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ORIGINAL PAPER

Factors driving dispersal and habitat use of loggerhead sea turtle post-hatchlings and its conservational implications

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Abstract

Nesting events of loggerhead sea turtles (*Caretta caretta*) are on the rise in the Western Mediterranean Sea, far from their usual nesting areas in the Mediterranean and Atlantic basins. The study of dispersal behavior toward potential developmental areas of loggerhead post-hatchlings from this new nesting area is crucial to comprehend this colonization process and determining grounded conservation strategies. To fill this gap, we investigated, for the first time in the Mediterranean Sea, the dispersal strategies and habitat use based on data from 19 head-started loggerhead post-hatchlings released from the Spanish Mediterranean coast and satellite-tracked between 2016 and 2018. Turtles dispersed over large areas and showed active swimming phases, as they frequently dispersed against sea currents. Dispersal routes varied for each individual, although they consistently dispersed south-eastwards, especially during the coldest periods. Several post-hatchlings traveled through the Sicilian Channel to reach deep and warmer areas in the eastern Mediterranean basin. The most year-round suitable areas corresponded to the Ionian and Levantine Seas, which correspond with those found in their traditional nesting areas. Therefore, conservation measures focused on this stage should be taken in the path toward and these developmental areas.

Keywords *Caretta caretta* · Dispersal · Habitat model · Mediterranean Sea · Post-hatchling · Satellite tracking · Sea turtle

Introduction

Reports of nesting events of loggerhead sea turtles (*Caretta caretta*) have been increasing during the last decade in the Western Mediterranean Basin, outside the usual nesting range in the eastern Mediterranean (Tomás et al. 2008; Maffucci et al. 2016; Carreras et al. 2018; Hochscheid et al. 2022). These reports suggest that the species is expanding its nesting range through a potential colonization process (Wyneken and Lolavar 2015; Abella et al. 2016; Maffucci et al. 2016; Carreras et al. 2018), probably led by the global warming (Witt et al. 2010; Maffucci et al. 2016; Hochscheid et al. 2022).

Monitoring dispersal of post-hatchlings (turtles with a size below 40 cm straight carapace length, SCL) shall provide the data to understand the dispersal patterns of newly hatched turtles from these new rookeries on the westernmost part of the Mediterranean Basin, and to identify the way through and the main developmental areas used by these immature individuals. The protection of these pathways and the development areas will be instrumental to safeguard recruitment into adult breeding populations (Hays et al. 2016; Jeffers and Godley 2016; Maffucci et al. 2016; Rees et al. 2017). Identifying these areas is especially relevant in those threatened species, such as the loggerhead sea turtle, listed as 'Vulnerable' under the IUCN Red List categories (Casale and Tucker 2015).

Satellite tagging has become the most common approach to studying species dispersal and identifying developmental areas of large, highly motile marine animals (e.g.,Godley et al. 2008; Abecassis et al. 2013; Sequeira et al. 2018; March et al. 2020; Kot et al. 2022). In accordance, during the last decades, satellite telemetry

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data allowed assessing movement patterns and habitat use of adult and juvenile loggerhead sea turtles in the Mediterranean Sea (Bentivegna 2002; Cardona et al. 2005, 2009; Revelles et al. 2007a, b; Mansfield et al. 2009; Cardona and Hays 2018; Luschi et al. 2018; Abalo-Morla et al. 2022a). The recent advances and the miniaturization in satellite tags allowed studying the dispersal of sea turtle post-hatchlings (below 40 cm SCL) in the Atlantic (Putman and Mansfield 2015; Mansfield et al. 2014, 2017) and Pacific oceans (Kobayashi et al. 2014; Briscoe et al. 2016; Saito et al. 2018). However, this life stage has been largely neglected in the Mediterranean Sea (see Abalo-Morla et al. 2018, 2022a, b). The few available studies based on satellite-tracked turtles in this region shed some light on post-hatchlings' survival and dispersal, although they were carried out for short time spans and a limited number of individuals (Abalo-Morla et al. 2018). Additionally, previous research about hatchlings dispersal was conducted in the Mediterranean Sea (i.e., Hays et al. 2010; Casale and Mariani 2014; Maffucci et al. 2016; Cardona and Hays 2018), although such studies essentially relied on numerical simulations instead of satellite-tracked individuals. Consequently, there still needs to be more information about preferred developmental and foraging areas for post-hatchlings, particularly those from new nesting places in the western Mediterranean. Knowledge of these preferences will help address potential threats for this life stage in the Mediterranean Sea and implement proper management and conservation measures for the species.

Loggerhead post-hatchling movements result from the combination of physical (ocean currents) and behavioral processes (swimming), which may drive the balance between passive drift to active swimming (Putman et al. 2016, 2018). In order to predict distributions, and the responses to the environmental variability, it is necessary to determine the relative contribution of both processes in the ultimate movement (Putman 2018). It has been generally assumed that hatchlings and small juveniles have limited swimming and diving abilities. Consequently, their dispersal and distribution were assumed to result from passive drifting along prevailing currents (Witherington 2002; Bolten 2003; Hays et al. 2010). However, recent studies support that turtle hatchlings and post-hatchlings have active directional swimming, leading to dispersal routes and distribution differing from those obtained with passive dispersal models (Putman et al. 2012a; Scott et al. 2012; Abecassis et al. 2013; Kobayashi et al. 2014; Christiansen et al. 2016; Robson et al. 2017; Chambault et al. 2019; Le Gouvello et al. 2020; Harrison et al. 2021), even in head-started loggerhead sea turtles, which are turtles reared in captivity for several months before release (Mansfield et al. 2014, 2017).

In this study, we investigated the dispersal and habitat use of loggerhead post-hatchlings. In particular, we used circular statistics to elucidate the existence of preferential bearings and the balance between active and passive swimming, which were studied with linear models and trajectory segmentation. Finally, factors driving habitat selection during post-hatchlings' dispersal have been investigated with habitat models based on decision trees. The study employed satellite-tracking data from 19 loggerhead post-hatchlings from two nests laid on the Spanish Mediterranean coast, released and satellite-tracked between 2016 and 2018. Results from our research provide new insights about loggerhead post-hatchling dispersal and habitat use that will improve conservation and management actions for the species.

Methods

Turtle data and satellite tagging

Loggerhead hatchlings were collected from two nesting events: Clutch A, laid in July 2015 in Almería (Spain), and Clutch B, laid in July 2016 in València (Spain). Several hatchlings from these clutches were reared within the framework of a head-starting program (see details in Table 1). After the head-starting period (which ranged from 9 to 13 months), post-hatchlings for this study ($n = 19$, Table 1) were selected randomly among those with appropriate size for tagging, in which tags are very unlikely to hinder behavior or turtle growth (Mansfield et al. 2012). The individual sizes ranged between 16.6 and 23.0 cm SCL and the weight ranged between 0.9 and 1.2 kg. Post-hatchlings were tagged with small solar-powered platform transmitting terminals (PTT) without duty cycle, model SEATAG-TurtleTag and manufactured by Desert Star Systems LLC (Monterey Bay, CA, USA), following the attachment and tagging procedure described in Abalo-Morla et al. (2018). We used two tags with similar characteristics but different weights: 18 and 26 g but tag weight was below 4% of turtle weight in any case (Mansfield et al. 2014; Abalo-Morla et al. 2018). Except for turtles ID 9 Valencia and 19 Morla, tracking data are publicly available at the EMODNet repository (Abalo-Morla et al. 2022b).

Data acquisition and processing

Location data (LC) were collected using the Argos satellite system and state-space models (SSM) were used to estimate positions from the observed data accounting for measurement errors and variability in movement dynamics (Jonsen et al. 2005, 2007, 2013). A hierarchical correlated random walk-switching state-space model (hDCRWS) was fitted to the data based on the whole dataset (Jonsen et al. 2007, 2016; Christiansen et al. 2016). We used the ‘bsam’ R package (Jonsen et al. 2005) in R 3.6.0 (R Development Core

Table 1 Post-hatchling loggerhead data information: Clutch (A or B), name of each turtle, turtle identity number (ID), weight (kg), straight carapace length (SCL) in cm, total tag weight (g) [which is the sum of both Platform Transmitter Terminal (PTT) tag and attachment material weights], percentage of total tag weight regarding turtles' weight, release date, number of days transmitted [which include all transmissions received with or without location], distance traveled (km) [which is the sum of the minimum distance between all consecutive locations of each turtle] and standard deviation (±sd), mean speed traveled (km/h) and standard deviation (±sd), and incubation type (electric incubator or protected beach)

Clutch	Name	Turtle identity number (ID)	Weight (kg)	SCL (cm)	Total tag weight (g)	% Total tag weight	Release date	Days transmitted	Distance traveled (km) ± sd	Mean speed (km/h) ± sd	Incubation type	Headstarting duration (months)
A	Benicarlo	1	1.526	21.0	45	2.95	19/10/2017	152	2617.3 ± 12.8	0.7 ± 0.5	Electric incubator	13
	Borriana	2	1.839	22.0	49	2.99	19/10/2017	276	5248.5 ± 15.8	0.8 ± 0.5	Electric incubator	13
	Castello	3	1.682	22.2	49	2.91	19/10/2017	285	3681.9 ± 12.0	0.7 ± 0.5	Electric incubator	13
	Cullera	4	1.897	22.4	50	2.64	19/10/2017	69	1244.0 ± 11.7	0.8 ± 0.5	Beach	13
	Denia	5	1.841	22.7	52	2.82	19/10/2017	271	4904.6 ± 13.5	0.8 ± 0.5	Beach	13
	Gandia	6	1.696	22.0	50	2.95	19/10/2017	290	5586.5 ± 11.6	0.8 ± 0.5	Beach	13
	Santa Pola	7	1.178	22.3	56	2.79	19/10/2017	279	5202.2 ± 12.5	0.8 ± 0.5	Beach	13
	Torrevieja	8	1.951	22.2	42	2.15	19/10/2017	339	6834.0 ± 18.3	0.9 ± 0.6	Beach	13
	Valencia	9	1.861	22.8	53	2.85	19/10/2017	181	NA	NA	Electric incubator	13
	Vinaros	10	1.922	23.0	55	2.86	19/10/2017	269	4698.5 ± 12.2	0.7 ± 0.5	Electric incubator	13
B	Cocedora	11	1.013	17.5	26+	NA	16/06/2016	82	3626.6 ± 22.7	3.3 ± 2.7	Electric incubator	9
	Rabiosa	12	1.097	17.5	26+	NA	16/06/2016	83	3743.4 ± 13.8	3.3 ± 2.7	Electric incubator	9
	Pichirichi	13	0.953	16.6	26+	NA	16/06/2016	79	4107.8 ± 17.6	3.9 ± 2.7	Electric incubator	9
	Serena	14	0.879	16.8	26+	NA	16/06/2016	102	4163.5 ± 24.8	2.8 ± 2.6	Electric incubator	9
	Toby	15	0.940	17.0	35	3.72	28/09/2016	106	4381.1 ± 52.5	3.2 ± 2.9	Electric incubator	12
	Dora	16	1.000	17.5	31	3.10	28/09/2016	115	2574.5 ± 85.8	1.7 ± 1.8	Electric incubator	12
	Vendetta	17	1.102	18.1	41	3.72	28/09/2016	108	5580.3 ± 48.0	3.3 ± 2.8	Electric incubator	12
	Bonita	18	1.030	17.5	39	3.79	28/09/2016	123	3981.2 ± 43.7	1.9 ± 1.7	Electric incubator	12
	Morla	19	1.308	18.7	43	3.29	28/09/2016	105	341.3 ± 32.8	1.6 ± 1.8	Electric incubator	12

Hatchlings were kept in a head-starting program after hatching: (i) Clutch A during 13 months in ARCA del mar (Área de Recuperación y Conservación de Animales del mar, Fundación Oceanogràfic de València, Spain); (ii) Hatchlings IDs 11 to 14 from Clutch B during 9 months in CEGMA (Andalusian Marine Environment Management Center, Consejería de Medio Ambiente y Ordenación del Territorio, Junta de Andalucía, Algeciras, Spain); and (iii) Hatchlings IDs 15 to 19 from Clutch B during 12 months in Aquarium of Sevilla (Spain). The release location for Clutch A was on a protected beach in El Saler (València, Spain) [39.32° N, 0.31° W], and on the nesting beach for Clutch B in Pulpí (Almería, Spain) [37.38° N, 1.64° W]. NA means not available data. + means that weight of attachment material was not measured. Unless turtles ID 9 and 19, tracking data are publicly available at the EMODNet repository (Abalo-Morla et al. 2022b)

Team 2019) to create this model. In our fitted hDCRWS model, two Markov Chain Monte Carlo (MCMC) chains for 120,000 iterations were run by dropping the first 60,000 samples as a burn-in and retaining every 10th sample from the remaining 60,000 assumed post-converge samples from each chain to reduce sample autocorrelation. Thus, the model parameters and the estimated locations were calculated using 12,000 MCMC samples. A 24-h time step was used to generate one daily location of the tracking period from the posterior means of the resultant distributions. The resulting SSM locations were post-processed to remove land locations (Arendt et al. 2012; Hoenner et al. 2012).

Dispersal analyses

Trajectories were performed to analyze turtles' movement patterns using the 'adehabitatLT' package (Calenge 2006) in R version 3.6.0 (R Development Core Team 2019). For each daily step length (distance between two consecutive post-processed SSM locations), we obtained a turning angle (angle between two consecutive steps). To identify movement phases characterized by a homogeneous behavior, a segmentation of trajectories was done using the method of Gueguen (2000). We set 15 models corresponding to 15 values of the mean distance traveled by turtles (i.e., from 0 to 100 at an increase rate of 10, 150, 200, 250, and 300 km), with a standard deviation of 3 km. For each trajectory, we computed the probability density for each step to be generated by each model of the set. Then, we estimated the optimal number of segments for each trajectory. In addition, for each track, we computed the segmentation from 2 up to 100 segments, and the pertaining residuals for each segmentation. We also tested the independence of the residuals of each segmentation through a Wald and Wolfowitz test (Calenge 2006). Finally, for each route, we selected a number of segments, based on the closest number to the optimal number of segments estimated in each case for which the Wald and Wolfowitz test suggested independence of the residuals.

The distance traveled and the bearing of each turtle were estimated from the tracks, considering each segment defined by two successive post-processed SSM locations. We obtained sea current velocity components data (meridional,v, and zonal,u) at a 1/24° of horizontal grid resolution from Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu) (Escudier et al. 2020). Sea current magnitude (Mc) and sea current direction (Hc) were estimated from the obtained data through vector computing. Following, sea current velocity component values, estimated sea current magnitude (Mc) and estimated sea current direction (Hc) were extracted along each post-processed SSM turtle track. The observed velocity of a swimming animal (Vf) is the sum of the animal's own velocity (V) and the velocity of the sea current (Vc). To study the turtles' active movements, and separate swimming from drifting, we inferred turtle swimming velocity (V) by subtracting sea current velocity (Vc) from track velocity (Vf) between successive post-processed SSM locations along turtle tracks, for each component value of velocity (Gaspar et al. 2006; Abecassis et al. 2013), following Eq. 1:

$$V = \mathrm{Vf} - \mathrm{Vc} \tag{1}$$

We used the estimated turtle velocity components (Vu and Vv) between two successive post-processed SSM locations to infer the turtle heading (Ht) through vector computing. Therefore, we obtained daily bearing values for each track, which shows the direction of the net displacement between two consecutive days. The existence of turtles' directional bearing was investigated using functions implemented in the R packages 'circular' and 'CircStats' (Agostellini and Lund 2017). Finally, we compared bearing differences among individuals and between Clutches A and B using the multi-sample and standard Mardia–Watson–Wheeler's tests, respectively (Batschelet 1981).

The influence of sea currents on turtles' movement was quantified by computing the sea current assistance between two successive post-processed SSM locations. The method to calculate it was modified from the tail-wind assistance in Åkesson and Hedenström (2000), following Eq. 2:

$$\text{Current assistance} = \mathrm{Mc} \times \cos(\mathrm{Ht} - \mathrm{Hc}) \tag{2}$$

where Mc is the sea current magnitude in km/h, Ht is the turtle heading and Hc is the sea current direction. Details on computing these variables from Copernicus ocean data product are shown above.

To study the influence of sea currents on post-hatchlings trajectories, we used a linear regression model, employing the R function lm, of the estimated sea current assistance and distance traveled by sea turtles between two successive post-processed SSM locations.

Habitat use modeling

We modeled the species habitat use with C5.0 decision trees (Quinlan 1992), a machine learning approach for decision tree induction, to determine the most important variables, their effects, and identify the suitable areas over the entire Mediterranean Sea (i.e., areas or habitats with values of the chosen variables similar to those in the habitats selected by the tracked post-hatchlings). To accomplish with these objectives, habitat use models were optimized to include only a subset of relevant environmental predictor variables able to discriminate satellite-tracking data (i.e., real observations) from a set of random routes (pseudo-absences) generated with random walks based on the collected satellite-tracking data (Hazen et al. 2017, 2021).

Random routes generation

We generated and combined two sets of random routes for each individual. The first consisted of 10 correlated random walks (Codling et al. 2008; Hazen et al. 2021) starting at the releasing date and position and lasting until the day transmission stopped definitively. The second set consisted of 10 reverse correlated random walks (Hazen et al. 2021), with the same duration as the number of days transmitted from each turtle but ending in the last recorded position (20 routes per individual and 30,976 data in total; Supplementary Information S4). In both cases, we obtained the step or distance traveled and the angle by independently resampling the observed angles and displacements of the corresponding individual to generate the random walks (Hazen et al. 2021).

Environmental predictor variables

Based on former literature and data availability (i.e., Hazen et al. 2012; Pikesley et al. 2015; Patel et al. 2021), a set of 14 variables that presumably could influence post-hatchlings dispersal and habitat selection were tested as potential predictor variables: bathymetry, bathymetry slope, sea current magnitude, sea current direction, salinity, sea surface temperature, chlorophyll a, primary productivity, sea surface height, earth magnetic anomaly, eddy kinetic energy, current assistance, month, and individual. Bathymetry data were obtained using the 30 arc-second resolution GEBCO global bathymetric model (GEBCO 2021; Weatherall et al. 2015). Environmental data about ocean currents, salinity, sea surface temperatures, sea surface height (SSH) (Escudier et al. 2020), and chlorophyll-a and primary productivity (Feudale et al. 2021) were obtained at 1/24° of horizontal grid resolution from Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu). We also calculated the frequency of locations by sea surface temperature to observe if there was a preferential temperature niche. In addition, we considered the local variations in the Earth's magnetic field through the Earth magnetic anomaly grid at 2 arc-minute-resolution, which was obtained from the National Oceanic and Atmospheric Administration of the USA (NOAA) (Meyer et al. 2017). Current assistance was obtained as described in Methods (3.3 Dispersal analysis). Eddy Kinetic Energy was computed as following:

$$\text{Eddy Kinetic Energy} = 0.5 \times \rho 0 \times \left(u^2 + v^2\right)$$

where ρ_0 is a constant reference density, which is chosen to be $\rho_0 = 1000$ kg m^{-3} in this study, and v and u correspond to the sea current velocity components (Richardson 1983; Kang and Curchitser 2017). Finally, we considered the temporal changes in the habitat use by including month as a predictor and included the individual to account for intrinsic behavioral differences.

Habitat use modeling with C5.0 decision trees

We used C5.0 (Quinlan 1992), as implemented in the R package 'C50' (Kuhn et al. 2015), to develop the habitat use models. C5.0 is a fast decision-tree induction approach able to deal with different data types (i.e., categorical or continuous) and to model non-linear relationships and variable interactions (Olden et al. 2008), which proved able to outcompete other popular decision-tree induction approaches (e.g., Muñoz-Mas et al. 2016).

Two elements interact with the training dataset and ultimately drive the predictive capability and generalization (i.e., the ability to correctly predict new unseen data) of machine learning approaches: the (hyper-)parameters (i.e., parameters controlling the learning process) and the set of selected predictor variables (Muñoz-Mas et al. 2016). Machine learning approaches rarely render AIC-like indices to rate models. Therefore, we performed hyper-parameter tuning (i.e., adjusted the parameters controlling the tree growth process), to maximize model predictive capability and generalization, and carried out variable selection to determine the most relevant predictors through cross-validation. Cross-validation approaches, such as the k-fold approach used in this study, split the data into k disjoints groups and iteratively use $k-1$ groups to train the model and the k group set out to validate the performance of a given set of variables and hyper-parameters (Arlot and Celisse 2010). Once the different combinations of these two elements are evaluated, a single model is generated employing the hyper-parameters and variables that rendered the best mean/median performance. Turtle routes may present intrinsic behavioral differences and temporal dependencies. Therefore, we split the route series considering these two elements to break down any dependency among the training data (Roberts et al. 2017) (Fig. 1).

Training machine learning approaches on large datasets (e.g., $n = 30{,}976$ data) can be computationally costly (Ozyildirim and Avci 2016). Therefore, to reduce the computational burden during the hyper-parameters' tuning and variable selection, we first ranked the environmental variables using the four algorithms of the Relief family implemented in the R package 'CORElearn' (Robnik-Sikonja and Savicky 2017; Kira and Rendell 1992). Then, we tested different combinations of the parameters *CF* [0.05, 0.45] and minCases [5, 105] and selected the best hyper-parameters after a forward variable selection approach based on the variables rank obtained with the four Relief-based rankings of variables (See Supplementary Information S5 and S6 for additional information about the rank of predictor variables and

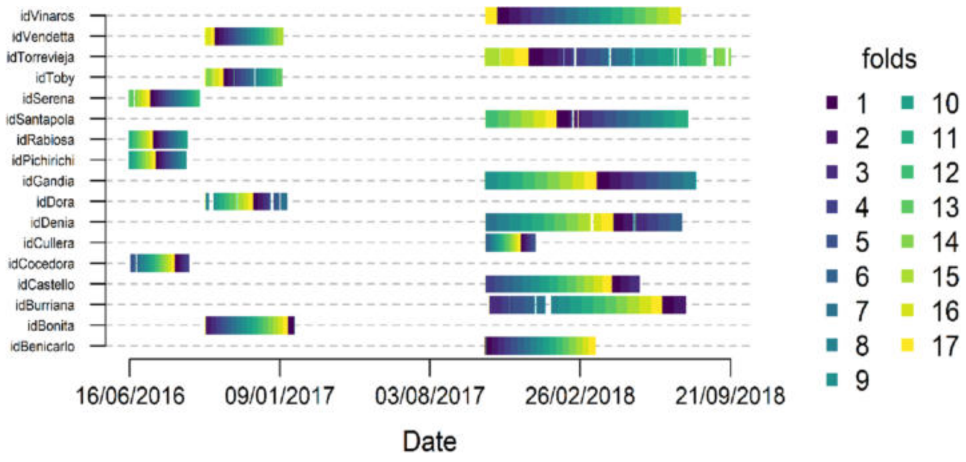

Fig. 1 Period of data collected for each individual considered in the present study. The figure highlights the data partition (folds) used during the process of hyper-parameters' tuning and variable selection through cross-validation used to optimize the habitat use model. Hyper-parameters control the learning process of the habitat model, and each fold corresponds to a set of data set out and used to recursively validate the tested combinations of hyper-parameters for each set of variables

tested hyper-parameters). The data of the observed routes was outnumbered by those of the correlated random walks (1/20). Therefore, we selected the balanced accuracy as the performance criteria to select the most relevant set of variables and hyper-parameters (Muñoz-Mas et al. 2019). When the best hyper-parameters and set of variables were determined, we carried out a sensitivity analysis to scrutinize the modeled habitat suitability (Friedman 2001) and developed habitat suitability maps, based on ten-year variable means (2010–2020), covering the entire Mediterranean Sea. This habitat evaluation over the entire Mediterranean Sea allowed identifying highly suitable areas (not necessarily visited) with similar environmental conditions than the areas frequented preferentially by the satellite-tracked turtles.

Results

Dispersal analyses

Individuals with very sparse and few locations were excluded from movement analyses ($n=2$, turtle IDs: 9 Valencia and 19 Morla). The remaining post-hatchlings ($n=17$) were remotely tracked on average for 174 ± 95 days, $n=17$, and traveled a mean distance of 4246 ± 1331 km, $n=17$, with a resultant mean speed of 1.79 ± 1.21 km h^{-1}, $n=17$ (Table 1). On average, $85\pm17\%$, $n=17$, of locations were off the continental shelf (> 200 m depth). Overall, post-hatchlings dispersed widely around the Mediterranean Sea following highly variable dispersal routes (Fig. 2a), although several differences were observed among clutches (Fig. 2b). Turtles from Clutch A mainly dispersed northwards after release and then moved eastwards, even crossing the Sicilian Channel and reaching the eastern basin (Fig. 2b). Most turtles from Clutch B released in June mainly dispersed southwards after release and dispersed across the Alboran Sea (ID: 11 Cocedora, 12 Rabiosa, and 14 Serena). Turtles from Clutch B released in September followed different dispersal patterns, although two turtles (ID: 16 Dora and 17 Vendetta) dispersed eastwards and reached waters close to the Sicilian Channel (Supplementary Information S1). Nonetheless, considering that post-hatchlings were released from June to September, dispersal patterns along the Mediterranean Basin were quite similar among individuals when considering the month of monitoring (Fig. 2c, Supplementary Information S1). After release, from June to October, turtles from both clutches mainly dispersed along the Spanish coasts, the Alboran Sea and/or the Balearic Sea. During November/December latitudinal displacements to south were observed, mainly located at the Balearic Sea and the Algerian Basin. From December/January, monitored post-hatchlings mainly dispersed eastwards along the Algerian Basin, reaching waters close the Sicilian Strait and even, in several cases ($n=7$), turtles crossed the Sicilian Strait to reach the Eastern Mediterranean Basin. Most long-term tracked post-hatchlings were observed from February/March and further months until stop monitoring dispersing along the eastern basin after crossing the Sicilian Channel. Nonetheless, there was a long-term tracked individual (ID: 5 Denia) which remained in the Tyrrhenian Sea until stop transmission.

Orientation values and mean bearing for each turtle are shown in Supplementary Information S2. Mean turtle's bearing considering all turtles showed that turtles dispersed eastwards (Fig. 3). If we consider clutches separately, no significant difference in orientation was found among individuals from Clutch A (multi-sample Mardia–Watson–Wheeler test, $W=20.969$ d.f $=16$, $P=0.179$). However, turtles from Clutch B, showed differences in orientation among them (multi-sample Mardia–Watson–Wheeler test, $W=43.525$, d.f $=14$, $P<0.001$). Differences in bearing were observed among all individuals (multi-sample Mardia–Watson–Wheeler test, $W=76.208$ d.f $=32$, $P<0.001$) and between nests (Mardia–Watson–Wheeler test, $W=7.9941$ d.f $=2$, $P=0.018$).

Post-hatchlings from Clutch A followed a similar dispersal pattern after release (October to December), traveling

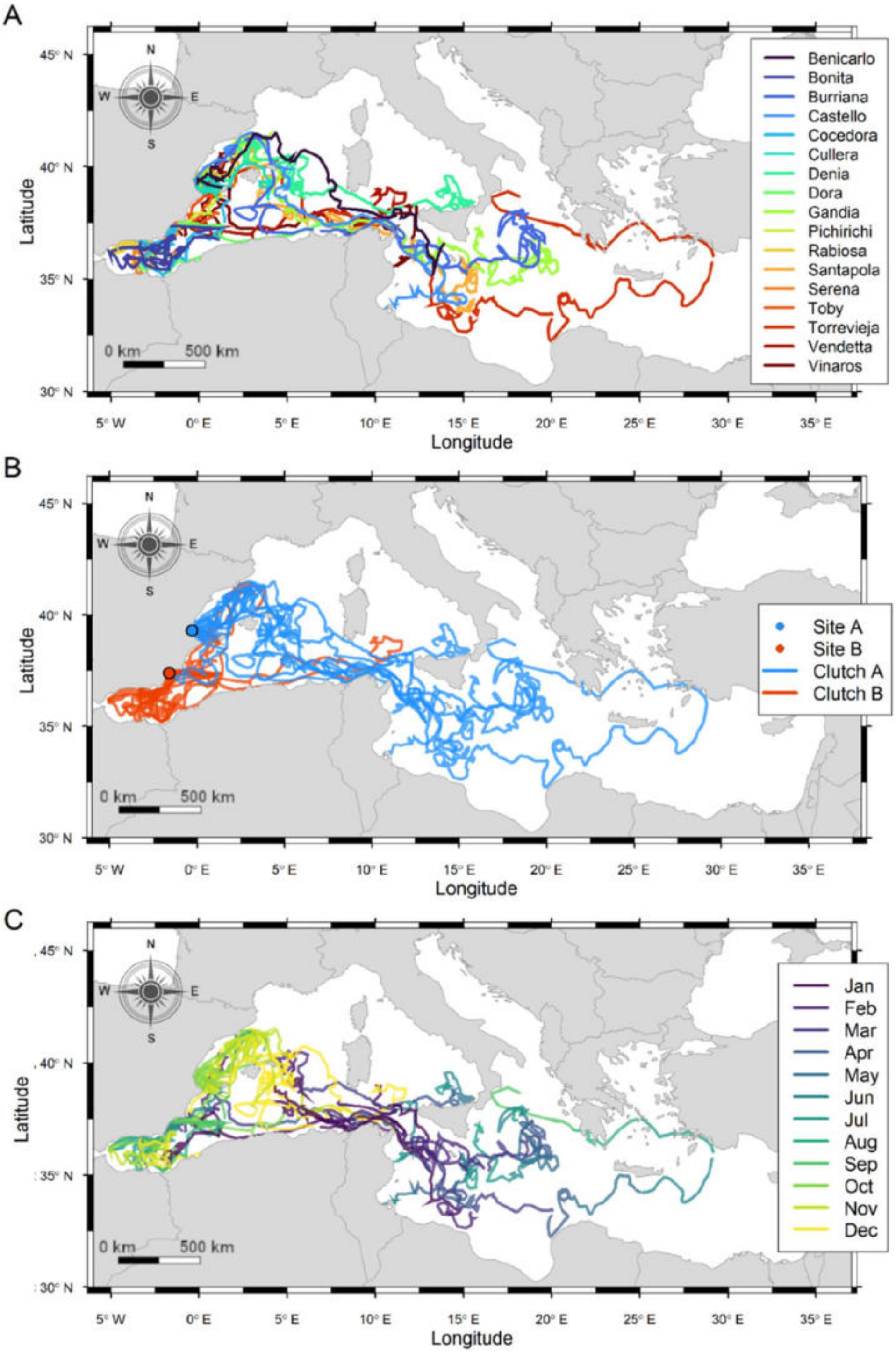

Fig. 2 **a** Turtle trajectories by turtle ID in the Mediterranean Sea. **b** Turtle trajectories by clutch and release location. Clutch A release was at Sueca (València, Spain) [39.32° N, 0.31° W] (blue circle) and Clutch B release was at Pulpí (Almería, Spain) [37.38° N, 1.64° W] (red circle). **c** Turtle trajectories by month of monitoring. Note that turtles were released in June and September (Clutch B) and October (Clutch A). Further details about release dates are shown in Table 1

through the northern waters of the Balearic Archipelago. Besides, long-term monitored post-hatchlings from Clutch A ($n=8$) traveled consistently eastwards, crossed the Sicilian Strait, and reached Central Mediterranean, except turtle ID 5 Denia, that remained in the Tyrrhenian Sea until transmission was lost. Most of these turtles ($n=6$) started traveling consistently eastwards since December/January, and the others ($n=2$) since March. Post-hatchlings from Clutch B presented two types of dispersal patterns after release: remained in the Alboran Sea ($n=7$) or traveled to the Balearic Sea ($n=1$). Long-term monitored post-hatchlings from Clutch B ($n=4$) exhibited different dispersal routes, although two of them traveled consistently eastwards during winter (December to January), similar to post-hatchlings from Clutch A (Supplementary Information S2). Overall, monitored turtles traveled through areas with sea surface

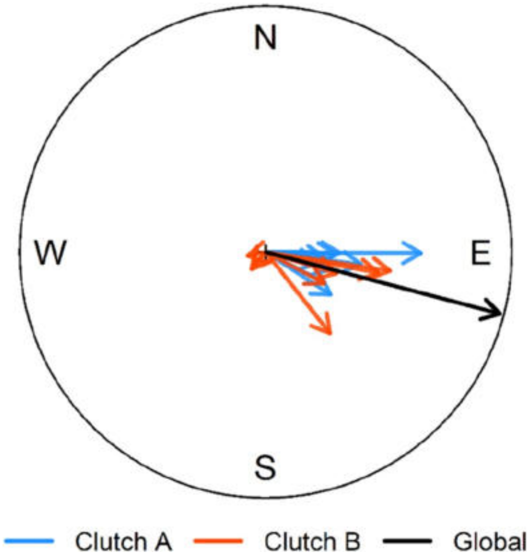

Fig. 3 Mean bearing by turtle and nest. Mean bearing for each turtle is represented by arrows (blue: turtles from Clutch A; red: turtles from Clutch B). Black arrow shows overall mean bearing. The length of vectors are proportional to the *r*-value obtained. Letters are cardinal points

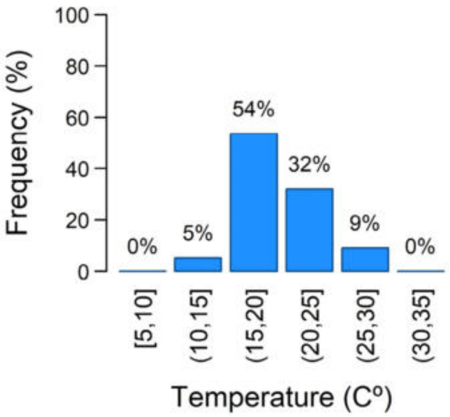

Fig. 4 Frequency (in percent) of turtles' locations by sea surface temperature ranges. Percentage of locations is above, and below each temperature range

temperatures ranging between 10 and 30 °C and most locations were located on waters with temperatures above 15 °C (95%) (Fig. 4). Daily mean sea surface temperatures in the Mediterranean Basin over the period of satellite-tracking ranged between 5 and 32 °C.

Turtles alternated among faster and slower movement phases during their monitoring (Fig. 5). The residuals of track segmentation analysis were independent in all turtles confirming the validity of the approach, as the elements of the sequence were mutually independent (Wald and Wolfowitz test $P > 0.05$), except one of them (turtle ID 7 Santapola), whose trajectory could not be significantly segmented in different movement phases.

Monitored turtles showed both active dispersal and passive drifting. Turtles traveled both long and short distances along the sea currents (in cases, even faster than sea current velocity) or against them (Fig. 6, Table 2, Supplementary Information S3). We removed from this analysis 16 data with daily distances above 100 km, as when such long distances are involved, a single current vector is not a reliable estimation of the currents encountered by tracked turtles. Current assistance values were around zero, suggesting that turtles traveled along or against sea currents.

Habitat use modeling

The process of hyper-parameters' tuning and the variable selection through of cross-validation indicated that the most relevant predictors were, in decreasing order, the individual (ID), sea surface temperature, salinity, bathymetry, the month of monitoring, and sea surface height, sea current magnitude and primary production were of minor importance (Supplementary Information S5 and S7). The sensitivity analysis indicated a temperature threshold at 15 °C because the probability of presence (suitability) was very low (<0.2) below this limit (Fig. 7). The higher suitability was observed above 39 ‰ salinity and the lowest suitability occurred below 37 ‰. Waters above deeper areas exhibited higher suitability for post-hatchings, especially in areas more than 3000 m deep, where the suitability was higher. Sea surface height, current magnitude, and primary production, although selected, were of minor relevance, as their influence depended on the clutch/individual and did not exhibit any clear and common selection pattern.

The habitat suitability maps by month indicated that the Eastern Mediterranean Sea (Ionian Sea and Levantine Sea) might be key year-round developmental areas for post-hatchlings (Fig. 8). Other suitable areas for loggerheads post-hatchlings were only for certain periods/seasons: the Tyrrhenian Sea (from April to December), the Sicilian Channel (from July to October), the Algerian Basin (during September, October and January), the North Adriatic Sea and the Gulf of Lion (from July to August), and the South Adriatic Sea (during September). Mediterranean Sea areas are detailed in Supplementary Information S8.

Discussion

Satellite-tracked loggerhead post-hatchlings dispersed over large areas, traveled long distances, exhibited highly variable routes, and showed an eastward directional movement, as in other similar studies (i.e., Okuyama et al. 2011; Mansfield et al. 2014, 2017; Abalo-Morla et al. 2018, 2022a). Only

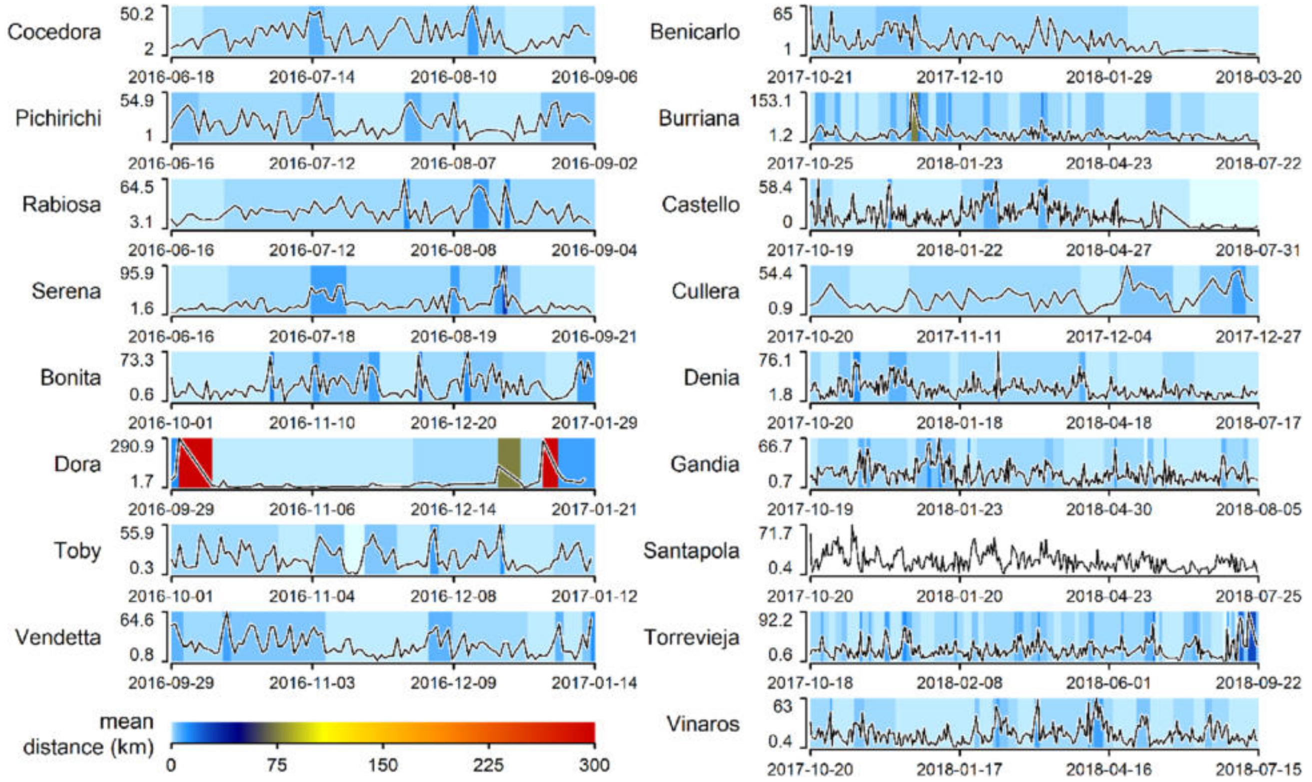

Fig. 5 Movement segmentation analyses of trajectories for post-hatchlings of loggerhead sea turtle. Y-axis represents the mean distance traveled by turtles in km. X-axis shows date and time. Black lines show the mean distance traveled per day. Background colors indicate the movement model as shown in legend. Track segmentation analysis is shown only if significant. Turtle identity (ID) is shown next to each segmentation

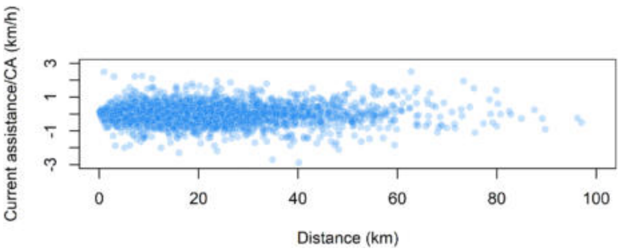

Fig. 6 Distance traveled by turtles (km) and current assistance (km/h) experienced by turtles. Negative values of current assistance indicate that turtles traveled against sea current, and positive values of current assistance indicate that turtle traveled along sea currents

Table 2 Linear model used to test the relation among the current assistance and the distance traveled by turtles

	Model
Linear model	Current assistance = A × Distance + B
P	0.9925
Adjusted R^2	− 0.0003353

Obtained adjusted squared *R* values (Adjusted R^2) and *P*-values (*P*) are shown

three turtles from Clutch B did not dispersed consistently to the east and remained in the Alboran Sea until transmission was lost. This result might be influenced by possible post-hatchlings genetic differences as nesting females in the Spanish Mediterranean Coast may have Mediterranean or Atlantic origin, and multiple paternities in the same clutch were observed in most cases (Carreras et al. 2018). Previous studies satellite-tracking loggerhead juveniles (Revelles et al. 2007a), and post-hatchlings, from Spanish nests revealed the absence of directional movement over the entire monitoring period (Abalo-Morla et al. 2018), although in this last study track duration was in general much shorter than those analyzed in the present study, especially during the coldest months in western Mediterranean.

Our findings suggest that active dispersal movements of loggerhead post-hatchlings in the Western Mediterranean are more relevant than expected, as was observed in recent studies in the Atlantic and Pacific oceans (Mansfield et al. 2014, 2017; Putman and Mansfield 2015; Briscoe et al. 2016; Chambault et al. 2019). In the Mediterranean Sea,

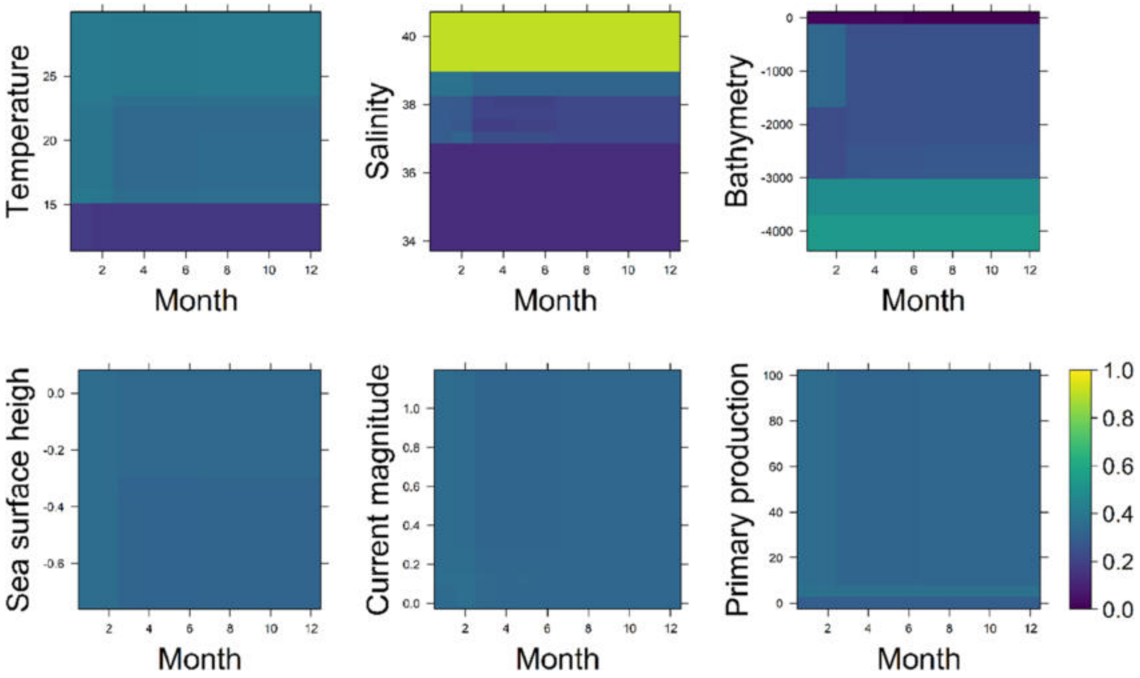

Fig. 7 Suitable habitat probability of loggerhead post-hatchlings by environmental variables and month. Units of variables: temperature is in °C, salinity in ‰, bathymetry in meters (m), sea surface height in m, current magnitude in m/s, and primary production in mg/m^3.day. Color scale of probability is shown at right

previous studies have suggested that strong currents (i.e., Algerian Current) may force immature loggerheads to drift along them (Revelles et al. 2007b). However, we observed that turtles swam actively, rather than passively, and even at a higher velocity than ocean currents, probably driven by their physiological need to remain in (or travel to) suitable developing areas, which altogether emphasizes previous observations (Chambault et al. 2019).

Our results support that post-hatchlings had the ability to disperse long distances, enabling them to travel across vast areas and reach any part of the Mediterranean Sea. However, turtles did not reach specific regions such as the Adriatic Sea or the North Ligurian Sea. This outcome may be attributed to their avoidance of these areas, possibly due to colder sea temperatures, as suggested by Maffucci et al. (2016). We recorded for the first-time post-hatchlings from Spanish nests crossing the Sicilian Channel and reaching the Eastern Mediterranean Basin, where seawater temperatures are warmer than in other Mediterranean Sea regions. A limited exchange between the two eastern and western Mediterranean basins has been traditionally estimated for hatchlings and post-hatchlings originating in the western Mediterranean. Consequently, turtles would be expected to be retained in the South Tyrrhenian Sea (Maffucci et al. 2016), which is considered an important foraging and overwintering area, due to the presence of volcanic islands and seamounts (Blasi and Mattei 2017; Luschi et al. 2018; Chimienti et al. 2020). By contrast, although the timing of movements away from the beach of our tracked post-hatchlings could not correspond to that of the natural hatchling dispersal, our results showed that at least seven of our tracked turtles were able to pass through the Sicilian Channel to reach de Eastern Mediterranean Basin, and only one post-hatchling was retained in the South Tyrrhenian Sea, proving the dispersal capability of post-hatchlings to reach an appropriate developmental area. No post-hatchling crossed the Gibraltar Strait during the monitoring period, which supports the hypothesis that small loggerheads (< 36 cm) are unlikely to cross the Gibraltar Strait toward the Atlantic Ocean (Revelles et al. 2007c; Abalo-Morla et al. 2018). However, ongoing studies on new satellite-tracked post-hatchlings could show different dispersal patterns due to the exceptionally high sea surface temperatures recorded in the 2020–2022 period at the western Mediterranean.

Turtles make latitudinal displacements to forage and escape extreme temperatures (Hawkes et al. 2011; Zbinden et al. 2011) in order to remain in their suitable temperature thermal range (Chambault et al. 2019), as we observed in our satellite-tracked post-hatchlings during the periods of coldest sea surface temperatures. Such latitudinal displacements were observed between November and January mainly at the Balearic Sea or the Algerian Basin. The habitat model corroborated that seawater temperature is an important variable driving the species habitat selection,

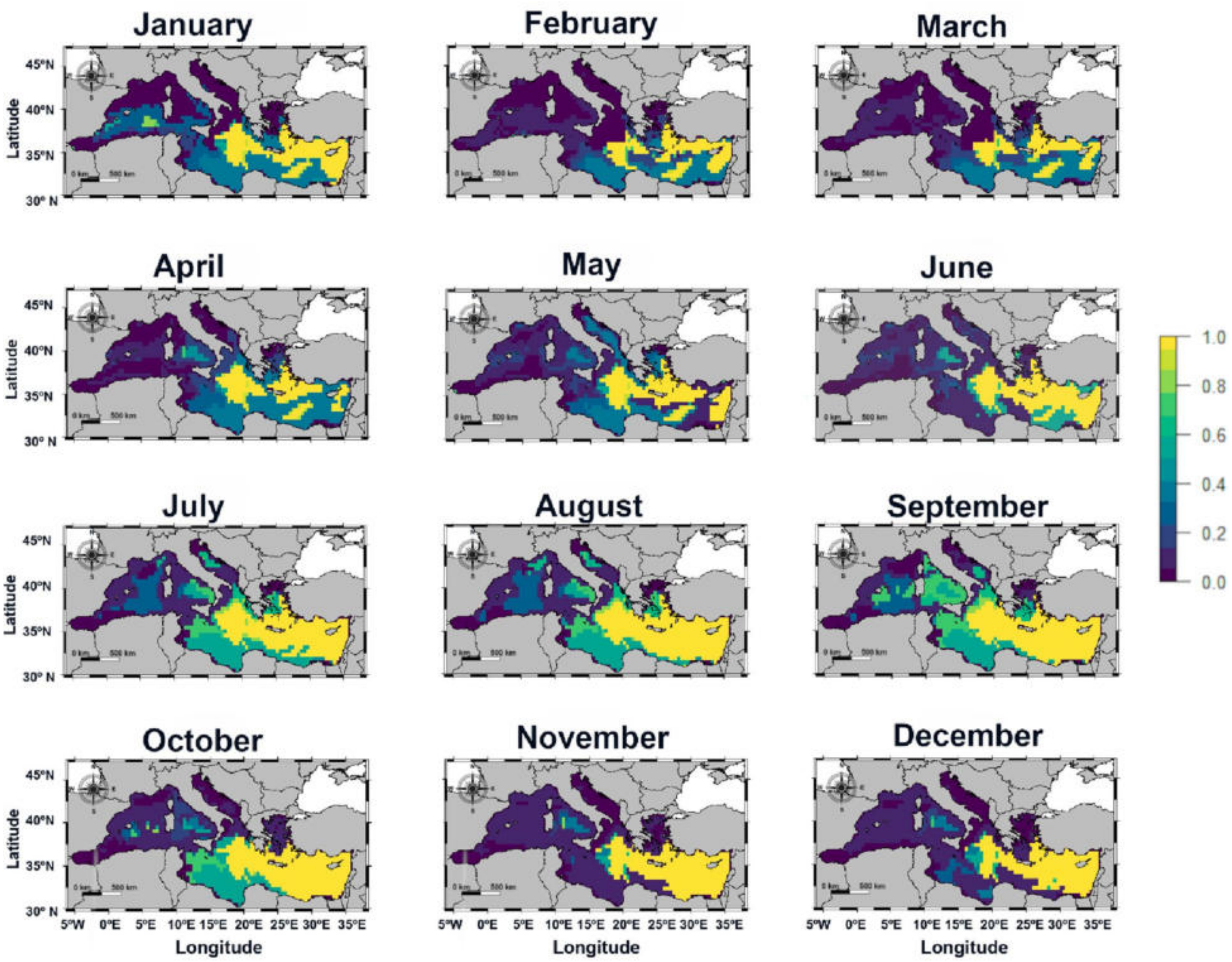

Fig. 8 Monthly habitat suitability maps for loggerhead post-hatchlings in the Mediterranean Sea (0 = unsuitable and 1 completely suitable). Habitat evaluation is based on ten-year variable means (2010–2020) covering the entire Mediterranean Sea

especially during its early life stage (Mansfield et al. 2009; Varo-Cruz et al. 2016). It has been observed that marine turtles select temperatures which maximizes its growth and swimming capability between 30 and 10 °C, which has been established as the threshold before hypothermic stunning (O'Hara 1980; Coles and Musick 2000). In concert with these results, our habitat model established a temperature threshold at 15 °C, and our tracked post-hatchlings traveled along sea surface areas across the expected temperature range (10–30 °C), supporting the aforementioned studies (Coles and Musick 2000; McMahon and Hays 2006; Abecassis et al. 2013; Patel et al. 2021).

The habitat model indicated the preferential use of high salinity areas most probably due to the typical higher seawater salinity concentrations found in the Eastern Mediterranean Basin (Ionian Sea and Levantine Sea) where likely developmental areas are placed. Although the physiological causes of this preferential use are less clear, this result disagrees to previous studies, which concluded that loggerhead sea turtles of Atlantic origin show high fidelity to low salinity regions (Carreras et al. 2006). Further genetic studies will allow elucidating whether these preferences are conditioned by the origin of the individuals or are general for the species or are caused by the spatial arrangement of seawater salinity concentrations in the Mediterranean Sea.

The habitat model also indicated that post-hatchlings in the Mediterranean Sea spent more time in oceanic areas over deep areas and generally avoided neritic zones. This result support that post-hatchlings belong to the oceanic phase of sea turtle life history (Bolten 2003; Mansfield et al. 2014), which suggests that early life stages of turtles can spend more than a decade in the open ocean (Chambault et al. 2019). Other predictor environmental variables, of minor relevance in this study, might be important when considering the individual separately. Former studies in the Pacific Sea found that satellite-tracked juvenile turtles were distributed in more productive waters (Polovina et al. 2006; Abecassis et al. 2013). By contrast, in the Western Mediterranean Sea, immature turtles did not aggregate in productive areas, probably because those regions are not more favorable than the adjoining areas or because immature turtles fail to recognize them (Revelles et al. 2007b). However eastern Mediterranean waters are very oligotrophic when compared to western Mediterranean waters (Bosc et al. 2004). Sea surface height has been related with seawater productivity, but only larger turtles respond to variations in sea surface height in the Mediterranean Sea (Eckert et al. 2008). Furthermore, despite previous studies suggested the effect of the Earth's magnetic field over dispersal of small loggerheads due to their innate magnetic sense (Lohmann et al. 2012; Putman et al. 2012b; Scott et al. 2012), our results showed that other environmental variables had a stronger effect in post-hatchlings dispersal. However, it should be noted that the directional headings we observed in our satellite-tracked turtles are consistent with the navigational behavior hypothesized for sea turtles (Putman and Mansfield 2015).

Recorded loggerhead sea turtle nesting events in western Mediterranean took place from June to September, and hatchlings emergence occurred from July to October (Tomás et al. 2002, 2008; Bentivegna et al. 2008; Benabdi and Belmahi 2020; González-Paredes et al. 2021). Considering these emerging dates, the predictions obtained with the habitat suitability model, point out the Algerian Basin and the Sicilian Channel as suitable habitats for loggerhead post-hatchlings during the period after emergence (from July to October), although this result could be biased by the release date of our monitored turtles. Nonetheless, our results support our hypothesis that post-hatchlings from western Mediterranean nests disperse eastwards after entering the sea, probably driven by environmental conditions (i.e., temperature) and occasionally taking advantage of sea currents, in order to reach suitable developmental areas in the eastern Mediterranean.

The predictions carried out with the habitat model evidenced how the Eastern Mediterranean Basin, especially the deep waters of the Ionian Sea and the Levantine Sea are key year-round developmental areas for loggerhead post-hatchlings from western Mediterranean nests. These regions, and their environmental conditions, coincide with the historical nesting areas of the loggerhead sea turtle in the Eastern Mediterranean Sea (Tomás et al. 2008; Maffucci et al. 2016; Carreras et al. 2018; Hochscheid et al. 2022), which suggests the process of adaptation to the new conditions encountered in the western Mediterranean is an ongoing phenomenon. Nonetheless, the tagged post-hatchlings actively sought the conditions (habitats) they would have encountered in the historical nesting areas. This conclusion can be most probably extended to post-hatchlings from eastern Mediterranean as such basin is also a known foraging ground for adults of loggerhead turtle (Zbinden et al. 2008; Schofield et al. 2010; Mingozzi et al. 2016; Almpanidou et al. 2022). Other suitable areas identified in this study were the Algerian Basin and the deep waters of the Sicilian Channel, which are presumably foraging grounds for the loggerhead turtle (Bentivegna 2002; Casale et al. 2012). Nevertheless, further research is needed to fully understand the movement patterns not only of post-hatchling but also of hatchling loggerheads in the western Mediterranean to develop more effective conservation strategies for the species. To achieve this goal, it will be necessary to improve the monitoring technologies to track sea turtle hatchlings since their emergence, and over longer periods of their oceanic stage. Nevertheless, our results provide the first picture about the habitat use and the preferred developmental areas for loggerhead post-hatchlings from Spanish nests.

Conclusions

The present study contributes to fill the gap in the knowledge about dispersal and habitat use of post-hatchlings from recent nesting events in Spain (western Mediterranean). Head-started post-hatchlings dispersed over large areas and showed active swimming phases, as they frequently dispersed against sea currents. They traveled consistently eastwards and, for the first time, we observed they reached optimum developmental areas in the Eastern Mediterranean Sea. Habitat models corroborated that the eastern Mediterranean (Ionian Sea and Levantine Sea) are key year-round developmental areas for loggerhead post-hatchlings, and probably also for hatchlings, from western Mediterranean nests. Consequently, the Sicilian Channel and the Algerian Basin could be important seasonal transit areas for these post-hatchlings in the way to reach the Eastern Mediterranean Basin after emergence. Our results may have implications on the loggerhead sea turtle management and conservation strategies, especially about the areas where conservation efforts should be applied for the early life stages of loggerhead sea turtle coming from potential new breeding areas in the western Mediterranean.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-023-04285-2.

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Author contributions All authors contributed to the study conception and design. Material preparation and satellite tagging were performed by EB, JT, and SA-M. Data collection was done by SA-M and EB. Data analysis was performed by SA-M and RM-M. The first draft of the manuscript was written by SA-M and all authors revised and made inputs on the manuscript. All authors read and approved the final manuscript for publication.

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Data availability The datasets generated during and analyzed during the current study are available in the EMODNET repository, https://cloud.emodnet-ingestion.eu/index.php/s/wF4jn2ypDiAgJ2U. Only data from two satellite-tracked turtles (ID 9 Valencia and 19 Morla) are not publicly available in repository. Data from these turtles were not used in analysis due to sparse and few locations, likely due to tag malfunction.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval The authors declare that animals were treated according to all applicable international, national, and/or institutional guidelines for the care and use of animals. Animal ethics approval was granted by Universitat Politècnica de València. Tagging of post-hatchlings was done under permit from local environmental authorities (Generalitat Valenciana, Generalitat de Catalunya, and Consejeria de Medio Ambiente y Ordenación del Territorio de la Junta de Andalucía).

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