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Abalo-Morla, S.; Marco, A.; Tomás, J.; Revuelta, O.; Abella, E.; Marco, V.; Crespo-Picazo, J.... (2018). Survival and dispersal routes of head-started loggerhead sea turtle (Caretta caretta) post-hatchlings in the Mediterranean Sea. Marine Biology. 165(3). https://doi.org/10.1007/s00227-018-3306-2



The final publication is available at https://doi.org/10.1007/s00227-018-3306-2

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Additional Information

- 1 Survival and dispersal routes of head-started loggerhead sea turtle (Caretta caretta) post-
- 2 hatchlings in the Mediterranean Sea

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# **Abstract**

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Several loggerhead sea turtle (Caretta caretta) nesting events have been recorded along Spain's Mediterranean coast, outside its known nesting range, in recent years. In view of the possible expansion of its nesting range and considering the conservation status of this species, management measures like nest protection and head-start programs have been implemented. To study the dispersal behavior and survival of head-started loggerheads, 19 post-hatchlings from three nesting events were satellite-tracked after their release in three consecutive years (2015-2017). This paper presents the first study of survival probabilities and dispersal movements of loggerhead post-hatchlings in the Mediterranean basin. Monitored post-hatchlings dispersed over large areas using variable routes, mainly off the continental shelf. Nonetheless, post-hatchlings dispersed to high productivity warmer areas during the coldest months of monitoring. These areas might be optimum for their survival and development. We observed differences regarding dispersal orientation and routes among individuals, even from the same nest, release date, and location. Our survival models contributed to improving current survival estimates for sea turtle post-hatchlings. We observed a high probability of survival in head-started individuals during the first months after release, usually the most critical period after reintroduction. The data did not support an effect of habitat (neritic or oceanic) in survival, neither an effect of the region (Balearic sea or Alboran sea) in survival probability. Differences in survival between nests were observed. These differences might be related to parasitic infections suffered during the head-starting period. This study shows that nest management measures may contribute to the conservation and range expansion of the loggerhead turtle population in the western Mediterranean.

# 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 20<sup>th</sup> 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 behavior 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 behavior and ecology and to design effective conservation strategies (Hays et al. 2016).

Most nesting events recorded in Spain have been found in touristic beaches, and so 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 behavioral 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. 2012). 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 this study, 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.

# Methods

### Turtle data and satellite tagging

Loggerhead post-hatchlings were collected from three nests (Clutch A (n = 8), Clutch B (n = 2), Clutch C (n = 9) along Spain's Mediterranean coast (Fig. 1). All hatchlings were reared in a head-starting program (see details in Table 1). Individuals from Clutch A suffered from a parasitic outbreak of the copepod *Balaenophilus manatorum* (Crespo-Picazo et al. 2017; Domènech et al. 2015) 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 behavior (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 1).

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At-sea movements of 19 post-hatchlings were tracked during 2015-2017 (Table 1). Post-hatchlings were 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 (Fig. 2) and an acrylic-silicone-neoprene attachment method 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 5-12% of the animal weight. There was 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 the turtles with identity numbers (ID) 15 to 19). The behavior (including swimming and diving ability) of the turtles tagged in advance was observed. Turtles behaved normally at release. 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 specify the tag weight (9.5 g), but do not provide any explicit information on total tag weight or the weight of the acrylic-silicone-neoprene attachment. The authors only provide 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 1). Our total added weight ranged between 31 and 72 g and our turtle size ranged between 489.9 and 4314 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).

## 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 1500 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 are stored in Seaturtle.org database. We used all locations except locations that required a high traveling speed, > 10 km h<sup>-1</sup> (González et al. 2016) and land locations (Arendt et al. 2012), which were filtered with Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley 2005). Then, we used the Douglas Argosfilter 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, MAXREDUN = 15, MINRATE = 10, and RATECOEF = 25.

# 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 behavior 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).

## 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) usingsoftware Mark 7.1 (White and Burnham 1999). In this way, survival probability ( $\Phi$ ) 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).

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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. In order to compare survival among nests, we started from the best model previously selected. Clutch B 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).

Most locations received were B (32.96%) and Z (25.90%); > 28.80 % of messages received had associated LCs

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#### Results

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## **Turtle movements**

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230 between 0 and 3 (Fig 3). Turtles were remotely tracked on average for  $74.2 \pm 35.5$  days, n = 19, and travelled a 231 minimum mean distance of 2,372.45  $\pm$  1,724.24 km, n = 19, with a resultant mean speed of 2.22  $\pm$  0.94 km h<sup>-1</sup>, n = 19232 = 19 (Table 1). Given the low accuracy of locations these swimming values should be considered as estimates. 233 Individuals with few locations were excluded from further movement analyses (n = 4, turtle IDs: 3, 7, 8 and 19). 234 On average 75.5  $\pm$  25.1 %, n = 15, of locations were off the continental shelf. However, when excluding turtles 235 from Clutch A,  $88.0 \pm 9.5\%$ , n = 15, of locations were off the shelf (>200 m depth). Turtles from Clutch A have 236  $50.4 \pm 28.7$  %, n = 5, of locations within continental shelf waters. 237 The track of each turtle (n = 15) showed no directional movement throughout the track duration (Rayleigh's test, 238 Z; P > 0.05, in all cases). Nonetheless, in several instances dispersal movement was consistently directional during 239 certain week periods (Raleigh's test, Z; P < 0.05). Differences in orientation were significant between nests 240 (Mardia-Watson-Wheeler test, W = 11.736, d.f = 4, P = 0.019), and individuals (Mardia-Watson-Wheeler test, W = 11.736, d.f = 4, d.f241 = 64.814, df = 28, P < 0.0001). Release date did not affect orientation (Mardia-Watson-Wheeler test, W = 3.291, df = 2, P = 0.193). Overall, post-hatchlings did not disperse following a similar pattern after release, except during 242 243 the coldest months. This was true even when considering releases by clutch or date (Fig. 4). The most frequented 244 areas were the Alboran and Balearic Seas. From Clutch A (n = 5) two turtles (IDs: 1, 2) moved northwards to the 245 Balearic Islands, Turtle ID 2 traveled south during winter. The other three (IDs: 4, 5, 6) moved southwards to the 246 Alboran Sea, and Turtle ID 4 traveled possibly taking a North African eddie. Turtles from Clutch B (IDs: 9, 10), 247 remained in the Balearic Sea, and Turtle ID 9 travelled northwards to the French coast reaching the Gulf of Lion. 248 From clutch C (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 C (IDs: 13, 15) traveled northwards from the release point to the Balearic Sea. Finally, only two turtles from Clutch C (IDs: 16, 17) moved eastwards along the north African coast to the Algerian subbasin approaching the Sicilian Strait (Fig. 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 (Online Resource S1 and S2).

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 (Fig. 5). Some individuals (IDs: 9, 10, 18) alternated between faster phase movements and slower ones (Fig. 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.

#### Survival analyses

All post-hatchlings were included to assess survival. We obtained 6235 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 C (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  $\Phi$  (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 ( $\Phi$ (t) p(m\*t); model 10, Table 2).

In the survival analysis, the model that best fitted the data considered constant survival and trap-dependence in recapture (Table 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 2). The model suggested that recapture probability declined with time since last encounter (Table 2). Models including a trend in survival were not supported (models 12, 14, 15, Table 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. Extrapolating these minimum

survival estimates ( $\Phi$  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 2) were fitted. In models 18 to 26, the two individuals from Clutch B 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 2). Thus, model 25 (Table 2) was used as the starting model to compare survival between clutches A and C. Models considering the region, Alboran Sea or Balearic Sea, were fitted (models 19 and 22, Table 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 ( $B = 0.76 \pm 0.83$ ; 95% Confidence interval (CI): -0.88 - 2.39). Models considering the habitat association, neritic or oceanic habitat, were fitted (models 21 and 25, Table 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 ( $B = 1.06 \pm 0.67$ ; 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 ( $B = 6.17 \pm 0.95$ ; 95% Confidence interval (CI): 4.32 - 8.03). Daily survival probabilities were significantly different between nests ( $\chi 2 = 5.3011$ , 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 C. 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 C.

# Discussion

#### **Turtle movements**

This study 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 tracks 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). 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-hatchlings 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 behavior 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 behavior 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 growing rate and individual size and, therefore, their behavior. Smaller or weaker individuals might not confront coastal currents to reach oceanic zones.

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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 behavioral 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.

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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: (1) southwards to the western Alboran Sea where the surface temperature is warmer due to the inflow of Atlantic waters (Skliris and Beckers 2009), or (2) 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 in order to avoid zones with low temperatures (Coles and Musick 2000). Furthermore, we observed that individuals from Clutch B 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 agrees with previous studies which suggest that small loggerheads (< 36 cm) are unable to pass the Gibraltar Strait from the Mediterranean basin 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 its 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 behavior. The lack of recent studies in the southern part of the western Mediterranean Sea impeded to confirm this hypothesis. 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. 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 predation or other reasons (Christiansen et al. 2016; Gaube et al. 2017).

## 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. 2012) 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 C. 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 behavior 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 behavior, 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) estimate 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 use 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 in order 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 (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, unpubl 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.

In conclusion, the present study 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.

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Compliance with Ethical Standards The authors declare that there is no conflict of interest and that consent was obtained from all parties. The authors declare that animals were treated according to all applicable international, national, and/or institutional guidelines for the care and use of animals. Animal ethics approval was granted by Universitat Politècnica de València. Tagging of post-hatchlings was done under permit from local environmental authorities (Generalitat Valenciana, Generalitat de Catalunya, and Consejeria de Medio Ambiente y Ordenación del Territorio de la Junta de Andalucía).

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Acknowledgments This satellite study was funded by Universitat Politècnica de València, Ministerio de Agricultura y Medio Ambiente (ref: 16MNSV006), Ministerio de Economía, Industria y Competitividad (ref: CGL2011-30413), Fundación CRAM, Fundación Hombre y Territorio and Eduardo J. Belda. Corresponding author, S. Abalo, was supported by a Ph.D. grant (FPU) from Ministerio de Educación, Cultura y Deporte (Spain). J. Tomás is also supported by project Prometeo II (2015) of Generalitat Valenciana and project INDICIT of the European Commission, Environment Directorate-General. We are extremely thankful to the entities that have collaborated: we thank all professionals at the Oceanogràfic, especially at the ARCA Rehabilitation Center, for their many efforts and whole-hearted dedication to the best animal care. In particular, we are grateful to the Conselleria d'Agricultura, Medi Ambient, Canvi Climàtic i Desenvolupament Rural of the Valencia Community Regional Government. We also thank professionals at Centro de Recuperacion de Animales Marinos (CRAM) for their dedication and animal care. We are thankful to the Marine Zoology Unit of the University of Valencia, NGO Xaloc, EQUINAC, Aquarium of Sevilla, Doñana Biological Station (EBD-CSIC) and to involved professionals at Consejería de Medio Ambiente y Ordenación del Territorio (CMAOT) of Junta de Andalucía, especially at the Andalusian Marine Environment Management Center (CEGMA) for their efforts with animal care, logistics for release events and necropsy of "Rabiosa". We are particularly grateful to the people who called 112 to report a nesting event and to the nest custody volunteers. Thanks to the staff of Parador de El Saler for volunteering logistical support. The authors wish to acknowledge the use of the Maptool program for analysis and graphics in this paper. Maptool is a product of SEATURTLE.ORG (Information is available at www.seaturtle.org). Also, we acknowledge the use of the Douglas Argos Filter (DAF) utility in Movebank (www.movebank.org), and especially to David Douglas for his help and recommendations. Finally, we thank the reviewers for their reviewing efforts.

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# 823 Figures

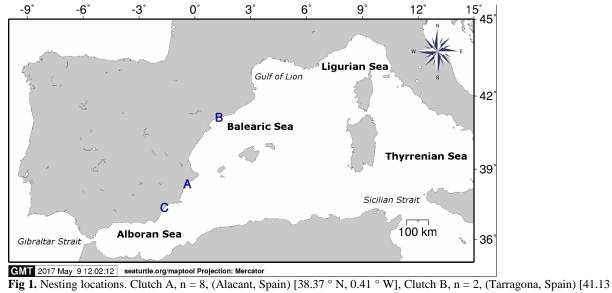


Fig 1. Nesting locations. Clutch A, n = 8, (Alacant, Spain) [38.37 ° N, 0.41 ° W], Clutch B, n = 2, (Tarragona, Spain) [41.13 ° N, 1.30 ° E] and Clutch C, n = 9, (Almería, Spain) [37.38 ° N, 1.64 ° W]. Map obtained with SeaTurtle Maptool (www.seaturtle.org/maptool)



Fig. 2 Post-hatchling identity number (ID): 21 satellite-tagged with a solar-powered platform transmitter terminal (PTT) by Desert Star S.L. a few moments after release

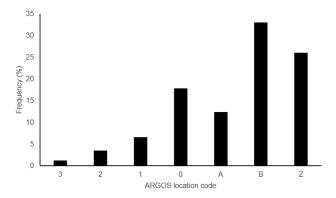
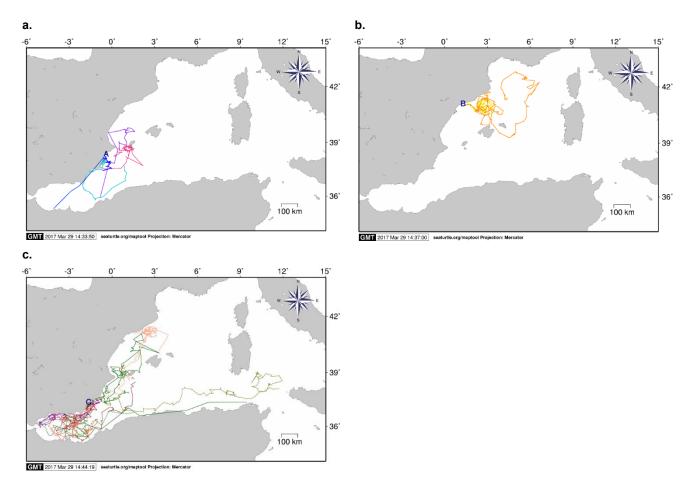
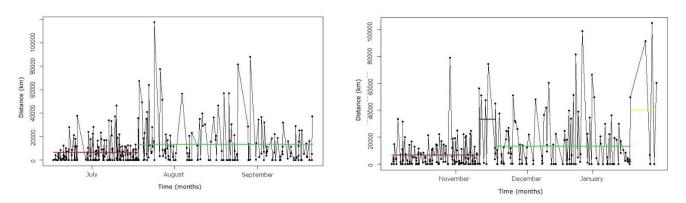


Fig. 3 Frequency (%) of Argos location codes reported with satellite track locations from loggerhead sea turtle post-hatchlings released in the Western Mediterranean.



**Fig. 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 C). Therefore, figures 4a, 4b, and 4c represent the dispersion routes for clutches A (n = 8), B (n = 2) and C (n = 9), respectively. Track colors represent different turtles. In 4c green colors represent post-hatchlings released in September and the other colors represent post-hatchlings released in June. Maps obtained with SeaTurtle Maptool (www.seaturtle.org/maptool)

a. b.



**Fig. 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), yellow (higher travel distance). Different mean travel distances point to different types of movement. Figure 5a: Turtle identity number (ID): 14; Figure 5b: Turtle ID: 18

Table 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 at ARCA (8 months) and at CEGMA (5 months). Clutch C 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 Tarragona, Barcelona (41.129 N, 1.302 E) and Clutch C in Pulpí, Almería (37.375 N, 1.636 W).

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 tra (km) ± s		Mean : (km/h)	-
	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
Α	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
В	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
ь	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
	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	$3.34 \pm$	2.68
	Pichirichi	13	952.6	16.6	NA	26.0	26+	CSIC / CEGMA	9	16/06/2016	79	4107.8 ±	17.64	$3.85 \pm$	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
С	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

Table 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
	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 In trend}	1349.36	223.83	0.00	91	608.30
Modeling Recapture probability	5. {Phi(t) p(c)}	1352.28	226.75	0.00	90	613.63
modeling Recapture probability	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
	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
Modeling Survival probability	13. {Phi(c) p(m)}	996.02	21.92	0.00	3	448.79
(considering all clutches)	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	92 91 91 91 90 91 91 91 264 177 4 6	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
	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
Madalina Cuminal probability	20. {Phi(c) p(m3)}	924.15	5.62	0.04	4	916.10
Modeling Survival probability	21. {Phi (nest+habitat association) p(m3)}	925.24	6.71	0.02	6	913.15
(considering nest origin and or	22.{Phi(region) p(m3)}	925.98	7.46	0.01	5	915.92
region)	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	2 5 6 4 6 5 4 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 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 C.

Model	Daily survival	p1	p2	р3
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)	$0.901 \pm 0.010$	$0.622 \pm 0.052$	$0.264 \pm 0.0428$
Considering nest influence for Clutch C	0.998 ± 0.002	(0.879 0.919)	(0.516 0.718)	(0.189 0.356)
{Phi(nest) p(m3)}	(0.987 1.000)			