



Atlantic connectivity of a major green sea turtle *Chelonia mydas* foraging aggregation at the Banc d'Arguin, Mauritania

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ABSTRACT: Understanding population connectivity is paramount for effective conservation. While genetic tools have elucidated sea turtle migration patterns, notable data gaps limit our understanding of ocean-wide connectivity, especially regarding east Atlantic green turtles. We characterized the genetic composition of a globally important green turtle foraging aggregation at the Banc d'Arguin, Mauritania, incorporating data from 323 individuals captured between 2018 and 2021. Using extended mitochondrial DNA D-loop (738 base pairs [bp]) and mitochondrial short tandem repeat (mtSTR; ~200 bp) markers, we assessed the genetic structure of Atlantic green turtle foraging aggregations and estimated the most likely origin of immature green turtles from the Banc d'Arguin using mixed stock analyses (MSAs). We identified 6 D-loop haplotypes, with a clear dominance of CM-A8.1 (91.8%) followed by CM-A5.1 (6.3%) and 4 rare haplotypes: CM-A1.4, CMA6.1, CM24.1 and CM36.1. We found 13 mtSTR haplotypes, with '7-12-4-4' being dominant (89.0%). The genetic composition at the Banc d'Arguin differed significantly from the only foraging aggregation studied in West Africa to date — in the archipelago of Cabo Verde (located ca. 750 km from the Banc d'Arguin) — dominated by haplotype CM-A5. The MSA combining both genetic markers indicated that 87.6% of immature green turtles at the Banc d'Arguin originate from the major East Atlantic rookery at Poilão (Guinea-Bissau), but 11.6% come from more distant rookeries in South America (8.1%) and potentially Ascension Island (3.4%). We suggest that green turtle transatlantic movements may be more common than previously thought and highlight the importance of the Banc d'Arguin as a regional foraging hub for this species.

KEY WORDS: Sea turtles · Population genetics · Migratory connectivity · Dispersal · Foraging grounds · Mixed-stock analysis · mtDNA · Atlantic Ocean

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1. INTRODUCTION

Across different stages of their life cycles, migratory species often rely on multiple habitats that can span 100s to 1000s of km (Webster et al. 2002). They can be exposed to a wide range of threats that can vary geographically (Halpern et al. 2008), such that local conservation efforts may be insufficient to protect an entire population (Dunn et al. 2019). Understanding migratory connectivity between distant regions is thus essential to identifying threats and designing effective conservation strategies at a regional or trans-oceanic scale (Dunn et al. 2019), while also providing valuable insights into species' ecology and behaviour (Scott et al. 2014). Genetic tools have been instrumental in uncovering the movements and connectivity of marine migratory species of conservation concern, including cetaceans (Pomilla & Rosenbaum 2005), elasmobranchs (Sandoval Laurrabaquio-A et al. 2019), seabirds (Burg et al. 2017) and sea turtles (Carreras et al. 2011, Shamblin et al. 2012, Vargas et al. 2016, Chambault et al. 2018), enhancing our understanding of their ecology and vulnerability to human stressors.

Among these marine migrants, the green turtle *Chelonia mydas* is a globally distributed species, nesting on tropical, subtropical and warm temperate sandy beaches (Wallace et al. 2010). After emerging from their nests, post-hatchlings disperse in the open ocean and undertake a pelagic phase that lasts about 3–5 yr (Reich et al. 2007) before establishing in coastal feeding grounds when they reach a carapace length of approximately 25–45 cm (Musick & Limpus 1996, Bolten 2003, Patrício et al. 2014). The process by which juveniles select coastal habitats remains unclear. Prevailing oceanic currents may aid initial dispersal of post-hatchlings (Putman & Naro-Maciel 2013), yet small juveniles are capable of oriented swimming and do not behave as passive drifters (Putman & Mansfield 2015). Immature turtles may display ontogenic shifts among foraging grounds. These shifts can be linked to the exploration of different habitats (e.g. larger turtles using deeper waters; Brette et al. 2010) or to juvenile natal homing (i.e. larger juveniles establishing in foraging areas closer to their natal region), where turtles gradually move closer to their rookery of origin as they grow (Eckert et al. 2008, Meylan et al. 2011, Naro-Maciel et al. 2012, Hays & Scott 2013).

Most green turtle populations remain as neritic foragers for the rest of their lives, using shallow coastal feeding areas (but see Parker et al. 2011, Turner Tomaszewicz et al. 2018), but adults undertake cyclic reproductive migrations that can involve extensive

oceanic crossings (Hays et al. 2001). Juvenile dispersal and adult reproductive migrations thus frequently connect distant geographic locations, which are often under different jurisdictions and protection levels (Dunn et al. 2019).

Population genetic approaches can provide insights into this connectivity by comparing the genetic compositions of foraging and nesting aggregations. Since adult green turtles display natal homing (i.e. returning to their natal region to reproduce), nesting aggregations are often demographically isolated and genetically distinct (Bowen & Karl 2007, Lee et al. 2007, Naro-Maciel et al. 2012), although varying levels of interpopulation gene flow and common ancestry can result in deviations from this pattern (Naro-Maciel et al. 2014, Bourjea et al. 2015). Juvenile foraging aggregations, on the other hand, are typically composed of individuals originating from multiple nesting populations (i.e. mixed stocks; Bowen & Karl 2007). However, regional patterns of connectivity (Bolker et al. 2007, Godley et al. 2010, Patrício et al. 2017a) suggest some level of natal homing among subadults.

Previous population genetic studies suggest that the migratory connectivity of green turtles in the Atlantic is predominantly regional (Patrício et al. 2017a, Shamblin et al. 2017, Vásquez-Carrillo et al. 2020), agreeing with the 'closest to home' hypothesis wherein sea turtles recruit as juveniles to foraging grounds close to their natal rookeries (Bolker et al. 2007). Some studies, however, have found that green turtles—like their close relative, the loggerhead turtle *Caretta caretta* (Putman et al. 2012)—can perform transatlantic migrations during their early dispersal stage, recruiting to foraging grounds very far from their natal sites (e.g. Monzón-Argüello et al. 2010, Patrício et al. 2017b). Such long-distance movements imply a far more connected ocean. However, the extent of this basin-wide connectivity remains uncertain due to geographic data gaps and the limitations of available genetic markers in separating some populations (Patrício et al. 2017b). Genetic similarities between populations can indicate ongoing gene flow but can also result from the significant population expansion following the Last Glacial Maximum, resulting in the widespread distribution of similar mitochondrial lineages across the southern Atlantic and South Caribbean (Naro-Maciel et al. 2014).

Green turtle population connectivity has mainly been assessed using sequences of approximately 486 bp of the mtDNA D-loop region (within the mtDNA control region). Yet recent studies have found that extended mtDNA D-loop sequences (~800 bp) and, particularly, a marker of 4 'AT' short tandem repeats

(mtSTRs; ~200 bp) at the end of the mtDNA improve assignment resolution (Tikochinski et al. 2012, 2018, Shamblin et al. 2015, Barbanti et al. 2019, Karaman et al. 2022). Genetic characterization of data-poor regions with improved genetic markers is thus necessary to allow robust assessments of migratory connectivity and clarify the extent of transatlantic links. The origins of east Atlantic green turtle foraging aggregations located along the African coastal shelf are particularly poorly known, which limits our comprehension of Atlantic-wide connectivity.

The east Atlantic is home to one of the largest green turtle foraging aggregations globally, located at the Banc d'Arguin in Mauritania (Catry et al. 2023). Most of the Banc d'Arguin lies within the boundaries of the National Park of the Bank d'Arguin (PNBA in its French acronym), where sea turtles are fully protected by law and only the local Imraguen people are permitted to fish, using sailboats (Catry et al. 2023). Despite regulations in place, low levels of illicit local consumption and bycatch occur within the park, although the exact extent of these threats is challenging to assess (Hama et al. 2019). In a recent study combining satellite tracking and field assessments, the Banc d'Arguin was estimated to harbour approximately 150 000 green turtles, mostly (>90%) individuals of immature sizes (Catry et al. 2023). Satellite tracking has demonstrated that mature female and male green turtles that are resident at the Banc d'Arguin breed at Poilão Island, in the Bijagós Archipelago of Guinea-Bissau (Beal et al. 2022, Patrício et al. 2022, Catry et al. 2023). Considering this link with Poilão and the magnitude of this rookery (13 293 nesting females; Catry et al. 2023, Instituto da Biodiversidade e Áreas Protegidas unpubl. data), it is reasonable to assume that a large proportion of the immature green turtles foraging at the Banc d'Arguin also originate from this nesting population. However, the only other green turtle foraging aggregation studied to date in the West Africa region, located in the Cabo Verde archipelago (ca. 750 km southwest the Banc d'Arguin), was estimated to have stronger genetic links with nesting populations in Suriname than with Guinea-Bissau (Monzón-Argüello et al. 2010). Given the proximity of these foraging aggregations and the broader dispersal patterns of juvenile green turtles compared to adults (Hays & Scott 2013), other important source populations for the Banc d'Arguin green turtle aggregation cannot be dismissed.

Here, we assess the genetic composition of green turtles foraging in the Banc d'Arguin using 2 genetic markers: the extended mtDNA D-loop and mtSTRs. We compare the genetic diversity between immature-

sized turtles foraging in the Banc d'Arguin and other foraging aggregations across the Atlantic. Mixed stock analysis (MSA) is then used to estimate the source populations of immature green turtles foraging at this site, combining existing data from several major east, central and west Atlantic rookeries with novel genetic data from 3 Atlantic nesting sites: Poilão (Guinea-Bissau), Cayenne (French Guiana) and São Tomé island (São Tomé and Príncipe).

2. MATERIALS AND METHODS

2.1. Study site

The Banc d'Arguin is a large (ca. 10 000 km²) shallow marine area off the northern coast of Mauritania in West Africa, located approximately between Cap Blanc (20° 46' N, 17° 02' W) and Cap Timiris (19° 23' N, 16° 32' W; Fig. 1a). The vast majority of the Banc d'Arguin lies within a marine protected area, the PNBA, covering approximately 6000 km². The seabed is characterized by macroalgae and seagrass meadows of *Zostera noltei*, *Cymodocea nodosa* and *Halodule wrightii* (Chefaoui et al. 2021). Average sea surface temperature in the Banc d'Arguin is 20.3°C (ranging from 17.8° to 22.7°C). Its waters are turbid, limiting seagrass growth to depths up to approximately 4 m (Chefaoui et al. 2021).

2.2. Capture methods and sample collection

We conducted in-water captures at various locations in the Banc d'Arguin (Fig. 1a) between 2018 and 2021. Research permits were secured from PNBA authorities (details can be found in the Acknowledgements). Capture sites were identified by local fishers and previous satellite tracking data (Patrício et al. 2022). To capture turtles, a net (300–500 m long, 4 m deep, 32 cm half mesh size) was deployed from 1 or 2 lanches (traditional sailing boats operated by local Imraguen fishers), encircling turtles in a seine. The net was immediately removed from the water without any soaking time. Captured turtles were then processed on-board the fishing vessels. We collected epidermis samples (0.5 mm diameter) from the shoulder region of each turtle using a sterile scalpel blade disinfected with a diluted povidone–iodine solution. The samples were then stored in 96% ethanol inside uniquely labelled 2 ml screw-cap microcentrifuge tubes. To avoid double sampling and allow the possibility of detecting movements between foraging and breeding sites

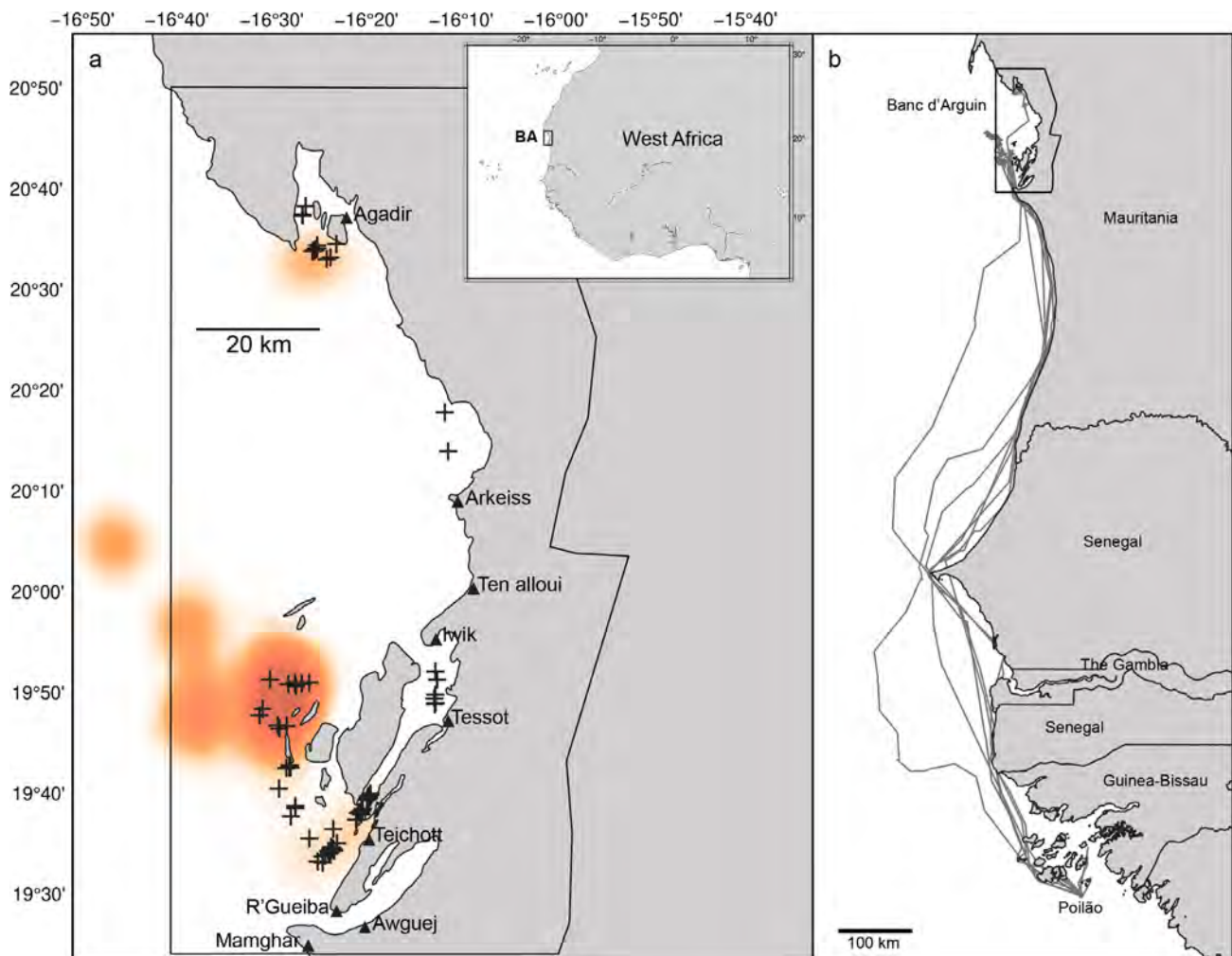


Fig. 1. (a) Banc d'Arguin, in northern Mauritania, with limits of the National Park of the Banc d'Arguin (PNBA, solid black line), villages within the park, capture locations of foraging green turtles *Chelonia mydas* (black crosses) and kernel density distribution of foraging adult green turtles (see Patricio et al. 2022). (b) Example of migration paths ($n = 7$; 2018) of adult female green turtles from their breeding ground at Poilão Island in Guinea-Bissau to the Banc d'Arguin (see Patricio et al. 2022 for tracking methods)

through mark–recapture, each turtle was tagged with inconel tags (NationalBand) on both front flippers. Additionally, their curved carapace length (CCL) was measured using a flexible measuring tape to the nearest 0.1 mm. Turtles were kept in the shade until processing, and handling was kept to a minimum (average 10 min ind.⁻¹). Each turtle was released near its capture location immediately after sampling.

In addition to the Banc d'Arguin, we also collected novel samples from 2 Atlantic green turtle rookeries: Poilão Island in Guinea-Bissau ($n = 118$) and Cayenne in French Guiana ($n = 25$). To minimize disturbance of nesting activity, these samples were collected while turtles covered the egg chamber, following the same protocol as above, and each turtle was flipper-tagged to avoid double sampling.

2.3. Laboratory procedures and haplotype assignment

We extracted DNA with the DNeasy Blood and Tissue Kit (Qiagen) following manufacturer's protocols. We then amplified 2 regions of the mtDNA control region with PCR: an ~800 bp fragment of the mtDNA D-loop (hereafter the extended D-loop) and an ~200 bp fragment of short tandem repeats of 'AT' (the mtSTR). For extended D-loop amplification, we used the primers LCM15382 and H950 (Abreu-Grobois et al. 2006). For mtSTRs, we used the primers CM-D-1 F and CM-D-5 R (Tikochinski et al. 2012). For both markers, the final reaction volume of the PCRs was 15 μ l, consisting of 3 μ l of deionized water, 7.5 μ l of Qiagen MasterMix, 0.75 μ l of forward primer

(10 μ M), 0.75 μ l of reverse primer (10 μ M) and 3 μ l of DNA. The annealing temperatures were 52°C for the D-loop and 56°C for mtSTRs. All PCR products (5 μ l) were purified with Exoprostar (2 μ l) using a single cycle of 37°C for 15 min and 80°C for 15 min. DNA extractions and PCRs were conducted at the laboratory of MARE-Ispa (Lisbon, Portugal), and PCR products were sequenced at Macrogen (Netherlands or Spain). D-loop sequences were aligned, truncated to the most common overlapping region (738 bp) and compared with haplotype sequences published in the database maintained by the Archie Carr Center for Sea Turtle Research (ACCSTR; <http://accstr.ufl.edu/>) using BioEdit v.7.2.5 (Hall 2011) and BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>). To score the mtSTRs, we counted the number of 'AT' repeats in each of the 4 loci described by Tikochinski et al. (2012). Haplotypes were named using the 4-number barcoding system. Following the standardized nomenclature for D-loop control region and mtSTR haplotypes is crucial to ensure comparability across studies. Detailed guidelines can be found on the ACCSTR website and in Tikochinski et al. (2012). In addition to the newly collected samples, we further amplified the mtSTR region from samples of green turtles from Poilão ($n = 171$; Patricio et al. 2017b) and from São Tomé, São Tomé and Príncipe ($n = 96$; Hancock et al. 2019), previously analysed for the extended D-loop marker.

As larger immature turtles may leave their distant developmental grounds to forage closer to their natal region (Eckert et al. 2008, Meylan et al. 2011, Hays & Scott 2013), subadults and adults can be more similar to nearby rookeries compared to juveniles. Thus, we tested for significant differences among Banc d'Arguin green turtles across size classes. To do so, we calculated pairwise genetic distances (F_{ST}) between juvenile, subadult and adult-sized turtles, followed by exact tests of differentiation. We used the most comprehensive data set of extended D-loop and mtSTRs pooled, and due to unclear relationships among mtSTR haplotypes and the potential for multiple mutation steps to lead to identical haplotype states, only frequency-based statistics were considered (Tikochinski et al. 2018, Karaman et al. 2022, Shamblin et al. 2023b).

The adult size class was defined based on the CCLs of nesting green turtles from Poilão Island (Fig. 1b), as satellite tracking showed that 50% of breeding females from this population forage in the Banc d'Arguin (Cтры et al. 2023). Following Stewart et al. (2007) and Phillips et al. (2021), we calculated the average minimum adult size (\bar{x} min) as 2 standard deviations below mean nesting female size (i.e. \bar{x} min

$= \bar{x} - 2SD\bar{x}$). Juvenile ($CCL \leq 65$ cm) and subadult ($CCL \leq 65$ cm) size classes followed a previous study in this foraging area ($65 \text{ cm} < CCL < 90 \text{ cm}$; Monteiro et al. 2021). To avoid bias when estimating the immature stock composition and allow comparisons with similar studies, turtles within breeding sizes were excluded from structure and MSAs.

2.4. Genetic structure of immature green turtle foraging aggregations in the Atlantic

We estimated the haplotype and nucleotide diversities of immature green turtles foraging in the Banc d'Arguin using Arlequin v.3.5.1.3 (Excoffier & Lischer 2010) and compared it to other immature foraging aggregations in the Atlantic. Given the scarcity of data available from green turtle foraging aggregations for the extended D-loop haplotype ($n = 12$ foraging aggregations), particularly for the East Atlantic ($n = 1$), we opted to also analyse the shorter D-loop haplotype (486 bp) uniquely for the structure analyses. This resulted in a sample size of 30 foraging aggregations. Genetic characterization with mtSTRs has only been published for one foraging ground to date (South Florida; Naro-Maciel et al. 2017); thus, structure analysis using this marker is not possible. To assess the genetic structure of Atlantic immature green turtle foraging aggregations, we calculated genetic distances (F_{ST} and Φ_{ST}) for the short and extended D-loop haplotypes and conducted exact tests of differentiation to determine whether distances were significant. A false discovery rate (FDR) correction was applied to find the most fitting threshold for the p-value significance, accounting for the number of multiple comparisons involved in the tests, under an expected original threshold of $p < 0.05$ (Narum 2006).

The R package 'gplots' (Warnes et al. 2016) was used in RStudio (RStudio Team 2020) to create heatmaps with dendrograms based on F_{ST} distances. Additionally, we conducted a spatial analysis of molecular variance (SAMOVA, in SAMOVA 2.0; Dupanloup et al. 2002) that groups foraging grounds based on geographical location and genetic composition. We obtained the coordinates of the foraging grounds from Google Earth and ran the SAMOVA with 100 simulated annealing processes. The resulting F_{CT} statistic was compared for different numbers of groupings (K , range: 2–30 for short D-loop haplotypes and 2–12 for extended D-loop haplotypes) to determine the optimum value for K , corresponding to the highest F_{CT} . We tested the significance of the resulting groupings with an AMOVA in Arlequin using 10 000 permutations.

2.5. Origin of immature green turtles from the Banc d'Arguin

We compared the Banc d'Arguin foraging aggregation with the rookery at Poilão using F_{ST} distances and our D-loop + mtSTR data set, to confirm that the former is indeed a mixed stock (rather than being uniquely from Poilão, the only significant nesting site within a radius of 3000 km). We then estimated the most likely origin of immature green turtles foraging in the Banc d'Arguin with 'many-to-one' MSAs, run in the BAYES program (Pella & Masuda 2001). 'Many-to-one' MSA estimates the contribution of multiple populations to a single mixed sample (i.e. the Banc d'Arguin). We ran MSAs using the extended D-loop and combining the extended D-loop and mtSTRs. Baseline data on extended D-loop and mtSTR haplotype frequencies of Atlantic nesting populations (Tables S1–S3 in the Supplement at www.int-res.com/articles/suppl/n054p365_supp.pdf) were obtained from the literature and added to our newly generated data from Cayenne in French Guiana, Poilão in Guinea-Bissau and São Tomé Island in São Tomé and Príncipe. Rookery size, defined as the number of nesting females per rookery, was used to establish weighted priors in one set of MSAs. We also ran the same MSAs without priors for comparison. Four independent Markov chain Monte Carlo (MCMC) chains were run for 500 000 iterations, with a burn-in period of 250 000. Lack of convergence of MCMC chains to posterior distribution was assessed with the shrink factor of Gelman & Rubin (1992), assuming that there was no evidence of non-convergence at values <1.2 (Pella & Masuda 2001). For the purposes of the MSA, the D-loop and mtSTR frequencies from Cayenne were assumed for the total number of nesting females in French Guiana.

3. RESULTS

3.1. Haplotype composition of green turtles from the Banc d'Arguin

We captured 323 green turtles foraging in the Banc d'Arguin, with CCLs ranging from 36.5 to 115.0 cm (mean \pm SD: 65.3 \pm 15.4 cm). The mean CCL of nesting females at the linked rookery of Poilão was 101.7 \pm 5.8 cm (range: 81.6–121.5 cm; n = 409) and the average minimum adult size (\bar{x} min) was 90.0 cm CCL (101.7 $- 2 \times 5.8$). Using this threshold, 9.6% of the turtles captured at the Banc d'Arguin were classified as adults. Of the remaining 90.4% of turtles classi-

fied as immatures, 57.9% were considered juveniles (i.e. CCL \leq 65 cm; Monteiro et al. 2021) and 32.5% were within the subadult size class (65 cm < CCL < 90 cm). Including all size classes, we identified 6 extended D-loop haplotypes from 304 green turtles within the Banc d'Arguin, with a clear dominance of CM-A8.1 (91.8%), followed by CM-A5.1 (6.3%) and 4 rare haplotypes (Table 1). For the mtSTR marker, we identified 13 different haplotypes in 296 individuals, with haplotype '7-12-4-4' being dominant (89.0%; Table 1). This dominant mtSTR haplotype was found in combination with 5 different D-loop haplotypes (Table 1). We were not able to identify the D-loop haplotype of 19 individuals or the mtSTR haplotype of 27 individuals due to the low quality of DNA.

The haplotype diversities (based on haplotype frequencies within samples) of Banc d'Arguin green turtles for the combined extended D-loop and mtSTRs were (mean \pm SD) 0.325 \pm 0.048, 0.270 \pm 0.060 and

Table 1. Frequency of mitochondrial DNA haplotypes per size class (adult sizes \geq 90 cm in curved carapace length) — D-loop and mitochondrial short tandem repeat (mtSTR) — of green turtles *Chelonia mydas* foraging in the Banc d'Arguin, Mauritania. 'No ID' means that it was not possible to identify the haplotype. Highlighted in **bold** are 3 individuals within adult sizes that had a combination of haplotypes only found to date in rookeries at >3000 km from the Banc d'Arguin

Genetic marker		Frequency per size class	
D-loop	mtSTR	Immature	Adult
CM-A1.4	7-8-4-4	1	0
CM-A5.1	6-12-4-4	2	0
	6-13-4-4	3	0
	6-14-4-4	1	0
	7-12-4-4	10	1
	7-13-4-4	1	0
	No ID	1	0
CM-A6.1	5-13-4-4	1	0
	7-7-4-4	1	0
	7-12-4-4	1	0
CM-A8.1	6-12-4-4	1	0
	6-13-4-4	1	0
	7-11-4-4	9	0
	7-11-5-4	3	1
	7-12-4-4	219	25
	7-13-4-4	5	0
	7-14-4-4	1	0
	7-16-3-5	1	0
	7-16-4-4	1	0
	No ID	10	2
CM-A24.1	7-12-4-4	0	1
CM-A36.1	7-12-4-4	1	0
no id	7-12-4-4	8	0
Total		282	30

0.206 ± 0.101, for the juvenile, subadult and adult size classes, respectively. There were no significant pairwise differences between these groups (juvenile × subadult: $F_{ST} = -0.004$, $p = 0.780$; juvenile × adult: $F_{ST} = -0.006$, $p = 0.551$ and subadult × adult: $F_{ST} = -0.012$, $p = 0.789$); regardless, subsequent structure analyses and MSAs use only the data set of immature-sized turtles to allow direct comparison with previous studies.

3.2. Genetic structure of immature green turtle foraging aggregations in the Atlantic

Haplotype and nucleotide diversities in the Banc d'Arguin were lower than other immature foraging aggregations in the Atlantic and significantly below the mean diversity indices both for the short and extended D-loop haplotypes (Table 2).

Using Φ_{ST} , there were no significant differences between the Banc d'Arguin and the Ubatuba and Uruguay foraging areas in South America when analysed with the short D-loop. When using the extended D-loop, no significant differences were found between the Banc d'Arguin and the foraging areas of Alagoas and Uruguay. When applying frequency-based genetic distances (i.e. F_{ST}), the Banc d'Arguin showed significant differentiation from all other Atlantic foraging areas (Fig. 2). See Tables S4–S7 for F_{ST} and Φ_{ST} values.

The SAMOVA considering short D-loop haplotypes separated the 30 foraging aggregations into 3 main groups ($F_{CT} = 0.739$, $p < 0.001$ for $K = 3$) — Group 1: southwest and east Atlantic; Group 2: Northwest Atlantic; and Group 3: Caribbean (Fig. 3). Two foraging aggregations located in the Caribbean fell outside Group 3: Puerto Rico was grouped with the northwest Atlantic, while Martinique was grouped with the southwest and east Atlantic. The AMOVA using this *a priori* grouping was highly significant ($F_{ST} = 0.754$, $p < 0.001$). We found similar results when considering the extended D-loop haplotypes (SAMOVA: same 3 groups, $F_{CT} = 0.757$, $p < 0.001$; AMOVA: $F_{ST} = 0.770$, $p < 0.001$).

3.3. Origin of immature green turtles from the Banc d'Arguin

Haplotype diversities were much higher in the Banc d'Arguin (0.295 ± 0.035), compared to Poilão (0.081 ± 0.022), and genetic distances between these sites were

highly significant ($F_{ST} = 0.027$, $p < 0.001$), supporting that this foraging aggregation is a mixed stock.

A total of 2217 sequences were included in the extended D-loop 'many-to-one' MSA, of which 410 are novel from this study (136 sequences from rookeries and 274 from the Banc d'Arguin). In the combined extended D-loop and mtSTR MSA, we included a total of 1799 sequences, of which 635 are novel from this study (375 from rookeries and 260 from the Banc d'Arguin). In the D-loop MSA, we included 16 rookeries as potential sources for the Banc d'Arguin foraging aggregation, while in the MSA with the D-loop and mtSTRs pooled, a total of 12 rookeries were included, as mtSTRs were not available for 4 rookeries (see Table 3 for the list of potential sources). Gelman-Rubin shrinkage factors were <1.2 for all stocks, confirming convergence of chains. The MSA based on extended D-loop haplotypes alone with population size as a prior estimated that the Poilão rookery was the most important source of immature green turtles foraging in the Banc d'Arguin, with a mean contribution of 91.4%, followed by Suriname at 7.6% (Fig. 4, Table 4). The MSA based on extended D-loop and mtSTR haplotypes combined, using priors, estimated a mean contribution from Poilão of 87.6%, followed by French Guiana with a mean contribution of 8.1% and Ascension Island at 3.4% (Fig. 4, Table S8). No significant differences were observed between the outputs of MSAs conducted with and without priors. For the D-loop MSA with no priors, the estimated contributions from Poilão and Suriname decreased by approximately 2 and 1%, respectively, while the estimated contributions from French Guiana and São Tomé each increased by approximately 1% (Table 4). In the MSA using combined D-loop and mtSTRs with no priors, changes were observed primarily for Ascension Island (decreasing from 3.4 to 2.3%) and São Tomé (increasing from ca. 0 to 1.2%; Table 4).

4. DISCUSSION

In this study, we used mtDNA markers to describe the genetic composition of a major West African green turtle foraging aggregation in the Banc d'Arguin, Mauritania. Interestingly, we found striking differences between the Banc d'Arguin and the only other West African foraging aggregation studied to date, in the Cabo Verde archipelago. A comprehensive 'many-to-one' MSA combining extended D-loop and mtSTR haplotypes revealed the origins of immature green turtles foraging in the Banc d'Arguin, highlighting the critical role of this site for the re-

Table 2. Haplotype diversity (h , mean \pm SD) and nucleotide diversity (π , mean \pm SD) of Atlantic green turtle *Chelonia mydas* immature foraging aggregations, assessed with the short (486 bp) and extended (738 bp) mitochondrial DNA D-loop haplotypes. n: sample size; hap: number of haplotypes, NA: not applicable (genetic marker not sequenced). The study population is shown in **bold**

Foraging grounds	Short D-loop (486 bp)		Extended D-loop (738 bp)		References				
	n	h	n	h					
Northwest Atlantic									
North Carolina, USA	106	12	0.729 \pm 0.030	0.005 \pm 0.003	NA	NA	Bass et al. (2006)		
Central eastern Florida, USA	62	6	0.486 \pm 0.067	0.003 \pm 0.002	NA	NA	Bass & Witzell (2000), Bagley (2003)		
South Florida, USA	138	15	0.715 \pm 0.030	0.005 \pm 0.003	138	21	0.751 \pm 0.032	0.004 \pm 0.002	Naro-Maciel et al. (2017)
Big Bend region, Florida, USA	177	10	0.682 \pm 0.024	0.004 \pm 0.002	177	15	0.723 \pm 0.026	0.003 \pm 0.002	Chabot et al. (2021)
St. Joseph Bay, Florida, USA	255	13	0.711 \pm 0.022	0.004 \pm 0.003	174	16	0.734 \pm 0.029	0.003 \pm 0.002	Foley et al. (2007)
Santa Rosa Island, Florida, USA	45	7	0.643 \pm 0.049	0.003 \pm 0.002	45	7	0.643 \pm 0.049	0.002 \pm 0.002	Shamblin et al. (2023a)
Port Fourchon, Louisiana, USA	127	10	0.554 \pm 0.041	0.002 \pm 0.002	127	13	0.584 \pm 0.041	0.002 \pm 0.001	Shamblin et al. (2023a)
South Texas, USA	382	16	0.537 \pm 0.025	0.002 \pm 0.002	168	10	0.576 \pm 0.032	0.002 \pm 0.001	Anderson et al. (2013), Shamblin et al. (2017, 2023a)
The Bahamas	560	23	0.612 \pm 0.021	0.006 \pm 0.003	NA	NA	NA	NA	Shamblin et al. (1998), Lahanas et al. (1998), Bjørndal & Bolten (2008)
Caribbean									
Culebra, Puerto Rico	103	10	0.680 \pm 0.040	0.008 \pm 0.005	103	17	0.834 \pm 0.023	0.007 \pm 0.004	Patrício et al. (2017a)
Guajira and Sta Marta, Colombia	43	7	0.729 \pm 0.041	0.011 \pm 0.006	42	6	0.715 \pm 0.041	0.008 \pm 0.005	Vásquez-Carrillo et al. (2020)
Barbados	60	8	0.773 \pm 0.028	0.010 \pm 0.006	NA	NA	NA	NA	Luke et al. (2004)
Martinique, French West Indies	40	6	0.674 \pm 0.064	0.008 \pm 0.005	NA	NA	NA	NA	Chambault et al. (2018)
Southwest Atlantic									
Almofala, Brazil	117	13	0.717 \pm 0.031	0.007 \pm 0.004	NA	NA	NA	NA	Naro-Maciel et al. (2007)
Rocas Atoll, Brazil	101	8	0.688 \pm 0.036	0.005 \pm 0.003	NA	NA	NA	NA	Naro-Maciel et al. (2012)
Fernando de Noronha, Brazil	117	12	0.650 \pm 0.028	0.004 \pm 0.003	NA	NA	NA	NA	Naro-Maciel et al. (2012)
Alagoas, Brazil	133	11	0.447 \pm 0.050	0.002 \pm 0.001	95	10	0.430 \pm 0.061	0.001 \pm 0.001	de Almeida et al. (2021)
Bahia, Brazil	45	6	0.648 \pm 0.053	0.002 \pm 0.002	NA	NA	NA	NA	Naro-Maciel et al. (2012)
Espirito Santo, Brazil	157	9	0.595 \pm 0.031	0.003 \pm 0.002	NA	NA	NA	NA	Naro-Maciel et al. (2012)
S.Francisco Itabapoana, Brazil	190	13	0.493 \pm 0.038	0.002 \pm 0.002	NA	NA	NA	NA	Jordao et al. (2017)
Ubatuba, Brazil	113	10	0.446 \pm 0.056	0.002 \pm 0.002	NA	NA	NA	NA	Naro-Maciel et al. (2007)
Parana, Brazil	285	12	0.498 \pm 0.032	0.002 \pm 0.002	NA	NA	NA	NA	Savada et al. (2021)
Arvoredo Island, Brazil	115	12	0.583 \pm 0.045	0.002 \pm 0.002	NA	NA	NA	NA	Proietti et al. (2012)
Cassino Beach, Brazil	101	12	0.586 \pm 0.050	0.003 \pm 0.002	NA	NA	NA	NA	Proietti et al. (2012)
Rio de la Plata, Uruguay	197	12	0.382 \pm 0.043	0.002 \pm 0.001	10	57	0.454 \pm 0.045	0.001 \pm 0.001	Prosdocimi et al. (2024)
Buenos Aires, Argentina	93	9	0.553 \pm 0.051	0.002 \pm 0.002	NA	NA	NA	NA	Prosdocimi et al. (2012)
Eastern Atlantic									
Canary Islands, Spain	17	3	0.588 \pm 0.062	0.004 \pm 0.003	NA	NA	NA	NA	Monzón-Argüello et al. (2018)
Cabo Verde	44	5	0.588 \pm 0.045	0.004 \pm 0.003	NA	NA	NA	NA	Monzón-Argüello et al. (2010)
Banc d'Arguin, Mauritania	274	5	0.157 \pm 0.029	0.000 \pm 0.001	274	6	0.157 \pm 0.029	0.001 \pm 0.001	This study
São Tomé and Príncipe	43	7	0.547 \pm 0.079	0.002 \pm 0.002	43	7	0.547 \pm 0.080	0.009 \pm 0.005	Hancock et al. (2019)

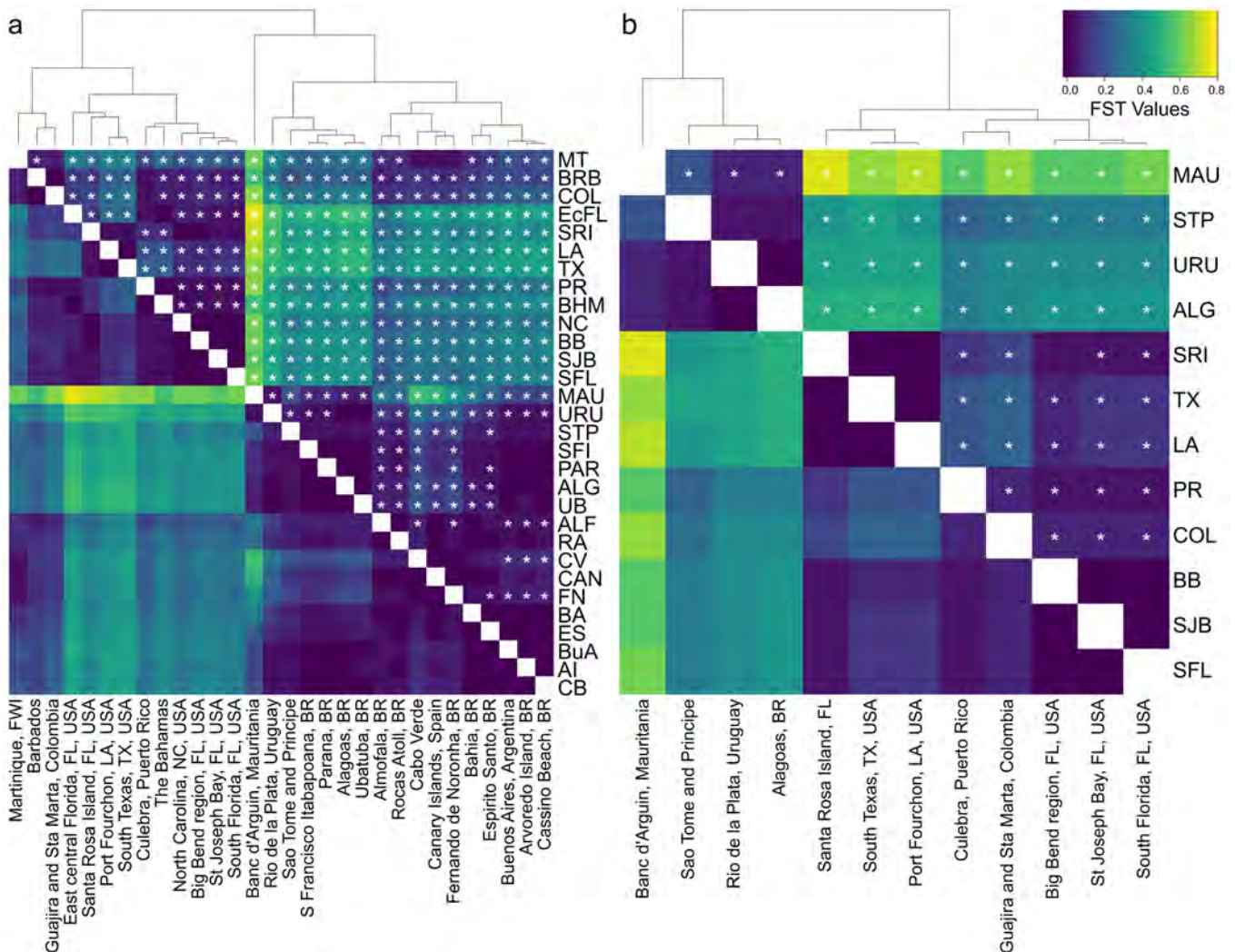


Fig. 2. Heatmaps and dendrograms based on F_{ST} pairwise distances between (a) 30 Atlantic green turtle *Chelonia mydas* foraging aggregations based on 486 bp sequences of the D-loop in the control region of the mitochondrial DNA (mtDNA) and (b) 12 Atlantic green turtle foraging aggregations based on 738 bp sequences of the D-loop in the control region of the mtDNA (extended D-loop). Dark purple: low F_{ST} values and therefore a low level of genetic similarity; yellow: high F_{ST} values and therefore a high level of genetic similarity. Asterisks in the top right diagonal indicate significant pairwise comparisons after false discovery rate (FDR) correction (Narum 2006), for an original significance value of $p \leq 0.05$: (a) 0.0075 and (b) 0.0105. The same F_{ST} values are shown in the bottom left diagonal without asterisks for ease of viewing. The acronyms on the vertical axis corresponds to the name of foraging grounds provided in full on the horizontal axis. BR: Brazil; FWI: French West Indies; US states are represented by their official abbreviations

gional conservation of green turtles and providing valuable insights into the Atlantic-wide migratory connectivity of this species.

4.1. Genetic structure among immature Atlantic green turtle foraging aggregations

Primarily comprising immature individuals, as reported in Catry et al. (2023), the green turtle foraging aggregation at the Banc d'Arguin presented the low-

est genetic diversity of all Atlantic immature foraging groups, consistent with the low genetic diversity of its main source rookery in Poilão, Guinea-Bissau. By contrast, mixed-stock groups on the west side of the Atlantic and in the Gulf of Guinea (São Tomé and Príncipe) likely exhibit greater admixture from several nearby rookeries with substantial numbers.

The Banc d'Arguin foraging aggregation was genetically different from all other Atlantic foraging aggregations when using F_{ST} , yet no significant differences were detected between this site and 2 South

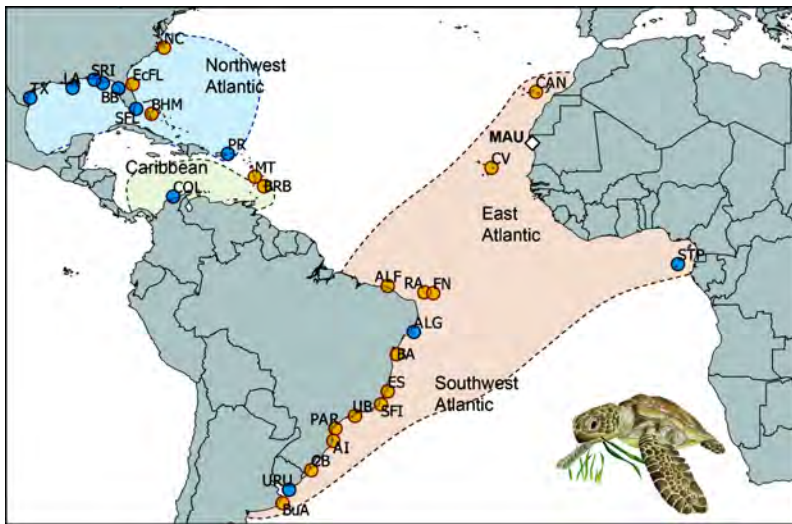


Fig. 3. Immature green turtle *Chelonia mydas* neritic foraging aggregations in the Atlantic Ocean genetically characterised only for the mtDNA control region short D-loop haplotype (486 bp); n = 18 (yellow circles) and for both the short and the extended mtDNA D-loop haplotype (738 bp), n = 12 (blue circles and white diamond). The study site is indicated by a white diamond and bold initials. Shaded areas with dashed lines broadly represent 3 genetic groups retrieved by spatial analyses of molecular variance using both haplotype groups; blue: Northwest Atlantic; green: Caribbean; brown: South-west and East Atlantic. See Fig. 2 and Table 2 for foraging site abbreviations

Table 3. List of Atlantic green turtle *Chelonia mydas* rookeries that were used in mixed stock analyses as putative source populations of the foraging aggregation in the Banc d'Arguin, Mauritania. For the mixed stock analyses, we considered that the haplotype frequency observed in Cayenne applied to all nesting sites in French Guiana, thus we used the total nesting female abundance

Rookery location	Short name	No. nesting turtles	Haplotypes	Source	
				Haplotype frequencies	Nesting population size
Northwest Atlantic					
Central East Florida, USA	CEFL	16305	D-loop + mtSTRs	Shamblin et al. (2020)	Seminoff et al. (2015)
South East Florida, USA	SEFL	9215	D-loop + mtSTRs	Shamblin et al. (2020)	Seminoff et al. (2015)
Dry Tortugas National Park, Florida, USA	DRT	390	D-loop + mtSTRs	Shamblin et al. (2020)	Seminoff et al. (2015)
Campeche and Yucatán, Mexico	EBCMX	4318	D-loop	Millán-Aguilar (2009), Shamblin et al. (2018)	Seminoff et al. (2015)
Caribbean Sea					
Southwest Cuba	CUB	2226	D-loop	Azanza-Ricardo et al. (2023)	Seminoff et al. (2015)
Tortuguero, Costa Rica	CR	131751	D-loop + mtSTRs	Shamblin et al. (2023b)	Seminoff et al. (2015)
Cayman Islands	CI	77	D-loop + mtSTRs	Barbanti et al. (2019)	Seminoff et al. (2015)
Aves Island, Venezuela	AV	2833	D-loop	Shamblin et al. (2012)	Seminoff et al. (2015)
Southwest Atlantic					
Matapica and Galibi, Suriname	SUR	13067	D-loop	Shamblin et al. (2012)	Seminoff et al. (2015)
Cayenne, French Guiana	FG	100	D-loop + mtSTRs	This study	Lasfargue et al. (2021)
All nesting sites: French Guiana		2682			
Rocas Atoll, Brazil	RA	275	D-loop + mtSTRs	Shamblin et al. (2015)	Seminoff et al. (2015)
Fernando de Noronha, Brazil	FN	70	D-loop + mtSTRs	Shamblin et al. (2015)	Seminoff et al. (2015)
Trindade Island, Brazil	TRI	2016	D-loop + mtSTRs	Shamblin et al. (2015)	Seminoff et al. (2015)
Ascension Island, UK	ASC	13417	D-loop + mtSTRs	Ascension Island Government, Conservation and Fisheries Directorate (unpubl.)	Weber et al. (2014)
Eastern Atlantic					
Poilão Island, Guinea-Bissau	GB	13293	D-loop + mtSTRs	Patrício et al. (2017b), this study	Catry et al. (2023), IBAP (unpubl.)
São Tomé Island, São Tomé and Príncipe	STP	376	D-loop + mtSTRs	Hancock et al. (2019), this study	Seminoff et al. (2015)

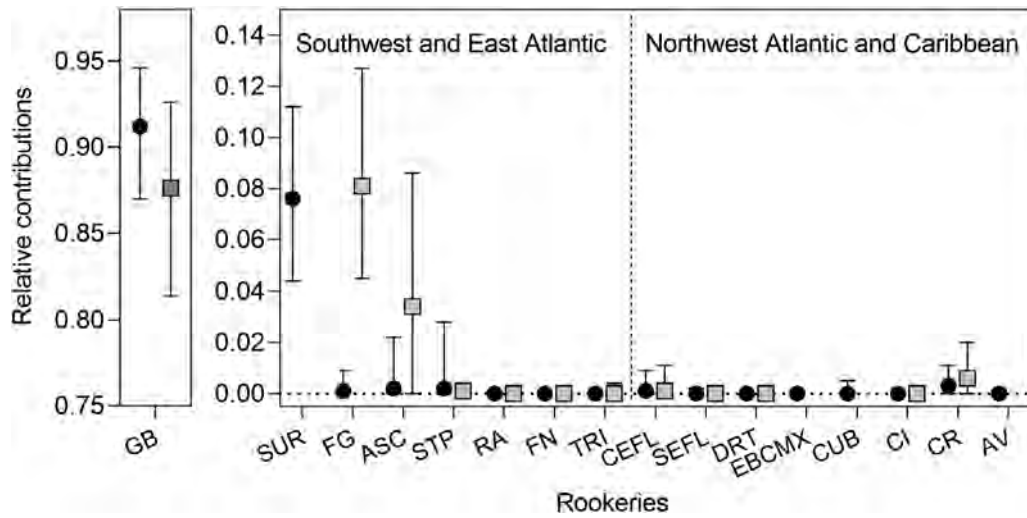


Fig. 4. Relative contributions from 16 Atlantic green turtle *Chelonia mydas* rookeries to the Banc d'Arguin foraging ground in Mauritania estimated using a 738 bp sequence of the mitochondrial DNA (mtDNA) control region (extended D-loop haplotype, black circles), and the combined extended D-loop and short tandem repeats (mtSTRs) haplotypes (grey squares). No mtSTR data is available for the following populations: SUR, EBCMX, CUB and AV, so the contribution of these populations was only assessed with one genetic marker. GB: Poilão, Guinea-Bissau; SUR: Matapica and Galibi, Suriname; ASC: Ascension Island, UK; FG: Cayenne, French Guiana; STP: São Tomé Island, São Tomé e Príncipe; TRI: Trindade Island, Brazil; RA: Rocas Atoll, Brazil; FN: Fernando de Noronha, Brazil; CEFL: Central eastern Florida, USA; SEFL: South east Florida, USA; DRT: Dry Tortugas National Park, Florida, USA; EBCMX: Campeche and Yucatán, Mexico; CR: Tortuguero, Costa Rica; CI: Cayman Islands; AV: Aves Island, Venezuela

Table 4. Estimated mean, maximum and minimum relative contributions of green turtle *Chelonia mydas* Atlantic rookeries to a foraging ground in the Banc d'Arguin, Mauritania, estimated through mixed stock analyses (MSAs) using either a single marker — the mtDNA extended D-loop (738 bp) — or a combination of 2 markers — the extended D-loop + the mtSTR (~200 bp). Each MSA was run (a) using population size as a prior and (b) without priors (all populations as equal in abundance)

Rookery location	— (a) Nesting population size as prior —						— (b) No priors —					
	D-loop			D-loop + mtSTR			D-loop			D-loop + mtSTR		
	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.
Poilão Island, Guinea-Bissau	0.914	0.946	0.871	0.876	0.926	0.814	0.895	0.940	0.833	0.875	0.925	0.812
Matapica and Galibi, Suriname	0.076	0.112	0.044				0.065	0.107	0.000			
Cayenne, French Guiana	0.001	0.009	0.000	0.081	0.127	0.045	0.008	0.078	0.000	0.080	0.125	0.044
Ascension Island, UK	0.002	0.022	0.000	0.034	0.086	0.000	0.002	0.020	0.000	0.023	0.076	0.000
São Tomé Isl., São Tomé and Príncipe	0.002	0.028	0.000	0.001	0.004	0.000	0.015	0.054	0.000	0.012	0.053	0.000
Rocas Atoll, Brazil	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.010	0.000	0.003	0.025	0.000
Fernando de Noronha, Brazil	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.046	0.000	0.001	0.007	0.000
Trindade Island, Brazil	0.000	0.000	0.000	0.000	0.004	0.000	0.001	0.006	0.000	0.004	0.028	0.000
Central eastern Florida, USA	0.001	0.009	0.000	0.001	0.011	0.000	0.001	0.007	0.000	0.001	0.009	0.000
South eastern Florida, USA	0.000	0.002	0.000	0.000	0.002	0.000	0.000	0.003	0.000	0.000	0.003	0.000
Dry Tortugas National Park, FL, USA	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.004	0.000
Campeche and Yucatán, Mexico	0.000	0.001	0.000				0.000	0.002	0.000			
Southwest Cuba	0.000	0.005	0.000				0.002	0.010	0.000			
Cayman Islands	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.004	0.000
Tortuguero, Costa Rica	0.003	0.011	0.000	0.006	0.020	0.000	0.000	0.004	0.000			
Aves Island, Venezuela	0.000	0.001	0.000				0.001	0.009	0.000	0.001	0.010	0.000

American foraging aggregations when using Φ_{ST} . This indicates that while haplotype frequencies are distinct in Banc d'Arguin compared to other foraging aggregations, the haplotypes found there share a recent evolutionary history with the South American

aggregations (Naro-Maciel et al. 2014). Additionally, our genetic structure analysis shows a regional affinity, indicating that the Banc d'Arguin clusters with the Southwest and East Atlantic groups. This clustering, driven by shared haplotypes such as CM-A5.1

and CM-A8.1, likely arises from similarities among Atlantic rookeries, attributed to common ancestry (Naro-Maciel et al. 2014, Reid et al. 2019), combined with contemporary hatchling dispersal and mixing across the Atlantic (Bolker et al. 2007, Jordao et al. 2017, Patrício et al. 2017b, Prosdocimi et al. 2024) and potential occasional deviations from natal homing (Bourjea et al. 2015).

The statistically significant genetic distance between the Banc d'Arguin and the nearest studied foraging ground in Cabo Verde's Boa Vista Island was a striking observation. This disparity arises from the much higher proportion of CM-A5 haplotypes—a trait from the Caribbean and Southwest Atlantic rookeries—found in Boa Vista turtles (52%; Monzón-Argüello et al. 2010) compared with that reported here (7%), a surprisingly large difference. With Cabo Verde being an offshore archipelago, it is potentially the first destination offering suitable foraging conditions encountered by pelagic juveniles during their eastward dispersal phase from rookeries located in the West Atlantic. A considerable time gap between the samples from Boa Vista (dating back to 2001, 2007 and 2008) and our samples (2018 to 2021), along with recent increases in several rookeries within the South Atlantic subpopulation (including Poilão, Guinea-Bissau, Broderick & Patrício 2019), could potentially contribute to the observed differences; linked to changes in contributions from source populations to these foraging aggregations (Hamabata et al. 2023). However, juvenile green turtles sampled in 2014 in the Canary Islands, another oceanic archipelago in the East Atlantic (located approximately 800 km northwest of the Banc d'Arguin), also exhibited a high proportion of the CM-A5 haplotype (47%; Monzón-Argüello et al. 2018). Thus, the substantial differences observed in the proportion of CM-A5 haplotypes between these sites seem to support a spatial rather than temporal pattern.

It will be relevant to reassess the genetic composition of some foraging grounds, namely that of Boa Vista Island, to detect any changes, preferably using the extended D-loop and mtSTRs combined to potentially improve resolution. It is also important to extend sampling efforts to encompass other foraging aggregations along the west coast of Africa, as this region has been historically underrepresented in genetic studies.

Notably, our sample does not reflect the complete range of sizes of foraging green turtles in the Banc d'Arguin. Smaller individuals ($29 < \text{CCL} \leq 35$ cm) have been found stranded (Catry et al. 2023). It is likely that smaller turtles managed to escape the seine nets due to the large mesh sizes, or they forage in different areas not sampled here. However, only 3% of the stranded turtles were within these sizes. Therefore, while future efforts at the Banc d'Arguin should aim to include smaller turtles, potentially by sampling freshly stranded individuals, their absence from our current sample does not raise significant concerns.

4.2. Atlantic-wide connectivity of West African green turtles

Previous tracking and tagging studies have demonstrated strong adult migratory connectivity between the Banc d'Arguin foraging ground and the regionally important breeding aggregation at Poilão Island rookery (Godley et al. 2010, Beal et al. 2022, Catry et al. 2023). The population genetic data presented here reaffirm this important migratory link, with ca. 88% of immature green turtles foraging at the Banc d'Arguin also estimated to have hatched at Poilão (Fig. 5). This is substantially higher than contributions of 50–75% to other immature foraging aggregations located along the Atlantic coast of Africa (i.e. Corisco Bay in Equatorial Guinea, Liberia to Benin, and São Tomé and Príncipe; Patrício et al. 2017b) estimated through many-to-many MSA using the short D-loop (486 bp). In addition, a very strong connectiv-

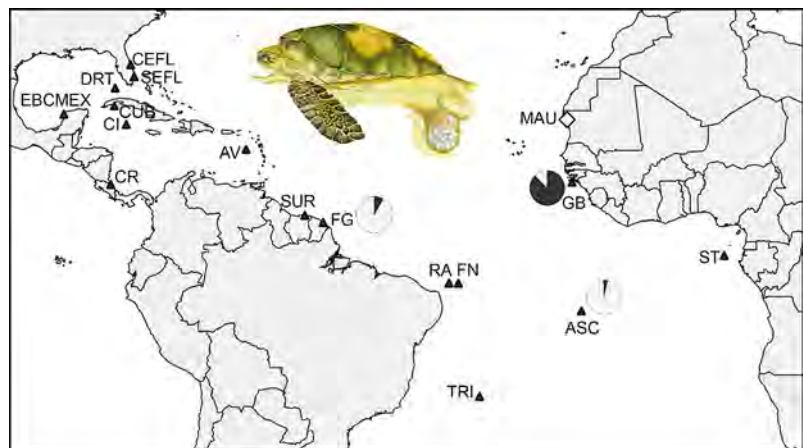


Fig. 5. Relative contributions of 16 green turtle *Chelonia mydas* nesting populations (black triangles) to a major foraging ground in the Banc d'Arguin, Mauritania (white diamond). Pie charts show in black the contribution of each rookery to the Banc d'Arguin. See Fig. 4 and Table 3 for rookery abbreviations

ity between Poilão and the Banc d'Arguin was also estimated through particle drift models (Putman & Naro-Maciel 2013).

The high proportion of juvenile turtles originating from Poilão is perhaps unsurprising given the large size and geographic proximity of this rookery (ca. 1000 km from the Banc d'Arguin) and provides some support for the 'closest to home' hypothesis. However, it is noteworthy that ca. 10% of immature green turtles foraging at the Banc d'Arguin were estimated to have originated from more distant rookeries located in the central and western Atlantic (Fig. 5), including Suriname (ca. 4300 km from the Banc d'Arguin), French Guiana (ca. 4200 km) and Ascension Island (ca. 3000 km). The dispersal of immature green turtles from west to east followed by recruitment at coastal waters of East Atlantic oceanic archipelagos was inferred by Monzón-Argüello et al. (2010, 2018) through genetic analyses and Lagrangian drifter data. Here, we find that it is highly likely that some of these turtles also recruit to neritic foraging grounds in mainland Africa. Using the mtSTR marker combined with the extended D-loop revealed a higher contribution from these distant rookeries, underscoring the value of utilizing diverse genetic markers to enhance migratory connectivity assessments. Particularly, with the mtSTR marker, the estimated mean contribution from Ascension Island increased from near 0 to 3.4%. This is because the mtSTR marker, combined with the predominant CM-A8.1 haplotype, allowed better discrimination of the rookeries of Poilão and Ascension Island. East-to-west dispersal of green turtles, from Poilão to foraging grounds in South America, has also been previously inferred using the short D-loop haplotype (Bolker et al. 2007, Jordao et al. 2017, Patrício et al. 2017b, Prosdocimi et al. 2024). Incorporating mtSTRs in future MSAs could improve estimates of relative contributions to these foraging sites, particularly from Ascension Island and Poilão.

There are some unresolved questions about Suriname's contribution, as mtSTR data from this significant rookery is missing. Most likely, the increase in the estimated relative contribution of French Guiana to the Banc d'Arguin when the combined D-loop and mtSTRs were used (from near 0 to 8.1%) is a direct result of the absence of Suriname's mtSTR data. In any case, our MSAs confirm that a substantial portion of the Banc d'Arguin's immature turtles originate from Suriname and/or French Guiana—2 nesting populations that are geographically proximate and have previously been shown to be genetically similar (Jordao et al. 2017).

It should be noted that as in previous studies (e.g. Proietti et al. 2012, Kynoch et al. 2022, Stahelin et al. 2022), our MSA estimates had large confidence intervals, indicating a degree of uncertainty in the exact contributions from each source population. These wide intervals likely stem from several factors; namely, an underrepresentation of potential source populations, considerable gene flow within regions of the Atlantic resulting in low genetic structure at smaller geographic scales and population mixing following the Last Glacial Maximum combined with a slow molecular evolution (Naro-Maciel et al. 2014). This lack of differentiation can make it difficult to distinguish between current and historical connectivity.

Future studies might benefit from increased sample sizes, inclusion of additional source populations, particularly from Suriname, as well as integration of other genetic markers such as mitogenomic SNPs and nuclear DNA. Mitogenomic single nucleotide polymorphism (mtSNP) sequencing has proven effective in revealing structure within dominant haplotypes (e.g. Shamblin et al. 2012, 2023a). Combining mtSTR and targeted mtSNP sequencing could significantly increase the likelihood of detecting fine-scale structural variations, especially within the CM-A8 haplotype group. Furthermore, as finer-scale genomic data becomes more accessible, it holds great potential to further refine our understanding of historical and current green turtle Atlantic-wide connectivity. Lastly, integrating genetic approaches with satellite tracking and tagging would greatly enhance the robustness of the findings.

4.3. Movements of larger turtles

Several previous studies have indicated that adult green turtles typically establish in foraging areas closer to their breeding grounds, abandoning their developmental feeding areas if these are too distant (Eckert et al. 2008, Hays & Scott 2013, Scott et al. 2014, Chambault et al. 2018). We thus expected that turtles within the adult sizes in our sample would have significantly lower haplotype diversities than juveniles, matching the closest source population of Poilão. This was not the case, and the 3 size classes (juvenile, subadult and adult) were not genetically different. Notably, 3 adult-sized turtles possessed a set of mtDNA haplotypes exclusively identified in more distant rookeries; namely, in São Tomé and Príncipe (CM-A8.1 '7-11-5-4'; female, 91 cm CCL), Ascension Island (CM-A24.1 '7-12-4-4'; male, 97 cm CCL) and Trindade and French Guiana (CM-A5.1 '7-

12-4-4'; female, 115 cm CCL). The latter was found nesting at Poilão Island 3 mo after being tagged and sampled in the Banc d'Arguin, indicating that despite extended sampling efforts, we have failed to identify some rare haplotypes in this rookery. To explore how results would be affected by incorporating this individual into the Poilão rookery database, we conducted an additional MSA for the combined extended D-loop and mtSTRs. The results revealed negligible differences, with less than 0.5% changes in estimated relative contributions from distant rookeries (Table S8). Another explanation for the remaining 2 unexpected observations would be that these turtles are large subadults that have not initiated their ontogenetic migration to adult foraging grounds, since green turtles can mature at a range of sizes, variable between and within populations (Phillips et al. 2021).

Alternatively, these could correspond to mature individuals undertaking longer reproductive migrations than the previously proposed threshold of 2850 km for hard-shelled sea turtles (Hays & Scott 2013). Compelling evidence from tagging data supports this possibility. Marcovaldi et al. (2000) recorded the recapture of a green turtle in Senegal, originally tagged (with metallic flipper tags) while nesting in Trindade Island of Brazil. This migration, exceeding 4000 km, evidences that some turtles breeding in the Southwest Atlantic use foraging grounds in West Africa. Transatlantic migrations between rookeries in Brazil and foraging areas in West Africa were also reported for olive ridley turtles (Santos et al. 2019). Thus far, no direct links between French Guiana, Suriname or Ascension Island nesting beaches and West African foraging grounds have been recorded in adult tracking or tagging data. Yet genetic data may exhibit greater sensitivity in detecting rarer migrations due to the larger sample sizes achievable through genetic analyses compared to traditional tracking studies.

4.4. Final considerations

This study demonstrated that the Banc d'Arguin is a vital developmental habitat for immature green turtles originating from the Bijagós archipelago of Guinea-Bissau. The PNBA of Mauritania and the biodiversity managing authority of Guinea-Bissau, the Instituto da Biodiversidade e das Áreas Protegidas, are already engaged in regional conservation efforts to protect this green turtle population, spurred by the adult migratory links identified through satellite tracking (Godley et al. 2010, Catry et al. 2023). Our findings are expected to strengthen ongoing re-

gional initiatives. Furthermore, other green turtle foraging grounds in West Africa, namely the Joal Fadiouth marine protected area (MPA) and the National Park of the Saloum Delta in Senegal, are also linked to Poilão through reproductive migrations (Beal et al. 2022, Patrício et al. 2022) but remain to be genetically characterized. It is likely that, as found here, most turtles in these foraging grounds originate from Poilão. Significantly, both the breeding sites at Poilão and the identified foraging locations in Mauritania and Senegal are part of a regional network of MPAs known as RAMPAO (Patrício et al. 2022), underscoring the importance of this network for sustaining this significant turtle population.

Furthermore, for the first time, this study established a genetic link between a neritic foraging aggregation in mainland West Africa and rookeries from South America and the mid-South Atlantic. These newly identified links will bolster future research partnerships and can potentially facilitate broader conservation efforts. Our results, along with previous work (Monzón-Argüello 2010, 2018, Patrício et al. 2017b, Chambault et al. 2018), suggest that transatlantic dispersal and possibly reproductive migration of green turtles may be more prevalent than previously believed. Considering the Banc d'Arguin foraging aggregation's numerical significance, comprising an estimated 137 442 immature green turtles (Catry et al. 2023), the relatively low mean contributions estimated for Ascension Island (ca. 3%) and French Guiana and Suriname (ca. 8%) translate into substantial numbers of immature individuals originating from each of these rookeries; 4123 and 10995 turtles, respectively. Thus, this site plays a significant role in supporting large numbers of turtles that will possibly recruit to these breeding populations.

This study emphasizes the importance of continuing the protection of the Banc d'Arguin foraging ground for regional turtle populations but also as a significant hub connecting Atlantic green turtles across large spatial scales. Sea turtles are integrally protected by Mauritanian law, and within the PNBA, strict fishing regulations are enforced (see Patrício et al. 2022). While the local Imraguen fishers historically consumed sea turtle meat, this practice has diminished to sporadic consumption for subsistence purposes, with no commercial trade. Significantly, the Poilão Island nesting population, with half of adults frequenting the Banc d'Arguin for foraging, has seen growth in recent times (Barbosa et al. 2018), signalling the effectiveness of conservation measures at these locations, despite considerable mortality linked to fisheries along the Mauritanian coast (Hama et al. 2019).

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