



Climate change on sea currents is not expected to alter contemporary migration routes of loggerhead sea turtles

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ABSTRACT

For marine species, traveling with the current potentially reduces energetic costs. Still, the extent to which organisms adjust routes to follow current flow remains an open question. Moreover, the extent to which climate change is altering sea currents, and in turn species migration routes, remains unknown, representing a major challenge to spatial ecology and conservation efforts.

We developed an approach to assess the extent to which projected optimal paths and corridors overlap with the observed migration routes of loggerhead sea turtles (*Caretta caretta*), minimizing exposure to opposing sea currents. To illustrate this approach, we used migratory tracks of the species traveling between breeding and foraging areas in the Mediterranean Sea. We calculated the energetic costs to sea turtles based on actual tracks and corresponding optimal paths. We also explored whether projected changes in ocean currents, driven by climate change, would alter the spatial patterns of optimal routes.

The energetic cost of observed tracks was, on average, 1.25 times higher than that of corresponding optimal paths. While optimal corridors differed spatially to observed corridors used by loggerheads, some positive correlations still existed for three cases ($r_s = 0.43, 0.42, 0.30$). Climate change projections showed no significant change to the migratory movement of sea turtles, as corridors for different climatic conditions overlapped by at least 70%.

Our results show that loggerheads do not explicitly take advantage of ocean currents to facilitate long distance migrations and reduce energetic demands. The contemporary and future migration routes are characterized by similar energetic demands and together with their strong spatial overlap suggest that climate change is expected to minimally alter the species migration routes in the future. The approach presented here could be applied to different spatial scales and marine taxa, allowing possible mechanisms between sea currents (or other environmental characteristics) and species movements to be elucidated.

1. Introduction

Many organisms perform repeated, directional, and persistent movements, with migration being one of the most impressive phenomena in nature (Nathan, 2008). Seasonal migration allows animals to find suitable environmental conditions for foraging and breeding (Dingle and Drake, 2007; Louzao et al., 2015; Nathan, 2008). As such, migration allows animals to meet their biological needs and avoid adverse conditions, contributing to their persistence (Alerstam and Bäckman, 2018;

Dingle and Drake, 2007). Still, traveling to reach a suitable area potentially generates high energy demands (Hays and Scott, 2013). Thus, species must choose routes that are efficient, minimizing energetic costs and exposure to potential environmental pressures (Hein et al., 2012). However, knowledge of whether species follow optimal migration paths remains limited, representing a major scientific challenge.

Optimal migratory paths depend on species traits and environmental factors constraining movement (e.g., unsuitable habitats, high human activity) (Adriaensen et al., 2003; Halpern et al., 2019). Given that

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climatic features largely determine seascape opposition to movement between two patches (e.g., sea temperature, (Almpanidou et al., 2019); sea surface winds, (González-Solís et al., 2009; Liechti and Bruderer, 1998)), climate change could alter the optimal routes currently used by animals, constraining alternative migratory corridors, or even favoring previously unsuitable routes (Robinson et al., 2009). Altered climate could either raise thermal barriers, leading to biophysical changes that potentially constrain species physiological limits, or lead to spatiotemporal shifts in environmental parameters (e.g., sea currents) that could facilitate or hinder movement.

Sea currents are among the most influential oceanographic features that largely determine the flow of energy and material in the marine environment (Gaspar et al., 2006; Hays et al., 2010; Kumagai et al., 2018; Luschi et al., 2003). Sea currents strongly affect connectivity (i.e., the extent to which landscape/seascape facilitates or impedes species movement among habitat patches; (Taylor et al., 1993)), as they provide directionality. From an ecological perspective, sea currents often promote dispersal and colonization (Tremblay et al., 2008), and affect the food chain by concentrating prey in specific areas (Foster and Vincent, 2004; Luschi and Casale, 2014). Nevertheless, the extent to which sea currents affect migratory routes might vary among species, because animals could move with them to reduce energetic costs or against them (e.g., to approach prey or avoid other unfavorable conditions), requiring higher energetic demands (Caldwell and Gergel, 2013).

Sea turtles are an ideal species to explore how sea currents affect migratory movement, and to detect whether changes to sea currents in the future would impact contemporary migratory routes positively or negatively. Sea turtles are migratory species that periodically travel up to 1000s kilometers between distinct breeding and foraging areas (Hays and Scott, 2013). Sea currents strongly affect the movement of sea turtles, as they influence where sea turtle nesting areas are located, as well as the drift trajectories of offspring after hatching on beaches (Boyle et al., 2009; Putman et al., 2010). Yet, the extent to which sea currents affect the migratory movement of adult sea turtles remains controversial, with studies demonstrating both positive (Bentivegna et al., 2007) and negative results (Hays et al., 2014; Hays et al., 2010). This effect also differs across the sea turtle species (i.e., green and loggerhead sea turtles, (Mestre et al., 2014)). Most of these studies are based on a limited number of individuals; thus, assembling observed migratory tracks from multiple sources could provide new insights on whether and to what extent sea turtles follow optimal migratory routes that minimize exposure to opposing sea currents.

Here, we delineated the optimal migratory routes of sea turtles spatially, in form of paths and corridors that minimize exposure to sea currents, and compared them against actual migratory routes. Four pairs of breeding and foraging areas of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea were selected. The study was performed for two different 20-year periods, reflecting present (2000–2019) and projected future (2040–2059) conditions. We built upon the algorithms of least-cost path (Adriaensen et al., 2003) and randomized shortest path (Saerens et al., 2009), evaluating opposing sea currents depending on the direction of turtle movement at any given point of the seascape. We compared projected optimal outputs with 39 actual migratory tracks extracted from tracking studies, and inspected whether optimal corridors overlapped with observed corridors. As energetic cost is a major determinant of sea turtle movement, we compared the amount of energy required for the observed tracks versus corresponding optimal paths. We also assessed the spatial overlap of the optimal corridors in the two time periods, to evaluate their persistence over time under climate change. The results provided by this analysis could be used for effective conservation planning, while our methodological framework can be applied to other marine taxa over various spatial scales.

2. Materials and methods

2.1. Data on migratory tracks

We extracted satellite telemetry data from studies on loggerhead sea turtles in the Mediterranean Sea using Google Scholar (Fig. 1). We used the keywords ("satellite telemetry" OR "satellite tracking") AND ("sea turtles" OR "C. caretta" OR "marine turtles") AND ("Mediterranean"). The temporal interval that was searched spanned 1991 to 2020, as the first relevant study was published in 1991 (Hays et al., 1991). We retained studies that included maps presenting the movement of individual turtles. We focused our analysis on the post-breeding migrations of female turtles (i.e., migrations initiated in a breeding habitat and ending at a foraging ground), as more data were available (Supplementary Data S1). We selected four (4) pairs of breeding–foraging areas, with 39 migratory tracks (hereafter called “observed tracks”). In brief, there were 8 tracks from Alagadi (Cyprus) to Gulf of Gabes (Tunisia); 8 tracks from Crete (Greece) to Gulf of Gabes; 10 tracks from Zakynthos (Greece) to the Adriatic Sea; and 13 tracks from Zakynthos to Gulf of Gabes. To digitize the observed turtle tracks, we georeferenced the maps in the studies in the WGS84 coordinate system (Fig. 2). These tracks were used to create migratory corridors for each breeding–foraging area pair (hereafter called “observed corridors”). We created four kernel density maps, with values indicating the number of detected observed tracks within the cell’s proximity. This procedure was performed in ArcMap v10.7, with the search radius for these maps being extracted following Silverman’s rule of thumb (Harpole et al., 2014).

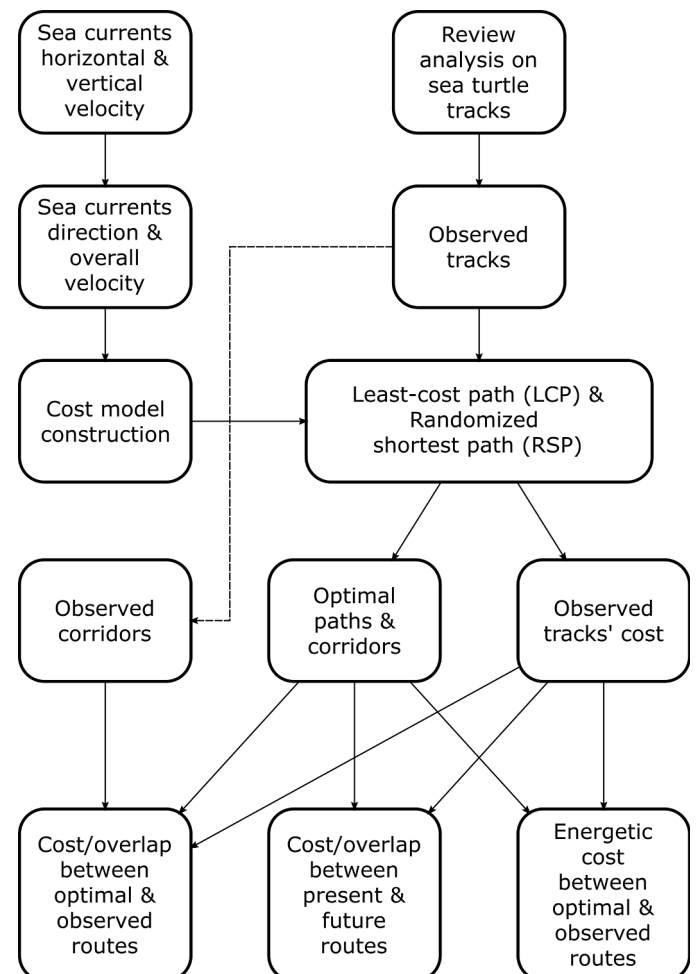


Fig. 1. Conceptual diagram presenting the methods used.

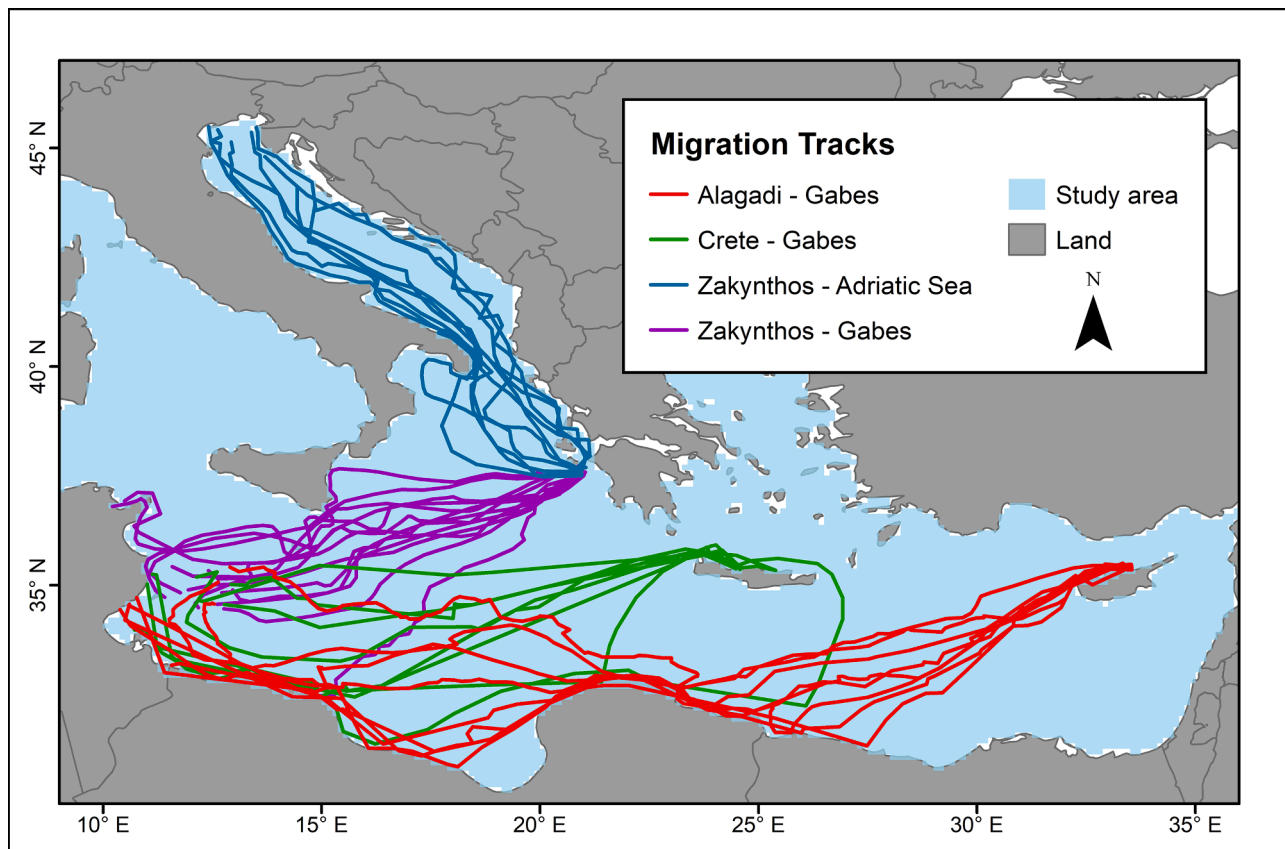


Fig. 2. Post-nesting migration tracks of female loggerhead sea turtles. The tracks are classified in four pairs of breeding – foraging areas. The study area is presented in transparent blue.

2.2. Sea current data

We extracted surface sea current data from the CNRM-CM5 model derived by MEDCORDEX (medcordex.eu). This model provides daily data on horizontal and vertical velocity of surface sea currents at a resolution of $1/8^\circ$ degrees. We used historical sea current projections and future projections based on the RCP 8.5 scenario. First, we extracted sea current data for the time interval spanning 2000 to 2019. For each year, we extracted sea current data from July 20 to August 31, when the post nesting migrations of adult female turtles commonly occur in this region (Schofield et al., 2013; Zbinden et al., 2011). The second time interval spanned 2040 to 2059, and we extracted future projections on surface sea currents considering the same dates as in the previous interval. For the third time interval, we used the same period (i.e., 2040 to 2059), but extracted data between June 10 and July 22, to account for a potential shift in the onset of migration due to climate change, which might cause migration to start one day earlier per year (Mazaris et al., 2008). For each time interval, we extracted the mean horizontal and vertical sea current velocity values for all days and years. This input was utilized to obtain sea current direction and overall sea current velocity (hereafter called “velocity”). Direction values were estimated in azimuth degrees, within the interval of $[0, 360]$, with 0 indicating direction to North. Velocity values were estimated in m/s.

2.3. Modeling seascape opposition to movement

To project optimal migration paths and corridors from breeding to foraging areas, we used the least-cost path (LCP) (Adriaenssen et al., 2003) and the randomized shortest path (RSP) (Saerens et al., 2009) algorithms, respectively. Both approaches evaluate the transition between two points based on seascape opposition to movement. In our case

study, land masses are considered as impermeable matrix; thus, the model only allowed for movement within the Mediterranean Sea. Initially, LCP was used to identify an optimal migratory path that minimized the cumulative cost between the source and end point of the observed track (hereafter called “optimal path”) (Adriaenssen et al., 2003). The output path has two attributes, its length and its cumulative cost. The cumulative cost of the optimal path quantifies the effort required to perform the movement. In contrast, RSP provides a map that evaluates each cell of the seascape with the probability that an individual passes through it (hereafter called “optimal corridors”). This map delineates corridors that promote the transition between the two points. This approach is similar to circuit theory (McRae et al., 2008), but incorporates a parameter called theta (θ), which is used to tune the degree of randomness when an individual selects the next cell to move (van Etten, 2017).

Both LCP and RSP evaluate the transition between two points based on the costs of multiple transitions between neighboring cells. These costs are typically derived from a cost layer, indicating cell-wise opposition to movement (Adriaenssen et al., 2003; McRae et al., 2008). In former studies, these cost layers were used to evaluate opposition to movement based on differences to sea current direction and the direction towards the target area (Afán et al., 2015; Dambach et al., 2016). Nevertheless, this approach might occasionally be misleading, as there might be an impenetrable matrix between the moving individual and target area (such as terrestrial masses); thus, the individual should not move directly to the target, but should follow an alternative path to pass the matrix.

We created a more comprehensive model that accounted for the direction of individual movement at each step of migration. Unlike previous approaches, we could not use a single cost layer to evaluate the opposition of sea currents to movement, as the cost of each cell differed

depending on the direction it was approached (Fig. 3). For example, if the direction of a current at a given site was towards the east, eastward turtle movement would require minimal effort, whereas westward movement would be highly impeded by the current. Therefore, the transition cost for movement between two neighboring cells was calculated based on the direction of the sea current and the direction of movement between neighboring cells. The transition cost c_{ij} between neighboring cells i and j was calculated using the formula:

$$c_{ij} = 1 + \frac{1}{2} \{ c_{dir}(d_{ij}, \varphi_i) * c_{vel}(v_i) + c_{dir}(d_{ij}, \varphi_j) * c_{vel}(v_j) \} \quad (1)$$

The transition cost is affected by the cost of the current direction c_{dir} and the cost of its velocity c_{vel} . Here, d_{ij} denotes the azimuth movement direction from cell i to cell j , φ_i and φ_j denote the azimuth sea current direction, while v_i and v_j denote sea current velocity. It is evident that c_{ij} differs from c_{ji} , as the cells would be approached from a different direction. Since the transition between cells begins from the center of cell i to the center of cell j , we account for the mean cost of the two cells, and thus we multiply by 1/2. The functions c_{dir} and c_{vel} transform the parameters of movement direction and velocity to cost, ranging from 0 to maximum cost k . To calculate current direction cost c_{dir} , we used a parabolic equation derived by (Afán et al., 2015):

$$c_{dir}(d_{ij}, \varphi_i) = a_1 * dif(d_{ij}, \varphi_i) + a_2 * dif(d_{ij}, \varphi_i)^2 \quad (2)$$

The term $dif(d_{ij}, \varphi_i)$ denotes the difference between the movement direction angle from cell i to cell j and sea current direction angle in cell i . Its value ranges between 0 (i.e., the individual is moving with the current) to 180 (i.e., the individual is moving against the current). As the difference increases, the opposition to movement increases. Coefficients a_1 and a_2 were calculated based on the parameter of maximum cost k , by solving the equation system with two initial conditions:

$$\begin{cases} dif(d_{ij}, \varphi_i) = 180 \rightarrow c_{dir}(d_{ij}, \varphi_i) = k \\ dif(d_{ij}, \varphi_i) = 360 \rightarrow c_{dir}(d_{ij}, \varphi_i) = 0 \end{cases} \quad (3)$$

The case of 360° is equivalent to the case of 0°, and is only used to solve the equation system. In essence, if the direction of an individual is with the current, the cost is zero, whereas if directions are opposite (i.e., 180°), the cost is given the maximum value of k .

The velocity cost c_{vel} given by the formula is:

$$c_{vel}(v_i) = k * \frac{v_i - v_{min}}{v_{max} - v_{min}} \quad (4)$$

where v_{min} and v_{max} are the minimum and maximum velocity values. Velocity increases movement cost linearly (Afán et al., 2015). In our

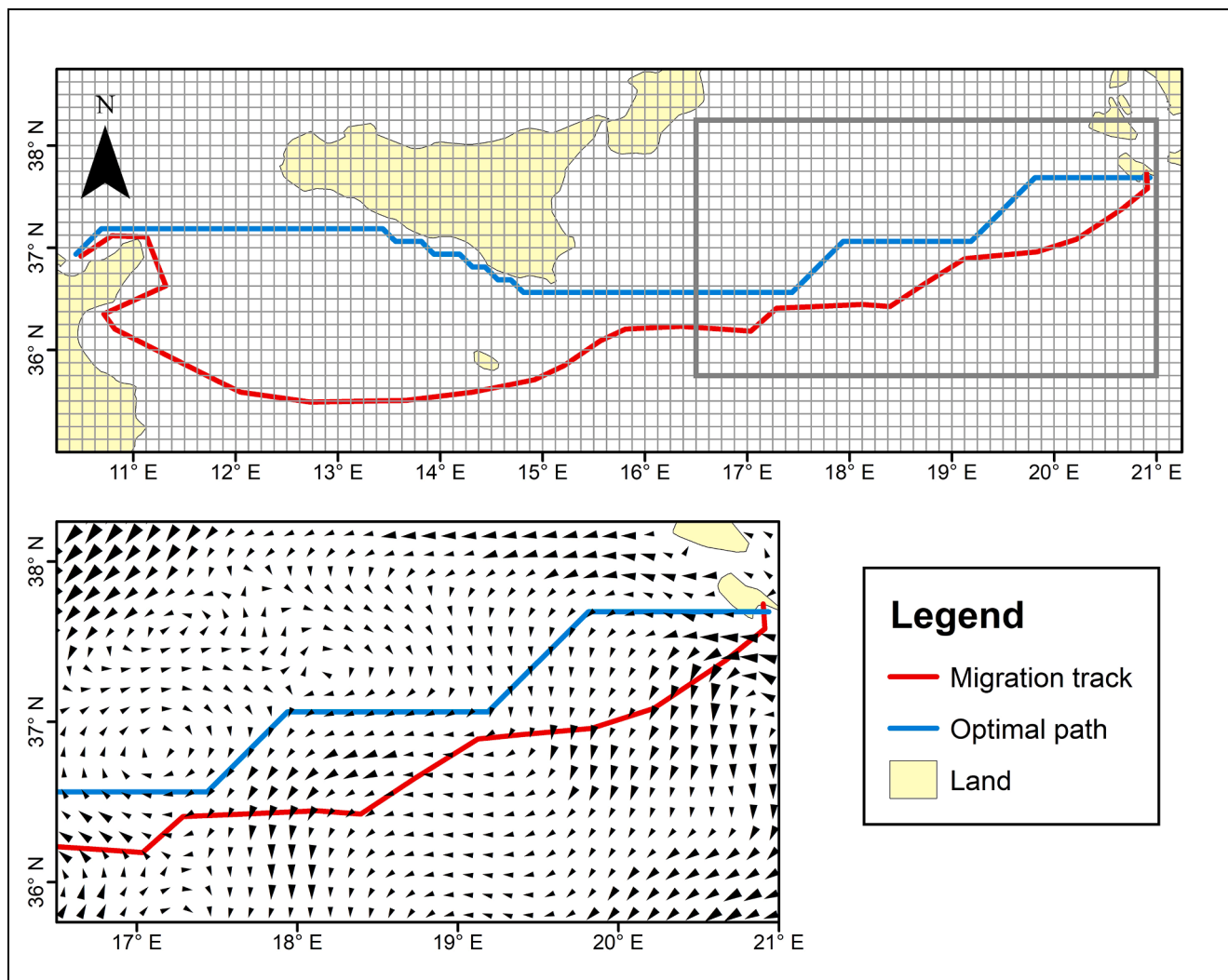


Fig. 3. Comparison of an observed track (red), initiated from the nesting sites in Zakynthos, towards the breeding areas in Gabes, with its corresponding least-cost path (blue), between the same start and end points. The lower panel highlights how these routes follow the sea currents (black arrows showing sea current direction, with size analogous to its velocity).

case, we chose $v_{min} = 0$ and $v_{max} = 0.8$ m/s, as it is the rounded maximum velocity value calculated over all three time intervals. For $v_i = v_{min}$, we receive a cost of 0, whereas for $v_i = v_{max}$, we receive the maximum cost k . Based on Eq. (1), the overall minimum cost is 1, whereas the maximum cost is affected by k , being equal to $1 + k^2$.

2.4. Identification of projected optimal paths and corridors

To project optimal migration paths and corridors, we applied LCP and RSP algorithms, respectively. The algorithms were applied for all time intervals, between the start and end points of each observed track. To quantify the energy required for turtles to travel between breeding and foraging areas by accounting for sea currents opposing movement, we also computed the cumulative cost of the observed tracks for all time intervals, by adjusting them in the cell grid of the study area (Supplementary Analysis S1, Fig. S1). To compare the optimal corridors derived from RSP with the observed corridors, we considered the RSP outputs for each foraging–breeding area pair, and computed mean probability values per cell, resulting in four ensemble optimal corridors. Regarding the parameter values, we selected $k = 4$ and $\theta = 0.3$, and conducted a sensitivity analysis for these parameters with respect to the model outputs (Supplementary Analysis S2, Fig. S2). We also projected optimal paths and corridors under a uniform model, where sea currents are absent (i.e., no seascape opposition to movement), and compared them to the paths and corridors presented here (Supplementary Analysis S3, Fig. S3).

2.5. Comparison between observed and optimal routes

We used Spearman correlation analysis to investigate whether the costs of observed tracks increase with the optimal paths, and we assessed whether the cell-wise probability values of the optimal corridors increased with the density values of the observed corridors derived from kernel density. We used Spearman correlation analyses between the time intervals for each attribute of the observed tracks (i.e., cumulative cost and length), optimal paths (i.e., cumulative cost), and corridors (i.e., cell-wise probability values), to examine whether they share similar properties among the tested climatic conditions.

2.6. Comparison of optimal corridors among the three time intervals

To assess the extent to which the optimal corridors between foraging and breeding areas were similar for the different time intervals, we used the Jaccard index of similarity. This index estimates the overlap between two maps by calculating the proportion of cells for which the two maps give similar results. The Jaccard index ranges from 0 to 1, with values close to 1 being indicative of high proportions of cells identified as corridors by both time intervals. For this procedure, we initially normalized the RSP raster values to a common value interval of [0, 1]. For each pair of foraging and breeding areas, we calculated the 80th percentile of RSP values for all three time intervals, and maintained their minimum values as the threshold used to calculate this index. In a given time interval, cells with values equal to, or higher than, this threshold were considered as corridor cells.

Data analysis of digitized observed tracks was conducted in ArcMap v10.7 (ESRI). The connectivity models and statistical analyses were conducted in R v4.0.3, using “raster” (Hijmans et al., 2013), “ncdf4” (Pierce and Pierce, 2019), “gdistance” (van Etten, 2017) and “tidyverse” (Wickham et al., 2019) packages.

2.7. Energetic cost of migration

To estimate the amount of energy that could be saved if the optimal path was preferred over the observed one, we applied a mechanistic approach that allowed us to transfer differences in travel days to

reproductive output. The key concept of our models relies on the assumption that one day less spent at sea could be used to produce more eggs. Assuming that individuals cover 50 km/day on average (Hays et al., 2014), we estimated the travel days of each observed track. Using the cost ratio of observed tracks and their corresponding optimal path, we estimated the travel days of the corresponding optimal paths derived by LCP algorithm. The difference in travel days between observed tracks and optimal paths indicated the travel days that could be saved if the optimal path had been chosen. To transfer the gain of these days to a potential difference in egg production, we estimated the amount of energy that would be required to ensure key metabolic processes.

We calculated the minimum energetic cost spent per day, based on the Dynamic Energy Budget (DEB) theory (Kooijman and Kooijman, 2010). Since loggerheads do not feed while migrating from foraging to breeding grounds in the Mediterranean, individuals use their reserves to cover basic metabolism and produce eggs (Hays et al., 2014). We considered an average Mediterranean turtle with a straight carapace length (SCL) of 78.5 cm (Margaritoulis et al., 2003), which corresponds to a structural length (L) of 29.045 cm ($L = SCL \cdot \partial M$ with $\partial M = 0.3744$) (Marn et al., 2017, 2017), with L being a measure of the turtle size used in DEB models that reflects the size and thus, the energetic demand of an individual. Based on Marn et al. (Marn et al., 2017, 2017), the daily metabolic cost of structure maintenance was equal to 13.25 J/cm^3 . Considering that the energetic value of a sea turtle egg is on average 209,640 J (Marn et al., 2017, 2017), we estimated a minimum number of eggs that could be produced per day. Next, we summed the number of eggs that could be saved if a certain number of days could be saved if the optimal path is chosen.

As an alternative estimate of the actual number of eggs that could be produced, we applied the approach of Hays et al. (Hays et al., 2014), where spent energy is translated to days away from foraging grounds. We estimated that one day of travelling would correspond to the production of 7.33 eggs, assuming that mean clutch size is 110 eggs (Hays and Scott, 2013) and is produced within 15 days (Hays et al., 2014).

3. Results

3.1. Observed and optimal routes

Our analysis revealed a significant, positive relationship between the cumulative cost of observed tracks and the cumulative cost of corresponding optimal paths ($r_s = 0.86$, $p < 0.05$). However, the observed tracks incurred, on average, 1.25 times (± 0.15) the cost of corresponding optimal paths. Comparing optimal routes with and without sea currents revealed that the presence of sea currents highly increased the effort required for loggerheads to migrate from breeding to foraging areas (Supplementary Analysis S3, Fig. S3). Overall, we observed medium to low correlations between observed and the optimal corridors, i.e., Crete-Gabes ($r_s = 0.43$, $p < 0.05$), Zakynthos-Gabes ($r_s = 0.42$, $p < 0.05$) and Zakynthos-Adriatic Sea ($r_s = 0.30$, $p < 0.05$). For the Alagadi-Gabes route, the most notable difference was detected in the direction of observed and optimal corridors, with the association reaching a negative sign ($r_s = -0.18$, $p < 0.05$) (Fig. 4).

3.2. Optimal routes among the three time intervals

The optimal paths exported by LCP had a positive degree of association among the three time intervals ($r_s > 0.99$, $p < 0.05$ for both cumulative cost and length, for each pair of time intervals, Supplementary Table S1). Similarly, positive correlations were obtained for the cumulative cost of observed tracks, as well as the probability values of RSP maps among the three time intervals ($r_s > 0.97$, $p < 0.05$, Supplementary Table S1). The Jaccard index of similarity provided values exceeding 0.70 (Supplementary Table S2), indicating that corridors among the three time intervals were relatively similar in terms of spatial extent. The main differences were detected along sub-corridors that

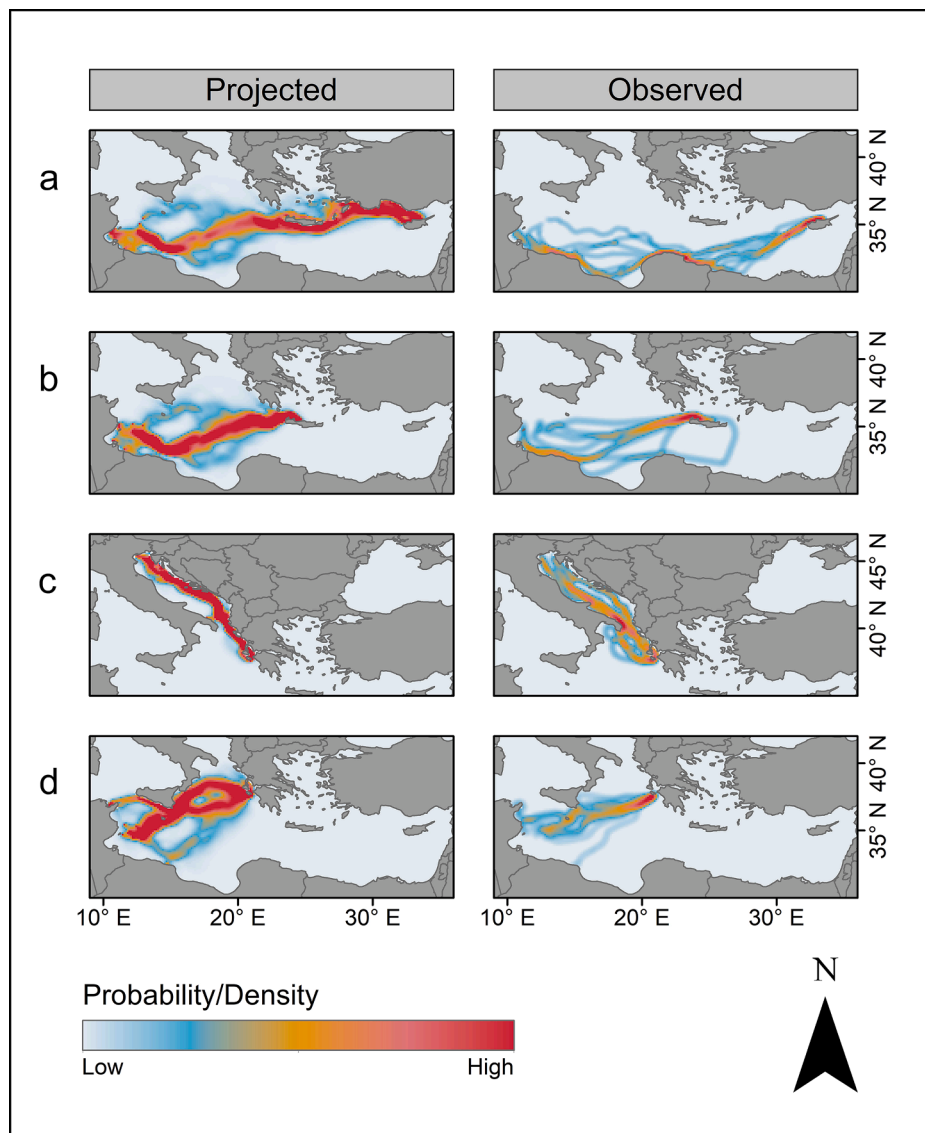


Fig. 4. Comparison of optimal corridors, derived from randomized shortest path (RSP) algorithm with kernel density map derived from the observed tracks. Each row corresponds to a pair of foraging – breeding areas, being a) Alagadi (Cyprus) to Gages (Tunisia), b) Crete (Greece) to Gages c) Zakynthos (Greece) to the Adriatic Sea and d) Zakynthos to Gages. Cell values indicate probability that an individual traversing between the areas passes through it (left panels), and number of detected observed tracks within the cell's proximity (right panels).

emerged in proximity to main corridors (Fig. 5). For example, visual inspection of the optimal corridors for Alagadi-Gages and Crete - Gages indicated that projected future movement through the coastal areas of Libya and Tunisia will increase (Fig. 5a-b). In comparison, optimal corridors projected under a potential phenological shift would more likely take place along southern coast of Italy. The optimal corridor that connected the Zakynthos nesting sites to Adriatic Sea foraging sites was projected to be narrower under a potential earlier onset of migration (Fig. 5c). In addition, for the optimal corridors between Zakynthos and Gages, we observed that a small sub-corridor from the coast of southern Sicily had lower probability to be selected, if a phenological shift occurs in the future (Fig. 5d).

3.3. Theoretical considerations on energetic costs

A turtle following the optimal path between breeding and foraging areas could save, on average, 4.87 days (Fig. 6). Using DEB theory, we estimated that the daily metabolism of loggerhead females would be equal to 324,660.9 J. This means that, for each day that a turtle is migrating, there would be a minimum energetic loss that corresponded to 1.55 eggs per day. Thus, on average, the optimal path could result in turtles saving energy for 7.55 eggs (± 6.99). Considering that this energy comes from existing reserves, for each additional day spent migrating,

additional time would be needed to replenish reserves at the foraging ground before any energy is allocated to subsequent reproduction. This is a conservative estimate, as it only considers basic metabolism, and does not account for any of the added cost of swimming against currents, changes to metabolism based on sea temperature, or any other factors that increase energetic cost. Our alternative approximation on the number of eggs that could be produced under the shorter, optimal path, showed that the energy saved could be translated to a mean number of 35.74 eggs (± 34.02).

4. Discussion

Here, we assessed optimal paths and corridors for sea turtle migration based on sea currents. Our study demonstrated a cost mismatch between the observed tracks and their corresponding optimal paths. A previous study revealed that sea turtles do not follow the optimal path, as they correct their direction during the final stage of migration, when close to the destination habitat (Hays et al., 2014, 2014). Furthermore, sea turtle navigation during migration might be affected by additional parameters, such as geomagnetic fields (Painter and Plochocka, 2019). Other marine species also travel independent of sea currents. For instance, whale sharks travel against sea currents, counter-balancing energetic costs with regular foraging (Sleeman et al., 2010), while

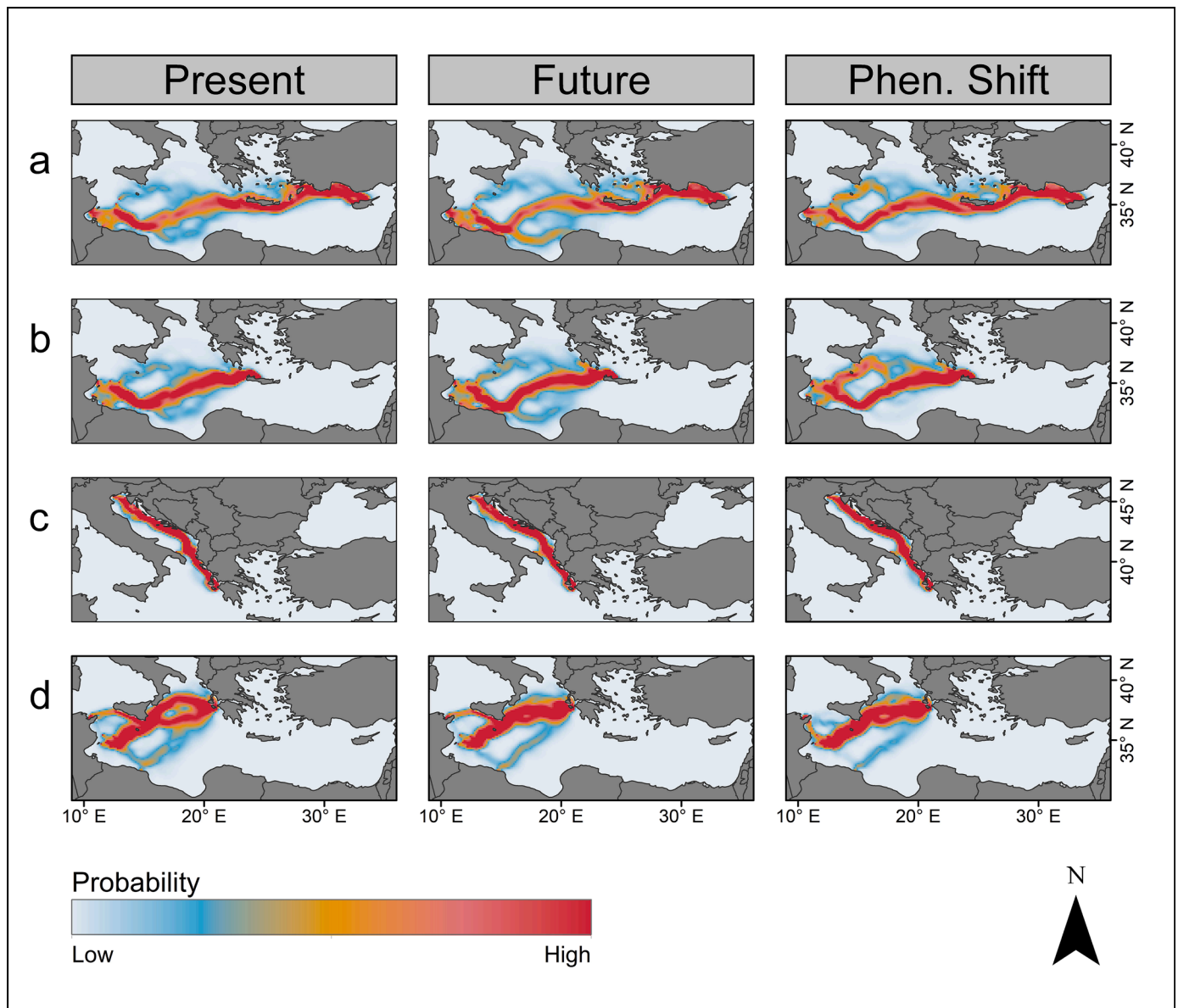


Fig. 5. Optimal corridors derived from randomized shortest path (RSP) algorithm for three different climatic conditions. Each row corresponds to a pair of foraging – breeding areas, being a) Alagadi (Cyprus) to Gages (Tunisia), b) Crete (Greece) to Gages c) Zakynthos (Greece) to the Adriatic Sea and d) Zakynthos to Gages. Cell values indicate probability that an individual traversing between the areas passes through it.

humpback whales exhibit highly directional movement in open sea, constantly adjusting displacement caused by sea currents and bathymetry (Horton et al., 2011).

The optimal corridors, in which individuals move randomly across a broader mosaic, only partially overlapped with the observed corridors. The most notable differences were observed for the corridors between Alagadi (Cyprus) and Gages (Tunisia). While we projected approximately linear optimal corridors passing along southern Turkey and Crete, the observed corridor actually passed along the coastal area of northern Africa. Previous studies showed that turtles migrating from breeding areas in Cyprus pass along this coastal area (Broderick et al., 2007; Godley et al., 2002; Snape et al., 2016; Stokes et al., 2015). There is also substantial evidence that loggerhead turtles minimize the time spent in open sea (Cheng, 2000; Dujon et al., 2017; Iverson et al., 2020). The preference for coastal areas over open sea could be explained by the potential for opportunistic feeding while travelling (Cheng, 2000; Godley et al., 2002). However, while this might occur for green turtles (Cheng, 2000), loggerhead turtles also feed in the open sea (Foley et al.,

2013).

Both empirical evidence and models show that climate change alters the migratory routes of marine species (Anderson et al., 2013; Robinson et al., 2009). Yet, our analysis showed that optimal corridors based on present sea current data were similar to future ones, even when considering a potential phenological shift due to climate change (Fig. 5). The only notable differences were identified in sub-corridors, which had different climatic conditions in each time interval (Fig. 5). The cumulative cost of both optimal paths and observed tracks minimally differed among the three time intervals. While the exact location of optimal paths might change over time due to climate change, suitable oceanographic conditions could probably be found within the surroundings. Nevertheless, climate change could affect the location of nesting areas, as climatic conditions strongly affect hatchling success and sex ratios (Fuentes et al., 2011; Pike, 2013; Turkozan et al., 2021), regulating population viability (Mazaris et al., 2005). Furthermore, certain climatic factors, such as marine heatwaves, could constrain food availability at contemporary foraging grounds (Konsta et al., 2022), forcing them to

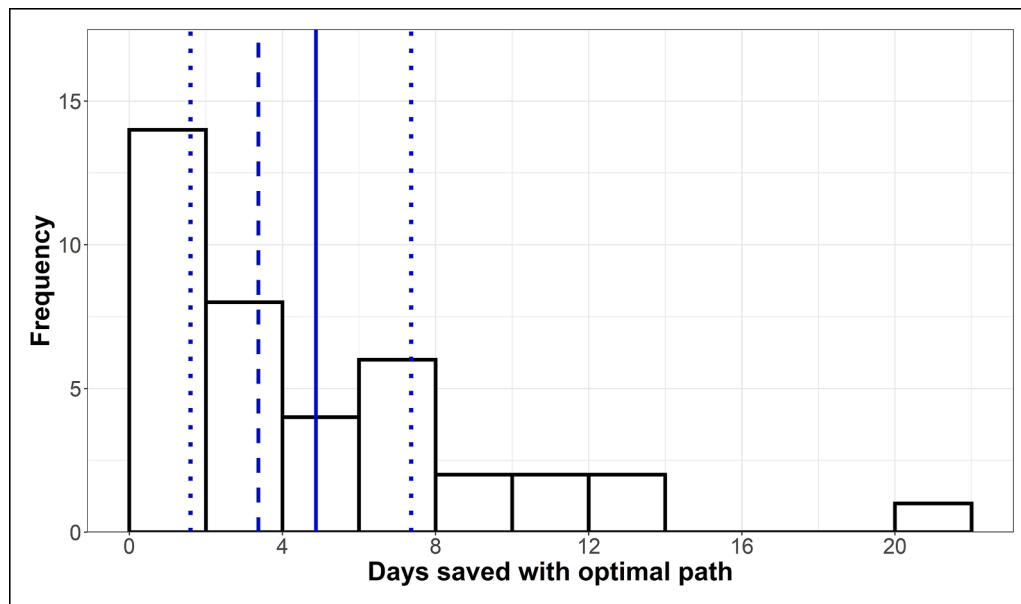


Fig. 6. Number of days saved if an individual would follow the optimal path instead of its tracked movement. The solid line indicates the mean value, the dashed line indicates the median value, while the dotted lines indicate 25th and 75th percentiles.

shift to alternative, suitable, foraging locations. Such changes to foraging and breeding areas would, in turn, alter the migratory routes between them. In addition, climate change could affect migrating turtles through other facets, such as increased warming (Almpanidou et al., 2019), hindering their movement, which would significantly impact the energetics of the migration and, by extension, the reproductive effort of turtles (Hays et al., 2002).

The amount of energy that could be saved when the optimal path is used would translate to the production of more eggs. We estimated that 8 to 36 eggs (corresponding to 1/14 to 1/3 of average clutch size in loggerheads) are jeopardized by potential energetic costs during migration. These estimates might co-vary with other parameters, such as the velocity or fitness of individuals; however, it is a reasonable estimation of energy reserves that could be allocated to reproduction. The observed tracks were post-nesting; thus, more energy could be saved if turtles migrated to the breeding areas following the optimal path, leading in higher egg productivity or shorter breeding periodicity (Hays et al., 2014). Older and bigger turtles also likely migrate further (Hays and Scott, 2013), and have higher metabolic requirements. This phenomenon would increase potential egg loss and increase the time interval between breeding years, to balance the energetic cost of spending more time at feeding ground (Hays et al., 2014).

The optimal paths and corridors presented here were projected for the observed tracks of post-nesting female loggerhead turtles in the Mediterranean Sea. Male turtles spend less time at the breeding grounds, and might so not necessarily follow the same migration routes (Hays et al., 2014; Schofield et al., 2010). This is also the case for pre-nesting migrations when animals travel towards breeding areas. Due to demographic stochasticity (Kendall and Fox, 2002), optimal paths and corridors might differ depending on the traits of individuals, such as species, age/life stage, dispersal capacity, and weight (Luschi and Casale, 2014; Schofield et al., 2020). In addition, modelled optimal paths were projected based on the assumption that individuals have complete knowledge of the area they encounter during migration, which might not always be the case for animals in real life. The models were simplified, such as assuming movements were linear from one cell to another, which obviously departs from actual turtle movement. Also, depending on the resolution of the analysis, currents might noticeably vary within a given cell area (Hays and Hawkes, 2018). Therefore, using one representative current value per cell, as we did here, could provide

biased estimates of sea currents opposing turtle movement. Although our analysis was based on a high-resolution sea current regional model, downscaled based on global circulation models, we acknowledge that the use of an ensemble multiple-model approach should be implemented in future analyses to reduce the bias of single models (Petsas et al., 2022). Despite these limitations, our analysis showed that loggerheads do not seem to use sea currents to adjust their post-nesting migratory routes. Finer resolution analyses might shed additional light in the possible mechanisms linking sea current and loggerhead movement patterns in the future.

While our methodology was developed and applied for sea turtles, it could be adapted for other species potentially affected by sea currents (Afán et al., 2015; Dambach et al., 2016). By fine tuning the parameterization of k or θ , unique models could be created, depending on how given species interact with sea currents (Caldwell and Gergel, 2013). While our models were conservative, reflecting only the effects of sea currents, they delineated optimal corridors, and assessed the extent to which loggerheads used them. By including additional data on other oceanographic features, more robust models could be produced, providing a more informed assessment and, thus, more effective conservation plans. For example, bathymetry and sea surface temperature might affect sea turtle movement, as turtles tend to avoid cold water masses (Stokes et al., 2015). Adapted modeling approaches, like using a weighting scheme among features (Petsas et al., 2020) is essential to properly quantify the extent to which each feature affects species' movement.

5. Conclusion

The current study modeled the actual tracks of sea turtles from breeding to foraging areas in the Mediterranean Sea based on sea currents. We found projected optimal corridors that are likely to be used by the species, as well as modeled optimal paths that minimize opposing sea currents. We revealed that, in general, optimal corridors only partially overlapped with observed tracks. The energy cost of observed tracks was estimated to be on average 1.25 times the cost of corresponding optimal paths. Ultimately, more data is required to examine how sea turtles are affected by sea currents during migration, and what other factors affect movement. Understanding the ecology of migration is key to providing insights for conservation and management

(Schofield et al., 2013). Incorporating connectivity assessments, such as this work, to conservation planning approaches is crucial for future conservation design under climate change.

Author contributions

ADM, PP and MT conceived the ideas and designed the methodology. PP and MT led the analysis and coding. AD and SS contributed to ecological knowledge and statistical analyses. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

All data needed to evaluate the conclusions of the paper are presented in the paper and supplementary material. Additional data related to this paper may be requested from the corresponding author.

Data sources

Sources on sea turtle migration tracks are provided in supplementary material (Supplementary Data S1). Surface sea current data were extracted from the CNRM-CM5 model, provided by the MEDCORDEX (medcordex.eu).

CRediT authorship contribution statement

Panagiotis Petsas: Conceptualization, Methodology, Software, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Marianna Tzivanopoulou:** Software, Data curation, Formal analysis, Writing – original draft. **Aggeliki Doxa:** Writing – original draft, Writing – review & editing, Supervision. **Sévrine F. Sailley:** Formal analysis, Writing – original draft, Writing – review & editing. **Antonios D. Mazaris:** Conceptualization, Methodology, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2022.110220](https://doi.org/10.1016/j.ecolmodel.2022.110220).

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