

# Title: Abundance and distribution of the white shark in the Mediterranean Sea

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**Running Head:** Mediterranean Great White Sharks

## ABSTRACT

Conservation of apex predators is a key challenge both in marine and terrestrial ecosystems. The white shark is a rare but persistent inhabitant of the Mediterranean Sea and it is currently assessed as “critically endangered” in the region. However, the population trends and dynamics of this species in the area are still unknown. Little is known about white shark distribution, habitat use, and population abundance trends, aspects that are critical for conservation and management. In this study, we built the most comprehensive database of white shark occurrence records in the region. We collected 773 different records from different sources and used them to characterize the spatial and temporal patterns of abundance of Mediterranean white sharks between 1860 and 2016. We analyzed these data by using generalized additive models and used spatially disaggregated information on human population abundance as a proxy of observation effort. Our results suggest a complex trajectory of population change characterized by a historical increase and a more recent reduction (61%, range 58-72%) since the second half of the 20th-century. In particular, analyses reveal a 52% (range 37-88%) to 96% (range 92-100%) overall decline in different Mediterranean sectors and a contraction in spatial distribution. Here, we provide the first reconstruction of abundance trends and offer

39 new hypotheses regarding the drivers of change of white sharks in the Mediterranean. Our approach can be  
40 broadly applied to data-poor contexts to reconstruct change and inform the conservation of endangered top  
41 predators in the Mediterranean Sea and other intensely used marine regions.

42 **Keywords:** Mediterranean Sea, observation effort, opportunistic and sparse data, spatiotemporal patterns,  
43 standardized trends, white shark  
44

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## 64 **INTRODUCTION**

65 The loss of top predators is one of the most challenging forms of global environmental change, with still un-  
66 recognized and not well-understood ecosystem effects (Estes et al., 2011). The decline of large predators on  
67 land started approximately 50 kya with the great demographic and geographic human expansion (Dirzo et  
68 al., 2014; Ripple et al., 2014). In the oceans, recent increases in resource exploitation by high seas industrial  
69 fishers as well as artisanal fleets, habitat degradation, and climate change pose unprecedented challenges also  
70 to marine predators (Worm & Tittensor, 2011). In the Mediterranean Sea, predator loss is more severe than  
71 other ocean sectors due to thousands of years of human impact on marine communities (Coll et al., 2010) and  
72 currently high cumulative human pressure on marine ecosystems (Micheli et al., 2013). However, it is only in

73 the last 50 years that systematic data started to be gathered to evaluate the impact of fishing on exploited  
74 marine populations and ecosystems (Ferretti et al., 2015; McClenachan et al., 2012). This lack of historical  
75 baselines hampers our ability to fully understand the ecology of habitats and species, and consequently, our  
76 ability to evaluate the conservation status of Mediterranean ecosystems and marine populations.

77 Among marine animals, sharks are one of the marine taxa with the highest percentage of threatened species  
78 (Dulvy et al., 2014). They are generally vulnerable animals, with very low resilience and biological  
79 productivity, strongly susceptible to fishing pressure (Ferretti et al., 2010; Queiroz et al., 2019), though  
80 examples of sustainable shark fishery also exist (see for details Simpfendorfer & Dulvy, 2017). Because of these  
81 features, in the past decades, many shark populations showed rapid declines in multiple marine regions  
82 mostly because of the direct effect of targeted and bycatch fisheries (Baum & Blanchard, 2010). An among  
83 global ocean sectors, the Mediterranean Sea showed the worst population declines and conservation statuses  
84 for many populations (Cavanagh & Gibson, 2007; Ferretti et al., 2008). In 2016, the International Union for  
85 Conservation of Nature (IUCN) compiled the second regional assessment of sharks and rays in the  
86 Mediterranean Sea, reporting that after ten years the situation had not improved and the conservation status  
87 of these species remained probably the worst in the world (Dulvy et al., 2016). In fact, 39 of the 73 assessed  
88 species are still threatened and 13 are still considered Data Deficient (Dulvy et al., 2016). Moreover, for most  
89 non-data-deficient species, the risk assessment was based on suspected trends and not adequately supported  
90 by quantitative analyses. For instance, the conservation status of the white shark (*Carcharodon Carcharias*,  
91 Lamnidae) was raised from Endangered to Critically Endangered in both Mediterranean and European  
92 Regional Red Lists (Dulvy et al., 2016; Nieto et al., 2015) solely on the ground of its current sporadic occurrence  
93 in the region and suspected declines.

94 The white shark is one of the largest and most widespread top predators in the ocean. It is broadly  
95 distributed between the sub-polar and sub-tropics in both hemispheres, with major coastal aggregation sites  
96 in temperate latitudes (Compagno, 2001). Most of the biological and ecological research on white sharks have  
97 been carried out in three coastal aggregation sites (Huvneers et al., 2018): California (Chapple et al., 2011;  
98 Tinker et al., 2016), southern Australia (Bruce & Bradford, 2012) and South Africa (Kock et al., 2013). Here,

99 satellite and acoustic tagging, genetics, and isotopes analyses have deepened our ecological understanding of  
100 the species' migrations, preferred habitats, population structure, abundance, and distribution patterns (Bruce  
101 & Bradford, 2012; Carlisle et al., 2012). Even if a general assessment of the white shark abundance trends is  
102 challenging to achieve, there have been several attempts in different areas to assess the status of the sharks.  
103 Locally, different data sources and modeling approaches have been adopted (Christiansen et al., 2014; Curtis  
104 et al., 2014; Dudley & Simpfendorfer, 2006; Lowe et al., 2012; Reid et al., 2011). Most of these attempts showed  
105 a slow increase in white shark populations or sub-populations relative abundance in recent years due to the  
106 presence of local protecting measures (Curtis et al., 2014; Dudley & Simpfendorfer, 2006; Lowe et al., 2012;  
107 Reid et al., 2011). By contrast, relative declines have been detected in regions lacking these measures  
108 (Christiansen et al., 2014). Despite both the protecting provisions existing and the actual conservation status,  
109 no white shark population trend analyses have been carried out in the Mediterranean basin, so far.

110 In the Mediterranean Sea, white sharks have been sporadically but regularly detected throughout history.  
111 Several authors (Fergusson, 1996; Gubili et al., 2011) hypothesized the existence of a distinct Mediterranean  
112 population, and phylogeographic analyses showed a large genetic distance and scarce genetic flow between  
113 the Mediterranean and northwestern Atlantic white sharks (Gubili et al., 2011, 2015). However, little is known  
114 about the ecology and biology of the Mediterranean population. Studying white sharks in the Mediterranean  
115 Sea is challenging because of the low population density and the absence of conventional aggregation sites,  
116 such as around pinnipeds colonies (Klimley & Anderson, 1996). This makes it challenging to conduct  
117 monitoring studies with the use of electronic tagging, and limits the scope of genetic and isotopic analyses  
118 (Gubili et al., 2011). However, opportunistic occurrence records exist (Boldrocchi et al., 2017; De Maddalena  
119 & Heim, 2012; Fergusson, 1996; Serena et al., 2008). Regional reviews of these data generated interesting  
120 hypotheses on patterns in population structure, movements, and abundance. For example, several catches of  
121 young-of-the-year white sharks reported for the Sicilian Channel suggested the presence of a nursery area in  
122 this sector (Fergusson, 1996, 2002). The reduction in white shark sightings through the years from areas with  
123 a parallel strong decline of tuna populations, combined with recent and historical sightings in and around  
124 farm pens and tuna traps (Galaz & De Maddalena, 2004; Storai et al., 2011), suggested a close relationship



125 between Atlantic Bluefin tuna (*Thunnus thynnus*, Scombridae) and white shark occurrence in the  
126 Mediterranean Sea (Boldrocchi et al., 2017; De Maddalena & Heim, 2012; Kabasakal, 2016). Yet, more research  
127 is needed to understand population structure, size, movements and distribution within the area and their  
128 relations with environmental and biological variables.

129 Mediterranean white shark observation records are opportunistic because they are often collected from  
130 fishers' anecdotes or newspaper articles (Pearce & Bouyce, 2006), and, hence, obtained without a specific and  
131 systematic sampling effort. Nevertheless, in the absence of systematic surveys, opportunistic data provide  
132 valuable insights on species distribution, habitat requirements and population trends (Christiansen et al., 2014;  
133 Curtis et al., 2014; Ferretti et al., 2015). For example, McPherson & Myers (2009) used white shark sightings  
134 collected between 1868 and 2005 to infer population changes in the Adriatic Sea. They estimated temporal  
135 trends of occurrence records under different scenarios of observation effort and estimated an 84% decline (CI:  
136 +27% and -98%). These estimates were highly uncertain as the authors had no direct information on  
137 observation effort but provided a first quantitative estimate of white shark population change in a sector of  
138 the Mediterranean Sea. Here we expand on this approach to produce the first regional assessment at the  
139 Mediterranean scale. We assembled the most comprehensive database of white shark's occurrence records  
140 currently available for the Mediterranean Sea and estimated trends controlling for observation effort, which  
141 was directly estimated with long-term trend models of coastal human population censuses in the region. We  
142 used these standardized records to infer trends in population abundance and asked whether, how and how  
143 much the white shark population has changed in abundance and spatial distribution over the last two  
144 centuries.

## 145 **METHODS**

### 146 *Shark database construction and exploratory analysis*

147 We built a database containing all the white shark records in the Mediterranean Sea using different sources  
148 and multiple search strategies (Supporting Information), also including existing institutional databases, such  
149 as MEDLEM (Mediterranean Large Elasmobranchs Monitoring) currently under the auspices of the General

150 Fisheries Commission for the Mediterranean Sea (GFCM, Serena et al., 2008). We followed through citations  
151 in the listed references to delineate the history of each account and to determine whether the record was  
152 original or redundant (reporting records from other publications) (Ferretti et al., 2016). For each observation  
153 we recorded: date and location; total length; weight; sex; age (adapted from Bruce & Bradford, 2012;  
154 Supporting Information); record type (stranding, catch, sighting, signs of predation on other marine animals);  
155 stomach contents; fishing gear involved in the capture; and bibliographic reference for published accounts.  
156 Then, we performed an exploratory data analysis in order to evaluate the most immediate ecological  
157 information, such as the sightings' temporal and spatial distribution, length frequency, length-weight  
158 relationship, and a qualitative stomach content analysis (Supporting Information).

### 159 *Model framework*

160 We stratified the Mediterranean sea in spatio-temporal statistical units of different resolution (e.g. FAO or  
161 GFCM statistical sectors and year) and following McPherson & Mayers (2009)'s approach, we assumed that  
162 the expected number of sightings per statistical unit (year  $t$  and geographic sector  $s$ ) was related to the  
163 following variables: number of possible observers (observation effort),  $O_{ts}$ , their propensity to report a  
164 sighting,  $P_{ts}$ , white sharks population abundance,  $N_{ts}$ , and shark detectability,  $D_{ts}$ . In systematic and dedicated  
165 surveys these factors can be controlled. Conversely, this information is incomplete for opportunistic data  
166 (McPherson & Myers, 2009). In this work, we chose the human population size ( $H_{ts}$ ) as a proxy of observation  
167 effort. Therefore, we treated  $O_{ts}$  and  $P_{ts}$  as a joint process, essentially assuming that all observers had a constant  
168 probability to report a record (McPherson & Myers, 2009) and that the number of observers is proportional to  
169 the human population size ( $O_{ts} = cH_{ts}$ , where  $c$  is constant). Hence, we assumed that detectability,  $D_{ts}$ , has a  
170 proportional relationship with abundance ( $D_{ts} = kN_{ts}$ ), assuming, in other words, that a specific amount of  
171 observation effort is needed to detect a fixed proportion of the individuals present in the study area  
172 (McPherson & Myers, 2009). This represents the simplest possible scenario to infer standardized abundance  
173 trends of the shark population. In fact, under these assumptions, the probability of a recorded sighting

174 depends only on  $H_{ts}$  and  $N_{ts}$ . We tested deviations from such an assumption in the following inferential  
175 analysis.

176 Given that Mediterranean white shark sightings are rare and discrete events, we assumed that the expected  
177 number of sharks per statistical unit follows either Poisson or Negative Binomial (NB, in case of overdispersed  
178 data) distributions where their means are a function of predictors describing  $N_{ts}$  and  $H_{ts}$ . However, it is  
179 important to note that factors other than  $H_{ts}$  can affect the observation effort variability over space and time.  
180 For example, the marine area covered by the potential observers and the technological innovations in fisheries  
181 and boating may have played a pivotal role in changing the sightings probability (fisheries have expanded in  
182 distance from shore and overall range over time (Rousseau et al., 2019)). So, the sighting probability may have  
183 increased during the 20th-century, but testing this hypothesis was not possible with the available data.  
184 Therefore, since this issue arises when interpreting the frequency of occurrence of many other Mediterranean  
185 species, we explored the performance of a single, readily available and systematic proxy of observation effort.

#### 186 *Collecting observation effort data*

187 In order to investigate trends in the spatiotemporal distribution of our proxy of observation effort, we  
188 divided the Mediterranean coastline into 202 coastal regions, belonging to 23 different countries and retrieved  
189 the human population in each coastal region (Supporting Information) (Fig.1a-b). Historical time series of the  
190 human population were collected for each coastal region over a time range of 156 years (1860-2016). Multiple  
191 sources, such as national census reports or international databases (Eurostat, World Bank), were consulted to  
192 rebuild each human population time-series (Supporting Information). As not all considered regions had  
193 annual census estimates for the whole time period, we interpolated missing years with a regression approach.  
194 Annual population size estimates for each region were obtained by fitting GAMs (Wood, 2011) and log-scale  
195 regressions to the historical population censuses data. Then, we selected estimates according to the best fitting  
196 model in each region (details are in the Supporting Information).

197 *Estimating standardized shark sighting trends*

198 In order to identify the spatial and temporal patterns characterizing the sighting data, we considered a time  
199 range of 156 years (between 1860 and 2016) and different levels of resolution for spatial strata. We chose 1860  
200 as our initial observation year because earlier sightings were scarce and previous human population data in  
201 most Mediterranean countries were unavailable. Observation effort and shark occurrences were spatially  
202 aggregated using both the GFCM's Mediterranean Geographic Sub-area stratification (GSAs,  
203 <http://www.fao.org/gfcm/data/map-geographical-subareas/en/>) (Fig.2a) and the coarser FAO Major Fishing  
204 Area 37's stratification of eight divisions (<http://www.fao.org/gfcm/data/map-geographical-subareas/en/>)  
205 (Fig3b). In order to find the best fitting model, we tested multiple model structures (Supporting Information)  
206 with various levels of temporal aggregation, functional relationships between response and predictors (e.g.  
207 linear or more complex with polynomials and splines) and the two statistical distributions of the response  
208 variable (NB and Poisson). GAMs with 1-year time bins resulted as the best model class in terms of AIC, fitting  
209 deviance and residuals analysis. Model fits were performed by using the R package mgcv (Wood, 2011). We  
210 fitted a GAM with a Negative Binomial Distribution and a log link function to the annual number of shark  
211 occurrences recorded in each GSA, using the observation effort (annual number of people for that GSA) as an  
212 offset term and the GSAs as spatial sectors (hereby referred as GSA model). The model structure was

213 
$$\log(z_{ij}) = f(y_i) + [GSA]_j + \log(H_{ij}) + \varepsilon_{ij} \quad (1)$$

214 where  $z_{ij}$  is the  $i$ th observed number of sharks in year  $y_i$  ( $i=1,\dots,156$ ) and GSA  $j$ ,  $f$  is a smooth function  
215 estimated using penalized likelihood maximization (with a smooth parameter estimated by Restricted  
216 Maximum Likelihood) (Wood, 2011),  $[GSA]_j$  is a factor with 27 levels ( $j=1,\dots,27$ ), corresponding to the GSAs),  
217  $\log(H_{ij})$  is the offset term and  $\varepsilon_{ij}$  is the error term for  $i$ th observation in GSA  $j$ , assumed to be normally  
218 distributed around 0 and with variance to estimate.

219 In our modeling exercises, we faced several issues. First, in order to verify the assumption of a linear  
220 relationship between the response variable and the offset term, we fitted a parallel model with a spline on the  
221 human population abundance and compared the two model's prediction errors through RMSEs (Root-mean-  
222 square-error, Supporting Information). Second, although we could expect the observation effort to increase

223 with time, we supposed there could be stages in our observation period where sighting effort changed  
224 abruptly (i.e. start of ocean use for bathing, interest in marine science, conflicts and epidemics). Therefore, we  
225 tested for the effect of these discrete important events dividing our temporal range in bins characterized by  
226 different hypothetical sighting effort regimes (Supporting Information). Finally, there was a tradeoff between  
227 spatial and temporal resolution. Because of the limited number of sightings from specific Mediterranean  
228 sectors, the use of a complex spatial stratification, such as the GSA scheme, with a high temporal resolution,  
229 allowed us only to detect a common temporal trend throughout the basin and a sector-specific spatial effect  
230 on shark's abundance. It was

$$231 \quad \log(z_{ij}) = f_j(y_i) + [FAO\ Division]_j + \log(H_{ij}) + \varepsilon_{ij} \quad (2)$$

232 where all terms are the same as in the GSA model except for  $f_j$ , which here is sector-specific  
233 ( $[FAO\ Division]_j$ , with  $j = 1, \dots, 8$ ). In this way, we obtained sub-regional temporal trends, though with a lower  
234 spatial resolution. However, this kind of model parametrization assigns the same number of knots to each  
235 sub-regional curve via REML (Restricted Maximum Likelihood). In this way, the trajectories estimated for  
236 well-represented sectors (with a high number of records) could have leverage on the others with fewer  
237 occurrences recorded. Thus, in order to validate the curves obtained with the FAO Model and to avoid the  
238 presence of artifacts related to the sparse nature of data, we chose to fit, parallelly, a single-sector model for  
239 each Division (Supporting Information). Finally, we predicted the expected number of sharks in each  
240 spatiotemporal model unit considering a fixed amount of observation effort (5 million people), in order to  
241 standardize the shark abundance trend on easily interpretable values.

#### 242 *Testing for spatial range contraction*

243 Given its "Critically Endangered" status, it is expected the species went through a range contraction together  
244 with a decline in population abundance (Worm & Tittensor, 2011). To test for this scenario, we aggregated the  
245 data in two main periods (1945 – 1975, 1976 – 2016), deemed to have the most comparable regimes of  
246 observation effort. We excluded from the analysis all the sightings from before 1945 in order to minimize the  
247 bias linked to unaccountable variations of the observation effort, such as the two World Wars presence. In  
248 addition, our aim was to test for a relatively recent decline associated with a spatial range contraction. Hence,

249 we fitted a Negative Binomial Generalized Linear Model (GLM) (R package MASS, Venables & Ripley, 2002)  
250 to the annual number of shark occurrences (considered as replicates) for each time bin in each FAO Division,  
251 still maintaining the observation effort as an offset term. The model structure was

$$252 \quad \log(z_{ij}) = \beta_0 + \beta_1(T_i) \cdot \beta_2[FAO\ Division]_j + \log(H_{ij}) + \varepsilon_{ij} \quad (3)$$

253 where  $z_{ij}$  is the observed number of sharks in period  $T_i$  and FAO Division  $j$ ,  $\beta_0$  is the intercept,  $\beta_{1-2}$  are  
254 regression coefficients,  $T_i$  is the time bin,  $[FAO\ Division]_j$  is a factor with eight levels ( $j= 1, \dots, 8$ , corresponding  
255 to the spatial sectors),  $\log(H_{ij})$  is the offset term and  $\varepsilon_{ij}$  is the error term for  $i$ th observation in each FAO  
256 Division  $j$ . Hence, we predicted the expected number of sharks in each FAO Division for each period  
257 considering a fixed value of observation effort (5 million people) and compared this index for each sector  
258 between the two different time bins.

## 259 **RESULTS**

### 260 **Exploratory data analysis**

261 We identified a total of 773 white shark records within the Mediterranean Sea, spanning from the end of the  
262 Middle Ages (1453) to 2016. However, 93% (718) of these occurred after 1860, which is the period when we  
263 had the most reliable data and, consequently, was used for our trend analyses. Fisheries catches accounted for  
264 66% of the records, 48% coming from tuna traps, followed by gillnets (23.0%), hand lines (8%), harpoons  
265 (6.4%), purse seines (5.6%) and longlines (5.2%) (Fig1e). The remaining portions came from strandings,  
266 sightings, recorded predation events, and bites to humans. Records were mainly distributed in the western  
267 Mediterranean Sea, in particular, the Northern Adriatic sea (GSA 17, 20.9%), Ligurian and North Tyrrhenian  
268 Sea (GSA 9, 13.8%), Southern Sicily (GSA 16, 9.5%) and off the Balearic Islands (GSA 5, 8.5%); and pertained  
269 mainly to adults (42.8%), sub-adults (10.5%) and juveniles (9.6%) (adapted from Bruce & Bradford 2012) with  
270 the majority of individuals of being from 4 to 6 meters long (Fig1b). However, it is important to emphasize  
271 that more than a third (32.8%) of records were lacking length information and, consequently, we could not  
272 address the age class. Sex ratio was biased toward females (64.1% of the 142 records having sex), and the  
273 individuals that had also information on stomach contents ( $n = 122$ ) suggested that bony fish were the main

274 prey (27.3%), followed by odontocetes (25.0%), scavenging carcasses of other animals (principally farm  
275 animals, pets - 5.7% and humans - 10.2% ) and chelonians (6.8%) (Fig1d).

276 Coastal human population increased six-fold since 1860, rising from 29.6 million to 183.8 million in 2016,  
277 though this increase was geographically heterogeneous (Fig1a). The highest increases were detected in the  
278 eastern basin sectors, with the maximum rise around the Marmara Sea (319.4-fold). By contrast, the lowest  
279 rates of change were observed in the western and central Mediterranean sectors, such as the Northern Adriatic,  
280 Southern Sicily, and Corsica, where the human population doubled throughout the same period (Fig1a).

281

## 282 **Model fitting results**

283

284 *Temporal trends.* Shark observations increased throughout the period (Supporting Information Fig.2), but  
285 when we controlled for changes in the potential number of observers (Fig2a), we detected an initial increase,  
286 characterized by two peaks in the 1880s and a higher one in the 1980s, followed by a 61% (range 58-72%)  
287 decline between 1975-2016. Similarly, to the changes in the human population, this trajectory was not  
288 homogeneous throughout the basin. At the FAO Divisions' level, the non-linear smoothing term for year  
289 (Fig3a-c) was significant for seven of the eight considered sectors (five with  $\alpha = 0.05$  and two considering  $\alpha =$   
290 0.1) and five of these six significant trajectories ended in recent declines (Fig3b). These declines began earlier  
291 and were more intense in the peripheral sectors, such as the Marmara Sea (1961 – 96.0%, range 92-100%),  
292 Adriatic Sea (1883 – 94.1%, range 90-100%) and the Balearic (1954 – 82.5%, range 76-98%) than central  
293 Mediterranean sectors (Ionian from 1988 a 52.1% decline, range 37-88%, and Sardinia from 1980 a 76.4%  
294 decline, range 75-91%).

295 *Spatial patterns and distribution shrinkage.* Our standardized indices of shark abundance identified  
296 heterogeneous spatial distribution landscapes. The main hotspots were located in the western Mediterranean  
297 sectors (Fig2b), especially in the Balearic Islands (0.73, CI 0.51 – 1.05), Maltese waters (0.37, CI 0.21 – 0.64) and  
298 Corsica (0.34, CI 0.18 – 0.65). Shark abundance cold spots were in all eastern Mediterranean GSAs, except for  
299 the Marmara and Aegean Sea. When we aggregated the records in two time bins (1945 – 1980; 1980 – 2016),

300 we detected a significant contraction of the species' spatial distribution. All the Mediterranean Sea peripheral  
301 sectors recorded a decrease in shark abundance in the second period (Fig4c), with the highest difference  
302 detected in the Marmara Sea (-96.6%, CI -95.2% – -99.9%), followed by the Balearic (-73.1%, CI -72.5% – -  
303 74.7%) and the Gulf of Lions (-38.0%, CI -41.4% – -18.3%). All the central sectors instead, highlighted an  
304 increase in the shark abundance (Fig4c), with the highest value detected in the Ionian Division (+ 222.6%, CI  
305 +191.6% – +322.4%).

## 306 **DISCUSSION**

307 Conservation actions and recovery plans for threatened and endangered marine top predators are broadly  
308 limited by a lack of information on the population status and trends at the scale of whole ecoregions and over  
309 multi-decadal time scales. By analyzing 156 years of white shark records in the Mediterranean Sea we were  
310 able, for the first time, to estimate large-scale and long-term trajectories of white shark abundance indices  
311 across the entire region. The use of all the available sources of information, integrated with a proxy controlling  
312 for the observation effort change within space and time, permitted us to standardize our trends. These  
313 standardized indices of population abundance suggested that the species went through a complex trajectory  
314 of change, characterized by an increasing phase followed by a sharp decline since the 1980s. The recent decline,  
315 together with a detected range contraction in the spatial distribution of records (Worm & Tittensor, 2011), and  
316 stronger and more prolonged declines estimated in peripheral regions compared to central sectors, suggest an  
317 overall rapid decline of the white shark population in the region in the last 3-4 decades. Our results are in  
318 contrast with population abundance increases inferred in other regions, such as California (Lowe et al., 2012),  
319 North-western Atlantic (Curtis et al., 2014), South Africa (Dudley & Simpfendorfer, 2006) and Australia (Reid  
320 et al., 2011). Conversely, they are in line with regions where the white shark occurrence data are sparse and  
321 infrequent, such as the Northwest Pacific Ocean (Christiansen et al., 2014). These results confirmed earlier  
322 evidence of regional declines provided by McPherson & Myers (2009), Boldrocchi et al., (2017), and Ferretti et  
323 al. (2008) for a larger taxonomic group, but scaled-down recent Red List assessments carried out by the IUCN,  
324 which classified the white shark as critically endangered in the Mediterranean Sea and European waters



325 (Dulvy et al., 2016; Nieto et al., 2015). Our results suggest instead an overall decline of 61.5% over the last 10  
326 years or three generations, which would classify the species as endangered (EN) “if the reduction causes may  
327 not have ceased or well understood”, as stated in IUCN Criteria Version 3.1 (A2-bc). Taken together, our  
328 results and those of studies conducted elsewhere highlight the importance of regional analyses and the risk of  
329 extrapolating trends across different geographies. It is easily perceivable that each region has peculiar  
330 characteristics, history of human impact and drivers of change. An informative regional assessment would  
331 prevent wastage of both conservation efforts and resources.

332 Similarly, we confirmed previous evidence of the prevalence of Mediterranean white sharks in western  
333 sectors (Boldrocchi et al., 2017), characterized by distinct bio-ecological and physical oceanographic  
334 characteristics from the Eastern Mediterranean. The west-east temperature (Bosc et al., 2004) and productivity  
335 (Coll et al., 2010) gradients would make the warmer eastern Mediterranean waters a sub-optimal habitat for  
336 adult endothermic white sharks (Carey et al., 1982). By contrast, the colder and productive western sectors  
337 could represent resource hotspots for the species. These are in fact important breeding and feeding ground for  
338 bluefin tunas (Cermeño et al., 2015) and small cetaceans (Gnone et al., 2011; Lauriano et al., 2014), which are  
339 important food items for the white sharks (Fig1d, Boldrocchi et al., 2017). This result highlights the critical  
340 importance of the western sectors for the persistence of white shark populations.

341 The white shark ecology in the Mediterranean Sea is still poorly characterized and these analyses are a step  
342 forward addressing this important issue. Among the multiple hypotheses that may explain the estimated  
343 trajectories of change, we highlight three potential drivers. First, over the last 200 years, coastal fishing in the  
344 Mediterranean Sea has notably increased and expanded throughout the region (Piroddi et al., 2015) impacting  
345 both juvenile and adult white sharks, but contemporarily increasing the number of occurrence records. Young-  
346 of-the-year and juvenile white sharks are vulnerable to inshore gears such as trammel or gill nets (Bruce &  
347 Bradford, 2012; Curtis et al., 2014; Lowe et al., 2012), which have been massively used all along the  
348 Mediterranean shores also for targeting sharks (Ferretti et al., 2013). Adult individuals were frequently  
349 reported in tuna traps (>50% of catches on record, Fig1e), which were fixed gears historically used to catch  
350 bluefin tunas on their migratory routes in the Mediterranean Sea (Bombace & Lucchetti, 2011) and could have

351 represented a source of mortality for white sharks for centuries. Since the 1960s, tuna traps ceased to be  
352 profitable and most have been closed as an effect of tuna overexploitation by industrial purse seining and  
353 other pelagic fisheries (Fromentin & Powers, 2005; ICCAT, 2017; Rouyer et al., 2018). This may have reduced  
354 the impact on adult white sharks as well as the number of catches we had on record. Meanwhile, white sharks  
355 began to be exposed to offshore fishing, especially tuna and swordfish longlining, which greatly escalated in  
356 the region during the last 50 years (Ferretti et al., 2008). In this period white sharks were exposed to both  
357 inshore and offshore fishing and could not benefit from sheltering offshore which was practically unexploited  
358 historically (Ferretti et al., 2008). Similar patterns have been observed in South Africa and Australia (Dudley  
359 & Simpfendorfer, 2006; Ferretti et al., 2010; Reid et al., 2011).

360 It is also possible that Mediterranean white sharks have followed the population trajectory of Bluefin tuna,  
361 one of their most frequent prey in the region (Boldrocchi et al., 2017; De Maddalena & Heim, 2012; Kabasakal,  
362 2016). In our data, 27.3% of the white sharks with stomach content data ate bony fish and 47% of these fishes  
363 were tunas (Fig1d, Supporting Information Tab. 6). Tunas are suitable prey for white sharks (Hussey et al.,  
364 2012) and the bluefin tuna's overexploitation in the last 50 years may have reduced one of the most important  
365 prey resources for this species in the area (ICCAT, 2017; Rouyer et al., 2018). The long-term trajectory we  
366 estimated for the white shark records has a temporal phase similar to the time series of Mediterranean bluefin  
367 tuna abundance estimated from centuries of tuna trap data (Ravier & Fromentin, 2001). The bluefin tuna  
368 decline detected in recent decades (Fromentin & Powers, 2005; Rouyer et al., 2018) coincides with the recent  
369 decline of the white shark sighting rate, supporting the plausibility of a predator-prey dynamic between the  
370 two species. Yet tuna overexploitation also caused the end of the tuna trap fishery. Therefore, it is unclear  
371 whether such a contemporary decline in sighting rate has been caused by the end of an important source of  
372 white shark mortality in the region (i.e. decline in catch records from tuna traps), or by an underlining  
373 population decline through indirect bottom-up effects (because of the decline of an important prey), or both  
374 factors combined. However, no differences in GAM's trajectories were detected by fitting the FAO Model with  
375 and without the tuna trap catches (Supporting Information, Fig. 9) in all sectors but the Balearic (Division 1.1),  
376 a piece of evidence against the decline in catch record hypothesis. Whereas, the predator-prey hypothesis is

377 corroborated by the fact that adult white sharks' preferential prey, such as pinnipeds and whale carcasses  
378 (Hussey et al., 2012), have been much scarcer or essentially absent in the Mediterranean Sea for most of the  
379 period considered in this analysis. The only pinniped in the region, the monk seal (*Monachus monachus*,  
380 Phocidae), has small remnant populations only in the eastern Mediterranean sectors (Karamanlidis &  
381 Dendrinos, 2015) and was considered rare (heavily depleted by centuries of overhunting) in most of the  
382 Mediterranean Sea by the 18th century (Johnson, 2004). Whale abundance is also much lower than in other  
383 ocean sectors where white sharks occur (Notarbartolo di Sciara, 2002). It is, therefore, possible that adult white  
384 sharks adapted to feed mainly on tunas in the Mediterranean Sea; a hypothesis that would make this  
385 population unique respect other global populations and should be formally tested in future research.

386 The above explanations are confounded by the change in observation effort expected from the spatial and  
387 temporal expansions of fisheries and other factors affecting the probability to detect records. We used  
388 trajectories of human population change along the Mediterranean coasts as a single and practical proxy of  
389 observation effort, but human population abundance is one of its multiple components. For example, linguistic  
390 barriers and political instability may have limited the number of records we found in North-African and  
391 Middle Eastern regions, as well as the two World Wars and the 1918 Flu Pandemic may have acted similarly  
392 in Europe during these periods (D'Ancona, 1949; Thurstan et al., 2010). In addition, episodic events, such as a  
393 19th-century reward program issued by the Imperial Maritime Austrian Government to cull white sharks in  
394 the Adriatic Sea (De Marchesetti, 1882), could have boosted the probability to have occurrence records  
395 independent of human population changes. Similarly, the expansion of the use of the Internet and social  
396 networks in the last 20 years has likely increased the probability that a record of a white shark capture is  
397 reported. International (CITES, CSM, Barcelona and Bern Conventions) and national legislation (in Malta,  
398 Israel, Croatia, Montenegro, and Slovenia) to protect this species may have deterred Mediterranean fishermen  
399 in reporting catches, fearing disruptive or legal consequences for their activities. Although these factors may  
400 have acted in different direction (i.e. biasing upward or downward the estimated trends), and the probabilistic  
401 distribution we used to handle the response variable allows clustered observations, quantifying these sources  
402 of bias is now a top priority to further explaining, and reducing uncertainty of the general large-scale spatial

403 and temporal patterns we identified. Nevertheless, our modelling approach represents an innovation in  
404 analyzing opportunistic data, by testing observation effort regimes that are not simulated, as done so far  
405 (Christiansen et al., 2014; Curtis et al., 2014; McPherson & Myers, 2009), but quantitatively estimated through  
406 the use of a proper observation effort proxy. Indeed, most of the cited features affecting observation effort are  
407 in some ways related to demographical changes of the human population (i.e. fishing pressure, technological  
408 development). Hence, adopting an observation effort proportional to the human population mitigates the  
409 confusing effects of the mentioned factors.

410 Reconstruction of the Mediterranean white shark spatio-temporal patterns of abundance, obtained by using  
411 all available occurrence records, generated new hypotheses on the species' population structure and predator-  
412 prey dynamics in the region. Testing these hypotheses with further dedicated research will further contribute  
413 to reconstruct population baselines of this species and deepen our understanding of its life-history, ecology,  
414 and biogeography. These aspects are crucial to ensure the conservation of white sharks in the region and across  
415 the planet. We also identified occurrence hotspots that would represent important sampling locations for  
416 collecting high-quality biological data, including tracking data to directly assess distribution, foraging, and  
417 habitat use. These field studies are expensive and require careful planning on where and when white sharks  
418 are most likely detected.

419 Globally, there are multiple species of conservation concern with a similar scantiness of abundance data that  
420 would benefit from our approach of combining all available occurrence data. Our study shows that a careful  
421 examination of these data, even if opportunistic, can reveal important ecological patterns, particularly  
422 regarding trends in abundance and spatial distribution, that are critical to inform adequate conservation  
423 actions and science-based recovery plans.

424

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426

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432

### 433 **Data Availability Statement**

434 The data that support the findings of this study are available from the corresponding author  
435 (stefano.moro@uniroma1.it) upon reasonable request.

436

### 437 **SUPPORTING INFORMATION**

438 Data collection and management, detailed description of the models, exploratory analysis (Appendix S1),  
439 human population size trends (Appendix S2).

440

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610

## 611 **Figure legends**

612 **Fig.1** Observation effort and exploratory analysis. (a) Absolute variation of coastal regions human population size calculated between  
613 1860 and 2016 and expressed in logarithmic scale. The red dots correspond to the white sharks sighting locations. (b) Length frequency.  
614 The absolute frequency is reported over each bar. (c) Sex distribution within age classes (YOY = young-of-the-year, JUV = Juveniles, SUB  
615 = Sub-adults, ADL = Adults, UND = Undetermined). (d) Diet composition. The absolute frequency is reported over each bar. (e) N° of  
616 specimens caught by each fishing gear category per age class.

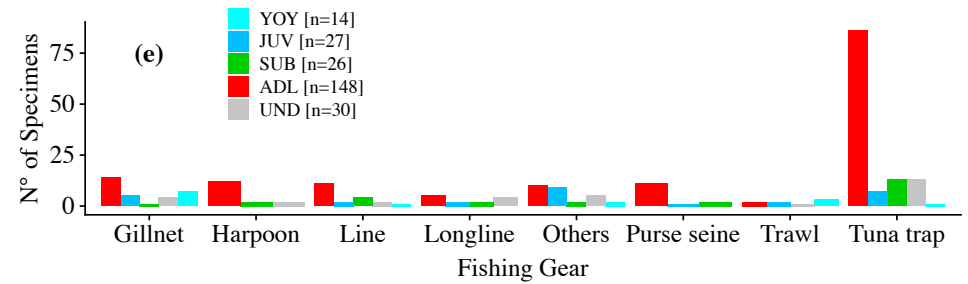
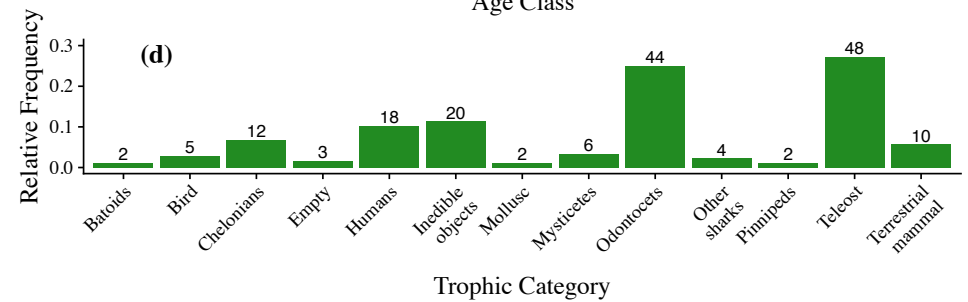
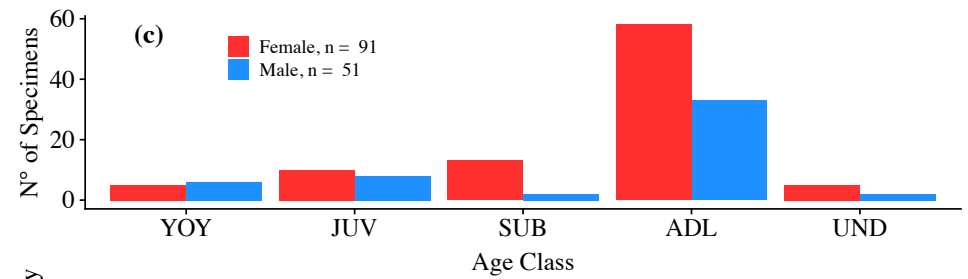
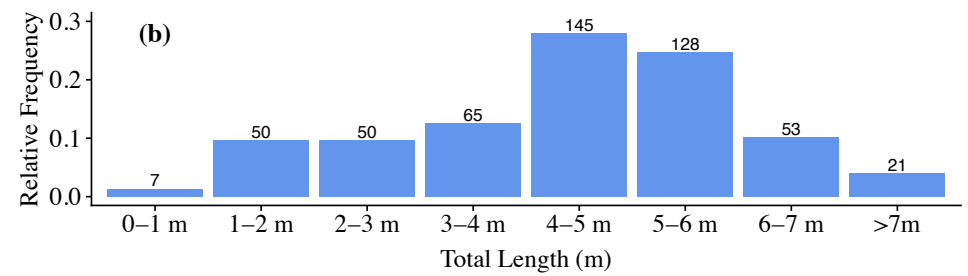
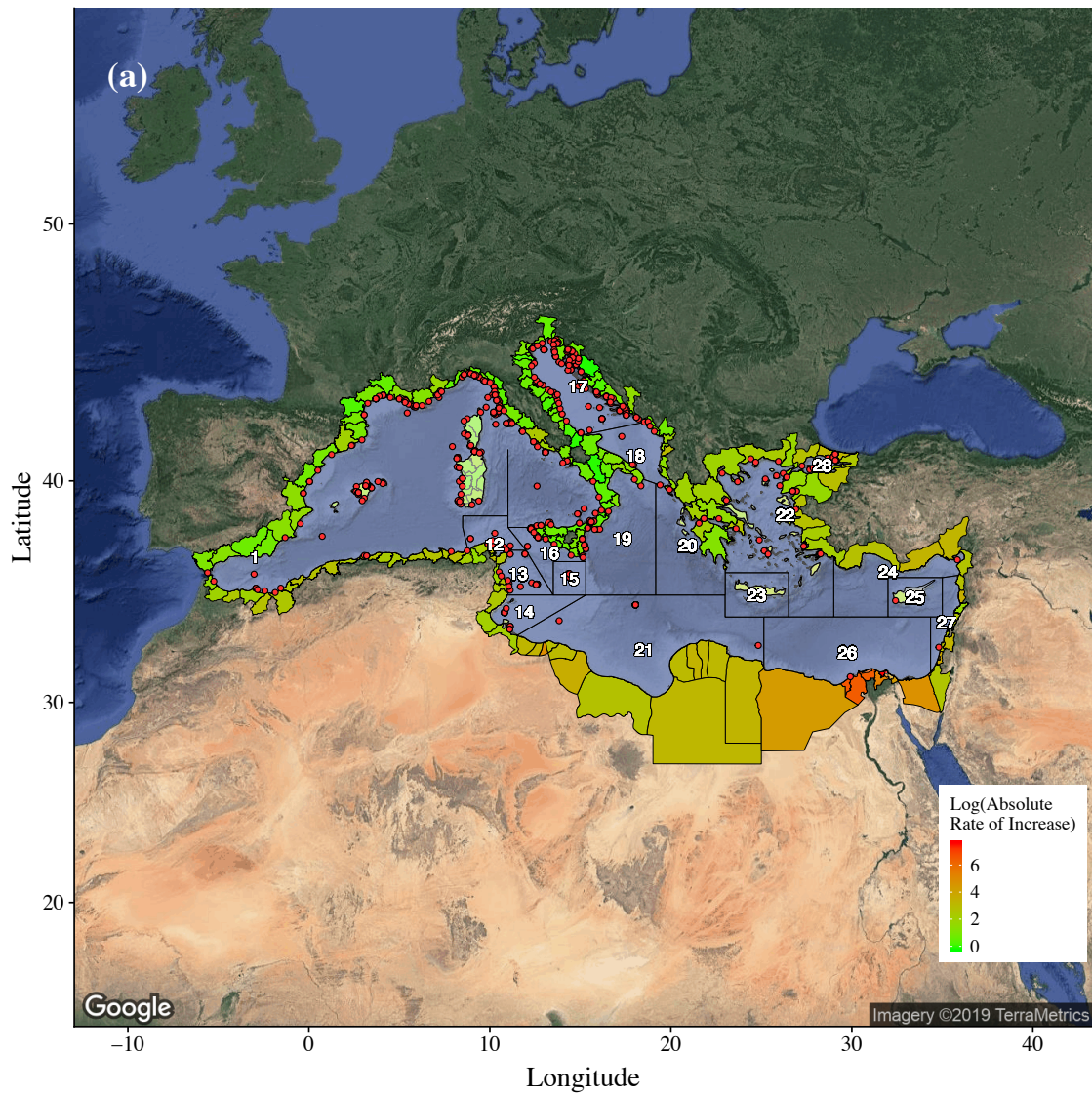
617 **Fig.2** Temporal and spatial changes of sighting rate estimated by the GSA Model. (a) Temporal effect: expected shark sighting rate between  
618 1860 and 2016 predicted by using a fixed observation effort of 5 million people. Magnitude of the detected decline, starting year, and p-  
619 value for the smooth term are shown in the top-right corner. The red line is the overall mean sighting rate. (b) Spatial effect: dots are the  
620 average variations in mean n° of shark detected in each GSA. Point color matches colors in the map. Segments indicate the confidence  
621 boundaries. (c) Spatial unit used in the model: GFCM Geographic Sub-Areas (as indicated in the Res. GFCM/33/2009/2). The green dots  
622 in the map correspond to the white sharks sighting locations extracted from a variety of source observations.

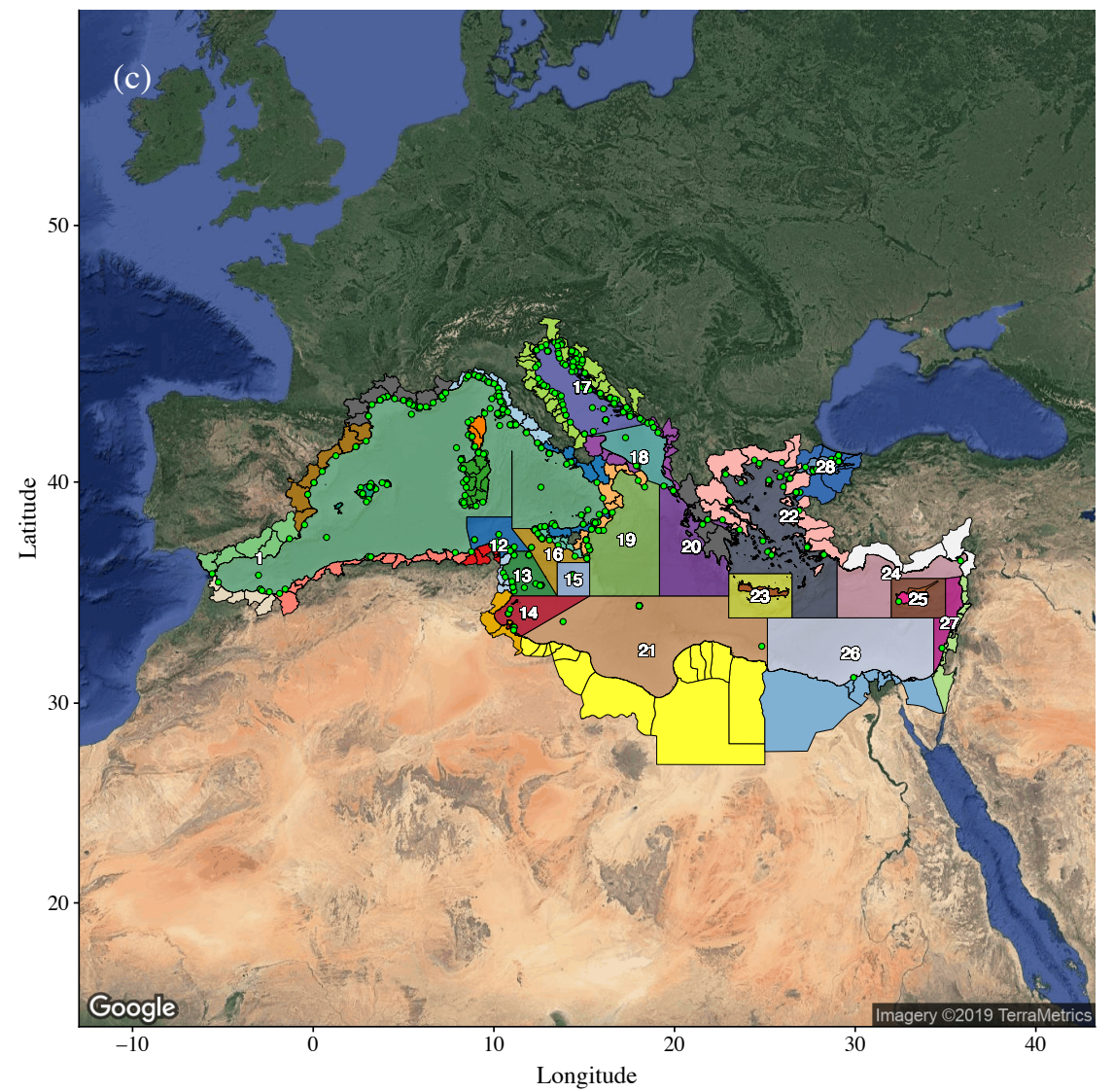
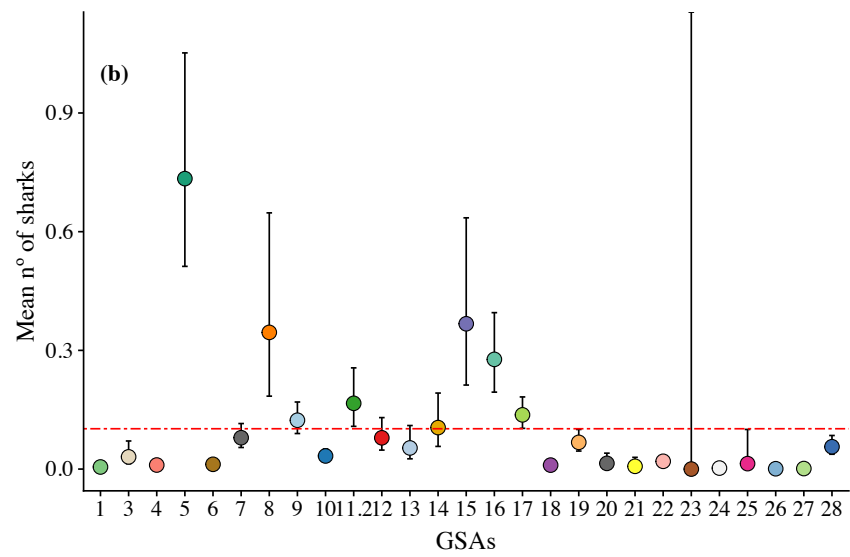
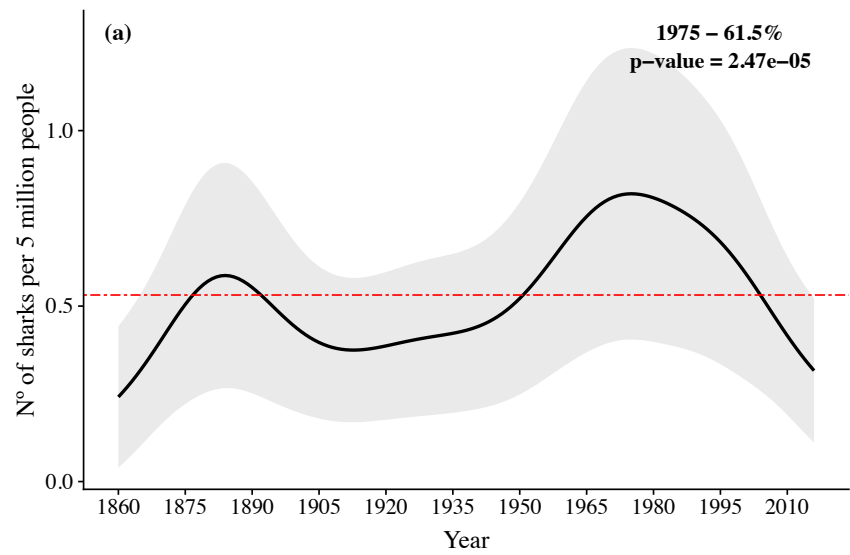
623 **Fig.3** FAO Model. (a) Mediterranean white shark temporal abundance trend (1860-2016) predicted by the FAO model in each FAO  
624 Division, considering a fixed observation effort value (5 million people). The black dots represent the actual sighting rates (expressed as  
625 n° of sightings per 5 million people) (b) Spatial unit used in the model: FAO Major Fishing Area 37 (Mediterranean and Black Sea)  
626 Divisions. The green dots in the map correspond to the white sharks sighting locations.

627 **Fig.4** Spatial range contraction. Predicted mean annual n° of sharks every 5 million people for each FAO Division in time intervals: (a)  
628 1945-1975, (b) 1976-2016. The red dots in the maps show the white sharks sighting locations in each period. (c) Variation between 1945-  
629 1975 and 1976-2016 time bins. Red sectors correspond to abundance rise, while blue sectors correspond to abundance decline.

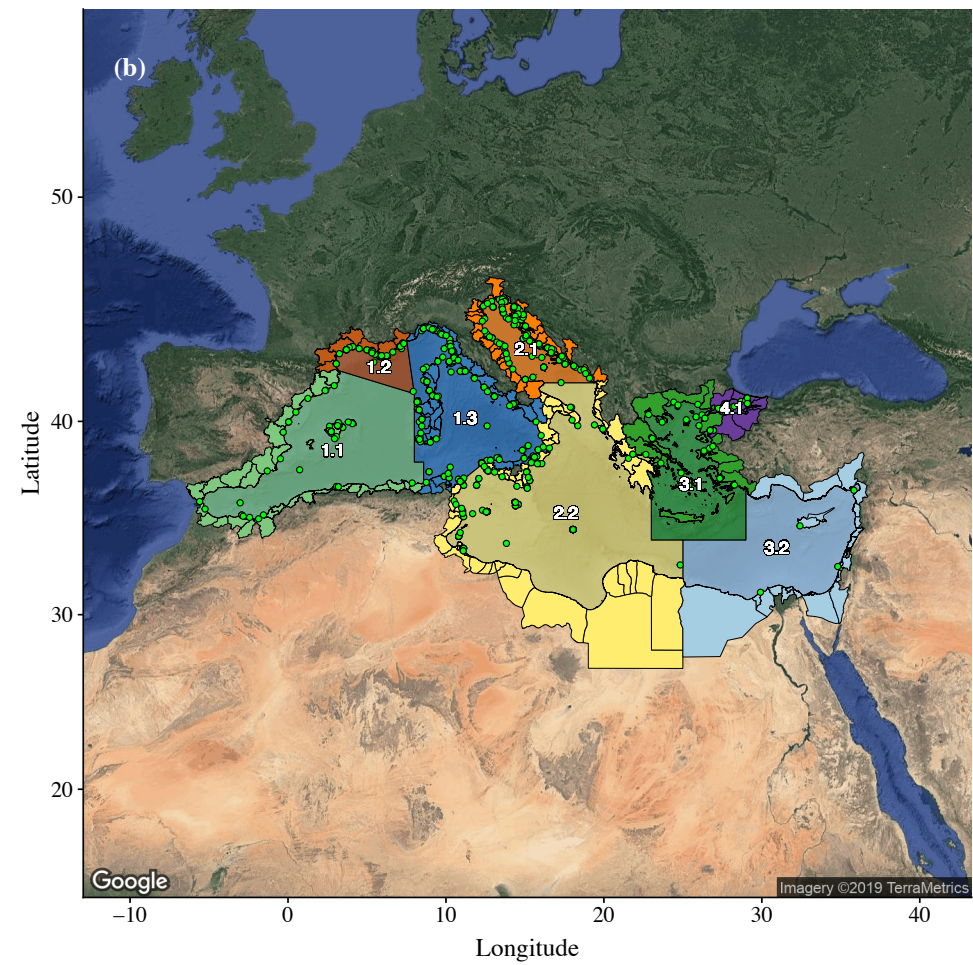
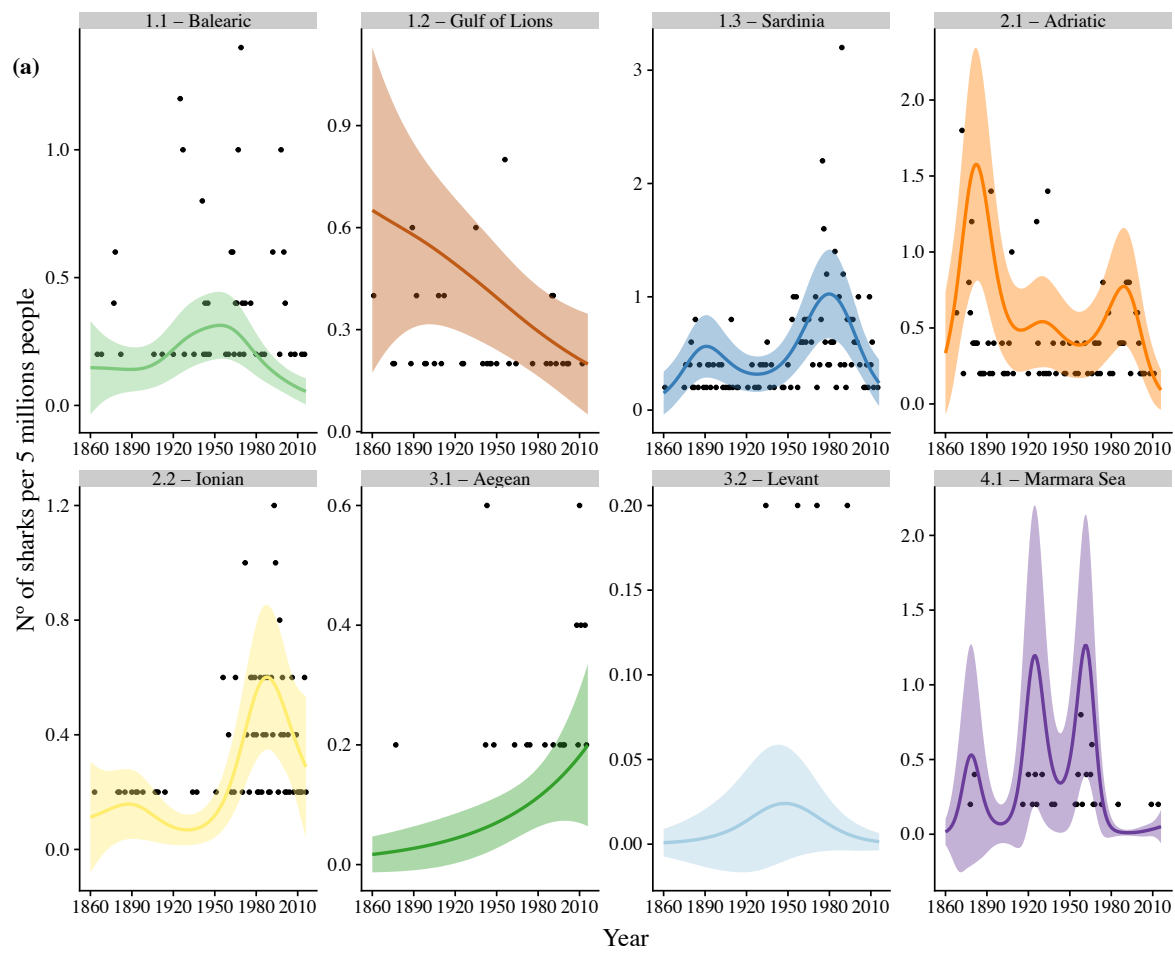
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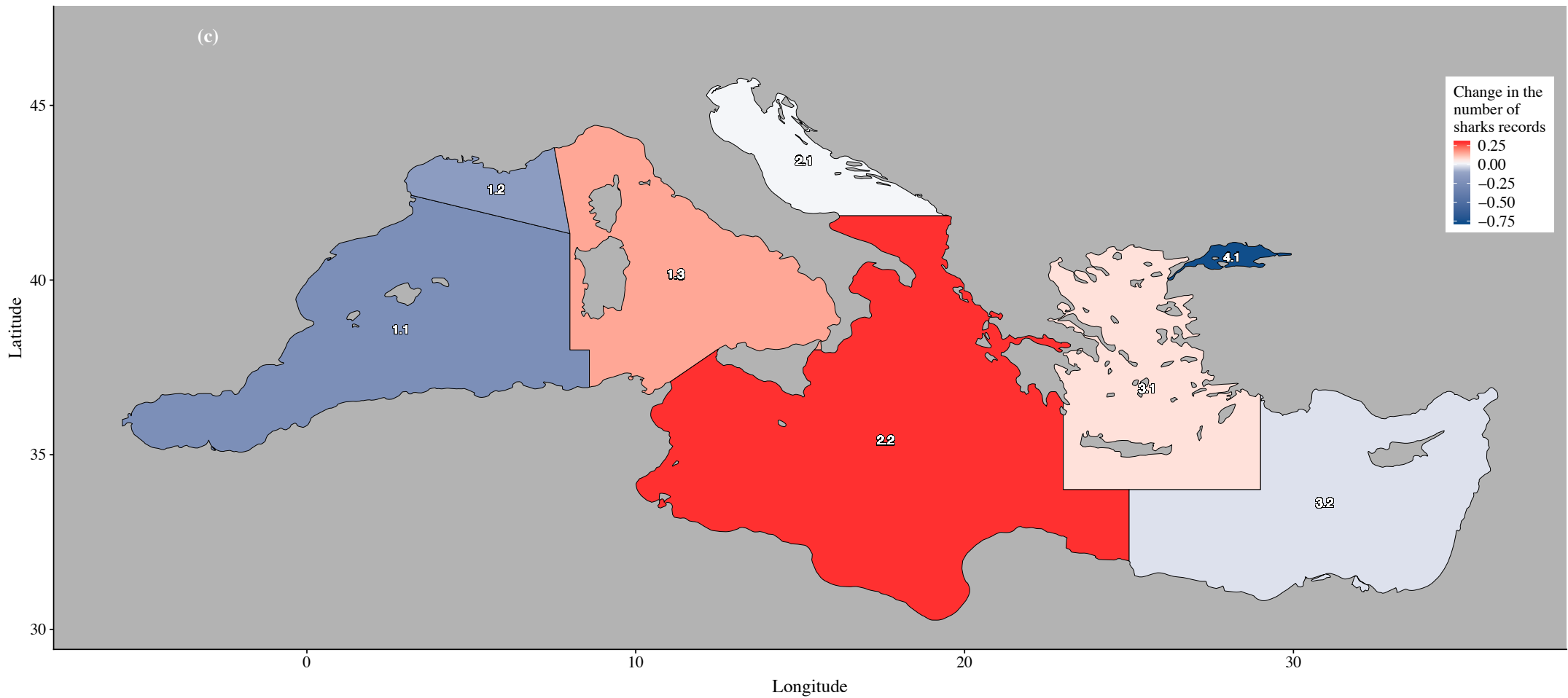
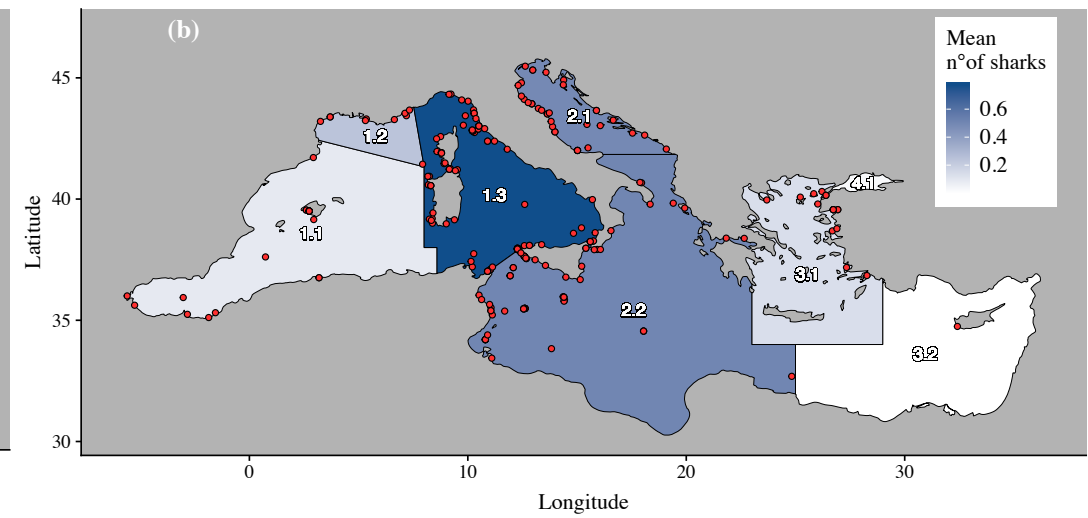
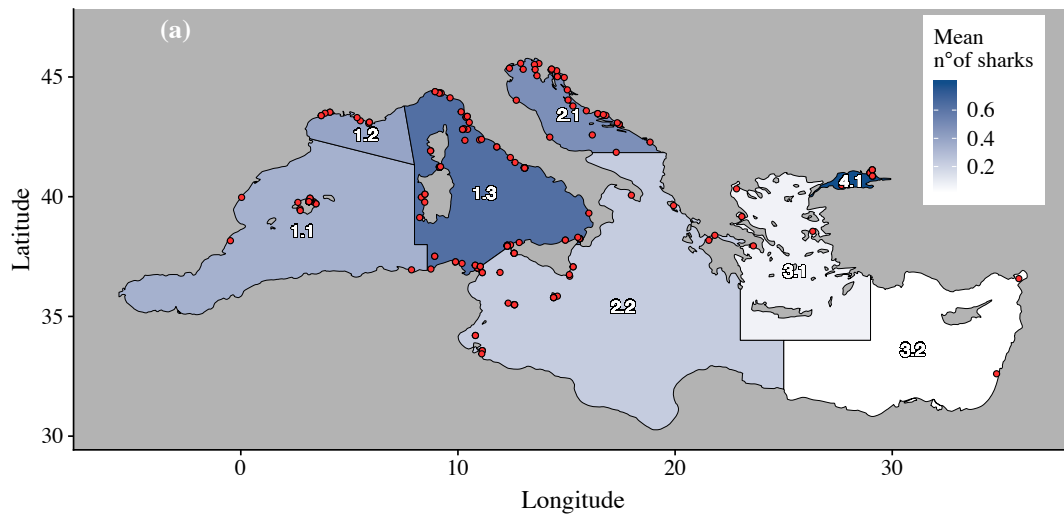
631











## 656 SUPPORTING INFORMATION

### 657 Shark data

#### 658 *Data collection*

659 Mediterranean white shark database was built up using multiple sources and different strategies. First, we  
660 reviewed all available historical and actual bibliographic references, including books and scientific papers.  
661 Second, we referred to the MedLem (Mediterranean Large Elasmobranchs Monitoring) database (Serena et al.  
662 2006) and collected all the records referring to *C. carcharias*. MedLem is a monitoring program, coordinated by  
663 the FAO's General Fisheries Commission for the Mediterranean Sea (GFCM), of large elasmobranch captures  
664 and sightings, collected by a network of Mediterranean research institutions, coastal enforcement and  
665 monitoring bodies (Serena et al. 2006). Third, we sifted through local news and fishing specialized websites  
666 (such as [www.sharkyear.com](http://www.sharkyear.com)), well-known online portals such as YouTube ([www.youtube.com](http://www.youtube.com)) and  
667 Facebook ([www.facebook.com](http://www.facebook.com)), and personal communications of shark sightings from local scientists, in  
668 order to identify unpublished records.

669 We validated each record by cross-checking each source reference. Furthermore, accordingly with other  
670 historical ecology bibliographic researches (Ferretti et al. 2016), we followed through each observation history  
671 to determine whether a record was original or redundant meaning that it was not reporting an undetected  
672 record but existing bibliographic references. Throughout this validation we have been able to erase all source-  
673 less observations and duplicates, assuming that each record of the dataset was referred to a unique specimen.  
674 After all, differences in size estimates joined with the fact that most of the shark sighted had been caught and  
675 then killed, reduce the likelihood that any single shark caused multiple records per year (McPhearson & Myers  
676 2009).

#### 677 *Data management*

678 Now, we will present all the variables included in the database and all criteria used to assemble them.

679 **ID – Identification number.** As assumed above, any record is referred to a single specimen. Consequently,  
680 we appointed each record to a specific identification number.

681 **Date and Season.** If available in the sources, year, month and day have been collected. Sighting date was not  
682 precisely reported from the original in most of the records referring to more than 150 years-old observations.  
683 Consequently, in such cases, the date has been approximated with the following criteria:

684 a) if original reference reported “before” – year, 1 year has been subtracted to referenced date; b) both in the  
685 case that original reference reported a time interval (instead of a specific year) and there were incongruities  
686 between sources, an average value has been taken in account.

687 The year was divided into four different seasons: winter (January through March), spring (April through  
688 June), summer (July through September) and fall (October through December).

689 **Specimen size.** Considering both the anecdotal nature characterizing the majority of our data and the long  
690 time passed from the direct observation for the oldest records, it may be expected that just in few cases size  
691 measurements have been taken using rigorous and modern techniques. Length and weight values, thus, has  
692 overall to be considered as approximations. However, although we do not have any control over the  
693 approximation degree used at the record collection time, it is necessary to explain the criteria we used to  
694 approximate the size data of our database. We used the following criteria:

- 695 1. We applied simple arithmetic mean to measurement values to solve source conflicts (sources  
696 indicating different values for the same specimen).
- 697 2. In case of measurement information associated with “>” or “<”, we added or subtracted one centimeter  
698 to the reported value.
- 699 3. If length or weight values were reported as “ca.” (circa), we assumed the source value as precise  
700 information.
- 701 4. If specimen length was measured using a different length type than Total Length (PRC – Precaudal  
702 Length, FOR – Fork Length, TOT – Total Length taken with caudal fin upper lobe lying on the main  
703 body axes), we converted it in Total Length through methods shown in

Country	Regional Data Source	National Data Source
Albania	INSTAT; worldbank; populstat.info	populstat.info
Algeria	worldbank; populstat.info	populstat.info
Bosnia and Herzegovina	worldbank; populstat.info	populstat.info
Croatia	eurostat; populstat.info	eurostat; populstat.info
Cyprus	eurostat; populstat.info	
Egypt	worldbank; populstat.info	populstat.info
France	INED; populstat.info	INED; populstat.info
Gibraltar	Gibraltar Government	
Greece	eurostat; populstat.info	eurostat; populstat.info
Israel	citypopulation.de; populstat.info	populstat.info
Italy	ISTAT	
Lebanon	worldbank; populstat.info	populstat.info
Libya	populstat.info	populstat.info
Malta	eurostat; populstat.info	
Monaco	eurostat; populstat.info	
Montenegro	worldbank	worldbank
Morocco	populstat.info	worldbank
Palestina	populstat.info; ONU (for Gaza Strip)	
Slovenia	eurostat; populstat.info	eurostat; populstat.info
Spain	INE; populstat.info	
Syria	citypopulation.de; populstat.info	populstat.info
Tunisia	INS; populstat.info	INS; populstat.info
Turkey	eurostat; worldbank; populstat.info	eurostat; populstat.info

704 5. .

705 *Predicting total length and weight missing values*

706 We investigated the length-weight relationship to predict missing values belonging to these two variables.  
707 This relationship tends to have two main characteristics in a fishing stock. First of all is not linear. This can be  
708 easily understood considering length as a linear measure, while weight is related to a volume. Second, the  
709 variance of weight increases with fish development. Thus, mainly for these two features, length-weight data  
710 use to violate the linearity and homoscedasticity assumption of a simple linear model. Commonly the  
711 relationship is modeled as a two-parameter power function with a multiplicative error term, as:

$$712 \quad W_i = aL_i^b e^{\epsilon_i} \quad (1)$$

713 where  $a$  and  $b$  are constants and  $\epsilon_i$  is the multiplicative error term for  $i$ th measurement. This model (1) can be  
714 linearized applying a logarithmic transformation in both side of the equation, as:



715 
$$\log(W_i) = \log(a) + b\log(L_i) + \epsilon_i \quad (2)$$

716 Thus, with  $y = \log(W)$ ,  $x = \log(L)$ , slope =  $b$ , e intercept =  $a$ , the model assumes the form of a simple linear  
717 regression. The other benefits of this transformation, beyond of linearity, is to make the errors additive and  
718 stabilizing the variance about the model. We used our observed length and weight data to examine the  
719 Mediterranean white shark length-weight relationship (Fig. 5c). Furthermore, the obtained regression line  
720 has been used to predict the total length and weight missing values included in the database. Normally, back-  
721 transforming the estimates on the log scale with a simple exponentiation use to underestimate the value in the  
722 original scale. Indeed, the back-transformed mean value from the log scale corresponds to the geometric mean  
723 values on the original scale. The geometric mean is always less than the arithmetic one, thus, a correction factor  
724 is needed to obtain rigorous estimates. The most common "correction" used for log-transformed data is that  
725 suggested by Baskerville (1972), multiplying the exponentiated back-transformed value by:

726 
$$e^{\frac{s^2_{y|x}}{2}} \quad (3)$$

727 Finally, the "observed" data regression line has been compared with the already existing regression lines  
728 describing the same relationship for other white sharks populations worldwide (Fig. 5a-b-d).

729 **Gender and Age.** We reported, if available, the specimen sex collected by the original source. In the case of  
730 source conflicts, gender information has not been considered reliable and, consequently, it has not included  
731 in the dataset.

732 Age distribution has been assessed using both predicted and observed length values. Four age classes have  
733 been established on the basis of Bruce and Bradford (2012) categorization: young-of-the-year (YOY -  $\leq 1.75$  m  
734 total length, TL), juvenile (JUV -  $>1.75$ - $3.0$  m TL), subadult (SUB -  $>3.0$ - $3.6$  m TL for males and  $>3.0$ - $4.8$  m TL  
735 for females), adult (ADL -  $>3.6$  m TL for males and  $>4.8$  m TL for females). When sex was not recorded, sexual  
736 maturity threshold was set to the average value between males and females ( $>4.2$  m TL). All records lacking  
737 length estimate were classified as "Undetermined".

738 **Geographic position.** Coordinates of sightings or catch were sometimes included in the record. In most cases,  
739 landing harbor or sighting location was reported. When precise coordinates were not available, we geocoded

740 the occurrences using the Google Map Geocoding API and searching for location reported as text strings (eg  
741 “Capo Testa, Sardinia, Italy”).

742 **Record type.** We distinguished between six different occurrence type: sighting, catch, catch and release,  
743 stranding, attack on humans or boats, signs of predation on other marine species.

744 **Fishing gear.** To facilitate the analysis, in addition to the fishing gear reported by the original source, we  
745 aggregated fishing techniques in macro-categories, as follows: trawl, purse seine, gill nets (included trammel  
746 net), longline, tuna trap, harpoon, line (rod and line; hand-line), others.

747 **Stomach contents.** This variable includes all information reported by the original source: species (if identified)  
748 or common name; quantity (if reported); weight (if reported).

749 **Museum collections.** We collected museum of provenance and catalog number of each Mediterranean white  
750 shark item hosted in European museums.

751 **Source and Reference.** Record origins have been distinguished in two different variables. Reference is referred  
752 to the scientific publication or database which record has been taken from, while source indicates all other  
753 authors reporting the same occurrence. In addition, a third variable reporting direct sighting observers’ names  
754 was attached to the data table. All records lacking one of this information have been rejected.

755 **Additional information.** For each record, if available, the following information has been collected:  
756 pregnancy, distance from the shore, depth, availability of photographic or video material, any additional  
757 information reported in original sources.

## 758 **Exploratory Analysis**

759 Here we report the main additional patterns showed by the exploratory analysis. First, we analyzed the  
760 temporal distribution of the sightings for the entire temporal range spaced by the data. As expected, the  
761 sighting rate increased significantly in the last 150 years and consequently, we considered time bins not  
762 homogeneously distributed. Temporal classes were subdivided in the following way: 100 years between 1500  
763 – 1700; 25 years between 1700 – 1800; 10 years after 1800. Data showed an asymmetric distribution with most

764 of the observations concentrated in the last 100 years. From 1900 to today 617 specimens were recorded, which  
765 corresponds to 79.81% of the total observations in the database. The nineteenth century counted for 140  
766 observations, corresponding to 18.11% of the total records, while only 16 were attributable to the previous 300  
767 years, representing 2.07% only. Decades with the highest number of observations corresponds to the period  
768 1960 – 2000. The sum of the sightings recorded during this 40-year bin accounts for 44.63% of the total number  
769 of sightings. Referring to the 19<sup>th</sup> century, decades 1870 – 1880 showed the highest number of observations,  
770 corresponding to 35% of all sightings recorded in that century. Decades 1910 – 1920 and 1940 – 1950 exhibited  
771 a lower number of specimens recorded which could indicate a contemporary reduction of the observation  
772 effort in the area due to historical reasons (World Wars, 1918 Flu Pandemic).

773 Aggregating sightings in function of different Mediterranean countries, data showed a heterogeneous  
774 frequency distribution, with most of the records referring to just a few countries. For example, records located  
775 in Italian waters accounted for almost half of the total sightings. The sum of observations of the first six most  
776 represented countries (Italy, Croatia, Spain, France, Tunisia, and Turkey) corresponded to the 92.2% of the  
777 whole number of sightings. Consequently, the ten countries left accounted for less than 8%, with 2.5% of it  
778 formed by just the sightings recorded in Greek waters.

779 The descriptive analysis also showed a rare but constant presence of the species in the area throughout all  
780 seasons. Summer (36.57%) and Spring (30.74%) accounted for almost two-thirds of the observations, while  
781 Winter (19.26%) and Fall (13.42%) for the remaining third. In terms of monthly distribution, August (16.84%),  
782 May (12.06%), September (12.06%) and June (11.43%) were the most represented. The increase in the sighting  
783 rate detected during summer is probably imputable to touristic movements and a generalized increase of all  
784 ocean anthropogenic activities during these months.

785 We investigated the length-weight relationship of observed values through the linearization shown in  
786 equation 2. The high  $R^2$  (0.78) underlined a good adaptation of data to the model. The regression line was  
787 described by the following equation:

$$788 \quad y = -8.31 + 2.48x \quad (5)$$

789 where  $y$  is the  $\log(\text{Total Length})$  and  $x$  is the  $\log(\text{Total Weight})$ . Our results seemed to indicate that  
790 Mediterranean white sharks could be on average bigger than other conspecifics inhabiting the oceans  
791 worldwide. However, this result is likely partially biased by the fact that our database is unbalanced toward  
792 adult and sub-adult specimens.

### 793 **Stomach Content Analysis**

794 Normally, the stomach content analysis constitutes an important component of ecological investigation and is  
795 performed on the basis of robust both quantitative and qualitative data. Given the opportunistic nature of our  
796 data, we could count exclusively on qualitative data. First, we extracted from data all information regarding  
797 122 specimens reporting stomach content data ( $n = 95$ ), direct hunting episodes and opportunistic scavenging  
798 on carcasses ( $n = 27$ ) (Tab. 6). We identified 45 different prey item typologies, rarely identified to species level,  
799 and in 3 cases the stomach was empty. To simplify the analysis prey items have been gathered in main trophic  
800 categories, as follows: odontocetes, mysticetes, teleosts, other sharks, batoids, chelonians, terrestrial mammals  
801 (human being included), pinnipeds, birds, empty, inorganic matter.

### 802 **Observation effort data**

803 We collected historical population time series referring to 202 coastal regions included in our sampling design.  
804 First, we listed all administrative regions belonging to the 23 different Mediterranean countries, considering  
805 both the first and second level of administrative division. Administrative divisions correspond to the entire  
806 nation, regions, provinces, governorates, depending on the specific country. In order to obtain spatial strata  
807 spacing as much as possible the same surface, we selected different administrative levels for different  
808 countries, including, for example, the entire country extension for small nation (e.g. Monaco, Malta, Gibraltar),  
809 whereas provinces or regions were considered for large nations like Spain, France or Italy.

810 A time bin of 156 years has been taken into account, ranging between 1860 and 2016. Data has been collected  
811 using different sources (Tab. 2) that include both national census data and international databases.

812 As expected, considering the long time range we chose for our model, many regional time-series were largely  
813 incomplete, reporting regional census data just for recent years. By contrast, national census data were more  
814 complete, reporting data even for the earliest part of the time series. Consequently, in order to obtain better  
815 estimates, if possible, we inferred the regional population size starting from the national census data, assuming  
816 a simple proportional relationship between them, with the following method:

$$817 \quad P = \frac{P_r}{P_n} \quad (4)$$

818 where  $P_r$  is the regional population size of the earliest year available in the series,  $P_n$  is the national population  
819 size of the same year and  $P$  is the ratio between the two terms. We assumed that this ratio was constant in time  
820 and inferred the regional population size for all the previous years where national census data were available.  
821 Hence, we fitted a log-scale linear regression and a GAM (Generalized Addictive Model) to a dataset including  
822 all the 202 regional time series, to obtain annual estimates of human population size in each coastal region. In  
823 this way, the model guarantees the same error term for any regional time series. Both models were set to  
824 estimate a different trajectory for each coastal region. GAM models have been performed using “mgcv” R  
825 package. Restricted Maximum Likelihood (REML) was used to determine the number of GAM knots and AIC  
826 (*Akaike Information Criterion*) as the overall model selection criterion. Despite a little over-fit in some splines,  
827 GAM performed the best approximation in all regions but Gaza Strip (Palestine). GAM predictions previous  
828 to 1936 in this region were remarkably close to zero and, consequently, we preferred, in this case, log-  
829 regression predicted values.

830 Then, we aggregated the regional time series following the spatial stratification included in the shark  
831 abundance models, obtaining human population size trends between 1860 and 2016 both for Geographic Sub-  
832 Areas and FAO Divisions (**Errore. L'origine riferimento non è stata trovata.**).

### 833 **Trend Models in details**

834 In order to evaluate the best fitting model, we considered various methods and different strategies. The  
835 investigated parameters are:

836 **Temporal units.** We started using an annual time bin to evaluate the population abundance trajectory. Then  
837 we considered time bins of 5yr and 10yr. Two years bins were rejected because not significantly different from  
838 1yr bins.

839 **Spatial units.** In our models, we considered two different spatial stratifications.

840 1) **Mediterranean Geographic Sub-Areas (GSA)** ([http://www.fao.org/gfcm/data/map-geographical-](http://www.fao.org/gfcm/data/map-geographical-subareas/en/)  
841 [subareas/en/](http://www.fao.org/gfcm/data/map-geographical-subareas/en/)) - First, we took into account 27 of the 31 Mediterranean GSA, excluding GSAs 2-11.1-29-  
842 30 from the analysis. The first two are entirely surrounded by other GSAs and, consequently, the  
843 absence of coastline made impossible to associate them with an observation effort value. The latter  
844 two represent the Black Sea and Azov Sea, where no sightings were recorded. The only record  
845 belonging to GSA 2 was moved to GSA 3, while all records of GSA 13 spotted around the Pelagie  
846 Islands were moved to GSA 16 as part of the Italian territorial waters and, hence, related to the  
847 Agrigento province human population size.

848 2) **FAO Fishing Area 37 Divisions** (<http://www.fao.org/gfcm/data/map-geographical-subareas/en/>) - In  
849 order to increase the spatial aggregation level, we used eight of ten Mediterranean FAO Divisions as  
850 new spatial grids, excluding Black and Azov Sea areas as above.

851 **Model selection procedure.** In our modelling exercise we started from the simplest possible choice, then going  
852 towards more complex functions. Our main goal was to select a model framework supporting the finest  
853 possible spatiotemporal resolution. Firstly, we investigated linear relationships, considering Poisson and  
854 Negative Binomial as representative distribution and fitting GLMs, zero-inflated regressions (ZIP and ZINB)  
855 and Hurdle models to our data. Hence, we explored non-linear relationships, still maintaining the same  
856 reference distributions, through Generalized Additive Models (GAM). AIC, fitted deviance,  $R^2$ , log-likelihood,  
857 residuals analysis, and dispersion parameter have been computed as criteria to assess the overall model  
858 performance. We repeated this procedure for each temporal and spatial aggregation unit. Negative Binomial  
859 GAMs with 1-year as spatial resolution returned the best fitting results in terms of fitted deviance, residuals  
860 analysis, and AIC. Details of the fitting criteria of the best models are reported in Tab. 3.

861 **Relationship between response and observation effort.** In all our models we considered the observation  
862 effort as an offset term, assuming a linear relationship with the response variable. To verify this assumption,  
863 we fitted a second model including a spline on the human population abundance. We proceeded by dividing  
864 the dataset into training and testing sets, where the latter was obtained by building a simple random sample  
865 of 10% of the entire dataset. This resampling procedure was carried out 150 times and RMSEs were computed  
866 on the test sets for both models. Eventually, we compared the average RMSEs in order to evaluate the  
867 prediction errors of both models. Given that the two means differed at the third decimal figure (Tab. 5), we  
868 chose to include the observation effort as an offset term as it is the simpler model structure and would not  
869 entail any serious prediction loss. Furthermore, this model setting permitted us to estimate a standardized  
870 index of abundance for the Mediterranean white shark population (#records/coastal people).

871 **Random/hierarchical spatiotemporal effect.** We explored the possibility of a random effect related to the  
872 spatial or temporal unit. In spatial terms we included both spatial stratifications (GSAs and FAO Divisions),  
873 while, in order to test temporal effects, we divided our 156-year range in the following time bins:

- 874 - pre-war (1860 – 1913), WWI (1914-1918), inter-war (1919 – 1938), WWII (1939 – 1945), post-war (1946-  
875 2016);
- 876 - pre-war (1860 – 1913), war (1914 – 1945), post-war (1946 – 2016);
- 877 - pre-war (1860 – 1945), post-war (1946 – 2016);
- 878 - pre-industrial fishery (1860 – 1959), post-industrial fishery (1960 – 2016).

879 Hence, we discriminated our models in two different groups:

- 880 • M1 → models considering only fixed effects: GSA (or FAO Division) + temporal effect
- 881 • M2 → models gathering fixed and random effects.

882 M2 models were computed using both GAMMs (Generalized Additive Mixed-Effect Models) and LMEMs  
883 (Linear Mixed-Effect Models). Eventually, we combined all possible temporal and spatial effects for both  
884 model's classes. No significant differences were detected between time bins for M1 models, while none of the  
885 models converged, even after a high number of iterations, in M2 models.

886 **Number of knots for the smooth function.** In both models (FAO and GSA Model) we started estimating the  
887 number of knots for the GAM's smooth function via REML (Restricted Maximum Likelihood), testing our  
888 choice through the gam.check function (Wood, 2017). In this procedure we allocated the same number of knots  
889 to each sector's smooth function. Hence, including a factorial variable in the model and asking to the algorithm  
890 to estimate a different spline in each sector, some artifacts may be introduced when only few records are  
891 available for a specific sector. To validate our patterns, we estimated parallelly single-sector models and  
892 compared the trajectories of the two modelling approaches. As expected, the abundance trend locally  
893 estimated coincided with the general model in 6 out of 8 sectors (Fig. 7). Only Divisions 2.1 (Adriatic) and 4.1  
894 (Marmara Sea) returned different trajectories with more smoothed curves. However, it is important to  
895 underline that the two approaches gave back very similar results if considering the curves' tendencies and the  
896 magnitude of the decline inferred (Fig. 8).

897 **Tuna traps exclusion.** We found in our analysis that tuna traps surely represented a strong source of mortality  
898 for Mediterranean white sharks. Consequently, their dismantling in the second half of the 20<sup>th</sup> century could  
899 constitute a source of bias for our trend analysis. To test for this, we fitted the same model (FAO Model) to our  
900 data excluding, this time, all catches coming from tuna traps. No strong differences were detected between  
901 the two models in most of the sectors (Fig. 9) but the Balearic (1.1). This is expected because more than a half  
902 of records in that particular sector comes from tuna traps.

903

## 904 **Figures and Tables**

### *Length - Length*

Unknown Length	Known Length	a	b	Formula	Reference
PCR	TOT	7.975	1.245	TOT = a + b PRC	Compagno, 1984
TL	PRC	-0.095	0.855	PCR = a + b TL	Mollet & Caillet, 1996
TL	FOR	-5.744	0.944	TL = a + b FOR	Kohler <i>et al.</i> , 1996

905 Tab. 1 Methods used to convert length values in Total Length

Country	Regional Data Source	National Data Source
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<b>Albania</b>	INSTAT; worldbank; populstat.info	populstat.info
<b>Algeria</b>	worldbank; populstat.info	populstat.info
<b>Bosnia and Herzegovina</b>	worldbank; populstat.info	populstat.info
<b>Croatia</b>	eurostat; populstat.info	eurostat; populstat.info
<b>Cyprus</b>	eurostat; populstat.info	
<b>Egypt</b>	worldbank; populstat.info	populstat.info
<b>France</b>	INED; populstat.info	INED; populstat.info
<b>Gibraltar</b>	Gibraltar Government	
<b>Greece</b>	eurostat; populstat.info	eurostat; populstat.info
<b>Israel</b>	citypopulation.de; populstat.info	populstat.info
<b>Italy</b>	ISTAT	
<b>Lebanon</b>	worldbank; populstat.info	populstat.info
<b>Libya</b>	populstat.info	populstat.info
<b>Malta</b>	eurostat; populstat.info	
<b>Monaco</b>	eurostat; populstat.info	
<b>Montenegro</b>	worldbank	worldbank
<b>Morocco</b>	populstat.info	worldbank
<b>Palestina</b>	populstat.info; ONU (for Gaza Strip)	
<b>Slovenia</b>	eurostat; populstat.info	eurostat; populstat.info
<b>Spain</b>	INE; populstat.info	
<b>Syria</b>	citypopulation.de; populstat.info	populstat.info
<b>Tunisia</b>	INS; populstat.info	INS; populstat.info
<b>Turkey</b>	eurostat; worldbank; populstat.info	eurostat; populstat.info

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**Tab. 2 Table reporting both national and regional population census data sources for each Mediterranean country.**

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Code	C	D	N	TU	SU	R <sup>2</sup> or FD	LL	AIC	Theta	R
GSA Model	GAM	NB	4239	1 year	GSAs	35.6		3216.6	0.445	normality
ZINB-1C	Zero-inflated GLM	NB	4239	1 year	GSAs		-1589	3240.7		non-normality
GLM_2	GLM	NB	4239	1 year	GSAs	34.10		3236.7	0.418	non-normality
ZIP-1C	Zero-inflated GLM	Poisson	4239	1 year	GSAs		-1663	3386.5		non-normality
GLM_1	GLM	Poisson	4239	1 year	GSAs	29.82		3529.5		non-normality
FAO Model	GAM	NB	1256	1 year	Divisions	36.8		2083.4	1.327	normality
ZINB-N1A	Zero-inflated GLM	NB	1256	1 year	Divisions		-1086	2210.2	1.574	non-normality
GLM_3	GLM	NB	1256	1 year	Divisions	20.47		2232.6	0.756	non-normality

908 **Tab. 3 Model fit statistics of the best models used to estimate the abundance trends. Code = model's identifier; C =**  
 909 **model's class; D = statistical distribution; N = number of observations; TU = temporal unit; SU = spatial unit; R<sup>2</sup> or FD**  
 910 **= adjusted R-square or fitted deviance; LL = log-likelihood; Theta = dispersion parameter; R = residuals analysis.**

911

Code	Fitted Deviance	N° of Knots (GCV)	Smooth Term P-value
FAO Model	36.8	10	
- Sector 1.1		10	0.01022
- Sector 1.2		10	0.07214
- Sector 1.3		10	0.00113
- Sector 2.1		10	0.00134
- Sector 2.2		10	4.25e-05
- Sector 3.1		10	0.02946
- Sector 3.2		10	0.44554
- Sector 4.1		10	1.03e-05
Single-sector 1.1	7.29	10	0.106
Single-sector 1.2	3.57	10	0.075
Single-sector 1.3	18.80	10	4.82e-05
Single-sector 2.1	3.86	10	0.0185
Single-sector 2.2	32.0	10	7e-08
Single-sector 3.1	7.92	10	0.0408
Single-sector 3.2	12.6	10	0.438
Single-sector 4.1	31.4	10	0.00031

912 **Tab. 4 FAO Model and Single-sector models in details.**

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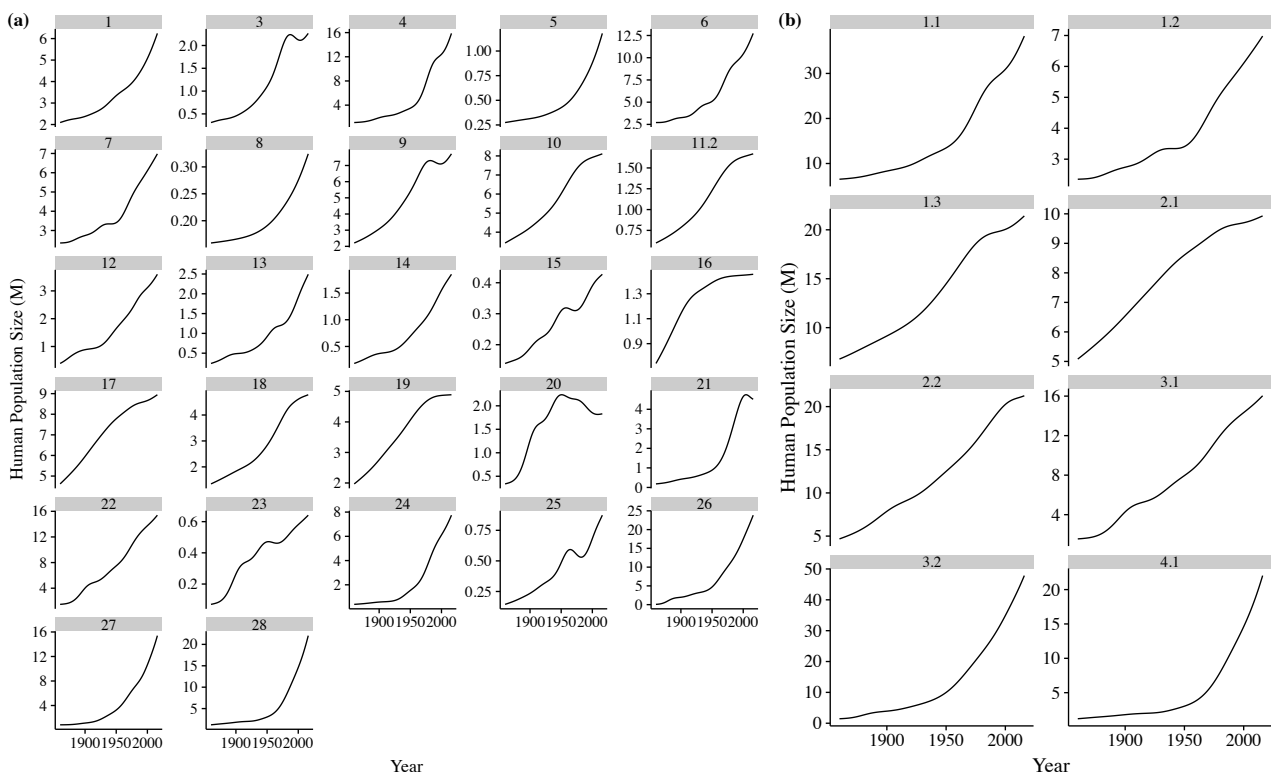
Model Type	Mean Value of RMSE
GAM with Obs. Effort as offset term	0.599
GAM with a spline on the Obs. Effort	0.640

916 **Tab. 5 Mean value of RMSEs for the two tested models calculated after 150 resampling procedure.**

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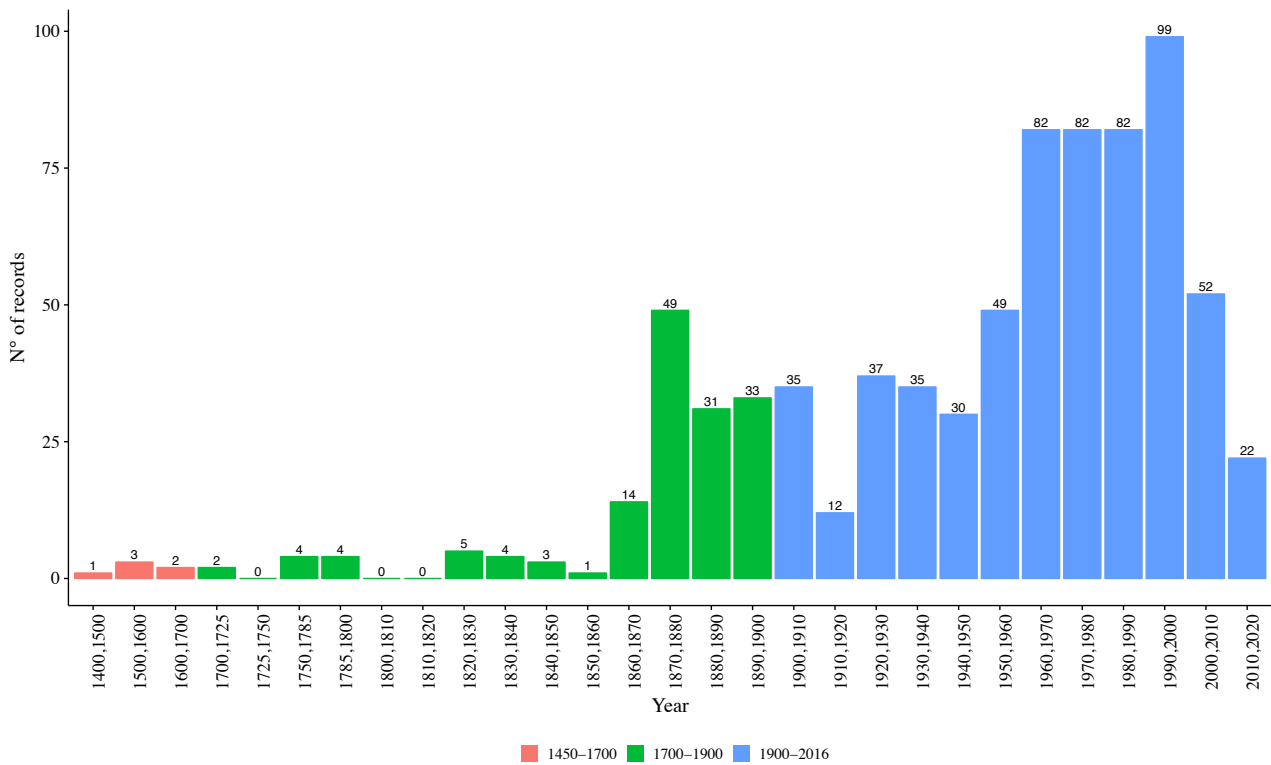
Taxonomic Group	Trophic Category	Family	Species	TOT	YOY	JUV	SUB	ADL
Bird	Bird	Laridae	Unidentified seagull	3				1
Bird	Bird	Unidentified bird	Unidentified bird	1			1	
Bird	Bird	Diomedidae	Unidentified albatross	1				1
Chondrichthyans	Batoids	Unidentified family	Unidentified ray	2				2
Chondrichthyans	Other sharks	Alopiidae	<i>Alopias vulpinus</i>	2			1	1
Chondrichthyans	Other sharks	Carcharhinidae	<i>Prionace glauca</i>	1				1
Chondrichthyans	Other sharks	Lamnidae	<i>Isurus oxyrinchus</i>	1				1
Empty	Empty	Empty	Empty	3			1	2
Inedible object	Inedible object	Inedible object	Inedible object	20	2	1	2	13
Marine mammal	Mysticetes	Balaenopteridae	<i>Balaenoptera physalus</i>	2				1
Marine mammal	Mysticetes	Physeteridae	<i>Physeter macrocephalus</i>	2				
Marine mammal	Mysticetes	Unidentified family	Unidentified Mysticete	2				
Marine mammal	Odontocetes	Delphinidae	<i>Delphinus delphis</i>	1				1

Marine mammal	Odontocets	Delphinidae	<i>Stenella coeruleoalba</i>	7	1	2
Marine mammal	Odontocets	Delphinidae	<i>Tursiops truncatus</i>	5	2	1
Marine mammal	Odontocets	Delphinidae	<i>Grampus griseus</i>	1		
Marine mammal	Pinnipeds	Phocidae	<i>Monachus monachus</i>	2		2
Marine mammal	Odontocets	Phocoenidae	<i>Phocoena phocoena</i>	2	1	1
Marine mammal	Odontocetes	Unidentified family	Unidentified Odontocete	28	1	23
Mollusca	Mollusc	Unidentified mollusc	Unidentified mollusc	1	1	
Mollusca	Mollusc	Unidentified squid	Unidentified squid	1		1
Reptile	Chelonians	Cheloniidae	<i>Chelonia mydas</i>	1		1
Reptile	Chelonians	Cheloniidae	<i>Caretta caretta</i>	5	1	2
Reptile	Chelonians	Cheloniidae	Unidentified turtle	6		4
Teleost	Teleost	Belonidae	<i>Belone belone</i>	1	1	
Teleost	Teleost	Clupeidae	<i>Sardina pilchardus</i>	1		1
Teleost	Teleost	Lophiidae	<i>Lophius spp.</i>	1	1	
Teleost	Teleost	Merlucciidae	<i>Merluccius merluccius</i>	1	1	
Teleost	Teleost	Molidae	<i>Mola mola</i>	1		1
Teleost	Teleost	Scombridae	<i>Thunnus spp.</i>	19		17
Teleost	Teleost	Scombridae	<i>Thunnus thynnus</i>	3		3
Teleost	Teleost	Scombridae	<i>Sarda sarda</i>	3	1	2
Teleost	Teleost	Scombridae	<i>Auxis rochei</i>	1		1
Teleost	Teleost	Scombridae	<i>Thunnus alalunga</i>	1	1	
Teleost	Teleost	Scorpaenidae	<i>Scorpaena spp.</i>	1		1
Teleost	Teleost	Sparidae	<i>Dentex dentex</i>	1		1
Teleost	Teleost	Unidentified family	Unidentified teleost	8	1	6
Teleost	Teleost	Xiphiidae	<i>Xiphias gladius</i>	6		4
Terrestrial mammal	Terrestrial mammal	Bovidae	<i>Ovis aries</i>	1		1
Terrestrial mammal	Terrestrial mammal	Bovidae	<i>Capra hircus</i>	3		3
Terrestrial mammal	Terrestrial mammal	Bovidae	<i>Bos taurus</i>	1		1
Terrestrial mammal	Terrestrial mammal	Canidae	<i>Canis lupus familiaris</i>	2	1	1
Terrestrial mammal	Terrestrial mammal	Equidae	<i>Equus caballus</i>	1		
Terrestrial mammal	Terrestrial mammal	Felidae	<i>Felis silvestris catus</i>	1	1	
Terrestrial mammal	Terrestrial mammal	Hominidae	<i>Homo sapiens</i>	18	2	10
Terrestrial mammal	Terrestrial mammal	Suidae	<i>Sus scrofa domesticus</i>	1		1



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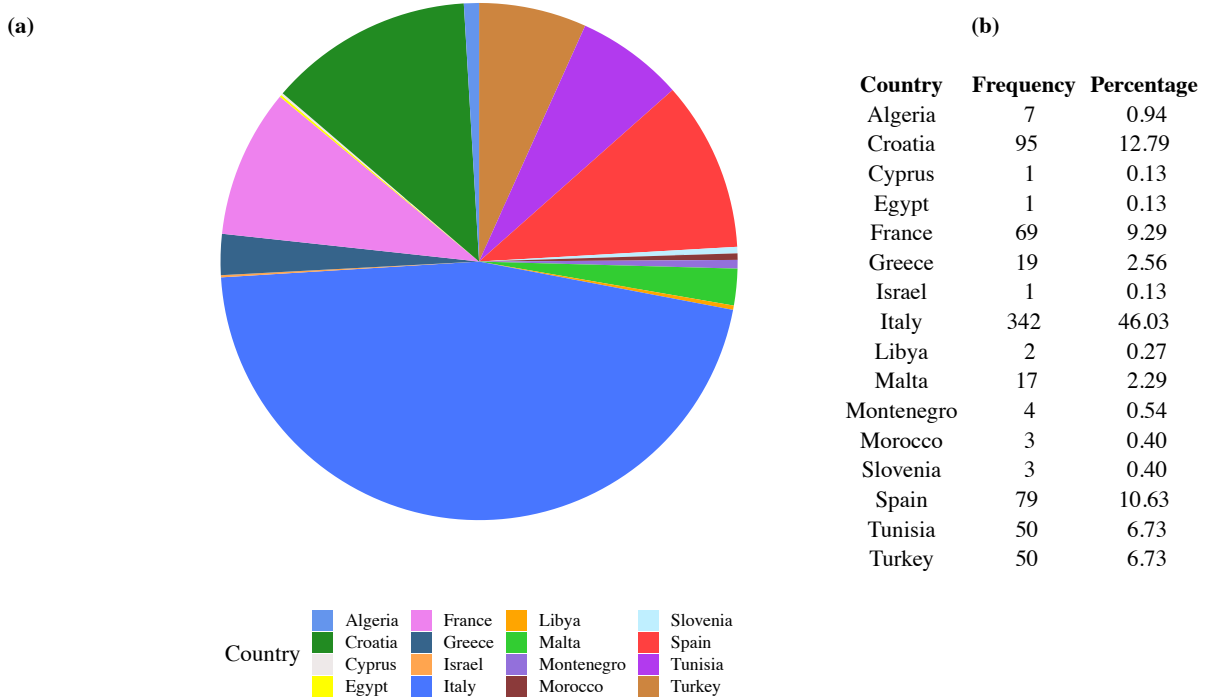
920 Fig. 1 Human population size trajectories both for GSAs (a) and FAO Divisions (b).



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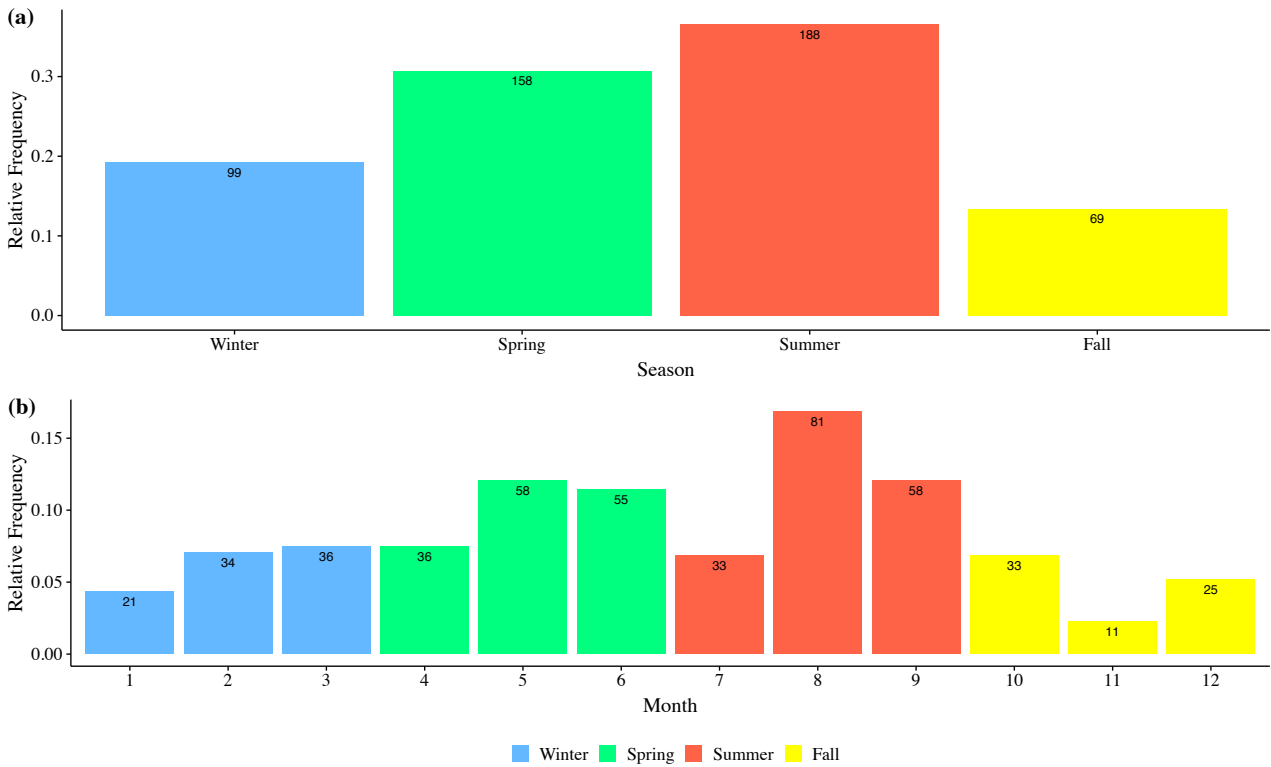
Fig. 2 Sightings temporal distribution. Colors correspond to macro-temporal periods. The specific number of recorded sightings is reported over each bar.

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Fig. 3 (a) Pie chart reporting the sightings distribution in function of Mediterranean countries. (b) Table reporting the number of specimens recorded in each country and the relative percentage.

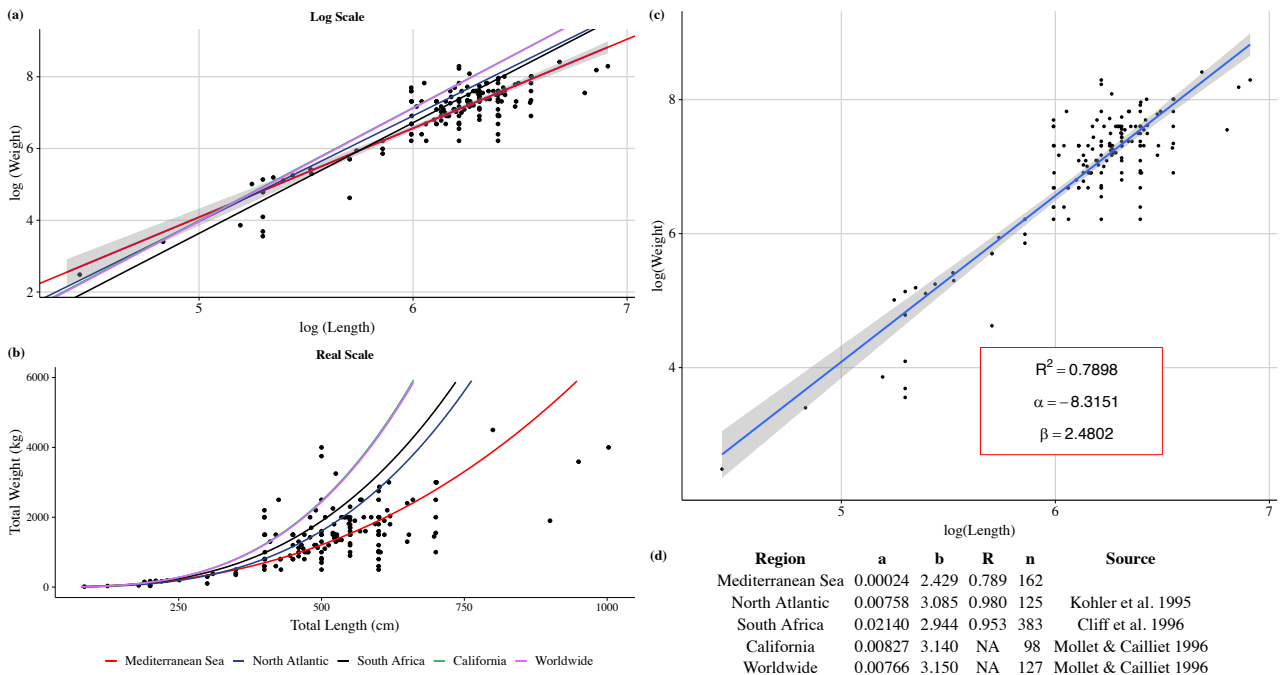


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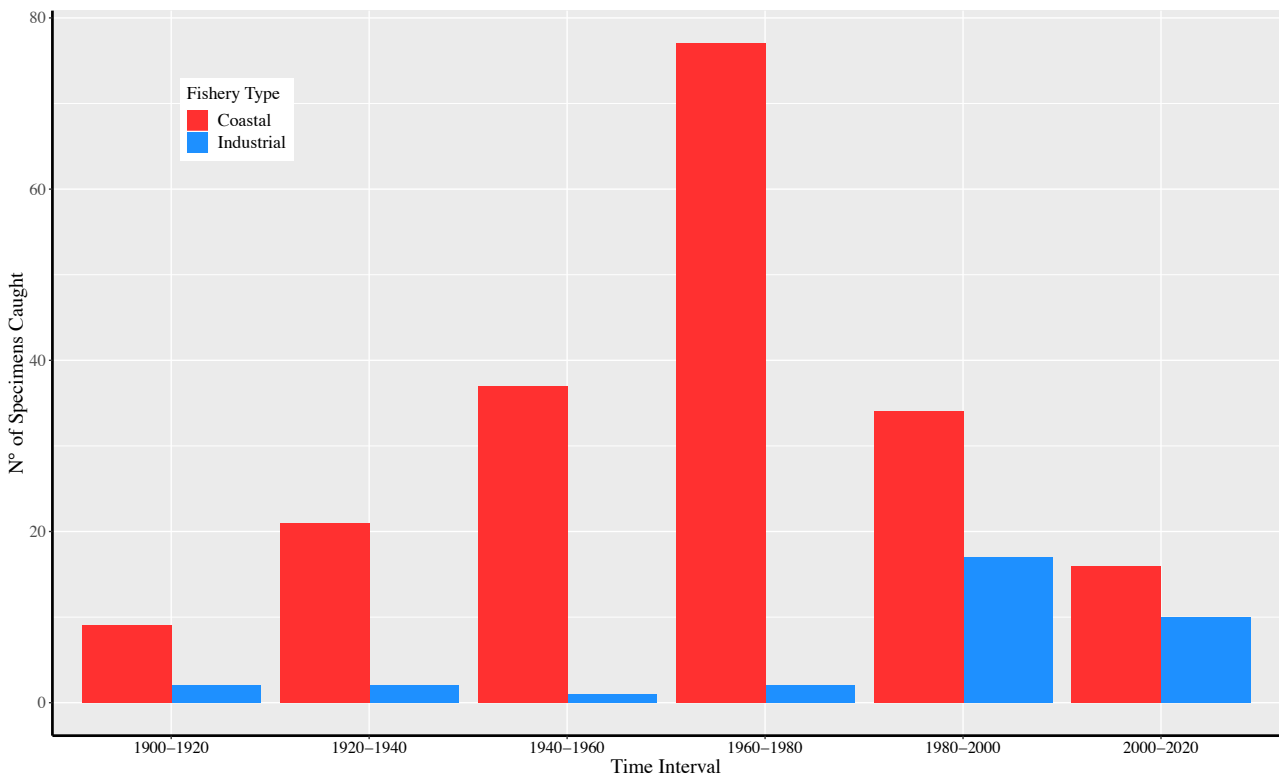
Fig. 4 Seasonal (a) and monthly (b) distribution of the shark sightings. The precise number of specimens recorded is reported over each bar. Colors match with seasons in both panels.

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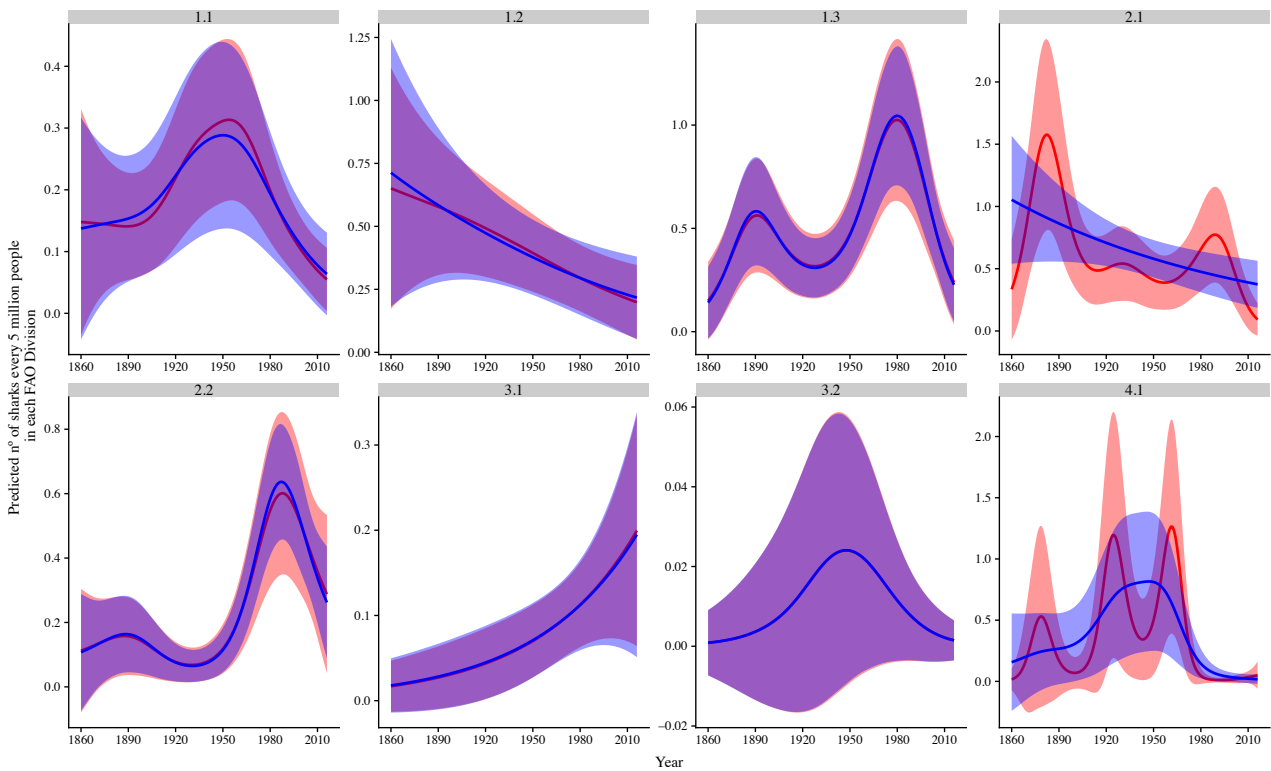
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937 **Fig. 5** Length-Weight Relationship in log scale (a) and natural scale (b) for Mediterranean white sharks (c) and other  
 938 white shark populations (a-b) distributed worldwide. (d) Table reporting intercept, a, slope, b, R<sup>2</sup>, number of specimens  
 939 sampled, n, and source of each regression line.



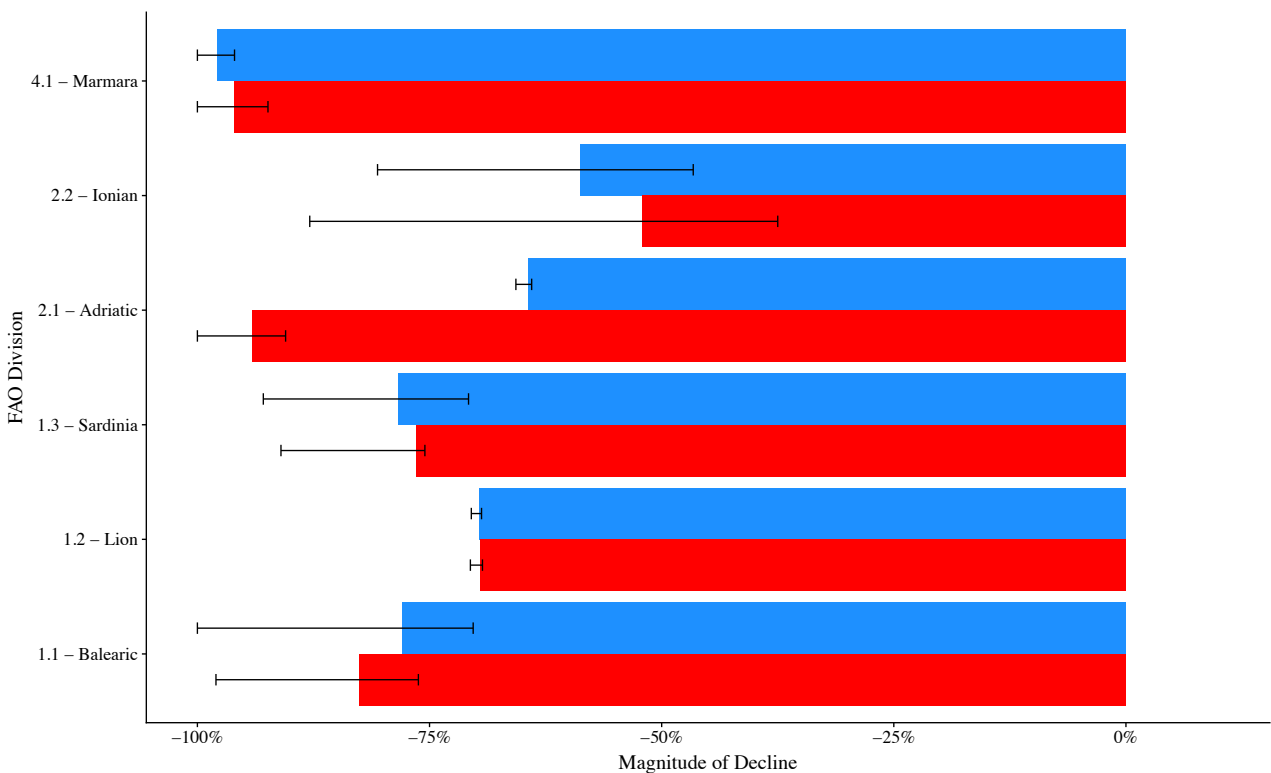
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941 **Fig. 6** White shark catches produced by coastal and industrial fishery in the period 1900-2016. Fishing gears have been  
 942 categorized in the following way: Industrial – Trawl, Purse Seine and Longline; Coastal – Gillnets, Harpoon, Tuna  
 943 Trap, Line, Others.



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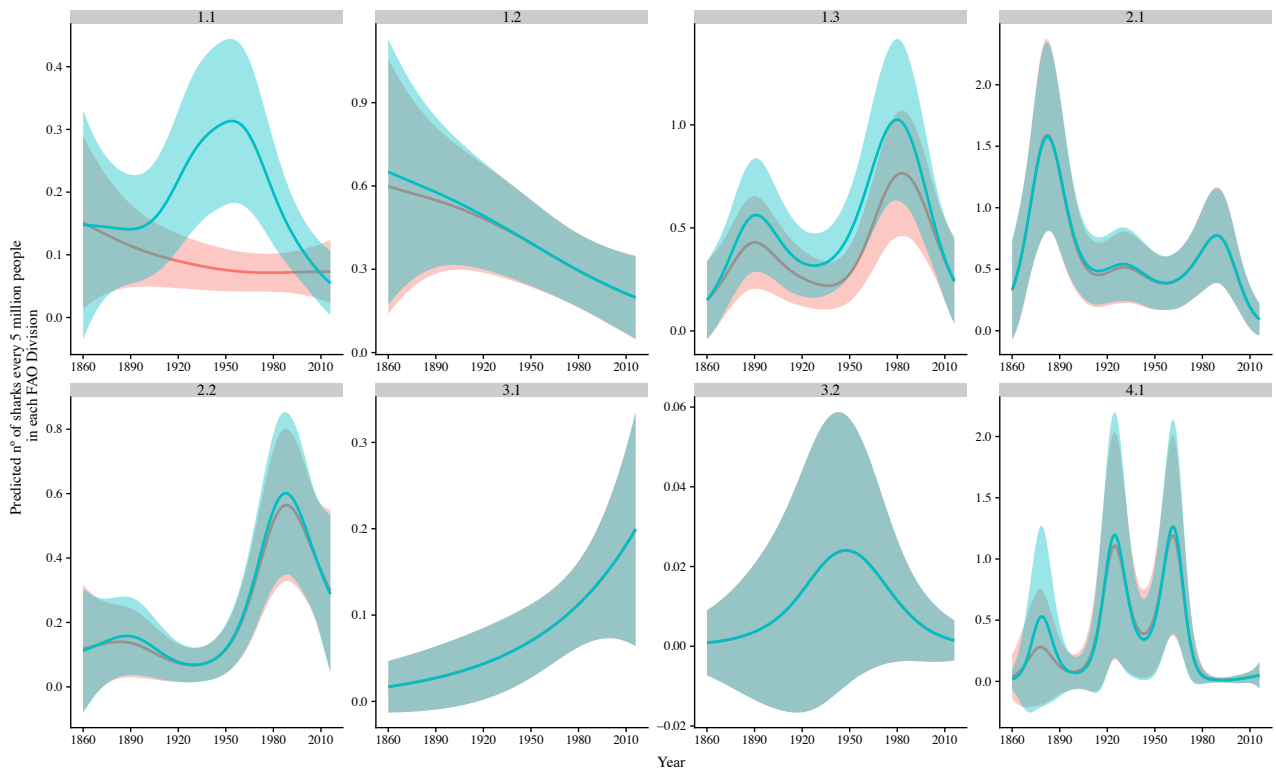
**Fig. 7 Single-sector models (blue) and FAO Model (red) trajectories comparison in each FAO Division.**



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**Fig. 8 Comparison between the Single-sector models (blue) and the FAO Model (red) in terms of magnitude of decline.**

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**Fig. 9 Comparison between the trajectories predicted by the FAO Model (aquamarine) and trajectories obtained excluding from the analysis all the tuna trap catches (red).**

954 **Literature Cited**

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