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Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles

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Abstract

1. Light-level geolocators are popular bio-logging tools, with advantageous sizes, longevity and affordability. Biologists tracking seabirds often presume geolocator spatial accuracies between 186 and 202 km from previously innovative, yet taxonomically, spatially and computationally limited, studies. Using recently developed methods, we investigated whether assumed uncertainty norms held across a larger-scale, multispecies study.
2. We field-tested geolocator spatial accuracy by synchronously deploying these with GPS loggers on scores of seabirds across five species and 11 Mediterranean Sea, east Atlantic and south Pacific breeding colonies. We first interpolated geolocations using the geolocation package `FLightR` without prior knowledge of GPS tracked routes. We likewise applied another package, `probGLS`, additionally testing whether sea-surface temperatures could improve route accuracy.
3. Geolocator spatial accuracy was lower than the ~200 km often assumed. `probGLS` produced the best accuracy (mean ± *SD* = 304 ± 413 km, *n* = 185 deployments) with 84.5% of GPS-derived latitudes and 88.8% of longitudes falling within resulting uncertainty estimates. `FLightR` produced lower spatial accuracy (408 ± 473 km, *n* = 171 deployments) with 38.6% of GPS-derived latitudes and 23.7% of longitudes within package-specific uncertainty estimates. Expected inter-twilight period (from GPS position and date) was the strongest predictor of accuracy, with increasingly equatorial solar profiles (i.e. closer temporally to equinoxes and/or spatially to the Equator) inducing more error. Individuals, species and geolocator model also significantly affected accuracy, while the impact of distance travelled between successive twilights depended on the geolocation package.
4. Geolocation accuracy is not uniform among seabird species and can be considerably lower than assumed. Individual idiosyncrasies and spatiotemporal dynamics (i.e. shallower inter-twilight shifts by date and latitude) mean that practitioners

should exercise greater caution in interpreting geolocator data and avoid universal uncertainty estimates. We provide a function capable of estimating relative accuracy of positions based on geolocator-observed inter-twilight period.

KEYWORDS

animal tracking, archival tags, bio-logging, FLightR, probGLS, sea-surface temperature, solar geolocation

1 | INTRODUCTION

Light-level geolocators ('geolocators') are one of the most popular and practical tools available to study animal movement, with well-established, open access standards and techniques available to guide analyses of geolocation data (see Lisovski et al., 2020). However, there can be considerable uncertainty associated with the accuracy of location estimates derived from light-level data. Geolocators are small (i.e. ~0.3–3.3 g) archival data loggers that measure and record solar intensity at regular intervals, some with the capability of measuring and archiving other information such as water temperature, wet/dry events and barometric pressure. When geolocators are retrieved, light-level data are downloaded and directed into astronomical equations that estimate spatial locations based on the timing of twilight events (i.e. sunrises and sunsets). Geolocator data can be interpolated into one or two positions per day with latitude estimated by day length, and longitude estimated by the timing of local midday or midnight relative to Greenwich Mean Time and Julian day (Hill, 1994).

Geolocators were first applied to tracking the movements of marine vertebrates including elephant seals (Delong et al., 1992), fish (Block et al., 1998), seabirds (Croxall et al., 2005; Egevang et al., 2010; González-Solís et al., 2007; Guilford et al., 2009; Phillips et al., 2006; Shaffer et al., 2006; Tuck et al., 1999) and sea turtles (Fuller et al., 2008). Recently, geolocators have undergone considerable miniaturisation and improvements to onboard storage capacity, which has stimulated an increase in studies that use light-level data to infer spatial information about both marine and terrestrial species that were otherwise too small to be burdened with tracking devices (Bridge et al., 2011). The number of ecologists using geolocators to study seabird movements has increased in tandem with these sensor improvements and newly designed geolocation methods implemented in several R packages for processing and analysing light-level data (e.g. Merkel et al., 2016; Rakhimberdiev et al., 2017; Sumner et al., 2009).

Despite the growing volume of geolocator data, the spatial accuracy of geolocators used on seabirds has to-date been empirically tested relative to more precise technologies only on three species of albatross with limited latitudinal breadth (Phillips et al., 2004; Shaffer et al., 2005). These studies employed older geolocator sensors that recorded light levels more infrequently and previous threshold method geolocation software that, unlike modern methods, did not incorporate movement models or probabilistic algorithms. These studies measured the distances of satellite Platform Terminal Transmitter (PTT) locations to corresponding geolocation estimates and assessed mean accuracies ± standard deviation (*SD*) of 186 ± 114 km (Phillips et al., 2004) to 202 ± 171 km (Shaffer et al., 2005). These estimations of geolocation accuracy are coarse relative to those obtained from satellite loggers that fix positions from orbiting Advanced Research and Global Observation Satellites (ARGOS), which have a typical 1–3 km accuracy (Burger & Shaffer, 2008) or the Global Positioning System (GPS), which regularly has average location accuracies of less than 10 m (Hulbert & French, 2001) to ~15 m (Forin-Wiart et al., 2015). However, tracking instruments that use satellites tend to be too large for many species and may be prohibitively expensive. Satellite tracking instruments typically have limited power capacity and on-board memory storage, and depending on the species, can place unreasonable burdens on birds in terms of wing-loading and hydrodynamic drag (Phillips et al., 2004; Shaffer et al., 2005). Furthermore, attaching satellite instruments to feathers for long-term deployments is not suitable for most seabirds because they periodically moult. For many seabird species the use of harness attachment to remedy this constraint is not recommended (Phillips et al., 2003) and may increase mortality and device-induced behaviours (Barron et al., 2010). Light-level geolocation has therefore offered an attractive year-round alternative to satellite tracking that tackles many of the constraints associated with using larger, more spatially accurate technology.

Light-level geolocation is inherently prone to coarse spatial accuracy, particularly for estimates of latitude which are generally considered to become less accurate under increasingly 'equatorial' solar profiles; that is, either nearer the Equator (spatial variation) or solar equinox (temporal variation) where and when day length changes more shallowly with latitude (Ekstrom, 2004; Hill, 1994; Lisovski et al., 2020). The inherent accuracy of latitudinal geolocations fluctuates by date, even if the amount of sensor shading remains constant (Lisovski et al., 2012). Weather (e.g. cloud cover) and behavioural patterns such as roosting at twilight periods can induce errors in estimates of day or night length and are thus thought to affect accuracy in geolocation (Lisovski et al., 2012). In addition, light-level data collected during breeding stages are often thought to have reduced spatial accuracy due to specific behaviours that might affect light curves (Lisovski et al., 2012, 2020). For example, some species roost on the ground (Corre & Jouventin, 1997; Schreiber & Chovan, 1986), brood their young at twilights (Howell & Bartholomew, 1969) which can shade sensors, or nest underground in burrows (Shaffer et al., 2006). Geolocators fitted on birds that go to roost before last light or depart nest sites after first light could therefore exhibit abnormal transitions between light and dark at twilight times in light curve data (Gow, 2016).

Another typical behaviour of seabirds is wide-ranging movement that can occur within a single day or night (Clay et al., 2018; McDuie et al., 2015). Such large-scale movement between twilights can impact interpolations of longitude by shifting the solar noon, or latitude by compressing or elongating day length, all depending on the speed and direction of travel and time of year (Lisovski et al., 2012). Furthermore, data collected by geolocators fitted to wide-ranging seabirds, generally on leg rings, are likely to have idiosyncratic differences relative to being collected at a stationary location (Lisovski et al., 2012; Welch & Eveson, 1999). Accordingly, it has been suggested that the performance of geolocators might be species dependent (Shaffer et al., 2005) and that the choice of geolocation algorithm might affect the accuracy of position estimates (Musyl et al., 2001).

Despite the well-known and hypothesised limitations of light-level geolocation, geolocators have generally been considered satisfactory for studying foraging ranges (Phillips et al., 2004), and habitat preferences and distributions of pelagic seabirds (Egevang et al., 2010; González-Solís et al., 2007; Guilford et al., 2009; Halpin et al., 2018; Lascelles et al., 2016; McDuie & Congdon, 2016; Pollet et al., 2014; Quillfeldt et al., 2017; Shaffer et al., 2006). Here, we sought to evaluate for the first time the accuracy of modern geolocation algorithms on a large and diverse sample of free-flying seabirds and assess whether accuracy is affected by the species being tracked and movement behaviours. Past studies of geolocation accuracy have used older technology and/or geolocation algorithms (e.g. Phillips et al. 2004; Shaffer et al. 2005), evaluated static deployments of tags either carried by resident birds or fixed in the environment (e.g. Fudickar et al., 2012), or been carried out on single species with sample sizes that are likely too small to have adequate statistical power to disentangle patterns in accuracy (e.g. Rakhimberdiev et al., 2016).

Our objectives were to (a) investigate if the spatial accuracy typically reported in geolocation studies of seabirds is applicable in the context of a large-scale, multi-species study; (b) test uncertainty estimates of more advanced geolocation models; (c) test whether sea-surface temperature (SST) interpolation improved average accuracy in these new methods and d) model which situational factors most affected geolocator spatial accuracy. To address these aims, we conducted a field test using synchronous deployments of GPS loggers and geolocators fitted to individual seabirds from around the world. We measured the spatial accuracy of geolocator-interpolated routes from GPS tracks, tested for effects of species and individuals, and whether the inter-twilight distances travelled by birds affected the spatial accuracy of geolocation.

2 | MATERIALS AND METHODS

2.1 | Study species & locations

We analysed synchronous location data from 151 chick-provisioning individual seabirds that were tracked concurrently with GPS and light-level geolocator loggers (i.e. 'double tagged') using the geolocation packages, `FlightR` (Rakhimberdiev et al., 2017) and `probGLS` (Merkel et al., 2016). Tracking data represent 200 deployments across five species from 11 separate seabird colonies between 2011 and 2019 (Table 1). We originally had access to 278 double-tagged deployments (some individuals were tagged more than once within and between years), but we reduced the dataset to 200 deployments after excluding those with insufficient data to produce stationary calibrations, or where light curve transitions were poor. Breeding colonies were located in several marine regions including in Southern Europe (Mediterranean Sea), West Africa (east Atlantic Ocean) and Australia (south Pacific Ocean). In the northern hemisphere, we analysed double-tagged deployments from Cape Verde Shearwaters (*Calonectris edwardsii*, $n = 11$; 2014 and 2018), Cory's Shearwaters (*C. borealis*, $n = 100$; 2011 and 2013–2018), Scopoli's Shearwaters (*C. diomedea*, $n = 61$; 2014–2018) and Red-billed Tropicbirds (*Phaethon aethereus*, $n = 7$; 2017–2018) on 10 breeding colonies between latitudes 15°N–40°N. In the southern hemisphere, we analysed double-tagged deployments from White-necked Petrels (*Pterodroma cervicalis*, $n = 21$; 2018 and 2019) on a single colony at latitude 29°S.

2.2 | Double tagging

We fitted birds with one of five light-level geolocator immersion sensors: BAS_MK19 (British Antarctic Survey) or Biotrack_MK3005 [formerly BAS_MK19] (Biotrack Ltd), which sample light intensity every minute and record the maximum value every 5 min with water temperature recorded when the sensor is immersed continuously for 25 min; and Intigeo-C330, Intigeo-C250 or C65-SUPER (Migrate Technology Ltd), which sample light intensity every minute, storing the maximum value every 5 min and record water temperature when the sensor is immersed continuously for 20 min. The conductivity (wet/dry) sensor sampling rate was 6 s for all models. Devices were leg mounted and fitted to the tarsus by mounting to either a darvic or metallic ring using a plastic cable tie, or a Velcro© (38 mm; Paskal) hook-and-loop harness. GPS loggers were fitted to birds using Tesa© tape (4651; Tesa Tape Inc.) by taping either to contour feathers between scapulae, or at the base of the two to four central rectrices on shearwaters and petrels and six rectrices on tropicbirds.

2.3 | Data preparation and analysis

All data were processed in the statistical software environment R, version 3.5.1 (R Core Team, 2020), and spatial measurements were

TABLE 1 The species, individuals, regions and respective colonies where seabirds were tracked synchronously with light-level geolocators and GPS loggers. The sample size of geolocation estimates used in analyses of each geolocation algorithm isprovided

					Number of geolocations[a]	
Colony name	**Latitude**	**Country**	**Marine Region**	**Species (no. individuals)**	**FLightR**	**probGLS**
Cala Morell (Menorca)	40.1°N	Spain	Mediterranean	Scopoli's Shearwater (52)	574	626
Islas Columbretes	39.9°N	Spain	Mediterranean	Scopoli's Shearwater (4)	73	77
Isla de Cabrera	39.2°N	Spain	Mediterranean	Scopoli's Shearwater (2)	24	26
Isla de las Palomas	37.6°N	Spain	East Atlantic	Scopoli's Shearwater (3)	41	44
Islote de Montaña Clara	29.3°N	Spain	East Atlantic	Cory's Shearwater (32)	441	501
Timanfaya (Lanzarote)	29.0°N	Spain	East Atlantic	Cory's Shearwater (6)	92	43
Veneguera (Gran Canaria)	27.8°N	Spain	East Atlantic	Cory's Shearwater (62)	598	1,206
Ilhéu Raso	16.6°N	Cabo Verde	East Atlantic	Red-billed Tropicbird (2)	8	10
Ilha Boa Vista	16.2°N	Cabo Verde	East Atlantic	Red-billed Tropicbird (5)	48	52
Ilhéu de Curral Velho	15.9°N	Cabo Verde	East Atlantic	Cape Verde Shearwater (11)	189	199
Phillip Island (Norfolk Island)	29.1°S	Australia	South Pacific	White-necked Petrel (21)	993	410

[a]The number of geolocations per package (i.e. `FLightR` or `probGLS`) differs depending on the suitability of the data for analysis in a given package. For example, whether the geolocator recorded water temperature exclusively when immersed, and calibration data from a stationary location.

calculated on the World Geodetic System (WGS 1984) ellipsoid. The processing of geolocation data was carried out by an analyst who had no knowledge of the spatial attributes of the paired GPS tracking data so that decisions about parameterising geolocation algorithms were not influenced by prior knowledge of the birds' underlying movements. This was done to ensure that geolocation positions in our study would be comparable to those of other geolocation studies for which practitioners typically have no knowledge of where the bird travelled. GPS tracks were standardised using the package `adehabitatLT` (Calenge, 2006) by resampling all GPS locations to an equal 10 min interval because the GPS sample rates varied among species and colonies. We gap-filled GPS tracks except when periods of more than 1 hr occurred between fixes. To account for erroneous positions that may have been caused by poor satellite reception, we applied a standard maximum allowable flight velocity of 27.8 m/s (100 km/hr) between consecutive locations for all seabird taxa. We considered this to be a maximum realistic speed for wide-ranging seabirds (Lascelles et al., 2016).

Depending on the brand of geolocator, we first imported raw light-level data using the functions `readMTlux` in the package `TwGeos` (Wotherspoon et al., 2016) or `ligTrans` in the package `GeoLight` (Lisovski & Hahn, 2012). We then automated twilight event (i.e. sunrises and sunsets) annotation in raw light-level data using the function `preprocessLight` in the package `TwGeos` (Wotherspoon et al., 2016) with a threshold level of 1, which presented as a suitable level above which to differentiate twilights from night time noise in log-transformed data. Following guidelines in Lisovski et al. (2020), we visually reviewed raw light data to identify any areas of the time series affected by shading and manually inspected each twilight event, subsequently deleting such events that we deemed to be falsely annotated in the automated procedure, or those with poor transitions between dark and light. Indistinguishable or unclear transitions between dark and light can occur due to the light sensors becoming shaded by weather, individual bird behaviours or bird plumage. This procedure resulted in an average rate of transition exclusion of 33.6% for Cape Verde Shearwaters, 29.1% for Cory's Shearwaters, 33.9% for Red-billed Tropicbirds, 32% for Scopoli's Shearwaters and 14% for White-necked Petrels. We expected to see a greater proportion of twilights excluded in these data because birds were in their breeding phase. Contrary to non-breeding, migratory seabirds, those in their breeding phase regularly visit nests, or raft on the water before visiting nests which can cause obscured light curves at twilight times.

We used two geolocation analysis packages to estimate the spatial locations of tracked seabirds: `FlightR` and `probGLS`. Using the annotated twilight data, we produced 'TAGS' files using the `TwGeos2TAGS` function in the `FLightR` package in preparation for light-level analyses. We analysed light-level data from 171 deployments in `FLightR` and 185 deployments in `probGLS`, which included 156 of the same datasets used in `FLightR` (15 deployments analysed in `FLightR` were excluded from `probGLS` because they did not collect SST data exclusively when the device was immersed in water). Data from sensors that recorded light and temperature, but did not have light data recorded from a stationary location were included in `probGLS` but excluded from `FLightR` analyses. While on-bird geolocator calibration is possible for some centrally placed species (see Rakhimberdiev et al., 2017), we considered that it may not be suitable for seabirds due to the large distances travelled during foraging. Calibrations were therefore conducted as 'rooftop calibrations' (see Lisovski et al., 2012). All species reported were included in analyses by both geolocation packages.

2.4 | Estimating spatial locations from light-level data

We parameterised both geolocation algorithms (FlightR and probGLS) to calculate seabird locations within a bounding box extending from the breeding colony by 35° of longitude in each direction, and 25° of latitude in the direction of the nearest pole and 50° of latitude in the direction of the Equator.

The geolocation analysis package, FLightR was used first to estimate the spatial likelihood of locations from annotated light-level data. To model movements, FLightR uses a hidden Markov model with the true location as the unobserved state. Inference is performed using a particle filter, with a template-fit method to allow the algorithm to use all available light measurements around annotated twilight events (Rakhimberdiev et al., 2017). FLightR also incorporates biologically relevant behavioural parameters to improve location estimates. To function, FLightR requires calibration data from each geolocator with which it measures the relationship between observed light levels (i.e. calibration data) and theoretical light levels estimated from current solar elevation angles (Ekstrom, 2004; Rakhimberdiev et al., 2017). When executing the FLightR algorithm, we included only data from geolocators that were calibrated by measuring light levels at a stationary location prior to deployment on a seabird. Analyses in FLightR were run with and without spatial masks to explore how land masking affected accuracy. We set the algorithm to allow maximum daily flight distances of 1,500 km on a 50 km grid. To estimate locations, we ran the FLightR particle filter with 1 million particles and used the median of the posterior probability distribution as the estimates of daily seabird relocations.

For light-level data from geolocators that also recorded SST, we analysed the same annotated twilights with the package, probGLS (Merkel et al., 2016), to investigate whether SST interpolation improved the spatial accuracy of geolocations. The probGLS algorithm estimates locations using an iterative forward step selection process, computing a weighted probability cloud of potential locations (10,000 particles for each point cloud) and producing the most likely movement path with 200 iterations for each track (Merkel et al., 2016). We included flight speed parameters for when the loggers were dry (probable maximum and *SD* (m/s), see supplementary metadata) based on Spear and Ainley (1997) and a maximum allowable dry-logger flight speed of 27.8 m/s, thus matching the speed used to filter GPS relocations; and wet speed parameters to allow for modest drift on the ocean if the bird was roosting on the water for long periods (fastest most likely = 1 m/s, *SD* = 1.3 m/s, maximum = 5 m/s). Geolocations were estimated using probGLS with a land mask to prevent the algorithm from estimating locations more than 1 km inland of coasts. We also used the daily median SST encountered by each bird, which was computed from that recorded by geolocators every 4 hr (Merkel et al., 2016) and matched this to satellite-derived SST (0.25° × 0.25°, NOAA OI SST V2 High-Resolution Dataset). We also ran probGLS both with and without SST matching and spatial masks.

2.5 | Measuring and modelling spatial accuracy

To measure the spatial discrepancy between geolocations and GPS positions, we calculated the distance between the geographic mean of all GPS fixes that occurred within ±30 min, respectively, of a given pair of twilights (i.e. sunset–sunrise or vice versa) and the geolocator-estimated solar noon/midnight position for that same period. This measure of accuracy is expressed as the great-circle distance in kilometres from an individual's GPS location to its corresponding geolocation for a given set of twilight events. To investigate the potentially nonlinear effects of predictor variables on the spatial accuracy of geolocation estimates, we constructed generalised additive mixed-effects models (GAMM) with a gamma distribution and a log link function. We separately modelled geolocation accuracy in position estimates computed by both the FLightR and probGLS analysis packages. We considered two predictors of geolocation accuracy: spatial displacement as the great-circle distance (kilometres) between successive twilight locations (from GPS) for individuals, and the expected inter-twilight period as the expected duration of day or night calculated from day of year and GPS latitude using the daylength function in the package geosphere (Hijmans, 2019). We modelled these as nonlinear effects using univariate thin-plate regression splines. We initially considered two other potential predictors of geolocation error: latitudinal position and closeness in time to the March and September equinoxes; but we could not consider these as independent variables due to strong concurvity with the inter-twilight period predictor, which we considered an equatorial solar profile index and the more proximate mechanism governing geolocation accuracy. We included the model of geolocator as a fixed effect. To account for potential effects of species and individuals, we also included the identity of each tracked individual nested under species type as random effects in the model.

Both geolocation packages contain spatial mask functions to avoid the algorithms estimating positions over land. In our data, this would likely have masked the effects of modelled covariates on spatial error, particularly for birds restricted to the relatively small Mediterranean Sea. Therefore, we modelled the effects of covariates on geolocation accuracy only on the position estimates produced without a land mask (both packages), SST (probGLS) or inbuilt outlier detection (FLightR). We used a correlogram to examine for residual autocorrelation in the time series of geolocations. Some evidence of autocorrelation was evident at the first time lag, but thinning the dataset to include only every second or third observation had no effect on the overall model results. Thus, we did not thin time series of geolocations.

We fitted the models by restricted maximum likelihood using the package mgcv (Wood, 2011). We used the inbuilt checks of the mgcv package to ensure that the models converged and that the basis dimension was sufficiently large (using a permutation test for the presence of a residual pattern along predictors). The residuals of the fitted models were inspected to ensure that residuals followed the gamma distribution assumption and that there was no evident structure or heterogeneity of variances against candidate predictors.

3 | RESULTS

Our initial geolocation results were implemented without applying land masks or SST interpolation and produced mean spatial accuracy (±*SD*) of 432 ± 460 and 372 ± 290 km for `FLightR` and `probGLS`, respectively (Table 2). When we applied land masks (for both analysis packages), and SST (`probGLS` only) mean accuracies were improved to 408 ± 473 and 304 ± 413 km, for `FLightR` and `probGLS` respectively (Table 2). As an additional test to investigate the effect of equinoxes on location accuracy, when we excluded from accuracy measurements the locations within 3 weeks (21 days) of the March or September equinoxes the mean spatial accuracies (km ± *SD*) were reduced to 227 ± 250 and 290 ± 369 for `FLightR` and `probGLS` respectively (Table 2).

GPS-derived latitude was within package-specific geolocation uncertainty estimates 38.6% and 84.5% of the time for `FLightR` (parameter set 4, see Table 2) and `probGLS` (parameter set 3, see Table 2), respectively, and GPS-derived longitude fell within uncertainty estimates for 23.7% and 88.8% of geolocations, for `FLightR` and `probGLS` respectively. Estimated uncertainties derived from package functions for each geolocation produced by each method are provided as supplementary material. We also provide as supplementary material the spatial accuracies for individual species within (i.e. ≤21 days) and outside (i.e. ≥21 days) of equinox periods. Results outputs with different parameters from the geolocation analyses are also provided as Supporting Information.

We found strong evidence of a bell-shaped effect of expected inter-twilight period on the spatial accuracy of geolocations (Figure 1a, `FLightR`: $F_{6 \cdot 47} = 993$, $p < 0.001$; Figure 2a, `probGLS`: $F_{7.1} = 718$, $p < 0.001$). Results demonstrated that spatial accuracy in both `FLightR` and `probGLS` drastically declines as expected inter-twilight periods approach 12 hr (i.e. closer to an equinox or the Equator) and best at approximately 9 and 15 hr (Figures 1a and 2a). Mean spatial accuracy (±*SD*) calculated on geolocation results associated with inter-twilight periods ≤10 and ≥14 hr was reduced to 243 ± 232 and 202 ± 239 km (±*SD*) for `probGLS` (with spatial land mask and SST) and `FLightR` (with spatial land mask and outlier detection) respectively.

We found significant effects of differences among species and individuals on the spatial accuracy of geolocations when individuals were fitted as random effects nested within their respective species type (Figure 1c, `FLightR`: $F_{154.7} = 25.7$, $p < 0.001$; Figure 2c, `probGLS`: $F_{158.2} = 11.8$, $p < 0.001$). The model of geolocator used also affected the accuracy (Figure 1d, `FLightR`: $F_{4.0} = 5$, $p < 0.001$; Figure 2d, `probGLS`: $F_{4.0} = 16.8$, $p < 0.001$). We found that there was an effect of an individual's spatial displacement within expected inter-twilight periods on the accuracy of geolocations when using `FLightR` (Figure 1b, $F_{2.3} = 40.3$, $p < 0.001$), but not for `probGLS` (Figure 2b, $F_{0.5} = 0.35$, $p = 0.111$).

TABLE 2 Spatial accuracy for each geolocation algorithm with specified package parameters. Accuracy is expressed as the great-circle distance between the GPS position and corresponding geolocator-derived position for a given twilight. GPS position was defined as the geographic mean of all GPS positions recorded within ±30 min of the given twilight

Geolocation package	Parameter set	Number of deployments included	Land mask[a]	SST[b]	Outlier detection[c]	Mean absolute latitudinal accuracy ± *SD* (°)	Mean absolute longitudinal accuracy ± *SD* (°)	Mean great-circle accuracy (km ± *SD*): All data	Equinox periods (<21 days)	Non-equinox periods (>21 days)
`FLightR`	1	171	No	N/A	No	2.9 ± 3.7	2.1 ± 3.1	432 ± 460	670 ± 564	286 ± 300
	2	171	Yes	N/A	No	2.9 ± 4.1	2.1 ± 3.2	430 ± 508	707 ± 635	260 ± 305
	3	171	No	N/A	Yes	2.7 ± 3.8	2.2 ± 3.2	416 ± 474	659 ± 576	267 ± 318
	4	171	Yes	N/A	Yes	2.7 ± 3.7	2.3 ± 3.2	408 ± 473	702 ± 587	227 ± 250
`probGLS`	1	185	No	No	N/A	3.0 ± 2.6	1.2 ± 1.3	372 ± 290	484 ± 388	344 ± 253
	2	185	Yes	No	N/A	3.7 ± 3.5	1.3 ± 1.3	449 ± 381	713 ± 465	384 ± 325
	3	185	Yes	Yes	N/A	2.4 ± 3.7	1.1 ± 1.5	304 ± 413	364 ± 554	290 ± 369

[a]Spatial mask restricting estimation of locations >1 km inland;
[b]Sea-surface temperature (not currently available in `FLightR`);
[c]Inbuilt outlier detection is not currently a function in `probGLS`.

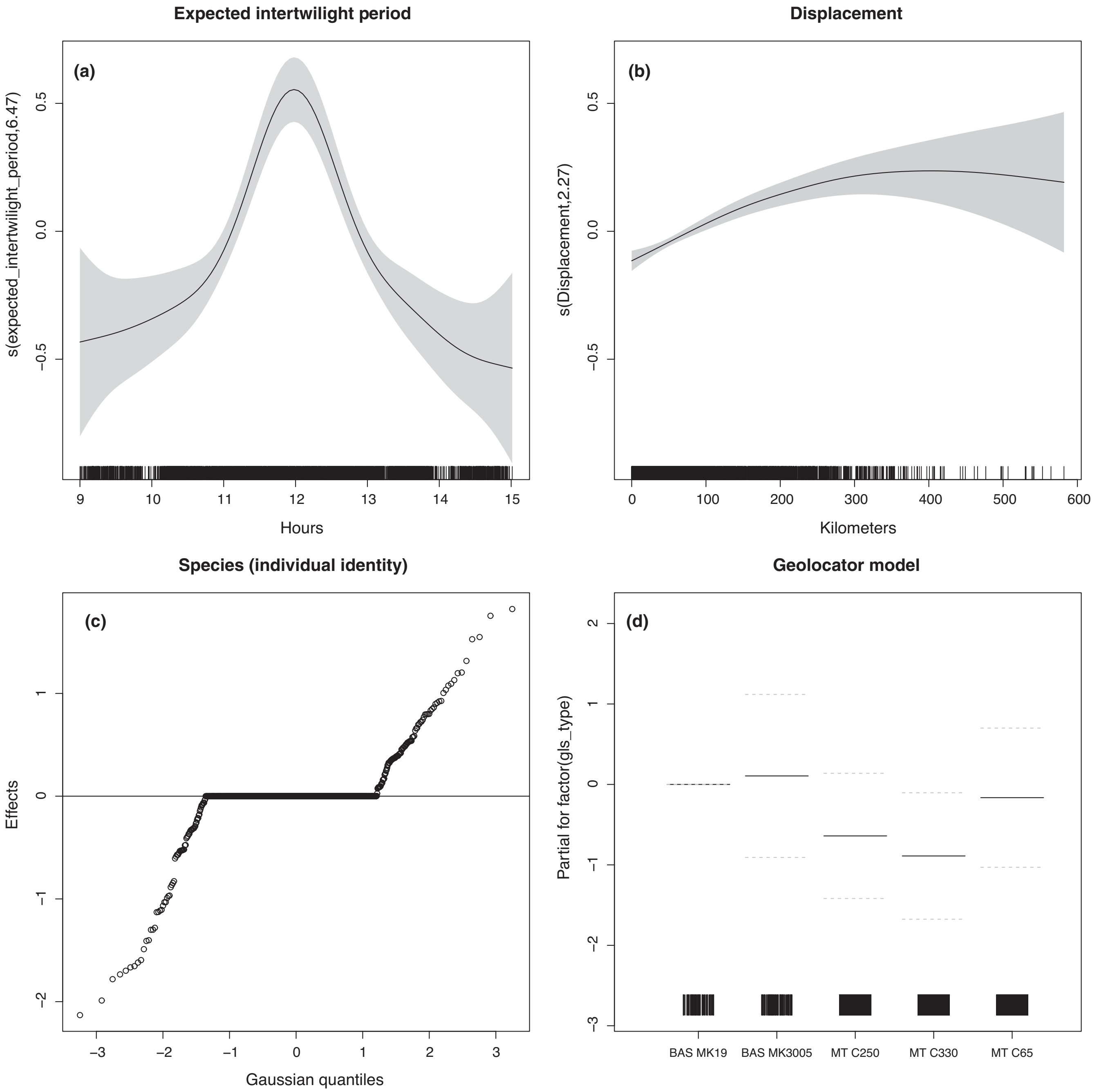

FIGURE 1 Response curves for spatial accuracy in `FLightR` geolocations as a function of expected inter-twilight period (a) and spatial displacement (b) with individual identity nested within species (c) and geolocator model as a fixed effect (d). Tick marks on the horizontal axis of the expected inter-twilight period (a) and displacement (b) plots are observed datapoints. For each predictor with a smooth term (a and b), the effect on spatial accuracy is shown on the *y*-axis and represented as a spline (s) of the predictor variable with the estimated degrees of freedom. Shaded grey areas in the expected inter-twilight period (a) and displacement (b) plots indicate 95% confidence intervals

The average spatial accuracy differed depending on species and geolocation package (Figure 3), with Red-billed Tropicbirds producing the poorest accuracy between GPS and corresponding geolocator positions in the `probGLS` results, whereas White-necked Petrel geolocations had the poorest accuracy in the `FLightR` results. Scopoli's Shearwater geolocations had consistently better spatial accuracy relative to other species (Figure 3) in all model runs of both geolocation packages, including when SST and spatial land masks were not applied.

4 | DISCUSSION

We provide the first large-scale assessment of the spatial accuracy of modern geolocation algorithms under field conditions. The advance in understanding our findings provide contextualises the results and hypotheses of past tests of geolocation accuracy that have until now been limited in field testing (e.g. static tags, small sample sizes, single species studies and outdated methods). Our results

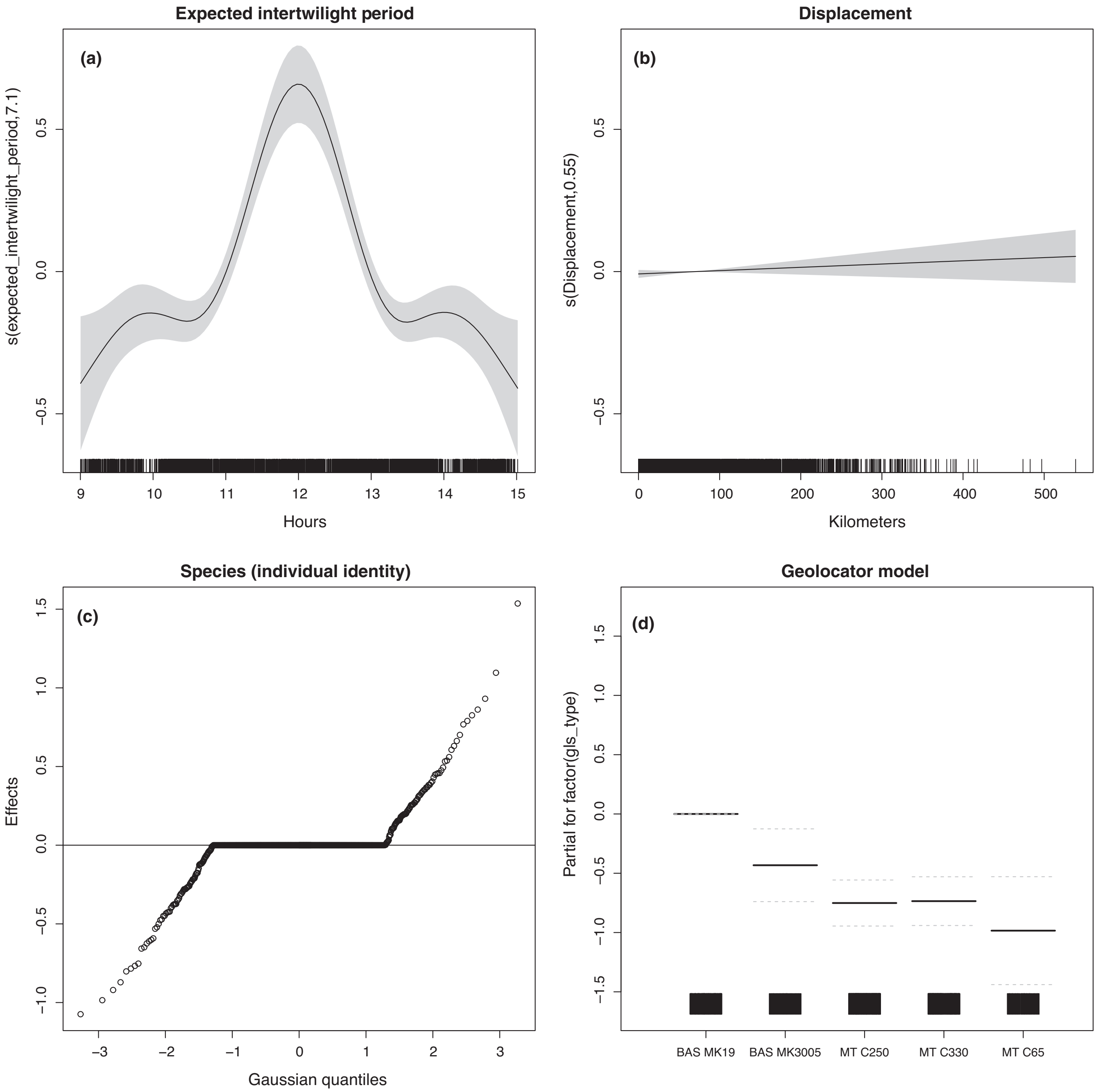

FIGURE 2 Response curves for spatial accuracy in probGLS geolocations as a function of expected inter-twilight period (a) and spatial displacement (b) with individual identity nested within species (c) and geolocator model as a fixed effect (d). Tick marks on the horizontal axis of the expected inter-twilight period (a) and displacement (b) plots are observed datapoints. For each predictor with a smooth term (a and b), the effect on spatial accuracy is shown on the *y*-axis and represented as a spline (s) of the predictor variable with the estimated degrees of freedom. Shaded grey areas in the expected inter-twilight period (a) and displacement (b) plots indicate 95% confidence intervals

emphasise the need for practitioners to account for species and spatiotemporal effects on geolocation accuracy by considering both when (i.e. temporal effects) and where (i.e. equatorial effects) they might expect a species to travel. If the former is either a wandering, circuitous or tropical path, the practitioner should be adequately aware of what scale their data could be analysed. This is particularly true of land birds, which do not have the luxury of using SST to enhance the accuracy of interpolation. We observed lower mean spatial accuracy in light-level geolocation of seabirds than what is typically reported as the expected accuracy in studies that use this tracking method. Moreover, the true location of a seabird was often outside of package-specific uncertainty estimates (as much as 76.3% of the time for `FLightR` and 15.5% of the time for `probGLS`). We also observed that the spatial accuracy in light-level geolocation of seabirds varies among species. As previously suggested by Lisovski et al. (2020) and Shaffer et al. (2005), it is likely that inconsistent

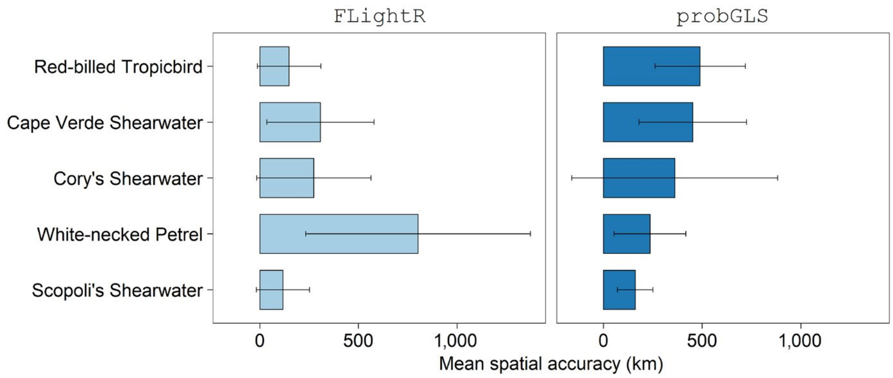

FIGURE 3 Mean spatial accuracy for each double-tagged seabird species as derived from the `FLightR` package (left) with a spatial land mask applied (parameter set 4, see Table 2) and `probGLS` package (right) using SST correction and a spatial land mask (parameter set 3, see Table 2). Accuracy is expressed as the great-circle distance between the GPS position and corresponding geolocator-derived position for a given twilight. GPS position was defined as the geographic mean of all GPS positions recorded within ±30 min of the given twilight. Distances were measured on the WGS 1984 ellipsoid. Error bars represent the standard deviation

accuracy is the result of species-dependent geolocator performance, which relates to the way in which the geolocator light sensors are affected by a combination of species-specific behaviour, morphology, plumage and habitat use. It is possible that smaller geolocator models are more prone to sensor shading than larger models, but we could not reliably test this hypothesis due to the confounding effects of species and individuals.

The method and quality of calibration can influence geolocation accuracy (see Lisovski et al., 2012 for a detailed discussion), so it is important that geolocation practitioners carefully consider calibration when planning their study. In particular, the calibration period should capture the complete variability in twilight transitions and care must be taken to ensure that the calibration method is suitable for the focal species (Lisovski et al., 2012). It is possible that calibration effects contributed to the poor accuracy seen in the `FLightR` results of some of the species we tracked—particularly in the case of White-necked Petrels due to their very long distance, looping trips away from the colony whence the geolocators were calibrated. However, we used standard 'rooftop' calibration methods that are commonly used by seabird biologists. Therefore, we expect our geolocation accuracies to be directly comparable to those obtained by seabird biologists in other geolocation studies.

Our modelling results showed that differences in species and individuals affected how accurate geolocations were. For example, in `probGLS` geolocation, Red-billed Tropicbirds had the poorest mean spatial accuracy. This could be explained by the species' morphology (i.e. extremely short tarsi) and nesting habits, which often include returning to the nest before or during sunset and sunrise, affecting geolocator performance. Conversely, White-necked Petrels had the poorest mean spatial accuracy in `FLightR` geolocation, which our models suggest is explained by their wide-ranging movement habits and large spatial displacement between twilights. The vastly different performance between `FLightR` and `probGLS` for this species supports the assertion that using SST correction is important for geolocation of wide-ranging marine species (Shaffer et al., 2005).

Mean spatial accuracy in Scopoli's Shearwater geolocations was good relative to other species possibly due to the species being restricted to a relatively small marine area (i.e. the Mediterranean Sea) compared to the other open ocean-foraging species that we tracked in this study. Spatial displacement of individuals between sunrises and sunsets affected the accuracy of geolocations produced by both packages, but was strongest in `FLightR`. Scopoli's Shearwaters made short-range movements within a small marine basin, and hence displacement did little to diminish their geolocation accuracy in either package. In the case of `probGLS`, the application of a land mask will have forced the algorithm to produce these geolocations within a small marine area, thus improving the latitudinal accuracy when using a spatial land mask. However, the species still had the highest mean spatial accuracy when a land mask was not applied. The spatial displacement of individuals between sunrises and sunsets appeared to be weakest in its effect on accuracy of geolocations estimated by the `probGLS` package, which suggests that the accuracies we observed for this package are not only applicable to breeding seabirds that exhibit central place foraging behaviour, but also for non-breeding or migratory seabirds. For these reasons, researchers working on coastal-foraging seabirds or seabirds in small marine basins will likely achieve useful results using either the `FLightR` or `probGLS` packages, whereas `probGLS` seems most suitable for researchers working on open ocean-foraging seabirds.

The `FLightR` package sometimes did not produce uncertainty estimates at the start of deployments, or for short-term deployments. This may have occurred because, for a given geolocation, `FLightR` determined low probability of movement between twilights (Rakhimberdiev et al., 2017). It is important to recognise that `FLightR` was designed to track migratory paths, therefore the algorithm may not calculate a probability of movement away from a capture location when tracking duration is short and when the tracked individual is in a state of central place foraging.

Our results suggest that the effect of spatial displacement on `FLightR` geolocations was driven by White-necked Petrels, which had the largest mean spatial displacement between twilights (more than double that of all other included species). This effect was likely due to the inbuilt Bayesian priors of the movement model incorporated by the `FLightR` algorithm. For geolocation of marine species, the `FLightR` package may benefit from the inclusion of SST as an optional model prior.

We found that the strongest predictor of accuracy was the duration of day or night between twilight events, with this pattern broadly consistent between expected day or night length (i.e. expected inter-twilight period calculated from GPS latitude) contrasted with the empirical geolocator-observed duration of day or night (i.e. calculated from raw light-level data). Our results empirically demonstrate why those using light-level geolocators should not only expect spatial accuracy to be lower during periods of solar equinox when day and night length is similar across the globe, but also as tracked animals move nearer the Equator where day and night length changes ever more shallowly per degree of latitude (Ekstrom, 2004; Hill, 1994; Lisovski et al., 2012).

Our results imply that practitioners should adopt variable spatial uncertainties by estimating a relative spatial accuracy based on observed inter-twilight period calculated from geolocator data, rather than by excluding data from an arbitrary duration either side of the March and September equinox dates, as is done in many geolocation studies (e.g. Van Bemmelen et al., 2017; Fayet et al., 2016; Jones et al., 2020). This approach not only tackles the issue of reduced spatial accuracy during solar equinoxes, but also of equatorial solar profiles and is a particularly important advance for geolocation of animals that migrate to, or reside on or near the Equator. The spatial accuracy of geolocation differs between species and inference method, but the relationship between geolocator-observed inter-twilight period and relative accuracy is consistent between periods of 9 and 15 hr, and closely follows a Gaussian function. We can therefore provide a rule-of-thumb for estimating the relative spatial accuracy of geolocations depending on the apparent inter-twilight period, which can be computed directly from geolocator data. The equation:

$$\exp\left(-0.5\left(\frac{d-12}{1.2}\right)^2\right)$$

where d is the duration in hours between the first and second twilight, gives the spatial accuracy in an estimate, relative to the accuracy with a duration of 12 hr. For example, when $d = 12$ the relative accuracy is 1, but at $d = 9$ or $d = 15$, the relative accuracy is 0.044, a 95.6% improvement in accuracy relative to when the duration of an inter-twilight period is 12 hr and accuracy is at its worst. When $d > 15$ or $d < 9$, this rule is not generalisable.

Our results present mean spatial accuracies that are within the order of magnitude of the reported average spatial errors (94–1,043 km) in studies of other marine vertebrates (Beck et al., 2002; Delong et al., 1992; Hull, 1999; Teo et al., 2004), but, in some species, are considerably larger than those that have previously measured accuracy in geolocation of pelagic seabirds (186–202 km; Merkel et al., 2016; Phillips et al., 2004; Shaffer et al., 2005). Based on our results, and considering previous studies that improved geolocations with SST (Delong et al., 1992; Gunn et al., 1994; Hill, 1994; Le Boeuf et al., 2000; Shaffer et al., 2005; Teo et al., 2004), we suggest that for pelagic seabirds, using SST as a prior in geolocation models might be essential to achieve better results and to increase spatial accuracy in light-level geolocation. Furthermore, the variation we observed between geolocation packages and geolocator types, and among outputs resulting from differently parametrised geolocation analyses (e.g. use of a land mask, SST interpolation etc.) validate the recommendations of Lisovski et al. (2020) concerning reporting of study parameters. Specifically, practitioners should clearly and unambiguously report assumptions and package-specific model parameters used to compute geolocations along with estimates of uncertainty associated with the data.

Light-level geolocation and geolocators are unquestionably important tools for studying the movement ecology and behaviour of marine organisms, and in many cases are the only available options to track small or sensitive species. Based on our results, we urge greater caution and consideration of the limitations of light-level geolocation when using geolocator data to draw inferences about regional spatial use and behaviour of wide-ranging marine species. Light-level geolocation is not an exact science and different combinations of geolocation packages, parameterisation, study species and data quality can yield different results and uncertainties. The key message in this study is not a criticism of light-level geolocation due to its inherent spatial uncertainty, but a demonstration that this can be reduced if practitioners adopt a dynamic approach to estimating uncertainty using duration of the inter-twilight period. While the spatial accuracy of geolocation may vary between packages, species and the quality of calibration data, the influence of the inter-twilight period on relative accuracy will be valid irrespective of the geolocation package chosen, or the species tracked. In particular, practitioners should make use of dynamic uncertainty estimates based on equatorial solar profiles and be aware that the average accuracy that one can expect will vary by species and might be greater than what is typically reported in seabird geolocation studies. This is especially important in the context of using geolocator-derived tracking data when precise, spatially explicit conservation or management actions are to be implemented.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

L.R.H. and J.D.R. conceived the project idea and co-designed the research; L.R.H. acquired funding and scientific permits, collected Pacific data, analysed the data and led the writing of the manuscript; J.D.R. generated positions of geolocator data, performed data analysis and contributed to writing the manuscript; R.M. helped with data analysis and contributed to project development and writing the manuscript; N.C. contributed to project development and ideas, permit acquisition and funding and assisted with Pacific data collection and writing the manuscript; N.G. helped with data analysis and contributed to writing the manuscript; R.R. was responsible for collating the Atlantic and Mediterranean tracking data; R.R. and J.G.-S. acquired funding and scientific permits, collected Atlantic and Mediterranean data, and assisted with writing the manuscript; J.M.R.-G., T.M., Z.Z., M.C.-F., S.S., V.M.-P., and L.Z. collected Atlantic data; F.D.F. and L.N.-H. collected Mediterranean data; R.H.C. contributed to project development, acquisition of scientific permits and funding and assisted with Pacific data collection and writing the manuscript. All authors contributed critically to manuscript drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code used in these analyses are archived on the Dryad Digital Repository https://doi.org/10.5061/dryad.gb5mkkwpf (Halpin et al., 2021).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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