Delphinid spatial distribution and abundance estimates over the shelf of the Bay of Biscay

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The small delphinid community (bottlenose *Tursiops truncatus*, common *Delphinus delphis*, and striped *Stenella coeruleoalba* dolphins) of the Bay of Biscay (100 000 km^2 of continental shelf along the French Atlantic coast) has been studied here by combining strip-transect aerial surveys conducted between 2001 and 2004 and ship-based surveys conducted between 2003 and 2006. Distribution was modelled spatially in relation to several large-scale descriptors of the environment. Highest densities of small delphinids were associated with the shelf break, in particular in two hotspots located in the north and the south of the bay. Using ship-based data, we found strong spatial segregation between common and bottlenose dolphins in spring, with common dolphins associated with coastal areas (and especially river plumes) and bottlenose dolphins on the outer shelf and the shelf break. Assuming a detection probability of 1, a strip-transect abundance estimate for the small delphinid community was obtained in August 2002 with 56 500 (95% CI 29 100–90 400), but relative abundance varied across months.

Keywords: abundance estimates, Bay of Biscay, dolphins, small delphinids, spatial distribution, transect surveys.

Received 17 April 2007; accepted 28 February 2008; advance access publication 3 April 2008.

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Introduction

Sustainable harvesting of natural resources and ecosystem-based management not only require long-term management of the marketed species, but also the mitigation of indirect effects on non-target species (Jennings *et al.*, 2001). The latter relies on accurate information on the status of non-commercial species, especially in terms of distribution and abundance. Both parameters are crucial in identifying potential interaction in space and time with harvesting activities. One of the most important conservation issues in marine ecosystems deals with interactions between marine megafauna and fisheries (reviewed by Lewison *et al.*, 2004). Interactions may be direct or indirect. For instance, overexploitation of marine species leads to changes in the pelagic community (Jennings *et al.*, 1999; Jennings and Blanchard, 2004), and it may affect top predators through prey availability (Trites and Donnelly, 2003). Moreover, clear identification of high-density areas of marine mammals is required to investigate direct interactions (i.e. bycatch) between cetaceans and fisheries. Study on spatio-temporal distribution of cetaceans requires the implementation of monitoring programmes over large spatio-temporal scales (Defra, 2003). In this context, assessment of the absolute abundance and the identification of critical habitat are crucial.

The continental shelf of the Bay of Biscay is exploited by many fishing fleets using different fishing gears, including lines, traps, gill- and trammelnets, bottom and pelagic trawls (Léauté, 1997). Such extensive fishing activities may affect marine life and

ecosystems, and the presence of many stranded dolphins along the French and English coasts provides evidence of the bycatch of small delphinids in some fisheries (mainly short-beaked common dolphin, *Delphinus delphis*), because many beached animals show clear bycatch marks (Tregenza and Collet, 1998). Pusineri (2006) identified diet overlaps between fisheries and small delphinids in the Bay of Biscay.

Previous studies conducted in European shelf waters (SCANS and SCANS II surveys; Hammond *et al.*, 2002, 2006) encompassed a greater (near 1 000 000 km^2) area and provided summer abundance estimates for the harbour porpoise (*Phocoena phocoena*) and several small delphinids, including common and bottlenose dolphin (*Tursiops truncatus*). Here, we document a complementary approach, based on repeated extensive surveys across different seasons and years (2001–2006) of a particular area, the continental shelf of the Bay of Biscay (100 000 km^2 on the French Atlantic coast). We provide detailed information on the small delphinid population, including spatial distribution, population size, specific composition, and temporal variation. Our surveys used both aerial and ship-based platforms. Aerial surveys were conducted in various seasons and years, and were used to assess the most important habitats for the small delphinid community and to quantify temporal variability in relative abundance. One aerial survey dedicated to small cetaceans provided an estimate of small delphinid abundance for the Bay of Biscay in August 2002. Ship-based surveys are used to model species-specific habitat and to allow interspecific comparison in distributions between

the two most important small delphinid species of the Bay of Biscay, common and bottlenose dolphins. These two species have different diets, common dolphins feeding on small pelagic fish (Pusineri, 2006), and bottlenose dolphins relying on demersal prey (Spitz *et al.*, 2006). The spatial distribution of both species is investigated in spring, during the spawning season of small pelagic fish such as sardine and anchovy. We have designed our analyses to provide results for key habitat identification, trophic web modelling and, in the longer term, for ecosystem-based fisheries management of the Bay of Biscay.

Material and methods
Area and data acquisition
The continental shelf of the Bay of Biscay (Figure 1a) has several habitats: two major sources of primary production are located along the eastern and western boundary of the shelf (Planque *et al.*, 2004; Puillat *et al.*, 2004). To the east, in coastal areas, river run-offs (Loire and Gironde) discharge nutrient-rich fresh water ($\sim 1\,km^3$ of fresh water per $1000\,km^2$ of continental shelf). To the west, at the shelf break, bathymetry increases sharply to 5000 m. Deep, cooler waters break through the surface under the influence of internal tides and waves (Gerkema *et al.*,

2004), and enhance primary production as they reach the euphotic layer (Laborde *et al.*, 1999). The shelf break is also characterized, in the south, by the presence of two deep canyons, Cap Ferret and Cap Breton. Coastal and shelf break areas are the most productive systems of the bay.

Data were collected along 55 430 km of transects over the continental shelf, by aerial and ship-based surveys conducted between 2001 and 2006 (see Table 1 for a summary). The surveys involved 15 observers, who recorded seabirds, cetaceans, and fishing activity. Aerial surveys were specifically designed for top predators, and aimed at investigating both spatial distribution and abundance. An absolute abundance was calculated using one aerial survey specifically designed for marine mammals (ATLANCET). Ship-based surveys involved the use of the RV "Thalassa" as a platform of opportunity, with three observers. Ship-based data were used to complement aerial-survey data, especially to describe species-specific habitat.

Aerial surveys
After an experimental survey conducted in March 2001, one survey per month was carried out from October 2001 to March 2002, then two additional surveys were conducted in June 2003 and
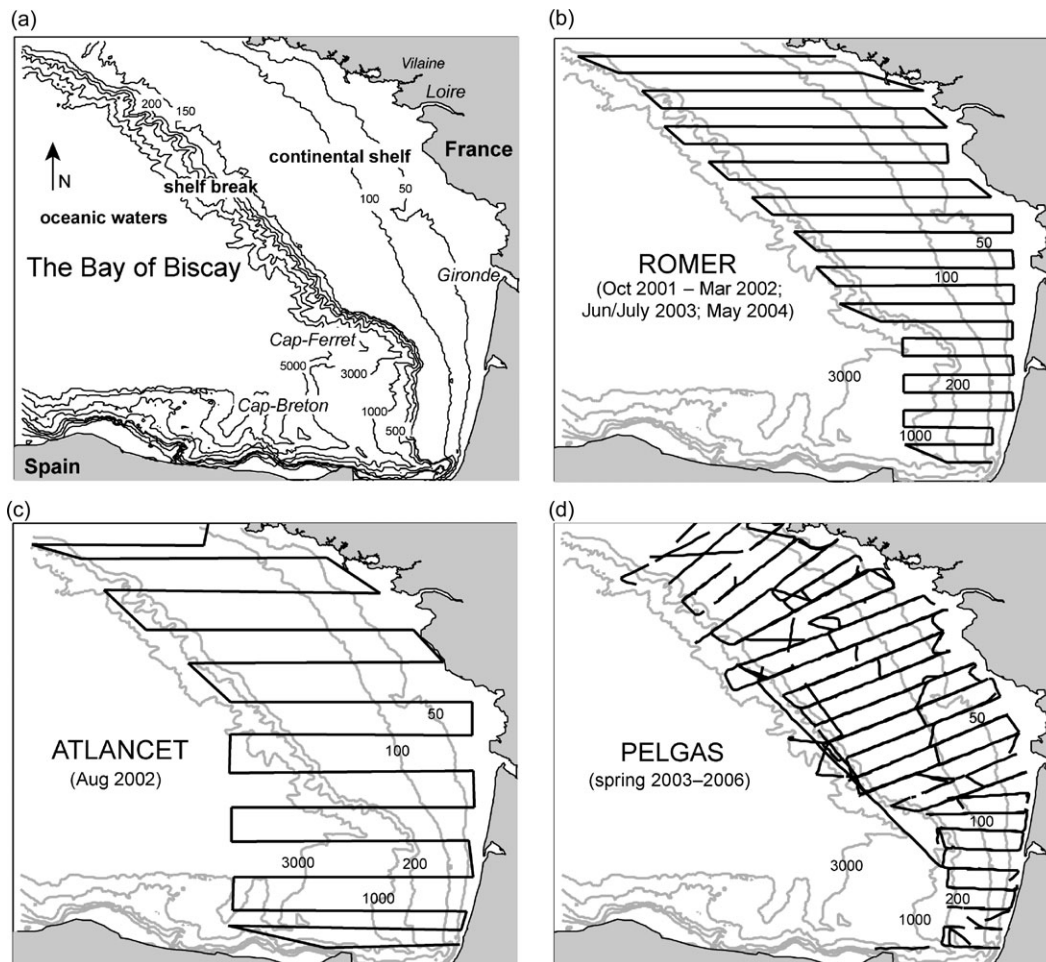

Figure 1. (a) Study area: the Bay of Biscay, between the French and the Spanish Atlantic coast. (b) ROMER sampling scheme (4600–4900 km of aerial transect, 6 monthly surveys between October 2001 and March 2002, 1 survey in June/July 2003, and 1 in May 2004). (c) ATLANCET sampling scheme (3400 km of aerial transect, 1 survey in August 2002). (d) PELGAS sampling scheme (3500–4000 km of ship-based transect, three annual surveys in spring of 2003, 2004, 2005, and 2006).

Table 1. Summary of the 13 surveys carried out in the Bay of Biscay between 2001 and 2006.

Effort (km)	Start date	End date	Duration (d)	Platform	Sampling scheme
4 650	24 October 2001	02 November 2001	7	Aircraft	ROMER
4 680	17 November 2001	27 November 2001	7	Aircraft	ROMER
4 745	07 December 2001	19 December 2001	7	Aircraft	ROMER
4 600	25 January 2002	01 February 2002	7	Aircraft	ROMER
4 705	09 February 2002	18 February 2002	7	Aircraft	ROMER
4 710	16 March 2002	25 March 2002	6	Aircraft	ROMER
3 430	03August 2002	14 August 2002	7	Aircraft	ATLANCET
3 950	29 May 2003	24 June 2003	25	Ship	PELGAS
4 900	28 June 2003	06 July 2003	5	Aircraft	ROMER
3 700	28 April 2004	22 May 2004	23	Ship	PELGAS
4 590	20 May 2004	29 May 2004	4	Aircraft	ROMER
3 475	05 May 2005	25 May 2005	19	Ship	PELGAS
3 550	02 May 2006	30 May 2006	26	Ship	PELGAS

May 2004. The first survey design ("ROMER", see Figure 1b) encompassed 4500 km of transects (Table 1). The same tracks were surveyed during every ROMER survey. In addition to ROMER surveys focused on both seabirds and cetaceans, one survey dedicated to cetaceans ("ATLANCET"; Figure 1c) was carried out in August 2002. The ATLANCET survey followed a slightly different sampling scheme, and encompassed 3430 km of transects over a wider study area (120 000 km²), incorporating oceanic water in the south. Both ROMER and ATLANCET surveys were designed under a systematic sampling scheme of 24 and 15 east–west orientated lines, spaced every 20 and 40 km, respectively. The survey design was drawn to achieve a homogeneous coverage of the Bay of Biscay. A complete survey of the Bay was achieved in 6–8 d.

The aircraft (a PA 34 Seneca) was a 6-seat, low-wing, twin-engined aircraft. Although high-wing aircraft are usually recommended (Buckland *et al.*, 2001), no such aircraft was available at the time surveys were carried out. The two observers were placed at the back of the aircraft, so that they could see below the wings. Data were collected using the strip-transect method. The strip-transect method assumes that all animals within the strip (i.e. a band of sea of fixed width each side of the transect line) are detected. Strip width was 230 m to each side of the aircraft for ROMER surveys, but was slightly reduced during ATLANCET surveys (200 m), to satisfy the assumption of homogeneity of detection probability better across the whole strip (see Pollock *et al.*, 2006). Visual marks on the wings ensured accurate estimates of strip bandwidth.

Flights were carried out from 09:00 to 17:00 local time, and their duration ranged between 150 and 180 min. Speed (150 km h⁻¹; i.e. 80 knots) and altitude (150 m; 500 feet) were determined during trial flights in March 2001 as a trade-off between sighting comfort and safety. In these conditions, the time-window to locate, identify, and assess group size was between 4 s at the inner limit of the strip and 7 s at the outer limit.

Surveys were conducted only under weather conditions categorized as good to excellent, i.e. all flights started with Beaufort Sea state 2 or less, an absence of rain or fog, and very good visibility. On board, two observers (one on each side), equipped with a GPS (Garmin 12) connected to a laptop computer, continuously recorded sightings within the strip (group size, species identity). When sightings were made outside the strip, lateral distance

was estimated by eye. Exact location and time of observation were recorded automatically. Observers were experienced field observers, and ATLANCET observers were all specialists in marine-mammal sightings. ROMER observers were chosen according to their experience of both seabird and marine-mammal sightings.

Ship-based surveys

Ship-based surveys were conducted in spring during "PELGAS" cruises (Figure 1d) on board the RV "Thalassa". The primary aim of PELGAS cruises is to assess stocks of small pelagic fish in the Bay of Biscay acoustically (Massé *et al.*, 1996; Petitgas, 2003). Surveys were in spring from 2003 to 2006 and followed a scheme of 26 transects perpendicular to the coast (4000 km; Figure 1d). The area surveyed was restricted to the continental shelf, and incursions on the shelf break were exceptional and limited to the middle of the bay. Sightings of top predators were recorded during daylight. During the first two PELGAS cruises (2003 and 2004), two observers were sited 14 m above sea level. During the 2005 and 2006 survey, observers had access to the upper bridge of the ship, 16 m above sea level. Ship's speed was maintained at 10 knots. Two observers searched for cetaceans and seabirds within an angle of 180° ahead of the bow, and were renewed every 2 h. For each sighting, the number, species composition, and GPS position were recorded, and the distance and angle was estimated by eye and with an angleboard.

Spatial analysis

Aerial and ship-based surveys were analysed separately, because survey protocol and data collected were not directly comparable. Both aerial and ship-based cetacean sightings were used to model small delphinid distributions against environmental covariates. Species identification was not always possible during aerial surveys, so we pooled all sightings of small delphinids. In contrast, ship-based sightings were identified to species level in almost all cases, allowing us to build two different models comparing common and bottlenose dolphin distributions. For spatial analysis, all sightings (including aerial observations recorded out of the strip) were used.

We split the data into bins of 20 km, a trade-off between spatial accuracy and the number of zero values in the data. The number of dolphin sightings was reported in each bin, so corresponding to an index of sightings, which is much easier to model than number of

individuals. Indeed, dolphins may be encountered in very large schools (up to several hundred animals). Cetacean schooling behaviour is often response to ecological factors such as prey distribution or specific behaviour (foraging, reproduction), which cannot easily be incorporated into a spatial model of large-scale distribution. Therefore, we restricted our spatial analyses to dolphin occurrence. We assumed that the number of sightings per 20 km bin approximates to a Poisson distribution (i.e. the number of sightings per bin range between 0 and 7 in aerial data, and between 0 and 3 in ship-based data). This index of occurrence was modelled with a generalized additive model (GAM; Hastie and Tibshirani, 1990; Wood and Augustin, 2002), using broad-scale descriptors of the environment, including latitude, distance to coast, distance to the nearest estuary (Loire or Gironde; Figure 1a), distance to the nearest canyon (Cap Ferret or Cap Breton; Figure 1a), and distance to the 200 m isobath (used as a proxy for shelf break location). Even if latitude is not a biological variable, it can be used to model possible north–south gradients in species distribution. We assumed a Poisson error distribution for our models. The spatial analysis followed the same methodology as Planque *et al.* (2007). First, we used GAM models with single predictors to identify the relationships between individual broad-scale descriptors of the environment and the relative abundance of dolphins. The outputs of the GAMs are smoothed fits for each predictor. Then we searched for the models that best incorporated multiple predictors with a forward selection procedure, using Akaike's information criteria (AIC; Wood and Augustin, 2002). Each covariate was tested individually, and the most significant ones were added in order. The procedure stopped when adding a new covariate did not further decrease the AIC. Three models were built, for three response variables. The first describes the global distribution of small delphinids (using aerial data) over the whole year, and the other two highlight specific habitats of common and bottlenose dolphins (using ship-based data) in spring.

Predicted relative abundances were calculated from the final model to map habitat within the bay. The predictions are spatially distributed into a grid. We used 40-km grid cells, because smaller cells result in a decrease in a model's predictive power. Model predictive power was tested using cross-validation, an iterative procedure carried out for every grid cell. For each grid cell, a model was built without the data being in the grid cell. Dolphin occurrence within the missing grid cell was predicted by the model. Then, predicted occurrences were compared with observations (i.e. the mean number of sightings per 20-km bin calculated with all bins that were removed) using a linear regression model. Model predictive power was measured by the regression parameters. In a perfect case, the slope of the linear model is expected to equal 1, with an important adjusted r^2. The modelling procedure was implemented using R software (R Development Core Team, 2003) and the mgcv package (Wood, 2001).

Abundance estimates

Absolute abundance estimates were calculated with a strip-transect estimator (Eberhardt, 1978), only from ATLANCET data. This estimate covered the ATLANCET area (i.e. 120 000 km^2), slightly larger than the ROMER area. Southward or westward sightings were potentially affected by sun glare (Yoshida *et al.*, 1998), but no glare index was recorded. Therefore, we provide two abundance estimates: one, termed "glare uncorrected", used all data collected within the strip on both sides of the aircraft (a 2×200-m strip width) and the other, termed "glare corrected" used only data collected on the side of the aircraft that was not subject to glare (i.e. located to the north or the east of the track line; a 1×200 m strip). Distance data were not recorded within the strip, so we made the assumption that detection probability was homogeneous across the whole strip. This assumption has already been tested during other aerial surveys, focusing on dugongs (see Pollock *et al.*, 2006), and was found to be satisfactory. Also, our survey protocol did not allow detection probability to be estimated, so we carried out a sensitivity analysis of our abundance estimate under detection probability values ranging from 0.5 to 1. To calculate confidence intervals of the abundance estimate, we used a non-parametric block bootstrap (Hall *et al.*, 1995). Transects were first divided into bins of 1 km, then blocks of 15 km were built using 15 adjacent 1-km bins (see Hall *et al.*, 1995, for block-size determination). These 15-km blocks were used to build 999 pseudo-samples of the ATLANCET survey, for which 999 abundance estimates were made, and 95% confidence intervals (CIs) were determined from these 999 estimates.

Temporal variability

Winter surveys were analysed to assess temporal variability in population abundance, using the mean number of individuals per 20-km bin. We used data collected on the north side of the plane only, to control for potential glare in the measure of relative density. The aim was to detect possible seasonal trends in relative abundance of the small delphinid community. This index was calculated for every survey, with CIs estimated by the same block bootstrap procedure as for absolute abundance.

Results

Excluding large whales, a total of 393 cetacean sightings was made during aerial surveys and 189 sightings during PELGAS cruises (Table 2). Almost 50% of the aerial sightings were unidentified small delphinids, probably mainly common dolphins, but also possibly striped dolphins (*Stenella coeruleoalba*), Atlantic white-sided dolphins (*Lagenorhynchus acutus*), or bottlenose dolphins, even if the two latter are more easily distinguishable. These four species constituted our ecological group "small delphinids" and accounted for 316 aerial and 145 ship-based sightings. Among them, common and bottlenose dolphins were by far the most frequent, striped dolphins were rare (in terms of number of sightings), and Atlantic white-sided dolphins were anecdotal (Table 2). Long-finned pilot whales (*Globicephalas melas*) were also quite often observed (56 aerial sightings and 37 ship-based sightings). In spring, the specific composition of the small delphinid community includes 48.3% common dolphins, 30.4% bottlenose dolphins, and 20.4% striped dolphins (with <1% of unidentified small delphinids).

Aerial sightings were widely distributed throughout the bay, but the largest groups were on the outer shelf, close to the shelf break (Figure 2a). Common dolphins were sighted over the shelf, the slope, and in oceanic deep water, but the largest groups were close to the shelf break. No bottlenose dolphin was observed in oceanic waters. The four sightings of striped dolphins were also on the slope, at the northern and southern limits of the study area. Sightings of long-finned pilot whales were exclusively on the shelf break, with the largest groups in the southwestern part of the study area.

By comparison, ship-based sightings suggested strong spatial segregation between common and bottlenose dolphins on the

Table 2. Summary of sightings made on aerial and ship-based surveys between 2001 and 2006.

Type of survey	Number	Species										
		Dsp	Tt	Dd	Gm	Zsp	Sc	Ha	Pp	La	Gg	Msp
Aerial	Sightings	166	72	71	56	9	7	5	3	2	1	1
	Animals	1 960	631	1 280	480	18	119	7	7	20	3	3
Ship-based	Sightings	11	68	57	37	0	9	0	2	0	5	0
	Animals	29	910	1 447	357	0	610	0	3	0	55	0

Dsp, Unidentified small delphinid; Tt, *Tursiops truncatus*; Dd, *Delphinus delphis*; Gm, *Globicephalas melas*; Zsp, *Ziphius* sp.; Sc, *Stenella coeruleoalba*; Ha, *Hyperoodon ampullatus*; Pp, *Phocoena phocoena*; La, *Lagenorhynchus acutus*; Gg, *Grampus griseus*; Msp, *Mesoplodon* sp.

shelf (Figure 2b): most common dolphins were found around the 50-m isobath, whereas bottlenose dolphins showed a more offshore distribution (between the 100- and the 200-m isobaths). Striped dolphins and long-finned pilot whales were sighted exclusively over the shelf break.

Spatial modelling

Individual relationships between dolphin relative abundance and broad-scale descriptors of the environment are summarized in Figure 3 (see Table 3 for the corresponding AIC and percentage of explained deviance). Globally, the dolphins (Figure 3a) were more abundant in the north and the south of the bay, away from the coast and estuaries, with an affinity for canyons and the shelf break area. In spring, the distribution of bottlenose dolphins reflects these properties (Figure 3c), but the distribution of common dolphins (Figure 3b) differed, in particular that they were more abundant closer to the coast and estuaries.

Using these broad-scale descriptors, three models with multiple predictors were built. The model-selection procedure is shown in Table 3. Model 1 describes the small delphinid distribution throughout the year, using aerial data. Models 2 and 3 focus on ship-based counts obtained in spring, model 2 describing common dolphin and model 3 bottlenose dolphin distributions, respectively. All models retained three covariates among the five tested. Model 1 retained distance to the nearest estuary, distance to the nearest canyon, and distance to the coast, and explained a fairly small proportion of data deviance (9.25%). Model 2 retained

distance to the coast, latitude, and distance to the nearest canyon, and explained 23.6% of data deviance. Model 3 retained distance to the slope, latitude, and distance to the nearest estuary, and explained 29.9% of data deviance.

Figure 4 presents the distribution maps resulting from model predictions, together with the results of the cross-validation procedure. Predictions from model 1 show that areas of high abundance of small delphinids are expected over the shelf break, mainly in two patches in the northern and southern parts of the bay. Predictions from models 2 and 3 clearly show spatial segregation between common and bottlenose dolphins in spring, common dolphins being mainly distributed in two coastal areas, located in the centre and the north of the bay, and bottlenose dolphins mainly associated with the central and southern shelf break. The cross-validation procedure highlighted differences in model predictive power, with the model based on aerial surveys offering satisfactory predictions ($r^2 = 0.375$, slope 0.70; Figure 4) along with the model predicting bottlenose dolphin distribution ($r^2 = 0.20$, slope 0.63; Figure 4). The model predicting common dolphin distribution performed less well ($r^2 = 0.07$, slope 0.36; Figure 4).

Abundance estimates

Glare-corrected absolute estimates of abundance calculated from ATLANCET survey data (August 2002) revealed that the continental shelf of the Bay of Biscay (ATLANCET area, 120 000 km^2) contained 66 000 small delphinids then (CV: 0.29;
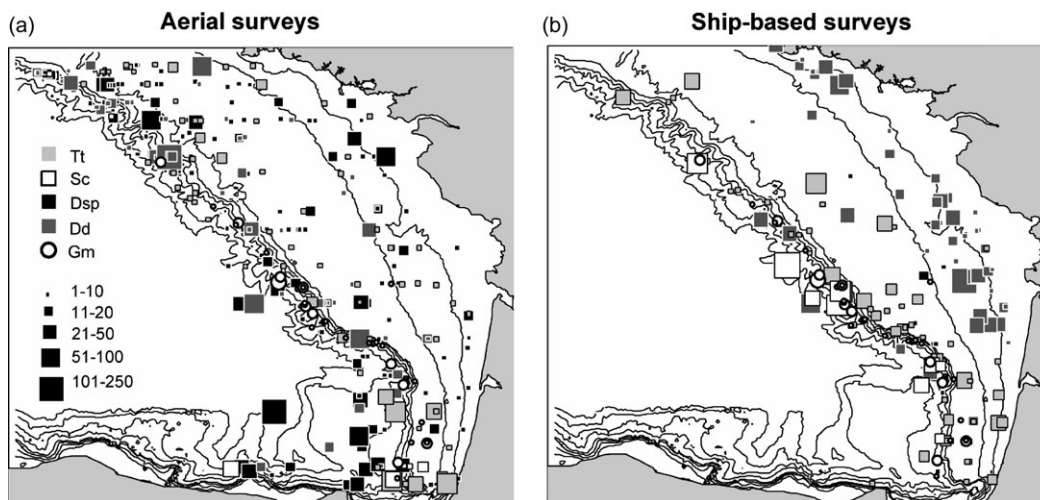

Figure 2. Spatial distribution of sightings of small delphinids (Dsp, unidentified small delphinid; Tt, *Tursiops truncatus*; Dd, *Delphinus delphis*; Sc, *Stenella coeruleoalba*) and pilot whales (Gm, *Globicephalas melas*) made during aerial and ship-based surveys.
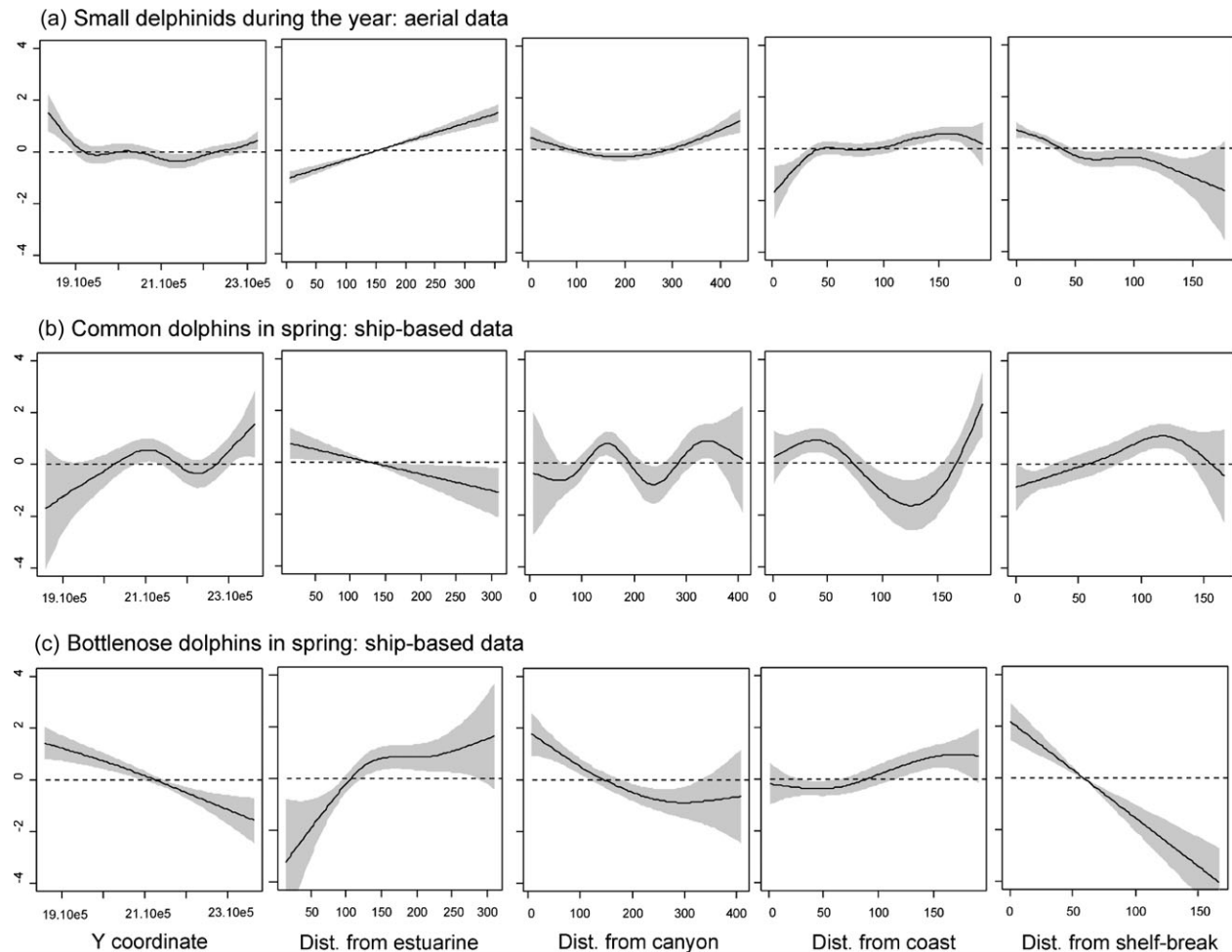
Figure 3. Coefficients of the GAMs for (a) small delphinids, (b) common dolphins, and (c) bottlenose dolphins against broad-scale descriptors of the environment. The black line indicates the value of the GAM coefficients, and grey shading the 95% CIs. The horizontal dotted line indicates a zero level.

95% CI 35 500–103 100). The corresponding glare-uncorrected estimate was 38 700 (CV: 0.26; 95% CI 20 700–61 600), confirming that glare can have a large influence on detection probability. Figure 5b shows the effect of a decrease in detection probability on absolute abundance, taking as starting point the glare-corrected estimate.

Temporal variability
Figure 5 shows the evolution of our index of relative abundance (and its associated variability) between months. Relative abundances were greatest in August (during the ATLANCET survey) and to a lesser extent in January/February. Relative abundance was lower in spring (late May to early June) and in autumn (October–December).

Discussion
Aerial vs. ship-based surveys
Ship-based and aerial surveys provided different patterns of species distribution across the shelf (Figure 4). However, the area covered by both platforms differed: during ship-based sampling, the shelf break was sampled up to the 1000-m isobath only in the middle of the bay. In contrast, aerial surveys always crossed the 1000-m isobath and detected important areas for

small delphinids around the northwestern and southwestern shelf breaks that were not detected by ship-based surveying owing to the poor sampling effort in these slope areas. Aerial surveys also suggested some common dolphins around the shelf break, whereas ship-based observations showed striped dolphins as the dominant shelf break species. Discriminating common and striped dolphins is difficult from the air, so interpretation of our results at a species level is difficult with aerial data. We are more confident, however, in the spatial segregation we found in spring between common and bottlenose dolphins. Abundance estimates were not calculated for our ship-based data, because our protocol could not take responsive movements into account (i.e. attraction/repulsion). Such availability biases can greatly overestimate abundance, especially with species such as common dolphins that are reported to be attracted to ships (Hammond et al., 2006). These response movements are negligible when the survey platform is an aircraft, for which speed far exceeds that of dolphins. The relatively poorer predictive power we found with ship-based surveys may be related to the differences in survey effort, 40 000 km with the aircraft vs. 16 000 km aboard ship. This issue highlights one indirect advantage of aerial over ship-based surveys: the ability to collect a large amount of data in less time and with reduced costs.

Table 3. Forward-selection procedure used to find the best set of predictors for each model.

Model	Predictors	AIC	Dev
1	y	1 883.632	2.16
	distest	1 829.348	5.24
	distcan	1 860.631	4.04
	distslope	1 846.47	4.47
	distcoast	1 866.683	3.3
	distest+y	1 823.186	5.8
	distest+distcan	1 805.018	8.16
	distest+distslope	1 824.407	6.06
	distest+distcoast	1 824.868	6.31
	distest+distcan+y	1 805.058	8.58
	distest+distcan+distslope	1 802.123	9.64
	distest+distcan+distcoast	**1 799.755**	**9.25**
	distest+distcan+distcoast+y	1 800.522	9.48
	distest+distcan+distcoast+distslope	1 801.799	9.24
2	y	406.9	6.03
	distest	413.11	1.99
	distcan	406.9	5.69
	distcoast	389.94	11.2
	distslope	397.3	9.39
	distcoast+y	375.12	18.5
	distcoast+distest	390.07	11.8
	distcoast+distcan	381.43	11.5
	distcoast+distslope	381.43	15.3
	distcoast+y+distest	375.31	21.4
	distcoast+y+distcan	**368.7**	**23.6**
	distcoast+y+distslope	375.63	18.8
	distcoast+y+distcan+distest	371.01	21.3
	distcoast+y+distcan+distslope	371.51	23.6
3	y	427.67	8.88
	distest	428.46	9.64
	distcan	427.57	9.41
	distcoast	442.87	5.27
	distslope	387.97	20.3
	distslope+y	386.63	21.3
	distslope+distest	389.03	21.6
	distslope+distcan	387.29	21.1
	distslope+distcoast	388.35	21.9
	distslope+y+distest	**379.21**	**29.9**
	distslope+y+distcan	388.25	21.4
	distslope+y+distcoast	384.55	24.2
	distslope+y+distest+distcan	385.99	22.8
	distslope+y+distest+distcoast	384.01	25.9

Model 1, small delphinids during the year (aerial data); Model 2, common dolphins in spring (ship-based data); Model 3, bottlenose dolphins in spring (ship-based data). AIC is the Akaike information criterion, and Dev indicates the percentage of deviance explained by each model. Abbreviations for predictors are: y, latitude; distest, distance from the nearest estuary; distcan, distance from the nearest canyon; distslope, distance from the shelf break; distcoast, distance from coast. The models emboldened were selected for prediction purposes.

To summarize, our combination of aerial and ship-based data allowed us to solve problems associated with the choice of a single methodology. Aerial surveys allowed repetition for different seasons and covered a larger area, so provided relative or absolute abundance, whereas ship-based data were well-suited to highlight species-specific habitat issues that do not appear in aerial data.

Spatial distribution of delphinids

In the Bay of Biscay, the shelf break appeared clearly, in aerial surveys, as the main habitat of the small delphinid community. More than 50% of the population concentrates around the 150-m isobath, in <20% of the study area, and species such as striped dolphins and long-finned pilot whales were sighted only over the shelf break. Bathymetry is known to influence dolphin distribution and has been used for modelling their habitat (Yen et al., 2004; Hastie et al., 2005). Indeed, shelf breaks and slopes are highly productive habitats that frequently support high densities of marine predators (Briggs et al., 1987; Schoenherr, 1991; Springer et al., 1996; Croll et al., 1998), and moreover constitute predictable oceanographic features involved in processes determining prey concentration (Joiris, 1991; Joiris et al., 1996; Hunt, 1997; Croll et al., 1998; Mehlum et al., 1998). Abrupt topographical features such as shelf breaks and canyons can concentrate zooplankton, which tend to aggregate by adopting counter-current swimming behaviour against up- or downwelling events (Genin, 2004; Shanks and Brink, 2005). Zooplankton aggregations, if sufficiently persistent, can attract organisms belonging to high trophic levels (Kaartvedt et al., 2005) and have been reported on the upper shelf break of the Bay of Biscay (Albaina and Irigoien, 2004), near the location of a stable, thermohaline front (Castaing et al., 1999). Young adult hake (Merluccius merluccius) are abundant along the slope of the northern bay in autumn and winter (Poulard, 2001), and the shelf edge is used by mackerel (Scomber scombrus) as a migratory pathway (in the Bay of Biscay, Uriarte and Lucio, 2001; also north of Scotland, Reid et al., 1997). The Bay of Biscay shelf break is also a key spawning area for sardine (Sardina pilchardus) and anchovy (Engraulis encrasicolus; Bellier et al., 2007). The pelagic community around the shelf break can also be dominated by blue whiting (Micromesistius poutassou; Gomes et al., 2001). All these species are typical prey of common and bottlenose dolphins in the neritic domain of the bay (Silva, 1999; Pusineri, 2006; Spitz et al., 2006).

Small delphinids were more abundant in the southern and northern parts of the bay around the shelf break in aerial surveys, and over the northern and central part of the shelf in ship-based surveys. The southwestern Bay of Biscay is influenced by a poleward current, an important mechanism allowing offshore fertilization (Gil, 2003; Sanchez and Gil, 2004) and a determinant of hake recruitment (Sanchez and Gil, 2000). In addition, the Cap Ferret and Cap Breton canyons are located in the area: the Cap Ferret canyon is involved in the formation of seasonal eddies (Durrieu de Madron et al., 1999). The heterogeneous topography is therefore likely to provide suitable habitat for small delphinids. The northern part of the shelf could be an important transition area for small delphinids moving between the Bay of Biscay and the Celtic Sea or the English Channel (which hosts some 25 000 common dolphins; Hammond et al., 2006), which is connected oceanographically to the Celtic Sea (Planque et al., 2004). In the area of the northwestern shelf break of the bay, satellite imagery shows colouration characteristic of deep blooms (Gohin et al., 2003), which is induced by cold water that comes to the surface
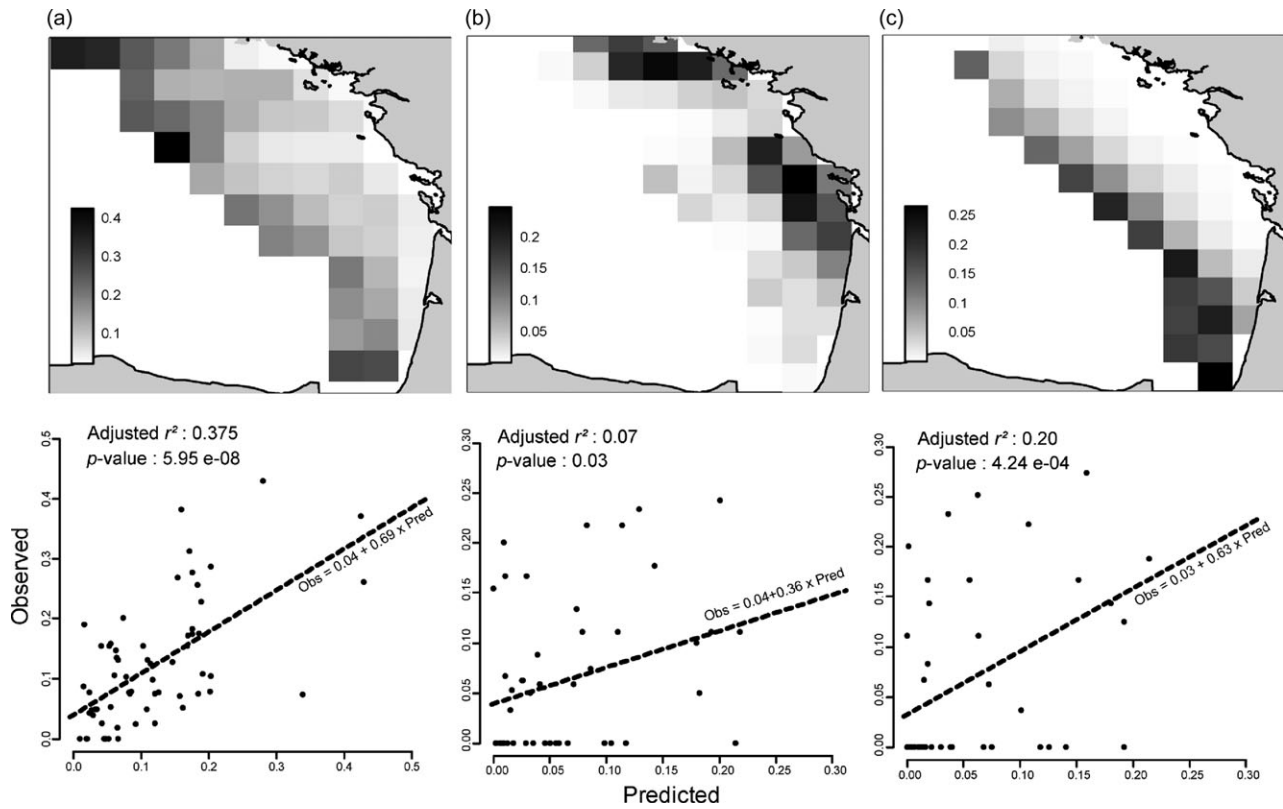
Figure 4. Index of the spatial distribution of dolphins (number of sightings per 20 km bin) for (a) small delphinids throughout the year (aerial data), (b) common dolphins in spring (ship-based data), and (c) bottlenose dolphins in spring (ship-based data). The maps represent predictions from the GAMs, and beneath them are the results of the cross-validation procedure (see text) that tests the predictive power of each model. The linear regression model between observed and predicted dolphin occurrence is reported, along with the regression parameters, r^2, and the significance level.
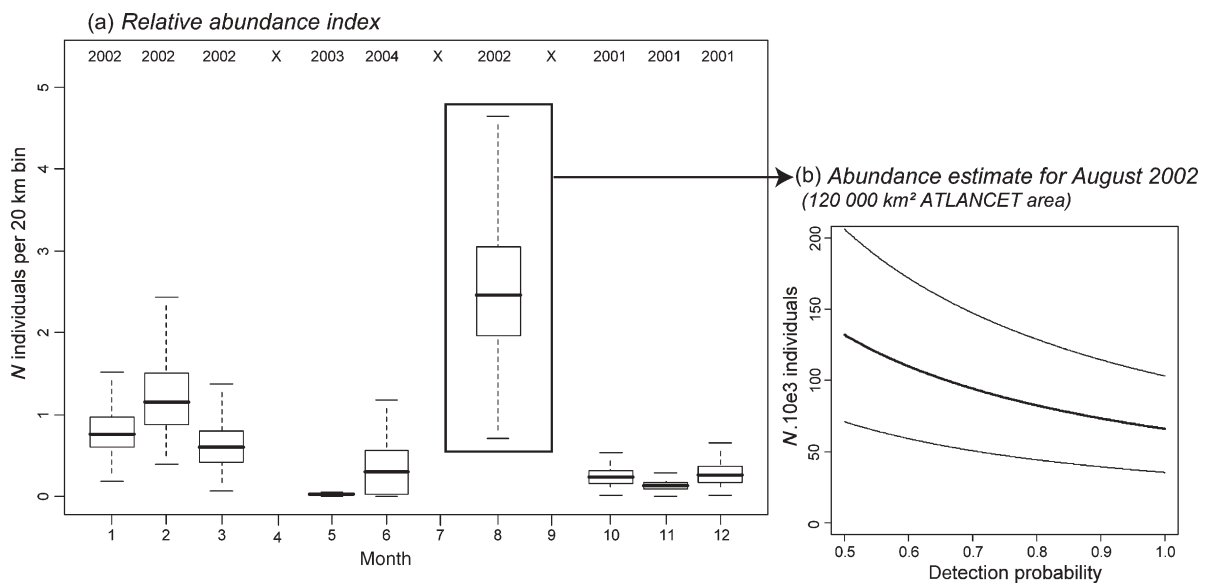
Figure 5. Monthly estimates of relative abundance of small delphinids in the Bay of Biscay. Each boxplot corresponds to the 95% CIs of the estimate, obtained by block bootstrap. Years of sampling are indicated at the top of the boxes. For August 2002, for which absolute abundance was also calculated, there is also a sensitivity analysis of the effect of a decrease of detection probability on the absolute estimate.

under the action of internal waves breaking on the slope (Gerkema et al., 2004).

In spring, the ship-based surveys revealed clear spatial segregation between common and bottlenose dolphins. In the Bay of Biscay, the two species rely on different prey: common dolphins mainly target small pelagic fish (sardine, sprat, anchovy, and mackerel; Pusineri, 2006), whereas bottlenose dolphins feed on larger demersal species, especially hake (Spitz et al., 2006). We hypothesize that the spatial segregation we found reflects this trophic segregation through preferred prey distributions.

Abundance estimates

The significance of our abundance estimates has to be assessed, and particularly its robustness to potential bias. The homogeneity of detection probability across the strip is a reasonable assumption for marine mammals (Pollock et al., 2006). However, our absolute abundance estimate has been calculated under the assumption that the detection probability equalled 1. This assumption cannot be tested here because we do not collect aerial data from two independent platforms. Therefore, our abundance estimate must be considered as a low one. Because we cannot calculate precisely the detection probability we carried out a sensitivity analysis to show how much the abundance estimate would increase as detection probability decreases (Figure 5b).

Recent results provided in July 2005 by SCANS II surveys (Hammond et al., 2006) give abundance estimates for common and bottlenose dolphins over a much wider area than the Bay of Biscay (virtually all European waters from the Shetland Islands to Gibraltar, i.e. 1 000 000 km^2). However, most bottlenose and common dolphins are found at the southern end of the SCANS II study area, in the Bay of Biscay and adjacent waters (Celtic Sea, English Channel, and over the Spanish continental shelf). Abundance calculated for bottlenose and common dolphins within European waters was 12 600 (CV 0.27) and 63 400 (CV 0.46) for bottlenose and common dolphins, respectively. These numbers are in accord with our ATLANCET estimate for the small delphinid community of the Bay and Biscay (66 000, CV 0.29), although SCANS II estimates cover a much wider area. Even if we considered the uncertainty and potential biases associated with both surveys, this suggests that a large part of the small delphinid community concentrates in the Bay of Biscay, at the season when our summer survey was carried out. The distributions of small delphinids around Europe can vary, however, leading to local variations in abundance when focusing on a specific area such as the Bay of Biscay, as we observed during winter 2001/2002 (Figure 5a).

These changes in distribution have to be characterized and quantified in future, to take efficient management measures. When and where do fisheries and cetaceans interact? Such a question requires modelling the movements of cetacean populations between seasons and years. It is costly to monitor European waters thoroughly every year. Instead, specific and smaller areas relevant to a particular cetacean community (such as the Bay of Biscay for common and bottlenose dolphins) could be monitored each year to provide, at several places within the European waters, temporal trends at medium and large spatial scales.

Conclusions

For the Bay of Biscay, areas of primary interest for dolphins were identified as the shelf break, canyon areas, and river plumes. These areas are also largely targeted by fisheries, mainly hake, sea bass, anchovy, and tuna fisheries (Morizur et al., 1999). We also detected extensive spatial segregation between common and bottlenose dolphins that we attributed to the spatial distribution of their preferred prey. Future prey/predator analysis could test this hypothesis. We obtained a minimum abundance estimate for a particular date (August 2002). A further step forward for cetacean management in European waters would be to study, understand, and model this seasonal and annual variability, to know precisely when and where specific management measures (such as bycatch mitigation or reduction in fishing effort) would be required and effective.

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