



Bidirectional migration routes of *Chelonia mydas* from the northern Great Barrier Reef

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ABSTRACT

Understanding the full migration dynamics of highly migratory marine species is essential for effective conservation and management. In sea turtles, research has largely focused on one-way, post-nesting migrations, leaving key gaps in knowledge regarding return movements and overall route fidelity. This study investigated the route fidelity of Northern Great Barrier Reef (nGBR) green turtles (*Chelonia mydas*) by comparing outward migrations from foraging grounds to nesting sites with return migrations to foraging areas. Satellite tracking data from eight individuals were analysed using ArcGIS to map migration routes, with comparisons made based on migration distance, duration, and speed. Route overlap between outward and return journeys was quantified using a 5 km pairwise buffer analysis. Outward migrations to nesting beaches (mean: 372 ± 136 km) were significantly longer than return migrations (mean: 252 ± 28 km) ($P < 0.05$). Route overlap was low, ranging from 2 to 17%, indicating limited reuse of migration pathways. These findings demonstrate that in our study nGBR green turtles do not consistently use the same routes between foraging and nesting sites, suggesting more complex spatial behaviour than previously recognised. As conservation strategies increasingly emphasise the protection of migratory corridors, these results highlight the importance of accounting for variability in movement patterns and the potential for exposure to spatially diverse anthropogenic threats.

Keywords: Argos, biologically important areas, Fastloc-GPS, foraging, nesting, nesting foraging, roundtrip migration, satellite-tagging, sea turtle.

Introduction

Understanding the nuances of migratory patterns in marine megafauna, such as sea turtles, is crucial for effective management and conservation (Hays *et al.* 2019). The green turtle (*Chelonia mydas*) life cycle can be categorised through a series of migrations. Green turtle hatchlings migrate to the open ocean; juveniles migrate into coastal areas to establish foraging grounds; and adult green turtles migrate between these foraging grounds and their nesting beaches (Bowen *et al.* 1992; Read 2015) while displaying high fidelity to their respective adult foraging areas and their breeding sites (Shimada *et al.* 2020). These migrations, sometimes spanning vast oceanic distances, are vital to the species' reproductive success and long-term survival (Limpus 2009). However, many of the specific dynamics of these migrations remain understudied (Hays *et al.* 2021).

In recent years, with advancements in satellite tag technology and increased accessibility, we have started to unravel the secrets of these vast migrations (Jang *et al.* 2018; Kim *et al.* 2022; Mann *et al.* 2024). This technology enables continuous remote monitoring of animals across the globe through satellite systems (Mettler *et al.* 2019; Perez *et al.* 2022). Although satellite-based data can be received and transmitted only when tags are above water, it still suits some aquatic species, such as green turtles, that surface regularly to breathe, allowing frequent and accurate location acquisition (Baudouin *et al.* 2015; Metz *et al.* 2020). Satellite tracking has allowed researchers to analyse turtle movements in unprecedented detail, revealing high site fidelity to foraging grounds across a few years (Shimada *et al.* 2020; Al-Mansi *et al.* 2021; Webster *et al.* 2022), and long-term flipper-tagging studies have

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demonstrated fidelity to their respective foraging areas over decades (Queensland Turtle conservation database, unpubl. data). Of the many migrations undertaken by green turtles, their post-nesting migrations have been the most thoroughly studied (Troëng *et al.* 2005; Mettler *et al.* 2020; Barr *et al.* 2021). The increased study of post-nesting migration routes in Australia has sparked interest in protecting these migratory pathways using Biologically Important Areas (BIAs) (Commonwealth of Australia 2017). However, despite this initiative, bidirectional migrations remain poorly studied, and although loggerheads have been shown to follow different routes on each trip (Schofield *et al.* 2010), it is commonly implicitly assumed that turtles follow the same route in both directions.

One of the few studies focused on bidirectional migrations between foraging and nesting grounds in the United Arab Emirates demonstrated significant differences between the outward and return routes of three green turtles tracked (Pilcher *et al.* 2020). Pre-nesting migrations were typically longer and more circuitous (Pilcher *et al.* 2020). Other tracking or capture–mark–recapture studies have included bidirectional migrations and/or site fidelity, and even if not the primary focus of that research, they have sparked interest. Although limited by small sample sizes, these studies have also found substantial differences in the routes taken (Balazs *et al.* 2017; Dutton *et al.* 2018) and collectively highlight the need for additional research on bidirectional migrations. In Australia, although fidelity to foraging and nesting areas has been documented (Shimada *et al.* 2020), no studies to date have specifically compared the bidirectional migration routes between green turtles' foraging and nesting grounds.

This study explores bidirectional migration routes between foraging and nesting grounds used by green turtles from the nGBR genetic stock. This research addresses two key questions: (1) Do green turtles utilise the same migration route for each direction of their nesting migrations? And if not, (2) is there an overlap between the two paths?

Methods

Data preparation

A total of eight satellite tags containing bidirectional migrations were identified from various taggings placed on turtles in their foraging grounds in 2009 ($n = 3$), 2012 ($n = 2$) and 2018 ($n = 3$), containing a mix of Fastloc-GPS (hereafter GPS) ($n = 2$) and Argos ($n = 6$) tags. Attachment methods followed Shimada *et al.* (2012). The data from the eight tags were plotted in ArcGIS Pro ver. 3.3.0 to separate the migration location fixes from internesting and foraging data. Migration fixes were characterised as successive fixes that illustrate long-distance directional travel, distinct from internesting and foraging movements, which are both characterised by an aggregation of fixes (Christiansen *et al.* 2017; Shimada *et al.* 2020; Perez *et al.* 2022). Migration fixes were then further split into nest-to-forage migrations and forage-to-nest migrations.

The migration files were then combined into individual files by tag type (ARGOS or GPS) and migration type (forage–nest or nest–forage) and cleaned using the *SDLfilter* package in R ver. 4.41 (R Core Team 2024), which is designed to filter satellite-derived location data (Shimada *et al.* 2012). Low-quality locations were removed, retaining only locations derived from more than four satellites and with a residual error below 30 for GPS tags and locations with a location class of ≥ 1 for ARGOS (doppler shift locations) tags, which generally results in location accuracy of 10 s of metres and 100 s metres for GPS and ARGOS tags respectively (Dujon *et al.* 2014; Perez *et al.* 2022; Webster *et al.* 2022). Spatial and temporal duplicates were removed, along with biologically impossible locations. The latter were identified using a maximum travel speed threshold and individual turning angles estimated via maximum likelihood, following a well-established methodology for filtering tracking data (Shimada *et al.* 2012; Perez *et al.* 2022; Webster *et al.* 2022; Shimada 2023).

Migration routes

Spatial analyses were conducted using ArcGIS Pro 3.3.0, with specific functions described for each procedure, unless otherwise stated. Filtered migration data were plotted using the Point-to-Line feature tool. Migration metrics were then calculated for both directions of each route. Migration distances were computed using the Calculate Geometry function in GDA2020 MGA Zone 54. Duration was also determined using the date/time for each route associated with the migration start and end points. Migration speed (in km/day) was calculated as the total distance travelled divided by the migration duration. Interindividual mean and standard deviation were calculated for each of the three metrics: distance, duration and speed. Migration distances were exported for further analysis in R version 4.41 (R Core Team 2024). Because each turtle contributed measurements for both forage-to-nesting and nesting-to-foraging migrations, migration distance, duration and speed were analysed as paired observations. Normality of the within-turtle differences was assessed using Shapiro–Wilk tests. Paired *t*-tests were then used to compare the two migration directions. Given the small sample size, Wilcoxon signed-rank tests were also conducted as sensitivity analyses.

Route overlap

A 5 km buffer was applied to each migration track (to both sides) using the Pairwise Buffer tool in ArcGIS Pro ver. 3.3.0. This distance was selected based on previously used grid sizes (Pendoley *et al.* 2014; Shaver *et al.* 2016; Ferreira *et al.* 2020) to encapsulate location variation from the satellite tags while being narrow enough to be biologically meaningful. After applying the buffers, a spatial overlay was performed to remove any areas where the buffers overlapped land. This step ensured no buffer zones encompassed terrestrial areas, including mainland Australia and the surrounding islands. The Calculate Geometry feature was then used to calculate the area of each migration route (km²). The intersect tool was then used to

identify areas where each turtle's forage–nest (F–N) and nest–forage (N–F) routes overlapped. The area (km²) of the resulting overlap layers was calculated using the Calculate Geometry feature, and the percentage route overlap was then calculated from the calculated combined route area and overlap area.

Ethical approval

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Results

Migration routes

Of the eight tracked green turtles, six migrated from foraging grounds in the Torres Strait, and two migrated from foraging grounds in the GBR to Raine Island (Fig. 1). All eight turtles

began and ended their migrations in relatively similar areas, demonstrating fidelity to foraging areas.

F–N migrations covered significantly greater distances than N–F migrations, with a mean within-turtle difference of 120 km (Table 1) (paired *t*-test: *P* = 0.03). Mean migration duration was longer for F–N migrations than for N–F migrations (296.8 versus 250.3 h), but this difference was not statistically significant (paired *t*-test: *P* = 0.49). Mean migration speed was similar between F–N and N–F migrations (1.28 versus 1.25 km h⁻¹; paired *t*-test: *P* = 0.91). The greatest within-turtle difference in migration distance was 312 km (Table 1).

Migration corridors

The degree of overlap varied across tracks, ranging from 2 to 17%, with a mean overlap of 8.6% ± 4.6%. Overlap was observed to be concentrated primarily at the start and end points of each turtle's track (Fig. 2).

Discussion

This study documented bidirectional migrations of eight nGBR green turtles (*Chelonia mydas*), shedding light on the

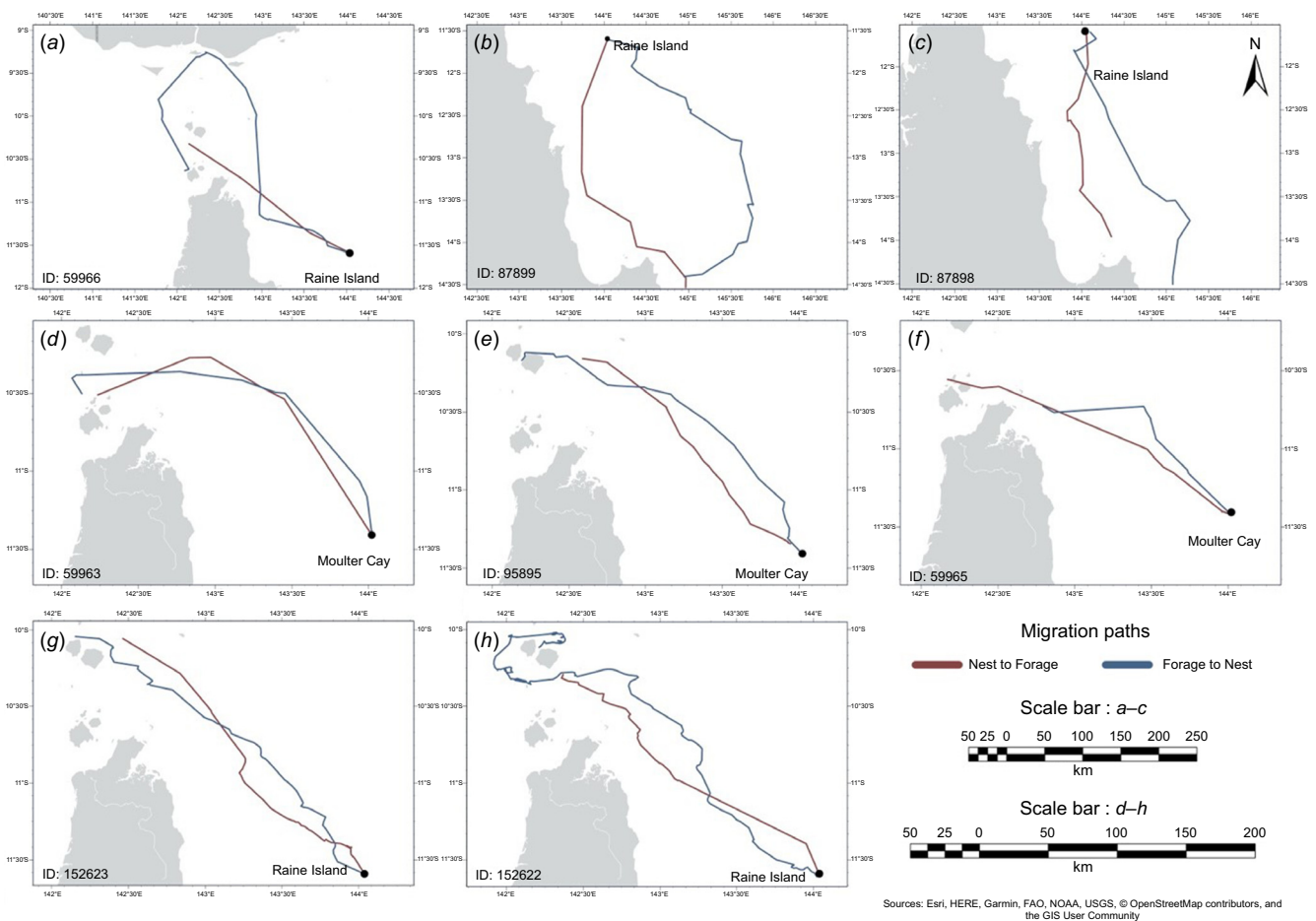


Fig. 1. Bidirectional migration routes of eight green turtles tracked from Raine Island in north-eastern Australia. Migration start location, F–N routes are depicted in blue and N–F routes and migration end location in red. Raine Island is marked in black.

Table 1. Individual migration characteristics for each of the eight tracked turtles.

Turtle ID	Distance (km)			Duration (h)			Speed (km/h)		
	F–N	N–F	Difference	F–N	N–F	Difference	F–N	N–F	Difference
59963	292.31	265.57	−26.74	200.99	392.96	+191.97	1.45	0.68	−0.78
59965	173.53	223.24	+49.71	129.11	155.86	+26.75	1.34	1.43	+0.09
59966	564.91	252.15	−312.77	389.14	199.08	−187.05	1.46	1.27	−0.20
87898	393.08	250.04	−143.04	304.78	218.08	−86.7	1.29	1.15	−0.14
87899	452.49	308.74	−143.75	369.57	598.50	+228.93	1.22	0.52	−0.71
95895	281.38	206.90	−74.48	399.80	144.20	−255.60	0.7	1.43	+0.73
152622	528.93	255.82	−273.11	348.32	168.90	−179.42	1.52	1.51	−0.01
152623	287.90	254.43	−33.46	233.03	125.19	−107.84	1.24	2.03	+0.80

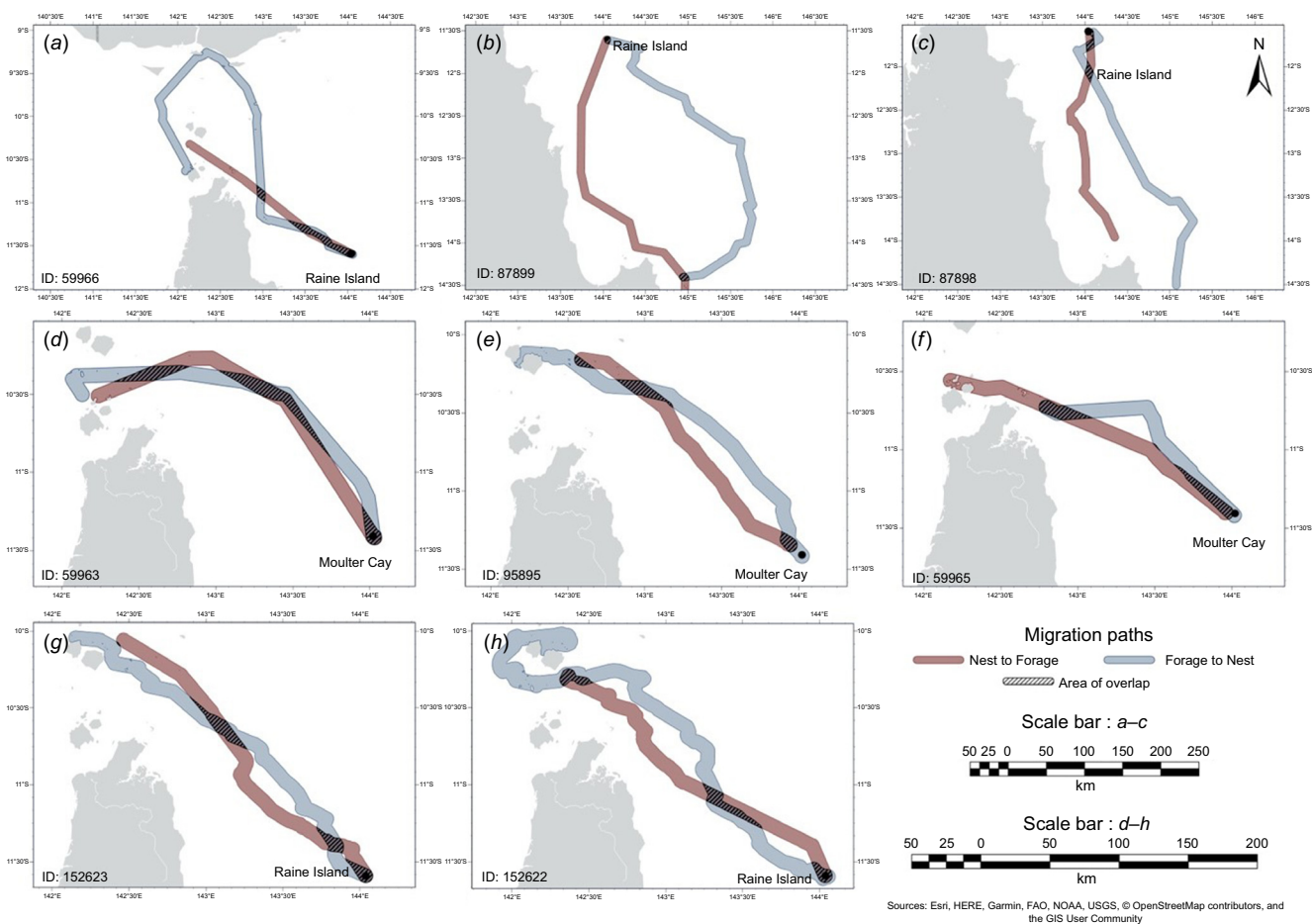


Fig. 2. Route overlap for the 5 km buffered migration routes of eight green turtles tracked from foraging grounds to Raine Island and back. F–N routes are depicted in blue, N–F routes in red, and areas of overlap are hashed. The area of overlap ranges from 2 to 17%.

variability of these pathways. Routes varied in both length and path similarity. Visually, forage-to-nest (F–N) and nest-to-forage (N–F) routes differed, with F–N routes being more irregular. F–N routes were also consistently longer than N–F routes, all in line with the limited body of published work on this topic (Balazs *et al.* 2017; Dutton *et al.* 2018; Pilcher *et al.* 2020). One previous study suggested that the variability in

length may be driven by turtles overshooting their nesting beaches during inbound migrations (Pilcher *et al.* 2020); however, this was not observed among the tracked turtles examined here. Given that the female must be inseminated at courtship before arriving at the nesting beach and given that courtship can occur at sites up to 200 km from an individual female’s nesting beach (Limpus 1993), the additional travel

via courtship to nesting sites may contribute to the irregularity and greater length and duration of the F–N migrations. Other potential drivers of variation could be energetic, with post-nesting turtles taking the most direct route back to their foraging grounds; however, navigation during migration is not exact, rather their map sense during migration likely has a resolution of 10 s to 100 s of km so environmental factors such as ocean currents, temperature, or resource availability are all likely to play a role (Morreale *et al.* 1996; Luschi *et al.* 2003; Hays *et al.* 2020; Pilcher *et al.* 2020).

Minimal overlap was observed among all tracked green turtles, with a significant proportion occurring at the migration's start and end points. This limited overlap reinforces findings from other studies (Balazs *et al.* 2017; Dutton *et al.* 2018; Pilcher *et al.* 2020) demonstrating significant differences in pre- and post-nesting routes. The documented spatial separation of outward and return migration routes further supports the idea that green turtles do not use the same routes for both directions of their migrations.

The findings of this study underscore the complexity of designing targeted management measures for highly migratory species such as green turtles. With increasing interest in using the Biologically Important Areas (BIAs) designation to protect turtle migration routes in Australia, our results suggest that more work is needed to ensure that protections do not neglect half of the migratory pathway when only tracks outward from nesting sites are used. The distinct differences between F–N and N–F routes highlight the need for conservation strategies that account for the dynamic nature of these migrations, rather than assuming a single pathway explains the entire migration. In the interim, BIAs are a valuable tool for identifying migratory pathways. Still, more work is needed to establish robust buffers along outward tracks to ensure migratory paths are optimised and used as effectively as possible.

Although our sample size exceeded that of previous studies comparing bidirectional migration routes, it remains relatively small. With a sample of only eight turtles, the specific pathways mapped are not widely generalisable, although they reflect the inherent differences in this migratory pathway. The limited data available in this study and in the existing literature indicate the difficulty of obtaining bidirectional migration datasets. Tagging turtles in their foraging grounds requires significantly more effort and higher costs than tagging on nesting beaches, with relatively lower reward (i.e. fewer turtles caught). Future studies could increase sample size to better assess variability in bidirectional migration routes. This may be achieved efficiently by selecting individuals preparing for the coming breeding season from their foraging areas, rather than randomly selecting individuals for satellite tracking (Limpus and Limpus 2001; Limpus *et al.* 2020). Vitellogenic females and spermatogenic males can be identified by laparoscopic (both sexes) or ultrasound (females) examination of the gonads (Limpus *et al.* 2020). An investigation into the drivers of these differences and potential temporal variability is necessary to fully understand the dynamics of this migratory pathway.

This study is one of the largest to date and the first to examine bidirectional migration routes in green turtles in Australia. Our findings reveal that green turtles use distinct routes for each leg of this migration, suggesting that bidirectional migrations are more complex than previously assumed. These results highlight the need for further research and more comprehensive bidirectional tagging efforts to fully understand the nuances of green turtle migration and ensure migration pathways are effectively protected in Australia.

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Data availability. Tracking data compiled in this study can be made available by request with permission from the individual data owners.

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