Deep–Sea Research Part II 141 (2017) 31–40

Contents lists available at ScienceDirect

Deep–Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Seasonal distribution and abundance of cetaceans within French waters- Part II: The Bay of Biscay and the English Channel

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A R T I C L E I N F O

Keywords:
Cetaceans
Bay of Biscay
English Channel
Harbour porpoise
Common dolphin
Bottlenose dolphin
Aerial survey

A B S T R A C T

From the Habitat Directive to the recent Marine Strategy Framework Directive, the conservation status of cetaceans in European water has been of concern for over two decades. In this study, a seasonal comparison of the abundance and distribution of cetaceans was carried out in two contrasted regions of the Eastern North Atlantic, the Bay of Biscay and the English Channel. Estimates were obtained in the two sub-regions (375,000 km²) from large aerial surveys conducted in the winter (November 2011 to February 2012) and in the summer (May to August 2012). The most abundant species encountered in the Channel, the harbour porpoise, displayed strong seasonal variations in its distribution but a stable abundance (18,000 individuals, CV=30%). In the Bay of Biscay, abundance and distribution patterns of common / striped dolphins varied from 285,000 individuals (95% CI: 174,000–481,000) in the winter, preferentially distributed close to the shelf break, to 494,000 individuals (95% CI: 342,000–719,000) distributed beyond the shelf break in summer. Baleen whales also exhibited an increase of their density in summer. Seasonal abundances of bottlenose dolphins were quite stable, with a large number of 'pelagic' encounters offshore in winter. No significant seasonal difference was estimated for pilot whales and sperm whale. These surveys provided baseline estimates to inform policies to be developed, or for existing conservation instruments such as the Habitats Directive. In addition, our results supported the hypothesis of a shift in the summer distributions of some species such as harbour porpoise and minke whale in European waters.

1. Introduction

The conservation status of cetaceans has been of concern for many years in the North Sea and adjacent waters, but discussions have mainly been focused on the two species of cetaceans listed in Annex II of the Habitat Directive (HD), namely the harbour porpoise (*Phocoena phocoena*) and the common bottlenose dolphin (*Tursiops truncatus*), with all other cetaceans being listed in the Annex IV. While Annex II lists species that can justify the designation of Special Areas of Conservation, Annex IV lists all species under strict, albeit not site-based, protection. European Union Member States have to implement a surveillance programme for species listed under HD-Annexes II and IV, as well as to monitor man-induced causes of death for species under Annex IV. Since the beginning of the 1990s, several studies have documented the large impact of incidental catches of cetaceans in Eastern-North Atlantic (ENA) fisheries (Peltier et al., 2016; Rogan and Mackey, 2007), with a risk of entanglement in different types of nets (Tregenza et al., 1997). While driftnets have been restricted in the area, trawling, particularly pelagic pair-trawling, has become the main threat for delphinids (de Boer et al., 2012). In addition, the development of marine renewable energy facilities could potentially affect marine mammals (Madsen et al., 2006; Thomsen et al., 2015). Finally, global warming is also expected to have a substantial impact on cetacean communities (MacLeod et al., 2005).

To address and mitigate these threats, the European Union issued the Marine Strategy Framework Directive (hereafter MSFD) to restore the European marine ecosystem. The MSFD (Directive 2008/56/EC) capitalises on former conservation instrument such as the HD, but addresses their shortcomings (e.g. a bias toward terrestrial habitats and species, a focus on administrative boundaries instead of ecosystem ones, etc…). The MSFD sets deadlines and requires Member States to achieve or maintain 'Good Environmental Status' of their waters by 2020.

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http://dx.doi.org/10.1016/j.dsr2.2016.12.012

Available online 22 December 2016
0967-0645/

Because of the high mobility of cetacean species, their protection can only effectively be achieved by means of international cooperation, which the MSFD encourages through existing conservation bodies such as the Regional Sea Conventions. For example, the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) promotes close cooperation between countries to achieve and maintain favourable conservation status for small cetaceans in the area. A prerequisite for effective conservation is information on important parameters such as abundance and distribution. If past large scale surveys such as SCANS and CODA (Hammond et al., 2013; MacLeod et al., 2009) have provided estimates for some species of community interest (*e.g.* harbour porpoises) or large whales. Some knowledge gaps, however, remain. Here, we report the results from two large scale aerial surveys designed to provide baseline estimates for the initial assessment of several cetacean species and their seasonal changes in abundance and distribution patterns in two contrasting areas of the Eastern North Atlantic Ocean (ENA): the English Channel and the Bay of Biscay. Among the detected species, two are considered in European waters as *Vulnerable* according to the IUCN Red List Criteria, the harbour porpoise and the sperm whale (*Physeter macrocephalus*), and one is *Near Threatened,* the fin whale (*Balaenoptera physalus*). In addition, these surveys allowed us to provide estimates for six currently *Data Deficient* species: common (*Delphinus delphis*) and striped dolphins (*Stenella coeruleoalba*), pooled together as small-sized delphinids; common bottlenose dolphin, Risso's dolphin (*Grampus griseus*), long-finned pilot whale (*Globicephala melas*) and Cuvier's beaked whale (*Ziphius cavirostris*), pooled in the beaked whales group. Finally, they provided estimates for the common minke whale (*Balaenoptera acutorostrata*), which is considered as *Least Concern*.

2. Materials and methods

2.1. Study area and survey design

Two contrasted sub-regions of the Eastern-North Atlantic were covered during this study. (1) The English Channel (EC), characterised by strong tides and freshwater inputs, which create well-mixed and turbid waters, joins the North Sea on its eastern partwith shallow depths, while its western end joins the Celtic Sea. Seasonal stratification along the English coast permits extensive blooms during the summer, while offshore southern Celtic Sea waters remained well mixed. (2) In the Bay of Biscay (BoB), the continental shelf is broader in the north, off France, while relatively narrow along the Iberian coast finishing with a wide complex of submarine canyons (Fig. 1). Blooms first occur in early summer, followed by shelf summer blooms along the Ushant front and coastal blooms on the shelf, related to river outflow or salinity fronts (Pingree and Garcia-Soto, 2014). The Ushant front (west of Brittany coasts) represents a transitional zone between cooler, tidally well mixed Channel water and the warmer stratified water of the Atlantic (Pingree and Garcia-Soto, 2014).

The study area was focused on the French EEZ, but for the sake of ecological consistency it also included Spanish waters in the south of the Bay of Biscay characterised by a complex topography due to numerous canyons and English Channel waters in the north to cover the whole epicontinental Channel. The study area spanned 375,000 km² including the English Channel (92,900 km²) and the Bay of Biscay (282,100 km²). These two sub-regions were stratified in four bathymetric strata (Fig. 1): two continental shelf strata less than 200 m deep (EC and BoB_Shelf); one continental slope stratum within the 200 m and 2000 m isobaths (BoB_Slope); and the oceanic stratum (BoB_Oceanic) with depth > 2000 m.

2.2. Data collection

Data were collected during two large dedicated aerial surveys, named SAMM (*Suivi Aérien de la Megafaune Marine;* aerial survey for marine megafauna) over three geographic sub-regions: the EC, the BoB (within ENA) and North-Western Mediterranean Sea. Target species were the main taxa of marine megafauna, *i.e.* marine mammals, sea turtles, large fish as elasmobranchs collected in line transect mode, while seabirds in strip transect. This study only presents results obtained for cetaceans within the two ENA sub-regions. Detailed methodology and results for the North-Western Mediterranean Sea are presented in a companion paper (Laran et al., 2017).

Transect were drawn manually but in order to approximate an equal coverage probability within each strata. A systematic zig-zag sampling design (Buckland et al., 2001; Strindberg and Buckland,

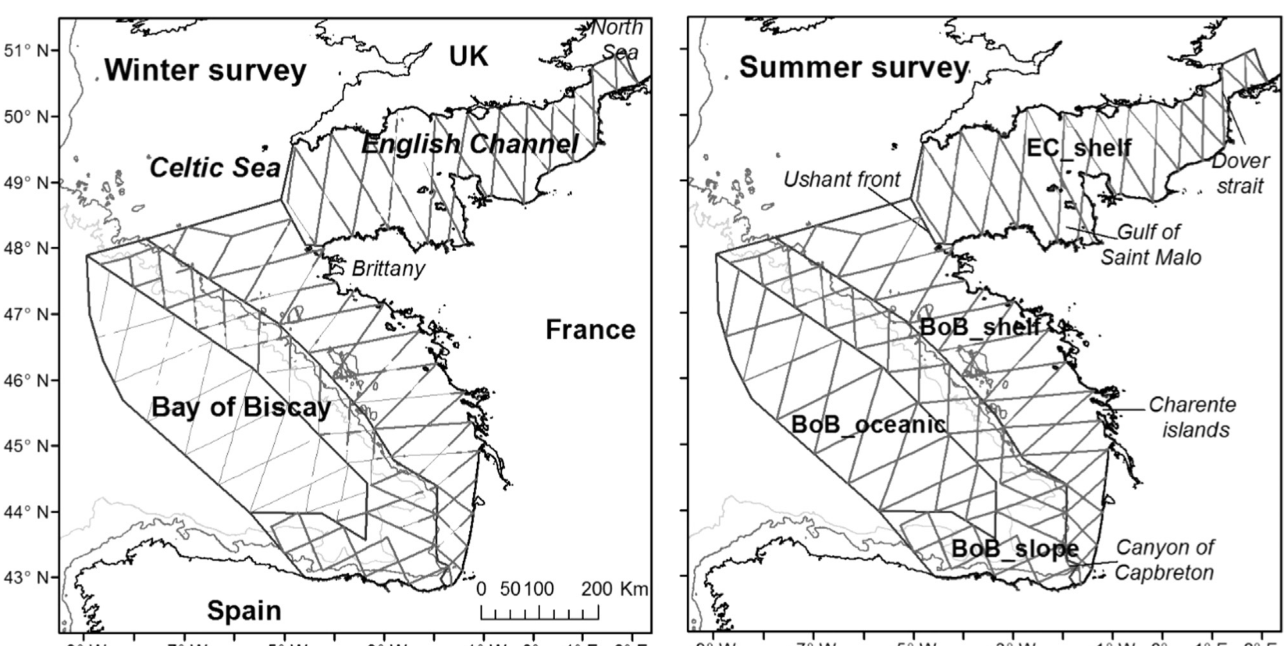

Fig. 1. Survey blocks with bathymetric strata and effort conducted during the winter survey (left) and summer (right) in good condition (selected for analyses: with sea state ≤3 Beaufort and subjective condition greater than *medium*). In bold transect done with a replicate.

Table 1
Blocks sizes, total effort (in km) and effort used for analysis (collected in good sighting conditions: Beaufort sea state ≤3 and subjective conditions > medium).

Sub-region	Bathymetric strata	Surface area (km²)	Winter		Summer	
			Total effort	Effort in good condition	Total effort	Effort in good condition
Bay of Biscay	BoB_Shelf	103,374	7341	6355	7134	6772
	BoB_Slope	87,584	6411	5375	6419	6389
	BoB_Oceanic	91,183	2599	2595	5087	4844
		282,141	16,351	14,325	18,640	18,005
English Channel	EC_Shelf	92,875	7162	7141	6471	6393

2004) was adopted for winter and summer surveys (Fig. 1). Transects were flown at a target altitude of 182 m (600 feet) and a ground speed of 167 km h^{-1} (90 knots), see Laran et al. (2017) for details.

2.3. Abundance estimates

Only transects flown with adequate sighting conditions were considered for the analysis (Beaufort sea state ≤ 3 and subjective condition greater than *Medium*). Data for the three sub-regions (EC, BoB and North-Western Mediterranean Sea) were pooled and effect of covariates incorporated into the function estimate on Distance 6.2 (Thomas et al., 2010). The best models were selected using minimum AIC (see Laran et al., 2017).

For each season and bathymetric strata school size, *E(s)*, was regressed (on a logarithmic scale) on *(x)* when significant ($p < 0.05$) or simply averaged.

In addition, density estimates were adjusted to account for availability bias on the trackline (D_{cor}) using previous availability correction factors estimated on similar aerial surveys. Selected factors and sources are summarised in Table A.1. For harbour porpoise, we used a previously estimated *g(0)* (including availability and perception bias) of 0.45 (Coefficient of Variation: CV=30%) obtained by "racetrack" under good conditions (Hammond et al., 2013). We used: 0.676 (CV=24%) when averaged (or regressed) group size was inferior or equal to 15 individuals of common or striped dolphins and no bias for *E(s)* > 15 individuals; 0.778 (CV=4%) for bottlenose dolphin; 0.407 (CV=30%) for fin whale; 0.12 (CV=28%) for minke whale; and 0.074 (CV=30%) for beaked whale (Carretta et al., 2000; Forcada et al., 2004; Gomez de Segura et al., 2006; Heide-Jorgensen et al., 2010). For others, the fraction of time spent in surfacing series (from the literature) was considered as a crude estimate of the availability bias: 0.167 (CV=17%) for sperm whale (Drouot et al., 2004) and a correcting factor of 0.763 (CV=24%) for long-finned pilot whale (Alves et al., 2013) and Risso's dolphin (in the absence of published value). Uncertainty of this factor was incorporated into the coefficient of variation (CV) and the confidence interval. Due to the constant team of observers over the two seasons, the perception bias (from observers) was assumed minor and was ignored (excepted for harbour porpoise for which a *g(0)* estimate was available).

Finally, to assess the effect of ignoring sightings of unidentified delphinids on abundance estimates, we conducted a sensibility analysis, whereby we imputed species identity (striped dolphin, bottlenose dolphin or Risso's dolphin) (see Laran et al., 2017, Text A.1).

3. Results

3.1. General

The two seasonal surveys covered 23,512 km in the winter (November 17th 2011–February 12th 2012) and 25,111 km in the summer (May 16th to August 8th 2012), with 91% of the effort conducted within sea condition Beaufort 3 or less in winter and 97% in the summer (Table 1).

3.1.1. Encounter rates

A total of 12 different species have been identified within the Bay of Biscay (BoB) and only 6 within the English Channel (EC), where harbour porpoise was dominant, accounting for more than 79% of all cetacean sightings (Table 2). In BoB, small-sized delphinids represented more than 49% of the sightings, and harbour porpoises accounted for only 20%. Cumulative encounter rates varied significantly between seasons in BoB, from 2.9 sightings per 100 km in the winter and 4.4 sightings/100 km in the summer. While, were quite stable in EC with 1.9–2.5 sightings/100 km in both seasons (Table 2). Harbour porpoise in EC and small-sized delphinids in BoB were the most prevalent species in both seasons.

3.1.2. Detection functions

Most of the detection functions were estimated for the three pooled sub-regions and presented in the companion paper (for small-sized delphinids, bottlenose dolphin, Risso's dolphin, pilot- and sperm whales). Detection function and corresponding effective strip half-width (μ) was estimated for harbour porpoise (μ=140 m, CV=5%), minke whale (μ=190 m, CV=23%) and beaked whales (μ=227 m, CV=21%) with no significant covariate selected for the three models (Fig. A.1).

3.2. Harbour porpoise

A total of 551 sightings was collected on effort within ENA (Table 2). Harbour porpoise exhibited contrasted seasonal distribution (Fig. 2). In the winter, porpoises were preferentially encountered in coastal waters, distributed from the southern Bay of Biscay to the North Sea, with more sightings in the Dover Strait (Fig. 2). This hotspot persisted in the summer, when porpoises were also found offshore, from the western EC to the Celtic Sea (Fig. 2). Calves were sighted in the Dover strait and along the French coast of EC in winter, as well as on the shelf break of the Celtic Sea and western EC in June and July (Fig. 2). Mean school sizes were comprised between 1 and 2 individuals (Table 3). Despite changes in their spatial distribution, harbour porpoises showed no seasonal change of their abundance in the EC, with a corrected abundance of about 18,000 individuals (CV=30%, Table 3). However their abundance in BoB increased five-fold from 2700 individuals (95% CI: 1300–5800) in winter to 13,400 individuals (95% CI: 8400–21,700) in summer.

3.3. Small-sized delphinids

This group included sightings of common dolphins (76%), striped dolphins (1%) and unidentified small-sized delphinids (23%). A total of 1122 sightings were collected on effort within ENA, without any sightings in the Eastern Channel (east of 1°W; Fig. 2). In the winter, small-sized delphinids were distributed mostly on the shelf and slope of BoB, with a hotspot in the southern Celtic Sea (Fig. 2). In the summer, small-sized delphinids were encountered more offshore, on the slope and oceanic strata of BoB. Moreover, few sightings were recorded north of 48°N in the summer, in contrast with the winter distribution (Fig. 2).

Mean school sizes varied from 9.5 to 18.7 individuals in the BoB,

Table 2
Total number of sightings collected in effort per species, corresponding proportion of sightings (%) and encounter rates (ER, sightings/100 km with coefficient of variation) during winter and summer surveys.

	Species	Bay of Biscay				English Channel				Total
		# Sightings		ER (CV)		# Sightings		ER (CV)		
		Wint.	Sum.	Wint.	Sum.	Wint.	Sum.	Wint.	Sum.	
Balaenopteridae	Minke whale	–	11	0.01 (0.57)	0.12 (0.19)	1	3	0.008 (1)	0.03 (0.58)	15
	Fin whale	3	16			–	–			19
	Blue whale	–	1			–	–			1
	undetermined w.	–	1			–	–			1
Harbour porpoise		52	99	0.25 (0.18)	0.43 (0.14)	227	173	1.95 (0.15)	1.58 (0.11)	551
Small-sized delphinids	Common dolphin	304	473	1.45 (0.15)	2.05 (0.11)	34	6	0.29 (0.21)	0.05 (0.47)	817
	Striped dolphin	9	3	0.47 (0.15)	0.87 (0.12)	–	–			12
	Striped / Common dolphin	90	198			5	–	0.04 (0.44)	–	293
Bottlenose dolphin		43	50	0.21 (0.18)	0.22 (0.16)	5	13	0.04 (0.45)	0.12 (0.38)	111
Globicepha-linae	Risso's dolphin	8	16	0.04 (0.47)	0.07 (0.33)	3	4	0.03 (0.74)	0.04 (0.50)	31
	Pilot whale	20	37	0.14 (0.21)	0.16 (0.24)	–	–			57
	Large Globicephalinae	9	–			–	–			9
Deep divers	Kogia spp.	4	2	0.02 (0.61)	0.01 (0.71)	–	–			6
	Sperm whale	4	4	0.02 (0.50)	0.02 (0.61)	–	–			8
	Cuvier's beaked whale	6	13	0.03 (0.41)	0.06 (0.27)	–	–			19
	Ziphiidae	–	1			–	–			1
Undetermined	Delphinidae	56	64			9	6			135
	Large cetacean	1	2			–	–			3
	Medium cetacean	5	5			–	–			10
	Small cetacean	2	10			4	3			19
	Cetacean	–	1			–	–			1
Total cetaceans		**616**	**1007**	**2.95 (0.08)**	**4.37 (0.07)**	**288**	**208**	**2.47 (0.12)**	**1.91 (0.10)**	2119
	Seals	–	1			15	19			35

with significant regression for the slope strata (Table 3). Seasonal densities of small-sized delphinids varied significantly in the EC and BoB (z-test > 2.1, $p < 0.05$). In the winter, a higher density was encountered in the shelf strata, in contrast to summer, where slope and oceanic were preferred (Table 3). Summer density of small-size delphinids decreased in the EC, while increased in BoB. Total corrected abundances of small-size delphinids in ENA were 300,800 individuals (95% CI: 181,500–516,600) in the winter and 494,600 (95% CI: 342,300–722,700) in the summer.

3.4. Common bottlenose dolphin

A total of 111 sightings of common bottlenose dolphins was collected on effort in ENA (Table 2). In the winter, sightings were concentrated south of 47°N, and mainly concentrated over the slope and oceanic strata in the summer (Fig. 2). Mean school size varied from 2.6 to 6.2 individuals (Table 3). There was no significant seasonal difference in bottlenose dolphin densities (Table 3). Corrected abundances of bottlenose dolphins within ENA were estimated at 18,700 individuals (95% CI: 7500-47,000) in the winter and 13,900 individuals (95% CI: 6700–31,000) in the summer (Table 3). EC accounted for 5% of the total estimated abundance in the winter and 26% in the summer.

3.5. Balaenopteridae

A total of 36 sightings of Balaenopteridae were collected on effort (Table 2), including 19 identified as fin whales, 15 as common minke whales, one as a blue whale (*Balaenoptera musculus*), and one unidentified whale, assumed as a fin whale from its location (Fig. 2). Baleen whale sightings exhibited strong seasonal variations, with 89% of the sightings recorded in summer (Table 2).

Fin whales were only sighted in BoB at depths > 2000 m, with a clearly oceanic distribution in the summer (Fig. 2). In the winter, only lone whales were encountered, whereas the mean summer school size varied from 1.0 to 1.3 (Table 3). Estimated seasonal densities of fin whales in BoB differed significantly (z-test=2.3, $p < 0.05$), especially in the oceanic strata, while estimates were similar over the slope. The corrected abundance of fin whales increased from about 250 in winter to one thousand in the summer in BoB (Table 3).

Minke whales were preferentially encountered in the continental shelf (Fig. 2), always as lone individual. Only one sighting was collected in winter, in the EC. Their summer corrected abundance was estimated to 1,100 whales (95% CI: 400–3300) in EC, while 3000 individuals (95% CI: 1200–7900) were estimated in the BoB (Table 3). EC accounted for 26% of the summer abundance of minke whales in our study area.

3.6. Globicephalinae

Long-finned pilot whales were frequently sighted, but in BoB only, with 66 sightings collected on effort (Table 2). Sightings included 57 identified as pilot whales plus 9 which could not be distinguished from potential false killer whales (*Pseudorca crassidens*) but pooled for analysis. Long-finned pilot whales were mostly encountered along slope and in oceanic strata in both seasons (Fig. 2). Mean school sizes varied between 1.5 and 4 individuals (Table 4). Seasonal densities were quite stable, with corrected abundances estimated to about 4000 individuals (95% CI: 1900–8900) for BoB in both seasons.

The Risso's dolphin, readily identifiable from the air by their colour compared to large Globicephalinae, accounted for 31 sightings on effort in the ENA but none were east of 2°W of longitude (Fig. 2). Their distributions did not revealed strong differences between the two seasons (Fig. 2). Risso's dolphins were encountered around Brittany and in shelf and oceanic strata of BoB in the winter and summer (Fig. 2). Mean school size varied from 1 to 5 individuals and seasonal densities did not vary significantly between seasons (Table 4). The total ENA corrected abundance for Risso's dolphins was estimated between 900 individuals (95% CI: 200–4500) in the winter, with EC accounting for 14%, and 2300 individuals (95% CI: 700–7800) in the summer only in BoB, as no estimate was computed for EC with only one sighting.

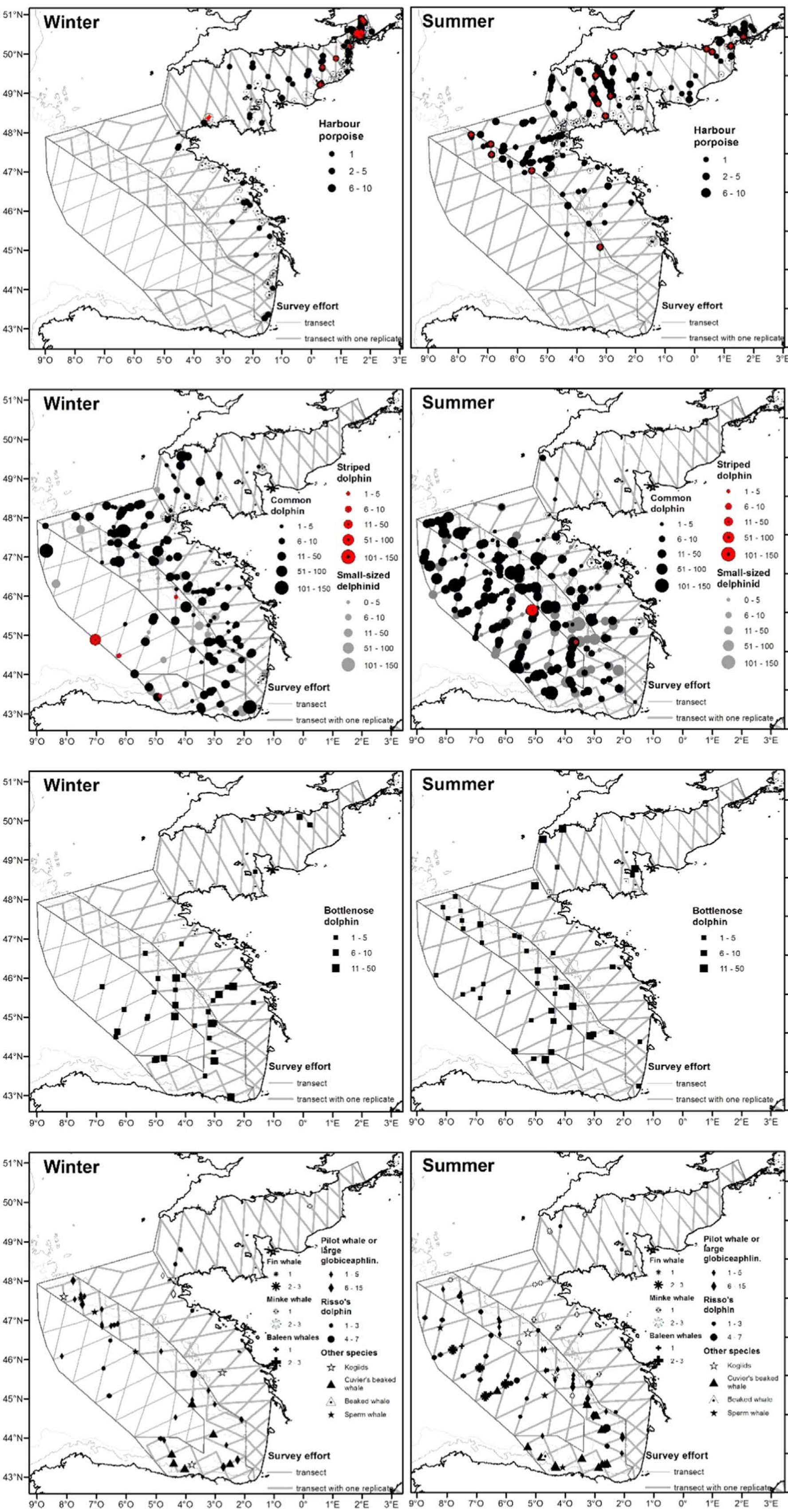

Fig. 2. Distribution of sightings and effort for winter and summer surveys, for harbour porpoise (with red dot for calf/young occurrence), common dolphin, small-sized delphinids, bottlenose dolphin, Balaenopteridae, sperm- and beaked whales, long-finned pilot whale and Risso's dolphin (sightings collected on a simultaneous coastal survey are represented by empty symbol). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Estimates of abundances for harbour porpoise, small-sized delphinids, bottlenose dolphin, fin whale and minke whale. Sightings numbers after truncation (*n*), mean school size (*Es*) with respective coefficient of variation (CV%), or regressed (*E(s)** when log(*s(i)*) on (*x*) is significant with $p < 0.05$), animal density (D in individual km^{-2} and CV) and density corrected for availability bias (D_{cor} and CV) and abundance adjusted too (N_{cor} and its 95% Confidence Interval).

	Strata	n	E(s)	CV	D	CV	D_{cor}	CV	N_{cor}	95% Confidence interval	
Harbour porpoise											
Winter	BoB_Shelf	14	1.4	14%	0.012	40%	0.026	50%	2724	1273	5836
	BoB_Slope	0									
	BoB_Oceanic	0									
	Total BoB	14			0.004	40%	0.010	30%	2724	1273	5836
	English Channel	93	1.6	7%	0.086	23%	0.192	30%	17,829	11,340	28,031
Summer	BoB_Shelf	49	1.5	7%	0.042	20%	0.093	36%	9624	6573	14,089
	BoB_Slope	17	2.0	17%	0.019	38%	0.043	48%	3733	1824	7638
	BoB_Oceanic	0									
	Total BoB	66			0.021	18%	0.047	30%	13,358	8398	21,727
	English Channel	103	1.4	5%	0.089	16%	0.198	30%	18,429	13,496	25,167
Small-sized delphinids (Common and striped dolphins)											
Winter	BoB_Shelf	246	9.5	10%	1.173	21%	1.736	32%	179,421	119,638	269,079
	BoB_Slope	91	9.8*	17%	0.443	25%	0.656	35%	57,450	35,206	93,750
	BoB_Oceanic	22	18.7	37%	0.527	48%	–	–	48,022	19,580	117,783
	Total BoB	359			0.738	17%	1.010	23%	284,894	174,423	480,612
	English Channel	23	10.5	36%	0.116	44%	0.171	50%	15,908	7033	35,986
Summer	BoB_Shelf	79	17.3	23%	0.646	32%	–	–	66,780	36,286	122,900
	BoB_Slope	306	13.7*	10%	1.994	17%	2.950	29%	258,360	185,338	360,152
	BoB_Oceanic	167	17.7	11%	1.847	17%	–	–	168,451	120,471	235,542
	Total BoB	552			1.453	11%	1.749	17%	493,591	342,094	718,593
	English Channel	4	3.5	53%	0.007	81%	0.011	84%	1023	255	4092
Bottlenose dolphin											
Winter	BoB_Shelf	7	7.0	40%	0.024	58%	0.03	58%	3255	1131	9372
	BoB_Slope	17	7.6	31%	0.074	43%	0.09	44%	8444	3735	19,087
	BoB_Oceanic	10	4.1	36%	0.051	52%	0.07	52%	6125	2348	15,979
	Total BoB	34			0.048	29%	0.062	30%	17,824	7214	44,437
	English Channel	4	4.0	27%	0.008	57%	0.010	57%	915	323	2589
Summer	BoB_Shelf	4	3	24%	0.006	65%	0.01	65%	751	234	2409
	BoB_Slope	22	4.7	18%	0.048	29%	0.06	30%	5567	3173	9766
	BoB_Oceanic	14	3.9	16%	0.034	33%	0.04	34%	4023	2127	7609
	Total BoB	40			0.028	21%	0.036	21%	10,340	5534	19,784
	English Channel	9	6.2	39%	0.029	64%	0.037	64%	3544	1121	11,202
Fin whale											
Winter	BoB_Shelf	0									
	BoB_Slope	2	1.0	0%	0.0005	71%	0.001	77%	117	33	411
	BoB_Oceanic	1	1.0	0%	0.0006	100%	0.001	104%	133	26	683
	Total BoB	3			0.0004	63%	0.001	30%	250	59	1094
Summer	BoB_Shelf	0									
	BoB_Slope	3	1.0	0%	0.001	57%	0.002	65%	143	50	409
	BoB_Oceanic	11	1.3	11%	0.004	32%	0.010	44%	914	494	1694
	Total BoB	14			0.0015	29%	0.004	30%	1058	544	2102
Minke whale											
Summer	BoB_Shelf	6	1.0	0%	0.0025	47%	0.02	55%	2129	890	5096
	BoB_Slope	3	1.0	0%	0.0012	62%	0.01	68%	911	296	2799
	BoB_Oceanic	0									
	Total BoB	9			0.001	38%	0.002	38%	3040	1186	7895
	English Channel	3	1.0	0%	0.001	62%	0.012	68%	1077	351	3299

3.7. Deep divers

Deep divers were only seen in BoB. Cuvier's beaked whales amounted to 19 sightings overall, plus one unidentified beaked whale (Table 2). In both seasons, sightings were mostly located along the Iberian coast, south of 46°N and along the 2000 m isobath (Fig. 2). Seasonal densities of Cuvier's beaked whales did not vary significantly with 483 and 590 individuals estimated without correction for availability bias in the winter and summer, respectively. But once the availability bias factor is applied about 7000 individuals (95% CI: 2700–21,400) were estimated whatever the season (Table 4).

The 8 sightings of sperm whales were located close to the 2000 m isobath (Fig. 2). Corrected abundances were few hundred of sperm whales within BoB whatever the season with confidence interval between 100 and 2600 individuals (Table 4).

On effort, 6 sightings of kogiids were collected, for which distinction between dwarf sperm whale (*Kogia sima*) and pygmy sperm whale (*K. breviceps*) was not possible from the air. Kogiids were all sighted within the slope strata, except one sighting over the continental shelf (Fig. 2). In the winter two close atypical sightings of kogiids of three individuals (including a calf) were detected in the Celtic Sea. Their encounter rate of 0.24 sightings per 1000 km (CV=61%) in winter was not significantly different from 0.10 sightings per 1000 km (CV=71%) in summer.

4. Discussion

4.1. General

The present work provided new information of a large panel of cetacean species in the ENA. We estimated corrected abundances (for availability bias only) for several species in the Bay of Biscay and the English Channel, documented their seasonal variations, and better characterised their seasonal distribution. These results are crucial for assessing the conservation status of species listed under Annex II of the Habitat Directive (HD), such as the common bottlenose dolphin, but also other species (listed in HD-Annex IV). Given the important and homogeneous sampling effort deployed during the SAMM surveys, our

Table 4
Estimates of abundances for Risso's dolphin, pilot whale, beaked whales and sperm whale. Sightings numbers after truncation (n), mean school size (Es) with respective coefficient of variation (CV%), or regressed ($E(s)$* when $\log(s(i))$ on (x) is significant with $p < 0.05$), animal density (D in individual.km^{-2} and CV) and density corrected for availability bias (D_{cor} and CV) and abundance adjusted too (N_{cor} and its 95% Confidence interval).

	Strata	n	E(s)	CV	D	CV	D_{cor}	CV	N_{cor}	95% Confidence interval	
Risso's dolphin											
Winter	BoB_Shelf	1	2.0	0%	0.001	101%	0.001	104%	103	20	532
	BoB_Slope	3	3.0	51%	0.004	112%	0.005	115%	457	78	2685
	BoB_Oceanic	2	1.0	0%	0.002	71%	0.003	75%	232	66	810
	Total BoB	6			0.002	69%	0.003	73%	793	164	4026
	English Channel	3	1.0	0%	0.001	75%	0.001	79%	133	36	492
Summer	BoB_Shelf	2	5.0	60%	0.004	93%	0.005	96%	486	103	2288
	BoB_Slope	9	3.1	32%	0.010	54%	0.013	60%	1164	428	3162
	BoB_Oceanic	5	3.0	33%	0.005	75%	0.007	79%	625	169	2313
	Total BoB	16			0.006	40%	0.008	47%	2274	700	7763
	English Channel	1	1.0	0%	0.000	101%					
Pilot whale											
Winter	BoB_Shelf	0									
	BoB_Slope	21	4.0	27%	0.032	39%	0.042	46%	3693	3665	3721
	BoB_Oceanic	2	1.5	33%	0.003	78%	0.003	82%	305	300	309
	Total BoB	23			0.011	36%	0.014	43%	3997	3965	4030
Summer	BoB_Shelf	0									
	BoB_Slope	30	3.4	11%	0.032	28%	0.042	37%	3675	3654	3695
	BoB_Oceanic	1	3.0	0%	0.001	101%	0.002	104%	149	146	152
	Total BoB	31			0.010	28%	0.014	37%	3824	3801	3847
Beaked whales											
Winter	BoB_Shelf	0									
	BoB_Slope	6	2.2	22%	0.006	50%	0.079	69%	6905	2715	17,559
	BoB_Oceanic	0									
	Total BoB	6			0.002	50%	0.024	59%	6905	2715	17,559
Summer	BoB_Shelf	0									
	BoB_Slope	12	1.9	16%	0.006	39%	0.083	49%	7236	3447	15,191
	BoB_Oceanic	1	2.0	0%	0.001	102%	0.013	107%	1187	226	6227
	Total BoB	13			0.002	37%	0.030	47%	8423	3673	21,418
Sperm whale											
Winter	BoB_Shelf	0									
	BoB_Slope	3	1.3	25%	0.001	67%	0.005	69%	429	131	1407
	BoB_Oceanic	0									
	Total BoB	3			0.0003	67%	0.0015	69%	429	131	1407
Summer	BoB_Shelf	0									
	BoB_Slope	1	1.0	0%	0.0002	103%	0.0010	104%	88	17	463
	BoB_Oceanic	3	1.5	19%	0.0011	81%	0.0066	82%	599	150	2396
	Total BoB	4			0.0004	71%	0.0024	73%	687	167	2859

analyses yielded fairly precise estimates of the abundance (CV < 45%) for four species in the Bay of Biscay (harbour porpoise, small-sized delphinids, bottlenose dolphin, and pilot whale). Our estimates contributed to the assessment of 'Good Environmental Status' in the ENA as they inform (i) on bottlenose dolphin abundances in the area, or (ii) biodiversity of the cetacean community, two candidate MSFD indicators (Azzellino et al., 2014; Lauriano et al., 2014). Moreover, our results could be compared to other summer surveys dedicated to abundance estimates (see Section 4.3).

4.2. Aerial survey methodology

One important limit intrinsic to aerial surveys is species identification. For example, our data did not allow common and striped dolphins to be distinguished for all sightings. Striped dolphins are restricted to deep oceanic waters, beyond the 1000 m isobath (Forcada et al., 1990; Hobbs, 2004), while common dolphins, have a more ubiquitous distribution in both deep and shallow waters (Kiszka et al., 2007). This spatial segregation did not show up in our data, because only a few sightings were unambiguously identified as striped dolphins. Overcoming this limitation will be a major way to improve future surveys (with e.g. autonomous digital picture, circle manoeuvre, etc.).

Because of possible misidentification between small-sized delphinids, bottlenose or Risso's dolphins, 65 and 70 sightings were classified as delphinids, and were discarded in the winter and summer, respectively. To assess the underestimation in abundance induced by these discarded sightings, we imputed species identity for these sightings and generated ten complete datasets (Fig. A2, Table A2) which were analysed and averaged to obtain abundance estimates. This procedure resulted in an increase of 2 to 20% in abundances estimates (Table A3). Abundance estimates for rarely occurring species, such as Risso's dolphins in the winter in the EC, were unsurprisingly most sensitive with a downward bias of up to one fifth.

The survey coverage do not respect completely the equal coverage probability, but density was estimated using design-based methods. Another step was then to obtained a distribution model of their densities using model-based methodology (Lambert et al., 2017).

4.3. Distribution and abundance

Spatial distribution of cetaceans in the Bay of Biscay and western English Channel have previously been investigated by several dedicated surveys, some of them which were conducted for absolute abundance estimation. Nevertheless each has its specific sampling areas, and between-survey comparison is often difficult.

4.3.1. Harbour porpoise

As a species listed under the HD-Annex II, the harbour porpoise is of community interest. In the English Channel we did not find any evidence of any seasonal change in estimated total abundance, contrary to Bay of Biscay, where summer abundance increased strongly, probably as a result of a southward migration of animals from the Celtic Sea. Despite stable abundances of porpoise in the Channel between winter and summer, the harbour porpoises exhibited a strong seasonal variation in their distribution. In the winter, they were mainly confined to the shelf waters of the Channel, with high densities in the Dover Strait as previously known (Reid et al., 2003), but were also present along the Atlantic coast, down to the South of the Bay of Biscay. The latter result was more surprising but not unexpected as stranding data reveal the presence of the species in the southern of the Bay in the winter (Peltier et al., 2013). In the summer, the Dover strait hotspot persisted, but the western part of the English Channel and North of the Bay of Biscay revealed a large number of sightings, probably as the south of the Celtic Sea. These results in Channel contrasted with those of the 1994 and 2005 SCANS I and II surveys, showing absence of low densities of harbour porpoise in the area (Hammond et al., 2002; Hammond et al., 2013; Kiszka et al., 2004). In Bay of Biscay, while porpoises were encountered during our summer survey until 45°N in the south, porpoises were absent south of 47°N in previous surveys in the same area (Hammond et al., 2002; Hammond et al., 2013; Kiszka et al., 2007). This summer distribution would confirm the southward shift in distribution shown by the SCANS II surveys (Hammond et al., 2013). Our density estimates in the Channel and Bay of Biscay were in agreement with those estimated previously (Table 5), such as in the neighbouring North Sea where 0.29 ind km^{-2} were estimated in 2008 (Scheidat et al., 2012).

4.3.2. Small-sized dolphins

The common and the striped dolphins are the most common cetaceans inhabiting the ENA (Forcada et al., 1990), nevertheless both are almost absent from the eastern Channel (De Boer et al., 2008; Hobbs, 2004; Reid et al., 2003), a result corroborated by strandings (Peltier et al., 2014). Strong seasonal variations were previously described for the common dolphin, being more widely dispersed in deep offshore waters in summer, while peaking in the Western Channel and Celtic Sea in winter (Hobbs, 2004) or along the southern Iberian coast (Marcos et al., 2010). Previous studies on habitat partitioning between the common and striped dolphins reported a wide degree of spatial overlap in certain seasons. In the spring, common dolphins were most abundant on the shelf of the Bay of Biscay at depths < 100 m (Certain et al., 2008), suggesting transient spatial segregation of the two species. Despite the uncertainty in species identification from the air, the winter and summer distributions of sightings of small delphinids were not congruent with the spring pattern described above. A large-scale aerial survey conducted during the spring may help to understand small delphinids ecology and their seasonal movements.

In the summer, our density of small-sized dolphins in the Channel was three times lower than estimates for common dolphins during SCANS-II in a larger survey block (B, including our EC_shelf, Table 5). However, both estimates have a large uncertainty. In the Bay of Biscay our estimate for the oceanic and slope strata is twice the density obtained from the 2007 CODA survey (Table 5). Alternatively, 2012 could be an unusual year for common and striped dolphins' distribution in the Bay, which would explain the differences observed with previous estimates. We observed a northward extension of small delphinids distribution on the continental shelf in the summer, but harbour porpoises and small-sized delphinids did not overlap in the southern Celtic Sea (Fig. 2).

4.3.3. Common bottlenose dolphin

In the NEA, two distinct bottlenose dolphin ecotypes (*i.e.* 'coastal' and 'pelagic') have been recently identified with genetic markers: a "Coastal South population" inhabits the Gulf of Saint Malo in the Western Channel and would be present further south down to Galicia, a "Pelagic Atlantic population" in the Bay of Biscay (Louis et al., 2014). In the Channel, where bottlenose dolphins are genetically distinct from northern conspecifics around the British Isles (Louis et al., 2014). Their population sizes in the Channel are not well known, except in the Gulf of Saint Malo, where 420 dolphins (95% CI: 331–521) were estimated by photo-identification-based Capture Mark Recapture analyses (Louis

Table 5
Densities (with CV when available) obtained in the English Channel and the Bay of Biscay in summer as inferred from existing literature.

Area	**Campaign**	**Plateform**	**Year**	**Harbour porpoise**	**Common dolphin**	**Bottlenose dolphin**	**Minke whales**	**References**
English Channel (Summer)	SAMM	Aircraft	2012	0.20 (CV=30%)	0.011* (CV=84%)	0.037 (CV=64%)	0.012 (CV= 68%)	This study, corrected for availability
	SCANS II-Block B		2005	0.33 (CV=38%)	0.04 (CV=82%)	0.0032 (CV=74%)	0.010 (CV=98%)	Hammond et al. 2013
Area	**Campaign**	**Plateform**	**Year**	**Striped dolphin**	**Common dolphin**	**Bottlenose dolphin**	**Fin whales**	**References**
BoB Shelf & slope (summer)	Atlancet	Aircraft	2002		0.55 (CV=29%)			Ridoux et al. 2003; Certain et al. 2008
BoB/ Slope & oceanic (summer)	CODA - Block IV	Ship	2009		1.2 (CV=38%) *	0.01 (CV=45%)	0.006 (CV=70%)	MacLeod et al. 2009; CODA, 2009
BoB/ Slope & oceanic (summer)	SAMM (Slope & OCE)	Aircraft	2012	0.02 (CV=30%)	2.38 (CV=12%)	0.053 (CV=15%)	0.001 (CV=48%)	This study, corrected for availability

* estimates including stripped dolphins.

et al., 2015). In addition there are two other small communities (less than a hundred individuals in total) in the Iroise Sea (Liret, 2001), while along the southern English coast, groups were considered as wider-ranging (Reid et al., 2003). Even if transect-based estimate is not well-suited for resident groups, our estimates (between 900 and 3500 individuals; total 95% CI: 300–7600) were consistent with knowledge for the area.

In the Bay of Biscay, bottlenose dolphins were homogenously distributed in the summer, contrary to the winter, when oceanic population distribution was south of 47°N, matching the narrow distribution (46°–48°30' N) obtained from long-term ferry-based surveys (Kiszka et al., 2007). In the summer in the Bay, our density was five times higher than during CODA survey (Table 4). In the winter, despite a consistent encounter rate of bottlenose dolphins over the continental shelf during ROMER survey, there were differences in timing. Most bottlenose dolphins were sighted between January and February 2002 during ROMER, with an encounter rate of 0.45 sightings per 100 km (Certain et al., 2008). We obtained 0.05 sightings per 100 km in the shelf stratum in January–February 2012, with an almost complete coverage of this sampling area at this period (4000 km of effort). This possible change in distribution between the beginning of 2002 and the beginning of 2012 needs to be confirmed, but could be associated with variation in prey distribution, resulting in a later inshore movement of dolphins, than in the beginning of the 2000s. In addition, in both seasons, we observed a wider distribution of the bottlenose dolphins than expected, with a peak abundance in the oceanic and shelf strata, as also found in the North-Western Mediterranean survey (Laran et al., 2017).

4.3.4. Baleen whales

The present summer estimate of fin whales density in the oceanic stratum of the Bay of Biscay is in agreement with that obtained from the ship survey CODA, in July 2007 (Table 5). It appeared that some fin whales overwinter in the area.

Minke whales are known to occur in the Western Channel and west of Brittany (MacLeod et al., 2007; Reid et al., 2003), inhabiting the continental shelf. In European Atlantic waters, minke whale occurrence peaks in summer throughout shelf waters of Eastern North Atlantic Ocean, suggesting that seasonal patterns of minke whale are not just a simple north-south seasonal movements of individuals (MacLeod et al., 2007). For the Channel, our estimate of density was in agreement with SCANS II (Table 5) but minke whales were not sighted on the shelf of the Bay of Biscay during the SCANS I and II surveys (in July 1994 and in 2005) and only distributed north of 50°N in the Celtic Sea (Hammond et al., 2002; Hammond et al., 2013). In contrast, the summer 2012 sightings that we collected southward (45°–48°N), may correspond to individuals migrating towards feeding areas.

4.3.5. Other species

Long-finned pilot whales were encountered over the shelf break in both seasons, and our results confirmed their deep water distribution in the Bay of Biscay (Kiszka et al., 2007; Reid et al., 2003). The winter peak of their occurrence around the Canyon of Capbreton compared to their low occurrence during the rest of the year (Marcos et al., 2010) was in agreement with the diffuse distribution along the shelf break in winter, while pilot whales seemed restricted between 44° and 47°N in summer. Regular incursions in coastal areas are confirmed for the species, in the Gulf of Saint Malo (Western Channel; Kiszka et al., 2004), between Charente islands and mainland or along Brittany coasts (PELAGIS Observatory unpublished data).

Risso's dolphins inhabit the Western Channel (Kiszka et al., 2004), notably in winter (De Boer et al., 2008), a pattern consistent with our winter estimate and distribution. In Western Europe, their occurrence peaks between July and September, and they appear to be more frequently offshore near the continental shelf in winter (Reid et al., 2003). In the Bay of Biscay their density increase slightly in summer but not significantly, but whatever the season the shelf break remain preferential area for Risso's dolphins.

Beaked whales were observed along the Iberian coast and in canyon areas, which matches previous results in the area well (Kiszka et al., 2007; Marcos et al., 2010).

S*perm whale* abundance seemed quite stable throughout the year in the Bay of Biscay, despite a small number of sightings, confirming previous results in the area (Hobbs et al., 2007).

There are very few sightings of kogiidsin European waters, mostly fromthe Bay of Biscay and Western Channel (Reid et al., 2003). Most of available information about kogiid distribution come from strandings (Santos et al., 2006). However, aerial surveys seems particularly adapted to detect their occurrence, nevertheless sighting number was still too limited to allow any estimation of their abundance at this stage.

5. Conclusion

These two seasonal surveys provided robust estimates of abundance and pattern of distribution for the main species of cetaceans inhabiting the Bay of Biscay and the English Channel. These baseline data are of paramount importance not only for designating new marine protected areas, or for marine spatial planning but also for conservation management in general. These data are also paramount for Member State requirements to provide an initial assessment of marine biodiversity under the Marine Strategy Framework Directive (MSFD). Nevertheless, the interpretation of abundance estimates depends on auxiliary information on population structure; complementary approaches, such as genetic or ecological markers, are needed to elucidate the spatial connectivity, if any, of populations. A clear example among cetaceans is that of bottlenose dolphins for which offshore and coastal populations, which are genetically distinct, can occur close in space (Allen et al., 2016; Louis et al., 2014).

Large scale surveys can reveal distributional shifts such as the one observed in harbour porpoises between the first and second SCANS surveys (Hammond et al., 2013). The SAMM surveys confirmed the abundance of this species in the English Channel in both the winter and summer. Abundance estimates are crucial in those regions for monitoring purposes, and *in fine* to assess human impacts. For example, a recent study on common dolphins in the area suggested a very high level of bycatch with about 4000 individuals year^{-1} (Peltier et al., 2016). Furthermore the ongoing development of offshore wind farms in the North Sea and Channel is becoming a growing concern for harbour porpoises (Madsen et al., 2006). Cooperation between countries will be crucial to monitor, asses and mitigate impacts on marine mammals. Supra-national management will be needed to achieve'Good Environmental Status' of marine ecosystems as required by the European MSFD. In this context, large scale surveys remain a tool of choice to document such crucial parameters as distribution and abundance of cetaceans.

Acknowledgements

The French Ministry in charge of the environment (*Ministère de l'Ecologie, du Développement Durable, et de l'Energie*) and the French Marine Protected Areas Agency (*Agence des aires marines protégées*, AAMP) funded the project. The PELAGIS observatory, with the help of the AAMP, designed, coordinated and conducted the survey. We thank all the observers: Léa David, Thomas Barreau, Ariane Blanchard, Vincent Bretille, Alexis Chevalier, Cécile Dars, Olivier Dian, Nathalie Di-Méglio, Emilie Durand, Marc Duvilla, Emmanuelle Levesque, Alessio Maglio, Marie Pellé, Morgane Perri, and Sandrine Serre. We are indebted to all aircraft crew members of Pixair Survey and to SINAY for its logistic support. We also thank the two anonymous reviewers for their insightful comments and suggestions.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr2.2016.12.012.

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