

1 **Distribution and abundance of bottlenose dolphin (*Tursiops truncatus*) over the French**

2 **Mediterranean continental shelf**

3

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## 20 **Abstract**

21 The Mediterranean bottlenose dolphin (*Tursiops truncatus*) sub-population is listed as  
22 vulnerable by the International Union for Conservation of Nature. This species is strictly  
23 protected in France and the designation of Special Areas of Conservation (SAC) is required  
24 under the European Habitat Directive. However, little information is available about the  
25 structure, dynamic and distribution of the population in the French Mediterranean waters. We  
26 collected photo-identification data over the whole French Mediterranean continental shelf all  
27 year round between 2013 and 2015. We sighted 151 groups of bottlenose dolphins allowing  
28 the individually photo-identification of 1,060 animals. The encounter rate distribution showed  
29 the presence of bottlenose dolphins over the whole continental shelf all year round. Using  
30 capture-recapture methods, we estimated for the first time the size of the bottlenose dolphin  
31 resident population at 557 individuals (95% confidence interval: 216-872) along the French  
32 Mediterranean continental coast. Our results were used in support of the designation of a new  
33 dedicated SAC in the Gulf of Lion and provide a reference state for the bottlenose dolphin  
34 monitoring in the French Mediterranean waters in the context of the Marine Strategy  
35 Framework Directive.

36

## 37 **Keywords**

38 Abundance, bottlenose dolphin, capture-recapture, distribution, French Mediterranean Sea,  
39 photo-identification, *Tursiops truncatus*

#### 40 **Introduction**

41 The Common bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821; hereafter bottlenose  
42 dolphin) is considered as a common species in the Mediterranean Sea. It has been observed  
43 along most of Mediterranean coast (Bearzi *et al.* 2009), preferentially over the continental  
44 shelf (Di Sciara *et al.*, 1993; Gannier, 2005; Gnone *et al.*, 2011), even though groups have  
45 also been observed offshore (Laran *et al.*, 2016). Both resident populations and transient  
46 individuals have been reported (Gnone *et al.*, 2011). Mediterranean bottlenose dolphins sup-  
47 population is genetically differentiated from populations inhabiting the contiguous eastern  
48 North Atlantic and the Black Sea and is structured into a Western and an Eastern population  
49 corresponding to habitat boundaries (Natoli *et al.* 2005).

50 The bottlenose dolphin Mediterranean sub-population is considered as "vulnerable" on the  
51 Red List of the International Union for Conservation of Nature (IUCN). It is listed in Annex II  
52 of the Washington Convention on International Trade in Endangered Species, in Appendix II  
53 of the Bern Convention for the Conservation of European Wildlife and Natural Habitats, in  
54 Appendix II of the Protocol to the Barcelona Convention on Specially Protected Areas of  
55 Mediterranean Importance (SPAMI) and is one of the only two species of cetaceans listed in  
56 Appendix II of the European Habitats Directive (92/43/CEE). It is also strictly protected in  
57 France by the decree of 1<sup>st</sup> July 2011 prohibiting, among other things, the destruction, capture  
58 and intentional disturbance of marine mammals. In addition, the bottlenose dolphin is the  
59 subject of a specific action plan under development by the Agreement on the Conservation of  
60 Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic Area (ACCOBAMS).  
61 In order to reach legal conservation objectives, the implementation of conservation strategies  
62 or action plans for a species requires the assessment of the population conservation status and  
63 the identification of trends in the population. Population indicators (e.g., distribution,

64 abundance) should be regularly evaluated and compared with reference values through  
65 standardized long-term monitoring (Cairns *et al.* 1993; Dale & Beyeler, 2001).

66 In France, the monitoring program set up for the implementation of the European Marine  
67 Strategy Framework Directive (2008/56/EC; MSFD) recommends specific monitoring by  
68 photo-identification of resident coastal populations of marine mammal species, including  
69 bottlenose dolphins. Photo-identification is a methodology commonly used to monitor  
70 bottlenose dolphins (Shane *et al.*, 1986; Defran & Weller, 1999; Gnone *et al.*, 2011;  
71 Karczmarski & Cockcroft, 2014; Louis *et al.*, 2015)□. Photo-identification allows individual  
72 monitoring for inferring population social structure, identifying movements and assessing  
73 population dynamics through the estimation of abundance and demographic parameters via  
74 capture-recapture (CR) methods (Hammond *et al.*, 2019; Hammond, 2009; Hammond *et al.*,  
75 1990; Rosel *et al.*, 2011)□.

76 In French Mediterranean waters, several studies on bottlenose dolphins have been conducted  
77 since the 1990s, mainly based on photo-identification (Bompar *et al.*, 1994; Dhermain *et al.*,  
78 1999; Labach *et al.*, 2015; Labach *et al.*, 2011; Ripoll *et al.*, 2001), but remain local and  
79 punctual. The knowledge of the population's structure, ecology and dynamic remain very  
80 poor and unequal.

81 In this study, we conducted the first large-scale survey of bottlenose dolphin based on photo-  
82 identification in the French Mediterranean waters. Standardized photo-identification data  
83 were collected all over the French Mediterranean continental shelf in each season over two  
84 years through a homogenized protocol by a network of organizations. The objectives of our  
85 study were to evaluate the distribution of bottlenose dolphin over the French continental shelf  
86 and to provide the first abundance estimate of the resident population.

87

## 88 **Methods**

89

## 90 *Study area*

91 The French Mediterranean waters present a great diversity and richness of habitats and  
92 seabed. The Gulf of Lion, from the Spanish border to Marseille, is a vast continental shelf  
93 limited to the north by a sandy and lagoon coastline and to the south by a broad slope cut by  
94 numerous canyons. The Corso-Liguro-Provençal basin (Riviera and west coast of Corsica)  
95 presents a rocky coastline prolonged by a very narrow continental shelf quickly giving way to  
96 an abrupt slope, cut by deep canyons, which debouches on the abyssal plain. To the east of  
97 Corsica, the reliefs are shallower with a larger continental shelf. The Corso-Liguro-Provençal  
98 basin and the Gulf of Lion are highly productive areas attracting a great diversity of species  
99 (D'ortenzio and Ribera Dalcaì, 2009)□.

100 The study area covers the continental shelf of the French Mediterranean waters between the  
101 coast and the 500 m isobath, bounded by the Spanish border to the west, the Italian border to  
102 the east, and includes the whole Corsican coastline (Fig 1). The overall study area covers  
103 24,481 km<sup>2</sup> that was divided in three regions according to their geographic and topographic  
104 characteristics: Gulf of Lion (14,731 km<sup>2</sup>), Riviera (2,866 km<sup>2</sup>) and Corsica (6,884 km<sup>2</sup>).

105

## 106 *Data collection*

107 To ensure a homogeneous sampling over the whole study area, each region was divided in  
108 sub-regions of similar area (4 in Gulf of Lion, 2 in Riviera and 3 in Corsica) and assigned to 5  
109 local structures involved in marine mammals monitoring (BREACH, CARI, EcoOcean  
110 Institut, GECEM and Parc naturel regional de Corse). Each partner conducted 4 days of boat-  
111 based survey in good weather conditions in each season during 2 years in the sub-regions  
112 assigned to it. We carried out surveys between summer 2013 and summer 2015 using small  
113 sailing and motor boats. We designed these surveys to locate and photo-identify bottlenose

114 dolphins and optimize the study area's sampling coverage. All partners applied a standard  
115 common protocol using a digital application for the data collection specifically designed with  
116 Cybertracker (<https://www.cybertracker.org/>), systematically recording survey tracks with a  
117 GPS receiver. When we encountered a group of bottlenose dolphins, we recorded the position  
118 of first contact, group size and composition along with group main activity. Whenever  
119 possible, we took pictures of both sides of dorsal fins of all individuals of the group with  
120 digital reflex camera. We gathered all data and best pictures of each sighting in a common  
121 database and uploaded the data on the international web database INTERCET  
122 (<http://www.intercet.it/>).

123

#### 124 *Photo-identification*

125 We identified individuals using natural marks: scars, nicks, and scratches on their dorsal fins  
126 (Würsig and Jefferson, 1990; Würsig and Würsig, 1977)□. We selected best quality pictures  
127 (methodology described below in *Abundance estimation* paragraph) of both profiles of each  
128 individual for each sighting and created catalogs of dolphins identified with the history of  
129 their sightings. Each partner compared its own catalog with all the others, hence leading to  
130 three regional catalogs and one global catalog containing the encounter history of each  
131 dolphin photo-identified during the study period.

132

#### 133 *Survey effort*

134 We defined the survey effort as the length (in km) of track actively traveled prospecting the  
135 area with naked eyes by three observers in favorable weather conditions (wind speed lower  
136 than Beaufort 3 and good visibility).

137

#### 138 *Group size*

139 We defined a group as all the dolphins seen with naked eyes during the sighting. The  
140 estimated group size is the estimated number of individuals observed or photo-identified  
141 whenever the latter figure is greater than the estimated one.

142

#### 143 *Distribution*

144 We calculated the encounter rate (ER) as the number of sightings per km of effort traveled in  
145 each region and within each 5'x5' cell of the Marsden grid WGS 84. All maps and spatial  
146 analyses were done in R 3.5.0 (R Core Team, 2018)□.

147

#### 148 *Abundance estimation*

149 To estimate the abundance of bottlenose dolphins occurring within the study area, we fitted  
150 CR models to the photo-identification data (Hammond *et al.*, 1990)□. We defined a capture  
151 as the time an individual was identified with photo-identification, and a recapture as the  
152 resighting of an individual already seen during the project.

153 We scored best pictures of each dolphin sighting according to their quality and the  
154 distinctiveness of animals using 1 for good, 2 for medium and 3 for bad (Ingram, 2000)□. We  
155 used only medium and good quality photos (quality scores = 1 or 2) of moderately and well-  
156 marked individuals (distinctiveness score = 1 or 2).

157 Because mortality most likely occurred during the study period, we used the Cormack-Jolly-  
158 Seber (CJS) (Cormack, 1964; Jolly, 1965; Seber, 1965)□ model to estimate abundance while  
159 accounting for apparent survival (the product of true survival and fidelity) and a recapture  
160 probability less than one. We considered the eight seasons as our capture occasions. The main  
161 assumptions underlying the CJS model (Lebreton *et al.*, 1992) are 1) the population is  
162 demographically open (i.e. natality and mortality events occur) during the study period; 2) all  
163 individuals are correctly identified at each capture occasion and 3) the marks are considered

164 permanent. Although these assumptions were unlikely to be violated in our study, we formally  
165 evaluated the quality of fit the CJS model to the data at hand (see next paragraph).  
166 We performed three distinct analyses corresponding to the sightings made in the Gulf of Lion,  
167 the Riviera and along the continental coast (Gulf of Lion plus Riviera). We did not pursue CR  
168 analyses with the Corsican sightings because of the insufficient number of recaptures (Table  
169 1). To fit CR models, we used the RMark package (Laake and Rexstad, 2008) which calls the  
170 MARK program (White and Burnham, 1999) in program R. We use the R package R2ucare  
171 (Gimenez *et al.*, 2018) to assess the quality of fit of the CJS model to data (Pradel *et al.*,  
172 2005)□. While trap-dependence was not detected, we detected a transient effect that we  
173 accounted for by using a two-age class for survival (Roger Pradel *et al.*, 1997). Individuals  
174 that were sighted only once were part of the first age-class (transients were included in this  
175 class) while all the others were part of the second. The age in CR analysis was considered as  
176 the time passed since the animal was first sighted (Madon *et al.*, 2012)□. The proportion of  
177 transients was estimated and the abundance estimate amended accordingly (Madon *et al.*,  
178 2012)□. To test and account for the presence of heterogeneity in the detection probability, we  
179 used CR mixture models (Pledger *et al.*, 2010) in which animals belong to different classes of  
180 detection in proportions to be estimated (Gimenez *et al.*, 2017). For each analysis, we fitted  
181 four models incorporating a season and/or heterogeneity in the recapture probability while  
182 survival was considered constant over time. To determine the most parsimonious model, the  
183 model with the lowest AICc score (Akaike Information Criterion corrected for small sample  
184 sizes) (Burnham and Anderson, 2002) was selected (Appendix 1). The selected model was  
185 then used in a non-parametric bootstrap procedure (with 500 iterations) to calculate 95%  
186 confidence interval for population size (Cubaynes *et al.*, 2010)□.  
187 Because we used only well and moderately marked individuals (assumed to be adults) in the  
188 CR analyses, the total abundance including poorly marked individuals (juveniles and



189 neonates) was obtained by correcting the CR-estimated abundance by the proportion of poorly  
190 marked individuals (Williams *et al.*, 1993)□.

191

## 192 **Results**

### 193 *Survey effort*

194 We traveled a total of 21,464 km in survey effort. The distribution of the effort between the 3  
195 regions was heterogeneous with a high coverage of Riviera but low coverage of Corsica and  
196 the offshore areas of Gulf of Lion. Summer was the best prospected season, autumn and  
197 winter being less prospected in the three regions (Fig 2).

198

### 199 *Sightings and photo-identification*

200 We sighted 151 groups of bottlenose dolphins during the project. Group size was highly  
201 variable in the three regions, mean group size was similar in Riviera and Gulf of Lion and  
202 lower in Corsica (Table 1).

203 We made a total of 1,705 photo-identifications of 1,060 dolphins (Table 1), of which 32%  
204 were observed more than once during the project. The percentage of individuals recaptured  
205 was higher in Riviera and lower in Corsica. We did not record any recapture between  
206 continental and Corsican coast during the project, while we observed 53 individuals in both  
207 Riviera and Gulf of Lion.

208

### 209 *Distribution*

210 We sighted bottlenose dolphins in the whole study area all year round (Fig. 3). Global ER was  
211 higher in Corsica and lower in Riviera (Table 1). In Riviera, ER was higher in spring, while in  
212 Gulf of Lion and Corsica, ER was higher in summer.

213

## 214 *Abundance estimates*

215 We excluded 15% of the pictures from the analyses because of their low quality (score 3). The  
216 percentage of moderate and well-marked individuals was 59% in Riviera, 77% in Gulf of  
217 Lion and 76% in the whole continental coast. Many dolphins (68% in continental coast) were  
218 seen only once. The maximum number of captures was 6 for two dolphins (Table 2).

219 According to AICc values (Appendix 1), the model best supported by the three datasets was  
220 the model considering two age classes in survival and season-dependent recapture  
221 probabilities. The mean ratio of transient animals was estimated to 0.69 (95% CI 0.36-0.85) in  
222 Riviera, 0.45 (95% CI 0.37-0.53) in Gulf of Lion and 0.41 (95% CI 0.33-0.50) in continental  
223 coast.

224 Mean total abundance (corrected by the ratio of moderately and well-marked individuals) of  
225 resident population has been estimated at 43 (95% CI 4-58) individuals in Riviera, 444 (95%  
226 CI 304-555) in Gulf of Lion and 557 (95% CI 216-872) along the continental coast.

227

## 228 **Discussion**

229 Our study provides the first large-scale dedicated photo-identification survey for the  
230 bottlenose dolphin in the French Mediterranean waters. We demonstrate the power of a  
231 collaborative and coordinated survey to study a mobile species at the scale of a population.  
232 Our results show that the whole continental shelf is frequented by bottlenose dolphins,  
233 including the entire Gulf of Lion, all year round. We also confirmed the presence of a resident  
234 population along the French Mediterranean coasts, for which we provided the first abundance  
235 estimate in Riviera and Gulf of Lion.

236 The prospecting effort of 21,464 km covered 87% of the study area. We found heterogeneity  
237 in this effort between the three regions which we explained by a later start of the survey in  
238 Corsica and more difficult survey conditions in the Gulf of Lion because of the important

239 offshore area which demands long-distance offshore survey trips. The entire coastline of the  
240 French Mediterranean is often subject to difficult weather conditions limiting survey effort,  
241 especially in Winter.

242 The global encounter rate (0.007) was higher than the encounter rates (0.0041 with CV = 0.17  
243 in winter and 0.0028 with CV = 0.2 in summer) obtained with the program “Surveillance  
244 Aérienne de la Mégafaune Marine” (SAMM), a comprehensive aerial survey of marine  
245 megafauna conducted by the French Biodiversity Agency in 2011 and 2012 over the whole  
246 French Exclusive Economic Zone (EEZ), encompassing continental shelf, slope and oceanic  
247 waters (Laran *et al.*, 2016)□. The ER in Riviera (0.003) and in Corsica (0.012) was also  
248 higher than the maximum ER obtained by (Gnone *et al.*, 2011)□ between 1994 and 2007 in  
249 Provence (ER = 0.0006) and in Corsica (ER = 0.0086), which might be due to an increase in  
250 dolphin abundance in these two regions, but the different time scale and different sampling  
251 methods make the comparison difficult.

252 The distribution of ER showed that bottlenose dolphins were present over the entire French  
253 Mediterranean continental shelf all year round. The higher ER in summer in Gulf of Lion and  
254 Corsica was consistent with the results of the SAMM survey, which showed higher ER in  
255 winter than in summer in the global EEZ, but a distribution more important in offshore waters  
256 in winter and in coastal waters of Gulf of Lion and Corsica in summer (Laran *et al.*, 2016)□.  
257 These results, together with the detection of a strong transient effect in the CR analyses,  
258 suggest a seasonal migration of bottlenose dolphins between offshore waters in winter to  
259 coastal waters in summer, especially in Gulf of Lion and Corsica. The sighting of 53 dolphins  
260 both in Riviera and Gulf of Lion also points towards eastward and westward movements. No  
261 movement between the continental areas and Corsica was observed during the project,  
262 although 5 individuals were identified both in Corsica and along continental coast in previous  
263 studies (Gnone *et al.*, 2011). The identification of distinct units and the characterization of

264 connections between them is the object of ongoing work using population genetic and social  
265 structure analyses based on photo-identification and biopsy data collected during the present  
266 study. The higher percentage of badly marked individuals (41%) suggests, in Riviera, a higher  
267 percentage of immature dolphins than in Gulf of Lion (23%).

268 The robust estimation of abundance relies on the validation of CR model assumptions. The  
269 two-year sampling period and the fact that newborns were observed in the study area suggest  
270 that assumption 1 of the CJS model is likely to have been respected. Assumptions 2 and 3 are  
271 ensured by the fact that only moderately and well-marked individuals with good-quality  
272 photographs were included in the analysis. Also, if the marks evolve, the short sampling  
273 period would allow to recognize the animals.

274 The average total population along the continental coast between 2013 and 2015 estimated at  
275 557 (95% CI 216-872) individuals was higher than the estimates of the only previous census  
276 campaign dedicated to bottlenose dolphins in the same area, which estimated by observed  
277 count (ignoring imperfect detection), the number of bottlenose dolphins between 200 and 209  
278 in the Gulf of Lion and 16 in Provence (Ripoll et al., 2001)□. These figures are not  
279 inconsistent with our abundance estimates which were corrected to account for imperfect  
280 detection. Our abundance estimates are coherent with the results obtained from the program  
281 SAMM with the distance sampling methodology, which estimated the absolute abundance of  
282 bottlenose dolphins in French territorial water (within 12 miles of the coast) at 350 (95% CI  
283 150-900) dolphins inside the Pelagos Sanctuary and 500 (95% CI 115-2,500) outside in  
284 Winter and at 1,800 (95% CI 900-3,500) individuals inside the Pelagos Sanctuary and 450  
285 (95% CI 120-1,700) outside in Summer (Laran *et al.*, 2016)□.

286

### 287 *Implications for conservation*

288 Our study provides an operational framework as well as a reference state for the  
289 implementation of a long-term large-scale monitoring of the resident bottlenose dolphin

290 population in the French Mediterranean waters in the framework of the Marine Strategy  
291 Framework Directive. We shared the data on the international webGIS platform INTERCET  
292 (<http://www.intercet.it/>) which will allow to enlarge the study of this species beyond French  
293 boundaries to the basin and Mediterranean scale.

294 The results of our study together with those from the SAMM survey (Laran *et al.*, 2016) led  
295 to an update of the Mediterranean bottlenose conservation status in the national IUCN Red  
296 List which was changed from “vulnerable” in 2009 to “nearly threatened” in 2017 because of  
297 knowledge improvement. Our demonstration of the presence of bottlenose dolphins in the  
298 entire Gulf of Lion led France to submit the designation of a dedicated offshore SAC  
299 encompassing the whole Gulf of Lion continental shelf beyond the territorial waters and to the  
300 recognition of this area as an important marine mammal area (IMMA) for bottlenose dolphins  
301 (<https://www.marinemammalhabitat.org/imma-eatlas/>). Our results will also contribute to  
302 update the ACCOBAMS bottlenose dolphin conservation plan.

303 We recommend that the photo-identification monitoring of bottlenose dolphins over the  
304 French Mediterranean continental shelf is continued in the long term to allow the  
305 identification of trends in the population and the implementation of adaptive management of  
306 the species at the sub-regional scale.

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309 Sanctuary, who financially supported the GDEGeM project and also thank Fondation de  
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312 Parc naturel régional de Corse as well as all the people who participated to the survey. We  
313 also acknowledge Guido Gnone and Michela Bellingeri for their support in the use of the  
314 INTERCET platform.

315 **Tables**

316

317 **Table 1:** Sightings and photo-identification of bottlenose dolphins

	Sightings	ER	Group size (SD)	Right profiles	Left profiles	Captures	Recaptures	Identified individuals	Recaptured individuals
Corsica	41	0.012	5.3 (4.5)	140	130	167	35 (21%)	132	26 (20%)
Riviera	18	0.003	15.7 (10.3)	227	207	260	113 (43%)	147	45 (31%)
Gulf of Lion	92	0.007	16.6 (13.2)	920	895	1278	446 (35%)	834	248 (30%)
Global	151	0.007	13.6 (12.5)	1287	1,232	1705	648 (38%)	1060	334 (32%)

318

319 Number of sightings, encounter rates (ER), mean group size and standard deviation (SD),

320 number of right and left profiles pictures, number of captures and number and percentage of

321 recaptures, number of individuals identified, number and percentage of individuals captured

322 more than once.

323

324 **Table 2.** Distribution of individuals per number of captures.

	1	2	3	4	5	6	Total
Riviera	79	9	5	3	1	0	97
Gulf of Lion	411	100	51	15	1	2	580
Continental coast	458	123	61	21	6	2	671

325

326 Number of dolphins identified 1, 2, 3, etc. times in each dataset.

327

328 **Tableau 3:** Abundance estimates (N) and 95% confidence intervals in Riviera, Gulf of Lion

329 and Continental coast in each season. For Winter and Summer 2014 in Riviera, the recapture

330 probabilities were estimated very low, which impeded the estimation of abundance.

331

		Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
		2013	2013	2013-2014	2014	2014	2014	2014-2015
Riviera	N	57.74	33.86	NA	57.78	NA	52.63	58.39
	2.5%	25.52	18.85	NA	21.56	NA	22.65	23.17
	97.5%	98.45	54.12	NA	151.24	NA	128.96	113.43
Gulf of Lion	N	377.36	297.87	539.56	338.44	558.28	499.50	494.55
	2.5%	124.21	147.82	266.82	236.38	453.18	399.50	412.48
	97.50%	875.67	631.09	1395.10	481.26	679.21	596.49	604.17
Continental coast	N	199.47	307.38	888.72	446.28	775.44	646.10	635.20
	2.5%	134.17	221.38	491.81	349.91	613.78	520.81	516.36
	97.5%	297.51	460.92	1717.56	535.68	963.60	788.23	748.54

332



333 **Figure legends**

334

335 **Figure 1:** Study area (in blue) encompassing the French Mediterranean continental shelf in  
336 north-western Mediterranean Sea. The bathymetry is also displayed on the map.

337

338 **Figure 2:** Seasonal distribution of survey effort (number of kilometers actively traveled per  
339 5'x5' cell) between 2013 and 2015 over the French Mediterranean continental shelf.

340

341 **Figure 3:** Seasonal distribution of bottlenose dolphins over French Mediterranean waters  
342 between 2013 and 2015. Encounter rates (number of sightings/km) per 5'x5' cell.

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462 Appendix 1

463

464 Table of AICc values

465

	Model*	number of parameters	QAICc	Deviance	c-hat
Gulf of Lion	1	9	983.89	126.80	1.39
	2	3	1002.54	157.67	1.39
	3	11	987.54	126.38	1.39
	4	5	1006.58	157.67	1.39
Riviera	1	9	211.15	68.91	0.87
	2	3	254.54	125.70	0.87
	3	11	214.72	67.82	0.87
	4	5	258.83	125.70	0.87
Continental coast	1	9	1130.85	129.72	1.60
	2	3	1154.71	165.75	1.60
	3	11	1132.26	127.03	1.60
	4	5	1156.45	163.45	1.60

466 \* Models were built as follows:

467 Model 1 considers two age classes in survival and season-dependent recapture probabilities

468 Model 2 considers two age classes in survival and constant recapture probabilities

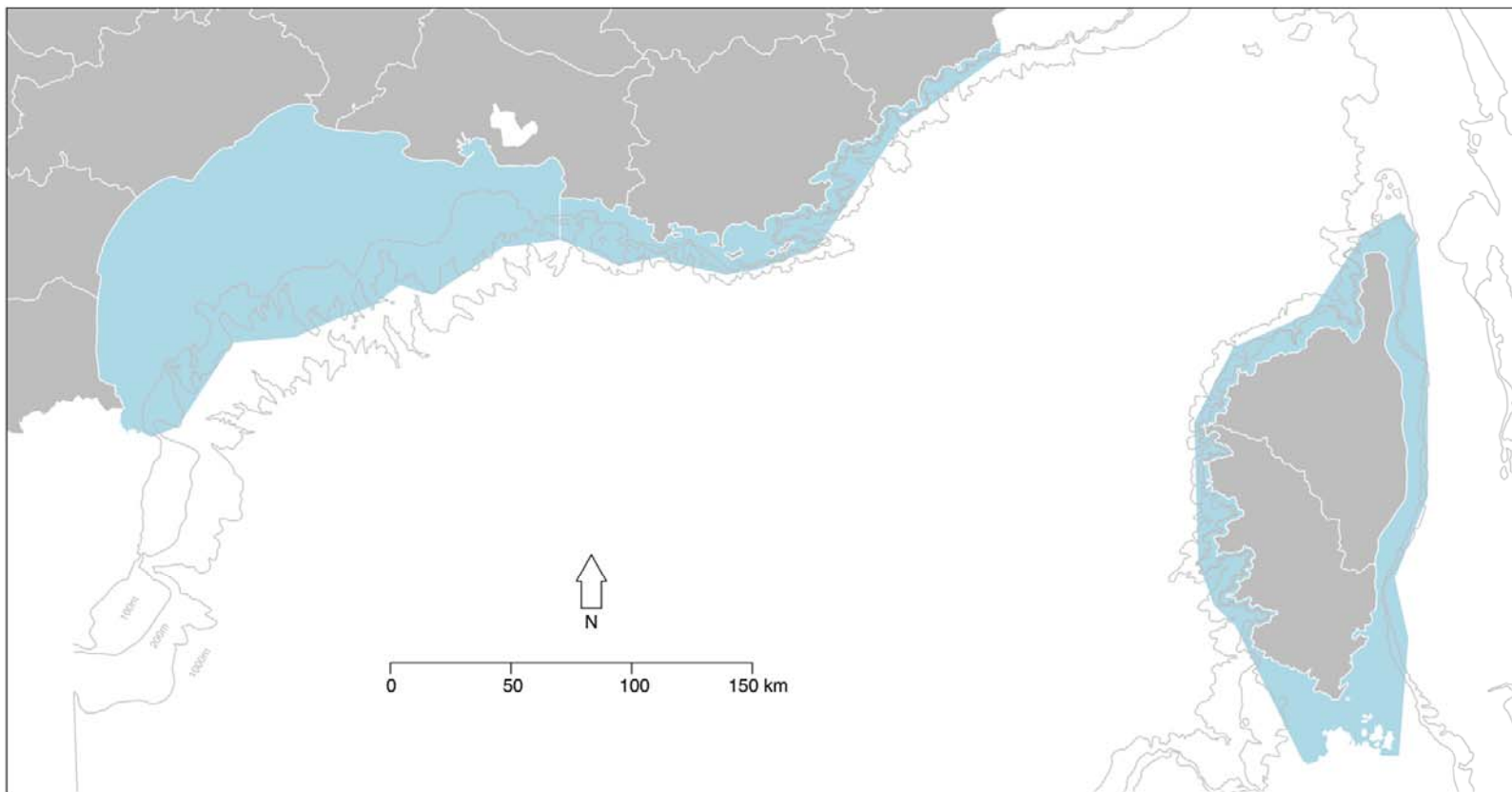
469 Model 3 considers two age classes in survival, heterogeneous and season-dependent

470 recapture probabilities

471 Model 4 considers two age classes in survival and heterogeneous recapture probabilities

472

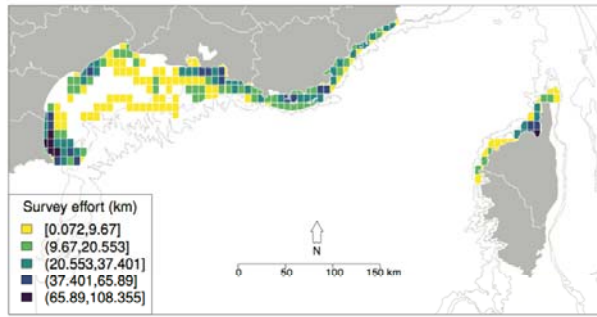




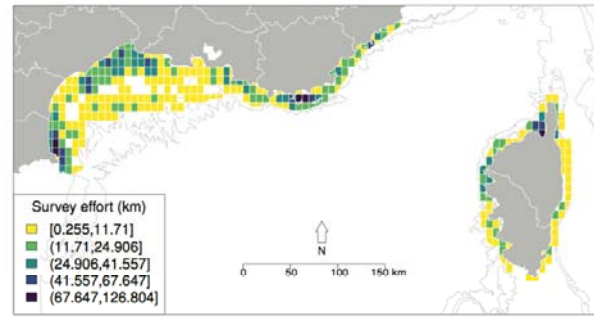
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Figure 1

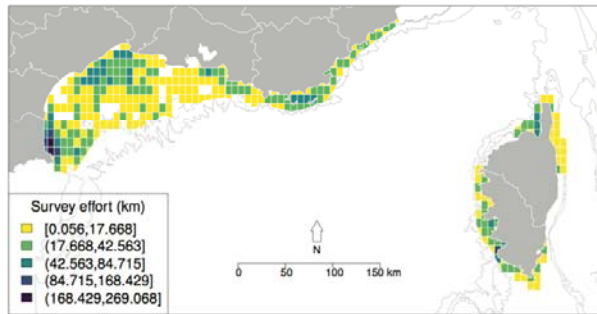
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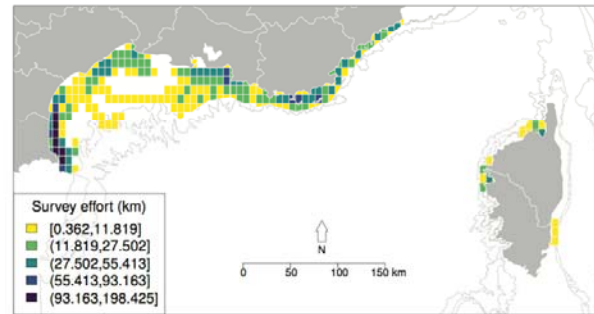
(a) Autumn



(b) Spring



(c) Summer

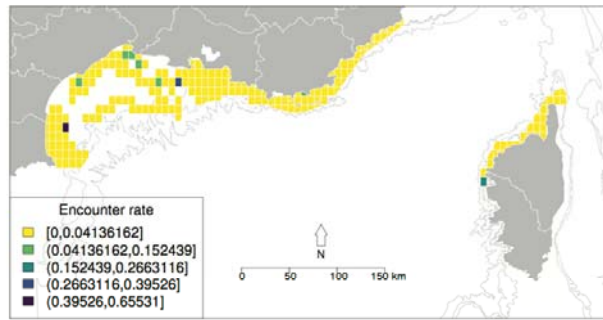


(d) Winter

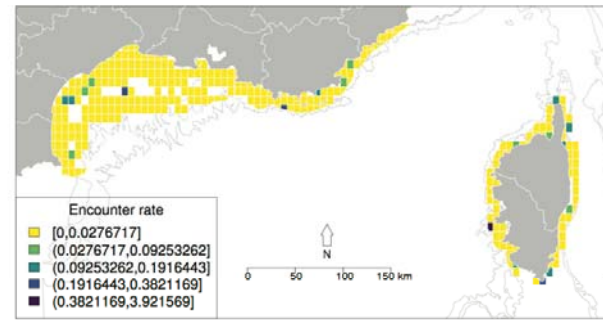
475

Figure 2

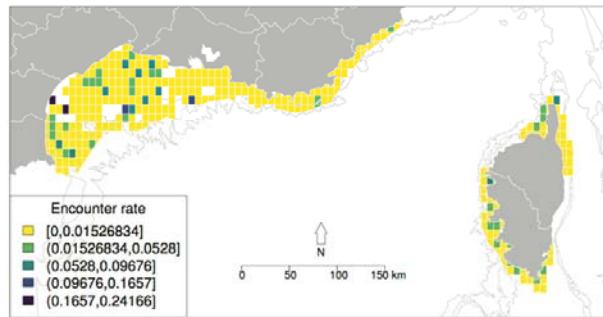
476



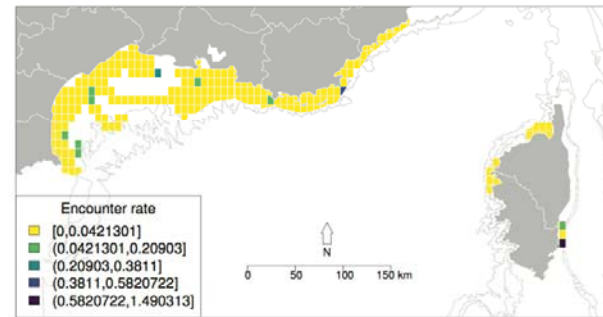
(a) Autumn



(b) Spring



(c) Summer



(d) Winter

477

Figure 3