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# Local differentiation in the origin of stranded loggerhead turtles, *Caretta caretta*, within an eastern Turkey foraging area



Oguz Turkozan<sup>a,\*</sup>, Can Yılmaz<sup>a</sup>, Aşkın Hasan Uçar<sup>b</sup>, Carlos Carreras<sup>c</sup>, Serap Ergene<sup>d</sup>, Cemil Aymak<sup>e</sup>, Sezgin Karaman<sup>a</sup>

<sup>a</sup> Adnan Menderes University, Faculty of Arts and Science, Department of Biology, 09010, Aydın, Turkey

<sup>b</sup> Mersin University Sea Turtles Application and Research Center, Mersin, Turkey

<sup>c</sup> Departament de Genètica, Microbiologia i Estadística and IRBio, Universitat de Barcelona, Av.Diagonal 643, 08028, Barcelona, Spain

<sup>d</sup> Mersin University, Faculty of Arts and Science, Department of Biology, Mersin, Turkey

<sup>e</sup> Bulancak Technical and Industrial Vocational High School, Giresun, Turkey

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# ABSTRACT

The eastern Mediterranean Sea is frequently visited by nesting and foraging loggerhead turtles and is also a nursery zone although the origin of these foraging animals has not yet been assessed. In order to estimate the natal origin of eastern Turkey foraging individuals we analysed a long fragment of the mtDNA control region from 135 loggerhead turtles and we performed a Bayesian mixed stock analysis to estimate the contributions from rookeries in the Mediterranean to the foraging grounds studied. A total of 5 haplotypes were identified but they were not homogeniously distributed across the sampling geographical range thus suggesting an east-west differentiation. The mixed stock analysis revealed that the turtles from the eastern feeding ground come mostly from the western nesting populations of Turkey (49%), while those from the western feeding ground come from Cypriot stocks (62%). These results show that anthropogenic activities on this area may have an impact on different populations depending on were this activities are located and overall pose threat to the survival of the western Turkish and Cypriot nesting beaches.

## 1. Introduction

The loggerhead turtle is a highly migratory animal (Bolten, 2003; Plotkin, 2003) with complex life cycle involving series of ontogenetic habitat shifts (Bolten, 2003; McClellan and Read, 2007). However, recent findings of Casale et al. (2008) suggested a relaxed model with general plasticity of habitat use. Thus, in the Mediterranean the proximity of different habitats of allow loggerhead turtles to feed upon benthic prevs very early. This complex life history covers different geographical regions and habitats around the world. It is, therefore, vital to understand the links among different life stages to provide effective conservation strategies for the conservation of species (Rees et al., 2016). Assessing the natal origin of the sea turtles in foraging grounds are one of the key information for the conservation of sea turtles. In this sense many studies has been done in the Mediterranean (Carreras et al., 2006; Garofalo et al., 2013; Clusa et al., 2014; Karaa et al., 2016; Rees et al., 2017) but little is known about the composition of eastern Mediterranean foraging areas. The Mediterranean loggerhead turtles have been described as a Regional Management Unit (Wallace et al., 2010) that is considered to be at low risk but under high threat (Wallace et al., 2011). It has recently been listed under the IUCN criteria as Least Concern, but with the caveat of being conservation dependent (Casale, 2015). Today, the largest sea turtle nesting aggregations occur in Greece, Turkey, Cyprus, Syria and Libya (Casale and Margaritoulis, 2010). Turkish populations host almost one third of nesting abundance in the Mediterranean (Casale and Margaritoulis, 2010) and they are genetically differentiated from other Mediterranean populations (Shamblin et al., 2014). Within Turkey, the eastern Mediterranean coast has low numbers of loggerhead turtle (Caretta caretta) nests while concentrate the main nesting activity of green sea turtles (Chelonia mydas) in the Mediterranean (Turkozan and Kaska, 2010). Despite this low loggerhead nesting abundance, this part of the coast has been identified as a foraging ground for both loggerhead and green sea turtles (Oruç 2001) and thus the loggerhead individuals using this area may potentially originate in distant nesting areas. Dispersal simulations using particle modelling have predicted that the neighbouring Levantine zone was a nursery zone for the Mediterranean sea turtles while individuals born in Turkey nesting populations dispersed

E-mail address: turkozan@adu.edu.tr (O. Turkozan).

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<sup>\*</sup> Corresponding author.

to Aegean and Levantine zones (Casale and Mariani, 2014). Although the predicted importance of Levantine foraging grounds, there is a lack of studies in terms of natal origin of turtles in foraging grounds, as only the south east Levantine area has been considered in previous studies (Clusa et al., 2014). Thus, the north east Levantine area remains being an important gap due to the proximity of the abundant nesting areas of Turkey. The use of mixed stock analysis initially designed to assess the stock origin of fish mixed aggregation (Grant et al., 1980), has proved to be useful for identifying the contribution of each rookery to foraging grounds in Mediterranean loggerhead turtles (Carreras et al., 2006; Clusa et al., 2014). Since bycatch of the sea turtles in foraging grounds is one of the most important factors (Casale, 2011) the information on the composition of the fishing ground is essential for the impact assessment. The aim of this study is to fulfil this gap of knowledge by analysing an important loggerhead foraging ground in eastern Turkey and to provide a baseline data from a less known life stage of the species for the conservation of the loggerhead turtles in Turkey.

#### 2. Material and methods

#### 2.1. Sample collection

Samples were obtained from 135 loggerhead sea turtles stranded on the seven locations namely Aykap (Ayaş and Kapızlı) (AYP), Davultepe (DTP), Limpoz (Liman and Pozcu) (LMP), Akyatan (AKY) and Kazanlı (KZL) between the years 2009 and 2012 (Table 1, Fig. 1). Tissue samples were preserved in 96% ethanol until DNA extraction. Furthermore, curved carapace length (CCL) of the strandings were measured in cm from the notch of nuchal scute to the outermost projection of supracaudals.

## 2.2. Laboratory procedures

Total DNA was isolated from skin and muscle tissues of stranded turtles with a modified version of the standard phenol-chloroform protocol (Hillis and Moritz, 1990). A fragment of 862 base-pair (bp) of the mtDNA d-loop region was amplified by polymerase chain reaction (PCR Mastercycler Personel, Eppendorf, Germany) using the primer pair LCM15382 (5'- GCT TAA CCC TAA AGC ATT GG -3') and H950 (5'-GTC TCG GAT TTA GGG GTT TG -3') (Abreu-Grobois et al., 2006). The PCR protocol was carried out according to Yilmaz et al. (2011), PCR products were visualized in agarose gel and purified with the GenElute PCR Clean-Up Kit, (Sigma, Germany). Purified PCR products were sequenced in both forward and reverse directions using a 3730xl capillary system automatic sequencer (Macrogen Inc., S. Korea). Sequences were aligned by eye using the program BioEdit ver 7.0.9 (Hall, 1999) and compared with previously described haplotypes recorded in the Archie Carr Center for Sea Turtle Research database (http://accstr.ufl.edu/) and GenBank (http://ncbi.nlm.nih.gov). Haplotype diversity (h) and nucleotide diversity (p) (Nei, 1987) were calculated for each sampling location using the program DNAsp 5.10 (Rozas et al., 2003).

#### 2.3. Stock composition

BAYES software (Pella and Masuda, 2001) with MMC (Markov-Chain Monte Carlo) method was used to carry out mixed stock analysis (MSA). This analysis estimates the proportion of individuals in the stock coming from different rookeries. We used a baseline that includes all populations from the Atlantic ocean and the Mediterranean sea (Shamblin et al., 2014). Estimates on the size of each rookery (mean number of nests per year) were included in the Bayesian approach as a weighting factor as suggested by previous studies (Bass et al., 2004; Clusa et al., 2014). Furthermore, we explored two possible sources of genetic subdivision within our data, size and sampling location. Individuals were clustered in two size classes considering the minimum size at maturation of 70 cm CCL and each location was analysed separatedly. Pairwise genetic distances among groups  $(F_{ST})$  were calculated using Arlequin 3.52 (Excoffier and Lischer, 2010) and significant genetic differentiation was assessed across the different groupings. Furthermore, we carried out principal coordinate analysis (Fig. 2) based on genetic distances  $(F_{ST})$  among the different sampling localities to define geographical subdivision. Finally, partial MSAs were performed when significant genetic subdivision was found in our data following the same procedure described above for the complete dataset.

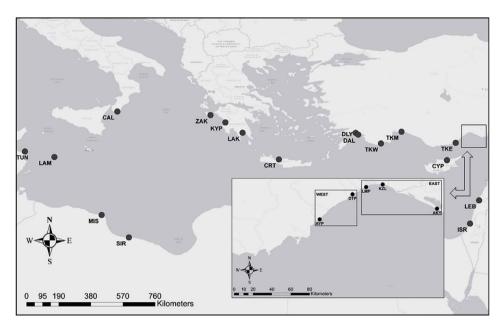
## 3. Results

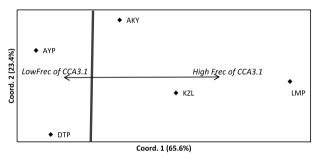
The mean CCL of the stranded turtles was  $65.4 \pm 072$ (range = 13.5-81) cm. There was no bias between the size and location (Man Whitney U test, p > .05). A total of 5 haplotypes were identified in 135 stranded turtles one of them was novel (CCA2.14) and another one (CCA44.1) previously recorded from Atlantic foraging area but reported for the first time in the Mediterranean. The remaining haplotypes (CCA2.1, CCA3.1 and CCA53.1) have been previously recorded from the Mediterranean (Carreras et al., 2007; Garofalo et al., 2009; Yilmaz et al. 2011). The most frequent haplotypes were CCA2.1 (83.7%) and CCA3.1 (14.1%). The haplotype and nucleotide diversity were 0.281 (0.000-0.338) and 0.00035 (0.0000-0.0006) respectively (Table 1). When we performed a MSA considering all the dataset we found that all the individuals from our feeding ground originated in Mediterranean nesting beaches (Supplement 1) with the exception of some contribution from the Atlantic population of Cay Sal, Bahamas (CSL) (Supplement 2), that has low sample size and presented only common haplotypes (Shamblin et al., 2014). Such cases of strange contributions from distant and low variable nesting populations have been previously reported as being artifacts (Engstrom et al., 2002; Godley et al., 2010). For this reason, we removed the Atlantic populations from our baseline and we used as a baseline only the 13 Mediterranean rookeries described in the literature (Garofalo et al., 2009; Yilmaz et al. 2011; Saied et al., 2012; Clusa et al., 2013; Carreras et al., 2014) as done also in other studies of foraging areas in the Mediterranean (Rees et al., 2017). When using the regional baseline, most of the turtles were predicted to be originated in Turkey (TKW = 42%, TKE = 34%) with some contribution of other Levantine populations (Supplement 3) and with no major differences when using the population size as a weighting factor with the exception of some reduction of

Table 1

Distribution of haplotypes occurring in Turkish foraging grounds. KZL; Kazanlı, AKY: Akyatan, LMP: Limpoz, DTP: Davultepe and AYP: Aykap, h: haplotype diversity, n: nucleotide diversity.

		CCA2.1	CCA2.14	CCA3.1	CCA44.1	CCA53.1	Total	h	n
EAST	KZL	65		16		1	82	0.338	0.0004
	AKY	8	1				9	0.222	0.0005
	LMP	3		1			4	0.500	0.0006
WEST	AYP	2					2	0.000	0.000
	DTP	35		2	1		38	0.152	0.0002
	Total	113	1	19	1	1	135		





**Fig. 2.** Principal coordinate analysis based on genetic distances  $(F_{ST})$  among the loggerhead turtles from the sampled locations. The thick vertical line represents the selected subdivision into east and west locations used for the partial MSAs. Foraging ground acronyms as shown in Table 1.

the predicted contribution of the smallest populations. No subdivision of our data was found according to the size of the animals (Fst = -0.0104 p > .05) but a subdivision close to significance was found according to sampling location (Global Fst = 0.0421 p = .051) thus suggesting that the analysis should be done at local scale. The PCoA clustered the populations along an east west axis that explained 65.6% of the variability and that corresponded to an eastward increase of the frequency of the CC-A3.1 haplotype (Fig. 2, Table 1). Considering this result, we divided our data in two groups (Table 1), East (KZL, AKY and LMP) and West (DTP and AYP). The partial MSA performed to the east group of samples showed that this area is inhabited mainly by turtles from the Turkish stocks of TKW (49%), TKM (14%) and TKE (12%) while the partial MSA performed to the west group showed that this area is inhabited mainly by turtles from Cyprus (62%) (Fig. 3A and B and Table 2).

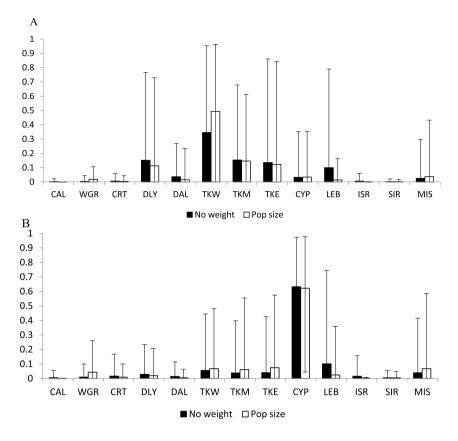
## 4. Discussion

Linking foraging aggregations with reproductive areas is a key information for the conservation of highly migratory marine organisms. This information is specially relevant for endangered species, as threats may be localised in certain foraging areas and have an impact in distant populations. For this reason, gaps in the knowledge of such links may lead to indiagnosed population sinks in these foraging areas. In this sense our study provided crucial information about the habitat use of one of the major loggerhead nesting areas (Turkey) by analysing by first time the foraging aggregations of this species in the eastern Fig. 1. Mediterranean nesting areas CAL (Calabria), LAM (Lampedusa), CRT (Crete), KYP (Kyparissia Bay), ZAK (Zakynthos), LAK (Lakonikos Bay), DLY (Dalyan), DAL (Dalaman), TKW (west Turkey), TKM (mid Turkey), TKE (east Turkey), CYP (Cyprus), LEB (Lebannon), ISR (Israel), SIR (Sirte), MIS (Misurata). The inset shows the locations of foraging turtles sampled in the present study including AYP (Aykap), DTP (Davultepe), LMP (Limpoz), KZL (Kazanlı) and AKY (Akyatan).

Mediterranean coast of Turkey. Furthermore, we revealed an heterogeneous composition of individuals in our study area showing the importance of fine scale analysis of foraging grounds to avoid missing important connections, like the one that connects Cyprus nesting population with the closest foraging areas of Aykap and Davultepe.

Unsurprisingly, most of the individuals were determined to be originated in Mediterranean nesting areas with a negligible contribution of Atlantic nesting areas. Atlantic visitors have previously been reported in western Mediterranean foraging areas (Carreras et al., 2006; Garofalo et al., 2013; Clusa et al., 2014) and central Mediterranean foraging areas (Casale et al., 2008). However, no exclusive Atlantic haplotypes have been found in the eastern Mediterranean foraging areas (Casale et al., 2008; Clusa et al., 2014) in comparison to western and central Mediterranean thus suggesting that the contribution of individuals from Atlantic nesting areas to eastern Mediterranean foraging areas is very low or negligible. North Atlantic populations are connected to the European coast through the Gulf Stream (Bolten et al., 1998) and negative water balance of Mediterranean Sea generates eastward flow of Atlantic water at the Strait of Gibraltar (Millot and Taupier-Letage, 2004) that connects Mediterranean with Gulf Stream. However, this Atlantic water dilutes within the Mediterranean and hardly influences the eastern Mediterranean surface water masses (Robinson et al., 2001; Millot and Taupier-Letage, 2004), thus it is not surprising not to detect Atlantic individuals in the eastern Mediterranean foraging areas considering that juvenile loggerheads are strongly influenced by surface currents (Carreras et al., 2006). However, this general result contrasts with the presence of one individual from Davultepe presenting the CCA44.1 haplotype. This haplotype has been previously found in North Atlantic foraging grounds (LaCasella et al. unpubl.) and thus may be the first evidence of Atlantic individuals reaching the eastern Mediterranean foraging grounds. Further sampling in nesting areas is needed to identify the population of origin of this orphan haplotype. Regardless the population of origin if this orphan haplotype, the global MSA (Supplement 1) showed the importance of the studied foraging area for Turkish populations. Furthermore, no differences were found within sampling locations related to the size of the individuals, indicating that the origin of the animals is independent of the developmental stage. This result is not unprecedented and agrees with the Learned Migration Goal Theory that postulates that adult individuals tend to use the same foraging areas that used as juveniles (Hays et al., 2010).

The absence of individuals from non Turkish nesting populations



Bayesian estimates of contributions by Mediterraenan stocks to the eastern and western Turkish aggregate. CAL: Calabria, Italy; WGR: western Greece; CRT: Rethymno, Crete; DLY: Dalyan, Turkey; DAL: Dalaman, Turkey; TKW: western Turkey (Fethiye to Çıralı); TKM: middle Turkey (Tekirova to Gazipaşa); TKE: eastern Turkey (Anamur to Samandağ); CYP: Cyprus; LEB: El Mansouri; ISR:scattered beaches, Israel; SIR:Sirte, western Libya; MIS: Misurata, western Libya. Standard deviation and 95% confidence intervals are also indicated.

East				West				
Stock	Mean	SD	2.5%	97.5%	Mean	SD	2.5%	97.5%
CAL	0.0001	0.0015	0.0000	0.0000	0.0002	0.0040	0.0000	0.0000
WGR	0.0180	0.0307	0.0000	0.1062	0.0434	0.0732	0.0000	0.2604
CRT	0.0041	0.0188	0.0000	0.0439	0.0091	0.0399	0.0000	0.1004
DLY	0.1126	0.2176	0.0000	0.7291	0.0194	0.0570	0.0000	0.2067
DAL	0.0153	0.0578	0.0000	0.2337	0.0045	0.0203	0.0000	0.0633
TKW	0.4940	0.3546	0.0000	0.9633	0.0679	0.1345	0.0000	0.4819
TKM	0.1462	0.1766	0.0000	0.6133	0.0615	0.1446	0.0000	0.5543
TKE	0.1230	0.2163	0.0000	0.8425	0.0745	0.1564	0.0000	0.5743
CYP	0.0338	0.0965	0.0000	0.3510	0.6220	0.2577	0.0437	0.9776
LEB	0.0138	0.0844	0.0000	0.1630	0.0244	0.1012	0.0000	0.3587
ISR	0.0006	0.0065	0.0000	0.0023	0.0016	0.0166	0.0000	0.0075
SIR	0.0015	0.0063	0.0000	0.0164	0.0042	0.0161	0.0000	0.0474
MIS	0.0371	0.1174	0.0000	0.4326	0.0675	0.1504	0.0000	0.5859

agrees with satellite telemetry studies. Tracked turtles from Greece moved either to north foraging areas in the Adriatic Sea and the Gulf of Amvrakikos or headed south to the areas off the coast of North Africa (Zbinden et al., 2011). A review of general migratory routes of 63 adult loggerhead turtles released mainly from Greece and Cyprus showed that only a few of them oriented to Turkish coasts (Luschi and Casale, 2014). The tracking studies from Northern Cyprus showed that only early nesters visited other Turkish rookeries (Snape et al., 2016). It is, therefore, not surprising that most of the turtles found in our foraging grounds had either a Turkish or Cyprus origin. The contribution of multiple nesting populations to a foraging ground is consistent with the patterns observed for the loggerhead turtles in the North Atlantic Fig. 3. Partial mixed Stock Analyses (MSA) of the stranded individuals found in the A) eastern or B) western foraging area. Each bar represents the percentage of individuals that come from each one of the Mediterranean nesting populations. Two different analyses were run including no weighting factor (dark bars) and including the population size as weighting factor (white bars). Error bars show the 95% confidence interval. Nesting areas: CAL (Calabria), WGR (western Greece), CRT (Crete), DLY (Dalyan), DAL (Dalaman), TKW (west Turkey), TKM (mid Turkey), TKE (east Turkey), CYP (Cyprus), LEB (Lebannon), ISR (Israel), SIR (Sirte), MIS (Misurata).

(Bowen et al. 2004; Reece et al., 2006), central Mediterranean (Garofalo et al., 2013) and Italian aggregates (Carreras et al., 2006). However, one of our most surprising results came when we performed a fine scale analysis of our data and thus the local contribution of Cyprus to Aykap and Davultepe was confirmed. This contribution was previously undetected when combining all samples and only became evident when screening our data for possible internal genetic subdivision and highlights the fact that mixing samples from genetically different foraging grounds may obscure the results and thus should be analysed independently. The eastern Mediterranean shows a complex pattern of ocean circulation and adult tracking suggests strong heterogeneity in the dispersal of individuals. The South to North sea surface currents (Hecht et al., 1988) might be one of them. Our results show the importance to check for possible internal subdivisions when analysing foraging grounds and to have as accurate geographical information of sample locations as possible.

Fisheries bycatch is the main threat to loggerhead turtles globally, and bycatch rate is the one of the highest in the Mediterranean among the world (Wallace et al., 2008; Casale, 2011). In the eastern Mediterranean, as much as 1000 turtles were estimated to be caught by fishery with a 60% mortality (Snape et al., 2013). Forty-seven percent of the carcasses were potential adult loggerhead turtles (Snape et al., 2013). Sixty percent of the strandings in the eastern Mediterranean coast of Turkey had a CCL of 61-80 cm meaning that strandings from this region represent mainly adults and subadults (Türkozan et al., 2013). The satellite tracking studies and present study detect that this area is mainly used by turtles originated in Turkey and Cyprus and thus the studied foraging area is a hotspot for these nesting areas as the bycatch will be affecting mainly these stocks. Furthermore, this bycatch affects a high proportion of adults (23%) an important life stage for the reproductive output of populations (Crowder et al., 1995; Lewison and Crowder, 2007). Furthermore, our study showed that the possible impact of fisheries on Cyrus was detected only when a fine scale analysis was done, stressing the need of fine scale analysis everywhere as failing to do it may lead to erroneous conservation actions. Furthermore, there are still missing analysis from foraging grounds along the Mediterrnean (Casale and Mariani, 2014) as the link among different habitats can be better explained by using multiple methods (Rees et al., 2017). Therefore, satellite telemetry studies in the Mediterrnean especially in Turkey should be increased. In conclusion, protecting defined important foraging sites can provide considerable conservation benefit. It is, therefore, vital to investigate potential foraging grounds and define their contributions to nesting colonies in fine scale in order to provide effective conservation and management.

## Compliance with ethical standards

### Conflict of interest

The authors declare that they have no conflict of interest.

## Ethical approval

This article does not contain any studies with human participants. All applicable international, national, and institutional guidelines for the care of animals found stranded alive were followed. We did not conduct experiments with animals.

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# Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx. doi.org/10.1016/j.ocecoaman.2017.12.011.

#### References

- Abreu-Grobois, F.A., Horrocks, J.A., Formia, A., Dutton, P., LeRoux, R., Vélez-Zuazo, X., Soares, L., Meylan, P., 2006. New mtDNA dloop primers which work for a variety of marine turtle species may increase the resolution capacity of mixed stock analyses. In: Poster Presented at the 26th Annual Symposium on Sea Turtle Biology and Conservation, Crete, Greece, 2–8 April 2006.
- Bass, A.L., Epperly, S.P., Braun-McNeill, J., 2004. Multi-year analysis of stock composition of a loggerhead turtle (*Caretta caretta*) foraging habitat using maximum likelihood and Bayesian methods. Conserv. Genet. 5, 783–796. http://dx.doi.org/10. 1007/s10592-004-1979-1.
- Bolten, A.B., 2003. Variation in sea turtle life history patterns: nertic vs. oceanic developmental stages. In: In: Lutz, P., Musisck, J.A., Wyneken, J. (Eds.), The Biology of Sea Turtles, vol. II. pp. 243–257.
- Bolten, A.E., Bjorndal, K.A., Martins, H.R., Dellinger, T., Biscoito, M.J., Encalada, S.E., Bowen, B.W., 1998. Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. Ecol. Appl. 8, 1–7. http://dx.doi.org/10. 1890/1051-0761.
- Bowen, B.W., Bass, A.L., Chow, S.-M., et al., 2004. Natal homing in juvenile loggerhead turtles (*Caretta caretta*). Mol. Ecol. 13, 3797–3808. http://dx.doi.org/10.1111/j. 1365-294X.2004.02356.x.
- Carreras, C., Pont, S., Maffucci, F., Pascual, M., Barceló, A., Bentivegna, F., Cardona, L., Alegre, F., SanFélix, M., Fernández, G., Aguilar, A., 2006. Genetic structuring of immature loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea reflects water circulation patterns. Mar. Biol. 149, 1269–1279. http://dx.doi.org/10.1007/ s00227-006-0282-8.
- Carreras, C., Pascual, M., Cardona, L., Aguilar, A., Margaritoulis, D., Rees, A., Turkozan, O., Levy, Y., Gasith, A., Aureggi, M., Khalil, M., 2007. The genetic structure of the loggerhead sea turtle (*Caretta caretta*) in the Mediterranean as revealed by nuclear and mitochondrial DNA and its conservation implications. Conserv. Genet. 8, 761–775. http://dx.doi.org/10.1007/s10592-006-9224-8.
- Carreras, C., Rees, A.F., Broderick, A.C., Godley, B.J., Margaritoulis, D., 2014. Mitochondrial DNA markers of loggerhead marine turtles (Caretta caretta) (Testudines: Cheloniidae) nesting at Kiparissia Bay, Greece, confirm the western Greece unit and regional structuring. Scentia Marina 78 (1), 115–124. http://dx.doi. org/10.3989/scimar.03865.27B.

 Casale, P., 2011. Sea turtle by-catch in the Mediterranean. Fish Fish. 12, 299–316.
Casale, P., 2015. Caretta caretta (Mediterranean Subpopulation). The IUCN Red List of Threatened Species 2015. http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS. T83644804A83646294.en.

- Casale, P., Margaritoulis, D., 2010. Sea Turtles in the Mediterranean Distribution, Threats and Conservation Priorities. IUCN/SSC Marine Turtle Specialist Group, Gland, Switzerland.
- Casale, P., Mariani, P., 2014. The first 'lost year' of Mediterranean Sea turtles: dispersal patterns indicate subregional management unit for conservation. Mar. Ecol. Prog. Ser. 498, 263–274. http://dx.doi.org/10.3354/meps10640.
- Casale, P., Freggi, D., Gratton, P., Argano, R., Oliverio, M., 2008. Mitochondrial DNA reveals regional and interregional importance of the central Mediterranean African shelf for loggerhead sea turtles (*Caretta caretta*). Sci. Mar. 72, 541–548. http://dx.doi. org/10.3989/scimar.2008.72n3541.
- Clusa, M., Carreras, C., Pascual, M., Demetropoulos, A., Margaritoulis, D., Rees, A.F., Hamza, A.A., Khalil, M., Aureggi, M., Levy, Y., Türkozan, O., Marco, A., Aguilar, A., Cardona, L., 2013. Mitochondrial DNA reveals Pleistocenic colonisation of the Mediterranean by loggerhead turtles (*Caretta caretta*). J. Exp. Mar. Biol. Ecol. 439, 15–24. http://dx.doi.org/10.1016/j.jembe.2012.10.011.
- Clusa, M., Carreras, C., Pascual, M., Gaughran, S.J., Piovano, S., Giacoma, C., Fernández, G., Levy, Y., Tomás, J., Raga, J.A., Maffucci, F., Hochscheid, S., Aguilar, A., Cardona, L., 2014. Fine-scale distribution of juvenile Atlantic and Mediterranean loggerhead turtles (*Caretta caretta*) in the Mediterranean sea. Mar. Biol. 2014 (161), 509–519. http://dx.doi.org/10.1007/s00227-013-2353-y.
- Crowder, L.B., Hopkins-Murphy, S.R., Royle, A., 1995. Effects of turtle excluder devices (TEDs) on loggerhead sea turtle strandings with implications for conservation. Copeia 1995, 773–779.
- Engstrom, T.N., Meylan, P.A., Meylan, A.B., 2002. Origin of juvenile loggerhad turtles (*Caretta caretta*) in a tropical developmental habitat in Caribbean Panamá. Anim. Conserv. 5, 125–133. http://dx.doi.org/10.1017/S1367943002002184.
- Excoffier, L., Lischer, H.E.L., 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol. Ecol. Resour. 10, 564–567. http://dx.doi.org/10.1111/j.1755-0998.2010.02847.x.
- Garofalo, L., Mingozzi, T., Micò, A., Novelletto, A., 2009. Loggerhead turtle (*Caretta caretta*) matrilines in the Mediterranean: further evidence of genetic diversity and connectivity. Mar. Biol. 156, 2085–2095. http://dx.doi.org/10.1007/s00227-009-1239-5.
- Garofalo, L., Mastrogiacomo, A., Casale, P., Carlini, R., Eleni, C., Freggi, D., Gell, D., Knittweis, L., Mifsud, C., Mingozzi, T., Novarini, N., Scaravelli, D., Scillitani, G., Oliverio, M., Novelleto, A., 2013. Genetic characterization of central Mediterranean stocks of the loggerhead turtle (*Caretta caretta*) using mitochondrial and nuclear markers and conservation implications. Aquat. Conserv. Mar. Freshw. Ecosyst. 23, 868–884. http://dx.doi.org/10.1002/aqc.2338.
- Godley, B.J., Barbosa, C., Bruford, M., Broderick, A.C., Catry, P., Coyne, M.S., Formia, A., Hays, G.C., Witt, M.J., 2010. Unravelling migratory connectivity in marine turtles using multiple methods. J. Appl. Ecol. 47, 769–778. http://dx.doi.org/10.1111/j. 1365-2664.2010.01817.x.
- Grant, W.S., Milner, G.B., Krasnowski, P., Utter, F.M., 1980. Use of biochemical genetic variants for identification of sockeye salmon (*Oncorhynchus nerka*) stocks in Cook Inlet, Alaska. Can. J. Fish. Aquat. Sci. 37, 1236–1247. http://dx.doi.org/10.1139/ f80-159.
- Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl. Acids. Symp. Ser. 41, 95–98.
- Hays, G.C., Fossette, S., Katselidis, K.A., Mariani, P., Schofield, G., 2010. Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. J. R. Soc. Interface 7, 1319–1327. http://dx.doi.org/10.1098/rsif.2010. 0009.
- Hecht, A., Pinardi, N., Robinson, A.R., 1988. Currents, water masses, Eddies and Jets in the Mediterranean Levantine basin. J. Phys. Oceanogr. 18, 1320–1353. http://dx.doi. org/10.1175/1520-0485.

Hillis, D.M., Moritz, C., 1990. Molecular Systematics. Sinauer, Sunderland, Mass.

- Karaa, S., Maffucci, F., Jribi, I., Bologna, M.A., Borra, M., Biffali, E., Bradai, M.N., Hochscheid, S., 2016. Connectivity and stock composition of loggerhead turtles foraging on the North African continental shelf (Central Mediterraenan): implications for conservation and management. Mar. Ecol. 37, 1103–1115. http://dx.doi.org/10. 1111/maec.12375.
- Lewison, R.L., Crowder, L.B., 2007. Putting longline bycatch of sea turtles into perspective. Conserv. Biol. 21, 79–86. http://dx.doi.org/10.1111/j.1523-1739.2006. 00592.x.
- Luschi, P., Casale, P., 2014. Movement patterns of marine turtles in the Mediterraenan Sea: a review. Ital. J. Zool. 81 (4), 478–495. http://dx.doi.org/10.1080/11250003. 2014.963714.
- McClellan, C.M., Read, A.J., 2007. Complexity and variation in loggerhead sea turtle life history. Biol. Lett. 3, 592–594. http://dx.doi.org/10.1098/rsbl.2007.035.

Millot, C., Taupier-Letage, 2004. Circulation in the Mediterranean Sea. The Handbook of Environmental Chemistry, vol. I Springer, Berlin.

Nei, M., 1987. Molecular Evolutionary Genetics. Columbia University Press, New York. Oruç, A., 2001. Trawl fisheries in the eastern Mediterranean and their impact on marine turtles. Zool. Middle East 24, 119–125. http://dx.doi.org/10.1080/09397140.2001. 10637890.

Pella, J., Masuda, M., 2001. Bayesian methods for analysis of stock mixtures from genetic characters. Fish. Bull. 99, 151–167.

Plotkin, P., 2003. In: In: Lutz, P., Musisck, J.A., Wyneken, J. (Eds.), Adult Migrations and Habitat Use in the Biology of Sea Turtles, vol. II. pp. 225–241.

Reece, S.J., Ehrhart, L.M., Parkinson, C., 2006. Mixed stock analysis of juvenile loggerheads (*Caretta caretta*) in Indian River Lagoon, Florida: implications for conservation planning. Conserv. Genet. 7, 345–352. http://dx.doi.org/10.1007/s10592-005-9046-0.

Rees, A.F., Alfaro-Shigueto, J., Barata, P.C.R., Bjorndal, K.A., Bolten, A.B., Bourjea, J.,

Broderick, A.C., Campbell, L.M., Cardona, L., Carreras, C., Casale, P., Ceriani, S.A., Dutton, P.H., Eguchi, T., Formia, A., Fuentes, M.M.P.B., Fuller, W.J., Girondot, M., Godfrey, M.H., Hamann, M., Hart, K.M., Hays, G.C., Hochscheid, S., Kaska, Y., Jensen, M.P., Mangel, J.C., Mortimer, J.A., Naro-Maciel, E., Ng, C.K.Y., Nichols, W.J., Phillott, A.D., Reina, R.D., Revuelta, O., Schofield, G., Seminoff, J.A., Shanker, K., Tomas, J., van de Merwe, J.P., Van Houtan, K.S., Vander Zanden, H.B., Wallace, B.P., Wedemeyer-Strombel, K.R., Work, T.M., Godley, B.J., 2016. Are we working towards global research priorities for management and conservation of sea turtles? Endang. Species Res. 31, 337–382. http://dx.doi.org/10.3354/esr00801.

- Rees, A.F., Carreras, C., Broderick, A.C., Margaritoulis, D., Stringell, T.B., Godley, B.J., 2017. Linking loggerhead locations: using multiple methods to determine the origin of sea turtles in feding grounds. Mar. Biol. 164, 30. http://dx.doi.org/10.1007/ s00227-016-3055-z.
- Robinson, A.R., Leslie, W.G., Theocharis, A., Lascaratos, A., 2001. Ocean circulation currents: Mediterranean sea circulation. In: Turekian, K.K., Thorpe, S.A. (Eds.), Encyclopedia of Ocean Sciences. Academic Press, London, pp. 1689–1703.
- Rozas, J., Sánchez-DelBarrio, J.C., Messeguer, X., Rozas, R., 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics 19, 2496–2497. http://dx.doi.org/10.1093/bioinformatics/btg359.
- Saied, A., Maffucci, F., Hochscheid, S., Dryag, S., Swayeb, B., Borra, M., Oureghi, A., Procaccini, G., Bentivegna, F., 2012. Loggerhead turtles nesting in Libya: an important management unit for the Mediterranean stock. Mar. Ecol. Prog. Ser. 450, 207–218. http://dx.doi.org/10.3354/meps09548.
- Shamblin, B.M., Bolten, A.B., Abreu-Grobois, F.A., Bjorndal, K.A., Cardona, L., Carreras, C., Clusa, M., Monzon-Arguello, C., Nairn, C.J., Nielsen, J.T., Nei, R., Soares, L.S., Stewart, K.R., Vilaça, S.T., Türkozan, O., Yılmaz, C., Dutton, P.H., 2014. Geographic patterns of genetic variation in a broadly distributed marine vertebrate: new insights into loggerhead turtle stock structure from expanded mitochondrial DNA sequences. PLOS ONE 9 (1), 1–12. http://dx.doi.org/10.1371/journal.pone.0085956.
- Snape, R.T.E., Beton, D., Broderick, A.C., Çiçek, B.A., Fuller, W., Özden, Ö., Godley, B.J., 2013. Strand monitoring and anthropological surveys provide insight into marine turtle bycatch in small scale fisheries of the eastern Mediterranean. Chelonian

Conserv. Biol. 12 (1), 44–55. http://dx.doi.org/10.2744/CCB-1008.1.

- Snape, R.T.E., Broderick, A.C., Çiçek, B.A., Fuller, W.J., Glen, F., Stokes, K., Godley, B.J., 2016. Shelf life: neritic habitat use of a turtle population highly threatened by fisheries. Divers. Distrib. 1–11. http://dx.doi.org/10.1111/ddi.12440.
- Turkozan, O., Kaska, Y., 2010. Turkey. In: Casale, P., Margaritoulis, D. (Eds.), Sea Turtles in the Mediterranean: Distribution, Threats and Conservation Priorities. IUCN/SSC Marine Turtle Specialist Group, Gland, Switzerland, pp. 257–293.
- Türkozan, O., Özdilek-Yalçın, Ş., Ergene, S., Uçar, A.H., Sönmez, B., Yılmaz, C., Kaçar, Y., Aymak, C., 2013. Strandings of loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles along eastern Mediterranean coast of Turkey. Herpetol. J. 23, 11–15.
- Wallace, B.P., Heppell, S.S., Lewison, R.L., Kelez, S., Crowder, L.B., 2008. Impacts of fisheries bycatch on loggerhead turtles worldwide inferred from reproductive value analyses. J. Appl. Ecol. 45, 1076–1085. http://dx.doi.org/10.1111/j.1365-2664. 2008.01507.x.
- Wallace, B.P., DiMatteo, A.D., Hurley, B.J., Finkbeiner, E.M., Bolten, A.B., Chaloupka, M.Y., Hutchinson, B.J., Abreu-Grobois, F.A., Amorocho, D., Bjorndal, K.A., Bourjea, J., Bowen, B.W., Briseño Dueñas, R., Casale, P., Choudhury, B.C., Costa, A., Dutton, P., Fallabrino, A., Girard, A., Girondot, M., Godfrey, M.H., Hamann, M., López-Mendilaharsu, M., Marcovaldi, M.A., Mortimer, J.A., Musick, J.A., Nel, R., Pilcher, N.J., Seminoff, J.A., Troëng, S., Witherington, B., Mast, R.B., 2010. Regional Management Units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. PLoS One 5, e15465.
- Wallace, B.P., DiMatteo, A.D., Bolten, A.B., Chaloupka, M.Y., Hutchinson, B.J., et al., 2011. Global conservation priorities for marine turtles. PLoS One 6, e24510.
- Yilmaz, C., Turkozan, O., Bardakci, F., 2011. Genetic structure of loggerhead turtle (*Caretta caretta*) populations in Turkey. Biochem. Systemat. Ecol. 39 (2011), 266–276. http://dx.doi.org/10.1016/j.bse.2011.08.018.
- Zbinden, J.A., Bearhop, S., Bradshaw, P., Gill, B., Margaritoulis, D., Newton, J., Godley, B.J., 2011. Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. Mar. Ecol. Prog. Ser. 421, 291–302. http://dx.doi.org/10.3354/meps08871.