

Tagging reveals limited exchange of immature loggerhead sea turtles (*Caretta caretta*) between regions in the western Mediterranean

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SUMMARY: Exchange of immature loggerhead sea turtles (*Caretta caretta*) between the northern and southern regions of the western Mediterranean was investigated using data obtained from several Spanish tagging programmes. Tagged turtles ranged in straight carapace length from 23.0 to 74.0 cm. Thirty-six turtles were recaptured after an average interval of 390.5±462.6 days (SD). As the mean dispersal distance (MDD) of a turtle population that spreads over the western Mediterranean would stabilize after 117 days (CI 95%: 98 to 149), two analyses were conducted that included data from turtles recaptured after 98 and 149 days respectively. In both analyses, turtles were recaptured more often than expected in the same region where they had been tagged. No difference was found in either of the two regions between the average distance between the capture and recapture locations and the expected MDD if the turtles were to remain in the region where they were first captured. Turtles recaptured after 15 and 25 days respectively were excluded from the analysis to ensure data independence. The overall evidence indicates that immature turtles exhibit strong site fidelity to certain areas and that there is a strong barrier to dispersal between the northern and southern parts of the western Mediterranean. Therefore, loggerhead turtles in the western Mediterranean should be split into at least two management units.

Keywords: biogeography, loggerhead sea turtle, capture-mark-recapture, flipper tags, dispersal, Mediterranean.

RESUMEN: EL MARCAJE REVELA UN INTERCAMBIO LIMITADO DE INMADUROS DE TORTUGA BOBA (*CARETTA CARETTA*) ENTRE REGIONES EN EL MEDITERRÁNEO OCCIDENTAL. – Se investigó el intercambio de inmaduros de tortuga boba (*Caretta caretta*) entre las regiones septentrional y meridional del Mediterráneo occidental a partir de los datos obtenidos por varios programas españoles de marcaje. El rango de la longitud recta de caparazón de las tortugas marcadas fue de 23 a 74 cm. 36 de ellas se recapturaron tras un intervalo medio de 390,5±462,6 días (DS). Como la distancia media de dispersión (MDD) de una población de tortugas que se dispersan por el Mediterráneo occidental se estabilizaría al cabo de 117 días (IC 95%: 98-149), se llevaron a cabo dos análisis incluyendo los datos de las tortugas recapturadas después de 98 y 149 días, respectivamente. En ambos análisis, la frecuencia de recaptura en la misma región donde fueron marcadas fue mayor a la esperada. En un segundo análisis se comparó la distancia media entre las localizaciones de captura y recaptura de las tortugas de cada región con la MDD esperada si permanecieran confinadas en la región de la primera captura. Se excluyeron de este análisis aquellas tortugas recapturadas en un plazo inferior a 15 días (región septentrional) y 25 días (región meridional) para garantizar la independencia entre la localidad de primera captura y de recaptura. No se hallaron diferencias significativas entre la MDD esperada y la distancia media entre las localizaciones de liberación y captura para ninguno de los dos grupos de tortugas. El

conjunto de los datos disponibles demuestran la fidelidad de las tortugas inmaduras a ciertas áreas y la existencia de una fuerte barrera a la dispersión de tortugas entre las regiones septentrionales y meridionales del Mediterráneo occidental, por lo que las tortugas bobas del Mediterráneo occidental se deben dividir en al menos dos unidades de manejo.

Palabras clave: biogeografía, tortuga boba, captura-marca-recaptura, marcas de aleta, dispersión, Mediterráneo.

INTRODUCTION

The loggerhead sea turtle (*Caretta caretta* (Linnaeus, 1758)) is the most common sea turtle in the Mediterranean. However, regular nesting only occurs in the eastern Mediterranean (Margaritoulis *et al.*, 2003), while the western Mediterranean is mainly used by immature individuals as a feeding ground (Laurent *et al.*, 1998; Carreras *et al.*, 2006). An indeterminate but probably large number of immature turtles from North American rookeries cross the Strait of Gibraltar and also use the western Mediterranean as a feeding ground, thus mixing with individuals of eastern Mediterranean origin (Laurent *et al.*, 1998; Carreras *et al.*, 2006). Unexpectedly, immature loggerhead sea turtles do not occupy the western Mediterranean homogeneously. Genetic analyses have revealed that turtles from North American rookeries prevail along the southern coast of the western Mediterranean while those from the eastern Mediterranean prevail along the European shore north of Cape La Nao (Carreras *et al.*, 2006; Revelles *et al.*, 2007a).

Understanding the movements of immature loggerhead sea turtles within the western Mediterranean is crucial for determining how such deep genetic structuring has emerged within such a small area for animals that are able to disperse as early juveniles across entire oceans. Carreras *et al.* (2006) suggested that water circulation within the western Mediterranean might be involved in generating a heterogeneous admixture of loggerhead sea turtles, as southward locations have a much stronger Atlantic influence than the basins along the European shore north of Cape La Nao (Millot, 1999). Satellite tracking of immature loggerhead sea turtles from the Balearic Islands confirms that turtles in the southern part of the western Mediterranean seldom approach the European shore north of Cape La Nao (Cardona *et al.*, 2005; Revelles *et al.*, 2007b). However, there is little information about the movements of the many immature loggerhead sea turtles along the shore north of Cape La Nao (Gómez de Segura *et al.*, 2006). Only a few tag recoveries have been reported to date (Bertolero, 2003). The four loggerhead sea turtles that

were satellite tracked in the Tyrrhenian Sea by Benítez-Vegna (2002) only provided information about the site fidelity patterns of early adult loggerheads, and the dispersal behaviour of loggerhead sea turtles is known to change with developmental stage (Bolten, 2003). Further insight into the dispersal pattern of the immature loggerhead sea turtles found along the European shore of the western Mediterranean north of Cape La Nao is essential in order to determine whether the genetic structuring observed in the western Mediterranean is simply the consequence of the homing behaviour of North American loggerhead sea turtles that have been trapped by currents within the Mediterranean (Revelles *et al.*, 2007a) or due to the existence of a powerful, symmetrical barrier between the northern and southern regions of the western Mediterranean.

Flipper tags have been widely used for studying migration in sea turtles (Balazs, 2000), in the eastern Mediterranean (Margaritoulis *et al.*, 2003), and off Italy (Casale *et al.*, 2007). Huge tagging programmes have also been conducted in the western Mediterranean (Roca and Camiñas, 2000; Bertolero, 2003; Camiñas, 2005), but most of the results have not yet been published. In this study we use the information provided by these tagging programmes to test whether there is a symmetrical barrier for loggerhead sea turtles within the western Mediterranean. In this a scenario, the loggerhead sea turtles found in southern locations would be more likely to disperse to the Atlantic than to northern locations, whereas those in the northern locations would be more likely to disperse to the eastern Mediterranean than to southern locations.

MATERIAL AND METHODS

Description of the study area

There are two major regions in the western Mediterranean: a southern area filled with Atlantic water and a northern area with a much lower Atlantic influence (Millot, 1999). The limit between them varies seasonally and annually (Pinot *et al.*, 2002), but

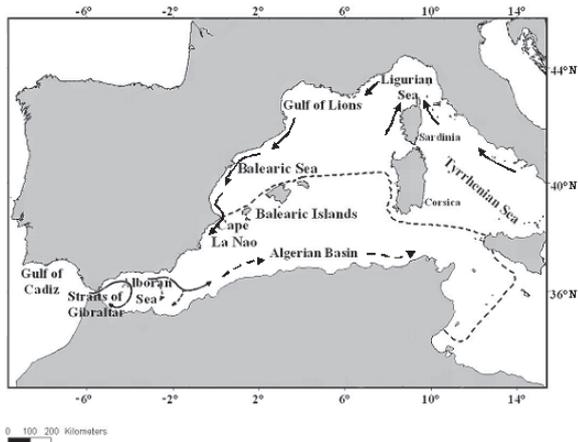


FIG. 1. – Basins within the western Mediterranean, the limit between the northern and southern regions (dashed line), and the prevailing currents in agreement with Millot (1999) (arrows).

the 37.8 isohaline, as established in MEDATLAS II climatology (<http://www.ifremer.fr/sismer/program/medar/>), seems to be a convenient frontier between the two regions (Fig. 1).

Analysis of tagging results

Several types of passive tags have been used to mark loggerhead sea turtles in the western Mediterranean since 1988: plastic tags, Monel tags, Inconel tags and internal transponders (Camiñas, 2005). Data examined here include information from several Spanish tagging programmes (Instituto Español de Oceanografía (IEO), Asociación Herpetológica Española (AHE), Instituto para la Conservación de la Naturaleza (ICONA), Centro de Recuperación de Animales Marinos de Andalucía (CREMA), Centre de Recuperació d'Animals Marins (CRAM) and University of Barcelona) in the western Mediterranean, independently of the recapture location, and from turtles recaptured by Spanish researchers in the western Mediterranean, independently of the location where they had been tagged. Some of these data have already been published (Roca and Camiñas, 2000; Tomás *et al.*, 2001; Bertolero, 2003; Camiñas, 2005).

In order to ensure independence between the release and subsequent recapture locations for any given turtle, we calculated the estimated time needed by a turtle population to disperse to the limits of the western Mediterranean (TDWM), to the limits of the northern region (TDNWM) and the limits of the southern region (TDSWM). Turtles recaptured in a period shorter than TDWM, TDNWM or TDSWM

were not included in the corresponding analyses (see below), as independence between the release and recapture locations could not be guaranteed. To calculate TDWM, TDNWM and TDSWM it was first necessary to determine the mean dispersal distance (MDD) of a population spreading over each of the considered regions by means of the Bovet and Benhamou (1988) equation:

$$MDD = L\sqrt{0.79n(1+r)/(1-r)} \quad (1)$$

where L is the average step size (distance between two consecutive locations) of the population (in kilometres), n is the number of steps, and r is a measure of route straightness, which can be calculated as:

$$r = \exp\left(\frac{-SDA^2}{2}\right) \quad (2)$$

where SDA is the standard deviation of the turning angles of the population expressed in radians. The MDD for a population confined to a region the size of the western Mediterranean will stabilize at 285 km (Fig. 2), once the entire available surface has been occupied. Likewise, the MDD for a population confined to regions the size of the northern and southern parts of the western Mediterranean will stabilize at 102 km and 132 km respectively (Fig. 2). Satellite tracking of loggerhead sea turtles in the western Mediterranean (Cardona *et al.*, 2005; Revelles *et al.*, 2007b) has revealed that $L=22.25$ km and $SDA=71.67^\circ$ for a step duration of 36.37 h; therefore, independence between the locations of consecutive capture is guaranteed after 117 days (CI 95%: 98 to 149) for a population confined to the western Mediterranean. Likewise, independence between the locations of consecutive capture is guaranteed after 15 days (CI 95%: 12 to 20) and 25 days (CI 95%: 20 to 32) for turtles confined to the northern and southern regions of the western Mediterranean respectively. A bias-corrected percentile bootstrap (Dixon, 2001) was used to find the 95% confidence interval in all cases.

Statistical analysis

The symmetrical barrier hypothesis implies that immature loggerhead sea turtles tagged within the western Mediterranean i) are unlikely to disperse to other regions within the western Mediterranean, but ii) may disperse to other regions in the Atlantic and

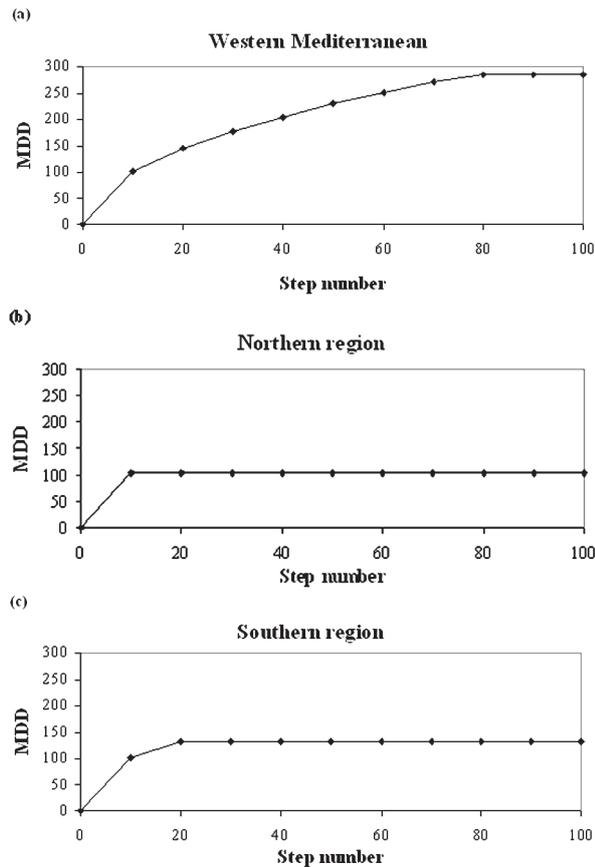


FIG. 2. – Expected MDDs of a population of loggerhead sea turtles dispersing over (a) the western Mediterranean, (b) the northern region and (c) the southern region of the western Mediterranean.

eastern Mediterranean. Thus, we have tested these predictions independently.

The Chi-square test was used to check whether the ratio of northern-tagged to southern-tagged turtles (NT/ST) in both the northern and southern regions differed from that expected due to chance in the absence of any barrier to dispersal within the Mediterranean, as predicted by the first part of the symmetrical barrier hypothesis. Only the turtles recaptured within the Mediterranean or the adjoining eastern Atlantic after a period longer than the TDWM were included in the analysis. This analysis was conducted twice using the lower (98 days) and higher (149 days) limits of the 95% confidence interval of TDWM.

To check whether turtles actually disperse far from the tagging area, as suggested by the second part of the symmetrical barrier hypothesis, the Student's *t*-test was used to compare the MDD of the turtle populations confined to the northern and southern regions of the western Mediterranean with the

mean distance between the turtles' release and recapture locations. Only the turtles recaptured after a period longer than the TDWM and TDSWM were included in the analysis. As the 95% CIs were small, only one analysis was used for each group of turtles.

Differences between straight carapace length (SCL) of individuals tagged in the northern region and in the southern region were assessed using the Student's *t*-test.

Prior to any statistical comparison between groups, normality and homogeneity of variance were tested with the Lilliefors test and Levene's test respectively (Zar, 1984).

RESULTS

Tagged and recaptured turtles ($n=36$, 19 northern-tagged, 17 southern-tagged; Table 1) ranged from 23.0 to 74.0 cm SCL and were recaptured in the Gulf of Lions, the Balearic Sea, the Alboran Sea, the Gulf of Cadiz, the Algerian basin, the Tyrrhenian Sea, the Caribbean Sea, and northern Cuba (Fig. 3), after an average interval between successive captures of 390.5 ± 462.6 days (SD). The recaptured turtles tagged in the southern region (mean SCL=53.3 cm, SD=12.2 cm) were significantly larger than those tagged in the northern region (mean SCL=39.6 cm, SD=12.6 cm) (Student's $t=-2.701$, $df=23$, $p=0.013$).

If dispersal were unlimited within the western Mediterranean, the ratio of northern-tagged to southern-tagged turtles (NT/ST) would be the same for any sample of recaptured turtles anywhere in the western Mediterranean after TDWM, i.e. 15 northern-tagged to 11 southern-tagged in the 98-days-independence scenario or 15 northern-tagged to 10 southern-tagged in the 149-days-independence scenario, once the turtles recaptured too early and those moving away from the western Mediterranean and the adjoining eastern Atlantic were removed from the analysis. However, turtles were recaptured in the same region where they had been tagged more often than expected, independently of the scenario considered (Table 2).

The average distance between the release and recapture locations of the northern-tagged turtles was 136.6 ± 180.6 km and was not significantly larger than a MDD of 102 km (Student's $t=0.878$, $df=21$, $p=0.211$). No northern-tagged turtle was recaptured earlier than 15 days and hence none was removed for the analysis. Once the two southern-tagged tur-

TABLE 1. – Loggerhead sea turtles tagged and recaptured in the northern and southern regions of the western Mediterranean. N, northern region; S, southern region; WA, western Atlantic.

Turtle (SCL cm)	Northern-tagged turtles			Number of days	Turtle (SCL cm)	Southern-tagged turtles			Number of days
	Release date	Recapture date	Recapture region			Release date	Recapture date	Recapture region	
#1(24.9)	18/11/1993	23/07/1995	N	612	#20(68.0)	27/07/2000	18/02/2002	WA	571
#2(23.0)	15/07/1995	20/06/2002	N	2533	#21(42.7)	02/08/2000	10/07/2001	S	317
#3(46.7)	9/10/1995	7/05/1998	N	941	#22(51.7)	02/08/2000	05/08/2000	S	3
#4(25.8)	10/07/1996	27/06/1997	N	353	#23(33.0)	13/03/2002	02/02/2003	S	327
#5(28.6)	27/10/2001	20/05/2003	N	571	#24(60.2)	14/05/2002	01/02/2005	WA	995
#6(60.2)	11/09/2002	27/09/2002	N	17	#25(49.2)	17/05/2000	24/05/2000	S	7
#6(60.2)	23/04/2003	10/05/2003	N	18	#26(64.0)	18/08/1999	06/06/2000	S	291
#6(60.2)	27/08/2003	7/06/2005	N	651	#27(46.0)	19/08/2000	02/07/2001	S	317
#7(45.1)	15/11/2002	22/05/2003	N	189	#28(46.0)	19/08/2000	02/07/2001	S	317
#8(39.8)	10/11/2003	5/01/2005	N	421	#29	2/12/1993	10/03/1994	S	106
#9(30.9)	27/08/2003	29/03/2004	N	216	#30(60.0)	20/05/2000	03/06/2001	S	379
#10(55.6)	6/04/2004	26/09/2004	N	174	#31(49.5)	20/08/2002	18/05/2004	S	1360
#11(26.6)	26/05/2004	20/06/2004	N	26	#32(64.0)	21/06/2001	24/04/2002	S	300
#12(38.8)	5/06/2004	13/12/2005	N	557	#33	21/09/2001	25/05/2003	S	612
#13(35.1)	15/07/2004	4/09/2004	N	52	#34(64.0)	22/05/2002	16/06/2002	S	26
#13(35.1)	5/07/2003	5/07/2004	N	367	#35(74.0)	24/05/2000	07/10/2000	S	136
#14(48.1)	23/06/2005	18/08/2005	N	56	#36(53.7)	4/08/1999	2/09/2000	S	183
#15(45.3)	23/06/2005	12/08/2005	N	50					
#16(29.5)	25/08/2004	8/11/2004	N	76					
#17(36.0)	6/11/2004	8/06/2005	N	215					
#18(62.6)	29/10/1999	1/06/2001	S	580					
#19(40.7)	13/07/2000	15/07/2001	S	367					

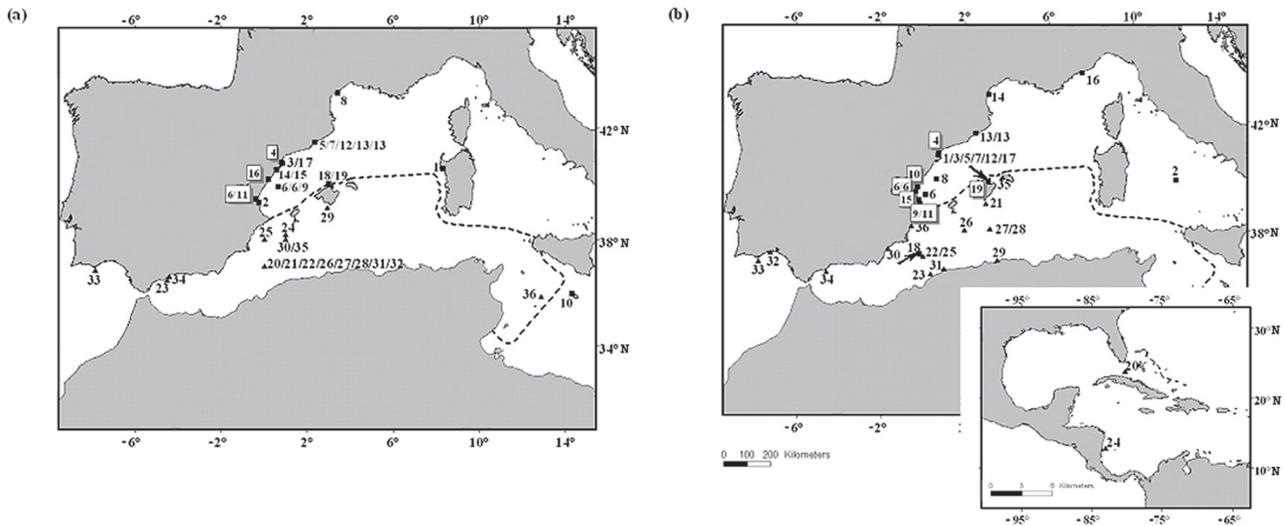


FIG. 3. – Locations of (a) release and (b) recapture of the northern tagged (squares) and southern tagged (triangles) turtles. Numbers identify individual turtles as in Table 1.

TABLE 2. – Expected and observed frequency of northern-tagged and southern-tagged loggerhead sea turtles recaptured in the northern and southern regions of the western Mediterranean and results of the Chi-square tests.

	Northern-tagged turtles		Southern-tagged turtles		Chi-square	df	p
	Expected	Observed	Expected	Observed			
98 days scenario							
Northern region	8	13	5	0	8.125	1	0.004
Southern region	8	2	5	11	11.700	1	0.001
149 days scenario							
Northern region	8	13	5	0	8.125	1	0.004
Southern region	7	2	5	10	8.571	1	0.003

tles recaptured earlier than 25 days were removed, the average distance between the release and recapture locations of the southern-tagged turtles was 632.9 ± 1245.0 km. This huge standard deviation was due to two of the turtles being recaptured in the western Atlantic, but most of the remaining turtles did not travel far from the release location. As a consequence, the average recapture distance was not significantly larger than a MDD of 132 km (Student's $t=1.497$, $df=14$, $p=0.105$), although the result was on the verge of similarity and differences would have been statistically significant if just a third turtle had moved to the western Atlantic.

DISCUSSION

Loggerhead sea turtles inhabit the oceanic zone in their early life (Bolten, 2003), recruit to neritic habitats as late immature turtles, with a SCL of 40 to 60 cm, and remain there as adults (Bolten, 2003), although they can periodically travel across oceanic areas as part of migrations to and from nesting beaches (Broderick *et al.*, 2007). Mediterranean loggerhead sea turtles approach adulthood at a smaller size (minimum SCL of nesting females: 58.0 cm; Margaritoulis *et al.*, 2003) than those from the Atlantic (minimum SCL of nesting females: 70.0 cm; Dodd, 1988). Most of the loggerhead sea turtles tagged for this study in the northern region of the western Mediterranean were first caught by bottom trawlers or entangled in bottom trammel nets over the continental shelf and hence were probably in the neritic stage. Turtles in this stage typically show a high degree of site fidelity to particular feeding grounds both as immatures (Avens *et al.*, 2003; Casale *et al.*, 2007) and adults (Broderick *et al.*, 2007), so it is hardly surprising that most of them were recaptured in the same region of the western Mediterranean after several months. Furthermore, the only two individuals that moved from the northern to the southern region were caught for the first time in the oceanic zone, and turtles in the oceanic stage are known to disperse across entire oceans (Bolten, 2003). Conversely, none of the turtles tagged in the southern region was recaptured in the northern region, although most of them were first caught in the oceanic zone. This fidelity to a broad oceanic area agrees with the results of the satellite tracking studies conducted by Cardona *et al.* (2005) and Revelles *et al.* (2007b) in the same region, although it is certainly temporary,

as rookeries do not exist in the western Mediterranean and turtles will finally leave the area when approaching adulthood (Revelles *et al.*, 2007a). Nevertheless, this localized residence of immature loggerhead turtles is shared by some other species, such as green turtles (*Chelonia mydas*) (Godley *et al.*, 2003). In contrast, some other species of sea turtles, such as leatherbacks (*Dermochelys coriacea*) and olive ridleys (*Lepidochelys olivacea*), seem to be far more mobile and may constantly move around oceanic areas throughout their lives (Luschi *et al.*, 2003).

Casale *et al.* (2007) called nomad turtles those individuals that move between different oceanographic areas and reported that this behaviour is common for the oceanic loggerhead sea turtles off Italy, although others exhibited a high level of site fidelity both to oceanic and neritic feeding grounds. Casale *et al.* (2007) hypothesized that nomad turtles were Atlantic turtles that continuously moved through different oceanic areas across the Atlantic and the Mediterranean. However, this nomadic behaviour is extremely uncommon in the turtles tagged in the southern region of the western Mediterranean, despite the overwhelming prevalence of Atlantic turtles in this area (Carreras *et al.*, 2006). This fact evidences the fidelity of immature loggerhead sea turtles to particular oceanic areas and supports the hypothesis of limited exchange of loggerhead sea turtles between adjoining regions. However, other patterns cannot be excluded and truly nomadic turtles may exist.

Carreras *et al.* (2006) hypothesized that the deep genetic structuring observed in the foraging aggregations of immature loggerhead sea turtles in the western Mediterranean reflect that immature turtles are limited to water masses with certain characteristics, as individuals of Mediterranean origin tend to remain associated with the higher salinity waters of the northern region, while those from the Atlantic show preference for the lower salinity waters of the southern region. The results reported here are consistent with this hypothesis, as the barrier between the northern and southern parts of the Mediterranean is symmetrical and loggerhead sea turtles of either origin seldom cross it, although they may. This indicates that the nomad turtles reported by Casale *et al.* (2007), which typically move from the central and eastern Mediterranean to the western Mediterranean, would be individuals coming back to their preferred region after an excursion to another region. Satellite tracking also provides evidence of this behaviour (Cardona *et al.*, 2005; Revelles *et al.*, 2007b).

Assigning tagged and satellite tracked turtles to Atlantic or Mediterranean populations precisely would provide a powerful tool for gaining further insight into the relation between site fidelity and turtle origin. Unfortunately, genetic data are only available for two of the turtles reported here, although all the tagging programmes collected samples for genetic analysis. This is because samples were only collected from a few individuals for each programme, as traditional mtDNA markers are suitable for analysis at the population or stock levels, but not for individual assignment in the Mediterranean due to the overwhelming prevalence of a haplotype shared by all the rookeries (Carreras *et al.*, 2006, 2007). As a consequence, the sampling effort was sufficient for conducting a mixed stock analysis but most individuals were not sampled because individual assignment was often impossible. Recently, the situation has improved due to the development of a new method for individual assignment (Revelles *et al.*, 2007a), but as tissue samples only exist for two of the recaptured turtles, a consistent analysis is not possible.

The results of this study also shed light on movements of turtles between the Mediterranean Sea and the Atlantic Ocean. Although it is known that immature loggerhead sea turtles cross the Strait of Gibraltar in both directions (Camiñas, 1997), movement of small individuals to the Atlantic appears to be restricted by the permanent eastward flow of surface water at the sill (Revelles *et al.*, 2007a). Two of the turtles tagged in the southern region migrated to the western Atlantic and although genetic information of these turtles is not available, this behaviour would be consistent with the putative Atlantic origin of turtles from the southern stock (Carreras *et al.*, 2006). Conversely, none of the turtles tagged in the northern region moved to the Atlantic, which is also in agreement with their putative Mediterranean origin (Carreras *et al.*, 2006).

In conclusion, the information provided by satellite tracking (Bentivegna, 2002; Cardona *et al.*, 2005; Revelles *et al.*, 2007b), genetic markers (Carreras *et al.*, 2006) and tagging (this study) strongly supports the hypothesis of limited exchange of immature loggerhead sea turtles between the northern and southern regions of the western Mediterranean. This conclusion is highly relevant for managing the loggerhead sea turtles in the western Mediterranean, as the overall stock should be divided into at least two distinct management units: one that is mostly composed of turtles from the eastern Mediterranean

that inhabit the European shore north of cape La Nao, and another that is mostly composed of individuals from Atlantic rookeries that occupy the Alboran sea, the Balearic Islands and the Algerian basin. This means that human activities in the southern management unit may negatively affect the loggerhead sea turtles nesting in the Atlantic, whereas impacts on the northern management unit are more relevant for the populations nesting in the eastern Mediterranean. Furthermore, as most of the turtles in the southern unit are in the oceanic stage and those in the northern unit are in the neritic stage, the precise nature of the anthropogenic impacts threatening turtles in these two areas is not the same.

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