements produced significantly lower errors overall, in

location estimates (Table 1). This trend was similar for Laysan albatrosses at both study locations. However, the variability in location errors for black-footed albatrosses was larger than for Laysan albatrosses and there was overlap in the 95% CI of the mean errors of locations determined with each methodology (Table 1).

Longitude errors in geolocations were less than latitude errors (Table 1). Thus, errors in geolocation positions compared to Argos locations were mostly attributed to larger inaccuracies of latitude estimations. In addition, these latitudinal errors were larger and more variable for estimates calculated from light level data compared to SST measurements for all birds combined (Table 1). This trend also influenced the distribution of errors with respect to Argos-based Reference locations for each geolocation method and albatross species (Fig. 2). The trend was similar for Laysan albatross from both study sites, but was opposite for black-footed albatrosses.

Given the measurement errors of each geolocation method, it was possible to compare the utility of each to recreate the track of an albatross at sea. Figure 3 (a & b) shows the at-sea movements of two albatrosses where each track was created using locations determined with the Argos-based Reference location, and each geolocation method. Although light-based geolocation estimates were comparable to the Reference location in some cases (e.g. Fig. 3), estimates based on SST/light appeared to more accurately represent the movement patterns of each albatross.

Testing the effects of archival tag placement

A total of 36 comparable tracking days were obtained from archival tags simultaneously deployed on the backs and legs of eight albatrosses (six Laysan and two black-footed). There was no significant effect of tag placement on light-based geolocation estimates after data were filtered ($n = 21$ comparable days).

Stationary trials

The mean geolocation error in stationary trials with the archival tags was 109 ± 58 km ($n = 24$ d) from the true location measured with GPS. The SD in light-based longitude error was 0.48° and the SD in light-based latitude error was 2.25° .

Discussion

Our results demonstrate that geolocating archival tags can be used to track basin-scale movements of free-ranging albatrosses with an average accuracy of 202–400 km from a “true” location. The accuracy of geolocation estimates, however, can be influenced by the method used to determine latitude (light levels vs. SST). Interestingly, our error measurements for light-based geolocation of flying albatrosses were greater than those reported in a similar study on black-browed albatrosses (*Thalassarche melanophrys* Temminck) at South Georgia Islands (54°S , 38°W) (Phillips et al. 2004). Employing a similar study design to ours, mean geolocation error using light-based methods was 186 ± 114 km, or less depending on the amount of post processing (Phillips et al. 2004). When light levels and SST measurements were combined to determine geolocation, however, the inaccuracies in our light-based estimates were reduced to a level comparable to those of Phillips et al. (2004).

The results of our stationary trials were similar to static trials reported elsewhere (DeLong et al. 1992; Wilson et al. 1992; Welch and Eveson 1999; Musyl et al. 2001; Beck et al. 2002; Phillips et al. 2004) suggesting that there were no major differences in the quality of our geolocation archival tags compared to those used in other validation studies.

Potential sources of error in geolocation estimates

Albatrosses in our study originated from breeding colonies at sub-tropical latitudes ($23\text{--}28^\circ\text{N}$) and while at sea, modal latitudes of both species were between 30°N and 40°N . These latitudinal

ranges are considerably lower than those of albatrosses studied at South Georgia. This latitudinal difference could partially explain why our light-based geolocation estimates exhibited larger errors than those reported by Phillips et al. (2004) because the calculation of light-based latitude is subject to larger errors when day/night differences are less pronounced (e.g. lower latitudes). Thus small differences in day length determination can cause substantive errors in latitude calculations, particularly of moving objects (DeLong et al. 1992; Hill 1994; Welch and Eveson 1999; Ekstrom 2004). In contrast, stationary tags deployed at low latitudes can estimate geographical positions with lower errors (this study; Musyl et al. 2001). Nevertheless, implementation of a latitude correction based on SSTs measurements can substantially reduce geolocation errors for subjects studied at low latitudes (this study; Teo et al. 2004) because SST changes sharply between 20°N and 30°N (Pickard and Emery 1990).

Another potential source of error in our geolocation estimates could be related to the fact that many birds in our study, especially Laysan albatrosses from Tern Island, exhibited a pronounced tendency for broad longitudinal movements (nearly 60°). Albatrosses are capable of traveling at least 500 km d⁻¹ (determined from satellite data) and significant movement in a longitudinal direction can affect geolocation estimates by either increasing or decreasing day length (Hill 1994; Ekstrom 2004).

In the present study, our calculation of geolocation error was based upon comparisons to an Argos-based Reference location rather than the average of all Argos locations over a given day. The absolute difference between comparisons of geolocation errors to the Reference location vs. averaging Argos locations was 27 km. We believe that the Reference location was a more accurate comparison to geolocation estimates because it encompassed the location of the albatross that was based upon the time period used to estimate longitude by the archival tag.

Thus, future validation studies should weigh carefully the potential errors in averaging Argos locations in comparison to an interpolated location when comparing geolocation estimates to Argos data.

The results of our trials on albatrosses fall within the range of estimated geolocation errors (94–1,043 km) measured on other marine vertebrates (DeLong et al. 1992; Hull 1999; Beck et al. 2002; Phillips et al. 2004; Teo et al. 2004). Unlike our study and that of Phillips et al. (2004), however, all previous validation studies were performed on diving and swimming vertebrates that travel at slower speeds than the albatrosses. For example, Beck et al. (2002) compared SST/light-based geolocation to Argos locations in a validation study on grey seals (*Halichoerus grypus* Fabricius) and measured errors in geolocation of only 94.2 ± 8.22 km from the satellite derived positions. The small errors were likely due to the fact that the seals were studied at latitudes above 40°N and were moving much more slowly (< 148 km d⁻¹) than the albatrosses. Similar results were also observed in validation experiments on sharks and tunas (Teo et al. 2004). Seals, sharks, and tunas spent a considerable amount of time at or near the surface, so sensors on these vertebrates would collect more SST data. This would allow greater precision and accuracy of latitude estimates based on SST measurements (Teo et al. 2004). Even though albatrosses fly rapidly over the sea surface with sporadic landings on the sea surface, our study and that of Phillips et al. (2004) demonstrate that light- and SST/light-based geolocation can be used to study albatross movements over broad spatial and temporal scales with results that are comparable to those of other marine vertebrates.

Population differences in geolocation errors of Laysan albatrosses were only apparent in light-based estimates. Larger errors in light-based geolocation were observed in Laysan albatrosses from Guadalupe Island, which may have been due to latitudinal regions frequented

by each population (mode = 40°N vs. 30°N for Tern and Guadalupe Islands, respectively) and the effect this had on light-based latitude estimates. Furthermore, each population of Laysan albatross utilized distinctly different oceanographic provinces of the North Pacific Ocean (Y Tremblay and WR Henry unpubl.), yet geolocation errors based on SST/light measurements were nearly identical. Albatrosses from Tern Island traveled within oceanic regions of the central North Pacific (Y Tremblay unpubl.) whereas albatrosses from Guadalupe Island traveled mainly within the eastern North Pacific (WR Henry unpubl.), which is heavily influenced by the California Current system. Thus, we might expect the stratification of SSTs within each oceanic province to vary considerably. Nevertheless, the SST/light-based geolocation algorithm of Teo et al. (2004) produced comparable results for albatrosses that utilize broadly different oceanic regions.

Our study suggests that geolocation accuracy, or more correctly tag performance, could be species-dependent. A high proportion of locations obtained from archival tags deployed on black-footed albatrosses were discarded compared to locations obtained from Laysan albatrosses. We offer three hypotheses to explain this difference. Black-footed albatrosses frequented oceanic regions that were typically 5° lower in latitude than Laysan albatrosses breeding at the same island, which could have influenced light-based estimates. Black-footed albatrosses also have dark feather plumage whereas Laysan albatrosses have white plumage. If feathers obscure the light sensor on the tag, dark feathers will absorb more ambient light than white feathers, which should reflect ambient light. Behavioral differences between species could also have influenced location quality. For example, if black-footed albatrosses were more active at dawn or dusk, measures of sunset and sunrise could be subject to error, which would affect longitude estimates.

Archival tag placement

Many factors can influence the accuracy of light-based geolocation. These include season, latitude, weather, the precision of the clock and oscillator temperature corrections used by the tags, and algorithms used to calculate geolocation (Hill 1994; Welch and Eveson 1999; Musyl et al. 2001; Ekstrom 2004). Tag placement on a subject's body has received less attention. Our dual deployments with an archival tag on the back and leg of the same individual were designed to examine this. The results indicated no effect of tag placement on the performance of our geolocation devices. This was important to determine because it is generally not practical to deploy archival tags onto the back feathers of albatrosses since the birds molt between breeding events (Warham 1996). Thus, for deployments of 6–12 months, archival tags need to be attached to a bird's leg to ensure tag retention, and our results demonstrate that this would not likely change the accuracy of the measurements. Furthermore, tags placed on the backs of the albatrosses would not collect SSTs.

The utility of combining measures of light level and SST to estimate location and behavior. Our analyses show that SST/light-based geolocation improves the accuracy of location estimates over light-based geolocation in North Pacific albatrosses. Similar improvements have been reported in studies on free-ranging marine mammals (Le Boeuf et al. 2000; Beck et al. 2002), and sharks and tuna (Teo et al. 2004). A major advantage of using SST-based latitudes in geolocation is the ability to determine an individual's location during the autumnal or vernal equinoxes when day/night cycles are nearly equivalent at all latitudes on the globe.

Consequently, latitude estimates are indeterminate whereas longitude estimates are unaffected (Wilson et al. 1992; Musyl et al. 2001; Phillips et al. 2004). Our study ended just prior to the vernal equinox so we did not test this directly. However, we are confident that our method of combining light-based longitude and SST-based latitude would have yielded viable locations

with similar accuracy. Studies on free-ranging fish (e.g. Teo et al. 2004) have already validated this method to study movements during equinox periods.

Although mean errors from light-based longitudes and SST-based latitude geolocation were lower compared to light-based estimates, SST/light-based estimates did produce larger errors in some instances (Fig. 2). This may have resulted from albatrosses frequenting regions with an abundance of surface mixing. For example, these birds' quite possibly sampled areas with fine scale mixing along constant latitudes, such as oceanographic frontal system or eddy (Hunt et al. 1999). Ultimately, this can lead to more variability in SSTs measured by orbiting satellites and by the archival tags placed on the albatrosses, which may reduce the algorithm's ability to estimate latitude for a given longitude. Nevertheless, when surface waters are stratified by temperature along latitudinal gradients, the SST/light algorithm is robust (Teo et al. 2004). In the future, it would be interesting to determine if the SST/light algorithm is as robust at high latitudes where water temperatures are lower and more uniform compared to the range of latitudes and SSTs measured by the albatrosses in our study (2–29°C). Significant cloud cover can also obscure remotely sensed SSTs. Thus, on days with considerable cloud cover in a region where our albatrosses were tracked (9 total), the algorithm could not produce a valid latitude estimate, resulting in the loss of daily locations or the inflation of latitudinal errors.

Another advantage of using archival tags that record SST is the ability to link an individual's geographic location with a measure of its physical environment (Weimerskirch et al. 1995). This information is useful for describing habitat preferences and/or foraging grounds. Numerous studies have linked individual behavior to specific oceanographic features based on environmental temperatures recorded by an archival tag attached to an individual (e.g. Weimerskirch et al. 1995; Guinet et al. 1997; Block et al. 2001; Beck et al. 2002; Pütz 2002). In

our study, archival tags mounted to leg bands on the albatrosses recorded SSTs when birds landed on the sea surface for extended periods (Fig. 1b). A previous study (Fernández and Anderson 2000) determined that Laysan and black-footed albatrosses land on the sea surface 30–60 times a day. Therefore, it is likely that we obtained several thousand SST measurements from each bird during our study. These data could be used to establish preferred foraging zones based on latitudinal stratification of SSTs, meso-scale oceanographic features, and current transition zones.

Temperature changes measured by the archival tags can also be used to distinguish activity patterns of the albatrosses (Fig. 1b; Wilson et al. 1995; Weimerskirch et al. 1997; Weimerskirch and Guionnet 2002). These changes in activity may be useful for establishing foraging effort and metabolic costs (Weimerskirch et al. 2000; Shaffer et al. 2001).

In conclusion, archival tags that record light level longitude and animal-collected SSTs can be used in combination to provide geolocations within 202 km of positions determined with satellite telemetry. Although location accuracy is much lower and more variable using archival tags compared to conventional satellite telemetry, the spatial scales over which albatrosses operate are substantially greater than the errors obtained using geolocation. Thus, it is possible to obtain long-range movement patterns of albatrosses with an accuracy that is comparable to meso-scale oceanographic processes occurring on a scale of several hundred kilometers (present study; Weimerskirch and Wilson 2000; Phillips et al. 2004). Consequently, archival tags offer an inexpensive alternative to conventional satellite telemetry with the advantage of potential long duration records, and the additional benefit of recording environmental temperature and pressure. This may be useful for linking species habitat preferences to oceanic features or behavioral

effort. In the future, these small geolocation archival tags will provide new opportunities for studies on smaller seabirds that have more severe mass restrictions.

Acknowledgements

We thank D. Barton and K. Lindquist for assistance in the field, Dr. B. Flint and the US Fish & Wildlife Service for logistical support on Tern Island, and Grupo Ecologica Conservación de Islas and the Mexican Navy for logistical support on Guadalupe. We also thank Dr. P. Raimondi for statistical advice, P. Robinson for programming assistance, and L. Hutnick for assistance with graphics. This research was part of the Tagging of Pacific Pelagics (TOPP) program, funded in part by the National Ocean Partnership Program (N00014-02-1-1012), and the Office of Naval Research (N00014-00-1-0880 & N00014-03-1-0651). All protocols employed in this study were approved by the Institutional Animal Care and Use Committees at UCSC. This paper is dedicated to AMS (b 19 October 2004).

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Figure Legends

Fig. 1 *Phoebastria immutabilis*. a) Relative light level measured by a Lotek LTD 2400 archival tag attached to leg band of Laysan albatross 132, from Tern Island (23° 52'N, 166° 17'W), 01 February 2003. Solar midnight occurred at 10:55:30 UTC. Variability in light level measurements during the day is likely attributed to changes in bird activity or weather. b) Activity pattern of Laysan albatross 132 on 01 February 2003, determined from changes in temperature, measured by the Lotek LTD 2400 archival tag every 32 s. Changes in temperature were assumed to represent activities like landing or taking off from sea surface. Red dots indicate temperatures when tag was in air or tucked under bird's feathers in flight. Blue dots indicate temperatures (or SSTs) when bird was sitting on the water and tag temperature was stable for >20 min. A total of 984 valid SSTs were recorded on this date, where temperatures ranged from 23.2–23.4 °C. Note that SSTs were recorded during solar night when bird sat on sea surface for most of the night. Temperatures lower than measured SSTs were probably caused by evaporative cooling of tag when bird took off from sea surface (Wilson et al. 1995)

Fig. 2 *Phoebastria immutabilis* and *P. nigripes*. Geolocation errors determined using light-based longitude and latitude vs. light-based longitude and SST-based latitude. Each point represents the error (Great Circle distance) of a filtered location established with each geolocation method and compared to a corresponding Argos-based Reference location, for a single albatross on a given day at sea. All data collected by albatrosses equipped with a satellite transmitter and geolocating archival tag for a single trip to sea. Solid line represents equality in geolocation error for both methods (i.e. slope = 1 passing through the origin). Number in each corner signifies total number of data points above and below the line of equality.

Symbols for each species are as follows: Laysan albatrosses from Tern Island (○), black-footed albatrosses from Tern Island (□), and Laysan albatrosses from Guadalupe Island (Δ)

Fig. 3 *Phoebastria immutabilis*. a) Comparison of methods used to determine at-sea locations of Laysan albatross 122, tracked from Tern Island, northwest Hawaiian Islands. b) A similar comparison of all three methods used to determine at-sea locations of Laysan albatross 300, tracked from Guadalupe Island, Baja, Mexico. For both birds, at-sea locations were determined by double tagging each bird with a 30-g satellite transmitter and a 6-g geolocating archival tag that measured ambient light levels and environmental temperatures. All locations shown were filtered as described in Methods. Note variability in location estimates for each bird with each method. Images were created with Ocean Data View 2.0 (Schlitzer 2004)

Fig. 1 a & b

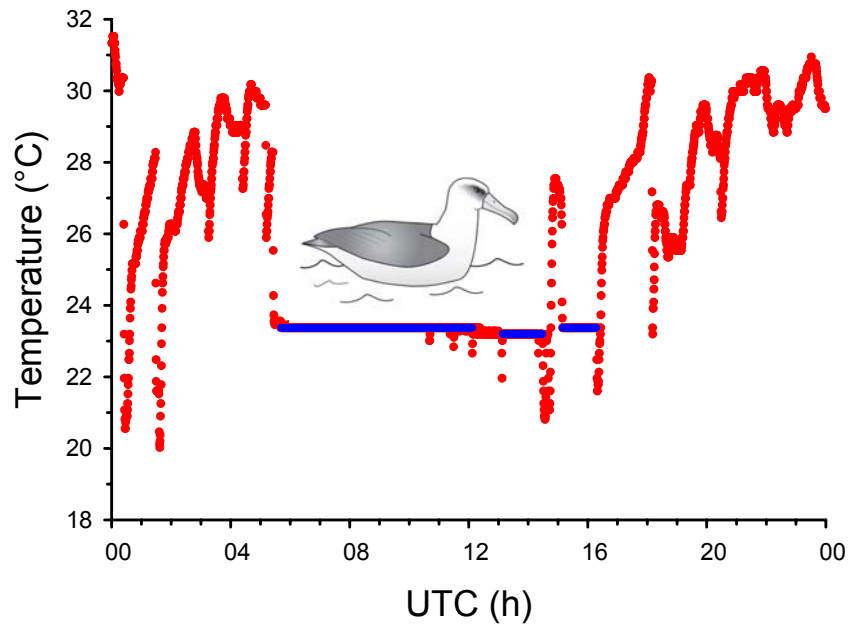
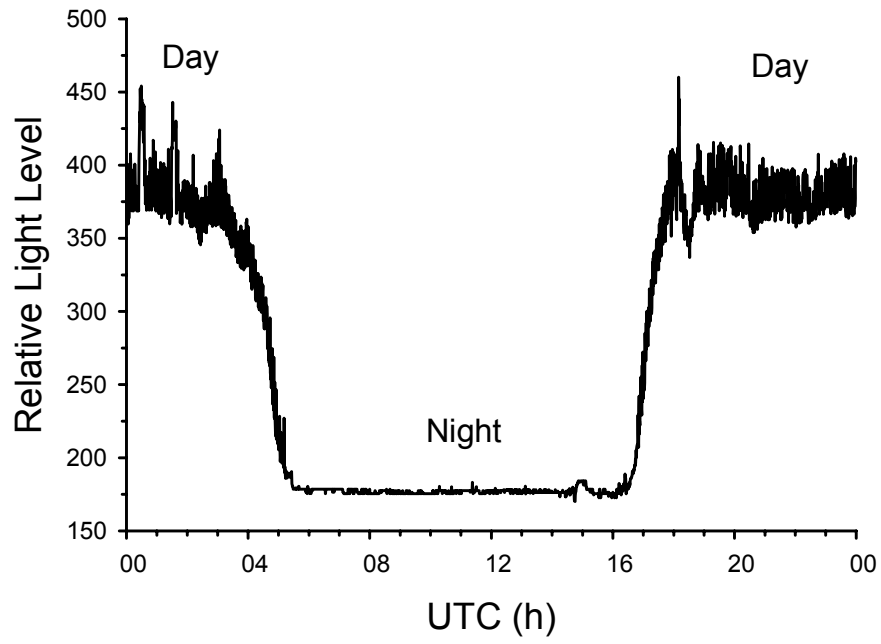


Fig. 2

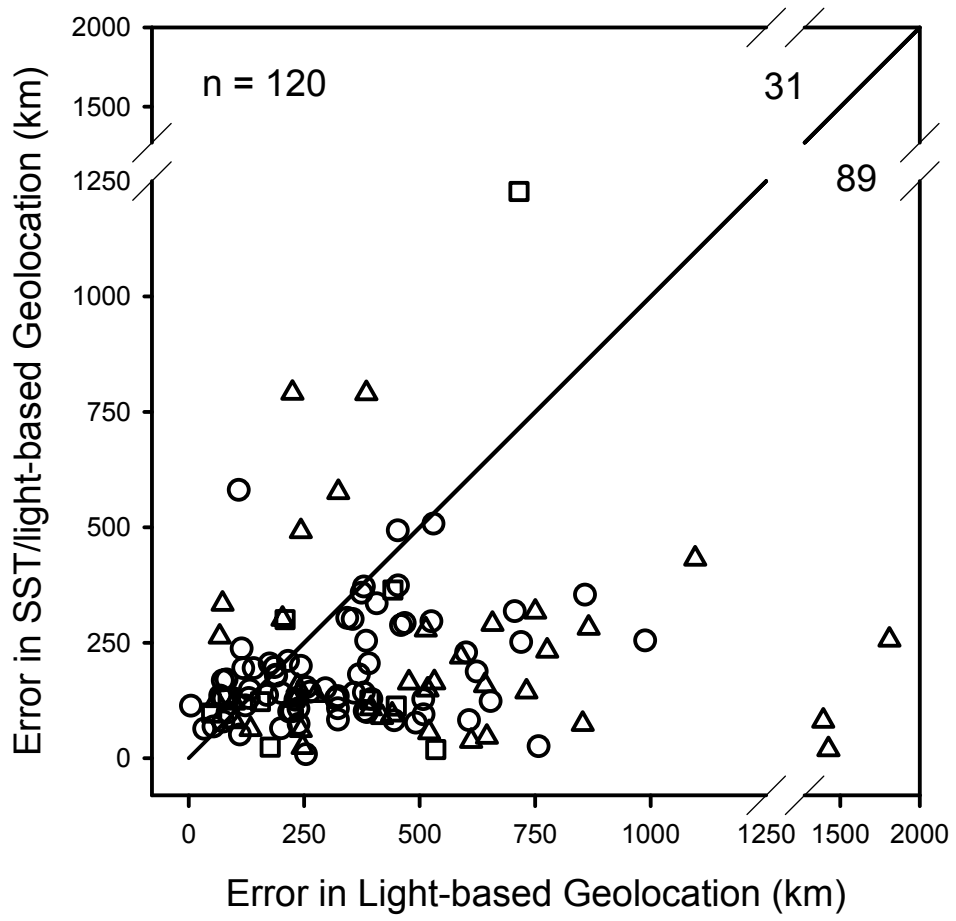


Fig. 3 a & b

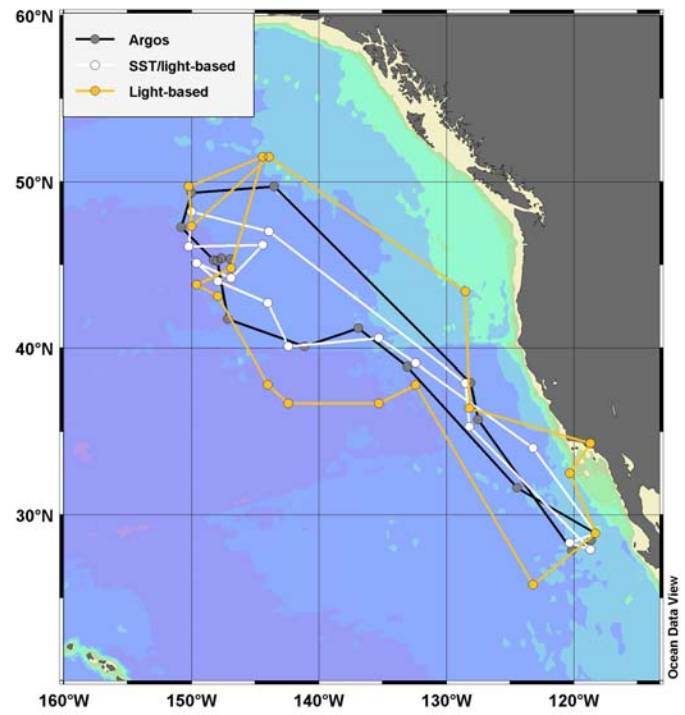
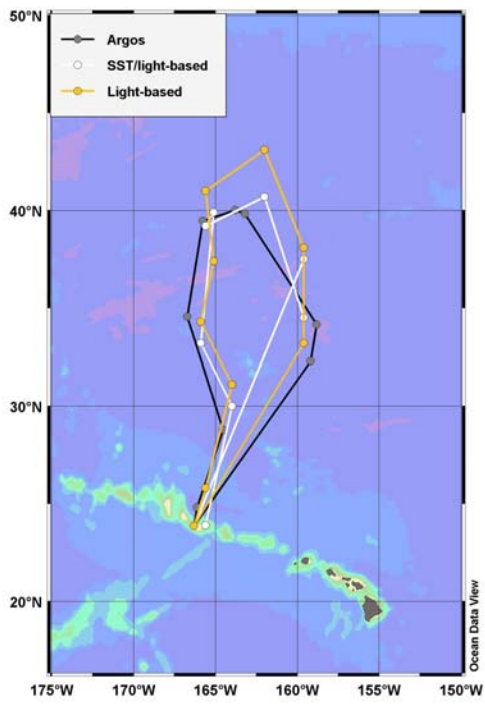


Table 1 *Phoebastria immutabilis* and *P. nigripes*. Estimated errors (Great Circle distances) in bird location using light- and SST-based geolocation in comparison to Argos Reference locations (see Methods). Presented are the median (med), minimum (min), and maximum (max) of raw unfiltered errors, and mean error \pm SD, 95% Confidence Intervals (CI) of mean, and standard deviations of longitudinal and latitudinal errors (in $^{\circ}$), from filtered locations. Each location was checked for (1) interference in light level threshold curve recorded by the archival tag, (2) interference of remotely sensed SST data from cloud cover that affected comparison with SST measured by the tag, and (3) unreasonable travel speeds ($>35 \text{ km h}^{-1}$) between positions determined with a speed filter. Locations failing any of these steps were excluded

Method	Raw data					Filtered data			
	n	Great Circle distance	Total (n) after quality check			Great Circle distance	Standard Deviation		
		med (min–max) (km)	(1)	(2)	(3)	mean \pm SD (km)	95% CI (km)	Longitudinal Error ($^{\circ}$)	Latitudinal Error ($^{\circ}$)
Laysan albatrosses – Tern Island									
Light	123	407 (5–17,516)	103		80	344 \pm 224	294–394	1.76	3.15
SST/light	123	203 (9–12,061)	103	94	85	189 \pm 120	163–214	1.79	1.43
Black-footed albatrosses – Tern Island									
Light	40	5,259 (50–16,659)	10		10	321 \pm 218	165–477	0.67	3.20
SST/light	40	3,248 (19–13,729)	10	10	10	253 \pm 359	-4.5–510	0.67	3.88
Laysan albatrosses – Guadalupe Island									
Light	63	477 (40–3,294)	61		41	529 \pm 393	405–653	1.60	5.07
SST/light	63	164 (14–2,806)	61	61	59	212 \pm 189	163–262	1.61	1.96
All Birds									
Light	226	504 (5–17,516)	174		131	400 \pm 298	349–452	1.65	3.89
SST/light	226	230 (9–13,729)	174	165	154	202 \pm 171	175–229	1.68	1.95