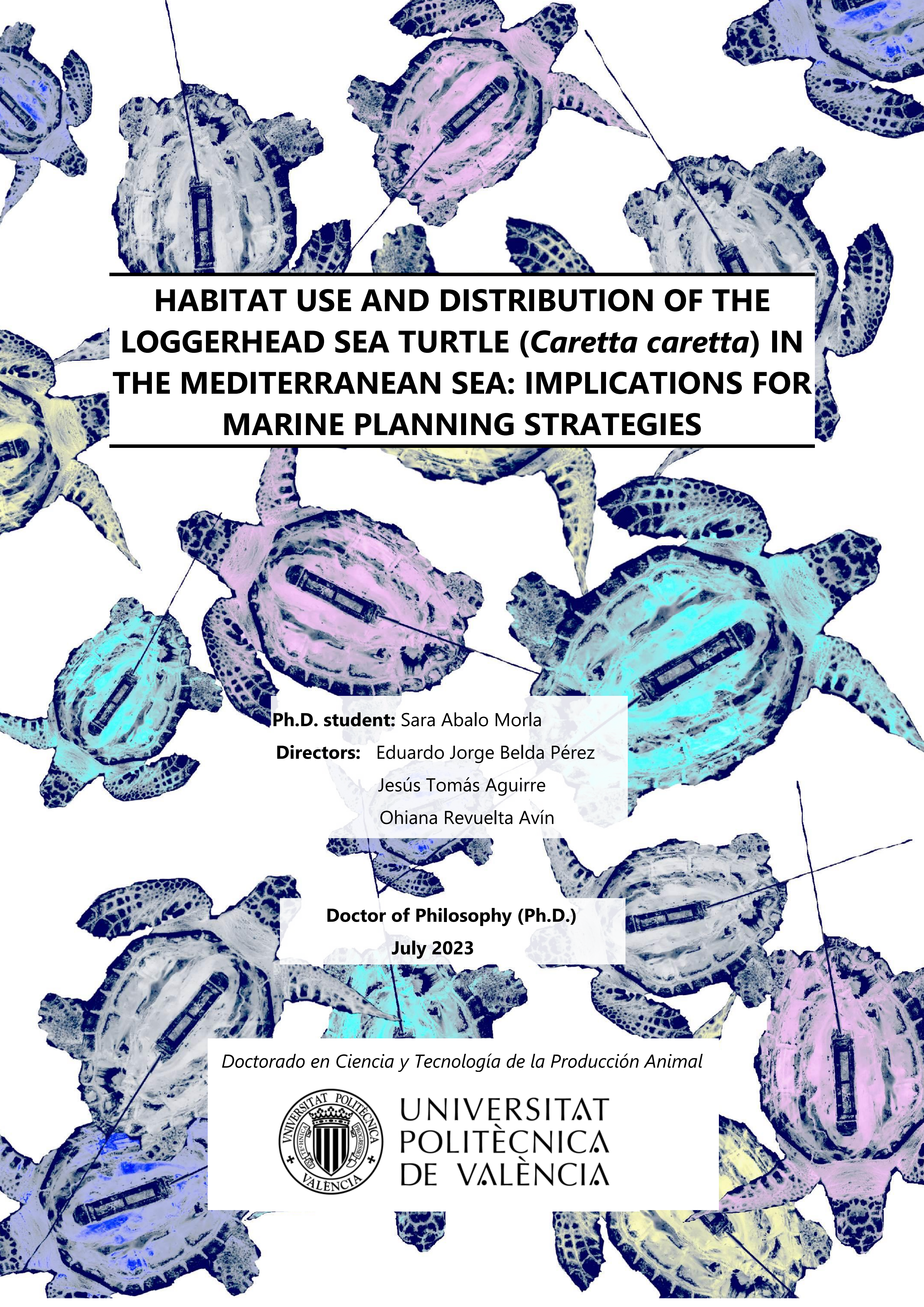

HABITAT USE AND DISTRIBUTION OF THE LOGGERHEAD SEA TURTLE (*Caretta caretta*) IN THE MEDITERRANEAN SEA: IMPLICATIONS FOR MARINE PLANNING STRATEGIES

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The cover image was self-produced using an own photography of a satellite-tagged loggerhead sea turtle.

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DISTRIBUCIÓN Y USO DEL HÁBITAT DE LA TORTUGA BOBA (*Caretta caretta*) EN EL MEDITERRÁNEO: IMPLICACIONES PARA LAS ESTRATEGIAS DE PLANIFICACIÓN MARINA

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Habitat use and distribution of the loggerhead sea turtle (*Caretta caretta) in the Mediterranean Sea: Implications for marine planning strategies*

Ph.D. thesis presented by Sara Abalo Morla and directed by Dr. Eduardo Jorge Belda Pérez, Professor at the Department of Animal Science (Universitat Politècnica de València), and codirected by Dr. Jesús Tomás Aguirre and Dra. Ohiana Revuelta Avín (Marine Zoology Unit at Universitat de València). The thesis was developed in the Institut d' Investigació per a la Gestió de Zones Costaneres (IGIC) research group to obtain the title of Doctor in Animal Production Science and Technology.

The thesis has been completed by reaching all requirements from the doctoral program. In total there have been three publications already published in scientific journals, along with one currently under review and another one being prepared. Furthermore, there have been ten international and national conference participations and publications, and attendance to several seminars, courses and transverse activities with more than 1100 hours recognized as specific and transverse activities, exceeding the requirement of 600 hours.

During her research, the candidate was a guest scientist during three months at the Department of Biological Sciences, Faculty of Science and Engineering at the Macquarie University (Australia). In addition, the candidate spent three months at the Department of Biology, University of Pisa (Italy). These international stays contribute to the recognition of the international mention of the present thesis.

Furthermore, the candidate co-directed two master thesis: 1) "*Cambios estacionales en la distribución del uso del hábitat en juveniles de un año de tortuga boba (Caretta caretta) nacidas en playas del Mediterráneo occidental*" presented by Carlos Pina Cubells at the Universitat Politècnica de València in 2022, and 2) "*Estudio de las poblaciones de cetáceos y tortugas marinas en la Zona de Especial Conservación Valles submarinos del Escarpe de Mazarrón*" presented by Gonzalo Martínez Fornos at the Universitat Politècnica de València in 2020.

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ABSTRACT

Loggerhead sea turtles (*Caretta caretta*) are highly mobile organisms, which occupy diverse habitats that often span large distances, exposing them to threats that can negatively impact the ability of their populations to persist. Delineating conservation priority measures for this species is challenging since integrated knowledge on survival, habitat use and the relative exposure to threats remains scarce, especially during the early life stages. In the western Mediterranean basin this is particularly relevant when considering the current colonization process taking place in the area within the last decade. During recent years, records on nesting females and clutches have increased and, when possible, management measures such as nest relocation and head-starting programs have been undertaken. This offers a unique opportunity to fill in the knowledge gaps on survival, dispersal routes and habitat use of loggerhead nesting females and post-hatchlings. No research prior to this thesis has satellite-tracked nesting and post-nesting females in the western Mediterranean, nor Mediterranean post-hatchlings smaller than 35 cm.

The present thesis aims to address the aforementioned knowledge gaps and enhance marine planning strategies for loggerhead conservation in the Mediterranean Sea. The main objectives were: i) to provide the first empirical survival estimates for head-started post-hatchlings, ii) to elucidate the dispersal routes and habitat use at different life stages, iii) to identify areas that should be considered for protection, iv) to assess the effectiveness of current marine protected areas (MPAs) and other protection measures for loggerhead conservation, and v) to propose spatial conservation measures based on research findings. To achieve these objectives, trajectories of 117 turtles satellite-tracked between 2003 and 2022 were analyzed. This dataset includes the first tracking data of nesting and post-nesting females in Spain and Mediterranean post-hatchlings, which have been made publicly available in a data repository. Moreover, the first assessment of habitat use and the use of MPAs for loggerhead sea turtles tracked from western Mediterranean thorough their life cycle was conducted.

The outcomes of this thesis revealed, for the first time, the survival, the dispersal routes and the habitat use of post-hatchlings in the Mediterranean Sea. Head-started post-hatchlings originating from western Mediterranean nests were able to survive in the wild after reintroduction (minimum daily survival probability 0.99), supporting the head-starting as a valuable management tool for hatchlings. Post-hatchlings were able to disperse across large oceanic areas, exhibiting highly variable routes, likely switching between active and passive dispersal. Most individuals displayed an eastward directional bearing, probably driven by environmental conditions, and some reached the eastern basin. The Ionian and Levant Seas were identified as potential developmental areas for post-hatchlings. Additionally, the Algerian basin, the Alboran Sea, the Tyrrhenian Sea and the deep waters of the Sicilian

Channel could be also important areas for loggerhead turtles from Spanish nests during the post-emergence period.

Dispersal and habitat use of new colonizer nesting females on the Spanish Mediterranean coast were also investigated for the first time. Females exhibited three different behaviours during the inter-nesting period: i) some degree of fidelity to a nesting area, ii) an exploratory nesting behavior, or iii) movement towards oceanic waters after tagging. In addition, the first-time remigration of this species to nest in Spain was recorded, confirming that females show some degree of nest site fidelity between breeding cycles. During the non-breeding stage, females remained in most cases foraging in oceanic waters of the Algerian basin, although we found evidence that nesting females in the western Mediterranean could temporarily travel to other foraging areas in the eastern basin.

The present thesis has validated the significance of the Algerian basin for loggerhead sea turtles satellite-tracked from the western Mediterranean, particularly for juveniles and adults. In addition, other important areas inhabited by the loggerhead turtles were identified in the southern Balearic Sea, the Alboran Sea, the Sicilian Channel, the Northeast Tunisia, Maltese waters, the Tyrrhenian Sea and the Ionian Sea, depending on the life stage. The analysis of the spatial distribution of the loggerhead sea turtle has also revealed that the current distribution and coverage of Mediterranean MPAs are not effective in achieving this species' conservation goals. Most MPAs are located in coastal zones, while loggerhead turtles in the western Mediterranean primarily inhabit oceanic areas. Furthermore, the main frequented areas by loggerhead turtles (Algerian basin, Sicilian Channel and Ionian Sea) lack protection. Furthermore, most MPAs in the western and eastern Mediterranean lack explicit management measures focused on minimizing threats that undermine sea turtle conservation. These findings underscore the need to modify and to add protected areas in the Mediterranean Sea with specific conservation measures focused on loggerhead turtles. Proposed new MPAs include the western part of the Algerian basin, the waters of the Northern Ionian Sea, the waters of the Northern Strait of Sicily, areas within the Tyrrhenian Sea, and the waters of Northeast Tunisia. Additionally, the expansion and interconnection of existing MPAs in Malta and the MPAs located in the Alboran Sea were also recommended.

Outcomes from the present thesis significantly enhance our understanding of the survival and spatial use of the loggerhead sea turtle throughout its life cycle in the Mediterranean Sea. Such outcomes hold particular importance for the management of potential new breeding areas in the western Mediterranean. Moreover, results from this thesis provide valuable and up-to-date scientific knowledge that can inform recommendations for the management and conservation of the species in the region. Additionally, these findings may have implications for updating marine planning strategies, particularly in areas where conservation priorities and mitigation efforts should be applied.

RESUMEN

Las tortugas bobas son organismos de gran movilidad que ocupan hábitats extensos y diversos, lo que las expone a varias amenazas que pueden afectar negativamente a la persistencia de sus poblaciones. Delinear medidas prioritarias de conservación para esta especie es todo un reto debido a la escasez del conocimiento integrado sobre su supervivencia, uso de hábitat y exposición relativa a amenazas, especialmente durante las primeras etapas de su ciclo vital. En la cuenca occidental del mar Mediterráneo esto adquiere mayor relevancia si se contextualiza en el proceso de colonización que está teniendo lugar en la zona durante la última década. Se ha registrado un aumento en el número de nidos y hembras nidificantes, para cuya protección se han tomado medidas de gestión como la reubicación de nidos y la inclusión de neonatos en programas de "*head-starting*". Esta coyuntura ha ofrecido una oportunidad única para incrementar el conocimiento sobre la supervivencia, dispersión y uso de hábitat de hembras nidificantes y post-neonatos de tortuga boba. Ninguna investigación previa ha realizado un seguimiento por satélite de hembras nidificantes en el Mediterráneo occidental, ni de post-neonatos mediterráneos con tamaño inferior a 35 cm.

La finalidad de esta tesis es abordar las lagunas de conocimiento mencionadas y aportar herramientas para mejorar las estrategias de planificación marina dirigidas a la conservación de la tortuga boba en el Mediterráneo. Los principales objetivos fueron: i) proporcionar las primeras estimaciones empíricas de supervivencia de post-neonatos, ii) dilucidar las rutas de dispersión y el uso de hábitat en las diferentes etapas del ciclo vital, iii) identificar áreas relevantes para su protección, iv) evaluar la eficacia de las actuales áreas marinas protegidas (AMPs) para la conservación de la tortuga boba, y v) proponer medidas de conservación basadas en el análisis espacial. Para ello, se analizaron las trayectorias de 117 tortugas seguidas vía satélite entre 2003 y 2022. Estos datos incluyen las primeras trayectorias de hembras nidificantes en España y de post-neonatos mediterráneos, que se han publicado en un repositorio. Además, se realizó la primera evaluación del uso de hábitat y de AMPs por tortugas bobas marcadas en el Mediterráneo occidental, a lo largo de su ciclo vital.

Los resultados de esta tesis muestran, por primera vez, la supervivencia, dispersión y uso de hábitat de post-neonatos de tortuga boba en el Mediterráneo. Dichos post-neonatos, procedentes de nidos del Mediterráneo occidental y liberados tras un período de *"head-starting"*, sobrevivieron en la naturaleza tras su reintroducción (probabilidad mínima de supervivencia diaria de 0.99), demostrando que el *"head-starting"* es una valiosa herramienta de gestión. Los post-neonatos se desplazaron por amplias áreas oceánicas, con rutas muy variables, alternando entre dispersión activa y pasiva. La mayoría mostraron una orientación preferente hacia el este, llegando algunos individuos a alcanzar la cuenca oriental, probablemente impulsados por las condiciones ambientales. Los mares Jónico y de Levante se identificaron como zonas potenciales de desarrollo de post-neonatos. Además, la cuenca argelina, el Mar de Alborán, el Mar Tirreno y las aguas profundas del Canal de Sicilia podrían ser zonas importantes para las tortugas procedentes de nidos españoles tras la eclosión.

También se investigó por primera vez la dispersión y el uso del hábitat de las hembras nidificantes en el mediterráneo español. Las hembras mostraron dos comportamientos diferentes durante el periodo de inter-anidación: i) fidelidad a la zona de nidificación, o ii) comportamiento exploratorio de nidificación. Además, se registró por primera vez la reemigración de esta especie para nidificar de nuevo en España, lo que confirma que las hembras pueden mostrar un cierto grado de fidelidad al lugar de nidificación entre ciclos reproductores. Durante la etapa no reproductora, la mayoría de las hembras permanecieron alimentándose en aguas oceánicas de la cuenca argelina, aunque se observó que algunas hembras nidificantes en el Mediterráneo occidental pueden desplazarse temporalmente a otras áreas de alimentación ubicadas en la cuenca oriental.

La presente tesis confirma la importancia de la cuenca argelina para las tortugas bobas del Mediterráneo occidental, en particular para los juveniles y adultos. Otras zonas identificadas como importantes son el sur del mar Balear, el mar de Alborán, el canal de Sicilia, el noreste de Túnez, las aguas de Malta, el mar Tirreno y el mar Jónico, según la etapa vital. El análisis de la distribución espacial de la tortuga boba también ha revelado que la distribución y cobertura actuales de las AMPs mediterráneas no contribuyen a alcanzar los objetivos de conservación para esta especie. La mayoría de las AMPs están situadas en zonas costeras, mientras que las tortugas bobas del Mediterráneo occidental habitan principalmente en zonas oceánicas. Además, las áreas más frecuentadas por estas tortugas (cuenca argelina, Canal de Sicilia y Mar Jónico) no están protegidas. Asimismo, la mayoría de las AMPs del Mediterráneo carecen de medidas de gestión explícitas centradas en minimizar las amenazas que socavan la conservación de las tortugas marinas. Estos hallazgos subrayan la necesidad de modificar y añadir AMPs en el mar Mediterráneo con medidas de conservación específicas dirigidas a la protección de esta especie. Las AMPs propuestas en esta tesis incluyen la parte occidental de la cuenca argelina, el mar Jónico septentrional, el estrecho septentrional de Sicilia, zonas del mar Tirreno y el nordeste de Túnez. Además, se recomienda la ampliación e interconexión de las AMPs existentes en Malta y en el Mar de Alborán.

Los resultados obtenidos en esta tesis contribuyen al conocimiento de la supervivencia y uso espacial de la tortuga boba a lo largo de su ciclo vital en el mar Mediterráneo. Estos resultados son especialmente importantes para la gestión de posibles nuevas zonas de nidificación en el Mediterráneo occidental. Además, aportan conocimientos científicos actualizados que pueden servir de base para elaborar recomendaciones de gestión y conservación de esta especie en la región. Asimismo, estos hallazgos pueden tener implicaciones para la actualización de las estrategias de planificación marina, particularmente en las áreas donde se deben aplicar prioritariamente acciones de conservación y esfuerzos de mitigación de impactos.

RESUM

Les tortugues babaues són organismes de gran mobilitat que ocupen hàbitats diversos i extensos, la qual cosa les exposa a diverses amenaces que poden afectar negativament la persistència de les seues poblacions. Delinear mesures prioritàries de conservació per a aquesta espècie és tot un repte, a causa de l'escassetat del coneixement integrat sobre la seua supervivència, ús d'hàbitat i exposició relativa a amenaces, especialment durant les primeres etapes del seu cicle vital. En la conca occidental de la mar Mediterrània això adquireix major rellevància si es contextualitza en el procés de colonització que està tenint lloc en la zona durant l'última dècada. S'ha registrat un augment en el nombre de nius i femelles nidificants, per a la protecció de les quals s'han pres mesures de gestió com la reubicació de nius i la inclusió de nounats en programes de "*head-starting*". Aquesta conjuntura ha oferit una oportunitat única per a incrementar el coneixement sobre la supervivència, dispersió i ús d'hàbitat de femelles nidificants i post-nounats de tortuga babaua. Cap investigació prèvia ha realitzat un seguiment per satèl·lit de femelles nidificants en el Mediterrani occidental, ni de post-nounats mediterranis amb grandària inferior a 35 cm. La finalitat d'aquesta tesi és abordar les llacunes de coneixement esmentades i aportar eines per a la millora de les estratègies de planificació marina dirigides a la conservació de la tortuga babaua al Mediterrani. Els principals objectius van ser: i) proporcionar les primeres estimacions empíriques de supervivència de post-nounats, ii) dilucidar les rutes de dispersió i l'ús d'hàbitat en les diferents etapes del cicle vital, iii) identificar àrees rellevants per a la seua protecció, iv) avaluar l'eficàcia de les actuals àrees marines protegides (AMPs) per a la conservació de la tortuga babaua, i v) proposar mesures de conservació basades en l'anàlisi espacial. Per a això, es van analitzar les trajectòries de 117 tortugues seguides via satèl·lit entre 2003 i 2022. Aquestes dades inclouen les primeres trajectòries de femelles nidificants a Espanya i de post-nounats mediterranis, que s'han publicat en un repositori de dades. A més, es va realitzar la primera avaluació de l'ús d'hàbitat i de les AMPs per les tortugues babaues marcades en el Mediterrani occidental, al llarg del seu cicle vital.

Els resultats d'aquesta tesi mostren, per primera vegada, la supervivència, dispersió i ús d'hàbitat de post-nounats de tortuga babaua al Mediterrani. Aquests post-nounats, procedents de nius del Mediterrani occidental i alliberats després d'un període de "*head-starting*", van sobreviure en la naturalesa després de la seua reintroducció (probabilitat mínima de supervivència diària de 0.99), demostrant que el "*head-starting*" és una valuosa eina de gestió. Els post-nounats es van desplaçar per àmplies àrees oceàniques, amb rutes molt variables, alternant entre dispersió activa i passiva. La majoria van mostrar una orientació preferent cap a l'est, arribant alguns individus a aconseguir la conca oriental, probablement impulsats per les condicions ambientals. Les mars Jònic i de Llevant es van identificar com a zones potencials de desenvolupament de post-nounats. A més, la conca algeriana, la Mar d'Alborán, la Mar Tirrena i les aigües profundes del Canal de Sicília podrien ser zones importants per a les tortugues procedents de nius espanyols després de l'eclosió.

També es va investigar per primera vegada la dispersió i l'ús de l'hàbitat de les femelles nidificants en el mediterrani espanyol. Les femelles van mostrar dos comportaments diferents durant el període de inter-nidificació: i) fidelitat a la zona de nidificació, o ii) un comportament exploratori de nidificació. A més, es va registrar per primera vegada la reemigració d'aquesta espècie per a nidificar de nou a Espanya, la qual cosa confirma que les femelles poden mostrar un cert grau de fidelitat al lloc de nidificació entre cicles reproductors. Durant l'etapa no reproductora, la majoria de les femelles van romandre alimentant-se en aigües oceàniques de la conca algeriana, encara que es va observar que algunes femelles nidificants en el Mediterrani occidental poden desplaçar-se temporalment a altres àrees d'alimentació situades la conca oriental.

La present tesi confirma la importància de la conca algeriana per a les tortugues babaues del Mediterrani occidental, en particular per als juvenils i adults. Altres zones identificades com a importants són el sud de la mar Balear, la mar d'Alborán, el canal de Sicília, el nord-est de Tunísia, les aigües de Malta, la mar Tirrena i la mar Jònica, segons l'etapa vital. L'anàlisi de la distribució espacial de la tortuga babaua també ha revelat que la distribució i cobertura actuals de les AMPs mediterrànies no contribueixen a aconseguir els objectius de conservació per a aquesta espècie. La majoria de les AMPs estan situades en zones costaneres, mentre que les tortugues babaues del Mediterrani occidental habiten principalment en zones oceàniques. A més, les àrees més freqüentades per aquestes tortugues (conca algeriana, Canal de Sicília i Mar Jònic) no estan protegides. Així mateix, la majoria de les AMPs del Mediterrani manquen de mesures de gestió explícites centrades en minimitzar les amenaces que soscaven la conservació de les tortugues marines. Aquestes troballes subratllen la necessitat de modificar i afegir AMPs en la mar Mediterrània amb mesures de conservació específiques dirigides a la protecció de la tortuga babaua. Les AMPs propostes en aquesta tesi inclouen la part occidental de la conca algeriana, la mar Jònica septentrional, l'estret septentrional de Sicília, zones de la mar Tirrena i el nord-est de Tunísia. A més, també es recomana l'ampliació i interconnexió de les AMPs existents a Malta i en la Mar d'Alborán.

Els resultats obtinguts en aquesta tesi contribueixen al coneixement de la supervivència i ús espacial de la tortuga babaua al llarg del seu cicle vital en la mar Mediterrània. Aquests resultats són especialment importants per a la gestió de possibles noves zones de nidificació en el Mediterrani occidental. A més, aporten coneixements científics actualitzats que poden servir de base per a elaborar recomanacions de gestió i conservació d'aquesta espècie a la regió. Així mateix, aquestes troballes poden tindre implicacions per a l'actualització de les estratègies de planificació marina, particularment en les àrees on s'han d'aplicar prioritàriament accions de conservació i esforços de mitigació d'impactes.

Chapter 1

Introduction

1.1 Background

1.1.1 The relevance of the marine biodiversity conservation

Biodiversity is a mechanism through which ecosystems respond to environmental changes, as high biodiversity buffers the effects of environmental variation and protects the ecosystem from disturbances (Bianchi et al. 2022). Therefore, marine biodiversity is an essential foundation for the structure and functioning of ocean ecosystems (Loreau et al. 2021) and for providing the full range of ecosystem services that benefit humans on local, regional, and global scales. These benefits include, for instance, the oxygen we breathe, the seafood we eat, the support of local livelihoods, the marine plants protecting our shorelines, or the biochemical compounds found in marine species, among others (Lotze 2021).

The Mediterranean region has been inhabited by humans for millennia, and consequently, ecosystems have been altered in many ways (Coll et al. 2010). Although the Mediterranean Sea only covers 0.7% of the world’s ocean area, it is a major marine biodiversity hotspot (Coll et al. 2010). The basin includes deep-sea and pelagic habitats that support unique species and ecosystems (Boudouresque 2004, Sardà et al. 2004, Danovaro et al. 2010), such as endemic seagrass meadows (Telesca et al. 2015), coralligenous assemblages (Ballesteros 2006), and species of global conservation concern, such as sea turtles and marine mammals (Casale and Margaritoulis 2010, Casale and Tucker 2017, Tetley et al. 2022). Temporal trends indicate that overexploitation (i.e., by fisheries) and habitat loss have been the main human drivers of historical changes in biodiversity (Bas 2009). At present, Mediterranean biodiversity is undergoing rapid alteration under the combined pressure of additional threats such as habitat fragmentation, pollution, marine traffic, coastal development, climate change, eutrophication, wildlife trade, and the establishment of alien species, which are the main factors causing the fast-paced loss of marine species and ecosystems (Bas 2009, FAO 2011, Wallace et al. 2013, O’Hara et al. 2021, Roberson et al. 2021).

Nonetheless, awareness of the risk of biodiversity degradation and loss has only recently grown (O’Hara et al. 2021). This risk is not only a biological or ecological problem but also a critical problem in economic and developmental terms due to the extremely high value of the biological resources of which human life depends (CBD 2010, Bianchi et al. 2022). Protection measures to minimize and mitigate the negative impacts of anthropogenic effects, either for Mediterranean marine species or ecosystems, are still scarce (Bianchi and Morri 2000, Fanelli et al. 2021). Therefore, the conservation measures taken were far from reaching the Aichi Biodiversity Target 11 of the Convention on Biological Diversity (CBD), whereby signatory countries agreed to protect and effectively manage 10% of coastal and marine areas by 2020 (CBD 2010, Boonzaier and Pauly 2016, Giménez et al. 2021). To adopt the necessary conservation and management measures, especially in relation to vulnerable species and ecosystems, it is required to bridge the gaps in knowledge that impede the effective implementation of such measures (FAO 2019, Lotze et al. 2021). Moreover, biodiversity undervaluing in national policies, planning, and budgets is another constraint to consider while gathering biodiversity knowledge (Bianchi et al. 2022).

Marine turtles have an essential ecological impact on ecosystem structure and function, as they play fundamental ecological roles in ocean ecosystems (Patel et al. 2022). These roles include providing a key habitat for other marine species and facilitating nutrient cycling from water to land (Bjorndal and Bolten 2003, Lazar et al. 2011, Lovich et al. 2018). Turtles also host parasites and pathogens (Santoro and Mattiucci 2009, Stacy et al. 2019, Ebani 2023) and serve as substrates for many species of epibionts, which can be consumed by fish, especially in nutrient-deficient areas (Ingels et al. 2020). Additionally, marine turtles provide nutrients to the ocean floor through a process called bioturbation, and when they forage, they facilitate aeration and nutrient distribution of sediments (Lazar et al. 2011, Lovich et al. 2018). Moreover, through nesting events, they can improve beach ecosystems by supplying essential nutrients from distant and dispersed foraging grounds, encouraging vegetation growth in the sand dunes, and contributing to the health of the ecosystem (Bouchard and Bjorndal 2000, Lovich et al. 2018). Eggs and hatchlings also provide a food source for predators (Lovich et al. 2018).

1.1.2 The loggerhead sea turtle in the Mediterranean Sea

The loggerhead sea turtle (*Caretta caretta*) is the most common marine turtle species in the Mediterranean Sea, occurring across the entire basin (Casale et al. 2018), although their traditional nesting areas are mainly concentrated in the eastern Mediterranean (Mancino et al. 2022). Despite its wide distribution range, the loggerhead turtle is listed as 'Vulnerable' globally in the IUCN Red List (International Union for Conservation of Nature, Casale and Tucker, 2017) and the Mediterranean population is categorised as 'Least Concern' by the same authority (Casale 2015). This 'Least Concern' status should, however, be considered as entirely conservation-dependent, because the current population is the result of decades of intense conservation programs, especially at nesting sites (Casale and Margaritoulis 2010), and the cessation of these programs would be followed by a population decrease (Casale et al. 2018). Fisheries by-catch and ingestion of plastic debris are considered the main causes of mortality for loggerhead sea turtles, which jeopardize the conservation goals for the species in the Mediterranean Sea (Tomás 2008b, Casale et al. 2010, 2018, Báez et al. 2014, 2019, Marco et al. 2020). Marine traffic, boat collision, coastal development, tourism related activities, beach erosion, predation of eggs and hatchlings by animals, egg infestation, climate change effects and marine debris and pollution are also other threats that put loggerhead sea turtle populations at risk (Casale and Margaritoulis 2010, 2014, Kaska et al.

2010, Margaritoulis and Panagopoulou 2010, Katselidis et al. 2013, Nelms et al. 2016, Casale et al. 2018 and references herein, Dimitriadis et al. 2018, Hochsheid et al. 2018, Monsinjon et al. 2019, DiRenzo et al. 2022, Novillo-Sanjuan et al. 2022, Pietrolungo et al. 2023, Sosa-Guedes et al. 2023).

The loggerhead turtle has a complex life cycle (Figure 1.1) (Bolten 2003, Rees 2013). After hatching on the beach, young turtles crawl into the sea and undergo an intense, but brief, swimming phase known as the "swimming frenzy". Then, they are rarely observed until they return to coastal waters as larger juveniles (Wyneken and Salmon 1992). During their early juvenile stage, loggerheads are distributed in oceanic habitats (depths > 200 m) and mainly feed on gelatinous zooplankton (Frick et al. 2009, Cardona et al. 2012a), but also on marine animals like fish, pelagic marine plants, terrestrial plants (mostly wood) or terrestial flying insects (Witherington et al. 2012, McClellan et al. 2010). The consumption of anthropogenic debris (i.e., plastics, tar) by post-hatchlings and early juveniles was also observed by previous reseach (Witherington et al. 2012). As the turtles grow in size, they gradually shift to feeding on benthic prey (Seney and Musick 2007, Casale et al. 2008a, Molter et al. 2022) recruiting to coastal habitats (depths < 200 m) (Bolten 2003). The time gap after young turtles hatch and head to sea, where they remain at a surface-pelagic or oceanic stage before returning to coastal waters as large juveniles, is referred to as the *lost years* because there is little information about this life period (Carr 1987, Bolten 2003, Mansfield et al. 2014, 2017). Late juvenile and adult loggerhead turtles of both sexes remain generally neritic in the Mediterranean (Zbinden et al. 2008, 2011, Casale et al. 2013, Luschi et al. 2013, Rees et al. 2013, Mingozzi et al. 2016, Snape et al. 2016), where they reach the sexual maturity at an estimated age of 21-34 years (Casale et al. 2020).

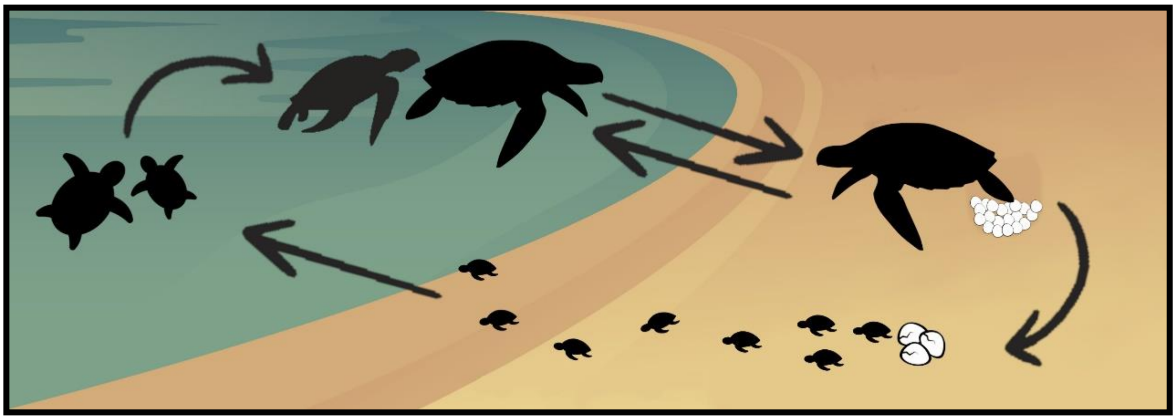

Figure 1.1 Generalized life cycle of the loggerhead sea turtle. This figure was created used using images from Flaticon.com.

Neritic loggerhead turtles typically exhibit smaller home ranges than those in oceanic habitats (Schofield et al. 2010, Snape et al. 2016). However, adult individuals from a given breeding rookery might use different foraging grounds, often separated by hundreds of kilometres (Bentivegna 2002, Zbinden et al. 2008, Schofield et al. 2010a, 2013). Moreover, at small seas, as the Mediterranean Sea, characterized by both oceanic and neritic habitats in close proximity, neritic and oceanic habitats are usually shared by loggerhead turtles of different life stages (Clusa et al. 2016, Luschi et al. 2018, Ten et al. 2019, Chimienti et al. 2020). Similarly, plasticity in habitat use was also observed for large subadults and juveniles of loggerhead in the Atlantic (i.e., Mansfield et al. 2009, McClellan and Read 2007) and Pacific oceans (i.e., Okuyama et al. 2022).

Only nesting females return to the beach to lay one or more clutches during the nesting season (Figure 1.1), although they usually do not nest every year (Bolten 2003). Average clutch size is about 110 eggs, and mean hatching success ranges between 56 and 86% (Casale et al. 2020). The major nesting aggregations of loggerheads, where over 96% of clutches are laid, are located in the central and eastern Mediterranean, specifically on beaches in Greece, Turkey, Libya and Cyprus where thousands of nests are recorded (Casale et al. 2018). Secondary nesting sites are found in Tunisia and Israel, while there are no recent reports on other countries where some nesting is known to occur, such as Lebanon and Egypt (Hoschsheid et al. 2018). These nesting aggregations correspond to distinct demographic sub-populations, which are genetically well-structured and differentiated (Carreras et al. 2018, Barbanti 2021), and have evolved independently from Atlantic loggerhead turtles (Clusa et al. 2013).

Sea turtles generally exhibit high philopatry, with adults homing to breeding sites, where males and females migrate periodically to reproduce close to their natal rookeries, and where females nest on their natal beach (Lohmann et al. 2013). However, there have been increasing observations of adults also frequenting secondary breeding sites (Schofield et al. 2010b, Casale et al. 2013), which may have important consequences for gene flow among different rookeries (Carreras et al. 2018, Casale et al. 2018). Indeed, it was hypothesized that loggerhead turtles may exhibit an exploratory non-phylopatric behaviour in order to colonize new nesting sites in the Mediterranean which could provide an adaptive advantage in response to possible environment changes (Carreras et al. 2018).

Such kind of colonising events were presumed to have also occurred when Atlantic loggerhead turtles colonised the Mediterranean waters during the late Pleistocene (Garofalo et al. 2009, Clusa et al. 2013). Thus, the regional population survived several cold periods using warm refuges across the southeastern parts of the sea (i.e., Libya, Greece, Turkey) where traditional major nesting aggregations are mainly concentrated (Clusa et al. 2013). During the Holocene, another independent colonization process from Atlantic individuals was presumed to have occurred in the Central Mediterranean (Southern Italy) (Garofalo et al.

2009, Clusa et al. 2013, Carreras et al. 2018). Nowadays, loggerhead turtles found in the Mediterranean Sea belong to three independent Regional Management Units (RMUs) with specific demographic and genetic features (Wallace et al. 2010): the Mediterranean, the northwestern Atlantic and, to a lesser extent, the northeastern Atlantic (Monzón-Argüello et al. 2010, Wallace et al. 2010, Clusa et al. 2014). Loggerheads from Atlantic RMUs enter the Mediterranean through the Strait of Gibraltar and mainly disperse across the south of the western basin up to the Ibiza channel (Carreras et al. 2006, 2011, Monzón-Argüello et al. 2009, Clusa et al. 2014), although they can be found at lower frequency on north Mediterranean Spanish waters. Juveniles from Atlantic RMUs reaching the Mediterranean mostly remain in the western basin of this sea (Casale et al. 2020), where they are supposed to stay, at least, until they reach a certain size (Revelles et al. 2007a). Loggerhead turtles from the Mediterranean RMU can be found throughout the sea, although their relative proportion is higher than 80% in the eastern, central and north-western Mediterranean and less than 45% in the Alboran Sea and the Algerian Basin (Clusa et al. 2014). Despite the admixture of loggerhead turtles from different origins, Atlantic and Mediterranean RMUs remain quite isolated (Carreras et al. 2011, Clusa et al. 2016).

In general, the highest density of loggerhead turtles appears to occur in the westernmost part of the Mediterranean Sea, the Sicily Straight, the Ionian Sea, the Gulf of Gabès in Tunisia, the Adriatic Sea, and the southeast coast of Turkey. Casale and Heppel (2016) estimated abundance of the loggerhead turtles in the Mediterranean Sea to be about 16,000 adult breeding turtles, resulting in a total Mediterranean population of around 2 million turtles, of which approximately 750,000 would be over 2 years old. The movements and habitat use of individual loggerhead turtles directly caught at sea have been well documented in the Mediterranean Sea, mainly for adults but also for immature individuals at their developmental habitats (Cardona et al. 2005, Revelles et al. 2007, Casale et al. 2012, Chimienti et al. 2020). Previous studies have suggested the Levantine Basin as a nursery area for turtles originating from eastern rookeries, while turtles hatched in Greece and in central Mediterranean nesting areas would disperse mainly in the Ionian, south-central Mediterranean (i.e., Gulf of Gabès) and Adriatic Seas (Casale and Mariani 2014). However, dispersal and high-density areas of post-hatchlings and early juveniles (< 40 cm SCL) of loggerhead sea turtle in the Mediterranean Sea essentially relied on numerical simulations of particle distribution (Hays et al. 2010, Casale and Mariani 2014, Maffucci et al. 2016, Cardona and Hays 2018). Recently, DiMatteo et al. (2022) estimated the abundance of the loggerhead turtles in the Mediterranean from data derived from line transect surveys, and observed higher abundance predicted in the northern Adriatic Sea, central Mediterranean basin, Tyrrhenian Sea, and south of the Balearic Islands. Research about habitat use of loggerhead breeding turtles which inhabit the Mediterranean Sea was mainly conducted on the eastern basin where the major nesting areas were reported for the species (Casale et al. 2018) while studies on nesting females in the westernmost part of the Mediterranean basin have not been developed yet.

Foraging sites of adult sea turtles are critical for population persistence, as they represent habitats where animals spend most of their time in order to replenish their reserves and be able to breed (Wallace et al. 2011). However, given that foraging sites are usually located in the coastal zone, they are subjected to multiple anthropogenic pressures, making their efficient protection particularly challenging (Wallace et al. 2011). For the loggerhead sea turtles, an ontogenetic dietary shift from oceanic to coastal waters has been described (Bolten 2003), although this shift can be gradual (Tomás et al. 2001, Domènech et al. 2019, Haywood et al. 2020a), with adult turtles also using open waters (Hawkes et al. 2006, Revelles et al. 2007d, Wallace et al. 2010, Ten et al. 2019). Based on different studies, such as satellite tracking data or fisheries bycatch, potential foraging areas have been described in the Mediterranean Sea for the species, including the Algerian Sea (Cardona et al. 2005, 2009, 2012b, Revelles 2007a, b, c, Hays et al. 2014), the deep waters of the Sicilian Strait (Bentivegna 2002, Casale et al. 2012d), the western Ionian Sea (Mingozzi et al. 2016), the central Ionian Sea (Zbinden et al. 2008, Schofield et al. 2010a), the central Spanish continental shelf (Cardona et al. 2009, Álvarez de Quevedo et al. 2010, Domènech et al. 2015, Casale et al. 2018), the Balearic Islands (Carreras et al. 2004) and the southwestern coasts of Italy (Hochscheid et al. 2007). Unfortunately, these studies do not cover the entire Mediterranean region, especially the Levantine Basin. Additionally, they do not encompass all life stages, particularly the earliest stages of development.

1.1.3 Marine turtle conservation in the Mediterranean Sea

Conservation challenges arising from the geopolitical complexity of the Mediterranean region, along with limited knowledge of some fundamental aspects of the loggerhead sea turtle biology has promoted conservation-oriented research about this species in the region (Margaritoulis et al. 2003, Casale and Margaritoulis 2010). Conservation projects typically involve monitoring nesting activity, mitigating threats in terrestrial and marine habitats, implementing education programs, and collaborating with fisheries (Hochscheid et al. 2018). Over the past 30 years, these efforts have not only prevented the decline of loggerhead populations but also led to an increase in nesting rookeries in the Mediterranean (Casale 2015). However, as mentioned earlier, the current status of the loggerhead turtle in the Mediterranean is entirely dependent on conservation efforts due to persistent threats at sea (Hochscheid et al. 2022 and references therein).

The primary conservation efforts in the Mediterranean Sea have focused on protecting nesting sites in the major nesting areas in Greece, Turkey and Cyprus (Casale and Margaritoulis 2010, Hochscheid et al. 2022). Nonetheless, due to the likely expansion of the nesting range of loggerhead turtles to the western Mediterranean, conservation measures have also been taken at less frequented nesting sites to ensure nest protection and survival in recent years (Báez et al. 2020). The most common conservation measures used to increase survival of loggerhead sea turtle nests at nesting sites are nest relocation or translocation and head-starting programs (Hochscheid et al. 2022). Nest relocation, despite the risk of motion-induced mortality of the developing embryos, is commonly applied to save nests that are at higher risk by one or multiple threats, to reach successful incubation and hatchling production, rather than losing some nests entirely (Venizelos 1989, Demetropoulos 2003, Kornaraki et al. 2006, Tuttle and Rostal 2010, Burke 2015, Revuelta et al. 2015, Hochscheid et al. 2022). However, even in cases where clutches are kept on the beach, several eggs may be moved to an electronic incubator at rescue centers to increase the hatching probability (i.e., Báez et al. 2020). Additionally, after hatching, head-starting programs have been applied as an *ex-situ* conservation strategy that involves the captive rearing of hatchlings for several months prior to their release, to avoid the high mortality rates of sea turtle hatchlings in their first year (Burke 2015, Shaver and Calliouet 2015).

However, preserving sea turtles in nesting areas alone is insufficient without considering other key habitats (Casale and Heppell 2016, Casale et al. 2018). In this sense, several by-catch mitigation measures are being implemented in recent years in the Mediterranean Sea to decrease sea turtle mortality derived from fisheries (Báez et al. 2019). Furthermore, the implementation of marine protected areas (MPAs) has recently increased in the region and, in several instances, the loggerhead turtle has been designated as flag species to support the MPA establishment, since this species is included in the Annex II of the Habitats Directive[1]. Although MPAs were primarily designed to manage fisheries (Weigel et al. 2014), they have proven to be effective in enhancing the status of species and habitats (Guidetti and Sala 2007, Fraschetti et al. 2013). Thus, they are viewed as the primary strategy for the conservation of marine biodiversity, some controversy notwithstanding (García-Charton 2008). However, only 31% of MPAs worldwide are considered effective for marine conservation, as the majority lack the implementation of management plans (Jameson et al. 2002). Consequently, there is still a need to assess the effectiveness of the MPAs for sea turtle conservation.

Despite the various conservation measures that are typically implemented for loggerhead sea turtle conservation, there are several constraints, mainly related to knowledge gaps, which make difficult to apply such measures in an efficient way. For instance, there is limited information about survival probability, habitat use and identification and delimitation of developmental areas during the *lost years*, foraging areas of adults in eastern Mediterranean,

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[1] Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora.

impacts of climate change on biotic and abiotic parameters affecting hatching success and hatchling survival on nesting sites, and about the use of MPAs by loggerheads at different life stages and time scales (Casale et al. 2013, Hochscheid et al. 2018).

1.2 Research justification

Designing and improving conservation measures focused on high-mobile and long-lived species as the loggerhead sea turtle has become one of the most important conservation challenges, not only in the Mediterranean, but worldwide. Therefore, addressing the lack of knowledge, especially about survival and habitat use during different life stages of this species and the effectiveness of the conservation measures taken, is crucial (Casale et al. 2018, Chimienti et al. 2020). In fact, there is still a significant gap in knowledge in understanding the earliest life stages of the loggerhead sea turtle. In particular, the location of oceanic developmental habitats, the most frequently used areas, and the types of movements performed during this stage, are mostly unknown in the Mediterranean basin (Casale et al. 2018). Furthermore, it remains mostly unknown which environmental factors may influence small turtles in reaching their developmental areas after hatching. Previous studies tried do shed some light on these topics (i.e., Soeiro et al. 2022); however, survival estimates, post-hatchling dispersal, high-density areas and habitat suitability for small oceanic juveniles have essentially relied on numerical simulations of particle distribution (Hays et al. 2010, Casale and Mariani 2014, Maffucci et al. 2016, Cardona and Hays 2018).

Another issue of concern is the increasing number of nesting events on the western Mediterranean that have been recorded since 2001 (Carreras et al. 2018 and references therein). Despite much research was done about nest success (Hochscheid et al. 2022 and references therein), there is a massive lack of information about the survival and habitat use of both hatchlings and nesting females out of the usual nesting range in the western Mediterranean. Furthermore, information about high-use areas remains scarce for other life stages and areas. Therefore, identifying accurate survival estimates and highly frequented areas, as well as the influence of environmental conditions on different life stages of the loggerhead sea turtle in the Mediterranean basin, is a key priority for turtle conservation (Casale et al. 2013). Indeed, the case of the nesting females out of the usual nesting range implies a new conservation challenge for the loggerhead sea turtle in a climate change context (Cardona et al. 2022, Hochscheid et al. 2022). Last but not least, it is crucial to evaluate the success of conservation management measures that are commonly implemented for the loggerhead sea turtle, such as the head-starting programs and the establishment of MPAs. Assessing the effectiveness of these measures is essential for improving management strategies and achieving conservation goals for this species.

1.3 Thesis outline

This document is organized in 9 chapters (Figure 1.2). First, this introductory chapter provides an introduction to the research background and justification. Then, the structure of the document is outlined. Chapter 2 presents the aim and objectives of the dissertation. Chapter 3 describes general methodology used in the research. Chapters 4 - 6 consist of edited versions of international scientific publications, which form the core of this dissertation. These chapters are complemented with results published in national and international conferences. Chapter 7 presents new insights and preliminary results that have not yet been published (publications in preparation). Finally, Chapters 8 and 9 provide the general discussion and conclusion of this research, respectively. Bibliographic references are at the end of the document.

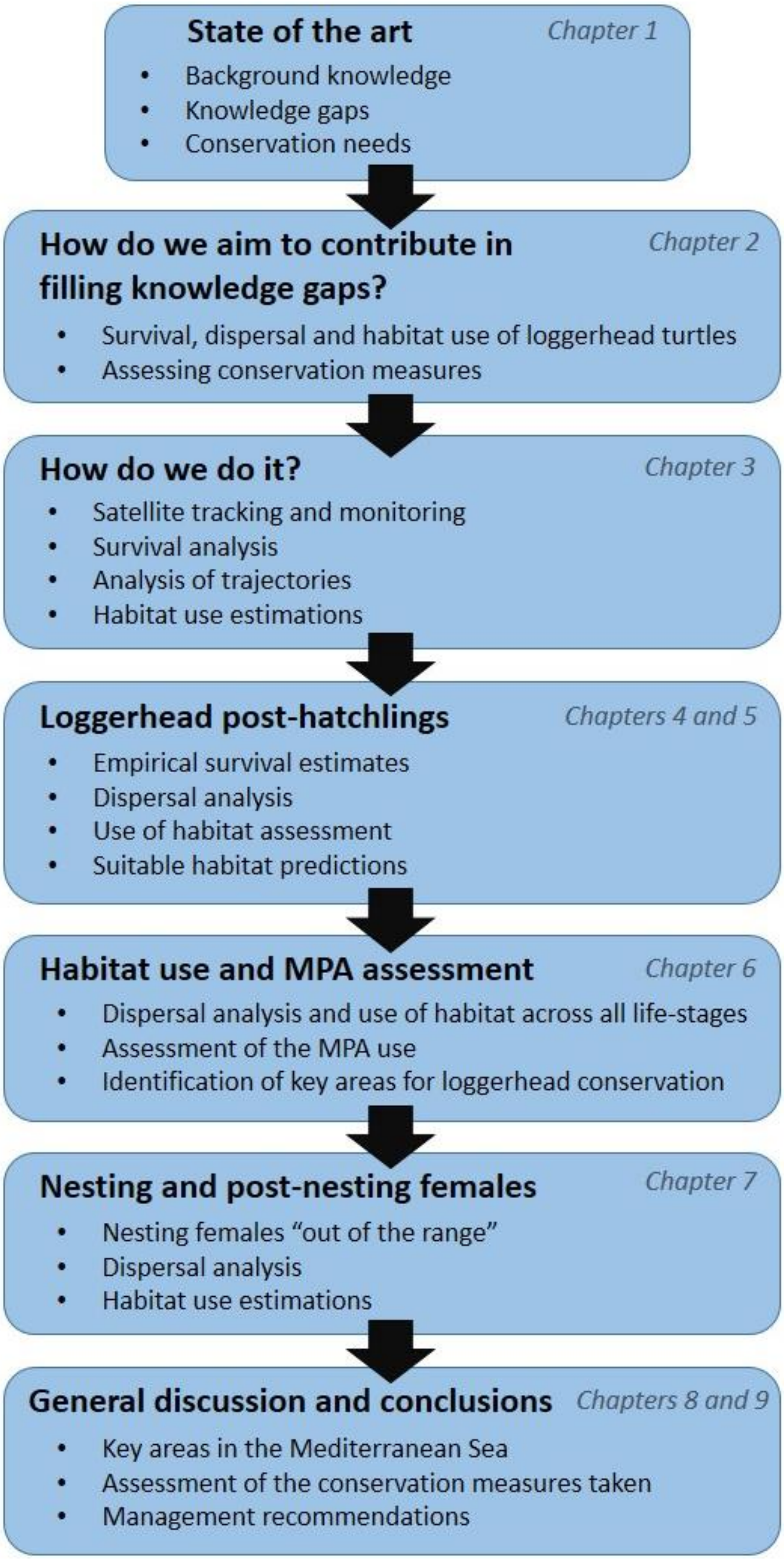

Figure 1.2 Flowchart of the Ph.D. thesis.

1.4 Scientific productions

This document is a compilation of the edited version of international scientific publications produced while developing this thesis. The publications are listed below with the approval of all co-authors. This compilation satisfies the requirements of the Ph.D. in in Animal Production Science and Technology of Universitat Politècnica de València, Spain.

- **Chapter 3**:

Abalo-Morla S, Belda EJ, Tomás J, Crespo-Picazo JL, Marco A, Revuelta O (2022) Satellite-tracking dataset of loggerhead sea turtles tracked from western Mediterranean. Data in Brief, 43: 108432. https://doi.org/10.1016/j.dib.2022.108432

- **Chapter 4:**

Abalo-Morla S, Marco A, Tomás J, Revuelta O, Abella E, Vicente Marco V, Crespo-Picazo JL, Fernández C, Valdés F, Arroyo MC, Montero S, Vázquez C, Eymar J, Esteban JA, Pelegrí J, Belda EJ (2018) Survival and dispersal routes of head-started loggerhead sea turtle (Caretta caretta) post-hatchlings in the Mediterranean Sea. Marine Biology 165:51. https://doi.org/10.1007/s00227-018-3306-2

- **Chapter 5**:

Abalo-Morla S, Muñoz Mas R, Tomás J, Belda EJ (2022) Factors driving dispersal and habitat use of loggerhead sea turtle post-hatchlings and its conservational implications. Marine Biology (under review). https://doi.org/10.21203/rs.3.rs-2660883/v1

- **Chapter 6**:

Abalo-Morla S, Belda EJ, March D, Revuelta O, Cardona L, Giralt S, Crespo-Picazo JL, Hochscheid S, Marco A, Merchán M, Sagarminaga R, Swimmer Y, Tomás J (2022) Assessing the use of marine protected areas by loggerhead sea turtles (Caretta caretta) in the western Mediterranean. Global Ecology and Conservation, 38, e02196. https://doi.org/10.1016/j.gecco.2022.e02196

Regarding the copy-rights for scholarly purposes, chapters 3 to 6 are edited versions of the abovementioned scientific papers, with full acknowledgement of the original publications and without any kind of commercial use. Other scientific publications produced during this research that complement this dissertation:

Peer-reviewed publications:

Mazaris A, Dimitriadis C, Papzekou M, Schofield G, Doxa A, Chatzimentor A, Katsanevakis S, Lioliou A, **Abalo-Morla S** et al. (2023) Priorities for Mediterranean sea turtle conservation and management in the face of climate change. Journal of Env. Management, 339: 117805. https://doi.org/10.1016/j.jenvman.2023.117805

Abalo-Morla S, Tomás J, Revuelta O, Belda E. Inter-nesting and post-nesting behaviour of loggerhead turtle colonizers in Spain (in preparation).

Cardona L, **Abalo-Morla S,** Cani A, Feliu B, Izaguirre N, Tomás J, Belda E. Identifying the foraging grounds of the new loggerhead turtle nesters in the western Mediterranean (submitted to Aquatic Conservation: Marine and Freshwater Ecosystems).

Conference papers:

- ***Poster presentations:***

Abalo-Morla S, Muñoz-Mas R, Tomás J, Revuelta O, Belda EJ (2022) Survival, dispersal strategies and habitat suitability of loggerhead sea turtle (Caretta caretta) post-hatchlings from Spanish nests. 7th Mediterranean Conference on Marine Turtles. Tetouan, Morocco.

Crespo-Picazo JL, Marco V, Belda EJ, Tomás J, **Abalo-Morla S**, Revuelta O, Eymar J, García-Párraga D (2019) Nesting females crawling into the beach: always to lay eggs? International Sea Turtle Symposium. Charleston, South Carolina, USA.

Abalo-Morla S, Crespo-Picazo JL, Tomás J, Merchán M, Eymar J, Marco V, Belda EJ, Revuelta O (2018) Exploring behaviour of loggerhead turtle nesting females in the Spain’s Mediterranean coasts through satellite tracking for clutch protection. Lazar B, Jancic M (eds). 2018. Book of abstracts, 6th Mediterranean Conference on Marine Turtles. Porec, Croatia, pp 68. ISBN: 978-953-6645-83-1

Abalo-Morla S, Tomás J, Fuentes O, Marco V, Belda EJ (2018) A second chance: The transoceanic journey of an amputee loggerhead sea turtle after 10 years in captivity. XV Congreso Luso-Español de Herpetología - XIX Congreso Español de Herpetología. 5-9 September 2018. Salamanca (Spain).

Peñalver-Duque P, León-Muez D, Marco A, Montero S, Gamero M, Baeza-Rojano E, **Abalo-Morla S**, Belda EJ (2018) The journey of Morla, a community experience. XV Congreso Luso-Español de Herpetología - XIX Congreso Español de Herpetología. 5-9 September 2018. Salamanca (Spain).

Abalo-Morla S, Belda EJ, Jonsen I, Marco A, Marco V, Crespo-Picazo JL, Tomás J, Revuelta O (2018) Dispersal patterns of loggerhead sea turtle post-hatchlings in the Mediterranean Basin. 38th Annual Symposium on Sea Turtle Biology and Conservation. 18-23 February 2018, Kobe (Japan).

Abalo-Morla S, Tomás J, Marco A, Marco V, Revuelta O, Crespo-Picazo JL, Belda EJ (2017) Long dispersal and large home ranges of loggerhead post-hatchlings in the Mediterranean basin. The 6th International Bio-Logging Science Symposium. 25-29 September 2017, Konstanz (Alemania).

Abalo-Morla S, Tomás J, Revuelta O, Esteban JA, Eymar J, Crespo JL, Pelegrí-Sebastiá J, Rodilla M, Belda EJ (2016) Survival of reintroduced post-hatchlings loggerheads using satellite monitoring. 36th Annual Symposium on Sea Turtle Biology and Conservation. 29 February - 4 March 2016, Lima (Peru).

- ***Oral presentations:***

Belda EJ, **Abalo-Morla S**, Revuelta O, Crespo-Picazo JL, Marco V, Abella E, Cardona L, Tomás J (2021) Nesting, inter-nesting and post-nesting behaviour of potential new colonizer loggerhead sea turtles in the Spain's Mediterranean coasts studied through satellite tracking. 7th International Bio-logging Symposium. Honolulu, Hawaii. Online.

Abalo-Morla S, Belda EJ, Revuelta O, Sagarminaga R, Cardona L, March D, Swimmer Y, Crespo JL, Marco A, Merchán M, Casquet A, Tomás J (2018) Are Marine Protected Areas (MPAs) an effective conservation measure for the loggerhead sea turtle (Caretta caretta) in the western Mediterranean? Lazar B, Jancic M (eds). 2018. Book of abstracts, 6th Mediterranean Conference on Marine Turtles. Porec, Croatia, pp.42 ISBN: 978-953-6645-83-1

Tomás J, Abella E, **Abalo-Morla S,** Revuelta O, Belda EJ, Marco A (2018) They keep coming: conservation strategies in response to the increasing number of loggerhead sea turtle nesting events in the Spanish Mediterranean. 38th Annual Symposium on Sea Turtle Biology and Conservation. 18-23 February 2018, Kobe (Japan).

Abalo-Morla S, Tomás J, Revuelta O, Crespo JL, Marco A, Belda EJ (2017) Home range estimation for post-hatchlings of Caretta caretta in the Mediterranean Sea. 14th Marine Biological Association Postgraduate Conference. 24–28 April 2017, Penryn (UK).

Abalo-Morla S, Tomás J, Marco A, Revuelta O, Abella E, Esteban JA, Vivas S, Eymar J, Arroyo MC, Crespo JL, Valdés F, Montero S, Belda EJ (2016) First satellite monitoring of head-started post-neonates loggerheads at the Mediterranean Sea. XIV Congreso Luso-Español de Herpetología – XVIII Congreso Español de Herpetología. 5-8 October 2016, Lleida (Spain).

Chapter 2

Aim and objectives

Aim

The approach advocated in this thesis is based on the fact that most information regarding survival, dispersal routes and habitat use of the loggerhead sea turtle along its whole life cycle is mostly unknown for the Mediterranean Sea. The loggerhead sea turtle is currently expanding its nesting range into the western Mediterranean through an ongoing new colonization process. This offers a unique opportunity to elucidate the survival, dispersal routes and habitat use of both loggerhead nesting females out of range and post-hatchlings in the area. There are no previous studies on both satellite-tracked nesting females in the westernmost part of the Mediterranean, nor satellite-tracked post-hatchlings with a size below 35 cm in the whole Mediterranean Sea. Gathering satellite tracking data from different life stages of loggerhead sea turtles could improve not only the development and implementation of appropriate conservation measures, but also the assessment of those measures in force for the species. Therefore, the present thesis aims to contribute in filling the abovementioned knowledge gaps to improve the marine planning strategies for loggerhead conservation in the Mediterranean Sea.

Objectives

The specific objectives of this study are as follows:

1. To provide, for the first time in the Mediterranean Sea, empirical survival estimates of loggerhead turtle post-hatchlings based on satellite-tracking data.
2. To elucidate the dispersal routes and habitat use of the loggerhead sea turtle at different life stages paying particular attention to both post-hatchlings and nesting females on the western Mediterranean as this information is completely unknown.
3. To identify important areas for the loggerhead sea turtle that should be considered for protection based on dispersal and habitat use.
4. To assess the effectiveness of current Mediterranean marine protected areas in achieving loggerhead sea turtle conservation goals.
5. To assess both the effectiveness and the conservation implications of implementing head-starting programs directed to loggerhead hatchlings from nesting events out of the usual nesting range in the Mediterranean.
6. To propose management recommendations based on grounded and updated scientific knowledge that can be considered to update of marine planning strategies.

Chapter 3

General materials and methods

Part of the chapter is an edited version of:

Abalo-Morla S, Belda EJ, Tomás J, Crespo-Picazo JL, Marco A, Revuelta O (2022) Satellite-tracking dataset of loggerhead sea turtles tracked from western Mediterranean. Data in Brief, 43: 108432. https://doi.org/10.1016/j.dib.2022.108432

3.1 Study area

The Mediterranean Sea is the largest and deepest semi-enclosed sea on Earth, with a mean depth of 1,500 meters and a maximum depth of 5,139 meters (Eakins and Sharman 2010). It is connected to the Atlantic Ocean in the west through the 14 kilometer-wide Strait of Gibraltar and to the Sea of Marmara and the Black Sea in the northeast through the Dardanelles (also known as Strait of Gallipoli). Since 1869 the Suez Canal links the Mediterranean Sea to the Red Sea and the Indian Ocean. In the Strait of Sicily, a shallow ridge at a depth of 400 m separates the island of Sicily from the coast of Tunisia, dividing the sea into two main sub-basins: the western Mediterranean and the eastern Mediterranean (Coll et al. 2010). Each sub-basin includes several regions which were considered in the present thesis: the Alboran Sea, the Algerian basin, the Balearic Sea, the Gulf of Lion, the Ligurian Sea and the Tyrrhenian Sea in the western Mediterranean basin, and the Sicilian Channel, the Adriatic Sea, the Ionian Sea, the Aegean Sea and the Levant Sea in the eastern basin (Figure 3.1).

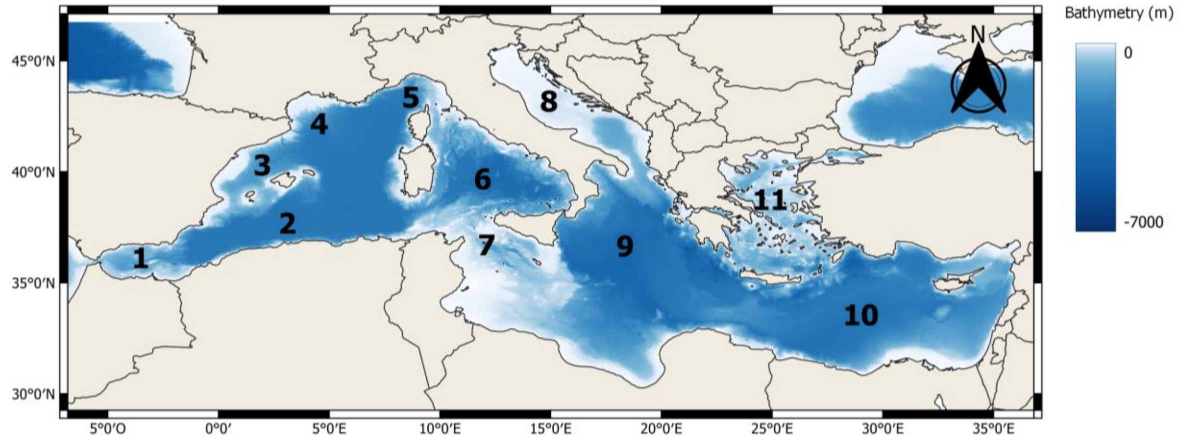

Figure 3.1 Regions of the Mediterranean Sea. On the western basin: 1) Alboran Sea, 2) Algerian basin, 3) Balearic Sea, 4) Gulf of Lion, 5) Ligurian Sea, and 6) Tyrrhenian Sea. On the eastern basin: 7) Sicilian Channel, 8) Adriatic Sea, 9) Ionian Sea, 10) Levant Sea, and 11) Aegean Sea.

The Mediterranean Sea has many narrow continental shelves (with some several exceptions as in the Aegean and Adriatic Seas and in the coast of Tunisia), and a large area of open sea, thus is classified as deep sea. Steep slopes, numerous submarine canyons and seamounts are characteristics of the Mediterranean Sea, particularly in its northern regions (Sarda et al. 2004). Overall, the basin is characterized by strong environmental gradients among sub-basins (Danovaro et al. 1999). The geophysical characteristics of the Mediterranean Sea offer a particular oceanic circulation (Figure 3.2) partly controlled by the density gradient and sea level differences between the Atlantic Ocean and the Mediterranean Sea. Evaporation, which is higher in the eastern basin, causes the water level to decrease and salinity to increase from west to east. The resulting pressure gradient pushes relatively cool, low-salinity water from the Atlantic across the Mediterranean basins. This water warms up to the east, where it becomes saltier, and then sinks in the Levantine Sea before circulating west and exiting through the Strait of Gibraltar (Pinardi and Masetti 2000, Testor et al. 2005). In addition to this important sea surface temperature gradient, the annual mean sea surface temperature shows high seasonality (Coll et al. 2010). Biological production also shows seasonal cycles with winter and spring blooms of phytoplankton (Bosc et al. 2004, Longhurst 2007). This biological production also shows a gradient across the sea basin as it decreases from north to south and west to east, which is more oligotrophic, and is inversely related to the increase in temperature and salinity (Pujo-Pay et al. 2011). Indeed, the Alboran Sea is a high-productivity area compared to the rest of the oligotrophic Mediterranean basin due to the input of rich Atlantic waters (Pinardi and Masetti 2000) and the permanent upwelling zone in the northwestern part of the Alboran Sea along the Spanish coast (Skliris and Beckers 2009). Moreover, regional features may enrich coastal areas through changing wind conditions, temporal thermoclines, currents and river discharges (Bosc et al. 2004, Tanhua et al. 2013).

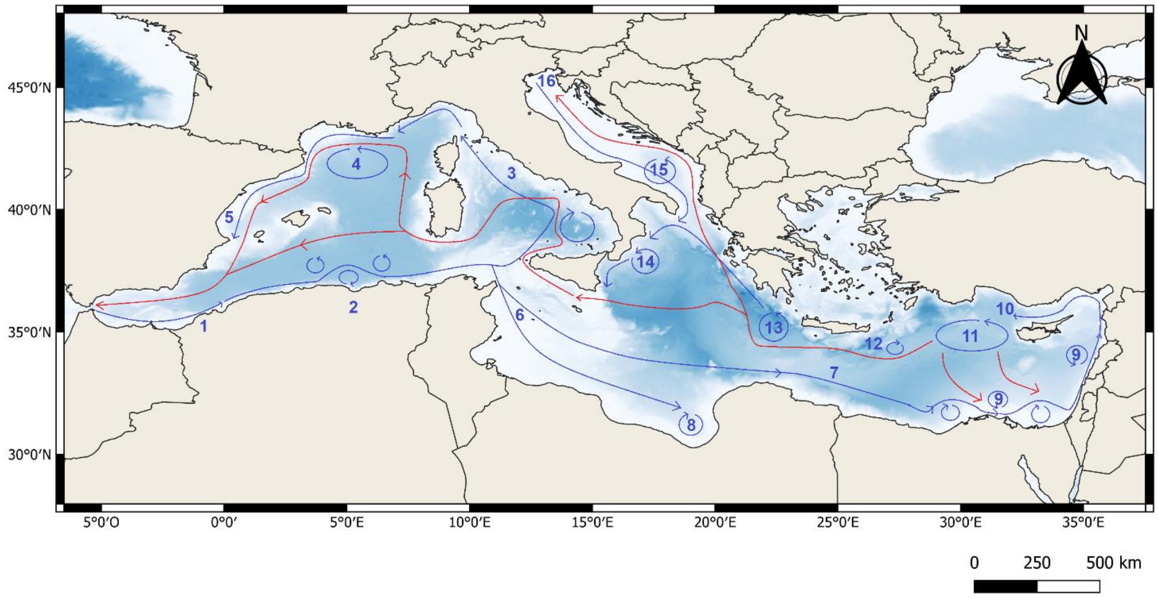

Figure 3.2 Main currents in the Mediterranean Sea. Blue arrows represent the surface currents and red arrows represent the deep water circulation. 1) Inflows of the Atlantic Ocean, 2) Algerian Current and eddies, 3) Tyrrhenian cyclonic circulation, 4) Lions Gyre, 5) Ligurian-provencal Current, 6) Atlantic Ionian Stream, 7) Mid-Mediterranean Jet, 8) Anticyclone in the Gulf of Syrte, 9) Shikmona and Mers a-Matruh gyres, 10) Cicilian and Asia Minor Current, 11) Rhodes Gyre, 12) Iera-Petra Gyre, 13) Pelops Gyre, 14) Western Ionian Gyre, 15) Southern Adriatic Gyre, 16) Western Adriatic Coastal Current. Adapted from Pinardi and Masetti (2000).

3.2 Data collection

3.2.1 Satellite tagging and monitoring

Data collection was performed by satellite-tagging loggerhead sea turtles of various sizes. In addition, for Chapter 6, we used our own collected data supplemented with datasets that are freely accessible and unpublished data, as described in Annex 1, which provides information on the origin of the data and other pertinent details about the dataset used in this thesis. Dataset summary information is shown in Table 3.1.

Table 3.1 Dataset summary information of satellite-tracked loggerhead sea turtles. Life stage, turtle size measured as Straight Carapace Length (SCL) in centimeters, turtle origin (whether they were collected directly from a nest, caught as by-catch, caught by hand at sea, or after a nesting event), range of deployment years and range of tracking years are shown.

Life stage	Size	Turtle origin	Deployment years	Tracking years
Post-hatchlings (*n* = 27)	Less than 24 cm SCL	Nest	2015 - 2017	2015 - 2019
Early juveniles (*n* = 10)	Between 24 - 40 cm SCL	Nest, by-catch or by hand	2003 – 2018	2003 - 2019
Late juveniles (*n* = 59)	Between > 40–70 cm SCL	By-catch or by hand	2003 – 2018	2003 - 2019
Adults (*n* = 21)	More than 70 cm SCL	By-catch, by hand on sea or after nesting event	2008 - 2022	2008 – 2022

Regarding to our own gathered data, each turtle was measured and weighed (if possible) before tag attachment, and additional information such as the type of capture, sex (if known), and nest location, among others, were recorded. The life stage of each turtle was classified based on the Straight Carapace Length (SCL) with post-hatchlings being those with SCL < 24 cm, early juveniles with SCL between 24 and 40 cm, late juveniles with SCL > 40–70 cm, and adult turtles with SCL > 70 cm, according to literature about loggerhead turtles in the Mediterranean (Casale et al. 2018 and references therein).

Post-hatchlings (*n* = 27) were collected from three different nesting events occurred on the Spanish Mediterranean coast over the period (2014 – 2016) (see Chapters 4 and 5). These individuals were aged from 9 to 13 months old. In addition, two two-year old turtles (22 months old) collected from another nest laid in the Mediterranean Spanish coast in 2014, considered as post-hatchlings in Chapter 4, but considered as early juveniles in Chapter 6 due to their age and size ≥ 24 cm SCL (see Clutch D in Annex I). Phenological information about these nests can be found in Hochscheid et al. (2022) and references therein. After being raised at a recovery center, post-hatchlings were tagged ensuring that satellite tags did not hinder behaviour or turtle growth movements (Mansfield et al. 2012). Juveniles (*n* = 69) were collected from: i) from fisheries by-catch or entanglements with drift nets (*n* = 24), ii) caught by-hand (*n* = 43), and iii) from nest (*n* = 2, see above references for Clutch D) (see Chapter 6). Adults (*n* = 21) were collected from: i) fisheries by-catch or entanglements (*n* = 4), ii) caught by-hand (*n* = 9) and iii) after nesting events (either successful or attempts) in the Mediterranean Spanish coast (*n* = 8). In these last cases, to avoid disturbance of the nesting behavior, tags were applied after nesting when turtles were heading back to sea (see Chapters 6 and 7). Only one female was tagged after being in a rescue center, where it was taken after following stranding protocol.

By-caught or entangled turtles were satellite-tagged and released immediately after capture or, if necessary, after they fully recovered at rescue centers to minimize the possibility of being compromised. Several data used to perform some analysis in the present thesis were obtained from publicly available datasets, as described in Annex I. Depending on life stage and availability of satellite tags, different types of satellite tags were attached to carapace of the loggerhead turtles according to size and stage of development, as detailed in Annex I. In this thesis: i) all solar-powered platform transmitter terminals (PPT-tags) without duty cycle[2] were attached (mostly to post-hatchlings) using an acrylic–silicone–neoprene attachment method adapted from Mansfield et al. (2012) (Figure 3.3A), which is described in Chapter 4, ii) all battery-powered SPOT and SPLASH tags were attached mainly to juvenile and adult turtles' carapaces using epoxy resin (Figure 3.3B), and iii) all solar-powered POP-UP tags were attached to juveniles at the edge of the most posterior scales using a nylon line through a drill-hole (Figure 3.3C). POP-UP tags remain attached to the turtles' carapace until the turtle dies, which is set by introducing a detachment order when temperature and depth parameters suddenly drop. In all cases, turtles were released near their capture location, if possible.

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[2] A duty cycle is the fraction of one period of time, commonly expressed as a percentage or a ratio, in which a signal or system is active.

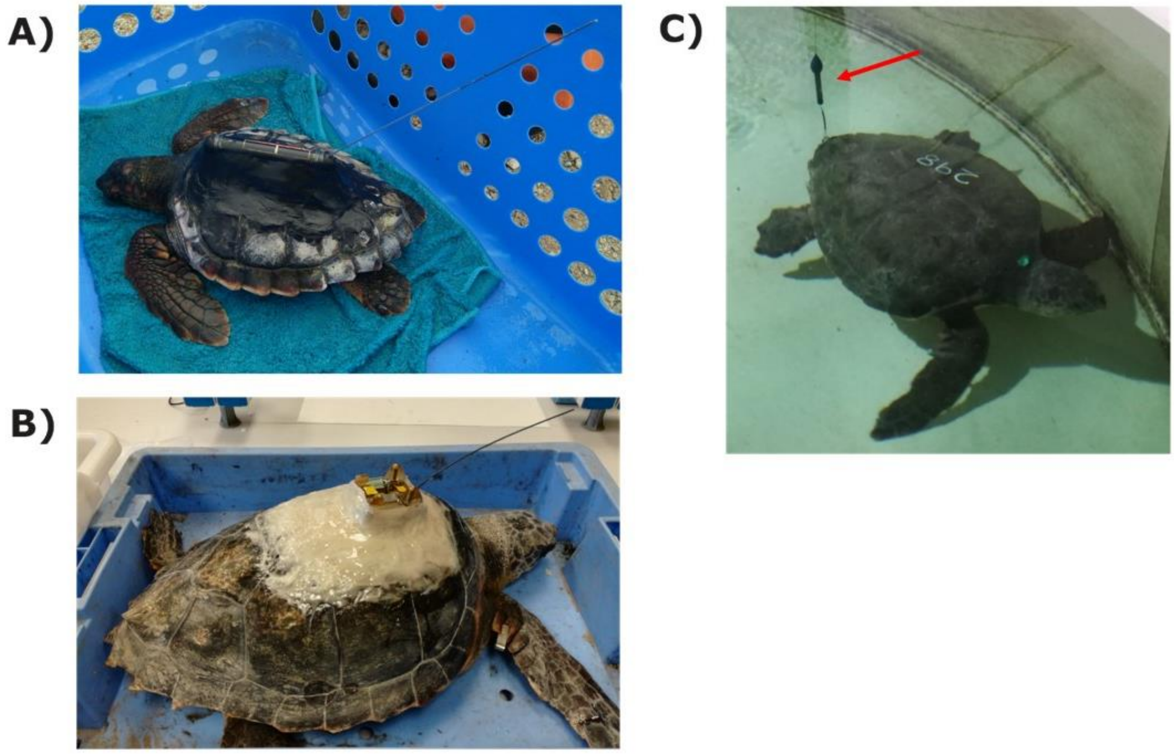

Figure 3.3 Types of satellite-tags and attachment methods used to tag loggerhead sea turtles in the present thesis: A) Solar-powered platform transmitter terminal (PPT-tag) attached on a post-hatchling by using acrylic, neoprene and silicone, B) Battery-powered tag attached on a juvenile by using epoxy resin, and C) Solar-powered POP-UP tag attached on a juvenile by using a nylon through a drill-hole.

Location data for our satellite-tracked turtles were collected during 2015–2022 until transmission stopped. As mentioned above, to perform several analyses our own data were complemented with free-access data and ceded unpublished data collected during 2003-2018 (see Annex I). In all cases, data were collected using the Argos system, which classifies locations into seven classes of decreasing accuracy (3, 2, 1, 0, A, B, Z) (CLS 2016).

Location data were post-processed to deal with outliers. In Chapter 4, high-speed and land locations were filtered and a Douglas Argos-filter algorithm (DAF) was performed. In Chapters 5 to 7, hierarchical State-Space Models (SSMs) were used to estimate daily or sub-daily positions from the observed data by accounting for measurement errors and variability in movement dynamics (Jonsen et al. 2005, 2007, 2013). Additionally, in Chapter 7 a behavioural state was assigned to each location. The detailed methodology is explained in the corresponding Chapters.

3.2.2 Environmental data

Environmental data was gathered from free-access available data sources as detailed in Table 3.2. Bathymetry data was obtained from the Satellite Tracking and Analysis Tool (Coyne and Godley 2005) in Chapter 4, and using the 30 arc-second resolution GEBCO global bathymetric model in Chapters 5 to 7 (GECBO 2014, 2015, Weatherall et al. 2015). Environmental data about ocean currents, salinity, sea surface temperatures, sea surface height (SSH) (Escudier et al. 2020), chlorophyll-a and primary productivity (Bolzon et al. 2019, Salon et al. 2019, Cossarini et al. 2021, Feudale et al. 2021, Teruzzi et al. 2021) were obtained at 1/24° of horizontal grid resolution from Copernicus Marine Environment Monitoring Service (https://marine.copernicus.eu). Earth magnetic anomaly grid at 2 arc-minute-resolution was obtained from National Oceanic and Atmospheric Administration of United States of America (NOAA) (Meyer et al. 2017).

Table 3.2 Environmental datasets used in this thesis. Type of environmental data, data source (CMS: Copernicus Marine Service, GEBCO: General Bathymetric Chart of the Oceans, or NOAA: National Oceanic and Atmospheric Administration of United States of America), spatial resolution, temporal coverage, temporal resolution, related thesis' chapter and dataset reference. Note: arc-second and arc-minutes are a units of measurement of angles in geometry, or units of angular measurement.

Environmental data type	Data source	Spatial resolution	Temporal coverage	Temporal resolution	Related Chapters	Dataset reference
Temperature Sea current velocity Salinity Sea surface height	CMS	1/24° (≈4 km)	from 01-01-1987 to present	Daily	Chapter 5	Escudier et al. (2020)
Phytoplankton Chlorophyll-a Primary production	CMS	1/24° (≈4 km)	from 04-05-2019 to present	Daily	Chapter 5	Salon et al. (2019) Feudale et al. (2021)
			from 01-01-2017 to 31-05-2019	Daily	Chapter 5	Bolzon et al. (2019)
			from 01-01-1999 to present	Daily	Chapter 5	Cossarini et al. (2021) Teruzzi et al. (2021)
Bathymetry	GEBCO	30 arc-second (≈1 km)	-	-	Chapter 6	GEBCO (2014) Weatherall et al. (2015)
					Chapters 5, 7	GEBCO (2021) Weatherall et al. (2015)
Earth Magnetic Anomaly	NOAA	2 arc-minute (≈3.5 km)	-	-	Chapter 5	Meyer et al. (2017)

3.3 Data analysis

3.3.1 Survival

In Chapters 4 and 5, we assessed the daily survival probability of sea turtles using capture–recapture models for open populations based on the Cormack–Jolly–Seber (CJS) model approach (Lebreton et al. 1992) using software Mark 7.1 (White and Burnham 1999). In this way, the survival probability (*Φ*) can be estimated independently of recapture probability (*p*) (Figure 3.4, Lebreton et al. 1992). Capture–recapture data were obtained from Argos messages and tracks information during 90 days from release (day 0). Days with no Argos message were coded as "not captured".

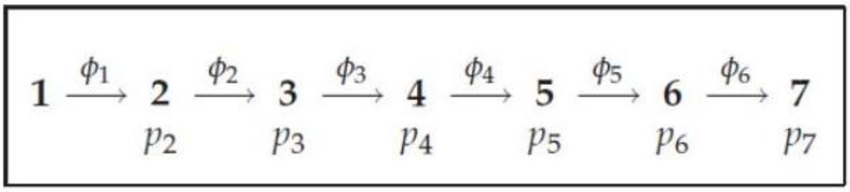

Figure 3.4 Cormack–Jolly–Seber (CJS) model approach, where numbers 1 to 7 are "capture" occasions, Φ are survival probabilities among capture occasions and *p* are recapture probabilities.

The goodness-of-fit test (GOF) of the CJS model was performed using U-CARE (Choquet et al. 2009). This was done to explore the fit of the CJS model to the data, and to identify a general model from which to start a suitable model selection. Trap dependence was analyzed following Pradel (1993). We used a linear model approach and a logit-link function to evaluate several models. The *a priori* set of models included different effects such as time dependence in survival or recapture, several trends (constant, linear, exponential, logarithmic and half-normal) in survival and/or recapture, differences in survival between months or trap-dependence effects on recapture. Model selection was based on the corrected Akaike's information criterion (AICc) (Burnham and Anderson 1998). We considered that models with a difference in AICc of less than two units were similarly supported by the data (Burnham and Anderson 1998). As we were mainly interested in survival, we first modeled recapture probabilities. Once we had the best model for recapture probability, we modeled survival. To compare survival among nests, we started from the best model previously selected. Covariates as nest origin, use of region and use of habitat were included in the models. Finally, we tested for significant difference in survival estimates between clutches with Contrast software (Hines and Sauer 1989).

3.3.2 Analysis of trajectories

A trajectory is made of successive steps traveled by an organism in the geographical space. These steps (the line connecting two successive relocations) can be described by a certain number of descriptive parameters (i.e., relative angles between successive steps, length of the step). One aim of the trajectory analysis is to identify the structure of the trajectory, for example, the parts of the trajectory where the steps have homogeneous properties. Indeed, homogeneous steps could help us to identify a variety of animals' behaviours (i.e., feeding, traveling, escape from a predator) (Calenge 2006, 2022). In this thesis, trajectories were analyzed in Chapters 4, 5 and 7, by using 'adehabitatLT' package (Calenge 2006, 2022) in R version 3.3.1 (R Core Team 2017). To identify movement phases, we segmented trajectory into segments characterized by a homogeneous behaviour by using the method of Gueguen (2000, 2009). This approach relies on a Bayesian partitioning of a sequence (which implies the Monte Carlo simulation of the independence of the steps in the trajectory), where positive autocorrelation in any of the descriptive parameters may mean that the animal behaviour is changing with time. Therefore, we may segment the trajectory of the animal into homogenous segments by finding both the number and the limits of the segments building up the trajectory, based on a given set of a priori Markov models (Figure 3.5, Calenge 2015). Independence of the residuals of the trajectory segmentation was tested using the Wald and Wolfowitz test, which tests the sequential autocorrelation. The null hypothesis is that residuals are independent and equally distributed (Wald and Wolfowitz 1943). Therefore, a p-value above 0.05 will confirm that the residuals of the segmentations are independent and, hence, the validity of the approach.

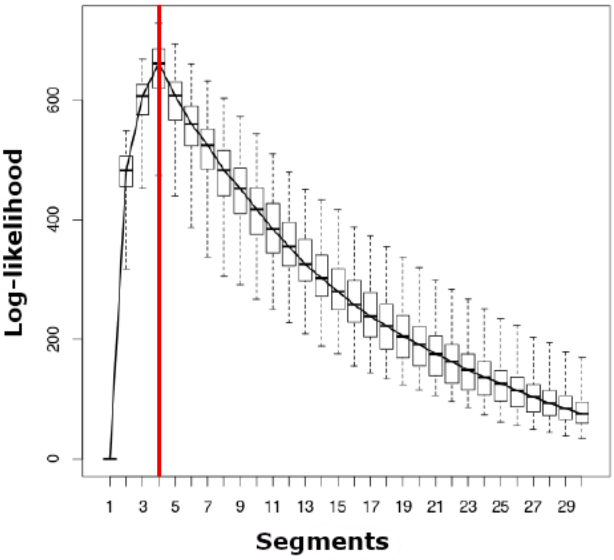

Figure 3.5 Example graph presenting the value of the log-likelihood (y) that the trajectory is actually made of *k* segments (x). Vertical straight red line indicates de number of segments that are a reasonable choice to compute segmentation in this example. Adapted from Calenge (2015).

Furthermore, orientation analyses were performed using 'circular' and 'CircStats' R-packages (Agostellini and Lund 2017). We computed the mean orientation followed by tracked turtles along the monitoring period. Additionally, we tested the significance of each circular mean through the Rayleigh's test of uniformity (Jammalamadaka and SenGupta 2001). If resultant p-value is under 0.05, implies that mean orientation obtained is significantly different from a random distribution. In Chapters 4 and 5 we tested the uniformity of distribution of the orientation among clutches, individuals and release dates using the Mardia–Wheeler–Watson's test for homogeneity on two or more samples of circular data (Batschelet 1981). In this case, a p-value less than 0.05 implies that the distribution of the circular data among groups are statistically different.

3.3.3 Habitat use analyses

Post-processed state-space model (SSM) locations were used to estimate the loggerhead turtle home ranges from our data in Chapters 6 and 7 (Hoenner et al. 2012, Pendoley et al. 2014, Queiroz et al. 2019). A home range is theoretically defined as the area in which an animal conducts its daily activities, and excludes atypical migrations or unpredictable movements (Worton 1989). We used the utilization distribution (UD) to define the spatial extent of an animal's home range and measure the spatial intensity of use. The core areas of UDs are high-use areas defined as portions of the home range that exceed equal-use patterns (Samuel et al. 1985). Kernel Utilization Distribution (KUD) (Worton 1989) was computed in Chapter 6 using the 'adehabitatHR' package in R (Calenge 2006), with the reference bandwidth as a smoothing parameter (Christiansen et al. 2016, Dujon et al. 2018). Whole home range areas were identified using KUD up to the 95% contour levels. Core areas were identified using KUD at two different levels, set up at 50% and 25% KUD (Powell 2000). In Chapter 6, KUD areas were estimated for the whole tracking dataset and for each life stage throughout the monitoring period (Lockhart and Barco 2015). Then, the terrestrial area that overlapped with home ranges areas was excluded from the home range estimations using QGIS 2.18.0 (QGIS Development Team 2019). In Chapter 7, 50% KUD areas were computed for each tracked loggerhead female, by using the Brownian Bridge Kernel method (Horne et al. 2007). In this case, the first month after tagging was analyzed separately as nesting females may present different behaviour during the nesting season. In both Chapters 6 and 7 home range results were plotted on maps of the Mediterranean Sea (Figure 3.6).

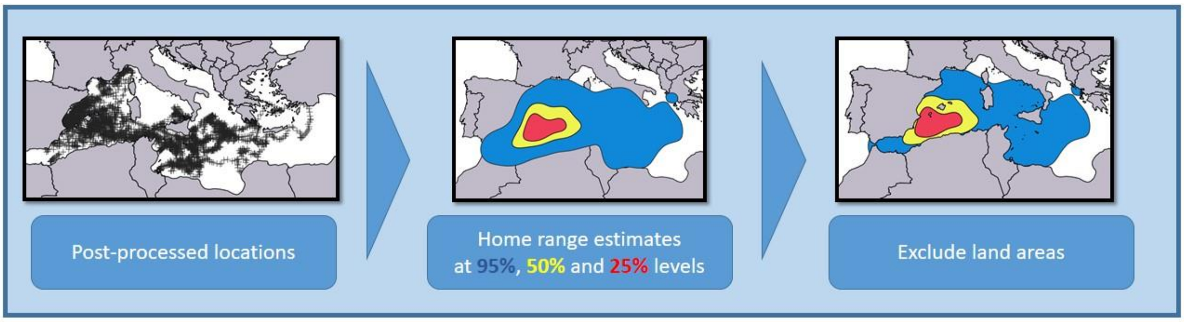

Figure 3.6 Workflow on computing home range estimates.

However, in Chapter 6 the habitat-use maps obtained from the tracking data are likely biased towards the tagging site. To address biases associated with variable track lengths and shorter tracks near the tagging location, we applied a time weighting procedure to compute less biased relative density estimates (Block et al. 2011, Queiroz et al. 2019). Following Queiroz et al. (2019), each daily location estimated for each individual was weighted by the inverse of the number of all individuals with location estimates for the same relative day of their track. Location weights after a threshold day of the number of tracking day were fixed equal to the weight on the day corresponding to the 85th percentile of track lengths in order to minimize bias in lower sample sizes (Queiroz et al. 2019). In this way, individual location estimates closer to the deployment location tended to receive a lower weight than later locations. All individuals contributed equally to the described global spatial density patterns because their weights were normalized so that they summed to 1. Hotspots were defined as areas within the upper 75% percentile of weighted daily location density. Relative density maps were obtained at a 0.25° x 0.25° grid-cell for i) the whole tracking dataset, and ii) each life stage throughout the monitoring period for Chapter 6 (see Chapter 6 for more detailed methods).

In Chapter 6 to analyze the use of Mediterranean MPAs by loggerhead sea turtles, the post-processed SSM turtle location point data were overlapped over the Marine World Database on Protected Areas (Revuelta et al. 2015, IUCN and UNEP-WCMC 2020). Furthermore, a residency index was estimated by dividing the number of days in which a turtle was detected within MPA boundaries by the total number of days that the turtle was monitored (Mason and Lowe 2010, Revuelta et al. 2015).

In Chapter 5, the species distribution was modelled with decision-trees to determine the areas of maximal suitability for post-hatchlings. Through this machine learning technique (Elith et al. 2008), classification trees are built using random subsets of the data (Figure 3.7).

Each decision-tree is fit to a bootstrap sample[3] of the observations, and the best split at each node is selected based on a randomly-chosen subset of predictor variables. Regression trees are used for response variables consisting of continuous data and classification trees for factor variables. For classification with presence-absence response data, decision trees can be used to predict the probability of a species' presence in non-sampled areas by identifying areas with similar environmental conditions (Kenchington et al. 2016, Valavi et al. 2021).

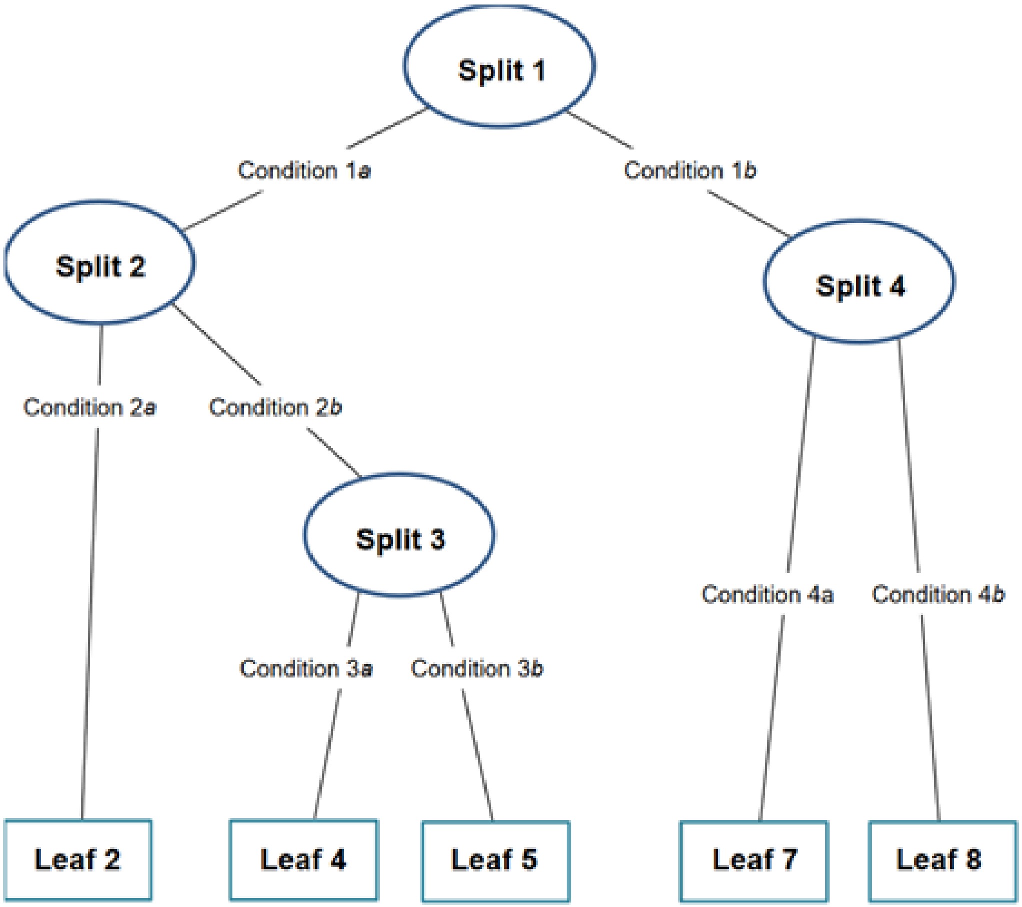

Figure 3.7 Example of a regression model tree. Split 1 is the root node, which represents the entire sample. A node that gets divided into sub-nodes is known as Parent Node (i.e., Split 2), and these sub-nodes are known as Child Nodes (i.e., Split 3). Leaf nodes do not have any child node and represent the Model. Splitting conditions are the subset of predictor variables in which data partitions are based. Adapted from Kuhn and Johnsen (2013).

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[3] A bootstrap sample is a smaller sample that is derived from a larger sample. Bootstrapping is a type of resampling where large numbers of smaller samples of the same size are repeatedly drawn, with replacement, from a single original sample.

Extrapolation of model predictions to areas outside of the range of data observations may produce unreliable predictions in those areas (Elith et al. 2010). When extrapolating outside the domain of the training data, where different physical conditions from those used to train the model likely exist, random forest models predict the same value as they would for the closest value in the tree for which they had training data (Breiman et al. 1984, Kenchington et al. 2016). Our approach modelled species distribution with C5.0 decision-trees (Quinlan 1992) by employing the environmental conditions associated to the turtles' presence (satellite-tracking data) and a randomly generated set of pseudo-absences to discriminate between them (Hazen et al. 2021). Pseudo-absences were generated as random walks based on the collected satellite-tracking data (Hazen et al. 2017, 2021). This analysis was done by using the 'C50' and 'COREIearn' R-packages (Kuhn et al. 2015, Robnik-Sikonja and Savicky, 2017) following Muñoz-Mas (2016, 2019) (see Chapter 5 for detailed methods).

Chapter 4

Survival and dispersal strategies of loggerhead post-hatchlings in the Mediterranean Sea

Edited version of:

Abalo-Morla S, Marco A, Tomás J, Revuelta O, Abella E, Vicente Marco V, Crespo-Picazo JL, Fernández C, Valdés F, Arroyo MC, Montero S, Vázquez C, Eymar J, Esteban JA, Pelegrí J, Belda EJ (2018) Survival and dispersal routes of head-started loggerhead sea turtle (*Caretta caretta*) post-hatchlings in the Mediterranean Sea. Marine Biology 165:51. https://doi.org/10.1007/s00227-018-3306-2

4.1 Introduction

In recent years, several loggerhead sea turtle (*Caretta caretta*) nesting events have been recorded in the western Mediterranean basin, outside the known nesting range in the Mediterranean Sea (Tomás et al. 2008a, Maffucci et al. 2016). Western Mediterranean nests may indicate that the species is exploring new locations to expand its nesting range (Maffucci et al. 2016). However, nothing is known yet about the survival and dispersal of post-hatchlings from these nests.

There is no evidence of supported nesting events in the past years. Nonetheless, despite the lack of scientific reports and nesting surveys, loggerhead nesting outside its range was sporadically reported in the western Mediterranean during the 20th century (Tomás et al. 2008). The increasing occurrence of these nesting events in the western Mediterranean may be a consequence of the higher sea temperatures recorded in recent decades (Witt et al. 2010a, Maffucci et al. 2016). Warmer temperatures during interglacial periods also seem to have facilitated the expansion of loggerhead turtles into higher latitudes (Bowen et al. 1993, Clusa et al. 2013). The warmer temperatures may also, hypothetically, imply the disappearance of the traditional nesting areas (Greece, Turkey, Cyprus, and Libya) in future (Hays 2000, Casale and Margaritoulis 2010). Therefore, colonization of new areas may be an important outcome for a threatened species (Wyneken and Lolavar 2015, Abella et al. 2016) like the loggerhead sea turtle, which IUCN considers ‘Vulnerable’ (Casale and Tucker 2015). These new nesting events may contribute to both the Mediterranean subpopulation, and the North Atlantic subpopulations (Revelles et al. 2007b, Clusa et al. 2014). Previous genetic analysis shows that hatchlings from the western Mediterranean basin have Atlantic and Mediterranean genotypes (Carreras et al. 2015).

Although several western Mediterranean nests have produced successful clutches (Tomás et al. 2008a, Maffucci et al. 2016) nothing is known about the dispersal behaviour and survival rates of the post-hatchlings from these nests. After hatching, young turtles crawl into the sea and swim offshore and are rarely observed until they return to coastal waters as larger juveniles. The time gap after young turtles hatch and head to sea, where they remain at a surface-pelagic or oceanic stage before returning to coastal waters as large juveniles, is referred to as the *lost years* (Carr 1987, Bolten 2003).

Few studies have tracked the dispersal movements of sea turtles during the *lost years*. Recent advances in satellite tags have allowed research in this area. For the rookeries in the Atlantic (Hays and Marsh 1997, Monzón-Argüello et al. 2012, Putman et al. 2012a, b, 2015, Putman and He 2013, Mansfield et al. 2014, 2017, Lamont et al. 2015) and Pacific oceans (Okuyama et al. 2011, Kobayashi et al. 2014, Briscoe et al. 2016, Christiansen et al. 2016) dispersal routes of young loggerhead post-hatchlings (< 2 years old) are starting to be elucidated by tracking, modeling or laboratory-based methods. However, for the Mediterranean Sea this information is lacking. There are some theoretical models for the rookeries at Greece and Italy (Hays et al. 2010, Luschi and Casale 2014, Casale et al. 2015, Maffucci et al. 2016). Cardona and Hays (2018) analyzed the tracks of young pelagic satellite tagged loggerheads (straight carapace length (SCL) ranged 41.2 to 68.5 cm) to assess their movements and the influence of currents in the Mediterranean Sea. Nonetheless, there are no previous studies based on post-hatchling tracked animals with size below 35 cm SCL, that is to say, younger than 2 years old (Bjorndal et al. 2000, Casale et al. 2009, 2011). Such information is relevant to assess the dispersal routes of loggerhead turtle post-hatchlings in the Mediterranean Sea since their routes may take them to unsuitable areas for their survival, that is, areas where low temperatures persist (Maffucci et al. 2016). Some authors support that directional swimming, even by small turtles, can influence their oceanic movements and may lead to hatchling distribution patterns that differ from the models (Putman et al. 2011, 2012a, b, Lohmann et al. 2012, Scott et al. 2012, Kobayashi et al. 2014, Mansfield et al. 2014, 2017, Christiansen et al. 2016). Thus, assessing the movement patterns of post-hatchlings would help to understand their behaviour and ecology and to design effective conservation strategies (Hays et al. 2016).

Most nesting events recorded in Spain have been found in touristic beaches, consequently, egg development and hatchling survival are threatened by human activities, as observed in other Mediterranean areas (Venizelos 1989, Demetropoulos 2003). Thus, management measures like nest relocation and head-starting programs were taken to protect Spanish clutches, as recommended in other areas (Kornaraki et al. 2006, Tuttle and Rostal 2010, Burke 2015, Revuelta et al. 2015). The head-starting program is an *ex-situ* conservation strategy that involves the captive rearing of hatchlings for several months. The objective of this strategy is to avoid the high mortality rates of sea turtle hatchlings in their first year (Burke 2015).

The head-starting technique is a frequent way of enhancing wildlife populations (Pritchard 1980, Heppell et al. 1996, Mestre et al. 2014, Burke 2015). There is evidence that head-started sea turtles can survive to adulthood and contribute to nesting events (Bell and Parsons 2002, Shaver and Rubio 2008). Nevertheless, head-starting programs might not always be as successful as expected, since several constraints like behavioural anomalies, lower growth rates or illness during the captivity period may limit the survival of post-hatchlings before and after release into the wild (Swingle et al. 1994, Heppell 1998, Addison and Nelson 2000, Cardona et al. 2012b). Evaluating the success of head-starting programs in sea turtles is challenging due to their long age to maturity (Burke 2015). One approach to assessing the short-term success of these programs is to evaluate the survival rate of reintroduced post-hatchlings during the first few months after release when their prospects of survival are expected to be the lowest (Armstrong and Seddon 2008). However, assessing the survival of post-hatchlings directly is challenging, and one of the major gaps in our knowledge of sea turtle population dynamics (Bolten 2003, Hazen et al. 2012, Casale et al. 2015).

In the study related to the present chapter, we satellite-tracked head-started loggerhead post-hatchlings to analyze and describe their dispersal routes and survival for the first time in the Mediterranean basin.

4.2 Methods

4.2.1 Turtle data and satellite tagging

Loggerhead post-hatchlings were collected from three nests (Clutch A (*n* = 8), Clutch B (*n* = 9) and Clutch D (*n* = 2) along Spain's Mediterranean coast (Figure 4.1). All hatchlings were reared in a head-starting program (see details in Table 4.1).

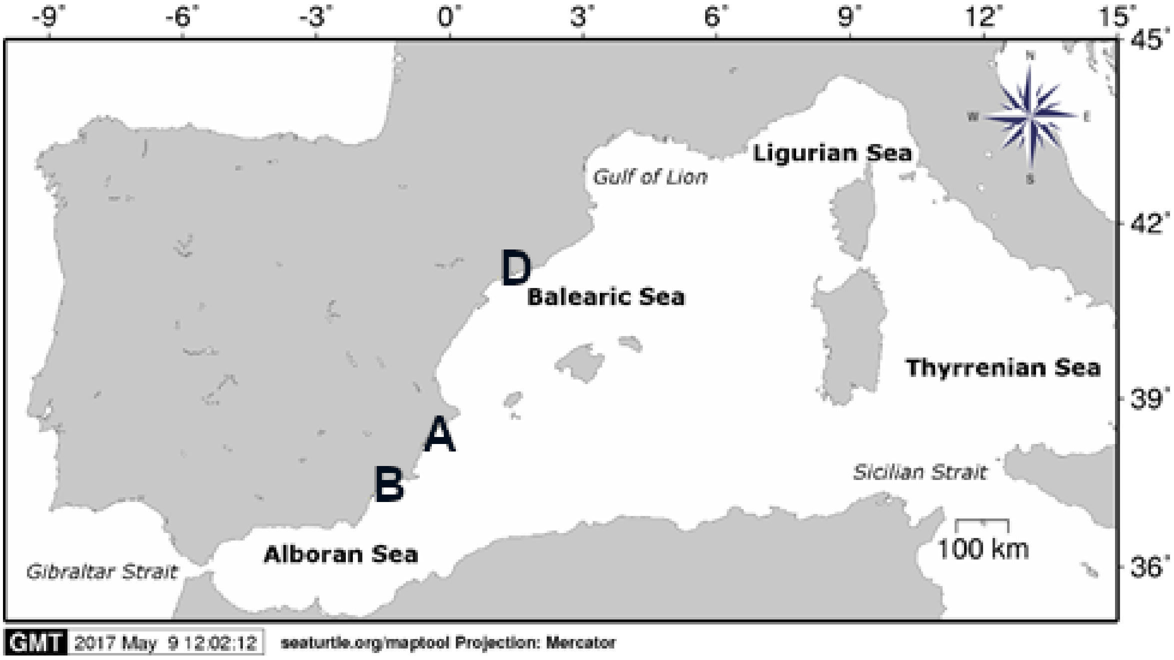


Figure 4.1 Nesting locations. Clutch A, *n* = 8, (Alacant, Spain) [38.37 ° N, 0.41 ° W], Clutch B, *n* = 9, (Almería, Spain) [37.38 ° N, 1.64 ° W] and Clutch D, *n* = 2, (Tarragona, Spain) [41.13 ° N, 1.30 ° E]. Map obtained with SeaTurtle Maptool (www.seaturtle.org/maptool).

Individuals from Clutch A suffered from a parasitic outbreak of the copepod *Balaenophilus manatorum* (Domènech et al. 2015, Crespo-Picazo et al. 2017) and spirorchiid blood fluke *Amphiorchis* sp. (Cribb et al. 2017) infections during the head-starting period. After the head-starting period, which lasted from 9 to 22 months, 19 post-hatchlings were selected based on appropriate size for tagging and their swimming and diving activities. Appropriate size is that which ensures that experimental tags do not hinder turtle growth movements, or behaviour (Mansfield et al. 2012). Individual sizes ranged between 13.3-29.1 cm straight carapace length (SCL) and weight between 0.490-4.314 kg (Table 4.1).

At-sea movements of 19 post-hatchlings aged from 9 to 22 months old were satellite-tracked during 2015-2017 (Table 4.1). Post-hatchlings were satellite tagged with small solar-powered platform transmitting terminals (PTT), model SEATAG-TurtleTag, manufactured by Desert Star S.L, without a duty cycle. We used three tags with similar characteristics but different weights: 18, 21 or 26 g and an acrylic-silicone-neoprene attachment method (Figure 4.2) modified from Mansfield et al. (2012).

The durability of the tag attachment on the carapace was tested in captivity with turtles from Clutch A over four weeks. Tags remained attached for a minimum of 18 days. We also examined the increase in weight of tagged animals over time relative to a control group to test if the tag affected the turtles' growth. The total weight added to the experimental animals ranged between 5-12% of the animal weight. There were no significant differences between experimental and control groups (t test, t = 0.757, df = 11.866, P = 0.4639). Prior to attaching the transmitter, the carapace was first cleaned with 70% isopropanol to remove natural oils, and allowed to air dry. Then, the carapace was sanded using mildly abrasive sandpaper (Godley et al. 2003), wiped with 2% chlorhexidine diacetate disinfectant solution, and air dried. The transmitter was attached between the second and the fourth vertebral scute with an acrylic base (Technovit 6091), two neoprene strips (7x0.8 cm, 5 mm thick), and finally aquarium silicone. Aquarium silicone was used in preference to epoxy resin because it is more flexible and allows the carapace to grow without deformations (Mansfield et al. 2012). Neoprene strips provide buoyancy and, with silicone, also provides a flexible base for the satellite tag. In most cases, we secured tags to the turtle's carapace with nylon line (0.4 mm) through a small hole drilled with a 0.6 mm sterilized needle through the keratin part of the crest of both second and fourth vertebral dorsal scutes (modified from Nagelkerken et al. 2003). Nylon was tied in a double knot. Turtles were tagged at least one day before their release so they could get used to the extra weight (except turtles with identity numbers (ID) from 15 to 19). The behaviour (including swimming and diving ability) of the turtles tagged in advance was observed (Figure 4.2).

Figure 4.2 General procedure for satellite tagging loggerhead sea turtle post-hatchlings.

Turtles behaved normally at release. They crawled along sand toward the seashore, entered the sea, and swam. Post-hatchlings were released preferentially on the same beach where the clutch was found. Tag weight was less than 5% of turtle weight, following previous studies (Mansfield et al. 2014). In methods, Mansfield et al. 2014 specified the tag weight (9.5 g), but did not provide any explicit information on total tag weight or the weight of the acrylic-silicone-neoprene attachment. The authors only provided information on the epoxy needed to protect the tag from the marine environment (epoxy added weight ranged from 1.5 – 3.5 g) (Mansfield et al. 2012). Nonetheless, we can estimate the total weight of the attachment they used from the information provided in Mansfield et al. 2012. They used approximately 15-22 mL of aquarium silicone (density = 1.03 g/L) and two neoprene strips (40 x 5 x 5 mm), approximate weight 1.5 g. Adding all these weights shows the total weight of the attached tag would range between 27.95 and 37.16 g. If turtle size in Mansfield were between 300 and 700 g, the added tag weight percentage could range between 3.99 and 12.39%. This percentage range of total added weight is similar to ours (Table 4.1). Our total added weight ranged between 31 and 72 g and our turtle size ranged between 489.9 and 4,314 g, so both weights were heavier than in Mansfield et al. (2014). However, in our case the percentage of added tag weight ranged from 1.29 to 8.81%. Therefore, our additional weight percentage was similar to Mansfield et al. (2014).

4.2.2 Data acquisition

Location data (LC) were collected using the Argos system, which classifies seven location classes of decreasing accuracy (3, 2, 1, 0, A, B, Z). LCs 3, 2, and 1 have Argos estimated errors of less than 250 m, 500 m, and 1,500 m, respectively (CLS 2016). Empirical studies by Hays et al. (2001) and Royer and Lutcavage (2008) found location class A comparable in accuracy to class 1. Witt et al. (2010b) found that LC B had poorer accuracy than LC A, and the worst level of accuracy was found in LC 0, such that LC3 < LC2 < LC1 < LCA < LCB < LC0 < LCZ. Facing shortages of LC 3, 2, and 1 locations, some researchers studying sea turtle movements have also included locations of LC 0, A, B and Z after extensive data screening (Mansfield et al. 2014, González et al. 2016). Data was stored in the Seaturtle.org database. We used all locations except locations that required a high traveling speed, > 10 km h^{-1} (González et al. 2016) and land locations (Arendt et al. 2012b), which were filtered with Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley 2005). Then, we used the Douglas Argos-filter algorithm (DAF) (Douglas et al. 2012) as implemented in the Movebank tracking database (Wikelski and Kays 2017). We used distance-angle rate filter (DAR), which retains spatially redundant locations and locations that pass movement rate and turning angle tests as the most appropriate approach for studying marine turtle movements (Douglas et al. 2012). Parameters were KEEP_LC = 2, MAXREDU*N* = 15, MINRATE = 10, and RATECOEF = 25.

Table 4.1 Post-hatchling loggerhead data information. Hatchlings were kept in a head-starting program. Head-starting locations were: ARCA del mar (Área de Recuperación y Conservación de Animales del mar, Oceanogràfic de València, Spain), CRAM (Centro de Recuperación de Animales Marinos, Tarragona, Spain), CEGMA (Andalusian Marine Environment Management Center, Consejería de Medio Ambiente y Ordenación del Territorio, Junta de Andalucía, Algeciras, Spain), and Aquarium of Sevilla (Spain). Several post-hatchlings from Clutch A were head-started first at ARCA (8 months) and then at CEGMA (5 months). All Clutch B was incubated at Doñana Biological Station (EBD-CSIC, Sevilla, Spain). Total tag weight includes both the Platform Transmitter Terminal (PTT) tag and attachment material. Days transmitted include all transmissions received with or without location. Distance traveled is the sum of the minimum distance between all consecutive locations of each turtle. Release location was on the beach: Clutch A in Elx, Alacant (38.234 N, 0.513 W), Clutch B in Pulpí, Almería (37.375 N, 1.636 W) and Clutch D in Tarragona, Barcelona (41.129 N, 1.302 E). SD is standard deviation of the mean.

Clutch	**Name**	**Turtle identity number (ID)**	**Weight (g)**	**SCL (cm)**	**% Total tag weight**	**PTT tag weight (g)**	**Total tag weight (g)**	**Head-starting locations**	**Age at release (months)**	**Release date**	**Days transmitted**	**Distance traveled (km) ±SD**	**Mean speed (km/h) ± SD**
A	Sali	1	970.6	17.5	4.07	26.0	39.5	ARCA / CEGMA	13	14/09/2015	98	2076.53 ± 17.97	1.91 ± 2.48
	Daniel	2	854.2	15.8	4.73	26.0	40.4	ARCA / CEGMA	13	14/09/2015	91	1429.58 ± 32.57	1.37 ± 1.83
	Espaikel	3	867.1	16.3	4.26	26.0	37.0	ARCA / CEGMA	13	14/09/2015	23	313.92 ± 2.94	1.28 ± 1.95
	Maya	4	718.3	15.3	5.35	21.0	38.5	ARCA / CEGMA	13	14/09/2015	43	1173.98 ± 11.18	1.50 ± 1.76
	Contxi	5	716.8	15.1	5.34	21.0	38.3	ARCA / CEGMA	13	14/09/2015	54	993.99 ± 31.58	1.70 ± 2.03
	Samy	6	700.4	15.0	5.18	21.0	36.3	ARCA	13	14/09/2015	42	262.73 ± 9.95	0.84 ± 1.13
	Lusi	7	489.9	13.6	8.81	21.0	42.2	ARCA	13	14/09/2015	34	383.86 ± 18.90	1.60 ± 1.62
	Carla	8	496.2	13.3	7.19	21.0	35.7	ARCA	13	14/09/2015	11	117.49 ± 15.26	1.23 ± 2.20
D	Seis	9	4314	25.6	1.29	26.0	72.0	CRAM	22	31/08/2016	123	3916.68 ± 12.15	2.23 ± 1.97
	Nueve	10	3381	29.1	2.17	26.0	56.0	CRAM	22	31/08/2016	37	1908.18 ± 15.99	3.51 ± 2.55
B	Cocedora	11	1012.8	17.5	NA	26.0	26+	CSIC / CEGMA	9	16/06/2016	82	3626.64 ± 22.68	3.27 ± 2.67
	Rabiosa	12	1096.7	17.5	NA	26.0	26+	CSIC / CEGMA	9	16/06/2016	83	3743.38 ± 13.84	3.34 ± 2.68
	Pichirichi	13	952.6	16.6	NA	26.0	26+	CSIC / CEGMA	9	16/06/2016	79	4107.8 ± 17.64	3.85 ± 2.72
	Serena	14	879.2	16.8	NA	26.0	26+	CSIC / CEGMA	9	16/06/2016	102	4163.46 ± 24.82	2.84 ± 2.59
	Toby	15	940	16.97	3.72	18.0	35.0	CSIC / Aq. of Sevilla	12	28/09/2016	106	4381.07 ± 52.49	3.18 ± 2.91
	Dora	16	1000	17.52	3.10	18.0	31.0	CSIC / Aq. of Sevilla	12	28/09/2016	115	2574.49 ± 85.76	1.70 ± 1.82
	Vendetta	17	1102	18.11	3.72	26.0	41.0	CSIC / Aq. of Sevilla	12	28/09/2016	108	5580.33 ± 48.00	3.31 ± 2.80
	Bonita	18	1030	17.47	3.79	26.0	39.0	CSIC / Aq. of Sevilla	12	28/09/2016	123	3981.24 ± 43.66	1.85 ± 1.69
	Morla	19	1308	18.65	3.29	26.0	43.0	CSIC / Aq. of Sevilla	12	28/09/2016	105	341.25 ± 38.20	1.58 ± 1.76

4.2.3 Dispersion analyses

Bathymetry data to analyze the use of neritic and oceanic habitats were obtained from the Satellite Tracking and Analysis Tool (Coyne and Godley 2005). Trajectories were analyzed using 'adehabitatLT' package (Calenge 2006) in R version 3.3.1 (R Development Core Team 2017). To identify movement phases we segmented trajectory into segments characterized by a homogeneous behaviour using the method of Gueguen (2000). Independence of the residuals of this segmentation was tested using the Wald and Wolfowitz test. Orientation analyses were performed using turtle bearing with 'circular' and 'CircStats' R-packages (Agostellini and Lund 2017). The significance of circular mean was tested through Rayleigh's test. Uniformity of distribution was tested using Watson's test. Finally, we compared orientation differences among clutches using Mardia-Wheeler-Watson's test (Batschelet 1981). Dispersion maps were produced using Maptool provided online by SEATURTLE.ORG (www.seaturtle.org/maptool).

4.2.4 Survival analyses

We assessed the daily survival probability of sea turtles using capture-recapture models for open populations based on the Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992) using software Mark 7.1 (White and Burnham 1999). In this way, survival probability (Φ) can be estimated independently of recapture probability (p) (Lebreton et al. 1992). Capture-recapture data were obtained from Argos messages and tracks information during 90 days from release (day 0). Days with no Argos message were coded as not captured. The goodness-of-fit test (GOF) of the CJS model was performed using U-CARE (Choquet et al. 2009). This was done to explore the fit of the CJS model to the data, and to identify a general model from which to start a suitable model selection. Trap dependence was analyzed following Pradel (1993).

We used a linear model approach and a logit-link function to evaluate several models. The *a priori* set of models included different effects such as time dependence in survival or recapture, several trends (constant, linear, exponential, logarithmic and half-normal) in survival or recapture, differences in survival between months or trap-dependence effects on recapture. Model selection was based on the corrected Akaike's Information Criterion (AICc) (Burnham and Anderson 1998). We considered that models with a difference in AICc of less than two units were similarly supported by the data (Burnham and Anderson 1998). As we were mainly interested in survival, we first modeled recapture probabilities. Once we had the best model for recapture probability, we modeled survival. To compare survival among nests, we started from the best model previously selected. Clutch D was excluded from this analyses due to low sample size (n = 2). Nest origin, use of region (Alboran Sea or Balearic

Sea) and use of habitat (neritic or oceanic) were included as covariates in these models. Finally, we tested for significant difference in survival estimates between clutches with Contrast software (Hines and Sauer 1989).

4.3 Results

4.3.1 Turtle movements

Most locations received were B (32.96%) and Z (25.90%), > 28.80% of messages received had associated LCs between 0 and 3 (Figure 4.3). Turtles were remotely tracked on average for 74.2 ± 35.5 days, *n* = 19, and travelled a minimum mean distance of 2,372.45 ± 1,724.24 km, *n* = 19, with a resultant mean speed of 2.22 ± 0.94 km h^{-1}, *n* = 19 (see Table 4.1). Given the low accuracy of locations these swimming values should be considered as estimates. Individuals with few locations were excluded from further movement analyses (*n* = 4, turtle IDs: 3, 7, 8 and 19). On average 75.5 ± 25.1%, *n* = 15, of locations were off the continental shelf. However, when excluding turtles from Clutch A, 88.0 ± 9.5%, *n* = 15, of locations were off the shelf (>200 m depth). Turtles from Clutch A have 50.4 ± 28.7%, *n* = 5, of locations within continental shelf waters.

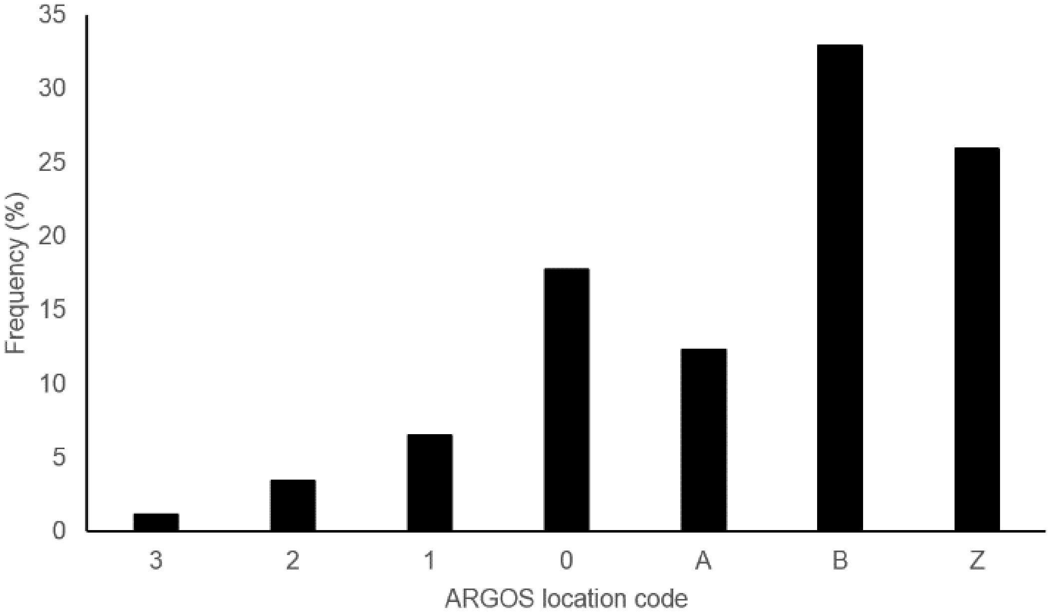


Figure 4.3 Frequency (%) of Argos location codes reported with satellite track locations from loggerhead sea turtle post-hatchlings released in the western Mediterranean.

The track of each turtle (*n* = 15) showed no directional movement throughout the track duration (Rayleigh's test, *Z*, *P* > 0.05, in all cases). Nonetheless, in several instances dispersal movement was consistently directional during certain week periods (Raleigh's test, *Z*, *P* < 0.05). Differences in orientation were significant between nests (Mardia-Watson-Wheeler test, *W* = 11.736, *d.f* = 4, *P* = 0.019), and individuals (Mardia-Watson-Wheeler test, *W* = 64.814, *d.f* = 28, *P* < 0.0001). Release date did not affect orientation (Mardia-Watson-Wheeler test, *W* = 3.291, *d.f* = 2, *P* = 0.193). Overall, post-hatchlings did not disperse following a similar pattern after release, except during the coldest months. This was true even when considering releases by clutch or date (Figure 4.4). The most frequented areas were the Alboran and Balearic Seas. From Clutch A (*n* = 5) two turtles (IDs: 1, 2) moved northwards to the Balearic Islands, Turtle ID 2 traveled south during winter. The other three (IDs: 4, 5, 6) moved southwards to the Alboran Sea, and Turtle ID 4 traveled possibly taking a North African eddie. Turtles from Clutch D (IDs: 9, 10), remained in the Balearic Sea, and Turtle ID 9 travelled northwards to the French coast reaching the Gulf of Lion. From Clutch B (*n* =8), four turtles (IDs: 11, 12, 14, 18) traveled south and moved into the Alboran Sea. One of them, Turtle ID 11, traveled at the end of its monitoring period northwards approaching the Balearic Islands. Two individuals from Clutch B (IDs: 13, 15) traveled northwards from the release point to the Balearic Sea. Finally, only two turtles from Clutch B (IDs: 16, 17) moved eastwards along the North African coast to the Algerian sub-basin approaching the Sicilian Strait (Figure 4.4). None of the turtles crossed the Gibraltar or Sicilian Straits or reached the Ligurian Sea during the tracking period. We only observed a common dispersal pattern during the coldest months of monitoring (December and January), when turtle movements were directed southwards to the western Alboran Sea or southeastwards to Sicilian Strait.

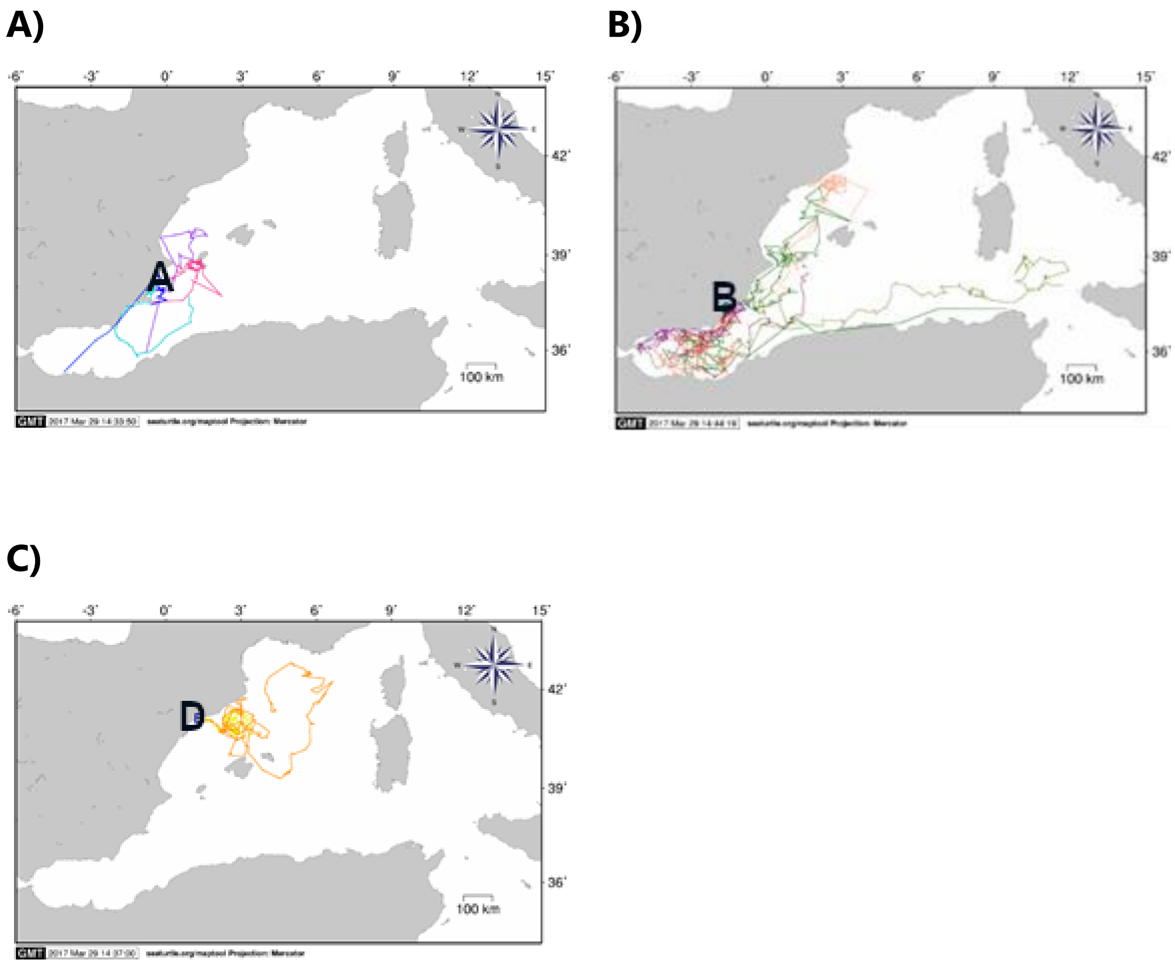
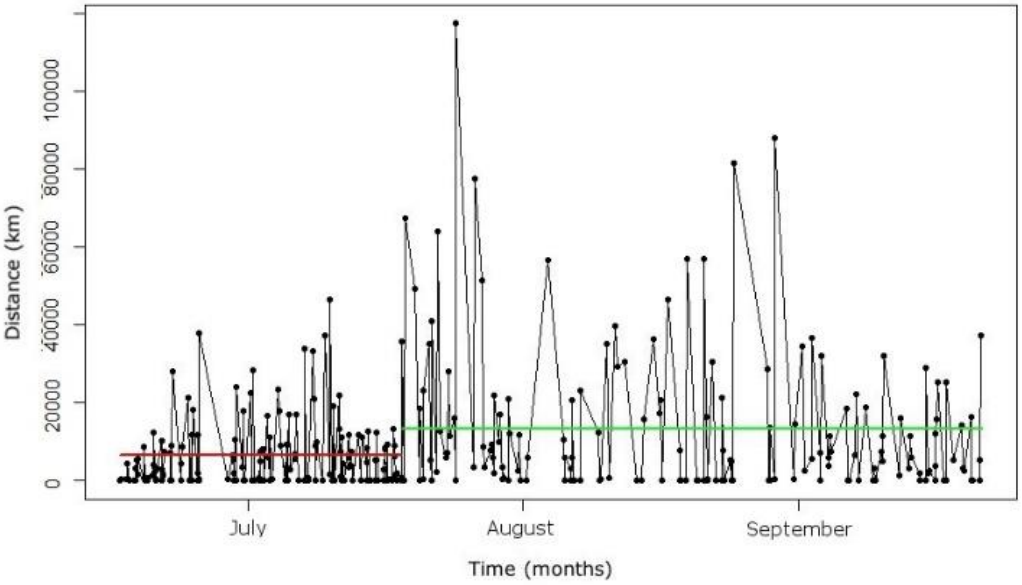


Figure 4.4 Dispersion patterns for loggerhead sea turtle (*Caretta caretta*) post-hatchlings in the western Mediterranean. Release point is marked by clutch letter (A, B or D) on map. Therefore, figures A), B), and C) represent the dispersion routes for clutches A (*n* = 8), B (*n* = 9), and D (*n* = 2), respectively. Track colors represent different turtles. In figure (B) green colors represent post-hatchlings released in September and the other colors represent post-hatchlings released in June. Maps were obtained with SeaTurtle Maptool (www.seaturtle.org/maptool).

Track segmentation analyses showed that in all analyzed individuals movements during the first days of monitoring (10-40 days) were slower than in the rest of the trajectory (Figure 4.5A and Figure 4.5B). Some individuals (IDs: 9, 10, 18) alternated between faster phase movements and slower ones (Figure 4.5B). In all cases (*n* = 15) the residuals of these segmentations were independent (Wald and Wolfowitz test *P* > 0.05), confirming the validity of the approach.

A)



B)

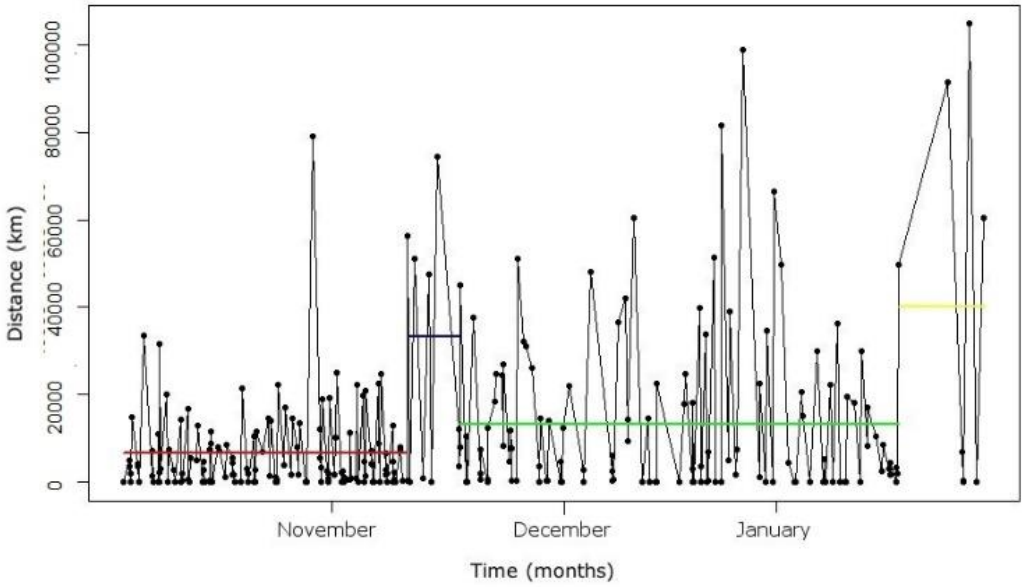


Figure 4.5 Movement segmentation analyses. Straight lines indicate mean travel distance through time, red (slower travel distance), green (low medium travel distance), blue (high medium travel distance), and yellow (higher travel distance). Different mean travel distances point to different types of movement. A) For turtle identity number (ID): 14, and B) For turtle ID 18.

4.3.2 Survival analyses

All post-hatchlings were included to assess survival. We obtained 6,235 locations and 887 transmissions without location. Two out of 19 satellite-tagged individuals were recaptured alive. The first one (ID 1), from Clutch A, was found 99 days after release stranded on a beach in Murcia (Spain). The second one from Clutch B (ID 12) was recaptured stranded on a beach in Málaga (Spain) after 83 days from release with its satellite transmitter attached. This individual was found with a high epibiotic colonization, and was taken to a rehabilitation center (CMAOT Junta de Andalucia, unpubl. data) and its satellite tag was removed. Both these post-hatchlings died a few weeks later at a rehabilitation center. Necropsy revealed plastic debris in the gastrointestinal track of both animals, but no clear cause of death was found. Therefore, the minimum estimated mortality was 11% after three months of tracking but at least 25% of monitored post-hatchlings were alive three months after release.

Our starting model to estimate survival was the CJS model which has survival and capture probabilities that vary with time (t, model Φ (t) p (t)). The overall GOF-test for daily survival was significant ($\chi 2$ = 191.20, P < 0.01). There was evidence for a significant trap dependence effect as revealed by the trap-dependence signed statistic (z = -11.37, P < 0.01). The negative sign of the statistic z indicated a trap-happiness effect, that is, recapture was more likely when a sea turtle had been located the day before. As we did not "capture" our turtles, this effect might be due to the likelihood of locating a tag by Argos or due to permanent tag loss or tag malfunction. Therefore, we fitted a model with capture probabilities dependent on time elapsed since last encounter ('m') and survival probability dependent on time (Φ(t) p(m*t), model 10, Table 4.2).

In the survival analysis, the model that best fitted the data considered constant survival and trap-dependence in recapture (Table 4.2, model 11). Model selection supported recapture probabilities being dependent on time elapsed since last encounter, considering three periods: whether capture occurred the day before, two days ago or three or more days ago (model 1, Table 4.2). The model suggested that recapture probability declined with time since last encounter (Table 4.2). Models including a trend in survival were not supported (models 12, 14, 15, Table 4.2). Other competing models had an AICc with a difference of more than two units compared with the selected model. Estimated mean daily probabilities of recapture and survival are shown in Table 4.3. Extrapolating these minimum survival estimates (Φ days), minimum monthly survival probability was 0.78 (95% CI: 0.63 – 0.87) and minimum survival for the study period was 0.59 (95% CI: 0.40 – 0.76). Similarly, minimum annual survival probability was estimated as 0.05 (95% CI: 0.003 – 0.20).

Models where survival differed between nests, habitat association and/or region (models 18, 19, 21, 22, 23 and 25, Table 4.2) were fitted. In models 18 to 26, the two individuals from Clutch D were not included because the clutch size (*n* = 2) was insufficient to compute an adequate estimate for survival rate. In this case, model assessment was started considering trap-dependence in recapture (model 25, Table 4.2). Thus, model 25 (Table 4.2) was used as the starting model to compare survival between clutches A and B. Models considering the region, Alboran Sea or Balearic Sea, were fitted (models 19 and 22, Table 4.2). Model 19 considered the influence of both nest and region. The influence of the region in survival was not clear, since the slope (*B)* of the linear model included zero (*B* = 0.76 ± 0.83, 95% Confidence interval (CI): -0.88 – 2.39). Models considering the habitat association, neritic or oceanic habitat, were fitted (models 21 and 25, Table 4.2). Model 21 considered the influence of both nest and habitat association. The influence of the habitat in survival was not clear, since the slope (*B)* of the linear model included zero (*B* = 1.06 ± 0.67, 95% Confidence interval (CI): -0.26 – 2.37). The best model in these analyses included a nest effect (model 18, Table 2). The effect, as determined by the slope (*B*) of the linear model for the covariate nest, was different from zero (*B* = 6.17 ± 0.95, 95% Confidence interval (CI): 4.32 - 8.03). Daily survival probabilities were significantly different between nests (*χ2* = 5.3011, *P* =0.0213). Minimum mean daily survival probability was 0.57 (95% CI: 0.30 – 0.76) for Clutch A and 0.94 (95% CI: 0.67 – 0.99) for Clutch B. Extrapolating these values, minimum annual survival estimates were 0.001 (95% CI: 5*10-7 – 0.04) for Clutch A and 0.47 (95% CI: 0.01 - 0.89) for Clutch B.

Table 4.2 Model selection for recapture and survival probabilities of loggerhead post-hatchlings. For each model, the values for deviance, the number of estimable parameters (Np), corrected Akaike's Information Criterion (AICc), differences between the first model and the model with the lowest AICc (ΔAICc) and AICc weights are shown. Model notation is as follows: Phi: post-hatchlings survival probability, p: recapture probability, c: constant, t: time dependence (days), linear trend: linear dependency, month: monthly dependency, ln trend: logarithmic dependency, exp trend: exponential dependency (positive or negative), half normal trend: half-normal dependency, age model for recapture (m2: considering two ages or m3: considering three ages), m*t: interaction recapture probability and time. Bold face denotes the selected models.

	Models	**AICc**	**ΔAICc**	**AICc weight**	**Np**	**Deviance**
Modeling Recapture probability	**1. {Phi(t) p(m3)}**	1125.53	0.00	1.00	92	382.06
	2. {Phi(t) p(m2)}	1146.21	20.68	0.00	91	405.16
	3. {Phi(t) p lineal trend}	1343.82	218.29	0.00	91	602.77
	4. {Phi(t) p ln trend}	1349.36	223.83	0.00	91	608.30
	5. {Phi(t) p(c)}	1352.28	226.75	0.00	90	613.63
	6. {Phi(t) p exp positive trend}	1353.25	227.72	0.00	91	612.19
	7. {Phi(t) p exp negative trend}	1354.33	228.80	0.00	91	613.28
	8. {Phi(t) p half normal trend}	1354.33	228.80	0.00	91	613.28
	9. {Phi(t) p(m*t)}	1418.76	293.23	0.00	264	166.66
	10. {Phi(t) p(t)	1479.36	353.83	0.00	177	510.20
Modeling Survival probability (considering all clutches)	**11. {Phi(c) p(m3)}**	974.10	0.00	0.88	4	424.86
	12. {Phi(month) p(m3)}	978.14	4.04	0.11	6	424.85
	13. {Phi(c) p(m)}	996.02	21.92	0.00	3	448.79
	14. {Phi(linear trend) p(m2)}	996.73	22.63	0.00	4	447.49
	15. {Phi(month) p(m2)}	1000.05	25.95	0.00	5	448.79
	16. {Phi(t) p(m3)}	1125.53	151.43	0.00	92	382.06
	17. {Phi (c) p(c)}	1199.44	225.35	0.00	2	654.23

Table 4.2 (continue) Model selection for recapture and survival probabilities of loggerhead post-hatchlings. For each model, the values for deviance, the number of estimable parameters (Np), corrected Akaike's Information Criterion (AICc), differences between the first model and the model with the lowest AICc (ΔAICc) and AICc weights are shown. Model notation is as follows: Phi: post-hatchlings survival probability, p: recapture probability, c: constant, t: time dependence (days), linear trend: linear dependency, month: monthly dependency, ln trend: logarithmic dependency, exp trend: exponential dependency (positive or negative), half normal trend: half-normal dependency, age model for recapture (m2: considering two ages or m3: considering three ages), m*t: interaction recapture probability and time. Bold face denotes the selected models.

	Models	**AICc**	**ΔAICc**	**AICc weight**	**Np**	**Deviance**
Modeling Survival probability (considering nest origin and or region)	**18. {Phi(nest) p(m3)}**	918.52	0.00	0.60	5	908.46
	19.{Phi(region+nest) p(m3)}	919.62	1.10	0.35	6	907.53
	20. {Phi(c) p(m3)}	924.15	5.62	0.04	4	916.10
	21. {Phi (nest+habitat association) p(m3)}	925.24	6.71	0.02	6	913.15
	22.{Phi(region) p(m3)}	925.98	7.46	0.01	5	915.92
	23. {Phi(nest) p(m2)}	942.60	24.07	0.00	4	934.55
	24. {Phi(c) p(m2)}	947.14	28.62	0.00	3	941.11
	25. {Phi (habitat association) p(m3)}	948.89	30.37	0.00	5	938.83
	25. {Phi(t) p(m3)}	1081.05	162.52	0.00	92	876.00
	26. {Phi(c) p(c)}	1131.51	212.99	0.00	2	1127.50

Table 4.3 Real estimate of daily survival parameters and 95% confidence intervals (CI), in brackets, for all covariates of the selected model. Model notation is as follows: Phi: post-hatchling loggerhead survival probability, c: constant, p: recapture probability (note that recapture probabilities are dependent on time elapsed since last encounter, thus, we considered three periods and therefore three recapture probabilities: capture the day before (p1), two days ago (p2) or three or more days (p3), nest: nest intrinsic influence on survival rates, m3: model age for recapture for three ages. Regarding nest influence, we show real estimate parameters for clutches A and B.

Model	Daily survival	p1	p2	p3
All clutches	0.991 ± 0.003	0.911 ± 0.009	0.625 ± 0.052	0.280 ± 0.044
{Phi(c) p(m3)}	(0.984 - 0.996)	(0.892 - 0.928)	(0.519 - 0.719)	(0.201 - 0.375)
Considering nest influence for Clutch A	0.981 ± 0.007			
{Phi(nest) p(m3)}	(0.961 - 0.991)	0.901 ± 0.010	0.622 ± 0.052	0.264 ± 0.0428
Considering nest influence for Clutch B	0.998 ± 0.002	(0.879 - 0.919)	(0.516 - 0.718)	(0.189 - 0.356)
{Phi(nest) p(m3)}	(0.987 - 1.000)			

4.4 Discussion

4.4.1 Turtle movements

The study related to this Chapter provides the first successful satellite tracks for post-hatchlings in the Mediterranean. It is also the first tracking of post-hatchlings from nesting events in the western Mediterranean, outside the loggerhead sea turtle's known breeding range (Tomás et al. 2008a).

Monitoring the movements of post-hatchlings was not easy because 59% of Argos LCs we obtained were B and Z, unlike other studies where > 70% of Argos LCs obtained where between 3 and 0 (Mansfield et al. 2014, 2017, Putman and Mansfield 2015). Given the lower accuracy of Argos LCs we obtained we should consider swim values as estimates. This highlighted that there remains a need to develop more accurate devices to assess sea turtle post-hatchling movements.

Assessing turtles' movements is challenging due to the relative contributions of the unique oceanic conditions encountered by each individual during the monitoring period, such as ocean currents, and the swimming behaviour of each turtle, that may influence their fate to passive drift or active dispersal (Putman et al. 2016). Overall, post-hatchlings spent much more time in oceanic zones and, generally avoided neritic areas supporting the loggerhead oceanic nursery paradigm (Carr 1987, Revelles et al. 2007a, Mansfield et al. 2014). Most turtles from Clutch A were an exception because they used the continental shelf extensively. Differences in behaviour observed between clutches could be caused by parasitic infections suffered at the rehabilitation center (Cribb et al. 2017). A weakened immune system and secondary lesions and infections caused by parasites could have affected their growth rate and individual size and, therefore, their behaviour. Smaller or weaker individuals might not confront coastal currents to reach oceanic zones.

It has been generally assumed that the distribution of sea turtle hatchlings and small juveniles is the result of passive drifting along prevailing currents, due to their limited swimming capacity (Witherington 2002, Bolten 2003). Nevertheless, recent studies also with head-started loggerhead sea turtles, have shown that post-hatchlings dispersal differed from what was predicted by passive drift alone (Mansfield et al. 2014, 2017). In previous studies, head-started post-hatchlings were able to disperse over large areas, could travel long distances (Bowen and Karl 2007, Mansfield et al. 2014) and exhibited highly variable routes (Okuyama et al. 2010), similarly to our results with loggerhead turtles in the western Mediterranean. In our study, monitored turtles did not show directional movement over the entire track, whether they were from the same nest, release date or location. However, in several instances dispersal movement was consistently directional during certain weeks. This could be explained by the turbulent current system in the Mediterranean Sea (MAGRAMA 2012, Balbín et al. 2014). Consequently, turtles may exhibit more convoluted routes and frequent changes in bearing (Cardona et al. 2009, Cardona and Hays 2018), in contrast to dispersal orientation of small loggerhead juveniles in the North and South Atlantic (Mansfield et al. 2014, 2017) and North Pacific oceans (Briscoe et al. 2016) where strong currents are present. Moreover, some turtles dispersed northwards along the western shore of the Balearic Archipelago, a direction opposite the average surface currents in this area (Balbín et al. 2012). This finding may suggest therefore that active dispersal is more relevant than expected in the at-sea movements of young loggerheads in the Western Mediterranean, as was observed in recent studies in the Atlantic and Pacific oceans (Mansfield et al. 2014, 2017, Putman and Mansfield 2015, Briscoe et al. 2016). Nonetheless, Cardona and Hays (2018) compared drifters and turtles' movements concluding that ocean flows profoundly impact the movements of juvenile loggerhead turtles (40-60 cm SCL), suggesting that surface advection is dominant in determining the trajectories of turtles in the Mediterranean Sea. Our hypothesis is that Mediterranean small juvenile sea turtles present behavioural plasticity, with passive drifting or directional swimming being tuned to local conditions as observed in other studies (Mansfield et al. 2014, 2017, Briscoe et al. 2016). Larger amounts of directional swimming may be required to avoid the less optimum areas as the northernmost part of the western Mediterranean basin during winter. Ongoing studies might confirm this hypothesis.

Post-hatchling movements appear to have been constrained by environmental variables such as sea surface temperature. Overall, we observed that during the coldest months of monitoring (December and January) turtles moved in two directions: i) southwards to the western Alboran Sea where the surface temperature is warmer due to the inflow of Atlantic waters (Skliris and Beckers 2009), or ii) southeastwards probably on the Algerian Current with its frontal systems of enhanced productivity (Pinardi and Masetti 2000, MAGRAMA 2012). This fact may be related to the habitat selection hypothesis (Christiansen et al. 2016), probably to avoid zones with low temperatures (Coles and Musick 2000). Furthermore, we observed that individuals from Clutch D moved northwards to the Gulf of Lion during the strong upwelling season in October (MAGRAMA 2012). Track segmentation analyses suggest that phases of lower speed at the beginning of the monitoring period may be related to an adjustment period to the new environment. Although oceanographic information was not assessed, alternation of faster and slower velocity phases may illustrate migration phases (direct swimming) and foraging phases (convoluted swimming), respectively (Cardona et al. 2005), or they might be a consequence of different speed currents.

None of the tagged individuals crossed the Gibraltar Strait during the monitoring period, even though three of the turtles spent most of the tracked time near the Strait area. This fact is consistent with previous studies which suggest that small loggerheads (< 36 cm) are unable to pass the Gibraltar Strait from the Mediterranean towards the Atlantic basin (Revelles et al. 2007b). It is assumed that most of small juvenile loggerheads found in this area come from the Atlantic Ocean (Bolten 2003, Revelles et al. 2007b), because transport of small juvenile turtles from eastern to western Mediterranean seems to be very unlikely (Putman and Naro-Maciel 2013, Casale and Mariani 2014, Maffucci et al. 2016). Our results suggested that the small juveniles frequenting the surrounding area of Gibraltar Strait might also come from western Mediterranean nests laid in Spain, France, Italy (Delaugerre and Cesarini 2004, Sénégas et al. 2009, Maffucci et al. 2016) and even from Algeria and the western Mediterranean coast of Morocco and Tunisia, though there were no recorded nesting events (Casale and Margaritoulis 2010). If we observe the prevailing currents in agreement with Millot (1999) we can notice that the Algerian current moves eastwards but it is convoluted as well, presenting a large number of gyres. This might permit hatchlings from North African coast to travel to the Alboran Sea by shifting passive drift and active swimming behaviour. The lack of recent studies in the southern part of the western Mediterranean Sea impeded to confirm this hypothesis. In this study we did not observe any tracked loggerhead crossing the Sicilian Strait from western Mediterranean to eastern Mediterranean during the monitoring period but we lost satellite transmission when two turtles were moving towards the Sicilian Strait, probably directed by the Algerian current (see Chapter 5). There is evidence of two southward conveyors connecting the south Tyrrhenian Sea with the Strait of Sicily, and therefore, with the favorable eastern Mediterranean developmental habitat (Casale and Mariani 2014, Maffucci et al. 2016).

We did not observe a common dispersal pattern, however, two confluence areas in the western Mediterranean were distinguished: The Balearic and Alboran Seas. The Alboran Sea is a high-productivity area in comparison with the rest of the oligotrophic western Mediterranean basin due to the input of rich Atlantic waters (Pinardi and Masetti 2000, MAGRAMA 2012) and the permanent upwelling zone in the northwestern part of the Alboran Sea along the Spanish coast (Skliris and Beckers 2009). We observed that our post-hatchlings do not frequent the Ebro’s Delta area, in contrast to previous studies on juveniles (Cardona et al. 2009), although our tracked individuals were younger, head-started and from a different rookery. Distribution in more productive areas like the Balearic and Alboran Seas may be related to directional swimming in young sea turtles to select more favorable habitats based on ambient temperatures, foraging conditions, decreased depredation or other reasons (Christiansen et al. 2016, Gaube et al. 2017).

4.4.2 Survival analyses

Estimating survival in the wild it is a difficult task, particularly when studying marine animals as it is not easy to find recoveries. One approach is the use of satellite locations to obtain capture and recapture data. Previous studies have suggested that head-started marine turtles may present low survival probabilities (Cardona et al. 2012b) as has been observed in other species of turtles, especially during the first weeks after release (Burke 2015). Our results show that the minimum daily survival probability of head-started turtles during the first three months after release is high (0.98 - 0.99). Additionally, we need to consider that we may have underestimated survival due to tag loss or tag malfunction (Lebreton et al. 1992). Therefore, if a tagged post-hatchling stopped transmitting we did not know whether it had lost the tag or died. Regarding our results, we can assume that at least within the first month, the likelihood of tags remaining attached was high, with decreasing likelihood in the next months of monitoring. Consequently, our estimates might be upper biased and should be considered conservative estimates due to an unknown, though not negligible, tag loss and failure rate, which increases substantially from the second month of monitoring after release. Nonetheless, estimated survival using capture-recapture methods is less biased than only using return rates.

We did not find real survival estimates for loggerhead turtle post-hatchlings to compare with. The only available estimates are found in status reviews and are broadly applied to all post-hatchlings worldwide. Hence, there is a need to assess the survival of loggerhead turtle post-hatchlings specifically. Conant et al. (2009) assumed that the oceanic survival rate during the first year was 0.4, however, this value was used for another species (*Lepidochelys kempii*) and, moreover, it was not empirically estimated. This assumed survival value is lower than the reported in our results when considering just Clutch B. Mansfield et al. (2014) present tracking data for satellite-tagged post-hatchlings in the North Atlantic. Although they did not analyze survival particularly, they tracked neonates for more than 80 days on average, which was similar to our results. Additionally, we need to consider whether tagging could have an effect on post-hatchling survival due the added weight or increase in drag. We used a similar attaching method and the proportional added weight was within the range used by Mansfield et al. (2012, 2014). These studies showed that the tagging method did not affect the growth of monitored individuals (Mansfield et al. 2012). We obtained the same results for differences in growing between captive tagged individuals and a control group. Moreover, our turtles were tagged in advance to the release and behaviour observed was normal for all individuals after a habituation period (usually 24 hours). In any case, even considering this possible effect of tagging on survival or behaviour, our survival estimates support that reintroduced head-started loggerhead turtle post-hatchlings were able to survive in the wild, at least during the most critical period after release (Armstrong and Seddon 2008). Although we cannot evaluate the long-term success of head-started turtles, our results support the short-term success of reintroduction into the wild (Armstrong and Seddon 2008).

Casale et al. (2007, 2015) estimate annual survival probability of juvenile loggerheads in the Mediterranean Sea using the capture-mark-recapture and the catch-curve method, respectively. They obtained survival estimates that ranged between 0.71-0.86. Sasso and Epperly (2007) estimated monthly and annual loggerhead survival rates (SCL ranged 43-60 cm) with the known-fate model, which upper-biases survival estimates when fate is unknown. Although our minimum mean estimates are lower than these previous studies, our range of estimates include these values. These previous studies focused on older individuals (> two years), whereas our study focuses mainly on younger individuals which are expected to have a lower survival probability. Additionally, Sasso and Epperly used a known-fate model instead of a Comarck-Jolly-Sebel model. This implies that they did not consider tag detachment probability, and therefore, the survival estimate was upper biased. The method we used to extrapolate minimum annual survival estimates is highly sensitive to small variations in daily survival. Our estimates, however, only cover a period between June to January, but do not include survival during the period of the year with the lowest sea surface temperature (March) in the western Mediterranean, when the survival of small loggerheads may be compromised (Maffucci et al. 2016). Further studies covering this cold period should be conducted to obtain annual survival probabilities for one-year-old individuals. Moreover, annual changes in oceanic circulation could impact post-hatchling survival rates (Putman et al. 2013). Therefore, possible annual changes in oceanic circulation should be considered in next studies to elucidate the more favorable periods and places to release head-started post-hatchlings, as this may influence their dispersal and survival.

Survival differences between clutches were most likely due to the condition of individuals. Lower survival probability of Clutch A was probably a consequence of parasitic infections caused by *Amphiorchis spp.* at the rehabilitation center (Cribb et al. 2017), although all infected individuals received proper veterinary treatment. Head-starting programs may have some constraints that limit their success (Burke 2015), especially during the initial years of implementation. Another condition that would contribute to different survival rates between clutches would be caused by a potential genetic bias, since turtles came from three different clutches. We did not observe any effect of the influence of region (Alboran Sea or Balearic Sea) or habitat association (oceanic or neritic habitat) on survival estimates.

Although fisheries by-catch is considered a major threat for juvenile and adult sea turtles in the Mediterranean Sea (Casale 2011, Baez et al. 2013, Casale and Heppell 2016), we have no evidence of interaction with fisheries of our monitored individuals during the monitoring period. Mortality induced by pelagic longline and bottom trawling gears is the most significant in the Mediterranean Sea (Casale 2011, Echwikhi et al. 2012). This threat becomes greater for larger juveniles (> 30 cm) because larger juveniles in the western Mediterranean exploit neritic habitats, therefore their main threat are the fishing gears typically deployed in this habitat (i.e., bottom trawls, set nets, demersal longlines). Pelagic longline is also a threat for larger juveniles because hooks used by longlines are smaller than turtles' mouth, increasing their chances of accidental capture. In contrast, the hooks are too big for small juvenile loggerheads, preventing their capture (Echwikhi et al. 2012, Casale et al. 2015). Several authors highlight the ingestion of debris and plastics as a major threat for immature turtles (Margaritoulis et al. 2003, Carreras et al. 2004, Cardona et al. 2009). Indeed, two of our satellite tagged turtles were found stranded after almost three months of tracking with several plastic items in their gastrointestinal track, but in these cases the significance remains unknown. One of these turtles also had a severe colonization of epibiotic barnacles in the Alboran Sea (CMAOT Junta de Andalucia, unpublished data). Epibiotic colonization have been described in the Adriatic basin, Aegean basin and, particularly, in the Alboran Sea (Vallini et al. 2011, Domènech et al. 2015). This phenomenon may be significant in certain areas and years, but this remains unclear. Further studies may highlight the importance of these threats for small loggerhead juveniles.

4.5 Conclusions

The study related to this chapter provides the first results on dispersal areas of head-started loggerhead post-hatchlings in the Mediterranean Sea and contributes to a better understanding of loggerhead post-hatchling survival and habitat use. These results are relevant for the management of potential new breeding areas in the western Mediterranean. Our survival estimates could be applied to model loggerhead sea turtle populations (Richards et al. 2011) or anthropogenic impacts (Putman et al. 2015). Management measures like nest translocation and head-starting programs for loggerhead hatchlings were successful when considered in terms of short-term survival. There was a high probability of survival of head-started individuals in the wild, and probably head-started turtles had the ability to forage natural prey and growth normally in its natural environment. Furthermore, post-hatchlings from the western Mediterranean may contribute not only to the Mediterranean subpopulation stock but also to the North Atlantic's, which are endangered. Further understanding of the movement ecology of post-hatchling loggerheads in the western Mediterranean is crucial for more effective conservation strategies. Nonetheless, as we said before, there remains a need for smaller, lighter and more accurate devices to help drive the science forward, especially about the monitoring of sea turtle post-hatchlings.

Chapter 5

Habitat suitability of loggerhead post-hatchlings in the Mediterranean Sea

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5.1 Introduction

Reports of nesting events of loggerhead sea turtle (*Caretta caretta*) have been increasing during the last decade in the western Mediterranean basin, outside the usual nesting range in eastern Mediterranean (Tomás et al. 2008a, Maffucci et al. 2016, Carreras et al. 2018, Hochscheid et al. 2022). These reports suggest the species is expanding its nesting range through a potential colonization process (Wyneken and Lolavar 2015, Abella et al. 2016, Maffucci et al. 2016), which is probably lead by global warming (Witt et al. 2010a, Maffucci et al. 2016, Hochscheid et al. 2022). Management measures are usually implemented to enhance eggs and hatchlings survival when nests are found (Kornaraki et al. 2006, Tuttle and Rostal 2010, Burke 2015, Revuelta et al. 2015), especially in new colonization areas, such as the western Mediterranean, where these measures have been undertaken during the last years (Hochscheid et al. 2022, and references therein). These management measures included: i) relocating eggs for protection (to safer places on the same beach, to different beaches or to incubators at rescue facilities), and ii) head-starting programs. Head-starting programs are *ex-situ* conservation management measures consisting in rearing hatchlings in captivity for several months before release. The primary aim of this strategy is to avoid the high mortality rates of hatchlings during their first year (Burke 2015). However, the effectiveness of such management measures should be assessed as they are not exempt of risks. For instance, head-starting programs could fail if hatchlings contract diseases, are parasitized, or the handling induce behavioural changes that hampers survival after reintroduction (Cribb et al. 2017, and also see Chapter 4 of this thesis). Survival estimates of reintroduced post-hatchlings during the first months after release, when their survival rate is expected to be the lowest, are good indicators to evaluate the success of head-starting programmes (Armstrong and Seddon 2008). Survival probability is, in turn, one of the major knowledge gaps of sea turtle population dynamics, in particular of post-hatchlings (Casale et al. 2015). Therefore, monitoring post-hatchlings survival and dispersal shall provide the data to evaluate head-starting programs and to identify the way through and the main developmental areas used by immature individuals. The protection of these pathways and developmental areas will be instrumental to safeguard recruitment into adult breeding populations (Hays et al. 2016, Jeffers and Godley 2016, Maffucci et al. 2016, Rees et al. 2017). This is especially relevant in those threatened species, such as the loggerhead sea turtle, listed as ‘Vulnerable’ under the IUCN Red List categories (Casale and Tucker 2017).

Satellite tagging has become the most common approach to study species survival and identify developmental areas of large, highly motile marine animals (Godley et al. 2008, Sequeira et al. 2018, March et al. 2019, Kot et al. 2022). In accordance, during recent decades satellite telemetry data allowed assessing survival rates, movement patterns, and habitat use of adult and juvenile loggerhead sea turtles (Bentivegna 2002, Cardona et al. 2005, 2009, Revelles et al. 2007a, c, Mansfield et al. 2009, Witt et al. 2010, see Chapter 6). The recent advances and miniaturisation in satellite tags allowed studying the survival and dispersal of loggerhead post-hatchlings in the Atlantic (Hays and Marsh 1997, Putman et al. 2012a, Putman and Mansfield 2015, Mansfield et al. 2014, 2017) and Pacific oceans (Abecassis et al.

2013, Kobayashi et al. 2014, Briscoe et al. 2016, Christiansen et al. 2016, Saito et al. 2018). However, this life stage has been largely neglected in the Mediterranean Sea until the development of the present thesis. Research conducted in Chapter 4 provides results about post-hatchlings' survival and dispersal although it was carried out for short time spans and a limited number of individuals. Nonetheless, there is still lacking information about preferred developmental and foraging areas for post-hatchlings, particularly those from new nesting places in the western Mediterranean. Knowledge of these preferences will help address potential threats for this life stage in the Mediterranean Sea and implement of proper management and conservation measures for the species.

Loggerhead post-hatchling dispersal might be influenced by ocean currents and phenotypic variation, which may drive the balance between passive drift to active swimming (Putman et al. 2016). It has been generally assumed that hatchlings and small juveniles have limited swimming and diving capabilities. Consequently, their dispersal and distribution was assumed to result from passive drifting along prevailing currents (Witherington 2002, Bolten 2003, Hays et al. 2010). However, recent studies support that turtle hatchlings have active directional swimming that influence their movement patterns, leading to dispersal routes and distribution differing from those obtained with passive dispersal models (Putman et al. 2012a, Scott et al. 2012, Abecassis et al. 2013, Kobayashi et al. 2014, Putman and Mansfield 2015, Christiansen et al. 2016, Robson et al. 2017, Chambault et al. 2019, Le Gouvello et al. 2020, Harrison et al. 2021), even in head-started loggerhead sea turtles, which are reared in captivity for several months before release (Mansfield et al. 2014, 2017).

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

5.2 Methods

5.2.1 Turtle data and satellite tagging

Loggerhead hatchlings were collected from two nesting events: Clutch B, laid in July 2015 in Almería (Spain), and Clutch C, laid in July 2016 in València (Spain). Several hatchlings from these clutches were reared within the framework of a head-starting program (see details in Table 1). After the head-starting period (ranged from 9 to 13 months), post-hatchlings for this study (*n* = 19, Table 5.1) were selected randomly among those with appropriate size for tagging, in which tags are very unlikely to hinder behaviour or turtle growth (Mansfield et al. 2012). The individual sizes ranged between 16.6 – 23.0 cm straight carapace length (SCL) and weight between 0.9 - 1.2 kg (Table 5.1). Post-hatchlings were tagged with small solar-powered platform transmitting terminals (PTT) without duty cycle, model SEATAG-TurtleTag and manufactured by Desert Star Systems LLC (Monterey Bay, CA, USA), following the attachment and tagging procedure described in Chapter 4. We used two tags with similar characteristics but different weights: 18 and 26 g but tag weight was below the 4% of turtle weight in any case (Mansfield et al. 2014, see Chapter 4). Release location for Clutch B was on the nesting beach in Pulpí (Almería, Spain) [37.38 ° N, 1.64 ° W]. Four turtles from this Clutch were released on June 2016 and five were released on September 2016. Release for Clutch C was on a protected beach in El Saler (València, Spain) [39.32 ° N, 0.31 ° W] in October 2017 (Table 5.1).With the exception of turtles ID 9 Valencia and 19 Morla, tracking data are publicly available at the EMODNET repository ([dataset] Abalo-Morla et al. 2022).

Table 5.1 (legend). Post-hatchling loggerhead data information: Clutch (B or C), name of each turtle, turtle identity number (ID), weight (kg), straight carapace length (SCL) in cm, total tag weight (g) [which is the sum of both Platform Transmitter Terminal (PTT) tag and attachment material weights], percentage of total tag weight regarding turtles' weight, release date, number of days transmitted [which include all transmissions received with or without location], distance travelled (km) [which is the sum of the minimum distance between all consecutive locations of each turtle] and standard deviation (± sd), mean speed travelled (km/h) and standard deviation (± sd), and incubation type (electric incubator or protected beach). Hatchlings were kept in a head-starting program after hatching: i) Hatchlings IDs 11 to 14 from Clutch B during 9 months in CEGMA (Andalusian Marine Environment Management Center, Consejería de Medio Ambiente y Ordenación del Territorio, Junta de Andalucía, Algeciras, Spain), ii) Hatchlings IDs 15 to 19 from Clutch B during 12 months in Aquarium of Sevilla (Spain), and iii) Hatchlings from Clutch C during 13 months in ARCA del mar (Área de Recuperación y Conservación de Animales del mar, Fundación Oceanogràfic de València, Spain). NA means not available data. + means that weight of attachment material was not measured. Unless turtles ID 9 Valencia and 28 Morla, tracking data are publicly available at the EMODNet repository ([dataset] Abalo-Morla et al. 2022).

Table 5.1 (continue).

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

5.2.2 Data acquisition and data processing

Location data (LC) were collected using the Argos satellite system and state-space models (SSM) were used to estimate positions from the observed data accounting for measurement errors and variability in movement dynamics (Jonsen et al. 2005, 2007, 2013). A hierarchical correlated random walk switching state-space model (hDCRWS) was fitted based on the whole dataset (Jonsen et al. 2007, 2016, Christiansen et al. 2016). We used the 'bsam' R-package (Jonsen et al. 2005) in *R* 3.6.0 (R Development Core Team 2019). In our fitted hDCRWS model, two Markov Chain Monte Carlo (MCMC) chains for 120,000 iterations were ran by dropping the first 60,000 samples as a burn-in and retaining every 10th sample from the remaining 60,000 assumed post-converge samples from each chain to reduce sample autocorrelation. Thus, the model parameters and estimated locations were calculated using 12,000 MCMC samples. A 24-hour time step was used to generate one daily location of the tracking period from the posterior means of the resultant distributions. SSM locations were post-processed to remove land locations (Hoenner et al. 2012, Arendt et al. 2012a).

5.2.3 Survival analyses

We assessed the daily survival probability of post-hatchlings using capture-recapture models for open populations based on the Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992). We performed this analysis as described in Chapter 4 (see "*4.2.4 Survival analysis*" for further details).

5.2.4 Dispersal analyses

Trajectories were performed to analyse turtles' movements using 'adehabitatLT' package (Calenge 2006) in R version 3.6.0 (R Development Core Team 2019). To identify movement phases characterized by a homogeneous behaviour, a segmentation of trajectories was done by using the method of Gueguen (2000). In this analysis, the validity of conclusions and independence of the residuals of this segmentation were tested using the Wald and Wolfowitz test. The existence of turtles' directional bearing was investigated using functions implemented in the R-packages 'circular' and 'CircStats' (Agostellini and Lund 2017). The significance of circular mean was corroborated through Rayleigh's tests. Finally, we compared bearing differences among individuals and between Clutches B and C using Mardia–Wheeler–Watson's tests (Batschelet 1981).

The influence of sea currents on turtles' movement was quantified by computing the sea current assistance. Method to calculate it was modified from the tail wind assistance in Akesson and Hedenströn (2000) as shown in Equation 1.

$$Current\ assistance = Mc \times cos(Ht - Hc)$$ (**Equation 1**)

where *Mc* is the magnitude of the current in km/h, *Ht* is the turtle heading and *Hc* is the sea current direction.

To study the influence of sea currents on post-hatchlings trajectories we used a linear regression model of sea current assistance and distance travelled by sea turtles. We also computed a linear regression model of the divergence (which is the difference in bearing between the turtle heading from sea current direction, ranged from 0 to 180 degrees) and the magnitude of the current to observe turtles' behaviour regarding the sea current intensity.

In addition, we computed the eddy kinetic energy (Richardson 1983, Kang and Curchitser 2017) (Equation 2).

$$Eddy\ Kinetic\ Energy = 0.5 \times \ \rho0 \ \times (u^2 + v^2)$$ (**Equation 2**)

where ρ_0 is a constant reference density, which is chosen to be ρ_0 = 1000 kg m^{-3} in this study, and v and u correspond to the sea current velocity components.

5.2.5 Habitat use modelling

We modelled the species distribution with decision tress (i.e., C5.0, Quinlan 1992) to determine the areas of maximal suitability for post-hatchlings. This approach employed the environmental conditions associated to the turtles' presence (satellite-tracking data) and a randomly generated set of pseudo-absences to discriminate between them (Hazen et al. 2021). Pseudo-absences were generated as random walks based on the collected satellite-tracking data (Hazen et al. 2017, 2021).

Random routes generation

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

Environmental predictor variables

A set of 14 variables that presumably could influence post-hatchlings dispersal were tested as relevant predictor variables in the process of habitat selection: bathymetry, bathymetry slope, magnitude of the current, sea current direction, salinity, sea surface temperature, chlorophyll a, primary productivity, sea surface height, earth magnetic anomaly, eddy kinetic energy, current assistance, month and individual. Bathymetry data were obtained using the 30 arc-second resolution GEBCO global bathymetric model (Weatherall et al. 2015, GEBCO 2021). Environmental data about ocean currents, salinity, sea surface temperatures, sea surface height (SSH), (Escudier et al. 2020), and chlorophyll a and primary productivity (Feudale et al. 2021) were obtained at 1/24° of horizontal grid resolution from Copernicus Marine Environment Monitoring Service (https://marine.copernicus.eu). We also calculated the frequency of locations by sea surface temperature to observe if there is a preferential temperature niche. Earth magnetic anomaly grid at 2 arc-minute-resolution was obtained from National Oceanic and Atmospheric Administration of the USA (NOAA) (Meyer et al. 2017). Current assistance and eddy kinetic energy were obtained as described in Equations 1 and 2 shown in "*5.2.4 Dispersal analysis*". We considered the temporal changes in the habitat use by including month as a predictor. In addition, we included the individual to account intrinsic behavioural differences.

Habitat modelling with C5.0 decision-trees

We used C5.0 (Quinlan 1992) implemented in the *R* package 'C50' (Kuhn et al. 2015) to determine the most relevant predictor variables of route selection. C5.0 is a kind of fast decision-tree induction approach able to deal with different data types (i.e., categorical or continuous) and to model non-linear relationships and variable interactions (Olden et al. 2008), which proved able to outcompete other popular decision-tree induction approaches (i.e., Muñoz-Mas et al. 2016). Though cross-validation, we performed hyper-parameter tuning, to maximise model generalization, and carried out variable selection to determine the most relevant variables. Cross-validation approaches, such as *k*-fold, split the data into *k* disjoints groups and iteratively use *k*-1 groups to train the model and the *k* group set out to validate the performance of a given set of variables and hyper-parameters (i.e., the parameter controlling the learning process). Turtle routes may present intrinsic behavioural differences and temporal dependencies. Therefore, we split the route series considering these two elements to break down any dependency (Roberts et al. 2017) (Figure 5.1).

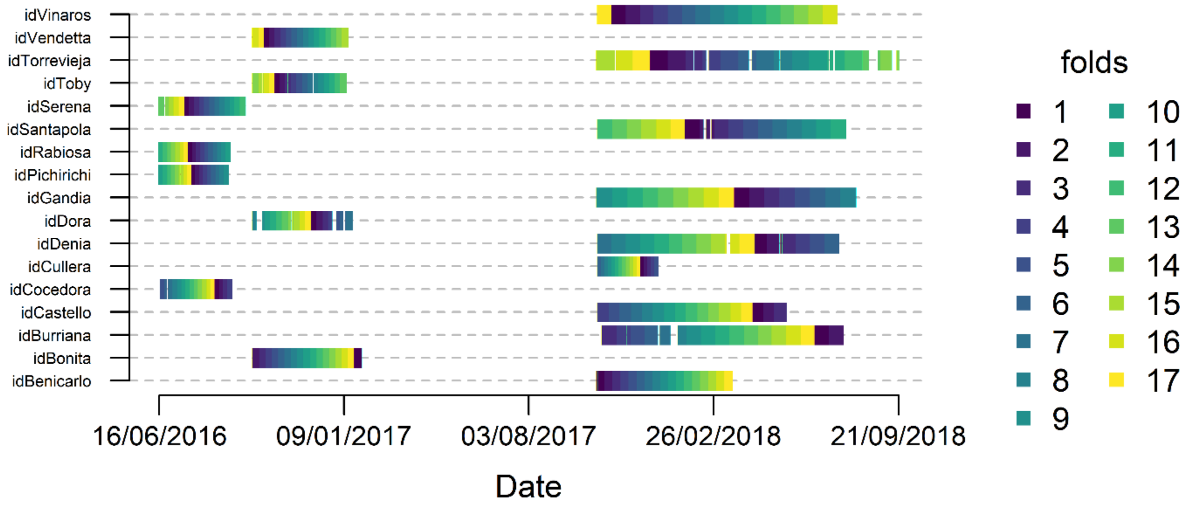

Figure 5.1 Period of data collected for each individual considered in the present study and data partition (folds) used during the process of hyper-parameters' tuning and variable selection through cross-validation. Hyper-parameters control the learning process of the habitat model, and each fold correspond to a set of data set out and used to recursively validate the tested hyper-parameters for each set of variables.

To carry out the hyper-parameters' tuning and variable selection we first ranked the environmental variables using the four algorithms of the *Relief* family implemented in the *R* package 'CORElearn' (Kira and Rendell 1992, Robnik-Sikonja and Savicky 2017). Then, we tested different combinations of the parameters *CF* [0.05, 0.45] and *minCases* [5, 105] and selected the best hyper-parameters after a forward variable selection approach based on the variables rank obtained with the four *Relief*-based rankings of variables. The data of the observed routes was outnumbered by those of the correlated random walks (1/20). Therefore, we selected the balanced accuracy as the performance criteria to select the most relevant set of variables and hyper-parameters (Muñoz-Mas et al. 2019). When the best hyper-parameters and set of variables were determined, we carried out a sensitivity analysis to scrutinize the modelled habitat suitability (Friedman 2001) and developed habitat suitability maps, based on ten years variable means, covering the entire Mediterranean Sea.

5.3 Results

5.3.1 Survival analyses

All satellite-tracked post-hatchlings (*n* = 19) were included to assess survival. Our starting model to estimate survival was the CJS model, which has survival and capture probabilities that vary with time (t, *model Φ (t) p (t)*). The overall GOF test for daily survival was significant (*P* < 0.01). As in Chapter 4, model selection suggested that recapture probabilities declined with time since last encounter ('m'), considering three periods: whether capture occurred the day before, two days ago or three or more days ago. Other competing models had an AICc with a difference of more than two units compared with the selected model. The best model selected included a nest effect and a trap-dependence effect (θ *(nest) p(m3)*), as in Chapter 4. Daily survival probabilities were significantly different between nests ($P < 0.05$). We extrapolated the minimum daily survival estimates, to minimum monthly and annual survival probabilities (Table 5.2).

Table 5.2. Real estimate of daily survival parameters, and monthly and annual survival extrapolated parameters, and 95% confidence intervals (CI), in brackets, for all covariates of the selected model for clutch B and clutch C. Model notation is as follows: θ is post-hatchling loggerhead survival probability, nest: nest intrinsic influence on survival rates, p: recapture probability (note that recapture probabilities are dependent on time elapsed since last encounter, thus, we considered three periods and therefore three recapture probabilities: capture the day before (p1), two days ago (p2) or three or more days (p3), m3: model age for recapture for three ages.

	Clutch B	**Clutch C**
Model	{ θ (nest) p(m3)}	
Daily survival	0.996 ± 0.003 (0.993 - 0.999)	0.999 ± 0.001 (0.998 - 1.000)
p1	0.901 ± 0.010 (0.879 - 0.919)	
p2	0.622 ± 0.052 (0.516 - 0.718)	
p3	0.264 ± 0.0428 (0.189 - 0.356)	
Monthly survival	0.880 (0.633 – 0.965)	0.966 (0.780 – 0.995)
Annual survival	0.213 (0.004 – 0.650)	0.654 (0.05 – 0.94)

5.3.2 Dispersal analyses

Individuals with very sparse and few locations were excluded from movement analyses (n = 2, turtle IDs: 9 Valencia and 28 Morla). The remaining post-hatchlings were remotely tracked on average for 174 ± 95 days, n = 17, and travelled a mean distance of 4,246 ± 1,331 km, n = 17, with a resultant mean speed of 1.79 ± 1.21 km h^{-1}, n = 17 (Table 5.1). On average, 85 ± 17%, n = 17, of locations were off the continental shelf (> 200 m depth). Overall, post-hatchlings dispersed widely around the Mediterranean Sea (Figure 5.2A), although several differences were observed among clutches (Figure 5.2B). Nonetheless, taking into account that post-hatchlings were released from June to September, dispersal patterns along the Mediterranean basin were quite similar among individuals when considering the month of monitoring (Figure 5.2C, Figure 5.3).

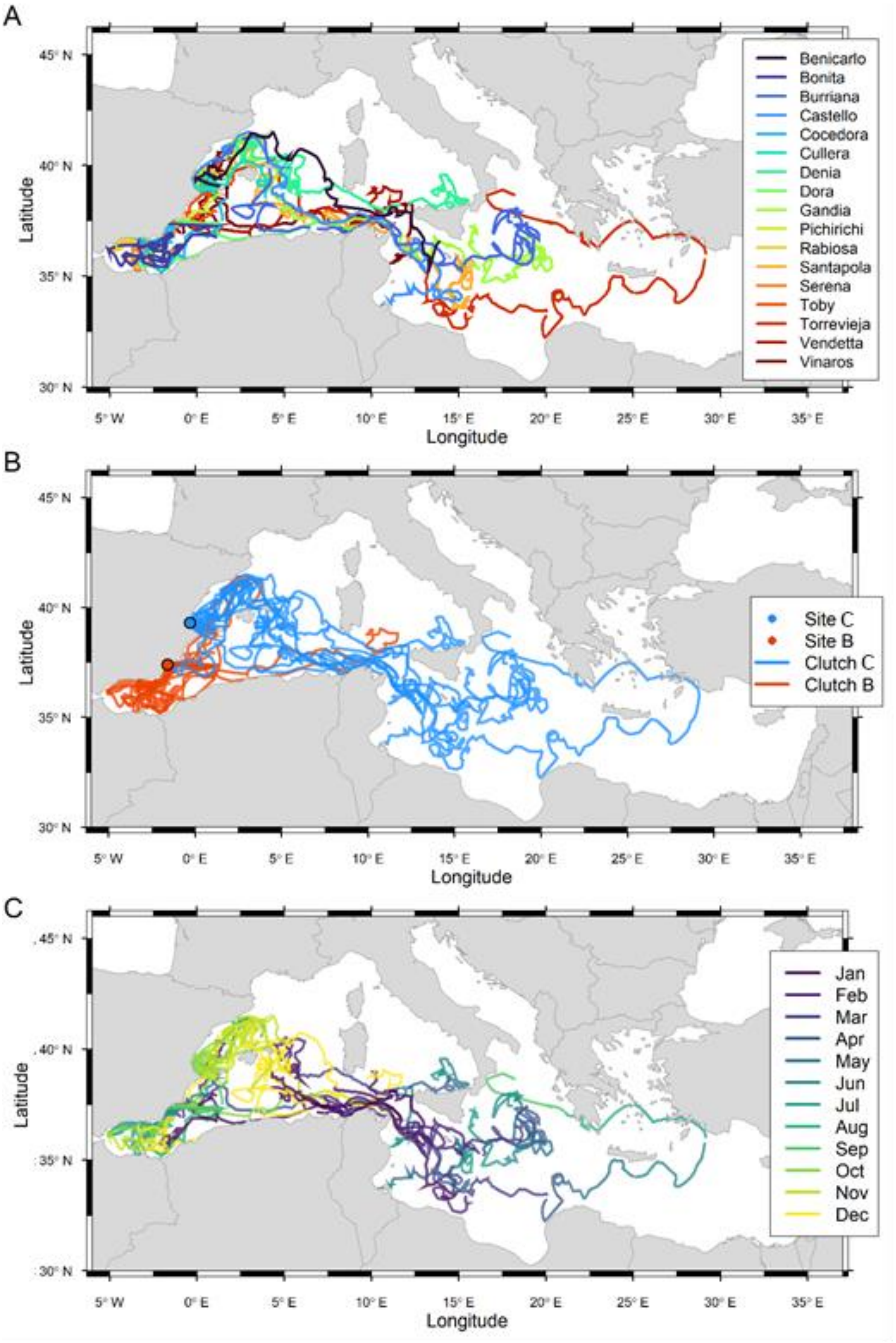

Figure 5.2 A) Turtle trajectories by turtle ID in the Mediterranean Sea. B) Turtle trajectories by clutch and release location. Clutch B release was at Pulpí (Almería, Spain) [37.38 ° N, 1.64 ° W] (red circle, site B), and Clutch C release was at Sueca (València, Spain) [39.32 ° N, 0.31 ° W] (blue circle, site C). C) Turtle trajectories by month of monitoring. Note that turtles were released in June and September (Clutch B) and October (Clutch C). Further details about release date are shown in Table 5.1.

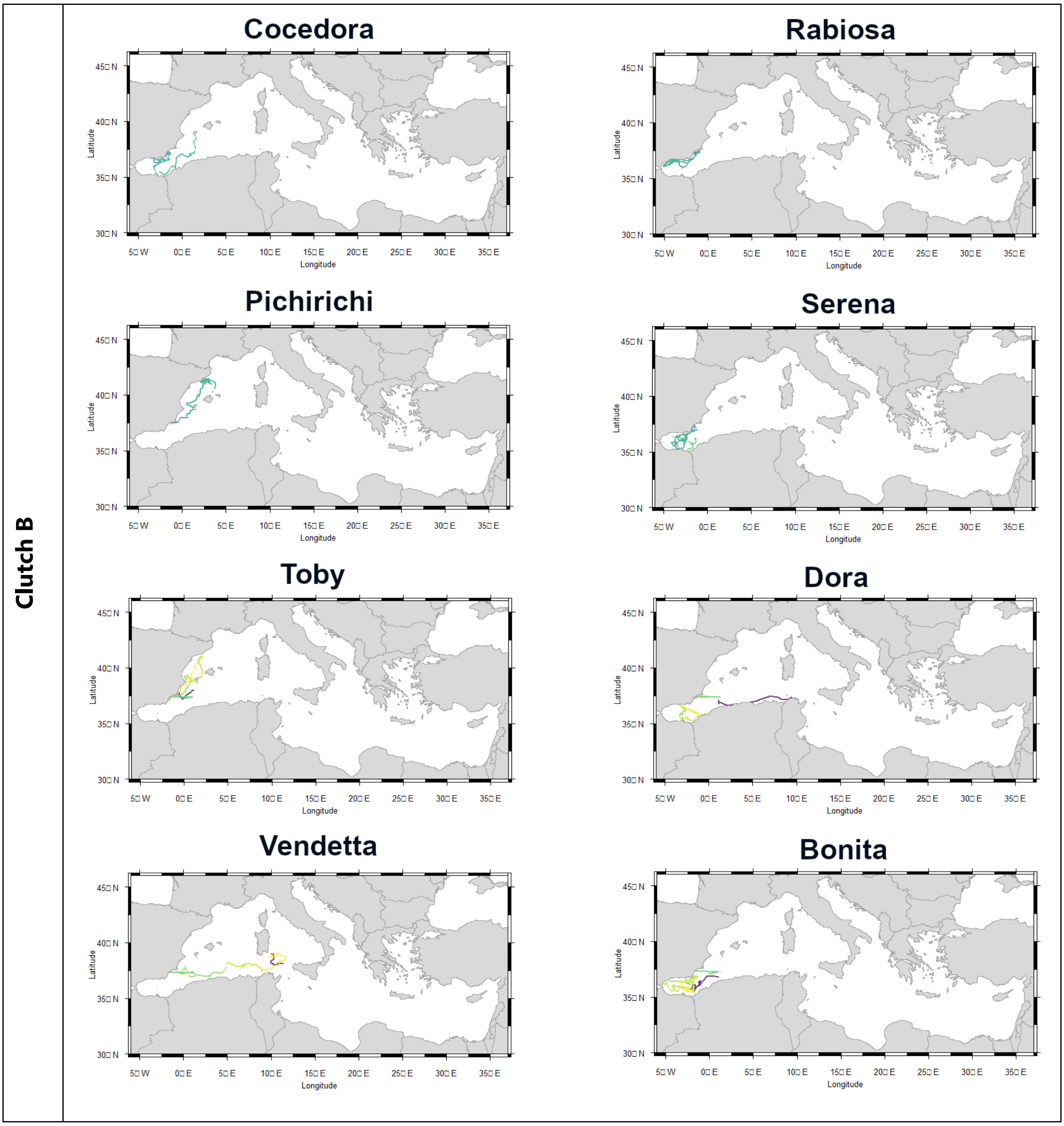

Figure 5.3 Dispersal trajectories for the monitored post-hatchlings in the Mediterranean Sea in the present study. Turtle ID is shown above each map. Colors in trajectories represent the month of the year as it is shown in the inset legend (continue).

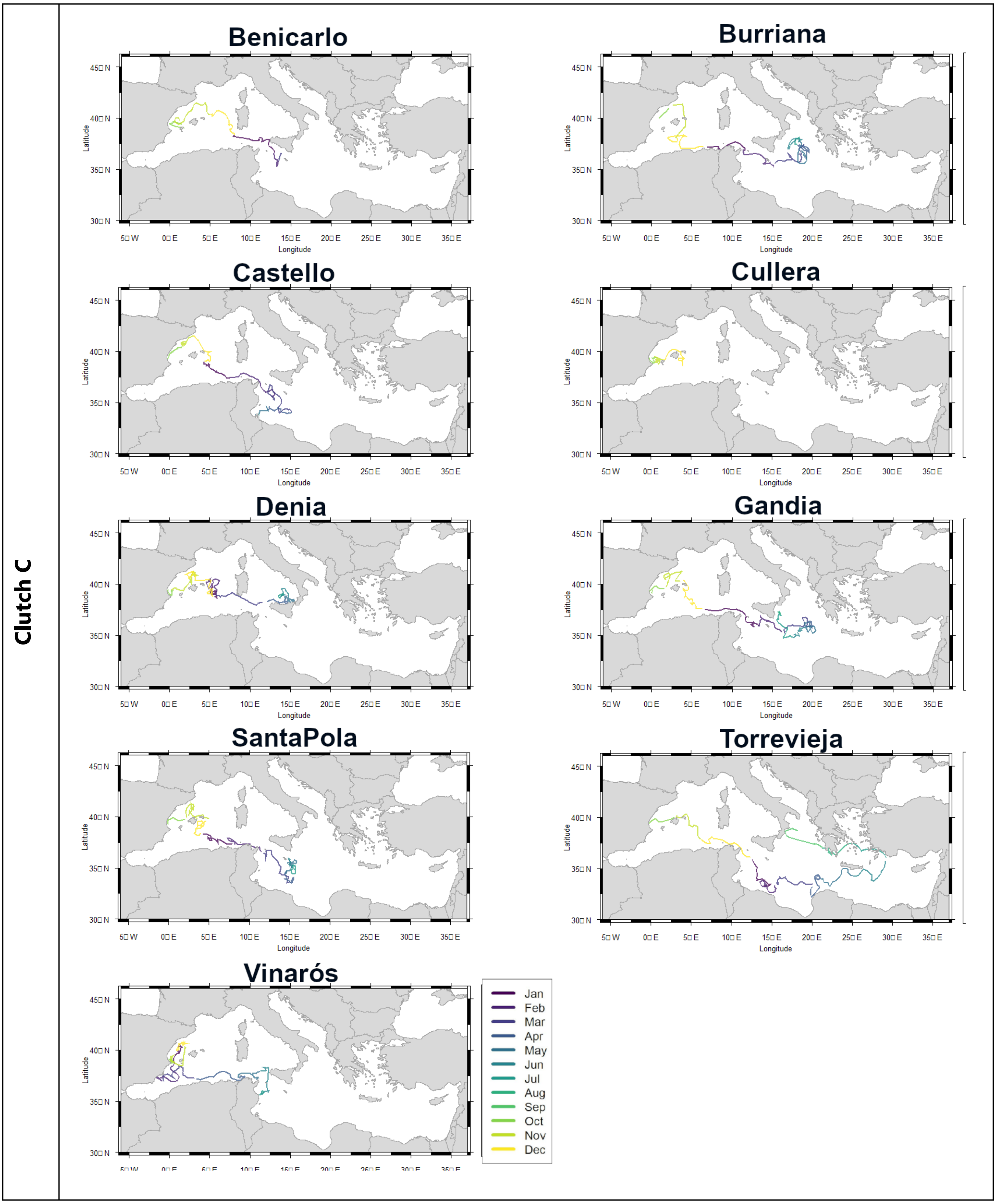

Figure 5.3 (continue) Dispersal trajectories for the monitored post-hatchlings in the Mediterranean Sea in the present study. Turtle ID is shown above each map. Colors in trajectories represent the month of the year as it is shown in the inset legend.

The Rayleigh's test of uniformity indicated preferential directions (non-random eastward directional movements) for all post-hatchlings from Clutch C and most individuals from Clutch B, except turtles ID: 12 Rabiosa, 14 Serena and 18 Bonita which had no preferential bearing (Figure 5.4) and remained in the Alboran Sea during the monitored period. Differences in bearing were observed among all individuals (Mardia-Watson-Wheeler test, $W = 76.208$ $d.f = 32$, $P < 0.001$) and between nests (Mardia-Watson-Wheeler test, $W = 7.9941$ $d.f = 2$, $P < 0.05$). However, if we consider clutches separately, dispersal movements were consistently directional for turtles of Clutch C (Rayleigh's test, $Z = 0.20$, $P < 0.001$) as there were no significant differences in orientation among them (Mardia-Watson-Wheeler test, $W = 20.969$ $d.f = 16$, $P > 0.05$). However, the mean bearing considering all turtles was consistently eastwards (Rayleigh's test, $Z = 0.66$, $P < 0.001$) (Figure 5.5).

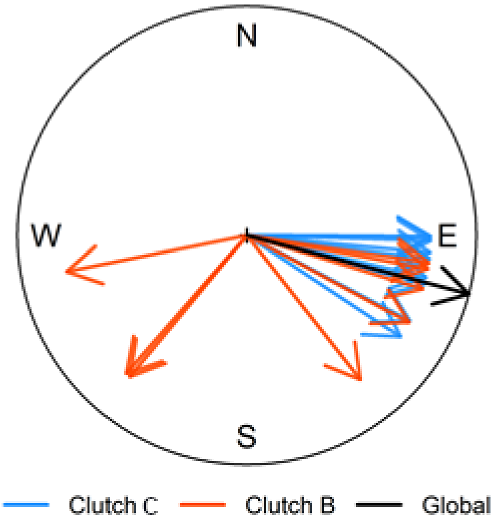

Figure 5.5 Mean bearing by turtle and nest. Mean bearing for each turtle is represented by arrows (red: turtles from Clutch B, blue: turtles from Clutch C). Black arrow shows overall mean bearing (Rayleigh's test, $Z = 0.66$, $P < 0.001$). Letters are cardinal points.

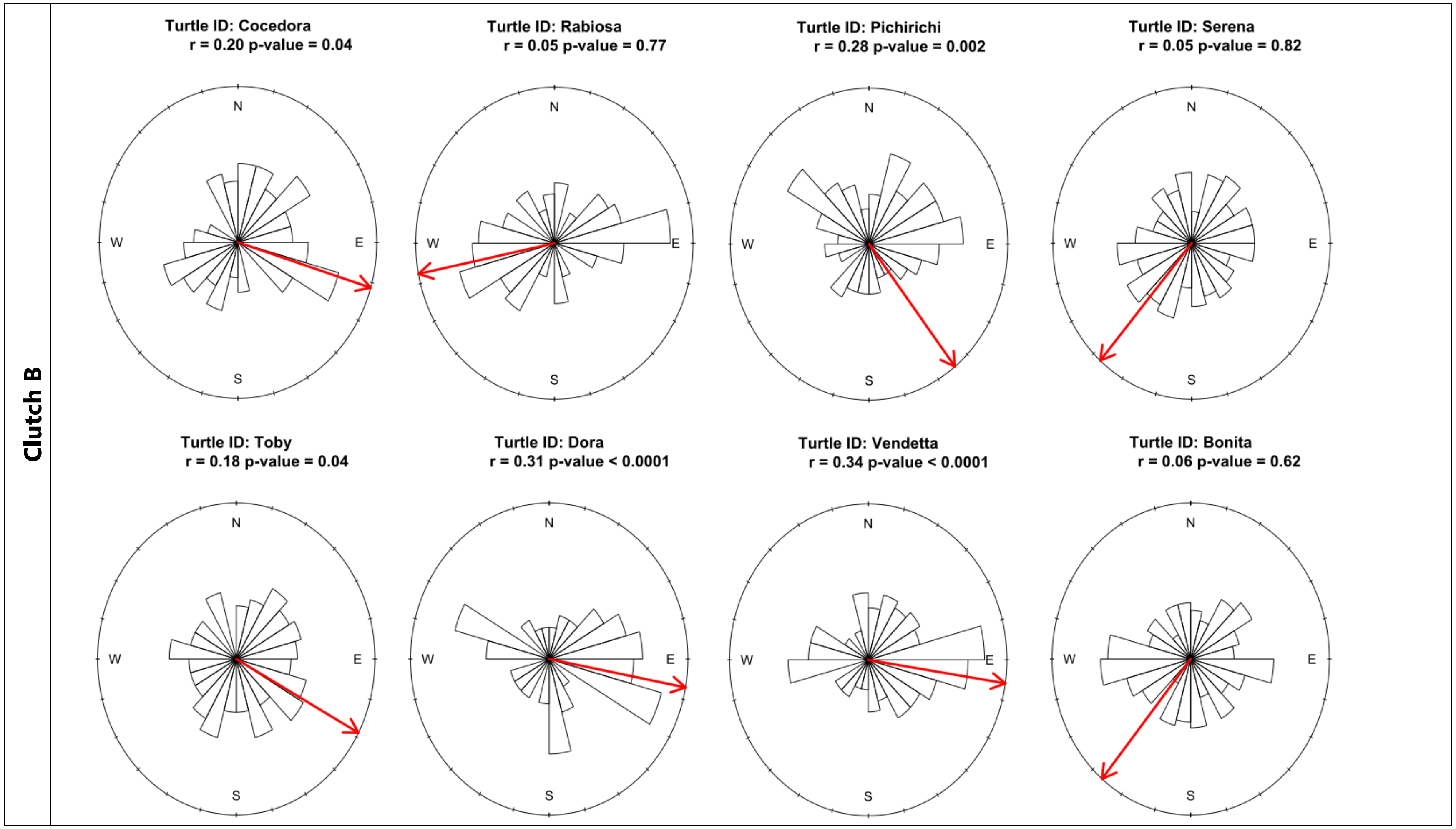

Figure 5.4 Circular plots of turtle bearing. Orientation values (white bars) and mean orientation (red arrow). Turtle ID and results of Rayleigh's test are shown on the top of each individual's plot. P-values < 0.05 indicate that turtles had significant and directional movement. The r value is also a measure of angular dispersion: This value can vary from 0 to 1, 0 indicating uniform dispersion and 1 indicating complete concentration of displacements in one direction.

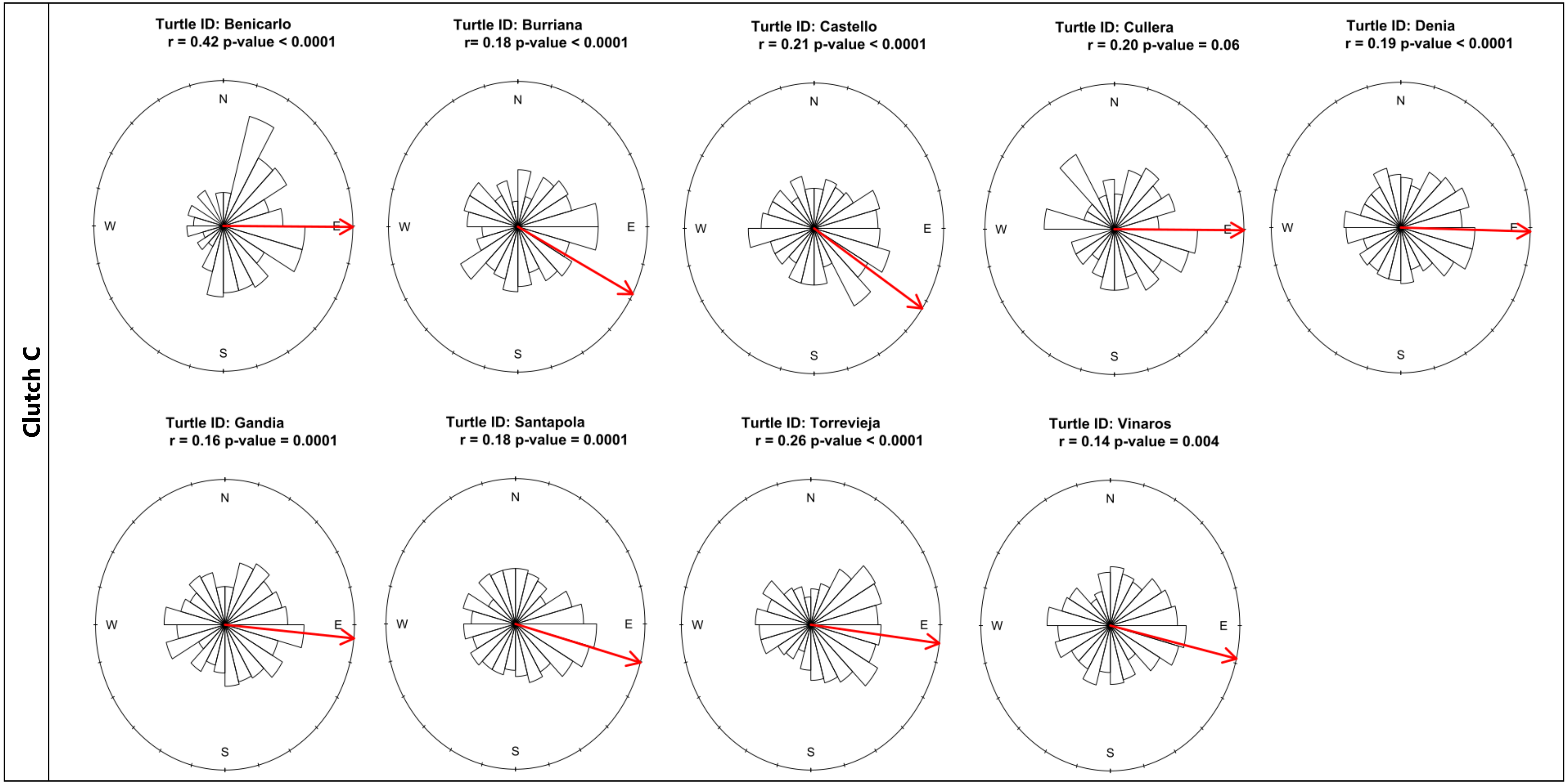

Figure 5.4 (continue) Circular plots of turtle bearing. Orientation values (white bars) and mean orientation (red arrow). Turtle ID and results of Rayleigh's test are shown on the top of each individual's plot. P-values < 0.05 indicate that turtles had significant and directional movement. The r value is also a measure of angular dispersion: This value can vary from 0 to 1, 0 indicating uniform dispersion and 1 indicating complete concentration of displacements in one direction.

Post-hatchlings from Clutch C followed a similar dispersal pattern after release (October to December), travelling through the northern waters of the Balearic Archipelago. Besides, long-term monitored post-hatchlings from Clutch C (*n* = 8) travelled consistently eastwards (Rayleigh's test, *P* < 0.001), crossed the Sicilian Strait, and reached Central Mediterranean, except turtle ID 24 Denia, that remained in the Tyrrhenian Sea until lost transmission. Most of these turtles (*n* = 6) started travelling consistently eastwards since December / January, and the others (*n* = 2) since March. Post-hatchlings from Clutch B presented two types of dispersal patterns after release: remained in the Alboran Sea (*n* = 7) or travelled to the Balearic Sea (*n* = 1). Long-term monitored post-hatchlings from Clutch B (*n* = 4) exhibited different dispersal routes, although two of them travelled consistently eastwards (Rayleigh test, *P* < 0.001) during winter (December to January), similar to post-hatchlings from Clutch C (Figure 5.4). Overall, monitored turtles travelled through areas with sea surface temperatures ranging between 10 - 30 º C and most locations were located on waters with temperatures above 15ºC (94.76%) (Figure 5.6). Daily mean sea surface temperatures in the Mediterranean basin over the period of satellite-tracking ranged between 5.1 – 31.7 º C.

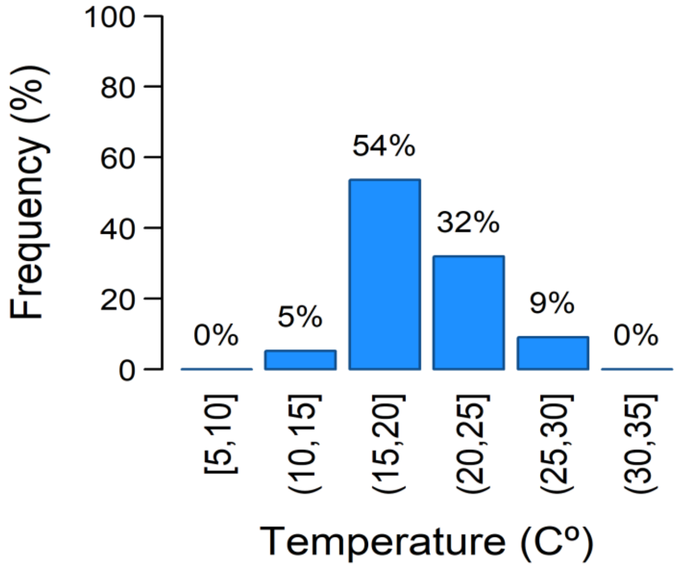

Figure 5.6 Frequency (in percent) of turtles' locations by sea surface temperature ranges. Percentage of locations is above and below each temperature range.

Turtles alternated among faster and slower movement phases during their monitoring (Figure 5.7). The residuals of track segmentation analysis were independent in all turtles confirming the validity of the approach (Wald and Wolfowitz test *P* > 0.05), except one of them (turtle ID: 7 Santapola), whose trajectory could not be significantly segmented in different movement phases.

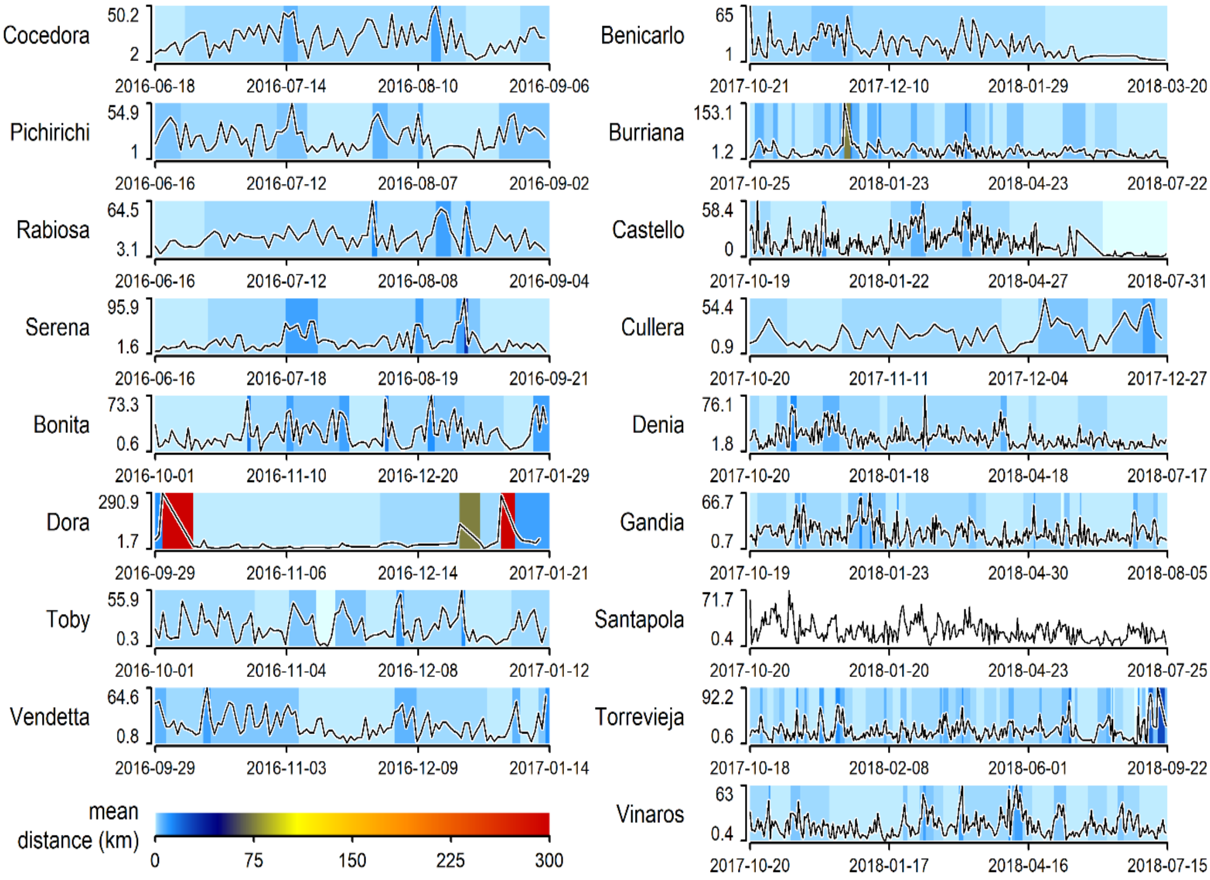

Figure 5.7 Movement segmentation analyses of trajectories for post-hatchlings of loggerhead sea turtle. Black lines show the mean distance travelled through time. Background colours indicate the movement model as shown in legend. Track segmentation analysis is shown only if significant. Turtle identity (ID) is shown next to each segmentation.

Monitored turtles showed both active dispersal and passive drifting. Turtles travelled both long and short distances along the sea currents (in cases, even faster than sea current velocity) or against them (Figure 5.8, Figure 5.9). Divergence of turtles' heading from current direction ranged from 0.01 to 179.85 degrees. However, we observed that the greater the magnitude of the current experienced by turtles, the divergence between turtles' heading and current direction decreased especially above 0.75 m/s of sea current velocity experienced (correlation coefficient = -0.30, t = -16.988, df = 2922, *P* < 0.001) (Figure 5.8, Figure 5.10).

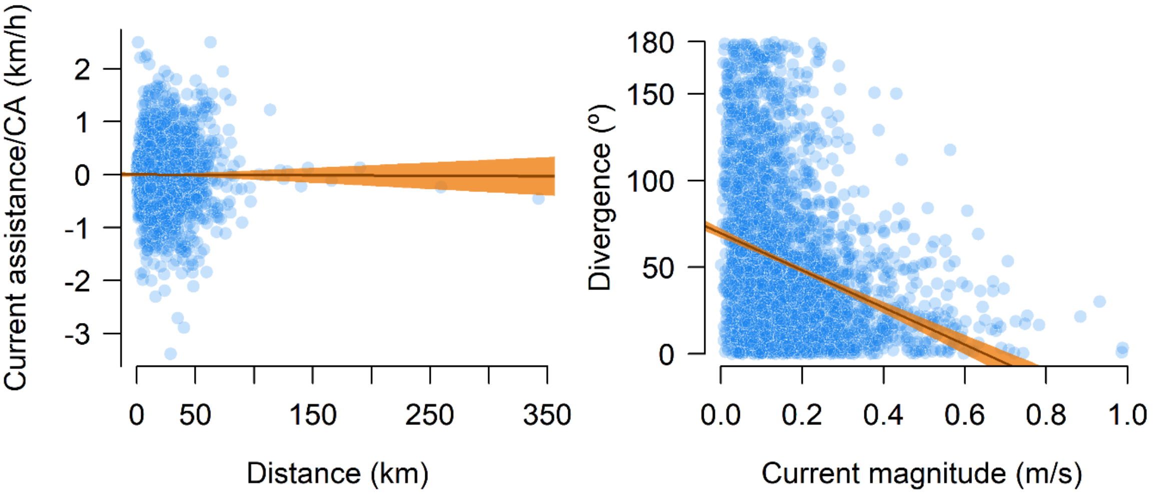

Figure 5.8 On the left: Distance travelled by turtles (km) and current assistance (km/h) experienced by turtles. Negative values of current assistance indicate that turtles travelled against sea current, and positive values of current assistance indicate that turtle travelled along sea currents. On the right: Divergence of turtle heading and current direction (in degrees) and the magnitude of the current (m/s). In each plot, blue dots are observations and the regression line and smoother are shown in orange.

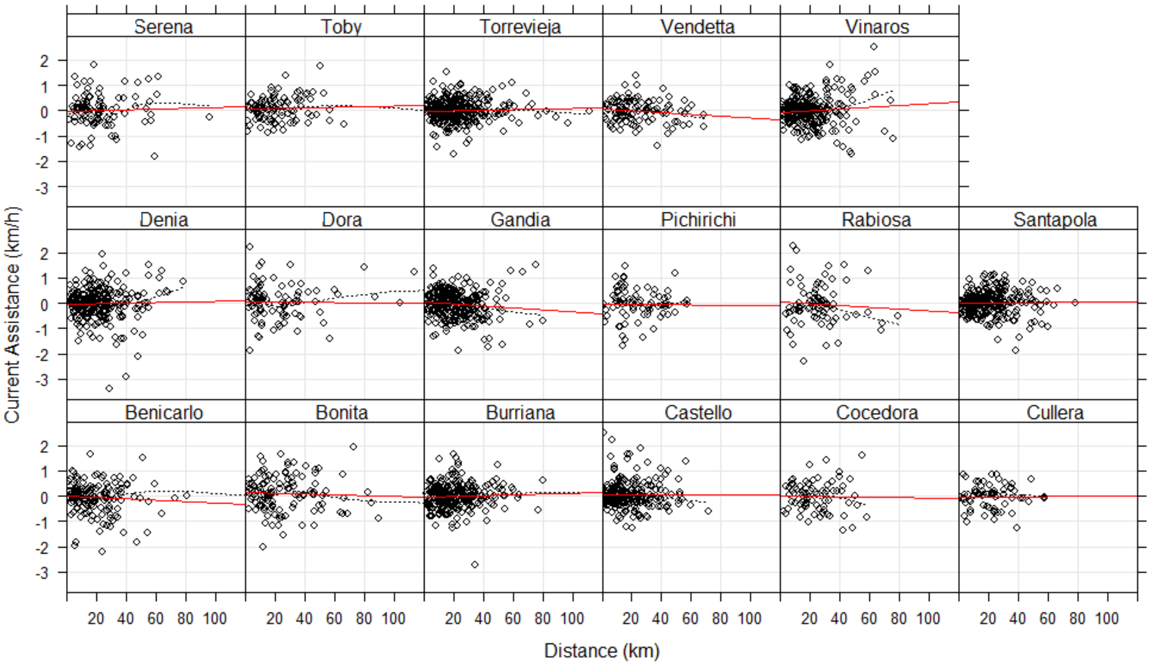

Figure 5.9 Distance travelled by turtles (km) and current assistance (km/h) experienced by turtles. Negative values of current assistance indicate that turtle travelled against sea current, and positive values of current assistance indicate that turtle travelled along sea currents. Turtle ID, regression line (red) and smother (dashed black line) are shown in each plot.

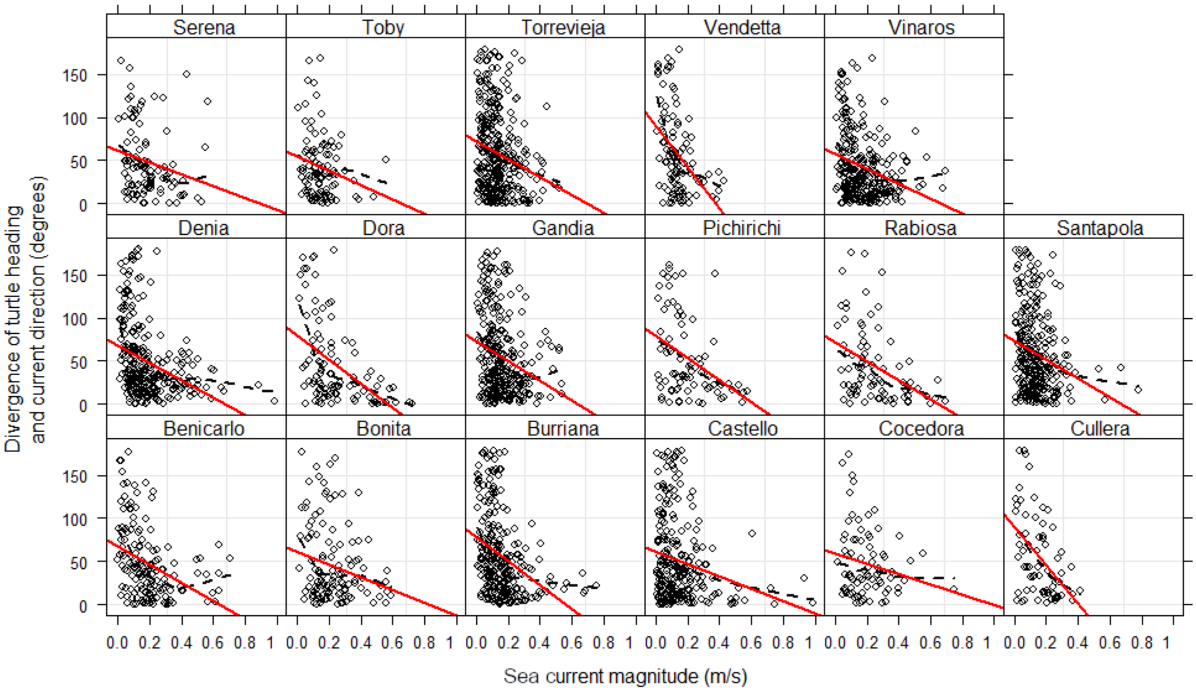

Figure 5.10 Divergence of turtle’s heading and current direction (in degrees) and the magnitude of the current (m/s). Turtle ID, regression line (red) and smother (dashed black line) are shown in each plot.

5.3.3 Habitat use modelling

The process of hyper-parameters' tuning and variable selection through cross-validation indicated that the most relevant predictors of habitat suitability were, in decreasing order, the individual, sea surface temperature, salinity, bathymetry, the month, sea surface height, the magnitude of the current and primary production were of minor importance (Figure 5.11). The sensitivity analysis indicated a temperature threshold at 15 °C because the probability of presence was very low (< 0.2) below this limit (Figure 5.12). The higher probability of presence was observed above 39 ‰ salinity and the lowest probability occurred below 37 ‰. Waters above deeper areas exhibited higher suitability for post-hatchings, especially in areas more than 3,000 meters deep, where the probability of presence was higher. Sea surface height, magnitude of the current and primary production were of minor relevance, as their influence depended on the clutch/individual.

Habitat suitability maps by month indicated that the eastern Mediterranean Sea (Ionian Sea and Levant Sea) might be key year-round developmental areas for post-hatchlings (Figure 5.13). Other suitable areas for loggerhead post-hatchlings were only for certain periods/seasons: the Tyrrhenian Sea (from April to December), the Sicilian Channel (from July to October), the Algerian basin (during September, October and January), the North Adriatic Sea and the Gulf of Lion (from July to August), and the South Adriatic Sea (during September).

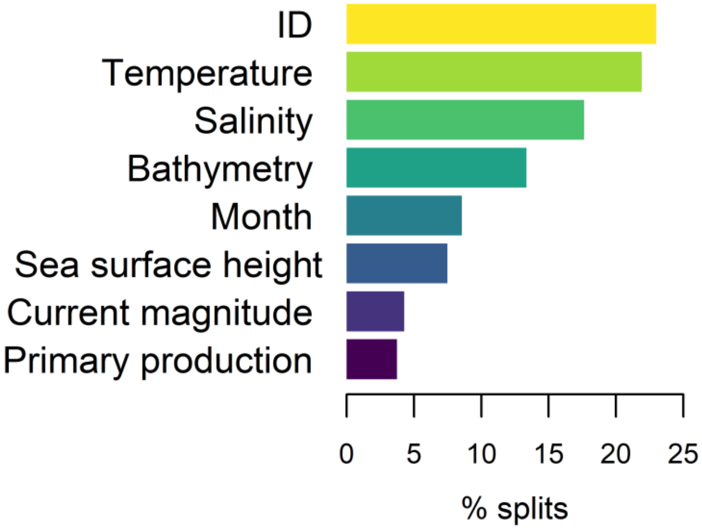

Figure 5.11 Ranking of variable importance considered in the habitat suitability analysis.

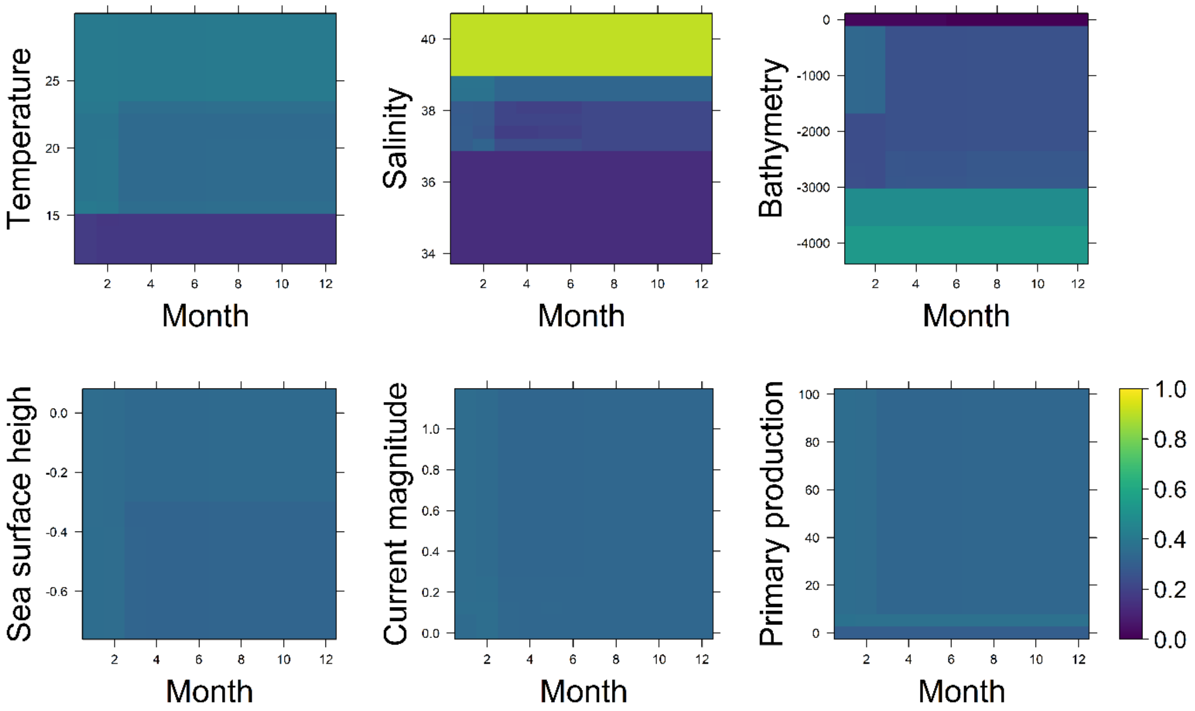

Figure 5.12 Suitable habitat probability of loggerhead post-hatchlings by environmental variables and month. Units of variables: temperature is in °C, salinity in ‰, bathymetry in meters (m), sea surface height in m, magnitude of the current in m/s and primary production in mg/m^3.day. Colour scale of probability is shown at right.

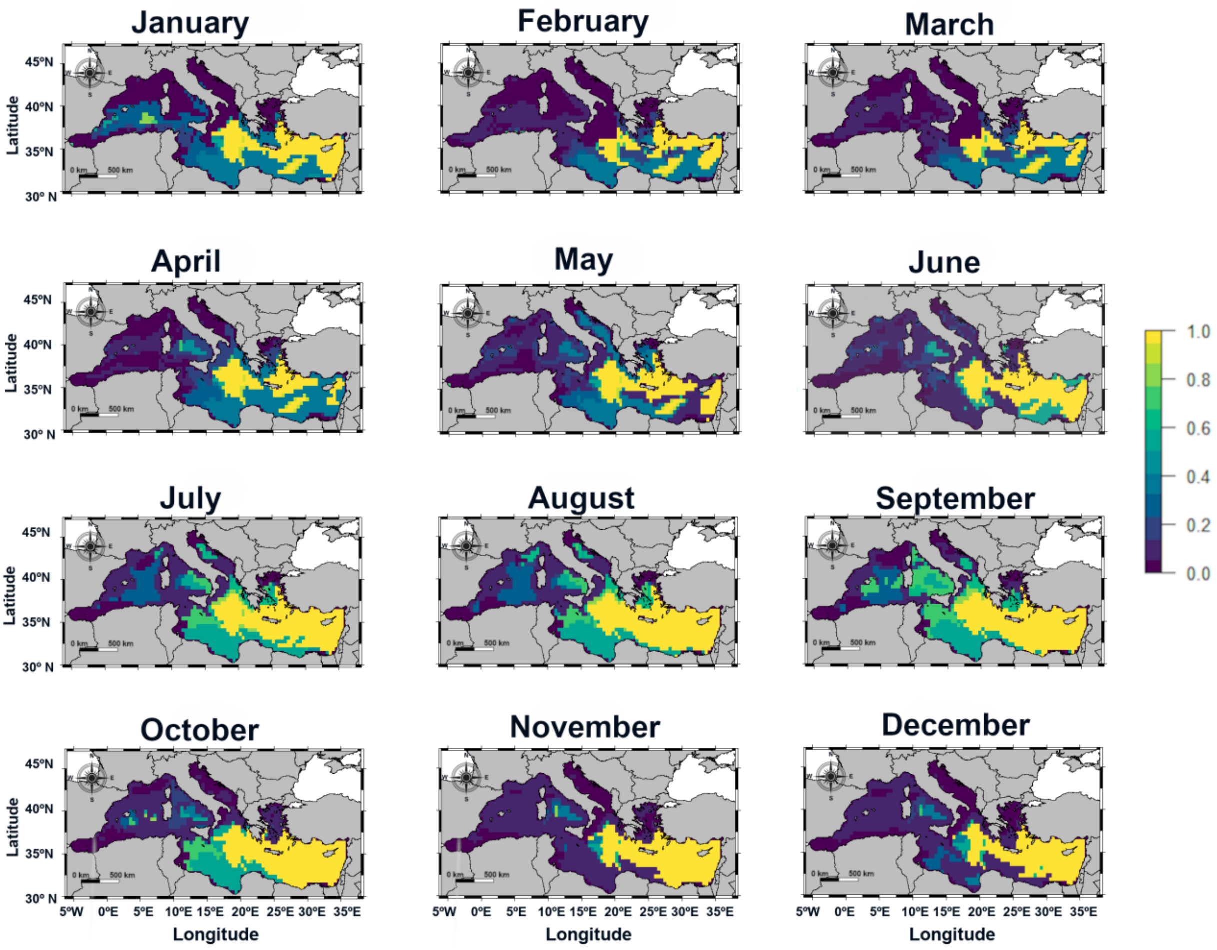

Figure 5.13 Suitable habitat probability maps by month of loggerhead post-hatchlings in the Mediterranean Sea. Colour scale are probability values.

5.4 Discussion

Several authors have suggested that head-started marine turtles may present low survival probabilities (Cardona et al. 2012), especially during the first weeks after release (Burke 2015). However, our results show high daily survival probability (0.99 – 1.00) of head-started loggerhead turtles during the first three months after release is high, supporting a previous study based on satellite-tracked loggerhead post-hatchlings in the Mediterranean Sea (see Chapter 4 of this thesis). Furthermore, survival estimates we obtained could be underestimated due to tag failure or tag loss (Lebreton et al. 1992), as we assumed that the likelihood of tags remaining attached decreased after the first month of monitoring (as in Chapter 4). Moreover, similar studies elsewhere showed that tagging method did not hinder the growth of post-hatchlings satellite tagged (Mansfield et al. 2012). Nonetheless, even considering a potential effect of tagging in survival or abnormal behaviour of the turtles, our survival estimates suggest that reintroduced head-started loggerhead post-hatchlings were able to survive in the wild, at least during the most critical period after release (as in Chapter 4), supporting the short-term success of reintroduction into the wild of head-started turtles (Armstrong and Seddon 2008).

Regarding dispersal movements, our satellite-tracked post-hatchlings dispersed over large areas, travelled long distances, exhibited highly variable routes and showed eastward directional movement, in the majority of cases, over the entire track (14 out of 17 turtles) as in other similar studies (i.e., Okuyama et al. 2010, Mansfield et al. 2014, 2017). Only 3 turtles from Clutch B had no directional movement over their track and remained in the Alboran Sea until transmission was lost. This result might be influenced by possible post-hatchling genetic differences as nesting females in the Spanish Mediterranean coast may have Mediterranean or Atlantic origin, and multiple paternities in the same clutch were observed in most cases (Carreras et al. 2018). Previous studies satellite-tracking loggerhead juveniles (Revelles et al. 2007a), and also post-hatchlings from Spanish nests revealed the absence of directional movement over the entire monitoring period (Chapter 4 of this thesis), although in this last study track duration was in general much shorter than those analysed in the present study, especially during the coldest months in the western Mediterranean.

Our findings suggest that active dispersal movements of loggerhead post-hatchlings in the western Mediterranean are more relevant than expected, as was observed in recent studies in the Atlantic and Pacific oceans (Mansfield et al. 2014, 2017, Putman and Mansfield 2015, Briscoe et al. 2016, Chambault et al. 2019). In the Mediterranean Sea previous studies have suggested that strong currents (i.e., Algerian current) may force immature loggerheads to drift along them (Revelles et al. 2007c). However, we observed that turtles swam actively rather than passively, and even at a higher velocity than ocean currents probably driven by their physiological need to remain in (or travel to) suitable developmental areas, which emphasize previous observations (Chambault et al. 2019).

We recorded for the first time post-hatchlings from Spanish nests crossing the Sicilian Channel and reaching the eastern Mediterranean basin, where seawater temperatures are warmer than other Mediterranean Sea regions. Traditionally, a limited exchange between the eastern and western Mediterranean basins has been estimated for hatchlings and post-hatchlings originating in the western Mediterranean. Turtles would be expected to be retained in the South Tyrrhenian Sea (Maffucci et al. 2016), which is considered an important foraging and overwintering area, due to the presence of volcanic islands and seamounts (Blasi and Mattei 2017, Luschi et al. 2018, Chimienti et al. 2020). By contrast, our results showed that at least 7 of our tracked turtles were able to pass through the Sicilian Channel to reach the eastern Mediterranean basin, and only one post-hatchling was retained in the South Tyrrhenian Sea, proving the dispersal capability of post-hatchlings to reach an appropriate developmental area. No post-hatchling crossed the Gibraltar Strait during the monitoring period, which supports that small loggerheads (< 36 cm) are unlikely to cross the Gibraltar Strait towards the Atlantic Ocean (Revelles et al. 2007b). However, ongoing studies on new satellite tracked post-hatchlings could show different dispersal patterns due to the exceptionally high sea surface temperatures recorded in the 2020-2022 period at the western Mediterranean.

Turtles make latitudinal displacements to forage and escape extreme temperatures (Hawkes et al. 2011, Zbinden et al. 2011) to remain in their suitable temperature thermal range (Chambault et al. 2019), as we observed in our satellite-tracked post-hatchlings during the periods of coldest sea surface temperatures. The habitat model corroborated that seawater temperature is an important variable driving the species distribution, especially during its early life stage (Mansfield et al. 2009, Varo-Cruz et al. 2016). It has been observed that marine turtles select temperatures that maximize their growth and swimming capability between 30 and 10 ºC, which has been established as the threshold before hypothermic stunning (O'Hara 1980, Coles and Musick 2000). In concert with these results, our habitat model established a temperature threshold at 15 ºC, and our tracked post-hatchlings travelled along sea surface areas across the expected temperature range (10 - 30 ºC), supporting the aforementioned studies (Coles and Musick 2000, McMahon and Hays 2006, Mansfield et al. 2009, Abecassis et al. 2013, Patel et al. 2021).

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

The habitat model also indicated that post-hatchlings in the Mediterranean Sea spent more time in oceanic areas over deep areas and generally avoided neritic zones. This result supports that post-hatchlings belong to the oceanic phase of sea turtle life history (Bolten 2003, Mansfield et al. 2014), which suggests that early life stages of turtles can spend more than a decade in the open ocean (Chambault et al. 2019). Other predictor environmental variables, of minor relevance in this study, might be important when considering the individual separately. Former studies in the Pacific Ocean found that satellite-tracked juvenile turtles were distributed in more productive waters (Polovina et al. 2006, Abecassis et al. 2013). By contrast, in the western Mediterranean Sea, immature turtles did not aggregate in productive areas (i.e., coastal waters, Gulf of Lion, Ligurian Sea, D'Ortenzio and Ribera d'Alcalà 2009), probably because those regions are not more favourable than the adjoining areas or because immature turtles fail to recognize them (Revelles et al. 2007c). However eastern Mediterranean waters are very oligotrophic when compared to western Mediterranean waters (Bosc et al. 2004). Sea surface height has been related to seawater productivity, but only larger turtles respond to variations in sea surface height in the Mediterranean Sea (Eckert et al. 2008). Furthermore, despite previous studies suggesting the effect of the Earth's magnetic field over dispersal of small loggerheads due to their innate magnetic sense (Lohman et al. 2012, Putman et al. 2012b, Scott et al. 2012), our results showed other that other environmental variables had a stronger effect in post-hatchlings dispersal.

The predictions generated with the habitat model evidenced how the eastern Mediterranean basin, especially the deep waters of the Ionian Sea and the Levant Sea are key year-round developmental areas for loggerhead post-hatchlings from western Mediterranean nests. This conclusion can be most probably extended to hatchlings because the eastern Mediterranean basin is also a known foraging ground for adults of loggerhead turtle (Zbinden et al. 2008, Schofield et al. 2010a, Mingozzi et al. 2016, Almpanidou et al. 2022). Other suitable areas identified in this study were the Algerian basin and the deep waters of the Sicilian Channel, which are presumably foraging grounds for the loggerhead turtle (Bentivegna 2002, Casale et al. 2012c).

Recorded loggerhead sea turtle nesting events in the western Mediterranean took place from June to September, and hatchling emergence occurred from July to October (Tomás et al. 2002, Tomás et al. 2008a, Bentivegna et al. 2008, Benabdi and Belhami 2020, González-Paredes et al. 2021). Considering these emergence dates, the predictions obtained with the habitat suitability model, point out the Algerian basin and the Sicilian Channel as suitable habitats for loggerhead post-hatchlings during the period after emergence (from July to October), although this result could be biased by the release date of our monitored turtles. Nonetheless, our results could support our hypothesis that hatchlings from western Mediterranean nests disperse eastwards after entering the sea, probably driven by environmental conditions (i.e., temperature) and occasionally taking advantage of sea currents, to reach suitable developmental areas in the eastern Mediterranean (i.e., Levantine Basin, the Ionian Sea, the Gulf of Gabès) (Casale and Mariani (2014). Nevertheless, further research is needed to fully understand the movement patterns of hatchling and post-hatchling loggerheads in the Western Mediterranean to develop more effective conservation strategies for the species. To achieve this goal, it will be necessary to improve the monitoring technologies to track sea turtle hatchlings since their emergence, and over longer periods of their oceanic stage. Our results provide the first picture about the habitat use and the preferred developmental areas for loggerhead post-hatchlings from Spanish nests.

5.5 Conclusions

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

Chapter 6

Marine protected areas and loggerhead turtles in the Mediterranean Sea

Edited version of:

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6.1 Introduction

The Mediterranean Sea is recognised as a hotspot of marine biodiversity because it comprises around 9% of the planet's marine species diversity (MedPAN and UNEP-MAP-SPA 2016). However, it faces many conservation challenges, like pollution, marine traffic, exploration and extraction of hydrocarbons, severe overexploitation of marine resources by fisheries (including bycatch), and impacts of both climate change and invasive species (Halpern et al. 2008, Coll et al. 2012). All these threats result in the decline and loss of the populations and habitats of marine species (MedPAN and UNEP-MAP-SPA 2016, FAO 2018). One of the measures currently at the forefront of marine conservation is to establish marine protected areas (MPAs). In recent decades, the number of proposed and designated MPAs increased in the Mediterranean Basin as a result of Aichi Biodiversity Target 11 of the Convention on Biological Diversity (CBD), whereby signature countries agreed to protect and effectively manage 10% of coastal and marine areas by 2020 (CBD 2010, Boonzaier and Pauly 2016). To date, there are 1,233 MPAs and other effective area-based conservation measures (OECMs) in the Mediterranean that cover 236,713 km^2, which means that 9.4% of the Mediterranean surface is legally designated as protected. These MPAs are not evenly distributed, they occur mainly (90%) in northwest, coastal European waters (MedPAN and UNEP-MAP-SPA 2016). There are also strong biases both for the geographic distribution of protected areas in the Mediterranean, mainly in the northwest, and for the type of protected ecosystems, mainly coastal (Micheli et al. 2013b, Amengual and Alvarez-Berastegui 2018). This distribution seems to poorly protect oceanic species or species with a large distribution range and broad mobility (Micheli et al. 2013a). In fact, there is a general lack of connectivity between Mediterranean MPAs. An interconnected MPA network is especially relevant when considering wide-ranged species with a complex life cycle involving different areas, including those beyond the boundaries of designated sites (Pendoley et al. 2014, Amengual and Alvarez-Berastegui 2018). The use of MPAs to protect highly mobile marine species can prove difficult as their ranges may encompass large areas, and even entire ocean basins (Block et al. 2011, Fortuna et al. 2018). Nonetheless, many mobile marine megavertebrates display high site fidelity to specific regions on a seasonal or yearly basis, which allows the protection of key areas (Pendoley et al. 2014).

Marine turtles may use distant areas in their different life stages (Bolten 2003). Given their long life cycle and their late reproductive maturity age (Bolten 2003, Casale et al. 2011), they are particularly vulnerable to threats, such as fisheries bycatch, boat strikes, seismic surveys, debris ingestion and climate change effects (Carreras et al. 2004, Tomás et al. 2008b, Casale and Margaritoulis 2010, Witt et al. 2010a, Baez et al. 2013, 2019, Camedda et al. 2014, Rees et al. 2016, Casale and Heppell 2016, Casale et al. 2018, Domènech et al. 2019). Consequently, marine turtle protection is challenging because their movements may span vast distances and cross international maritime borders (Mazor et al. 2016, Harrison et al. 2018).

The loggerhead sea turtle is a priority species listed in Annexes II and IV of the Habitats Directive (European Comission 2007) and is considered 'Vulnerable' by the IUCN (Casale and

Tucker 2017). Species listed in Annex II should be protected in the core areas of their habitat, that must be designated as Sites of Community Importance (SCIs) and included in the Natura 2000 Network (European Comission 2007). Species listed in Annex IV should be strictly protected across their natural range by ensuring that other activities will not lead to incidental killing or specimens being captured (European Comission 2007). In the Mediterranean, the loggerhead is catalogued as Least Concern, but this status should be considered to be conservation-dependent as the current population in this sea is the result of decades of intense conservation programmes, especially at nesting sites (Casale et al. 2018), and cessation of these programmes could be followed by a declining population (Casale and Tucker 2017).

The western Mediterranean, which comprises the waters from the east Gibraltar Strait up to the west Sicilian Channel, is an important foraging area for Mediterranean and Atlantic management units of loggerhead sea turtle (Clusa et al. 2014). Furthermore, in the last decade, nesting events have been recorded in this basin, out of the nesting range of the species (Tomás et al. 2008b, 2015, Báez et al. 2020). These nesting events are probably the result of an incipient colonization process guided by global warming (Tomás et al. 2008a, Maffucci et al. 2016, Carreras et al. 2018).

Despite management plans of 40 Mediterranean MPAs mention the loggerhead turtle as a priority species to protect, few studies about the suitability and use of Mediterranean MPAs by this species have been published, and those that exist have focused on specific regions and life stages (Schofield et al. 2010b). Thus, far from the nesting protected areas in eastern Mediterranean, MPAs contribution to loggerhead conservation remains unknown and should be assessed in order to protect important areas for this species that might remain unprotected and, thereby, contribute to reach MPAs stated goals.

For this assessment, complete knowledge of the life history stages and understanding how loggerhead turtles use space is essential (Hazen et al. 2012, Maxwell et al. 2013, Edgar et al. 2014, Fortuna et al. 2018). MPAs contribution to conservation depends on the quality and level of enforcing the management measures undertaken to reduce the impact of threats on loggerhead turtles in their habitats (Agardy et al. 2011, Hooker et al. 2011, Di Franco et al. 2018). One methodology to assess the use of MPAs by loggerhead turtles involves computing the overlap of their high-use areas and the current MPAs by using data acquired in tracking studies (Casale et al. 2013, Schofield et al. 2013b, Revuelta et al. 2015, Casale and Simone 2017, Snape et al. 2018). Home range estimations and relative density maps are frequently used tools to reveal the distribution patterns and space-use hotspots of marine animals (Queiroz et al. 2019) and to assess conservation management measures of loggerhead sea turtles (Schofield et al. 2010a, 2013a, Gredzens et al. 2014). Thus, both methods can be used for identifying loggerhead sea turtle core areas of activity and underscoring hotspots that can be incorporated into conservation management strategies for their protection if they are not already protected (Casale et al. 2012a, Schofield et al. 2013a, Levy et al. 2017, Hays et al. 2019).

The study related to the present chapter used the satellite tracking data of a large sample size of loggerhead sea turtles of different life stages, captured and released in the western Mediterranean over the 2003-2018 period, to describe the species distribution in this sea. The aim was to analyse the overlapping of the loggerhead turtle distribution and its hotspots over the MPAs in the Mediterranean Sea, to assess whether current MPAs represents an effective conservation strategy for the wide-ranging transboundary loggerhead sea turtle.

6.2 Methods

6.2.1 Studied turtles

The satellite tracking data of 103 loggerhead sea turtles tagged and released in the western Mediterranean over the 2003-2018 period were used here: 17 post-hatchlings (headstarted yearlings, < 24 cm straight carapace length, SCL), 10 early juveniles (24 – 40 cm SCL), 59 late juveniles (> 40 - 70 cm SCL) and 17 adult-size turtles (> 70 cm SCL), four of which were nesting females (Table 6.1, further details can be found in Annex I, as well as in our own dataset, which is available at the EMODNet repository ([dataset] Abalo-Morla et al. 2022). All data described in Annex I were used in the present Chapter, except Clutch A and nesting turtles with Argos IDs 86260, 222027, 222028, and 232741, which were tagged after the completion of this chapter.

Table 6.1 Satellite tracking data information by life stage. Sex, percent of turtles taken from bycatch events, range of deployment years, mean track duration, standard deviation of the mean (SD), maximum and minimum tracking durations in days and Economic Exclusive Zone (EEZ) of release. Post-hatchlings had from 9 to 13 months old at the time of release.

Life stage	Sex	% Bycatch	Range of deployment years	Mean tracking duration (days)	SD (days)	Minimum (days)	Maximum (days)	EEZ release
Adults (*n* = 17)	2 male 5 female 10 unknown	24%	2008-2018	107	115	14	394	Spain
Late juveniles (*n* = 59)	1 male 1 female 56 unknown	34%	2003-2018	121	100	6	339	11 Italy 48 Spain
Early juveniles (*n* = 10)	All unknown	36%	2003-2018	111	89	22	317	Spain
Post-hatchlings (*n* = 17)	All unknown	0%	2016-2017	174	96	69	337	Spain

The post-hatchlings originated from sporadic nesting activity in different regions of the Spanish Mediterranean (see Chapter 4 for further details) were selected based on their swimming and diving activities, and the appropriate size for tagging, ensuring that tags did not hinder behaviour or turtle growth (Mansfield et al. 2012). Several (n= 28) juvenile and adult turtles originated from bycatch or entanglements and were tagged and released immediately after capture, or if needed, after full recovery in rescue centres to minimize the possibility to be compromised (see Annex I). It is possible that movement patterns displayed by these turtles may have been biased by time spent in confined spaces and maintenance conditions in rehabilitation centers, or by trauma, stress, and injuries inflicted during fishing operations or other human activities (Cardona et al. 2012). Otherwise, recent satellite-tracking studies about recovered turtles showed that behaviour of amputees and non-amputees turtles was similar after release, even with severed front flippers (Abalo-Morla et al. 2018, Robinson et al. 2021). Thus, we could infer that our recovered turtles could be used as a proxy for wild animals. Juvenile turtles were separated into early juveniles and late juveniles because the transition between passive drifting and active habitat selection seems to occur at an SCL of about 40 cm (Cardona et al. 2005). The turtles larger than 70 cm SCL were considered adults as 70 cm was assumed as the minimum SCL for adult loggerhead turtles from the Mediterranean or Atlantic populations inhabiting the Mediterranean Sea (Margaritoulis et al. 2003, Casale et al. 2011, and references therein). Nesting females were tagged avoiding disturbance on the nesting behaviour after the nesting event, when turtles were heading back to sea. Only one female (Turtle ID 160303) was tagged after being in a rescue center, where it was taken after applying a stranding protocol by local authorities. Nesting turtles with Argos IDs 86260, 222027, 222028, and 232741 which are present in the Annex I, were tagged after the completion of this chapter and, therefore, were not included in the data analyzed in this chapter. Tracking data were obtained from own tracking projects (available at data repository [dataset] Abalo-Morla et al. 2022) and from published satellite tracking datasets (Williard et al. 2015, Cardona and Hays 2018, see Annex I). We considered that our sample size could offer an approach about loggerhead dispersal and habitat use for individuals tracked from western Mediterranean.

6.2.2 Location data acquisition and data processing

As in previous chapters of the present thesis, the location data were collected by the Argos system, which classifies seven location classes (LC) of decreasing accuracy (3, 2, 1, 0, A, B, Z). LCs 3, 2, and 1 have Argos estimated errors of less than 250 m, 500 m, and 1,500 m, respectively (CLS 2016). However, in this case we used state-space models (SSM), which are a general and highly flexible statistical tool that allows position estimates to be inferred from the observed data by accounting for measurement errors and variability in movement dynamics (Jonsen et al. 2005, 2007, 2013). These models have been previously applied to model the movements of marine animals, including marine turtles (Jonsen et al. 2007, Hoenner et al. 2012). A hierarchical switching state-space model (hDCRWS) was fitted to our data to provide a position estimate at regular 24-hour intervals (Jonsen et al. 2007, 2016, Christiansen et al. 2016) using the 'bsam' R-package (Jonsen et al. 2005) in R 3.4.3 (R Development Core Team 2019). Two Markov Chain Monte Carlo (MCMC) chains for 120,000 iterations were ran by dropping the first 60,000 samples as a burn-in and retaining every 10th sample from the remaining 60,000 assumed post-converge samples from each chain to reduce sample autocorrelation. Thus, the model parameters and estimated locations were calculated using 12,000 MCMC samples. A 24-hour time step was used to generate one daily location of the tracking period from the posterior means of the resultant distributions. SSM locations were post-processed to remove terrestrial locations (Arendt et al. 2012a, Hoenner et al. 2012).

6.2.3 Home range estimation and relative density estimation

Post-processed state-space model locations were used to estimate the loggerhead turtle home ranges and relative density estimations from our data (Hoenner et al. 2012, Pendoley et al. 2014, Queiroz et al. 2019). A home range is theoretically defined as the area in which an animal conducts its daily activities, and excludes atypical migrations or unpredictable movements (Worton 1989). We used the utilisation distribution (UD) to define the spatial extent of an animal's home range and measure the spatial intensity of use. The core areas of UDs are high-use areas defined as portions of the home range that exceed equal-use patterns (Samuel et al. 1985). Kernel Utilization Distribution (KUD) (Worton 1989) was computed using the 'adehabitatHR' package in R (Calenge 2006), with the reference bandwidth as a smoothing parameter (Christiansen et al. 2016, Dujon et al. 2018). Home range areas were identified using KUD up to the 95% contour levels. Core areas were identified using KUD at two different levels, 50% and 25% KUD (Powell 2000), for the whole tracking dataset and for each life stage throughout the monitoring period (Lockhart and Barco 2015). The terrestrial area that overlaped with home range areas was excluded from the home range estimations using QGIS 2.18.0 (QGIS Development Team 2019). Home range and core areas were represented on maps of the Mediterranean Sea.

The habitat-use maps obtained from the tracking data are likely biased towards the tagging site. To address biases associated with variable track lengths and shorter tracks near the tagging location, we applied a time weighting procedure to compute less biased relative density estimates (Block et al. 2011, Queiroz et al. 2019). Following Queiroz et al. (2019), each daily location estimated for each individual was weighted by the inverse of the number of all individuals with location estimates for the same relative day of their track. Location weights after a threshold day of the number of tracking day (day 220) were fixed equal to the weight on the day corresponding to the 85th percentile of track lengths in order to minimize bias in lower sample sizes (Queiroz et al. 2019). In this way, individual location estimates closer to the deployment location tended to receive a lower weight than later locations. All individuals contributed equally to the described global spatial density patterns because their weights were normalized so that they summed to 1. Hotspots were defined as areas within the upper 75% percentile of weighted daily location density. Relative density maps were obtained at a

0.25º x 0.25º grid-cell for i) the whole tracking dataset and ii) each life stage throughout the monitoring period.

6.2.4 Use of MPAs

To analyse the use of Mediterranean MPAs by the loggerhead sea turtle, the post-processed SSM turtle location point data were overlapped in the Marine World Database on Protected Areas (Revuelta et al. 2015, IUCN and UNEP-WCMC 2020). To avoid MPA use overestimation that might be caused by MPAs whose areas overlap, we counted presence once in these cases. The turtle presence was assigned to the smaller area in which the presence point fell to observe possible important small MPAs. However, if the presence point was located in a border of a MPA which overlaps with another MPA that better englobed the presence point, the location was assigned to the last. A residency index was estimated by dividing the number of days in which a turtle was detected within MPA boundaries by the total number of days that the turtle was monitored (Mason and Lowe 2010, Revuelta et al. 2015). The abundance (total number of individuals) and density (individuals km^2) for our monitored turtles within limits of MPAs were also calculated (Fortuna et al. 2018). The estimated relative density, home ranges and core areas were mapped for each life stage and for the whole sample of tracked turtles to compute the percentage of overlapping between turtles locations and MPAs (Schofield et al. 2013a, Revuelta et al. 2015, Fortuna et al. 2018). Weighted location data by Economic Exclusive Zones (EEZ) extension were also overlaid over EEZ (Flanders Marine Institute 2018) to compare the use turtles made among countries' EEZ. Bathymetry data were obtained using the 30 arc-second resolution GEBCO global bathymetric model (GEBCO 2014, Weatherall et al. 2015). The classification between neritic and oceanic zones was divided by the 200 m isobath. A two-way ANOVA was conducted to test if the differences in the use of neritic and oceanic zones between life stages were significant. A 5% significance level was used in all the analyses. The considered Mediterranean regions are those shown in Chapter 3 (Figure 3.1).

6.3 Results

6.3.1 Tracking data

The monitored individuals travelled extensively the Mediterranean Sea, mainly throughout its westernmost region (Figure 6.1). Turtle trajectories by life stage and turtle trajectories over bathymetry data and release points are shown in Figures 6.2 and 6.3, respectively.

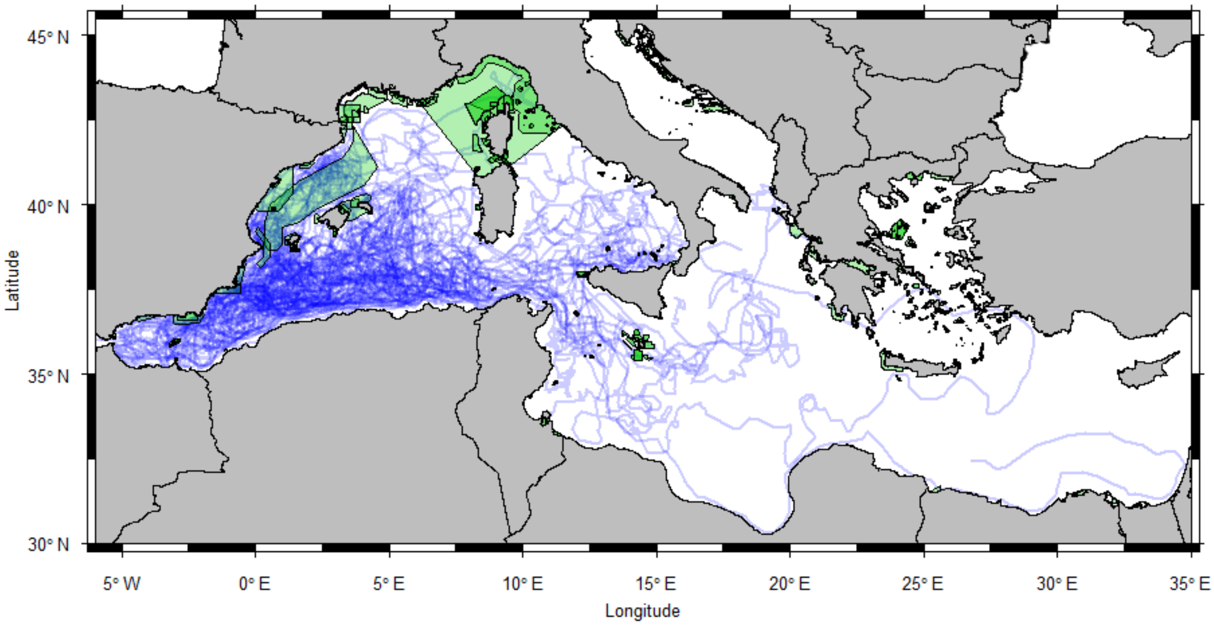


Figure 6.1 Tagged turtles' trajectories (in blue) and marine protected areas (green) in the Mediterranean Sea.

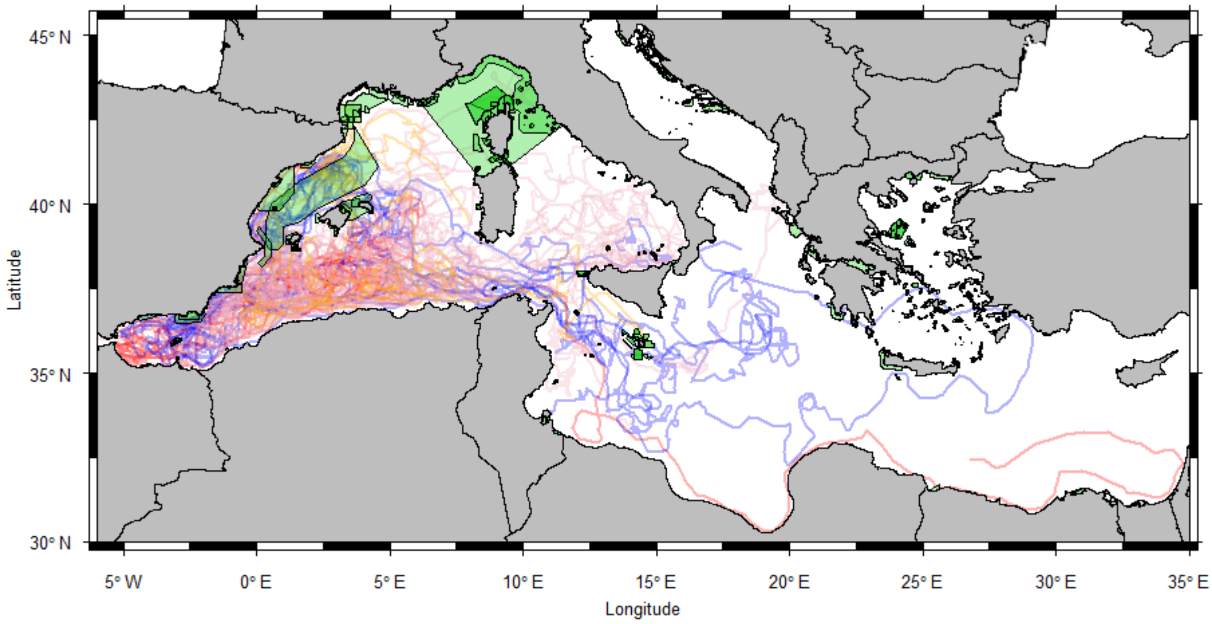


Figure 6.2 Tagged turtles' trajectories by life stage: post-hatchlings (blue), early juveniles (orange), late juveniles (pink) and adults (red); and marine protected areas (green) in the Mediterranean Sea.

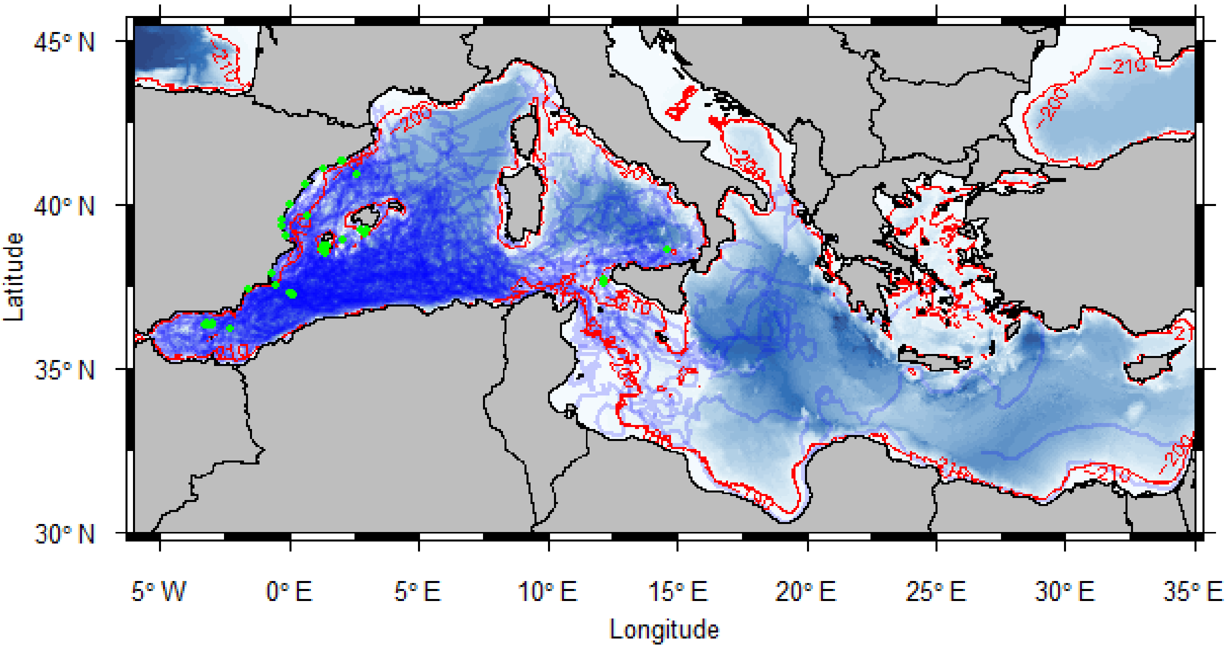


Figure 6.3 Turtle trajectories (in blue) over bathymetry data. Red line represents 200 m depth isobath. Green dots denote the turtle release locations.

The mean tracking duration (± standard deviation of the mean (SD)) was 133 days ± 109 SD. The details of tracking duration for loggerhead sea turtles are reported in Annex 1. After the data analysis and post-processing, a total of 13,039 locations were considered. Concerning habitat use, a total of 2,140 locations (16.4%, *n* = 103 turtles) were located in neritic waters (< 200 m depth). No significant differences were observed for the frequency of neritic locations among life stages (ANOVA, $F_{3,7}$ = 1.98, *P* = 0.30). Most weighted locations by EEZ extension fell inside the Algerian (29%) and Spain (26%) Exclusive Economic Zones (EEZ) (Figure 6.4).

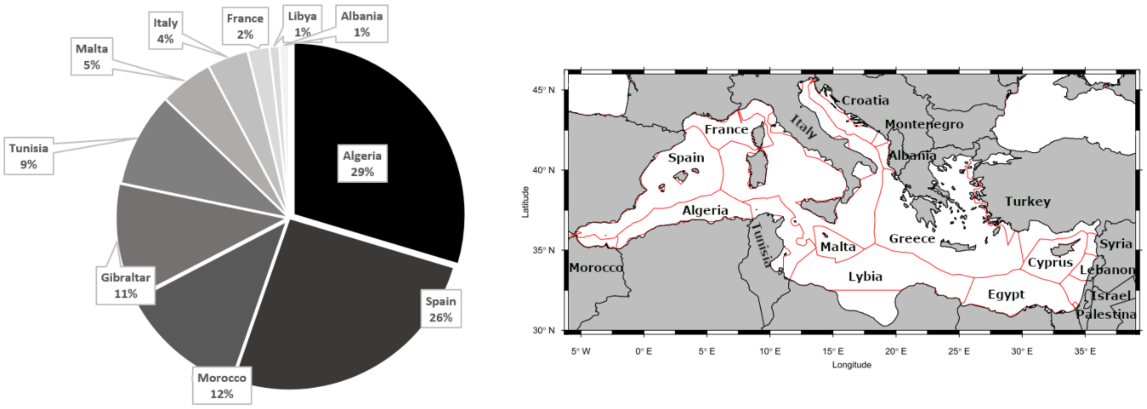


Figure 6.4 Percent of daily locations weighted by Economic Exclusive Zones (EEZ) extension that fell inside EEZ per country (map on the right).

6.3.2 Relative density, home range and core area estimates

The tracked loggerhead sea turtles generally covered large areas of the Mediterranean Sea. The individuals' 50% KUDs ranged from 139 km^2 to 1,397,226 km^2 and their 25% KUDs ranged from 0.01 to 451,068 km^2. Core area sizes by life stages are shown in Figure 6.5.

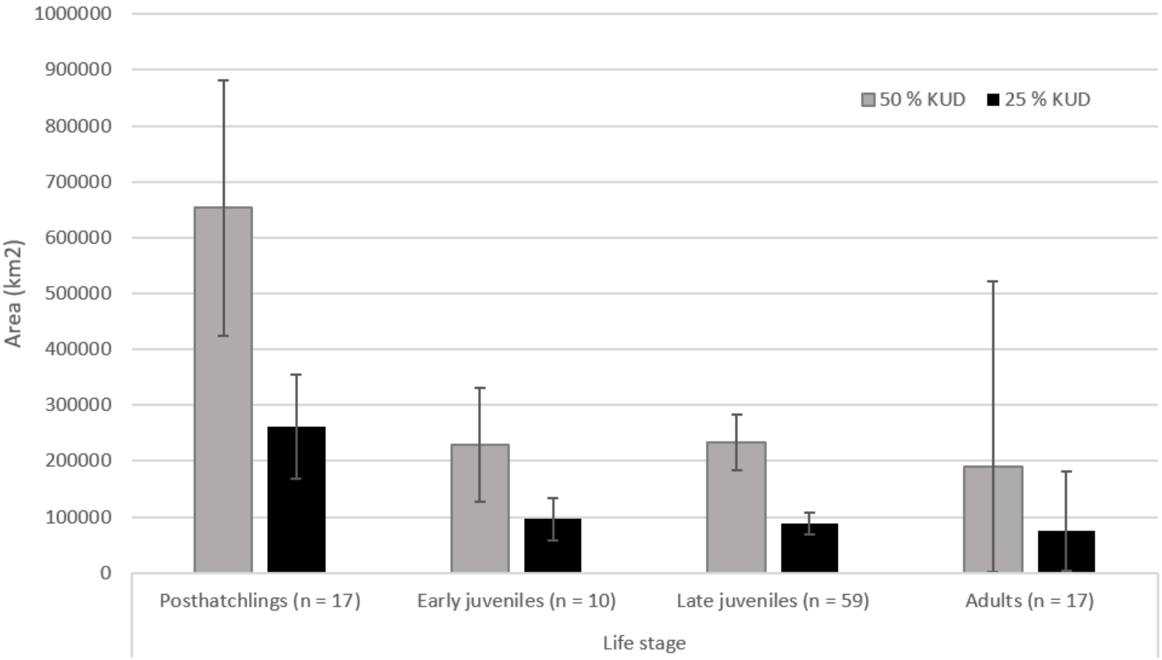
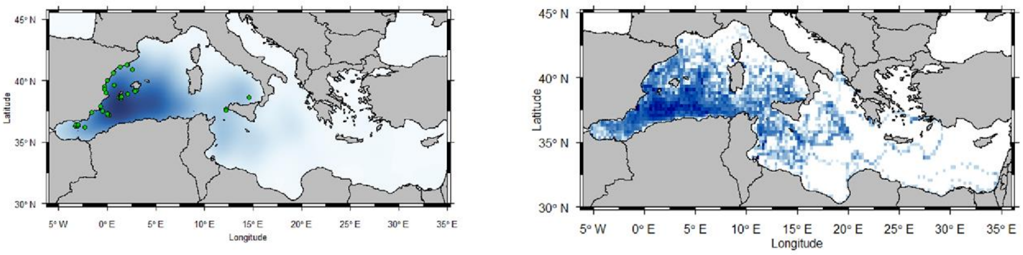


Figure 6.5 Mean kernel utilization distributions (KUD) at 50% and 25% and standard deviation by loggerhead turtle life stage. Sampling size is denoted by *n*.

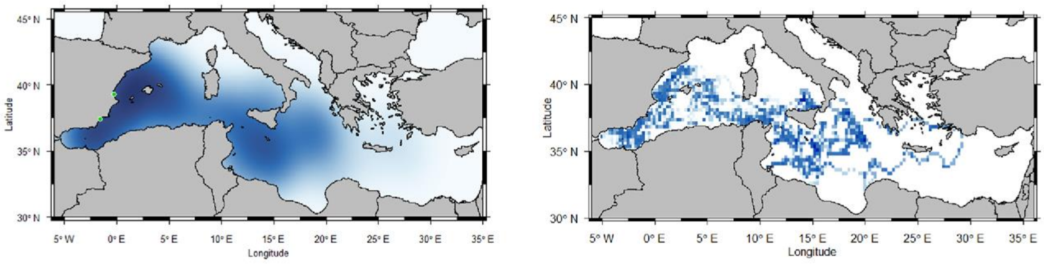
For the whole tracking dataset, core areas were observed in the Algerian Basin (Figure 6.6A). The estimated home ranges for each life stage showed a different habitat use among stages (Figure 6.6B). Post-hatchlings had the largest overall home range and two different core areas: one at the westernmost part of the Mediterranean Sea from the Alboran Sea to the Balearic Sea, and another to the southwest of the Ionian Sea (Figure 6.6B.1). For early juveniles, core areas concentrated in the western Mediterranean, in the Balearic Sea and the Algerian Basin (Figure 6.6B.2). Late juveniles (Figure 6.6B.3) and adults (Figure 6.6B.4) also had core areas in the Algerian Basin. Besides, adults were more likely to remain in the western Mediterranean basin where tagged.

A) **Global home range and global relative density map**
(*n* = 103, total daily locations =13039)

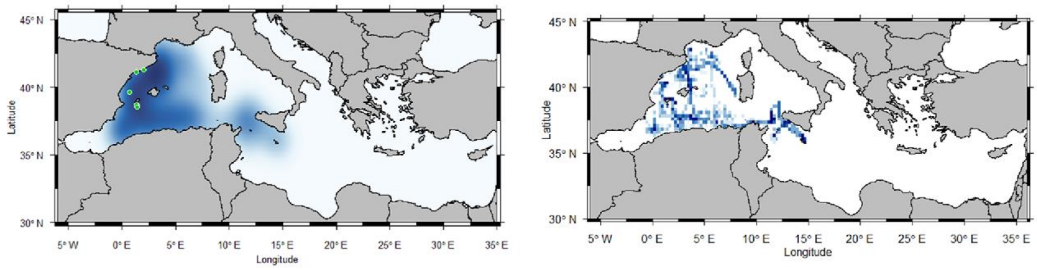


B) **Life stage home ranges and relative density maps**

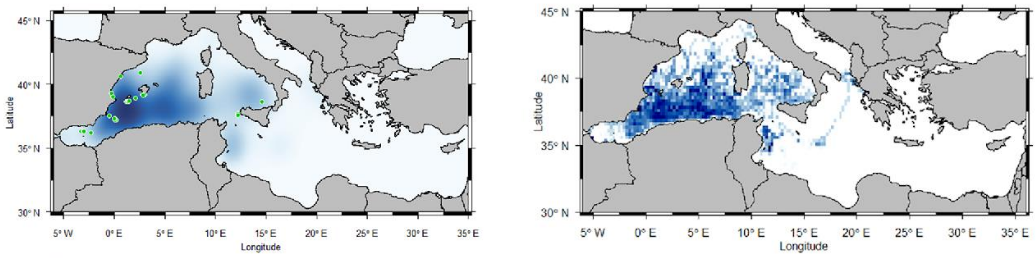
B1) **Post-hatchlings** (*n* = 17 total daily locations = 2 961)



B2) **Early Juveniles** (*n* = 10, total daily locations = 1 112)



B3) **Late Juveniles** (*n* = 59, total daily locations = 7164)



B4) **Adults** (*n* =17, total daily locations = 1 812)

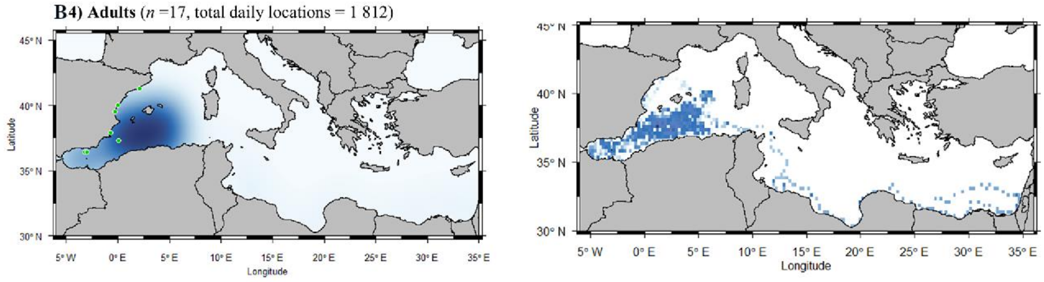


Figure 6.6 Home range estimates (on the left) and relative density maps (on the right) for loggerhead sea turtles in the Mediterranean Sea. Blue dark areas are high-density areas (25% KUD and percentile 75, respectively). Figure 6.6A shows the global home range and relative density for all the tracking data. The home ranges and relative density by life stage are shown in Figure 6.6B, B1: post-hatchlings, B2: early juveniles, B3: late juveniles and B4: adults. Release points are shown in green at the home range estimate map.

6.3.3 Overlap of turtles' home ranges and density maps over MPAs

Overall, tracked turtles visited 60 Mediterranean MPAs, which comprised a total protected area of 222,040 km^2 (Table 6.2). Tracked individuals spent only a mean of 12.6% ± 18.2 SD of their monitored days inside the limits of MPAs (range: 0 - 76%). Only nine turtles (8.7%) of all the monitored individuals spent more than 50% of their tracked days inside MPAs (Figure 6.7). The use of MPAs seemed to decrease with turtle development as the percentage of turtles that spent more than 50% of their time inside MPAs lowered among developmental stages (post-hatchlings: 17.7%, early juveniles 10%, late juveniles 6.8%, and adults 5.9%). Twenty-two turtles (22%) visited at least one MPA during their monitoring period. However this percent decreases as the number of MPAs which overlapped with the core area of each turtle increases (Figure 6.8). Moreover, 31 (30%) of the monitored individuals did not frequent any location inside the limits of MPAs (Figure 6.8). In addition, we observed that 5.9% of post-hatchlings, 10.0% of early juveniles, 51.0% of late juveniles and 23.5% of adults never used an MPA.

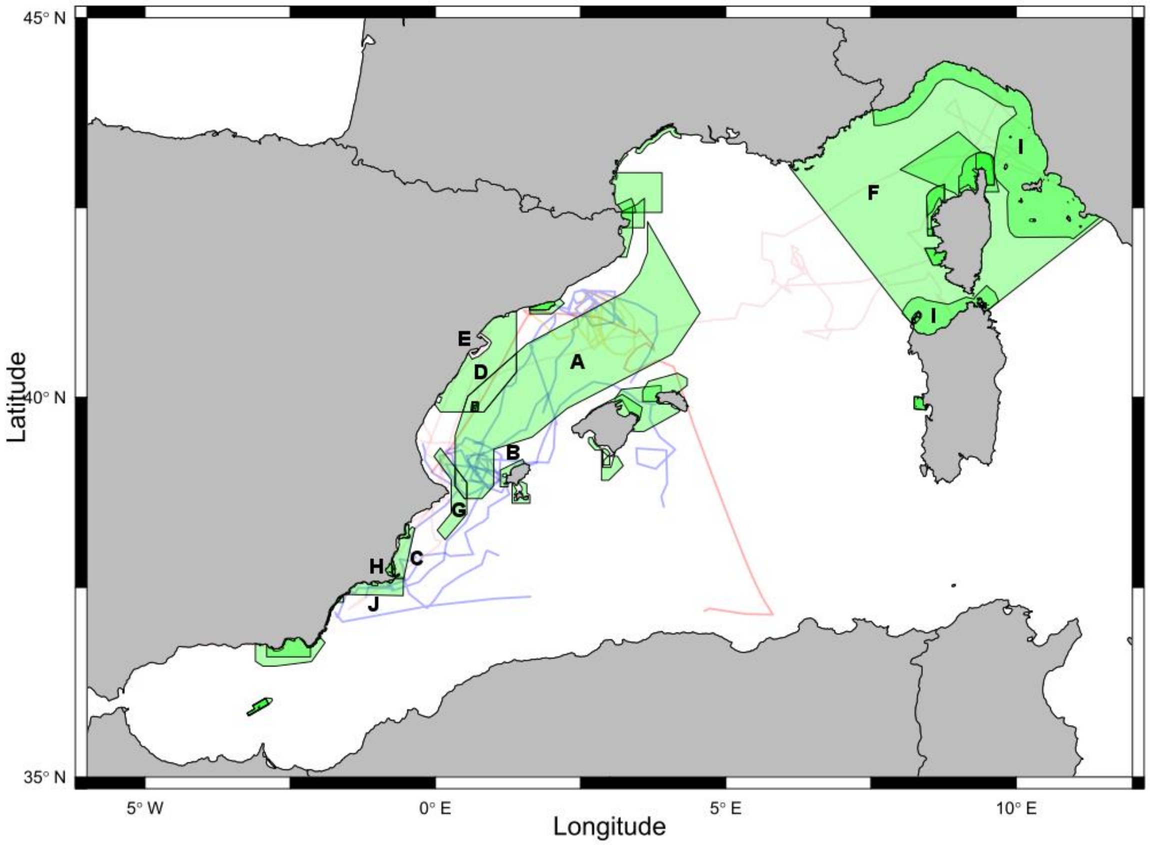


Figure 6.7 Trajectories of the turtles that spent more than the 50% of the monitoring time inside the limits of MPAs and overlapping marine protected areas (green) in the Mediterranean Sea. Results are shown by life stage (post-hatchlings (blue, *n* = 3), early juveniles (orange, *n* = 1), late juveniles (pink, *n* = 4) and adults (red, *n* = 1)). Most of the MPAs, ordered as highest use, used by these turtles were: A. Mediterranean Cetacean Corridor, B. Northwest Ibiza, C. Marine area of Tabarca-Cabo de Palos, D. Delta de l'Ebre –Columbretes Islands, E. Delta de l'Ebre, F. Pelagos Sanctuary for the conservation of marine mammals, G. Marine plataform Cabo de la Nao, H. Mar Menor, I. Santuario per i mammiferi marini, J. Submarine valleys of Mazarrón.

Table 6.2 Marine protected areas (MPA) visited by the monitored loggerhead sea turtles in the Mediterranean. Protection designation: Marine Protected Area (MPA), Special Protection Area – Habitats Directive (SPA), Specially Protected Areas of Mediterranean Importance – Barcelona Convention (SPAMI), Site of Community Importance – Habitats Directive (SCI), Special Areas of Conservation (SAC). * denotes specific conservation measures for the considered marine turtles.

Nº	**Marine Protected Area (MPA)**	**Designation**	**Designation type**	**Area (km^2)**	**Status**	**Status year**	**Country**
1	El Salum	MPA	National	293	Designated	2010	Egypt
2	Cap Corse et Agriate	Marine Nature Park	National	6,840	Designated	2016	France
3	Capu Rossu, Scandola, revellata, Calvi	SPA (Birds Directive)	Regional	996	Designated	2003	France
4	Gulf of Lion	Marine Nature Park	National	4,019	Designated	2011	France
5	Languedocienne coast	SPA (Birds Directive)	Regional	719	Designated	2006	France
6	Sanguinaires Islands, Ajaccio Gulf	SPA (Birds Directive)	Regional	465	Designated	2004	France
7	Pelagos Sanctuary For The Conservation Of Marine Mammals	SPAMI	Regional	87,500	Adopted	2001	France, Italy, Monaco
8	Coasts and Islets in the North West of Sardinia	SCI	Regional	17	Designated	1995	Italy
9	Egadi Islands Marine Nature Reserve	MPA	National	540	Designated	1991	Italy
10	Marine area Asinara Island	MPA	National	107	Designated	2002	Italy
11	Marine area Pelagie Island	MPA	National	41	Designated	2002	Italy
12	Marine area Peninsula of Sinis - Mal di Ventre Island	MPA	National	267	Designated	1997	Italy
13	Pantelleria Island and surrounding marine area	SPA (Birds Directive)	Regional	93	Designated	1995	Italy
14	Sanctuary for marine mammals	International significance Natural Marine Area	National	25,573	Designated	2001	Italy
15	Il-Bahar tal-Grigal	SPAs	National	626	Designated	2016	Malta
16	Il-Bahar tal-Lvant	SPAs	National	352	Designated	2016	Malta
17	Il-Bahar tan-Nofsinhar	SAC - International Importance	National	835	Designated	2016	Malta
18	Il-Bahar tax-Xlokk	SPAs	National	219	Designated	2016	Malta
19	Cap des 3 Fourches	Nature reserve	National	70	Proposed	2014	Morocco
20	Alguers de Borriana-Nules-Moncofa	SCI	Regional	41	Designated	2000	Spain
21	Cabrera Archipelago	Nacional Park	National	1,153	Designated	1991	Spain
22	Channel of Menorca	SCI	Regional	3,354	Designated	2014	Spain
23	Delta de l`Ebre	Protection Plan	National	360	Designated	1992	Spain

Nº	Marine Protected Area (MPA)	Designation	Designation type	Area (km^2)	Status	Status year	Country
24	Delta de l`Ebre	Natural Park	National	5	Designated	1983	Spain
25	El Saladillo-Punta de Baños	SCI	Regional	18	Designated	2007	Spain
26	Garraf's coast	Protection Plan	National	266	Designated	1992	Spain
27	Gata-Nijar Cape	Natura 2000	National	120	Designated	2012	Spain
		Marine Reserve	National	125	Designated	1995	Spain
28	Ibiza, Biodiversity and Culture	World Heritage Site	International	83	Inscribed	1999	Spain
29	Irta	Nature Reserve	National	25	Designated	2002	Spain
30	Malaga-Cerro Gordo Bay	SPA (Birds Directive)	Regional	613	Designated	2014	Spain
31	Mar Menor	Ramsar Site, Wetland of International Importance	International	131	Designated	1994	Spain
		SPA (Birds Directive)	Regional	135	Designated	2000	Spain
32	Marine area of Alboran	SCI	Regional	109	Designated	2014	Spain
33	Marine area of Alboran Island	SPA (Birds Directive)	Regional	663	Designated	2014	Spain
34	Marine area of Baix Llobregat-Garraf	SPA (Birds Directive)	Regional	387	Designated	2014	Spain
35	Marine area of Cabo Roig	SPA (Birds Directive)	Regional	47	Designated	2009	Spain
36	Marine area of Cape Hortes	SCI	Regional	43	Designated	1997	Spain
37	Marine area of Delta de l'Ebre-Columbretes Islands	SPA (Birds Directive)	Regional	9,017	Designated	2014	Spain
38	Marine area of Formentera y del sur de Ibiza	SPA (Birds Directive)	Regional	464	Designated	2014	Spain
39	Marine area of l'Emporda	SPA (Birds Directive)	Regional	854	Designated	2014	Spain
40	Marine area of los Islotes Litorales de Murcia y Almeria	SPA (Birds Directive)	Regional	123	Designated	2014	Spain
41	Marine area of North Mallorca	SPA (Birds Directive)	Regional	984	Designated	2014	Spain
42	Marine area of Northwest Ibiza	SPA (Birds Directive)	Regional	472	Designated	2014	Spain
43	Marine area of Northwest Menorca	SPA (Birds Directive)	Regional	1,613	Designated	2014	Spain
44	Marine area of South Mallorca and Cabrera	SPA (Birds Directive)	Regional	400	Designated	2014	Spain
45	Marine area of Tabarca	SCI	Regional	143	Designated	1997	Spain
46	Marine area of Tabarca-Cabo de Palos	SPA (Birds Directive)	Regional	1,261	Designated	2014	Spain
47	Marine Platform Cabo de la Nao	SPA (Birds Directive)	Regional	2,681	Designated	2014	Spain
48	Marine Reserve of Palos Cape-Hormigas Islands	Marine Reserve	National	19	Designated	1995	Spain
49	Marine Reserve of Tabarca Island	Marine Reserve	National	14	Designated	1986	Spain

Nº	Marine Protected Area (MPA)	Designation	Designation type	Area (km^2)	Status	Status year	Country
50	Mediterranean Cetacean Corridor	SPAMI	National	60,965	Designated	2018	
51	Roquetas de Mar Reefs	SCI	Regional	2	Designated	2000	Spain
52	Salinas y Arenales de San Pedro del Pinatar	Regional Park	National	1	Designated	1992	Spain
53	Seabed East Almeria	SCI	Regional	107	Designated	1997	Spain
54	Seabed of Punta Entinas-Sabinar	SCI	Regional	40	Designated	1997	Spain
55	Serra Gelada	Natural Park	National	50	Designated	2005	Spain
56	Ses Salines d Eivissa i Formentera	Natural Park	National	141	Designated	2001	Spain
57	South Almeria-Seco de los Olivos*	SCI	Regional	2,829	Designated	2014	Spain
58	Submarine valleys of Mazarrón	SCI	Regional	1,541	Designated	2000	Spain
59	Submerged coastal strip of the Murcia Region	SCI	Regional	135	Designated	1999	Spain
60	System of western submarine canyons of the Gulf of Lion	SCI	Regional	938	Designated	2014	Spain

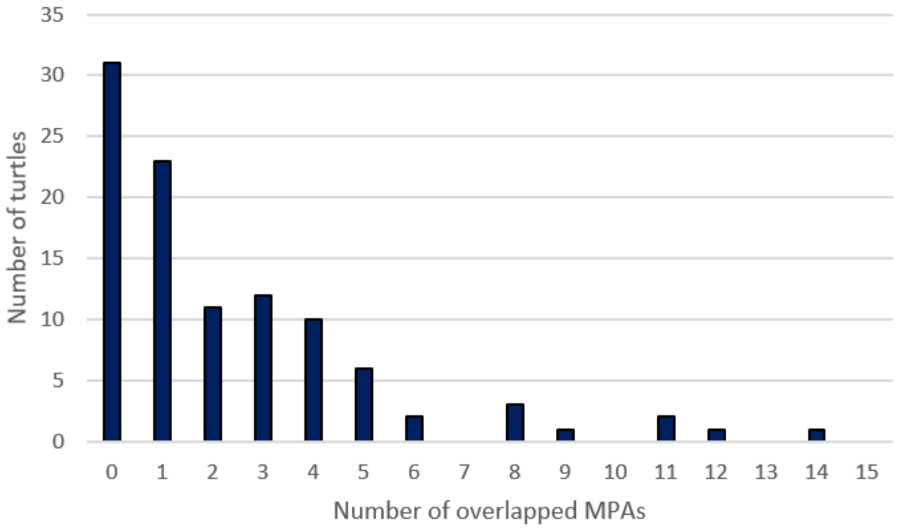


Figure 6.8 Number of turtles in relation to number of MPAs which overlapped with the core area of each turtle.

The residency indices of turtles by life stage are shown in Table 6.3. Post-hatchlings used 25 different MPAs, of which 17 were used immediately after they were released from the Spain's Mediterranean coasts. The highest residency index was observed in early juveniles, followed by post-hatchlings, late juveniles and adults, which spent less time in MPAs. A significant positive correlation was observed between the residency index in MPAs and frequency of neritic locations (correlatio*n* = 0.52, t-statistic = 2.1686, df = 13, *P*< 0.04926) as most MPAs are coastal. The MPA with most turtles using it and with the highest residence index, even when considered different life stages, was the SPAMI (Special Protected Area of Mediterranean Importance) "Mediterranean Cetacean Corridor" (Table 6.2), though on average the use was concentrated mainly in the southernmost part (Figure 6.9). The second most used was the Delte de l'Ebre and Columbretes Islands.

According to the low residence indices recorded, the other MPAs seemed to be used only during transit. Figure 6.9 shows homerange areas and relative density maps overlapped with MPAs. Among 9.2% to 15.7% of the global estimated core areas fell within protected areas, depending on whether we consider the 25% or the 50% KUD (Figure 6.9A). Estimated core areas at 25% KUD overlapped with only 1.5% (18 out of 1,233) Mediterranean MPAs (Figure 6.10A). It is relevant to note that 10 out of 18 MPAs which overlapped home ranges were small areas (< 50 km2). However, small protected areas (< 50 km2) were underused by tracked turtles, as only 0.2% of locations that fell on a protected area were in a small protected area. Regarding density areas, between 8.3% and 11.1% of the hotspots fell into protected areas, depending on whether we consider areas upper 75% percentile or 50% percentile of weighted daily location density, respectively (Figure 6.9B). Estimated density at 75% percentile overlapped with 3.7% (46 out of 1,233) Mediterranean MPAs (Figure 6.10B).

Table 6.3 Most widely used MPAs by monitored loggerhead sea turtles. MPA size is shown in squared kilometres and density in number of the monitored individuals that used the MPA per squared kilometre. The residency index is the number of locations inside the limits of MPAs *versus* the total location number. The Residence index is shown as a percent for all the stages and separated by stage. The percent of individuals is the number of individuals that used MPAs *versus* the total number of monitored individuals. MPA designations are: SPAMI (Specially Protected Areas of Mediterranean Importance), SPA (Special Protection Area, Birds Directive) and SCI (Site of Community importance, Habitats Directive). Global residency index considering all dataset are shown in the last row.

MPA	**MPA Area (km^2)**	**Designation**	**Density ($indv/km^2$)**	**Individuals (%)**	**Residency index (%)**				
					All	**Adults**	**Late juveniles**	**Early juveniles**	**Post-hatchlings**
Mediterranean Cetacean Corridor	60,965	SPAMI	0.001	33.0	6.8	1.1	4.6	18.2	2.6
Marine area of Delta de l'Ebre-Columbretes Islands	9,017	SPA	0.001	11.7	0.7	0.6	0.8	1.0	0.1
Marine area of Northwest Ibiza	472	SPA	0.017	7.8	0.6	0.0	0.8	1.3	0.0
Marine Plataform of Cabo de la Nao	2,681	SPA	0.007	19.4	0.6	0.7	0.5	0.1	0.2
Marine area of Tabarca-Cabo de Palos	1,260	SPA	0.008	9.7	0.6	0.7	0.7	0.0	0.1
Submarine valleys of Mazarrón	1,540	SCI	0.016	23.3	0.4	0.4	0.5	0.2	0.1
South Almeria-Seco de los Olivos	2,829	SCI	0.005	13.6	0.4	0.5	0.2	0.0	0.2
Pelagos Sanctuary For The Conservation Of Marine Mammals	87,500	SPAMI	0.00001	1.0	0.3	0.0	0.6	0.0	0.0
Menorca Channel	3,354	SCI	0.002	7.8	0.2	0.1	0.1	1.1	0.1
All MPAs				69.9	12.7	4.9	11.1	26.2	16.3

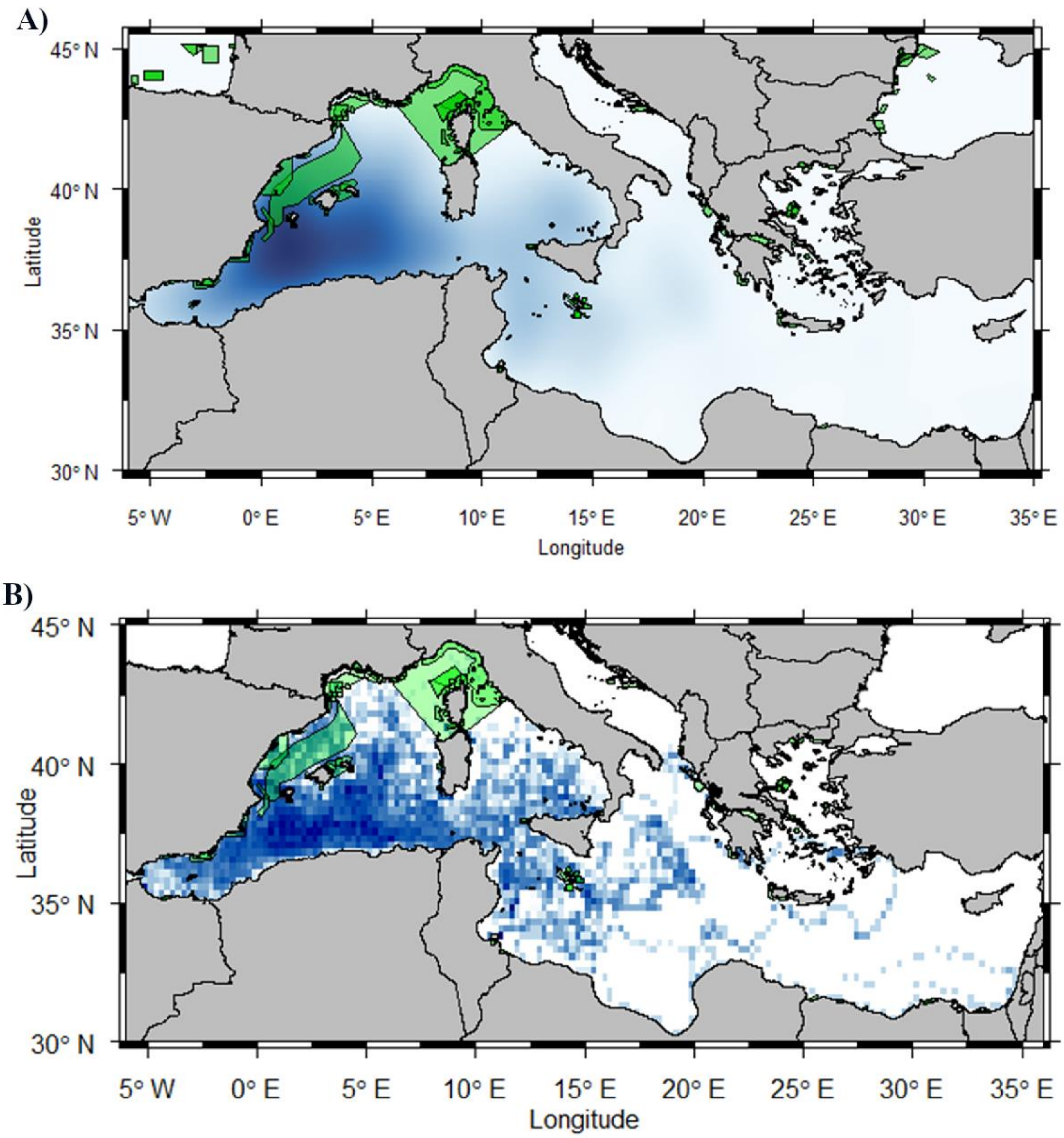


Figure 6.9. Overlapping of the kernel utilization distributions (KUD) and the relative density estimations of the monitored individuals with marine protected areas (green) in the Mediterranean Sea. A) Overall home range, B) Relative density map. Blue dark represents high density areas (25% KUD and percentile 75, repectively).

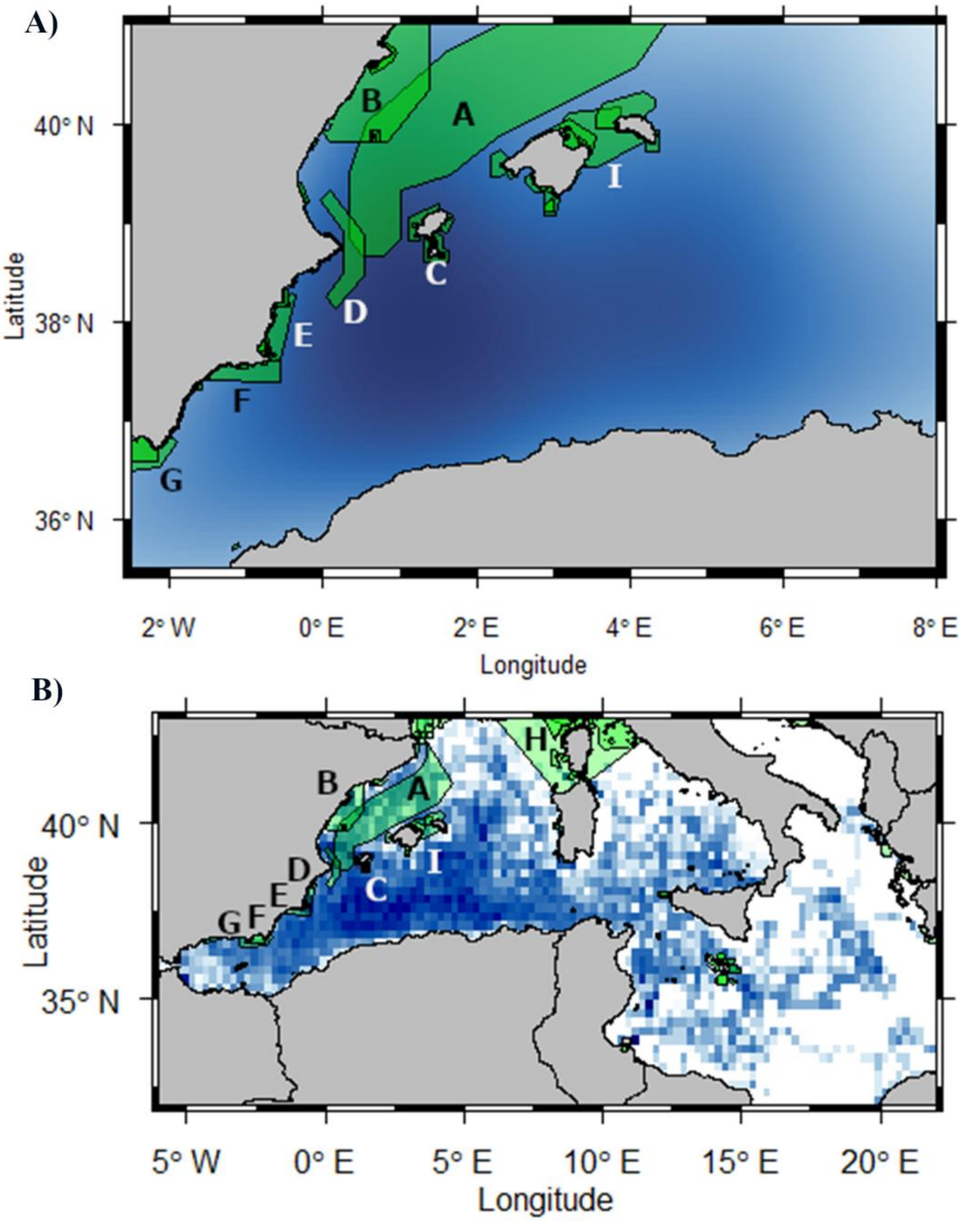


Figure 6.10 Overlapping of the kernel utilization distributions (KUD) and the relative density estimations of the monitored individuals with marine protected areas (green). Results zoomed in core areas: A) Home range maps zoomed over the 25% and 50% KUD core areas, B) Density map zoomed over percentile 75. The MPAs which overlapped turtles core areas with a higher residency index and listed decreasingly were: A. Mediterranean Cetacean Corridor, B: Delta de l'Ebre-Columbretes Islands, C: Northwest Ibiza, D: Marine plataform Cabo de la Nao, E: Marine area of Tabarca-Cabo de Palos, F: Submarine valleys of Mazarrón, G: South Almeria–Seco de los Olivos, H: Pelagos Sanctuary For The Conservation Of Marine Mammals, I: Menorca Channel.

Different use of MPAs by life stages was observed. Post-hatchlings most visited area was the Mediterranean Cetacean Corridor. The Platform Cabo de la Nao, Almería – Seco de los Olivos, Submarine valleys of Mazarrón and MPAs between the Balearic Islands and the Spanish coastline, including the Menorca Channel, were visited only during transit or migratory movements during the first months after release. After crossing the Sicilian Channel, the MPA most visited by posthatchlings was Il-Bahar tal-Lvant, inside the 25% KUD hotspot (Figure 6.6B.1).

Early juveniles showed the higher residency index in the Mediterranean Cetacean Corridor, Northwest Ibiza, Delte de l'Ebre – Columbretes Islands, Gulf of Lion, Menorca Channel and Maltese MPAs (Il-Bahar tal-Lvant and Il-Bahar tal-Grigal). All these MPAs fell inside home range and/or relative density hotspots (Figure 6.6B.2).

Late juveniles mostly visited the Cetacean Mediterranean Corridor, followed by the Delte de l'Ebre – Columbretes Islands, northwest Ibiza, Tabarca – Cabo de Palos, submarine valleys of Mazarrón and the Platform Cape de la Nao. Although these areas were the most used by late juveniles, the residency indexes were low compared to other life stages, as the hotspot was located in the Algerian basin (Figure 6.6B.3). Adults visited a few areas as the core area was at the Algerian basin (Figure 6.6B.4). In decreasing residency index the areas visited by adults were: Mediterranean Cetacean Corridor, Platform Cape de la Nao, Tabarca – Cabo de Palos, Delta de l'Ebre – Columbretes Islands, South Almería – Seco de los Olivos and submarine valleys of Mazarrón.

6.3.4 MPAs proposal for loggerhead sea turtle conservation in the Mediterranean Sea

According to the core areas and the relative density maps obtained, the areas to be considered for protection of the loggerhead sea turtle in the western and central Mediterranean would be located in open waters more than in coastal areas. As important areas obtained from our analysis comprises large areas across the Mediterranean basin, we suggested several candidates to be protected areas, whose shape was computed taking into account the minimum area which includes the closest cells of upper 75% percentile of relative density estimates: in first place of global estimates and in second place to completely define these areas taking into account life stage. Those proposed areas should be considered as the minimum area of interest that could be protected as no buffer area was added to MPAs proposal.

Here, we propose candidate areas to be considered as marine protected areas in the following zones: the west of the Algerian basin, the waters at the Northern Ionian Sea, waters at the Northern Strait of Sicily, areas at the Tyrrhenian Sea and waters at the Northeast Tunisia (waters in front of Hammamet Gulf in Tunisia) (Figure 6.11). Moreover, we propose an enlargement and a connection of the already existing Maltese MPAs (MPAs Il-Bahar tal-Lvant and Il-Bahar tal-Grigal), as the Maltese EEZ waters close to these areas seemed to be important, at least for early juveniles tracked from western Mediterranean and post-hatchlings from Spanish Mediterranean nests. Finally, we propose to protect the waters located at the Alboran Sea, which also would imply an enlargement and connection of the already existing areas: South Almeria – Seco de los Olivos, Marine Reserve of the Alboran Island and Marro – Cerro Gordo Cliffs (Figure 6.11). High-use areas identified in the Balearic Sea are in their most part already under several figures of protection, therefore, we do not propose any candidate in this area.

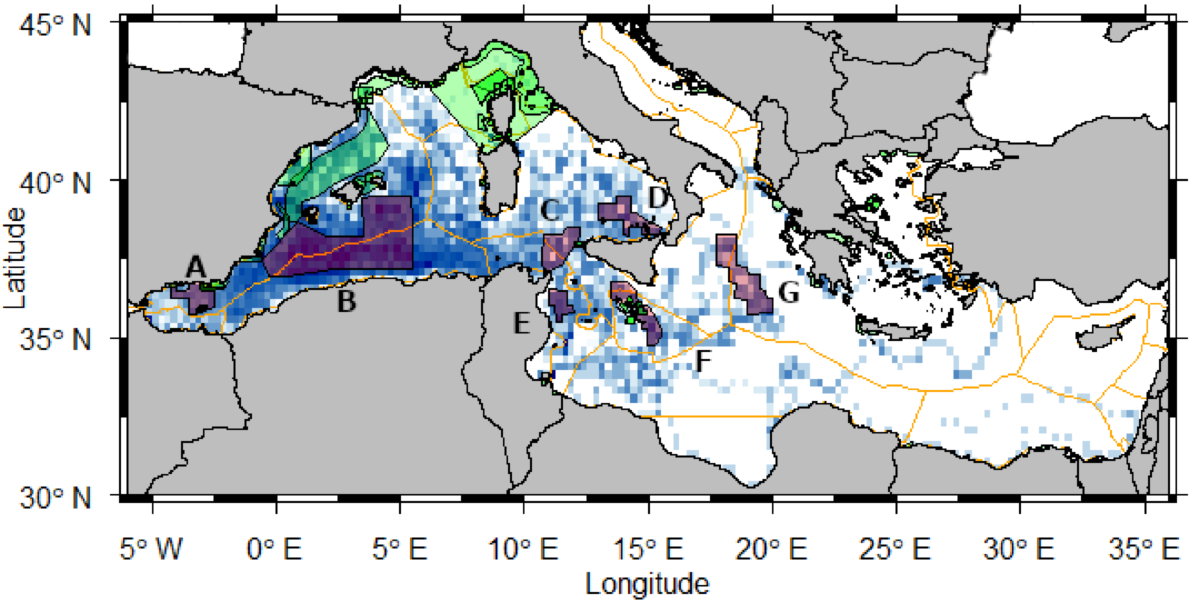


Figure 6.11 Specially Protected Areas of Mediterranean Importance (SPAMIs) proposed for loggerhead sea turtle conservation in the Mediterranean Sea and extension in km^2: A) Alboran Sea (13,064 km^2), B) Algerian basin (116,032 km^2), C) Northern Strait of Sicily (17,140 km^2), D) Tyrrhenian Sea (17,579 km^2), E) Northeast Tunisia (7,709 km^2), F) Malta (17,713 km^2), and G) Northern Ionian Sea (29,257 km^2). Current Marine Protected Areas are shown in green. Relative density estimates are shown in blue. Delimitation of countries Exclusive Economic Zones are shown in orange.

6.4 Discussion

The present study provides home range estimations, descriptions of core areas and relative density estimations for loggerhead sea turtles tracked from western Mediterranean, by relating them to the current MPAs' network in this sea to ascertain their effectiveness to protect this species.

6.4.1 Spatial distribution

Our results should be considered for satellite-tracked loggerhead sea turtles tracked from the western Mediterranean because despite tag bias was addressed in our methodology, it cannot be fully corrected. Most of the monitored individuals moved long distances and had wide home range areas that apparently decreased with life stage development, with post-hatchlings having the widest home ranges probably to dispersal movements. Early juveniles show more reduced home ranges probably because they move around feeding habitats. This coincides with the proposed model of ontogenetic reduction in home ranges, and agrees with previous literature (Carr 1987, Bolten 2003, Schofield et al. 2010a, Casale et al. 2012a). No transitions by late juveniles and adults to neritic areas were observed, as proposed in other areas (Bjorndal et al. 2000), because they remained in oceanic waters. In fact, long term studies on diet, debris ingestion, and epibionts suggest that the ontogenetic habitat shift in the loggerhead sea turtle are very flexible in the Spanish Mediterranean, with temporary exploitation of oceanic resources regardless of size (Tomás et al. 2001, Domènech et al. 2018, 2019, Ten et al. 2019).

The main identified core areas were located in the Algerian Basin, the southern Balearic Sea, the Alboran Sea, the Sicilian Channel, the Northeast Tunisia, Maltese waters, Tyrrhenian Sea and the Ionian Sea, depending on life stage. Our results support previous studies that have pointed out the Algerian Basin and the southern Balearic Islands as an important area for loggerhead sea turtle conservation in the western Mediterranean for juveniles and adults (Cardona et al. 2005, Revelles et al. 2007a , b, c, Casale et al. 2012a, b, Hays et al. 2014). The core areas observed for late juveniles and adults along the Algerian Basin may be related to the highly productive eddies of the Algerian current (Millot 1999, Obaton et al. 2000, Pinardi and Masetti 2000, Bosc et al. 2004, Balbín et al. 2014, Cardona and Hays 2018). In addition, a strong current like the Algerian current may act as a physical barrier in loggerhead dispersal movements by retaining some individuals in the Algerian basin (Revelles et al. 2007 b,c). Additionally, adults tracked from the western Mediterranean were more likely to remain in the same basin where tagged (Luschi et al. 2017). This could be related, for instance, to the turtle's Mediterranean or Atlantic genetic origin (Carreras et al. 2018), or to a possible adult fidelity to a foraging or breeding area (Casale et al. 2012c).

The Algerian basin and the Alboran Sea are also important areas for post-hatchlings, and maybe for hatchlings, of nests laid in the western Mediterranean (Chapter 4 and present study). Regarding post-hatchlings, the core area observed off the Spanish Mediterranean coast would be an important developmental area for hatchlings only immediately after entering the sea, before entering in the influence of currents that may transport them to the eastern Mediterranean, although we cannot discard a potential effect of release locations from the coast of Spain. The Tyrrhenian Sea could be an important area for post-hatchlings and juveniles for foraging (Chimienti et al. 2020). This sea presents robust cyclonic and anticyclonic gyres that change seasonally affecting sea productivity and turtle distribution (Blasi and Mattei 2017, Luschi et al. 2018). The Sicilian Channel, Northeast Tunisia, Malta and the Ionian Sea seem to be also important developmental areas for post-hatchlings coming from nesting events in the western Mediterranean, as has been proposed also for hatchlings from eastern Mediterranean nesting beaches (Hays et al. 2010, Casale and Mariani 2014), and also for juveniles and adult loggerhead tagged in other Mediterranean areas (Bentivegna 2002, Hochscheid et al. 2007, Schofield et al. 2010a, Bastari et al. 2016, Mingozzi et al. 2016, Casale et al. 2018, Luschi et al. 2018). Additionally, the identification of core areas for the loggerhead sea turtle in the Western Mediterranean results essential for the conservation of this species and the potential colonization process in the area, given the recent increase in nesting events in this basin (Tomás et al. 2008a, 2015, Carreras et al. 2018, Marco et al. 2018), possibly as result of adaptation of the species to global warming (Witt et al. 2010a, Maffucci et al. 2016).

6.4.2 Effectiveness of MPA for loggerhead sea turtle protection in the Mediterranean

There was very little overlapping between turtle’s core areas and tracks with the protected areas, and turtles spent very little of their monitored time inside them. Indeed, most of the core areas and high density areas estimated (> 85%) were not included within any of the MPAs. Furthermore, less than 5% of the Mediterranean MPAs were used by tracked loggerhead sea turtles.

Just one of the most used MPAs by loggerhead turtles tracked herein had a current management plan with specific conservation measures for the species (Submarine Valleys of Mazarrón). This is especially relevant because the loggerhead turtle is a priority species set out in the Habitats Directive of the European Commission (European Commission 2007). Applied conservation measures are unlikely to be enough to protect 60% of the loggerhead turtle populations in the Mediterranean, as required by the Natura 2000 Network (European Comission 2007, Fortuna et al. 2018). The identification of high-use areas would represent a spatial management opportunity, where specific threats could be reduced (Casale et al. 2012a, Rees et al. 2016, Fortuna et al. 2018).

Most of the MPAs are designed to protect waters near or not far from the coasts, and we have seen that tracked turtles barely used the waters included in many of them in the western Mediterranean. Small and coastal MPAs (< 50 km^2) were not used often. Similar results have been observed elsewhere. For instance, very little use of coastal MPAs has been observed by loggerhead turtle nesting females in Cyprus (Snape et al. 2018). On the other hand, large MPAs are difficult to manage given the diverse range of economic, political and legal obstacles that may impede the establishment and enforcement of large reserves, especially transnational ones (Agardy et al. 2011, Singleton and Roberts 2014, Gruby et al. 2016). Moreover, the lack of an inter-connected Mediterranean MPAs' network was pointed out as a main constraint for the conservation of wide-ranged species with complex life cycles (Amengual and Alvarez-Berastegui 2018). For all these reasons, current MPAs may offer unsuccessful protection for loggerhead sea turtles in the Mediterranean Sea, as proposed in previous studies at smaller geographical scales (i.e., Revelles et al. 2007b, Snape et al. 2018).

Previous sea turtle conservation efforts in the Mediterranean have primarily focused on protecting nesting sites (Casale and Margaritoulis 2010), although population models have indicated that only preserving sea turtle nesting areas is insufficient without considering other key habitats (Casale and Heppell 2016, Casale et al. 2018). Conservation planning for sea turtles must consider these species' ecological and ontogenetic developmental requirements (Hamann et al. 2010, Venter et al. 2014, Rees et al. 2016) and should explicitly protect all life stages (Bentivegna 2002, Beger et al. 2015) with large-scale conservation plans that explicitly incorporate their habitat needs and migratory behaviours (Mazor et al. 2016, Harrison et al. 2018). According to Art. 4.1 of the Habitats Directive, the core areas used by the species, and now identified in the present study, should be protected (European Comission 2007, Fortuna et al. 2018).

According to our results, the areas to maximize protection for the conservation of the loggerhead sea turtles tracked from the western Mediterranean were identified in the western and central Mediterranean. Therefore, we propose several areas as potential candidates to be protected in the Mediterranean. If protected, over 18% of the Mediterranean Sea would be under legal conservation figures of protection. This proposal will help to achieve the goal of the "*High Ambition Coalition for Nature and People*" (https://www.hacfornatureandpeople.org/home) of protecting at least 30 percent of world's land and ocean by 2030.

The most effective type of MPA in the Mediterranean Sea depends on the distribution and extension of the areas which are intended to protect. On the one hand, SPAMIs could be an option for those areas which include waters of the Economic Exclusive Zone (EEZ) of two countries. On the other hand, areas that fell in a country EEZ in the European Union (Alboran Sea and Tyrrhenian Sea) could be declared protected marine areas in the 2000 Nature Network framework, as the loggerhead sea turtle is a priority species under the Habitat Directive (European Comission 2007).

Both, existing protected areas and proposed areas to be protected should include the implementation of specific measures to enhance loggerhead sea turtle conservation. In the Mediterranean Sea there are 1,233 MPAs declared, of which 118 consider the loggerhead sea turtle as a priority species to protect. However, only 40 have current management plans including specific conservation measures focused on the loggerhead sea turtle. For example, in the Balearic Sea, the MPA "Mediterranean Cetacean Corridor" includes protection measures for cetacean species but do not include any conservation measures focused on sea turtles. We observed that the Balearic Sea could be an important area for loggerhead post-hatchlings and juveniles. Therefore, our proposal is to include specific protection measures for loggerhead conservation in the already existing MPAs in the Balearic Sea.

The MPA we propose in the Alboran Sea could contribute to the protection for post-hatchling and adult loggerhead sea turtles. The MPA in the Algerian basin could be of interest for the protection of juvenile and adult loggerhead turtles (Cardona et al. 2005, Casale et al. 2012c). The proposed MPAs Northern Strait of Sicily, Northeast Tunisia, Maltese waters, and Tyrrhenian Sea could be also important areas to be protected, particularly for juveniles tracked on western Mediterranean and post-hatchlings from clutches laid in the Spanish Mediterranean and probably also for post-hatchlings from the western Mediterranean in general. Traditionally, a limited exchange between the two Mediterranean basins has been estimated for hatchlings and post-hatchlings originating in the western Mediterranean, and turtles would be expected to be retained in the South Tyrrhenian Sea (Maffucci et al. 2016), which is considered an important foraging and overwintering area (Blasi and Mattei 2017, Luschi et al. 2018, Chimienti et al. 2020). Northeast Tunisia was also identified as a important foraging area for adults and subadults of loggerheads tracked on the western Mediterranean basin (Hochscheid et al. 2007). The proposed MPA in the Northern Ionian Sea could also act as a key area for loggerhead post-hatchlings, at least, from western Mediterranean nests, since similar research about post-hatchlings from eastern Mediterranean has yet to be conducted. Increasing nesting events in the western Mediterranean basin during last decades could be a consequence of global warming (Tomás et al. 2008, Maffucci et al. 2016, Carreras et al. 2018), therefore our results could be important for post-hatchlings conservation. Furthermore, proposed MPAs include important areas for other species of cetaceans, sharks and sea turtles, which could be benefited from conservation measures taken in this areas.

Our results agree with previous studies that pointed out the waters at the southwest of Balearic Islands, the west of the Algerian basin, the Alboran seamounts in the Alboran Sea, the northern side of the Strait of Sicily, the Tunisia Plateau and the northern Ionian Sea as potential SPAMIs (Notarbartolo di Sciara and Agardy 2009, Micheli et al. 2013). Previous studies also proposed the northern part of the Mallorca and Menorca Channel as Site of Community Importance (pSCI) for seabirds, cetaceans and loggerhead sea turtle conservation (Barberà et al. 2014), and this area partially overlaps with the early juvenile loggerhead core areas estimated herein. Proposed areas to be protected in the Central Mediterranean are based on the results showed in this paper and for turtles tracked from the western Mediterranean. However, further research and collaboration among researchers from both basins is needed to define important areas to be protected accurately, especially for juveniles and post-hatchlings, gathering satellite-tracking data from both eastern and western Mediterranean. For instance, similar research with satellite-tracked loggerhead post-hatchlings from eastern Mediterranean has yet to be conducted. Nonetheless, managers and conservation stakeholders from Central Mediterranean could use this research as a starting-point to define adequate protected areas for loggerhead post-hatchlings conservation.

6.5 Conclusions

The study related to the present chapter has revealed that the current distribution and coverage of Mediterranean MPAs seem to be insufficient to protect the loggerhead sea turtles in this sea. Core areas for the loggerhead turtles observed in the Algerian Basin, the Sicilian Channel and the Ionian Sea are currently beyond the limits of MPAs and, hence, remain unprotected. Moreover, most MPAs in the western and eastern Mediterranean lack explicit management measures focusing on minimizing threats that undermine sea turtle conservation. Therefore, conservation measures that focus directly on loggerhead turtle survival would be most beneficial if they were to include in the core areas described in this paper. The MPAs we propose in the Alboran Sea, Algerian basin, Northern Strait of Sicily, Northeast Tunisia, Malta, Tyrrhenian Sea and Northern Ionian Sea, could be interesting areas to be implemented for loggerhead sea turtle conservation in the western and central Mediterranean.

Chapter 7

Inter-nesting and post-nesting behaviour of loggerhead turtle colonizers in Spain

Part of this Chapter is related to the following peer-reviewed publications:

Abalo-Morla S, Tomás J, Revuelta O, Belda E. Inter-nesting and post-nesting behaviour of loggerhead turtle colonizers in Spain (in preparation).

Cardona L, **Abalo-Morla S,** Cani A, Feliu B, Izaguirre N, Tomás J, Belda E. Identifying the foraging grounds of the new loggerhead turtle nesters in the western Mediterranean (submitted to Aquatic Conservation: Marine and Freshwater Ecosystems).

7.1 Introduction

The major nesting aggregations of loggerhead sea turtles in the Mediterranean are located in the traditional nesting areas in the central and eastern basins, where thousands of nests are recorded from beaches in Greece, Turkey, Libya and Cyprus (Casale et al. 2018). However, since 2001, loggerhead nesting events have been increasing in the western Mediterranean basin, although it is not recognised as a frequent nesting area for the species, as there is no established nesting beach identified yet (Tomás et al. 2020, Hochscheid et al. 2022 and references therein). These nesting attempts, successful nesting events and/or hatchling emergence outside of the traditional nesting range were considered sporadic nesting, defined as unusual nesting events in uncommon nesting area (Chaieb et al. 2022). Nonetheless, recent research suggests that loggerhead nesting events in the western Mediterranean are a result of a nesting range expansion, as the western Mediterranean basin has become a suitable nesting area for loggerhead turtles (Hochscheid et al. 2022, Santidrián-Tomillo et al. 2022), likely driven by rising sea water temperatures due to global warming (Witt et al. 2010, Maffucci et al. 2016, Carreras et al. 2018, Girard et al. 2021) and improved thermal conditions for clutch development in local beaches (Cardona et al. 2022, Santidrián Tomillo et al. 2022). However, the origin of the loggerhead turtles currently nesting in the Spanish Mediterranean remains unknown.

Mediterranean nesting events out of range were recorded in Spain (Tomás et al. 2002, 2008a, 2015, Carreras et al. 2018, Marco et al. 2018a, b, Báez et al. 2020), France (Sénégas et al. 2009), Algeria (Benabdi and Belmahi 2020), North Tunisia (Bradai and Karaa 2017) and the western coast of Italy and Corsica Island (Delaugerre and Cesarini 2004, Bentivegna et al. 2008, Casale et al. 2012b, Maffucci et al. 2016, Denaro et al. 2022). In fact, in Spain's Mediterranean coast, 6-7 nesting records/attempts have been reported annually since 2014 (Marco et al. 2018a,b), and the tendency seems to increase yearly (Tomás et al. 2020). Most nests recorded in Spain have been found in touristic beaches, and so consequently, egg development and hatchling survival are threatened by human activities. Thus, management measures like nest relocation and other clutch protection actions are required.

Previous studies stated that Mediterranean loggerhead turtle nesting aggregations correspond to distinct demographic sub-populations, which are genetically well structured and differentiated (Carreras et al. 2018), and evolved independently from Atlantic loggerhead turtles (Clusa et al. 2013). Loggerhead sea turtles generally exhibit high philopatry, with adults homing to breeding sites, where males and females migrate periodically to reproduce close to their natal rookeries and where females nest on their natal beach (Lohmann et al. 2013, Clusa et al. 2018, Baltazar-Soares et al. 2020). However, nesting events at secondary breeding sites (Schofield et al. 2010b, Casale et al. 2013), may have important consequences for gene flow among different rookeries (Casale et al. 2018). In fact, western Mediterranean colonization events have been linked to both Mediterranean and northwestern Atlantic populations using genetic markers (Carreras et al. 2018). Moreover, it was hypothesized that loggerhead turtles may exhibit an exploratory non-phylopatric behaviour to colonize new nesting sites which could act as an adaptive advantage to possible environmental changes (Carreras et al. 2018). Such exploratory behaviour implies turtles to nest in areas far from their natal beaches and even nesting in distant locations during the same breeding period (as suggested by Carreras et al. 2018). In addition, the geomagnetic imprinting and the magnetic navigation map were found to shape the loggerhead population structure and long-distance migrations to reproduce in the Atlantic Ocean (Brothers and Lohmann 2015, 2018).

Few studies have tried to spatially delineate foraging grounds for adult turtles across the Mediterranean Sea with the aim of improving our understanding of the location and extent of the critical habitats for nesting female loggerheads. These studies have primarily been conducted on local scales through various approaches (i.e., satellite tracking in Tyrrhenian Sea, Italy, Luschi et al. 2018; stranding individuals in Fethiye-Gocek, Turkey, Başkale et al. 2018) or at broader extent through the analysis of telemetry post-nesting data derived from individuals using certain nesting sites (i.e., Zbinden et al. 2008, Schofield et al. 2010b, Almpanidou et al. 2022). Over the last decades, satellite tracking techniques have substantially advanced our understanding of sea turtle spatial behaviour, especially for the post-nesting migrations of females, although considerable gaps remain in our knowledge about females' behaviour during the remaining inter-reproductive period (Mingozzi et al. 2016). Adult loggerheads typically move between distinct foraging and nesting grounds, often undertaking long-distance migrations on a multi-annual basis (Godley et al. 2008). Previous studies have also observed a dichotomy in foraging behaviour that appears to be linked to body size, with larger turtles foraging in coastal waters while smaller turtles foraged oceanically. Such studies were conducted in the Atlantic (Hawkes et al. 2006, Mansfield et al. 2009, McClellan et al. 2010, Vieira et al. 2014), and Pacific oceans (Okuyama et al. 2022), and in the Mediterranean Sea (Zbinden et al. 2011). Moreover, adult females are known to perform extensive movements also between successive nesting events within the same breeding season, known as the inter-nesting period (Godley et al. 2008). During the breeding and/or inter-nesting period adults are usually aggregated in limited areas, being vulnerable to anthropogenic threats. Therefore, it is crucial to define these areas and the level of nest site fidelity shown by individuals during multiple breeding attempts within the same season (Godley et al. 2008). Almpanidou et al. (2022) found that the foraging grounds of adult loggerhead turtles in the Mediterranean Sea were mainly hosted within the neritic zone, with the most suitable sites being located at the Tunisian Plateau and the Adriatic Sea (Central Mediterranean), decreasingly followed by the Aegean Sea, the Levantine Sea, the French and Spanish coasts, the Ionian Sea and the Alboran Sea. Nevertheless, as shown in Chapter 6 of this thesis, in the western Mediterranean basin the highest concentrations of juveniles and adults of loggerhead turtles were located in open waters (Abalo-Morla et al. 2022).

However, to present date, information about the behaviour and use of habitat of female loggerhead turtles nesting at the western Mediterranean, is still very scarce. Therefore, it is necessary to better understand the nesting, inter-nesting and post-nesting behaviours, as well as the use of habitat by nesting females on the Spanish coast in order to identify potential threats to the species in the area and ensure future nesting activity in this potential colonization area. In the present study, we provide for the first time through satellite tracking, information on the movements and results about dispersal, habitat use and behaviour of nesting females in Spanish Mediterranean beaches.

7.2 Methods

7.2.1 Turtle data and satellite tagging

In recent years, the scientific community developed and established an encounter and notification protocol in case of sighting nesting females, trails or hatchlings after emergence on the Spanish coast, which were implemented by using the already existing regional stranding networks or through other public awareness initiatives (i.e., "Caretta a la vista", https://mon.uvic.cat/caretta-a-la-vista/es/). In fact, until now, this is the main tool for localizing nesting females in Spain to both protect and study clutches and nesting females. During five nesting seasons (years 2016, 2018, 2020, 2021, 2022), seven nesting loggerhead females were found on beaches along the Spanish coast. Tagging was done to avoid disturbance on the nesting behaviour as females were approached at the end of the egg-laying process or after a nesting attempt, and a satellite tag linked to Argos system (www.argos-system.org) was attached to their carapace using standardmethods when turtles were heading back to sea (see Chapter 3 for detailed methods, Mingozzi et al. 2016, Figure 7.1, Table 7.1). Only Mascletà2016 was tagged after being taken to a rescue center as a consequence of applying a stranding protocol due to the local authorities' unawareness of the possibility that it could be a nesting event. In addition, Mascletà was the only turtle that was tagged in two different years, in 2016 and 2020 (Turtle IDs: Mascletà2016 and Mascletà2020, respectively).

Details on tracked turtles, satellite transmitters, attachment methods, and deployment locations are shown in Table 7.1. Location data were collected using the Argos satellite system. We fitted a hierarchical switching state-space model (hDCRWS) to our data to provide a position estimate at regular 12 hours interval with an associated behavioural state (Jonsen et al. 2007, 2016, Christiansen et al. 2016). We ran two Markov Chain Monte Carlo (MCMC) chains for 120,000 iterations, dropping the first 60,000 samples as a burn-in and retaining every 10th sample from the remaining 60,000 assumed post-converge samples from each chain to reduce sample autocorrelation. Thus, model parameters and estimated locations were calculated using a total of 12,000 MCMC samples. A time-step of 12 h was used to generate 2 daily locations of the tracking period from the posterior means of resultant distributions.

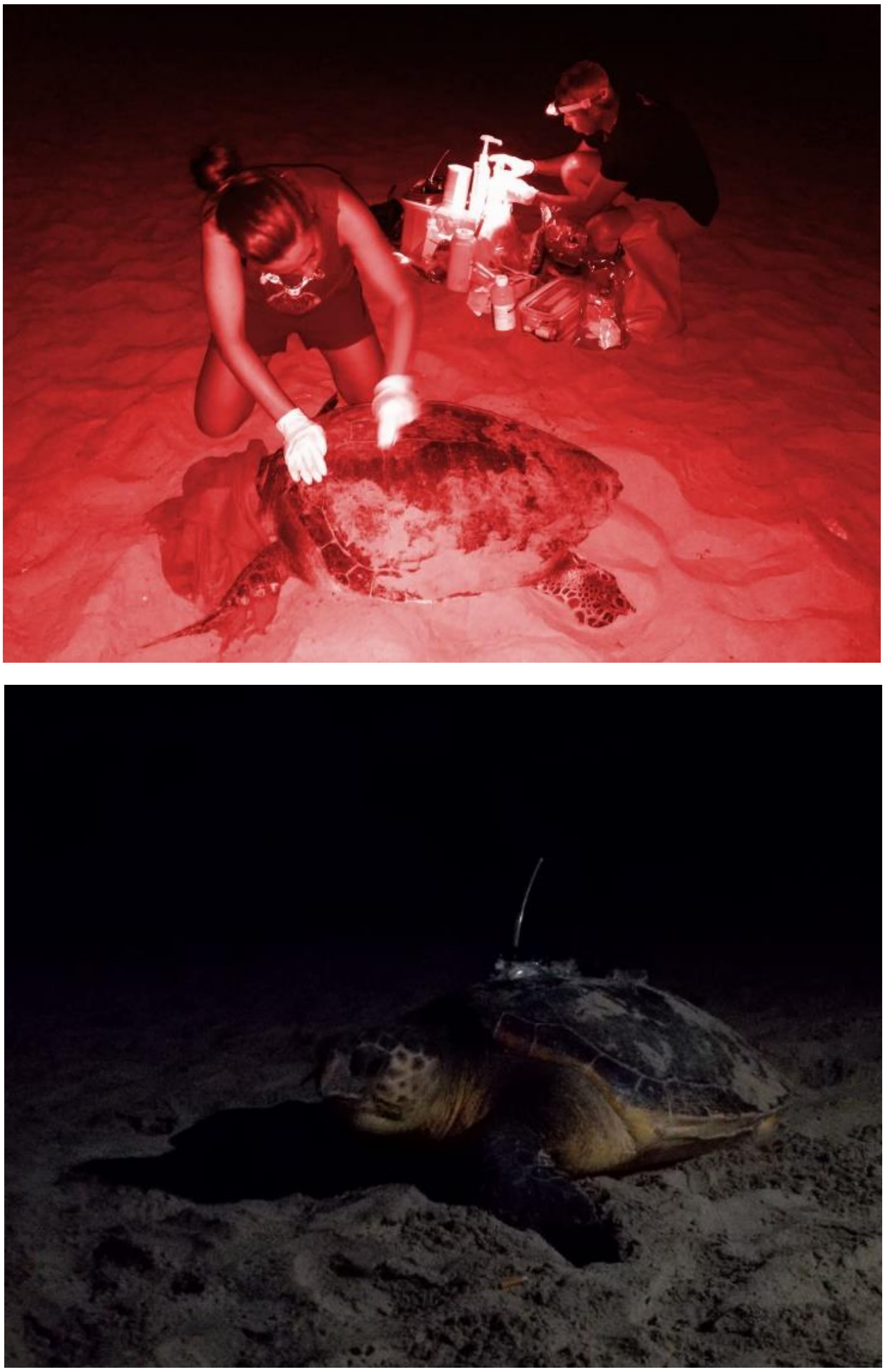


Figure 7.1 Nesting female ID Ana on nesting beach. On the top: Sanding turtle's carapace prior to tag attachment. On the bottom: Turtle with satellite transmitter attached on carapace just after release.

Table 7.1 Details on satellite-tracked nesting females: Argos ID number, name, CCL (curved carapace length), CCW (curved carapace width), date of deployment, deployment coordinates (latitude and longitude, in decimal degrees), date of end monitoring, days of monitoring, attachment method (epoxy resin or silicone), tag brand (SIRTRACK, DesertStar, or Wildlife Computers), and type of tag (solar powered PPT, SPOT, SPLASH, FASTLOC GPS). NA: not available data. *: still transmitting. Mascletà2016 and Mascletà2022 refers to the same turtle which was tagged in two different nesting events. Satellite-tracking data for turtle IDs Ana, María, Mascletà 2016 and Yaiza are publicly available at EMODNet repository ([dataset] Abalo-Morla et al. 2022).

Argos ID	Name	CCL (cm)	CCW (cm)	Deployment date	Latitude	Longitude	End monitoring date	Days of monitoring	Attachment method	Tag brand	Type tag
36422	Ana	80	76	08/07/2018	37.92	-0.72	15/11/2018	131	Epoxy	SIRTRACK	FASTLOC GPS
232741	Catherine	80	73	26/07/2022	38.04	-0.65	11/12/2022*	139	Epoxy	SIRTRACK	FASTLOC GPS
222028	Elena	NA	NA	10/07/2021	41.11	1.26	30/09/2021	83	Epoxy	SIRTRACK	FASTLOC GPS
60623	María	79	NA	30/06/2018	40.03	0.05	15/07/2018	16	Epoxy	Wildlife Computers	SPOT
160303	Mascletà_2016	61	77	24/06/2016	41.28	2.09	21/08/2016	59	Silicone	DesertStar	Solar PTT
84260	Mascletà_2020	60	NA	16/07/2020	41.08	1.18	13/09/2020	60	Epoxy	SIRTRACK	FASTLOC GPS
222027	Victoria	87	82	30/07/2020	39.18	-0.23	13/12/2022*	867	Epoxy	SIRTRACK	FASTLOC GPS
33052	Yaiza	79	72.5	27/06/2018	39.51	-0.32	03/01/2019	191	Epoxy	Wildlife Computers	SPLASH

7.2.2 Analysis of dispersal and habitat use

First, location data were split into two subsets: i) the first month after release, when an inter-nesting behaviour could be expected, and ii) the rest of the monitoring period. This was done because females might present different behaviour during the nesting season *versus* the rest of the year. Previous studies observed that females appear to: i) barely feed during the nesting and inter-nesting periods (Miller 1997, Hays et al. 2002, Hays 2008), and ii) to remain close to the nesting beach during the inter-nesting period (Zbinden et al. 2007). Area of restricted search patches (ARS) and migratory phases were identified for each individual (Lydersen et al. 2020). A migratory phase was defined when a transiting behaviour was predicted (behavioural estimated state < 1.25), and an ARS patch was defined when an ARS behaviour was predicted (behavioural estimated state > 1.75). To help to identify movement phases, we segmented turtle's trajectories into segments characterized by a homogeneous behaviour by using the method of Gueguen (2001, 2009) through the 'adehabitatLT' R-package (Calenge 2006). Independence of the residuals of the trajectory segmentation was tested using the Wald and Wolfowitz test (Wald and Wolfowitz 1943). Moreover, the distance to the coast (baseline isobath 0 meters) was plotted for each female. The Brownian Bridge approach of the kernel method implemented in the 'adehabitatHR' package was used for estimating the expected movement path of females and for identifying the core use areas for each female (50% Kernel Utilization Distribution, KUD) (Horne et al. 2007). This method considers the fact that between two successive relocations, the animal has moved through a continuous path, which was not necessarily linear. Therefore, a brownian bridge estimates the density of probability that this path passed through any point of the study area, with a certain amount of inaccuracy. Results were overlaid to identify overlapping core areas.

7.3 Results

Turtles were monitored during a range of 16 to 867 days (mean of 193 ± 260 days), and all turtles remained in the Mediterranean Sea during the monitoring period (Figure 7.2). Two turtles were still transmitting at the moment of the preparation of this Chapter (Turtle IDs Catherine and Victoria). Turtle ID Mascletà was tagged in two different years (2016 and 2020), at two different beaches 88 km apart. This was the first remigration record of a nesting female in the westernmost part of the Mediterranean basin and the first evidence that the same female has nested in this basin during two different nesting seasons. Both analyses of the foraging behaviour and trajectory segmentation supported the finding that the turtles alternated between faster and slower movement phases (Figures 7.3 and 7.4). Except for turtle ID Catherine, the residuals of these segmentations were independent (Wald and Wolfowitz test $P > 0.05$), confirming the validity of the approach (Figure 7.4). Fast movement model phases (high average displacement) would correspond to a migratory or displacement behaviour. Slow movement model phases (low average displacement) would correspond to ARS patches, likely related to a foraging or resting behaviour. In tracked females, slow movement phases appear to correspond to foraging periods in oceanic waters and to the period immediately previous to a coast approachment during the nesting season (Figure 7.5).

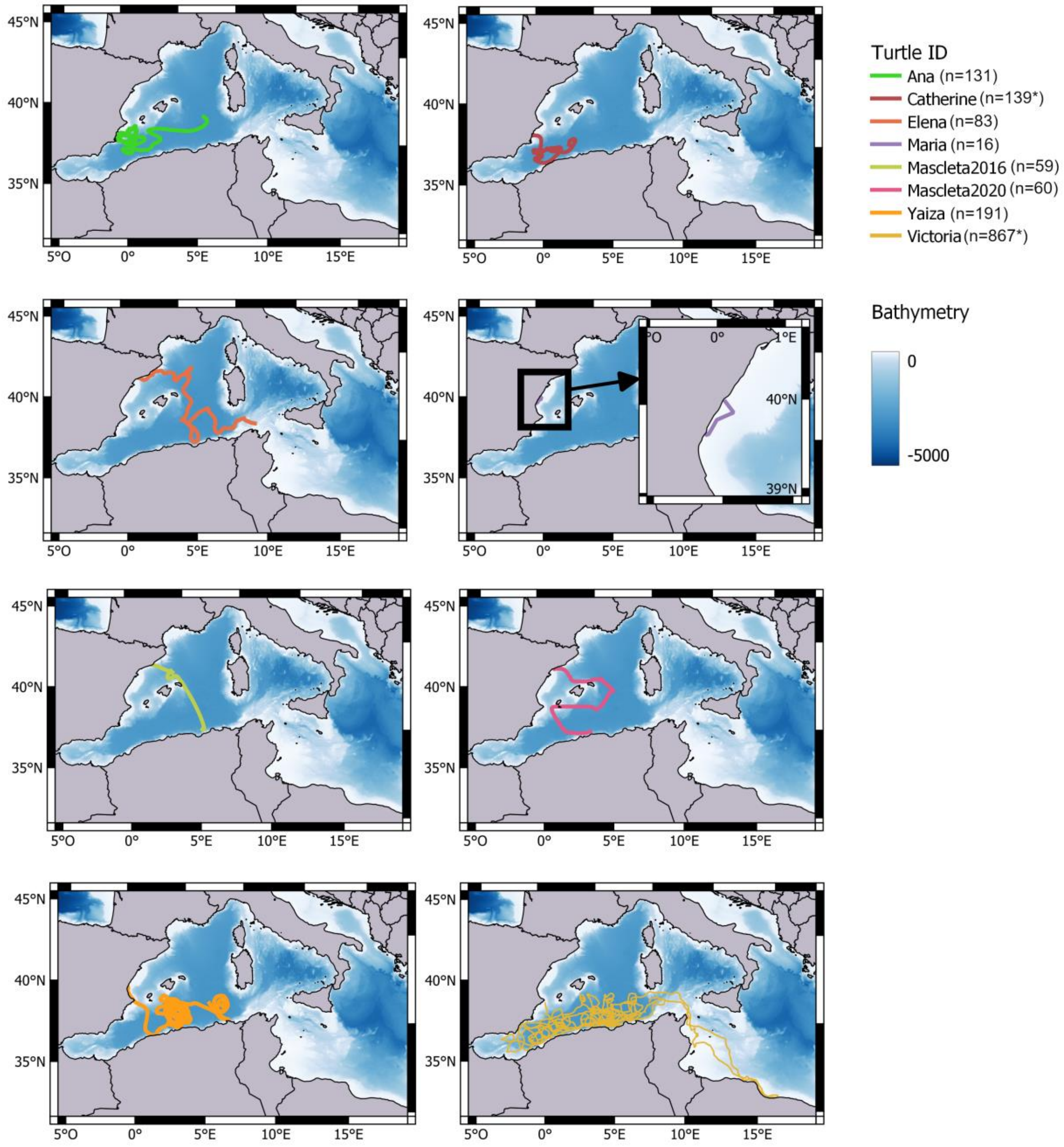


Figure 7.2 Tracks of the seven female loggerhead turtles satellite tracked from Spanish nesting beaches. Turtle IDs from top left to bottom right: Ana, Catherine, Elena, Maria, Mascletà2016, Mascletà2020, Yaiza, and Victoria. Days of transmission are shown in parenthesis next no each ID turtle. Bathymetry data is shown in blue scale.

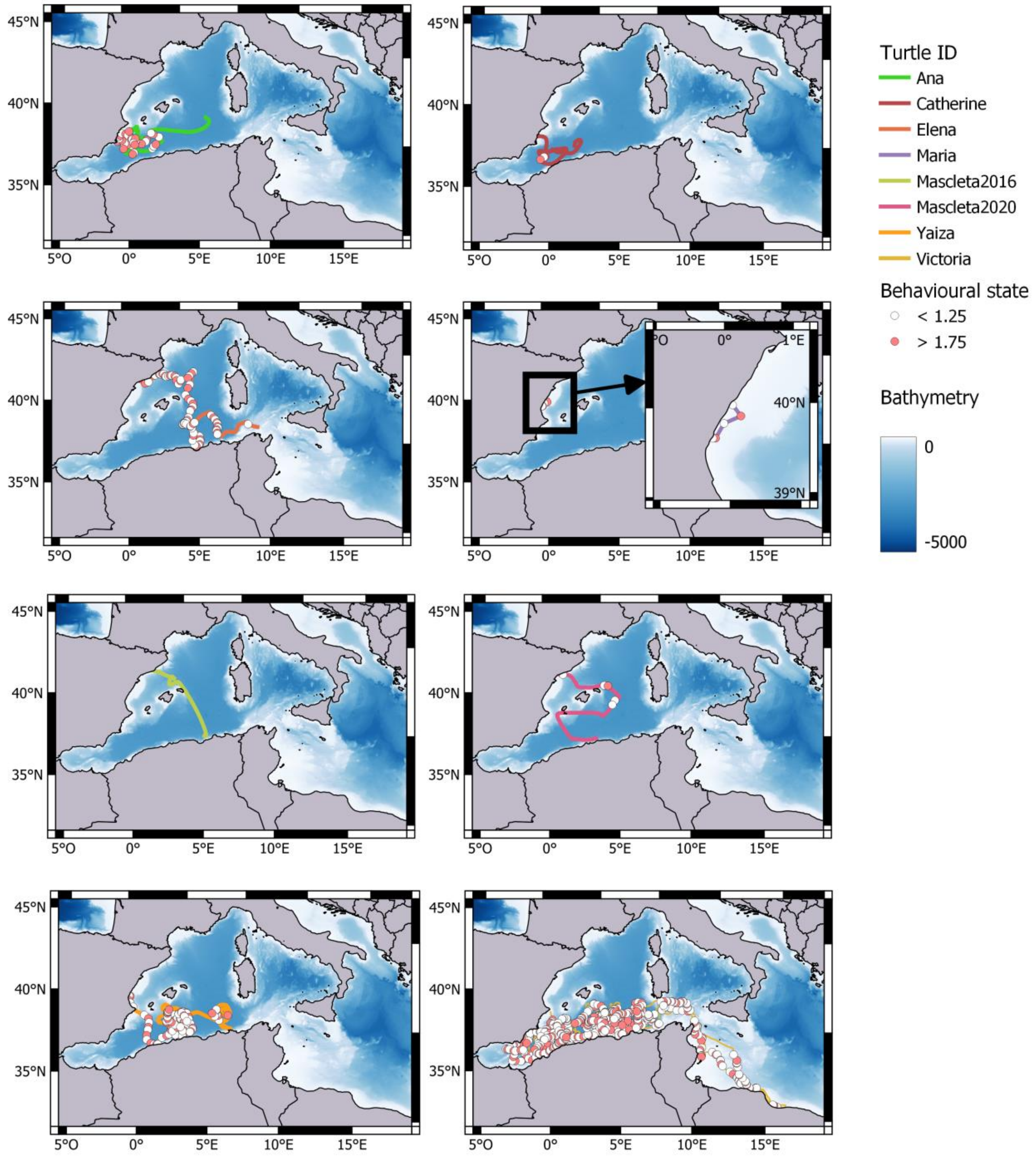


Figure 7.3 Tracks of the seven female loggerhead turtles satellite tracked from Spanish nesting beaches. Behavioural state is shown over turtle trajectories when migratory values (< 1.25) or Area Restricted Patch (ARS) values (>1.75) were reached. For Mascletà2016 migratory state nor ARS was associated. Turtle IDs from top left to bottom right: Ana, Catherine, Elena, Maria, Mascletà2016, Mascletà2020, Yaiza, and Victoria. Bathymetry data is shown in blue scale.

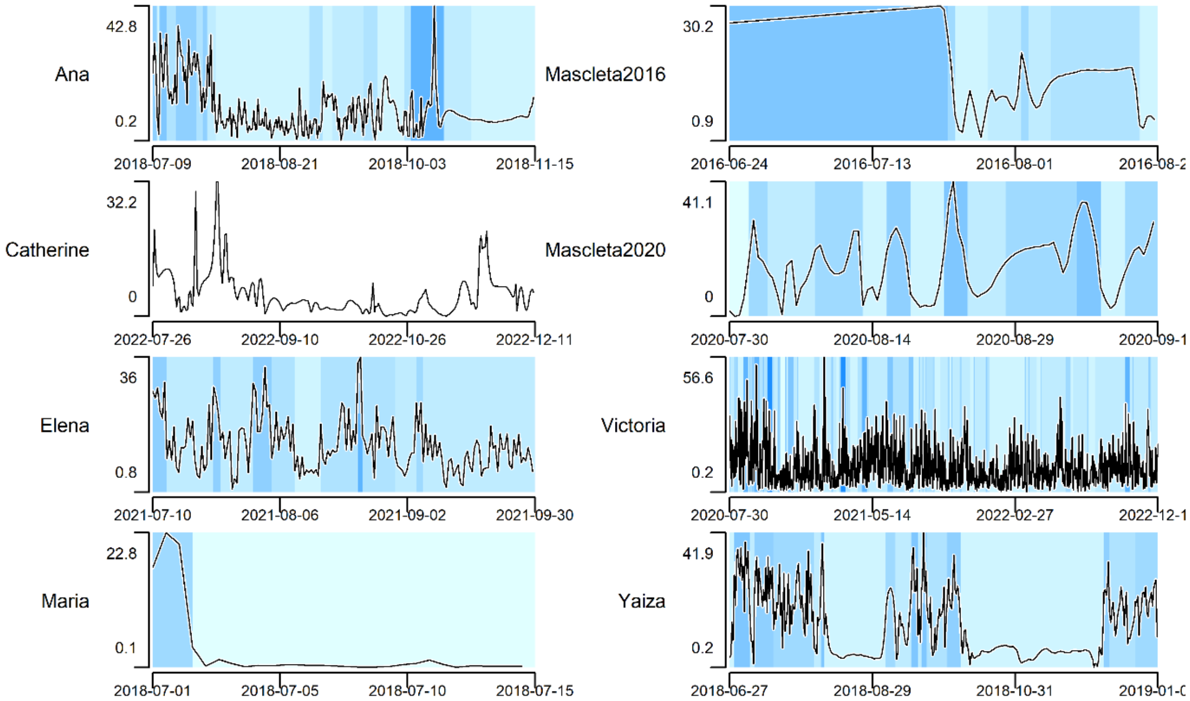


Figure 7.4 Results of the movement segmentation analysis, which shows the mean travel distance (y-axis) over time (x-axis). The background color represents different movement phases, with higher intensities of blue indicating greater average distances traveled and a faster movement model. Conversely, lower intensities of blue indicate shorter average distances traveled and a slower movement model. For Catherine, no significant movement segmentation analysis was found.

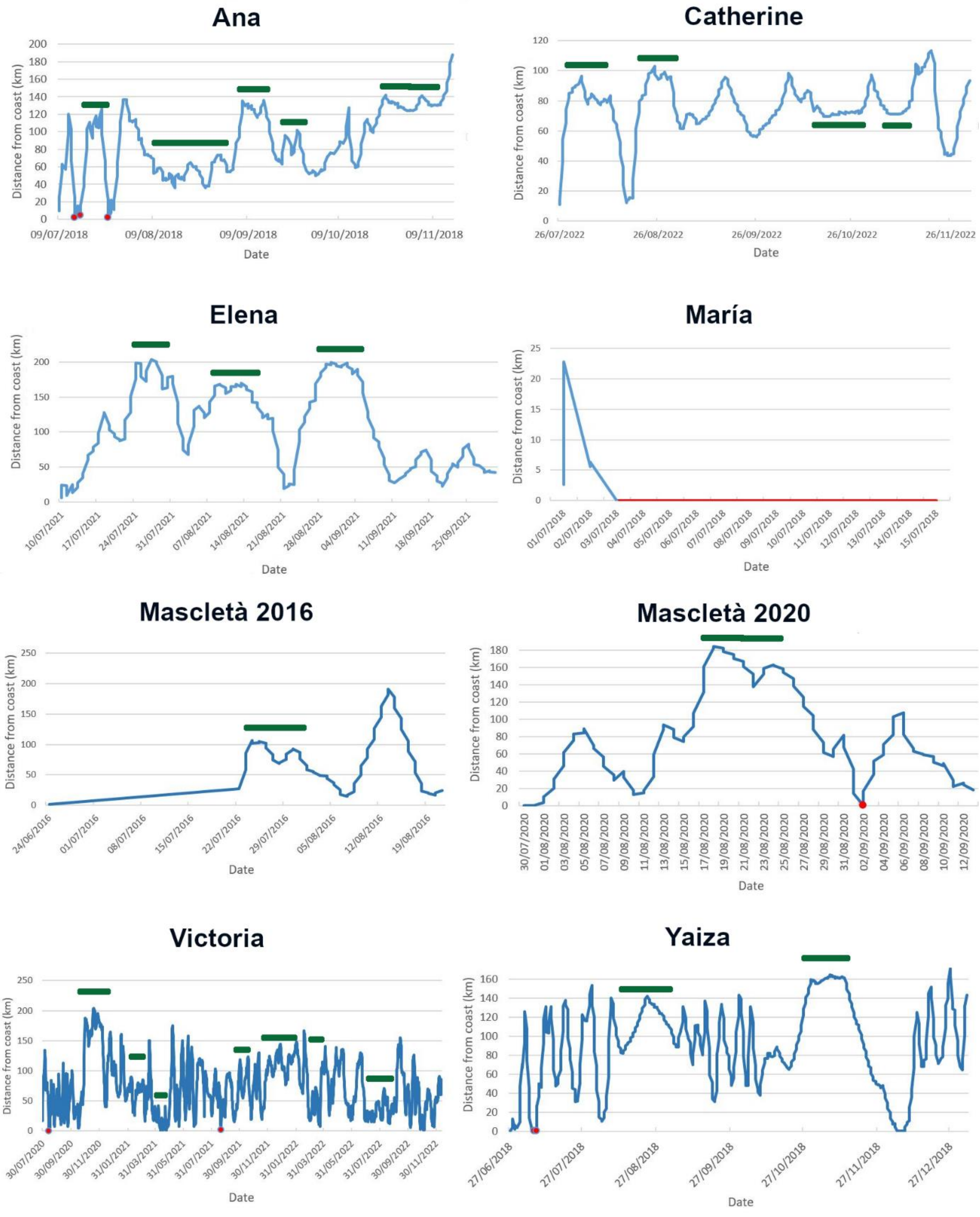


Figure 7.5 Distance from coast (baseline isobath 0 meters) over time for each nesting female. Red points indicate land locations during nesting period, suggesting a possible nesting event or nesting attempt. Likely foraging periods in oceanic waters are highlighted in green.

7.3.1 Behaviour during the nesting and inter-nesting periods

Different behaviour and use of habitat were observed in nesting females during the nesting and inter-nesting period. During the first month after tagging, we found three clear different behaviours (Figure 7.6). Some females remained close to the nesting beach where they were tagged (i.e., Turtles ID Mascletà in 2016, María, Ana), others were dectected exploring or trying to nest in distant beaches (more than 100 km away from the first recorded nesting beach) (i.e., Turtles ID Yaiza, Victoria), and other females moved towards oceanic waters after tagging (i.e., Turtles ID Catherine, Elena) (see Figure 7.7). Although nesting events were inferred from satellite-tracking data, none was confirmed by direct observation (turtle sighting on the beach).

For instance, for turtle ID Ana we inferred two potential nesting attempts in the same nesting season in a 30 km radius after release. The female was tagged on a beach in the Alicante province. The first recorded nesting attempt after tagging occurred 30 km south from the beach where the female was tagged. One week later was recorded the second nesting attempt, with emergences during 2 consecutive nights on the same beach where it was tagged and also 24 km north from there (see Figure 7.7). Turtle ID Mascletà was tagged after nesting in two different nesting seasons (2016 and 2020) on the coast of Catalunya, with nesting beaches being 88 km apart. In both instances, Mascletà exhibited similar post-nesting behaviour. This was the first record of a returning breeding female in the westernmost part of the Mediterranean basin and the first evidence that the same female nested in this basin during two different nesting seasons. Turtle ID María was tagged on a nesting beach located in the Castelló province while heading to sea after several unsuccessful attempts to lay eggs on the beach. The veterinary team examined this female by ultrasound and confirmed that she had shelled eggs present in her oviducts when she was tagged (Crespo-Picazo et al. 2019). Additionally, this female remained close to the beach where subsequent days after tagging turtle trails were recorded on the sand. However, transmission was lost 15 days after release, possibly due to tag detachment, tag failure or damage, or turtle death (Figure 7.7).

Other female turtles exhibited exploratory nesting behaviour (i .e., nested in distant locations during the same breeding period). For example, turtle ID Yaiza nested on the Spanish Mediterranean coast (Valencia province) where she was tagged. During the same nesting season, 11 days after tagging, we inferred a potential nesting event of this female on the Algerian coast, with emergences occurring over three consecutive nights. Additionally, turtle ID Victoria made nesting attempts on the Spanish coast more than 300 km away from female's initial nesting site, about two weeks later, indicating low nest site fidelity. While we recorded turtle emergences and turtle trails on the beaches, no nests were found. Habitat use varied during the first month of monitoring compared to the rest of the year, as indicated by the overlapping map of Brownian Bridge kernel estimations at 50% KUD (Figure

7.8). During the first month of monitoring, nesting females exhibited different habitat preferences. Some turtles remained relatively close to the coast in the Alboran or Balearic Seas, while other travelled to the oceanic waters of the Algerian basin.

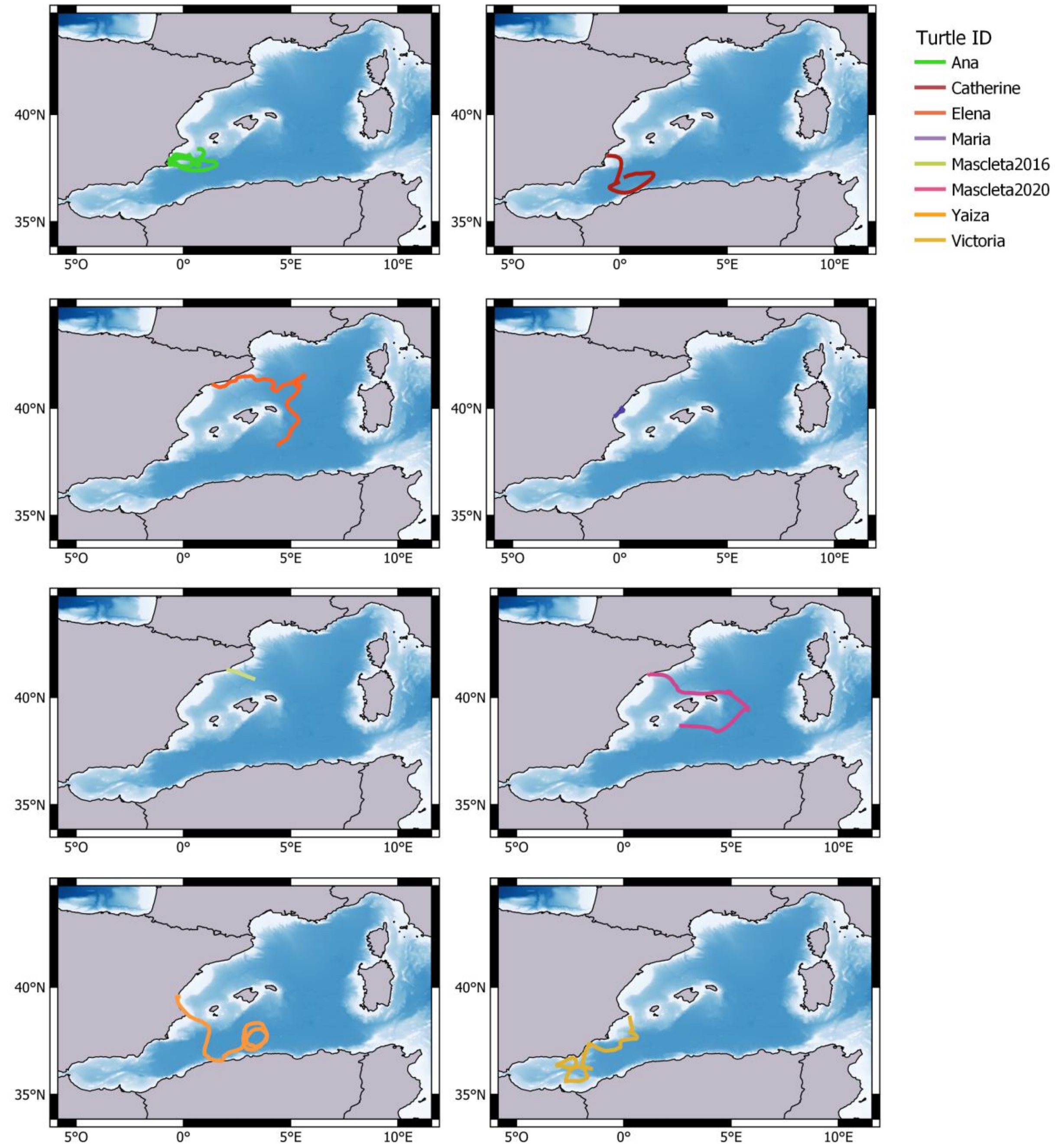


Figure 7.6 Tracks of the seven female loggerhead turtles satellite tracked from Spanish nesting beaches during the first month after tagging. Turtle IDs from top left to bottom right: Ana, Catherine, Elena, Maria, Mascletà2016, Mascletà2020, Yaiza, and Victoria. Bathymetry data is shown in blue scale.

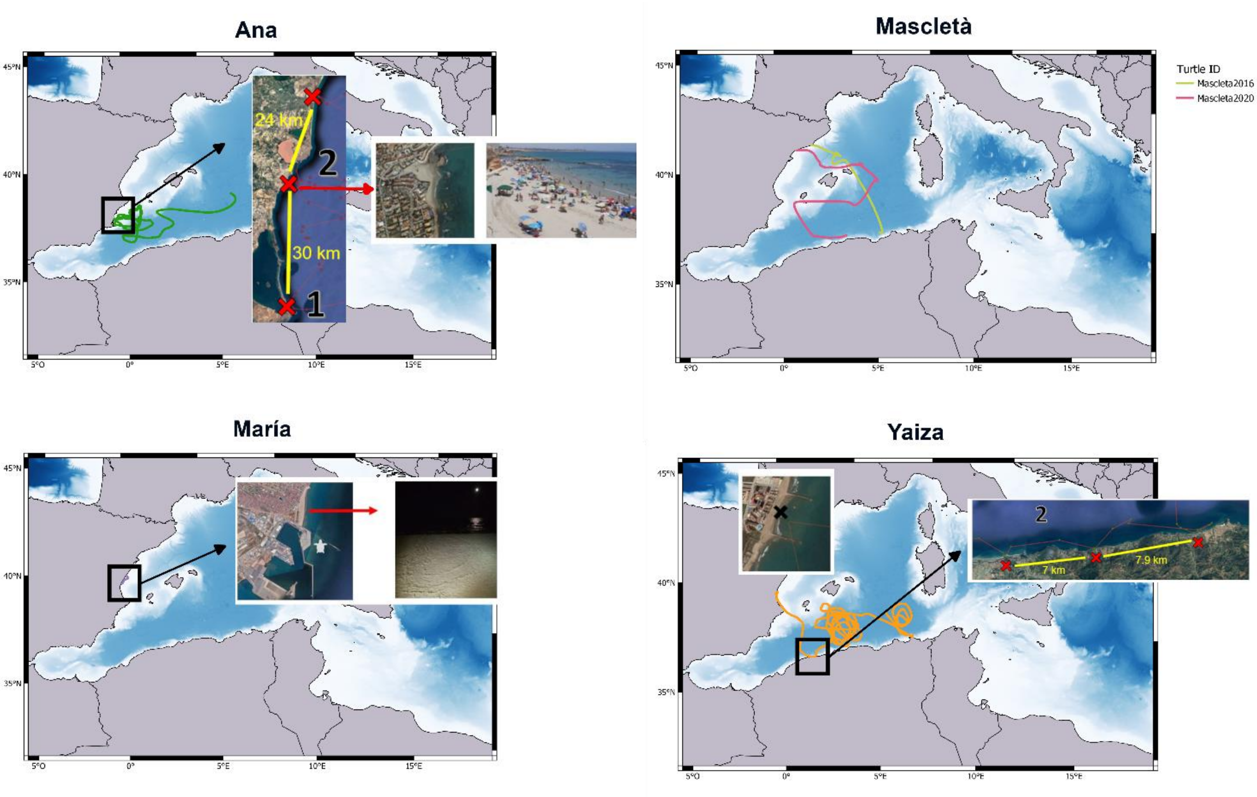


Figure 7.7 Satellite tracks of nesting females and satellite images of the site where first nesting attempt was recorded and turtles were tagged. Locations of subsequent nesting events are also marked, if available. Mascletà was tagged after nesting in two different nesting seasons (year 2016 in green, and year 2020 in pink).

7.3.2 Behaviour during the post-nesting period

Different post-nesting behaviours were observed among females, as they followed different dispersal routes. Nonetheless, when nesting season ended all turtles moved away from the nesting area (except turtle ID Maria from which we lost transmission close to the nesting beach, likely due to tag detachment or death), usually embarking in long-distance loops occurring mostly in oceanic waters (see Figure 7.2). Turtles ID Ana and Catherine traveled south and spent the most time in the western part of the Algerian Basin. Both times after tagging, Mascletà moved eastward and then southward, to reach the eastern part of the Algerian Basin. Both turtles ID Elena and Yaiza reached the central part of the Algerian Basin, although they followed different routes: Turtle ID Elena traveled eastward and the south, and turtle ID Yaiza traveled south and then eastward. Turtle ID Ana also reached the central Algerian basin at the end of monitoring. However, a year later, her satellite tag was found on the same nesting beach where she was tagged, suggesting that this female returned close to the nesting area. Finally, turtle ID Victoria used the western Mediterranean (Alboran Sea and Algerian basin) extensively, crossed the Sicilian Channel and spent 3.5 months in the eastern Mediterranean, before coming back to the Algerian Basin. To date, this is the longest record of a nesting female on the Spanish coast (2.4 years of monitoring and counting). Turtles spent most of the tracking time (92.3%) in areas of sea bottoms deeper than 200 m and hence were mainly oceanic foragers. The Algerian basin was the most frequented area by all turtles during the non breeding period, as indicated by the overlapping map of the Brownian Bridge kernel estimations at 50% KUD (Figure 7.8), although one female (turtle ID Victoria) also used the Tunisian plateau and the coast of Libya.

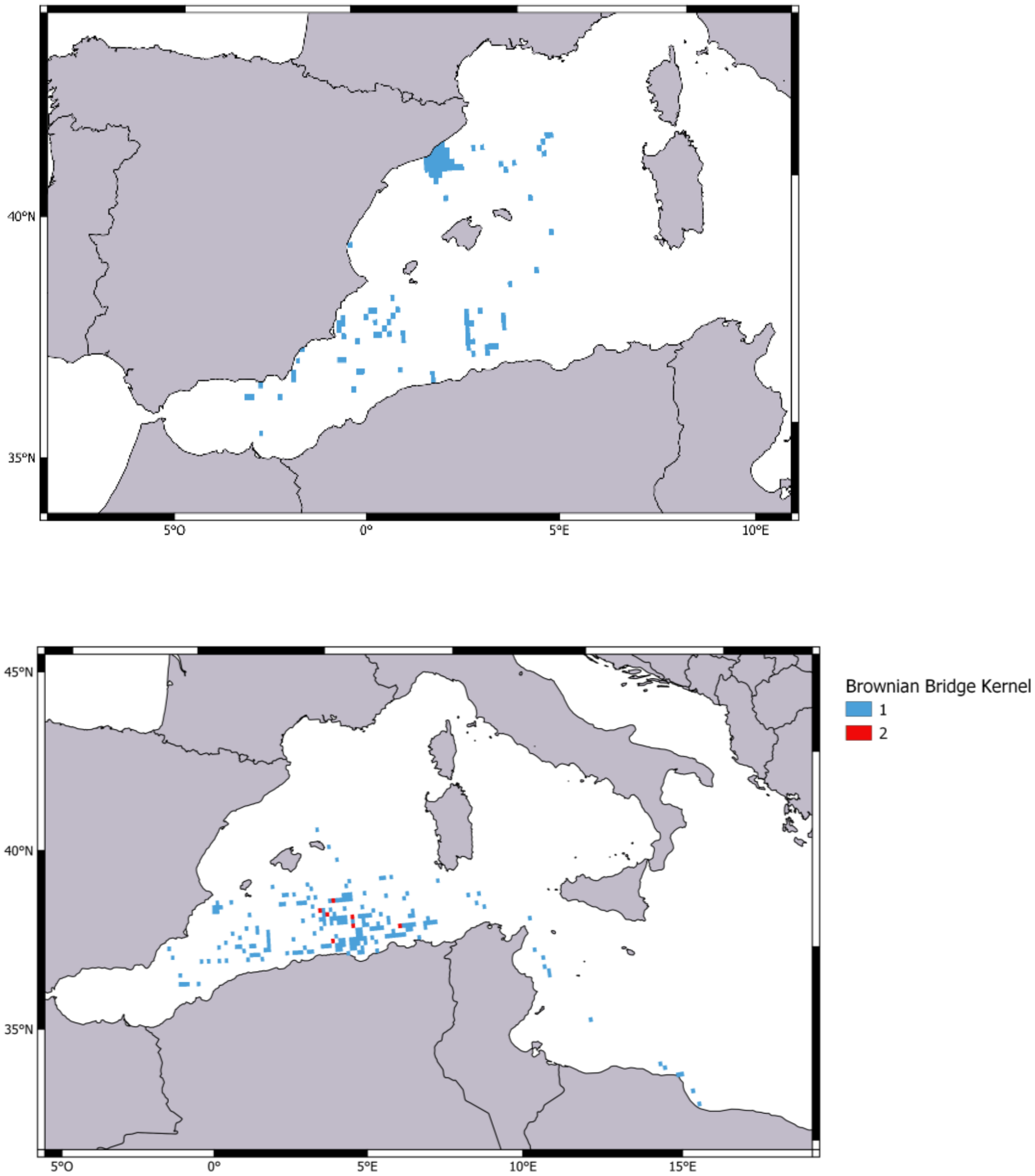


Figure 7.8 Kernel habitat use estimations obtained by the Brownian Brigde method. The color scale indicates areas with no overlapping kernels (blue) or two overlapped kernels (red). On the top: Kernel for the first month of monitoring period (inter-nesting period expected). On the bottom: Kernel for the rest of the monitoring period (non breeding period).

7.4 Discussion

Over the last decades, satellite tracking techniques have substantially advanced our understanding of sea turtle spatial behaviour, especially for the post-nesting migrations of females. However, substantial gaps about females' behaviour during the remaining inter-reproductive period remains in our knowledge. In fact, until now there are only a few studies providing information about the spatial behaviour of Mediterranean loggerheads during an entire reproductive cycle (Mingozzi et al. 2016). In addition to this, nesting events on the western Mediterranean basin are suggested to belong to an increasing colonizing process of turtles from eastern Mediterranean and even from the Atlantic, probably driven by the climate warming, which seems to induce changes in nesting behaviour of loggerhead turtles (Hochsheid et al. 2022). Such ongoing colonization process is recent and, therefore, there is not an established nesting beach identified yet in the western Mediterranean for the species (Tomás et al. 2020). This fact constrains the detection of nesting females to satellite-tag them in comparison with other Mediterranean areas (i.e., Greece, Cyprus, Lybia) where hundreds of nesting females are found on the beach at nesting season. However, since 2017, irregular monitoring of beaches were made by volunteers in several Spanish regions (i.e., Valencia, Murcia, Catalonia) (Hochsheid et al. 2022). Moreover, encounter and notification protocols were established in case of sighting a nesting female. Such protocols were crucial for reporting the presence of females or hatchlings or their tracks on the beach (Hochsheid et al. 2022) and, consequently, to conduct the research related to the present thesis.

Knowledge about behaviour and habitat use of nesting females in Spain was very scarce prior to our research, which provides, for the first time, insights about the habitat use of loggerhead nesting females on the Spanish Mediterranean coast. During the post-nesting period we observed that all turtles moved away from the nesting area, usually embarking in long-distance loops occurring mostly in oceanic waters (as observed by Migozzi et al. 2016, Godley et al. 2008). Previous studies suggested that adult loggerheads in the Mediterranean Sea inhabit foraging grounds usually hosted at the neritic zone (Wallace et al. 2011, Zbinden et al. 2008, 2011, Casale et al. 2013, Luschi et al. 2013, Rees et al. 2013, Mingozzi et al. 2016, Snape et al. 2016, Almpanidou et al. 2022), and exhibit smaller home ranges than those turtle life stages that inhabit oceanic habitats (Schofield et al. 2010, Snape et al. 2016). However, recent studies suggested that adult turtles in the Mediterranean may alternate between neritic and oceanic habitats due to the short distance between the two types of habitat in the Mediterranean basin (Ten et al. 2019, Cerritelli et al. 2022, Baldi et al. 2023).

Our results suggested that post-nesting females (and even females throughout the year) on western Mediterranean are mainly oceanic foragers, as they mainly inhabit the Algerian basin, showing high fidelity to this foraging ground, as observed in previous studies on Central Mediterranean (see Mingozzi et al. 2016). Foraging sites of adult sea turtles are critical for population persistence, as they represent habitats where animals spend most of their time so as to replenish their reserves and be able to breed (Wallace et al. 2011). The Algerian basin seems to be an important foraging ground not only for post-nesting females but also for adults in general and for juveniles (see Chapter 6). This result agrees with previous studies on feeding ecology of loggerhead turtles in the western Mediterranean, which highlighted the importance of the pelagic prey for loggerheads inhabiting western Mediterranean (i.e., Tomás et al. 2001, Revelles et al. 2007d). However, in the western Mediterranean, the presence of less controlled fisheries and the discarding of fishing gear from North African countries has been reported (Darmon et al. 2022). Therefore, management and conservation efforts should be held not only at the well-known foraging grounds (Migozzi et al. 2016, Almpanidou et al. 2022) but also at the Algerian basin, to ensure viable loggerhead populations at the western Mediterranean.

Only one female (turtle ID Victoria), which was satellite-tracked more than 2 years (and counting), frequented neritic foraging grounds for a 3-month period at the Tunisian Plateau and Libyan coastal waters before returning to the western basin, suggesting that this foraging area is used by females nesting on the western basin. The Tunisian Plateau and the coast of Libya are known foraging grounds for adult loggerhead turtles from other Mediterranean regions (see Mingozzi et al. 2016, Levy et al. 2017, Almpanidou et al. 2022, Cerritelli et al. 2022). This result supports previous studies in which adult individuals from a given breeding rookery might use different foraging grounds, often separated by hundreds of kilometres (Bentivegna 2002, Zbinden et al. 2008, Schofield et al. 2010a, Schofield et al. 2013). Even on some rare occasions, females that nested on eastern Mediterranean rookeries were satellite tracked into the western Mediterranean (Zbinden et al. 2011, Schofield et al. 2013b, Haywood et al. 2020b), so it may even be possible that they opportunistically explore nearby beaches for nesting in successive seasons. In addition, the aforementioned result supports that adults could display a dichotomy in foraging behaviour linked to body size (Hawkes et al. 2006, Mansfield et al. 2009, McClellan et al. 2010, Zbinden et al. 2011, Vieira et al. 2014, Okuyama et al. 2022), as we inferred from satellite tracking that the larger female (Turtle ID Victoria) was foraging in coastal waters, while the smaller females were predominantly inferred to were foraging in open ocean. Additionally, several authors pointed out climate change as a factor fostering the redistribution of adult loggerheads into western Mediterranean foraging habitats (Chatzimentor et al. 2021). Other authors pointed out that temperature plays a key role on foraging areas suitability, shaping the distribution of adult turtles (Almpanidou et al. 2022). However, it remains unknown if nesting sites are correlated with the distribution and number of adult turtles frequenting the nearby foraging habitats or other environmental factors such as sea surface temperature or warming trends (Hochsheid et al. 2022). Previous research in the Atlantic Ocean has found evidence that sea turtles use magnetic cues to return to their natal beaches for nesting through a combination of geomagnetic imprinting and magnetic navigation (Brothers and Lohmann 2015). Brothers and Lohmann (2018) observed that nesting beaches on opposite sides of the Florida peninsula are close to the same magnetic isoline and have similar magnetic signatures. Consequently, they suggested that a nesting turtle might nest on a beach that has the same magnetic field, even if it is far from its original natal location. Considering that the magnetic isolines in the Mediterranean Sea "bound" nesting sites from the eastern and western Mediterranean, the role of magnetic cues cannot be dismissed as a driver for nesting site selection in the Mediterranean Sea.

Despite the difficulties associated in monitoring females during the inter-nesting period due to transmitters failure as a result of mating and/or inter-nesting resting behaviour (i.e., under rocky ledges), and to the high risk of fisheries interaction (Godley et al. 2008), we successfully tracked several females during the inter-nesting period. We observed that during the inter-nesting period our tracked females showed three different behaviours. Some females remained close to coast prior to the next nesting event, which could be explained because females displayed some degree of fidelity to a nesting area, and/or because females do not probably forage between nesting events (Miller 1997, Hays et al. 2002, 2008, Zbiden et al. 2007). However, further research on turtle females' tracking is needed to corroborate this result. Other females travelled to other areas, displaying an exploratory nesting behaviour (as suggested by Hochsheid et al. 2022), nesting even on the south Mediterranean basin (i.e., Algeria). And other females moved towards oceanic waters after tagging, reaching foraging areas in the way through. In this last case, it was hypothesized that such long oceanic movements were induced by the need of replenishing the females' food stores after laying eggs (Mingozzi et al. 2016). In addition, such mentioned differences in females' behaviour could be influenced by a different genetic origin of females (Carreras et al. 2018). In addition, Hochsheid et al. (2022) found very unlikely that nesting females on western Mediterranean basin were recruitments from previously unnoticed nesting events, as temperature one generation ago would not allow to produce sufficient numbers of females to return to these beaches.

Finally, we observed for the first time in the western Mediterranean that nesting females on Spain's coast may display some degree of nest site fidelity between breeding cycles, as we registered the first-time remigration of this species to nest in Spain's beaches (Turtle ID Mascletà, in 2016 and 2020) four years after the first recorded nesting event for this turtle in the same region. Moreover, this female followed a similar route during both post-nesting migrations, in accordance with previous findings (Broderick et al. 2007, Mingozzi et al. 2016). Although we recorded turtle emergences and turtle trails on the beach, no nests were found. This could be caused by turtles attempt to nest but finally did not lay the clutch, or turtle might complete the egg-laying process but trails were not detected due to beach cleaning with heavy machinery.

7.5 Conclusions

We analyzed for the first time the dispersal of nesting females on the western Mediterranean during the inter-nesting and post-nesting periods. Females might display three different behaviours during the inter-nesting period: i) remain close to coast showing some degree of fidelity to a nesting area, ii) display an exploratory nesting behavior, or iii) moved towards oceanic waters after tagging. Furthermore, we observed that females might display some degree of nest site fidelity between breeding cycles, as we recorded the first-time remigration of this species to nest in Spain. Our outcomes support the hypothesis of the existence of a colonization process by loggerhead sea turtles in the western Mediterranean basin. We observed females reemigrating to nest in the same area, suggesting the possibility of unrecorded nesting events in these areas over 20 years ago. Another explanation could be that these females exhibit exploratory behaviour as a means to "avoid" the constraints of philopatry, for instance regarding the potential consequences of a climate change. During the non-breeding stage, females remained in most cases foraging in oceanic waters of the Algerian basin. However, we found evidence that nesting females in the western Mediterranean could temporary travel to other foraging areas in the eastern Mediterranean. Overall, findings from this chapter may contribute to identify areas frequented by nesting females, which are crucial for their protection, as these areas may face threats that undermine sea turtle conservation (i.e., fishing activity, coastal development, tourism, under-regulated countries). Ultimately, these results will contribute to the development of effective conservation measures not only for nesting females along Spain’s coast but also for nesting females along the entire western Mediterranean basin.

Chapter 8

General discussion

Conservation planning for sea turtles must consider the species' ecological and ontogenetic developmental requirements (Hamann et al. 2010, Venter et al. 2014, Rees et al. 2016) and should protect all life stages (Bentivegna 2002, Beger et al. 2015) with large-scale conservation plans that explicitly incorporate their habitat needs and migratory behaviours (Mazor et al. 2016, Harrison et al. 2018). However, until the development of this thesis, in the Mediterranean Sea there was a knowledge gap about the habitat use and behaviour of the loggerhead sea turtle across all life stages, which is crucial for implementing adequate conservation measures for the species. The new colonizing nesting events recorded in recent years on the Spanish coast have allowed in the context of the present thesis to satellite track, for the first time, post-hatchlings in the Mediterranean Sea and nesting females in the western basin. The analysis of such novel data contributes in filling gaps in knowledge about the survival, dispersal and habitat use of the loggerhead turtle along its life cycle in the Mediterranean Sea, and about the potential colonization process of loggerhead sea turtle nesting currently taking place in the area (Hochscheid et al. 2022).

In general, most of the monitored and analyzed individuals moved long distances and had wide home range areas that apparently decreased with life stage development, supporting the proposed model of ontogenetic reduction in home ranges for the species (Carr 1987, Bolten 2003, Schofield et al. 2010a, Casale et al. 2012a). The relevance of the Algerian basin for the loggerhead sea turtle in the western Mediterranean was broadly observed in the present thesis during all life stages, but especially for juveniles and adults (including nesting females) satellite-tracked from the western basin, as suggested by previous studies (Cardona et al. 2005, Revelles et al. 2007a, b, c, Casale et al. 2012a, b, Hays et al. 2014). Although the central-eastern Mediterranean basin is a known foraging ground for adult loggerhead turtles (Zbinden et al. 2008, Schofield et al. 2010, Mingozzi et al. 2016, Almpanidou et al. 2022), our results showed that such area is much less frequented by adult turtles tracked from the western Mediterranean. Such results supported previous studies where adults tracked from the western Mediterranean were more likely to remain in the same basin where tagged (Luschi et al. 2017). In addition, our late juvenile and adult monitored turtles showed a high fidelity to the oceanic waters of the Algerian basin, where they behaved mainly as oceanic foragers. This result supports recent studies that have suggested that adult loggerhead turtles in the Mediterranean basin may alternate between neritic and oceanic habitats (Tomás et al. 2001, Domènech et al. 2018, Luschi et al. 2018, Ten et al. 2019, Chimienti et al. 2020, Baldi et al. 2023), instead of inhabiting mainly neritic foraging grounds, as was proposed by other studies in the same region (Wallace et al. 2011, Zbinden et al. 2008, 2011, Casale et al. 2013, Luschi et al. 2013, Rees et al. 2013, Mingozzi et al. 2016, Snape et al. 2016, Almpanidou et al. 2022).

This thesis describes for the first time the inter-nesting and post-nesting behaviour of nesting females on the western Mediterranean basin. Overall, during the inter-nesting period females showed three main different behaviours: i) remained close to coast prior to the next nesting event, which could be explained because females displayed some degree of fidelity to a nesting area, and/or because females do not probably forage between nesting events(Miller 1997, Hays et al. 2002, 2008, Zbinden et al. 2007), ii) displayed an exploratory nesting behaviour (as suggested by Hochsheid et al. 2022), or iii) dispersed to oceanic water to reach foraging areas. Why females displayed such differences in inter-nesting behaviour remains unknown although it could be influenced by a different genetic origin of females (Carreras et al. 2018). Furthermore, we observed for the first time in the western Mediterranean that nesting females may display certain degree of nest site fidelity between nesting seasons, and even follow similar routes during post-nesting migrations, as reported in previous studies from other regions (Broderick et al. 2007, Mingozzi et al. 2016). During the post-nesting period females moved away from the nesting area, usually embarking in long-distance loops occurring mostly in Algerian oceanic waters (as observed by Godley et al. 2008, Migozzi et al. 2016).

The head-starting programs carried out with loggerhead clutches laid by nesting females along the Spanish coasts allowed us to study the *lost years* of this species (Bolten 2003) for the first time in the Mediterranean Sea through satellite tracking techniques, following previous research conducted in the Atlantic Ocean (Mansfield et al. 2014, 2017). We obtained the first empirical survival estimates for this life stage in the Mediterranean basin observing that most of our head-started post-hatchlings were able to survive in the wild, at least during the most critical period after release (Armstrong and Seddon, 2008). Indeed, the high daily survival probability estimated supported the head-starting programs, if appropriately implemented, as an effective conservation measure for hatchlings, especially of those coming from nests out of range which could be exposed to threats (i.e., predation, climatic conditions, tourism) (Hochscheid et al. 2022).

For the first time in the Mediterranean Sea, our conducted analysis of the routes followed by satellite tracked post-hatchlings also provides insights into post-hatchlings dispersal and habitat use. Post-hatchlings travelled mostly through oceanic waters, supporting the loggerhead oceanic nursery paradigm (Carr 1987, Bolten 2003, Chambault et al. 2019). All post-hatchlings remained in the Mediterranean basin, which supports previous studies suggesting that small loggerheads (< 36 cm) are unlikely to cross the inflow current from the Atlantic and leave Mediterranean Sea towards the Atlantic Ocean (Revelles 2007b). Moreover, although turtles exhibited highly variable routes, as seen in previous research in other regions (Okuyama et al. 2010), most post-hatchlings displayed an eastward directional movement, particularly when sea surface temperatures dropped below 15 ºC. This finding supports previous studies that have emphasized the importance of seawater temperature in shaping sea turtle dispersal movements (Coles and Musick, 2000, Varo-Cruz et al. 2016). Directional movements in head-started post-hatchlings have also been observed in previous studies conducted in the Atlantic Ocean (Mansfield et al. 2014, 2017). Most post-hatchlings travelled long distances, switching among active dispersal and passive drifting as observed in previous studies (Mansfield et al. 2014, 2017, Chambault et al. 2019), and some of them crossed the Sicilian Channel to reach potential developmental areas in Central Mediterranean (Northeast Tunisia, Ionian Sea, Maltese waters). The importance of the Central Mediterranean for juveniles and adults from other Mediterranean regions was also highlighted by previous literature (Bentivegna 2002, Hochscheid et al. 2007, Schofield et al. 2010a, Bastari et al. 2016, Mingozzi et al. 2016, Casale et al. 2012c, 2018, Luschi et al. 2018). The habitat analysis and prediction models performed in this thesis (see Chapter 5) identified the Ionian and Levant Seas as suitable areas for the development of post-hatchlings, at least for those coming from western Mediterranean nests. Previous research has also indicated the importance of the Central Mediterranean for hatchlings and post-hatchlings originating from central-eastern Mediterranean nesting beaches (Casale and Mariani 2014). However, it should be noted that, to the best of our knowledge, no similar research to that of this thesis involving satellite-tracked post-hatchlings from the eastern Mediterranean has been conducted. In addition, we suggested that the Algerian basin, the Alboran Sea, the Tyrrhenian Sea and the deep waters of the Sicilian Channel could be also important areas for post-hatchlings, and maybe for hatchlings, from Spanish nests during the period after emergence.

To cover the whole spectrum of conservation needs for this highly migratory species, we evaluated the efficiency of the current Mediterranean marine protected areas in protecting the loggerhead sea turtle. Our results revealed that the vast majority of the most used areas for loggerhead turtles tracked from the western Mediterranean were not under protection, in spite of the requirement of the Habitats Directive (Art 4.1) (European Comission 2007, Fortuna et al. 2018). In addition, in most cases protected areas do not implement any specific measure to enhance loggerhead sea turtle conservation. Our results agree with the statement that the current Mediterranean MPAs seems to be unlikely effective in protecting the species, as suggested in previous studies at smaller geographical scales (i.e., Revelles et al. 2007b, Snape et al. 2018). In the context of this issue, we went a step further in the research proposing several areas in the western and central Mediterranean where protection should be maximized for the conservation of the loggerhead sea turtle. Such areas are located at the Algerian basin, Alboran Sea and southern Balearic Sea, especially focused on juveniles and adults, and at the Sicilian Channel, the Ionian Sea, Northeast Tunisia, the Maltese waters, and the Tyrrhenian Sea, focused on post-hatchlings and small juveniles coming from western Mediterranean nests. Previous research conducted by Notarbartolo di Sciara and Agardy (2009) also proposed potential large-scale protected areas based on several criteria, including important areas for the loggerhead sea turtle. The areas they proposed in the Alboran Sea, the Balearic Sea, the northern part of the Algerian basin, the Sicilian Channel, the Tunisian Plateau, and in the North Ionian Sea are fully or partially coincident with the areas we propose in the present thesis for the protection of the loggerhead sea turtle. Furthermore, both the Sicilian Channel and the Tunisian Plateau are subjected to high or very high human pressure, which poses a significant threat to sea turtles (Micheli et al. 2013).

In summary, this thesis presents comprehensive information regarding the ecology, habitat use, and distribution of loggerhead turtles throughout various life stages in the Mediterranean. This valuable information is particularly relevant for identifying potential threats specific to each life history phase. Ultimately, these findings will contribute to the enhancement of conservation measures aimed at the protection of this species.

Chapter 9

Conclusions

9.1 Conclusions

The present Ph.D. thesis analyses the habitat use and distribution of loggerhead sea turtles throughout their life cycle in the Mediterranean Sea, as well as implications for conservation. The following section summarizes the main findings and conclusions:

1. We provided the first empirical survival estimates of head-started loggerhead post-hatchlings in the Mediterranean Sea, based on data from three different clutches laid in Spain between 2014 and 2016. The head-starting programs for loggerhead hatchlings were successful in terms of short-term survival. There was a high probability of survival of head-started individuals in the wild, and probably head-started turtles had the ability to forage on natural prey and grow normally in their natural environment.

2. The results mentioned above support the effectiveness of head-starting programs as a valuable management and conservation tool for hatchlings, if implemented appropriately. Furthermore, head-starting programs yield valuable information for the conservation of the species (i.e., habitat use, development areas), hitherto unknown in the Mediterranean.

3. We elucidated the dispersal routes and the habitat use of post-hatchlings, for the first time in the Mediterranean Sea. Post-hatchlings originating from western Mediterranean nests were able to disperse over large oceanic areas, exhibiting highly variable routes, likely switching between active and passive dispersal. Most individuals displayed an eastward directional bearing, probably driven by environmental conditions (i.e., temperature) and taking advantage of sea currents.

4. We identified potential developmental areas for Mediterranean for post-hatchlings, located at the Ionian and Levant Seas. Furthermore, the Algerian basin, the Alboran Sea, the Tyrrhenian Sea and the deep waters of the Sicilian Channel could be also important areas for loggerhead turtles from Spanish nests during the period after emergence.

5. We also investigated, for the first time, the new colonizer nesting females on the Spanish Mediterranean coast. Females displayed three different behaviours during the inter-nesting period: i) remained close to coast until the next nesting event, showing certain degree of fidelity to a nesting area, ii) travelled to reach other nesting areas, showing an exploratory nesting behavior, or iii) moved towards oceanic waters after tagging.

6. We recorded the first-time remigration of this species to nest in Spain, confirming that females could show some degree of nest site fidelity between breeding cycles. During the non-breeding stage, females remained in most cases foraging in oceanic waters of the Algerian basin, although we found evidence that nesting females on western Mediterranean could also temporary travel to other foraging areas in Central Mediterranean.

7. In the present thesis we validate the relevance of the Algerian basin for loggerhead sea turtles satellite-tracked from the western Mediterranean, particularly for juveniles and adults (including nesting females). Additionally, we identified other important areas inhabited by loggerhead turtles in the southern Balearic Sea, the Alboran Sea, the Sicilian Channel, the Northeast Tunisia, Maltese waters, Tyrrhenian Sea and the Ionian Sea, depending on life stage.

8. The analysis of the spatial distribution of the loggerhead sea turtle allows to state that the current distribution and coverage of the marine protected areas (MPAs) in the Mediterranean are not effective to achieve this species conservation goals. Most of these areas are located in coastal zones, while loggerhead turtles in the western Mediterranean are mainly oceanic foragers. Furthermore, their main frequented areas (Algerian basin, Sicilian Channel and Ionian Sea) remain unprotected, and most MPAs in the western and eastern Mediterranean lack explicit management measures focusing on minimizing threats that undermine sea turtle conservation.

9. Building upon the previous point, we have identified the need to expand and add new MPAs in the Mediterranean Sea with specific conservation measures focused on loggerhead turtles. We propose new areas to be considered as MPAs in the following regions: the western part of the Algerian basin, the waters of the Northern Ionian Sea, the waters of the Northern Strait of Sicily, areas within the Tyrrhenian Sea, and the waters of the Northeast Tunisia. Additionally, we propose the expansion and interconnection of existing MPAs in Malta and the MPAs located in the Alboran Sea.

10. Outcomes from the present thesis significantly enhance our understanding of the survival and spatial use of the loggerhead sea turtle throughout its life cycle in the Mediterranean Sea. Such outcomes hold particular importance for the management of potential new breeding areas in the western Mediterranean. Moreover, results from this thesis provide valuable and up-to-date scientific knowledge that can inform recommendations for the management and conservation of the species in the region. Additionally, these findings may have implications for updating of marine planning strategies, particularly in areas where conservation priorities and mitigation efforts should be applied.

9.2 Future research

Future research could expand in several directions. Further understanding of the movement ecology of loggerhead sea turtles in the western Mediterranean (especially regarding post-hatchlings and nesting females) is crucial for more effective conservation strategies. Developing smaller, lighter and more accurate devices could help drive the science forward, particularly about the monitoring of sea turtle post-hatchlings. Moreover, it would be important to conduct similar research to that of this thesis about post-hatchlings from eastern Mediterranean nests, because as far as we know there is not information about where they disperse or which their developmental areas are. Such research could be relevant to compare with the outcomes from the present thesis, and to robustly determine the developmental areas for loggerhead post-hatchlings in the Mediterranean Sea.

Furthermore, there is still a lack of satellite-track research on some turtle sizes, particularly in the range of 20-40 CCL (curved carapace length). This information would be valuable in determining when ontogenic shifts occur (if they do), as it is currently unknown at what size turtles transition from oceanic to neritic habitats.

Another research need is to investigate the impact of climate change on the survival, dispersal and habitat use of loggerhead sea turtles in the western Mediterranean. Continuing research on nesting females in the western basin would help identify important breeding areas on the western basin and provide valuable insights for improving management and conservation measures for adult turtles. Moreover, increase satellite tagging on nesting females would yield results that could be used to confirm inter-nesting intervals, nest site fidelity, interseasonal interval and fidelity and other aspects of nesting biology of females in the western Mediterranean.

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Annex I – Satellite tracking data information

Compilation of the satellite tracking data information used in the present thesis by life stage and data source: i) own data gathered during thesis development, ii) free access published datasets, or iii) unpublished data ceded for analysis. Turtle identity name or number (Turtle ID), straight carapace length (SCL, denoted by *) or curved carapace length (CCL, denoted by **), sex (M: male, F: female, U: unknown), type of capture (Nest: collected at nest, C: caught by hand for study, LL: longline bycatch and released, T: trawler bycatch, D: driftnet bycatch E: found entangled, RC: recovery at rescue centre, N: female after nesting event), deployment location, deployment date, total tracking days (‡ means still transmitting at the time of writing this thesis) and type of satellite-tag attached (PTT, POP-UP, SPOT, SPLASH, FASTLOC, ST and SRDL) of each monitored turtle are shown. PTT-tags were solar powered transmitter terminals and POP-UP-tags were satellite pop-up archival tags, both from Desert Star LLC (www.desertstar.com). SPOT and SPLASH were battery-powered data-archiving tags from Wildlife Computers Inc. (https://wildlifecomputers.com). FASTLOC GPS were battery-powered data-archiving tags from Sirtrack (www.sitrack.com). ST tags were Argos data-archiving tags from Telonics Inc. (www.telonics.com). SRDL were satellite relay data loggers from Sea Mammal Research Unit Instrumentation, Scotish Oceans Institute, University of St Andrews, Scotland (http://www.smru.st-andrews.ac.uk/). Own data (with exception of turtles ID Morla, València, Mascletà2020, Victoria, Elena and Catherine) are available at EMODNET repository ([dataset] Abalo-Morla et al. (2022)) and are part of the related publication of Chapter 3[4].

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[4] **Abalo-Morla S**, Belda EJ, Tomás J, Crespo-Picazo JL, Marco A, Revuelta O. 2022. Satellite-tracking dataset of loggerhead sea turtles tracked from western Mediterranean. Data in Brief, 43: 108432, https://doi.org/10.1016/j.dib.2022.108432

Life stage	Source	Turtle ID	SCL*/ CCL** (cm)	Sex	Type capture	Deployment location	EEZ release	Deployment date	Tracking days	Type of tag
Post-hatchlings	Own data: Clutch A	Sali	17.5*	U	Nest	37.375 N, 1.636 W	Spain	14/09/2015	98	PTT
		Daniel	15.8*	U	Nest	37.375 N, 1.636 W	Spain	14/09/2015	91	PTT
		Espaikel	16.3*	U	Nest	37.375 N, 1.636 W	Spain	14/09/2015	23	PTT
		Maya	15.3*	U	Nest	37.375 N, 1.636 W	Spain	14/09/2015	43	PTT
		Contxi	15.1*	U	Nest	37.375 N, 1.636 W	Spain	14/09/2015	54	PTT
		Samy	15.0*	U	Nest	37.375 N, 1.636 W	Spain	14/09/2015	42	PTT
		Lusi	13.6*	U	Nest	37.375 N, 1.636 W	Spain	14/09/2015	34	PTT
		Carla	13.3*	U	Nest	37.375 N, 1.636 W	Spain	14/09/2015	11	PTT
	Own data: Clutch B	Cocedora	17.5 *	U	Nest	37.375 N, 1.636 W	Spain	16/06/2016	82	PTT
		Rabiosa	17.5 *	U	Nest	37.375 N, 1.636 W	Spain	16/06/2016	83	PTT
		Pichirichi	16.6 *	U	Nest	37.375 N, 1.636 W	Spain	16/06/2016	79	PTT
		Serena	16.8 *	U	Nest	37.375 N, 1.636 W	Spain	16/06/2016	102	PTT
		Toby	17.0 *	U	Nest	37.375 N, 1.636 W	Spain	28/09/2016	106	PTT
		Dora	17.5 *	U	Nest	37.375 N, 1.636 W	Spain	28/09/2016	115	PTT
		Vendetta	18.1 *	U	Nest	37.375 N, 1.636 W	Spain	28/09/2016	108	PTT
		Bonita	17.5 *	U	Nest	37.375 N, 1.636 W	Spain	28/09/2016	123	PTT
		Morla	18.7*	U	Nest	37.375 N, 1.636 W	Spain	28/09/2016	105	PTT
	Own data: Clutch C	Benicarló	21.0 *	U	Nest	39.310 N, 0.290 W	Spain	19/10/2017	152	PTT
		Borriana	22.0 *	U	Nest	39.310 N, 0.290 W	Spain	19/10/2017	261	PTT
		Castelló	22.2 *	U	Nest	39.310 N, 0.290 W	Spain	19/10/2017	264	PTT
		Cullera	22.4 *	U	Nest	39.310 N, 0.290 W	Spain	19/10/2017	69	PTT
		Denia	22.0 *	U	Nest	39.310 N, 0.290 W	Spain	19/10/2017	270	PTT
		Gandia	22.3 *	U	Nest	39.310 N, 0.290 W	Spain	19/10/2017	291	PTT
		Santa Pola	22.2 *	U	Nest	39.310 N, 0.290 W	Spain	19/10/2017	276	PTT
		Torrevieja	22.8 *	U	Nest	39.310 N, 0.290 W	Spain	19/10/2017	337	PTT
		Vinarós	23.0 *	U	Nest	39.310 N, 0.290 W	Spain	19/10/2017	269	PTT
		València	22.8*	U	Nest	39.310 N, 0.290 W	Spain	19/10/2017	181	PTT

Life stage	Source	Turtle ID	SCL*/ CCL** (cm)	Sex	Type capture	Deployment location	EEZ release	Deployment date	Tracking days	Type of tag
Early juveniles	Own data: Clutch D	163910	25.6 *	U	Nest	41.129 N, 1.302 E	Spain	31/08/2016	123	PTT
		163909	29.1 *	U	Nest	41.129 N, 1.302 E	Spain	31/08/2016	37	PTT
	Own data	163348	37 .1 *	U	T, RC	39.010 N, 0.102 W	Spain	10/04/2017	215	POP-UP
		60624	31.6 *	U	RC	37.579 N, 0993 W	Spain	15/10/2018	82	SPOT
		64584	29.0 *	U	RC	37.579 N, 0993 W	Spain	15/10/2018	92	SPOT
		36539	37.0 *	U	RC	41.129 N, 1.302 E	Spain	03/07/2017	22	SPOT
	Unpublished data	96216	36.0 **	U	C	39.951 N, 4.54 E	Spain	12/09/2011	76	SPOT
	Cardona and Hays (2018)	17658	41.5 **	U	C	38.285 N, 1.697E	Spain	28/04/2003	78	ST
		17682	46.0 **	U	C	38.745 N, 1.4262 E	Spain	25/04/2003	79	ST
		56455	43.3 **	U	C	40.780 N 0.738 E	Spain	25/07/2005	317	ST
Late juveniles	Own data	163345	47.0 *	U	T, RC	39.000 N, 0.108 W	Spain	10/04/2017	223	POP-UP
		163346	58.0 *	U	T, RC	39.662 N, 0.205 W	Spain	03/02/2017	36	POP-UP
		163347	50.0 *	U	T, RC	39.310 N, 0.290 W	Spain	07/01/2017	106	POP-UP
		163350	52.0 *	U	T, RC	39 N, 0.108 W	Spain	10/04/2017	44	POP-UP
		163351	48.0 *	U	T, RC	39 N, 0.108 W	Spain	10/04/2017	83	POP-UP
		163352	47.0 *	U	T, RC	39 N, 0.108 W	Spain	10/04/2017	59	POP-UP
		163353	40.0 *	U	T, RC	38.639 N, 0.048 W	Spain	26/01/2017	169	POP-UP
		163354	44.0 *	U	T, RC	39.662 N, 0.205 W	Spain	03/02/2017	265	POP-UP
		62419	47.0 *	U	E, RC	36.712 N, 2.191 W	Spain	23/07/2018	24	SPOT
		45951	44.0 *	U	D	39 N, 0.108 W	Spain	27/11/2017	79	SPOT
		45952	45.0 *	U	T	39 N, 0.108 W	Spain	13/12/2017	49	SPOT
		60611	48.0 *	U	RC	39.310 N, 0.290 W	Spain	05/07/2018	200	SPOT
		45950	40.8 *	U	D	39 N, 0.108 W	Spain	13/12/2017	63	SPOT
		66604	45.0 *	U	RC	37.579 N, 0993 W	Spain	19/11/2018	22	SPOT
		64583	40.1 *	U	RC	37.579 N, 0993 W	Spain	15/10/2018	91	SPOT
	Unpublished data	95588	52.0 **	U	C	37.491 N, 3.625 W	Spain	12/09/2011	16	SPOT
		95589	63.0 **	U	C	37.000 N, 0.300 W	Spain	31/07/2012	67	SPOT

Life stage	Source	Turtle ID	SCL*/ CCL** (cm)	Sex	Type capture	Deployment location	EEZ release	Deployment date	Tracking days	Type of tag
Late juveniles	Unpublished data	96212	52.0 **	U	C	37.000 N, 0.300 W	Spain	01/08/2012	33	SPOT
		96215	57.0 **	U	C	37.000 N, 0.300 W	Spain	01/08/2012	105	SPOT
		138120	50.0 **	U	C	39.000 N, 3.000 E	Spain	05/08/2015	19	SPLASH
		138122	66.0 **	U	C	39.000 N, 3.000 E	Spain	21/06/2016	125	SPLASH
		151933	46.0 **	U	C	39.088 N, 3.13 E	Spain	09/07/2016	211	SPLASH
		151935	65.0 **	U	C	39.724 N, 2.178 E	Spain	22/06/2016	278	SPLASH
		151936	60.0 **	U	C	39.724 N, 2.178 E	Spain	26/06/2016	268	SPLASH
	Williard et al. (2015)	79824	49.5 **	U	C	36.303 N, 3.262 W	Spain	30/07/2008	8	SPOT
		79825	63.5 **	U	C	36.317 N, 3.146 W	Spain	30/07/2008	13	SPOT
		79827	56.0 **	U	C	36.299 N, 3.038 W	Spain	05/08/2008	89	SPOT
		79828	65.0 **	U	C	36.231 N, 2.266 W	Spain	06/08/2008	11	SPOT
		95584	53.0 **	U	C	37.260 N, 0.084 E	Spain	07/08/2009	86	SPOT
		95585	58.0 **	U	C	37.520 N, 0.466 W	Spain	11/08/2010	51	SPLASH
		96206	57.0 **	U	LL	37.320 N, 0.113 E	Spain	29/07/2009	19	SPOT
		96207	50.0 **	U	LL	37.319 N, 0.110 E	Spain	03/08/2009	6	SPOT
		96208	68.0 **	U	LL	37.250 N, 0.061 E	Spain	07/08/2009	7	SPOT
		96210	59.0 **	U	LL	37.214 N, 0.169 E	Spain	28/07/2009	41	SPOT
		96214	65.2 **	U	LL	37.252 N, 0.042 E	Spain	07/08/2009	339	SPOT
	Cardona and Hays (2018)	17744	55.0 **	U	C	38.620 N, 1.235 E	Spain	20/04/2003	155	ST
		40034	51.9 **	U	C	38.582 N, 1.348 E	Spain	29/06/2004	138	ST
		40035	55.8 **	U	C	38.764 N, 1.578 E	Spain	13/08/2004	132	ST
		40036	52.5 **	U	C	38.737 N, 1.272 E	Spain	03/10/2004	290	ST
		40037	66.5 **	U	C	38.649 N, 1.298 E	Spain	16/07/2004	163	ST
		40038	53.5 **	U	C	38.812 N, 1.073 E	Spain	07/10/2004	172	ST
		40039	51.5 **	U	C	38.659 N, 1.326 E	Spain	20/03/2004	278	ST
		40041	52.0 **	U	C	36.630 N, 1.401 E	Spain	24/03/2004	87	ST

Life stage	Source	Turtle ID	SCL*/ CCL** (cm)	Sex	Type capture	Deployment location	EEZ release	Deployment date	Tracking days	Type of tag
Late juveniles	Cardona and Hays (2018)	40043	68.5 **	U	C	39.197 N, 2.814 E	Spain	05/11/2004	143	ST
	Chimienti et al. (2020)	56454	58.5 **	U	C	40.585 N, 0.576 E	Spain	24/10/2005	246	SRDL
		56456	60.1 **	U	C	40.619 N, 0.722 E	Spain	29/07/2005	294	SRDL
		56259	59.6 **	U	C	40.944 N, 2.616 E	Spain	24/10/2005	304	SRDL
		17696	44.5 **	U	C	38.741 N, 1.332 E	Spain	29/04/2003	45	SRDL
		165766a	70.5 **	M	C	38.558 N, 14.565 E	Italy	04/11/2016	207	SRDL
		165767	65.5 **	F	C	38.558 N, 14.565 E	Italy	04/11/2016	270	SRDL
		165768	64.5 **	U	C	38.558 N, 14.565 E	Italy	13/10/2016	195	SRDL
		165769	62.0 **	U	C	38.558 N, 14.565 E	Italy	04/11/2016	217	SRDL
		162338	59.5 **	U	C	38.558 N, 14.565 E	Italy	04/11/2016	175	SRDL
		162341	55.0 **	U	C	38.558 N, 14.565 E	Italy	09/06/2017	33	SRDL
		162340	59.0 **	U	C	38.558 N, 14.565 E	Italy	09/06/2017	36	SRDL
		162342	58.0 **	U	C	38.558 N, 14.565 E	Italy	09/06/2017	49	SRDL
		162339	61.0 **	U	C	38.558 N, 14.565 E	Italy	09/06/2017	23	SRDL
		162343	75.0 **	U	C	38.558 N, 14.565 E	Italy	09/06/2017	37	SRDL
		165766b	62.0 **	U	C	38.558 N, 14.565 E	Italy	08/07/2018	117	SRDL
Adults	Own data	164928	97.0 *	M	E, RC	41.280 N, 2.090 E	Spain	18/09/2016	75	SPLASH
		60623	79.0 *	F	N	40.025 N, 0.049 E	Spain	01/07/2018	15	SPOT
		160303	61.0 **	F	N	41.280 N, 2.090 E	Spain	24/06/2016	55	PTT
		33052	79.0 **	F	N	39.508 N, 0.321 W	Spain	27/06/2018	87	SPLASH
		66605	71.0 **	U	RC	37.579 N, 0993 W	Spain	16/12/2018	28	SPOT
		36422	80.0 **	F	N	37.912 N, 0.722 W	Spain	09/07/2018	78	FASTLOC
		84260	60.0 **	F	N	41.080 N, 1.180 E	Spain	16/07/2020	60	FASTLOC
		222027	87.0 **	F	N	39.180 N, 0.230 W	Spain	30/07/2020	867‡	FASTLOC
		222028	NA	F	N	41.110 N, 1.260 E	Spain	10/07/2021	82	FASTLOC
		232741	80.0	F	N	38.400 N, 0.650 W	Spain	26/07/2022	139‡	FASTLOC
	Unpublished data	95586	72.0 **	U	C	37.300 N, 0.300 W	Spain	19/07/2012	52	SPLASH
		95590	75.0 **	U	C	37.300 N, 0.300 W	Spain	19/07/2012	57	SPOT
		96204	74.0 **	U	C	37.300 N, 0.300 W	Spain	19/07/2012	88	SPOT

Life stage	Source	Turtle ID	SCL*/ CCL** (cm)	Sex	Type capture	Deployment location	EEZ release	Deployment date	Tracking days	Type of tag
Adults	Unpublished data	138119	74.0 **	U	C	39.000 N, 3.000 E	Spain	12/05/2014	104	SPLASH
		138121	76.0 **	U	C	39.000 N, 3.000 E	Spain	06/05/2014	394	SPLASH
		151934	73. 0 **	U	C	39.724 N, 3.33 E	Spain	26/07/2016	280	SPLASH
		34319	83.0 **	F	C	39.724 N, 3.33 E	Spain	21/06/2017	86	SPLASH
	Williard et al. (2015)	79826	73. 0 **	U	C	36.400 N, 3.200 W	Spain	04/08/2008	14	SPOT
		79829	75.0 **	U	C	36.400 N, 3.000 W	Spain	04/08/2008	40	SPOT
		96205	75.0 **	U	LL	37.300 N, 0.100 E	Spain	07/08/2009	336	SPOT
		96209	76.0 **	M	LL	37.300 N, 0.100 E	Spain	03/08/2009	23	SPOT