Received: 6 January 2021 | Revised: 1 March 2022 | Accepted: 11 March 2022

DOI: 10.1002/aqc.3815

RESEARCH ARTICLE

WILEY

Seasonal niche and spatial distribution modelling of the loggerhead (*Caretta caretta*) in the Adriatic and Ionian seas

Arianna Zampollo[1,2] | **Antonella Arcangeli**[3] | **Matteo Costantino**[1] | **Chiara Mancino**[1,4] | **Roberto Crosti**[2] | **Guido Pietroluongo**[1,5] | **Cristina Giacoma**[6] | **Marta Azzolin**[1,6]

[1]Gaia Research Institute Onlus, Turin, Italy

[2]School of Biological Science, University of Aberdeen, Aberdeen, UK

[3]ISPRA, Department for Biodiversity Conservation and Monitoring, Rome, Italy

[4]Biology and Biotechnology Department "Charles Darwin", University of Rome, Rome, Italy

[5]Biomedicine and Food Science Department, University of Padua, Legnaro, Italy

[6]Life and System Biology Department, University of Turin, Turin, Italy

Correspondence
Arianna Zampollo, Gaia Research Institute Onlus, Corso Moncalieri 68B, 10133, Turin, Italy.
Email: zampolloarianna@gmail.com

Abstract

1. Although *Caretta caretta* is the most common turtle in the eastern Mediterranean Sea, its distribution is relatively difficult to assess due to the lack of data in offshore waters.
2. The ecological niches in the central-southern Adriatic Sea and the north-eastern Ionian Sea were investigated for loggerhead turtles with body sizes ≥20 cm during two periods: winter (W), which includes months from October to March, and breeding–nesting (BN), from April to September. Differences in the spatial distribution of loggerheads were explored between periods, and the environmental predictors driving habitat selection were examined.
3. Loggerheads mainly select habitats within the continental shelf (<200 m) differently, and exhibit: (i) a generalist behaviour in the Adriatic subregion during BN and a specific selection of environmental conditions during W; and (ii) a specialist behaviour in the Ionian Sea. The Adriatic niche appeared as an important foraging ground year-round, whereas the distribution of suitable areas in the Ionian Sea is patchy and limited to specific habitats close to shore. Extreme values of sea surface temperatures (SSTs) from October to March (W) influenced loggerhead distribution differently in the subregions: areas experiencing cold and warm SST peaks were selected, respectively, in the Adriatic and Ionian subregions. Moreover, SST in April largely contributed to defining the habitat suitability in BN for both subregions
4. This study further confirms the importance of the Adriatic and Ionian seas for the conservation of loggerhead sea turtles and the need for seasonal investigations to establish effective conservation measures. Here, the use of a cost-effective method (fixed line transects from ferries) to inform the distribution of sea turtles in offshore waters is a valuable methodology for long-term seasonal investigations of the habitat use of sea turtles.

KEYWORDS

breeding–nesting, habitat use, Maxent, Mediterranean Sea, SST, thermal ecology, winter

1 | INTRODUCTION

The loggerhead sea turtle (*Caretta caretta*) is a globally distributed species throughout the subtropical and temperate regions, where multiple types of threats affect its conservation status (Wallace et al., 2010). In the Mediterranean bio-region, the loggerhead turtle has been assessed as Least Concern (Casale & Tucker, 2017) due to decades of intensive conservation programmes on nesting sites, although recently an increasing level of anthropogenic and climatic threats (e.g. habitat degradation, habitat shift due to climate change, parachute underwater entrapment, entanglement in fishing gear, and ingestion of marine litter) has amplified the population's vulnerability. Reports from the EU member states for the period 2013–2018 (Article 17 of the Habitat Directive) assessed the overall conservation status of *C. caretta* as Unfavourable–Inadequate in the bio-region Marine Mediterranean (https://nature-art17.eionet.europa.eu/article17), revealing a high level of uncertainty in assessing population trends and its habitat use.

Loggerhead turtles exhibit a complex life cycle comprising a number of different stages (Bolten, 2003). The standard life-history model describes juveniles, subadults, and adults selecting for suitable areas that can be hundreds of kilometres apart through long-distance migrations (Casale et al., 2007; Revelles et al., 2007; Scales et al., 2015). Juveniles prey upon epipelagic animals occurring at oceanographic features such as gyre systems and oceanic fronts, whereas adults and subadults are known to have a higher site fidelity to neritic habitats (Polovina et al., 2000; Bolten, 2003; Scales et al., 2015). However, this model is flexible in the Mediterranean Sea, where juveniles and adults can switch their preferences and move between neritic (Casale & Simone, 2017; Haywood et al., 2020) and oceanic (Bentivegna, 2002; Zbinden et al., 2008; Schofield et al., 2010; Casale et al., 2012a; Hays, Mazaris & Schofield, 2014; Casale et al., 2020) habitats. To date, oceanic nursery areas for post-hatchlings and juveniles (<40 cm) are still unknown within the Mediterranean basin due to the difficulties in observing these stages at sea (Casale et al., 2018).

The Adriatic Sea (north-east Mediterranean Sea) is one of the four main dispersal/aggregation areas for loggerhead turtles that come from the nesting sites on the western Ionian beaches (Casale & Mariani, 2014), as well as a recognized hotspot of sea turtles year-round (Arcangeli et al., 2019). Aerial surveys performed during summer and winter (W) in 2009 reported a summer estimate of 4,083 animals at the surface (coefficient of variation (CV) = 14.59%; 95% confidence interval (CI) = 3,061–5,466), and a much lower estimate of 237 animals (CV = 34.33%; 95% CI = 122–461) during W (Lauriano et al., 2011). However, the habitat uses and the areas occupied by adults, juveniles, and rookeries throughout the year are less well investigated. Several studies reported inconsistent results in defining which foraging ecology (Bjorndal, 1996) is preferred by loggerheads inhabiting this region, which may be explained by seasonal selection of the foraging grounds by this species. Seasonal changes in loggerhead occupancy were recorded mainly in the northern (Zbinden et al., 2008; Zbinden et al., 2011; Casale et al., 2012a; Luschi et al., 2013; Schofield et al., 2013) and central (Luschi et al., 2013; Casale & Simone, 2017) Adriatic Sea, where a general pattern indicates turtles moving from deep offshore areas during W to shallow feeding grounds in summer (Broderick et al., 2007; Casale & Simone, 2017). During summer, movement patterns are mainly recorded in adults migrating from Ionian nesting sites to Adriatic foraging grounds at the end of the breeding season (July–August for females, May–June for males) (Zbinden et al., 2011; Schofield et al., 2013). On the other hand, though the Ionian coastline is recognized as nesting grounds, loggerheads nesting on the Adriatic beaches are rarely documented (citizen science records for Puglia, Abruzzo, Marche, and Molise, www.tartapedia.it; Mancino et al. (in preparation) listed all the nesting sites from 1960 to 2020 in the Mediterranean Sea). The Adriatic Sea is used by post-nesting and post-hatching turtles to overwinter in the proximity of easily available resources (Lazar, Margaritoulis & Tvrtković, 2004; Maffucci, Kooistra & Bentivegna, 2006). Recent studies identified the spatial overlap of adults and juveniles within the Adriatic Sea, where neritic and pelagic grounds offer both oceanic and neritic foraging strategies interchangeably (Casale & Simone, 2017; Haywood et al., 2020). In particular, the neritic area within the Adriatic Sea (depth <200 m) is an important foraging ground for both adults and juveniles (Casale et al., 2012a; Luschi et al., 2013; Casale & Simone, 2017) that tend to overwinter close to food resources (Zbinden et al., 2008; Schofield et al., 2013). Haywood et al. (2020) indicated that juveniles adopt oceanic and neritic foraging strategies interchangeably in the Adriatic Sea, feeding on a small range of foraging grounds and/or exhibiting a strong fidelity to the same geographical region. A stronger site fidelity is also found in juveniles feeding in neritic grounds (Casale et al., 2007; Revelles et al., 2007; Cardona et al., 2009; Casale et al., 2012b) than those individuals distributing in oceanic waters (Schofield et al., 2010).

The Ionian Sea has a shallow western region over the continental shelf that is separated from the oceanic zone (the deepest point at 5,267 m) by a steep continental slope. The Greek islands over the continental shelf are some of the most important nesting sites for loggerhead turtles in the Mediterranean Sea (Margaritoulis et al., 2003), with their proximity to oceanic grounds in the Ionian/South Adriatic. The Ionian basin is an important oceanic ground for juveniles during their developmental stages (Margaritoulis et al., 2003; Casale et al., 2005) that prompts the residency of post-nesting and post-hatching individuals due to the near location of an oceanic ground (south Adriatic/north Ionian), a neritic ground (north/central Adriatic), and a reproductive ground (Ionian coastlines) (Casale et al., 2007). The connection of Greek nesting sites and the northern Adriatic Sea is maintained via nearshore migration pathways (Casale et al., 2007; Luschi & Casale, 2014), especially by adult females (Lazar, Margaritoulis & Tvrtković, 2004), while genetic inflow and outflow in the Adriatic-Ionian region are maintained by migratory corridors in the oceanic waters of the Ionian Sea linking the eastern and western Mediterranean basins (Bentivegna, 2002; Schofield et al., 2013).

Since the current Habitats Directive 92/43/EEC and Marine Strategy Framework Directive 2008/56/EC require baseline information on the conservation status of protected species through standardized sampling and analytical methods, the potential use of monitoring carried out by fixed line transects (FLTs; Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), 2015) was investigated to assess the habitat use of individuals with life stages having body size ≥20 cm divided into two biological seasons: breeding–nesting (BN; April–September) and winter (W; October–March). This study aims to (i) model and predict the spatial distribution of *C. caretta* during two biological seasons in each subregion (Ionian and Adriatic seas), (ii) quantify the rates of overlap among the predicted distributions during the two seasons in each subregion, (iii) highlight differences among subregions and biological seasons, and (iv) characterize which environmental variables define the loggerhead turtle's niches within the seasons and subregions investigated. Two different analytical approaches—a within outlying mean indexes (WitOMI) analysis (Karasiewicz, Dolédec & Lefebvre, 2017) and Maxent predictions (Phillips & Dudík, 2008)—were used to authenticate the reliability of the outputs and maximize the information derived from an FLT dataset. The WitOMI analysis explored the ecological characteristics (marginality and tolerance) of niches (subregions) and subniches (biological seasons) by measuring their position in an *n*-dimensional space defined by environmental conditions, whereas Maxent predictions visualized the extension and occupancy of suitable areas for loggerhead turtles and their changes over time. Both WitOMI and Maxent methods inform on the influence of environmental variables on habitat selection, whose output's consistency was checked. To date, understanding the environmental conditions driving the habitat selection during W and BN, combined with predicting the extent of the area occupied by this species, is necessary to adopt proper management plans, including monitoring different life-stages and developing strategies to preserve the ecological features that define the niches occupied by the loggerhead turtles.

2 | METHODS

2.1 | Sea turtle data

From December 2014 to February 2018, data were collected along FLTs (ISPRA, 2015) in the central-southern Adriatic Sea and the north-eastern Ionian Sea (Figure 1) by employing ferries as a platform of observation. Monitoring activity was carried out for 3 days each month onboard cruises with no stops between Ancona in Italy and Patras in Greece. The analyses were performed with only on-effort tracks defined by monitoring during daytime with standard weather conditions (wind ≤3 on the Beaufort scale; sea ≤3 on the Douglas scale). Four observers recorded the GPS location of turtles following the ISPRA protocol for FLTs; see ISPRA (2015) and Arcangeli et al. (2020) for details. Data were collected from both sides of the ferry from the command deck (20 m above sea level) within a buffer of 50 m from each side. The GPS coordinates were not adjusted with the distance between the deck and the sighting, since further analyses were based on a resolution lower than 50 m (4 × 4 km^2 grid; see Section 2.2 for details). The size of turtles that is visible from the deck is estimated as ≥20 cm over the straight carapace length. Similar studies have reported this estimate (Arcangeli et al., 2020; Atzori et al., 2021) and compared the carapace with known litter items floating at sea (Arcangeli et al., 2020).

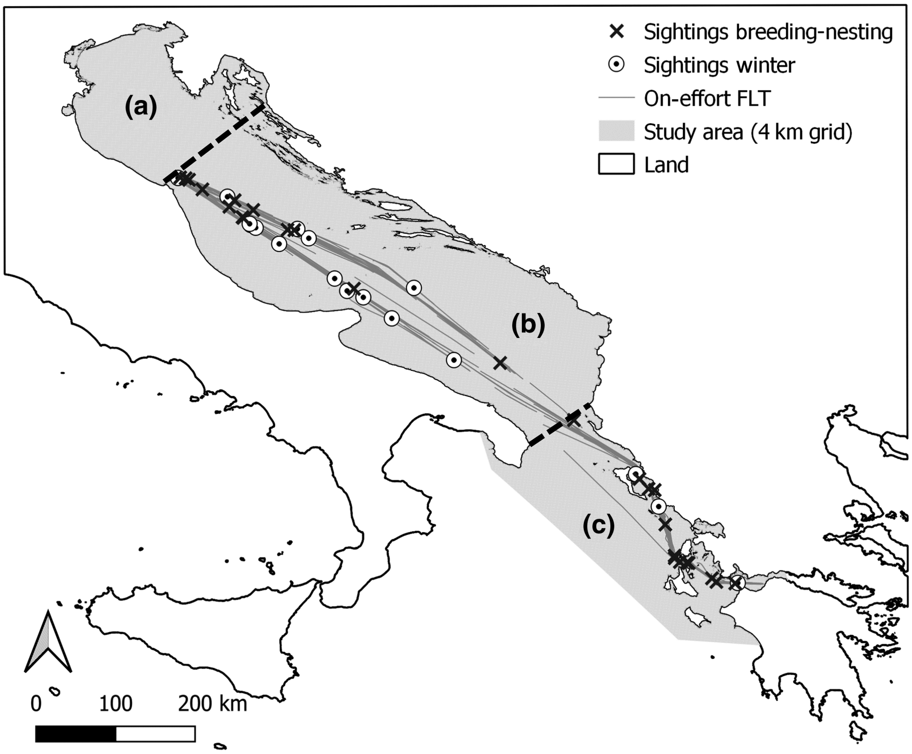

FIGURE 1 Map summarizing the sightings in the breeding–nesting (black cross) and winter (pointed circle) periods and the on-effort monitoring tracks (grey lines). The study area was divided into three subregions: northern (a) and central-southern (b) Adriatic Sea, and north-eastern Ionian Sea (c). The spatial domain of the Maxent and the within outlying mean indexes analyses is reported in light grey and includes the central-southern Adriatic Sea and the north-eastern Ionian Sea

The occurrence rate of sea turtles was estimated for the Adriatic–Ionian region by measuring the number of sightings per unit effort (SPUE) within the cells of a 4 × 4 km^2 grid overlaying the study areas (Figure 1) (see Section 2.3.1 for details about the spatial domain selection for Maxent predictions). The number of sightings and the kilometres of on-effort tracks were reported into each cell to measure SPUE. The seasonal distribution of loggerheads has been investigated by gathering loggerhead sightings into two 'biological seasons': W (October to March) and BN (April to September). Although the individuals sighted in this study may not be in reproductive phases, the sightings were divided into two periods characterized by different environmental conditions, loggerhead turtle behaviour, and availability of resources to check if differences in spatial distributions were occurring. A finer temporal resolution was not possible due to the limited number of sightings.

2.2 | Environmental variables

Topographic and oceanographic predictors were selected amongst the available and ecologically relevant environmental variables. Several studies have reported the effects of sea productivity and sea surface temperature (SST) on diving patterns in sea turtles (Iverson et al., 2019), overwintering (Hochscheid et al., 2007; Hochscheid, 2014), nesting phenology (Mazaris et al., 2004; Mazaris et al., 2009), and reproductive performance (Mazaris et al., 2008). The spatial domain (Figure 1) was overlapped with a 4 × 4 km^2 grid (see Section 2.3 for details) and the environmental conditions were reported for each cell of the grid.

Monthly oceanographic data were downloaded from NASA OceanColor (https://oceancolor.gsfc.nasa.gov): SST (°C), particulate organic carbon (POC; mg m^{-3}), and absorption due to phytoplankton at 443 nm (chlorophyll *a* (Chl-*a*); mg m^{-3}). Considering the temporal distribution of sightings (a few data per month), it was not possible to model the spatial distribution using a temporal resolution finer than a month. Moreover, Maxent requires rasters with values covering the whole extension of the study area as input files (layers), and 8-day composite rasters from OceanColor present several missing values during W. Therefore, loggerhead distribution was investigated using long-term averages of dynamic variables (SST and sea productivity). For clarity, we use 'pixel' for the downloaded rasters and 'cell' for the 4 × 4 km^2 grid. Each layer was obtained by (i) summarizing (see later) the values for each biological season per year, (ii) averaging values from (i) for the year range (2014–2018), and (iii) reporting values from (ii) to each 4 × 4 km^2 cell by mediating all the pixels within its border ('zonal statistics' plugin in QGIS v. 3.12.3). At step (i), Chl-*a* and POC values in each pixel within each biological season were summed, since primary production and carbonate content have a seasonal variation that is independent of the seasons considered here (e.g. phytoplankton blooms in spring and late summer); the coldest and warmest peaks within each biological season (SST min and SST max) were extracted; and the SST within each biological season (SST mean) was averaged. The averaged range of variation from the lowest to the highest peaks within each year was also included in the analyses (SST range). Moreover, April SST was considered as a single variable to investigate its influence in driving loggerhead distribution at the beginning of the reproductive season. Despite the relatively small number of sightings recorded in April ($n = 5$), the effect of April SST was evaluated in determining loggerhead distribution over the whole BN period (April–September), assuming that the April SST occurring in a certain region can affect loggerhead occupation in the following months due to, for example, increased productivity (plankton blooms) or favourable temperature conditions for mating (Schofield et al., 2009).

Bathymetry was downloaded as a digital terrain model from the EMODnet Bathymetry portal (http://www.emodnet-bathymetry.eu) with a grid resolution of 1/16 arc minutes (about 100 × 100 m^2). Seabed slope was extracted from bathymetry in QGIS v. 3.12.3, and bathymetry and slope were reported to 4 × 4 km^2 cells by mediating all the pixels within its borders ('zonal statistics' plugin in QGIS v. 3.12.3). The distance of the middle of each cell from shore was measured in QGIS v. 3.12.3 using the 'distance matrix' tool.

2.3 | Maxent

Loggerhead turtle distribution with presence-only data was investigated using Maxent (Phillips & Dudík, 2008) for each biological season at each subregion. Maxent can handle complex interactions between response and environmental variables with a small sample size, estimating fundamental ecological niches in regions where no systematic surveys are available. Since confirmed absences are difficult to collect, especially at sea, presence-only models rely on artificial absence data, named pseudo-absences, or background (Phillips & Dudík, 2008), to investigate species distribution. Maxent models predicted loggerhead distribution over a 4 × 4 km^2 grid (within a selected domain; see Section 2.3.1 for details) using a training dataset comprising presence (cells with sightings) and pseudo-absence data.

In this study, preprocessing investigations were carried out to reduce sampling biases and increase outputs' reliability. Bias corrections for restricted sampling methods (Fourcade et al., 2014) and a small dataset (Syfert, Smith & Coomes, 2013) were applied to the selection of the spatial domain (described in Section 2.3.1) and the training dataset (described in Section 2.3.2).

Loggerhead distribution was predicted for each subregion (the central-southern Adriatic Sea and the north-eastern Ionian Sea) during the BN and W periods. Linear, quadratic, and hinge relationships between presences and environmental variables were evaluated over 50 iterations to obtain a final ensemble model reporting the habitat suitability. We started from a model including all the environmental variables and excluded those correlated variables whose contribution and ecological relevance was valueless. Maxent was performed in R software (R Core Team, 2013) with the biomod2 package (Thuiller et al., 2009). Predictions were evaluated with the area under the receiver operating curve, and the overlap rate between the W and BN distributions for each subregion was measured with Schoener's *D* index (Schoener, 1968) (from 0 for no overlap to 1 for complete overlap) using the spaa package in R software (R Core Team, 2013). Two thresholds were selected to evaluate the ranges of environmental variables selected by the loggerheads by reclassifying the potential distribution of habitat suitability into two categories: high suitability (HS) areas from 60% to 100% of suitability, and low suitability (LS) areas from 0% to 40% suitability (Convertino et al., 2014; Zhang et al., 2019; Yan et al., 2020; Tang et al., 2021).

2.3.1 | Spatial domain

Obtaining reliable Maxent predictions is essential to correct the spatial domain of the prediction and the training dataset to the type of sampling bias. In this study, the monitoring was limited within a restricted portion of two areas: the central-southern Adriatic Sea and the north-eastern Ionian Sea (Figure 1 and Supporting information Figure S1). Many studies report the northern Adriatic Sea as an ecologically important site for loggerheads (e.g. Lazar, Margaritoulis & Tvrtković, 2004; Zbinden et al., 2011; Casale et al., 2012a; Fortuna et al., 2018; Haywood et al., 2020), although a priori inclusion of this region in Maxent would have been reckless because (i) the northern Adriatic Sea exhibits different oceanographic conditions from the central-southern Adriatic Sea and the north-eastern Ionian Sea (shallow bathymetry, high primary productivity, low salinity concentrations due to large freshwater inputs from the River Po), and (ii) FLT (ISPRA, 2015) did not cover this region (Supporting information Figure S1).

The variability of environmental variables among these three subregions (northern Adriatic Sea, central-southern Adriatic Sea, and north-eastern Ionian Sea; Figure 1) was checked using a principal component analysis (PCA) and significant differences among subregions were tested using a Tukey's HSD (honestly significant difference) analysis in R software (R Core Team, 2013).

2.3.2 | Training dataset

FLTs restricted loggerhead sampling to a fraction of the study area, which has been described as one of the sampling biases affecting the resulting predictions (Fourcade et al., 2014). This type of bias was reduced by using a restricted background (for pseudo-absences; see later) and a standardized density grid (for presences). Maxent was trained using SPUE values as presences per cell rather than by considering all the cells with sightings equally.

As background selection can strongly affect the resulting model, a bias correction of pseudo-absences was applied for monitoring restricted to a fraction of the study area (Fourcade et al., 2014). We randomly sampled 1,000 pseudo-absences from a buffer of 50 km along the ferry's tracks with a minimum distance of 4 km from each sighting to avoid pseudo-absences near presences (Supporting information Figure S1 shows the spatial distribution of the training dataset). The environmental characteristics at pseudo-absences were checked to be representative of the whole study area with a multivariate environmental similarity surfaces (MESS) analysis (Elith, Kearney & Phillips, 2010) for each model (subregion per biological season, $n = 4$). MESS analysis quantifies the similarity between each cell in the training (reference) dataset and those in the (predicted) spatial domain by returning negative values for localities with environmental conditions dissimilar to the reference region. We measured the similarity of advocated pseudo-absences to all the cells from the 4×4 km^2 grid used for predictions and deleted those pseudo-absences with negative values from the training dataset.

2.4 | Niche and subniche analysis with presence data

The investigation of the occupied niche and subniche was carried out using an outlying mean index (OMI) analysis (Dolédec, Chessel & Gimaret-Carpentier, 2000) combined with a *K*-select analysis (Calenge, Dufour & Maillard, 2005) into a WitOMI analysis (Karasiewicz, Dolédec & Lefebvre, 2017). Karasiewicz, Dolédec & Lefebvre (2017) defined OMI analysis as an ordination technique designed to 'seek combinations of environmental variables that maximize the average species marginality used by a species [..] and the mean habitat conditions of the sampling domain'. The position of the species in a multidimensional space is defined by 'its niche deviation from a uniformly distributed theoretical species, which would occur under all available habitat conditions (i.e. ubiquitous)' (Karasiewicz, Dolédec & Lefebvre, 2017). The WitOMI analysis is built on OMI results and includes the *K*-select analysis to investigate species niche dynamics within spatial and temporal subsets.

Here, an OMI analysis was performed on a single species by considering the central-southern Adriatic Sea and the north-eastern Ionian Sea as two sampling units—which are defined by Karasiewicz, Dolédec & Lefebvre (2017)—to evaluate the marginality of the ecological niches (one per sampling unit) to the overall average habitat conditions, represented by *G*. Once the ecological niches were fixed by OMI, the occupation of the species at different subsets (here we considered a temporal subset: biological seasons) was decomposed within the spatial domain using the *K*-select analysis within the WitOMI analysis. Therefore, OMI is used as the reference ordination technique and the subniches (here referring to biological seasons as a temporal subset) are evaluated in the same *n*-dimensional space. Therefore, the resulting niche and subniche parameters of the species are all in the same factorial plane. WitOMI returns two ecological parameters (marginality and tolerance) from the comparison of the ecological niche and ecological subniche to the overall habitat conditions (G) and the average subset habitat conditions (G_K) of the spatial domain. High values of marginality indicate a species selecting for a less common habitat within the spatial domain; on the contrary, low values describe species using habitats prevailing in the region (Hernández Fariñas et al., 2015). The deviations from G and G_K (WitOMIG and WitOMIG$_K$) are associated with a tolerance parameter

(Tol), or species' niche breadth, whose low values refer to a species that uses a limited portion of environmental conditions distributed across the region investigated (specialist species), and high values describe a species tolerating a wide range of environmental conditions (generalist species) (Hernández Fariñas et al., 2015; Karasiewicz, Dolédec & Lefebvre, 2017). The statistical significance for the species marginality was tested using a Monte Carlo test (Manly, 2006) with 1,000 permutations testing the following null-hypotheses: (i) the species selects the two subregions independently to its overall average habitat conditions (*G*; i.e. ubiquitous) (from the OMI analysis) (Dolédec, Chessel & Gimaret-Carpentier, 2000), and (ii) the species within a subset (biological seasons W and BN) were uninfluenced by the overall average habitat conditions (*G*) and the subset habitat conditions (G_K; from the WitOMI analysis) (Karasiewicz, Dolédec & Lefebvre, 2017). The analysis was performed using the 'subniche' package (Karasiewicz, Dolédec & Lefebvre, 2017) for R software (R Core Team, 2013).

3 | RESULTS

3.1 | Environmental conditions within presence data

From December 2014 to February 2018, 49 loggerhead turtles were sighted at 44 GPS locations (at each of five locations two individuals were sighted) falling into 44 out of 21,922 cells of the 4×4 km^2 grid. The project monitored 23,751 km along FLTs in the central-southern Adriatic Sea and the north-eastern Ionian Sea. The SPUE measured over the monitored cells is 0.0021 (sightings/km), and the mean SPUE (±*SD*) from cells with at least one sighting is 0.61 ± 0.89 (sightings/km). The spatial distribution of sightings varies among biological seasons and subregions: three out of 17 in the Ionian subregion and 13 out of 27 in the Adriatic subregion were from the W period (Figure 1). The subregions were equally monitored year-round (tracks lengths were 12,764 km in the Adriatic Sea and 10,987 km in the Ionian Sea). Between biological seasons, 58.6% of W monitoring effort occurred in the central-southern Adriatic Sea and 41.4% in the north-eastern Ionian Sea. In contrast, 53.6% of tracks were in the central-southern Adriatic Sea and 46.4% in the north-eastern Ionian Sea during the BN period. Comparable SPUEs were recorded between biological seasons in the Adriatic Sea (0.0019 in W and 0.0024 in BN) and the Ionian Sea (0.0027 in W and 0.0027 in BN). Although previous findings reported good performances of Maxent predictions with a small dataset (Syfert, Smith & Coomes, 2013), the number of sightings in the Ionian Sea during W is low ($n = 3$); therefore, care should be taken over any interpretation of the results.

Bathymetry, distance from shore, and sea-bed slope were not significantly different among subregions and biological seasons (Supporting information Table S1), and SST variables (min, max, and mean) were significantly different for all pairwise comparisons (subregions and W–BN) (Supporting information Table S1). The April SST recorded at the sightings' locations was 2 °C higher in the Ionian subregion than in the Adriatic subregion (Table 1). The total POC and Chl-*a* at loggerhead sightings were higher in W than in BN, with the highest production in the Adriatic Sea. Chl-*a* at sightings showed significantly different concentrations between W and BN in both subregions (Supporting information Table S1).

3.2 | Niche and subniche

The OMI analysis of the environmental conditions in presence cells revealed that the realized niches in the Adriatic and Ionian subregions are characterized by environmental variables that are not ubiquitous within the study area (three Monte Carlo tests, $P < 0.001$; the null

TABLE 1 Mean ± *SD* values of the environmental predictors at the sightings are reported for the winter (W) and the breeding-nesting (BN) periods

	Adriatic Sea		Ionian Sea	
Variable	W	BN	W	BN
Bathymetry (m)	−216.9 ± 238.3	−194.2 ± 258.8	−47.8 ± 28.2	−161.6 ± 134.2
Slope (°)	0.34 ± 0.69	0.58 ± 1.71	0.30 ± 0.11	2.18 ± 2.65
Distance from shore (km)	27.3 ± 19.7	10.5 ± 15	43 ± .21.1	37.2 ± 20.8
SST min (°C)[a]	13.7 ± 0.8	18.6 ± 0.2	15.2 ± 0.3	20 ± 0.3
SST max (°C)[a]	19.8 ± 0.4	27 ± 0.4	23.2 ± 0.2	27.6 ± 0.3
SST mean (°C)[a]	15.9 ± 0.4	23.9 ± 0.3	18.1 ± 0.2	24.8 ± 0.4
SST range (°C)	13.0 ± 2.2		12.2 ± 2.6	
April SST (°C)	–	15.3 ± 0.5	–	17.3 ± 0.3
Chl-*a* sum (mg m^{-3})	0.12 ± 0.03	0.07 ± 0.02	0.05 ± 0.02	0.03 ± 0.01
POC sum (mg m^{-3})	663.7 ± 287.8	468.9 ± 157.8	727.3 ± 193.6	313.3 ± 58

Abbreviations: Chl-*a*, chlorophyll *a*; POC, particulate organic carbon; SST, sea surface temperature.

[a] Indicates a significant difference of the values among biological seasons and subregion (Mann–Whitney tests reported in Supporting information Table S1).

hypothesis 'the species selects the two subregions independently to its overall average habitat conditions' is rejected). The first two axes of the OMI analysis accounted for 100% of the marginality, with a contribution of 98.6% for the first axis (OMI1) (Figure 2a). The total amount of POC, April SST, SST mean, and bathymetry define mainly the niches' distribution along the OMI2, while slope, SST min and max characterize the distribution along OMI1 (Figure 2b). The central-southern Adriatic niche is explained by distance from shore and the total amount of Chl-*a* and POC, while the north-eastern Ionian niche is influenced by temperature extremes (SST min and max), bathymetry, and slope (Figure 2a,b).

The WitOMI analysis was performed on OMI results to measure the realized subniches in the Adriatic–Ionian basin during the W (October–March) and BN (April–September) periods. The average habitat conditions for each biological season (G_K) were significantly different (Monte Carlo test, $P < 0.001$ for both W and BN) from the overall average habitat conditions (G) by comparing the distribution of 1,000 permutations following the null hypothesis $G_K = G$. Loggerhead distribution was determined by the environmental conditions during W in the central-southern Adriatic Sea (Monte Carlo test, $P = 0.043$; BN in the same subregion was $P = 0.481$) and during BN in the north-eastern Ionian Sea (Monte Carlo test, $P = 0.008$; W in the same subregion was $P = 0.215$). Among all the environmental variables, the statistical test highlighted three variables that significantly influence the species marginality during BN (Monte Carlo test, SST min, $P = 0.004$; POC, $P = 0.001$; Chl-*a*, $P = 0.001$) and W (Monte Carlo test, SST min, $P = 0.001$; POC, $P < 0.001$; Chl-*a*, $P < 0.001$).

Loggerhead turtles selected a more common habitat in the central-southern Adriatic Sea (OMI = 1.08) than in the north-eastern Ionian niche (OMI = 2.70), extending over a wide range of environmental conditions (Tol = 1.24 compared with Tol = 0.51 in the north-eastern Ionian Sea). Sea turtles appeared to distribute within a limited portion of the available habitat in the north-eastern Ionian Sea during both seasons (WitOMIG = 4.73 and 3.42 in BN and W respectively) and selecting for a small range of the environmental conditions occurring within each biological season ($\text{WitOMIG}_K = 2.53$ and 4.39 in BN and W respectively). The marginality, which is the distance between the ecological niche selected by loggerhead turtles and the average habitat conditions (G) or the subset average conditions (G_K), exhibited low tolerance values for W and BN in the Ionian subregion (Table 2), reinforcing the hypothesis that loggerhead turtles exhibit a specialist strategy year-round in the north-eastern Ionian Sea. In the central-southern Adriatic Sea, the loggerhead turtles' niche includes a wide range of environmental conditions of the subregion year-round (Tol = 1.34 and 2.11 in BN and W respectively), although the marginality to *G* (average habitat conditions) is higher in W (WitOMIG = 3.16) than in BN (WitOMIG = 0.84). Although the loggerhead turtles selected more

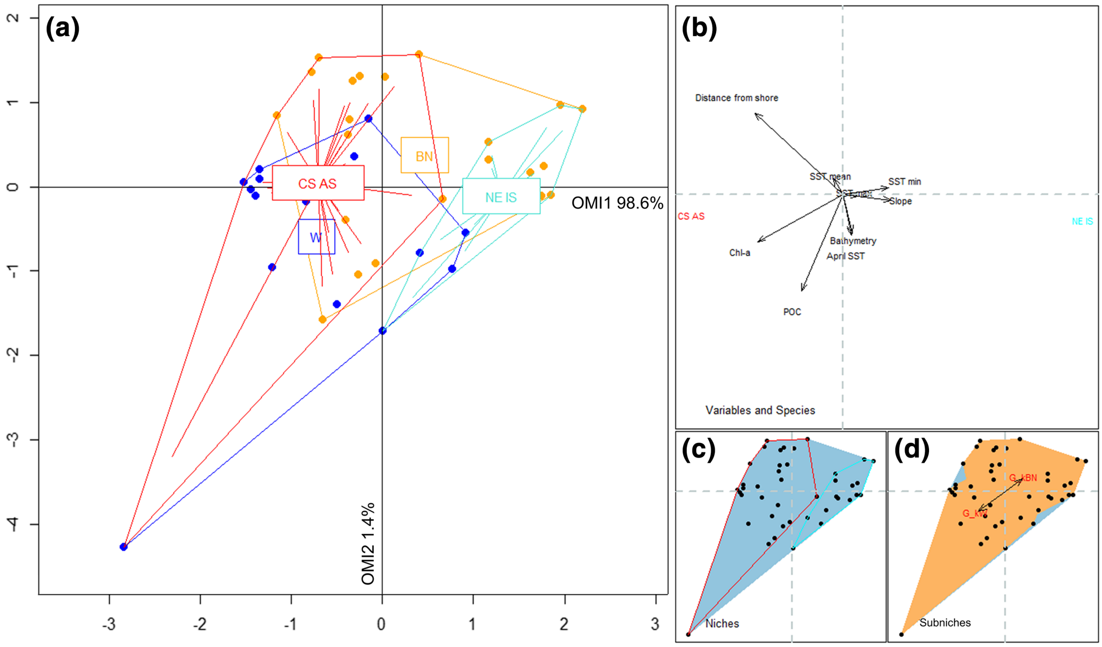

FIGURE 2 Plots with outlying mean index (OMI) and within outlying mean indexes (WitOMI) results on the first two factorial axes (OMI1 and OMI2) of a two-dimensional Euclidean space. (a) The niche positions of the central-southern Adriatic Sea (CS AS, red) and north-eastern Ionian Sea (NE IS, turquoise), and the subniche positions for the winter (W, blue) and the breeding–nesting (BN, orange) subsets. The labels represent the centroids of each niche and subniche, the points are the observations (presences) coloured according to the subniche (biological season), and the cut lines link the centroid of the niche to each observation. (b) The weight and direction of the contribution of environmental variables to OMI analysis. (c) The niches' constraints (red boundary for CS AS and light blue for NE IS) found within the overall available habitat conditions (blue polygon); black dots are observations (same in (d)). (d) The subniches' constraints (orange polygons) over all the available habitat conditions (blue polygon), with a graphical representation of the marginality vectors in the WitOMI analysis (WitOMIG_K). Chl-*a*: chlorophyll *a*; POC: particulate organic carbon; SST: sea surface temperature

specific environmental conditions in W than in BN (higher marginality to G in W than in BN), the niche in W is characterized by environmental conditions widely occurring over this subregion.

3.3 | Distribution of suitable habitat

Several papers have described the occurrence of loggerhead turtles in the northern Adriatic Sea (Figure 1) (e.g. Lazar, Margaritoulis & Tvrtković, 2004; Zbinden et al., 2011; Casale et al., 2012a; Fortuna et al., 2018; Haywood et al., 2020), although this subregion exhibited different environmental conditions from the monitored subregions (central-southern Adriatic Sea and northern-eastern Ionian Sea). The PCA pointed out significantly different environmental conditions in the northern Adriatic Sea for the first principal factor ($P < 0.001$ for PC1) (Supporting information Figure S2) from the Adriatic–Ionian region. Therefore, the northern Adriatic Sea was neither included in spatial modelling analyses with the central-southern Adriatic Sea nor considered alone (due to the lack of monitoring in this area). The correction for sampling bias on the selection of pseudo-absences was checked using MESS analysis, which returned only a few pseudo-absences exhibiting dissimilar environmental conditions from the predicted areas. Dissimilar conditions (negative values from MESS) were reported in two cells in the central-southern Adriatic Sea during BN and W, two cells in the north-eastern Ionian Sea during BN, and one cell during W (see Supporting information Figure S3 for details on other pseudo-absences). These cells were deleted from the training dataset and used for predictions.

TABLE 2 Parameters obtained from the within outlying mean indexes (WitOMI) analysis for each subregion and biological season

	WitOMI		Tolerance	
	G	G_K	G	G_K
Central-southern Adriatic Sea, BN	0.84	1.36	1.34	0.67
Central-southern Adriatic Sea, W	3.16	0.51	2.11	0.98
North-eastern Ionian Sea, BN	4.73	2.53	0.51	0.62
North-eastern Ionian Sea, W	3.42	4.39	0.21	0.06

Abbreviations: BN, breeding-nesting; W, winter.

Each Maxent model was built using a backward stepwise selection of the environmental variables. Although the variables defined by the SSTs (April SST, SST min and max) exhibited correlation values >0.7, they were included in the models owing to the interest in investigating the biological effects of temperature extremes on loggerhead distribution. This decision was supported by Sillero & Barbosa (2021), who described the occasional inclusion of correlated variables in the models as long as they explained a species' niche (e.g. when a species is affected by both maximum and minimum temperatures). SST mean and SST range were excluded from Maxent models. The evaluation coefficients for each variable that were included into Maxent models are reported in Table 3. The selected niches among subregions and biological seasons were compared by gathering the habitat suitability (0–100%) into two groups: cells with suitability ≤40% as LS areas, and cells with suitability ≥60% as HS areas. HS areas are found in waters between -1 m and -683 m depth (on average 50.18 ± 25.59 m), extending from shore to 63 km offshore in the central-southern Adriatic Sea and 8 km offshore in the north-eastern Ionian Sea. Bathymetry highly contributed to define HS areas in the central-southern Adriatic Sea (Table 3), and bathymetry values in the HS areas were significantly different from the LS areas in all subregions and biological seasons (Mann–Whitney test for Adriatic subregion in BN, $W = 516,627$, $P < 0.001$, and in W, $W = 304,149$, $P < 0.001$; Mann–Whitney test for Ionian subregion in BN, $W = 67,915$, $P < 0.001$, and in W, $W = 54,973$, $P < 0.001$) (Supporting information Figure S4). The central-southern Adriatic Sea was characterized by significant low values of SST min and max during W and BN (Mann–Whitney test for SST min between suitability ≥60% and ≤40%, $W = 516,627$, $P < 0.001$; Mann–Whitney test for SST max between suitability ≥60% and ≤40%, $W = 304,149$, $P < 0.001$)

TABLE 3 Evaluation coefficients for the environmental variables used in Maxent predictions for winter (W) and breeding–nesting (BN)

	Central-southern Adriatic Sea		North-eastern Ionian Sea	
Variable	W	BN	W	BN
Bathymetry	0.458	0	0.078	0.101
Slope	0	0	0	0.005
Distance from shore	0.052	0.015	0.32	0.605
SST min	0	0.345	0.006	0
SST max	0.483	0	0.522	0.07
April SST	–	0.433	–	0.139
Chl-*a* sum	0.150	0.051	0.055	0.101
POC sum	0.013	0.014	0.116	0.043
Model evaluation				
ROC	0.801	0.713	0.960	0.939

Abbreviations: Chl-*a*, chlorophyll *a*; POC, particulate organic carbon; ROC, receiver operating curve; SST, sea surface temperature.

(Supporting information Figure S4). SST max contributed highly to the model in W, whereas SST min affected loggerhead distribution only during BN (Table 3), suggesting a significant preference of loggerhead turtles for cold waters during BN (Mann–Whitney test for SST min in BN between suitability ≥60% and ≤40%, $W = 442{,}782$, $P < 0.001$) (Supporting information Figure S4). Loggerhead turtle niche in the north-eastern Ionian Sea was defined mostly by SST max during W, whereas distance from shore contributed most during BN (Table 3). HS cells were significantly characterized by a higher SST max than values in LS areas (Mann–Whitney test for SST max in W between suitability ≥60% and ≤40%, W = 218,306, $P < 0.001$; Mann–Whitney test for SST max in BN between suitability ≥60% and ≤40%, W = 221,188, $P < 0.005$) (Supporting information Figure S4), whereas SST min did not affect the models in this subregion during BN (Table 3). April SST defined habitat suitability in both subregions, especially in the central-southern Adriatic Sea (Table 3). Chl-*a* and POC marginally defined niches in both subregions and biological seasons (Table 3). In the central-southern Adriatic Sea, during W, higher concentrations of Chl-*a* and POC defined HS areas than those in the Ionian subregion (Mann–Whitney test for Chl-*a* between suitability ≥60% and ≤40% in the central-southern Adriatic Sea, $W = 962{,}474$, $P < 0.001$; Mann–Whitney test for POC between suitability ≥60% and ≤40% in the central-southern Adriatic Sea, $W = 1{,}025{,}019$, $P < 0.001$) (Supporting information Figure S4).

The distribution of habitat suitability differed slightly from W to BN in the north-eastern Ionian Sea (Schoener's $D = 0.717$) and remained almost the same in the central-southern Adriatic Sea (Schoener's $D = 0.879$) (see Supporting information Figure S5 for the changes of suitability from BN to W). The Adriatic subregion exhibited HS areas in coastal waters off the Croatian and Italian coastlines during BN (Figure 3a) and in the central portion of the basin during W (Figure 3b). The deep waters in the southern Adriatic Sea (>200 m) and the coastal waters off Montenegro and Albania showed LS year-round. In the north-eastern Ionian Sea, loggerhead turtles appeared confined to shallow waters between the Greek islands (Corfù, Kefalonia, and Zakynthos), in the Bay of Vlorë (Albania), and along the shoreline near Gallipoli (Italy) (Figure 3c,d).

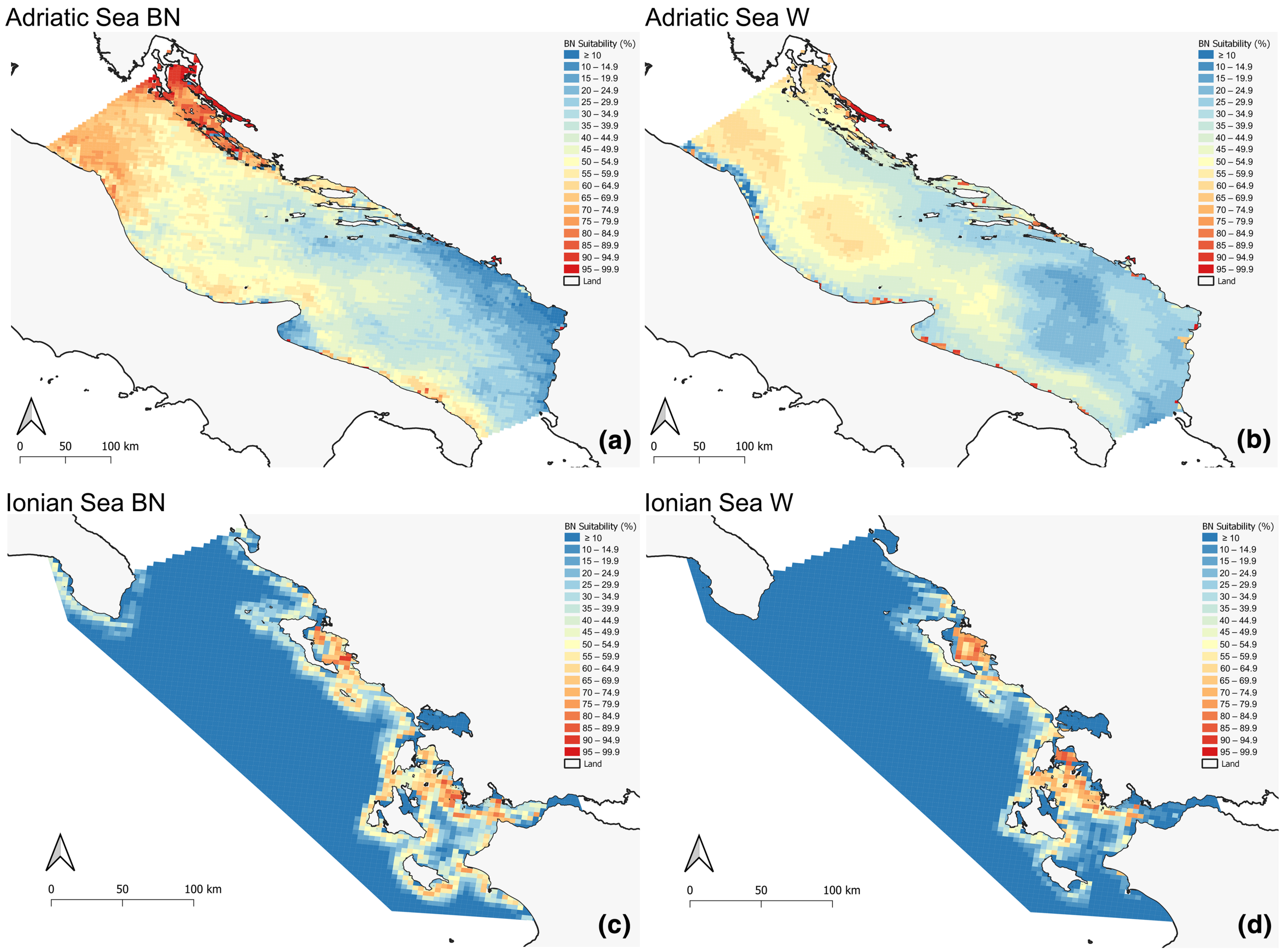

FIGURE 3 Predicted habitat suitability (0–100%) from Maxent in (a, b) the central-southern Adriatic Sea and (c, d) the north-eastern Ionian Sea. Colours from blue to red indicate the habitat suitability from 0% to 100%. Colours are grouped in ranges as described in the legend. BN breeding–nesting; W: winter

4 | DISCUSSION

Several studies (Zbinden et al., 2011; Casale et al., 2012a; Casale et al., 2012b; Luschi et al., 2013; Schofield et al., 2013; Casale & Mariani, 2014; Casale & Simone, 2017; Haywood et al., 2020) reported loggerhead populations migrating from Greek nesting sites to foraging and developmental areas in the Adriatic Sea, where there are suitable pelagic and neritic conditions year-round. To date, describing the movement patterns and habitat uses of sea turtles requires a composite dataset at a high temporal and spatial resolution that is difficult to obtain using a single sampling method. In this study, offshore data on sea turtles were collected using a cost-effective method: FLTs, onboard ferries; and the spatial occupancy of loggerheads was evaluated for two regions of the Mediterranean Sea: the central-southern Adriatic Sea and the north-eastern Ionian Sea (Figure 1). The proposed approach offers a standardized methodology to investigate the occurrence of loggerheads year-round and is considered complementary to tagging records, and isotopic and genetic analyses.

4.1 | Seasonal habitat selection in loggerhead sea turtles

The niche in the central-southern Adriatic Sea was characterized by Chl-*a*, POC, and SST variables, which are largely considered proxies for prey distribution and might indirectly drive loggerhead movements for foraging purposes. From W to BN, Maxent showed HS areas slightly shifting from offshore to coastal waters (Figure 3a,b). During W, loggerheads significantly selected waters on the continental shelf (Supporting information Figure S4), with SST max oscillating within the range 12.2–20.7 °C (values from cells with suitability ≥60%), which is compatible with previous studies on thermal tolerance (Lazar, Margaritoulis & Tvrtković, 2004; Hochscheid et al., 2007; Casale et al., 2012b). W foraging activities were described in shallow regions exhibiting cold SST (Hawkes et al., 2007; Hochscheid et al., 2007; Dodge et al., 2014; Narazaki, Sato & Miyazaki, 2015; Iverson et al., 2019); in particular, shallow diving behaviour was identified in highly productive cold waters (Chambault et al., 2016). Previous studies reported loggerheads to occur in waters up to 11.8 °C during W (Hochscheid et al., 2007), where they may take advantage of high concentrations of food. Oceanographic features can explain the association of cold SST with foraging grounds; for example, deep convection, fronts, and gyres that resuspend nutrient-enriched waters at the surface that trigger sporadic phytoplankton blooms (Goffart, Hecq & Legendre, 2002; Batistić et al., 2019). These sporadic events can serve as temporary hot spots of food patches during prolonged oligotrophic conditions in W, although monthly averaged SST data may not detect those patches that are too ephemeral. However, the SST max is the variable with the highest contribution in the central-southern Adriatic Sea during W, and its low values in HS areas (compared with LS cells, Supporting information Figure S4) may reflect the selection of cold waters that persist for months. Since the SST max is the value of the maximum monthly temperature recorded throughout the investigated time series (2014–2018), its influence on Maxent prediction can relate to the selection of areas with either prolonged cold temperatures or oceanographic features occurring repeatedly over time in the same spot. HS areas were also characterized by higher Chl-*a* in W than in BN (Supporting information Figure S5), which may reflect the selection of frequent productive regions and/or the prevalence of foraging behaviour during W (Schofield et al., 2006). On the other hand, the southern and deeper portion of the Adriatic Sea (>200 m) showed less suitability than the central one, probably due to the presence of strong currents coming from the cyclonic sub-gyre (Poulain, 2001; Zavatarelli & Pinardi, 2003) that disperses resources close to shores (Carlson et al., 2017), where the permanent north-westward current supports migratory routes along the eastern coastline and a south-westward current on the western one (Poulain, 2001; Zavatarelli & Pinardi, 2003; Casale et al., 2012a; Luschi et al., 2013). Overall, loggerhead turtles that selected the subniches in the central-southern Adriatic Sea during W and BN were tolerating a wide range of environmental conditions (generalist species) in the subregion (high tolerance values reported in Table 2). Isotope analyses on juveniles in the northern Adriatic Sea demonstrated foraging strategies involving a combination of several habitats and prey items, which are likely to remain in the same geographical region (Haywood et al., 2020). The selection of a small portion of the whole range of available environmental conditions in the Adriatic subregion is also reported by the WitOMI analysis, which indicates that loggerheads select a specific range of the investigated variables during W (marginality to overall average conditions, $G = 3.16$) that is very close to the seasonal subniche selected by the species (marginality to the subset average conditions $G_K = 0.51$). The similar distribution of habitat suitability in the Adriatic subregion from W to BN (Schoener's $D = 0.879$) (Figure 7c) suggests that the individuals occupy this subregion year-round and reinforces the current recognition of this area as an important foraging ground for juveniles and adults (Lazar, Margaritoulis & Tvrtković, 2004; Patel et al., 2016; Arcangeli et al., 2019).

Loggerhead turtles occurred in marginal niches in the north-eastern Ionian Sea compared with both the overall (G) and subset (G_K) average environmental conditions (Table 2). The small tolerance measured for loggerhead subniches during W and BN suggests the selection of a limited range of the available environmental variables in the Adriatic–Ionian region. Loggerhead distribution appeared to be slightly influenced by bathymetry and sea-bed slope, but mainly by distance from shore (Table 3) within coastal waters (<8 km from shore), where females, after mating, are described as staying until egg deposition (Miller, 1996). During the BN season, foraging events are set aside to allow for more resting, swimming, and reproduction behaviours (Schofield et al., 2006). The low foraging activity reflects Chl-*a* and POC's marginal contribution to Maxent modelling during BN (Table 3), supporting the hypothesis that loggerheads use this region mainly for breeding and nesting. Several studies reported a meaningful association of SST with movement patterns (Bentivegna, 2002) and reproductive phenology (Sato et al., 1998; Hays et al., 2003; Mazaris et al., 2008; Mazaris et al., 2009; Mazaris et al., 2013; Patel et al., 2016). Mating individuals have been observed to remain close to shore and nesting sites during the BN season and selecting specific thermal microhabitats (Schofield et al., 2009). However, the presence of loggerheads close to the shore is not random and aims to find warm water patches near-shore to speed up egg maturation in females (Schofield et al., 2009). The nesting population in Zakynthos exhibited a positive correlation between warm SST in April and early nesting and hatching (Mazaris et al., 2008; Mazaris et al., 2009; Patel et al., 2016). Although the effects on the fitness of early nesting remain unclear (positive effects described by Schofield et al. (2009) and negative effects described by Mazaris et al. (2008) and Monsinjon et al. (2019)), April SST contributed to the niche definition in the Ionian basin during BN, reinforcing the importance of this variable for selecting suitable niches. The warm temperature (SST max ranging between 26.5 °C and 28.7 °C) characterizing HS areas (suitability ≥60%) would also suggest the selection of waters <30 °C (range of SST max in LS areas is 22.0–31.0 °C) during BN helps females to improve their reproductive efficiency and extend the nesting season (Schofield et al., 2009). To date, the nesting season in the Greek islands extends from May to September (Margaritoulis, 1982; Rees & Margaritoulis, 2004; Adam et al., 2007; Zbinden et al., 2007; Katselidis et al., 2014), whereas a small number of nests were recorded on the Adriatic coastlines from June to August (citizen science records for Puglia, Abruzzo, Marche, and Molise, www.tartapedia.it; Mancino et al. (in preparation) listed all the nesting sites from 1960 to 2020 in the Mediterranean Sea). The short and late nesting seasons along the Adriatic coastline are consistent with a colder April SST in this area (average April SST in HS cells is 14.62 ± 0.48 °C) than in the Ionian subregion (17.32 ± 0.22 °C), whose April SST is outside the range of temperature that elicits female egg deposition (16.7–25.6 °C) (Mazaris et al., 2013).

Owing to the few sightings in the Ionian subregion during W ($n = 3$), the resulting Maxent prediction of loggerhead distribution for this period should be interpreted with caution. Despite the comparable amount of monitoring effort in the Ionian subregion during W (41.4% of tracks during W), the small number of individuals sighted in this area may reflect the findings from a few tagging records describing individuals passing through these areas rather than being resident (Bentivegna, 2002). The time and duration of loggerheads' establishment within the HS areas (Figure 3d) cannot be inferred by this study, and hence the HS areas for the W period identified by Maxent might be associated with transitory movements.

4.2 | Seasonal habitat selection in a climate change scenario

The tight relationships described by the analyses between habitat selection and SSTs point out the consequences of climate-change-related scenarios (e.g. increasing SST, the rise of sea level) on the survival of the Mediterranean loggerhead populations. Climate change appears to be a major threat to sea turtle populations around the globe, although little is known about the processes that influence turtle dispersal, growth, diet, sex determination, mating, and nesting (Hamann et al., 2013; Godley et al., 2020). Future predictions of global SST raise strong concerns for the loggerhead population in the Mediterranean Sea (Witt et al., 2010). Some studies have shown that changes in temperature conditions negatively affect the phenology of reproduction and the choice of nesting sites (Mazaris et al., 2013; Pike, 2013; Katselidis et al., 2014; Patel et al., 2016). Although the species may adapt its distribution at sea to rising temperatures by migrating polewards (Patel et al., 2021), the intricate habitat selection that involves proximal favourable conditions at sea and nesting sites during the BN season (Schofield et al., 2009) may not occur in more northern habitats. To date, late and short nesting seasons on the Adriatic coastline may coincide with the difference in April SST reported by HS areas in the Adriatic and Ionian subregions during BN: The suitable areas in the central-southern Adriatic Sea have an average April SST 2.5 °C lower than the northern-eastern Ionian Sea, suggesting that the Adriatic Sea is not currently ideal for extensive breeding and nesting purposes and may represent an alternative ground for a poleward shift of populations nesting. Previous studies reported that April SST has a positive correlation to early nesting and hatching (Mazaris et al., 2008; Mazaris et al., 2009; Patel et al., 2016), and spring SST influences the spatial distribution of gravid females (Schofield et al., 2009). Therefore, April SST may represent one of the influential factors determining the reproductive success of the loggerhead population in the Mediterranean basin and, hence, influencing the northward spatial migration. For this reason, long-term planning is essential for implementing management strategies, especially the habitat protection (including potential future habitat) of nesting sites.

4.3 | Conservation and management strategies

The extreme vulnerability of the loggerhead turtle to anthropogenic pressures led this species to becoming listed as Vulnerable on the Red List of protected species for the Mediterranean region and being chosen as an indicator of the impact of marine litter to assess the good environmental status (Marine Strategy Framework Directive, MSFD, 2008/56/EC) of marine ecosystems (Matiddi et al., 2017). Both MSFD and the Habitats Directive require a 6-year assessment of the conservation status of the loggerhead turtle in the Mediterranean Sea based on different criteria. The primary criteria (D1C5) of the MSFD imposes that ‘the habitat for the species has the necessary extent and condition to support the different stages in the life history of the species’; similarly, the Habitats Directive requires that ‘there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis’. In the last decades, numerous actions have been successfully carried out on protecting nest sites of the species (Casale & Margaritoulis, 2010), but information on the seasonal usage of offshore waters is still scarce (Casale et al., 2018).

Most of the measures for conserving the loggerhead turtle generally focused on protecting nesting beaches by establishing protected areas, eliminating disturbances, regulating beach nourishment, and limiting the impacts of people on the beach.

However, the hypothesis of a poleward shift of suitable habitats at the sea and land phases raises new questions that can be investigated by monitoring the environmental conditions of areas (e.g. the north and central Adriatic Sea and its coastline) that have not historically been reported as hotspots of nesting and reproduction or are known to be used exclusively for foraging and overwintering. The eastern Adriatic coastline lacks nesting activity by loggerhead turtles (Casale et al., 2018), and a late and short nesting season is reported for the western coastline (citizen science records for Puglia, Abruzzo, Marche, and Molise, www.tartapedia.it; Mancino et al. (in preparation) listed all the nesting sites from 1960 to 2020 in the Mediterranean Sea). Comparisons between the Adriatic and Ionian nests of the clutch sizes, sex ratio, hatching success, and the length of the nesting season may inform the reproductive success of loggerheads in the two subregions and allow for the implementation of further conservation activities against anthropogenic threats, such as tourism-related development, erosion of beaches, or recreational activities. New potential climate-induced nesting sites could indeed require the application of prompt conservation measures, such as the establishment of dedicated networks for the surveillance of beaches and the application of guidelines for the recovery, rescue, custody, and management of sea turtles coming onshore. Moreover, activities related to the habitat restoration of the coastline in the central-northern Adriatic Sea (e.g. nearby the Po river estuary) by cleaning the beaches of litter may improve the use of northern beaches by gravid females for nesting. The potential poleward shift of mature adults may also be threatened at sea by intensive fishing activities during the BN period, and therefore great attention should also be given to the potential impacts of the fisheries through gill net regulations, the use of dissuader devices, and the enforcement of surveillance. The Adriatic Sea exhibits the highest by-catch rates of loggerhead turtles in the Mediterranean basin (Casale et al., 2018), since post-hatching and post-breeding individuals tend to migrate from the Ionian Sea to overwinter in the Adriatic subregion (Zbinden et al., 2008; Schofield et al., 2013). Other threats relate to the potential entanglement of marine sea turtles in anthropogenic debris that could be mitigated by enforcing the law to regulate the dumping of pollutants and solid waste into the sea. Still, the identification of key areas and seasons and the driving forces that determine the ecological niches of the species at sea are crucial information to focus potential conservation and mitigation measures on the right place and the right time. To date, the urgent need of protecting this species covering all the life stages is a widely shared commitment by the EU countries bordering the Mediterranean Sea that are called to collect standardized data in coastal and offshore waters and develop standard methods to assess the conservation status at sea and on shore. An effective multidisciplinary study combining the ecological needs of sea turtles at sea and on shore is thus needed for the early detection of significant changes that require a redefinition of the conservation effort. In terms of conservation, this study offers a novel approach that can help in sharing the diversity of skills, knowledge, and information within a capacity-building point of view that can be shared by different countries. In addition, the distribution of these data is essential for the establishment of year-round or seasonal protection schemes for feeding and wintering grounds, as well as the main migratory corridors.

5 | CONCLUSION

This study presents an alternative, cost-effective method for collecting standardized data of subadults and adults along trans-border FLTs that currently cover most of the eastern Mediterranean basin (ISPRA, 2015; Arcangeli et al., 2020). The methodology proved to be useful to deliver information required by the legislative framework, especially regarding the criteria related to the habitat of the marine (criteria D1C5 in the MSFD and ‘Habitat for the species’ in the Habitats Directive), underlining also that a seasonal-based assessment is important to identify the ecological needs of the species. The analyses provide a baseline framework that can be extended to the basin scale, the developmental stage and sex of individuals, and provide long-term surveillance of the habitat for the species. The habitat suitability models enable the potential distribution of protected species to be described that can be used to develop intensive monitoring in HS areas or limiting maritime traffic during periods that are sensitive to the species (e.g. breeding and nesting). The Adriatic niche appeared as an important foraging ground year-round, calling for diffuse measures during all the seasons, whereas specific conservation and mitigation measures could be focused on the localized patchy niches observed in the Ionian Sea. A poleward shift of the Greek nesting population is further confirmed by the results of this study, where the increasing spring temperatures may redefine the distribution of suitable habitat for the loggerhead sea turtle. The results confirm that the Adriatic and Ionian seas are priority research areas where long-term transboundary monitoring programmes to assess abundance, movement patterns, and population trends need to be implemented.

ACKNOWLEDGEMENTS

We are thankful to the Minoan Lines ferry company who participated in this research programme and kindly hosted the researchers on board, and to all observers who participated in data collection.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

ORCID

Arianna Zampollo https://orcid.org/0000-0003-0402-2824
Antonella Arcangeli https://orcid.org/0000-0003-2156-9987
Chiara Mancino https://orcid.org/0000-0002-8212-9195
Guido Pietroluongo https://orcid.org/0000-0001-8578-6038

REFERENCES

Adam, V., Tur, C., Rees, A.F. & Tomás, J. (2007). Emergence pattern of loggerhead turtle (*Caretta caretta*) hatchlings from Kyparissia Bay, Greece. *Marine Biology*, 151(5), 1743–1749. https://doi.org/10.1007/s00227-007-0607-2

Arcangeli, A., David, L., Aguilar, A., Atzori, F., Borrell, A., Campana, I. et al. (2020). Floating marine macro litter: Density reference values and monitoring protocol settings from coast to offshore. Results from the MEDSEALITTER project. *Marine Pollution Bulletin*, 160, 111647. https://doi.org/10.1016/j.marpolbul.2020.111647

Arcangeli, A., Maffucci, F., Atzori, F., Azzolin, M., Campana, I., Carosso, L. et al. (2019). Turtles on the trash track: Loggerhead turtles exposed to floating plastic in the Mediterranean Sea. *Endangered Species Research*, 40, 107–121. https://doi.org/10.3354/esr00980

Atzori, F., Carosso, L., Cadoni, N., Frau, F., Gutiérrez, M.L.G., Lucia, G.A.D. et al. (2021). Loggerhead sea turtle, *Caretta caretta*, presence and its exposure to floating marine litter in the Sardinia Channel and the Strait of Sicily: Results from seven years of monitoring using ferry as platform of observation. *Mediterranean Marine Science*, 22(2), 422–435. https://doi.org/10.12681/mms.25579

Batistić, M., Viličić, D., Kovačević, V., Jasprica, N., Garić, R., Lavigne, H. et al. (2019). Occurrence of winter phytoplankton bloom in the open southern Adriatic: Relationship with hydroclimatic events in the eastern Mediterranean. *Continental Shelf Research*, 174, 12–25. https://doi.org/10.1016/j.csr.2018.12.011

Bentivegna, F. (2002). Intra-Mediterranean migrations of loggerhead sea turtles (*Caretta caretta*) monitored by satellite telemetry. *Marine Biology*, 141(4), 795–800. https://doi.org/10.1007/s00227-002-0856-z

Bjorndal, K.A. (1996). Foraging ecology and nutrition of sea turtles. In: P.L. Lutz, J.A. Musick (Eds.) *The Biology of Sea Turtles*. Boca Raton, FL: CRC Press, pp. 191–231.

Bolten, A.B. (2003). Active swimmers–passive drifters: The oceanic juvenile stage of loggerheads in the Atlantic system. In: A.B. Bolten, B.E. Witherington (Eds.) *Loggerhead Sea Turtles*. Washington, DC: Smithsonian Books, pp. 63–78.

Broderick, A.C., Coyne, M.S., Fuller, W.J., Glen, F. & Godley, B.J. (2007). Fidelity and over-wintering of sea turtles. *Proceedings of the Royal Society B: Biological Sciences*, 274(1617), 1533–1539. https://doi.org/10.1098/rspb.2007.0211

Calenge, C., Dufour, A.B. & Maillard, D. (2005). *K*-select analysis: A new method to analyse habitat selection in radio-tracking studies. *Ecological Modelling*, 186(2), 143–153. https://doi.org/10.1016/j.ecolmodel.2004.12.005

Cardona, L., Revelles, M., Parga, M.L., Tomás, J., Aguilar, A., Alegre, F. et al. (2009). Habitat use by loggerhead sea turtles *Caretta caretta* off the coast of eastern Spain results in a high vulnerability to neritic fishing gear. *Marine Biology*, 156(12), 2621–2630. https://doi.org/10.1007/s00227-009-1288-9

Carlson, D.F., Suaria, G., Aliani, S., Fredj, E., Fortibuoni, T., Griffa, A. et al. (2017). Combining litter observations with a regional ocean model to identify sources and sinks of floating debris in a semi-enclosed basin: The Adriatic Sea. *Frontiers in Marine Science*, 4, 78. https://doi.org/10.3389/fmars.2017.00078

Casale, P. & Margaritoulis, D. (Eds.) (2010). *Sea turtles in the Mediterranean: Distribution, threats and conservation priorities*. Gland, Switzerland: IUCN.

Casale, P., Affronte, M., Scaravelli, D., Lazar, B., Vallini, C. & Luschi, P. (2012a). Foraging grounds, movement patterns and habitat connectivity of juvenile loggerhead turtles (*Caretta caretta*) tracked from the Adriatic Sea. *Marine Biology*, 159(7), 1527–1535. https://doi.org/10.1007/s00227-012-1937-2

Casale, P., Broderick, A.C., Camiñas, J.A., Cardona, L., Carreras, C., Demetropoulos, A. et al. (2018). Mediterranean sea turtles: Current knowledge and priorities for conservation and research. *Endangered Species Research*, 36, 229–267. https://doi.org/10.3354/esr00901

Casale, P., Broderick, A.C., Freggi, D., Mencacci, R., Fuller, W.J., Godley, B.J. et al. (2012b). Long-term residence of juvenile loggerhead turtles to foraging grounds: A potential conservation hotspot in the Mediterranean. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22(2), 144–154. https://doi.org/10.1002/aqc.2222

Casale, P., Ciccocioppo, A., Vagnoli, G., Rigoli, A., Freggi, D., Tolve, L. et al. (2020). Citizen science helps assessing spatio-temporal distribution of sea turtles in foraging areas. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(1), 123–130. https://doi.org/10.1002/aqc.3228

Casale, P., Freggi, D., Basso, R. & Argano, R. (2005). Oceanic habitats for loggerhead turtles in the Mediterranean Sea. *Marine Turtle Newletter*, 107, 10–11.

Casale, P., Freggi, D., Basso, R., Vallini, C. & Argano, R. (2007). A model of area fidelity, nomadism, and distribution patterns of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea. *Marine Biology*, 152(5), 1039–1049. https://doi.org/10.1007/s00227-007-0752-7

Casale, P. & Mariani, P. (2014). The first 'lost year' of Mediterranean sea turtles: Dispersal patterns indicate subregional management units for conservation. *Marine Ecology Progress Series*, 498, 263–274. https://doi.org/10.3354/meps10640

Casale, P. & Simone, G. (2017). Seasonal residency of loggerhead turtles *Caretta caretta* tracked from the Gulf of Manfredonia, south Adriatic. *Mediterranean Marine Science*, 18(1), 4. https://doi.org/10.12681/mms.1663

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

Chambault, P., de Thoisy, B., Heerah, K., Conchon, A., Barrioz, S., Dos Reis, V. et al. (2016). The influence of oceanographic features on the foraging behavior of the olive ridley sea turtle *Lepidochelys olivacea* along the Guiana coast. *Progress in Oceanography*, 142, 58–71. https://doi.org/10.1016/j.pocean.2016.01.006

Convertino, M., Muñoz-Carpena, R., Chu-Agor, M.L., Kiker, G.A. & Linkov, I. (2014). Untangling drivers of species distributions: Global sensitivity and uncertainty analyses of MaxEnt. *Environmental Modelling & Software*, 51, 296–309. https://doi.org/10.1016/j.envsoft.2013.10.001

Dodge, K.L., Galuardi, B., Miller, T.J. & Lutcavage, M.E. (2014). Leatherback turtle movements, dive behavior, and habitat characteristics in ecoregions of the northwest Atlantic Ocean. *PLoS ONE*, 9(3), e91726. https://doi.org/10.1371/journal.pone.0091726

Dolédec, S., Chessel, D. & Gimaret-Carpentier, C. (2000). Niche separation in community analysis: A new method. *Ecology*, 81(10), 2914–2927. https://doi.org/10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2

Elith, J., Kearney, M. & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1(4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Fortuna, C.M., Cañadas, A., Holcer, D., Brecciaroli, B., Donovan, G.P., Lazar, B. et al. (2018). The coherence of the European Union marine Natura 2000 network for wide-ranging charismatic species: A Mediterranean case study. *Frontiers in Marine Science*, 5, 356. https://doi.org/10.3389/fmars.2018.00356

Fourcade, Y., Engler, J.O., Rödder, D. & Secondi, J. (2014). Mapping species distributions with MAXENT using a geographically biased sample of presence data: A performance assessment of methods for correcting sampling bias. *PLoS ONE*, 9(5), e97122. https://doi.org/10.1371/journal.pone.0097122

Godley, B.J., Broderick, A.C., Colman, L.P., Formia, A., Godfrey, M.H., Hamann, M. et al. (2020). Reflections on sea turtle conservation. *Oryx*, 54(3), 287–289. https://doi.org/10.1017/S0030605320000162

Goffart, A., Hecq, J. & Legendre, L. (2002). Changes in the development of the winter–spring phytoplankton bloom in the Bay of Calvi (NW Mediterranean) over the last two decades: A response to changing climate? *Marine Ecology Progress Series*, 236, 45–60. https://doi.org/10.3354/meps236045

Hamann, M., Fuentes, M.M., Ban, N.C. & Mocellin, V.J. (2013). Climate change and marine turtles. In: J. Wyneken, K.J. Lohmann, J.A. Musick (Eds.) *The Biology of Sea Turtles*, Vol. III. Boca Raton, FL: CRC Press, pp. 353–378.

Hawkes, L.A., Broderick, A.C., Coyne, M.S., Godfrey, M.H. & Godley, B.J. (2007). Only some like it hot—Quantifying the environmental niche of the loggerhead sea turtle. *Diversity and Distributions*, 13(4), 447–457. https://doi.org/10.1111/j.1472-4642.2007.00354.x

Hays, G.C., Broderick, A.C., Godley, B.J., Luschi, P. & Nichols, W.J. (2003). Satellite telemetry suggests high levels of fishing-induced mortality in marine turtles. *Marine Ecology Progress Series*, 262, 305–309. https://doi.org/10.3354/meps262305

Hays, G.C., Mazaris, A.D. & Schofield, G. (2014). Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Frontiers in Marine Science*, 1, 43. https://doi.org/10.3389/fmars.2014.00043

Haywood, J.C., Casale, P., Freggi, D., Fuller, W.J., Godley, B.J., Lazar, B. et al. (2020). Foraging ecology of Mediterranean juvenile loggerhead turtles: Insights from C and N stable isotope ratios. *Marine Biology*, 167(3), 28. https://doi.org/10.1007/s00227-020-3647-5

Hernández Fariñas, T., Bacher, C., Soudant, D., Belin, C. & Barillé, L. (2015). Assessing phytoplankton realized niches using a French national phytoplankton monitoring network. *Estuarine, Coastal and Shelf Science*, 159, 15–27. https://doi.org/10.1016/j.ecss.2015.03.010

Hochscheid, S. (2014). Why we mind sea turtles' underwater business: A review on the study of diving behavior. *Journal of Experimental Marine Biology and Ecology*, 450, 118–136. https://doi.org/10.1016/j.jembe.2013.10.016

Hochscheid, S., Bentivegna, F., Bradai, M.N. & Hays, G.C. (2007). Overwintering behaviour in sea turtles: Dormancy is optional. *Marine Ecology Progress Series*, 340, 287–298. https://doi.org/10.3354/meps340287

Istituto Superiore per la Protezione e la Ricerca Ambientale. (2015). Marine litter and marine macro-fauna protocol for the agreement 'Fixed line transect using ferries as platform of observation for monitoring cetacean populations'. Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), Technical Annex II, pp. 10.

Iverson, A.R., Fujisaki, I., Lamont, M.M. & Hart, K.M. (2019). Loggerhead sea turtle (*Caretta caretta*) diving changes with productivity, behavioral mode, and sea surface temperature. *PLoS ONE*, 14(8), e0220372. https://doi.org/10.1371/journal.pone.0220372

Karasiewicz, S., Dolédec, S. & Lefebvre, S. (2017). Within outlying mean indexes: Refining the OMI analysis for the realized niche decomposition. *PeerJ*, 5, e3364. https://doi.org/10.7717/peerj.3364

Katselidis, K.A., Schofield, G., Stamou, G., Dimopoulos, P. & Pantis, J.D. (2014). Employing sea-level rise scenarios to strategically select sea turtle nesting habitat important for long-term management at a temperate breeding area. *Journal of Experimental Marine Biology and Ecology*, 450, 47–54. https://doi.org/10.1016/j.jembe.2013.10.017

Lauriano, G., Panigada, S., Fortuna, C.M., Holcer, D., Filidei, J.R., Pierantonio, N. & Donovan, G. (2011). Monitoring density and abundance of cetaceans in the seas around Italy through aerial surveys: A summary contribution to conservation and the future ACCOBAMS survey. In 63rd Meeting of the IWC Scientific Committee, Tromsø, Norway (vol. 30).

Lazar, B., Margaritoulis, D. & Tvrtković, N. (2004). Tag recoveries of the loggerhead sea turtle *Caretta caretta* in the eastern Adriatic Sea: Implications for conservation. *Journal of the Marine Biological Association of the United Kingdom*, 84(2), 475–480. https://doi.org/10.1017/S0025315404009488h

Luschi, P. & Casale, P. (2014). Movement patterns of marine turtles in the Mediterranean Sea: A review. *The Italian Journal of Zoology*, 81(4), 478–495. https://doi.org/10.1080/11250003.2014.963714

Luschi, P., Mencacci, R., Vallini, C., Ligas, A., Lambardi, P. & Benvenuti, S. (2013). Long-Term tracking of adult loggerhead turtles (*Caretta caretta*) in the Mediterranean Sea. *Journal of Herpetology*, 47(2), 227–231. https://doi.org/10.1670/11-173

Maffucci, F., Kooistra, W.H.C.F. & Bentivegna, F. (2006). Natal origin of loggerhead turtles, *Caretta caretta*, in the neritic habitat off the Italian coasts, central Mediterranean. *Biological Conservation*, 127(2), 183–189. https://doi.org/10.1016/j.biocon.2005.08.009

Manly, B.F.J. (2006). *Randomization, bootstrap and Monte Carlo methods in biology*, Third edition, Vol. 70. Boca Raton, FL: Chapman &Hall/CRC. Texts in Statistical Science.

Margaritoulis, D. (1982). Observations on loggerhead sea turtle *Caretta caretta* activity during three nesting seasons (1977–1979) in Zakynthos, Greece. *Biological Conservation*, 24(3), 193–204. https://doi.org/10.1016/0006-3207(82)90057-X

Margaritoulis, D., Argano, R., Baran, I., Bentivegna, F., Bradai, M.N., Camiñas, J.A. et al. (2003). Loggerhead turtles in the Mediterranean: Present knowledge and conservation perspectives. In: A.B. Bolten, B.E. Witherington (Eds.) *Loggerhead Sea Turtles*. Washington, DC: Smithsonian Institution Press, pp. 175–198.

Matiddi, M., Hochsheid, S., Camedda, A., Baini, M., Cocumelli, C., Serena, F. et al. (2017). Loggerhead sea turtles (*Caretta caretta*): A target species for monitoring litter ingested by marine organisms in the Mediterranean Sea. *Environmental Pollution*, 230, 199–209. https://doi.org/10.1016/j.envpol.2017.06.054

Mazaris, A.D., Kallimanis, A.S., Pantis, J.D. & Hays, G.C. (2013). Phenological response of sea turtles to environmental variation across a species' northern range. *Proceedings of the Royal Society B: Biological Sciences*, 280(1751), 20122397. https://doi.org/10.1098/rspb.2012.2397

Mazaris, A.D., Kallimanis, A.S., Sgardelis, S.P. & Pantis, J.D. (2008). Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. *Journal of Experimental Marine Biology and Ecology*, 367(2), 219–226. https://doi.org/10.1016/j.jembe.2008.09.025

Mazaris, A.D., Kallimanis, A.S., Tzanopoulos, J., Sgardelis, S.P. & Pantis, J.D. (2009). Sea surface temperature variations in core foraging grounds drive nesting trends and phenology of loggerhead turtles in the Mediterranean Sea. *Journal of Experimental Marine Biology and Ecology*, 379(1), 23–27. https://doi.org/10.1016/j.jembe.2009.07.026

Mazaris, A.D., Kornaraki, E., Matsinos, Y.G. & Margaritoulis, D. (2004). Modeling the effect of sea surface temperature on sea turtle nesting activities by investigating seasonal trends. *Natural Resource Modeling*, 17(4), 445–465. https://doi.org/10.1111/j.1939-7445.2004.tb00145.x

Miller, J.D. (1996). Reproduction in sea turtles. In: P.L. Lutz, J.A. Musick (Eds.) *The Biology of Sea Turtles*. Boca Raton, FL: CRC Press, pp. 51–81.

Monsinjon, J., Lopez-Mendilaharsu, M., Lara, P., Santos, A., dei Marcovaldi, M.A.G., Girondot, M. et al. (2019). Effects of temperature and demography on the phenology of loggerhead sea turtles in Brazil. *Marine Ecology Progress Series*, 623, 209–219. https://doi.org/10.3354/meps12988

Narazaki, T., Sato, K. & Miyazaki, N. (2015). Summer migration to temperate foraging habitats and active winter diving of juvenile loggerhead turtles *Caretta caretta* in the western North Pacific. *Marine Biology*, 162(6), 1251–1263. https://doi.org/10.1007/s00227-015-2666-0

Patel, S.H., Morreale, S.J., Saba, V.S., Panagopoulou, A., Margaritoulis, D. & Spotila, J.R. (2016). Climate impacts on sea turtle breeding phenology in Greece and associated foraging habitats in the wider Mediterranean region. *PLoS ONE*, 11(6), e0157170. https://doi.org/10.1371/journal.pone.0157170

Patel, S.H., Winton, M.V., Hatch, J.M., Haas, H.L., Saba, V.S., Fay, G. et al. (2021). Projected shifts in loggerhead sea turtle thermal habitat in the northwest Atlantic Ocean due to climate change. *Scientific Reports*, 11(1), 8850. https://doi.org/10.1038/s41598-021-88290-9

Phillips, S.J. & Dudík, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, 31(2), 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Pike, D.A. (2013). Climate influences the global distribution of sea turtle nesting. *Global Ecology and Biogeography*, 22(5), 555–566. https://doi.org/10.1111/geb.12025

Polovina, J.J., Kobayashi, D.R., Parker, D.M., Seki, M.P. & Balazs, G.H. (2000). Turtles on the edge: Movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. *Fisheries Oceanography*, 9(1), 71–82. https://doi.org/10.1046/j.1365-2419.2000.00123.x

Poulain, P.-M. (2001). Adriatic Sea surface circulation as derived from drifter data between 1990 and 1999. *Journal of Marine Systems*, 29(1), 3–32. https://doi.org/10.1016/S0924-7963(01)00007-0

R Core Team. (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/

Rees, A.F. & Margaritoulis, D. (2004). Beach temperatures, incubation durations and estimated hatchling sex ratio for loggerhead sea turtle nests in southern Kyparissia Bay, Greece. *Testudo*, 6(1), 23–36.

Revelles, M., Cardona, L., Aguilar, A., San Félix, M. & Fernández, G. (2007). Habitat use by immature loggerhead sea turtles in the Algerian Basin (western Mediterranean): Swimming behaviour, seasonality and dispersal pattern. *Marine Biology*, 151(4), 1501–1515. https://doi.org/10.1007/s00227-006-0602-z

Sato, K., Matsuzawa, Y., Tanaka, H., Bando, T., Minamikawa, S., Sakamoto, W. et al. (1998). Internesting intervals for loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, are affected by temperature. *Canadian Journal of Zoology*, 76(9), 1651–1662. https://doi.org/10.1139/z98-107

Scales, K.L., Miller, P.I., Varo-Cruz, N., Hodgson, D.J., Hawkes, L.A. & Godley, B.J. (2015). Oceanic loggerhead turtles *Caretta caretta* associate with thermal fronts: Evidence from the Canary Current Large Marine Ecosystem. *Marine Ecology Progress Series*, 519, 195–207. https://doi.org/10.3354/meps11075

Schoener, T.W. (1968). The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. *Ecology*, 49(4), 704–726. https://doi.org/10.2307/1935534

Schofield, G., Bishop, C.M., Katselidis, K.A., Dimopoulos, P., Pantis, J.D. & Hays, G.C. (2009). Microhabitat selection by sea turtles in a dynamic thermal marine environment. *Journal of Animal Ecology*, 78(1), 14–21. https://doi.org/10.1111/j.1365-2656.2008.01454.x

Schofield, G., Dimadi, A., Fossette, S., Katselidis, K.A., Koutsoubas, D., Lilley, M.K.S. et al. (2013). Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. *Diversity and Distributions*, 19(7), 834–844. https://doi.org/10.1111/ddi.12077

Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K.S., Katselidis, K.A. & Hays, G.C. (2010). Biodiversity research: Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. *Diversity and Distributions*, 16(5), 840–853. https://doi.org/10.1111/j.1472-4642.2010.00694.x

Schofield, G., Katselidis, K., Dimopoulos, P., Pantis, J. & Hays, G. (2006). Behaviour analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. *Endangered Species Research*, 2, 71–79. https://doi.org/10.3354/esr002071

Sillero, N. & Barbosa, A.M. (2021). Common mistakes in ecological niche models. *International Journal of Geographical Information Science*, 35(2), 213–226. https://doi.org/10.1080/13658816.2020.1798968

Syfert, M.M., Smith, M.J. & Coomes, D.A. (2013). The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS ONE*, 8(2), e55158. https://doi.org/10.1371/journal.pone.0055158

Tang, X., Yuan, Y., Li, X. & Zhang, J. (2021). Maximum entropy modeling to predict the impact of climate change on pine wilt disease in China. *Frontiers in Plant Science*, 12, 764. https://doi.org/10.3389/fpls.2021.652500

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009). BIOMOD—A platform for ensemble forecasting of species distributions. *Ecography*, 32(3), 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Wallace, B.P., DiMatteo, A.D., Hurley, B.J., Finkbeiner, E.M., Bolten, A.B., Chaloupka, M.Y. et al. (2010). Regional management units for marine turtles: A novel framework for prioritizing conservation and research across multiple scales. *PLoS ONE*, 5(12), e15465. https://doi.org/10.1371/journal.pone.0015465

Witt, M.J., Hawkes, L.A., Godfrey, M.H., Godley, B.J. & Broderick, A.C. (2010). Predicting the impacts of climate change on a globally distributed species: The case of the loggerhead turtle. *Journal of Experimental Biology*, 213(6), 901–911. https://doi.org/10.1242/jeb.038133

Yan, H., Feng, L., Zhao, Y., Feng, L., Wu, D. & Zhu, C. (2020). Prediction of the spatial distribution of *Alternanthera philoxeroides* in China based on ArcGIS and MaxEnt. *Global Ecology and Conservation*, 21, e00856. https://doi.org/10.1016/j.gecco.2019.e00856

Zavatarelli, M. & Pinardi, N. (2003). The Adriatic Sea modelling system: A nested approach. *Annales Geophysicae*, 21(1), 345–364. https://doi.org/10.5194/angeo-21-345-2003

Zbinden, J.A., Aebischer, A., Margaritoulis, D. & Arlettaz, R. (2008). Important areas at sea for adult loggerhead sea turtles in the Mediterranean Sea: Satellite tracking corroborates findings from potentially biased sources. *Marine Biology*, 153(5), 899–906. https://doi.org/10.1007/s00227-007-0862-2

Zbinden, J.A., Bearhop, S., Bradshaw, P., Gill, B., Margaritoulis, D., Newton, J. et al. (2011). Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. *Marine Ecology Progress Series*, 421, 291–302. https://doi.org/10.3354/meps08871

Zbinden, J.A., Davy, C., Margaritoulis, D. & Arlettaz, R. (2007). Large spatial variation and female bias in the estimated sex ratio of loggerhead sea turtle hatchlings of a Mediterranean rookery. *Endangered Species Research*, 3(3), 305–312. https://doi.org/10.3354/esr00058

Zhang, J., Jiang, F., Li, G., Qin, W., Li, S., Gao, H. et al. (2019). Maxent modeling for predicting the spatial distribution of three raptors in the Sanjiangyuan National Park, China. *Ecology and Evolution*, 9(11), 6643–6654. https://doi.org/10.1002/ece3.5243

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Zampollo, A., Arcangeli, A., Costantino, M., Mancino, C., Crosti, R., Pietroluongo, G. et al. (2022). Seasonal niche and spatial distribution modelling of the loggerhead (*Caretta caretta*) in the Adriatic and Ionian seas. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 32(7), 1141–1155. https://doi.org/10.1002/aqc.3815