

Distribution, abundance, and movements of the bottlenose dolphin (Tursiops truncatus) in the Pelagos Sanctuary MPA (north-west Mediterranean Sea)

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ABSTRACT

1. The Pelagos Sanctuary is the largest marine protected area of the Mediterranean Sea (87 500 km²), and is located in the north-west part of the basin. The presence of the bottlenose dolphin in this area is well documented but its distribution and abundance are not well known.

2. The present study collected and analysed data from 10 different research groups operating in the Pelagos Sanctuary from 1994 to 2007. Photo-identification data were used to analyse the displacement behaviour of the dolphins and to estimate their abundance through mark–recapture modelling.

3. Results show that the distribution of bottlenose dolphin is confined to the continental shelf within the 200 m isobath, with a preference for shallow waters of less than 100 m depth.

4. Bottlenose dolphins seem to be more densely present in the eastern part of the sanctuary and along the north-west coast of Corsica.

5. Bottlenose dolphins show a residential attitude with excursions usually within a distance of 80 km (50 km on average). A few dolphins exhibit more wide-ranging journeys, travelling up to 427 km between sub-areas.

6. The displacement analysis identified two (sub)populations of bottlenose dolphins, one centred on the eastern part of the sanctuary and the other one around the west coast of Corsica.

7. In 2006, the eastern (sub)population was estimated to comprise 510–552 individuals, while 368–429 individuals were estimated in the Corsican (sub)population. It was estimated that in total, 884–1023 bottlenose dolphins were living in the Pelagos Sanctuary MPA in the same year.

8. The designation of a number of Special Areas of Conservation (SACs) under the Habitats Directive is discussed as a possible tool to protect the bottlenose dolphin in the Pelagos Sanctuary and in the whole of the Mediterranean Sea.

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Received 31 August 2010; Revised 30 March 2011; Accepted 09 April 2011

KEY WORDS: *Tursiops truncatus*; bottlenose dolphin; Pelagos Sanctuary; Mediterranean Sea; abundance; protection

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INTRODUCTION

The common bottlenose dolphin (*Tursiops truncatus* Montagu, 1821) is a cosmopolitan Delphinidae. Its distribution is usually contained within the 45th parallel in both hemispheres, in tropical and temperate waters, but in the North Atlantic it can reach the 65th parallel (Rice, 1998; Wells and Scott, 1999). This wide distribution is associated with a remarkable morphometric differentiation among populations, which led to 20 species being classified in the 1960s (Hershkovitz, 1966). Today most authors identify the majority of the forms in a single species, *Tursiops truncatus*; a second species of Indo-Pacific distribution, *Tursiops aduncus* (Ehrenberg, 1833), however, is still the subject of ongoing debate (Ross and Cockcroft, 1990; Hale *et al.*, 2000).

Within the species *Tursiops truncatus*, the presence of two genetically different ecotypes, one with primarily coastal habits and the other with primarily offshore habits, has been described by various authors in different areas of the world (Ross, 1977, 1984; Walker, 1981; Duffield *et al.*, 1983; Hersh and Duffield, 1990; Van Waerebeek *et al.*, 1990; Mead and Potter, 1995; Hoelzel, 1998).

The bottlenose dolphin is considered a commonly occurring species in the Mediterranean Sea (Pilleri and Gahr, 1969; Cagnolaro *et al.*, 1983; Notarbartolo di Sciara and Demma, 1994) and occurs in most coastal waters of the basin (Bearzi and Fortuna, 2006). No differing ecotypes of bottlenose dolphin have been described in the Mediterranean Sea. According to Notarbartolo di Sciara and Demma (1994) the Mediterranean population is more related to the inshore ecotype, because of its shallow water habits, while Cañadas *et al.* (2002), reporting the distribution of the bottlenose dolphin off southern Spain, suggested a closer link with the offshore Atlantic ecotype. Gnone *et al.* (2005) investigated the distribution of bottlenose dolphin strandings along the Italian peninsula over a period of 18 years (1986–2002) and found a strong positive correlation with the extent of the continental shelf facing the coast line, suggesting that bottlenose dolphins tend to be more abundant in shallow water areas, within the 100 m isobath. The presence of different ecotypes in the Mediterranean Sea cannot be excluded at this stage, since very few genetic studies have been conducted in the basin; Natoli *et al.* (2005) investigated the genetic diversity of bottlenose dolphin populations along a continuous distributional range from the Black Sea to the eastern North Atlantic and found clear population structures over the geographical range, coinciding with transitions between habitat regions.

The shallow water preference of the bottlenose dolphin could be related to the feeding habits of the species, preying mostly on benthic and demersal fishes (Voliani and Volpi, 1990; Orsi Relini *et al.*, 1994; Silva and Sequeira, 1997; Mioković *et al.*, 1999; Blanco *et al.*, 2001; Santos *et al.*, 2001).

Bottlenose dolphins can learn to get the fish from trawls, gillnets and fish cages for aquaculture. This behaviour can generate a partial dependence on human activity, triggering conflicts with fishermen and is a concern in many areas of the world including the Mediterranean Sea (Chilvers and Corkeron, 2001; Lauriano *et al.*, 2004; Diaz Lopez, 2006a, 2006b; Gonzalzo *et al.*, 2008).

Bottlenose dolphin in the Mediterranean Sea have been classified as DD (Data Deficient) IUCN category since 2006; in the last IUCN report on the Status of Cetaceans in

the Mediterranean and Black Sea (Reeves and Notarbartolo di Sciara, 2006) the species was classified as Vulnerable. *Tursiops truncatus* is also listed in the Annex II of the Habitats Directive (Council Directive 92/43/EEC), as a Species of Community Interest. According to Bearzi *et al.* (2004) deliberate killing, overfishing (prey depletion), and habitat degradation may have caused a considerable reduction (about 50%) of the bottlenose dolphin population in the northern Adriatic Sea. Bearzi and Fortuna (2006) and Bearzi *et al.* (2008b) suggest a similar reduction should be applicable to the whole of the Mediterranean basin, with a current total population of less than 10,000 animals representing a decrease of about 30% in the last 60 years. These results should be taken as the best possible estimate considering the extreme data shortage in the Mediterranean Sea.

The international agreement for the Pelagos Sanctuary MPA (marine protected area) was signed by the parties in 1999, to preserve the marine environment and the cetacean fauna in the north-west Mediterranean basin. The Pelagos Sanctuary is the biggest MPA in the Mediterranean Sea (about 87,500 km²), extending over waters belonging to three European countries (France, Italy and Monaco) including Corsican and north Sardinian coasts (for a complete report on the Pelagos Sanctuary and its history see Notarbartolo di Sciara *et al.*, 2008). The area comprises pelagic areas, deep water zones and the continental shelf, with remarkable oceanographic and physiographic differences. It supports a diverse cetacean fauna, including eight species regularly present: *Balaenoptera physalus*, *Physeter macrocephalus*, *Ziphius cavirostris*, *Globicephala melas*, *Grampus griseus*, *Delphinus delphis*, *Stenella coeruleoalba* and *Tursiops truncatus* (Reeves and Notarbartolo di Sciara, 2006).

The presence of the bottlenose dolphin in the Pelagos Sanctuary MPA has been reported along the west coast of France (Ripoll *et al.*, 2001; Gannier, 2005), east coast of Liguria (Gnone *et al.*, 2006), north Tuscany (Nuti *et al.*, 2006b), Tuscany Archipelago (Nuti *et al.*, 2007; Rosso *et al.*, 2006), west and south coast of Corsica (Dhermain *et al.*, 1999; Dhermain, 2004; Dhermain and Cesarini, 2007), and the north coast of Sardinia (Lauriano, 1997; Fozzi *et al.*, 2001). Occasional sightings have also been reported in the west coast of Liguria (Azzellino *et al.*, 2008; Bearzi *et al.*, 2008b).

A few attempts have been made to estimate the abundance of the bottlenose dolphin in the Pelagos area (see Table 1).

The data collected in the last decade led to a shared perception of a major abundance of the bottlenose dolphin in the east (shallow water) portion of the MPA and along the Corsican coasts.

Interactions between bottlenose dolphins and fishing activity has been reported in the Pelagos area: Bellingeri *et al.* (2008) reported opportunistic feeding from trawlers off the eastern Ligurian Coast, while Nuti *et al.* (2006a) and Alessi *et al.* (2008) reported analogous interactions off the north Tuscany coast and the Tuscany Archipelago. Opportunistic feeding on artisanal trammel nets has been described between Corsica and Sardinia (Bonifacio Strait Natural Reserve) by Rocklin *et al.* (2009).

The local dimension of these research activities does not give an exhaustive view of the status and ecological habits of the bottlenose dolphin in the Pelagos Sanctuary. This work represents the first attempt to aggregate most of the data collected in the area over the last 14 years in order to present a complete report on distribution, movements, and abundance of the bottlenose dolphin in the Pelagos Sanctuary MPA.

Table 1. Bottlenose dolphin abundance estimates in the Pelagos Sanctuary as inferred from existing literature

Geographic area	Reference	Abundance estimate, \hat{N}	Method
West coast of Liguria and North Tuscany	Nuti <i>et al.</i> (2006c)	250	Mark-recapture
Liguria, east coast	Manfredini <i>et al.</i> (2007)	170	Mark-recapture
Gulf of Lion, Hyeres Archipelago, Gulf of Genoa and Corsica	Ripoll <i>et al.</i> (2001)	424–515	Direct counting
Corsica	Dhermain <i>et al.</i> (2003)	130–173	Direct counting
Corsica, east coast	Bompar <i>et al.</i> (1994)	25–36	Direct counting
Corsica, west coast	Bompar <i>et al.</i> (1994)	102–118	Direct counting

Table 2. Data analysed in the present study

Organization	Research period	Research platform	Survey	Speed (km h ⁻¹)	Data	
					Photo-ID	Effort track records
Delfini Metropolitan 1 ⁽¹⁾	2001-2007	semi-rigid boat	random	13-15	yes	2001-2007
Delfini Metropolitan 2 ⁽¹⁾	2006-2007	tourist boat	random	20-22	no	2006-2007
CE.TU.S. ⁽²⁾	1997-2007	sailing boat	random	8-10	yes	2003-2007
Tethys Res. Institute ⁽³⁾	1999-2007	sailing boat	random	8-10	yes	1999-2006
WWF Liguria ⁽⁴⁾	2005	tourist boat	random	20-22	no	2005
NURC 1 ⁽⁵⁾	1999-2006	res. Ship	linear transect	8-10	no	1999-2006
NURC 2 ⁽⁵⁾	1999-2006	motor boat	random	18-20	no	1999-2006
GECEM ⁽⁶⁾	1996-2007	semi-rigid boat	random	10-12	yes	2004-2007
DIBIO ⁽⁷⁾	2005-2007	semi-rigid boat	random	12-14	yes	2005-2007
CRC ⁽⁸⁾	1999-2007	motor boat	random	20-22	yes	1999-2007
EcoOcean Institut ⁽⁹⁾	1994-2007	sailing boat	mix	10-12	yes	1994-2007
Ambiente Mare ⁽¹⁰⁾	2004-2007	sailing boat	random	8-12	yes	-

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METHODS

Data collection

The data analysed originate from 10 different research organizations, all operating within the Pelagos Sanctuary, over a total period of 14 years (1994–2007) (Table 2). Data were collected during specific visual surveys carried out by expert observers. All survey effort was carried out in a sea state <4 on the Douglas Scale. The effort tracks and the sighting positions (first contact with the animals) were recorded by GPS.

Since the aggregated data were from many different research groups, over a long period of time, it was decided to use a different dolphin species, the striped dolphin (*Stenella coeruleoalba*), as a control to test the suitability of the effort made by the vessels involved. The use of a control species made the results more robust (see the Results and Discussion).

During bottlenose dolphin sightings, photographic data were collected for individual photo-identification. The procedure to collect the photographic data was the same for all the research organizations involved. Every group was provided with a proper boat, appropriate to follow the dolphins and to photograph the

fins as perpendicularly as possible. On each encounter with the dolphins, attempts were made to obtain as many photographs as possible of all individuals in the school and if possible to collect at least one photo for each side (Wursig and Jefferson, 1990). Both optical reflex cameras (1999–2002) and digital reflex cameras (2003–2007) were used for photographic data collection.

The data were used to investigate the distribution, the movements and the abundance of the bottlenose dolphin in the Pelagos Sanctuary area. In the data analysis a sequential process was followed, where the results of a given analysis are used to start the following analysis process (see below).

Data analysis

Distribution

The GIS system ArcGis 9.3 was used to visualize the research effort (tracks) and the related research success (sightings) of the target and control species in the study area. The same GIS system was used to produce a Kernel density visualization of the aggregated sampling effort and to calculate the research effort (km) and the encounter rate (ER, sightings per km) in relation to bathymetric bands (0–100, 100–200, >200, see Table 3). It should be noted that not all the research partners recorded the effort tracks regularly during the surveys. This produced a lower proportion of sighting data with no associated effort track. These data were excluded from the ER analysis.

*The data set from CE.TU.S includes data belonging to Museo di Storia Naturale, Sezione Zoologia “La Specola”, Università degli Studi di Firenze - BIOMART

Table 3. Encounter rate (sightings per km) per bathymetric band of the target (*T. truncatus*) and control species (*S. coeruleoalba*)

Research group	0–100 m						100–200 m						>200 m						
	Effort (km)		T. t.		S. c.		Effort (km)		T. t.		S. c.		Effort (km)		T. t.		S. c.		
	n	E.R.	n	ER	n	ER	n	ER	n	ER	n	ER	n	ER	n	ER	n	ER	
DM 1	11676	0.0061	71	0.0004	1361	0.0029	4	0.0037	877	0	5	0.0016	877	0	0	0.0171	15	0.0274	
DM 2	640	0	0	0	120	0	0	0	1677	0	0	0	1677	0	0	0.0089	8	0.0236	
CETUS	5652	0.008	47	0.0002	621	0.0016	1	0.0009	897	0	0	0	897	0	0	0.0199	48	0.0169	
T.R.I.	6688	0.0012	8	0.0036	1658	0.0018	3	0.0013	47619	3	15	0.0009	47619	3	6E-05	1125	0.0134	3	0.0016
WWF	505	0.002	1	0	151	0	0	0	2414	0	0	0	2414	0	0	0.0305	331	0.0336	
NURC 1	297	0	0	0	95	0	0	0	15449	1	0	0	15449	1	6E-05	261	0.0169	2	0.0336
NURC 2	759	0.0053	4	0	1028	0.0058	6	0.001	2841	0	1	0.001	2841	0	0	0.0134	38	0.0134	
GECEM	11597	0.0077	89	0.0001	1556	0.0064	10	0.0013	1833	9	0	0.0049	1833	9	0.0049	3	0.0016	3	0.0016
DIBIO	3125	0.0102	32	0.001	1525	0.0079	12	0.0013	9718	1	2	0.0013	9718	1	0.0001	273	0.0281	273	0.0281
C.R.C.	416	0.0024	1	0.0048	405	0	0	0.0074	10866	1	3	0.0074	10866	1	9E-05	331	0.0305	331	0.0305
E.O.I.	1139	0.0009	1	0.0061	726	0.0014	1	0.0083	23841	2	6	0.0083	23841	2	8E-05	801	0.0336	801	0.0336
Total	42494	0.006	254	0.001	9248	0.004	37	0.0035	118032	17	32	0.0035	118032	17	0.0001	2949	0.0249	2949	0.0249

According to the distribution analysis per bathymetric band (see the results), the continental shelf (<200 m) was subdivided into eight zones of similar length (about 170 km). The encounter rate for the target species was measured in each of these zones in order to investigate the distribution of the bottlenose dolphins in the study area. In this case, only the effort produced by similar research platforms (sailing boats, motor boats, semi-rigid boats) and similar sampling method (random – see Table 2) was considered and the ER was calculated only in those zones where the total effort (km) exceeded the surface area (km²) of the same zone (km/km² > 1 km⁻¹). To test the statistical significance of the ER differences between zones, we were forced to use a non-parametric test, due to lack of homogeneity within the data set. The research tracks were sectioned into 100 km segments and the number of segments with sightings in each zone counted, following a 1–0 sampling method (every 100 km section with at least one sighting was counted as 1, while every section with no sightings was counted as 0). The final score was put into a contingency schedule, performing a chi square test (see Table 4).

Photographic data and matching process

Each research group independently selected the photo-ID data on the basis of (a) the quality of the image, and (b) the distinctiveness of the animals.

- Photographic quality was based on focus, lighting, angle of the fin to the photographer, contrast between dorsal fin and background, visibility of the fin (Whitehead *et al.*, 1997; Wilson *et al.*, 1999; Read *et al.*, 2003).
- Identification value was based on the presence of notches, deformities, unusual fin shapes, scars, discoloration (Chilvers and Corkeron, 2003). Notches, deformities and unusual fin shapes were considered to be permanent marks (Wilson *et al.*, 1999) and were used as primary distinctive elements for the photo-identification of the animals. Scars and discolorations were only used in association with primary distinctive elements.

All of the catalogues were then pooled to perform the matching process. Before this was started, a further selection of the data was implemented in order to normalize the separate catalogues; all of the photos not meeting the matching team standards were then removed. One single expert performed the matching process visually on a PC screen. If any doubt existed, then a second person was asked to confirm the match.

A discovery curve, showing the trend of the captures over time, was finally plotted.

Movements

The above mentioned matching process was used to analyse the displacement behaviour of the dolphins within the study area. The maximum displacement distance (the maximum distance between sightings of the same individual), was measured for each dolphin with at least two sightings.

In agreement with the individual displacement behaviour resulting from the matching process, discrete sub-areas were identified and the simple ratio index (SRI, Ginsberg and Young, 1992) between these (see below) was measured:

$$SRI = X/a + b - X$$

Table 4. Sighting distribution per 100 km in the different zones

Sightings per 100 km (<i>T.t.</i>)	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7	Zone 8
<i>n</i>	18	51	46	97	83	28	101	33
1	1	1	9	28	57	20	55	9
0	17	50	37	69	26	8	46	24
Mean	0.0556	0.0392	0.2173	0.3608	1.1325	1.2142	0.9108	0.3636
S.E.	0.0556	0.0392	0.0689	0.0642	0.1108	0.2143	0.1025	0.1136
Min	0	0	0	0	0	0	0	0
Max	1	2	2	3	4	4	4	2
1 st quartile	0	0	0	0	0	0	0	0
3 rd quartile	0	0	0	1	2	2	2	1

n=number of 100 km effort segments in the respective zone; 1=number of 100 km segments with at least 1 sighting following a 1–0 sampling method; 0=number of 100 km segments with no sightings, following a 1–0 sampling method.

where *a* = total number of individuals identified in sub-area A, *b* = total number of individuals identified in sub-area B, *X* = number of individuals shared between A and B.

The sub-areas with *SRI* > 0.15 were then aggregated to identify those with a certain level of isolation. Comparing the *SRI* of these same sub-areas, two macro-areas (A and B) with a high isolation level between them (see Table 5 and Figure 8) were identified.

Abundance estimate

Within the two macro-areas identified from the displacement analysis (macro-area A, macro-area B), a closed population mark–recapture model (Otis *et al.*, 1978) was fitted to produce single year abundance estimates of the bottlenose dolphin (sub)populations, using program Capture (White *et al.*, 1982; Rexstad and Burnham, 1991) within program Mark (White and Burnham, 1999); this model, applied to the annual data set, was considered the most appropriate approach in agreement with the previous displacement analysis (see the results) and literature consultation. The same model was used to produce a total abundance estimate of the whole Pelagos area, pooling all of the data. The abundance estimates were produced for a selection of three years (2005, 2006, 2007), in agreement with the best sampling effort and related sighting success (Table 6 and Figures 4 and 9). Each single sighting was considered a capture occasion.

Mark–recapture models for closed populations have already been used to estimate the abundance of bottlenose dolphins (Wilson *et al.*, 1999; Chilvers and Corkeron, 2003; Read *et al.*, 2003; Bearzi *et al.*, 2008a). These models rely on a series of assumptions: (a) the mark (or the recognition system) should be reliable during the study period; (b) the capture of an animal should not modify the probability of the same individual being captured again; (c) the population should be considered closed, meaning that emigration/immigration and birth/death events should not affect the size of the population during the study period, neither should the portion of marked and unmarked animals change within the population; (d) all of the individuals of the population should have the same probability of being captured at each sampling event.

Strong violations of these assumptions may lead to bias in the abundance estimate and therefore a proper validation of the data collected should be done in advance (Williams *et al.*, 1993).

- (a) Mark reliability: the recognition and matching process is based on different permanent natural marks, produced

by aggressive interactions between conspecifics. Although these may change over time (new marks may be added) the use of multiple elements to check the match guarantees the respect of this assumption, as long as a photographic history of the same individual is recorded.

- (b) Behavioural experience: the photographic capture technique does not affect the behavioural response of the individual to the next capture event.
- (c) Population closure: in relation to births and deaths, the bottlenose dolphins are long living and slow breeding animals; the annual birth rate is approximately 5–6% (Wells and Scott, 1999; Wilson *et al.*, 1999) and is usually compensated by a similar death rate. An imbalance between births and deaths may of course produce a change in the population size, but this will be modest within an annual time span, unless dramatic events occurred. Longevity and slow breeding rate also account for relative stability in the portion of marked and unmarked individuals within the year. In relation to immigration and emigration events, we based this assumption of closure on the previous spatial analysis. In fact, the individual movements between sub-areas are rare over the research period analysed (*SRI* < 0.15) and are minimal (if any are present) within the years selected for analysis (*SRI* < 0.05). This is consistent with the resident behaviour exhibited by the dolphins during the study period (Tables 5 and 6). As the abundance analysis is enlarged to macro-areas, the closure assumption becomes even stronger. Emigration/immigration events may still be possible in the border regions along the continental shelf (Côte d'Azur, south Corsica, south Tuscany), but dolphin displacements in these areas are unlikely to produce considerable variations in the population size of the entire area, owing to the resident attitude of the dolphins, evident from the maximum displacement analysis (see the results).
- (d) Capture probabilities: the assumption that all the individuals in the study area have the same probability of being captured on each sampling occasion is usually the most difficult to satisfy (Hammond, 1986; Wilson *et al.*, 1999). Violation of this assumption may lead to underestimation of the population size.

Within this study, capture probabilities are unlikely to be constant, owing to the multiple research groups conducting the data collection. For this reason a time dependent and/or heterogeneity model, which allows a certain tolerance of assumptions (b)

Table 5. Number of individuals shared between different sub-areas and related simple ratio index (in brackets). The numbers in bold represent the total number of dolphins captured in the respective sub-area. Only one dolphin moved between macro-area A and macro-area B (cell *) during the research period

Sub-area	Sightings	A1	A2	A3	As1	As2	A4	As3	B1	B2	B3	B4
A1	4	30	12 (0.13)	3 (0.014)	0	0	2 (0.01)	0	0	0	0	0
A2	28		74	30 (0.13)	0	0	6 (0.025)	0	0	0	1* (0.009)	0
A3	119			186	0	0	21 (0.062)	0	0	0	0	0
As1	1				6	0	3 (0.017)	0	0	0	0	0
As2	1					4	2 (0.011)	0	0	0	0	0
A4	41						173	1 (0.005)	0	0	0	0
As3	1							13	0	0	0	0
B1	70								170	10 (0.046)	5 (0.025)	2 (0.011)
B2	16									57	1 (0.011)	0
B3	13										38	4 (0.08)
B4	4											16

Table 6. Photo-ID data sampling effort and success in the different research sub-areas (number of photo-identified dolphins)

SUB-AREAS	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Tot. ind. per sub-area
A1	-	-	-	-	6	23	-	-	-	-	1	-	30
A2	-	-	-	-	-	17	2	7	-	23	30	20	74
A3	-	1	-	8	9	17	31	59	30	49	72	125	186
As1	-	-	-	-	-	-	-	-	-	6	-	-	6
As2	-	-	-	-	-	-	-	-	-	-	4	-	4
A4	-	-	-	-	4	-	-	1	2	48	88	68	173
As3	-	-	-	-	-	-	-	-	-	-	-	13	13
B1	1	1	-	-	47	-	4	12	30	54	65	108	170
B2	-	-	-	-	20	-	-	-	2	-	38	5	57
B3	-	2	-	-	-	-	-	-	-	24	4	20	38
B4	-	-	-	-	3	-	1	-	-	-	-	12	16
Total	1	4	-	8	89	57	38	79	64	204	302	371	767
Total ind. per year	1	3	-	8	86	47	38	75	64	199	284	360	670

The last line (total individuals per year) represents the total number of different individuals captured per year (Figure 6); comparison with the above line gives the number of animals shared between sub-areas.

and (d) should be used. Variants of the Chao model (Chao *et al.*, 1992) based on Wilson *et al.* (1999), Chilvers and Corkeron (2003) and Bearzi *et al.* (2008a) were chosen; time dependent (Chao M_t) and heterogeneity and time dependent (Chao M_{th}) were both considered for the estimation of population size.

To get a final estimate, also including the portion of unmarked or poorly marked individuals, this fraction should be known and added to the preliminary estimate. Williams *et al.* (1993) estimated this fraction by counting the proportions of pictures representing well marked and poorly marked individuals; Wilson *et al.* (1999) were able to improve this technique by counting the number of marked and unmarked (or poorly marked) individuals at each sighting. This method could not be used since complete photographic data sets (including the photos of unmarked or poorly marked animals) were not available from all the partners. Instead the Wilson *et al.* (1999) method was applied to the total number of dolphins visually estimated during the sighting. Therefore the total proportion of identifiable animals was calculated as an average of the proportion of animals captured at each sighting. Since the accuracy of the total animals in the group estimate decreases as the size of the group increases, only those sightings (72% of the total) with an estimate on site of at most 20 individuals were considered (see also the Discussion).

The preliminary estimates were then adjusted adding the number of unidentifiable individuals and the new variance was calculated using the delta method as suggested by Wilson *et al.* (1999):

$$\hat{N}_{total} = \frac{\hat{N}}{\hat{\theta}}$$

$$\text{var}(\hat{N}_{total}) = \hat{N}_{total}^2 \left(\frac{\text{var}(\hat{N})}{\hat{N}^2} + \frac{1-\hat{\theta}}{n\hat{\theta}} \right)$$

where \hat{N}_{total} = estimate total population size, \hat{N} = preliminary estimate produced by the mark-recapture model, $\hat{\theta}$ = estimated portion of animals identifiable in the population, n = total number of animals from which $\hat{\theta}$ was estimated.

RESULTS

In total, 170.000 km of effort tracks within the study area (Figure 1) were aggregated. The Kernel density analysis (Figure 2) shows a heterogeneous distribution of sampling effort within the study area; the effort is higher along the coasts and tends to decrease from north to south and from west to east. The research effort is also seasonally heterogeneous, since

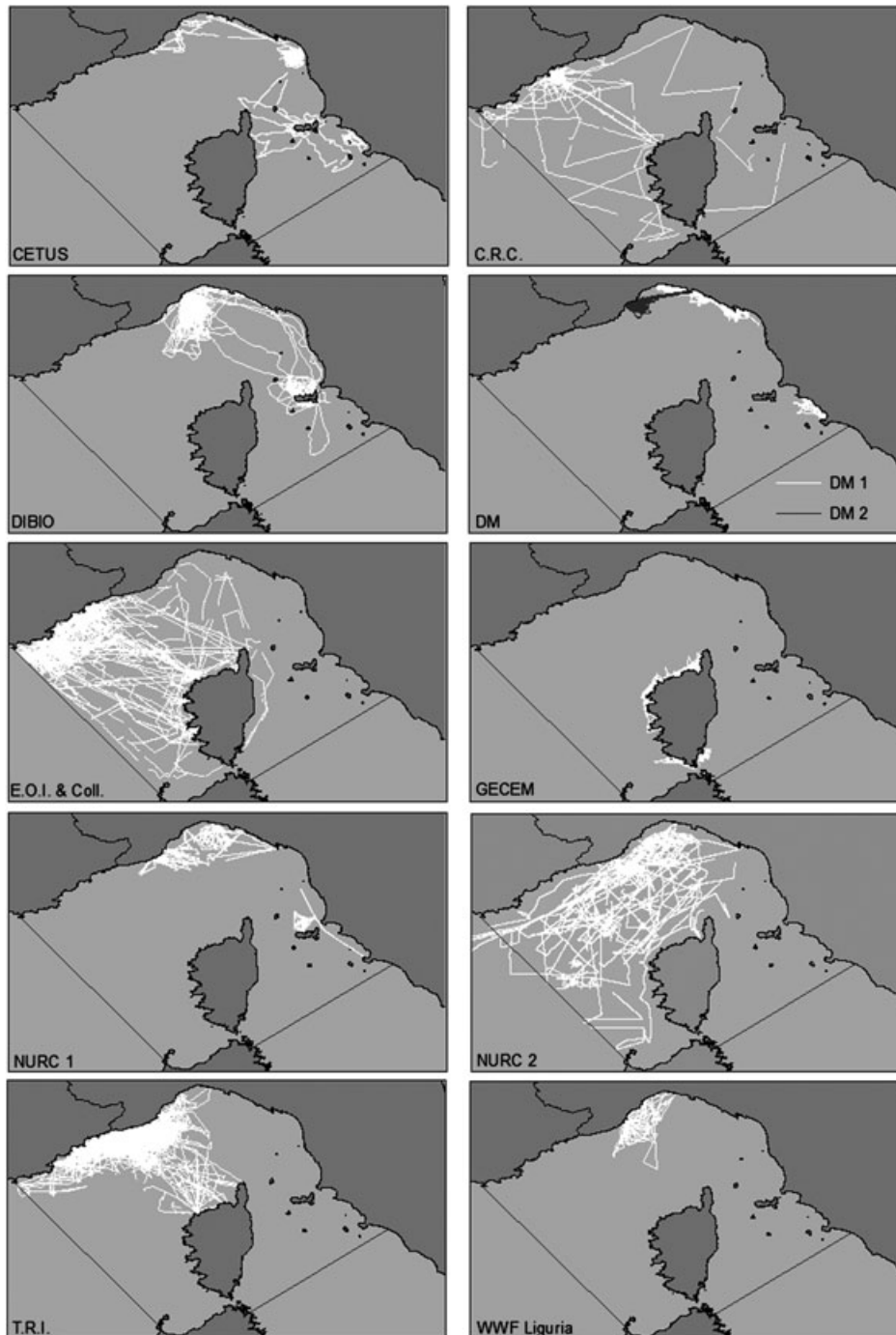


Figure 1. The research tracks recorded by the various research vessels from 1994 to 2007 (see Table 1 for details).

most of the surveys occurred between April and October (Figure 3).

The sampling effort increased from 1994 to 2007 (Figure 4) mainly due to the addition of new sampling activities in the Pelagos area coinciding with an enlargement of the total sampling area. The last three years (2005, 2006, 2007) show the best sampling effort, with most of the research groups active at the same time in the different areas (Table 2 and Table 6). These three years were selected as appropriate years of data for estimating abundance.

This sampling effort produced 308 bottlenose dolphin sightings (Figure 4) with an additional 170 bottlenose dolphin

sightings obtained during surveys with no effort track recorded, resulting in a total of 478 sightings of the target species.

Distribution

Table 3 shows the encounter rate (ER, sightings per effort in km) per bathymetric band (0–100 m, 100–200 m, >200 m) for the two species. The ER of the target species decreases abruptly beyond the 200 m isobath, while the control species' ER follows an inverse pattern. This distribution pattern can be observed also in Figure 5.

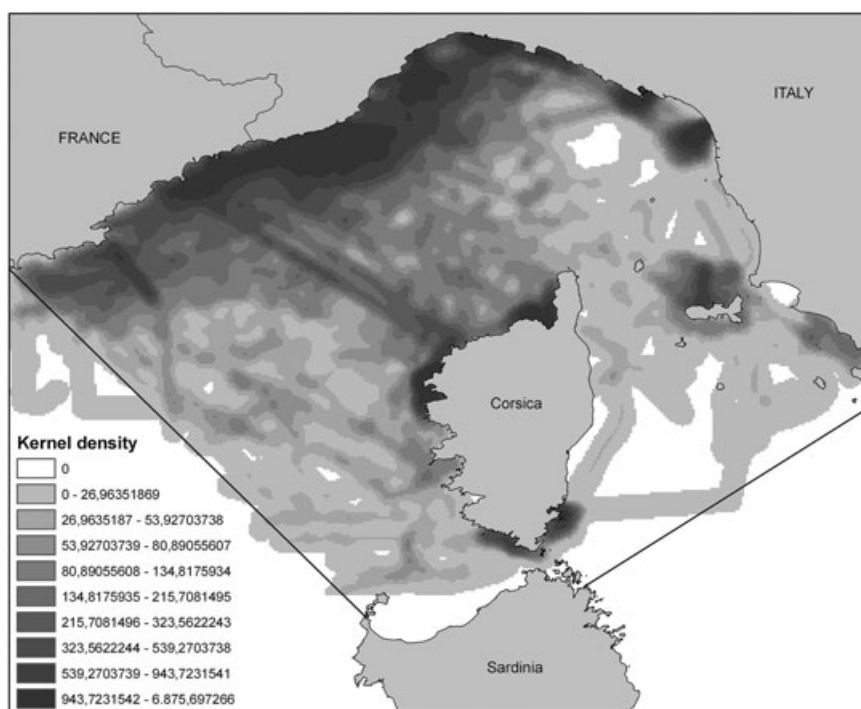


Figure 2. A Kernel density representation of the sampling effort in the study area (cell size x, y : degree 0.0133, 0.0133; radius: degree 0.1463).

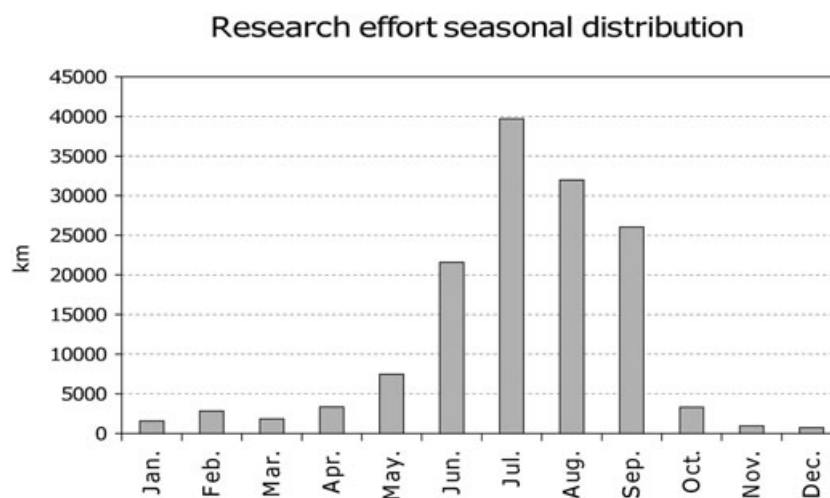


Figure 3. The seasonal distribution of the sampling effort over the entire research period (1994–2007).

Analysis of the ER of the target species in eight zones distributed along the continental shelf (<200 m) (Figures 6 and 7) shows an increasing ER for the bottlenose dolphin from west to east, in agreement with expectations (see the introduction), with the maximum sighting success in zone 6.

The statistical analysis of the contingency table, comparing the ER in zones 4, 5, 6, 7, and 8, (1–0 sampling method within 100 km track portions) confirms a significant ER difference ($P < 0.001$), with the maximum chi square value in zone 4 (observed < expected). The contingency table shows a significant difference also when comparing zones 5, 6, 7, and 8 ($P < 0.001$), with zone 8 having the maximum chi square

value (observed < expected); no statistical significance was found ($P > 0.05$) when comparing zones 5, 6, and 7 only (Table 4).

Photographic data and matching process

A total of 298 bottlenose dolphin sightings produced photo-ID data (Figure 8). The capture success was variable between years, with a clear increasing trend (Figure 9). The rise in the number of individuals captured annually is a consequence of the increased effort (Figure 4, Table 2) and improved techniques (i.e. the use of digital reflex cameras)

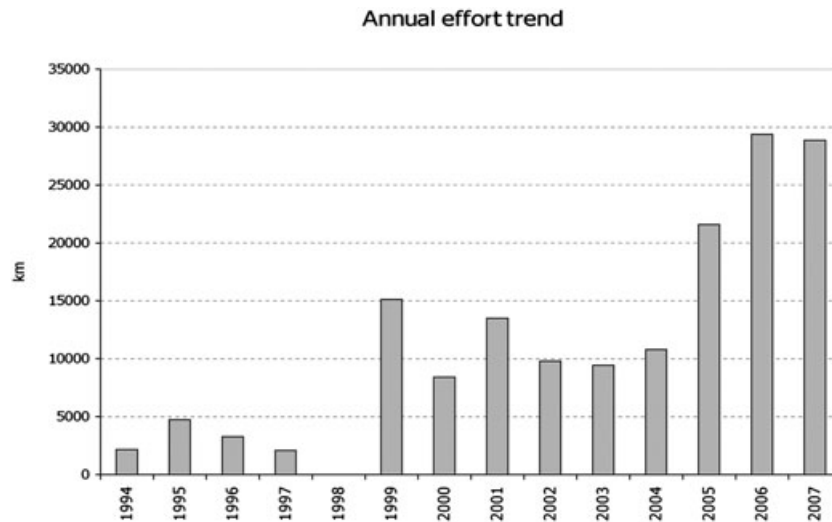


Figure 4. The annual distribution of the sampling effort (1994-2007).

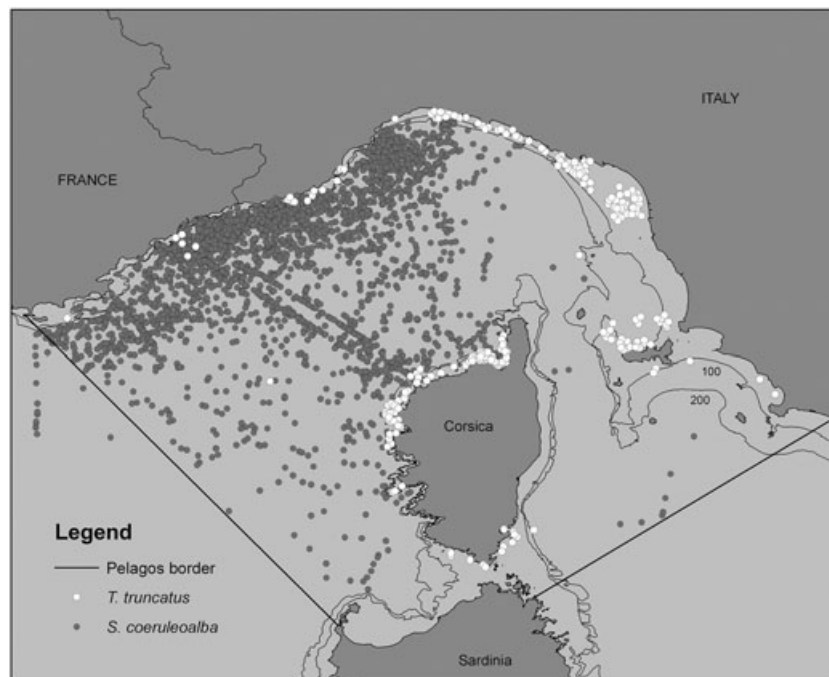


Figure 5. Bottlenose dolphin (308) and striped dolphin (3024) sightings associated with the effort tracks in Figure 1.

for data collection. A concurrent increasing trend in the number of dolphins within the study area cannot be excluded but such a trend cannot be tested through this type of analysis.

The cross-analysis of the photo-ID catalogues from the different research groups resulted in 670 different individuals identified (carrying long-lasting marks) over the entire research period. The discovery curve (Figure 10) resembles the increasing trend in the sampling effort and related capture success; the curve seems to find a first plateau at the end of 2004, but as the sampling effort spreads to other areas, the curve shows a new rise. At the end of the study period, however, the curve shows a flatter trend, suggesting the presence of a near new plateau.

Movements

In total, 360 dolphins were sighted at least two times and the maximum displacement analysis (the maximum distance between sighting points of the same individual) was calculated for these animals: 80% of the animals moved within 80 km and 90% within 120 km; only 2% of the dolphins analysed moved greater than 200 km in distance (Figure 11).

The average maximum distance covered by all of the individuals analysed ($n = 360$) was 50 km (50 ± 2.8 SE) with a maximum distance (individual P276) of 427 km covered in less than three years (this dolphin was sighted in the Gulf of Lion in 2008, but its displacement was included in the present spatial analysis, being the maximum ever recorded in the study area).

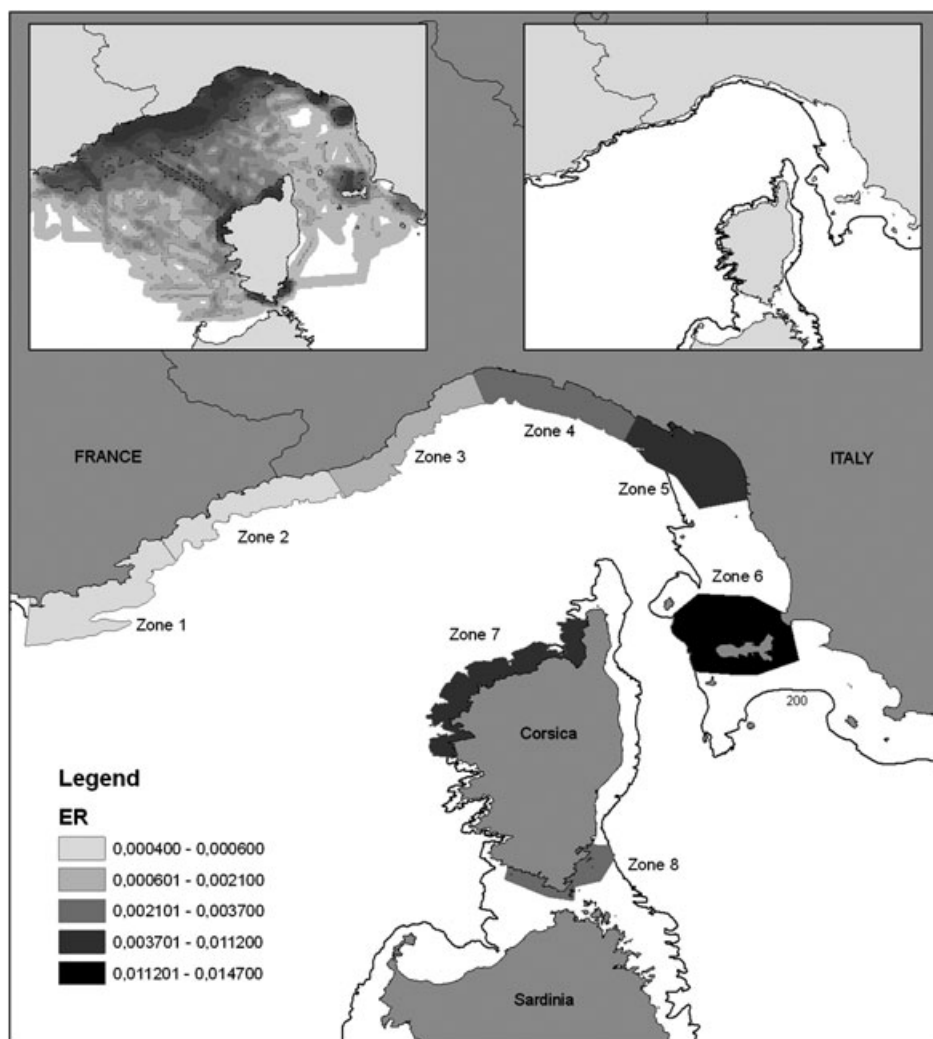


Figure 6. The encounter rate (sightings/km) per zone (1-8). The continental shelf (< 200 m) has been stretched for a better visualization of the colour tone in each zone. The top-right image shows the original position of the 200m isobath. The top-left image shows the total research effort according to the Kernel density analysis (see Figure 2).

According to the spatial behaviour analysis, eight sub-areas with $SRI < 0.15$ were identified (A1, A2, A3, A4, B1, B2, B3, B4) plus three single sighting events (As1, As2, As3) from occasional sightings in zones not regularly sampled (Figure 8, Table 5).

In relation to the displacements between sub-areas, the SRI tends to decrease as the distance between sub-areas increases (as expected) with one important exception: area B1 (north-west Corsica) shares 0 individuals with the close area A4 (Elba Island) and 5 individuals with the far off area B3 (Hyères – French coast). It is possible to identify two macro-areas: one in the north-east part of the sanctuary area (denoted by the letter A in Table 5 and Figure 8) and a second one in the Corsica and eastern-France coast (denoted by the letter B in Table 5 and Figure 8). Over the entire research period (Table 5) only one dolphin displacement between these two macro-areas was recorded.

The years 2005, 2006, and 2007 clearly show the best success in terms of number of animals captured in the different sub-areas. If we compare the total number of animals captured per year with the sum of individuals from each sub-area we have the number of animals shared between sub-areas (Table 6).

For the selected years (2005, 2006, 2007) the calculated SRI between sub-areas was always less than 0.05.

Abundance

For the selected years (2005, 2006, 2007) three different abundance estimates were produced for macro-area A, macro-area B and Pelagos, using the Chao mark-recapture model for closed populations. The closure assumption is supported by the small number (1 dolphin) moving between A and B over the entire research period (Table 5).

Table 7 shows the preliminary abundance estimates with Chao (M_t and M_{th}) models for the two macro-areas and Pelagos as a whole. A range of estimated capture probabilities associated with each of the models and data sets is also presented.

The abundance estimates obtained with the M_{th} model are higher than those obtained with the M_t model in years 2005 and 2006, while in year 2007 it is the opposite. The abundance estimate in macro-area B in 2006 is much higher if compared with the estimates in the same area in 2005 and 2007. This is probably the consequence of a wider sampling distribution, with

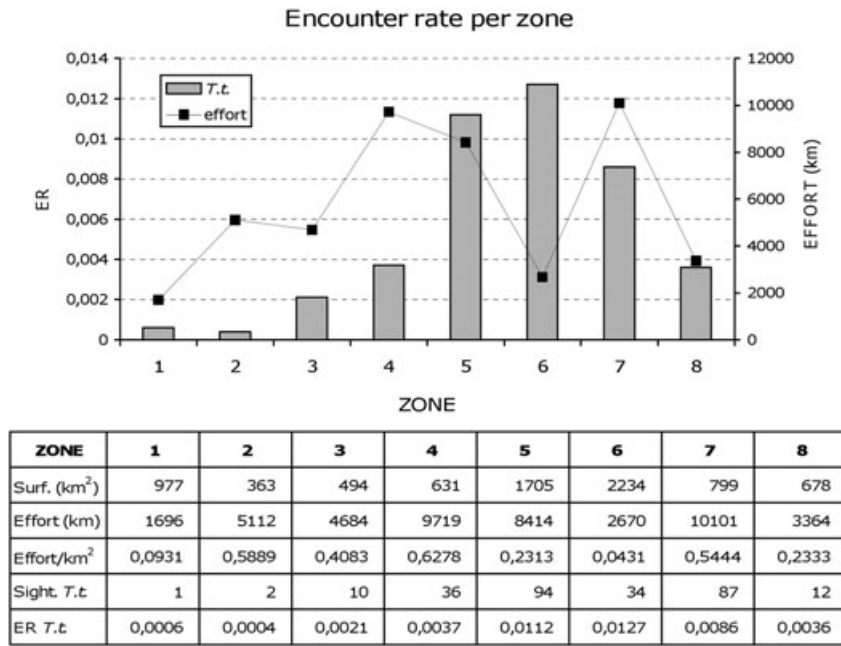


Figure 7. The encounter rate (ER) per zone (1-8) of the target species (*T. truncatus*) (see also Figure 6).

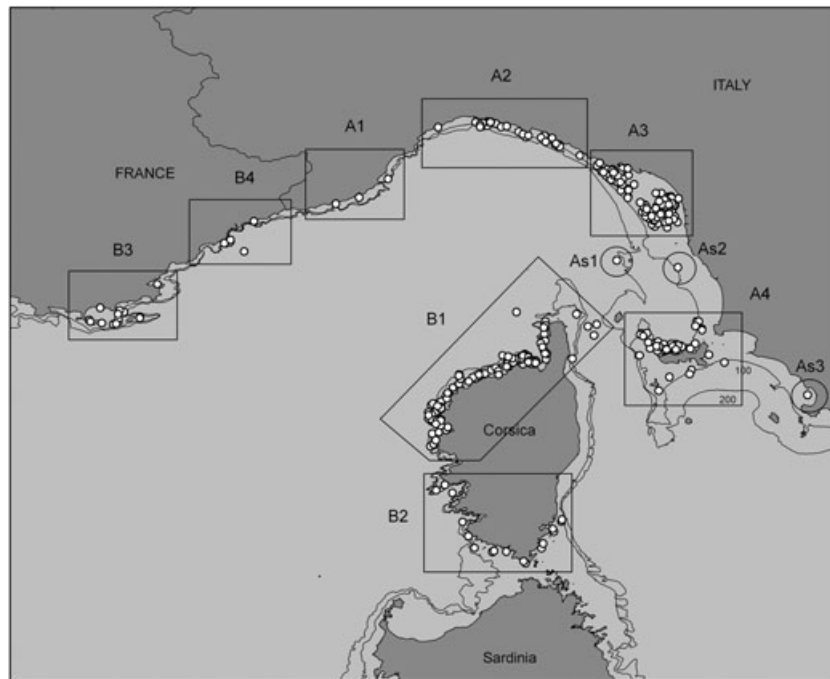


Figure 8. Sightings of bottlenose dolphins producing photo-ID data over the entire research period (298 in total).

sightings occurring in both sub-area B1 and B2 in 2006 (Table 6). As such, 2006 was considered the most representative year when producing the (best) final estimate, obtained by adding the unidentifiable animals to the preliminary estimate (Table 8, see also the discussion).

In 2006, it was estimated that macro-area A supported 510–552 (M_l – M_{th}) bottlenose dolphins, while macro-area B supported 368–429 (M_l – M_{th}) animals. A total of 884–1023 (M_l – M_{th}) bottlenose dolphins were estimated to live in the Pelagos area (Table 8).

DISCUSSION

Distribution

The distribution of the sightings indicates a strong affiliation of the bottlenose dolphin to living in relatively shallow waters, on the continental shelf, within the 200 m isobath. Furthermore, most of the sightings between the 100 m and 200 m isobaths occurred around Elba Island (37 out of 54), where the 100 m and 200 m isobaths follow a complex pattern, with shallow

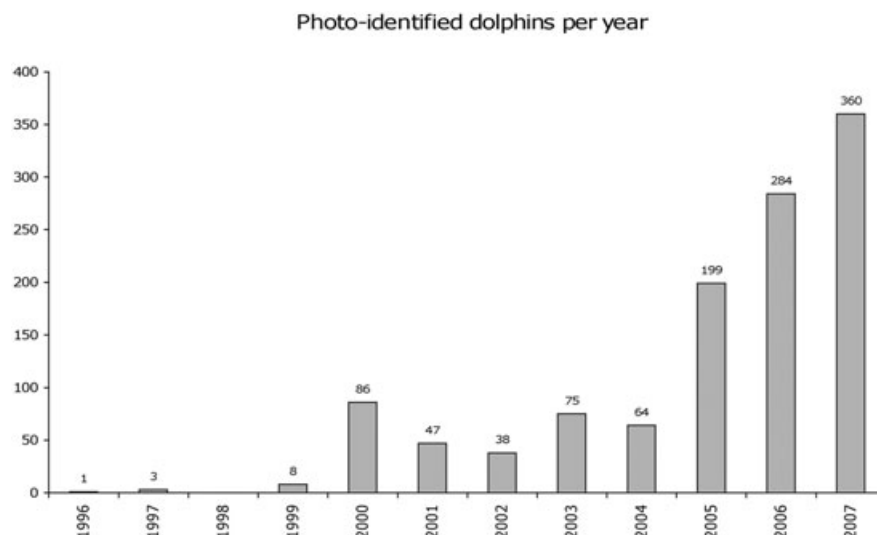


Figure 9. The annual trend (1996-2007, not cumulative) of the bottlenose dolphin captures in the study area.

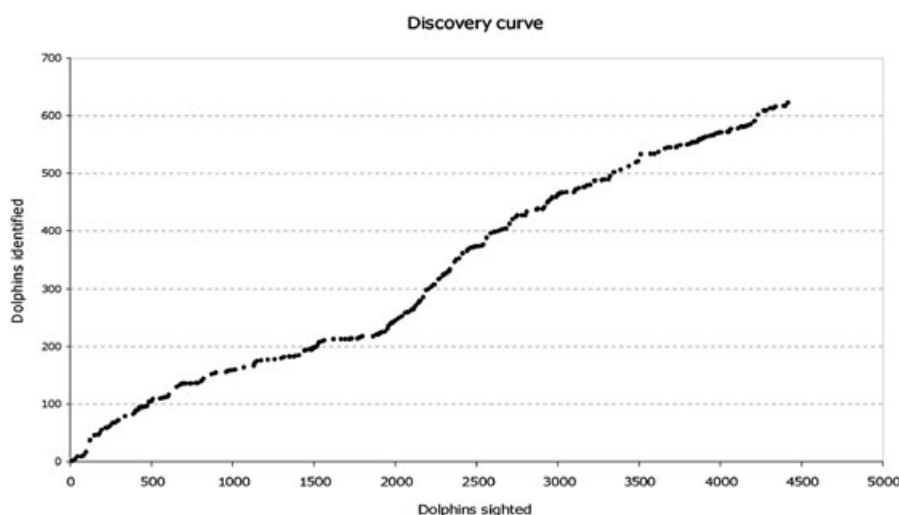


Figure 10. Discovery curve for the bottlenose dolphin (1996-2007).

water (<100m) extensions offshore. The encounter rate analysis per bathymetric line confirmed this pattern, with the sighting success falling beyond the 200 m isobath; only 17 sightings out of 308 (5.5%) occurred beyond the 200 m isobath and always (except one) very close to the 200 m isobath. This pattern seems quite consistent over the whole study area, with no evident differences between research groups (Figure 5, Table 3). The overall distribution pattern seems to strongly indicate that the bottlenose dolphin in the Pelagos area is a shallow water ecotype. Although the majority of data were collected between April and October, the data collected from November to March are not in conflict with these findings.

In relation to the presence (sighting probability) of the bottlenose dolphin in the different zones of the continental shelf, there seems to be a major density of dolphins in the east section of the Pelagos area, characterized by a wide continental shelf and shallow waters, and along the north-west part of the Corsican coast. The very low presence of dolphins in the north and north-west part of the Pelagos area could be the result of constriction of

the bottlenose dolphin habitat (the continental shelf <200 m) in these zones, where it is too small for the establishment of local resident (sub)populations, and/or of the interaction between local bathymetric traits and human activity such as boat traffic. In fact, the constriction of the continental shelf results in a complete overlap with the pleasure boating distribution, which is confined to within 4–6 km of the coast, as reported by Manfredini *et al.* (2007) along the Ligurian coast, and David and Di-Méglio (2008) along the Liguro-Provençale coast. Conversely, in the eastern part of the sanctuary area there is only a partial overlap, since the 200 m isobath runs off shore (about 12 km from the coastline); this could give the dolphins the possibility to bypass the disturbance produced by pleasure boating, moving offshore without leaving their preferred shelf habitat.

Movements

The cross-analysis of the photographic catalogues from the different sub-areas gave interesting and sometimes unexpected

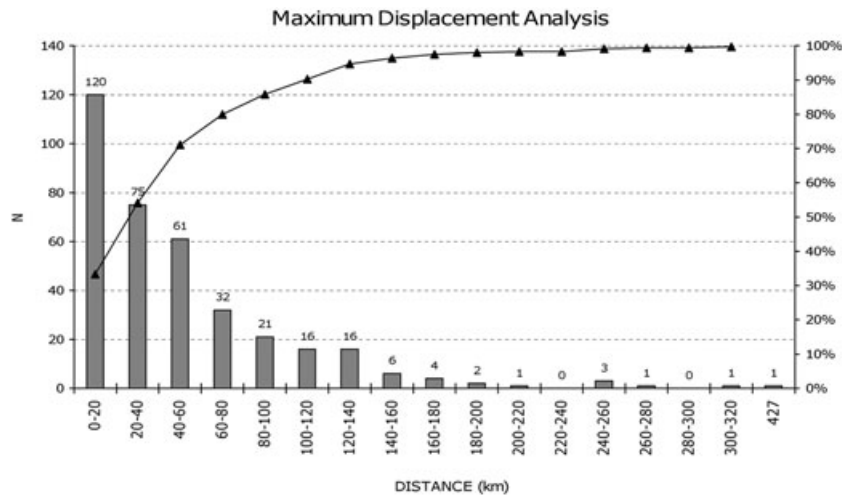


Figure 11. Maximum displacement analysis: the columns represent the number of dolphins per displacement interval (km); the line represents the percentage of animals per maximum displacement (km) (all individuals with at least 2 sightings, $n=360$).

Table 7. Abundance estimates from Chao mark–recapture model for closed population fitted to macro-area A, macro-area B and Pelagos data in 2005, 2006, 2007. The range of capture probability estimates are presented for each of the models

Area	Number of sightings	Chao model	Abundance estimate, \hat{N}	95% CI	Capture probability
2005					
Macro-area A	24	M_t	305	230-436	0.01-0.06
		M_{th}	333	246-486	0.01-0.05
Macro-area B	21	M_t	154	115-236	0.01-0.07
		M_{th}	161	120-242	0.01-0.07
All Pelagos	45	M_t	440	352-578	0.00-0.04
		M_{th}	461	369-603	0.00-0.04
2006					
Macro-area A	45	M_t	306	256-390	0.00-0.07
		M_{th}	331	280-411	0.00-0.06
Macro-area B	25	M_t	243	180-360	0.00-0.09
		M_{th}	283	210-407	0.00-0.07
All Pelagos	70	M_t	548	461-679	0.00-0.04
		M_{th}	634	532-776	0.00-0.03
2007					
Macro-area A	51	M_t	388	326-490	0.00-0.09
		M_{th}	381	328-462	0.00-0.09
Macro-area B	24	M_t	192	166-245	0.01-0.27
		M_{th}	179	162-209	0.01-0.028
All Pelagos	75	M_t	567	497-672	0.00-0.09
		M_{th}	521	473-587	0.00-0.10

results. Bottlenose dolphins show a general sedentary behaviour, with displacements usually within 80 km (50 km on average). Only a few animals moved between sub-areas up to 427 km in distance.

Some dolphins (five individuals) moved between north-west Corsica (area B1) and Côte d'Azur (area B3) (about 160 km in distance);* a greater number moved regularly between Elba (area A4) and north Tuscany and East Liguria (area A3), around 150 km. Despite the close distance between Corsica (north-west section, area B1) and Elba (area A4), no dolphins have been observed moving between these two sub-areas, neither are there dolphins moving from the Italian peninsula

(north Tuscany and Liguria, areas A1, A2, A3, A4) to Corsica (north-west and south section, areas B1, B2). These patterns strongly suggest that bottlenose dolphins cross the Ligurian Sea to move between Côte d'Azur (area B3) and Corsica (areas B1, B2); the sighting of a bottlenose dolphin group in the middle of the Ligurian Sea, on the route linking the east coast of France to the west coast of Corsica, may support this hypothesis, as already stated by Dhermain *et al.* (1999).

Even if the long distance movements involve only a few animals, this cannot be considered to be accidental behaviour for these individuals, since at least four dolphins crossed the Ligurian Sea at least twice (Table 9). These animals seem to have a geographic perception of the area which allows them to move from one continental platform to another.

The sharp separation between 'Italian' and 'Côte d'Azur-Corsican' dolphins would suggest the presence of two

*Three more dolphins have moved from Corsica to Côte d'Azur in 2009 (Dhermain, personal communication).

Table 8. Final estimates for macro-area A, macro-area B and the whole of Pelagos in 2006

Area	Model	2006				
		Pre est.	$\hat{\theta}$ (average)	$\hat{\theta}$ SE	Final est.	95% CI
Macro -area A	Chao M_t	306	0.60 ($n = 29$)	0.043	510	412-631
	Chao M_{th}	331			552	454-671
Macro -area B	Chao M_t	243	0.66 ($n = 18$)	0.047	368	259-522
	Chao M_{th}	283			429	307-599
Pelagos	Chao M_t	548	0.62 ($n = 47$)	0.044	884	729-1072
	Chao M_{th}	634			1023	848-1234

$\hat{\theta}$ represents the proportion of identifiable animals (see Methods).

Table 9. Displacements (sub-area – date) of the dolphins moving between Corsica and Côte d'Azur

Individual	Sub-area - Date			
	Corsica	Côte d'Azur	Corsica	Côte d'Azur
P416	B1 - 17/07/1997	B3 - 5/09/1997	B1 - 16/08/2000	
P417	B1 - 15/07/1996	B3 - 28/04/2005	B1 - 25/04/2007	
P342	B1 - 27/07/2003	B3 - 28/04/2005	B2 - 11/05/2006	
P276		B3 - 2/05/2005	B1 - 27/06/2005	B3 - 15/09/2005

(sub)populations, oddly coinciding with the French and Italian water territories. This could be due to the different physiographic and ecological characteristics of the two areas. The east-France and the west-Corsica coasts are characterized by a quite narrow platform and a steep slope while the north Tuscany coast and the Tuscany Archipelago present typical shallow water ecosystems. Despite the closeness, the north-west Corsica coast and the Elba and Tuscany coasts are very different in terms of ecological and physiographic traits. Our hypothesis (in agreement with Natoli *et al.*, 2005) is that ecological specialization in the foraging activity, possibly including opportunistic feeding on the discards from different fishing activities, may have caused a (partial) separation between the two (sub)populations. On the north side, around the Italy–France border, the ‘barrier’ could be represented by a habitat gap, since the continental shelf is so narrow that it almost disappears. However, the long distance travellers seem to be able to overcome these habitat gaps, providing a link between contiguous (sub)populations. Genetic analysis should be used to test the actual isolation level of the two (sub)populations.

Abundance

The abundance estimates appear to be consistent when comparing the two macro-areas (A, B) and the whole of Pelagos.

The abundance estimates produced with the M_{th} model are higher than those obtained with the M_t model estimate in 2005 and 2006; this would suggest some heterogeneity in the capture probability. In contrast, in year 2007 the estimate produced with the M_{th} model was lower than for M_t , suggesting that there is unlikely to be a heterogeneity effect in that year. This could be the consequence of improved data collection quality, making the data set more homogeneous. However, this is not conclusive as the confidence intervals for the estimates of N overlap.

It is not possible to compare the abundance estimates in the different selected years, due to differences in the sampling

distribution. This is why we chose 2006 for the final estimate as the only year with a sampling effort well distributed around Corsica (both in sub-area B1 and B2). In 2005 and 2007 the southern portion (sub-area B2) was not surveyed; this also justifies the higher abundance estimated in macro-area B in 2006.

When calculating the portion of unmarked animals, which was added to the preliminary estimates produced by the selected model, we used a method modified from Wilson *et al.* (1999) (see the Methods). However, when comparing our results with the results from the same authors, we found good consistency: Wilson and co-authors estimated a portion of unmarked individuals between 0.56 and 0.68, we estimated a portion between 0.60 and 0.66.

Since we do not have any historical data in relation to the abundance of the bottlenose dolphin in the whole study area, we are not able to infer possible positive or negative population trends. GECM (Groupe d'Etudes des Cétacés de Méditerranée) estimated about 198–242 dolphins by direct counting and photo-identification around Corsica in 2000 (Ripoll *et al.*, 2001), and 130–173 in 2003 (Dhermain *et al.*, 2003; low results biased by intense touristic activity and/or 2003 heat wave, according to the authors). These estimates are lower than those we produced in the same area, but this may be due to the different methodological approaches: direct counting, especially with only one boat, does not take into account the proportion of animals unsighted and may therefore underestimate the total number.

Implications for conservation

Bottlenose dolphins show a residential attitude, forming discrete (sub)populations distributed over the continental shelf, having their centre of distribution in special favourable areas. The shelf-limited distribution exposes the species to potential impacts from human coastal activity such as pleasure boating, overfishing and chemical pollution; these threats may produce

a habitat contraction and fragmentation, which in the end could result in the isolation of single (sub)populations.

An effective conservation programme should take into account these findings: the favourable areas for the bottlenose dolphin should be identified, the size of the resident (sub)populations should be estimated, and specific protection actions should be taken to conserve the habitat. At the same time a genetic continuity between (sub)populations should be guaranteed, by avoiding habitat fragmentation. Conservation programmes should therefore involve different countries in a coordinated effort to establish a system of protected areas over a continuous expanse, providing ecological corridors between (sub)populations.

Tursiops truncatus is listed in Annex II of the Habitats Directive; requiring the designation of SACs (Special Areas of Conservation) as an appropriate mechanism for bottlenose dolphin conservation. Cañadas *et al.* (2005) have already proposed this in southern Spain and Strait of Gibraltar.

The SACs should be designed around the special favourable areas, where local bottlenose dolphin (sub)populations are known to have their centre of distribution. The SACs should include the whole continental shelf (< 200 m) and should be big enough to support the energetic needs of the resident (sub)populations; each one should be part of a coordinated protection system which also provides ecological corridors between (sub)populations, taking into account the observed behaviour of the dolphins.

Within the Pelagos Sanctuary there are at least three areas that qualify for SAC designation. These correspond to the centres of distribution of the identified resident (sub)populations, namely: (a) the shelf area between Punta Mesco and Marina di Pisa (corresponding grossly to sub-area A3); (b) the shelf area around Elba Island (corresponding grossly to sub-area A4); (c) the north-west shelf of Corsica (corresponding grossly to sub-area B1) (Figure 8). These zones show the highest ER for the bottlenose dolphins and the highest capture success.

These areas are, at present, subject to different protection regimes (Cinque Terre Marine Protected Area in sub-area A3; Archipelago Toscano National Park in sub-area A4; Scandola Natural Reserve in sub-area B1). However, the protection measures in place are not specifically designed for bottlenose dolphin protection and may thus be poorly effective, since they are limited to a very thin coastal band, which covers only a proportion of the bottlenose dolphin distribution area.

Protection measures should be devoted to avoiding over-fishing, limiting the disturbance from pleasure boating, and reducing chemical pollution and toxic contamination, which are believed to be the main threats for the bottlenose dolphin in the Mediterranean Sea (Cañadas *et al.*, 2005; Bearzi *et al.*, 2008b). At the same time the size of the (sub)populations under protection should be monitored over time to check the effectiveness and adequacy of the measures adopted. The monitoring activity should be coordinated, to check for consistency or inconsistency in possible population trends recorded in the different SACs and/or to record possible emigration/immigration events from one area to another. This monitoring network will have to validate the effectiveness and adequacy of the protection measures and suggest changes to these measures and/or a revision of the SACs boundaries, if the bottlenose dolphin (sub)populations change their centre of distribution over time, as has been reported by Wilson *et al.* (2004) in the Moray Firth (North Scotland).

The Pelagos Sanctuary, as an international agreement, could facilitate coordination within the SAC system, as well as provide overall protection which should guarantee the ecological corridors between SACs.

Further studies will be needed to better identify the boundaries of each SAC and to identify other special propitious areas for the bottlenose dolphin, possibly deserving a protection action, either within the Pelagos Sanctuary or in adjacent zones.

ACKNOWLEDGEMENTS

The Delfini Metropolitan team would like to thank all the researchers who supported this project with their work on data collection. Special thanks to Giovanni Caltavuturo, who started the project in year 2001.

The GECEM wish to thank WWF-France for coordination of the Life LINDA on the Bottle-nosed Dolphin in Corsica (2005–2007), and Cathy Cesarini, who performed most of the surveys in the island during this period.

The EcoOcean Institut would like to thank all the observers taking part in data collection aboard their vessels and their collaborators: WWF-France, Fondation Nicolas Hulot, EPHE, the Swiss Cetacean Society and Cybelle Planète.

The DIBIO database has been collected in collaboration with CIMA Research Foundation during surveys partially funded by Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Provincia di Livorno, Comune di Capoliveri, ACCOBAMS and NURC, Nato Research Centre. DIBIO sincerely thanks all master and bachelor students who have assisted with the dolphin database.

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