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Movement patterns of marine turtles in the Mediterranean Sea: a review

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RUNNING HEAD
Movements of sea turtles in the Mediterranean

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ABSTRACT

Understanding the at-sea spatial behaviour of sea turtles is a priority for their conservation. In the present paper, the current information on the distribution and movement patterns of the two species breeding in the Mediterranean, the loggerhead and the green turtle, is reviewed, focusing mainly on the 195 published routes of satellite tracked turtles. A satisfactory level of knowledge about adults' migrations and other movements is reached only for loggerheads breeding at Zakynthos Is., Greece and for green and loggerhead females nesting in Cyprus, while studies at foraging grounds are limited to loggerheads in the western and central parts of the basin. Adult males and females mostly show quite uniform post-breeding migratory patterns, typically moving towards individually-specific neritic foraging grounds. A much higher variability is shown by loggerhead juveniles, which is probably associated with differences in their spatial behaviour while in oceanic or neritic waters. Evidence of seasonal migrations driven by lower temperatures in winter is available only for adult and juvenile loggerheads frequenting the two northernmost parts of the basin, i.e. the Ligurian and the northern Adriatic Sea. Current knowledge gaps and priority for further research in the Mediterranean are discussed.

INTRODUCTION

Marine turtles are characterized by an itinerant behaviour at all stages of their life cycle. Immediately after hatching, newborn turtles swim quickly away from their natal beaches and begin large-scale movements lasting several years which can extend over entire ocean basins, being strictly dependent on the course of the main ocean current systems (Musick & Limpus 1997). In the following juvenile stage, turtles exhibit a variety of movement behaviours associated with their specific feeding needs. Although variable in different turtle species, the juveniles' spatial behaviour often involves long-range movements, especially during the initial pelagic phase of development that occur in the oceanic environment (Musick & Limpus 1997). As adults, female turtles perform cyclical shuttling migrations between individually-specific foraging and breeding areas (Luschi et al. 2003; Godley et al. 2008), which are probably undertaken by males as well (Hays et al. 2010b; Casale et al. 2013a).

Understanding the spatial behaviour of marine turtles during their migrations and prolonged movement phases is therefore crucial to elucidate key aspects of their complex life cycle and ecology. Furthermore, this knowledge is crucial to define appropriate conservation measures for these species of conservation concern, which are listed in the IUCN Red List of Threatened Species (IUCN 2012) but whose protection status is often unsatisfactory, especially during their at-sea movements (Hamann et al. 2010). However, obtaining information on the movements performed by marine animals like sea turtles is not a straightforward task. Turtles spend the vast majority of their life in the water, often frequenting offshore or inaccessible areas, where even approaching or capturing them can be quite difficult. Moreover, they are known to stay submerged for 90-95% of time (Lutcavage & Lutz 1997), and this additionally creates huge technical problems, e.g. to remotely acquire information through radio signals. Sea turtle movements have been initially studied through capture-marking-recapture techniques since the 1950s (Hendrickson 1958), with the recoveries of marked individuals away from the capture area providing very general information on the extent and course of the movements performed (e.g. Meylan 1982). In the last 15-20 years, satellite telemetry has led to substantial progresses in the field, as this technique allows to reconstruct the actual routes followed by marked individuals (Godley et al. 2008). This provides quite detailed information on the spatial behaviour of individuals belonging to various life stages and on the main features of the movements performed by the single individuals in their natural environment (see below for further information on these methods).

Adult females represent the class of individuals that have been most studied in their movements, because they can be easily tagged and/or equipped with satellite transmitters during the nesting process and then tracked during the internesting movements between successive egg-layings and the subsequent migrations after the end of the nesting season (Godley et al. 2008). In most species, the prevailing migration pattern consists in a quick and direct movement towards specific foraging areas in the neritic environment (e.g., Papi et al. 1997; Limpus & Limpus 2001), where females stay for long periods feeding on benthic prey and which they show fidelity to in successive reproductive seasons (Broderick et al. 2007). The most recent results have however revealed numerous exceptions to this general pattern, including the possible prolonged residence of females in the oceanic habitat (Hatase et al. 2002; Hawkes et al. 2006; Hatase et al. 2007; Rees et al. 2010), suggesting the possibility of an epipelagic feeding in adults (Reich et al. 2010), the presence of seasonal migrations between different feeding and wintering areas (Hawkes et al.

2007; Zbinden et al. 2008; Zbinden et al. 2011), or of convoluted segments in the migratory routes (Dodd & Byles 2003; Hatase et al. 2007; Hawkes et al. 2007) of uncertain biological significance.

The information on the movements made by turtles other than adult females (i.e., adult males and juveniles) are limited (Godley et al. 2008), although growing. For males, the main difficulty lies in approaching the animals to tag them and deploy the satellite transmitters, since they very rarely leave the aquatic environment (e.g., Godley et al. 2008; Arendt et al. 2012a; Casale et al. 2013a; Schofield et al. 2013; and references therein). For juvenile turtles, the best available evidence on their spatial distribution has been obtained from genetic studies that have allowed to estimate the contribution of different rookeries to the aggregations of juveniles frequenting a certain foraging area (e.g., Bowen & Karl 2007), thus providing indirect but valuable information on the distribution and the general movement patterns in the juvenile stages. Tracking experiments on juveniles are fewer than those on adults, and mostly limited to larger turtles foraging at neritic areas, where they usually settle after spending the first years of their life in oceanic areas (Bolten 2003). Very little information is available on the movements of younger turtles during their pelagic developmental phase (but see Kobayashi et al. 2008; Howell et al. 2010; Mansfield et al 2014), when in fact it is believed that they move over large oceanic areas (Bolten 2003).

Three sea turtle species occur in the Mediterranean (Casale & Margaritoulis 2010): the leatherback turtle (*Dermochelys coriacea*), the green turtle (*Chelonia mydas*), and the loggerhead turtle (*Caretta caretta*). Just a few leatherback turtles enter the Mediterranean from the Atlantic and they can be found all over the basin, although they do not breed in the Mediterranean (Casale et al. 2003). The other two species have Mediterranean populations recognized as regional management units with the green turtle unit being considered at high risk (Wallace et al. 2011). The main identified threats at sea to these two Mediterranean populations are incidental catch in fishing gear, collision with boats, and intentional killing (Tomás et al. 2008; Casale et al. 2010; Casale 2011) that as a whole represent a high level of threat (Wallace et al. 2011). The impact on the populations of other potential threats like chemical contaminants (D'Ilio et al. 2011) and debris (e.g., Tomas et al. 2002; Lazar & Gračan 2011), is not clear yet.

The loggerhead turtle is the most common species in the Mediterranean Sea, where it nests mainly in the eastern part, from which juveniles then disperse widely throughout the basin (Margaritoulis et al. 2003; Casale & Margaritoulis 2010; Hays et al. 2010a; Casale & Mariani 2014). The Mediterranean loggerhead population shows a genetic divergence from the Atlantic populations (Bowen & Karl 2007) and a population substructure (Laurent et al. 1998; Carreras et al. 2007; Clusa et al. 2013), indicating the presence of independent management units for conservation. Loggerhead turtles are carnivorous: for the first period of life they mainly feed upon pelagic prey at the sea surface, then they increasingly shift towards benthic prey (Bjorndal 1997), although they also feed through the whole water column (e.g., Narazaki et al. 2013). The duration of the first strictly epipelagic period varies according to population and oceanographic features, being most extended in those turtles that disperse over wide oceanic regions (Musick & Limpus 1997). In the Mediterranean, where neritic (on the continental shelf) and oceanic areas (out of the continental shelf) are not widely separated', loggerhead turtles start feeding upon benthic prey rather early: an analysis of gut and faecal content has shown that benthic feeding occur in turtles as small as 26 cm of curved carapace length (CCL) (Casale et al. 2008a).

Green turtles breed exclusively in the Levantine basin (east of Libya and Crete), and primarily in Turkey, Cyprus and Syria (Casale & Margaritoulis 2010). At sea, green turtles have been observed mainly in neritic areas in the Levantine basin (e.g., Oruç 2001; Oruç et al. 2011), but also in Greece and north Africa (e.g., Broderick et al. 2007; Margaritoulis & Panagopoulou 2010). A limited number of individuals disperse as far as the Ionian, Adriatic and Tyrrhenian Seas (Lazar et al. 2004; Bentivegna et al. 2011). The Mediterranean green turtle population shows a genetic divergence from the Atlantic populations (Encalada et al. 1996) indicating a degree of isolation, and is affected by strong anthropogenic pressures primarily represented by incidental catches in fishery activities (Casale 2011). Like loggerheads, green turtles feed upon pelagic prey in the first period of their life but then they shift to a herbivorous diet, feeding upon benthic seagrasses and algae (Bjorndal 1997). Eventually, large juveniles become fully herbivorous: in the Mediterranean such a stage is reached at a size over 62 cm CCL (Cardona et al. 2010).

Relatively little is known about the spatial behaviour of Mediterranean loggerhead and green turtles: recapture studies and satellite tracking experiments have so far been conducted in a non-systematic manner and the available data is therefore quite fragmentary. However, taking all these findings together, an overall picture is starting to emerge of the movement routes, the habitat use and the most frequented areas of the Mediterranean populations of the two species, providing crucial information for a desirable management of marine areas and representing a research priority for sea turtle conservation (Hamann et al. 2010).

The aim of this review is to present the current state of knowledge on sea turtle movement patterns in the Mediterranean and to identify major gaps to be filled by future research. Only data available from peer-reviewed publications or obtained by the authors are considered, so to avoid the methodological, interpretative and data ownership issues associated to non-reviewed sources. Given the scarce occurrence of leatherback turtles in the Mediterranean and the lack of information on their movements, only information about loggerhead and green turtles is considered.

METHODS FOR STUDYING SEA TURTLE MOVEMENTS

The oldest system employed to study sea turtle movements is to apply a tag to one or more flippers of an individual and to wait for someone to recapture it somewhere at a later date. If the turtle is re-encountered, it can then be individually identified thanks to the unique code of the tag (Hendrickson 1958; Balazs 1999). This method, by its very nature, only gives general indications on the endpoints of the journeys made by tagged turtles. Also, even the simple recapture of a tagged turtle in the vastness of the sea may be rather an improbable event, and the geographic pattern of turtle captures is consequently biased towards the most populated (or most fishery-exploited) areas. In any case, such a capture-mark-recapture method has provided basic but most useful information on the movement patterns and migrations of many sea turtle populations (e.g., Meylan 1982) including Mediterranean ones (Margaritoulis et al. 2003; Casale et al. 2007a).

More recently, satellite telemetry has rapidly integrated and complemented the initial basic information obtainable with tag recoveries. This technique is a viable and quite effective solution to track air-breathing animals that spend at least some seconds at the sea surface, and turtles have been among the first animals to be studied in this way (Stoneburner 1982; Timko & Kolz 1982). Satellite telemetry has become a popular method to study sea turtles, despite its non-negligible costs, and the number of turtles so far tracked worldwide lies in range of a few thousands at least, with individuals being now routinely tracked for several months on the average, and up to a few years in the best cases.

Essentially, marine animal telemetry via satellite is presently only possible through the Franco-American Argos System, which employs a number of polar-orbiting satellites (eight in 2014) located at around 850 km above the Earth's surface. Upon receiving radio signals coming from special transmitters, called Platform Transmitters Terminals (PTTs), the Argos system is able to localise the animal carrying the PTT anywhere on the Earth's surface, through a complex computational process based on the Doppler effect of the received signals. Successive signals useful for localization are spaced in time (with 40-50 of seconds between them minimum), and this greatly increases the localization efficiency in surfacing animals like turtles, that can then be localized when they emerge only briefly, then dive and surface again after a few minutes. The determined locations have different accuracies, depending on various factors (especially on the number of PTT signals received within a single satellite overpass) and Argos itself classifies the fixes obtained in 6 location classes, with an accuracy ranging between 150 and over 1000 m. Recently, new models of Argos-linked PTTs have been developed also featuring a GPS receiver: these instruments can acquire GPS ephemeris even during the short surfacings of the turtle (thanks to special technologies allowing fast data acquisition, such as Fastloc; Hazel 2009). This information is then part-processed on board, and then relayed in a compressed form to the Argos system (thus using Argos satellites only as a communication channel), which subsequently determine the final GPS position. These units however have a higher costs, are heavier and their batteries last much less than standard PTTs, so that their usage in turtle studies is not widespread.

The PTT models currently available can either be attached to the top of the turtle carapace, commonly by an epoxy resin (e.g., Godley et al. 2002), or be towed by the turtle through a tether attached to the posterior part of the carapace (e.g., Sasso & Epperly 2007). In any case, PTTs will sooner or later detach from the carapace, although the gluing systems commonly employed guarantee quite long tag attachment durations, not uncommonly well over one year (e.g., Casale et al. 2013a; Schofield et al. 2013). PTTs can have an impact on turtle behaviour and energetics, especially during long movements, and carapace-attached tags have indeed been shown to increase the drag of marine turtles (Watson & Granger 1998; Jones et al. 2013). This effect is relevant only for relatively small turtles (juveniles), while it is minimal for the large adults. Impacts on other activities (e.g., feeding, mating) seem unlikely. Besides turtle localizations, other information can be obtained through the Argos satellites: for instance various kinds of sensor data (e.g. water temperature or depths reached) can be collected by the PTT on-board sensors and then transmitted every time the turtle surfaces or when the PTT detaches from the turtle as programmed (“pop-up units”; Swimmer et al. 2006). Tracking and sensor data can then be processed and displayed by through online platforms such as STAT (Satellite Tracking and Analysis Tool), originally designed for turtle studies (Coyne & Godley 2005).

Other tracking systems like visual-, radio- or acoustic- tracking can also be used (Lohmann et al. 2008), but they require to maintain a relatively close contact between the animal and the experimenter, and as such are quite tricky to be used in animals moving in the marine environment while staying mostly underwater. Data loggers recording GPS positions are useful only when chances are high to recover tagged individuals after some time, and so their application has basically been limited to females tracked during the period between successive egg depositions, the so-called internesting interval (Schofield et al. 2007; Schofield et al. 2010b; Schofield et al. 2010c).

Genetic methods can additionally contribute to understand the general movement patterns of turtle populations, usually over broad spatial scales (e.g., Bowen & Karl 2007). This is possible because turtles, and especially females, tend to display a natal homing behaviour, i.e. to breed at natal areas (Bowen & Karl 2007), and as a consequence the different rookeries tend to differentiate genetically with time and to be characterized by unique DNA sequences or by different proportions of specific DNA sequences. Analysing genetic differences can therefore provide information on the relative contribution of different rookeries to a common foraging ground, rather than on the origin of a single individual (e.g., for the Mediterranean: Carreras et al. 2006; Garofalo et al. 2013).

Finally, other sources of information able to provide clues on turtle distribution, are stranding data (Tomás et al. 2008; Casale et al. 2010; Türkozan et al. 2013), incidental catch in fishing gears (reviewed by Casale 2011), and aerial surveys (Gomez de Segura et al. 2006; Lauriano et al. 2011).

ADULT LOGGERHEAD TURTLES

Like for the other turtle species, the majority of the available information about movement patterns of adult loggerheads in the Mediterranean concerns nesting females, obtained either from recoveries of tagged individuals (Margaritoulis et al. 2003) or from satellite tracking experiments (summarized in Table 1). This is not surprising, since this class of individuals is the only one that come ashore for extended periods at predictable times and locations during the long and laborious egg-laying process, thus offering an easy way for students to approach and tag or equip them with electronic instruments.

Adult females in the Mediterranean Sea have been typically tracked during their postnesting migrations, having been equipped with satellite transmitters while at their nesting beach in the final part of the nesting season so to reduce the risk of losing the tag during mating. In a few cases, females have also been tagged early in the season to be tracked also during the internesting intervals, showing movements in close vicinity of the nesting beach (Hays et al. 1991; Godley et al. 2003; Zbinden et al. 2007; Fuller et al. 2008; Schofield et al. 2007; Schofield et al. 2010b; Schofield et al. 2010c) . In Greece, some females have however been shown to make excursions away from the nesting area during the internesting interval, with a turtle making a 200-km return trip (Schofield et al. 2010b; Schofield et al. 2010c).

Nearly all postnesting routes tracked so far in Mediterranean loggerheads conform to the most common migratory pattern known in loggerheads, i.e. a direct and rather quick migration away from the breeding site to reach a specific feeding area, usually located in the neritic environment, where the turtle is then localised for months (type A pattern in Godley et al. 2008). Most information is available for turtles belonging to the main rookery of Zakynthos Island, in western Greece (Table 1), with a total of 36 females having been tracked so far (Zbinden et al. 2008; Zbinden et al. 2011; Schofield et al. 2013). They have been shown to migrate towards two main destinations in the central Mediterranean (Fig. 1), the Adriatic Sea (especially in its northern portion) and the continental shelf area offshore Tunisia and Libya (often, but rather improperly, indicated as Gulf of Gabès, which actually only constitutes a small part of this area). These findings confirmed the information obtained through recoveries of turtles tagged in western Greece (Margaritoulis et al. 2003). Tracked Zakynthos turtles distributed about roughly equally between these two foraging areas (Zbinden et al. 2011; Schofield et al. 2013), which indeed represent the largest neritic areas suitable for turtle foraging in the whole Mediterranean (Schofield et al. 2013). Some of the turtles foraging in the northern Adriatic displayed seasonal migrations moving towards lower latitudes during the winter months (Zbinden et al. 2011). In a few cases, turtles were tracked for long enough to reconstruct also their movements back to the breeding areas (Zbinden et al. 2008; Hays et al. 2010b; Schofield et al. 2010a). This revealed precious details on the poorly-known pre-breeding migratory phenology of Mediterranean loggerheads. This information is particularly valuable since some migratory features (e.g., timing of pre-breeding migrations) might be flexible and controlled by the environment (e.g., by sea temperatures; Mazaris et al. 2013).

Some Zakynthos turtles however migrated towards other sites such as the close-by Amvrakikos Gulf in western Greece, the Aegean Sea and the coasts of Peloponnese, eastern and northern Greece (Fig. 1). Females breeding in Cyprus displayed much the same type A movement pattern, migrating towards more disparate foraging areas along the North African shelf, the Syrian coast or even remaining in Cyprus (Godley et al. 2003; Broderick et al. 2007) (Fig. 1). In both cases, it is not to be excluded that other foraging sites for these populations can be discovered in the future, given that the number of tracked females is still quite low with respect to the number of females breeding in these rookeries (Schofield et al. 2013). Information on the migrations of turtles from the other Mediterranean rookeries is limited and mostly unpublished. A single female migrated from Rethymno, northern Crete to Mykonos Island in the Aegean Sea, from where she then made a southward seasonal movement frequenting other islands during the winter before returning to Mykonos in the following spring (Margaritoulis & Rees 2011). Turtles nesting in Calabria, southern Italy, have been shown to migrate directly towards the Tunisian shelf, again following the type A pattern (T. Mingozzi and P. Luschi, unpublished data).

The other postnesting migratory pattern known in loggerheads, that of staying in offshore oceanic waters moving continuously over more or less extended areas (type B pattern in Godley et al. 2008), is much less represented in Mediterranean turtles, having so far been shown in only a few turtles tracked from Zakynthos (Zbinden et al. 2008; Hays et al. 2010b; Schofield et al. 2013). For example a female tracked by Zbinden et al. (2008) kept on the move for the 189 days of tracking while visiting various areas of the Adriatic and Ionian sea, apparently without heading towards a specific destination (but slowing down its movement rate while in the Northern Adriatic) (Fig. 2).

Quite a large number of adult males have been tracked in the Mediterranean, although to a slightly lesser extent than females (Table 1). Males breeding at Zakynthos have been captured while in coastal waters and tracked either during the breeding season or during the successive postbreeding migrations (Schofield et al.

2010a; Schofield et al. 2013). They showed a pattern fully correspondent to those of females (Fig. 1), as they i) remained in the waters close to the nesting site during the breeding period, which however lasted a few days only (Schofield et al. 2010b; Schofield et al. 2010c), ii) mostly migrated away from Zakynthos towards disparate feeding grounds predominantly located in the Adriatic or on the Tunisian shelf, as well as along the Greek coasts and in Western Turkey, with a few turtles foraging in oceanic sites (Schofield et al. 2010a; Schofield et al. 2013), iii) displayed a fidelity to the same foraging sites in successive years, often showing a remarkable consistency in the migratory route and an accurate homing behaviour (Schofield et al. 2010a); iv) undertook seasonal migrations when foraging in the Northern Adriatic Sea (Hays et al. 2010a; Hays et al. 2010b; Schofield et al. 2010a). Males were however found to remain more often than females in Zakynthos and nearby areas, without embarking in migrations (Schofield et al. 2010a; Schofield et al. 2013). Adult males have also been tracked from their foraging area in the Tunisian shelf area after having been captured by fisheries (Casale et al. 2013a). The reconstructed routes showed a combination of short-range foraging movements and of shuttling migrations towards breeding sites along the Libyan coast and even in Greece. In two cases, a strong fidelity to foraging sites on the Tunisian shelf and to a possible breeding site in Libya, was revealed, although the four males that were tracked during the complete return migrations followed different routes during the pre- and post-breeding movements. A protracted residency in specific foraging sites, likely indicative of site fidelity, have also been shown in males and females frequenting the enclosed basin of Amvrakikos Gulf, Western Greece (Rees et al. 2013).

Finally, a few adult-sized turtles (CCL between 68 and 87 cm) have been tracked upon release after a rehabilitation period in turtle rescue centers in Italy (Bentivegna 2002; Mencacci et al. 2006; Casale et al. 2012a; Luschi et al. 2013). These turtles displayed a variety of movements, including seasonal migrations over large spatial scales, often made independently and even against main surface currents (Bentivegna et al. 2007). The scarcity of information about the specific individuals prevents to precisely frame their movements within the turtles' life cycle, and in only two cases the reconstructed movements could be clearly identified as pre-nesting migrations towards a nesting site (Luschi et al. 2013). In many cases, turtles were found to wander over large distances while frequenting different, disparate areas during the non-breeding period: such a lack of a prolonged permanence in a fixed area may indicate that these turtles too displayed a type B movement pattern (Godley et al. 2008).

JUVENILE LOGGERHEAD TURTLES

Small juveniles: the 'lost years'

If movements and distribution of wide-ranging marine species like sea turtles are generally difficult to study, this is particularly true for their first period of life, the so-called 'lost-years' (Carr & Meylan 1980), when individuals are small, usually live in open waters and are chiefly difficult to observe. The Mediterranean turtles are no exception. The various empirical methods employed to study turtle distribution and movements in Mediterranean waters usually observe adults or large juveniles, thus leaving out loggerheads smaller than 40 cm CCL, roughly corresponding to the first seven years of life (Casale et al. 2009; Casale et al. 2011a; Casale et al. 2011b). The only method available to investigate their movement patterns is through simulations of particle dispersals in large-scale oceanographic models (e.g. Hays et al. 2010a) although new promising tracking techniques are for on small turtles are being developed (Mansfield et al. 2014).

In the Mediterranean, recent simulations of hatchling dispersal have indicated that hatchlings from the Levantine and central nesting sites are mainly retained in the same areas of origin, while those from the Ionian region disperse widely to the Ionian, Adriatic and south-central Mediterranean areas (Hays et al. 2010a; Casale & Mariani 2014).

Large juveniles

The number of satellite-tracked large juveniles (> 40 cm CCL) in the Mediterranean and the study areas are summarized in Table 1. These turtles showed a large variety of movements. Some just wandered across wide areas, with no sign of residence to any specific site (Bentivegna 2002; Casale et al. 2007a; Eckert et al. 2008; Cardona et al. 2009; Hochscheid et al. 2010) (Fig. 3). Others frequented somewhat smaller areas (Cardona et al. 2005; Revelles et al. 2007a; Revelles et al. 2007b; Eckert et al. 2008; Cardona et al. 2009; Hochscheid et al. 2010; Casale et al. 2012a; Casale et al. 2012b) (Fig. 3), in some cases remaining for long time in very restricted sites (Hochscheid et al. 2010; Mencacci et al. 2011). The areas frequented and the routes followed are the result of a combination of surface circulation patterns and the turtle active swimming (Bentivegna et al. 2007; Revelles et al. 2007b).

Juveniles frequenting oceanic areas may either show fidelity to an area or move across multiple areas. A degree of permanence in the same area was indicated by tag returns in the western and eastern Mediterranean (Casale et al. 2007a) and was directly observed through satellite tracking in some cases in the western Mediterranean (Revelles et al. 2007a) but not in others, both in the western (Cardona et al. 2005; Eckert et al. 2008; Cardona et al. 2009) and in the eastern Mediterranean (Bentivegna 2002). In general, resident areas of juveniles in oceanic zones are much wider than in neritic zones (Revelles et al. 2007b; Cardona et al. 2009; Casale et al. 2012a; Casale et al. 2012b) (Fig. 4), as also observed for adults in the Mediterranean and elsewhere (Hawkes et al. 2006; Schofield et al. 2010a). Long-term residence of juveniles in neritic foraging grounds seems more common than in oceanic areas and it has been observed in various locations through tag returns (Casale et al. 2007a; Revelles et al. 2008) and satellite tracking (Hochscheid et al. 2007; Cardona et al. 2009; Hochscheid et al. 2010; Casale et al. 2012a; Casale et al. 2012b; Hochscheid et al. 2013) (Fig. 3). The juvenile neritic foraging sites are however usually larger than the adult neritic sites, with juveniles showing a propensity to wander over quite large areas (e.g., Casale et al. 2012b) rather than to settle in a given location as adults usually do (e.g., Schofield et al. 2010a; Casale et al. 2013a).

The behavioural response of juvenile turtles to seasons, varies per location and per individual. In some areas, like the western Mediterranean (Revelles et al. 2007b) and the Tunisian shelf (Casale et al. 2012b), no seasonal movement patterns were observed through satellite tracking. Differently, individuals foraging in the north Adriatic have been found to move southwards in winter, as observed also in adults (see above) and in the Ligurian Sea (Lauriano et al. 2011). For instance, Casale et al. (2012a) tracked one individual during a complete migration cycle, with an autumn southwards migration along the Italian coast in the western Adriatic and a northwards spring return to very same site following a route along the eastern Adriatic coast (Fig. 2). However, the same study also showed that other individuals remained in the northernmost and coldest part of the basin during the whole winter (Casale et al. 2012a). Actually, there is evidence from bycatch (Casale et al. 2004) and stranding records (Casale et al. 2010) that at least some loggerhead turtles, mainly juveniles, frequent the wider north Adriatic area also in winter. Indeed, Mediterranean loggerhead turtles have been observed to maintain some level of activity at temperatures as low as 11.8°C, adopting a specific behavioural strategy known as overwintering (Hochscheid et al. 2007). Therefore, it seems that cold winter temperatures induce only part of the turtles to move southwards and only from the two northernmost areas (Fig. 5), i.e. the north Adriatic (Casale et al. 2012a and references therein) and the Ligurian Sea (Lauriano et al. 2011), where temperatures drop below 13°C in winter.

In the western Mediterranean, tag and genetic data indicate that turtle movements are affected by the prevailing currents that define two main "water masses": the northern and southern parts of the basin (Carreras et al. 2006; Revelles et al. 2008). It has been suggested that the Atlantic individuals entering from the Strait of Gibraltar (see below) frequent the southern part of the western basin, while Mediterranean loggerheads frequent the northern part (Carreras et al. 2006).

Atlantic loggerheads in the Mediterranean

Genetic analyses on mtDNA have shown that the Mediterranean is also frequented by loggerheads originating from the Atlantic Ocean. These turtles derive from western Atlantic rookeries (Carreras et al. 2006), and reach the eastern side during their long-distance developmental migrations helped by the Gulf Stream and related oceanic currents (Musick & Limpus 1997). The modal size of loggerheads found on the Atlantic coast of northern Europe is about 23 cm CCL (20.5 cm straight carapace length, Hays & Marsh 1997; converted according to Bjorndal et al. 2000), suggesting that Atlantic turtles enter the Mediterranean at this size or larger. The smallest turtle found in the eastern Mediterranean and carrying an mtDNA haplotype endemic to the western Atlantic was in the size range 30–34 cm CCL (Laurent et al. 1998). Genetic markers have shown that Atlantic loggerheads occur in high numbers, especially in the oceanic zone of the westernmost part of the Mediterranean basin, closer to the Strait of Gibraltar, through which they enter from the Atlantic (Fig. 5) (Carreras et al. 2006). However, individuals tagged in the Atlantic have been found in the eastern Mediterranean as well, as far as the Sicily Channel (Bolten et al. 1992) and the north Ionian Sea (Manzella et al. 1988). Genetic studies too have indicated high proportions of Atlantic individuals in the oceanic zone of the Sicily Channel (Laurent et al. 1998) as well as their occurrence in the neritic zone of the Tunisian continental shelf (Fig. 5), though at a lower proportion (Casale et al. 2008b). Current data suggests that Atlantic turtles do not enter the Adriatic or do so in very low numbers (Giovannotti et al. 2010; Garofalo et al. 2013). The occurrence of Atlantic loggerheads in other parts of the eastern Mediterranean basin is possible but has not yet been adequately assessed through genetic surveys.

Since genetic flow from the Atlantic to the Mediterranean is estimated to be low, these Atlantic turtles are thought not to breed in the Mediterranean and to return to the Atlantic to breed (Carreras et al. 2011). This hypothesis is corroborated by a few empirical findings: one loggerhead tagged in the western Mediterranean (Spain) was found in Cuba (Moncada et al. 2010), one turtle tagged in the eastern Mediterranean (north Ionian Sea) was found on the coast of Portugal, just outside the Mediterranean (Argano et al. 1992), and one turtle tagged in the central

Mediterranean was found in north America (Casale et al. 2013b). Moreover, three large juveniles were satellite tracked during their transatlantic migrations starting from the Mediterranean side of the Strait of Gibraltar: two of them stopped transmissions in the middle of the North Atlantic while the third one reached Nicaragua (Eckert et al. 2008). Notably, Atlantic turtles maintain a different growth rate from the Mediterranean one when they stay in the Mediterranean (Piovano et al. 2011). The occurrence of Atlantic loggerheads in the Mediterranean represents a good opportunity to understand the species behavioural patterns associated with fidelity to different habitats at different life stages, and information about backward migration to the Atlantic basin can contribute to understanding these patterns.

GREEN TURTLES

The current knowledge on the distribution and movements of green turtles in the Mediterranean is very limited in comparison to loggerhead turtles. Like loggerheads, information on the distribution of small turtles is particularly deficient, but in green turtles this applies to larger juveniles as well, given that no tracking experiment has been ever undertaken. Hatchling dispersal simulations indicated that green turtle hatchlings are mainly retained in the Levantine basin, where the nesting sites are (Casale & Mariani 2014). A high proportion of green turtles smaller than 30 cm CCL was reported to occur in southern Turkey waters (Türkozan et al. 2013) while low numbers of small turtles < 40 cm CCL frequent the Adriatic (Lazar et al. 2004), especially in the southern part, the Ionian and even the Tyrrhenian seas around Italy (Bentivegna et al. 2011). Larger juveniles and adults are mainly found in the Levantine zone (Casale & Margaritoulis 2010; Nada & Casale 2011; Türkozan et al. 2013), with foraging habitats having been identified also in the Aegean and Ionian (south Peloponnesus, Greece) seas (Margaritoulis & Panagopoulou 2010), as well as in Libyan and, to a lesser extent, in Tunisian waters (Broderick et al. 2007; Bradai & Jribi 2010; Hamza 2010; Turkecan & Yerli 2011).

A total of fourteen green turtles have been satellite-tracked in the Mediterranean (Table 1). Thirteen adult females have been monitored from nesting sites in Turkey (Turkecan & Yerli 2011; n=2), Cyprus (Broderick et al. 2007; n=10), and Syria (Rees et al. 2008; n=1). They all followed a type A pattern (Godley et al. 2008), performing a direct and rather quick migration away from the breeding site to reach individually specific neritic foraging areas in Libya, Turkey and Egypt (Fig. 6). These data indicate that the north African coast of Egypt and Libya is an important migratory corridor for green turtles (Broderick et al. 2007). Cyprus females tracked in different years showed a remarkable fidelity to the same foraging grounds in Libya (Broderick et al. 2007). No information on the internesting movements performed is unfortunately available. Finally, one adult male was tracked from Cyprus and showed a non-direct route to Egypt along the coast, that was interpreted as an evidence of multiple breeding areas (Wright et al. 2012) (Fig. 6).

DISCUSSION

<u>General considerations</u>

Despite the large knowledge gaps still remaining, the available information reviewed above allows to depict an overall picture of the spatial behaviour of Mediterranean sea turtles, that can be compared with what is known on turtles of other areas. Overall, adult females display a rather uniform migratory behaviour, especially in green turtles, as they leave the nesting beach to quickly move towards discrete foraging zones (type A pattern; Godley et al. 2008). These sites are often located quite far away from the breeding area, and are in neritic (frequently coastal) waters, in line with the tendency of both species to primarily feed on algae, seagrass or benthic prey (Bjorndal 1997). While the geographic course and extension of these migrations can be quite variable even within the same rookery (e.g., Schofield et al. 2013), the overall behavioural pattern is basically the same, and is shared by loggerhead males as well. This migratory behaviour is fully correspondent to that observed in other areas in female loggerhead (e.g., Papi et al. 1997; Blumenthal et al. 2006; Hawkes et al. 2007; Girard et al. 2009) and green turtles (e.g., Luschi et al. 1996; Cheng 2000; Craig et al. 2004; Seminoff et al. 2008), as are the short scale internesting movements performed by loggerheads, typically recorded also elsewhere (Stoneburner 1982; Limpus & Limpus 2001). Given that in the Mediterranean the largest extension of shallow areas offering suitable neritic foraging sites is in the northern Adriatic and in the Libyan/Tunisian shelf, these represent key areas for both Mediterranean green and loggerhead turtles, given that both areas are frequented by adults and juveniles. Other factors may however play a role in determining the movement patterns observed: for instance, recent evidence suggests that the foraging locations of adult turtles might be influenced by their drift scenarios as hatchlings (Hays et al. 2010a, Scott et al. in press), and this would for example explain why few adults forage in the western part of Mediterranean, given that rookeries are confined in the Eastern basin (see also Casale & Mariani 2014).Mediterranean adult loggerheads however do exhibit some variety in their movements, with some turtles foraging in offshore oceanic waters for at least part of their inter-reproductive phase, sometimes keeping on the move without fixing to any specific site (Zbinden et al. 2008; Luschi et al. 2013; Schofield et al. 2013). This pattern too is in general accordance with recent findings obtained elsewhere showing how loggerhead spatial behaviour is actually characterised by a considerable complexity (Hatase et al. 2002; Hawkes et al. 2006; Hawkes et al. 2007; Rees et al. 2010). This variability is likely linked to the loggerhead plastic and opportunistic foraging habits (McClellan et al. 2010; Reich et al. 2010; Narazaki et al. 2013), which allows them to exploit both neritic and oceanic foraging grounds.

The variety in spatial patterns reaches its peak in the case of Mediterranean loggerhead juveniles, which have been found to perform diverse movement patterns such as erratic movements over pelagic or neritic areas, prolonged stays in restricted zones or even long-distance migrations, frequently with a seasonal periodicity. Once again, this is in accordance with tracking data obtained on other loggerhead populations outside the Mediterranean (McClellan & Read 2007; Kobayashi et al. 2008; Mansfield et al. 2009; Arendt et al. 2012b). Basing on juvenile foraging ecology (Casale et al. 2008a) and on the difference in size of the residential oceanic and neritic areas, an ecological-behavioural model has been recently put forward (Casale et al. 2012b). The model proposes a gradual rather than abrupt shift from a pelagic-vagile to a benthic-sedentary life style leading to a progressive reduction of home ranges. This reduction in home ranges may be due to the higher availability and energy content of the benthic prey accessible in the neritic zone with respect to the epipelagic prey that are the only ones available to loggerheads in the oceanic environment. This model has been developed especially for loggerheads living in the Mediterranean Sea, whose oceanographic features, with a great extent of oceanic-neritic edges, would produce an 'edge effect' that may favour opportunistic feeding, early frequentation, settlement and residence in neritic feeding grounds. However, such a non-rigid, 'relaxed' model could be well applied to loggerheads of other areas as well: actually, the 'classic' models of a loggerhead life cycle with specific ontogenetic stages (Musick & Limpus 1997; Bolten 2003), probably represent just specific cases of a greater behavioural plasticity.

Research priorities

Only a few of the 42 major sea turtle nesting sites in the Mediterranean (Casale & Margaritoulis 2010) have been investigated regarding their connections with the marine areas, which is where turtles originating from a specific nesting sites spend the vast majority of their time. Due to the well-known phenomenon of sea turtle natal homing, in particular of females (Bowen & Karl 2007), each breeding site should be regarded as an independent management unit (Moritz 1994; Bowen et al. 2005), i.e. the fate of one nesting site has little or no consequences on other nesting sites. In such a context, one research priority is to assess the localization of the specific foraging areas for each major nesting site. Genetic markers can provide rough patterns of distribution from rookery aggregates (Garofalo et al. 2013; Clusa et al. 2014). However, this approach is made difficult by the relatively poor genetic characterization of Mediterranean rookeries (i.e., the presence of shared genetic markers), partly due to the recent colonization of the Mediterranean Sea by loggerheads (Clusa et al. 2013), the gaps in the sampled rookeries and others intrinsic methodological limits, which prevent a complete assessment of the dispersal and migratory patterns of individual rookeries. Satellite tracking, although intrinsically limited in sample size, can be helpful on this aspect and can also identify migratory connectivity, including the routes followed by single individuals. So far, however, satellite tracking experiments on Mediterranean loggerheads have been conducted in a non-systematic manner usually with a few individuals tracked each time (Table 1), thus limiting the significance of the findings obtained. Two complementary approaches can be used to overcome this limitations: tracking a large number of adults from one breeding site to identify multiple foraging areas (e.g., Schofield et al. 2013) and tracking adults from one foraging area to identify multiple breeding sites (e.g., Casale et al. 2013a). This strategy should not be limited to females, but more attention and efforts should be given to adult males as well. Considering the previous studies (Table 1), the next priority nesting areas should be eastern Greece, Turkey, Libya and Syria.

Also, it has to be considered that sea turtle populations are made mostly by juveniles, and anthropogenic threats at sea, mainly fishing, mostly affect the juvenile class and the consequent reduction of survival rate (e.g., Casale et al. 2007b; Casale et al. in press) can be detrimental for the population (Heppell 1998). Hence, a comprehensive knowledge on the distribution of juveniles is fundamental for implementing sound conservation measures. In order to identify important oceanic and neritic foraging grounds, satellite tracking studies should complement other source of information, such as stranding and bycatch records, which may be intrinsically biased. A priority goal should be identifying movement patterns and neritic foraging areas of juveniles of both species, and especially in the Levantine basin (e.g., Turkey, Egypt, Cyprus, and Libya), for which information is particularly lacking (Table 1).

Finally, it should be noted that many unpublished tracks do exist in addition to those reviewed here. For instance we estimate that roughly 140 Mediterranean tracks of those available on seaturtle.org's "Satellite tracking" service as of April 2014, have not been included in any peer-reviewed paper. It is therefore to be expected that an amount of information nearly as much as the one reviewed here, still awaits a proper publication. This represents a missed opportunity to improve the overall picture of Mediterranean turtle spatial behaviour and may even causes incidental redundancy and waste of resources when planning future research. We therefore recommend the prompt publication of satellite tracking data in peer-reviewed journals.

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LEGEND TO FIGURES

Fig. 1. General migratory routes of the 63 adult loggerhead turtles satellite tracked in the Mediterranean (Table 1) and showing type A movement pattern (Godley et al. 2008). Only groups of ≥ 10 animals released from the same site are considered, while releases of single individuals (Table 1) are not shown. Arrows represent the approximate, general courses and do not show the actual reconstructed routes. Circles represent the release breeding sites in Greece (32 females and 23 males) and Cyprus (8 females; 2 turtles remained along the Cyprus coast). Number of individual females (F) and males (M) reaching different destinations are shown in boxes. The 200 m isobath is shown. AL, Albania; BA, Bosnia and Herzegovina; EG, Egypt; GR, Greece; HR, Croatia; IL, Israel; IT, Italy; LB, Lebanon; LY, Libya; ME, Montenegro; SI, Slovenia; SY, Syria; TN, Tunisia; TR, Turkey.

Fig. 2. Seasonal migrations in Mediterranean loggerheads. Blue track: migration of a rehabilitated juvenile turtle that left the release site in the North Adriatic (blue dot) in autumn 2007, remained in the Ionian Sea during winter and early spring and returned to northern Adriatic in May 2008 (from Casale et al. 2012a). Red track: seasonal migration of an adult female that moved to the northern Adriatic after completing nesting in Zakynthos island (red dot) and then migrated south during winter (from Zbinden et al. 2008). Arrows indicate direction of movement. Symbols and abbreviations as in Fig. 1.

Fig. 3. Examples of variable movements in juvenile loggerheads in the Mediterranean. Turtles released from Southwestern Italy performed long distance erratic movements over large oceanic areas (brown, orange and green tracks; Hochscheid et al. 2010). Conversely, turtles released from the Tunisian (fuchsia and dark blue; Casale et al. 2012b) and Adriatic shelves (red and light blue; Casale et al. 2012a) displayed convoluted movement over more restricted areas. Release sites are indicated by open circles. DZ, Algeria; other abbreviations and symbols as in Fig. 1.

Fig. 4. Schematic examples of the areas frequented by satellite-tracked juvenile loggerheads in the Mediterranean. All turtles considered were tracked for minimum 120 days. The areas frequented by juveniles in the oceanic zone north to Algeria (a; Revelles et al. 2007b; Cardona et al. 2009) tend to be larger than areas of juveniles in the neritic zones along the Spanish coast (b; Cardona et al. 2009), the Tunisian (c; Casale et al. 2012b) and Adriatic shelves (d; Casale et al. 2012a), and the western Italian coast (e; the arrows indicate the areas frequented by two turtles; Mencacci et al. 2011). FR, France; MA, Morocco; SP, Spain; other abbreviations and symbols as in Figs. 1 and 3.

Fig. 5. Specific cases of distribution and movements of loggerhead turtles in the Mediterranean. The main movement routes and the areas possibly visited by Atlantic individuals entering the Mediterranean are shown by grey arrows. Black arrows indicate the course of the possible seasonal movements from the two northernmost and coldest areas of the Mediterranean, the Ligurian Sea (a; only juveniles) and the

north Adriatic (b; both adults and juveniles). Symbols and abbreviations as in Figs. 1, 3 and 4.

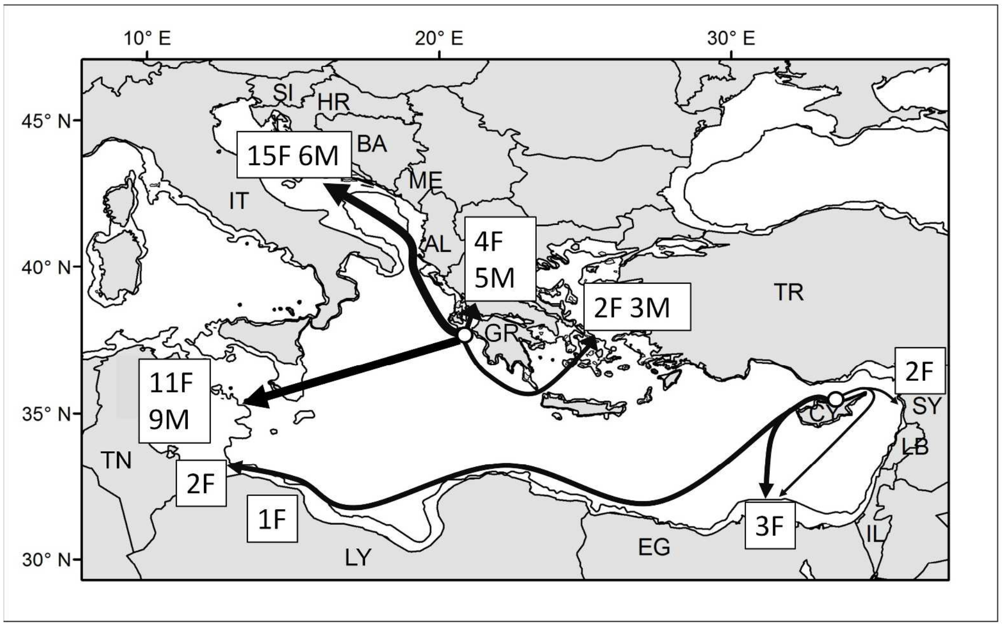
Fig. 6. Migratory routes of 13 adult green turtles satellite tracked in the Mediterranean (Table 1). Arrows represent the approximate, general courses and do not show the actual reconstructed courses. Routes of females and male are represented by black and grey lines respectively. Circles indicate the release sites of 10 females and one male (Cyprus), two females (Turkey), and one female (Syria). The area of Turkey, Syria and Cyprus is shown enlarged in the top-right box. Symbols and abbreviations as in Fig. 1.

Table 1. Summary of the 195 loggerhead and green turtles tracked by satellite in the Mediterranean (data presented in published papers, up to 2013).

Release area	Western/ Eastern Mediterranean	Release breeding/ Foraging area	Adult females	Adult males	Juveniles/ unknown	Source
Caretta caretta						
Alagadi + Esentepe (Cyprus)	Eastern	Breeding	10			Broderick et al. (2007)
Rethymno (Crete, Greece)	Eastern	Breeding	1			Margaritoulis & Rees (2011)
Cephalonia (Greece)	Eastern	Breeding	1			Hays et al. (1991)
Zakynthos (Greece)	Eastern	Breeding	18*	33*		Schofield et al. (2013)
Zakynthos (Greece)	Eastern	Breeding	18			Zbinden et al. (2011)
Amvrakikos Gulf (Greece)	Eastern	Foraging	2	2	2	Rees et al. (2013)
Adriatic	Eastern	Foraging	1		6	Casale et al. (2012a)
Adriatic	Eastern	Foraging	2			Luschi et al. (2013)
Adriatic	Eastern	Foraging		1		(Mencacci et al. 2006)
North Ionian	Eastern	Foraging			1	Hochscheid et al. (2007); Hochscheid et al. (2010)
Libya	Eastern	Foraging			2	Hochscheid et al. (2010)
Tunisian shelf	Eastern	Foraging			2	Hochscheid et al. (2007)
Tunisian shelf	Eastern	Foraging		10		Casale et al. (2013)
Tunisian shelf	Eastern	Foraging			6	Casale et al. (2012b)
Tyrrhenian	Western	Foraging			1	Luschi et al. (2013)
Tyrrhenian	Western	Foraging	3		1	Bentivegna (2002); Bentivegna et al. (2007)
Tyrrhenian	Western	Foraging			10	Hochscheid et al. (2007); Hochscheid et al. (2010)
Tyrrhenian	Western	Foraging			1	Hochscheid et al. (2010)
Tyrrhenian	Western	Foraging			3	(Mencacci et al. 2011)
Balearic Archipelago	Western	Foraging			5	Cardona et al. (2005); Revelles et al. (2007a)
Balearic Archipelago	Western	Foraging			10	Revelles et al. (2007a); Revelles et al. (2007b); Cardona et al. (2012)
Balearic Archipelago	Western	Foraging			3	Cardona et al. (2012)
Spanish shelf	Western	Foraging			7	Cardona et al. (2009)
Alboran Sea	Western	Foraging			19	Eckert et al. (2008)
Total *C. caretta*			56	46	79	

Chelonia mydas					
Akyatan (Turkey)	Eastern	Breeding	2		Turkecan & Yerli (2011)
Alagadi + Esentepe (Cyprus)	Eastern	Breeding	10		Broderick et al. (2007)
Latakia (Syria)	Eastern	Breeding	1		Rees et al. (2008)
Cyprus	Eastern	Breeding		1	Wright et al. (2012)
Total *C. mydas*			13	1	

*Actual numbers of turtles presented in the study (different numbers were declared, probably referring to the number of tracks obtained).



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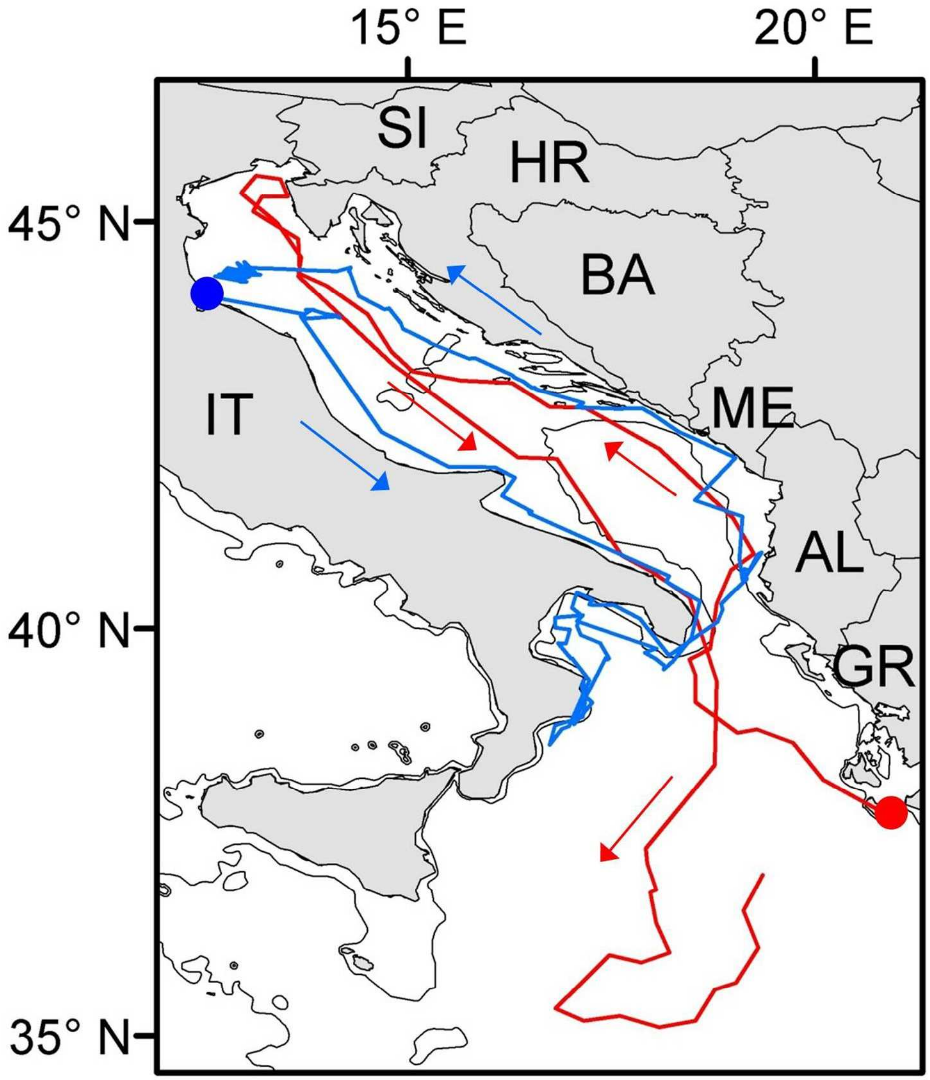

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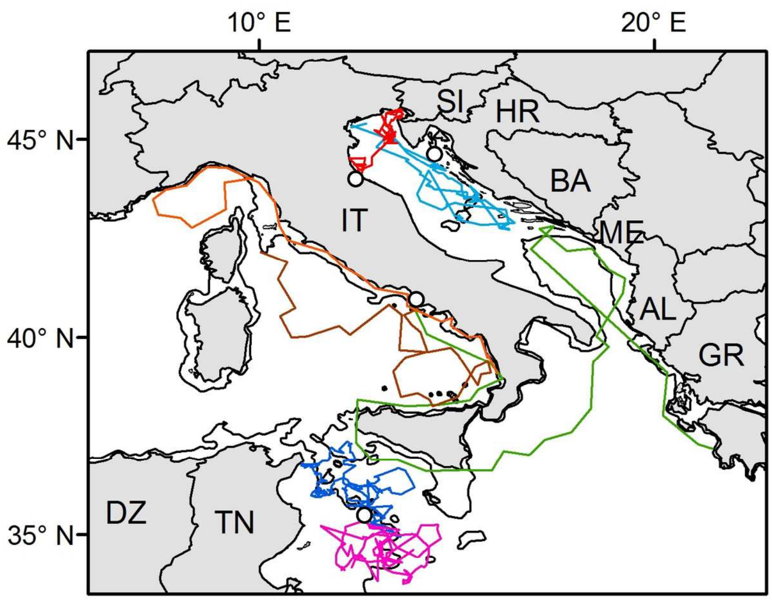

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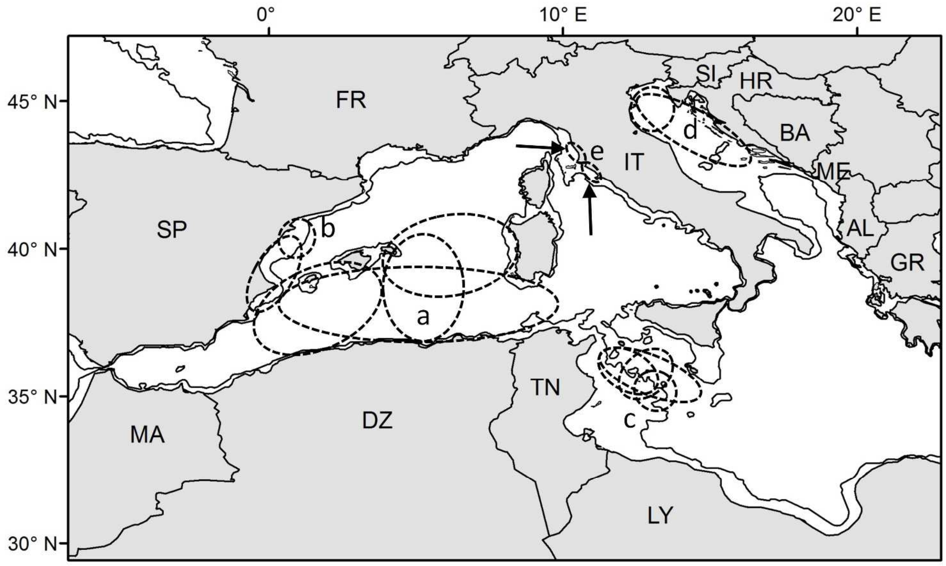

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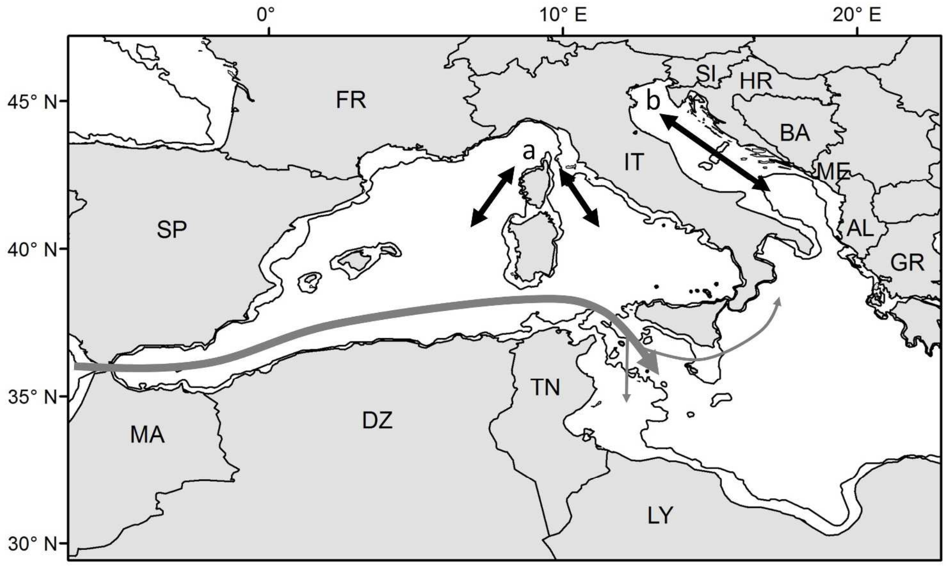

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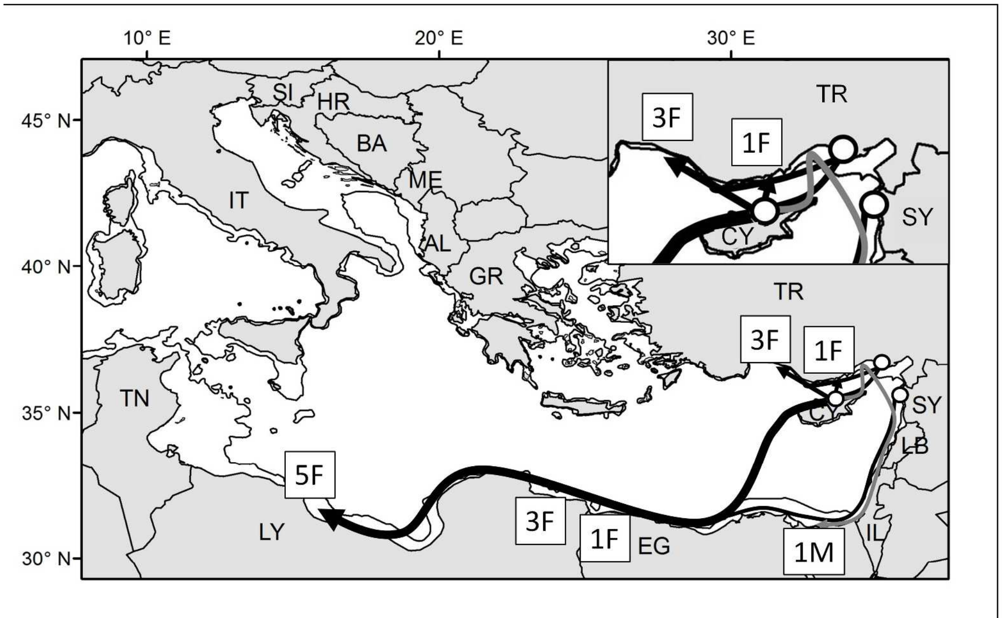

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