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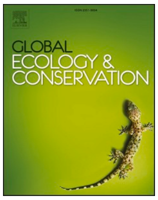

Little migrants: Assessment of stranded loggerhead turtles (*Caretta caretta*) source populations found in the north-east Atlantic

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ABSTRACT

Maritime activities affect the migratory routes of marine organisms, including loggerhead turtles (*Caretta caretta*). The coastal waters of mainland Portugal lie along these routes, providing foraging grounds but lacking nesting beaches, making them ideal for studying turtle migration. This study presents the first assessment of the natal origins of loggerheads in the North-East Atlantic. We analysed the genetic diversity of 127 stranded loggerhead turtles along the Portuguese coast, sequencing the mitochondrial DNA control region (776 bp). Sixteen haplotypes were identified, including a previously unknown one. Mixed-stock analysis revealed that loggerhead turtles stranded in Portuguese mainland coastal waters appear to originate predominantly from the Western Atlantic, with possible contributions from other regions including Cape Verde and the Eastern Mediterranean, though the latter remains uncertain. The primary sources were Florida rookeries, particularly Canaveral National Seashore, Melbourne Beach, Juno Beach, and Ft. Lauderdale. Our findings underscore the role of oceanic circulation patterns in shaping migration routes, as turtles predominantly followed major currents across the Atlantic. The predominance of juveniles among stranded individuals in areas with known high fishing pressure indicates that Portuguese waters may pose significant anthropogenic risks for this life stage. This study highlights the vulnerability of juvenile loggerheads in Portuguese waters and underscores the need for conservation strategies, including bycatch mitigation and fisheries management. Further ecological studies, such as tag tracking, are essential to understanding migratory patterns and improving conservation efforts in this critical migratory corridor.

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1. Introduction

There are seven marine turtle species worldwide, five of which can be found roaming the Atlantic (Avise and Hamrick, 1995). Although they have been essential to marine ecosystems for millions of years, six of the seven marine turtle species are currently listed as either critically endangered, endangered, or vulnerable due to human activities, while the flatback turtle (*Natator depressus*) remains data deficient (IUCN, 2015). The major threats to the survival of marine turtles in many parts of the world include diverse fisheries impacts (collision, accidental capture), direct take, loss of nesting habitats, diseases, and marine pollution (Mast et al., 2005; Nicolau et al., 2016a, 2016b).

The species exhibits strong natal homing behavior, with adult loggerheads typically returning to the general region of their natal beaches to nest, a phenomenon believed to be guided by geomagnetic imprinting (Lohmann et al., 2008; Lohmann and Lohmann, 2019). Migration patterns of loggerhead turtles are marked by long-distance movements across ocean basins, with some populations travelling thousands of kilometres from their natal beaches to reach specific foraging grounds (Foley et al., 2013).

The relevance of the species' migratory patterns and life cycles promotes the study of their original rookeries and migratory routes, which became an important element in their conservation. Because loggerhead turtles can migrate thousands of kilometres, using genetic markers to track their migratory patterns and understand population structures becomes crucial for conservation efforts (Bolker et al., 2003).

The Atlantic Iberian coast, particularly the Algarve region, located on the Portuguese southern coast, is considered a "high-use area", playing a central role in the feeding ecology of juvenile loggerhead turtles (Nicolau et al., 2016a, 2016b). Over a 36-year period (1978–2013), loggerheads accounted for 57 % of all sea turtle strandings in the region, making them the most frequently observed species. Stranding density for loggerheads was notably highest along the southern coast, with peaks during spring and summer (Nicolau et al., 2016a, 2016b). The waters surrounding the Iberian Peninsula are critical to loggerhead turtles due to two factors: (1) they contain upwelling zones that support epipelagic foraging opportunities for turtles (Cameron et al., 2019), and (2) they constitute a migratory corridor for the adjacent Mediterranean and the North Atlantic regions, both of which offer suitable habitats and productive foraging grounds (Bellido López et al., 2018; Carreras et al., 2006). The Portuguese continental waters encompass overlapping migratory routes from three main source regions of loggerhead populations - the Mediterranean (major nesting areas in Greece, Turkey, Cyprus, and Israel), the North West Atlantic (major nesting areas in the south-eastern United States and México) and the North-East Atlantic (major nesting area in Cape Verde) (Wallace et al., 2023). In the past decade, bycatch by artisanal fisheries has shown to be the leading cause of turtle mortality in the coastal waters of Portugal, especially in demersal long lines and passive gears (set nets-gill or trammel nets) (Nicolau et al., 2016a, 2016b). The absence of suitable nesting beaches in this area confirms that loggerheads foraging here originate from distant rookeries in the Mediterranean, the NW Atlantic and Cape Verde. This scenario offers a valuable opportunity to implement origin-tracing techniques to assess the natal origins of individuals in this foraging area.

Recent advances in satellite telemetry have revealed complex migration routes and site fidelity patterns among Atlantic loggerhead turtles (Evans et al., 2019; Goodwin et al., 2024). Notably, isotopic analyses corroborate telemetry-based findings, suggesting stable use of multiple foraging areas (Ceriani et al., 2023). Coupled with climate-driven dispersal models, these insights demonstrate that loggerhead juveniles are sensitive to shifts in ocean currents, potentially exacerbated by climate change (Patrício et al., 2021; Maglietta et al., 2024). Habitat suitability models forecast redistribution of loggerhead foraging areas under warming scenarios (Dellinger et al., 2022; Abalo-Morla et al., 2023). Moreover, integration of active swimming behavior with hydrodynamic models suggests turtles can partially counter passive drift, modifying predicted dispersal pathways (Quattrocchi et al., 2021). These findings emphasize the need to incorporate dynamic oceanography and ongoing climate variability when interpreting loggerhead juvenile dispersal and mixed stock compositions in the North Atlantic.

Differences in the haplotype frequency of the maternally inherited mitochondrial DNA (mtDNA) control region between sufficiently differentiated rookeries (baseline data) can be used to estimate the natal origins of individuals in mixed feeding aggregations (Clusa et al., 2014; Encalada et al., 1998; Karaa et al., 2016). Mixed stock analysis (MSA) provides a statistical framework to infer the proportional contributions (not individual assignments) of source populations to such aggregations based on haplotype frequency distributions. Initially developed for general applications in migratory species and fisheries (Jensen et al., 2016; Leroux et al., 2012), it yields population-level estimates with associated uncertainty. In loggerhead turtles, MSA based on mtDNA control region sequences has been widely used to assess stock composition across multiple regions, revealing trans-Atlantic connectivity and foraging ground use (Bolker et al., 2003; Bolten et al., 1998; Shamblin et al., 2014). Numerous studies have successfully applied this approach to trace loggerhead population origins in regions of high turtle activity (Engstrom et al., 2002; LaCasella et al., 2013; Loisier et al., 2021; Rankin-Baransky et al., 2001; Stewart et al., 2019; Tolve et al., 2018; Turkozan et al., 2018). These findings support the hypothesis loggerheads, upon reaching sufficient maturity, are capable of trans-Atlantic migration, navigating through the Gibraltar Strait to the North Atlantic (Bellido et al., 2009; Clusa et al., 2014).

This study aims to determine the putative natal origin of stranded loggerhead turtles found along the Portuguese mainland coast. Understanding the demographic parameters of sea turtle populations, which are critical for assessing their status and trends, may be affected by individual foraging preference areas. Individuals who regularly visit these areas face heightened risks if these areas are subject to significant anthropogenic pressure. To investigate, we sequenced 127 samples of stranded loggerhead turtles in the Portuguese coasts for a fragment of the mtDNA control region. Our objectives were to characterize these individuals' haplotype composition and determine their natal origins, contributing to knowledge about the populations frequenting the Portuguese coastal waters.

2. Materials and Methods

2.1. Sample collection and laboratory procedures

Samples were obtained from an agreement between the Portuguese Marine Animal Tissue Bank (MATB) and the Centre for Marine Sciences (CCMAR). Over 10 years (2008–2017), 194 loggerhead tissue samples were collected from stranded turtles (Supplementary Material S1) by the regional stranding networks operating along the Portuguese coast (Fig. 1). For each individual, information on the date, place of sampling, cause of stranding and tissue condition was recorded. Sex was not determined, but both curved carapace length (CCL) and straight carapace length (SCL) measurements were collected. To divide turtles into stage classes, we used the SCL recommendations in the 2009 TEWG report (Turtle Expert Working Group) as a guideline. We divided turtles into two main categories:

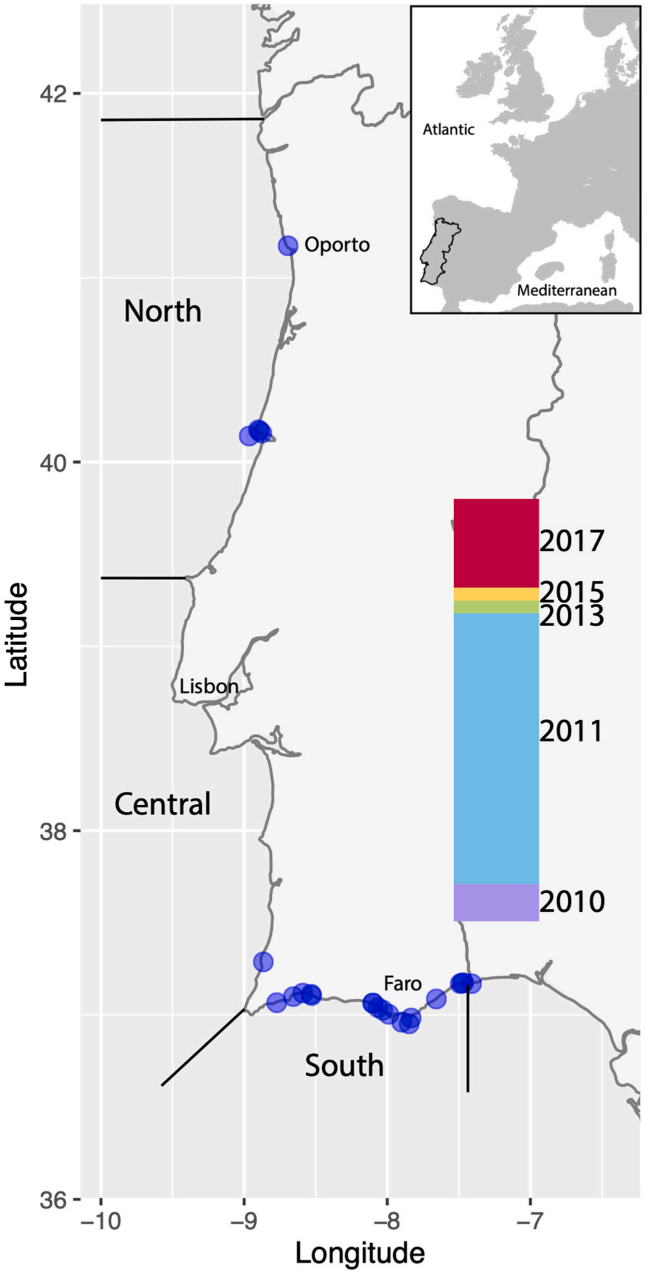

Fig. 1. Maps showing *Caretta caretta* strandings along the Portuguese coast and the annual distribution of strandings. Inset, displays Portugal's location in Europe. Colored bar indicates proportion of individuals recorded in each year. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

small turtles (≤ 63 cm), including first years, oceanic juveniles and juveniles that may alternate between oceanic and neritic habitats and large turtles (> 63) (including larger juveniles alternating between oceanic and neritic habitat, and adult turtles in both habitats). Skin biopsies were taken from all dead turtles. Tissue samples were preserved in 70 % ethanol at 4 °C.

According to manufacturer instructions, DNA extraction from the muscle tissue was done using the Qiagen DNeasy Blood & Tissue Kit (QIAGEN GmbH, Hilden, Germany). The ~800 base pairs of the mitochondrial control region (CR) were amplified using primers LCM-15382 (5′ - GCTTAACCCTAAAGCATTGG - 3′) and H950g (5′ - GTCTCGGATTTAGGGGTTTG - 3′) (Abreu-Grobois et al., 2006). PCRs were conducted on Biometra thermocycler, using the following cycling parameters: 3-min denaturation at 94 °C, followed by 30-s denaturation at 94 °C, 30-s annealing at 50 °C, and 1-min extension at 72 °C for 35 cycles and ending with a final extension at 72 °C for 10 min. PCR volumes of 25 µl included 1 µl of genomic DNA, 0.2 mM (=0.5 µl) dNTPs (Promega, Madison, WI, USA), 1 U (=0.2 µl) GoTaq polymerase (Promega, Madison, WI, USA), 5 mM de Gotaq Buffer (5x) (=5 µl), 1.5 mM (=1.5 µl) MgCl2 and 10 pmol (=0.5 µl) of forward and reverse primers. Negative controls were run alongside positive samples to identify contamination from the extraction step. PCR products were visually verified using 2 % agarose gels with GelGreen®.

Samples were precipitated before sequencing, using 10 µl Sodium acetate 3 M in a volume of 100 µl, containing 20 µl of our PCR product. After two steps of mixing with Ethanol (100 % on the first step and 70 % on the second) and high-speed centrifugation, we eluded the dry pellet with miliQ H_2O. Only forward strands were cycle sequenced using an ABI ® Big Dye Terminator v3.1 or a v3.1 ABI Prism Terminator Cycle Sequencing Kit and evaluated with Applied Biosystems ® (models 3130 and 3730) automated genetic analysers (Foster City, CA, USA) at CCMAR.

2.2. Data analysis

Raw sequence chromatographs were edited and aligned in Geneious Prime (Biomatters, New Zealand (https://www.geneious.com) using MUSCLE version 3.6 (Edgar, 2004) with default values selected and visually verified. Sequences were cropped at a standard cropping site of 776 bp (Abreu-Grobois et al., 2006). We also trimmed sequences to 380 bp to match the short mtDNA control region fragment (Norman, 1994). We also compared sequence diversity parameters to values reported for *C. caretta* in the earlier studies.

Haplotypes were assigned by comparing sequences from the samples to a reference library of long 776-bp haplotypes of published loggerhead sequences from the Atlantic and Mediterranean, using the standardised nomenclature of the Archie Carr Center for Sea Turtle Research (https://accstr.ufl.edu/resources/mtdna-sequences/). Haplotype network was constructed using the minimum-spanning algorithms (Bandelt et al., 1999) in PopART v.1.7 (Leigh and Bryant, 2015).

The standard measures of genetic diversity were computed separately for the primary location sites. We used *pegas* R-package (Paradis, 2010) to estimate standard descriptive measures of genetic diversity, including the number of haplotypes and private haplotypes, haplotype diversity (h) and nucleotide diversity (π) (Saitou and Nei, 1987) and respective standard deviations.

To estimate the contribution of each origin region to the sampled stock, we used a Bayesian many-to-one MSA approach (Pella and Masuda, 2001), implemented via the mixstock R package (Bolker et al., 2007). For each dataset, we ran as many parallel MCMC chains as source populations (e.g. dataset 1, three source populations, three chains; dataset 2, six source populations, six chains), primarily to facilitate convergence diagnostics across different data partitions. While this is not a methodological requirement, it provided practical transparency in assessing model behavior. Each chain was run for 2,000,000 iterations, with 100,000 of the iterations discarded as burn-in. Convergence of the MCMC chains was evaluated using the Gelman–Rubin shrink factor, with all parameter estimates exhibiting values below 1.2, indicating adequate convergence. Simulated mixture data were generated using the simmixstock2 function from the R-based mixstock framework (Bolker et al., 2007), which creates mixture datasets based on user-specified haplotype frequencies, source sizes, and sampling parameters. Simulations were based on the number of nests reported in published assessments of loggerhead rookeries. Specifically, nesting abundances for the Western Atlantic and Gulf of Mexico were drawn from Stewart et al. (2019), while estimates for other Atlantic and Mediterranean rookeries were compiled from Shamblin et al. (2014), which synthesized nesting data across a broad geographic range to support MSA and stock structure modeling. Two dataset configurations were used to explore source contributions: Dataset 1 grouped the primary source regions into the Eastern Mediterranean (EMED), Cape Verde (CAP), and Western Atlantic (WAT), which included all western rookeries—comprising the U.S. east coast, Gulf of Mexico, Mexico, Bahamas, and Brazil and Dataset 2 subdivided these regions into finer subunits: Eastern US (EUS), the Bahamas (BAH), the Gulf of Mexico (GME), the Brazilian coast (BRA), the Cape Verde (CAP) and the Eastern Mediterranean which holds all Mediterranean rookeries (EMED). Dataset 1 served as the primary model, satisfying the key assumption that all significant contributing rookeries are included while datasets 2 disaggregated the Western to assess finer-scale contributions within that basin.

3. Results

3.1. Sampling information

Of the 194 loggerhead turtles sampled from strandings, 163 individuals (84 %) were found along the Southern coast of Portugal. Length measurements were recorded for 185 turtles, revealing that 170 were juveniles with CCL ranging from 22.0 to 63 cm, while 15 were adults, the largest measuring 83 cm. Annual strandings fluctuated across the study period (2008–2017), peaking in 2011 with 88 recorded turtles and declining to a low of one turtle in 2008 (Fig. 1).

3.2. Mitochondrial haplotypes

Long fragments of 776 bp were obtained from 127 individuals (9 adults, 114 juveniles, and 4 of unknown age). The overall nucleotide diversity was 0.022 (± 0.001), and the haplotype diversity was 0.739 (± 0.027). We identified 16 different haplotypes (Fig. 2). The most common haplotype was CC-A1.1 (N = 53), the most prevalent Atlantic haplotype of *C. caretta*, primarily found along the Eastern US coast and the Gulf of Mexico. The second most abundant haplotype was CC-A2.1 (N = 34), the most common haplotype in the Mediterranean Sea. The third haplotype identified was CC-A1.3 (N = 16), predominantly seen in Cape Verde rookeries. Haplotypes CC-A3.1 and CC-A14.1 were found in nine and four individuals, respectively, while the remaining haplotypes were singletons. One new haplotype detected in one individual differed from CC-A1.1 for one T-to-G transversion at nucleotide site 15,699 of the published *C. caretta* mitochondrial genome sequences (ACCN FR694649, KP256531 and NC_016923). The new haplotype was submitted to the ACCSTR (and named A76) and to GenBank (PV593174). The new haplotype was not considered in the MSA as its rookeries of origin have yet to be identified.

For the network analysis, 217 sequences previously published by Shamblin et al. (2014) and Splendiani et al. (2017) were added to our dataset. These sequences represent 57 haplotypes of the long mtDNA control region fragment and include samples from both Atlantic and Mediterranean nesting rookeries.

The parsimony network we built for the control region with minimum spanning distance (Fig. 2) indicated two main haplogroups (nomenclature according to Shamblin et al., 2014) that mainly represented geographic groups. Haplogroup IB, clustered around CC-A1.1, included a majority of Atlantic haplotypes, and haplogroup II, clustered around CC-A2.1, encompassed haplotypes from the Atlantic Ocean and the Mediterranean Sea. Haplogroups II and IB are separated by 26 substitutions.

3.2.1. Mixed stock analysis

The MSA of the relative contribution of three main regions (Western Atlantic, Cape Verde and Eastern Mediterranean Sea) to the turtles found in Portuguese waters exhibited a shrink factor equal to 1 (according to the mixstock manual - http://shorturl.at/pBCOQ, the Gelman-Rubin criterion should be below 1.2 for all parameters for the chain to be judged to have converged properly) and narrow confidence intervals. While dataset 1 provides the most robust and comprehensive estimate by incorporating all major population sources grouped into three regions, while the additional dataset 2 disaggregates the Western Atlantic components allowing a finer resolution of contributions within that region. The analysis showed a substantial difference between the large ($p = 0.82$, 95 % CI = 0.59–0.93) contribution estimates of Western Atlantic rookeries, Cape Verde rookeries ($p = 0.12$, 95 % CI = 0.06–0.26) and Eastern Mediterranean rookeries ($p = 0.06$, 95 % CI = <0.01–0.25) based on simulated mixtures reflecting source population sizes. The wide confidence interval for the Eastern Mediterranean, including values near zero, suggests a high degree of uncertainty in the contribution, and it should therefore be interpreted cautiously (Fig. 3A, and Supplementary Material S2). The following analysis, albeit with very wide confidence intervals, allowed us to pinpoint specific contributions in each major geographic region. According to the MSA with priors weighted by population abundance within the Western Atlantic, the Gulf of Mexico had the highest contribution ($p = 0.69$, 95 % CI = <0.01–0.86) (dataset 2, Fig. 3B, and Supplementary Material S2).

4. Discussion

Before interpreting the biological implications of our results, it is important to acknowledge a methodological limitation. As with

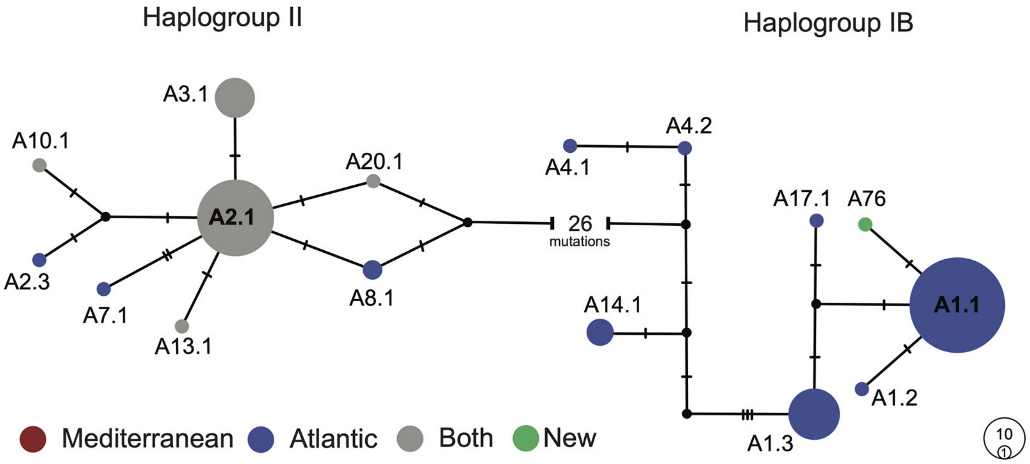

Fig. 2. Haplotype network obtained for the long fragment of the control region for 127 individuals of *Caretta caretta*. Each sequenced haplotype is represented by a circle, the size of which is proportional to its overall frequency in the dataset (Supplementary Material S1). Black lines on the branches indicate the number of mutational changes between two different haplotypes. Haplotype colours correspond to the sampling localities annotated on the legend. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

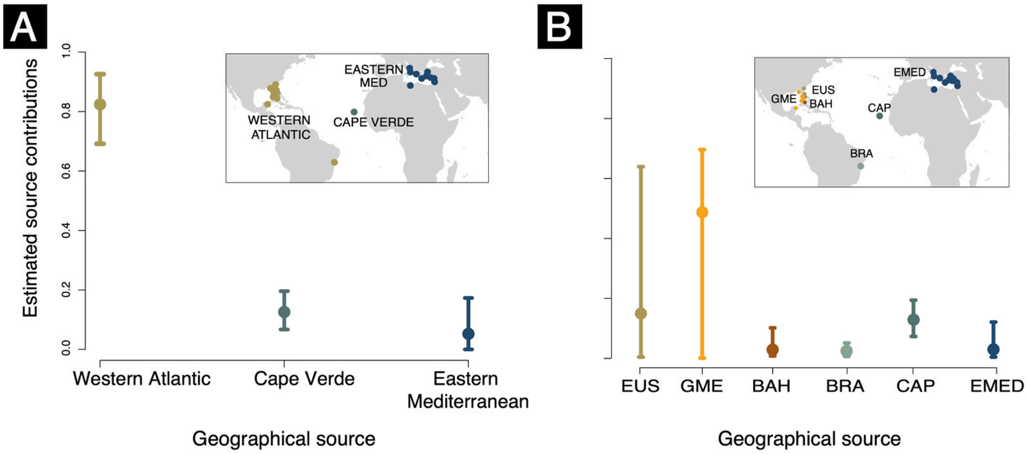

Fig. 3. Estimated proportional contributions of nesting rookeries to the Portuguese foraging aggregation based on mixed stock analysis (MSA) using four datasets. (A) Dataset 1: grouped contributions from Western Atlantic, Cape Verde, and Eastern Mediterranean rookeries. (B) Dataset 2: disaggregated contributions from major regional subunits. Confidence intervals (95 %) are shown for each estimate. Dataset 1 provides the most comprehensive model including all major source regions. Notably, the estimated contribution from the Eastern Mediterranean in Dataset 1 includes a wide confidence interval extending nearly to zero, indicating substantial uncertainty; this contribution should be interpreted with caution.

all mtDNA-based MSA approaches, our estimates reflect population-level probabilities and do not permit the assignment of individual turtles to specific rookeries, due to the widespread sharing of haplotypes among populations. The present contribution is particularly valuable since no prior data were available for the Southern Portuguese Coast in the Northeastern Atlantic Ocean, a region lacking local rookeries and hosting only foraging individuals. Our mixed-stock analysis reveals that loggerhead turtles stranded in Portuguese mainland coastal waters have diverse geographic origins at least from Western Pacific and Cape Verde. Our mixed-stock analysis reveals that loggerhead turtles stranded in Portuguese mainland coastal waters have diverse geographic origins. The primary estimated contribution is from the aggregations of the Western Atlantic Ocean (82 %). While our results suggest that loggerhead turtles stranded along the Portuguese coast originate predominantly from the Western Atlantic, contributions from Cape Verde (12 %) and potentially the Eastern Mediterranean (6 %) are also inferred. However, the estimated contribution from the Eastern Mediterranean displays a wide 95 % confidence interval (nearly including zero), indicating high uncertainty. Therefore, although this region appears in the posterior distribution, its contribution should be interpreted with caution and cannot be considered conclusive without further supporting evidence.

These samples' nucleotide (π) and haplotype diversity (h) is notably high compared to values reported for global management units. In fact, the nucleotide diversity observed in this study is comparable to values reported in other Atlantic foraging aggregations based on similar 774-bp mtDNA fragments, such as Clusa et al. (2014), which obtained an h range of 0.095–0.668 and a π range of 0.0001–0.0248. While Encalada et al. (1998) provided foundational data on loggerhead population structure, their diversity estimates were calculated using shorter 380-bp sequences, which limits direct comparison with our results. Likewise, in the Mexican aggregations, where we observe many of the loggerheads' haplotypes, our samples' haplotype diversity (h) is also high (Monzón-Argüello et al., 2010). Such results are expected from a mixed stock of many different origins and indicate that we can obtain much information from genetic analysis on this mtDNA marker. Furthermore, the parsimony network reveals two main groups of haplotypes: those that exist specifically in the Atlantic Ocean and those that appear in the Mediterranean Sea along with the Atlantic. Notably, we found a new haplotype that is one mutation away from CC-A1(Fig 2.3), leading us to hypothesise that the individual with this haplotype likely originates from the Western Atlantic, where CC-A1 is most abundant.

Previous studies have revealed that older loggerheads tend to forage close to their natal grounds, with only a limited number of individuals known to migrate further away (Pajuelo et al., 2012). In contrast, younger loggerheads are more likely to migrate to distant foraging grounds (Hatase et al., 2002; Hawkes et al., 2006; Mansfield et al., 2009). These tendencies align with previous observations where individuals from the Gulf of Mexico and surrounding rookeries follow currents to reach the Azores and Madeira islands (Bolten et al., 1998). Studies conducted in the Mediterranean suggest similar turtle migration behaviour. In the Adriatic Sea, loggerheads who frequent the coastal waters are born in Greece, Cyprus and Turkey (Lazar et al., 2004; Splendiani et al., 2017; Tolve et al., 2018) following the Eastern-Southern Adriatic current (Zavatarelli and Pinardi, 2003). Some of those turtles from Greece and Turkey go west to the French coast, following Mediterranean currents in search of upwellings rich in prey (Carreras et al., 2006; Loisier et al., 2021).

While the species is characterised by philopatry, the Iberian coast does not contain any nursing rookeries hence all the turtles found in these waters are most likely foraging. The coastal upwelling provides an abundance of prey for marine migratory species, like turtles. The loggerhead turtles stranded in Portuguese waters consist mainly of young and subadults between 22 and 83 cm CCL (Nicolau et al., 2016a, 2016b). The turtles' size is found to be positively correlated with diet volume and variety (Frick et al., 2009; Hatase et al., 2002), which relates their arrival to their need for more prey after their oceanic stage is over. Nonetheless, it is not clarified at which point the turtles change their diet, and it is also speculated that sometimes, their change of prey uptake leads to faster growth (Hatase et al., 2002). The latter can explain why seven small individuals (<32 cm) are also found in Portugal.

The observation that many turtles come to the Iberian coast from the western part of the Atlantic aligns with prior expectations for two main reasons. Firstly, the Florida and Gulf of Mexico management units are some of the largest in the world, counting thousands of turtles every year (Ceriani et al., 2019). Secondly, besides the contribution in numbers, the dominant currents of the North Atlantic Drift lead turtles from the American to the European side, facilitating the species dispersal (Monzón-Argüello et al., 2009). To facilitate a better understanding of the movement patterns of stranded individuals, we recommend readers consult the detailed visual summary maps of source rookeries and inferred oceanic routes presented in Cani et al. (2025) in addition to the overview map of the Atlantic provided herein (Supplementary Material S3). The North Atlantic drift starts to form intensely in the Gulf of Mexico, where most of the loggerheads we sampled originate (Reverdin et al., 2003). This movement agrees with the hypothesis that turtles tend to use currents to travel to tread great distances with minimum energy expansion. It is noteworthy that the lack of older adults in our samples can be because adult females from the Gulf of Mexico do not travel far from their natal sites after giving birth (Girard et al., 2009; Renaud and Carpenter, 1994). Unfortunately, our samples were missing data on their gender and reproduction phase, thus hindering an accurate estimation of whether this is the reason older loggerheads (>83 cm) are absent from the strandings.

Sea turtles can also orient themselves and memorise parts of their journeys (Bowen and Karl, 2017; Monzón-Argüello et al., 2012). This is demonstrated by the fact that 50 of the turtles found in Portuguese waters share haplotypes with turtles from Cape Verde, which is located South of the Portuguese waters. The North Atlantic Current splits in two directions: North to waters too cold for the loggerhead turtles and South towards Cape Verde (Reverdin et al., 2003). This constitutes another example of these turtles moving counter-current. The haplotype CC-A17.1, which is uniquely found in the Cape Verde rookeries, along with the CC-A1.3, which frequently appears in those rookeries, imply that turtle-s indeed travelled northwards. Moreover, Cape Verde is one of the most important loggerhead turtle rookeries, recently characterised as a stepping stone for the species' dispersal in the Atlantic (Baltazar-Soares et al., 2020). The contribution of Cape Verde indicates that the turtles can navigate across or even against currents in whatever direction they choose, matching their hatchlings' orientation and travelling behaviour (Avens and Lohmann, 2003; Salmon and Wyneken, 1987). However, the sample size was insufficient to allow us to draw definite conclusions on how these aggregations can be affected by activities on the European Atlantic coasts.

Considering these findings, the rookeries most adversely affected by threats in the North-East Atlantic are those located in the Gulf of Mexico. Loggerhead turtles have to overcome similar challenges on both sides of the Atlantic Ocean, as the leading cause of stranding in the Gulf of Mexico is also bycatch by fisheries, followed by marine litter digestion and the loss of nesting habitat (Lewison et al., 2003; Reece et al., 2013). Implementing bycatch reduction measures, such as turtle-excluding devices, has helped conserve loggerhead turtles on the American continental coast, increasing the population (Lewison et al., 2003).

This study suggests that conservation strategies and regulations should be implemented in areas like the Portuguese coast, which, while lacking nesting sites, serves as a vital foraging ground for these turtles. In addition, collecting data on gender and reproduction stage can provide insights into the absence of older loggerheads from Portuguese waters. Nonetheless, evidence of extensive oceanic migrations remains clear. Satellite tagging will confirm the species' tendency to follow currents and reveal all the ecosystems they affect. Data collected from stranded individuals may reveal new haplotypes, like the one discovered in our study, and contribute to the global database.

In conclusion, studying sea turtle populations underscores that effective management and conservation rely on coordinated global efforts, especially for highly migratory and widely dispersed species like the loggerhead turtle (Wallace et al., 2011, 2023). Regional management is the first shield for conservation; however, it becomes ineffective when organisms travel to regions lacking robust protective measures (Wallace et al., 2023). Ultimately, studies on populations and ecosystems consistently point to their inseparable connection.

CRediT authorship contribution statement

Ana Marçalo: Writing – review & editing, Writing – original draft, Resources, Investigation, Conceptualization. **Pereira Andreia:** Writing – review & editing, Resources. **Sá Sara:** Writing – review & editing, Resources. **Lídia Nicolau:** Writing – review & editing. **Cunha Regina:** Writing – review & editing, Investigation, Conceptualization. **Adam Galatoulas:** Writing – review & editing, Methodology, Investigation. **Corona Luana:** Writing – review & editing, Methodology, Investigation. **Rita Castilho:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of Competing Interest

None.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03878.

Data availability

Data will be made available on request.

References

Abalo-Morla, S., Muñoz-Mas, R., Tomás, J., Belda, E.J., 2023. Factors driving dispersal and habitat use of loggerhead sea turtle post-hatchlings and its conservational implications. Mar. Biol. 170, 155. https://doi.org/10.1007/s00227-023-04285-2.

Abreu-Grobois, F., Horrocks, J., Formia, A., LeRoux, R., Vélez-Zuazo, X., Dutton, P., Soares, L., Meylan, P., Browne, D., 2006. New mDNA Dloop primers which work for a variety of marine turtle species may increase the resolution capacity of mixed stock analysis. 178-179. In: Proceedings of the twenty Sixth Annual Symposium on Sea Turtle Biology and Conservation. Archelon, Creta.

Avens, L., Lohmann, K.J., 2003. Use of multiple orientation cues by juvenile loggerhead sea turtles Caretta caretta. J. Exp. Biol. 206, 4317–4325. https://doi.org/10.1242/jeb.00657.

Avise, J.C., Hamrick, J.L., 1995. Conservation Genetics: Case Histories from Nature. Chapman & Hall, New York.

Baltazar-Soares, M., Klein, J.D., Correia, S.M., Reischig, T., Taxonera, A., Roque, S.M., Dos Passos, L., Durão, J., Lomba, J.P., Dinis, H., Cameron, S.J.K., Stiebens, V.A., Eizaguirre, C., 2020. Distribution of genetic diversity reveals colonization patterns and philopatry of the loggerhead sea turtles across geographic scales. Sci. Rep. 10, 18001. https://doi.org/10.1038/s41598-020-74141-6.

Bandelt, H.-J., Forster, P., Röhl, A., 1999. Median-joining networks for inferring intraspecific phylogenies. Mol. Biol. Evol. 16, 37–48.

Bellido, J.J., Castillo, J.J., Pinto, F., Martín, J.J., Mons, J.L., Báez, J.C., Real, R., 2009. Differential geographical trends for loggerhead turtles stranding dead or alive along the andalusian coast, Southern Spain. J. Mar. Biol. Assoc. U. K. 90. https://doi.org/10.1017/s0025315409990361.

Bellido López, J.J., Torreblanca, E., Baez, J.C., Camiñas, J.A., 2018. Sea turtles in the eastern margin of the north atlantic: the Northern Ibero-Moroccan gulf as an important neritic area for sea turtles. Medit. Mar. Sci. https://doi.org/10.12681/mms.15835.

Bolker, B., Okuyama, T., Bjorndal, K., Bolten, A., 2003. Sea turtle stock estimation using genetic markers: accounting for sampling error of rare genotypes. Ecol. Appl. 13 (3), 763–775.

Bolker, B.M., Okuyama, T., Bjorndal, K.A., Bolten, A.B., 2007. Incorporating multiple mixed stocks in mixed stock analysis: "many-to-many" analyses. Mol. Ecol. 16, 685–695. https://doi.org/10.1111/j.1365-294X.2006.03161.x.

Bolten, A.B., Bjorndal, K.A., Martins, H.R., Dellinger, T., Biscoito, M.J., Encalada, S.E., Bowen, B.W., 1998. Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. Ecol. Appl. 8 (7), 1. https://doi.org/10.1890/1051-0761(1998)008[0001:TDMOLS]2.0.CO;2.

Bowen, B.W., Karl, S.A., 2017. Population genetics, phylogeography, and molecular evolution. In: in: The Biology of Sea Turtles, I. CRC Press, pp. 39–50.

Cameron, S.J.K., Baltazar-Soares, M., Stiebens, V.A., Reischig, T., Correia, S.M., Harrod, C., Eizaguirre, C., 2019. Diversity of feeding strategies in loggerhead sea turtles from the Cape Verde archipelago. Mar. Biol. 166, 130. https://doi.org/10.1007/s00227-019-3571-8.

Cani, A., Besén, C., Carreras, C., Pascual, M., Cardona, L., 2025. The journey of loggerhead turtles from the northwest Atlantic to the Mediterranean Sea as recorded by the stable isotope ratios of O, C and N of their bones. Mar. Environ. Res. 203, 106851. https://doi.org/10.1016/j.marenvres.2024.106851.

Carreras, C., Pont, S., Maffucci, F., Pascual, M., Barceló, A., Bentivegna, F., Cardona, L., Alegre, F., SanFélix, M., Fernández, G., Aguilar, A., 2006. Genetic structuring of immature loggerhead sea turtles (Caretta caretta) in the Mediterranean Sea reflects water circulation patterns. Mar. Biol. 149, 1269–1279. https://doi.org/10.1007/s00227-006-0282-8.

Ceriani, S.A., Casale, P., Brost, M., Leone, E.H., Witherington, B.E., 2019. Conservation implications of sea turtle nesting trends: elusive recovery of a globally important loggerhead population. Ecosphere 10, e02936. https://doi.org/10.1002/ecs2.2936.

Ceriani, S.A., Murasko, S., Addison, D.S., Anderson, D., Curry, G., Desjardin, N.A., Eastman, S.F., Evans, D.R., Evou, N., Fuentes, M.M.P.B., Godfrey, M.H., Hart, K.M., Hillbrand, P., Hirsch, S.E., Mott, C.R., Mansfield, K.L., Mazzarella, K.T., Norris, S.V., Pate, S.M., Phillips, K.F., Rusenko, K.W., Shamblin, B.M., Stevenson, A., Sloan, K.A., Tucker, A.D., Welsh, R.C., Casale, P., 2023. Monitoring population-level foraging distribution of a marine migratory species from land: strengths and weaknesses of the isotopic approach on the northwest Atlantic loggerhead turtle aggregation. Front. Mar. Sci. 10, 1189661. https://doi.org/10.3389/fmars.2023.1189661.

Clusa, M., Carreras, C., Pascual, M., Gaughran, S.J., Piovano, S., Giacoma, C., Fernández, G., Levy, Y., Tomás, J., Raga, J.A., Maffucci, F., Hochscheid, S., Aguilar, A., Cardona, L., 2014. Fine-scale distribution of juvenile atlantic and Mediterranean loggerhead turtles (Caretta caretta) in the Mediterranean Sea. Mar. Biol. 161, 509–519. https://doi.org/10.1007/s00227-013-2353-y.

Dellinger, T., Zekovic, V., Radeta, M., 2022. Long-Term monitoring of in-water abundance of juvenile pelagic loggerhead sea turtles (Caretta caretta): population trends in relation to north Atlantic oscillation and nesting. Front. Mar. Sci. 9, 877636. https://doi.org/10.3389/fmars.2022.877636.

Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res 32, 1792–1797. https://doi.org/10.1093/nar/gkh340.

Encalada, S., Bjorndal, K., Bolten, A., Zurita, J., Schroeder, B., Possardt, E., Sears, C., Bowen, B., 1998. Population structure of loggerhead turtle (Caretta caretta) nesting colonies in the atlantic and Mediterranean as inferred from mitochondrial DNA control region sequences. Mar. Biol. 130, 567–575. https://doi.org/10.1007/s002270050278.

Engstrom, T., Meylan, P., Meylan, A., 2002. Origin of juvenile loggerhead turtles (Caretta caretta) in a tropical developmental habitat in Caribbean Panama. Anim. Conserv. 5, 125–133. https://doi.org/10.1017/S1367943002002184.

Evans, D.R., Carthy, R.R., Ceriani, S.A., 2019. Migration routes, foraging behavior, and site fidelity of loggerhead sea turtles (Caretta caretta) satellite tracked from a globally important rookery. Mar. Biol. 166, 134. https://doi.org/10.1007/s00227-019-3583-4.

Foley, A., Schroeder, B., Hardy, R., MacPherson, S., Nicholas, M., Coyne, M., 2013. Postnesting migratory behavior of loggerhead sea turtles Caretta caretta from three Florida rookeries. Endang. Species Res. 21, 129–142. https://doi.org/10.3354/esr00512.

Frick, M., Williams, K., Bolten, A., Bjorndal, K., Martins, H., 2009. Foraging ecology of oceanic-stage loggerhead turtles Caretta caretta. Endang. Species Res. 9, 91–97. https://doi.org/10.3354/esr00227.

Girard, C., Tucker, A.D., Calmettes, B., 2009. Post-nesting migrations of loggerhead sea turtles in the Gulf of Mexico: dispersal in highly dynamic conditions. Mar. Biol. 156, 1827–1839. https://doi.org/10.1007/s00227-009-1216-z.

Goodwin, G., Hart, K., Evans, A., Burkholder, D., 2024. Satellite telemetry reveals high-use internesting areas and international foraging extent for loggerhead turtles tagged in southeast Florida, USA. Endang. Species Res. 54, 245–259. https://doi.org/10.3354/esr01339.

Hatase, H., Takai, N., Matsuzawa, Y., Sakamoto, W., Omuta, K., Goto, K., Arai, N., Fujiwara, T., 2002. Size-related differences in feeding habitat use of adult female loggerhead turtles Caretta caretta around Japan determined by stable isotope analyses and satellite telemetry. Mar. Ecol. Prog. Ser. 233, 273–281.

Hawkes, L.A., Broderick, A.C., Coyne, M.S., Godfrey, M.H., Lopez-Jurado, L.-F., Lopez-Suarez, P., Merino, S.E., Varo-Cruz, N., Godley, B.J., 2006. Phenotypically linked dichotomy in sea turtle foraging requires multiple conservation approaches. Curr. Biol. 16, 990–995. https://doi.org/10.1016/j.cub.2006.03.063.

IUCN, 2015. In: Casale, P., Tucker, A.D. (Eds.), Caretta caretta. The IUCN Red List of Threatened Species 2017. https://doi.org/10.2305/IUCN.UK.2017-2.RLTS.T3897A119333622.en.

Jensen, M., Bell, I., Limpus, C., Hamann, M., Ambar, S., Whap, T., David, C., FitzSimmons, N., 2016. Spatial and temporal genetic variation among size classes of Green turtles (*Chelonia mydas*) provides information on oceanic dispersal and population dynamics. Mar. Ecol. Prog. Ser. 543, 241–256. https://doi.org/10.3354/meps11521.

Karaa, S., Maffucci, F., Jribi, I., Bologna, M.A., Borra, M., Biffali, E., Bradai, M.N., Hochscheid, S., 2016. Connectivity and stock composition of loggerhead turtles foraging on the north African continental shelf (Central Mediterranean): implications for conservation and management. Mar. Ecol. 37, 1103–1115. https://doi.org/10.1111/maec.12375.

LaCasella, E., Epperly, S., Jensen, M., Stokes, L., Dutton, P., 2013. Genetic stock composition of loggerhead turtles Caretta caretta bycaught in the pelagic waters of the north Atlantic. Endang. Species Res. 22, 73–84. https://doi.org/10.3354/esr00535.

Lazar, B., Margaritoulis, D., Tvrtković, N., 2004. Tag recoveries of the loggerhead sea turtle Caretta caretta in the eastern adriatic sea: implications for conservation. J. Mar. Biol. Ass. 84, 475–480. https://doi.org/10.1017/S0025315404009488h.

Leigh, J.W., Bryant, D., 2015. Popart: full-feature software for haplotype network construction. Methods Ecol. Evol. 6, 1110–1116. https://doi.org/10.1111/2041-210X.12410.

Leroux, R.A., Dutton, P.H., Abreu-Grobois, F.A., Lagueux, C.J., Campbell, C.L., Delcroix, E., Chevalier, J., Horrocks, J.A., Hillis-Starr, Z., Troëng, S., Harrison, E., Stapleton, S., 2012. Re-examination of population structure and phylogeography of hawksbill turtles in the wider Caribbean using longer mtDNA sequences. J. Hered. 103, 806–820. https://doi.org/10.1093/jhered/ess055.

Lewison, R.L., Crowder, L.B., Shaver, D.J., 2003. The impact of turtle excluder devices and fisheries closures on loggerhead and Kemp's ridley strandings in the Western Gulf of Mexico. Conserv. Biol. 17, 1089–1097.

Lohmann, K.J., Lohmann, C.M.F., 2019. There and back again: natal homing by magnetic navigation in sea turtles and salmon. J. Exp. Biol. 222, jeb184077. https://doi.org/10.1242/jeb.184077.

Lohmann, K.J., Putman, N.F., Lohmann, C.M.F., 2008. Geomagnetic imprinting: a unifying hypothesis of long-distance natal homing in salmon and sea turtles. Proc. Natl. Acad. Sci. USA 105, 19096–19101. https://doi.org/10.1073/pnas.0801859105.

Loisier, A., Savelli, M., Arnal, V., Claro, F., Gambaiani, D., Senegas, J., Cesarini, C., Sacchi, J., Miaud, C., Montgelard, C., 2021. Genetic composition, origin and conservation of loggerhead sea turtles (Caretta caretta) frequenting the French Mediterranean coasts. Mar. Biol. 168. https://doi.org/10.1007/s00227-021-03855-6.

Maglietta, R., Caccioppoli, R., Piazzolla, D., Saccotelli, L., Cherubini, C., Scagnoli, E., Piermattei, V., Marcelli, M., De Lucia, G.A., Lecci, R., Causio, S., Dimauro, G., De Franco, F., Scuro, M., Coppini, G., 2024. Habitat suitability modeling of loggerhead sea turtles in the Central-Eastern Mediterranean Sea: a machine learning approach using satellite tracking data. Front. Mar. Sci. 11, 1493598. https://doi.org/10.3389/fmars.2024.1493598.

Mansfield, K.L., Saba, V.S., Keinath, J.A., Musick, J.A., 2009. Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the northwest Atlantic. Mar. Biol. 156, 2555–2570. https://doi.org/10.1007/s00227-009-1279-x.

Mast, R.B., Bailey, L.M., Hutchinson, B.J., 2005. SWoT report: the State of the World's Sea Turtles,I. State of the World's Sea Turtles, Washington DC.

Monzón-Argüello, C., Dell'Amico, F., Morinière, P., Marco, A., López-Jurado, L.F., Hays, G.C., Scott, R., Marsh, R., Lee, P.L.M., 2012. Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal. J. R. Soc. Interface 9, 1725–1732. https://doi.org/10.1098/rsif.2011.0788.

Monzón-Argüello, C., Rico, C., Carreras, C., Calabuig, P., Marco, A., López-Jurado, L.F., 2009. Variation in spatial distribution of juvenile loggerhead turtles in the eastern atlantic and Western Mediterranean Sea. J. Exp. Mar. Biol. Ecol. 373, 79–86. https://doi.org/10.1016/j.jembe.2009.03.007.

Monzón-Argüello, C., Rico, C., Naro-Maciel, E., Varo-Cruz, N., López, P., Marco, A., López-Jurado, L.F., 2010. Population structure and conservation implications for the loggerhead sea turtle of the Cape Verde islands. Conserv. Genet. 11, 1871–1884. https://doi.org/10.1007/s10592-010-0079-7.

Nicolau, L., Ferreira, M., Santos, J., Araújo, H., Sequeira, M., Vingada, J., Eira, C., Marçalo, A., 2016a. Sea turtle strandings along the Portuguese mainland coast: spatio-temporal occurrence and main threats. Mar. Biol. 163, 21. https://doi.org/10.1007/s00227-015-2783-9.

Nicolau, L., Marçalo, A., Ferreira, M., Sá, S., Vingada, J., Eira, C., 2016b. Ingestion of marine litter by loggerhead sea turtles, Caretta caretta, in Portuguese continental waters. Mar. Pollut. Bull. 103, 179–185. https://doi.org/10.1016/j.marpolbul.2015.12.021.

Norman, J.A., 1994. Mitochondrial DNA control region polymorphisms: genetic markers for ecological studies of marine turtles. Mol. Ecol. 3, 363–373.

Pajuelo, M., Bjorndal, K.A., Reich, K.J., Vander Zanden, H.B., Hawkes, L.A., Bolten, A.B., 2012. Assignment of nesting loggerhead turtles to their foraging areas in the northwest atlantic using stable isotopes. Ecosphere 3, 1–18. https://doi.org/10.1890/ES12-00220.1.

Paradis, E., 2010. Pegas: an r package for population genetics with an integrated-modular approach. Bioinformatics 26, 419–420. https://doi.org/10.1093/bioinformatics/btp696.

Patrício, A., Hawkes, L., Monsinjon, J., Godley, B., Fuentes, M., 2021. Climate change and marine turtles: recent advances and future directions. Endang. Species Res. 44, 363–395. https://doi.org/10.3354/esr01110.

Pella, J., Masuda, M., 2001. Bayesian methods for analysis of stock mixtures from genetic characters. Fish. Bull. 99, 151. –151.

Quattrocchi, G., Cucco, A., Cerritelli, G., Mencacci, R., Comparetto, G., Sammartano, D., Ribotti, A., Luschi, P., 2021. Testing a novel aggregated methodology to assess hydrodynamic impacts on a High-Resolution marine turtle trajectory. Front. Mar. Sci. 8, 699580. https://doi.org/10.3389/fmars.2021.699580.

Rankin-Baransky, K., Williams, C.J., Bass, A.L., Bowen, B.W., Spotila, J.R., 2001. Origin of loggerhead turtles stranded in the northeastern United States as determined by mitochondrial DNA analysis. J. Herpetol. 35, 638. https://doi.org/10.2307/1565903.

Reece, J.S., Passeri, D., Ehrhart, L., Hagen, S.C., Hays, A., Long, C., Noss, R.F., Bilskie, M., Sanchez, C., Schwoerer, M.V., et al., 2013. Sea level rise, land use, and climate change influence the distribution of loggerhead turtle nests at the largest USA rookery (Melbourne Beach, Florida). Mar. Ecol. Prog. Ser. 493, 259–274.

Renaud, M.L., Carpenter, J.A., 1994. Movements and submergence patterns of loggerhead turtles (Caretta caretta) in the Gulf of Mexico determined through satellite telemetry. Bull. Mar. Sci. 55, 1–15.

Reverdin, G., Niiler, P.P., Valdimarsson, H., 2003. North Atlantic Ocean surface currents. J. Geophys. Res. 108. https://doi.org/10.1029/2001JC001020.

Saitou, N., Nei, M., 1987. The neighbor-joining method: a new method for reconstructing phylogenies. Mol. Biol. Evol. 4, 406–425.

Salmon, M., Wyneken, J., 1987. Orientation and swimming behavior of hatchling loggerhead turtles Caretta caretta L. During their offshore migration. J. Exp. Mar. Biol. Ecol. 109, 137–153. https://doi.org/10.1016/0022-0981(87)90012-8.

Shamblin, B.M., Bolten, A.B., Abreu-Grobois, F.A., Bjorndal, K.A., Cardona, L., Carreras, C., Clusa, M., Monzón-Argüello, C., Nairn, C.J., Nielsen, J.T., Nel, R., Soares, L.S., Stewart, K.R., Vilaça, S.T., Türkozan, O., Yilmaz, C., Dutton, P.H., 2014. Geographic patterns of genetic variation in a broadly distributed marine vertebrate: new insights into loggerhead turtle stock structure from expanded mitochondrial DNA sequences. PLoS One 9, e85956. https://doi.org/10.1371/journal.pone.0085956.

Splendiani, A., Fioravanti, T., Giovannotti, M., D'Amore, A., Furii, G., Totaro, G., Nisi Cerioni, P., Lucchetti, A., Caputo Barucchi, V., 2017. Mitochondrial DNA reveals the natal origin of Caretta caretta (Testudines: Cheloniidae) stranded or bycaught along the southwestern Adriatic coasts. Eur. Zool. J. 84, 566–574. https://doi.org/10.1080/24750263.2017.1400597.

Stewart, K.R., LaCasella, E.L., Jensen, M.P., Epperly, S.P., Haas, H.L., Stokes, L.W., Dutton, P.H., 2019. Using mixed stock analysis to assess source populations for at-sea bycaught juvenile and adult loggerhead turtles (Caretta caretta) in the north-west Atlantic. Fish Fish. 20, 239–254. https://doi.org/10.1111/faf.12336.

Tolve, L., Casale, P., Formia, A., Garofalo, L., Lazar, B., Natali, C., Novelletto, A., Vallini, C., Bužan, E., Chelazzi, G., Gaspari, S., Fortuna, C., Kocijan, I., Marchiori, E., Novarini, N., Poppi, L., Salvemini, P., Ciofi, C., 2018. A comprehensive mitochondrial DNA mixed-stock analysis clarifies the composition of loggerhead turtle aggregates in the Adriatic sea. Mar. Biol. 165, 68. https://doi.org/10.1007/s00227-018-3325-z.

Turkozan, O., Yılmaz, C., Uçar, A.H., Carreras, C., Ergene, S., Aymak, C., Karaman, S., 2018. Local differentiation in the origin of stranded loggerhead turtles, Caretta caretta, within an eastern Turkey foraging area. Ocean Coast. Manag. 153, 70–75. https://doi.org/10.1016/j.ocecoaman.2017.12.011.

Wallace, B., Posnik, Z., Hurley, B., DiMatteo, A., Bandimere, A., Rodriguez, I., Maxwell, S., Meyer, L., Brenner, H., Jensen, M., LaCasella, E., Shamblin, B., Abreu-Grobois, F., Stewart, K., Dutton, P., Barrios-Garrido, H., Dalleau, M., Dell'Amico, F., Eckert, K., Mast, R., 2023. Marine turtle regional management units 2.0: an updated framework for conservation and research of wide-ranging megafauna species. Endanger. Species Res. 52, 209–223.

Wallace, B.P., DiMatteo, A.D., Bolten, A.B., Chaloupka, M.Y., Hutchinson, B.J., Abreu-Grobois, F.A., Mortimer, J.A., Seminoff, J.A., Amorocho, D., Bjorndal, K.A., Bourjea, J., Bowen, B.W., Briseño Dueñas, R., Casale, P., Choudhury, B.C., Costa, A., Dutton, P.H., Fallabrino, A., Finkbeiner, E.M., Girard, A., Girondot, M., Hamann, M., Hurley, B.J., López-Mendilaharsu, M., Marcovaldi, M.A., Musick, J.A., Nel, R., Pilcher, N.J., Troëng, S., Witherington, B., Mast, R.B., 2011. Global conservation priorities for marine turtles. PLoS One 6, e24510. https://doi.org/10.1371/journal.pone.0024510.

Zavatarelli, M., Pinardi, N., 2003. The adriatic sea modelling system: a nested approach. Ann. Geophys 21, 345–364. https://doi.org/10.5194/angeo-21-345-2003.