Thermal heterogeneity along the migration corridors of sea turtles: implications for climate change ecology

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12   **Abstract**

13

14   Increased temperatures caused by anthropogenic climate change are becoming a

15   major challenge for species. In particular, species that migrate over long distances

16   are affected by altered climatic conditions at the various sites they frequent and en

17   route. Here, we investigated whether climatic conditions experienced by sea turtles

18   during their migration would change in the future. We focused on the post-nesting

19   migrations of female loggerhead sea turtles (*Caretta caretta*) in the Mediterranean

20   region, to explore climatic variability along four main corridors and their surrounding

21   environment. We also modeled the impact of earlier onset of migration, as a potential

22   adaptive behavioral response of Mediterranean loggerheads. We found that over the

23   next 80 years, sea turtles will be exposed to significant increases in sea surface

24   temperatures (SSTs) along their key migration corridors and the surrounding area

25   (mean rate of 0.24 ºC increase per decade). The projected increase in SST falls

26   outside the range of SSTs currently reported within the examined corridors, but falls

27   below the threshold defined as the upper thermal limit for this species. A highly

28   variable climatic mosaic was identified within the distinct segments of the corridors.

29   We found no evidence to support that phenological shifts might result in turtles being

30   exposed to climatic conditions that are similar to current levels in the future. Our

31   outputs offer the first comprehensive spatial assessment of climatic patterns along

32   extended areas used for the migration of sea turtles and highlight the need to quantify

33   the relationship between altered conditions and species physiological and energetic

34   status. This regional analysis could provide a background methodological framework

35   for mapping and assessing spatiotemporal patterns of climatic variability along

36   migratory areas of marine megafauna.

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1. Introduction

The rapidly changing climate means that species must develop adaptive responses fast enough to ensure a window of favorable conditions for their activities, or go extinct (Visser and Both, 2005; Bellard et al., 2012). This challenge is particularly great for migratory species, while even though they are mobile and they might be expected to track changes, they are affected by altered climatic conditions at the various sites they frequent (e.g., breeding, foraging, wintering grounds) on an annual basis (Santangeli and Lehikoinen, 2017). For such species, long distance travel is an enormous physical task, with high energy demands (Hays and Scott, 2013), which could further increase the temporal and spatial window that individuals are exposed to changing climatic characteristics. Therefore, it is important to explore the dynamics of climatic conditions during migration to evaluate the full range of potential impacts of climate change on mobile species (Ahola et al., 2004; Both, 2010).

Migratory marine species are prone to altered climatic conditions in oceanic habitats with increased temperatures also altering their distributional range (e.g., whale shark; Sequeira et al., 2014) and triggering behavioral responses such as phenological shifts (e.g., beluga whales; Hauser et al., 2017). In addition, variability in ocean temperatures cause changes in migration routes (e.g., elephant seal; Bestley et al., 2012), with pelagic marine species migrating through alternative habitats to capture favorable conditions (Beaugrand and Kirby, 2018). Ocean temperature is also tightly related to the physiological responses and energy expenditure, especially for marine ectothermic species (Williard, 2013), with the low metabolic rate allowing the efficient use of their energy reserves, particularly during long periods of migration (Hays et al., 2014). Yet, most studies for migratory species continue to focus on climatic effects at departure and arrival destinations (e.g., Muhling et al., 2011; Hauser et al., 2017) or at intermediate sites (i.e., stopover sites, Dias et al., 2010; Studds et al., 2017) during migration.

The ability to quantify how environmental conditions vary during the course of migration is critical towards assessing species fitness and performance (Anderson et al., 2013). At the same time, such information could inform us of whether phenological shifts (i.e., changes on the timing of seasonal biological events; Walther

76 et al., 2002) are efficient mechanisms for coping with climate change at different

77 periods of life cycle. For example, an onset of the seaward migration of young

78 anadromous Atlantic salmon (*Salmo salar*), driven by environmental cues in the

79 freshwater habitat (e.g., water temperature, flow, turbidity), leads to adverse

80 conditions in the marine environment (predators, pathogens, feeding opportunities,

81 ocean temperatures), posing serious limitations to individuals' performance (Otero et

82 al., 2014). Under this context, phenological responses that are provoked by cues (e.g.,

83 energy reserves, climate) perceived at sites located far from the destination could

84 result in maladaptation, such as asynchrony with trophic resources or anticipation of

85 unfavorable weather conditions (Thackeray et al., 2010; Åkesson et al., 2017).

86 Therefore, it is important to understand whether potential changes to the initiation of

87 migration will ensure that favorable climatic conditions are maintained throughout the

88 migration route.

89

90 Sea turtles represent an ideal model for exploring the dynamics of climate change

91 during migration. They have a complex life cycle with distinct foraging and breeding

92 grounds that may be distant (up to 2800 km for hard-shelled sea turtles; Hays and

93 Scott, 2013). Research on the potential impacts of sea turtles to climate change has

94 focused on various aspects at breeding (e.g., Poloczanska et al., 2009; Witt et al.,

95 2010), and foraging sites (e.g., Hazen et al., 2013; Pikesley et al., 2015). There is also

96 evidence that an earlier onset of nesting could serve as an effective mechanism in

97 order for sea turtles to capture favorable climatic conditions during breeding period

98 (Almpanidou et al., 2016, 2018; Rees et al., 2016). Still, while information on

99 migration routes and main corridors is increasing (Hays et al., 2016), there is a

100 knowledge gap on the dynamics of climatic conditions during sea turtle migration.

101

102 Here, we investigated whether sea surface temperature (SST) experienced by sea

103 turtles during their migration would change in the future. We focused on the post-

104 nesting migrations (i.e., from breeding to foraging grounds) of female loggerhead sea

105 turtles (*Caretta caretta*) in the Mediterranean region. We developed a dynamic

106 multifaceted process to assess the potential exposure of individuals to variability in

107 SST, by successively comparing the current climatic properties of segments of

108 corridors and the surrounding area, considered as "baseline conditions", to projected

109 conditions, while animals move in the seascape. Next, to examine whether variation

110   in climatic conditions confronted during post-nesting migrations would be limited by

111   an earlier onset of migration, we projected future SSTs considering an advance in the

112   initiation of migration. The proposed approach could be applied for modeling climatic

113   exposure along other critical migration travels (e.g., post hatchling, adult pre-

114   breeding, juvenile developmental migrations), but also for other highly migratory

115   marine species. Thus, this spatiotemporal framework could be used to advance our

116   understanding on the impacts of climate change during migration, which is a highly

117   demanding physical task.

118

119   **2. Material and methods**

120   **2.1. Migration tracks**

121

122 To determine the spatial distribution of post-nesting migration corridors of loggerhead

123 sea turtles in the Mediterranean region, we compiled a database of all available

124 satellite tracked data. We initially searched Google Scholar using the terms "sea

125 turtles" (or "marine turtles"), "satellite telemetry" and "Mediterranean". In the search,

126 we included scientific papers and grey literature (i.e., conference proceedings, theses

127 and reports). Since 1982 that the first reference for tracking sea turtles by satellite was

128 made (Timko and Kolz, 1982), with a total of 916 records being identified (by 20

129 December 2017). In addition, we validated our research against the sources provided

130 by Luschi and Casale (2014), adding more recent publications.

131

132 Sources that were for species other than loggerheads or were described part of

133 movement other than the route from breeding to foraging grounds of adult animals,

134 were excluded. Similarly, as female and male sea turtles demonstrate different

135 temporal patterns of departure from breeding sites (i.e., in the Mediterranean region,

136 males depart from nesting sites after mating in early summer, while females depart a

137 few months later after finishing nesting; Schofield et al., 2010b, 2013), we focused

138 our analyses on post-nesting females only.

139

140 From the sources identified (see Appendix A), we extracted all the maps that

141 illustrated migration routes. These maps were georeferenced and migration routes

142 were digitized (n=89), using ArcGIS (ESRI, 2011).

143

144 **2.2.   Delineating migration corridors**

145

146   Four main migratory corridors leading to key foraging sites for adult loggerheads in

147   the Mediterranean were identified, reflecting more than 80% of collected tracks. To

148   define the spatial extent of each migration corridor, we applied a line kernel density

149   estimate (KDE) approach (Steiniger and Hunter, 2013; Demšar et al., 2015) by using

150   the tracking data as set of distinct lines. In the KDE algorithm, the selection of density

151   parameters determines the final output (Demšar et al., 2015). Hence, to avoid any

152   such bias in determining the width of the corridors, we used three different smoothing

153   parameters (i.e., search radius distance known as bandwidths): a) the average of the

154   maximum distance between different pairs of routes that had the same origin and

155   destination, in the same year (100km; Broderick et al., 2007; Zbinden et al., 2011), b)

156   the average travel distance per day (Steiniger and Hunter, 2013), based on speed data

157   reported for the studied loggerheads (i.e., mean speed of 40km/day; e.g., Zbinden et

158   al., 2011; Patel et al., 2015), and c) the mean of the two values generated by the

159   previous methods (70km).

160

161   A 0.0625° x 0.0625° (approximately 7km x 7km) cell size was applied for the KDE

162   analysis, to ensure agreement with the resolution of the climatic data used (see section

163   2.3). For reproduction, sea turtles exhibit high fidelity to nesting areas (or beaches),

164   inhabiting the marine area around these sites between each nesting event (termed

165   internesting period; with usually 2-3 nests/female/season in the Mediterranean;

166   Poloczanska et al., 2009). Therefore, many animals initiate their movement from

167   similar locations, with a high density of tracking data being expected during the initial

168   phase of migration before animals disperse more broadly. Hence, to ensure that KDE

169   outputs were not be driven by higher data densities in these areas, the selection of less

170   strict percentages for the KDE distribution was applied. Therefore, the volume of the

171   KDE distribution was determined at 75%, which is considered a more representative

172   threshold for studying broader movement patterns (Pendoley et al., 2014). The

173   analysis was performed using Geospatial Modelling Environment software (Beyer,

174   2012).

175

176   **2.3.   Climatic data**

177

178   Sea turtles, as air breathing animals, tend to swim just below the surface during

179   migration, to replenish oxygen stores regularly and avoid the energetic costs of

180   vertical transport (Hays et al., 2001; Enstipp et al., 2016). Therefore, in order to

181   examine climatic conditions along migration corridors, we used high spatial

182   resolution SST data. SSTs for the Mediterranean region were derived from the Centro

183   Euro-Mediterraneo sui Cambiamenti Climatici (CMCC) (Gualdi S., Centro Euro-

184   Mediterraneo sui Cambiamenti Climatici, personal communication). The dataset

185   contained historical and projected mean daily SST, covering the Mediterranean Sea

186   for the period 1950-2100, at 0.0625° spatial resolution. Data were derived from the

187   regional ocean-atmosphere coupled model COSMONEMO_MFS, generated by

188   CMCC (Cavicchia et al., 2015, 2016). Future climatic data were based on projections

189   of the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate

190   Change (IPCC) and emission scenario rcp45, which represents an intermediate

191   emission scenario (Moss et al., 2010). To extract SST time-series for the identified

192   corridors, we generated mean daily SST values under current conditions, covering the

193   period from 1987 to 2016. Mean daily SSTs were also calculated for 10-year intervals

194   from 2017 to 2096 (i.e., 2017-2026, 2027-2036, 2037-2046, and so on until 2096).

195

196   **2.4.   Current and future climate along corridors**

197

198   In the Mediterranean, the nesting season of sea turtles generally extends from mid-

199   May to early August, with a peak in June and July (Schofield et al., 2013). After the

200   completion of nesting, female sea turtles depart from breeding grounds and migrate to

201   foraging grounds (Zbinden et al., 2008). Taking into account that July 20 was

202   estimated as a mean departure date from breeding areas for most female sea turtles

203   after peak nesting (Zbinden et al., 2011; Schofield et al., 2013), we considered this

204   date as the onset of migration.

205

206   Individuals migrate for up to four weeks, and experience SSTs that change both

207   spatially and temporally. The Mediterranean region represents the northernmost edge

208   of the distribution for loggerheads, and thus, individuals there encounter lower water

209   temperature compared to other regions of their global range. To capture the exposure

210   of loggerheads to this heterogeneous climatic environment, we developed and applied

211 an approach that accounts for the patterns of climatic variability along migration

212 corridors. This approach builds on three types of analyses.

213

214 Initially, we split each corridor into segments. To do so, we first drew a line that was

215 equidistant between the edges of the corridor, as these were delineated based on the

216 KDE approach (see section 2.2). Next, this line was divided into parts of 120km

217 length to split the migration corridor into segments. These 120km were used as an

218 approximation of the distance covered by an animal over a 3-day period, assuming a

219 constant travel speed of 40km/day. The first segment represented a distance of 120km

220 from each nesting ground, and was characterized by the mean SST of July 20, 21, and

221 22. The second segment represented the distance of 120-240km from the nesting

222 ground, and was characterized by the mean SST of July 23, 24, and 25. We followed

223 the same procedure to estimate the future SSTs for all the studied future 10-year

224 periods, considering July 20 as the onset of migration. Sea turtles exhibit consistent

225 movement strategies during post-nesting migration, adjusting travel speeds based on

226 day/night, stage of migration and oceanic conditions (Dujon et al., 2017), with a wide

227 range of reported speeds for loggerheads (e.g., from 33.6 to 45.6km/day; Zbinden et

228 al., 2008; from 36 to 52.8km/day; Patel et al., 2015). Therefore, to account for this

229 potential source of variability on the conditions experienced over different travelled

230 distances and to alleviate the impact of daily SST variations that occur at spatial and

231 temporal scales, we also split the corridors and averaged SST values using 5- and 7-

232 day steps.

233

234 Of note, the different bandwidths (i.e., search radius distance) used to delineate the

235 width of the corridors did not alter the patterns of SST ranges (see Appendix B, Fig

236 B.1-B.4). Thus, we maintained the migration corridors delineated with bandwidth of

237 70km for the subsequent analyses, as the intermediate approach. In addition, the

238 observed patterns in SST range of each corridor, under current and all the future

239 periods, were similar when using 5- and 7-day steps for splitting corridors to different

240 segments and calculating SST values (see Appendix B, Fig. B.5-B.8).

241

242 While empirical information on the optimal conditions for migration of sea turtles is

243 not available, we compared future SSTs to SSTs currently experienced by turtles in

244 the Mediterranean, which were considered "baseline conditions." Thus, to investigate

245   whether the SSTs experienced by loggerheads in the Mediterranean during their

246   migration from breeding to foraging grounds significantly change in the future, we

247   ran two analyses. First, we compared the distribution of current SSTs (1987–2016) in

248   all cells of the four main corridors with the distribution of projected SSTs for each of

249   the 10-year periods of future climate. This analysis allowed us to summarize the

250   climatic properties experienced at the population level. Next, to investigate for

251   potential differences in the SST range patterns among different corridors, we assessed

252   changes to current and future SSTs for each corridor separately. The Kolmogorov-

253   Smirnov test used to detect significant differences in SST distributions for both

254   analyses.

255

256   To examine potential differences in SST changes for each segment of each corridor,

257   we used a sign test. For this test, we applied a cell by cell comparison for each

258   segment, comparing current conditions and all of the 10-year periods of future

259   climate. To define the range of current conditions, and to avoid outliers and extreme

260   values, we only considered cells with SSTs that fell within 95% of the distribution of

261   all cells in each corridor.

262

263

264   **2.5.   Current and future climate around corridors**

265

266   To examine differences in the potential changes of SSTs inside and outside the

267   delineated corridors, we created buffer zones around the corridors to a distance of

268   70km (i.e., to be consistent to the bandwidth used for the delineation of the corridors.

269   section 2.2), wherever feasible (i.e., excluding parts of buffer zones located over the

270   land). Following the same approach used in section 2.4, we split each buffer zone into

271   120km segments, as an approximation of the distance covered by an animal over a 3-

272   day period. Each segment was characterized by the mean SST over three days, under

273   current conditions, considering July 20 as the onset of migration. We followed the

274   same procedure to estimate the future SST for all the studied future 10-year periods.

275

276   To examine potential differences regarding future SST changes between each

277   segment of the delineated corridors and the surrounding area, we used a Mann-

278   Whitney test. For this test, we applied a segment by segment comparison, by

comparing each segment of the corridor with its adjacent sites for all of the 10-year periods of future climate. We further calculated the percentage of the cells within each segment of the adjacent sites, for which projected SST fell outside the range of the current conditions reported within the same corridor (i.e., SSTs within the 95% of the distribution of all cells within each corridor).

To investigate whether a potential spatial shift of the existing corridors could ensure that future climate conditions would be similar to the current level, we assessed changes to current SSTs within each corridor and future conditions surrounding each corridor. For this analysis, we compared the distribution of current SSTs (1987–2016) by using all cells of each corridor with the distribution of projected SSTs for each 10-year period of future climate in the surrounding sites using Kolmogorov-Smirnov test.

2.6. Efficiency of phenological shifts

To investigate whether variation in climatic conditions experienced during post-nesting migrations would be limited by an earlier onset of migration, we projected future SSTs considering an advance in the onset of migration by one day per year. The rate of one day per year was recorded for the earlier onset of nesting at a major nesting site for loggerheads in the region (i.e., Zakynthos Island, Greece; Mazaris et al., 2008). Mazaris et al. (2008) also found that the duration of the nesting season did not significantly change over time. Thus, for the purposes of this study, we assumed that departure from the breeding site would shift to one day earlier too, although a number of individual life-history components and environmental components might impact this behavior. Therefore, by advancing migration by one day per year, July 10 was set as the departure date for the period 2017-2026, June 30 was set as the departure date for 2027–2036 and so on.

At the population level, we examined whether phenological shifts in departure after nesting could contribute in maintaining thermal conditions by comparing current to projected distributions of SSTs along the four migration corridors. The comparisons were performed for all 10-year future periods, by applying a Kolmogorov–Smirnov test.

313 To assess potential changes at each corridor separately, we used a sign test to run cell

314 by cell comparisons for each segment of the delineated corridors between current

315 SSTs and future SSTs projected under the earlier onset of migration. We further

316 calculated the percentage of cells within each segment, for which projected SST with

317 phenological shifts fell outside the range of current conditions (i.e., SSTs within 95%

318 of the distribution of all cells in each corridor).

319

320 A more strict view on the effectiveness of earlier onset of migration could support the

321 hypothesis that, even if future SSTs fall within the distribution of the current climatic

322 conditions, future SSTs will be at lower levels than the SSTs projected under no

323 advancement of migration. To test this hypothesis, we applied a cell by cell

324 comparison for projected SSTs, with and without phenological shifts, using the sign

325 test.

326

327

328 **3. Results**

329

330 **3.1. Current and future SST conditions**

331

332 Comparisons of the distribution of SSTs that are currently experienced by sea turtles

333 along the main migration corridors with projected SSTs demonstrated significant

334 increases ($p<0.05$). Over the next 80 years, future SSTs will rise by a mean rate of

335 0.24 ºC per decade (Fig. 1 and Fig. 2). This was also the case when repeating the

336 analysis separately for each migration corridor, with the distribution of current SSTs

337 shifting towards higher temperatures in the near future (for all corridors and for all

338 future decadal periods, $p<0.05$).
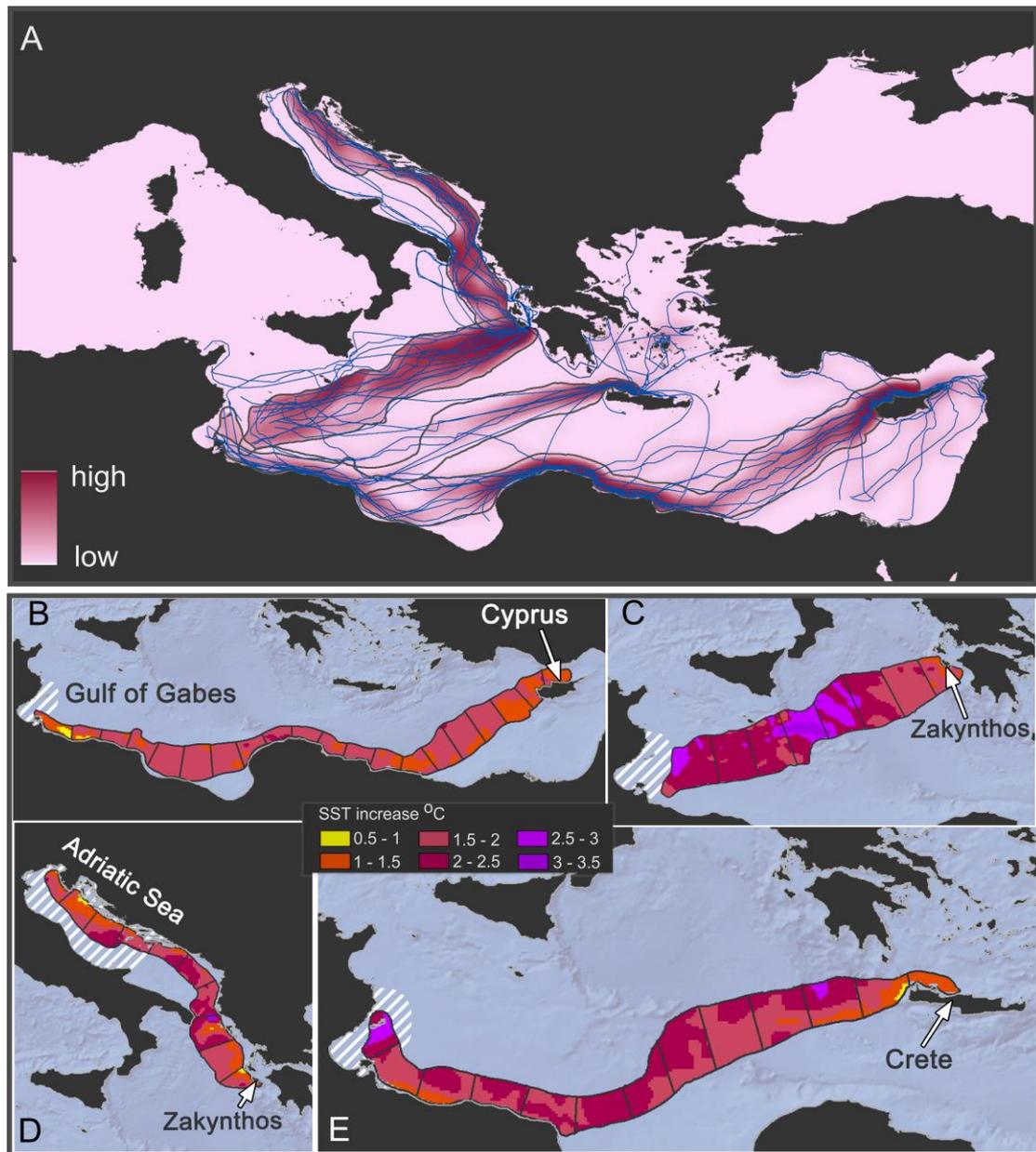
Fig. 1: The main identified post-nesting migration corridors for female loggerheads (*Caretta caretta*) in the Mediterranean region. (A) The migration routes used to determine the corridors (blue lines) and kernel density estimates of the migration tracks (red gradient) are presented. (B) - (E) Sea surface temperature increase between the current period (i.e., 1987-2016) and the end of century (i.e., 2087-2096) for the four migration corridors. Each segment of each corridor represents a 3-day step based on a mean speed of 40km/day, departing the breeding area on 20 July. The locations of the nesting sites from which migration begins are shown. The white striped areas represent the locations of foraging areas, where migration ends up.
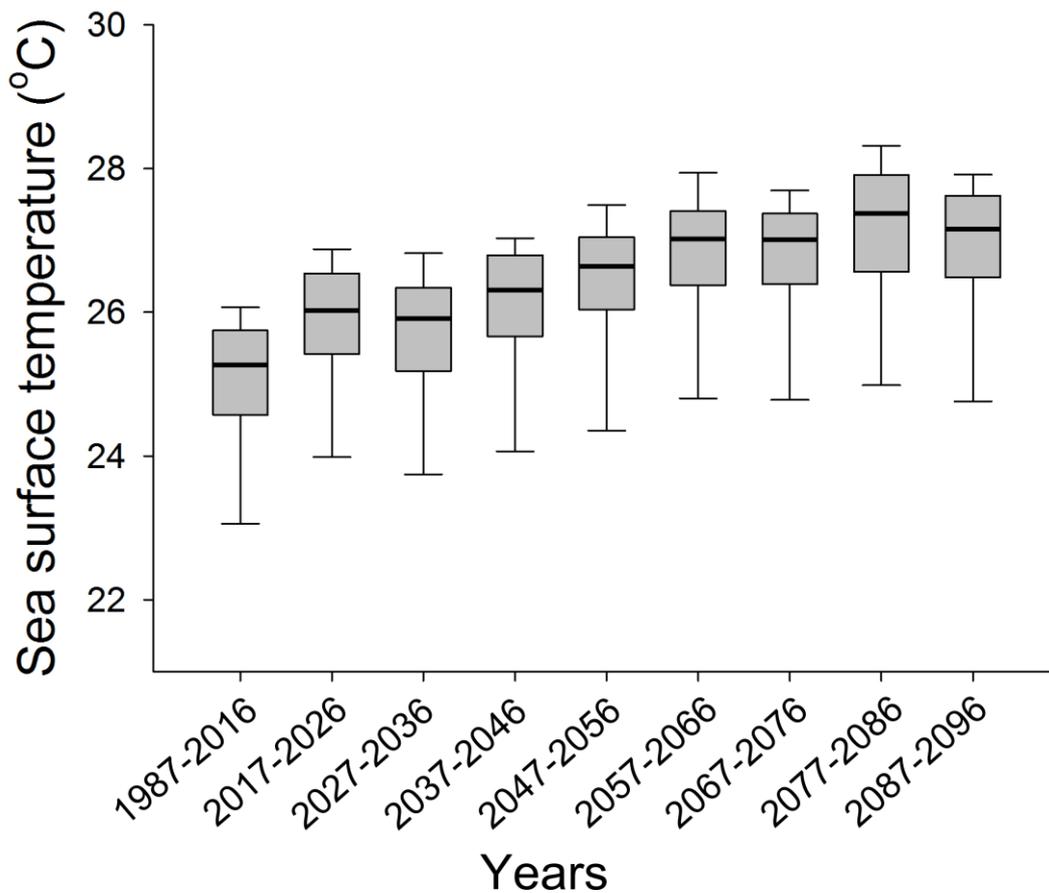
Fig. 2: Sea surface temperature along the main post-nesting migration corridors for female loggerheads (*Caretta caretta*) in the Mediterranean region over time, i.e. current 1987-2016 and future from 2017 to 2096 by 10-year periods. The thick black lines represent the median values, the upper and lower boundaries of the box represent 75 and 25 percentiles, and the vertical lines represent the 90th and 10th percentiles.

Significant increases obtained when performing a cell by cell comparison of current and projected SSTs within each segment of a given corridor (p<0.05; Fig. B.9A). Still, at this finer scale, the results did not support a clear spatiotemporal pattern. For example, during the first half of the century (i.e., 2017-2056), most cells in the segments had SSTs that fell within the range of currently observed SSTs (ranging from 48.07% to 87.39% for the four corridors). However, during the second half of the century, a smaller percentage of projected SSTs fell within the current range (ranging from 4.87% to 63.11% for the four corridors), with most exceeding the values currently obtained.

369   The distribution of the projected SSTs in the surrounding areas of the corridors was

370   also higher compared to current SSTs along the corridors (in all cases, for all future

371   decadal periods, $p<0.05$; Fig. B.10). For the first half of the century, these increased

372   temperatures in many cells from the surrounding segments fell within the SSTs

373   detected under current conditions along each entire corridor (mean percentage of cells

374   equal to 64.53%). However, during the second half of the century, most cells in the

375   surrounding segments had projected SSTs beyond current levels (mean percentage of

376   cells equal to 70.72%).

377

378   Significant differences were obtained when comparing projected SSTs between

379   segments inside and outside the same corridor ($p<0.05$) for most pair-wise

380   comparisons (n=532 out of the 568 segments analyzed). These changes were

381   heterogeneous, with 44.54% and 49.12% of the segments in the surrounding area

382   exhibiting higher and low temperatures, respectively, compared to the segments

383   inside the corridors.

384

385   **3.2.   Efficiency of phenological shifts**

386

387   Comparison of current SSTs in the corridors versus the future SSTs with an earlier

388   onset in the migration period demonstrated significant differences ($p<0.05$). The pair-

389   wise comparison of current and future SSTs obtained under an earlier onset of

390   migration significantly differed in most (99%) segments ($p<0.05$).

391

392   For the next three decades (up to 2046), many cells of segments exceed current SSTs

393   (mean percentage of cells equal to 51.77%) (Fig. B.5B). About 12.94% (ranging from

394   6.02-20.53%) of the cells in all segments had significantly higher SST values when

395   comparing SSTs under earlier migration versus no phenological shift in the same

396   period ($p<0.05$; Fig. 3).

397

398
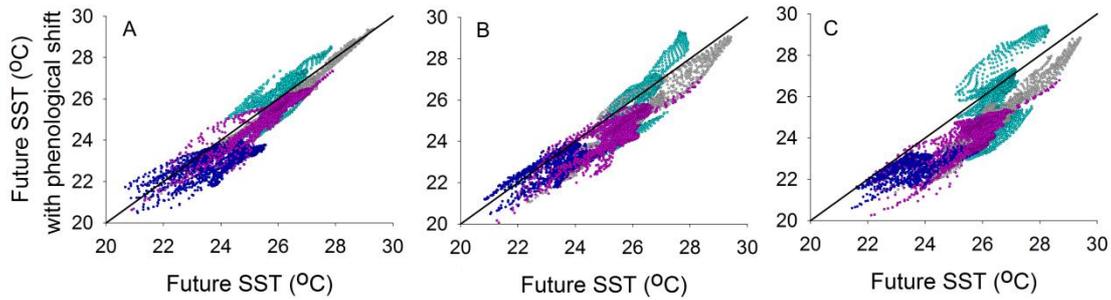
Fig. 3: Relationship between projected sea surface temperature (SST) considering an onset of migration on 20 July and projected SST accounting for phenological shifts towards an advance onset of migration by one day per year. Dots represent all the cells that comprise the main identified post-nesting migration corridors for female loggerheads (*Caretta caretta*) in the Mediterranean region for future periods of (A) 2017-2026, (B) 2027-2036 and (C) 2037-2046. Different colors represent different corridors, i.e., light blue is the corridor from the northern coast of Cyprus to Tunisia, grey is the corridor from Crete (Greece) to Tunisia, dark blue is the corridor from Zakynthos (Greece) to the northern Adriatic Sea, and pink is the corridor from Zakynthos (Greece) to Tunisia. The straight line represents an expected 1:1 relationship. The deviations from the straight line towards the upper part are indicative of cells with higher SST values, considering an earlier migration compared to SST without accounting for phenological shifts.

From 2047 onwards, the percentage of the segments that fall within the range of SST currently detected along each corridor noticeably dropped (from 27% at 2056 to 0% from 2076 onwards). For these decades, SSTs might be much lower than those found under current conditions. At the end of the century (2086-2096), a shift in the onset of migration would lead to lower SSTs in most segments of all corridors compared to those in the range of the current SSTs.

4. Discussion

The spatiotemporal framework used in the current study delineated a highly heterogeneous climatic mosaic along and around the corridors used for the long distance, post-nesting migration of sea turtles. Future SSTs tended to be higher in all of the segments. At the end of century, the temperature exceeded that of current ranges in each corridor, but remained below the upper thermal limit for this species globally. The multi-faceted approach developed here, demonstrated that phenological

429   shifts might not result in turtles being exposed to climatic conditions that are similar

430   to current levels in the future along the post-nesting migration corridors.

431

432   Warmer temperatures affect all the physiological rates and biological processes of

433   ectothermic species (Williard, 2013), with even small temperature changes having a

434   relatively large effect on the metabolic rates of sea turtles (Marn et al., 2017). For

435   example, higher temperatures (along with energy richer environments) could

436   positively affect the growth, maturation, and reproduction of loggerheads (Marn et al.,

437   2017). For temperate regions, such as the Mediterranean, where sea turtles experience

438   lower water temperature compared to the tropics, rising temperatures could affect

439   behavioral mechanisms, life cycle processes and activities of turtles at different life

440   cycle stages. For example, rising temperature could reduce the length of winter

441   dormancy (Hochscheid et al., 2007), extend the foraging period (Witt et al., 2010),

442   and improve nesting conditions, but reduce post-hatchling survival (Mafucci et al.,

443   2016). Our analyses showed that, during migration, loggerheads in the Mediterranean

444   might confront higher temperatures in the future (~31°C to the maximum), but with

445   these temperatures being lower than the upper thermal limits and thus, they would not

446   be threatened by hyperthermia (i.e., 37.5°C; Heath and McGinnis, 1980; ~40°C;

447   Spotila et al., 1997). During the post-nesting migration, body condition is not

448   expected to be optimal, as females do not generally forage during the breeding

449   periods (Hays et al., 2014). Thus, the faster consumption of energy reserves, due to

450   increased sea temperatures, might impact fitness. For example, for an adult individual

451   with a mean body mass of ~68.5kg (Hays et al., 1991), a mean increase of ~ 2.3 °C

452   between current conditions and the end of the century (i.e., from 24.8 °C to 27.1 °C,

453   along the corridor that connects the breeding grounds on Zakynthos, Greece, with the

454   foraging grounds in Tunisia; Fig 1C), could cause oxygen consumption to increase by

455   47% VO_2 in mL O_2/min (based on the equation provided by Hochscheid et al., 2004).

456   Thus, this increase in temperature along the entire route could increase daily energy

457   expenditure from 470kJ/day to 690kJ/day (equations used for loggerheads by Hatase

458   & Tsukamoto, 2008). This demonstrates the importance of understanding how higher

459   SSTs could impact sea turtles during migration from a physiological perspective.

460

461   Migration behavior is innate for adult sea turtles (Scott et al., 2014). Still, individuals

462   exhibit different levels of fidelity to the same corridors during successive post-nesting

463   travels, varying from low to high depending on oceanic or neritic migration,

464   respectively (Broderick et al., 2007; Schofield et al., 2010a). Global climate change

465   has already led to poleward range expansion of foraging habitats of sea turtles (e.g.,

466   leatherbacks at North East Atlantic; McMahon and Hays, 2006). Thus, adult sea

467   turtles might gradually shift their migration corridors spatially. For example,

468   loggerheads that migrate through open ocean habitats might move towards higher

469   latitudes and benefit from smaller SST changes. However, probably this behavioral

470   response could not be the case when sea turtles moving along the shore. In addition,

471   given that our findings on the surrounding area of the main corridors revealed an

472   heterogeneous pattern of SST change compared to the temperatures inside the

473   corridors, it might be tricky for the animals to detect and track favorable temperatures,

474   even if they exhibit potential spatial shifts in routes, within this highly variable

475   climatic mosaic.

476

477   In the present study we focused on the post-nesting migration of loggerheads in the

478   Mediterranean region, which hosts a distinct population, with specific demographic

479   and genetic features (i.e., Regional Management Unit - RMU). The Mediterranean

480   region represents the northernmost edge of the distribution for loggerheads, with most

481   of breeding populations found in tropical areas where sea temperatures tend to be

482   higher and more stable year round. Thus, this population might be subject to different

483   evolutionary pathways to other loggerhead populations globally (Wallace et al.,

484   2010). Still, given that climatic preferences of sea turtles are differentiated (e.g.,

485   Mazaris et al., 2015; Almpanidou et al., 2017) across RMUs, exhibiting various levels

486   of resilience to climate change (Fuentes et al., 2013), it is important

487   to explore potential differences in the sensitivity and the ability of distinct populations

488   to adapt to climate change. Information on populations in warmer environments could

489   also be used to predict behavioral future responses of populations currently inhabiting

490   cooler habitats as these habitats warm under climate change.

491

492   To track the changing climate, sea turtles might adjust the overall travel speed based

493   on conditions en-route (e.g., SST, currents), make stopovers, or regulate the arrival to

494   foraging areas based on climatic conditions (see Åkesson et al., 2017, for birds). For

495   example, sea turtles have been detected to exhibit stopovers during migration at other

496   regions, primarily near the tropics (e.g., north-eastern coast of South America;

497 Baudoin et al., 2015; Western Indian Ocean; Dujon et al., 2017) as a potential strategy

498 for resting and feeding in order to replenish body supplies. Thus, loggerheads in

499 temperate regions, such as the Mediterranean, might also adopt this behavior, as a

500 response to warmer temperatures in the future. For regions near the tropics, the use of

501 cold waters at depth by leatherbacks (i.e., in Costa Rica) during the internesting

502 period might be a behavioral response to avoid very warm waters and to conserve

503 energy for reproduction (Wallace et al., 2005). In the Mediterranean region, the

504 duration of the nesting season for loggerheads is stable through time, despite the

505 earlier initiation (Mazaris et al., 2008); thus, the departure of turtles from the breeding

506 grounds might initiate earlier, in parallel; however, a number of individual life history

507 and environmental factors might influence this. In other regions, shorter (Atlantic

508 coast of central Florida, US; Pike et al., 2006; Weishampel et al., 2010) or longer

509 (Northwest Florida, US; Lamont and Fujisaki, 2014) nesting seasons have been

510 recorded as a response to warmer temperatures. Such an increase in temperature could

511 result in time adjustments while animals begin their post-nesting migration. The

512 current study showed that the climatic environment in the Mediterranean would be

513 highly variable in the future; thus, behavioral and biological responses to warming

514 temperatures must be monitored to determine whether they could be adopted as a

515 population strategy in the Mediterranean.

516

517 Phenological responses do not always guarantee the synchronization of species

518 activities with favorable conditions for growth or survival (Zipkin et al., 2012;

519 Tomotani et al., 2018). For example, following an early departure from Africa,

520 migratory birds might be subjected to poor food supplies or adverse weather

521 conditions at temperate breeding sites (Both, 2010; Åkesson et al., 2017). With earlier

522 nesting, sea turtles track current climatic conditions, during nesting and incubation,

523 which might ensure suitable habitat under climate change (Poloczanska et al., 2009).

524 However, the current study showed that climatic conditions during the post-nesting

525 migration might not necessarily be favorable under these phenological shifts. Thus,

526 different life-history stages must be evaluated to elucidate the impacts of such

527 behavioral responses.

528

529 Many other environmental factors (e.g., changes in productivity, prey distribution,

530 ocean currents) could affect movement patterns (Putman, 2018); thus, potential future

531   changes of these parameters could impact the observed spatiotemporal patterns. For

532   example, there is evidence that sea turtles assess their position along their migratory

533   routes based on geomagnetic fields (Putman and Lohmann, 2008; Brothers and

534   Lohmann, 2015). This is also the case for other marine migrants (e.g., pink and

535   sockeye salmon), for which geomagnetic navigation contributes to long-distance

536   movements, along with SST and ocean currents (Putman et al., 2014). Therefore, a

537   better understanding of the interaction between marine migratory species and their

538   environment is needed to understand current patterns. Such information would help

539   improve mechanistic and hybrid modeling approaches to forecast potential species

540   responses to climate change.

541

542   The incorporation of climate change into systematic conservation planning has largely

543   been overlooked, despite being highlighted as a high priority (Jones et al., 2016). The

544   proposed approach could be used as a first step towards identifying areas that would

545   be subjected to minor changes and thus, serve as climate refugia or potential favorable

546   stepping stones through which species are likely to move in the future. However, we

547   emphasize that further investigation is crucial to evaluate the actual impacts of these

548   temperature changes on species performance. Under this context, we encourage future

549   studies to apply this framework to investigate climatic variability along the migration

550   routes used by sea turtles at the different stages of their life cycles (e.g., post

551   hatchling, juvenile developmental, adult breeding migrations) to generate more

552   integrated assessments.

553

554   **5.   Conclusions**

555

556   This study demonstrated that Mediterranean loggerheads are going to encounter

557   increasing temperatures along and around their post-nesting migration corridors,

558   which might impact the effectiveness of potential phenological shifts. The

559   multifaceted approach developed and applied here could be used to model climate

560   exposure of other highly migratory marine organisms with complex life cycles that

561   inhabit multiple areas. We suggest that it is essential to improve our understanding of

562   the potential impact of rising temperatures on metabolic rates, physiological

563   responses, energetic constraints, and the overall performance of marine species,

564   particularly ectotherms like sea turtles. Studies on climate change impacts along

565 migration corridors should be conducted in other regions, applying the proposed

566 methodological framework, as well as on other highly mobile marine species, to

567 prioritize conservation actions under a changing climate.

568

569

Appendices

570

571   Appendix A. Data sources

572   Appendix B. Supplementary figures

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