

Potential bycatch impact on distinct sea turtle populations is dependent on fishing ground rather than gear type in the Mediterranean Sea

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Abstract Bycatch is one of the main threats affecting marine megafauna worldwide, not only because of its prevalence, but also because the impact of high levels of bycatch in small oceanic regions may spread over whole oceans due to the complex dispersal patterns of bycaught species. Here, we use intrinsic and genetic markers to understand the impact of bycatch on the Atlantic and Mediterranean populations of the loggerhead turtle sharing the same foraging grounds in the western Mediterranean Sea. Turtles of Atlantic origin settle on the continental shelf later and at a larger size than turtles of Mediterranean origin and hence have been suggested to be more vulnerable to pelagic fishing gears, whereas those of Mediterranean origin would

be more vulnerable to neritic ones. To assess whether this hypothesis holds true, we compared the genetic make-up of turtle bycatch from drifting longlines and bottom trawl/trammel nets in three different regions (eastern mainland Spain, southern Balearic Islands and southern Italy). A total of 176 incidentally caught turtles were considered, and size and habitat use, as revealed by stable isotopes, were incorporated to the analysis. No genetic, size or isotopic differences were found between turtles caught with drifting longlines and bottom trawl/trammel nets within any of the three regions. However, genetic, size and isotopic differences were detected among regions, regardless of the fishing gear. Thus, the population make-up of loggerhead bycatch depends on the area where the fishing operations are conducted, but not on the fishing gear used. Accordingly, the actual impact of loggerhead bycatch in the Mediterranean Sea will depend not only on the total number of turtles taken, but also on the geographic distribution of the fishing effort.

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Introduction

Fishing activity is a well-known threat to many endangered marine species because of a combination of overfishing and habitat disturbance (Pauly et al. 2005). However, fisheries not only may affect targeted species, but also un-targeted species, threatened through overfishing of food resources or lethal direct interactions. Bycatch, the unintentional capture of non-targeted species during fishing operations, has been described as one of the most important factors causing the decline of marine species worldwide, especially of large marine vertebrates: birds, sharks, marine mammals and sea turtles (Lewison et al. 2004). The vulnerability of many large marine vertebrate populations to fisheries interactions is also accentuated by their long lifespan, late age at maturity and low reproductive output (Heppell et al. 1999).

In order to assess the impact of bycatch on marine megafauna, it is crucial to evaluate the number of animals incidentally caught and to estimate the demographic effects of such catch rates for each of the threatened populations (Bache 2003). However, spatial division among populations is not always clear, particularly as these species usually occur in remote oceanic habitats, are distributed across entire oceans and often have complex life cycles involving migrations that cover thousands of kilometres (Anderson et al. 2013). Thus, assignment of caught individuals to specific populations often cannot be carried out based on geographical divisions, and the need to use different approaches such as the use of genetic markers arises (Bowen et al. 1995; Edwards et al. 2001).

Sea turtles present complex life cycles involving several habitat shifts and long-distance migrations (Plotkin 2003). Loggerhead turtles (*Caretta caretta*), for instance, spend several years in the open ocean during early life and recruit to neritic habitats as late juveniles or immatures (Bolten 2003), although, in some populations, a number of adults may remain oceanic throughout their entire lives (Watanabe et al. 2011; Eder et al. 2012). Sea turtle bycatch has been of strong concern among scientists for decades (Hamann et al. 2010), especially considering that most sea turtles are listed as endangered under the IUCN Red List of Threatened Species. Among all fisheries, drifting longlines targeting large pelagic fish (Lewison and Crowder 2007) and bottom trawling in neritic areas (Casale 2011; Wallace et al. 2013) have been the focus of most of the research on turtle bycatch due to the large number of captures worldwide. Mid-water trawls have also been identified as relevant threats to sea turtle populations in certain areas (Lewison and Crowder 2007). However, due to the implementation of turtle excluder devices in mid-water trawls (particularly in prawn fisheries) in many countries, bycatch numbers associated with this type of gear have plummeted down to 90 % (northern Australia; Robins et al. 2002).

The foraging grounds in the Mediterranean Sea are used by juvenile loggerhead turtles of Atlantic and Mediterranean origin (Carreras et al. 2006; Clusa et al. 2014), and hence, turtle bycatch in this area may have broad implications across the North Atlantic and Mediterranean nesting stocks (Álvarez de Quevedo et al. 2013). Pioneering research on the origin of the loggerhead turtles using the Mediterranean foraging grounds indicated that drifting longlines captured a mixture of turtles of Atlantic and Mediterranean origin, whereas bottom trawling captured only turtles of Mediterranean origin (Laurent et al. 1998). Unfortunately, it is unclear whether that pattern was real and emerged from the earlier settlement of Mediterranean turtles into neritic habitats (Casale et al. 2008; Piovano et al. 2011) or was an artefact caused by the eastward decreasing abundance of turtles of Atlantic origin within the Mediterranean Sea (Maffucci et al. 2006; Clusa et al. 2014). This is extremely relevant to the conservation of loggerhead turtles because each scenario leads to a different management strategy, focused either on fishing gear types or on fishing grounds.

To disentangle whether fishing ground and/or fishing gear has a differential impact on turtles from different origins present in the Mediterranean as juveniles, we collected samples of loggerheads caught by drifting longline and bottom trawling/trammel nets within three areas (eastern mainland Spain, southern Balearic Islands and southern Italy). These areas corresponded to three sub-basins differing in salinity, sea surface temperature, primary productivity and surface circulation (Millot 1999; Bosc et al. 2004). We measured the size of bycaught turtles, and through the use of stable isotope ratios and genetic mitochondrial and nuclear DNA markers, we assessed whether juvenile loggerhead turtles caught with different gears in the same region consistently differ (1) in size, (2) in patterns of habitat use and (3) in haplotype frequencies and natal origin. With this approach, we aimed to assess the impact that different fishing gears on different foraging grounds might have on Atlantic and Mediterranean rookeries.

Materials and methods

Bycatch sampling

A total of 176 juvenile loggerhead turtles incidentally caught from 2001 to 2012 in three major regions of the western and central Mediterranean (Fig. 1) were sampled: 55 from eastern mainland Spain (SPA), 85 from southern Balearic Islands (BAL) and 36 from southern Italy (SIT). Muscle samples were collected from dead animals and stored in 95 % ethanol, whilst blood samples were taken from live animals and stored frozen. Live animals sampled

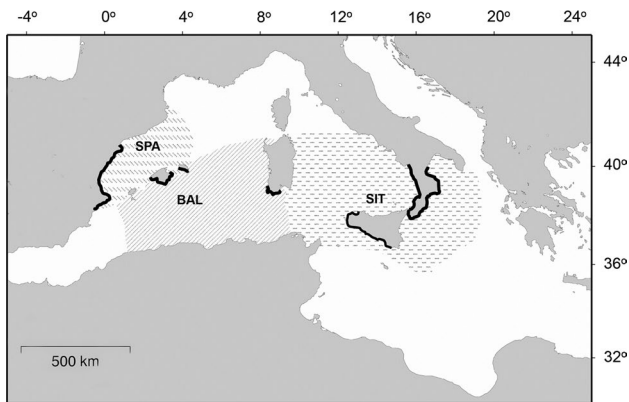


Fig. 1 Study area with shaded zones representing three basins used by the juvenile loggerhead turtles analysed: SPA (eastern mainland Spain), BAL (southern Balearic Islands) and SIT (southern Italy). Black lines identify the ports and coastlines surveyed

were flipper-tagged to make sure that each individual was only sampled once.

Turtles were divided into two groups for each region, according to bycatch source: turtles caught by drifting longline (DLL) and turtles caught by trawl and trammel fisheries (TWL). Samples were collected over 10 years (Supplementary Table 1), and even if the type of gear and fishing effort (number of boats and hours at sea) might have changed during this period, these did not affect the results and main conclusions of this study. This was shown by the lack of significant differences between two groups on the distribution of number of samples per group analysed through time (sign test; $Z = 0.917$, $P = 0.359$).

Genetic characterisation of loggerhead turtle bycatch

DNA from bycaught turtles ($N = 176$) was extracted with the QIAamp extraction kit (QIAGEN®) and sequenced to assign their natal origin (Atlantic or Mediterranean). A fragment of the mtDNA control region was amplified by polymerase chain reaction (PCR) using the primer pairs TCR1–TCR2 (short fragment; Norman et al. 1994) and LCM15382–H950 (long fragment; Abreu-Grobois et al. 2006) following the protocols described in Carreras et al. (2006) and Clusa et al. (2013), respectively. The samples amplified by the primer pairs TCR1–TCR2 came from previous surveys, and hence, no long fragments could be amplified due to sample degradation. All samples were sequenced in forward and reverse directions to confirm variable sites on both strands of DNA on an ABI 3730 automated DNA analyser.

Sequences were manually aligned with BioEdit v7.2.5 (Hall 1999) and compared to the short (380bp) and long (815bp) haplotypes previously described for the species, compiled at the Archie Carr Center for Sea Turtle Research

of the University of Florida (ACCSTR; <http://accstr.ufl.edu>).

Individual assignments to natal origin were undertaken following the sequential method described in Carreras et al. (2011). Whenever an individual carried an mtDNA haplotype exclusive to an Atlantic or Mediterranean nesting area, this individual was assumed to have originated from the corresponding nesting area, without any further analysis. Individuals carrying shared haplotypes, orphan haplotypes (not described in any nesting area to date), or individuals that failed to amplify for the long mtDNA fragment were genotyped at seven microsatellite loci. Control individuals with known origin carrying exclusive haplotypes were tested by Carreras et al. (2011) with both techniques, and controls were correctly reassigned when genotyped. This sequential approach highly reduced the analysis cost.

Seven microsatellites had previously been used in *C.caretta*: Cc117, Cm72, Cm84 and Ei8 (FitzSimmons et al. 1995); Cc7 and Cc141 (FitzSimmons et al. 1996); and Ccar176 (Moore and Ball 2002; modified by Carreras et al. 2007). These individuals were assigned with STRUCTURE v2.3.4 (Pritchard et al. 2000) by comparison with the baseline individual genotypes used in Carreras et al. (2011). Origin assignments were only considered valid when the probability of belonging to the Atlantic or Mediterranean stock was higher than 0.7 for one of the two groups.

Overall differences in origin frequencies (Atlantic or Mediterranean) between fishing gears among the three sampled regions (Fig. 1) were assessed with an analysis of molecular variance (AMOVA) using ARLEQUIN v3.5 (Excoffier and Lischer 2010). The same program was used to estimate genetic differentiation between groups of juveniles caught with different fishing gears in each sampled region. Based on short mtDNA control region sequences, pairwise F_{ST} values were computed and its significance was assessed with an exact test.

Size characterisation of loggerhead turtle bycatch

Curved carapace length notch-to-tip (CCL_{n-t}) was measured for all individuals. Mediterranean turtles only smaller than 69 cm CCL_{n-t} were used for size and isotopic comparisons of the juvenile stage, as this is the mean minimum size of nesting females in the Mediterranean (Margaritoulis et al. 2003). On the contrary, all turtles assigned to an Atlantic origin were used for subsequent analyses, as Atlantic turtles start nesting at sizes much larger (87–104 cm CCL_{n-t} ; Turtle Expert Working Group 2009) than the ones recorded in this study. A two-way ANCOVA, with gear and region as fixed factors and year as a covariate, was used to test for differences in size (CCL_{n-t}) of turtles caught by the different fishing gears in three regions analysed. In this study, year was always chosen as a covariate according to its

independence from the other two factors (gear and region) and the fact that year was not different across the groups as revealed by the sign test above (Miller and Chapman 2001).

Stable isotope characterisation of loggerhead turtle bycatch

Ethanol-preserved muscle samples from 11 juvenile individuals from each fishing gear and region were thoroughly rinsed with distilled water (periodical changes of water over 12 h) to avoid the presence of ethanol—even if this has minimal effects on stable isotope analyses (Arrington and Winemiller 2002). Subsequently, samples were oven-dried at 60 °C for 48–72 h. They were ground into fine powder, and lipids were extracted from all tissues with a chloroform–methanol (2:1) solution. This was undertaken as lipids are depleted in ^{13}C in comparison with other molecules, and hence, changes in the lipid contents of the sample may bias the $\delta^{13}\text{C}$ values (Logan and Lutcavage 2008).

Approximately 0.3 mg of each dry and powdered sample was combusted at 1000 °C. The analyses were performed in a continuous-flow isotope ratio mass spectrometer (Flash 112 IRMS Delta C Series EA Thermo Finnigan) at *Serveis Científics i Tecnològics* at the University of Barcelona. Stable isotope ratios were expressed in the following delta notation (δ) in parts per thousand (‰):

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio of the heavier to the lighter isotope (i.e. $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$). International isotope standards of known $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios were used to a precision of 0.2 ‰: IAEA CH6 ($\delta^{13}\text{C} = -10.3$ ‰), USGS 40 ($\delta^{13}\text{C} = -25.8$ ‰) and IAEA CH7 ($\delta^{13}\text{C} = -31.6$ ‰) for carbon and USGS 40 ($\delta^{15}\text{N} = -4.3$ ‰), IAEA N1 ($\delta^{15}\text{N} = +0.8$ ‰), IAEA 600 ($\delta^{15}\text{N} = +1.0$ ‰) and IAEA N2 ($\delta^{15}\text{N} = +20.4$ ‰) for nitrogen.

A two-way ANCOVA, considering gear and region as fixed factors and sampling year as a covariate, was used to test for statistical differences in the nitrogen and carbon stable isotope ratios of turtles caught by the different fishing gears in three regions analysed. Relationships between size and isotopic signatures of bycaught individuals were assessed with Pearson's correlation tests in three regions analysed.

Results

Genetic characterisation of loggerhead turtle bycatch

Individual assignment through the amplification of mtDNA and nDNA allowed us to assign 153 individuals (87 %) to

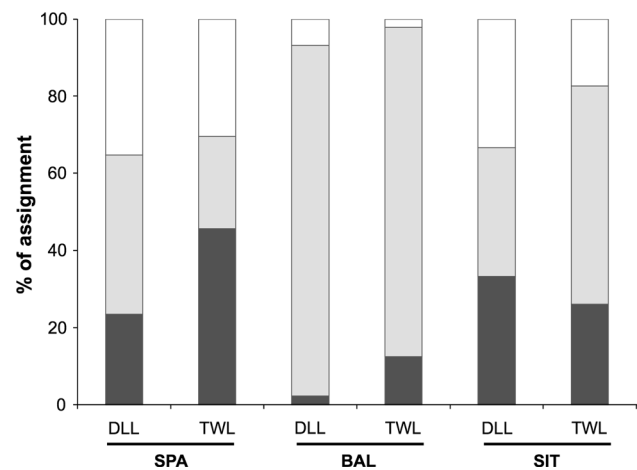


Fig. 2 Individual assignment results showing the percentage of juvenile individuals incidentally caught in the studied regions (SPA: eastern mainland Spain, BAL: southern Balearic Islands, SIT: southern Italy) by drifting longlines (DLL) and trawling/trammel nets (TWL) from Mediterranean (dark grey) and Atlantic (light grey) rookeries. The proportion of unassigned individuals is shown in white

their natal stocks (Atlantic or Mediterranean origin), a similar successful assignment ratio to previous studies (Carreras et al. 2011). Of these, short mtDNA control region haplotypes allowed assigning the origin of 47 individuals. Whilst only one individual carried an exclusive Mediterranean short mtDNA haplotype (CC-A6), the remaining 46 assigned individuals carried exclusive Atlantic haplotypes: CC-A1 (39 individuals); CC-A5 (1); CC-A6 (1); CC-A10 (1); CC-A14 (4). The rest of analysed individuals carried haplotypes found in both Atlantic and Mediterranean rookeries (CC-A2, CC-A3, CC-A20) and hence could not be assigned with just short mtDNA haplotypes. Furthermore, in regards to the long mtDNA haplotypes, these allowed the assignment of another 12 individuals, all carrying the CC-A2.9 haplotype—only found in Mediterranean rookeries until the moment (Clusa et al. 2013). A total of 94 individuals were further assigned with microsatellite markers, but the remaining 23 individuals (13 %) could not be assigned due to low assigning probabilities mostly caused by amplification failure of some of the microsatellite loci.

Juvenile individuals of Atlantic and Mediterranean origin were not homogeneously distributed among groups (Fig. 2). Marginal differences were detected among regions (AMOVA; percentage of variation = 33.54 %, $P = 0.062$), but there were no statistically significant differences between fishing gears within each region (AMOVA; percentage of variation = 2.91 %, $P = 0.181$). The exact tests revealed that pairwise genetic distances between fishing gears within the same region were not significant, and the only significant differences were detected between the southern Balearic Islands and the other two regions

Table 1 Genetic differentiation (F_{ST}) between regions (SPA, BAL and SIT) and fishing gears (DLL and TWL)

Region	Gear	SPA		BAL		SIT	
		DLL	TWL	DLL	TWL	DLL	TWL
SPA	DLL	0					
	TWL	0.029	0				
BAL	DLL	0.463*	0.581*	0			
	TWL	0.248*	0.456*	0.017	0		
SIT	DLL	-0.011	-0.050	0.636*	0.466*	0	
	TWL	-0.067	0.097	0.345*	0.162*	0.056	0

Acronyms as in Figs. 1 and 2, respectively

* $P < 0.05$ as assessed with an exact test

regardless of fishing gear (Table 1). Juvenile turtles of Atlantic origin caught in the southern Balearic Islands represented 87.8 % of the turtle bycatch of drifting longlines and 81.8 % of the turtle bycatch of bottom trawls/trammel in the same area. Conversely, the proportion of juvenile turtles of Atlantic origin was always lower than 65 % both for drifting longlines and for trammel nets/bottom trawls off eastern mainland Spain and southern Italy (Fig. 2).

Size characterisation of loggerhead turtle bycatch

The size of turtles captured with drifting longlines (Fig. 3) ranged between 25 cm (in SIT) and 76 cm (in BAL), whilst those captured with trawling/trammel nets ranged between 22 cm (in SIT) and 80 cm (in SIT).

No significant differences in size were observed between fishing gears nor for the interaction between regions and fishing gears (Table 2). However, significant size differences were found among regions, with turtles caught in southern Italy being significantly smaller than turtles caught in eastern mainland Spain and southern Balearic Islands (Fig. 3), as assessed by a post hoc Tukey's test ($P = 0.031$ and $P < 0.01$, respectively).

Stable isotope characterisation of loggerhead turtle bycatch

Sampling year did not affect the values of $\delta^{13}\text{C}$, which did not differ among fishing gears or regions (Table 2; Fig. 4). Likewise, sampling year did not affect the $\delta^{15}\text{N}$ values, which were significantly different among regions, but not between fishing gears (Table 2). The post hoc Tukey's test revealed much lower $\delta^{15}\text{N}$ values for the turtles caught in the central Mediterranean (SIT) than for those captured in the western Mediterranean, but no differences between eastern mainland Spain and southern Balearic Islands (Fig. 4). Nevertheless, there was a significant interaction term because in southern Italy turtles caught with drifting longlines were more enriched in ^{15}N than turtles caught

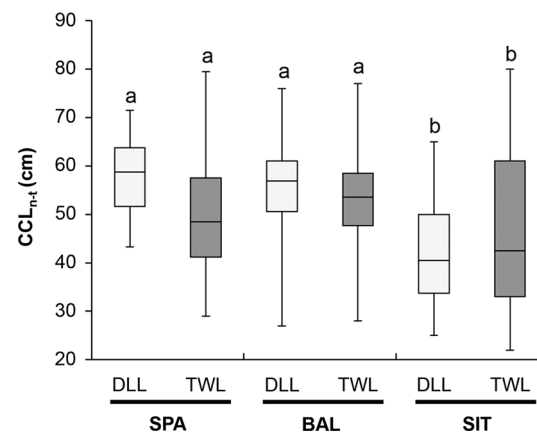


Fig. 3 Size ranges (CCL_{n-t}) of loggerhead turtles incidentally caught in the studied regions by drifting longlines (DLL, light grey) and trawling/trammel nets (TWL, dark grey). Bars labelled with the same letter do not differ significantly according to Tukey's post hoc test

with bottom trawls/trammel nets, whereas the opposite was true for eastern mainland Spain and southern Balearic Islands. No correlation was found between the size of an individual and its $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in any of the three studied regions analysed (Pearson's correlations, all $P > 0.05$).

Discussion

The complex dispersal patterns of many marine predators sometimes hinder the understanding of the broad significance of high levels of bycatch in small geographic areas. The western Mediterranean has supported some of the highest sea turtle bycatch levels worldwide since the 1980s (Lewison et al. 2004; Wallace et al. 2013), and its potential significance for sea turtle conservation is much larger than suggested simply by its geographic extension, as loggerhead turtles from two different regional management units are regularly bycaught there (Laurent et al. 1998; Carreras

Table 2 Effect of region and fishing gear on size, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of captured juvenile turtles in the western and central Mediterranean

	<i>df</i>	Size		<i>df</i>	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Covariate (year)	1	0.13	0.723	1	0.12	0.820	0.43	0.574
Region	2	8.56	<0.001	2	0.24	0.646	12.69	<0.001
Fishing gear	1	1.35	0.248	1	0.54	0.347	0.13	0.724
Region \times gear	2	2.26	0.108	2	0.36	0.639	5.24	<0.001
Error	154			154				

Bold typing denotes statistical significance

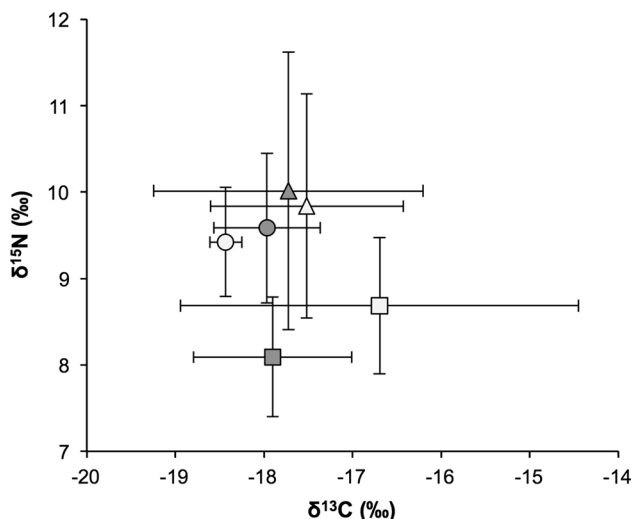


Fig. 4 Stable isotope composition of juvenile loggerhead turtles from the regions analysed. Samples pooled by fishing gear (light grey: drifting longline; dark grey: trawling/trammel net) and region (triangles: eastern mainland Spain; circles: southern Balearic Islands; squares: southern Italy). Sample size is 11 turtles for each category

et al. 2006, 2011; Clusa et al. 2014). The same might be true for other marine predators with complex, non-univocal migratory connections between nesting and foraging grounds (e.g. Gómez-Díaz and González-Solís 2007; Valenzuela et al. 2009; Sequeira et al. 2013).

Our results revealed no significant differences in size, stable isotopic ratios or origin of the juvenile loggerhead turtles caught with drifting longlines and bottom trawling/trammel nets within any of the three regions considered, although differences existed among regions. This indicates that vulnerability to fishing gear does not differ between turtles of Atlantic and Mediterranean origin inhabiting any given region. Accordingly, all the fisheries that incidentally catch juvenile sea turtles in the Mediterranean Sea (Casale 2011) may potentially impact both the Northwest Atlantic and Mediterranean management units. Thus, the actual impact on each management unit will depend on the total number of turtles taken and the geographic distribution of the catch within the Mediterranean, but not on the

composition of the fleets involved. This is because of the heterogeneous composition of loggerhead turtle stocks within the Mediterranean Sea (Carreras et al. 2006, 2011; Maffucci et al. 2006; Clusa et al. 2014). Thus, the differences in the genetic characterisation of longline and trawling bycatch previously reported by Laurent et al. (1998) might have emerged because fishing gears were regionally nested, and hence, the gear and region factors were confounded.

The absence of differences in the size and stable isotope ratios of loggerhead turtles caught by drifting longlines and neritic gears off southern Balearic Islands and eastern mainland Spain revealed that turtles behave similarly in each area regardless of their natal origin. These results strongly corroborate previous satellite telemetry data that suggested that juvenile turtles inhabiting the southern Balearic Islands spend most of the time in oceanic waters and only occasionally visit the continental shelf (Cardona et al. 2005; Revelles et al. 2007b). Similarly, in southern Italy, tracked small and large juvenile turtles regularly moved between oceanic and neritic habitats (Bentivegna 2002). On the other hand, significant differences were found among areas for $\delta^{15}\text{N}$ values. The lower values observed off southern Italy are consistent with the eastward pattern of particulate organic matter within the Mediterranean Sea (Pantoja et al. 2002), and the results found in three regions fit within the values found for other marine vertebrates of the Mediterranean Sea (Pinnegar and Polunin 2000; Navarro et al. 2011). The eastward pattern found, combined with the turnover rate of stable isotopes in muscle (Reich et al. 2008), is congruent with a limited exchange of turtles between adjoining basins on a monthly scale, previously suggested by tagging (Revelles et al. 2008) and satellite telemetry (Bentivegna 2002; Cardona et al. 2005; Revelles et al. 2007b). The Algerian basin has been described as a hot spot for Atlantic juveniles, with a decreasing relative abundance of turtles of Atlantic origin from the Strait of Gibraltar to the Adriatic Sea (Carreras et al. 2006; Maffucci et al. 2006; Clusa et al. 2014). The presence of turtles of Atlantic origin in the western Mediterranean would also explain the individual size differences found among areas. Turtles bycaught in eastern mainland Spain and southern Balearic Islands are

significantly larger than those from southern Italy probably because turtles of Atlantic origin are forced to stay in the area and grow until they are large enough to overcome the currents in the Alboran Sea and the Strait of Gibraltar to settle in the western Atlantic (Bowen et al. 2005; Revelles et al. 2007a).

Relatively lower proportions of turtles assigned to Mediterranean nesting areas were found in the sample sets of eastern mainland Spain and southern Italy in comparison with the proportion expected by mixed stock analyses. Former mixed stock analyses from the same area estimated a presence of 80–90 % of turtles of Mediterranean origin (Carreras et al. 2006) against the 50 % found through individual assignment (Carreras et al. 2011; present work). This is likely a consequence of the high proportion of unassigned individuals in both regions and the lower probability of assignment of turtles of Mediterranean origin as compared to those of Atlantic origin. Haplotype CC-A1.1 is the most frequent haplotype in Atlantic rookeries and is also exclusively from that area (Shamblin et al. 2014). Conversely, haplotype CC-A2.1 might be the most common in Mediterranean rookeries (Clusa et al. 2013), but is also shared with Atlantic rookeries. Thus, the power of assignment is higher on foraging grounds with a high proportion of turtles carrying CC-A1.1 than for foraging grounds with a high proportion of turtles carrying CC-A2.1 (the most abundant haplotype in eastern mainland Spain and southern Italy). As a consequence, a higher proportion of unassigned individuals are expected when turtles of Mediterranean origin are common as most Mediterranean individuals carry shared haplotypes. This hypothesis is supported by the congruence found between direct assignment and mixed stock analysis on the proportion of turtles of Atlantic origin (Clusa et al. 2014).

Genetic tools have been previously used to track the origin of specific individuals to certain populations for management and conservation purposes of multiple species (Manel et al. 2005; Schwartz et al. 2007; Benestan et al. 2015). However, the results here presented highlight the need to use multiple markers not only in loggerhead turtle research, but also in all megafauna studies in general. In the case of the loggerhead turtle, the majority of previous studies that analysed short mtDNA haplotypes found inconclusive results due to lower resolution capacity and high numbers of shared haplotypes between different rookeries (Maffucci et al. 2006, Carreras et al. 2007, Casale et al. 2008, Saied et al. 2012). Thus, by using a combination of mtDNA and nuclear markers, there has been a remarkable increase in the power of individual assignment in this study. Even if the use of microsatellite markers in sea turtle research has been slowly increasing during this decade (Carreras et al. 2007, 2011; Monzón-Argüello et al. 2008; Dutton et al. 2013; Garofalo et al. 2013, Naro-Maciél

et al. 2014), there is still an over-dominance of studies that only focus on mtDNA analyses. Accordingly, the re-analysis of turtles from certain areas with primers that amplify for longer fragments, together with the use of multiple microsatellite markers, would be highly recommendable. This would help increase the resolution of genetic differentiation not only among rookeries, but also among foraging grounds. Only by having a complete knowledge on the genetic structuring of nesting areas will individual assignments to natal origin be successful.

Implications for future conservation

The heterogeneous presence of individuals of Atlantic and Mediterranean origin in Mediterranean bycatch, as found in the present study, highlights that bycatch impact will strongly depend on turtle distribution, spatio-temporal overlap with fishing activities and mortality associated with each fishing gear. Casale (2011) estimated that over 132,000 sea turtles are caught every year in the Mediterranean Sea, of which 44,000 (the majority loggerhead turtles) are killed due to fatal interactions with fisheries. However, post-release mortality has been assessed for drifting longlines only recently (Álvarez de Quevedo et al. 2013), and nothing is known about other fishing gears.

Drifting longlines have been defined as the most threatening of all fishing gears for juvenile loggerhead turtles in the Mediterranean Sea (Deflorio et al. 2005), mainly impacting areas of Spain, Morocco, Tunisia, Italy, Greece and Libya (Jribi et al. 2008; Casale 2011). The estimated bycatch rate is of approximately 70,000 turtles caught per year (Casale 2011), and the mortality rate is approximately 35 % (Álvarez de Quevedo et al. 2013). However, that figure is probably not up to date, as the total number of turtles bycaught annually by the Spanish fleet has decreased from some 20,000 in the early 1990s to 6000 in 2006–2007 (Álvarez de Quevedo et al. 2014; Báez et al. 2014) and less than 1000 in recent years (Báez, personal communication). No recent figures exist for the rest of the Mediterranean to our knowledge. In any case, the Spanish fleet used to be the one with the highest rate of loggerhead longline bycatch (Casale 2011), and the current study reveals that Spain longliners might capture mainly turtles of Atlantic origin, thus potentially impacting primarily on the populations nesting in south Florida. Conversely, the Italian fleet might capture a larger proportion of turtles of Mediterranean origin, as this fleet operates primarily in the Ionian Sea (Deflorio et al. 2005; Casale 2011) where the prevalence of turtles of Mediterranean origin is higher (Clusa et al. 2014).

On another front, countries involved in trawling activities are Spain, Italy, Tunisia, Croatia, Greece, Turkey, Egypt and Libya (Lazar and Tvrtkovic 1995; Oruç 2001; Álvarez de Quevedo et al. 2010; Casale 2011; Domènech

et al. 2014) with a particular presence in the northern Adriatic Sea (Lazar and Tvrtkovic 1995; Casale et al. 2004). Even if bycatch derived from trawling activities has been considered less of a threat than that coming from longlines because of its lower bycatch rates in the Mediterranean Sea (39,000 captures per year; Casale 2011), it should not be ignored. According to Wallace et al. (2013), on a global scale mortality rates associated with trawling (0.26 ± 0.29) and set nets (0.32 ± 0.3) are significantly higher than in longlines (0.07 ± 0.19), although rates vary depending on fishing depth (from 0.01 ± 0.01 in surface/drift longlines to 0.54 ± 0.32 in bottom set nets), and little is known about post-release mortality rates (Álvarez de Quevedo et al. 2013; García-Párraga et al. 2014). Accordingly, fishery interactions can represent a significant threat for sea turtle populations (Lewison et al. 2004; Lewison and Crowder 2007), and there is a growing need to understand the effects of bycatch on wild populations. However, this can become a difficult subject as reliable data on fishing effort and bycatch quantification in some areas are irregular or scarce.

In the current study, even if the analysed fishing gears caught turtles of both Atlantic and Mediterranean origin, we can conclude that the impact that fisheries may have on wild populations will differ depending on the foraging grounds used by each of these populations, even if the analysed gears caught turtles of both Atlantic and Mediterranean origin. This is shown by the lack of differentiation between turtles caught with drifting longlines and trawl/trammel nets within each region but the existence of composition differentiation among regions. Accordingly, the type of fishing gear used in each region determines the mortality rate of the caught turtles and the susceptibility of being caught, but does not determine the origin of its individuals.

With hatchlings and juvenile turtles using foraging grounds located in faraway areas from their rookeries, insufficiency of focusing all the conservation measures in nesting beaches comes to light. Further research should focus on determining the composition of each foraging ground, as proper identification of the affected populations is essential. Thus, the use of multiple intrinsic and genetic marker characterisation of bycatch should be implemented in new conservation plans as populations with distinct origins and conservation statuses may share the same foraging grounds.

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