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ARTICLE

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Distribution and abundance of common bottlenose dolphin (*Tursiops truncatus*) over the French Mediterranean continental shelf

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Abstract

The common bottlenose dolphin (*Tursiops truncatus*) subpopulation in the Mediterranean is listed as vulnerable by the International Union for Conservation of Nature. This species is strictly protected in France and the designation of Special Areas of Conservation (SAC) is required under the EU Habitats Directive (92/43/EEC). However, little information is available about the structure and dynamics of bottlenose dolphins in French Mediterranean waters. We collected photo-identification data over the whole French Mediterranean continental shelf year-round between 2013 and 2015. We sighted 151 groups of bottlenose dolphins allowing the individual photo-identification of 766 animals. The encounter rate distribution showed the presence of bottlenose dolphins over the whole continental shelf year-round. We estimated for the first time, using capture-recapture methods, the size of this bottlenose dolphin population at 2,350 individuals, 95% credible interval [1,827, 3,135]. Our results were used in support of the designation of a new dedicated SAC in the Gulf of Lion and provide a baseline for the bottlenose dolphin monitoring in the French Mediterranean waters in the context of the Marine Strategy Framework Directive.

KEYWORDS
abundance, bottlenose dolphin, capture-recapture, distribution, French Mediterranean Sea, photo-identification, *Tursiops truncatus*

1 | INTRODUCTION

The common bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821; hereafter bottlenose dolphin) is considered as a regular species in the Mediterranean Sea (Reeves & Notarbartolo di Sciara, 2006). It has been observed along most of the Mediterranean coast (Bearzi et al., 2009), most often over the continental shelf (Gannier, 2005; Gnone et al., 2011; Notarbartolo Di Sciara et al., 1993), even though groups have also been observed offshore (Laran et al., 2016). Both resident populations and transient individuals have been reported (Gnone et al., 2011). The Mediterranean bottlenose dolphin subpopulation is genetically differentiated from populations inhabiting the contiguous eastern North Atlantic and the Black Sea and is structured into a Western and an Eastern population, corresponding to habitat boundaries (Natoli et al., 2005).

The Mediterranean bottlenose dolphin subpopulation is considered as vulnerable on the IUCN (International Union for Conservation of Nature) Red List. It is listed in Annex II of the Washington Convention on International Trade in Endangered Species, in Appendix II of the Bern Convention for the Conservation of European Wildlife and Natural Habitats, in Appendix II of the Protocol to the Barcelona Convention on Specially Protected Areas of Mediterranean Importance (SPAMI), and is one of only two species of cetaceans listed in Appendix II of the European Habitats Directive (92/43/CEE). It is also strictly protected in France by the decree of July 1, 2011, prohibiting, among other things, the destruction, capture, and intentional disturbance of marine mammals. In addition, the bottlenose dolphin is the subject of a specific action plan under development by the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea, and contiguous Atlantic Area (ACCOBAMS).

In this context the population's conservation status, including population trends, needs to be assessed. Population indicators (e.g., distribution, abundance) should be regularly evaluated and compared with reference values through standardized long-term monitoring (Cairns et al., 1993; Dale & Beyeler, 2001).

In France, the monitoring program set up for the implementation of the European Marine Strategy Framework Directive (2008/56/EC; MSFD) recommends specific monitoring of resident coastal populations of marine mammal species using photo-identification, including bottlenose dolphins. Bottlenose dolphins can be identified individually from their natural markings, and the resulting longitudinal sighting histories of individuals can be analyzed with capture-recapture (CR) models (Hammond, 2009; Hammond et al., 1990; Rosel et al., 2011) to estimate population abundance and survival. Photo-identification data have been used widely to monitor populations of bottlenose dolphins (e.g., Defran & Weller, 1999; Gnone et al., 2011; Karczmarski & Cockcroft, 2014; Louis et al., 2015; Shane et al., 1986).

In French Mediterranean waters, several studies on bottlenose dolphins have been conducted since the 1990s, and many of them were based on photo-identification (Bompar et al., 1994; Dhermain et al., 1999; Labach et al., 2011, 2015; Ripoll et al., 2001). The knowledge of the population structure, ecology, and dynamics remains poor and unequal, in part because these studies were limited to small areas over short periods.

In this study, we conducted the first large-scale bottlenose dolphin photo-identification survey in French Mediterranean waters. Standardized photo-identification data were collected throughout the French Mediterranean continental shelf year-round over 2 years through a standard protocol by a network of organizations. The objectives of our study were to evaluate the distribution of bottlenose dolphins and to provide the first population abundance estimate over the French continental shelf.

2 | METHODS

2.1 | Study area

The French Mediterranean waters contain high diversity and a richness of habitats and seabed. The Gulf of Lion, from the Spanish border to Marseille, is a vast continental shelf limited to the north by a sandy and lagoon coastline and to the south by a broad slope cut by numerous canyons. The Corso-Liguro-Provençal basin (Riviera and west coast of Corsica) presents a rocky coastline prolonged by a narrow continental shelf quickly giving way to an abrupt slope, cut by deep canyons. To the east of Corsica, the reliefs are shallower with a wider continental shelf. The Corso-Liguro-Provençal basin and the Gulf of Lion are highly productive areas, attracting a high diversity of species (D'Ortenzio & Ribera d'Alcaì, 2009).

The study area covers the continental shelf of the French Mediterranean waters between the coast and the 500 m isobath, bounded by the Spanish border to the west, the Italian border to the east, and includes the whole Corsican coastline (Figure 1). The overall study area covers 24,481 km^2 and was divided into three regions based on geographic and topographic characteristics: Gulf of Lion (14,731 km^2), Riviera (2,866 km^2), and Corsica (6,884 km^2). To ensure homogeneous sampling over the whole study area, each region was divided into subregions of similar area, covering on average 2,500 (±500) km^2 (four in Gulf of Lion, two in Riviera, and three in Corsica) and assigned to five local organizations associated with marine mammal monitoring (BREACH, CARI, EcoOcéan Institut, GECEM, and Parc naturel régional de Corse) according to their location and usual study areas, with each organization covering one or two subregions.

2.2 | Data collection

The objective of the survey was to conduct 4 days of boat-based survey effort per season within each subregion. We defined the survey effort as the length (in kilometers) of track actively traveled, prospecting the area with naked eyes by

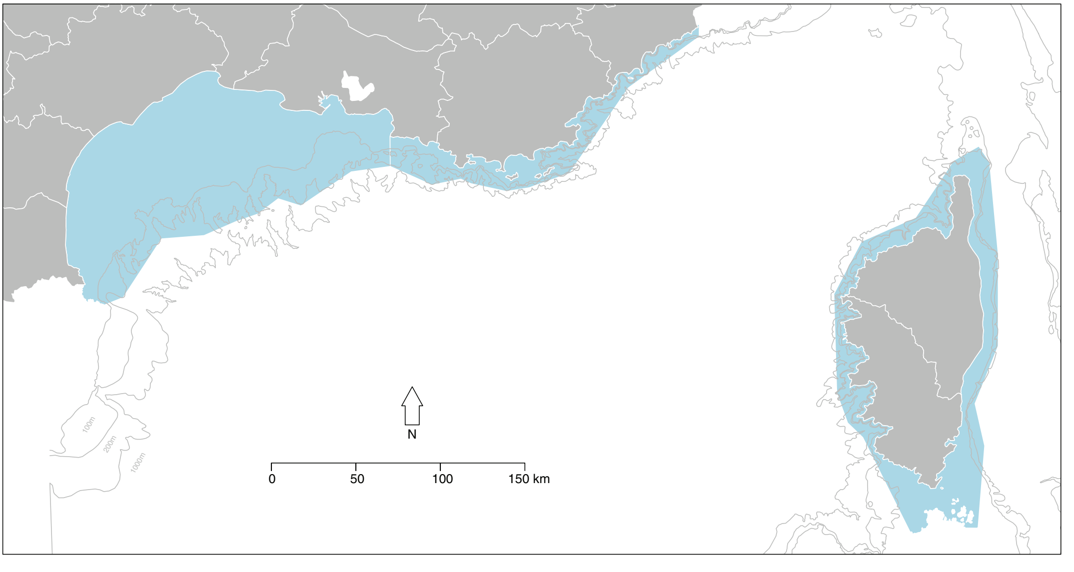

FIGURE 1 Study area (in light blue) encompassing the French Mediterranean continental shelf in the northwestern Mediterranean Sea. The Pelagos sanctuary boundaries appear in dark blue. The bathymetry is also displayed on the map.

three observers. Surveys were conducted only in favorable weather conditions (Beaufort scale 0–3 and good visibility). Seasons were defined as spring (March 22–June 21), summer (June 22–September 21), autumn (September 22–December 21), and winter (December 22–March 21). This survey design was conducted twice between 2013 and 2015 using small sailboats and motorboats. Routes were planned on a variable basis, according to weather conditions, to optimize the study area sampling coverage. All partners applied a standard common protocol using a digital application for the data collection specifically designed with Cybertracker (https://www.cybertracker.org/), systematically recording survey tracks with a GPS receiver. When we encountered a group of bottlenose dolphins, we recorded the position of first contact, group size, and composition along with the group's main activity. We defined a group as all dolphins seen with naked eye during the sighting. The estimated group size is the estimated number of individuals observed or photo-identified when the latter figure is greater than the estimated one.

Whenever possible, we took photographs with a digital reflex camera of both sides of the dorsal fins of all individuals of the group, regardless of their markings.

2.3 | Photo-identification

We identified individuals using natural marks: scars, nicks, and scratches on their dorsal fins (Würsig & Jefferson, 1990; Würsig & Würsig, 1977). The best photographs of each side of each individual at every encounter were selected and scored according to their quality (Q1 for good, Q2 for medium, and Q3 for bad) and the distinctiveness of animals (D1 for well-marked, D2 for moderately marked and D3 for poorly marked) (Berrow et al., 2012; Ingram, 2000) to generate catalogs of identified dolphins. Catalog and associated data were incorporated into a common database which was uploaded onto the international web database INTERCET (http://www.intercet.it/). Each partner compared its own catalog with all the others compiled within the project, and a global matching was conducted by one additional scientist, ensuring that matching was conducted by at least three people, minimizing bias due to false positive and negative matching. The matching process led to three regional catalogs and one global one. A matrix of sighting histories was associated with each catalog gathering all the sighting data and information of all the dolphins identified. For the analyses, we used only medium and good quality photographs (quality scores = 1 or 2) of moderately and well-marked individuals (distinctiveness score = 1 or 2). The proportion of moderately and well-marked individuals was evaluated as the number of individuals identified during the project, considering each side (right or left side) separately, that scored D1 or D2 (removing all pictures scored D3) among individuals identified by at least one photograph scored Q1 or Q2 (removing all pictures scored Q3) (see also the Abundance estimation section).

2.4 | Distribution

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

2.5 | Abundance estimation

To estimate the abundance of bottlenose dolphins occurring within the study area, we fitted CR models to the photo-identification data (Hammond et al., 1990). We defined a capture when an individual was identified using photo-identification, and a recapture as the resighting of an individual already identified during the project. Because some individuals were sighted both in Gulf of Lion and in the Riviera during the study period, we performed three separate analyses, corresponding to the sightings made in the Gulf of Lion, in the Riviera, and along the continental coast (Gulf of Lion plus Riviera). We did not pursue CR analyses with the Corsican sightings because of insufficient recaptures (Table 1).

We used Bayesian closed population models (McClintock, 2015) to estimate abundance while accounting for a capture probability less than one. We considered the eight seasons as our capture occasions. The main assumptions underlying closed population CR models are (1) the population is demographically closed (i.e., natality and mortality events do not occur) during the study period, (2) all individuals are correctly identified at each capture occasion, and (3) the marks are considered permanent.

To fit CR models, we used the package *multimark* (McClintock 2015) in R (R Core Team, 2018), which implements Markov Chain Monte Carlo (MCMC) simulations. We performed an analysis for each data set, that is the Gulf of Lion, the Riviera, and the continental coast (Gulf of Lion plus Riviera). For each analysis, we fitted eight models, including a model with constant detection probability (M0), a model with time variation in the detection probability (Mt), a model with heterogeneity in the detection probability (Mh) under the form of an individual random effect, a model with behavioral response in the detection probability (Mb), and combinations of these effects (Mbt, Mht, Mbh, Mbht). To determine the model best supported by the data, we calculated posterior model probabilities (Barker & Link, 2013). More precisely, we relied on an extension of the standard Bayes theorem where the posterior distribution of all parameters is now defined over both the parameter and model space. In addition to posterior summaries for parameters (abundance and detection probabilities), we also obtained the posterior probability for each model obtained as the proportion of the time the MCMC simulations spend in each model. Because we used only moderately and well-marked individuals (assumed to be adults) in the CR analyses, the abundance, including poorly marked individuals (juveniles and neonates), was obtained by correcting the CR abundance by the proportion of moderately and well-marked individuals (Williams et al., 1993) estimated as: $\Delta = n\text{QD12}/n\text{Q12}$, where Δ is the proportion of moderately and well-marked individuals, nQ12 is the number of individuals identified after removing bad quality photographs (Q3), and nQD12 is the number of individuals identified after removing bad quality photographs (Q3) and poorly marked individuals (D3) evaluated on the global data set (all captures included) for each data set. We estimated this proportion for left- and right-side photographs then calculated the average of these two proportions for each data set. The standard error was obtained with the formula $\widehat{p}(1 - \widehat{p})/n$ for a proportion estimate $\widehat{p}$ where n is the sample size. In practice, the Bayesian approach using MCMC made it easy to propagate the uncertainty in the proportion of moderately and well-marked individuals. We divided each MCMC value drawn in the posterior distribution of abundance by a random draw from a normal distribution with mean Δ and standard deviation the standard error, therefore providing the posterior distribution of the corrected CR abundance. We reported posterior means and 95% credible intervals for abundance and detection probabilities.

3 | RESULTS

3.1 | Survey effort

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

TABLE 1 Distribution of individuals per number of captures.

Location	1	2	3	4	5	6	Total
Corsica	78	16	0	1	0	0	95
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

Note: Number of moderately and well-marked individuals identified (based on good and medium quality photographs) 1, 2, 3, etc. times in each data set. Continental coast refers to Riviera plus Gulf of Lion.

3.2 | Distribution

We sighted bottlenose dolphins across the study area in all seasons (Figure 3). Global ER was higher in Corsica (0.012) than in Gulf of Lion (0.007) and in Riviera (0.003) (Table 2). In Riviera, ER appeared higher in spring (Figure 3), while in Gulf of Lion and Corsica, ER appeared higher in summer (Figure 3).

3.3 | Sightings and photo-identification

We sighted 151 groups of bottlenose dolphins during the project. Group size was highly variable in the three regions, mean group size was similar in Riviera (15.7, *SD* 10.3) and Gulf of Lion (16.6, *SD* 13.2) and lower in Corsica (5.3, *SD* 4.5) (Table 2).

After photos scoring and sorting, 766 different moderately and well-marked dolphins were identified based on good and medium quality photographs (Table 2), of which 30% were observed more than once during the project. The percentage of individuals recaptured was higher in Gulf of Lion (29%) than in Riviera (19%) and in Corsica (18%). Six individuals were sighted in both the Gulf of Lion and Riviera, while no recaptures were made between continental and Corsican coast.

3.4 | Abundance estimates

We excluded 15% of the 1,705 photographs from the analyses because of their low quality (Q3). The proportion of moderately and well-marked individuals was 0.73 in Riviera ($SE = 0.02$), 0.84 ($SE = 0.01$) in Gulf of Lion and 0.86

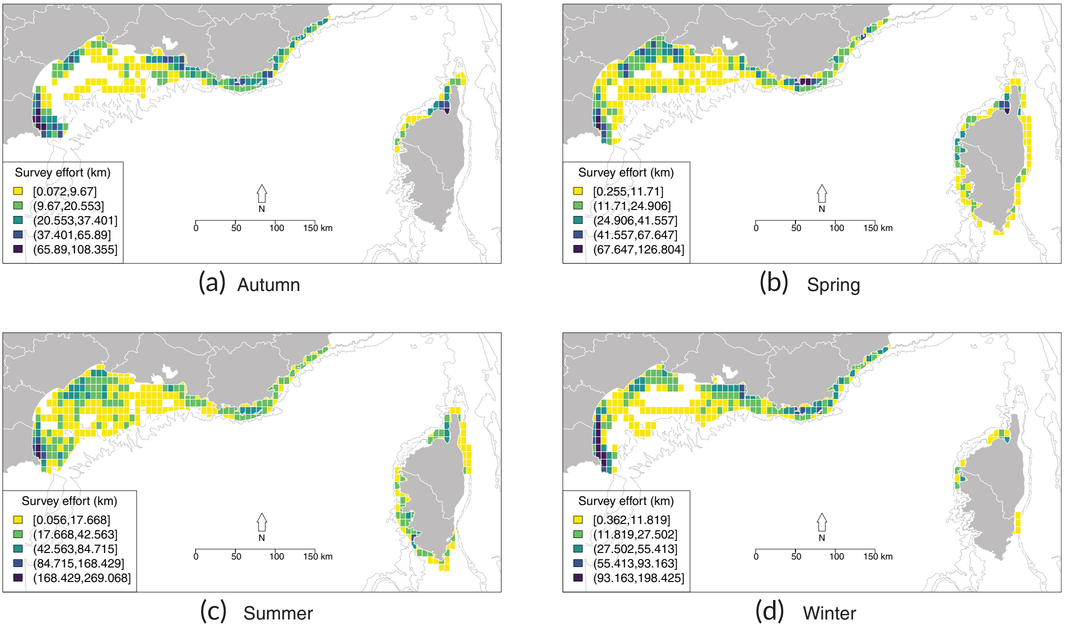

FIGURE 2 Seasonal distribution of survey effort (number of kilometers actively traveled per 5′ × 5′ cell) between 2013 and 2015 over the French Mediterranean continental shelf.

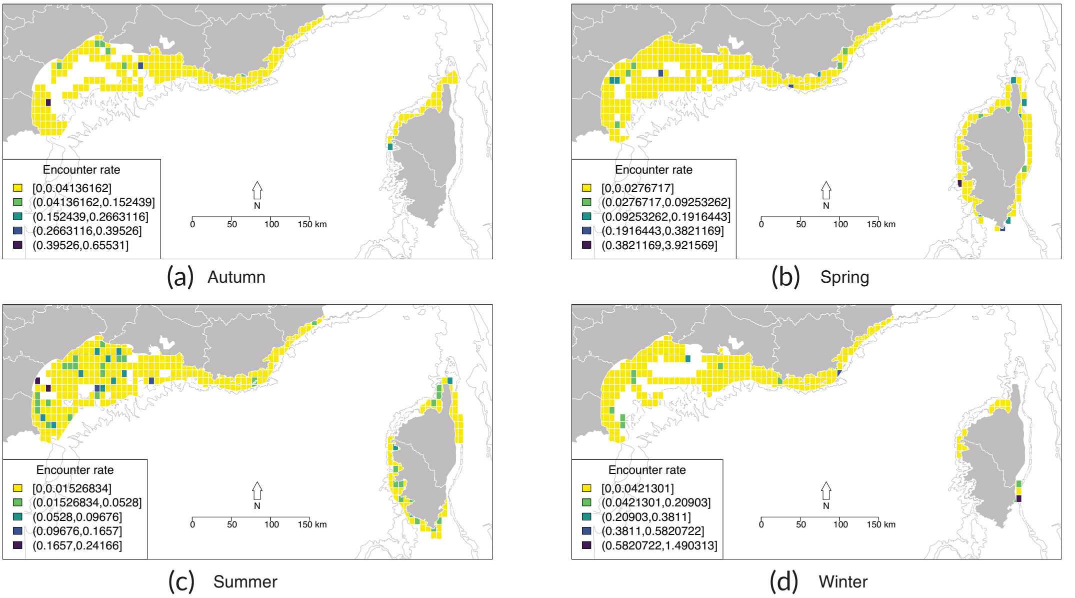

FIGURE 3 Seasonal distribution of bottlenose dolphins over French Mediterranean waters between 2013 and 2015. Encounter rates (number of sightings/km) per 5′ × 5′ cell.

TABLE 2 Sightings and photo-identification of bottlenose dolphins.

Location	Sightings	Encounter rate	Mean group size (*SD*)	Identified individuals	Recaptured individuals
Corsica	41	0.012	5.3 (4.5)	95	17 (18%)
Riviera	18	0.003	15.7 (10.3)	97	18 (19%)
Gulf of Lion	92	0.007	16.6 (13.2)	580	169 (29%)
Global	151	0.007	13.6 (12.5)	766	230 (30%)

Note: Number of sightings, encounter rates, mean group size and standard deviation (*SD*), number of moderately and well-marked individuals identified based on good and medium quality photographs, and number of recaptured individuals (sighted more than once) in each region.

(*SE* = 0.01) in the whole continental coast (Riviera and Gulf of Lion). Many dolphins (68% in continental coast) were seen only once. The maximum number of captures was 6 for two dolphins (Table 1).

The model best supported by the Gulf of Lion and whole continental coast data included heterogeneity and temporal variation in the detection probability (posterior probability = .70 and .78, respectively), while the model best supported by the Riviera data was the one considering heterogeneity, a behavioral response and temporal variation in the detection probability (posterior probability = 1). Detection probabilities varied between .02 (.01–.03) and .16 (.11–.22) for Gulf of Lion, between .07 (.01–.19) and .44 (.19–.68) for Riviera, and between .02 (.02–.03) and .15 (.11–.19) for the whole continental coast.

Abundance (corrected by the proportion of moderately and well-marked individuals) of population was estimated at 223 (152–385) individuals in Riviera, 2,231 (1,590–3,175) in Gulf of Lion and 2,350 (1,827–3,135) along the whole continental coast.

4 | DISCUSSION

Our study provides the first large-scale dedicated photo-identification survey for the bottlenose dolphin in the French Mediterranean waters. We demonstrate the power of a collaborative and coordinated survey to study a mobile species at population's scale. Our results show that the whole continental shelf is frequented by bottlenose dolphins, including the entire Gulf of Lion, all year round and provides the first abundance estimate of bottlenose dolphins frequenting the French continental shelf of Riviera and Gulf of Lion.

The effort of 21,464 km covered 87% of the study area. We found heterogeneity in this effort, mainly between Corsica and the continental coast, which we explain by a later start of the survey in Corsica and difficult survey conditions during the study. The results obtained in Gulf of Lion and Riviera show that the survey effort is sufficient to provide consistent estimates of abundance and distribution.

The global encounter rate (0.007) was higher than the encounter rates obtained with the program "Surveillance Aérienne de la Mégafaune Marine" (SAMM) (0.0041 in winter and 0.0028 in summer; Laran et al., 2016). This difference could be explained by the fact that this comprehensive aerial survey of marine megafauna conducted by the French Biodiversity Agency in 2011 and 2012 over the whole French Exclusive Economic Zone (EEZ), encompasses continental shelf, slope, and oceanic waters (Laran et al., 2016). Another likely reason might be that aerial surveys consistently have lower encounter rates than boat-based surveys because of the order of magnitude difference in survey speed. The ER in Riviera (0.003) and in Corsica (0.012) were also higher than the maximum ER obtained by Gnone et al. (2011) between 1994 and 2007 in Provence (ER = 0.0006) and in Corsica (ER = 0.0086), which suggest an increase in dolphin abundance in these two regions.

The distribution of ER showed that bottlenose dolphins were present over the entire French Mediterranean continental shelf all year round. The higher ER in summer in the Gulf of Lion and Corsica was consistent with the results of the SAMM survey, which despite showing higher ER in winter than summer in the global EEZ, also showed contrasting seasonal distributions, with encounters concentrating in coastal areas of the Gulf of Lion and Corsica in the summer (Laran et al., 2016). These results suggest a seasonal migration of bottlenose dolphins between offshore waters in winter to coastal waters in summer, especially in Gulf of Lion and Corsica. The sighting of dolphins both in Riviera and Gulf of Lion also points towards some eastward and westward movements. No movement between the continental areas and Corsica was observed during the project. In previous studies (Gnone et al., 2011), 5 individuals were identified both in Corsica and the continental coast, highlighting that some dolphins perform long distance travels. The high percentage of dolphins captured only once (70%) during the project can be explained by the short period and the large study area of the project decreasing the recapture probability. It may also highlight that an important proportion of bottlenose dolphins sighted over the French Mediterranean continental shelf are transient animals coming from remote areas, as suggested by the seasonal differences in the ER and the movements identified, whereas other animals are resident, as suggested by sightings of some individuals all year round for more than 20 years (authors unpublished data). Pursuing photo-identification at this scale over the long term will allow further exploration of and characterizing residency patterns. In their study, Gnone et al. (2011) identified two subpopulations inside the Pelagos Sanctuary coinciding with the national boundaries between French and Italian territories. The identification of distinct units and the characterization of connections between them along the French continental coast is the object of ongoing work using population genetic and social structure analyses based on photo-identification and biopsy data collected during the present study. Sharing photo-identification catalogs and associated metadata through the INTERCET platform will make possible the characterization of bottlenose dolphin movements and social structure at wider Mediterranean scale. The higher percentage of poorly marked individuals in Riviera (27%) suggests a higher percentage of immature dolphins in this region than in Gulf of Lion (16%).

The robust estimation of abundance relies on the validation of CR model assumptions. The 2-year sampling period and the fact that newborns were observed in the study area suggest that assumption 1 of the capture-recapture model is likely to have been violated. We expect little underestimation bias in the abundance estimates because of birth occurring during the study, as we considered adults only, and they have high survival probability. Mortality occurring during the study could also lead to abundance overestimation, nevertheless we expect little bias considering the relative short period for this long-lived species and the high survival probability. Assumptions 2 and 3 are ensured by the fact that only moderately and well-marked individuals with medium and good quality photographs were included in the analysis. Also, if the marks evolve, the short sampling period would allow recognition of the animals.

The population abundance along the continental coast was higher than the estimates of the only previous census dedicated to bottlenose dolphins in the same area, which estimated based on observed count (not corrected by imperfect detection) the number of bottlenose dolphins between 200 and 209 in the Gulf of Lion and 16 in Provence (Ripoll et al., 2001). These figures are not inconsistent with our abundance estimates which accounted for imperfect detection by correcting the observed counts by the estimated detection probability. Our abundance estimates are coherent with the results obtained from the program SAMM with the distance sampling methodology, which estimated the absolute abundance of bottlenose dolphins in the Gulf of Lion at 63, 95% CI [17, 241] in winter and at 1,331, 95% CI [466, 3,805] in summer and over the continental slope inside the French EEZ waters and including some Italian and Spanish waters at the eastern and western borders at 1,795, 95% CI [769, 4,190] in winter and 10, 95% CI [3, 30] in summer (Laran et al., 2016).

Further efforts should be implemented to complete the survey planned for this study in Corsica to provide consistent estimates for this region also.

4.1 | Implications for conservation

Our study provides an operational framework as well as a baseline for the implementation of a long-term large-scale monitoring of bottlenose dolphin population in the French Mediterranean waters. We therefore recommend pursuing the monitoring initiated in this study for the long-term, taking into consideration the evaluation of the efficacy of the survey design, on which we are currently working, to allow the identification of trends in the population as required for the surveillance program of the MSFD.

We shared the data on the international webGIS platform INTERCET (http://www.intercet.it/), which will allow enlarging the study of this species beyond French boundaries to the basin and Mediterranean scale.

The results of our study, together with those from the SAMM survey (Laran et al., 2016), led to an update of the Mediterranean bottlenose conservation status in the national IUCN Red List, which was changed from “vulnerable” in 2009 to “near threatened” in 2017 because of the improved knowledge. They also contributed to the update of the Mediterranean subpopulation status initiated in 2020. Our demonstration of the presence of bottlenose dolphins in the entire Gulf of Lion led France to submit the designation of a dedicated offshore SAC encompassing the whole Gulf of Lion continental shelf beyond the territorial waters and to the recognition of this area as an important marine mammal area (IMMA) for bottlenose dolphins (https://www.marinemammalhabitat.org/imma-eatlas/). Our results will also contribute to updating the ACCOBAMS bottlenose dolphin conservation plan.

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AUTHOR CONTRIBUTIONS

Hélène Labach: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; validation; visualization; writing – original draft; writing – review and editing. **Caroline Azzinari:** Data curation; investigation; writing – original draft. **Maxime Barbier:** Data curation; investigation; writing – original draft. **Cathy Cesarini:** Data curation; investigation; writing – original draft. **Boris Daniel:** Resources; writing – original draft. **Léa David:** Conceptualization; data curation; investigation; methodology; writing – original draft. **Frank Dhermain:** Data curation; investigation; writing – original draft. **Nathalie Di-Méglio:** Conceptualization; data curation; investigation; methodology; writing – original draft. **Benjamin Guichard:** Resources; writing – original draft. **Julie Jourdan:** Data curation; investigation; writing – original draft. **Nicolas Robert:** Data curation; investigation; writing – original draft. **Marine Roul:** Data curation; investigation; writing – original draft. **Nicolas Tomasi:** Data curation; investigation; writing – original draft. **Olivier Gimenez:** Formal analysis; methodology; supervision; validation; visualization; writing – original draft; writing – review and editing.

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