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Off-the-shelf GPS technology to inform marine protected areas for marine turtles

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ABSTRACT

The financial expense of tracking solutions often impedes effective characterisation of habitat use in threatened marine megavertebrates. Yet some of these taxa predictably aggregate at coastal breeding sites, providing conservation opportunities. Toward a low-cost solution for tracking marine megavertebrates, we trial conventional GPS data loggers against Argos satellite transmitters for assessing inter-nesting habitat use of marine turtles. Devices were attached to green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles nesting at a study site in Cyprus, where patrol teams were in place to retrieve GPS loggers from turtles returning to lay subsequent clutches. GPS tracking revealed loggerhead turtles to predominantly use areas outside the boundaries of an MPA proposed for the region, while both species under-used much of the MPA area. Due to high location error, Argos data were considered unsuitable for such fine-scale assessments (all location classes except Z were included in our analysis). However, Argos tracking showed half the loggerhead turtles sampled also nested outside of the patrolled study area, demonstrating connectivity with other proposed MPAs. This was not accounted for by GPS tracking, because females exhibiting this behaviour rarely returned to the study beach, precluding GPS retrieval, thus, demonstrating the power of remote data access. The low-cost GPS technology could be considered in similar cases, where recapture is likely and where funding barriers preclude the use of Argos-relay fast-acquisition GPS technology. In combining the accuracy GPS and the continuity of Argos, the latter provides the best solution in most scenarios, but at far greater cost.

1. Introduction

Marine megavertebrates typically disperse over large spatial scales, across which anthropogenic threats are diverse, difficult to assess and therefore challenging to mitigate (Block et al., 2001; Croxall et al., 2005; Maxwell et al., 2013; Scales et al., 2014). As conservation becomes increasingly important to human development, animal tracking studies have become key in establishing priority areas at sea for addressing loss of biodiversity (Anadón et al., 2011; Coll et al., 2012; Ramos et al., 2017). To meet the demand of growing research and need, biologging solutions for marine megavertebrates have evolved to encompass a broad range of species, scenarios and biological questions (reviewed by Crossin et al., 2014 and Hays, 2014).

Prior to the inception of Argos-based satellite tracking in the 1980s, marine megavertebrate habitat use studies were reliant on mark-recapture methods (Godley et al., 2008). Under many circumstances recapture of study animals is highly improbable, and their movements may be broad, unpredictable and remote with great effort and extended durations needed (eg. Horrocks et al., 2016). Animal tracking in the marine realm has therefore become heavily reliant on the Argos satellite system for real time global location estimation and data retrieval (Gredzens et al., 2014; Martínez-Miranzo et al., 2016; Reynolds et al., 2017; Thums et al., 2017). The cost of taxon-bespoke Argos platform transmitter terminals (PTTs) along with the associated Argos system fees is typically $2000–6000 USD per study animal, depending on the type of unit used and the duration of tracking. This has meant that understanding the habitat requirements of many populations of conservation concern has been fiscally unachievable (Jeffers and Godley, 2016). In some cases, protected areas could have been more effective, had tracking data been incorporated in their design (Witt et al., 2008;

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Hays et al., 2014., Mazor et al., 2016).

While their broad dispersal poses a management challenge, many marine megavertebrate taxa aggregate to breed/nest/rear young at predictable locations and during set seasons, often in human-populated coastal areas, where the diversity and magnitude of anthropogenic threats can be elevated (Barlow et al., 2002; Castillo-Géniz et al., 1998; Haynes, 1987). At breeding sites, human effects (such as direct harvesting, habitat degradation) are acute because reproductive individuals and/or the process of reproduction are impacted. Conversely, breeding aggregations present a valuable opportunity for conservation. If priority coastal areas can be identified and human activities within these areas managed, then reproduction can be safeguarded and, indeed, some populations have shown significant and sustained recovery after cessation of decades or centuries of human pressures at breeding sites (Staniland et al., 2011; Weber et al., 2014).

Aggregation at breeding sites may provide an opportunity for data loggers to be deployed and subsequently retrieved, negating the requirement for remote data links. For example, onboard data loggers have been used to study incubating seabirds (Scheffer et al., 2012), whelping seals (Jeanniard-du-Dot et al., 2017) and nesting marine turtles (Houghton et al., 2002). Such taxa show fidelity to terrestrial breeding sites which they visit repeatedly within seasons, allowing adequate recapture rates for biologging studies. The reduction in size of low-cost (approximately $75 USD), off-the-shelf GPS loggers, developed for the more competitive human tracking market, has increased the financial feasibility of animal tracking (e.g. when modified to track birds: Bodey et al., 2014). Such units require extended surface time to acquire satellite ephemerides and almanac data, so for diving marine megavertebrates that surface only briefly to breathe, tags use fast-acquisition GPS logging technology such as FastLoc® (eg. Hoskins et al., 2015). But such tags are relatively expensive due to technology copyrighting and the cost of calibrating and individually testing tags for specific taxa (eg $3300 USD pers. comm Kevin Lay, Wildlife Computers). Even at discrete breeding sites where probabilities of recapture are relatively high, a proportion of tags will be lost, as not all animals will be recaptured. Given the expense of fast-acquisition GPS tag losses, an Argos-relay to upload archived GPS data is thus advisable, again at significant additional cost per study animal (eg $5000 USD pers. comm Kevin lay, Wildlife Computers), plus monthly Argos payments.

Among diving marine megavertebrate taxa, marine turtles are an appropriate group for tracking studies using archival data loggers, because they migrate from dispersed foraging grounds to aggregate off discrete beaches, onto which females emerge predictably to lay multiple nests. During mating and inter-nesting periods (the period between subsequent nesting events), marine turtles usually spend many weeks or months within habitats proximal to their nest sites, where Marine Protected Areas (MPAs) can be established to mitigate threats such as fisheries bycatch (Casale et al., 2017; Casale and Heppell, 2016), industrial activities such as seismic surveys (Nelms et al., 2016) or dredging (Whittock et al., 2017), limited or prolonged pollution events (Lauritsen et al., 2017; Wallace et al., 2017), boat strikes (Denkinger et al., 2013), human exploitation (Stringell et al., 2015) and human disturbance (Schofield et al., 2010; Zbinden et al., 2007). Many of these are prevalent in the Mediterranean (Casale et al., 2018).

To delimit priority marine turtle habitat-use zones, telemetry is often the most efficacious method. Where habitat use is being studied at such fine scales as during inter-nesting movements, GPS-quality location estimates have been advised (Thomson et al., 2017; Witt et al., 2010), but, due to the short surfacing periods of marine turtles, these have to date required Argos-relay fast-acquisition GPS devices (Schofield et al., 2007, 2009a; Shimada et al., 2017., Thomson et al., 2017). Considerable funding barriers (tens to hundreds of thousands of dollars per site) therefore exist to establishing well managed MPAs off the thousands of protected nesting beaches identified and monitored around the world (Hamann et al., 2010).

At a monitored nesting site in northern Cyprus, where nearly all nesting turtles are encountered by an established field team (Stokes et al., 2014), we set out to trial and compare the utility of conventional GPS loggers and Argos-only satellite telemetry (PTTs), in assessing the inter-nesting habitat use of sympatric green (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta*). Using marine turtles as a case example for diving marine megavertebrates, our goals were to determine whether Argos-linked fast-acquisition GPS technology was necessary, or whether either Argos PTTs or conventional GPS loggers could be used at lower cost.

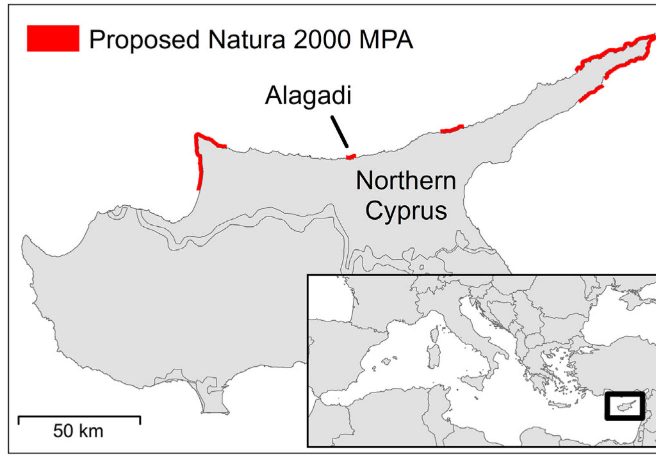

Fig. 1. Location of study site in the Eastern Mediterranean and proposed Natura 2000 MPAs.

2. Methods

2.1. Study area

In northern Cyprus, nesting of green turtles and loggerhead turtles is sympatric; some nesting beaches are used more intensively by one species than the other, but both species use all monitored beaches at least occasionally. Intensive night-time monitoring and tagging has been undertaken at Alagadi Beach (Fig. 1) since 1993. These two bays of 1.2 and 0.8 km in length, form part of a locally designated Specially Protected Area and boundaries have been delineated for a proposed Natura 2000 site (European Union network of protected areas; Fuller et al., 2009a). The Natura 2000 site management plan includes an MPA, within which fisheries and other human pressures are to be regulated to protect marine turtles while they are aggregating off the nesting beaches (Fig. 1). To prevent disturbance of nesting females the Department for Environmental Protection enforce closure of the Alagadi beaches between 20:00 and 08:00 and the Society for the Protection of Turtles (SPOT) in partnership with the Marine Turtle Research Group at University of Exeter, are permitted to undertake studies. An international team of volunteers are hosted by SPOT near Alagadi beaches and beach patrols are made at 10 min intervals throughout each night to ensure that all nesting females of both species are identified, monitored and tagged (Broderick et al., 2002; Stokes et al., 2014). The mean annual number of green and loggerhead turtles nesting at the study site are 74 and 35 females respectively (2013 to 2017).

2.2. Deployment method and location data handling – Argos PTT

Twenty-six female green turtles and 18 female loggerhead turtles were tracked after nesting at Alagadi between 1998 and 2015 (for post-nesting analysis see Stokes et al., 2015; Snape et al., 2016, Bradshaw et al., 2017). Argos PTTs ((Platform Terminal Transmitters) for details see online Appendix Table A1) were attached using epoxy resin according to the method described by Godley et al. (2002). Of the tracked females 17 green turtles and 11 loggerhead turtles laid subsequent clutches prior to their post-nesting departures and hence provided inter-nesting datasets. These sample sizes represent 23% and 31% (respectively) of the mean annual nesting population of green and loggerhead turtles recorded at Alagadi.

For each nesting female, data were included until the turtle's final clutch and subsequent departure from beaches in northern Cyprus. Where movement from a previous location would have required swimming speeds of $> 5\,km{\cdot}h^{-1}$ (a commonly used expected threshold for marine turtles; Witt et al., 2010; Hart et al., 2013) these data were removed. Locations were then filtered according to the location class (LC) error estimates assigned by Argos (LC 3: < 250 m; LC 2: 250–500 m; LC 1: 500–1500 m; LC 0: > 1500 m; LC B: unknown; LC A; unknown; CLS, 2008), although, when compared to simultaneously recorded Argos-relay fast-acquisition GPS locations from tracked marine megavertebrates, these Argos LC errors have differed considerably (Witt et al., 2010). LC Z (invalid; CLS, 2008) were removed. To examine any differences between habitat use during day and night periods, while also limiting the effect of auto-correlation on habitat utilisation mapping, data were allocated into 12-hour tracking periods and further processed to one location per 12-h period (Day: 07:01–19:00; Night: 19:01–07:00). Within these periods, where available, a single location (with descending preference LC 3,2,1,A, B, 0) was used. If two or more locations of the same preferred LC remained within a given 12-h period, the median location was used (Revuelta et al., 2015).

2.3. Deployment method and location data handling - GPS

Based on the success of their use with seabirds (e.g. Wakefield et al., 2013., Soanes et al., 2016; Bodey et al., 2014., Froy et al., 2015) iGotU GT600 (Mobile Technology; GPS locations generated within minimum 35 s from cold start) GPS trackers were used to track 16 female green turtles and 26 female loggerhead turtles during inter-nesting intervals at Alagadi in 2013 and 2014. Various user-definable data acquisition schedules and two housing methods were used and to conserve battery life, devices were programmed to undergo periods of inactivity (see online Appendix Table A2). Following a method similar to Walcott et al. (2012), plastic platforms were fastened to turtle carapaces using epoxy resin to enable mounting and removal of housed GPS trackers, which were fastened with cable ties (for detailed method see online appendix Table A2). Twenty-nine deployments were made on green turtles and 36 deployments were made on loggerhead turtles using 50 GPS trackers, resulting in 20 inter-nesting data sets for 13 green turtles and 15 inter-nesting data sets for 13 loggerhead turtles (see online appendix Table A3 for details of failed deployments). These sample sizes represent 18% and 38% (respectively) of the mean annual nesting population of green and loggerhead turtles recorded at Alagadi.

Nesting emergence was assumed where > 1 terrestrial location was logged in succession at a beach, indicating an extended haul out. Such data were removed and separated from the at-sea location data, for which one location per 12-hour period was retained (Section 2.2).

2.4. Nesting emergences outside of the monitored study beach

Some of the females tracked by PTT stayed within the coastal waters of Cyprus, to lay further clutches on beaches other than Alagadi. The approximate nest site was visually assigned to the nearest potential nesting beach by monitoring the number of messages received from transmitters (Rees et al., 2010; Tucker, 2010; Stringell et al., 2015) while using inter-nesting interval duration as a guide to expected clutch deposition (for green and loggerhead turtles nesting at Alagadi, respectively, mean = 12.5 days, SD = 1.65 and 13.4 days, SD = 1.62; Broderick et al., 2002). Any turtles tracked by GPS that subsequently nested at remote beaches, were not recaptured at Alagadi, thus such data were lost. However, some animals tracked by GPS emerged to nest, without success, at other beaches, prior to returning to nest successfully at Alagadi, and the locations of these nesting attempts were mapped using the resulting emergence data (Section 2.3).

2.5. Habitat utilisation mapping

A single coordinate, the midpoint of the Alagadi nest site, was used to estimate displacement of tracked turtles according to the processed Argos and GPS data. Data were pooled by species and by tracking method. The Kernel Density tool (ArcGIS 10.2.2) was used to determine habitat utilisation distributions (UDs; 25%, 50% and 75%) to view and compare the spatial extent of turtle habitat use. We used the default search radius setting for this package which computes the bandwidth parameter specifically for each input dataset, using Silverman's Rule of Thumb (Sheather, 2004). Habitat utilisation distributions and filtered locations were mapped alongside the proposed Alagadi Natura 2000 (European Union network of protected areas; Fuller et al., 2009a) site marine boundaries, to assess the degree of protection afforded to each species in their respective marine zones, and to compare inter-specific habitat use and the utility of the two tracking methods.

3. Results

3.1. Tracking data availability

3.1.1. Turtles tracked by Argos PTT

The 17 green turtles were tracked by PTT for 378 days across an estimated 31 inter-nesting intervals, yielding 1760 locations, from which 628 locations (one in each 12-h turtle tracking period for which data were available) were derived for analysis (see online appendix Table A4). Most of these 12-h locations were derived from LC's A and B (A-B: 86.9%; 3: 3.0%; 2: 5.3%; 1:4.6%; 0: 0.2%). Across turtles, the majority of 12-h turtle tracking periods provided one or more locations (mean: 82%, ± SD: 18; range: 36–100%) and the frequency of data-available 12 h tracking periods was relatively consistent during inter-nesting intervals (Fig. 2a).

The 11 loggerhead turtles were tracked by PTT for 319 days across an estimated 25 inter-nesting intervals, yielding 493 locations, from which 308 locations (one in each 12-hr tracking period for which data were available) were derived for analysis (see online appendix Table A4). Most of these 12-hr locations were derived from locations of LC A and B (A–B: 79.3%; 3: 4.9%; 2: 7.4%; 1:4.9%; 0: 3.6%). Compared to green turtles, fewer 12-h tracking periods provided one or more location (39%; ± 25, 7–72%). The frequency of data-available 12-h tracking periods was relatively consistent during inter-nesting intervals with fewer 12-h tracking periods providing data than for green turtles (Fig. 2b).

3.1.2. Turtles tracked by GPS

The 13 green turtles were tracked by GPS for 254 tracking days across 20 inter-nesting intervals, yielding 844 locations from which 120 12-hr tracking locations were used in analysis (see online appendix Table A4). Across deployments, data were available for approximately one quarter of 12-h tracking periods (27% ± 20; range: 9–77%). The frequency of data-available 12-hr tracking periods was skewed, with fewer locations toward the end of inter-nesting intervals (Fig. 2c).

The 13 loggerhead turtles were tracked by GPS for 217 tracking days across 15 inter-nesting intervals, yielding 504 locations from which 97 12-hr tracking locations were used in analysis (see online appendix Table A4). Across deployments, location data were available for 21% of 12-hr tracking periods (± SD: 19; range: 6–77%). The frequency of data-positive 12-hr tracking periods was relatively skewed, with fewer locations toward the end of inter-nesting intervals (Fig. 2d).

3.2. Nesting emergences outside the Alagadi study beaches

Of the turtles tracked by PTT, three (18%) green turtles laid one

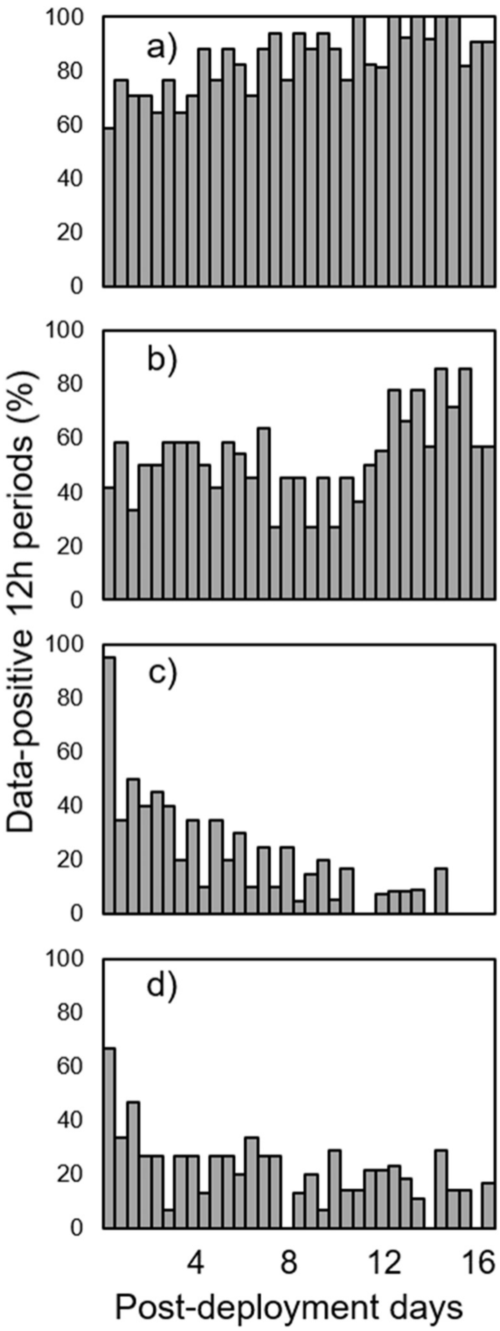

Fig. 2. Twelve-hour tracking intervals across study turtles at large for which data were available as a proportion of tracking intervals of turtles at large. Green and loggerhead turtles tracked by PTT (a and b respectively) and GPS (c, and d respectively). Data availability was temporally more consistent for PTT tracking compared to GPS tracking, where data were skewed toward the first days of tracking due to battery failures.

clutch (Fig. 3a and c) and six (56%) loggerhead turtles laid 1–3 subsequent clutches (Fig. 3b and d) away from Alagadi. Only one of these females, a loggerhead, returned to nest at Alagadi after nesting elsewhere. Of the recaptured turtles tracked by GPS, one green turtle made a nesting attempt at another sandy beach (Fig. 3g), and five loggerhead turtle females made nesting attempts across a 20 km area of coastline surrounding Alagadi (Fig. 3h) prior to returning to nest and recapture at Alagadi.

3.3. Marine habitat use

When assessed by PTT (Fig. 3a and b), 25%, 50% and 75% habitat UDs were at least an order of magnitude greater for both species than when using GPS (Fig. 3e and f; Table 1). UDs were relatively more inflated for green turtles than for loggerhead turtles. The PTT derived 25% habitat UD (Fig. 3c and d) almost encompasses the entire GPS derived dataset for green and loggerhead turtles, except for outlying locations (Fig. 3.e and f).

Despite these differences, some species-specific inter-nesting habitat use patterns were common among tracking methods. Green turtles tended to remain in the close vicinity of the nesting beach while loggerhead turtles made both local and wide-ranging coastal movements. Loggerhead turtles were therefore shown to occupy markedly broader habitat UDs (Table 1, Fig.3) and displaced further (Fig.4) than green turtles, using both methods. However, because PTTs provided data for three green turtles using subsequent nest sites, not shown by GPS, UDs were spread across a markedly broader coastal area (Fig. 3a). In contrast, UDs of green turtles tracked by GPS were almost entirely restricted to the close vicinity of the nesting beach (Fig. 3e, g and i), with very low displacement values (Fig. 4). Meanwhile, loggerhead turtles tracked by PTT moved over a wider area than green turtles (Fig.3b), across which over half were considered to be nesting. This habitat connectivity was better demonstrated by PTT, with two other proposed MPAs being used by loggerhead turtles and one by green turtles (Fig. 3a–b). One other MPA was used by loggerhead turtles tracked by GPS, Fig. 3f). Broad loggerhead turtle habitat use and displacement was also indicated by loggerhead GPS tracking, although no nesting events were detected outside Alagadi by this method (Fig.3, Fig. 4).

The median displacement of green turtles tracked by PTT and GPS respectively was 2.3 km (inter-quartile range (IQR): 1.0–7.0, range: 0.1–89.9) and 0.6 km (IQR: 0.4–0.8, range: 0.1–5.2; Fig. 4). The median displacement of loggerhead turtles tracked by PTT and GPS respectively was 14.3 km (IQR: 4.7–30.9, range: 0.2–97.8) and 2.6 (IQR: 1.1–9.4, range: 0.0–56.9; Fig.4).

Around the Alagadi nesting beaches, most GPS locations occurred within the 30 m bathymetric contour. Green turtles utilised habitats generally shallower than 10 m, with an apparent diel movement from Alagadi's western embayment into deeper waters between 10 and 30 m by day (Fig. 3g and i). Loggerhead turtles remained largely within the 10 to 30 m bathymetric contours. Eighty-nine percent of GPS derived locations for green turtles were within the proposed Alagadi marine Natura 2000 area, while only 30% of loggerhead locations were within this area. Because of the low location accuracy of Argos data, no inferences can be made to the bathymetric bands occupied or fine-scale movements of either species when tracked by PTT.

4. Discussion

The study of two marine turtle species at the same location has afforded insights regarding the utility of conventional GPS logger to gather short-term marine megavertebrate habitat use data, at reduced cost compared to Argos or Argos-relay fast-acquisition GPS tracking. While clearly being relevant to the study of inter-nesting movement of marine turtles, similar techniques could be applied to the foraging excursions of colonially breeding penguins and pinnipeds. Even at low volumes, the high accuracy GPS data were of greater value in home range analysis than Argos data, as to account for autocorrelation, data are filtered to one location per unit time (typically per 24 h period) (Griffin et al., 2013; Hart et al., 2013; Revuelta et al., 2015; Thomson et al., 2017; Witt et al., 2010). With modifications (see Section 4.4), this low-cost equipment could become much more relevant in the realm of marine megavertebrate tracking.

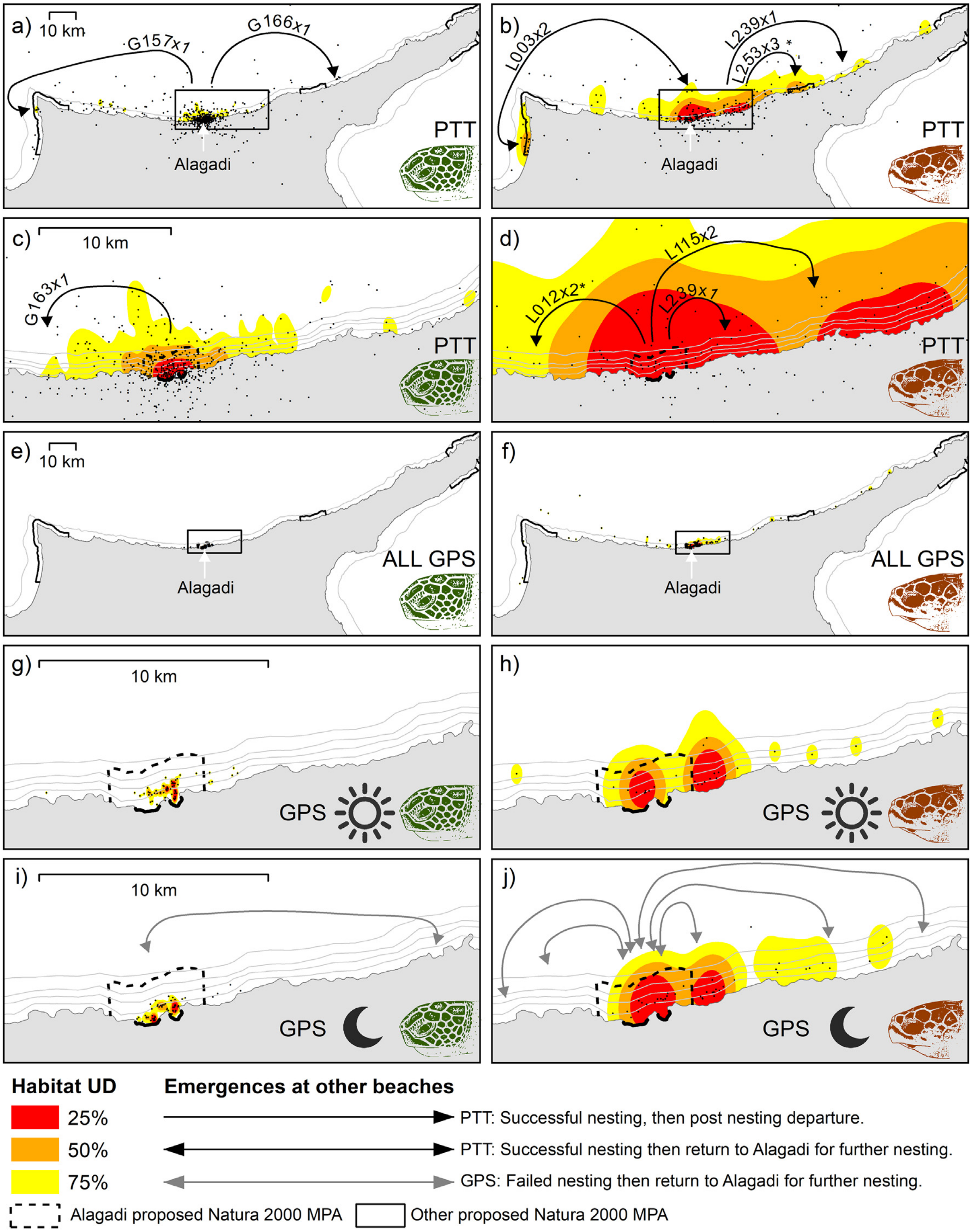

Fig. 3. Habitat utilisation distributions (UDs), filtered location data and schematic movements to alternative nesting sites (see legend for details) by species and tracking method. Left and right columns show green and loggerhead turtle tracking respectively and maps in the same rows are at equal scale. Argos PTT tracking of a) green turtles and b) loggerhead turtles, where insert boxes show the areas depicted subsequently at higher resolution for c) green turtles and for d) loggerhead turtles. GPS tracking of e) green turtles and f) loggerhead turtles, where insert boxes show the areas depicted subsequently at higher resolution for g) green turtles by day and h) loggerhead turtles by day and i) green turtles by night and j) loggerhead turtles by night. Thick black coastal embayments represent Alagadi nesting beaches. Bathymetric contours are 100 m in a–b, e–f and 10, 30, 50 and 100 m in c–d and g–j. *labels denote female ID and estimated number of clutches laid at distant site (see online appendix Table A4). See Snape et al. (2016) for one loggerhead turtle, tracked by PTT which laid further clutches in the Antalya region of Turkey, not drawn here for clarity.

4.1. Habitat use

General patterns of habitat use were common among the two tracking methods with green turtles remaining relatively close to the nesting beach and loggerhead turtles using a broader area and dispersing to distant coastal areas (both methods), where over half were shown to be nesting (PTT), including within other Natura 2000 areas. Loggerheads regularly emerged onto beaches near to Alagadi (GPS) presumably to investigate nesting opportunities. This low nest site fidelity was particularly highlighted when three loggerhead turtles

Table 1
Area (km^2) of habitat utilisation distributions for green and loggerhead turtles assessed by PTT and GPS.

Habitat UD	Green turtles		Loggerhead turtles	
	PTT	GPS	PTT	GPS
25%	4.5	0.1	117.1	4.0
50%	18.2	0.4	370.1	12.8
75%	90.3	0.9	1081.6	47.0

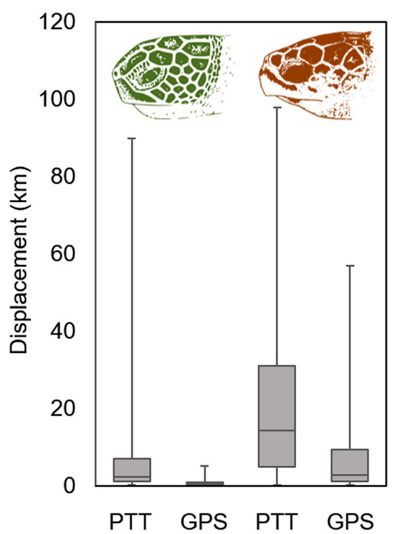

Fig. 4. Displacement (km) values of PTT and GPS locations (one location per 12-hr period). Horizontal line on boxes indicates median value, upper and lower edges of boxes represent first and third quartiles respectively and whiskers represent range.

tracked by PTT early in the nesting season subsequently nested in three other countries (Snape et al., 2016). Conversely, due to their high nest site fidelity, green turtle rookeries on Cyprus exhibit significant genetic stock structuring (Bradshaw et al., 2018), which is supported by both tracking methods.

Conventional GPS tracking showed that green turtles remained close (almost entirely within 1 km) to the nesting beach, generally using waters < 10 m deep, supporting previous dive logging studies of Hays et al. (2002) and Fuller et al. (2009b) at this site. The latter study observed diel habitat use of green turtles, with turtles using greater depths during the day, which again supports the findings of our conventional GPS tracking. These diel patterns may be attributed to human disturbance, as the near-shore areas vacated during daylight hours, correspond to those most heavily used by bathers (lead author personal observations). Diurnal patterns could also be tied to natural behaviour such as thermal niche selection (Schofield et al., 2009b), or foraging behaviour, with turtles moving out to forage on sea grass beds during the day (Christiansen et al., 2017; Gredzens et al., 2014; Fuller et al., 2009b). Loggerhead turtles used deeper waters, between the 10 and 30 m bathymetric contours, with few GPS locations occurring in waters > 50 m deep and this supports the results of a dive study by Houghton et al. (2002) at Alagadi, which found two breeding loggerhead turtles to be using waters of < 20 m. Argos satellite tracking (PTT) failed to provide such spatial detail but did show that some green turtle females used broader areas when visiting other nest sites on Cyprus, a feature of their behaviour which GPS tracking missed.

4.2. Critical appraisal of methods

Although the current study does not examine the accuracy of the GPS devices used, the difference in home range size resulting from GPS and Argos data was of the same order reported by Thomson et al. (2017), who compared FastLoc® Argos-relay fast-acquisition GPS data and Argos data, suggesting a GPS accuracy comparable to FastLoc® when used in this way. Thomson et al. (2017) also compared FastLoc® GPS and Argos tracking data when only high-quality Argos locations are retained (LC:1, 2 and 3). During that analysis, home ranges sizes were found to approach those derived from GPS data, but due to low data volumes, even over extended tracking durations, habitat UDs poorly defined spatial use. During the current study, high-quality Argos locations were few per individual or absent which is typical of Argos tracking studies with marine turtles (Witt et al., 2010). Retaining only these both reduced our sample size and resulted in insufficient data volumes. The accuracy of the available Argos data was therefore deemed not high enough to undertake detailed home range analysis.

Due to their great costs, sample sizes for marine turtle habitat use studies are usually fiscally dependent and although more tracks are always preferable (Godley et al., 2008; Jeffers and Godley, 2016), small numbers of tracks are valuable to conservation plans (Mazor et al., 2016). We therefore consider our tracking sample sizes (13 individuals of each species; 18–38% of females nesting annually), appropriate for advising management to protect nesting turtles according to core habitat UDs. Provided that similarly representative sample sizes can be attained, the conventional GPS devices are useful for the description of inter-nesting habitat use and to define localised MPAs for the protection of turtles aggregating off important nesting beaches. However, the trackers are less likely to detect habitat use at and around other subsequently visited nest sites. As we found with PTT tracking of similar numbers of individuals, this is because nesting attempts outside the Alagadi study site were usually followed by post-nesting migration without the opportunity for recapture. The strength of PTT tracking here is its utility in determining habitat connectivity, metapopulation structure, in estimating overall fecundity and population estimates based on nest counts, where nesting attempts can be identified (Tucker, 2010; Weber et al., 2013).

4.3. Conservation recommendations

In 2009 and 2010 through the European Union's aid programme for the Turkish Cypriot Community (EU regulation No. 389/2006: http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32006R0389&from=EN), five potential Natura 2000 sites were identified for coastal areas of northern Cyprus (Fuller et al., 2009a, 2009c, 2009d, 2010a, 2010b). The sites were selected according to the presence of important terrestrial biotypes, marine turtle nesting beaches, Mediterranean monk seal (*Monachus monachus*) haul out sites and seabird colonies (Audouins gull (*Larus audouinii*) and Mediterranean shag (*Phalacrocorax aristotelis desmarestii*)). MPAs were allocated to 1.5 km offshore, to also protect seagrass beds (*Posidonia oceanica*), which are ubiquitous around the island (Bianchi et al., 1999). The proposed MPA management plans include no information on the habitat use of the marine megavertebrates they aim to protect, nor on any fisheries activities. Yet they advise that fishing using set nets, which are the mainstay of the small-scale fishing industry (Snape et al., 2018) should not be permitted in these broad areas. The five proposed MPAs cover over a quarter of the northern Cyprus coastline. Despite the perceived cost of tracking marine megavertebrates, biologging studies may have paid dividends in this case, because the current management plans require extensive fisheries bans, potentially affecting the livelihoods of hundreds of fishers and requiring huge annual budgets to police fisheries closures across large areas. The value of marine megavertebrate habitat use studies should therefore be fully considered prior to designing such management plans, with appropriate analysis of available tracking technologies according to the long-term economic impacts of potential management decisions (Mazor et al., 2016; McGowan et al., 2017).

In the current study, a major area of core loggerhead UD fell eastward of the proposed Alagadi MPA and large areas were not used intensively by turtles. We propose that to protect the nesting turtles, the eastern boundary should be extended eastward by 1.7 km (to longitude 33.523°) to encompass this important loggerhead area, increasing the coverage of filtered turtle locations from 89% to 97% for green turtles and from 30% to 50% for loggerhead turtles. Meanwhile zoning in western areas of the MPA could permit human activities as appropriate where there are few aggregating turtles. Further inter-nesting habitat use studies are required to similarly address inter-nesting habitat use and connectivity among the four other MPAs.

Given its low cost, if there are suitable questions to be answered using conventional GPS technology alone, they can clearly be investigated with greater power for much less financial outlay, other than the labour involved in retrieving the units, which in this case, was already in place. Conventional GPS could provide a useful tool with which established local marine turtle conservation stakeholder groups could directly drive tracking studies, thus, tackling a communication gap between academic practitioners who traditionally drive such research and marine managers (Jeffers and Godley, 2016). However, in combining large GPS data volumes and remote data access, fast-acquisition GPS is the best solution in scenarios where large fiscal resources are available.

4.4. Recommendations for further tracking

The observed temporal skewing of GPS data was attributed to battery failure of some devices during the inter-nesting period and this short longevity is a major limitation. However, technical modifications could be used to overcome this. A conductivity switch could be integrated so that power-consuming satellite searches are only made during periods at the surface, and for large study animals (e.g. for all adult marine turtles), a larger battery size could be afforded. With a custom-built housing and a more appropriately placed antenna, more data could be acquired per unit time. The problem of study animals not returning to the precise study beach or colony for data recovery, may be overcome by integration of a UHF (Ultra High Frequency) and/or GSM Global System for Mobile connection) link, to transmit GPS data packages to a base station at the breeding site or via GSM networks respectively; such devices are used with solar cells for tracking large flighted birds (Ponchon et al., 2017) and have been used with success for tracking loggerhead turtles (Schofield et al., 2013). These data upload methods may incur lower monetary costs than the Argos satellite relay typically used to upload datasets logged onboard in marine turtle tracking.

Given the increased longevity of Argos devices and improvements in attachment methods, we recommend that Argos PTTs are deployed at or as close to the first clutch as possible, to maximise the value of satellite tracking programmes. Thus, additionally allowing provision of more accurate information on life history traits such as nest site fidelity and clutch frequency (Rees et al., 2012; Snape et al., 2016; Tucker, 2010), both critical parameters of population ecology and a global research priority for marine turtles (Rees et al., 2016).

5. Conclusion

Argos tracking, is clearly of great relevance in tracking animals over larger spatial scales, addressing habitat connectivity and identifying migration routes, but has limited value for assessing habitat use of species using relatively small areas such as in coastal MPAs. By providing both high resolution data and information on habitat connectivity, Argos-relay fast-acquisition GPS tags provide the best overall solution in most tracking scenarios where sufficient funds are available. Where funding barriers exist, the fact that conventional GPS devices can provide high-quality at-sea data for marine turtles is useful and shows their utility for informing MPA planning, where diving marine megavertebrates can be reliably recaptured after periods of weeks at sea.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.09.029.

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