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Original Article

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Behavioural plasticity in the use of a neritic foraging area by loggerhead sea turtles: insights from 37 years of capture–mark–recapture in the Adriatic Sea (Mediterranean Sea)

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Assessing sea turtle movements and connectivity among different areas is pivotal to understanding their biology and implementing efficient conservation actions. In the Adriatic Sea, one of the most important sea turtle foraging areas in the Mediterranean, a total of 311 capture–mark–recapture (CMR) records (mostly bycatch) from 294 loggerhead turtles (*Caretta caretta*) in the period 1984–2021 were analysed. A general fidelity pattern to Adriatic subareas was indicated by a significantly shorter CMR distance than the potential dispersal distance and by the significantly higher proportion of re-encounters in the same area of release than expected. No seasonal pattern was detected between subareas, and shorter re-encounter distances were observed in turtles released and re-encountered in the same season, suggesting different winter and summer residential areas. Results suggest that turtles frequenting the Adriatic can go anywhere in the Mediterranean basin and may exhibit a wandering behaviour regardless of their size. A substantial connectivity with nesting sites in Greece was observed, confirming with empirical evidence that this is the most important breeding area for turtles foraging in the Adriatic Sea. This study highlights the value of cooperation among different groups and shows a main behavioural pattern of fidelity to neritic foraging grounds.

Keywords: Adriatic Sea, *Caretta caretta*, connectivity, fidelity, flipper tagging, Mediterranean Sea.

Introduction

Large marine vertebrates have a long life span and often migrate long distances, making it challenging to disclose ecological characteristics that are crucial for conservation and management (Heppell *et al.*, 2005). Distribution is one of the most important and cryptic aspects to uncover in order to understand their behavioural ecology. A better knowledge of distribution has important conservation implications, especially for highly vagile animals.

This is the case for sea turtles, which use different habitats in the various stages of their life cycle, which may be thousands of kilometres apart. Loggerhead sea turtles (*Caretta caretta*) tend to wander in open oceanic habitats when small (Bolten, 2003), while larger turtles are known to display fidelity to nesting and foraging sites (Musick and Limpus, 1997; Broderick *et al.*, 2007), with adults periodically migrating between the two (e.g. Hawkes *et al.*, 2006; Rees *et al.*, 2010; Abalo-Morla *et al.*, 2022; Cerritelli *et al.*, 2022).

In the Mediterranean Sea, the loggerhead sea turtle is the most abundant species (Casale and Margaritoulis, 2010; Casale *et al.*, 2018). Juveniles are distributed in the oceanic habitats throughout the basin (Carreras *et al.*, 2006; Revelles *et al.*, 2008; Abalo-Morla *et al.*, 2022), although data in the eastern area are still scarce. Nesting grounds are mostly distributed in the eastern basin, with the most important sites being in Greece, Turkey, Libya, and Cyprus (Casale *et al.*, 2018),

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while low nesting levels, although increasing, are reported from the western basin (Hochscheid *et al.*, 2022; Prato *et al.*, 2022). The eastern basin also hosts the most important neritic foraging grounds for turtles nesting in the Mediterranean, like the Tunisian Shelf and the Adriatic Sea (Margaritoulis *et al.*, 2003; Luschi and Casale, 2014; Casale *et al.*, 2018). In the Adriatic Sea, sea turtles are subject to high anthropogenic pressure, especially by incidental capture in fishing gears (Lucchetti, Vasapollo, and Virgili, 2017). Here, mortality affects larger sea turtles in particular, considered important for their high reproductive value (Heppell *et al.*, 2005). Such threats mainly affect turtles from the Greek nesting sites that are known to frequent these waters (Lazar, Margaritoulis, and Tvrtkovic, 2004; Zbinden *et al.*, 2011; Schofield *et al.*, 2013; Tolve *et al.*, 2018). Assessing sea turtle distribution at a fine scale as well as turtle movements and connectivity among different areas can contribute to the development of adequate conservation measures for the Adriatic Sea; however, the current knowledge is limited to large-scale migratory movements of adults (Casale *et al.*, 2018).

Currently, sea turtle distribution and movements are investigated worldwide through several methods, notably satellite tracking (Godley *et al.*, 2008; Hays and Hawkes, 2018), genetic markers (Bowen and Karl, 2007; Komoroske *et al.*, 2017), and capture–mark–recapture (CMR; Avens *et al.*, 2003; Shimada *et al.*, 2020). CMR has been largely used since the earliest studies on sea turtles (Hendrickson, 1958) and is still carried on despite the onset of more informative technologies. Due to logistical constraints, CMR is mostly used at nesting grounds, where adult females come on land and are easier to reach. For instance, a previous study on nesting females showed the connectivity between the nesting grounds in Greece and the foraging grounds of the eastern Adriatic (Lazar *et al.*, 2004). However, this approach leaves a large gap in the information that is possible to infer from these studies because juvenile turtles are not covered. CMR studies at foraging grounds allow a broader coverage of size classes but are much fewer (e.g. López-Castro *et al.*, 2010; Rees *et al.*, 2013; Shimada *et al.*, 2020) because of the challenges represented by lower densities and logistic limitations.

In Italy, a sea turtle CMR programme at foraging grounds was launched in 1981 by the University of Rome "La Sapienza" and provided insights on the movements of juvenile turtles (Argano *et al.*, 1992; Casale *et al.*, 2007). Taking advantage of long-term CMR activity in the Adriatic, the present study aims to provide novel insights on the behaviour of sea turtles foraging in the Adriatic Sea, and in particular to assess: (i) potential fidelity to sub-areas of the Adriatic and connectivity among them; (ii) seasonal patterns; and (iii) connectivity to other areas.

Material and methods

Data collection

CMR records of loggerhead sea turtles found by five organizations working along the Italian coasts of the Adriatic Sea (group A: Arché, ARC; Fondazione Cetacea, FC; Centro Studi Cetacei, CSC; Legambiente, LEG; Associazione Panda Molfetta, MOL) were assembled (Figure 1). These CMR records included both turtles tagged by group A and turtles only re-encountered by group A but originally tagged by other organizations (group B: ARCHELON, ARL; CRTM Lampedusa, LMP; Herpetofauna Albanian Society, HAS; Stazione Zoologica Anthon Dohrn, SZN; University of Primorska, UP). Specifically, 254 records were of turtles tagged by Group A (ARC, $n = 36$; FC, $n = 21$; CSC, $n = 9$; LEG, $n = 110$; MOL, $n = 78$); and 35 records were of turtles originally tagged by Group B (ARL, $n = 10$; LMP, $n = 4$; HAS, $n = 9$; SZN, $n = 8$; UP, $n = 4$). Moreover, 22 records already published (Casale *et al.*, 2007) were also included in the present study. Tags stamped with an alphanumeric code and return address were applied on the front or rear flippers of the turtles. Tag model and style varied among the organizations, including: small plastic, jumbo plastic, jumbo roto plastic (Dalton, England), 49 monel, 681 monel, 681 inconel, 681 metal (National Band and Tag Company, KY, USA), and titanium (Stockbrands, Australia).

For each turtle encounter, the following parameters were considered: date of release/re-encounter, location, type of encounter (incidental capture in fishing gears, stranding, gathering while floating at sea, nesting), and size (carapace length). Carapace measurements differed among the organizations, including curved or straight-line methods, notch to tip (n–t), total (T), or minimum (min; Bolten, 1999). Only CCLn–t measures were considered for the analyses, including records where the type of measurement was not explicitly specified, but on the basis of the context (e.g. the specific tagging project), it was likely CCLn–t.

Data analysis

A minimum route between the release and re-encounter sites was created through the following two steps. First, routes at sea (i.e. not over land) were created through the function *shortest Path* of the package *gdistance* (van Etten, 2017) in R (R Core Team, 2021), which uses the Dijkstra algorithm to assess the shortest distance between a cell and the 16 neighbouring cells. However, the function favours N–S and W–E routes, making the overall path longer than the minimum. Thus, as a second step, the tracks were edited in QGis (QGIS Development Team 2021) to allow for diagonal paths. Finally, the minimum route length (L) between capture and re-encounter sites was calculated in Qgis.

For turtles with multiple recaptures, Spearman's rank correlation was computed between L of the first re-encounter and L of the second or third re-encounter, and given that no autocorrelation was detected, each re-encounter event was treated independently even when the same turtle was re-encountered more than once. To investigate differences in L of turtles released in the Adriatic among organizations in group A, a Kruskal–Wallis test was performed through the function *kruskal.test* of the package *stats*, followed by a post-hoc test carried out with the function *kruskalmc* of the package *pgirmess* (Giraudoux, 2013). To investigate the possible area fidelity of this subset of CMR turtles, L was compared to a theoretical potential distance (D) covered by the same turtles, assuming they had a wandering, non-fidelity behaviour. To estimate D, we referred to ten turtles satellite tracked in other Mediterranean seas close to the Adriatic: nine in the Tyrrhenian (Mencacci *et al.*, 2011; Luschi *et al.*, 2013; Luschi *et al.*, 2018; Mencacci *et al.*, 2020) and one in the Ionian Sea (Mingozzi *et al.*, 2016). These turtles were selected as models of such wandering non-fidelity behaviour because they showed undirected wandering movements mostly over oceanic marine areas. For each satellite-tracked turtle, the following move-

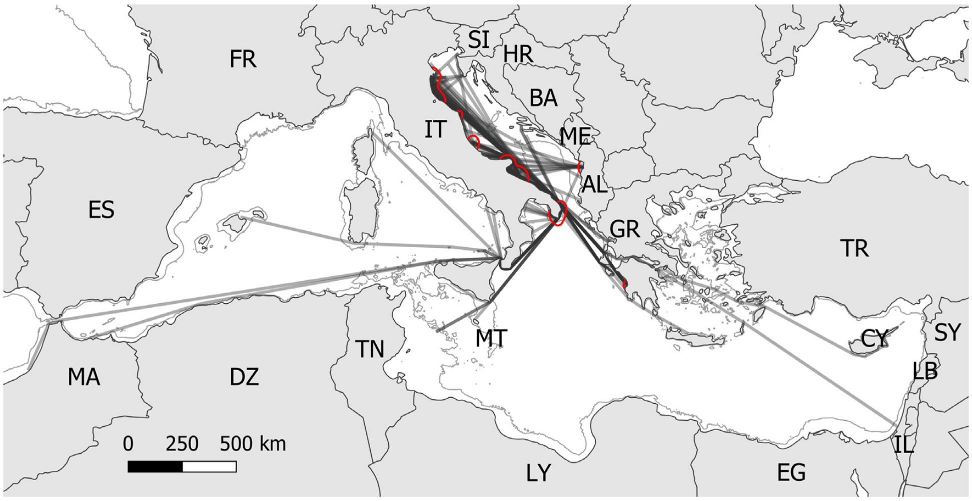

Figure 1. Minimum paths between release and re-encounter sites for 295 turtles (311 tracks, of which 26 are not visible due to L = 0). Darker colour indicates higher track density. A total of 90% KDE of the release sites are shown in red colour. The 200-m isobath is shown in grey. Country codes (clockwise): ES = Spain, FR = France, IT = Italy, SI = Slovenia, HR = Croatia; BA = Bosnia and Herzegovina; ME = Montenegro, AL = Albania, GR = Greece; TR = Turkey; CY = Cyprus; SY = Syria; LB = Lebanon, IL = Israel, EG = Egypt; LY = Libya; MT = Malta. TN = Tunisia; DZ = Algeria; and MA = Morocco.

ment parameters (see Bovet and Benhamou, 1988; Revelles *et al.*, 2008) were calculated: mean step size *S* (distance between consecutive fixes; km); mean time interval between steps *t* (hours); and sinuosity of the path *C* (rad km^{-2}), calculated as

$$C = \text{SDA}\sqrt{S},$$

and route straightness (*r*), calculated as

$$r = \exp\left(\frac{-\text{SDA}^2}{2}\right),$$

where SDA (radians) is the standard deviation of the angle between consecutive steps. Then, $\bar{S}$, $\bar{t}$, $\bar{C}$, and $\bar{r}$ were calculated as means of *S*, *t*, *C*, and *r* for all satellite-tracked turtles. These values were assumed to describe the theoretical wandering of turtles showing a non-fidelity behaviour and were applied to each CMR turtle to estimate its potential dispersal (*D*) as follows:

$$D = \bar{S}\sqrt{\bar{C}n\,(1+\bar{r})\,/\,(1-\bar{r})},$$

where *n* is the number of steps of CMR turtles calculated from *d* (the number of days elapsed between release and re-encounter of CMR turtles) as

$$n = \frac{d}{\bar{t}/24}.$$

This process produced paired values of L and D for each CMR turtle that were compared through a Wilcoxon signed-rank test.

The Adriatic was divided into three areas according to the current system and bathymetry of the sub-basins: north (NA), centre (CA), and south (SA; Figure 2). Only NA and SA had an adequate sample size and were considered for the following analysis. To explore patterns of connectivity between these two subareas, the proportion of turtles released in one area and re-encountered in the same or in the other area (NN, NS, SS, and SN) were compared through a Fisher exact test. Since time may affect the probability of re-encounters in the same areas, only turtles re-encountered after a period longer than the median interval for a re-encounter in a different area were used in this analysis.

To investigate a potential seasonality in the spatial distribution of sea turtles in the Adriatic Sea, only turtles released and re-encountered in the Adriatic were considered, and the year was divided into two periods: cold (Oct–Mar) and warm (Apr–Sep). Since time may affect the probability of re-encountering in the same period (season), only turtles re-encountered after the duration of a season (180 d) were used in this analysis. First, the proportion of turtles released in one period and re-encountered in the same or another season (CC, CW, WW, and WC) were compared through a Fisher exact test. Given that turtles frequenting different areas might have different seasonalities, the test was conducted separately for turtles released in NA and SA. Then, to investigate intra-season versus inter-season spatial fidelity, potential differences in L among the groups (CC, WW, WC, and CW) were explored with a Kruskal–Wallis test, followed by a post-hoc test and a Mann–Whitney test.

To investigate habitat utilization in different size classes, we compared the size of the turtles released inside the Adriatic Sea and re-encountered inside versus outside the Adriatic Sea through a Mann–Whitney test. Turtles re-encountered while nesting (in Greece) were excluded because they may induce a bias to the larger size. All the above tests were performed in R (v. 4.0.1).

Results

From August 1984 to July 2021, 294 individual loggerhead sea turtles were either released or re-encountered in the Adriatic Sea (Figure 1). These turtles were re-encountered once ($n = 279$), twice ($n = 13$), and thrice ($n = 2$), for a total of 311 release/re-encounter pairs. Most of the multiple re-encounters occurred in the Gulf of Manfredonia, in SA. Encounters in NA, CA, SA, and outside the Adriatic were 122, 30, 422, and 48, respectively (Figure 1; Supplementary Table S1). A total of 263 turtles were both released and re-encountered in the Adri-

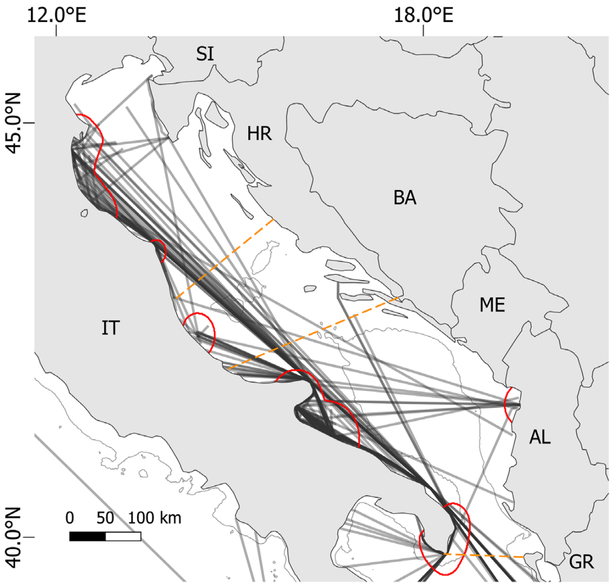

Figure 2. Minimum paths between release and re-encounter sites for 263 turtles (only the parts within the Adriatic Sea). Darker colour indicates higher track density. A total of 90% of the KDE release sites are shown in red colour. Orange broken lines show the boundaries between three subareas of the Adriatic Sea (from the top: NA, CA, and SA). The 200-m isobath is shown in grey. Country codes (clockwise): IT = Italy, SI = Slovenia, HR = Croatia, BA = Bosnia and Herzegovina, ME = Montenegro, AL = Albania, and GR = Greece.

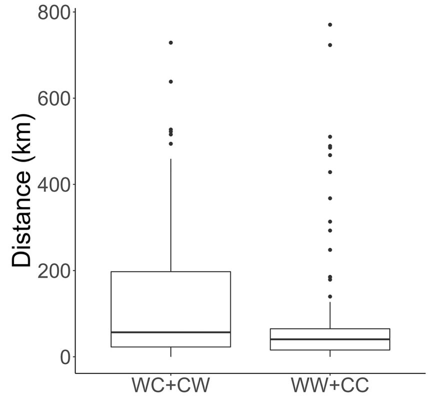

Figure 3. Distance between release and re-encounter sites (L; see text) of 186 sea turtles encountered in different or same seasons (W: warm; C, cold). The bar represents the median; the upper and lower limits of the box are the 25th and 75th percentiles. The whiskers extend up to a value of ±1.5 × IQR. Black dots are outliers.

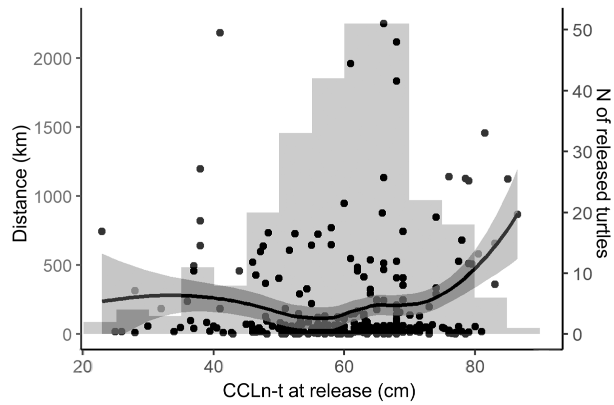

Figure 4. Distance between release and re-encounter sites (L; see text) of 272 sea turtles for which size (CCL) at release was available (black dots; left axis). Regression line in black with 95% *CI*. Grey bars represent the frequency distribution (right axis) of the released turtles by 5-cm CCL size classes.

atic Sea (Figure 2). Turtles were re-encountered after 1–4584 d (median = 396 d, IQR 177–810, $n = 311$). Type of first encounter and re-encounter was respectively: bycatch (mostly in bottom trawls; $n = 265, 181$), stranding ($n = 9, 103$), gathered while floating at sea ($n = 11, 13$), nesting ($n = 9, 2$), unknown ($n = 17, 12$). Of the nesting turtles, seven were found in NA, three in SA, and one in CA.

There was no significant correlation between L of the first re-encounter and L of the second or third re-encounter (Rho = −0.007, $P = 0.98$, $n = 17$). Distance (L) ranged from 0 to 2561 km (median = 56.6 km; IQR = 19–272.2; $n = 311$). For each organization in group A, the median L was 26.7 (LEG), 59.5 (MOL), 70.4 (ARC), 86.0 (FC), and 221.4 (CSC) km. L was significantly different among release organizations (Kruskal–Wallis chi-squared = 29.9, $P < 0.001$, $n = 244$), and the post-hoc test showed that the L of turtles released by LEG was significantly lower than all the other organizations. Potential dispersal (D) had a median of 579 km (range = 29.5–1955.5 km; IQR = 377.4–812.4, $n = 253$) (Supplementary Figure S1) and was significantly larger than L (median = 42.4, range 0–2115.5, IQR = 16.8–101.9, $n = 253$; Wilcoxon signed-rank test; V = 30 708, $P < 0.001$, $n = 506$).

The median number of days elapsing between release and re-encounter for turtles released in the NA and re-encountered in the SA, and vice versa, was 472 d. Among turtles with interval above this value, the proportion of turtles re-encountered in the same area of release was significantly higher than the proportion of those re-encountered in the other area (Fisher Exact test, $P < 0.001$, $n = 98$).

The proportion of turtles released and re-encountered in the same season (CC and WW) was not significantly different from those re-encountered in a different season (CW and WC) (Fisher exact test; NA: $P = 0.33$, $n = 38$; SA: $P = 0.16$, $n = 143$). L was significantly different among the three groups (WW, CC, and WC + CW) (Kruskal–Wallis chi-squared = 8.24, $P < 0.05$, CC = 62, CW = 32, WC = 54, WW = 38), but the post-hoc test showed that CC and WW were not significantly different; therefore, they were aggregated into an intra-season group. L was significantly lower in the intra-season group (WW + CC) than in the inter-season group (WC + CW) (Mann–Whitney U = 5279, $P < 0.01$, Figure 3).

At release, sea turtles mean size was 60.2 cm CCLn–t ($SD = 12$; range = 23–86.5, $n = 272$; Figure 4). No significant difference in size was detected between sea turtles released in the Adriatic and re-encountered inside versus outside the Adriatic Sea (excluding turtles re-encountered while nesting) (Mann–Whitney $U = 653.5$, $P = 0.08$, $n = 204$).

Discussion

This study provides new insights about the behavioural patterns of loggerhead sea turtles foraging in the Adriatic Sea—one of the most important foraging grounds for this species in the Mediterranean (Casale *et al.*, 2018 and references therein)—in terms of connectivity with other areas, fidelity, and seasonality. This was possible through assembling datasets from several long-term monitoring programmes, and it shows the potential value of CMR of sea turtles at foraging grounds (versus the most common CMR at nesting sites) and of regional cooperation.

The present study expands a previous study (Lazar *et al.*, 2004) focused on the eastern Adriatic regarding the origin of turtles frequenting the Adriatic Sea. So far, CMR studies are the only ones that can provide direct evidence of connectivity between breeding and foraging grounds across multiple years (López-Castro *et al.*, 2010). Present data indicate that nesting sites in Greece represent the main origin of turtles found on both sides of the Adriatic, although nesting sites with less CMR effort than in Greece may be underrepresented just for this reason. These results are consistent with genetic and satellite tracking studies that, however, can only estimate proportions based on a likelihood approach (Garofalo *et al.*, 2013; Clusa *et al.*, 2014; Splendiani *et al.*, 2017; Tolve *et al.*, 2018; Bertuccio *et al.*, 2019) or are limited by sample size, duration, and tagging effort (Zbinden *et al.*, 2011; Schofield *et al.*, 2013; Haywood *et al.*, 2020); respectively. The present and previous CMR studies and genetic data also suggest a minor connectivity with Turkey, Cyprus, and Israel (Garofalo *et al.*, 2013; Splendiani *et al.*, 2017; Tolve *et al.*, 2018; Bertuccio *et al.*, 2019).

Results show that turtles frequenting the Adriatic can go anywhere in the Mediterranean basin, and such movements do not seem to be size-related. While in the Mediterranean, nomadic behaviour of immature turtles can be expected (Luschi and Casale, 2014; Abalo-Morla *et al.*, 2022), and adults periodically undergo breeding migrations (Zbinden *et al.*, 2008; Hays *et al.*, 2010; Schofield *et al.*, 2010), large juveniles generally show fidelity to their foraging grounds (Casale *et al.*, 2012a, b; Snape, Schofield, and White, 2020). Several individuals were found exiting the Adriatic, suggesting a plasticity in the behaviour that was already proposed in previous studies in juveniles (Tomas, Aznar, and Raga, 2001; Casale *et al.*, 2008; Arendt *et al.*, 2012; Casale *et al.*, 2012a) as well as adult females (Hatase *et al.*, 2002; Hawkes *et al.*, 2006; Rees *et al.*, 2010; Reich *et al.*, 2010; Mingozzi *et al.*, 2016; Cerritelli *et al.*, 2022), which were observed frequenting oceanic foraging grounds. It appears that turtles may alternate between a wandering behaviour, more typical of oceanic habitats, and periods of fidelity, usually associated with neritic habitats, which in the Mediterranean Sea could be facilitated by the relatively short distance between the two (Casale *et al.*, 2008; Ten *et al.*, 2019).

Two results indicate that in the Adriatic, turtles tend to remain in a sub-area. First, re-encountered turtles moved less than their potential capabilities, as shown by the significantly shorter distances covered with respect to the potential dispersal values. Second, they tend to be re-encountered in the same area of release. A few individuals were even re-encountered multiple times in the same area (mostly in the SA). Hence, the present study supports the general pattern of fidelity to foraging sites reported from this (Casale *et al.*, 2012a; Casale and Simone, 2017) and other areas for both juveniles (Avens *et al.*, 2003; Casale *et al.*, 2007) and adults (Schofield *et al.*, 2010; Rees *et al.*, 2017; Shimada *et al.*, 2020).

A wide latitudinal range and different features along the Adriatic coasts may determine variability in the choice of habitat at a finer scale. Such an individual preference for a certain area probably does not depend on the turtle's origin, because all turtles enter the Adriatic through a rather narrow strait, and, accordingly, the available genetic data do not show any significant structure within the Adriatic (Tolve *et al.*, 2018; Bertuccio *et al.*, 2019). There are two possible explanations for turtles choosing a specific subarea: (i) dispersal in the first stages of life is governed by currents, and later turtles will keep frequenting the foraging ground(s) they have previous knowledge of; (ii) turtles actively choose the NA or SA for particular environmental features regardless of dispersal in their early stages of life. Since in the Mediterranean, turtles may start using neritic habitats at a small size (Casale *et al.*, 2008; Lazar *et al.*, 2008), two lines of evidence support the first hypothesis. First, the Adriatic current system (Poulain, 2001; Zavatarelli and Pinardi, 2003) favours the movements of turtles entering the Adriatic toward the NA through the northward-flowing East Adriatic Current. A portion of the turtles entering the Adriatic during this phase may not be able to counter the currents of the south Adriatic gyre (Poulain, 2001) and may keep using that area as their foraging ground. As suggested by Shimada *et al.* (2020), turtles do not invest energy in finding other foraging areas when the current trophic resources are adequate. Second, based on the distribution of chlorophyll a, particulate organic carbon, and sea surface temperature, Zampollo *et al.* (2022) modelled a lower general habitat suitability in the SA, except for a few restricted areas. If turtles were affected by such features, they would concentrate in the NA, moving away from the SA even if the currents brought them there in their early stages. This is not the case, as the present results and recent studies show that the SA is largely frequented by sea turtles, in particular in the Gulf of Manfredonia (Casale *et al.*, 2012c; Baldi *et al.*, 2022).

Present results also show that the Adriatic Sea is used as a foraging/development area year-round. No clear southward wintering migration pattern (NA–SA) was observed, supporting the same conclusions by a previous satellite tracking study based on a relatively small sample size (Casale *et al.*, 2012a). As Hochscheid, Bentivegna, and Hays (2005) suggested, undergoing migrations for a small increase in temperature may not be cost-efficient. However, the significantly lower L values recorded in turtles released and re-encountered in the same season than in different seasons suggests that turtles may have different winter and summer residential areas, as observed in other areas (e.g. Broderick *et al.*, 2007; Mansfield *et al.*, 2009; Narazaki, Sato, and Miyazaki, 2015; Mingozzi *et al.*, 2016).

CMR is a low-cost method that can provide an adequate sample size to inform on residency and connectivity. Such information, especially on juvenile turtles, is more difficult to obtain through satellite tracking, which typically is based on a small sample size and on adults (Godley *et al.*, 2003). On the other hand, CMR can only inform about the release and re-encounter site, without possibility to infer on the movement patterns or the origin of the individuals (as allowed by satellite tracking and genetic data, respectively). Other challenges for CMR studies are the management of long-term datasets, as re-encounters may span several years after release (e.g. max 12.6 years in this study, 14.9 years in Casale *et al.*, 2007), and the standardization of data collection among different organizations, which can influence data analysis. Uneven monitoring efforts or reporting to the tagging organization also affect encounter distribution. For instance, the relatively low number of encounters in CA observed in this study may be an artefact of different monitoring efforts (e.g. collaboration with fishers is more developed in NA and SA). The lower L of turtles released by LEG than the other organizations (especially compared to MOL, which is in the same area) suggests that distant re-encounter reports did not reach this organization. Previous studies in the SA (Casale *et al*., 2012c; Baldi *et al*., 2022) showed how monitoring programmes and cooperation with fishers are essential to unveil distribution patterns of this elusive species. In this respect, flipper tagging is less expensive at release and more accessible at re-encounter than passive integrated transponders (Omeyer *et al*., 2019), and therefore, it is more suitable for opportunistic tag recoveries. Flipper tag loss can be reduced with double tagging and has just a minor effect on tag return in comparison with the reporting rate and turtle survival (Casale, Freggi, and Salvemini, 2017).

CMR studies at sea can provide useful information, especially when performed in synergy with satellite tracking and genetic studies to balance their different biases. CMR can greatly benefit from standardization of type of tagging and size measure, and from increasing the reporting rates to make the most out of the huge tagging effort carried out by CMR projects. In this respect, in-water CMR efforts have the best chances of success in a semi-closed basin like the Mediterranean, and any public awareness campaign focused on sea turtles or marine animals in general should explain the importance of reporting tagged animals.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest statement

The authors have no conflicts of interest to declare.

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Author contributions statement

Conceptualization: PC and GB; methodology: GB and PC; formal analysis: GB; investigation: GF, MDV, PS, CV, VA, SP, KLM, CP, VO, DM, AFR, AÇ, SH, DF, BL, PL; Writing—Original Draft: GB, PC; Writing—Review and Editing: GF, MDV, PS, CV, VA, SP, KLM, CP, VO, DM, AFR, AÇ, SH, DF, BL, PL; Visualization: GB; Supervision: PC.

Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

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SUPPLEMENTAL MATERIALS

Behavioral plasticity in the use of a neritic foraging area by loggerhead sea turtles: insights from 37 years of capture-mark-recapture in the Adriatic Sea (Mediterranean Sea)

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Table S1. Summary of the sea turtles that were released or re-encountered outside the Adriatic (n = 48). NA = North Adriatic, CA = Central Adriatic, SA = South Adriatic, IS = Ionian Sea, TS = Tyrrhenians Sea, SC = Sicily Channel, a = gathered while floating at sea, b = bycatch, n = nesting, s = stranding. Size is CCL except for T (total length), where available type of measurement is stated. Number in parentheses are the N per sub-area.

N	Release	Re-encounter	Re-encounter type	Re-encounter size
1	NA	Balearic Islands, Spain	b	n/a
1	NA	Crete, Greece	n	84
8	NA (2) CA (1) SA (5)	Gulf of Taranto, Italy, IS	s, s s s, n/a, s, s, a	60, 50 59 50, 81, n/a, 70, 73 n-t
3	NA (2), SA (1)	Kyparissia Bay, Greece	n, s s	86 n-t, 87.5 n/a
1	CA	Eolian Archipelago, Italy, TS	a	62.2
3	CA (1) SA (2)	Kefalonia, Greece	s s, a	83 65, 84.3
3	SA	Zakynthos, Greece	a, s, s	n/a, n/a, 76
1	SA	Campania, Italy, TS	n/a	89.5 n-t
1	SA	North Corsica, France, TS	b	n/a
1	SA	Atlantic Morocco	n/a	n/a
1	SA	Med. Morocco	n/a	n/a
1	SA	Malta	n/a	n/a
1	SA	Cyprus	b	n/a
1	SA	Israel	s	69
1	SA	Amvrakikos Gulf, Greece	a	66.5 n-t
5	Gulf of Taranto, Italy, IS	NA (4) SA (1)	s, b, s, a b	38, 76, 53, 56 74 n-t
1	Campania, Italy, TS	SA	a	76.5 n-t
1	North Sicily, Italy, TS	SA	b	68 n-t
1	South Sicily, Italy, SC	CA	n/a	47
2	Pelagian Archipelago, Italy, SC	CA	s, s	47 n-t, n/a
1	Amvrakikos Gulf, Greece	SA	b	70 n-t
2	Zakynthos, Greece	NA (1) SA (1)	s b	89 86.7 n-t
7	Kyparissia Bay, Greece	NA (4) CA (1) SA (2)	s, s, b, s b b, b	80, 81, 79.5 min, 75 T 86.5 n-t 79, 83 n-t

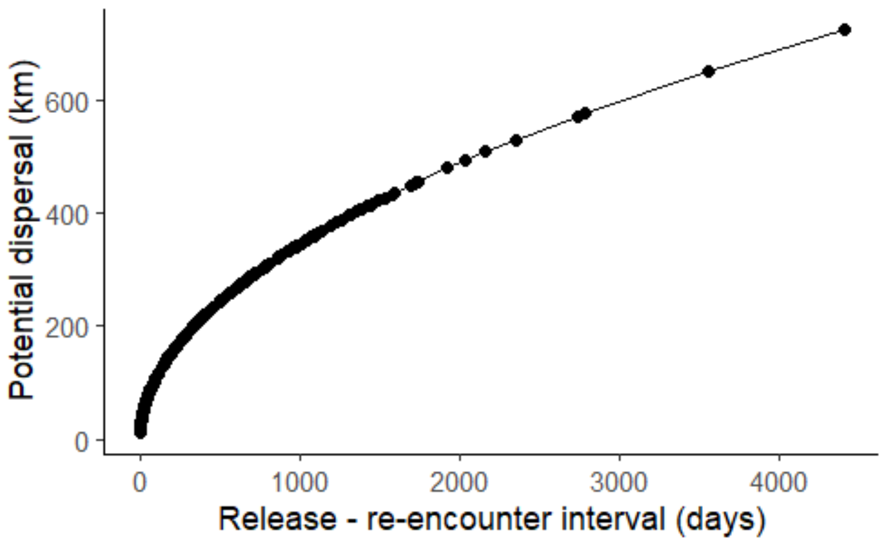

Figure S1. Potential dispersal (D) estimated for each CMR sea turtle (n = 253) from its time interval between release and re-encounter (days).