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REVIEWS

Distribution, ecology, and status of the white shark, *Carcharodon carcharias,* in the Mediterranean Sea

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Abstract The occurrence of the white shark, *Carcharodon carcharias*, in the Mediterranean Sea has been reported since the Middle Ages (476–1453). Several studies have documented its presence in various areas of the basin, but no comprehensive review of the distribution and status of this species is available for the area. We compiled a total of 628 white shark records from 476 to 2015. Data suggests that the white shark is more common in the western Mediterranean Sea, especially in the Adriatic Sea and in the Sicilian Channel and is more frequently observed during summer months. However, analysis using night-time satellite imagery showed the existence of an anthropogenic bias in the distribution of white sharks. All size classes have been recorded in the region. However, the highest occurrence of young of the year has been recorded in the Sicilian Channel, in the Adriatic Sea and in the Aegean Sea, in summer, suggesting these areas might serve as nursery grounds. In the Mediterranean Sea, the white shark exhibits a broad diet. The most common prey found include small cetaceans (*Tursiops truncatus*, *Stenella coeruleoalba*), tuna (*Thunnus* spp.), swordfish (*Xiphias gladius*) and loggerhead sea turtle (*Caretta caretta*). A total of 53 white shark records refer to interactions between sharks and humans that resulted in a detrimental impact on humans, which include 42 bites and 11 reports of the presence of human remains in the stomach of captured animals. Analysis of the temporal variation in mean total lengths of white sharks found a decreasing trend from 1913 to 2012. The decreasing length of white sharks suggests this species might be declining in the Mediterranean Sea.

Keywords Spatio-temporal distribution · Nursery grounds · Size distribution · Human interactions · Feeding ecology

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Introduction

The white shark, *Carcharodon carcharias* (Linnaeus, 1758), occurs worldwide from temperate to tropical waters of all oceans and in enclosed seas such as the Mediterranean Sea (Compagno 1984, 2002). However, its distribution appears to be discontinuous and major aggregations tend to occur in the vicinity of highly productive habitats with high marine mammal abundance (particularly pinnipeds) (Compagno 1984). Major white shark aggregations have been documented in central California (Ainley et al. 1985; Klimley 1985; Klimley et al. 1992; Long 1994), the shelf waters of the mid-Atlantic bight (Casey and Pratt 1985), the south and west coast of Australia (McCosker 1987; Bruce 1992; Strong et al. 1992), in New Zealand (Duffy et al. 2012; Francis et al. 2015) and South Africa (Cliff et al. 1989; Ferreira and Ferreira 1996), especially in the Western Cape province (Martin et al. 2005, 2009; Kock et al. 2013). White sharks have only been studied in regions of highest abundance resulting in limited knowledge of their movements, ecology and biology in areas with lower densities (Fergusson 1996).

White sharks have been documented in several areas of the Mediterranean Sea since the Middle Ages (476–1453) (De Maddalena and Heim 2012). They have been recorded from all coasts of the western basin, with frequent captures and sightings off the Balearic Islands, the Gulf of Lions (France) and in the Tyrrhenian Sea (Fergusson 1996; Mojetta et al. 1997; Barrull and Mate 2001; Morey et al. 2003; Storai et al. 2005; De Maddalena and Zuffa 2008; De Maddalena and Heim 2012) (Fig. 1). Sightings have also been reported in the Sicilian Channel, off Tunisia and Malta (Fergusson 1996, 2002; Storai et al. 2000; Saidi et al. 2005) (Fig. 1). The Sicilian Channel has been hypothesized to be a nursery ground for this species (Fergusson 1996). Frequent captures and sightings have been documented in the Adriatic Sea since the early nineteenth century (Fergusson 1996; Mojetta et al. 1997; De Maddalena 2000; Soldo and Jardas 2002; Soldo and Dulcic 2005). In the eastern Mediterranean, white sharks have been recorded in Libya (Galaz and De Maddalena 2004), in the Marmara and Aegean Sea, as well as in the Bosphorus Strait (Kabasakal 2003, 2008, 2011, 2014; Kabasakal and Gedikoglu 2008; Kabasakal et al. 2009) (Fig. 1).

The white shark in the Mediterranean Sea has been considered an "occasional transient" from Atlantic waters, however the sighting reports suggest this species may be more common than previously thought (Fergusson 1996; Mojetta et al. 1997; Storai et al. 2000; Soldo and Jardas 2002). Several authors (Fergusson 1996; Storai et al. 2000) have also speculated on the existence of a Mediterranean population of white sharks separated from the Atlantic one. This hypothesis is consistent with analysis of the mitochondrial DNA control region of Mediterranean white sharks that showed little genetic differentiation from Indo-Pacific lineages, but strong separation from geographically closer Atlantic haplotypes, which dismisses a regular interchange between the Mediterranean Sea and the Atlantic Ocean (Gubili et al. 2010).

The white shark is listed under Appendix II of the Convention on International Trade in Endangered Species (CITES), and as globally Vulnerable on the International Union for Conservation of Nature (IUCN) Red List since 2000 (Cavanagh and Gibson 2007). However, the species is particularly Threatened in the Mediterranean Sea where, in the past, was targeted for sportfishing, commercial trophy hunting or captured for human consumption, and has therefore been classified as Critically Endangered by IUCN Red List in this region (Fergusson et al. 2005; Malak 2011; Soldo et al. 2016). Declines in shark populations have already been observed in the early twentieth century in the northwestern Mediterranean Sea due to direct exploitation and bycatch, whereas in the second half of the century the decrease was mainly due to the expansion of pelagic fisheries, particularly longlining, resulting in increasing number of incidental captures (Megalofonou et al. 2005; Tudela et al. 2005; Ferretti et al. 2008). In the Mediterranean, 42% of shark species are threatened compared to a global average of 17% (Cavanagh and Gibson 2007).

The white shark has the tendency to approach boats and to scavenge from fishing gear, increasing its vulnerability to capture (Fergusson et al. 2005). In addition to bycatch, white sharks are popular animals resulting in high market value of teeth, jaws, and fins which may pose an additonal threat to the species, even where protected (Compagno 2002; IUCN 2004; CITES 2004; Shivji et al. 2005). Another major concern for this species is habitat degradation (Cavanagh and Gibson 2007). This is especially acute in the Mediterranean, which has been inhabited by humans for millennia and has become one of the most sought after tourist destinations in the world (Lotze et al. 2006). Increased human population in this region has increased overlap with the white shark's range (Cavanagh and Gibson 2007). Additionally, high fishing pressure has caused a reduction of important prey, such as bluefin tuna *Thunnus thynnus* and other small cetaceans (Morey et al. 2003; Soldo and Dulcic

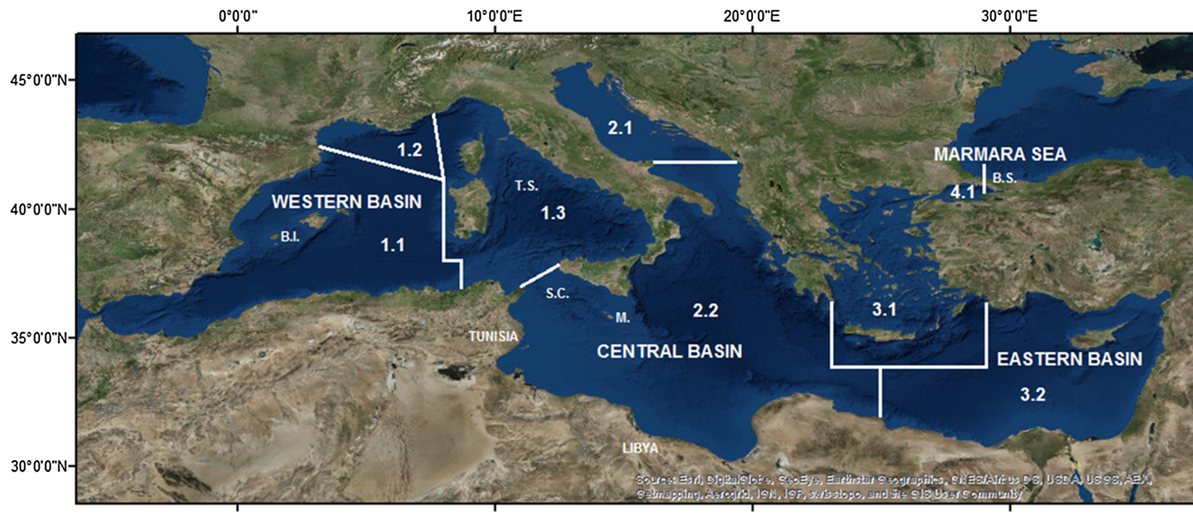

Fig. 1 Different basins and sub-areas of the Mediterranean Sea. *1.1* Balearic Sea (Division 37.1.1); *1.2* Gulf of Lions (Division 37.1.2); *1.3* Sardinia (Division 37.1.3); *2.1* Adriatic (Division 37.2.1); *2.2* Ionian (Division 37.2.2); *3.1* Aegean (Division 37.3.1); *3.2* Levant (Division 37.3.2); *4.1* Marmara Sea (Division 37.4.1). *B.I.* Balearic Islands, *T.S.* Tyrrhenian Sea, *S.C.* Sicilian Channel, *M.* Malta, *B.S.* Bosphorus Strait. Modified from FAO (http://www.fao.org/fishery/area/Area37/en)

2005), which may impact the white shark population (Cavanagh and Gibson 2007). Twenty-two nations share the Mediterranean coastline which makes conservation actions challenging by the inherent socio-political complexity of this region and the high diversity of jurisdictions (De Juan et al. 2012; Micheli et al. 2013b). In addition, conservation management of the white shark (and other elasmobranchs) in the basin is challenging as this species is rare, wide-ranging and diffusely distributed, with little known about seasonal movement patterns or key elements of its natural history (Fergusson 1996, 2002).

So far, most white shark data in the Mediterranean Sea have come from opportunistic records, including reports from the media, fishermen, and the general public (McPherson and Myers 2009; De Maddalena and Heim 2012). Opportunistic reports, despite having a number of caveats, provide a wide range of information. Nevertheless, when systematic surveys cannot be undertaken, long-term opportunistic data can provide valuable baseline information on the distribution and relative abundance of large and charismatic species such as large sharks (Case et al. 2007; McPherson and Myers 2009). This study provides a review of the existing literature and new records on the occurrence, distribution, and status of the white shark in the Mediterranean Sea. In addition to the most recent comprehensive study by De Maddalena and Heim (2012), in which the authors reported all available information, but without conducting any further investigation, this research aims to take one step further into the ecology of this species providing analysis of new sightings and captures.More specifically, this paper reviews (1) the spatial and seasonal distribution of white sharks in the Mediterranean, (2) patterns of intra-species segregation, particularly related to sex and size (including potential nursery areas), (3) feeding ecology and (4) human interactions.

Materials and methods

Study area

The Mediterranean Sea is the largest (2,969,000 km^2) and deepest (mean depth: 1460 m, maximum: 5267 m) enclosed sea in the world. It is surrounded by three continents: Africa (south), Europe (north), and Asia (east) and bordered by 22 countries. The Mediterranean is connected to the Atlantic through the Strait of Gibraltar in the west, to the Black Sea and the Sea of Marmara (Turkey) by the strait of Dardanelles in the northeast. In the southeast, the Suez Canal links the Mediterranean to the Red Sea. While the Mediterranean Sea accounts for <1% of the total water surface area of the planet, fish biodiversity is relatively high (about 6% global fish biodiversity, Fredj et al. 1992), including 84 cartilaginous fish species (Fredj et al. 1992; Serena 2005; Bradai et al. 2012).

In the present study, the Mediterranean Sea has been subdivided in the following sub-areas according to FAO's classification: Western basin which includes the Balearic, Gulf of Lions and Sardinia sub-areas; Central basin which comprises the Adriatic and Ionian sub-areas; and the Eastern basin which includes the Aegean and Levant regions (Fig. 1). For the Black Sea only the Marmara Sea sub-area was taken into consideration for this study.

Data sources and collection

Data on white sharks were collected from: (a) books and scientific papers published in peer-reviewed scientific journals, (b) newspaper articles, some of which have been grouped by authors in the past years, (c) local news websites and online portals including YouTube (www.youtube.com), and (d) unpublished records provided by researchers working in the Mediterranean Sea. For the data search, recreational fishing forums were also used in order to identify possible missing sources of information. From each source, the following information was collected: type of record (capture, sighting, stranding, or indirect record such as wounds observed on possible prey species, especially marine mammals and sea turtles), date and location of records and associated physiographical covariates (distance from shore, depth), total length (TL) in cm, weight (W) in kg, sex, stomach content (if available), presence of embryos, and in case of captures, information on gear involved was also recorded. To investigate the white shark reproduction in the Mediterranean Sea, information of pregnant females, embryos and neonates have been also collected. After compiling all records, a capture/sighting database was constructed (Online Resource 1).

Age distribution of white sharks was assessed using four length categories established and defined in Bruce and Bradford (2012), and modified following Fergusson (1996): young of the year (YOY) ($\leq$1.75 m total length, TL), juvenile (>1.75–3.0 m TL), subadult (>3.0–3.6 m TL for males and >3.0–4.5 m TL for females) and adult (>3.6 m TL for males and >4.5 m TL for females). Females were considered as adults at >4.5 m TL which agrees with values by Francis (1996) and the previous adult category classification parameters used in the Mediterranean Sea by Fergusson (1996) and Morey et al. (2003). Furthermore, following Fergusson (2002), when sex was not recorded, a threshold of maturity was set at >4.5 m which would include most adult females and mature males.

Records of white sharks were plotted using ArcGIS 10.2 (ESRI Inc. 2008; Redlands, California, USA). If a sighting did not include a GPS position, when possible, approximated geographical coordinates were identified using the geographic references provided by the record. Records that provided only generic spatial reference were rejected.

Remote sensing data, especially from night-time satellite imagery showing artificial light distributions can be used to identify urban centres, and characterize human population distribution and density (Elvidge et al. 1997; Sutton et al. 1997; Briggs et al. 2007). For this study night-time satellite imagery was obtained from Nasa Visible Earth. These maps were used to identify areas of dense human population that may result in a sighting bias (higher occurrence of sharks in more densely populated areas). Urban centres with a light profile of a 90 km^2 or greater (representing a large urban area approximately the size of the center of Genoa with a population of about 600,000 people) and metropolis of 455 km^2 (such as Rome with over two million people) were identified using ArcGIS 10.2. For each white shark position recorded, the shortest distances to the nearest urban centres and to the nearest metropolis was measured in kilometres to investigate this possible bias. By using a threshold light area cut-off, we could eliminate small towns that would result in great overlap and would not provide much insight into the survey. The frequency of occurrence was plotted as a function of the distance from the shark to the closest urban centre. Records of white sharks were plotted over a raster image showing cumulative fishing impact of the Mediterranean Sea, with the picture modified from Micheli et al. (2013a) (Fig. 2).

Data reliability and analysis

White shark data from the Mediterranean was compiled resulting in a total of 628 records, 615 were collected from peer-reviewed journals (n = 450) and books (e.g. Klimley and Ainley 1996; De Maddalena

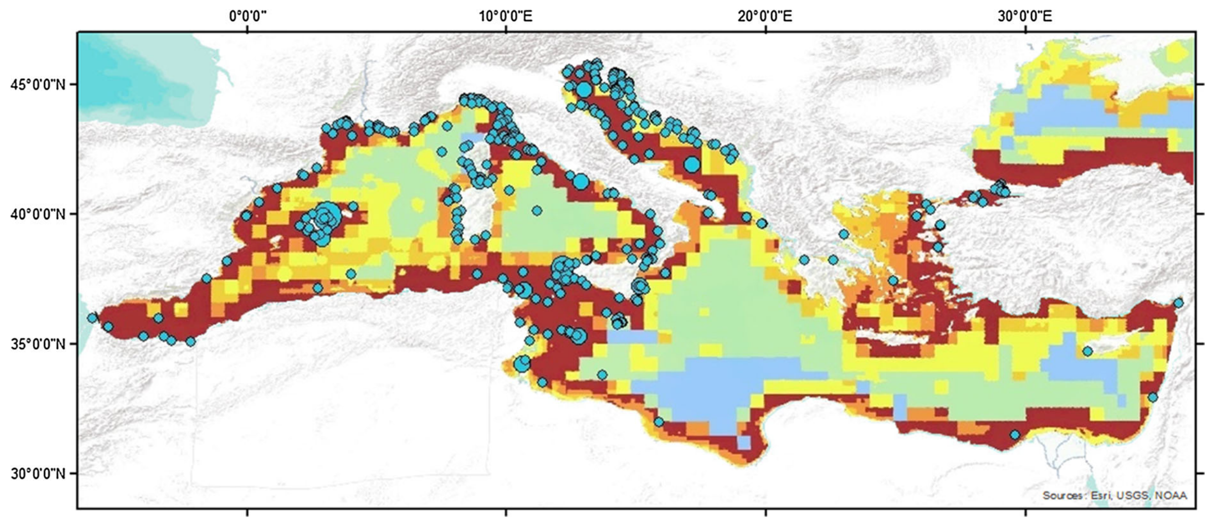

Fig. 2 Spatial distribution of white sharks (*circles*, n = 618) plotted over an image of the Mediterranean Sea showing cumulative fishing impact (artisanal, pelagic and demersal fisheries combined). Darker tones correspond to highest impact in compare to those lighter. Image modified from Micheli et al. (2013a)

and Heim 2012; n = 165), 5 from local newspapers, 5 through the Internet, 2 personal communications (Biaggi and Fozzi per com) and 1 unpublished record gathered from local research scientists. The majority of the primary reports include historical, anedoctal, and opportunistic testimonies. However, 98% (n = 615) of reported data have been published or cited in peer-reviewed scientific journals and therefore were considered as reliable to be included in this review.

White shark records were analysed for spatial and temporal distribution, investigated by shark size classes across the Mediterranean Sea to find any spatial patterns in the size of sharks between sub-areas of the Mediterranean, as well as any influence of season on the size distribution of sharks using using Wilcoxon and Steel–Dwass tests. A Welch Anova test was used to assess the influence of gear type of the size structure of shark caught. White shark records were binned in 25 year increments to assess the long term trends in mean shark length during the last 150 years. After ensuring that the assumptions for parametric tests were not violated, a one-way ANOVA was used to investigate the temporal patterns of shark length from 1863 to 2012. To examine the possible impact of increased fishing pressure in the Mediterranean during the last 100 years, a second analysis using 8 year bins was used. The narrower bins were created to more precisely identify any possible differences in mean length of white sharks from 1901 to 2012. A one way ANOVA was used to investigate a temporal change in mean length of white sharks for each survey zone and a Chi square test for Independence to identify any differences in the proportion of females and males between sub-areas.To investigate the white shark feeding ecology in the Mediterranean Sea, information on stomach contents were also collected (Online Resource 1).

Results

Spatial distribution

628 records of *C. carcharias* were collected for this study (Online Resource 1). Data ranged from the Middle Ages (476–1453) to 2015. The majority of records originated from Italy (44.7%), Croatia (13.2%), and Spain (10%) (see Online Resource 2; Table 1).

Of 618 records with geographical references, 331 occurred in the western, 236 in the central, 25 in the eastern part of the Mediterranean Sea and 26 in the Marmara Sea. In the western Mediterranean, the highest number of white shark reports originated from Sardinia sub-area (215 records, 34.8%), the Balearic Islands (71 records, 11.5%) and the Gulf of Lions (45 records, 7.3%), France. The central Mediterranean accounted for 236 records, including the Adriatic Sea

(139 records, 22.5%) and the Ionian Sea (97 records, 15.7%). The eastern Mediterranean Sea accounted for only 25 records, of which 21 (3.4%) from the Aegean Sea and 4 from the Levant Sea (0.6%). The Marmara Sea accounted for 26 records (4.2%) (see Online Resource 2; Table 2).

232 records with a defined geographical reference were used to account for any possible bias in shark distribution. Using a threshold of 455 km^2, the nearest distance from a shark to an urban centre was 10 meters, while the maximum recorded was 777 km. The frequency of occurrence plotted as a function of the distance from the shark to the closest urban centre showed a slightly skewed distribution to the right (skew = 0.67; mean = 199 km ± 133; median = 188 km; mode = 226 km) when considering urban areas >455 km^2. A potential reporting bias in relation to distance from an urban centre was more evident when the threshold was set to 90 km^2 (Fig. 3). The frequency histogram showed a stronger positive skewed trend (skewness = 1.3; mean = 80.7 km ± 75.9; median = 62 km; mode = 5 km).

Length distribution

A total of 403 records contained information on shark length. White shark length ranged from 80 to 100 cm (YOY) to an estimated 675 cm adult (this is likely exaggerated as this is longer than the scientifically accepted maximum size of the white shark). White sharks of all sizes occurred in the Mediterranean Sea. Adults have been recorded in all survey zones, but were mainly recorded in Sardinia sub-area and the Adriatic area. The distribution of subadults was similar to the adults, but they were also frequently found in the Ionian Sea, and have not been recorded in the Aegean Sea. Juveniles have been recorded in all regions except in the Marmara Sea, but were most prominent in Sardinia sub-area and in the Adriatic Sea. YOY were most frequently recorded in Adriatic and Ionian Sea and were not recorded in the Marmara Sea, Levant or in the Gulf of Lions (Fig. 4).

Significant spatial variations of the size structure of white sharks recorded in the Mediterranean Sea were found (W = 20.1, $p = 0.005$), in particular the Steel–Dwass All Pair test showed a statistical difference ($p = 0.0088$) in the mean length of sharks recorded in the Balearic which were significantly larger ($\bar{x} = 498.4$ cm ± 71.7) than those recorded in the Ionian ($\bar{x} = 387.6$ cm ± 151.9).

Gender and life history patterns

Gender was documented for 136 specimens (Online Resource 1). A total of 91 females and 45 males was recorded (see Online Resource 2; Table 3). 125 of these records provided reliable length data. Female length ranged from 85 to 653 cm ($\bar{x} = 456$ cm ± 142.7), while males ranged from 126 to 620 cm ($\bar{x} = 387$ cm ± 150.4) (Fig. 5). No spatial variations of the gender distribution of white sharks was found between sub-areas of the Mediterranean Sea ($\chi^2 = 12.51$, $df = 7$, $p > 0.05$).

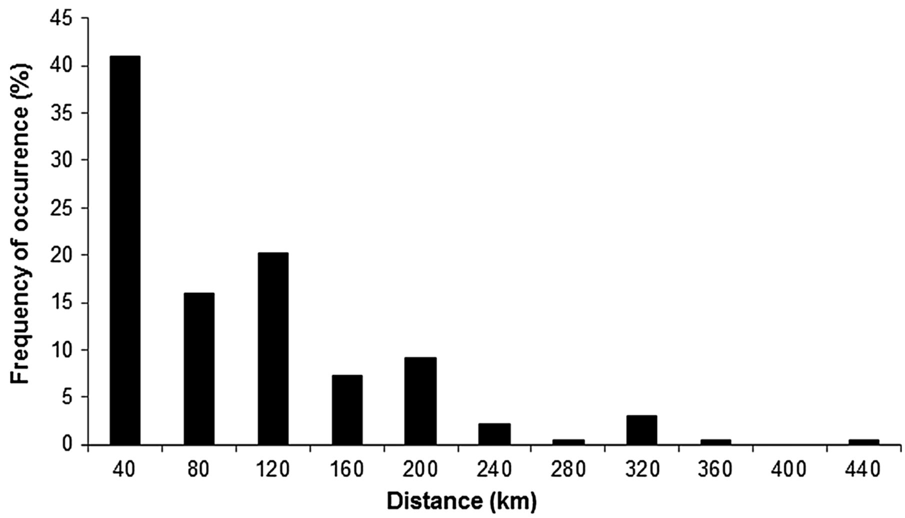

Fig. 3 Frequency distribution of distances (km) measured from each shark position to the closest urban centre. Threshold area of 90 km^2. Data ranged from 1900 to 2012 (n = 232)

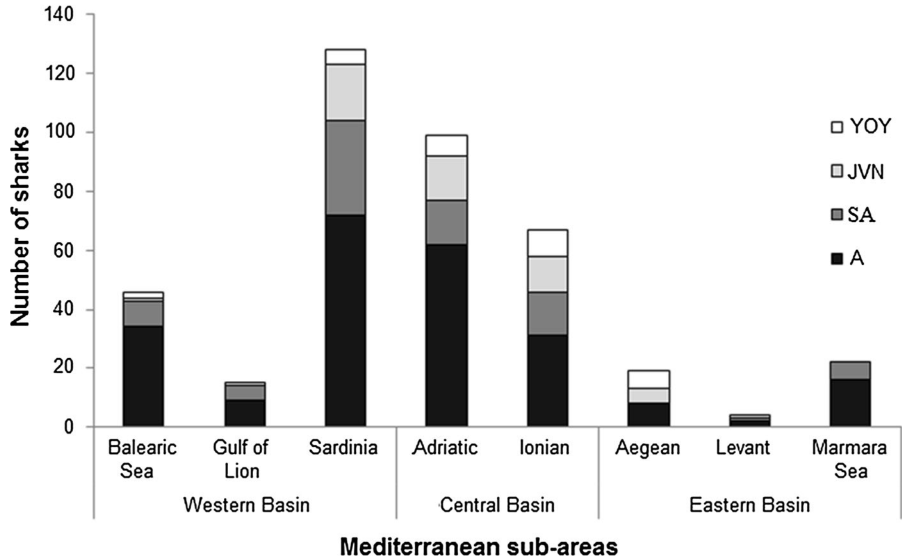

Fig. 4 Distribution of white sharks by age class for each basin from 1721 to 2015 (n = 400)

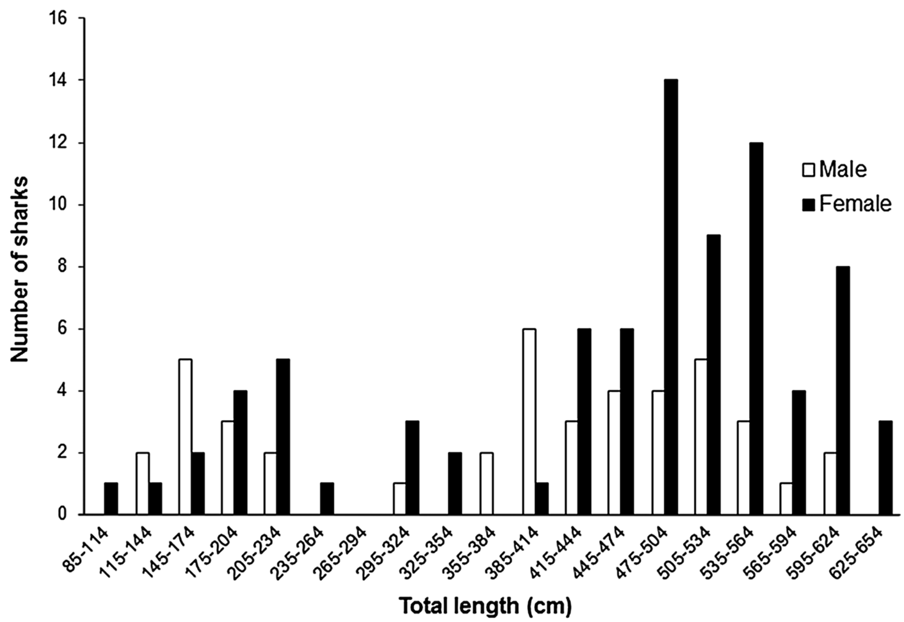

Fig. 5 The length-frequency distribution of white sharks in the Mediterranean Sea according to gender (n = 125)

Temporal trends

A total of 408 records included the date of sighting and/or capture. The majority of sharks were observed during spring (April–June, 31.9%) and summer (July–September, 35.5%), with a peak in May (13%) and August (16.4%), respectively. White shark records decreased during fall (October–December, 14.7%) and winter (January-March, 17.9%, Fig. 6).

A significant influence of season on white shark size distribution was found (W = 12.8, $p = 0.005$). The average length of sharks was larger during colder (fall $\bar{x} = 484.2$ cm ± 121.7; winter $\bar{x} = 466.8$ cm ± 131.5) than warmer months (spring $\bar{x} = 414.1$ cm ± 143.1; summer x = 411.2 cm ± 158). The post hoc Steel–Dwass All Pair test revealed a statistical difference between fall and spring ($p = 0.032$). In the Adriatic Sea, shark length was larger during summer ($\bar{x} = 500.6$ cm ± 117.1) than winter ($\bar{x} =$

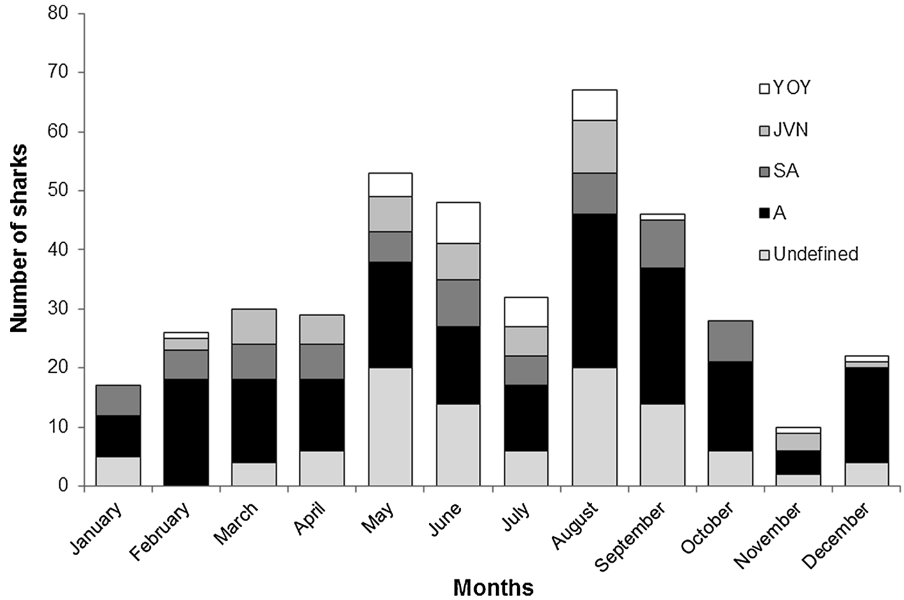

Fig. 6 Monthly distribution of white sharks by age class in the Mediterranean Sea from 1666 to 2015 (n = 408)

362.3 cm ± 175) and spring ($\bar{x}$ = 371.6 cm ± 151.1, ANOVA, $F_{3,77} = 5.3$, $p = 0.0023$). In the Aegean Sea, shark length was significantly smaller during summer ($\bar{x}$ = 155.1 cm ± 136.3, ANOVA, $F_{2,12} = 6.25$, $p = 0.0138$). In the Ionian Sea, shark length was smaller during summer than spring ($\bar{x}$ = 316.6 cm ± 160.6, ANOVA, $F_{3,53} = 3.35$, $p = 0.0258$). In Sardinia shark length was significantly smaller in spring ($\bar{x}$ = 410.1 cm ± 154.6) and summer ($\bar{x}$ = 420.6 cm ± 122.8) than in winter ($\bar{x}$ = 550.1 cm ± 93.74, ANOVA, $F_{3,98} = 4.13$, $p = 0.008$). No significant difference was found in shark length between seasons in the Balearic Sea (ANOVA, $F_{2,27} = 0.78$; $p = 0.468$), in the Gulf of Lions (ANOVA, $F_{3,6} = 1.7$; $p = 0.27$) and in the Marmara Sea (ANOVA, $F_{2,10} = 0.86$; $p = 0.45$).

The sighting and capture locations, mapped as a function of seasons, did not visually show any evident seasonal movements (see Online Resource 3; Fig. 1).

Fisheries interaction

Of the 628 records collected, 351 records were from individuals captured in fishing gears. Of these, 70.1% provided length data (n = 246) (Online Resource 2; Table 4). No effect of gear type on size of sharks was found (Welch Anova test, $F_{6,19.15} = 1.81$, $p = 0.1512$), however, data might be insufficient to detect any variance in shark TL taken by different gears (Online Resource 2; Table 4).

Temporal trend in mean length of white sharks

Temporal variation in mean length of white sharks was assessed over a 150 year time period (1863–2012). A decreasing trend in mean lengths of white sharks over time was found (ANOVA, $F_{5,347} = 5.38$, $p < 0.0001$) (Fig. 7). Inside this time period (1863–2012), the mean length of shark records showed a negative trend from 1913. Post hoc Tukey's HSD test showed that the mean length of white sharks recorded over the last 25 years (1988–2012) ($\bar{x}$ = 405.9 cm ± 152.9) was significantly lower than the 1913–1962 block. In particular, it showed a significant difference in the mean length of the 1988–2012 block with the one of 1913–1937 ($p = 0.019$) and 1938–1962 ($p = 0.014$). Post hoc Tukey's HSD test showed also a significant difference in the mean length of the 1863–1887 block with the one of 1913–1937 ($p = 0.004$), 1938–1962 (0.003) and 1963–1987 ($p = 0.044$).

A second analysis utilizing 8 year bins was conducted (n = 294). Using ANOVA with Tukey's HSD the negative trend held with records 2005–2012 showed a statistically significant decrease in length when compared to records from 1933 to 1972 (ANOVA, $F_{13,281} = 3.20$, $p = 0.0002$). In particular, the test showed a significant difference between the mean length of the 2005–2012 block with that of 1933–1940 ($p = 0.001$), 1941–1948 (0.003), 1949–1956 ($p = 0.033$), 1957–1964 ($p = 0.0006$) and 1965–1972 ($p = 0.001$). Finally, the test found a

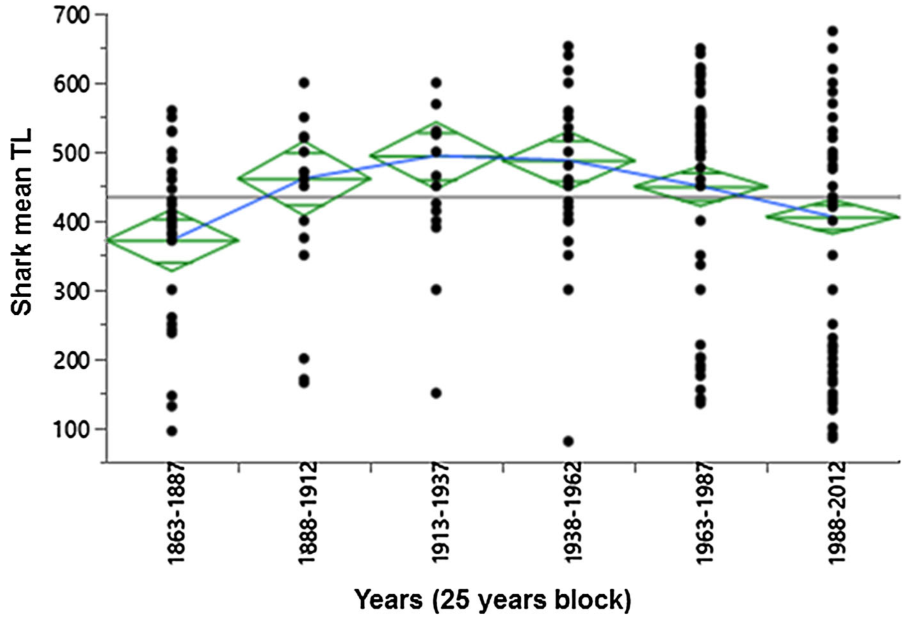

Fig. 7 Temporal variation in mean shark length from 1863 to 2012 (n = 353). The *Green Diamonds* are the mean diamond: The center *horizontal line* is drawn through the mean of each group proportional to its x-axis. The *top* and *bottom* points of the mean diamond show the upper and lower 95% confidence intervals for each group. The *Blue Line* connects the the group means to in this case show the trend in group means over time

significant difference in the mean length also between 1997–2004 and 2005–2012 ($p = 0.044$). The mean length for the 2005–2012 block was the lowest mean total length recorded for white sharks in the twentieth century ($\bar{x} = 317.4$ cm $\pm$ 152.8).

Finally, a temporal change in mean length of white sharks was investigated for each survey zone. In the Adriatic Sea, a significant increase (ANOVA, $F_{3,79} = 6.0$; $p = 0.001$) in the mean length was found between the end of nineteenth century and the beginning of the twentieth century. In Sardinia sub-area a significant decrease (ANOVA, $F_{2,108} = 3.96$; $p = 0.0219$) in the mean size of white sharks was found between the sharks caught in 1921–1966 and the ones in 1967–2012. No statistical differences were found for the Aegean Sea (ANOVA, $F_{2,14} = 1.26$; $p = 0.313$), the Gulf of Lions (ANOVA, $F_{2,11} = 2.62$; $p = 0.118$), Balearic (ANOVA, $F_{2,33} = 0.46$; $p = 0.6332$), Ionian (ANOVA, $F_{4,60} = 0.91$; $p = 0.465$) and Marmara (ANOVA, $F_{2,16} = 0.226$; $p = 0.801$) regions.

Reproduction

Four females were pregnant at the time of capture (Online Resource 1). One female was captured in 1934 near Alexandria (Egypt) during summer, measuring 425 cm and carrying 9 embryos measuring an average 61 cm length (Fergusson 1996). The second female was caught in 1981 in Sciacca (Italy) carrying 6 embryos measuring 40 cm length (De Maddalena and Heim 2012). The third female was captured in the north-western region of Cape Bon (Tunisia) in 1992, possibly in September. It was estimated to be more than 500 cm length and pregnant with 2 full-term embryos (Fergusson 1996). The fourth specimen was 587 cm length and its mass was estimated to be more than 2000 kg. The female was caught in the Gulf of Gabes (Tunisia) in February 2004 and was carrying 4 embryos, 1 male and 3 females, measuring respectively 134, 132, 133.5, and 135 length. The male weighted 30.40 kg, while the 3 females 27.65, 28.86 and 31.50 kg cm length (Saidi et al. 2005). Three of the 4 females were caught in the Sicilian Channel, 2 near the African coastline and 1 was caught on the Sicilian coast. The mean length of the pregnant sharks was 504 ± 81.1 cm. In order to identify possible nursery grounds, the distribution of YOYs was mapped (Online Resource 3; Fig. 2). They were recorded in Italy (n = 11, 37.9%), Croatia (n = 7, 24.1%), Turkey (n = 6, 20.7%), Tunisia (n = 3, 10.3%), Algeria (n = 1, 3.5%) and Spain (n = 1, 3.5%). Eight of the 11 YOYs recorded in Italy and all 3 Tunisian individuals were recorded in the Sicilian Channel. In Edremit Bay (Turkey), 4 small white sharks were recorded measuring approximately 80–100 cm length. The mean length of YOYs recorded was 151 ± 14.1 cm in the Sicilian Channel; 141 ± 25.4 cm in the Adriatic; 104 ± 24.9 cm in the Aegean; 150 cm in Balearic area and 110 ± 36.1 cm in Sardinia. Of the smaller total length records, 25 had a capture date. Most small animals were encountered during the warmer months, especially summer and spring (summer, n = 14; fall, n = 1; winter, n = 2; spring, n = 8).

As shown in Fig. 2 (Online Resource 3) the distribution of juveniles followed a pattern similar to the one of YOY, but as sharks increase their size, they featured a wider range.

Human interactions

A total of 53 white shark records referred to interactions between sharks and humans, where humans were negatively impacted or injured (Online Resource 1). Records included 42 bites, of which 23 were fatal, and 11 reports of the presence of human remains in the stomach of captured animals. Of the 42 bites, 14 involved swimmers, 6 referred to people who accidentally fell into the water, 7 to spearfishermen, 2 to scuba divers, 1 to a windsurfer, 1 to a surfer, and 1 to a kayaker. White shark interactions with humans were primarily during summer (n = 21) and fall (n = 5). They were rarer during winter (n = 4) and spring (n = 4).

New records

Ten new records (not previously reported in the scientific literature) have been recorded in the Mediterranean Sea since 1993 (Online Resource 2; Table 5). Five have been collected along the coast of Sardinia (Italy) from 1993 to 2011. Data included 2 sightings, 2 indirect records (wounds observed on a stranded *Stenella coeruleoalba* and teeth found on the seafloor), and 1 capture. Sharks were spotted in the northern and southern part of the island. Sharks ranged from 294–304 cm to approximately 400 cm length, the sex of these individuals was not recorded (see Online Resource 2; Table 5). The remaining five have been recorded in Tunisia (n = 2), Morocco (n = 1), Italy (n = 1) and France (n = 1) from 2012 to 2015 (Online Resource 2; Table 5).

Feeding ecology

We reviewed information on the diet of white sharks in the Mediterranean inferred from stomach content analyses from the Middle Ages (476–1453) to 2011 (Online Resource 1). Stomachs of 104 individuals (56 adults, 12 subadults, 2 juveniles, 2 YOY and 32 unknown) were examined and 103 stomachs contained prey items.

A total of 161 prey items were recorded (Table 1), including 73 (46%) mammal, 50 (31%) fish, 11 (7%) reptile, birds remains (2%), molluscs (1%) and inedible objects (13%). Mammal prey included both terrestrial (14%) and marine species (32%). Marine mammals included 51 prey items identified, including 50 cetaceans (primarily *Tursiops truncatus* and *Stenella coeruleoalba*) and 1 pinniped, the Mediterranean monk seal (*Monachus monachus*). Terrestrial mammals included several farm animals, pets and human remains (Table 1). Fishes comprise of 45 bony fish and 5 cartilaginous fish. The most common teleost prey groups were tuna (*Thunnus* spp.) and swordfish (*Xiphias gladius*). White shark stomachs also included 11 sea turtles, mainly the loggerhead turtle (*Caretta caretta*), seabirds, and molluscs (Table 1). Several inedible objects, such as clothes, plastic bag, bottles, trash, car license, fishing gears, hooks, broomstick and a wig, were also recorded (Table 1).

Discussion

Despite the fact that 98% of records of white sharks in the Mediterranean Sea came from scientific sources and, therefore were considered as reliable, data were collected opportunistically. Opportunistic and historical records used for this study lack quantifiable effort-related data to infer relative abundance, which would have come from systematic long-term research programmes and, therefore, limit the interpretation of results. Furthermore they often provide limited information and possible inaccuracy of measurements (McPherson and Myers 2009) however, when quantifiable scientific data are lacking (e.g. CPUEs), they have the potential to provide valuable insights on species' ecology (Rossi-Santo et al. 2006; Cotton et al. 2005) and population trends (Sáenz-Arroyo et al. 2005; McPherson and Myers 2009). In lieu of the potential limitations of opportunistic records, in our

Table 1 Diet composition of white sharks (n = 103) in the Mediterranean, expressed as percent by number (%N)

Prey		Total		YOY	Juvenile	Subadult	Adult
		N	N %	N	N	N	N
Marine mammal							
Phocidae	*Monachus monachus*	1	0.6				
Balaenopteridae	*Balaenoptera physalus*	2	1.2				1
Delphinidae	*Tursiops truncatus*	7	4.4			1	2
	Delphinus delphis	1	0.6				1
	Stenella coeruleoalba	6	3.7			3	1
	Grampus griseus	1	0.6				
Physeteridae	*Physeter macrocephalus*	2	1.2				
Phocoenidae	*Phocoena phocoena*	3	1.9			1	1
	Unidentified Mysticete	2	1.2				
	Unidentified Odontocete	26	16.2			2	20
	Total	51	32			7	26
Terrestrial mammal							
Canidae	*Canis lupus familiaris*	1	0.6			1	
Felidae	*Felis silvestris catus*	1	0.6			1	
Bovidae	*Capra hircus*	3	1.9				3
	Ovis aries	1	0.6				1
	Bos taurus	1	0.6				1
Equidae	*Equus caballus*	1	0.6				
Suidae	*Sus scrofa domesticus*	1	0.6				
Hominidae	*Homo sapiens*	12	7.5			3	4
	Unidentified	1	0.6				1
	Total	22	14			5	11
Teleost							
Scombridae	*Thunnus thynnus*	3	1.9			1	2
	Thunnus alalunga	1	0.6			1	
	Sarda sarda	2	1.2			1	1
	Auxis rochei	1	0.6				1
	Thunnus spp.	16	9.9				12
Xiphiidae	*Xiphias gladius*	6	3.7			1	4
Sparidae	*Dentex dentex*	1	0.6				1
Scorpaenidae	*Scorpaena* spp.	1	0.6				1
Serranidae	Unidentified	1	0.6				1
Clupeidae	*Sardina pilchardus*	1	0.6				1
Belonidae	*Belone belone*	1	0.6		1		
Merlucciidae	*Merluccius merluccius*	1	0.6		1		
Lophiidae	*Lophius* spp.	1	0.6		1		
	Unidentified teleost	9	5.6	1			6

Table 1 continued

Prey		Total		YOY	Juvenile	Subadult	Adult
		N	N %	N	N	N	N
	Total	4	28	1	3	4	30
		5					
Chondrichthyans							
Carcharhinidae	*Prionace glauca*	1	0.6				1
Lamnidae	*Isurus oxyrinchus*	1	0.6				1
Alopiidae	*Alopias* spp.	2	1.2			1	1
Unidentified	Unidentified mobulid	1	0.6				1
	Total	5	3			1	4
Reptile							
Cheloniidae	*Caretta caretta*	6	3.7				3
	Chelonia mydas	1	0.6				1
	Unidentified turtle	4	2.5				3
	Total	1	7				7
Bird		1					
Laridae	Unidentified	2	1.2				1
	Unidentified bird	1	0.6				1
	Total	3	2				2
Mollusca							
	Unidentified squid	1	0.6				1
	Unidentified mollusc	1	0.6			1	
	Total	2	1			1	1
Inedible object							
	Total	2	13	2	1	3	12
Stomach examined	Total	1		2	2	12	56

Records range from the Middle Ages (476–1453) to 2011

study it was possible to provide some alternative effort data using information on human population size and distribution as well as fishing impact and, thus, highlight the presence of an anthropogenic bias in the spatial and temporal distribution of white sharks in the Mediterranean Sea. Our study shows also a clear the directionality of changes in the white shark size structure over the time. In fact, this analysis shows a distinct declining trend in the mean length of the white shark in the Mediterranean Sea since the mid-twentieth century, suggesting a population decline. This result is particularly important considering the fact that scientific data on white sharks in the basin are sparse and mainly limited to incidental captures or sightings (McPherson and Myers 2009).

Most studies (Fergusson 1996; Mojetta et al. 1997; Storai et al. 2000, 2002; Barrull and Mate 2000; De Maddalena 2000, 2002; Soldo and Jardas 2002; Galaz and De Maddalena 2004; Cristo et al. 2006) have attempted to describe the distribution of the species and its natural history at the local level in multiple regions of the Mediterranean Sea. White sharks have been recorded across the basin but appear to be more common in the western basin, in the Adriatic Sea, and in the Sicilian Channel. The Mediterranean Sea exhibits a west-east decreasing trend in nutrient availability, where phytoplankton biomass and primary production is highest in the western reaches of the Mediterranean (Moutin and Raimbault 2002; Ignatiades et al. 2009). The Adriatic Sea and the Sicilian Channel are also areas of relatively high marine productivity (Umani 1996; Marasović et al. 1999), and represent biodiversity hotspots within the Mediterranean (De Juan and Lleonart 2010).

Therefore, the higher occurrence of white sharks in these areas might be related to higher productivity of these regions, which support higher biomasses of potential prey (Coll et al. 2007). Furthermore these regions are important breeding and feeding ground for tunas, including the Atlantic bluefin tuna (Cermeño et al. 2015) and several small cetacean species (Notarbartolo Di Sciara et al. 1993; Forcada et al. 1994; Gnone et al. 2011; Bearzi et al. 1997; Tringali et al. 2006; Pulcini et al. 2010). Although, an alternative explanation for the high number of sharks reported in these areas may be an artefact of anthropogenic bias, as all of these regions are highly populated. The concentration of human population measured in coastal regions around the Mediterranean is heaviest in the western Mediterranean, the Adriatic Sea, the eastern extent of the Levantine region and in the Nile Delta (UNEP/MAP 2012). In support to this explanation, the shark distribution bias analysis using night-time satellite imagery clearly shows that the number of shark sightings and captures increases approaching populated areas. In addition, the distribution of white shark records plotted in function of cumulative fishing impact also shows some overlap between areas with higher number of animals and those highly impacted by fisheries. Furthermore, temporal analysis of occurrence shows that white sharks are more frequently observed during summer months, with the highest sighting peak in August when the beaches and waterways are heavily utilized. The Mediterranean region is one of the most visited tourist destinations in the world. Tourist densities are heavily influenced by the season and experience a peak during the summer months (UNEP/MAP 2012), which coincides with the peak of the white shark's recorded presence. The results from this study clearly underline the existence of an anthropogenic bias and, therefore, some care should be used when describing the spatial and temporal distribution of white sharks in the Mediterranena Sea as it might not reflect the real assessment, but be just an artefact of anthropogenic presence.

In the Mediterranean, white sharks from all size classes have been recorded, including YOY. Adults, subadults and juveniles were distributed in most regions of the basin, except for the Levant sub-region and the Marmara Sea. YOYs were more commonly found in the Sicilian Channel. It has been hypothesized that this area could represent a nursery ground for this species during summer (Fergusson 1996; Fergusson et al. 2000). In the current study, this hypothesis is supported by both the high number of YOY recorded in the Sicilian Channel in comparison to other locations in the Mediterranean, and the almost exclusive presence of pregnant females in the latter area. Kabasakal (2014) suggested Edremit Bay (Aegean Sea) as another possible nursery ground, where 6 neonates from 85 to 145 cm length have been caught between 2008 and 2011 during summer. All YOY that have been recorded in the Adriatic Sea were caught in Croatia between the second half of the nineteenth and the beginning of the twentieth century. Most of these specimens were captured in the Sibenik Bay and in the nearby Kvarner Gulf suggest this area might also serve as a nursery ground. The recorded sightings presented here agree with other authors' findings (Fergusson 1996; Fergusson et al. 2000; Kabasakal 2014), with most YOY animals being caught during spring and summer, suggesting parturition occurs during this time of the year (Fergusson 1996). Moreover, the high number of small sharks caught during summer may explain why the mean length of white sharks is significantly smaller during summer than any other time of year. The distribution of juveniles showed a similar pattern to YOY, but with a wider range. This is consistent with the literature, suggesting an increasing individual home range of white sharks with age (Fergusson 1996).

Fergusson (2002) found variation in the mean length of individuals taken by different fishing gear types throughout the Sicilian Channel and in the nearby areas. Larger specimens were caught using tuna traps, while smaller sharks were caught primarily by trawl fisheries (Fergusson 2002). In this study no size variation based on fisheries gear type was found. However, as already reported for several regions, most of the white shark records in coastal waters have been associated with tuna fisheries, including in the Adriatic Sea (Soldo and Jardas 2002), in Catalonian waters (Barrull and Mate 2001), off Sardinia (Storai et al. 2006, 2011), in the Marmara Sea and in the Bosphorus Strait (Kabasakal 2014). Several captures or sightings have occurred in tuna traps near Favignana and Formica (Sicily), Sidi Daoub (Tunisia), Camogli and Portofino (Northwestern Italy), Kvarner Bay (Croatia), Gulf of Baratti (Italy), Capo Enfola (Elba Island, Italy), Mallorca Island (Spain), Capo Testa and Isola Piana (Sardinia) (Fergusson 1996; Cristo et al. 2006;

Mojetta et al. 1997; Storai et al. 2005, 2011; De Maddalena and Heim 2012). The Mediterranean Sea is one of two known spawning grounds for Atlantic bluefin tuna and since early civilization several Mediterranean countries have developed fisheries for individuals moving near shore (Longo and Clark 2012). Capture methods for these near shore tuna include construction of traps, called *tonnare* in Italian, *madrague* in French and *alamdraba* in Spanish (Longo 2011), which have been widely used around the Mediterranean coast until the first half of the twentieth century (Doumenge 1998; Pavesi 1889). Captures of white sharks in the Mediterranean Sea have been associated with both traditional and modern tuna fisheries. Since the 1970s, intensive fishing methods have been used instead in open waters (Longo 2011), which lead to the decline of the use of traps and a decrease of white sharks records in these areas. The tuna-white shark relationship has been investigated in the Sea of Marmara and Bosphorus Strait where the collapse of coastal tuna fisheries have led to the near disappearance of documented white sharks (Kabasakal 2014). This tight relationship has been also investigated in Catalonian waters (Spain) where seasonal variations of the occurrence of white sharks can be linked to the tuna migrations in this area (Barrull and Mate 2001). In the eastern Adriatic Sea a decline of reported white sharks coincides with the collapse of tuna fisheries in the region (Soldo and Jardas 2002; De Maddalena 2000). However since the mid-1990s, 8 new records have been documented along the Croatian coast. It is interesting to note that most of white shark records after the 1990s have occurred in the area between Zadar and Dubrovnik, where the Croatian tuna farming has expanded since the mid-1990s, further highlighting the potential relationship between bluefin tunas and white sharks in the Mediterranean (Iborra Martin and Kekez 2009). Few authors (Morey et al. 2003; Galaz and De Maddalena 2004; Storai et al. 2011; De Maddalena and Heim 2012; Kabasakal 2014;) have already highlighted a possible interaction between white sharks and tuna farming which is supported by data from this study. The importance of tuna to the diet of white sharks is apparent in the observed stomach contents, where tunas were found to have the highest numerical occurrence in the observed stomachs.

As shown by this study, white sharks exhibit a broad diet, targeting a large number of different prey items. This type of opportunistic feeding is common among large predatory sharks such as the porbeagle shark *Lamna nasus* (Bonnaterre, 1788) (Joyce et al. 2002), the blue shark *Prionace glauca* (Linnaeus, 1758) (Ellis et al. 1996), the tiger shark *Galeocerdo cuvier* (Lowe et al. 1996) and the bigeye thresher shark *Alopias superciliosus* (Lowe, 1840) (Preti et al. 2008). The high diversity of prey items found in the stomach of white sharks might indicate that sharks feed across multiple habitat types.

Across their range, white shark adults have been found to feed on both fishes and marine mammals (Compagno 1984; Tricas and McCosker 1984; Casey and Pratt 1985; Klimley 1985) which has been confirmed in the Mediterranean Sea with the most common prey types being cetaceans and teleost fishes. White sharks have been hypothesized to move from the Marmara Sea and Bosphrus Strait areas to the Aegean Sea to feed on cetacean prey after the collapse of tuna stocks (Kabasakal 2014). White sharks are considered sporadic feeders upon sea turtles and few records document shark predation on them, particularly on *C. caretta* (Long 1996; Fergusson et al. 2000; Morey et al. 2003; Cristo et al. 2006). Sea turtles are thought to be a low value prey in comparison to marine mammals or teleost fishes (Long 1996) and the relative high occurrence of predation upon chelonians in the Mediterranean Sea might be a result of a decrease in the abundance of white sharks' preferred prey items. However, the limited data from this study cannot confirm this hypothesis. Overfishing has been evident since the 1950s in the Mediterranean basin, when about 60% of the Mediterranean and Black Sea stocks were already being fully exploited and 40% were overexploited (Froese and Kesner-Reyes 2002). Since the 1950s, the exploitation rate in the basin has been steadily increasing and has led to a dramatic shrinking of fish stocks (Vasilakopoulos et al. 2014). Like fish stocks, cetacean and pinniped have shown large population declines over the last 70 years (Maynou et al. 2011). High fishing pressure resulting in a decrease in their preferred food base might explain why white sharks predate on chelonians more frequently in this area than in other parts of their range, where the preferred prey can still be found in higher abundance (Long 1996).

Predation upon humans is rare for sharks but has been recorded in several parts of the world; South Africa (Levine 1996; Cliff and Dudley 1992), New

Caledonia (Clua and Séret 2010), California (Collier 1992, 1993; Lea and Miller 1985), Chile (Egaña and McCosker 1984), Australia (West 2011) and in the Mediterranean Sea (Storai et al. 2005; De Maddalena and Heim 2012). In the Mediterranean Sea white sharks implicated in attack upon humans are mainly subadults and adults and the victims include divers, spearfishermen, swimmers, windsurfer, surfer and a kayaker. Although attacks occur throughout the year, they peak during summer months, when tourism and coastal activities are more common. In addition to bites on humans, between 1862 and 1998, 26 records documented boats that have being bitten by white sharks. In some cases the shark was trying to feed upon the prey at the hook of the fisherman, while in other, it attacked with no apparent reason.

Measuring changes in size structure has been shown to be an important step in identifying whether over-exploitation of a population has occurred (Shin et al. 2005; Greenstreet and Rogers 2006). In this study the size of white sharks appears to have decreased since the mid-twentieth century, with the most significant decrease experienced in the last 25 years. A more fine scale analysis of temporal trends in the Mediterranean indicated that the largest decrease in total length measurements started in the 1970s, resulting in the lowest length occurring at the beginning of the twenty-first century. Over the last 50 years, fishing pressure has increased considerably in the oceans all over the world, resulting in a decline of large predatory fish communities (Myers and Worm 2003). Shark's life history is characterized by slow growth, late maturity and low fecundity, which make them more vulnerable to modern fishing technology than teleost fishes (Stevens et al. 2000). Overfishing not only acts by reducing abundance, but also by changing sharks growth rate (Walker et al. 1998; Sminkey and Musick 1995), fecundity (Gauld 1979), population age structure and may selectively remove particular size classes (Walker et al. 1998). In some heavily exploited species, a decrease in mean length is observable as fishing gear is often size-selective (Pace et al. 1999), generally targeting the largest individuals (Baum and Myers 2004). Linkages between fish body size and effect of fisheries on marine populations have been investigated by several authors (Jennings et al. 1998; Dulvy et al. 2003; Reynolds et al. 2005) and found that species of large body size and slow growth rates have faster population declines (Jennings et al. 1998). Records of white sharks in the Mediterranean Sea are opportunistic sighting and capture records, which limit the interpretation of results (e.g. lack of effort-related data to infer relative abundance). However, despite a lack of quantifiable scientific data for white sharks in this region, from these opportunistic data it was possible to highlight a declining trend in the mean length of individuals of this species, which hints a population decline in the basin.

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