



**TRACKING THE DISPERSAL ECOLOGY OF JUVENILE GREEN SEA TURTLES  
FROM THE CAYMAN ISLANDS USING SATELLITE TELEMETRY**

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**Abstract:**

In movement ecology, juvenile marine animals, like sea turtles, are often understudied. We released 40 green turtle juveniles (*Chelonia mydas*, 1-4 years old) from two different sites off the Cayman Islands coast in January and July of 2023 with satellite tags to see how they dispersed and what impact the release had. The determinants of turtles' directional swimming persistence, including the effect of ocean current direction, were determined using a statistical model and vector plots. Within 6-22 days, almost half of the population ( $N = 22$ ) successfully migrated from the islands to the surrounding regions. In contrast to the July turtles' northward spread (27-396 km), the January turtles radiated out (185-1138 km) in different directions. Daily swimming persistence rose around track ends and coastal zones, according to statistical data and vector plots. Turtles mostly swam against ocean currents. These findings show that young greens raised in captivity may find its way to important coastal environments for growth and development. Dispersal differences between January and July provide further evidence that release site and timing are crucial. We provide recommendations for future research on sea turtle and juvenile mobility ecology, and our findings help with conservation efforts for Caymanian green turtles that are making a comeback.

**Keywords:** Juvenile dispersal; green sea turtle; head-started releases; generalized additive mixed models; satellite tracking.

**Introduction**

Attempts to catalogue every single movement phase that a person goes through over the course of their lifetime—the "lifetime track"—present a constant and formidable challenge to movement ecologists [1]. Understanding the lifetime movements of a single individual has been nearly impossible due to the fact that tag technology that can report animals' spatial-temporal positions is typically limited to time periods less than a year. However, progress is being made for certain taxa, such as white storks [2,3]. The traditional approach to studying ontogenetic behaviour, habitat usage, and migrations has been to follow individuals throughout age groups and then utilise quantitative tools and biological information to draw conclusions about the relationships between various life stages. The difficulties of tagging young animals—including higher mortality rates, large tag-to-body-size ratios, and, for animals that disperse long distances, accessibility to intermediate age classes—have also skewed active biotelemetry studies that aim to track multiple life stages towards larger and adult animals [4,5]. Several studies have been able to successfully track younger and smaller age groups, such as neonate caribou [13], juvenile green turtles [6], juvenile bearded seals [8], juvenile Scopoli shearwaters [9], juvenile cuckoos [10], juvenile king penguins [11]; juvenile silky sharks [12]; and neonate leatherback turtles [6]. However, due to the difficulties and costs associated with long-lasting tags, these studies often used smaller sample sizes, shorter tracking durations, or only monitored one age group at a time.

Little is known about the migrations of juvenile marine species due to the intricacy of their life cycles and the fact that they exist in a large, dynamic, and fluid medium. The sea turtle is an

interesting example of a long-lived taxonomic group since most species show ontogenetic changes in foraging locations [14,15] and migratory patterns that vary across species and even within populations [16]. A mysterious developmental period known as "The Lost Years" [17] occurs when the young animals, including newborns and younger juveniles, spend a considerable amount of time foraging distant from any nearshore reproductive or feeding areas. Research on sea turtle migration has mostly concentrated on adult females after nesting [5,16], but there is an increasing amount of literature devoted to this pelagic developmental period's "when" and "where" of movement [1], particularly regarding developmental habitat shifts that occur as larger juveniles.

Through a mix of mark-recapture, stable isotope, and tracking studies, it has been demonstrated that as larger juveniles, Chelonian sea turtles (including green, hawksbill, loggerhead, flatback, and Kemp's and olive ridley varieties) move from offshore pelagic to nearshore benthic developmental habitats, frequently in conjunction with patches of drifting Sargassum algae [15,17-19]. The developmental pelagic stage of the green sea turtle's (*Chelonia mydas*) life cycle is characterised by active orientation and swimming against ocean currents in order to stay in or find favourable foraging habitats, according to studies of its movement ecology [20-22]. Laboratory studies and simulated individual-based models (IBMs) have been the mainstays of research on young sea turtles' navigational ability and large-scale habitat usage [23-26].

Recently, empirical assessments of the movement of young sea turtles have been made possible by the advancement and miniaturisation of long-lasting satellite tags. These tags can currently record tracks for 100 days at a weight of 10 g or less [21,27-30]. Nevertheless, there has been very little empirical description of the physical causes and the role of ontogeny in dispersion for many sea turtle species and populations, and it is quite unusual to follow numerous age classes at the same time. To learn if there are ontogenetic variations in the way juveniles migrate and how those movements relate to physical factors such as ocean currents, fluctuating sea surface temperatures, and colonies of floating Sargassum algae, further research is required. The Cayman Islands were home to a massive green turtle breeding colony in the past, but by the late 1800s, the species had almost gone extinct due to human overexploitation and consumption [31]. New studies, nevertheless, have shown that prior large-scale

The successful reestablishment of a green turtle nesting population in the Cayman Islands was likely made possible by releases (over 30,000 individuals, Bell et al., 2005) of neonate and juvenile green turtles from the Cayman Turtle Conservation and Education Centre (CTCEC), a breeding and captive centre for green turtles of all age classes [32]. According to past mark-recapture research on similar large releases, the turtles went all over the Caribbean and then came back to lay their eggs [33,34]. Adult wild Cayman green turtles use hunting places off the coast of Central America, according to limited satellite tracking studies [35], but no research have yet used satellite tracking on newborns or juveniles from the CTCEC or the local wild population.

We satellite-tagged and released various classes of young green sea turtles from the Cayman Islands to study their ontogeny in terms of mobility ecology and dispersion. Being kept in captivity during their pelagic developmental stage, this experiment provided a rare chance to see how well juveniles raised in captivity, or "head-started," could disperse beyond the release site and into an unfamiliar ocean habitat. To further investigate the potential impacts of release, turtles were released at two separate times and places. This study aimed to assess (a) any ontogeny in the turtles' directional movements, (b) any differences in directional movements between release site locations and timing, and (c) any relationships between turtle directional swimming and key environmental variables. To measure persistence swimming velocity, a generalised additive mixed model (GAMM) was employed with a mixture of biotic and abiotic variables. New information on movement ecology for the juvenile life stages is added to the existing body of knowledge by our investigation. This is the first extensive tracking research on green turtle juveniles in the Caribbean that we are aware of, and it included many age groups. Furthermore, our findings will guide the development of future ex situ conservation programs, which will have far-reaching consequences for the protection of endangered sea turtle species like the nesting population of green turtles on Cayman Island.

## 2: Materials and Methods

### 2.1: Deploying Satellite Tags and Releasing Turtles

The Cayman Turtle Conservation and Education Centre (CTCEC) in Grand Cayman, Cayman Islands (Figure S1) provided the juvenile green sea turtles. In a controlled environment, the turtles were nurtured from hatching to maturity. They were housed in concrete tanks of varying sizes (up to 150 m<sup>2</sup>), filled with raw, unfiltered seawater, and given a balanced diet of floating, modified extruded fish. Turtles of the same age and size were kept together until they were ready to be released. (For more information on captive rearing, see the "Commercial Reptile Farming" section of Mader's Reptile Medicine and Surgery, [36]). Prior to their release, all turtles were quarantined and examined to make sure they were healthy and met all quarantine criteria (you may get the CTCEC's quarantine and health screening process if you ask).

Table S1 shows that forty turtles were released between January and July of 2022, divided into three age groups: 1-2 years, 2-3 years, and 3-4 years. It was determined that all of the turtles were physically healthy. The Institute for Animal Care and Use Committee (IACUC; study protocol No. S-CBL-2021-03) at the University of Maryland Centre for Environmental Science gave their approval for all procedures and handling of animals. We compared the performance of two kinds of turtle tags—miniature (~1 g) solar (N = 15 in January and N = 10 in July) and battery-powered Lotek satellite transmitter tags (N = 15). We used these distinct tags because they were available and because we wanted to see how the two types of tags compared. Table S1 shows that most of the turtles' carapaces had epoxy adhesives (N = 25), although a small number of them (N = 15, 1-2 years old) had marine adhesives from 3M 5200 Fast Cure™ (FC) instead. No less than forty tags communicated their whereabouts and any errors they encountered with the ARGOS satellite

network (argos-system.org). We used appropriate statistical tests to examine differences in tag performance (e.g., recorded tracking durations or daily positions reported) with tag and adhesive types. First, we compared the mean tracking duration between January solar tags, July solar tags, and January battery-powered tags using an analysis of variance (ANOVA). Then, we compared the mean number of positions reported per day between January solar tags, July solar tags, and January battery-powered tags using a repeated measures ANOVA. Finally, we compared the mean tracking durations and mean number of positions reported per day for Fast Cure™ adhesives with epoxy, using two sample Student t-tests. These tests ensured that the data was accurate and reliable.

Separate time periods (January and July 2022) were used to tag and release turtles of varying ages, depending on their availability. Ten more turtles from the youngest age group (1-2 years, 36-40 cm CCL; Table S1) were tagged and released on 20 July 2022, bringing the total number of turtles tagged and released that year to thirty. The age groups were as follows: 1-2 years, 44-62 cm CCL; 2-3 years, 35-40 cm CCL; and 3-4 years, 54-62 cm CCL. To maximise release success and survival by avoiding nearshore predation, all age groups were released by boat off the Grand Cayman shoreline. Figure S1 shows that the January turtles were released around 10 km north of Rum Point, Grand Cayman, and the July turtles were released approximately 10 km south of Spotts Beach, Grand Cayman, in order to examine the consequences of releasing the turtles in various places. To better understand the smaller scale surface current trajectories upon release and throughout the research zone, surface drifters (January, N = 1, Pacific Gyre REEF Drifter; July, N = 1, Microstar GPS Drifter) were released at the same time as the turtles and recorded their positions regularly (every 10 minutes). After being released, turtles were classified as either "residential" if their tracks stayed within ~10 km of Grand Cayman island or "dispersive" if their footprints went beyond that area. With R version 4.2.0, we processed and analysed all the data [37].

## 2.2: Annotating Environmental Data

Removed from the tracks of "dispersive" people (those who left the island's vicinity; N = 22) were any relocations within a 10-kilometer buffer of the island, in order to align with the resolution of environmental data products and to eliminate inaccurate positions. The remaining sites were then regularised and further filtered using the "fit\_ssm" function of the "foieGras" R package [38]. By fitting a basic random walk as a continuous-time (state space) process model, this function enables users to concurrently filter and forecast ARGOS positions at regular time intervals [39]. To avoid over-interpolation, we compared the predicted daily positions of each turtle with their actual locations using the ARGOS error ellipse variables and a 24-hour time step (to compensate for large positional gaps and match the temporal resolution of the environmental data) (Figure S2). Afterwards, the regularised trajectories of every single turtle were adjusted according to the procedures outlined by Gaspar et al. [40] to account for the impact of ocean currents. The Copernicus Marine Service (<https://marine.copernicus.eu/>, accessed on 2 February 2022) supplied all the most recent updates. To calculate the average swimming speeds and course corrections for each day, we first calculated the ground velocities using the locations that were recorded

throughout the day. Then, we subtracted the surface current velocities from this data, which came from ocean current observations [40]. The operational meridian ocean analysis and forecast system (product DOI: <https://doi.org/10.48670/moi-00016> accessed on 2 February 2022) and the PSY4V3 product were used to gather data on ocean surface currents. This system generates daily average estimates of sea surface temperature and surface current velocity at a resolution of 1/12th degree (~9.2 km).

Along with the daily turtle locations, we also collected data on the density of Sargassum and the sea surface temperature. The PSY4V3 ocean product was used to get the mean daily SST data. Weekly mean Sargassum biomass densities (g/m<sup>2</sup>) were derived from a processed product of the region's Sargassum biomass density (University of South Florida [41]). Estimates have been made using MODIS alternative floating algae index (AFAI) data at a resolution of 0.01 degree (~1.1 km), adjusting for inaccuracies caused by cloud cover, cloud shadows, sun glare, and gaps in satellite coverage [41]. Within a one-kilometer radius of the daily turtle sites, the density values of the underlying Sargassum were retrieved.

### 2.3. Visual Evaluations of Turtle Pathways

We used circular histograms on the first two recorded locations for each turtle with viable locations (N = 38) to compare the initial magnetic headings (degrees from magnetic north) of the turtles upon release between the two tracking periods (January and July). In January, the mean was 25 hours  $\pm$  53 SD, and in July, it was 18 hours  $\pm$  10 SD. The alignment of the turtles with the surface currents following release was evaluated by comparing their initial heads with the first direction of surface drifters.

To compare the daily headings of the 22 dispersive turtles with the mean daily directions of the ocean surface currents between the monitoring periods of January and July, circular histograms were applied to their regularised daily positions. A Watson's U<sub>2</sub> two sample test using the "circular" R package was used to further explore statistical differences between mean ocean current directions and mean turtle headings (January vs. July) [42].

The dispersion patterns were compared with regard to ocean currents, release location, and time by creating maps of individual trajectories and surface current fields for each monitoring period (January and July). To create these backdrop visualisations of mean current velocities, we used the PSY4V3 product and averaged the daily mean ocean surface currents throughout the maximum monitoring length for each tracking period (28 days in January and 10 days in July). The Copernicus Marine Service (<https://marine.copernicus.eu/>, accessed on 2 February 2022). supplied the surface current velocity fields.

Every one of the twenty-two turtles that left the island had their regularised trajectories plotted alongside the daily ocean surface current and turtle swimming vectors. This allowed researchers to see exactly where the turtles were swimming in relation to the currents, whether they were swimming against them or in the same direction and speed.

## 2.4 Mixed Model with Generalised Additive Features

To find out what factors influence the persistence of daily swimming in a certain direction, we used a generalised additive mixed model (GAMM) with a combination of biotic and abiotic variables to analyse the regularised daily data of all 22 dispersive turtles. To find the daily swimming persistence velocities of each turtle, we used their current-corrected trajectories and the following parameters: turning angles (in radians), step lengths (in km day<sup>-1</sup>), and the angle between two swimming speed vectors. Step lengths and daily turning angles were calculated with the help of the "amt" R package [43]. Multiplying the magnitude of each daily step length by the cosine of the corresponding daily turning angle [44] yielded the daily persistence velocity, which is the propensity and amplitude of a given movement to persist in a particular direction on a daily scale.

The model selection method took into account potential drivers of turtle daily persistence velocity, which were: variable (e.g., January or July) and constant (e.g., mean ocean surface current velocity, sea surface temperature, density of Sargassum biomass), turtle size (e.g., body weight). These were considered fixed effects in the model selection process.

The inclusion of individual turtles as a random effect allowed for the accounting of individual replication with the size variable. The inclusion of a smoother interaction between latitude and longitude allowed for the accounting of spatial autocorrelation. A correlation autoregressive moving average (ARMA) structure was included into potential models to handle temporal autocorrelation. The starting values of  $p$  and  $q$  were ascertained via the use of autocorrelation function (ACF) and partial autocorrelation function (PACF) plots.

A standard mixed effect model selection procedure was used to identify the most important covariates affecting turtles' daily persistence velocity. This procedure involved fitting an initial model with all potential covariates and structures using maximum likelihood estimation (MLE) and then comparing it with subsequent models that varied combinations of fixed effect variables. To choose the best fixed-effect structure, these candidate models underwent backward elimination using the Akaike information criterion (AIC). Additionally, this method was used to ascertain whether an ARMA structure was suitable and, if so, to choose the optimal structure for  $p$  and  $q$  according to the fits from a limited maximum likelihood estimate (REML). To validate the model's assumptions, we plotted the standardised residuals against the fitted values and re-fitted the model using the "mgcv" R package [45]. By comparing the GAMM-predicted values for daily persistence velocity with the fitted values for certain variables, the final model results could be shown graphically. Using a partial effects contour plot from the "itsadug" R package [46], we were able to visualise the predicted persistence velocity values as a function of the non-linear interaction between latitude and longitude.

## 3. Empirical Result

### 3.1. Summary of Tags

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Two turtles (Table S1) out of thirty that were released in January only reported a single position; these turtles were not included in the subsequent analysis since they were located outside of Grand Cayman island. All twenty-eight of the January turtles that were able to be released and were in a viable position returned to Grand Cayman island within twenty-four hours of their release, mostly in a southerly direction that was consistent with the surface drifter's trajectory (Figure 1A). After that, twelve turtles were marked as "dispersive" and distributed radially from the island (Table 1, Figure 1C), whereas sixteen turtles were marked as "residential" and kept within a 10-kilometer radius (Figure S1) of the island during the tag's lifespan. The January surface drifter was re-released on 26 January 2022 after washing ashore on Grand Cayman.

**Table 1: Results for the dispersed individuals' daily positions (N = 22) are summarised in the following columns: tracking period (January and July), age group (1-2, 2-3, and 3-4 years old), length of track (days, after island positions were removed), average 24-hour displacement (km), average heading (0-360 degrees from true north), average sea surface temperature (deg C), average surface current velocity (km/day), average swimming speed (km/day), and total displacement (km; from start location to end of track).**

| ID     | Period | Age Class | Track Duration (days) | Mean 24-Hr Displacement (km) | Mean Bearing (°) | Mean SST (°C) | Mean Current Velocity (km/day) | Mean Swimming Speed (km/day) | Total Displacement (km) |
|--------|--------|-----------|-----------------------|------------------------------|------------------|---------------|--------------------------------|------------------------------|-------------------------|
| 304512 | Jan    | 1-2 Yrs   | 7                     | 40 (±15)                     | 183              | 26 (±0.18)    | 20 (±7)                        | 35 (±12)                     | 185                     |
| 304513 | Jan    | 2-3 Yrs   | 10                    | 53 (±20)                     | 205              | 27 (±0.22)    | 25 (±10)                       | 42 (±18)                     | 295                     |
| 304514 | Jan    | 2-3 Yrs   | 12                    | 37 (±12)                     | 258              | 27 (±0.30)    | 28 (±9)                        | 33 (±15)                     | 325                     |
| 304515 | Jan    | 3-4 Yrs   | 8                     | 29 (±9)                      | 167              | 27 (±0.19)    | 18 (±6)                        | 31 (±14)                     | 210                     |

|            |     |            |    |                 |     |                         |                    |                 |     |
|------------|-----|------------|----|-----------------|-----|-------------------------|--------------------|-----------------|-----|
| 3045<br>16 | Jan | 3–4<br>Yrs | 13 | 45 ( $\pm 22$ ) | 300 | 26<br>( $\pm 0.2$<br>5) | 30<br>( $\pm 10$ ) | 36 ( $\pm 20$ ) | 392 |
| 3045<br>17 | Jul | 1–2<br>Yrs | 11 | 33 ( $\pm 11$ ) | 135 | 29<br>( $\pm 0.1$<br>6) | 22 ( $\pm 8$ )     | 39 ( $\pm 13$ ) | 250 |
| 3045<br>18 | Jul | 1–2<br>Yrs | 9  | 21 ( $\pm 13$ ) | 192 | 29<br>( $\pm 0.1$<br>2) | 15 ( $\pm 5$ )     | 26 ( $\pm 10$ ) | 130 |
| 3045<br>19 | Jul | 1–2<br>Yrs | 10 | 44 ( $\pm 14$ ) | 278 | 29<br>( $\pm 0.2$<br>1) | 24 ( $\pm 9$ )     | 40 ( $\pm 18$ ) | 370 |
| 3045<br>20 | Jul | 1–2<br>Yrs | 8  | 19 ( $\pm 6$ )  | 167 | 29<br>( $\pm 0.0$<br>9) | 13 ( $\pm 4$ )     | 22 ( $\pm 11$ ) | 105 |
| 3045<br>21 | Jul | 1–2<br>Yrs | 10 | 36 ( $\pm 17$ ) | 219 | 29<br>( $\pm 0.1$<br>8) | 21 ( $\pm 7$ )     | 38 ( $\pm 16$ ) | 290 |

Table 1 and Figure 1A,D show that the ten turtles released in July all had viable locations and dispersed away from the island in the same direction as the surface drifter, which was located northwest of the island. The number of individuals from each age class was unequally distributed among the 22 turtles that dispersed from the island in January and July ("dispersive" individuals, Figure 1C,D): 5 1-2 year olds, 4 2-3 year olds, and 3-4 year olds in January, and 10 1-2 year olds in July (Table 1). There was also an unequal distribution in the age classes among the remaining 16 turtles that remained within a 10-kilometer radius of Grand Cayman throughout the length of their tags ("residential"). Specifically, there were 5 turtles that were 1-2 years old, 4 turtles that were 2-3 years old, and 7 turtles that were 3-4 years old (Table S1). The average number of locations reported by dispersive turtles each day was 12.6 (range: 2.6-17.4), whereas the average number of positions reported by turtles that remained near the island, known as "residential," was 4.2 (range: 1.0-9.1) (Table S1).

Figure S3A shows that there were no statistically significant variations in the tracking length across the three tag types (January solar tags, July solar tags, and January battery tags) according to the analysis of variance model (ANOVA). Nevertheless, a repeated measures ANOVA revealed that, in comparison to the battery-powered tags ( $2.5 \pm 1.3$  SD, solely in January) (F-value: 54, p-value:

$3.8 \times 10^{-11}$ ), the solar tags recorded a noticeably greater average daily position count ( $6.4 \pm 4.7$  SD for January release,  $12.8 \pm 5.1$  SD for July release) (Figure S3C). A two sample Student's t-test did not support a significant difference (t-value:  $-1.5$ , p-value:  $0.18$ ), when comparing the different adhesive types tested with the tags on an equal number of 1-2 year old turtles released in January. However, turtles with Fast Cure™ adhesives had a longer mean tracking duration of 14.4 days ( $\pm 7.4$  SD) compared to 8.7 days ( $\pm 1.8$  SD) for those with epoxy adhesives (Figure S3B). The average number of positions reported per day for 1-2 year olds with Fast Cure™ attachment types and epoxy tags was similar ( $6.3 \pm 5.1$  SD) (Figure S3D), and a two sample Student's t-test found no significant difference (t-value:  $0.031$ , p-value:  $0.98$ ).

### 3.2. Visual Evaluations of Turtle Pathways

Results from statistical tests and circular histograms of daily magnetic headings for 22 "dispersive" turtles released from the island in January and July, respectively, demonstrated statistically significant differences in mean headings (Watson's U2 two sample test, t-value:  $0.620$ , p-value:  $<0.001$ ). The majority of turtles released in January (42% or 5/12 turtles) had a mean southwest heading throughout their dispersion, whereas a significant fraction of turtles released in July (50% or 5/10 turtles) had a mean northeast heading (Figure 1B:  $226 \text{ deg} \pm 101 \text{ SD}$ ,  $20 \text{ deg} \pm 94 \text{ SD}$ ). The means of the turtles' headings and the ocean currents' mean directions were found to be significantly different for every monitoring period (Figure 1B) according to Watson's U2 two sample test (t-value:  $0.703$  in January, t-value:  $1.101$  in July, p-values:  $<0.001$  in both months). The average current directions that turtles encountered on their tracks differed significantly between the different tracking periods (Watson's U2 two sample test, t-value:  $0.402$ , p-value:  $<0.001$ ). In July, the turtles' currents were mainly in a northwest direction, compared to the currents recorded in January ( $288 \text{ deg} \pm 76 \text{ SD}$ ,  $331 \text{ deg} \pm 75 \text{ SD}$ ; Figure 1B).

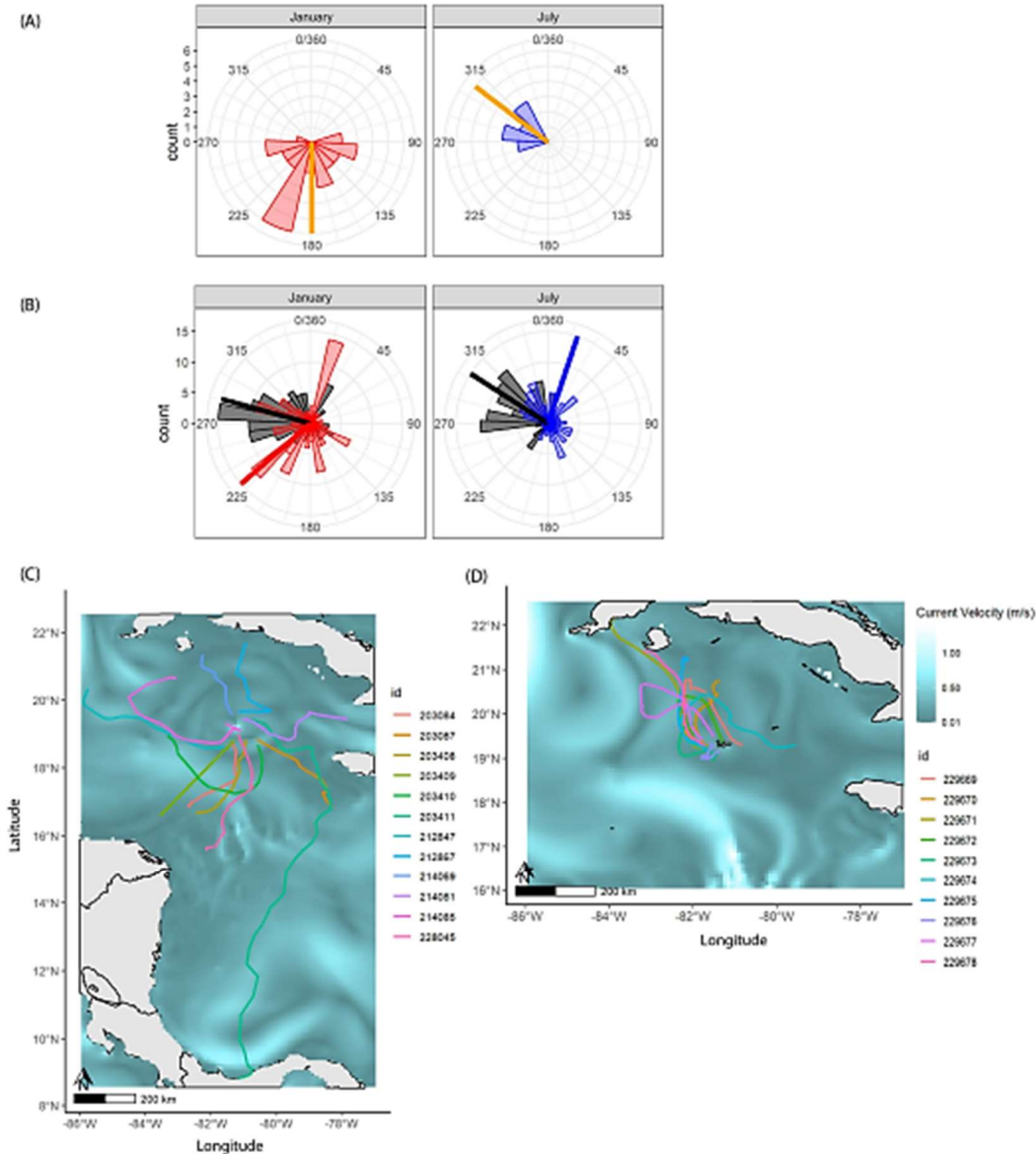


Figure 1: The starting direction of the surface drifter is displayed (orange) in the circular histograms of the first two reported locations of turtles released in January (N = 28 red) and turtles released in July (N = 10 blue). (B) Daily average surface current directions (black) in relation to the January and July tracks (blue and red, respectively), with thick coloured lines indicating the averages of each group. Ocean surface current fields averaged across the maximum duration of the tracks from each monitoring period (28 days in January and 10 days in July) were used to illustrate the trajectories of dispersive turtles in January (N = 28) (C) and July (N = 10) (D). As of 2 February 2022, the data for surface current velocity fields came from the Copernicus Marine Service, which may be found at <https://marine.copernicus.eu/>.

Figure 1C shows that the paths of the turtles released in January often went through areas with strong currents ( $>0.7 \text{ m} \cdot \text{s}^{-1}$ ) and then spread out in different directions from the island. Figure 1D shows that in July, the turtles generally scattered to locations north of the island with slower current velocities ( $<0.5 \text{ m} \cdot \text{s}^{-1}$ ). Figure 2A,B shows that between January and July, plots of daily ocean currents and turtle swimming vectors across regularised trajectories demonstrated that, for the most part, the turtles swam against the currents, with magnitudes comparable to the current vectors, in order to keep to their trajectories. Figure 2A,B shows that turtles did not always swim against the currents; in some instances, they did so (for example, IDs 203411, 212847, 229671, and 229678).

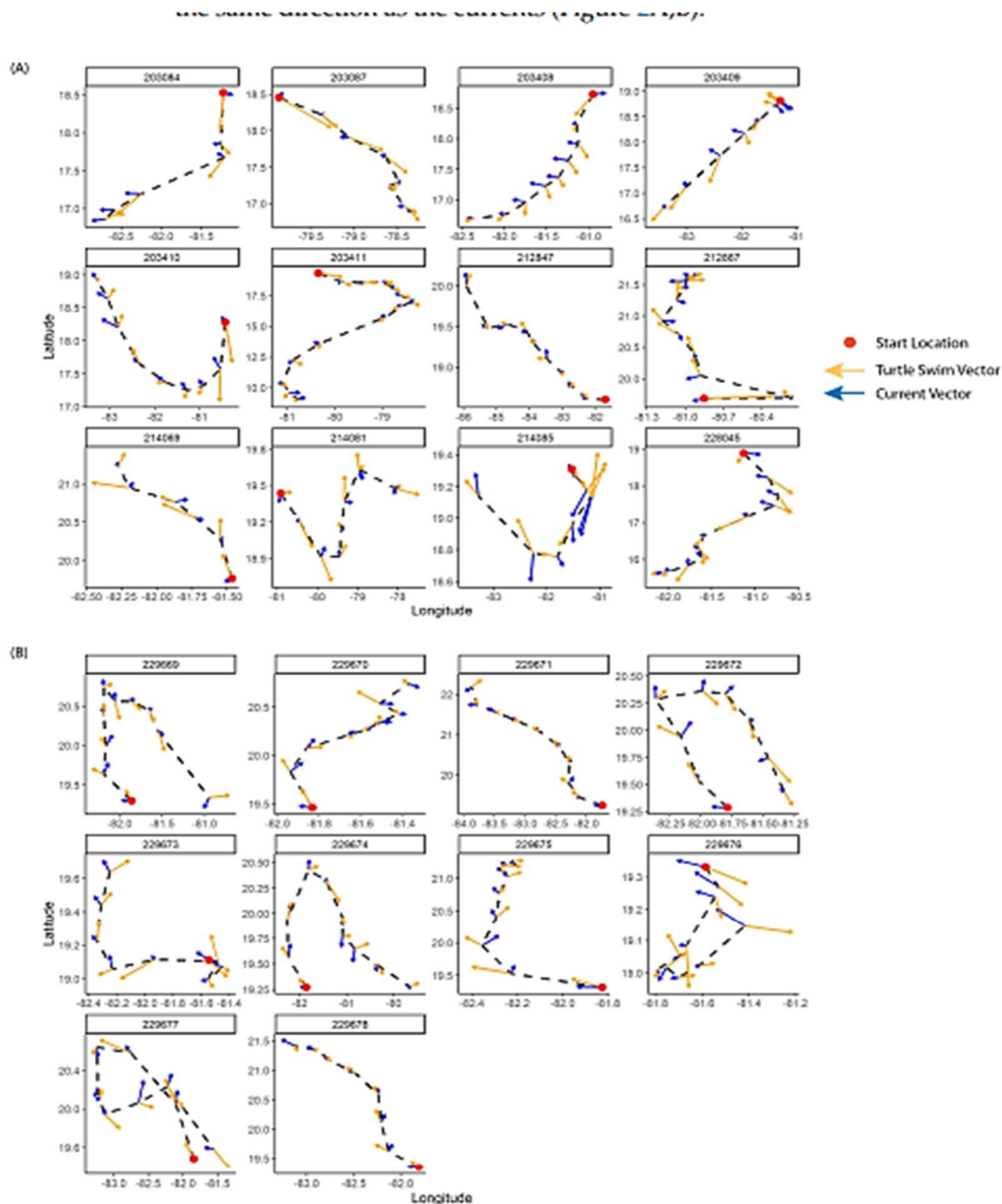


Figure 2: Figure 2 shows the individual trajectories of 22 turtles that swam away from Grand Cayman Island. The yellow vectors represent the turtles' daily swimming, while the blue vectors represent the ocean current. The plots are overlay for the monitoring periods in January and July, respectively. The beginning points of the trajectories are shown with red dots

### 3.3. A Mixed Model with Generalised Additives

A final GAMM of turtle daily persistence velocities as a function of the tracking period (January and July) and the smoothed interaction of latitude and longitude was produced by the model selection process. To account for temporal autocorrelation, the model employs an ARMA structure with parameters  $p = 4$  and  $q = 4$ , as shown in Table 2.

**Table 2 displays the outcomes of the generalised additive mixed model (GAMM) that was fitted to the data, which pertains to the swimming persistence velocity of turtles (km/day), the identity link function, and the Gaussian error. Using AIC comparison, the final model structures were chosen. An initial non-linear smoothing and interaction term for location (latitude, longitude) and a linear term for tracking period (July to January) were included in the final model. With  $p = 4$  and  $q = 4$ , the model additionally included individual turtle tracks as random effects and took temporal autocorrelation into consideration using an ARMA structure**

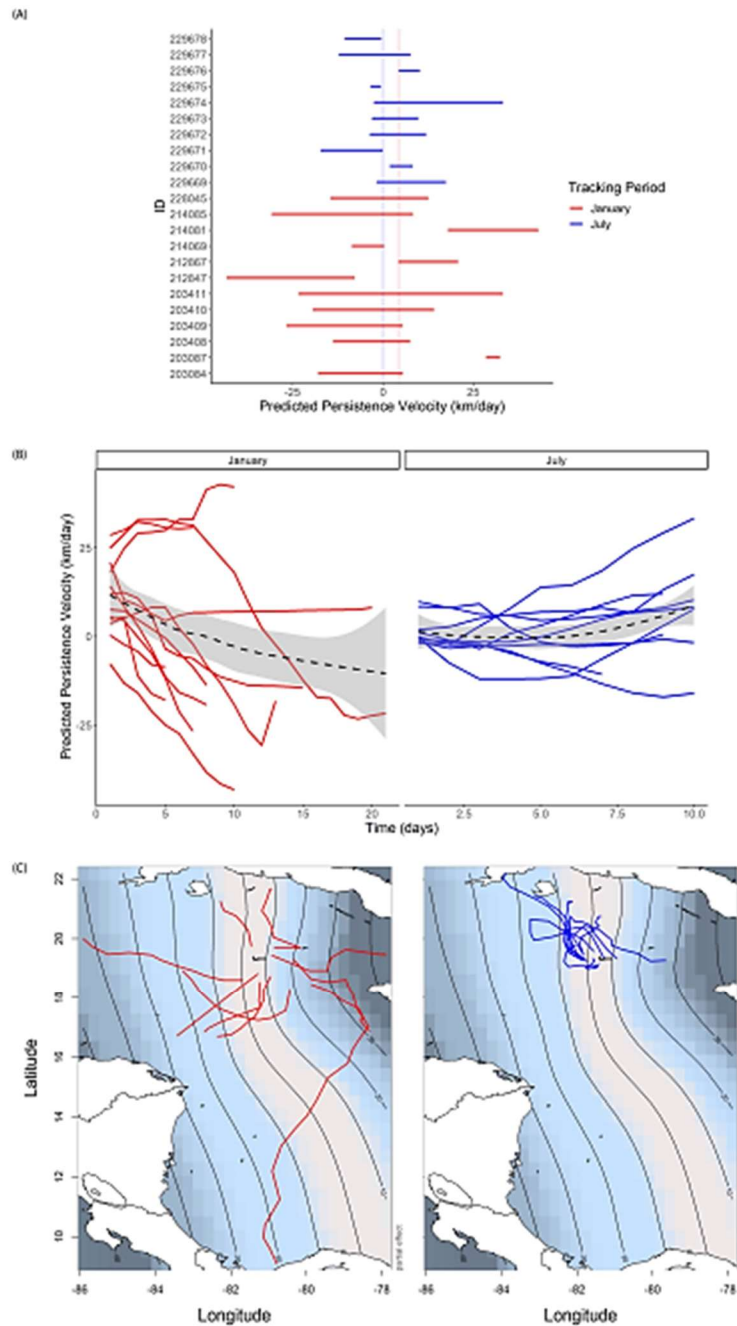
| Response Variable | Predictor                                        | Estimate | Std. Error | p-value |
|-------------------|--------------------------------------------------|----------|------------|---------|
| (Intercept)       | —                                                | −0.7     | 1.9        | 0.70    |
|                   | Persistence Velocity × Tracking Period (January) | 6.2      | 3.8        | 0.10    |

Between the monitoring periods, the predicted values of daily persistence velocity were  $2.0 \text{ km day}^{-1} \pm 19 \text{ SD}$  in January and  $1.8 \text{ km day}^{-1} \pm 9.0 \text{ SD}$  in July, with comparable means but different standard deviations. Figure 3A displays the expected values by individual and coloured by tracking period. It is evident that there is more variance among individuals and that the median is greater for turtles released in January ( $4.4 \text{ km day}^{-1}$ , July:  $-0.05 \text{ km day}^{-1}$ ). Figure 3B shows an additional plot of anticipated persistence values over time, which reveals that most people in both monitoring periods started with persistence velocities closer to zero and then progressively increased them.

By contrast, in July, the majority of turtles (nine out of twelve) maintained a westward velocity component (positive persistence velocity values) or saw their persistence velocities decrease or even go to zero (Figure 3B). Figure 3C shows that the predicted persistence velocities over the study area demonstrated a strong longitudinal gradient. Lower values were observed near the

beginning of the tracks and near Grand Cayman island and Cuban shelf areas, while larger values were observed towards the end of the tracks, particularly for those that seemed to be heading to the coast or nearshore areas of Cuba and Central American countries like Honduras, Costa Rica, and Panama. Figure 3C. Between the monitoring periods, the predicted values of daily persistence velocity were  $2.0 \text{ km day}^{-1} \pm 19 \text{ SD}$  in January and  $1.8 \text{ km day}^{-1} \pm 9.0 \text{ SD}$  in July, with comparable means but different standard deviations. Figure 3A displays the expected values by individual and coloured by tracking period. It is evident that there is more variance among individuals and that the median is greater for turtles released in January ( $4.4 \text{ km day}^{-1}$ , July:  $-0.05 \text{ km day}^{-1}$ ). Figure 3B shows an additional plot of anticipated persistence values over time, which reveals that most people in both monitoring periods started with persistence velocities closer to zero and then progressively increased them.

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**Figure 3** shows the predicted swimming persistence velocities for different turtles based on their tracking periods. In (A), the turtles are coloured by January (red) and July (blue). The vertical bars show the median persistence velocity values for each tracking period. In (B), the turtles in January (red) and July (blue) are shown over time with the generalised additive model smoothers (black line) and 95 percent confidence intervals (grey). Finally, in (C), there are contour maps that overlies the

As far as we are aware, this research is the first Caribbean-based large-scale satellite tagging attempt of young green turtles. Our data show that young green turtles that are head-started may disperse from release sites, even when the tag durations are limited. There was a marked change in the ontogenetic niches of several of the turtles in our study, with some swimming persistently through the open seas towards the Caribbean coast ("dispersive" turtles) and others staying close to the coast of the Cayman Islands the whole time ("residential" turtles). This provides further evidence that, had monitoring durations been longer, turtles would have been seen recruiting to various nearshore regions in the Caribbean and the Cayman Islands that are known to be developing environments. We tagged many different age groups of baby turtles, but our model still couldn't tell them apart when it came to dispersion.

There was a strong correlation between the timing and location of turtle releases and observed behavioural variations among the animals. This emphasises how crucial it is to release captive-bred green turtles at certain times and locations. We found that turtles may recruit to environments where dangers (such as bycatch or illegal take by fishermen) are more severe, which might have long-term consequences for turtle survival. This finding has crucial implications for research on turtles that are raised in captivity. Our research offers a framework for studying the ecology and behaviour of migrating juveniles that might be applied to other species whose migratory juvenile life phases are not well characterised.

### 3.4 How the Time and Place of Release Affect Dispersal

Distinct current configurations at the release sites may explain the striking variation in dispersion paths seen among turtles released at various times of year and locales. By releasing surface drifters at the same time as the turtles, researchers were able to determine that the turtles in January moved south of their release site back towards the island, while the turtles in July moved north-west of their release site towards waters north of the island. This pattern was consistent across both time periods (Figure 1A). Differences between January and July releases show that turtles may be helped to disperse away from the release site by favourable circumstances, such as surface currents [47]. Following the removal of two turtles with unhealthy postures, all thirty-eight turtles released in January returned to the region around the island within ten km of their release. Of these, sixteen turtles stayed put throughout the life of their tag. There were a lot of behavioural factors that made it impossible to get records of the turtles' dispersal from the Grand Cayman island area. For example, the turtles might have scraped or removed their tags from hard surfaces around the island [48] or the tags might have failed early on (the duration of the tags ranged from 3.0 to 32.5 days). Another theory, which is also hard to prove since the tag lengths were so short, is that the turtles that stayed close to the island adopted a more resident lifestyle and began recruiting from the surrounding areas. A previous research found that all of the "residential" turtles who stayed close to the island were of the same body size, with a mean of 55.7 cm CCL and a range of 32.8-80.7 cm CCL [49]. lived in a nearby southern lagoon and displayed a wide range of behaviours, including entering and leaving the lagoon as well as using seagrass and coral reefs throughout the day. It is possible that the 16 turtles that stayed close to the island during the time their tags were

attached were engaging in residential behaviours, such as less diving and more benthic resting or foraging, because the average number of positions reported per day for "dispersive" turtles was significantly higher (12.6 positions per day) than for these "residential" turtles (4.2 positions per day). Among the bigger age class of our research, which consisted of 3-4 year olds with a CCL of 54-62 cm (Table S1), there were more "residential" turtles ( $N = 7$ , 3-4 year olds) than "dispersive" turtles ( $N = 3$ , 3-4 year olds). Due to being closer in age and size to when the life stage change from pelagic to neritic developmental environment occurs, these older and bigger juveniles—which were near to the mean size of 55.7 cm CCL recorded by Blumenthal et al., [49]—may have been more likely to recruit locally [15,18,34]. This study highlights the significance of currents when selecting sites for turtle releases, even if we were unable to draw any firm conclusions on the long-term habits or residence of the turtles we released owing to the short length of the tags.

freeing marine and species raised in captivity. Because the turtles' initial responses to the direction of the currents were similar in both tracking periods (whether they stayed near the island or not), conservation programs that want to maximise the amount of time that released captive-reared individuals spend being tracked could use long-term sea turtle movement modelling (e.g., STAMM,25) or simulations run at different times of year to figure out when and where to release the turtles [47,50].

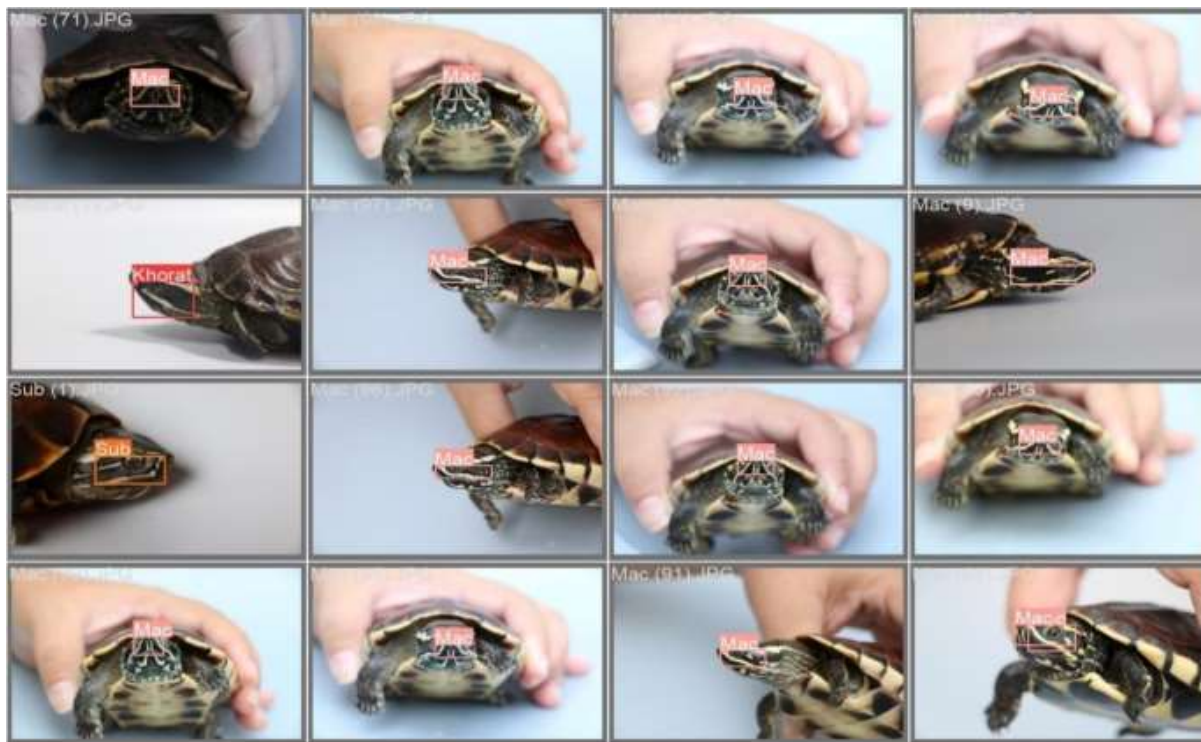
Given the relatively short length of the tracks (mean 15.2 days in January and 10.6 days in July), it is difficult to determine the impact of the changes in release site and timing on turtle long-term survival and migration, whether that impact is favourable or detrimental.

While 12 out of the 30 turtles released in January eventually left the island (after around 4.5–19.5 days), all 10 turtles released in July left their release site and the island promptly. It is common practice in captive-bred release programs to aim for successful dispersal of animals into new habitats as soon as possible after release [51]. The Cayman Islands are home to a vibrant natural population of green turtles, despite the fact that these animals are vulnerable to human poaching [32] and may engage in resource competition with older resident turtles [32,33].

Those who lingered close to the island had access to more resources, and the 16 "residential" turtles that were released in January may have attracted local Caymanian foragers and nesting sites [49].

It is possible to speculate about the impacts of different release locations and timings by drawing parallels to the "soft" and "hard" releases experienced by other caged animals. These procedures are often used in terrestrial investigations. In contrast to "hard" releases, which do not enable animals to acclimatise to their environment, "soft" releases allow them to do so, and the results may be more favourable [52]. While there is less research on the effects of "hard" vs. "soft" releases in marine and aquatic animals kept in captivity, the effects of "sea pens" or enclosed areas in their natural habitat can help marine mammals adjust to the ocean before a full release, reducing the likelihood of negative effects like startling, confusion, and starvation [52]. Our research suggests that turtles released in January may have experienced a more gradual return to the island, where

they could acclimatise to their new home and maybe even do some foraging. After that, they could either stay put in the Cayman Islands' local waters or leave at a predetermined time to migrate to other developmental habitats in the surrounding geographic areas, such as Central America or Cuba. Turtles that leave the island in January follow different paths as they travel around the Caribbean (Figure 1C). This could help them survive in the long run by attracting fewer individuals to crowded and resource-poor coastal and shelf areas, and by reducing the likelihood that any one turtle will be harmed by human interactions (such as bycatch or poaching). On the other hand, turtles that were released in July with a more forceful release seemed to float away from the island with the currents before moving on to other regions to the north (Figure 1D). Figure 3C shows that only 20% of the individuals released in July continued to travel towards the Cuban shelf's prolific coastline recruitment zones, even though this does meet certain requirements for a successful release by showing quick dispersion away from the release location [51]. A region with circular circulation known as the "Cuban Vortex," an extension of the Loop Current, seemed to be ensnaring the majority of them instead [56]. The turtles' movements away from the recruitment areas may have been impacted by the current structure. Even though the ocean surface currents were slower in this area in July compared to January, they still swam against the currents most of the time (Figure 2B) and were less directed than in January (Figure 3A-C).



**Figure 4: Sample outcome**

### 3.5 Past and Present Factors Affecting Dispersal

Our findings revealed that turtles exhibited individual heterogeneity in their dispersion patterns, in addition to variations in movement patterns with release period (January or July). In January, a few of turtles (IDs 203084, 203408, and 203409) swam against strong currents ( $>1 \text{ m}\cdot\text{s}^{-1}$ ) in order to retain their southwest trajectories heading towards Honduras and Nicaragua (Figure 2A; 21, 28, 40). Similar to 212867, 214069, and 214085, others swam counter-currents (Figure 2A) to reach the Cuban continental shelf from the more rapidly moving regions of the Cuban Vortex. On the other hand, it seemed that certain individuals (IDs 212847, 229671, and 229678, Figure 2A,B) were swimming against the currents, which might have been an attempt to "boost" their dispersion and save energy [28,40].

Figure 2A,B show that turtle swimming was clearly affected by the direction of the ocean current during both periods of tracking. However, according to our statistical model, turtles showed a directed drive to their movements regardless of the speed of the current, the sea surface temperature, the density of Sargassum algae, or their body size. While turtles' movement persistence varied significantly with longitude (Figure 3C) and time along their track (Figure 3B), it was most noticeable in January when turtles, on average, increased it near the end of their tracks and areas closer to coastal and shelf recruitment areas. In order to minimise bias from either spatial or temporal autocorrelation, our final model (Table 2) included both variables. However, it is important to note that no model completely accounts for the system complexity. In the Caribbean, turtles may have developed a more sophisticated sense of navigation as they approached land masses and coastal foraging areas. This sense could be aided by a variety of signals, such as smell, sound, sight, or even waves, which could guide the turtles closer to shore and away from current drift [57,58] (Hays et al., 2003, Lohmann et al., 2008). July turtle observations revealed that four individuals—IDs 229669, 229672, 229676, and 229677—had returned "home" (to the area around the Cayman Islands) by the end of their tracks. This raises the question of whether these turtles homing or imprinting on the rearing location for captive-raised and/or juvenile turtles is possible [59]. Figure 2B shows that all four of these individuals seemed to have swimming vectors directed towards the islands as their tracks came to a close. This may be more of a signal of the release strategy and current structures around the island in July than a reflection of the size or age of the turtles, as none of the 1-2 year old individuals released in January displayed this possible homing behaviour. These four turtles were in the youngest age class as in figure 4.

Previous laboratory studies have discovered evidence that turtles may use locational markers of the geomagnetic field (inclination and intensity) to imprint on and return to natal and foraging sites [60-62]. Although we were unable to test for relationships of turtle movements and behaviours with the magnetic field, we cannot rule out the possibility. Two of the turtles that were "homeward bound" in July (IDs 229676 and 229677) appeared to show a total change in their trajectory directions after about seven or eight days (Figures 1D and 2B), going only half a degree of latitude before turning around. This could be because of a "confusion" effect caused by the possible "hard" release in July, or the turtles might have discovered a resource, like Sargassum mats, and have been actively swimming around it to avoid drifting in the currents [22,28,40].

### 3.6 Proof of Prolonged Offshore Hiring

It is possible that the lack of a significant relationship between turtle swimming persistence velocity and Sargassum density was due to the fact that the model was using daily movement data, which is not very precise, as well as individual variability in movement persistence (Figure 3B). For example, in our turtle data, a daily interpolation of locations might conceal opportunistic feeding on the migration route, which is a fine-scale behaviour [63]. Animals reared in captivity sometimes end up bigger than their wild relatives, even though the pelagic developmental stage of green turtles is believed to last an average of three years (with a range of one to seven years [18,64]). Our research included turtles with a cumulative lifetime value (CCL) ranging from 35 to 65 cm (January: 1-2, 2-3, and 3-4 years; July: 1-2 years, CCL range: 36-40 cm) that were all this size range corresponds to the developmental habitats of young green turtles moving from pelagic to nearshore benthic environments, which they are traversing throughout their transitional recruitment period [15,18,34]. It is plausible that juvenile green turtles foraged or were associated with floating patches of Sargassum algae during dispersal, even though the resolution of our data may limit our ability to detect a relationship between Sargassum density and turtle swimming persistence [19]. In addition, as mentioned earlier (see Section 4.1, Effects of Release Location and Timing on Dispersal), most of the turtles released in January stayed close to Grand Cayman island for the whole time their tags were on. All sixteen turtles were around the same size as other juvenile greens, which have been found to inhabit nearby nearshore lagoons, sea grass beds, and coral reefs. Their mean central body length was 55.7 cm and their range was 32.8 to 80.7 cm [49].

whether we want to know whether head-started young greens are recruiting to the Cayman Islands' local foraging and resting habitats, we need further study that uses tags with extended tracking durations, maybe in combination with passive acoustic arrays or mark-recapture investigations [49].

Many of the turtles in our study probably ended up in other nearshore development habitats in the Caribbean. Of the 22 turtles that dispersed, the majority (68.2%, or 15 out of 22) had trajectories towards other coastal habitats after they left the Cayman Islands area (CCL range: 35-65 cm, Figure 1C,D). It has been demonstrated through a combination of adult and juvenile mark-recapture studies as well as small adult satellite tagging studies that turtles originating from the Cayman Islands will travel to regions off Nicaragua, Honduras, and Cuba in search of good feeding and nesting grounds [33–35]. It is possible that the turtles in our study were taking advantage of foraging opportunities along their tracks. This was particularly true for the July turtles, who had a more "hard" release; in January, the turtles returned to the island to forage nearby before dispersing, but in July, it took at least seven days (e.g., ID 229678, Figure 1D) to reach Cuba's productive shelf areas [34].

During this time, total fasting is expected to lead to significantly reduced metabolic rates, which would impede dispersion [68].

### 3.7 Head-Starting and Conservation Program Consequences

We found that animals who are raised in captivity, often known as "head-started," are capable of using a range of behaviours and directed movements to find their way around in an unfamiliar setting, which might be useful for finding food or finding a place to form a family. The Cayman Islands are home to a wild nesting population of green sea turtles that have been steadily making a comeback after decades of overhunting [32]. This discovery is significant for the species as a whole and for that population in particular. These findings show that other, more endangered species, including the Eastern Pacific leatherback turtle, might benefit from comparable ex situ head-starting experiments [69,70]. Some have argued that sea turtles' natural navigational abilities, natal imprinting, and nesting site choices could be disrupted by head-starting and release initiatives, which involve keeping animals in captivity from birth or hatching until they reach a large enough size to reduce the likelihood of natural mortality, and then releasing them into the wild.

While these concerns are understandable, it's possible that most head-starting initiatives don't do enough tracking or monitoring to back up claims of long-term effectiveness [73].

Furthermore, the impact of oceanography (such as ocean currents) on dispersion may have gone unnoticed in these research. In our study, we found that headstarted turtles released in January went back to their rearing site when the ocean currents took them in the opposite direction, whereas turtles released in July went in the opposite direction. This suggests that the timing and location of releases in relation to the directions of the ocean currents may have significant effects on the final destinations of released headstarted turtles. One major worry with headstarting and captive-reared programs is that the animals won't learn to navigate, forage, or recruit in crucial habitats since they've grown up in a lab [51]. People who participated in our research were able to use a variety of dispersion strategies and behaviours to independently travel to critical habitat regions. Individual spatial separation in foraging and developmental habitats may have provided resilience to the population in the face of high anthropogenic mortality or inter/intra-specific competition for resources, particularly during January and for those that dispersed from Grand Cayman island. In addition, as mentioned earlier, there are known habitats around the islands that can support the development of juvenile greens. Even though most of the individuals released in January seemed to follow ocean currents and remain near Grand Cayman island for the duration of their tags, there are other areas as well [49]. The local nesting population of Caymanian green turtles is believed to contain just 100-150 females [32], therefore their potential long-term presence might assist boost recruitment. To find out whether the people released in our research satisfy the criteria for "successful" head-starting programs, we need to conduct longer-term monitoring, maybe with the use of passive tags or mark-recapture initiatives [51].

The capacity to mingle with conspecifics during recruitment to nearshore developmental environments, long-term survival, and philopatry to one's birthplace are all examples of these

traits. Recent studies on Caymanian green turtles have shown that these turtles, whether released as neonates, juveniles, or adults, can and will fulfil all of these requirements [32–35].

To better understand the extent to which turtles in our Caribbean study area interact with fisheries, both while at sea and in their nearshore foraging and inter-nesting habitats, as well as to quantify the spatial overlap between the two, larger-scale tracking studies involving more age groups (e.g., neonates and adults) are required. The study's innovative satellite tags were too small to measure the spatial use of nearshore areas, but they were long enough to pinpoint where turtles went after they left the islands. This included places in Central America like the Caribbean coasts of Honduras, Costa Rica, and Panama, as well as the nearshore and shelf areas of Cuba and Grand Cayman. As a result of the high volume of fishing in these areas, green turtles are both accidentally trapped as bycatch and deliberately killed for human food, either legally or illegally (by poaching) [32–34]. There have been some successful repopulation and mass head-starting efforts of local green turtle populations, such as the Cayman Turtle Conservation and Education Centre (CTCEC) on Grand Cayman. However, predictive management tools that combine threat data with near real-time movement and habitat use data, also known as "dynamic management" [75,76], could provide additional strategies to reduce illegal hunting and bycatch in ocean habitats and nearshore shelf areas for these turtles.

#### 4. Conclusion

Improving the unique tiny tags used in this work will help future research minimise locational mistakes and increase monitoring durations, which will provide a better understanding of the ability to quantify fine-scale behaviours like foraging. In general, the locations given by the tags were somewhat inaccurate, particularly for the January turtles (Figure S4). In comparison to the solar-powered tags, the battery-powered ones showed a much smaller number of positions (Figure S3C). Based on these findings, future research should use updated versions of these tags, giving preference to the ones powered by solar energy. Regardless, we overcame these obstacles and obtained sufficient individual positions to forecast daily movements and overall trajectories (Figure S2A,B). We recognise that the data's quality naturally dictated the predictions' accuracy; for example, for IDs 203,409 and 212867, Figures 1C and S2A show that overinterpolation or unrealistically straight segments of the track may have occurred. In spite of these caveats, we think our results—the first empirical research of its kind in the Caribbean—offer useful coarse-scale predictions of dispersion and behaviour for young green turtles in this area. Future research into the factors that cause juvenile dispersion and swimming persistence at finer scales may benefit from this work.

Our approaches for identifying ecologically important movement-based behaviours may be applicable to other species' movement ecology research in the future. Research on this population, as well as other migratory animals that traverse fluid environments, could provide more detailed information. With this, we could expand our current statistical model to include multiple movement behaviours. This could be achieved through the use of more sophisticated behaviour

parsing techniques, such as discrete [77-79] or continuous time [39,80] state-space movement models. These models could account for hierarchical structures in the data, temporal autocorrelation, locational errors, and relationships with environmental variables all at once. Using environmental factors (such as ocean currents or sea surface temperature) and habitat-directed movements, individual based models (IBMs) might be used to further develop these methodologies by modelling long-term dispersion and survival probability. Studies of actual tracking might be used to parameterise models and compare them to real-world data [29,81].

While similar IBMs have been effectively used with other species (e.g., leatherbacks, [25,26]), they could be a good alternative to costly tracking studies and the scarcity of turtles of different ages for release with Caribbean green and head-started turtles. To the best of our knowledge, this research is the first Caribbean-wide attempt to monitor green sea turtles using biotelemetry over a range of juvenile ages. Although our tagging data has its limits, these findings nonetheless show that young green turtles may move about in different ways and might potentially find fruitful places along the beach much like their wild relatives. Our findings have substantial implications for both the present and the future of sea turtle tracking research and conservation initiatives. Future research involving the release of post-captive turtles should use caution when deciding when and where to release the animals. Given the under-representation of research using captive-reared (head-started) juveniles of other species in the domains of animal behaviour and movement ecology, we submit our results to serve as an example of how comparable methodologies might be used to such investigations.

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