Large-scale movements in the oceanic environment identify important foraging areas for loggerheads in central Mediterranean Sea

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Abstract

Loggerhead sea turtles (*Caretta caretta*) are known to display a wide range of movement patterns during the different stages of their life cycle, but empirical information to document this extensive behavioural plasticity is still limited. This is especially true for large, adult-sized individuals, that are thought to mainly forage in neritic areas. In the present paper, eight adult-sized loggerhead turtles were tracked using satellite telemetry to identify the location of their foraging grounds in the seas along the western coast of the Italian peninsula. Tracked turtles mostly stayed in the region between the Italian peninsula and the islands of Sicily and Sardinia, that was reached following quick, directed movements by the turtles from a release site to the north. In this area, two turtles took up residence in spatially-limited neritic sites along the coast, while the remaining six alternated circumscribed coastal stays with long-distance, circuitous movements in the oceanic environment. An utilization distribution analysis clearly identified an area, mostly comprising oceanic waters, that was continuously used by turtles in different seasons and years. The present results contribute to the still-limited knowledge of the spatial ecology of loggerheads frequenting the Western Mediterranean Sea and highlight the presence of a potentially important oceanic region in the Southern Tyrrhenian Sea where adult-sized turtles forage for extended periods. These findings increase our knowledge of complex life history traits of loggerhead turtles and provide important information to be considered for evidence-based conservation measures.

Keywords: adult-sized loggerheads; oceanic foraging; central Mediterranean Sea

Introduction

Satellite telemetry has provided a wealth of information on the movements of marine turtles which is radically changing our view of turtle movement ecology and spatial behaviour. This is especially true for loggerhead turtles (*Caretta caretta*), whose original life history model (Musick and Limpus 1997; Bolten 2003), largely accepted until a few years ago, is being questioned (e.g. McClellan and Read 2007; Casale et al. 2008). According to this model, after an initial phase of pelagic living in the oceanic environment, late juvenile loggerheads recruit to neritic areas where they remain until adulthood, while adults are thought to shuttle between residential neritic foraging grounds and the breeding sites. This view has been challenged by satellite telemetry findings that have shown a large amount of behavioural plasticity in both juvenile and adult loggerheads. In particular, large juveniles have been found not to always reside in neritic zones, but were rather often shown to display prolonged movements also over oceanic waters (e.g. McClellan & Read 2007; Arendt et al. 2012a; Varo Cruz et al. 2016). Adults, too, have been sometimes observed foraging in oceanic zones while displaying wandering movements, either when tracked soon after migrating away from breeding/nesting areas (Hatase et al. 2002; Hawkes et al. 2006; Schofield et al. 2010; Pikesley et al. 2015; Mingozzi et al. 2016) or in periods outside the breeding season (Bentivegna 2002; Kobayashi et al. 2011; Casale et al. 2013; Luschi et al. 2013).

Given this marked behavioural variability, it is mandatory to collect as much data as possible to document the main features of loggerhead movement patterns, especially for seldom-studied life stages such as juveniles (Godley et al. 2008). Indeed, it is particularly difficult to equip non-nesting turtles, including males and juveniles, with tracking instruments, since they do not come ashore at any time and cannot be easily accessed or captured (but see Van Dam et al. 2008; Arendt et al. 2012b; Schofield et al. 2013). The most commonly used way to study males and juveniles relies on accidentally or deliberately caught individuals, that are released soon after capture (e.g. Limpus et al. 1993; Howell et al. 2010; Barcelo et al. 2013; see also Ehrhart and Ogren 1999) or after a period spent in captivity for rehabilitation (e.g. Bentivegna 2002; Cardona et al. 2012; Dalleau et al. 2014). In this way, it has been possible to obtain an initial picture of the movements performed of loggerhead juveniles and adult males, but the available information remains scant and fragmentary, especially for large juveniles in the late stage of their developmental period.

In this study, we present satellite tracking data obtained for eight adult-sized loggerhead turtles that were incidentally captured while foraging in the Tyrrhenian Sea, western Mediterranean. Loggerheads are the most abundant turtle species in the Mediterranean, and are widely distributed throughout the whole basin, although nesting sites are mainly concentrated in its eastern part (Casale and Margaritoulis 2010). Studies involving mark and recapture, satellite tracking and distance sampling techniques have shown that Mediterranean loggerheads disperse widely, both as juveniles and as adults (Luschi and Casale 2014), frequenting virtually all the available areas of the basin, including the most northern ones (e.g. Casale et al. 2012a; Hochscheid et al. 2010; Lauriano et al. 2011). Data on the movements made in the Western Mediterranean (West of Sicily) are however not abundant, and are mainly restricted to turtles tracked in the westernmost area between Spain and Algeria (Cardona et al. 2005, 2009, 2012; Revelles et al. 2007a; Eckert et al. 2008), with only a few turtles (n=15 in total in 5 studies) having been tracked in the Ligurian and Tyrrhenian seas along the western coast of the Italian peninsula (Bentivegna 2002; Hochscheid et al. 2007, 2010; Mencacci et al. 2011; Luschi et al. 2013). Using this approach, we intended to investigate whether large turtles, which are presumably in their neritic developmental stage, still make extensive use of oceanic foraging areas and to identify the location and extension of the most frequented sites in the region. Such information is important to decipher complex life history traits of sea turtles and design ad-hoc management plans for this threatened species.

Materials and methods

Tracked turtles were captured in various areas of the Tyrrhenian Sea, having been incidentally caught by bottom trawlers, found floating (turtle T6) or entangled in nets (turtle T8). Before release, they had been kept in captivity for a variable period (range 30-463 days; table 1) to be rehabilitated by Rescue Centres operating in the areas.

Curved carapace length (CCL) of all turtles was above 60 cm, and so they can be considered in the subadult-adult stage of their life cycle, given that the minimum CCL of females nesting in Mediterranean rookeries is around 65-70 cm (Margaritoulis et al. 2003) and that males attains sexual maturity at a size of at least 75 cm CCL (Casale et al. 2005). Based on their size, external morphology and on the presence/absence of male sexual characteristics (Casale et al. 2005), turtles T2, T4, T5, T6 and T7 were considered adults and ultrasound scanning indeed revealed that turtle T2 had eggs developing in her ovary at the time of release. The other turtles, with CCLs ranging between 63 and 68 cm at the time of release, were likely approaching sexual maturity.

Turtles were released from locations close to the capture sites, after having been equipped with various models of Argos-linked satellite transmitters (table 1), that were attached using standard attachment procedures with epoxy resins. The units were programmed to transmit with different duty cycles (table 1).

The Argos system assigns a level of decreasing accuracy to locations obtained: classes 3, 2 and 1 are the most accurate (generally within 1 km of the true position; Witt et al. 2010), while low-quality classes 0, A and B have no accuracy estimation. The data were managed by STAT program (www.seaturtle.org; Coyne and Godley 2005) and the routes were reconstructed by filtering out low-quality locations that were on land or which inferred movement speeds above a pre-determined individual speed threshold. Speed thresholds were determined for each turtle by assessing the maximum speed between locations of classes 3, 2, and 1 that were obtained at least 1 h apart and then adding a 20% buffer to this value (see also Lambardi et al. 2008; Dujon et al. 2017). A minimum individual speed threshold of 4 km/h was applied. The number of locations obtained varied between 1.4 and 21.7 per day, with an average of 27% of fixes of appropriate quality having been obtained less than 1 h apart. Data filtering eliminated the 32% of locations on average (range 24-51%).

To identify high-use areas in the Tyrrhenian Sea, the utilization distribution (UD) of each turtle was estimated (Worton 1989) by selecting only one fix per day and choosing the one with highest accuracy and the one closest to midday if more than one fix had the same accuracy (Zbinden et al. 2008). Individual turtles' core areas were identified by applying the Area Independent Method developed by Seaman and Powell (1990). The method divides the home range in areas of high- and low- use using an objective criterion, and is based on a graphical representation of the home range area in relation to its use (Kernel UD volume contour). In this way it is possible to identify the dividing point between high- and low-use areas, as the point where the plot is maximally distant from a straight line of slope ±1, that represents a distribution of random use. We performed the analysis using steps of 5% and for all our turtles the point of maximum distance was reached at a value close to 30% volume contour. As a result, we defined the core areas as 30% Kernel UD. The core area polygons were calculated with a fixed kernel technique with reference smoothing parameter (Worton 1989). Calculations were made with the adehabitatHR package (Calenge 2006) in R 3.3.3 (R core team 2017).

Results

Six of the eight turtles were tracked for more than four months after release, up to a maximum of 314 days (table 1; Fig. S1). The three turtles from the Northern Tyrrhenian Sea moved southward soon after release, with turtle T3 taking a route closely following the coastline and the other two turtles moving in the open sea (Fig. 1). In this way they quickly reached an area south of 41° N, where the other turtles released in South Tyrrhenian Sea also remained for several months (Fig. 2). Turtles T3 and T1 took residence in limited coastal sites around the Gulf of Naples where they were tracked for 30 and 111 days (Fig. 1), while performing short-range movements in restricted (<50 km) sites, moving at low speed (mean ± SEM: 0.88±0.20 kmh^{-1} for T1, 0.76±0.02 kmh^{-1} for T3). Turtle T3 was then found dead after 44 days of tracking stranded along the coast north of Gulf of Naples; a successive necropsy did not reveal any evident cause of death.

The other six tracked turtles, conversely, alternated circumscribed movements in sites along the southwestern Italian peninsula with long-distance circuitous movements in oceanic waters in the area comprised between the peninsula, Sicily and Sardinia islands

(Fig. 1, 2). For these turtles, the percentage of locations occurring in oceanic (>200 m deep) waters ranged between 75% and 96%. Turtles frequented this oceanic area both during winter (e.g. turtles T2, T7, T8) and summer (e.g. turtles T2, T4, T5) months (Fig. S1), and they mostly performed movements at low speed (<2 kmh^{-1}).

Only two turtles left this general area while they were being tracked: turtle T8 to move northward in April 2007, and turtle T6 first to circumnavigate Sicily in Feb. 2010, and then to enter the south Ionian Sea in July 2010. During these legs, too, turtles moved at speeds below 2 kmh^{-1}.

The UD analysis identified an area in south-eastern Tyrrhenian Sea where all tracked turtles remained for long time (Fig. 3), despite having been tracked in different seasons and years. Each tracked turtle was localised inside this area for at least 3 weeks (range 3-34 weeks, corresponding to 60-100% of total tracking time; Fig. S1). Core areas of individual turtles were generally in this region (Fig. 4), although differences among turtles were also evident, with some individuals mostly frequenting coastal waters (T3, T5, T6) and others remaining in oceanic areas (Fig. 4). As a result, the overlap between different core areas was limited (Fig. S2): the mean proportion of overlap among individual core areas was 0.13 ±0.17 SD, with all overlaps smaller than 35%, except for the core areas of turtles T1 vs. T3 and T4 vs T5, which overlapped by about 80%. The size of individual core areas ranged between 2725 and 20682 km^2. Core area sizes were smaller in winter than in summer, both when considering the mean size for the whole sample (means ± SEM 9603 ± 911 km^2 vs 13125 ± 2150 km^2, n= 4 and 6, respectively) and for just the two turtles that had been tracked both in summer and winter months (turtle T2: winter, 8965 km^2; summer 17418 km^2; turtle T6: winter, 4979 km^2; summer 13736 km^2).

Discussion

The results of the present study further highlight the high behavioural plasticity of loggerhead turtles and provide a substantial contribution to increase our poor knowledge of the distribution and spatial ecology of loggerheads frequenting the Western Mediterranean Sea, and in particular its eastern portion. They also highlight the potential importance of the offshore area between the Italian peninsula, Sardinia and northern Sicily, where tracked turtles spent a large amount of their time in different months/seasons and in different years (Fig. 3, S1), even when they were released far from this location (Fig. 1). The seas adjacent to the west coast of Italy and around the two largest Mediterranean islands (Sardinia and Corsica) are known to host quite a large number of loggerheads, foraging in either coastal or pelagic areas (Casale and Margaritoulis 2010; Lauriano et al. 2011). These findings, although based on a limited sample size, help clarifying the locations of their preferred foraging/residential sites, providing the first evidence of the oceanic foraging areas used by loggerheads in the region. A recent survey covering a large part of the Tyrrhenian Sea has indeed reported a large number of loggerhead sightings in the offshore waters of its southern portion, that broadly correspond to those frequented by our tracked turtles (Fiori et al. 2016). Finally, loggerhead strandings are also not infrequent in the area, again especially along the southern coasts (Casale et al. 2010).

Information on the movements and at-sea behaviour of turtles in the seas west of Italy is limited to a few routes recorded in accidentally-caught and rehabilitated turtles (Bentivegna 2002; Hochscheid et al. 2010; Mencacci et al. 2011; Luschi et al. 2013). Turtles previously tracked in the area were somewhat smaller than those of our sample, and mostly displayed movements in the neritic areas, with prolonged residence in coastal sites being shown in all studies. Only a few turtles undertook long-distance movements in the oceanic environment (Bentivegna 2002), and most of these occurred outside the Tyrrhenian Sea (Bentivegna 2002; Hochscheid et al. 2010; Luschi et al. 2013). The tendency to leave the Tyrrhenian Sea was only noted in turtle T6 in our sample. Conversely, turtles tracked from other Mediterranean areas have rarely been found to enter the Tyrrhenian Sea. For instance, of the nearly 50 published routes for turtles released from the Spanish coast (Cardona et al. 2005, 2009, 2012, Revelles et al. 2007a, 2007b; Eckert et al. 2008), only one juvenile (CCL 53 cm) was tracked as it reached the waters northwest of Sicily and then moved northward (Eckert et al. 2008).

On the whole, the results of the present study further confirm the large behavioural variability shown in the movements of loggerhead turtles, especially during the juvenile/non-breeding stages. According to the widely accepted scheme of the loggerhead life cycle (Musick and Limpus 1997; Bolten 2003), large juveniles like those tracked in this study that likely were approaching sexual maturity, should inhabit neritic, mostly coastal, waters while foraging on benthic prey. Conversely, our data clearly show that large loggerhead juveniles spend most of their time foraging in the oceanic environment, although they can also frequent coastal areas for limited periods. These findings are in line with previous studies that have revealed similar prolonged offshore residences in large juvenile loggerheads (CCL >60 cm) moving in several different areas, like the western Atlantic Ocean (McClellan and Read 2007), the central Pacific Ocean (Kobayashi et al. 2008) and the Western Mediterranean Sea (e.g. Eckert et al. 2008; Cardona et al. 2009; Zbinden et al. 2011; Schofield et al. 2013). In our study area, the presence of adult-sized individuals has been documented by analyses of bycatch data, which have shown that turtles of this size are captured more often by pelagic longlines than by bottom trawls (Casale 2011). Offshore residence, often in conjunction to extended movements over large areas, should therefore be regarded as a common feature of the spatial ecology of late-juvenile loggerheads. It is worth recalling here that these turtles had been released after a rehabilitation period in rescue centres, so their behaviour might not completely correspond to that of individuals in the wild. However, no indications of any abnormal behaviour were evident for the turtles in this study, either with respect to their overall movement patterns or other aspects such as their diving or surfacing pattern (data not shown). This is in general accordance with previous studies with rehabilitated individuals that have shown no major anomalies in post-release behaviour (e.g. Polovina et al. 2006; Rees et al. 2013; Robinson et al. 2017; but see also Cardona et al. 2012).

It is clear that when moving for such long periods in oceanic waters, loggerheads will have to shift from their usual feeding habit on benthic prey to some form of epipelagic feeding (e.g. Hatase et al. 2002; McClellan and Read 2007), which further highlights the large behavioural plasticity of loggerheads. Epipelagic feeding will likely also affect the range of movements performed by the turtles, as it may be expected that feeding on patchy and highly dynamic food resources will require high mobility. Indeed, Mediterranean loggerheads have been shown to use multiple foraging areas (Schofield et al. 2010; 2013). Our results are in accordance with this view, showing that the most frequented areas of tracked turtles were indeed very large, typically spanning more than 13 000 km^2 (table 1). It is worth recalling that the volume contours used for these core area estimations (30%) were objectively determined through the Area Independent Method, and so they are more precise in representing the turtles' highly used areas than the commonly used 50% contours. Much smaller core areas (<4000 km^2, as determined by Kernel UD) have been described for loggerheads foraging in neritic (Marcovaldi et al. 2010 and references therein; Casale et al. 2013; Foley et al. 2013; Hart et al. 2015; Mingozzi et al. 2016), as well as in oceanic sites (Schofield et al. 2010, a single individual). Neritic juveniles, conversely, have been found to frequent areas larger than 10 000 km^2 (Casale et al. 2012b). The fact that our turtles stayed in smaller areas (still >4000 km^2) in winter than in summer is in accordance with previous findings in adult loggerheads (Broderick et al. 2007; Zbinden et al. 2008; Hawkes et al. 2011). Turtles T2 and T6 reduced their home range while remaining always in the same general area, a strategy previously shown in juveniles (Casale et al. 2012b).

The high variability of the oceanic habitats exploited by tracked turtles may also explain the limited overlap between high-use areas of different individuals: an area preferred by a turtle in one particular period/year might not be appealing to other turtles or at another time. Finally, it is worth noting that the Tyrrhenian Sea is characterised by quite a large number of seamounts, that represent foraging hotspots for marine fauna (Morato et al. 2010) and have indeed been found to attract top predators (Fiori et al. 2016). Interestingly, the core areas of tracked turtles did include several seamounts (Fig. S3), and on several occasions tracked turtles remained in close vicinity (<20 km) or passed over some of them (Fig. S4).

Recent conservation strategies for sea turtles highlight the need not only to ensure protection to coastal areas around well-known nesting/breeding sites (e.g. Schofield et al. 2009; Mazaris et al. 2014), but also to identify highly frequented offshore areas that are largely used by turtles outside the breeding season and where conservation efforts may be directed (Schofield et al. 2013). For instance, fishing activities and boat traffic constitute the major threats to sea turtles in the Mediterranean (Casale et al. 2010; Casale et al. 2011) and are likely to have a large impact on turtles frequenting the area identified in the current study, where fishing pressure and maritime traffic are high (Coll et al. 2012). Although it was not possible to definitively determine cause of death, turtle T3 was indeed found stranded after a period spent foraging in shallow waters very close to the coast (Fig. 1). The present findings, albeit obtained for only a few individuals, demonstrated the power of satellite telemetry as a tool for collecting direct observations of the areas actually frequented by marine turtles. We hope that future studies will confirm these findings: compiling the data yielded by the efforts of the different groups employing these techniques (e.g. Fossette et al. 2014) may then lead to identification of the main high-use areas in the Mediterranean basin, thus providing ground-truthed information to set up appropriate conservation plans for the Mediterranean Sea.

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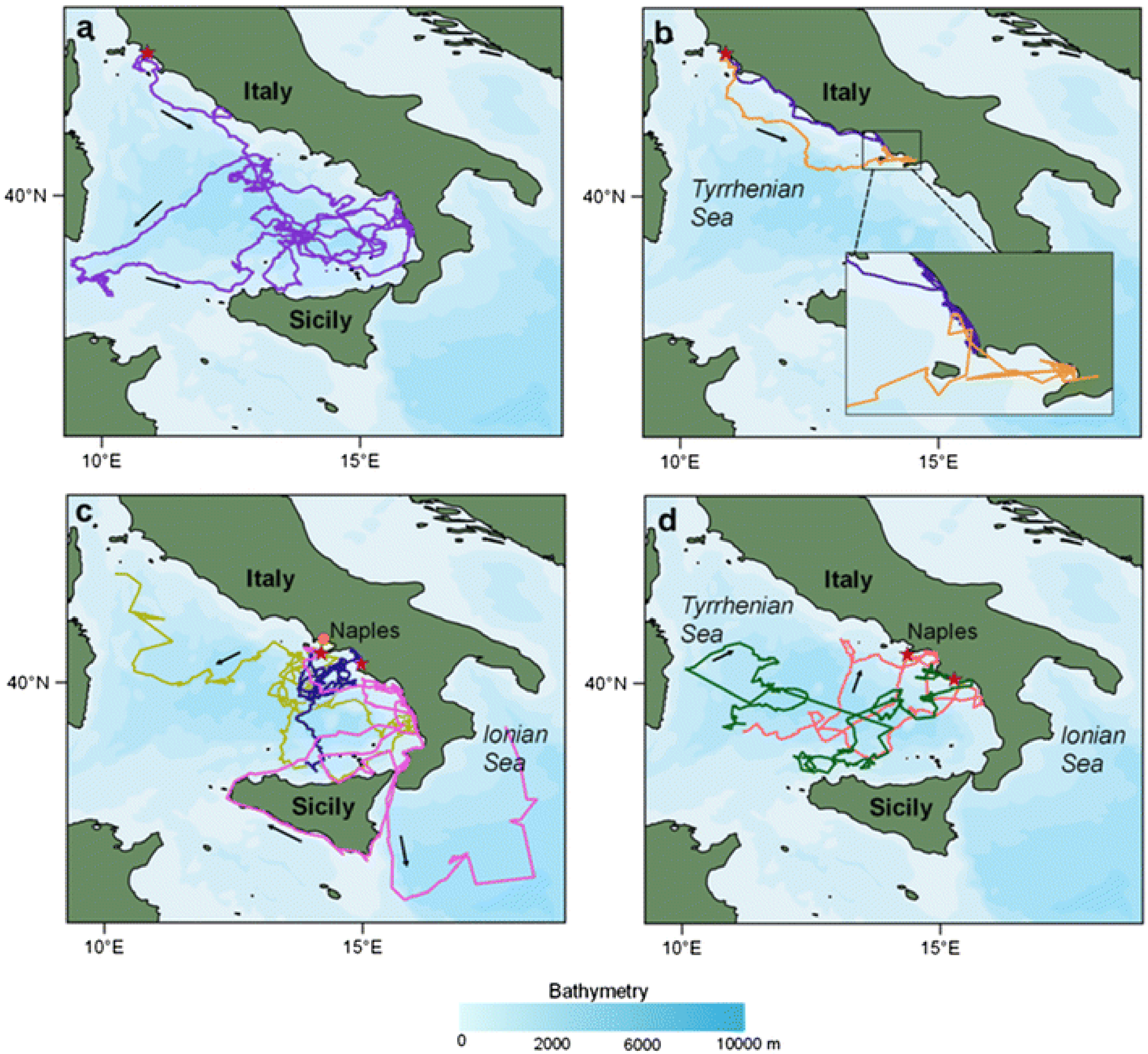
Figure captions

Fig. 1 Reconstructed routes of the tracked turtles. a) Turtle T2, b) T1 (orange line) and T3 (dark blue line), c) Turtle T5 (blue line), T6 (pink line) and T8 (yellow line), d) T4 (coral line) and T7 (green line). Bathymetric information was taken from Natural Earth (naturalearthdata.com).

Fig. 2 Utilization distribution (UD) of the eight turtles tracked. Red stars indicate the release sites.

Fig. 3 Individually-specific core areas (30% Kernel UD) for the tracked turtles.



a
Italy
Sicily
40°N
10°E
15°E
b
Italy
Tyrrhenian Sea
40°N
10°E
15°E
c
Italy
Naples
Ionian Sea
Sicily
40°N
10°E
15°E
d
Italy
Tyrrhenian Sea
Naples
Ionian Sea
Sicily
40°N
10°E
15°E
Bathymetry
0
2000
6000
10000 m

Fig. 1

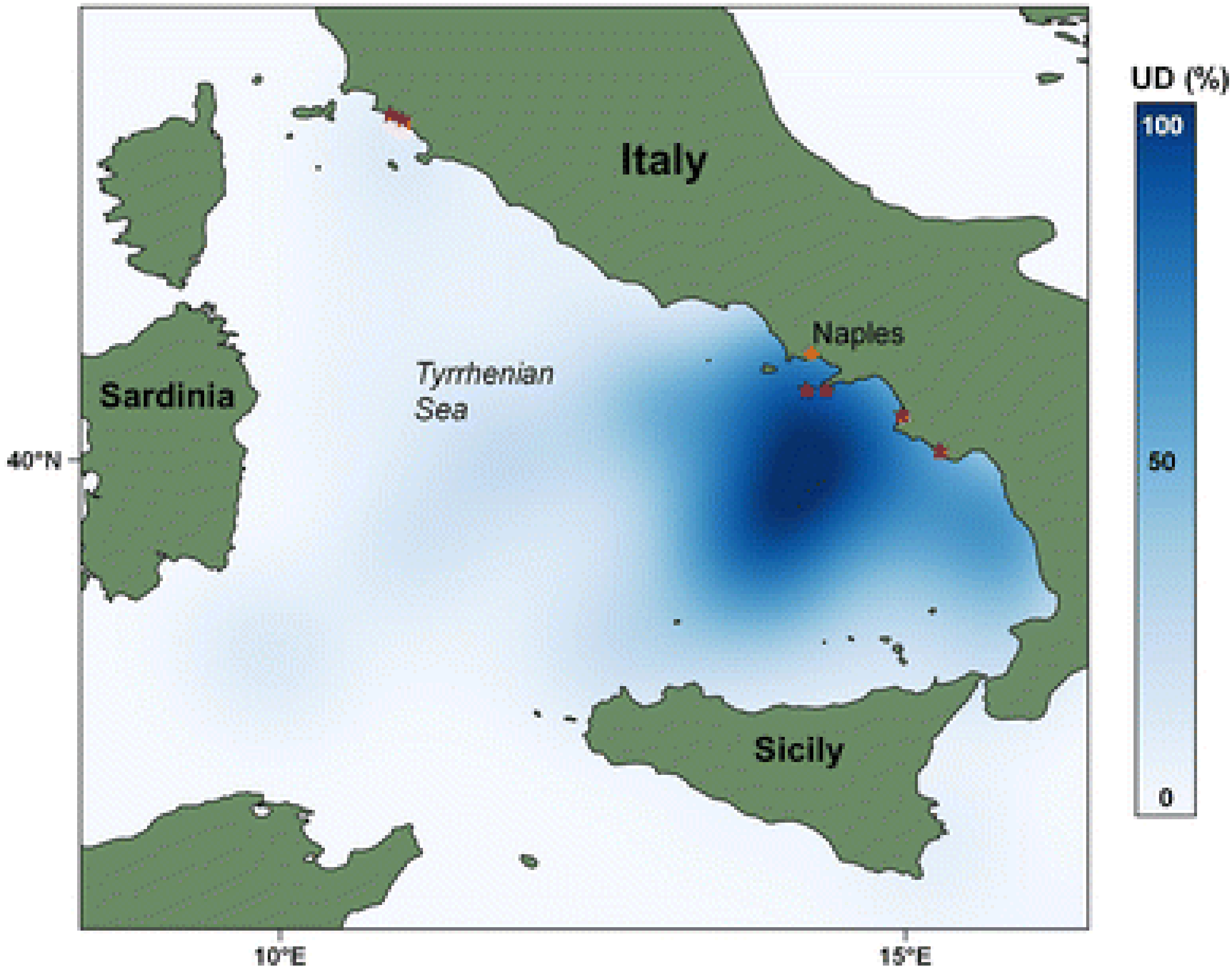

UD (%)
100
50
0
Italy
Naples
Tyrrhenian
Sea
Sardinia
Sicily
40°N
10°E
15°E

Fig. 2

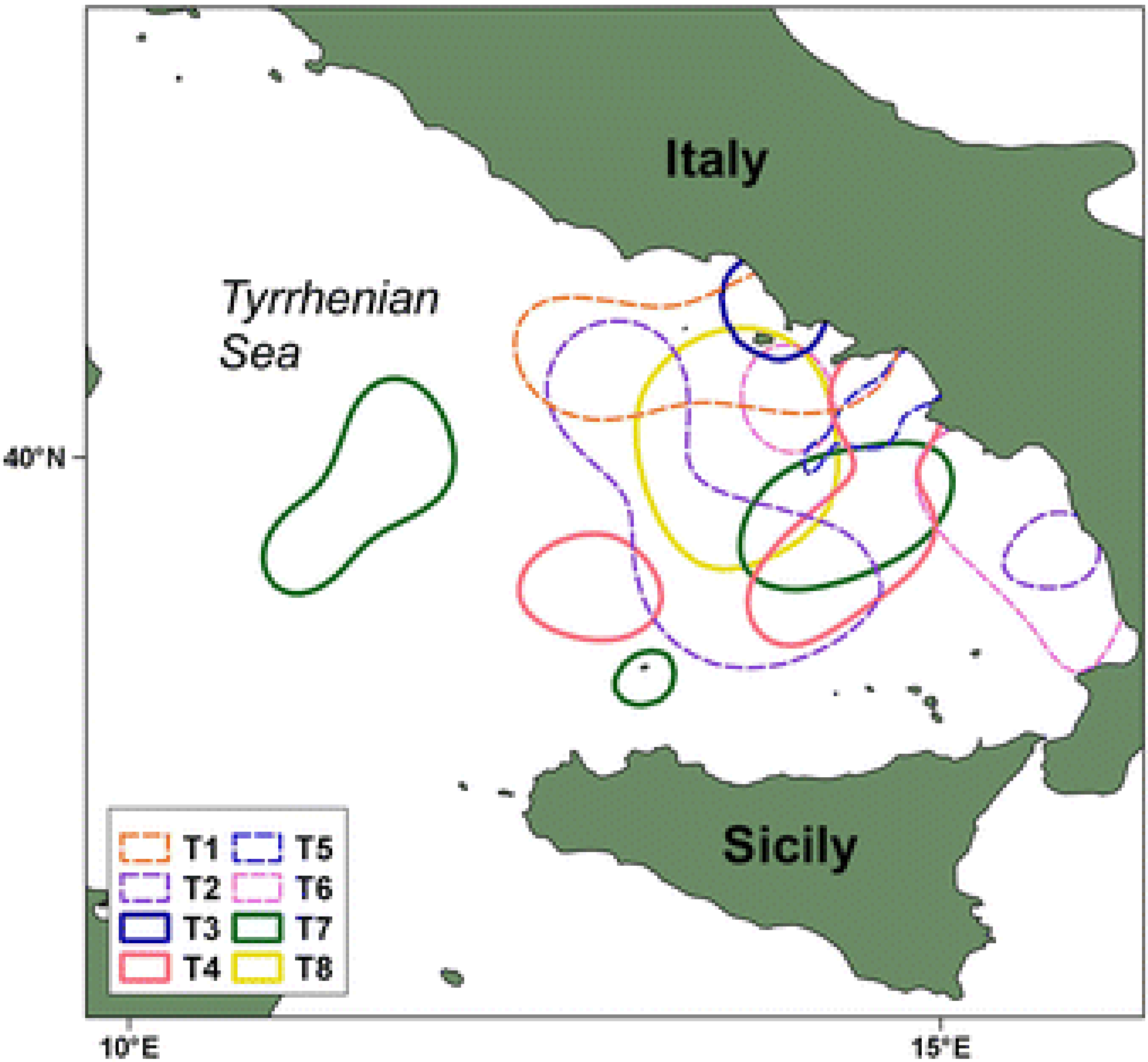


Fig. 3