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RESEARCH ARTICLE

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Assessing the impacts of satellite tagging on growth rates of immature hawksbill turtles

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Abstract

1. Animal-borne devices including transmitters, data loggers and identification tags are widely used across taxa to address important biological and ecological questions. Some of these devices may affect fitness, hence studies to assess device impacts are important across taxa and developmental stages.
2. We assessed the impact of satellite tagging on sea turtles at a foraging site in the Indian Ocean. Hawksbill turtles (*Eretmochelys imbricata*) were captured, and satellite tags (Fastloc-GPS Argos) attached to 25 individuals between 2018 and 2021, with a mean straight carapace length (SCLn-t) of 55.3 ± 6.9 cm (range = 47.9–69.5 cm; $N = 21$). We recaptured 12 tagged turtles and removed 11 tags between 2021 and 2023 and estimated growth rates of tagged ($N = 10$) and untagged ($N = 44$) animals (mean SCL range = 33.3–69.4 cm) using capture–mark–recapture of 54 individuals at liberty for 730–1095 days.
3. Growth rates decreased exponentially as turtle size increased, and we found no significant difference between tagged and untagged growth rates and body condition. We also found no damage to the carapace from the tag attachment.
4. We suggest that tagging does not impact growth rates at this study site because the turtles (i) typically maintain small home ranges in the lagoon and (ii) are benthic feeders, not actively pursuing prey. We encourage best practice to study the effects of satellite tagging on turtle populations around the world, as the outlook may be different for animals that swim long distances and/or carry large devices.

KEYWORDS
animal welfare, conservation, critically endangered, juvenile, marine megafauna, marine protected area, satellite tracking, Western Indian Ocean

1 | INTRODUCTION

Understanding animal behaviour, movement and distribution is essential for successful conservation and management planning (Hays et al., 2019). In terms of tagging, field biologists originally tracked animals using non-electronic external identification tags (e.g. plastic or metal tags with a unique identification number; Silvy et al., 2012), followed by the option of internal electronic identification tags (e.g. passive integrated transponders; Gibbons & Andrews, 2004). Although both tags are effective, and affordable techniques, these methods require recapturing animals, and information between captures is missing. Animal-borne tags (devices attached to animals that collect or transmit data) are now used widely to fill the knowledge gaps between recaptures and a range of sensors are available to collect a plethora of data, including location (e.g. telemetry), intrinsic (e.g. accelerometers) and environment sensors (e.g. video loggers; Williams et al., 2019).

The rise in reliable satellite technology and associated streamlined tags has overcome many challenges to studying marine animals that span large spatio-temporal scales (Hart & Hyrenbach, 2009). Marine animals are routinely tracked using satellite technology, including sea birds, fishes, marine mammals and sea turtles (Hussey et al., 2015) providing information on movement, dive behaviour (Luschi et al., 2013) and environmental conditions including sea temperature and depth (Hussey et al., 2015). Information obtained from satellite tracking data about migratory patterns and home ranges has been used widely in conservation management such as in the design of marine protected areas (MPAs) to encompass focal species home ranges (Dawson et al., 2017), informing fisheries management of movement patterns to reduce bycatch (Hussey et al., 2017) and reducing vessel strikes by monitoring vessel numbers and speed in high use areas to minimise interactions (Shimada et al., 2017).

Tag attachment methods vary between taxa, species and life stages. An adjustable leg harness might be the preferred attachment method for some birds to ensure both welfare and optimum data collection (Jirinec et al., 2021), whilst a transmitter at the sea surface tethered to a dugong (*Dugong dugon*) is common practice (Sheppard et al., 2006), and epoxy is typically used to attach satellite tags to the carapace of hard-shelled sea turtles (Hays & Hawkes, 2018).

Ideally, animal-borne devices will optimise data collection whilst minimising adverse impacts to the animal, and although some studies have reported no effect of tagging on reproductive success or growth of adult sea turtles (Omeyer et al., 2019), certain types of tag attachment can cause injuries (e.g. shoulder calluses from harnesses on leatherbacks, *Dermochelys coriacea*; Hamelin & James, 2018). Tags have also been shown to increase energy expenditure (as recorded for devices larger than 3% of seabird body mass; Vandenabeele et al., 2012), or have physiological effects such as elevated stress hormones in common and thick-billed murres (*Uria aalge*, *Uria lomvia*) equipped with small geolocators (Elliott et al., 2012). Some tags may disrupt movement as documented for pop-up satellite archival tags (PSATs) which increase drag on the European eel, *Anguilla anguilla* (Methling et al., 2011), change dive behaviour of great cormorants, *Phalacrocorax carbo* (Vandenabeele et al., 2015), and reduce growth in Atlantic salmon, *Salmo salar* (Hedger et al., 2017). It follows that negative effects of tag type and attachment mechanisms may undermine the quality of the data collected, and not accurately represent the population.

Tagging impacts may also increase with high tag retention. Whilst short-term deployments in which tags are removed several days or weeks after attachment (e.g. animal-borne video), may have little impact, long deployments over several months or years (e.g. satellite tags) and associated cumulative drag, may increase the risk of negative effects. Non-electronic, flipper bands were shown to increase mortality of king penguins (*Aptenodytes patagonicus*), likely through the impact of long-term (>10 years) increased drag leading to loss of fitness (Saraux et al., 2011).

Despite the increased use of animal-borne devices in sea turtle research (Godley et al., 2008) with >7000 sea turtles satellite tracked up to the end of 2017 (Hays & Hawkes, 2018), a review of 369 papers found 18% of studies examined welfare issues related to device attachment and <2% investigated welfare issues as the focus of their study (Jeffers & Godley, 2016).

Often there is little or no opportunity to re-observe tagged animals to assess changes in growth or body condition, or to identify injuries from tag attachment. Sea turtles which come ashore repeatedly to nest (Bjorndal et al., 1983) also often show high fidelity to their foraging grounds (e.g. immature green turtles in Martinique, Caribbean; Siegwalt et al., 2020), thereby providing opportunities for re-observation. Here we take advantage of the long-term fidelity of immature hawksbill turtles, *Eretmochelys imbricata*, to a foraging ground in the Indian Ocean (Hays et al., 2021) to assess the impacts of satellite tag attachment. We were also able to assess whether long-term attachment (2–3 years) caused any injury to the carapace. We highlight the importance of such assessments to evaluate the impact of animal-borne devices used to study various species and developmental stages around the world and hence to determine and encourage best practices.

2 | MATERIALS AND METHODS

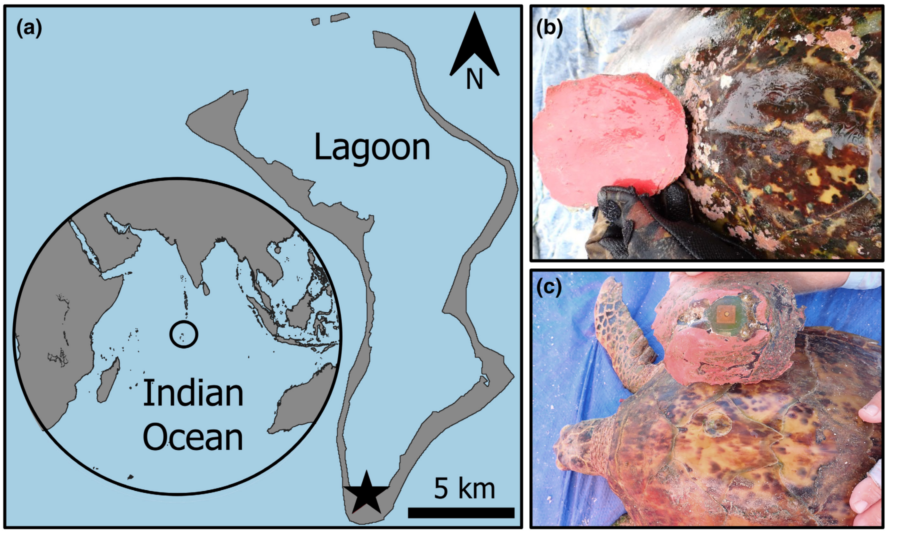
2.1 | Study site

Our research was undertaken on the island of Diego Garcia in the Chagos Archipelago, at Turtle Cove (7.4309° S, 72.4349° E; Figure 1a), a Ramsar site in the south of the Diego Garcia lagoon. Turtle Cove is an important developmental habitat for immature hawksbill and green turtles, *Chelonia mydas*, and both species have been protected at the site since 1968 and 1970, respectively (Mortimer et al., 2020). The site is shallow with a maximum depth of 3.22 m at the cove entrance (measured using a G5 depth logger, Cefas Technology Limited, Lowestoft, UK, 0.03 m resolution, attached to a concrete block on the seabed from 5 February to 10 August 2021).

2.2 | Capture–mark–recapture

Between 2018 and 2023, immature hawksbill turtles were captured ($N = 199$ individuals on 331 occasions) as part of a long-term in-water sampling programme underway between 1996 and the present. We waded in shallow water at low tide (<0.5 m) and quietly approached

FIGURE 1 (a) Diego Garcia with an inset map showing the location of the Chagos Archipelago (black circle) in relation to the wider Indian Ocean. The black star indicates where the hawksbill turtles were captured and equipped with a satellite tag (Fastloc-GPS Argos transmitter) at the south of the lagoon (Turtle Cove). (b) and (c) Examples of hawksbill turtle carapaces post satellite tag removal showing no signs of damage.



turtles from behind whilst they were feeding and captured them by hand. At the first encounter, each turtle was flipper tagged on both front flippers using Inconel (National Band and Tag Company, KY, USA) tags, and biometric measurements were taken. During subsequent recaptures, turtle tags were recorded, missing tags replaced as needed, and measurements repeated. These included curved carapace length (cm) notch-to-tip ($CCL_{n\text{-}t}$, hereafter CCL; Bolten, 1999) using a flexible measuring tape, straight carapace length (cm) notch-to-tip ($SCL_{n\text{-}t}$, hereafter SCL; Bolten, 1999) using Vernier callipers, and mass (kg) using a spring balance. Mean mass divided by mean SCL cubed was used as a metric for body condition (mass/SCL^3; Marn et al., 2019). If satellite tagged, the turtle was examined and photographed for evidence of damage at the attachment site on the carapace. Observations were recorded.

2.3 | Growth rates

Growth rate (cm/yr) was calculated for each turtle using SCL:

$$\left[SCL_{(\text{re-capture})} - SCL_{(\text{capture})}\right] / \text{recapture interval in years.}$$

Mean SCL (cm) was calculated by taking the mean of the initial and recapture SCL measurements. For growth rate analysis and the relationship between mass and SCL, outliers were identified and removed after plotting CCL against SCL when residual values from the positive linear relationship were >2 cm (9 out of 310 points; Figure S1), likely because of a mismeasurement or an error in transcription. The linear relationship between SCL and CCL was explored only using initial capture measurements from each individual ($N = 196$; Figure S1). For growth rate analysis and the relationship between mass and SCL, we set lower and upper limit intervals (730–1095 days) between capture and recapture. Including growth rates with short recapture intervals (<1 year) can increase sample size greatly, but measurement error can then dramatically impact estimated growth rate, particularly for slow-growing populations. On the contrary, including very long intervals between measurements increases the risk of missing size-specific growth rates. Negative values can arise due to measurement error or deterioration of the carapace (Bell & Pike, 2012), and as such were included in this dataset to avoid bias that could arise from exclusion. We also removed repeated measurements from the same individuals. The most recent measurements were retained unless the measurement removed was from an individual equipped with a satellite tag, and if so, preference was given to measurements from satellite-tagged individuals.

2.4 | Satellite tagging

Satellite tags with Fastloc-GPS (SPLASH10-BF-297B-01; Wildlife Computers, Seattle, Washington, USA) were attached to 25 hawksbill turtles between 2018 and 2021 (for detailed attachment methods see Hays & Hawkes, 2018). Length × width × height dimensions of the tags were 8.6 × 5.5 × 2.6 cm and their mass in air was 130 g (<1.2% total body mass of the smallest tagged turtle) and approximately 10 g in seawater (i.e. negatively buoyant). Satellite tags were only attached to individuals with a CCL >50 cm. As immature turtles in Diego Garcia lagoon generally show high fidelity to their foraging grounds (Hays et al., 2021), recaptures of the same individuals were frequent. Turtles were considered immature based on classification of immature hawksbills at other sites in the south-west Indian Ocean (e.g. Seychelles; <80 cm CCL; Sanchez et al., 2023). Tags were removed if there were signs of detachment from the carapace, for example, the epoxy was weak along the edges. To compare tagged and untagged individuals we filtered the data to reflect tagged turtle recapture intervals which were between 2 and 3 years (730–1095 days), and so all untagged turtles were only included if recaptures occurred between 730 and 1095 days. We plotted growth rates against SCL rather than CCL, as we more frequently had SCL measurements at both capture and recapture ($N = 10$).

2.5 | Review of studies investigating the impact of satellite tags on sea turtles

A literature search was conducted in June 2024 for studies investigating the potential effects of satellite tag attachment on sea turtles. We conducted a search on Google Scholar using the search terms: 'sea turtle' and 'satellite tag effects'. The first five pages of results were reviewed, and a forward and backward search was conducted for relevant papers from two recent studies (Hamelin & James, 2018; Omeyer et al., 2019). Papers were only included if they took an experimental approach (e.g. harness vs. direct attachment, Hamelin & James, 2018; tagged vs. untagged, Omeyer et al., 2019). For relevant studies, we recorded whether the study was conducted in the field or in laboratory conditions, tag attachment method, life stage, species, animal welfare measures investigated and if any, the effects reported.

2.6 | Ethical note

Our research was approved by Swansea University research ethics committee (AWERB reference numbers: IP-2018-01 and IP-2021-01). The study was endorsed through research permits (0006SE18, 0009SE18, 0004SE19, 0001SE21, 0001XSE22 and 0007SE23) from the Commissioner's Representative for BIOT and research complied with all relevant local and national legislation.

2.7 | Statistical analyses

We conducted a Pearson product–moment correlation test and fitted a quadratic model to examine the relationship between mean SCL and mean mass. All growth rates were increased by a value of 1 to transform negative values ($N=2$) into positive ones to fit the growth rate model with an exponential decay formula using log-growth rates. The relationship between growth rate, SCL and satellite tag attachment was explored using linear modelling with growth rate as the response variable, and SCL and tagged/untagged as fixed effects. Model comparison was performed using maximum likelihood estimates, and model residuals were checked for homoscedasticity and normality. A two-sample *t*-test was also conducted to explore whether there was a significant difference in body condition (mass/SCL^3) of individuals with and without a satellite tag between 50 and 60 cm SCL. All plots were created, and statistical analyses were performed in R (R Core Team, 2023; version 4.2.2). Data are presented as mean ± SD.

3 | RESULTS

3.1 | Capture–mark–recapture

Between 2018 and 2023, we captured 199 individual hawksbill turtles on 331 occasions in Turtle Cove, Diego Garcia. From these 331 captures, hawksbill turtle CCL was on average 46.4 ± 9.1 cm, range = 30.5–76.0 cm (SCL = 43.5 ± 8.2 cm, range = 28.8–70.3 cm; mass = 9.8 ± 6.3 kg, range = 2.5–36.7 kg; Figure S1). After removing recaptures that occurred outside 730–1095 days, and repeated measurements from the same individuals, we obtained 54 growth rates that were on average 918 ± 79 days apart (range = 736–1066 days). Mean SCL (mean of capture and recapture) was on average 44 ± 7.6 cm (range = 33.3–69.4 cm) for the remaining 54 individuals. As expected, turtle SCL and CCL have a strong linear relationship (SCL = 0.978 + 0.918 × CCL; $R^2=0.99$; $N=196$; $F_{1,194}=26{,}370$; $p<0.001$; Figure S1; Table 1), and turtle mass increased significantly with SCL (Mass = 11.7–0.73 × SCL + 0.02 × SCL^2; $R^2=0.98$; $N=54$; $F_{2,51}=1338$; $p<0.001$; Figure 2; Table 1).

3.2 | Recovery of satellite tags and assessment of individuals upon tag removal

From the 25 hawksbill turtles equipped with satellite tags (CCL = 60.2 ± 7.5 cm, range = 51.1–74.5 cm, $N=25$; SCL = 55.3 ± 6.9 cm, range = 47.9–69.5 cm, $N=21$; mass = 19.6 ± 8.0 kg, range = 10.5–36.0 kg, $N=25$), we recaptured 12 and examined the carapaces of 11 turtles post satellite tag removal, after 2–3 years of attachment (between 2021 and 2023). One tag was still fully secure to the turtle and so we did not remove the tag to avoid the risk of potentially damaging the carapace. On removal, we found no direct damage to the carapace, including no significant scute damage on the edges untoward of regular occurring damage and no significant thinning of keratin. Turtles in the cove are regularly found with algal build-up on their carapace and this can be seen built up around the tag (Figure 1c).

TABLE 1 Relationships between hawksbill turtle biometric measurements and growth rate in Turtle Cove, Diego Garcia, Chagos Archipelago.

Parameters	Equation	Test statistics	R^2
SCL, CCL	SCL = 0.978 + 0.918 × CCL	$F_{1,194}=26{,}370$, $p<0.001$	0.99
Mass, SCL	Mass = 11.7–0.73 × SCL + 0.02 × SCL^2	$F_{2,51}=1338$, $p<0.001$	0.98
Growth rate, SCL	Growth rate = 9.1192 × exp.(−0.0339 × SCL)−1	$F_{1,52}=40.91$, $p<0.001$	0.44

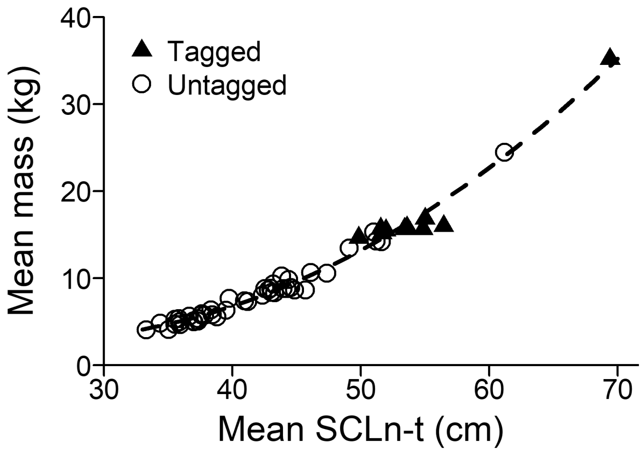


FIGURE 2 Mean mass of individual immature hawksbill turtles versus their mean straight carapace length (SCLn-t). The mean for each individual was calculated from the initial and recapture measurements. Black dashed line shows a fitted quadratic model (Mass = 11.7–0.73 × SCL + 0.02 × SCL^2; R^2 = 0.98; N = 54; $F_{2,51}$ = 1338; p < 0.001).

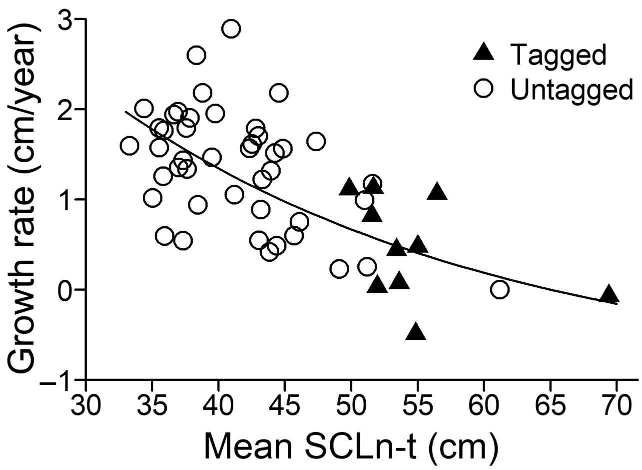


FIGURE 3 Relationship between mean straight carapace length (SCLn-t) and growth rate. Growth rate decays exponentially with turtle size (linear model: black line) for tagged (black triangles) and untagged (black circles) immature hawksbill sea turtles (growth rate = 9.1192 × exp.(−0.0339 × SCL)−1; R^2 = 0.44; N = 54; $F_{1,52}$ = 40.91; p < 0.001).

3.3 | Growth and body condition of tagged and untagged turtles

Hawksbill turtles grew on average 1.2 ± 0.7 cm, range = −0.5–2.9 cm per year (N = 54; Figure 2). Growth rate decreased exponentially as mean carapace size increased (growth rate = 9.1192 × exp(−0.0339 × SCL) -1; R^2 = 0.44; N = 54; $F_{1,52}$ = 40.91; p < 0.001; Figure 3; Table 1). For example, between 33.3 and 39.9 cm mean SCL, mean growth rate was 1.57 cm per year, whilst turtles between 50.0 and 59.9 cm grew on average 0.54 cm per year (Figure 2). We found no significant relationship between mass gain and mean SCL (Figure S2).

The 54 growth rates included 10 turtles with satellite tags. The tagged turtles mean SCL was on average 54.8 ± 5.5 cm, range = 49.9–69.4 cm and tagged turtle growth rates ranged between −0.5 and 1.12 cm per year. There was no significant effect of tagging when comparing growth rate models with and without an extra term describing which individuals were tagged ($F_{52,51}$ = 0.79; p = 0.38), suggesting that tagging did not impact turtle growth rates (Figure 3). Between 50 and 60 cm SCL, there was also no significant difference in the body condition of recaptured satellite-tagged turtles and unequipped turtles (t_5 = 1.05; p = 0.34).

3.4 | Review of satellite tagging impacts on sea turtles

From our review, we found seven papers that assessed the effects of satellite tag devices on live turtles in field (N = 4; Table S1) and captive (N = 3; Table S1) conditions. All studies assessing tag effects on free-living turtles were conducted on adult females and the majority of these studies were on leatherbacks, in particular comparing two attachment methods (harness vs. direct attachment). From laboratory and field-based studies, we found no papers investigating the effects of satellite tags on Kemp's ridley (*Lepidochelys kempii*), olive ridley (*Lepidochelys olivacea*) or flatback (*Natator depressus*) turtles. The main effects measured were injury, behavioural and growth. We also found no studies investigating the impacts on free-living immature turtles of any species.

4 | DISCUSSION

We report the first analysis of satellite tag impacts on growth rate, and body condition for free-living immature turtles. We found no significant impact from satellite tagging on growth rates or body condition as both tagged and untagged individuals grew at similar rates. Nor did we find that long-term attachment (2–3 years) physically damaged the carapace. Our findings are encouraging and suggest that satellite tracking can provide long-term behavioural data from small turtles (>50 cm CCL), without impacting their fitness.

We used two metrics to assess the impact of long-term satellite tag deployments. Firstly, we used the mass divided by the length cubed of individuals, an index of body condition used widely (e.g. fish, Stevenson & Woods Jr., 2006). If there were long-term effects of tagging, then we would predict that the weight of tagged turtles would be less than the weight of untagged turtles of a similar length. However, this was not the case and so this metric implies no measurable effect of long-term tagging. If there is any impact it is so small that it is not distinguishable from other factors driving individual variation in mass per unit body length. Secondly, we calculated growth rate, which again is a measure that integrates an animal's performance over long periods of time. The growth rate is broadly driven by the budget of energy expenditure versus energy acquisition (Werner et al., 2018). One possibility is that tags might increase the costs of swimming for turtles through increased drag, thereby raising their energy expenditure relative to their energy acquisition and so reducing their growth rates. However, growth rates in satellite-tagged individuals were not different to untagged turtles, likely because of the small size of tags and the fact that immature turtles on Diego Garcia only move small distances (Hays et al., 2021) and they are not pursuing prey, but rather forage on sedentary benthic animals and plants (Bjorndal, 1997; Mortimer & Day, 1999). We similarly encourage others tracking marine animals to develop objective criteria to investigate the effects of tags.

4.1 | Evolution of tag design and attachment methods for sea turtles

The drive to maximise tag performance through increased data collection and functionality under challenging conditions, together with minimising negative effects on animal welfare has led to the design of smaller tags (reduced tag mass and footprint) over the years (Holton et al., 2021). For example, early tag designs for sea turtles were large, heavy devices initially weighing several kilograms (Stoneburner, 1982) and over the past few decades some tags have miniaturised to ~11 to 13 g (total mass in air) meaning they can be attached to neonate turtles (e.g. loggerheads, Mansfield et al., 2012) to overcome the knowledge gaps of the understudied movement ecology of young sea turtles.

Early large tag designs were attached via long tethers which increased drag (Stoneburner, 1982) and harness attachments were trialled, particularly for soft-shelled turtles, such as leatherbacks, which increased drag as well as causing abrasions (Hamelin & James, 2018). Over time the advances in design and engineering of tags to be lighter and smaller has led to the direct attachment of tags to the turtle carapace (Balazs et al., 1996). From the three attachment methods used for sea turtles: harness, tether and direct attachment, the consensus is that direct attachment is the preferred method for hard and soft-shelled species and all life stages (Hamelin & James, 2018; Hays & Hawkes, 2018; Mansfield et al., 2012). Set against this backdrop of a general reduction in the size of satellite tags, the tags we used were 130 g in air, that is <1.2% of the mass of the smallest turtle we tagged. The size of these small tags likely contributed to their lack of measurable impact. The small tag size and longevity is facilitated by smart battery management. In older studies, tags were routinely duty-cycled (e.g. 6 h on and 48 h off; Parker et al., 2014). However, with our tags, a daily limit is set to the number of Argos transmissions and Fastloc-GPS acquisition attempts, which ensures that the batteries have a guaranteed longevity regardless of the surfacing behaviour of the turtles. Smart battery management on tags, allowing size reductions is clearly a positive attribute of modern tags.

4.2 | The effect of drag

Several elegant studies with animals, or models of animals, in wind tunnels to address device impacts (Jones et al., 2013; Vandenabeele et al., 2015; Watson & Granger, 1998) have shown that energy expenditure increases with the physical size of a tag in response to drag and mass. Since the impact on drag scales with the speed of travel, maximum tag impacts are expected for larger devices deployed on small, fast-moving animals. Studies of how devices impact free-living animals complement these drag and energy expenditure calculations from laboratory studies. For example, travel rate was 16% slower and dives 12% shorter for leatherbacks equipped with satellite tags via a harness attachment when compared to individuals with directly attached satellite tags (Fossette et al., 2008). Moreover, long-term increases in mortality in king penguins from flipper banding can be linked to the relatively small size of penguins and their fast-swimming speeds and hence even a small attachment can have negative impacts (Saraux et al., 2011). In contrast, the immature turtles that we equipped travel little, generally maintain small home ranges, and show high fidelity to the southern part of the lagoon (Hays et al., 2021), rarely moving outside of this area which lacks large sharks, making this a relatively safe foraging environment (Stokes et al., 2023). However, for turtles that travel faster, with long-distance movements (e.g. travelling outside the shallow lagoon) tagging effects may increase.

Many bird tagging studies follow the 3% or 5% rule, whereby the mass of the tag should be less than 3% or 5% of the body mass (Vandenabeele et al., 2012), and this has followed through into tagging studies of other terrestrial and marine organisms. The general rule of thumb for fish is less than 2% (Jepsen et al., 2005). The tags we used were <1.2% of the body mass of the smallest turtle satellite tagged and this in part could explain why we found no effects on growth and body condition from satellite tagging. Additionally, the combination of minimal movement and slow swim speeds of the turtles at our study site likely reduces the device impact that we recorded and helps explain why wind tunnel studies have suggested that whilst most external tags likely cause minimal drag to adults, larger devices might sometimes cause significantly increased drag for immature turtles when swimming quickly (Jones et al., 2013).

For some marine animals, the mass of the tag may be less important due to buoyancy control. Sea turtle buoyancy is regulated by the volume of air inspired in their lungs (Hays et al., 2004) and, since turtles adjust this volume to achieve the desired level of buoyancy on the bottom phase of dives, it is likely that they can alter their lung volume to compensate for the extra mass of the tag. Similarly, the buoyancy of some marine mammals varies within a dive, for example due to lung compression with depth, and with their body condition (Richard et al., 2014). So here again with marine mammals, the mass of the tag may lead to compensatory adjustments with buoyancy control. Still, to adjust for the additional tag mass, particularly for larger devices, there will be an increase in energy expended or an adjustment in behaviour to minimise energy expenditure (Rosen et al., 2017) which over time could result in reduced foraging, growth, and reproductive success (Schacter & Jones, 2017). In theory, this might lead to longer dives at shallow depths since they could inhale more and still achieve neutral buoyancy (Hays et al., 2004) and thereby increase their foraging success. However, this effect would be expected to be very small considering the low mass of tags in water.

4.3 | Physical injuries from attachment methods

As well as increasing drag, tag attachment can negatively impact free-living animals in several other ways. For example, in some cases the attachment itself may cause trauma at the point of contact, such as when darts are used to secure tethered tags to marine mammals (Andrews et al., 2019). Unlike other marine vertebrates, most marine turtles have a hard carapace and the preferred method is to directly attach tags using fibreglass or epoxy resin for slow-growing life stages or populations (Balazs et al., 1996; Seney et al., 2010). Epoxy alone is the most commonly used method of attachment as handling times are much shorter (Storch & Zankl, 2003). In this regard, it is reassuring that we found no long-term effects of the epoxy attachment to the turtles' carapace. Diggins et al. (2023) also found no effects to the attachment site under laboratory conditions although their attachment technique was epoxy in combination with neoprene and silicone for juvenile turtles to increase flexibility of the attachment for turtle growth. For neonates, various attachment techniques have been trialled to allow for the rapid growth rates of smaller turtles (Seney et al., 2010). For example, Mansfield et al. (2012) trialled harness, epoxy and neoprene-silicone attachments, rejecting both harness and epoxy, as these methods temporarily altered the shape of the carapace and opted for neoprene-silicone application as the preferential method as no effects were found.

The situation is different for soft-shelled marine turtles, such as leatherbacks and flatbacks, where harnesses were initially used but were found to cause abrasions (e.g. calluses on the front flippers for leatherbacks; Sherrill-Mix & James, 2008 or close to the hind flippers in flatbacks; Sperling & Guinea, 2004). Indeed, this concern from harnesses led to the development of a method of directly attaching satellite tags that is now used as the best practice for leatherback turtle satellite tracking (Fossette et al., 2008). However, the method of direct attachment for leatherbacks is to anchor the tag to the medial ridge through two small drill channels and so although direct injuries are reduced with direct attachment, there are reports of scarring from drill holes and discolouration of the epidermis from the footprint of the epoxy to support the tag (Hamelin & James, 2018). Our direct attachment of the tags to the carapace seemed to leave no damage. Indeed, epoxies of the type we used for tag attachment are often used by vets for repairing the damaged carapaces of individuals hit by boats (Bogard & Innis, 2008). For sea turtles, direct attachment of tags should always be favoured over the use of harnesses, whenever possible.

4.4 | Predation and entanglement risk

Another negative impact reported from animal-borne tagging is that tags and attachment methods might sometimes act as lures and increase the risk of predation for tagged animals. This impact has been noted, for example for immature loggerhead turtles (*Caretta caretta*) with tethered PSATs where the data and sudden termination of satellite uplinks were indicative of predation from sharks (Hall & James, 2021). Similarly, migrating eels have been observed being consumed, presumably by large predatory fish or by marine mammals (Koster et al., 2021). Tags could also increase the risk of entanglement from tether attachments, though, transmitters tethered to dugongs (*Dugong dugon*) in Australia (Sheppard et al., 2006) and green turtles at Laguna San Ignacio, Mexico (Senko et al., 2019), were designed with a fail-safe weak link so animals could still break free if the tether snagged (e.g. on vegetation). The immature hawksbill turtles that we tagged show high fidelity to Turtle Cove, a relatively safe, shallow habitat with no large sharks present (Stokes et al., 2023). Moreover, the tags we deployed are not tethered, further minimising the risk of predation or entanglement for this population.

4.5 | Studies investigating the impact of satellite tags on sea turtles

The effects reported from tagging studies vary depending on the attachment method, ability to re-observe or recapture the tagged individual for assessment, and the animal welfare measures assessed in a specific study. Some tagging studies on free-living turtles have simply resighted a tagged individual over a short period of time and reported normal behaviour and minimal device effects (Hart & Fujisaki, 2010; Stoneburner, 1982). More in-depth assessments have taken an experimental approach, for example, to compare harness versus direct attachment (e.g. leatherbacks, Hamelin & James, 2018) or tagged versus untagged (e.g. loggerheads and greens, Omeyer et al., 2019; hawksbills, Present study).

Although assessments have been conducted on the effects of tags and attachment to sea turtles, many studies are conducted in controlled laboratory environments (Diggins et al., 2023; Hoover et al., 2017; Mansfield et al., 2012) and natural environmental factors cannot be assessed. Furthermore, the advances in tag design and attachment methods for sea turtles over the last few decades have resulted in increasing tag attachment duration, and so it is important for us to understand the effects that long-term attachment may have on these individuals as was investigated for green and loggerhead nesting females in Cyprus (Omeyer et al., 2019). We encourage others to develop objective metrics of tag effects so that the effects can be quantitatively assessed for species and life stages that are frequently tagged around the world, particularly Kemp's ridley, olive ridley or flatback turtles, as we found no experimental studies on the effects of tags for these species.

5 | CONCLUSIONS

Tracking studies involving a range of marine animals have provided valuable information that has helped drive conservation planning and ultimately enhanced the conservation status of a range of species, including fish, mammals, birds and sea turtles (Hays et al., 2019). For sea turtles, there is a need for assessments and reporting of tag effects, particularly for long-term tag attachment. Studies at other sites around the world could also take advantage of the high fidelity of immature turtles to their foraging grounds (e.g. immature green turtles in Martinique, Caribbean; Siegwalt et al., 2020) in order to expand our assessment of tag effects on free-living immature turtles. Whilst animal tracking clearly has great merit, we echo the views of Walker et al. (2011) and Batsleer et al. (2020) who encourage practitioners to publish evidence of tagging impacts for each study species, environmental conditions, tag type, and attachment method regardless of whether they found no or little impact and, in this way, develop and refine best practices based on empirical evidence.

AUTHOR CONTRIBUTIONS

Graeme C. Hays, Nicole Esteban and Holly J. Stokes conceived the study. Holly J. Stokes, Graeme C. Hays, Nicole Esteban, Jeanne A. Mortimer and Jacques-Olivier Laloë completed the fieldwork. Holly J. Stokes compiled the data and review papers. Holly J. Stokes, Kimberley L. Stokes, Graeme C. Hays and Nicole Esteban conducted the statistical analysis. Holly J. Stokes and Graeme C. Hays led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no financial or competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available via the Dryad repository https://doi.org/10.5061/dryad.jh9w0vtmq (Stokes et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Straight carapace length notch-tip and curved carapace length notch-tip have a strong positive linear relationship.

Figure S2. A comparison of mass gain against mean straight carapace length (SCLn-t) showed no relationship for tagged (triangles) and untagged (circles) turtles.

Table S1. Reported effects of satellite tags and attachment methods on free-living and captive sea turtles from studies using an experimental approach (e.g. tagged vs. untagged; harness vs. direct attachment) including species, attachment method, and life stage.

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