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Distribution, encounter rates, and habitat characteristics of toothed cetaceans in the Bay of Biscay and adjacent waters from platform-of-opportunity data

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Abstract:

Data on the distribution and habitat utilization of oceanic marine mammals are difficult to collect and yet such information is beneficial for many conservation and management purposes. Data collected during ferry-based cetacean surveys in the English Channel and Bay of Biscay between 1998 and 2002 were analysed to investigate the distribution, encounter rate, and habitat characteristics of toothed cetaceans there. In all, 17 873 nautical miles were surveyed, and 1008 encounters of 13 identified species, including delphinids, ziphiids, harbour porpoise, and sperm whale, were recorded. The common dolphin was the commonest species, followed in decreasing occurrence by striped and bottlenose dolphins, pilot whale, harbour porpoise, Cuvier's beaked whale, and sperm whales. The distribution of harbour porpoises was restricted to the shallow waters of the western English Channel. Common and bottlenose dolphins were distributed mainly over the continental shelf, although there were some encounters along the shelf edge and in the open ocean. Striped dolphins and pilot whales were sighted in oceanic waters in the central and southern Bay of Biscay. Cuvier's beaked whales and sperm whales were recorded in the deep oceanic waters of the southern Bay of Biscay. Bathymetry clearly plays a significant role in the distribution and habitat partitioning of toothed cetaceans in the region.

Keywords: bathymetric preference, Bay of Biscay, distribution, encounter rate, English Channel, habitat characteristics, platforms of opportunity, toothed cetaceans

1. Introduction

Distribution and abundance data on cetaceans, particularly those occurring predominantly offshore, are generally difficult to collect. The cost of dedicated surveys using chartered research vessels often prohibits regular surveys. For this reason, vessels of opportunity can be used for opportunistic cetacean surveys. The cetaceans of the temperate waters of western Europe (Bay of Biscay and English Channel) have been the focus of opportunistic ferry surveys since the mid-1990s. These routes were targeted because 1) they allow surveying of shelf (mostly the western English Channel), slope (northern and southern Bay of Biscay) and deep oceanic waters representing a range of cetacean habitat and 2) there is a lack of data on the status of cetaceans in this area where considerable interactions occur, especially with pelagic fisheries (Tregenza *et al.*, 1997; Tregenza & Collet, 1998).

Western European waters constitute diverse water masses and topographical environments. The English Channel and Bay of Biscay exemplify this heterogeneity. The relatively shallow English Channel, situated between the northern coast of France and the south coast of the UK, is characterised by turbid, well-mixed waters and many local hydrological fronts (Southward *et al.*, 2005). The Bay of Biscay, situated between the southern coast of Brittany, the west coast of France and the northern Spanish coast, is more diverse in terms of topography and hydrology including shelf (especially in the north), shelf edge and oceanic habitats. A wide complex of submarine canyons distinguishes the southern part of the Bay (Quéro *et al.*, 1989). The area is also characterised by the presence of many hydrological fronts and localised upwellings due to the convergence of various water masses and the steepness of the topography in some sectors (Brylinski, 1997; P. Lazure, *pers. comm.*¹). The variety of habitats supports many of the toothed cetacean species occurring in the wider northeast Atlantic (Reid *et al.*, 2003).

Offshore populations of toothed cetaceans have been poorly studied in this area compared with coastal populations of bottlenose dolphins (*Tursiops truncatus*) in the English Channel (see for example Williams *et al.*, 1996; Lahaye & Mauger, 2000). A few investigations have also been conducted on long-finned pilot whales (*Globicephala melas*) in the coastal waters of the central Bay of Biscay and English Channel (CRMM, unpublished data; Kiszka *et al.*, 2004). Duguay (1983) generated one of the first descriptions of cetacean diversity and distribution in the Bay of Biscay, using, in particular, stranding records along the French coast. Additionally, there have been several opportunistic cetacean surveys of distribution and relative abundance of cetaceans in the English Channel and Bay of Biscay (Evans, 1980; Northridge *et al.*, 1995; Williams *et al.*, 2002; Kiszka *et al.*, 2004).

Quantitative studies using dedicated surveys to estimate cetacean abundance have also been conducted in the area. Summer abundance estimates of 62,000 [CI 95% (35,000-108,000)] common dolphins (*Delphinus delphis*) and 73,843 striped dolphins (*Stenella coeruleoalba*) [CI 95% (36,113-150,990)] were estimated in the Bay of Biscay and adjacent waters (Goujon, 1996). Buckland *et al.* (1993) estimated long-finned pilot whale (*Globicephala melas*) abundance as 12,335 individuals [CI 95% (3,924-38,148)] for a survey block in the oceanic Bay of Biscay and its adjacent waters during the North Atlantic Sighting Survey (NASS) that took place in summer 1989. The surveys of the Small Cetacean Abundance in the North Sea and adjacent waters (SCANS) project conducted during July 1994, did not record any cetaceans in the English Channel; common dolphin and harbour porpoise (*Phocoena phocoena*) abundance in the Celtic Sea was estimated as 75,000 individuals [CI 95% (22,900-248,900)] and 36,280 (CI 95%) individuals, respectively (Hammond *et al.*, 2002). Preliminary studies suggest that harbour porpoises, common and bottlenose dolphins are the most frequently encountered species in the English Channel and occur year-round. In the Bay of Biscay, the common dolphin seems to be the most abundant species, followed by striped, bottlenose dolphins and long-finned pilot whales (Goujon, 1996). Other odontocete species, such as the pygmy killer whale (*Feresa attenuata*), the false killer whale (*Pseudorca crassidens*), the melon-headed whale (*Peponocephala electra*) and the killer whale (*Orcinus orca*) (Williams *et al.*, 2002; CRMM, unpublished data) are rarely seen in the Bay of Biscay. The distribution and encounter rates of toothed cetaceans has not been described in detail in this area and their habitat preferences in terms of physiographical variables such as depth have never been investigated. The distribution of cetaceans is driven by many factors, but the primary influence is probably the aggregation of prey species (Hui, 1979; Forcada *et al.*, 1990; Baumgartner, 1997; Davis *et al.*, 1998, 2002; Hooker *et al.*, 1999; Macleod *et al.*, 2004). These authors also suggested the habitat of several cetacean species could be defined on the basis of physiography, i.e. depth and slope. The objective of this study is to provide an assessment of the distribution, encounter rates and habitat characteristics (related to bathymetric preferences) of toothed cetaceans using data collected onboard ferries operating through the English Channel and Bay of Biscay.

¹ Pascal LAZURE, Ifremer Brest, personal communication, Brest, April 2003.

2. Materials and methods

2.1. Survey method

Two ferry-lines operating between the southern coast of the UK and northern Spain (*The Pride of Bilbao*: Portsmouth-Bilbao and *Val de Loire*: Plymouth-Santander) were used as platforms of opportunity to conduct cetacean surveys. Both ships follow a relatively fixed route through the English Channel and Bay of Biscay and travelled at a speed of approximately 20 knots.

A survey is defined as a return ferry journey between the homeport and destination. Data were collected from July 1998 to September 2002, mainly during the summer months. The observation effort was significantly higher on the *Pride of Bilbao* than on the *Val de Loire* (see Table 1). At least two or more experienced observers carried out surveys, primarily on the “monkey island” (37m above sea level). Observers searched 180° ahead of the ship from the port and the starboard sides and forward of the bow. Surveys involved continuous scanning with the naked eye combined with occasional scans with 7 X 50 binoculars. Environmental data and survey effort were recorded at the start and end of each survey leg and at half hourly intervals or when sighting conditions changed. The environmental variables recorded were wind speed and direction, Beaufort sea state, cloud cover and precipitation. Only sighting data collected in good weather conditions (B<3) were included in the analysis as cetacean detectability tends to be biased downward in poorer survey conditions. Survey effort was quantified by recording the ship's position using a handheld Global Positioning System (GPS) *Garmin XII*. Additionally, for each sighting, observers recorded species and the certainty of their identification, GPS position of the ship at the time of sighting, group size and behaviour. Only definite identifications were considered in this study. Group sizes used to provide mean, SD and range values were best estimates recorded at sea. Considering the low amount of time spent with encountered groups at sea, it is possible that group sizes seen may not be the same as actual group sizes. Groups were defined as individuals having the same activity and being in close proximity to each other (less than 5 bodies). Differences group sizes between sub-regions were tested for using a non-parametric Kruskal- Wallis test. All data were collected on pre-prepared data sheets and were logged in an Excel database after the surveys.

2.2. Analysis: spatial distribution and encounter rates

To investigate the spatial distribution, encounter rates and habitat characteristics of odontocetes, maps of encounter rates per cell for the commonest species (≥ 40 encounters) were generated using *ArcView* 8.2. Encounter rates were calculated for each cells (20 nautical miles square) throughout the study area using the Spatial Analyst extension of *ArcGIS* 8.2. Encounter rate, was defined as:

$$\frac{n}{L} \times 100$$

where n is the number of encounters and L is the total distance travelled (i.e. survey effort) in nautical miles (nm). Global values of encounter rates were calculated for the whole study area. In addition, in order to provide regional differences of encounter rates, three sub-regions were defined:

- i) Shelf waters of the Western English Channel and Western Approaches (north of 47°30'N);
- ii) shelf, shelf edge, and deep oceanic waters of the northern Bay of Biscay (47°30'-45°30'N);
- iii) deep oceanic waters and submarine canyons (Santander and Torrelavega) of the southern Bay of Biscay (45°30'-43°30'N).

2.3. Habitat characteristics: bathymetric preferences

Values of the median, minimum and inter-quartile ranges of depth are provided to describe bathymetric preferences for each species. Depth is considered one of the primary habitat features explaining cetacean distribution (see for example Cañadas *et al.*, 2002). Depth data were provided by SHOM (*Service Hydrographique et Océanographique de la Marine*), and were included in the GIS procedure to obtain depth data for each cetacean sighting.

3. Results

Between 1998 and 2002, 147 surveys were completed through the English Channel and Bay of Biscay (Figure 1), totalling 17,873 nautical miles of survey effort. Most survey effort was conducted on the *Pride of Bilbao* (N=17,075 nm made on the *Pride of Bilbao* vs. 798 on the *Val de Loire*). The amount of survey effort varied between sub-regions; 15.9% of effort was in the western English Channel and western approaches, 54.6% in the northern Bay, and 29.5% in the southern Bay (Figure 1). There was also variability in survey effort between seasons and years (Figure 2). Effort increased significantly between 1998 and 2002 ($r=0.84$, $p<0.001$), and was concentrated between July and September (Figure 2).

1,008 odontocete encounters were recorded during the surveys which amounted to 20,481 individuals. We rejected all unidentified cetaceans in the analysis and considered only single species groups (Table 2). Small delphinids were the most frequently encountered (common and striped dolphins), followed by the bottlenose dolphin, the long-finned pilot whale and the harbour porpoise. Three large delphinids, the Risso's dolphin, the killer whale and the false killer whale were rare. The largest toothed whale species encountered were the sperm whale and four beaked whale species of which Cuvier's beaked whale was the commonest.

3.1. Distribution, encounter rates and bathymetric preferences

The spatial distribution of sightings is very heterogeneous between different species. Group size of these species also varied significantly. Delphinids were characterised by higher group size whereas the larger species were observed in small groups. Toothed cetaceans were encountered throughout the study area, with higher concentrations of sightings in the Bay of Biscay (Figure 3).

3.1.1. Harbour porpoise

The harbour porpoise was encountered on 114 occasions, with a total number of 313 individuals. Encounter rate throughout the area was 0.49/100nm. Of the 3 sub-areas, encounter rates peaked in the western English Channel and Western Approaches (Figure 4) and was lowest in the northern Bay of Biscay, where only one sighting was recorded (Figure 7). No sightings were made in the southern Bay of Biscay. The higher encounter rates were observed off the northern Brittany coast. Group size was generally small ($\bar{y}=2.75$; $SD=1.8$), although group size ranged from 1-10 individuals. Harbour porpoises showed a clear preference for shallow waters of the western English Channel and approaches (median=108; $Q1=96.5$; $Q3=125.2$; min=78; max=3,941). One sighting in the deep oceanic waters of the Bay of Biscay increases significantly the standard deviation value.

3.1.2. Common dolphin

The common dolphin was the most commonly sighted species, accounting for more than 50% of individuals sighted ($n = 329$ sightings; 11,297 individuals), with an average encounter rate of 1.84/100nm. Overall, regional encounter rate decreased from 2.46/100nm, 2/100nm and 0.95/100nm for the western Channel, northern Bay and southern Bay of Biscay, respectively (Figures 4, 5 & 6). Group size was highly variable ($\bar{y}=38.1$; $SD=73.5$) ranging from 1 to 600 individuals. There was significant variation between group size according to each sub-area, especially between the western Channel and the northern Bay of Biscay (Kruskal-Wallis; $H=4.38$; $p=0.036$), as well as between the northern and the southern Bay (Kruskal-Wallis; $H=3.975$; $p=0.04$). The largest aggregations were observed in the northern Bay of Biscay. Common dolphins were sighted both in shelf, slope and deep oceanic waters, with a preference for slope areas of the northern Bay of Biscay (median=874 ; $Q1=137$; $Q3=2,187$; min=67; max=4,385).

3.1.3. Striped dolphin

The striped dolphin was the second commonest species recorded with 187 sightings and 6,103 individuals. Over the entire survey region, the encounter rate of the striped dolphin was 1.05/100nm and increased from 0.03 - 2.18/100nm from the western Channel to the southern Bay of Biscay (Figures 4, 5 & 6). The highest encounter rates were observed in the central part of the bay. Group size varied from 1-250 individuals, with a mean of 32.7 ($SD=34.6$). The striped dolphin was distributed predominately in the Bay of Biscay (Figure 9) particularly the south and was encountered only once in the central English Channel. They were most common in deep oceanic waters of the Bay of Biscay (median=3,552; $Q1=2,633$; $Q3=3,975$; min=136; max=4,421).

3.1.4. Bottlenose dolphin

There were 110 sightings of bottlenose dolphins amounting to 1,556 individuals. Throughout the survey area, the encounter rate of the bottlenose dolphin was 0.62/100nm. Encounter rates decreased from 0.87/100nm, 0.66/100nm and 0.31/100nm from the western Channel to the southern Bay of Biscay (Figures 4, 5, 6 & 10). Mean group size was 14 (SD=11.9) and was not significantly different between the southern and northern Bay of Biscay (Kruskal-Wallis; $H=1.70$; $p=0.43$). Bottlenose dolphins showed a clear preference for shelf and slope waters of the northern Bay of Biscay (median=158; Q1=129; Q3=984; min=60; max=3,920).

3.1.5. Pilot whale

895 individual pilot whales (probably mostly *G. melas*) were recorded during 134 encounters. Occurrence was 0.09/100nm, 0.89/100nm and 0.92/100nm, in the western Channel, the northern Bay and the southern Bay of Biscay, respectively, and 0.75/100 nm overall (Figure 11). Group size was relatively small ($\hat{y}=6.8$; SD=5.1) with a maximum of 30 and did not vary between the sub-regions (Kruskal-Wallis; $H=0.01$; $p=0.94$). The species is widely distributed in the central and southern Bay of Biscay, with only two sightings in the western approaches of the English Channel. Pilot whales showed a clear preference for deep oceanic waters, despite sightings made on the continental shelf (median=2,726; Q1=1,088; Q3=3,641; min=103; max=4,237).

3.1.6. Sperm whale

The sperm whale was regularly sighted throughout the study area, with 42 encounters comprising 68 individuals. Group size ranged from 1-4 ($\hat{y}=1.6$; SD=0.9). Encounter rates throughout the survey area was 0.23/100 nm and higher in the southern Bay of Biscay (0.8/100nm), especially in the area of the Santander canyon, compared to the northern Bay (0.09/100 nm) (Figure 12). No sightings were made in the English Channel. Sperm whales showed a significant preference for deep oceanic waters (median=3,168; Q1=2,748; Q3=3,852; min=1,185; max=4,195).

Cuvier's beaked whale

The Cuvier's beaked whale showed similar patterns of distribution as for the sperm whale and an overall occurrence of 0.34/100 nm. Group size was larger and more variable than for the sperm whale ($\hat{y}=2.4$; SD=1.1). The Cuvier's beaked whale encounter rate was 0.09/100 nm in the northern Bay compared to 1.2/100nm in the southern Bay (Figures 5, 6 & 13). Sighting rates were particularly high in the area of the Santander canyon. Cuvier's beaked whales were observed in deep oceanic waters (median=3,238; Q1=2,771; Q3=3,770; min=685; max=4,259).

3.1.7. Less frequently seen species

The Risso's dolphin was rarely seen in the study area, with only 14 confirmed sightings of 58 individuals (0.08/100 nm). Group sizes were small ($\hat{y}=4$, SD=2.8). This species was more commonly sighted in the central and southern Bay of Biscay, but a few were recorded in the western English Channel. Risso's dolphin's sightings occurred primarily in deep oceanic waters, but three sightings were also made in the shelf waters of the western English Channel (median=2,392; Q1=431; Q3=2,844; min=81; max=3,852). Nine sightings of northern bottlenose whales were made in the deep oceanic waters of the southern Bay of Biscay (median=3,349; Q1=1,756; Q3=3,735; min=972; max=4,470) where the occurrence was 0.05/100 nm. Mean group size was 2.8.

In addition to the pilot whales, two other species of "black fish" were recorded: killer and false killer whales. The killer whale was sighted on five occasions in the central and southern Bay, with group sizes ranging from one to five individuals (SD=1.6). Two groups of false killer whales were sighted in the same area, with six and seven individuals in each group. Both killer and false killer whale sightings occurred in deep oceanic waters (>2,000m).

Two other beaked whale species were encountered on single occasions in the southern Bay of Biscay: True's beaked whale (*Mesoplodon mirus*) and Sowerby's beaked whale (*Mesoplodon bidens*). Two unidentified mesoplodon whale groups were encountered in July 1999, involving two and five individuals. Both sightings occurred in deep oceanic waters (>2,000m).

4. Discussion

Few studies have been conducted to assess the distribution, occurrence and habitat characteristics of cetaceans in the Bay of Biscay and English Channel. Platforms of opportunity, such as ferries, are a valuable means of monitoring cetaceans and can be used on a long-term basis. In this study, they enabled access to little known offshore areas for a very low cost. However, the use of platforms of opportunity often incurs limitations and biases in spatial and temporal coverage. Nevertheless, the ferry routes used in this study enabled surveying to be completed through several habitat types (shelf, shelf edge, and oceanic ecosystems) and record data to investigate how toothed cetaceans distribute in relation to different habitats, particularly of differing depth. The maps on encounter rates presented help to provide an accurate picture of the spatial distribution of the different species, with the use of effort-related data, in relation to the main habitat types.

The study area is highly heterogeneous, with the presence of both shelf, slope and oceanic waters. As a result, the diversity of toothed cetaceans is characterised by the presence of both typically shelf species, such as the harbour porpoise, as well as oceanic species such as beaked and sperm whales. Delphinids, especially common, striped, bottlenose dolphins and pilot whales are particularly common in the Bay of Biscay. In the western English Channel, the bottlenose dolphin, the common dolphin and the harbour porpoise are the most frequently encountered species (Evans, 1980; Kiszka *et al.*, 2004). The greater toothed cetacean species diversity in the Bay of Biscay may be attributable to its diverse range of habitats for these predators. The depth and seabed topography of the English Channel is comparatively uniform, while the Bay of Biscay comprises shelf, shelf edge and deep oceanic waters. The Bay of Biscay is also an area where cold and warm temperate waters mix. The odontocetes of Biscay are typified by cold temperate water species, such as the harbour porpoise, the northern bottlenose whale and the long-finned pilot whale as well as warm temperate water species such as the striped dolphin and the Cuvier's beaked whale. The other species such as the bottlenose dolphin, common dolphin, Risso's dolphin and the sperm whale are wide-ranging. They can occur both in cold, warm temperate and tropical waters (Rice, 1998).

4.1. Distribution and habitat characteristics

Water depth and the topography of the seabed can effect mixing within the water column and influence primary productivity of an area (St. John & Pond, 1992). Consequently, these physiographic features also drive the distribution of higher trophic levels, including intermediate predators and top predators like cetaceans (Hui, 1979; Davis *et al.*, 1998, 2002; Cañadas *et al.*, 2002; Macleod *et al.*, 2004). The analysis of bathymetric preferences of toothed cetaceans in the Bay of Biscay and adjacent waters showed some major trends.

The harbour porpoise is a typical shelf water species, restricted to the shallow waters of the western English Channel and the northern Bay of Biscay. No sightings were made in the southern Bay, even over the shelf waters, which suggest the absence or low densities of the species in this area. The harbour porpoise is generally considered as a coastal species occurring in shallow waters (Rice, 1998). Sightings of harbour porpoises beyond the continental shelf edge have also been recorded west of the UK (Bloor *et al.*, 1996; Macleod *et al.*, 2003). In the western English Channel and Bay of Biscay, the harbour porpoise has been observed essentially over and beyond the continental shelf in water depths less than 200m.

The distribution of the common dolphin is very broad in west European waters (Reid *et al.*, 2003). Our study reveals it occurs from the English Channel to the southern Bay of Biscay, with higher encounter rates in the western approaches of the Channel and the northern Bay of Biscay, a trend also described by other authors (Brereton *et al.*, 1999). Hui (1979) noted that common dolphin distribution was linked to regions of high topographic relief. In our dataset, we observe a substantial presence of common dolphins in the shelf edge area. The preference of common dolphins for the continental shelf edge may be related to the concentration of its main prey species in this area, especially of *Sardina pilchardus* and *Trachurus trachurus* (Meynier, 2004).

The striped dolphin is considered an oceanic species, occurring primarily off the continental shelf-edge (Perrin *et al.*, 1994). Forcada *et al.* (1990) found that the striped dolphin would occur in waters deeper than 1,000m depth. In the Bay of Biscay, the bulk of striped dolphin sightings were made beyond the 2,000m isobath, over the abyssal plain area. In the Bay of Biscay, the striped dolphin and the common dolphin exploit different habitats, which contrasts with the situation found in the eastern tropical Pacific where these two species occur in the same habitat (Reilly, 1990). The pattern of distribution in relation to depth for common and striped dolphin in the study area is similar to that found in the Alboran Sea, in the western Mediterranean (Cañadas *et al.*, 2002).

The bottlenose dolphin was a commonly sighted species in the offshore waters of the Bay of Biscay and western English Channel, both over the continental shelf, the continental slope and in oceanic waters.

The coastal and resident populations of bottlenose dolphins around the English Channel have been well documented whilst the populations found further offshore have not been studied. In the Northeast Atlantic, offshore bottlenose dolphins are thought to associate with the continental slope (Skov *et al.*, 1995). In the western Mediterranean, bottlenose dolphins occur essentially over the shelf edge, where the slope is accentuated (Cañadas *et al.*, 2002). In our study, we did not observe significant bathymetric preferences in bottlenose dolphins. The distribution of the bottlenose dolphin may be better predicted by other environmental variables. The wide distribution of this species could be the result of the opportunistic feeding behaviour of the species in the northeast Atlantic, and the wide variety of prey it can feed on (Klinowska, 1991; Spitz *et al.*, 2006).

Pilot whales were commonly recorded in small groups, especially in the deep waters of the Bay of Biscay, with few incursions in the English Channel. The sighted species is probably the long-finned pilot whale, as the tropical form *G. macrorhynchus* is rarely seen in the Bay of Biscay. This information is based on stranding records from the Atlantic coast of France (CRMM, unpublished data). This species is considered primarily as oceanic and frequently associated with the continental slope (Abend & Smith, 1999; Payne & Heinemann, 1993; Davis *et al.*, 1998; Bernard & Reilly, 1999; Cañadas & Sagarminaga, 2000). However, the species can occur, at least for short periods, in shallow coastal waters. This phenomenon has been described for the French coast of the English Channel and may be related to feeding or reproduction (Kiszka *et al.*, 2004). Our results suggest that this species is essentially oceanic in the area (essentially occurring beyond the 2,000m isobath), despite some incursions over the continental shelf. In the northeast Atlantic, pilot whale sightings have been mainly reported beyond the 1,000m isobath (Lewis *et al.*, 1998; Stone, 1998).

The sperm whale is a deep oceanic cetacean species (Whitehead, 2003) and occasionally occurs over the shelf edge. Males will incur onto the continental shelf, albeit rarely, and is attributed to their opportunistic feeding ecology (Whitehead *et al.*, 1992; Best, 1999; Gregr *et al.*, 2000). In the Bay of Biscay, sperm whales occur in deep waters, with no sightings over the continental shelf and few on the upper shelf edge. Highest encounter rates were concentrated in the southern Bay of Biscay, over the Santander canyon. This pattern of distribution is in accordance with previous studies on the species elsewhere (see for review Whitehead, 2003).

Four beaked whale species were recorded in this study: Cuvier's beaked whale, northern bottlenose whale, Sowerby's beaked whale and True's beaked whale. The presence of these beaked whale species has been previously reported in the area by several authors (Heyning, 1999; Walker *et al.*, 2004; Weir *et al.*, 2004). Cuvier's beaked whale was the most frequently encountered species. The species showed the highest encounter rate in the deep oceanic waters of the Santander canyon. It has been previously shown that submarine canyons are critical habitats for other species in cold temperate waters, such as the northern bottlenose whale in the Gully, north-western Atlantic (Hooker *et al.*, 1999, 2002). The northern bottlenose whale is distributed in subarctic waters of the North Atlantic, from Davis Strait, Jan Mayen, the west coast of Spitsbergen, and Bjørnøya, south to Nova Scotia and the western side of the British Isles (Rice, 1998). The presence of this species seems to be irregular in the Bay of Biscay, and could be linked to lower sea surface temperature.

The other species recorded during the study are rare. The Risso's dolphin is regularly sighted in the shelf temperate waters of northwest Europe (Reid *et al.*, 2003), but was relatively rare in the western Channel and in the Bay of Biscay. However, the species tend to occur seasonally in the shallow coastal waters of the western French Channel coasts (Kiszka *et al.*, 2004). Sightings are occasionally recorded in the English Channel and in the Bay of Biscay, and the species occurs both in shelf and oceanic waters. In other regions, such as the Gulf of Mexico, Risso's dolphin has a strong preference for the continental slope (Baumgartner, 1997). The species may be more ubiquitous in west European waters (Reid *et al.*, 2003).

The other rare species recorded are the killer whale and the false killer whale. The killer whale has a worldwide distribution, from tropical to polar pack-ice zones of all oceans, but greatest abundance is in coastal waters and cooler regions where productivity is high (Rice, 1998). The false killer whale has a worldwide distribution in tropical and temperate waters. This species is vagrant to these waters as its main distribution is in subtropical waters (Rice, 1998).

4.2. Limitations

This study described the main features of distribution and habitat characteristics for several toothed cetacean species. Data were limited for some species and meant that a relationship between species distribution and depth was not evident for some species. Data collected using platforms of opportunity are a cost-effective means of collecting monitoring data to assess relative abundance and habitat preferences. However, the spatial coverage throughout the area and survey effort in the different habitat types is strictly limited and heterogeneous. Therefore, the interpretation of habitat preferences of species cannot be inferred beyond the extent of the relatively fixed ferry route. The ferry also departs and returns

on its crossing at relatively fixed times throughout the year which further restricts and defines periods available for observations. In addition, the survey track runs approximately parallel to the central Biscay continental shelf that introduces bias in to our sampling effort. Effort should be made to extend survey coverage either through alternative opportunistic platforms or on a dedicated vessel. However, the results presented do suggest that valuable information can be collated from opportunistic platforms and offer an insight into the bathymetric preferences of cetaceans in the western Channel and Bay of Biscay.

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6. References

- Abend, A.G. & Smith, T.D. 1999. Review of distribution of the Long-finned pilot whale (*Globicephala melas*) in the North Atlantic and Mediterranean. NOAA Technical Memorandum NMFS-NE-117, 22 p.
- Baumgartner, M. F., 1997. The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. *Marine Mammal Science*, 13: 614-638.
- Bernard, H. J., and Reilly, S. B. 1999. Pilot whales *Globicephala* Lesson, 1828. In : S. H. Rigway & Sir R. Harrison (Eds). *Handbook of Marine Mammals. Volume 6. The second book of Dolphins and the porpoises*, 245-279.
- Best, P.B. 1999. Food and feeding of sperm whales *Physeter macrocephalus* off the west coast of South Africa. *South African Journal of Marine Science*, 21: 393-413.
- Bloor, P.D., Reid, J.B., Webb, A., Begg, G., and Tasker, M.L. 1996. The distribution of seabirds and cetaceans between the Shetland and Faeroe islands. Rep. 224, Joint Nature Conservation Committee, Aberdeen, Scotland, 138 p.
- Brereton, T.M., Williams, A. D., and Williams, R. 1999. Distribution and relative abundance of the common dolphin (*Delphinus delphis*) in the Bay of Biscay. *European Research on Cetaceans*, 13: 295-299.
- Brylinski, J. M. 1997. Les biocénoses planctoniques, introduction. In J.-C. DAUVIN (Ed.). *Les biocénoses marines et littorales des côtes Atlantique, Manche et Mer du Nord : synthèse, menaces et perspectives*. Laboratoire de Biologie des invertébrés marin et Malocologie. Service du patrimoine naturel / IEGB / MNHN, Paris, 17-20. [In French].
- Buckland, S.T., Bloch, D., Cattanach, K.L., Gunnlagsson, T., Hydal, K., Lens, S., and Sigurjonsson, J. 1993. Distribution and abundance of Long-finned pilot whales in the North Atlantic, estimated from NASS-87 and NASS-89 data. Report of the International Whaling Commission, (Special Issue 14): 33-49.
- Cañadas, A., and Sagarminaga, R. 2000. The northeastern Alboran Sea, an important breeding and feeding ground for the long-finned pilot whale (*Globicephala melas*) in the Mediterranean Sea. *Marine Mammal Science*, 16: 513-529.
- Cañadas, A., Sagarminaga, R., and Garcia-Tiscar, S. 2002. Cetacean distribution related with depth and slope in the Mediterranean off southern Spain. *Deep Sea Research Part I*, 49: 2053-2073.
- Davis, R.W., Fargion, G.S., May, N., Leming, T.D., Baumgartner, M., Evans, W.E., Hansen, L. J., and Mullin, K. 1998. Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. *Marine Mammal Science*, 14 : 490-507.
- Davis, R.W., Ortega-Ortiz, J.G., Ribic, C.A., Evans, W.E., Biggs, D.C., Ressler, P.H., Cady, R.B., Leben, R.R., Mullin, K.D., and Würsig, B. 2002. Cetacean habitat in the northern Gulf of Mexico. *Deep Sea Research Part I*, 49: 121-142.
- Duguy, R. 1983. Les cétacés des côtes de France. *Annales de la Société des Sciences Naturelles de la Charente-Maritime*, supplément, mars 1983. Contrat d'étude n° 80 01 417. Ministère de l'Environnement, Direction de la Protection de la Nature, Paris, France. [In French].
- Evans, P.G.H. 1980. Cetaceans in British waters. *Mammal Review*, 10: 1-52.
- Forcada, J., Aguilar, A., Evans, P.G.H., and Perrin, W.F. 1990. Distribution of common and striped dolphins in temperate waters of eastern North Atlantic. *European Research on Cetaceans*, 4: 64-66.
- Goujon, M. 1996. Captures accidentelles du filet maillant dérivant et dynamique des populations de dauphins au large du golfe de Gascogne. Thèse de l'Ecole Nationale Supérieure Agronomique de Rennes (PhD thesis), 239 p. [In French].

Gregg, E.J., Nichol, L., Ford, J.K.B., Ellis, G., and Trites, A.W. 2000. Migration and populations structure of northeastern Pacific whales off coastal British Columbia: an analysis of commercial whaling records from 1908-1967. *Marine Mammal Science*, 16: 699-727.

Hammond, P.S., Berggren, P., Benke, H., Borchers, D.L., Collet, A., Heide-Jørgensen, M.P., Heimlich, S., Hiby, A.R., Leopold, M.F., and Øien, N., 2002. Abundance of harbour porpoises and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology*, 39: 361-376

Heyning, J. E. 1989. Cuvier's beaked whale *Ziphius cavirostris* G. Cuvier, 1823. In : S. H. Rigway & Sir R. Harrison (Eds). *Handbook of Marine Mammals*. Volume 4. River dolphins and the Larger toothed whales, 289-308.

Hooker, S.K., Whitehead, H., and Gowans, S. 1999. Marine Protected Area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conservation Biology*, 13: 592-602.

Hui, C. A. 1979. Undersea topography and distribution of dolphins of the genus *Delphinus* in the southern California bight. *Journal of Mammalogy*, 60: 521-527.

Kiszka, J., Hassani, S., and Pezeril, S. 2004. Distribution and status of small cetaceans along the French Channel coasts: using opportunistic records for a preliminary assessment. *Lutra*, 47: 33-45.

Klinowska, M. 1991. Dolphins, porpoises and whales of the world. The Red IUCN data book, Eds IUCN, 425 p.

Lahaye, V., and Mauger, G. 2000. Site fidelity, movement patterns and group mixing in Normandy bottlenose dolphins (*Tursiops truncatus*). *European Research on Cetaceans*, 14: 335-338.

Lahaye, V., Bustamante, P., Spitz, J., Dabin, W., Das, K., Pierce, G.J., and Caurant, F. 2005. Long-term dietary segregation of common dolphins *Delphinus delphis* in the Bay of Biscay, determined using Cadmium as an ecological tracer. *Marine Ecology Progress Series*, 305: 275-285.

Lewis, T., Swift, R., Gozalbes, P., Butler, J., and Gordon, J. 1998. Report on passive acoustic monitoring of cetacean distribution north-west of the Hebrides 1997-1998, for Conoco UK. Hebridean Whale and Dolphin Trust, Isle of Mull, Scotland, UK, 60 p.

Macleod, K. Simmonds, M. P., and Murray, E. 2003. Summer distribution and relative abundance of cetacean populations off north-west Scotland. *Journal of the Marine Biological Association of the United Kingdom*, 83:1187-1192.

Macleod K., Fairbairns R., Fairbairns B., Gill A., Gordon J., Blair-Myers C., and Parsons E.C.M. 2004. The seasonal distribution of the Minke whale (*Balaenoptera acutorostrata*) in relation to physiographic factors and potential prey off the Isle of Mull, Scotland. *Marine Ecology Progress Series*, 277: 263-274.

Meynier, L. 2004. Food and feeding ecology of the common dolphin, *Delphinus delphis*, in the Bay of Biscay: intraspecific dietary variation and food transfer modelling. MSc thesis, University of Aberdeen, 63 p.

Northridge, S., M.L. Tasker, A. Webb, and J.M. Williams 1995. Seasonal relative abundance of harbour porpoises *Phocoena phocoena* (L.), white-beaked dolphins *Lagenorhynchus albirostris* (Gray) and minke whales *Balaenoptera acutorostrata* (Lacépède) in the waters around the British Isles. *ICES Journal of Marine Science*, 52: 55-66.

Payne, P.M., and Heinemann, D.W. 1993. The distribution of pilot whales (*Globicephala* sp.) in shelf/shelf-edge and slope waters of the northeastern United States, 1978-1988. Report to the International Whaling Commission, (Special Issue 14): 51-68.

Perrin, W.F., Wilson, C.E., and Archer, F. I. 1994. Striped dolphin *Stenella coeruleoalba* (Meyen, 1833). In: S. H. Rigway & Sir R. Harrison (Eds). *Handbook of Marine Mammals*. Volume 5. The first book of Dolphins and the porpoises, 129-159.

Quero, J.-C., Dardignac, J., and Vayne, J.-J. 1989. Les poissons du golfe de Gascogne. Rapport de l'Institut Français de Recherche pour l'Exploitation de la MER (I.F.R.E.M.E.R.), 229 p. [In French].

Reid, J.B., Evans, P.G.H., and Northridge, S.P. 2003. Atlas of cetacean distribution in north-west European waters. Joint Nature Conservation Committee, Aberdeen, 76 p.

Reilly, S.B. 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Marine Ecology Progress Series*, 66: 1-11.

Rice, D.W. 1998. *Marine Mammals of the World: systematics and distribution*. Special publication Number 4. The Society for Marine Mammalogy, 231 p.

Skov, H., Durink, J., Danielsen, F., and Bloch, D. 1995. Co-occurrence of cetaceans and seabirds in the north-east Atlantic. *Journal of Biogeography*, 22: 71-88.

Southward, A.J., Langmead, O., Hardman-Mountford, N.J., Aiken, J., Boalch, G.T., Genner, M.J., Joint, I., Kendall, M., Halliday, N.C., Harris, R.P., Leaper, R., Mieszkowska, N., Pingree, R.D., Richardson, A.J., Sims, D.W., Smith, T., Walne, A.W., and Hawkins S.J. 2005. Long-term oceanographic and ecological research in the western English Channel. *Advances in Marine Biology*, 47: 1-105.

Spitz, J., Y. Rousseau & V. Ridoux 2006. Diet overlap between harbour porpoise and bottlenose dolphin: an argument in favour of interference competition for food? *Estuarine, Coastal and Shelf Science*, 70: 259-270.

- St. John, M.A., and Pond, S. 1992. Tidal plume generation around a promontory: effects on nutrient concentrations and primary productivity. *Continental Shelf Research*, 12: 339-354.
- Stone, C.J. 1998. Cetacean observations during seismic surveys in 1997. Rep. 278, Joint Nature conservation Committee, Aberdeen.
- Tregenza, N.J.C., Berrow, S.D., Hammond, P.S., and Leaper, R. 1997. Harbour porpoise (*Phocoena phocoena*) by-catch in set gillnets in the Celtic Sea. *ICES Journal of Marine Science*, 54: 896-904.
- Tregenza, N.J.C., and Collet, A. 1998. Common dolphin *Delphinus delphis* by-catch in pelagic trawl and other fisheries in the northeast Atlantic. Report of the International Whaling Commission, 48: 453-459.
- Weir, C.R., Stokes, J., Martin, C., and Cermeño, P. 2004. Three sightings of *Mesoplodon* species in the Bay of Biscay: first confirmed True's beaked whales (*M. mirus*) for the north-east Atlantic? *Journal of the Marine Biological Association of the United Kingdom*, 84: 1095-1099.
- Wells, R.S., and Scott, M.D. 1999. Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). In: S. H. Rigway & Sir R. Harrison (Eds). *Handbook of Marine Mammals. Volume 6. The second book of Dolphins and the Porpoises*, 137-182.
- Williams, A., Williams, R., Heimlich-Boran, J.R., Evans, P.G.H., Tregenza, N.J.C., Ridoux, V., Liret, C., and Savage, S. 1996. A preliminary report on an investigation into bottlenose dolphins (*Tursiops truncatus*) of the English Channel: a collaborative approach. *European Research on Cetaceans*, 10: 217-220.
- Williams, A.D., Williams, R., and Brereton, T. 2002. The sighting of pygmy killer whales (*Feresa attenuata*) in the southern Bay of Biscay and their association with cetacean calves. *Journal of the Marine Biological Association of the United Kingdom*, 82: 509-511.
- Whitehead, H. 2003. *Sperm whales: social evolution in the oceans*. The University of Chicago Press. 431 p.
- Whitehead, H., Brennan, S., and Grover, D. 1992. Distribution and behaviour of male sperm whales on the Scotian shelf, Canada. *Canadian Journal of Zoology*, 70: 912-918.

Table 1: Observation effort conducted in the English Channel and Bay of Biscay from 1998 to 2002 (in nautical miles).

	February	March	April	May	June	July	August	September	October
1998	0	0	0	0	0	465.7	1 639.9	747.9	0
1999	0	0	0	0	0	1 059.4	532.9	82.2	0
2000	0	0	0	0	0	0	1 184.3	0	410.5
2001	0	368.3	0	0	713.5	606.6	2 778	1 026.3	0
2002	291.2	98.8	173.91	270.6	422.5	1 407.4	1 973.1	1 617.9	0

Table 2: Number of sightings and individuals (with their respective proportions) for each encountered toothed cetacean species recorded from 1998 to 2002.

Species	N sightings	N individuals	% sightings	% individuals
Common dolphin	329	11 297	32.6	55.2
Striped dolphin	187	6 103	18.6	29.8
Long-finned pilot whale	134	895	13.3	4.4
Harbour porpoise	114	313	11.3	1.5
Bottlenose dolphin	110	1 536	10.8	7.6
Cuvier's beaked whale	60	146	6	0.6
Sperm whale	42	68	4.2	0.3
Risso's dolphin	14	58	1.4	0,3
Northern bottlenose whale	9	32	0.9	0.2
Killer whale	5	16	0.5	0.1
False killer whale	2	13	0.2	0.1
Sowerby's beaked whale	1	3	0.1	0.02
True's beaked whale	1	1	0.1	0.005
TOTAL	1,008	20,481	100	100

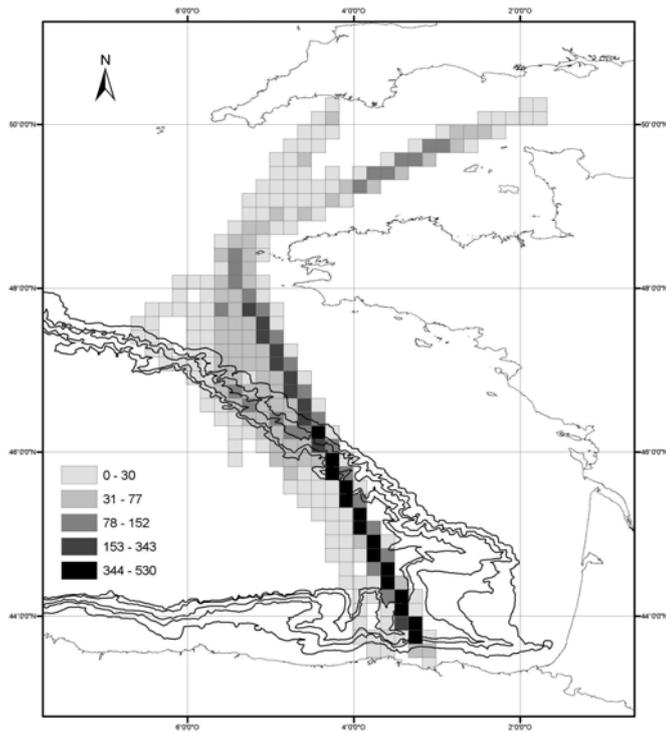


Figure 1: Survey coverage in the English Channel and Bay of Biscay onboard both of the platforms, from 1998 to 2002.

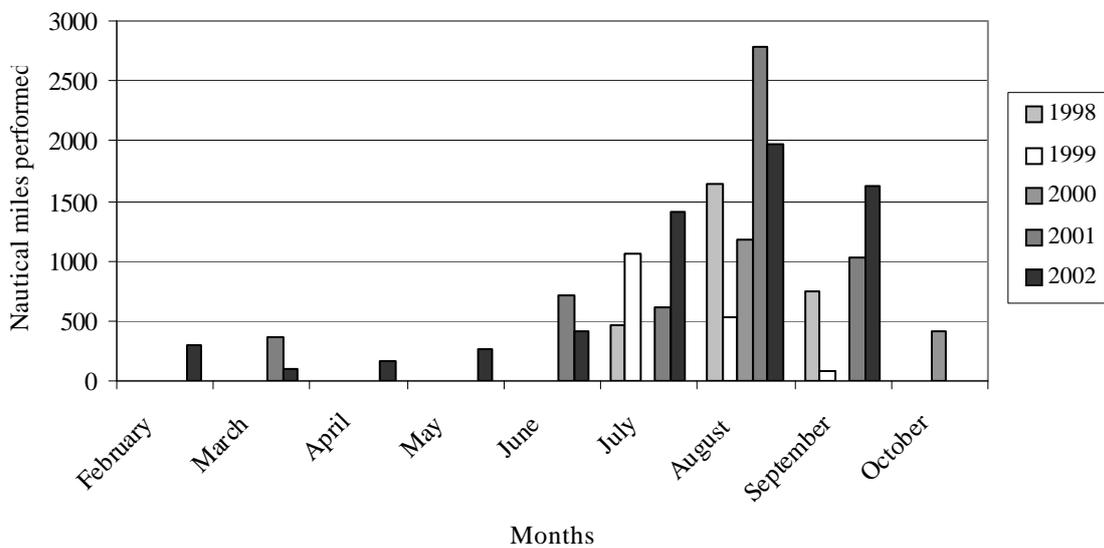


Figure 2: Variations of observation effort on both platforms according to years and seasons, from 1998 to 2002.

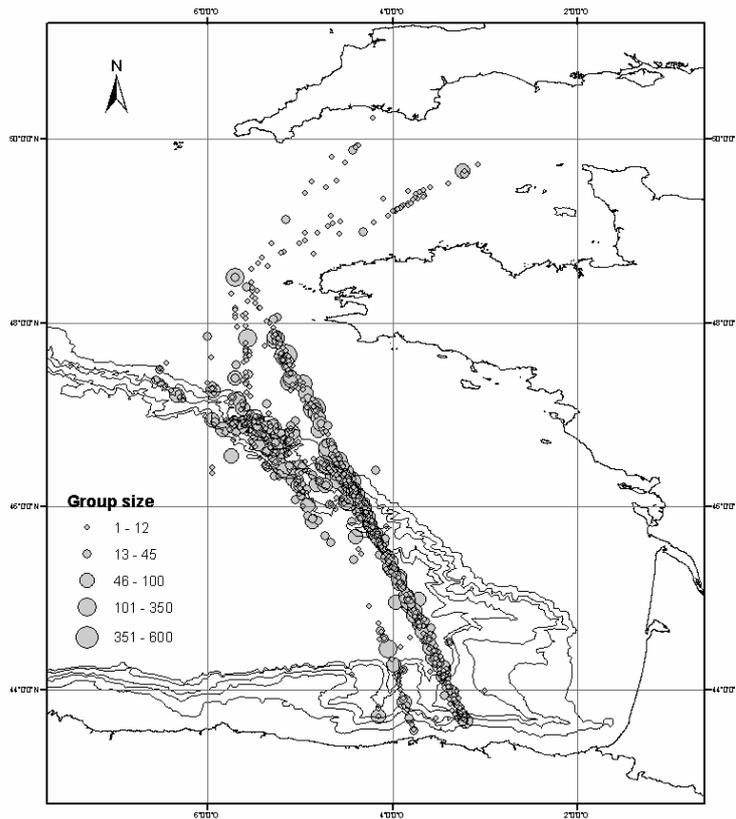


Figure 3: Distribution of all mono-generic groups of small cetaceans encountered from 1998 to 2002 (N=1,008).

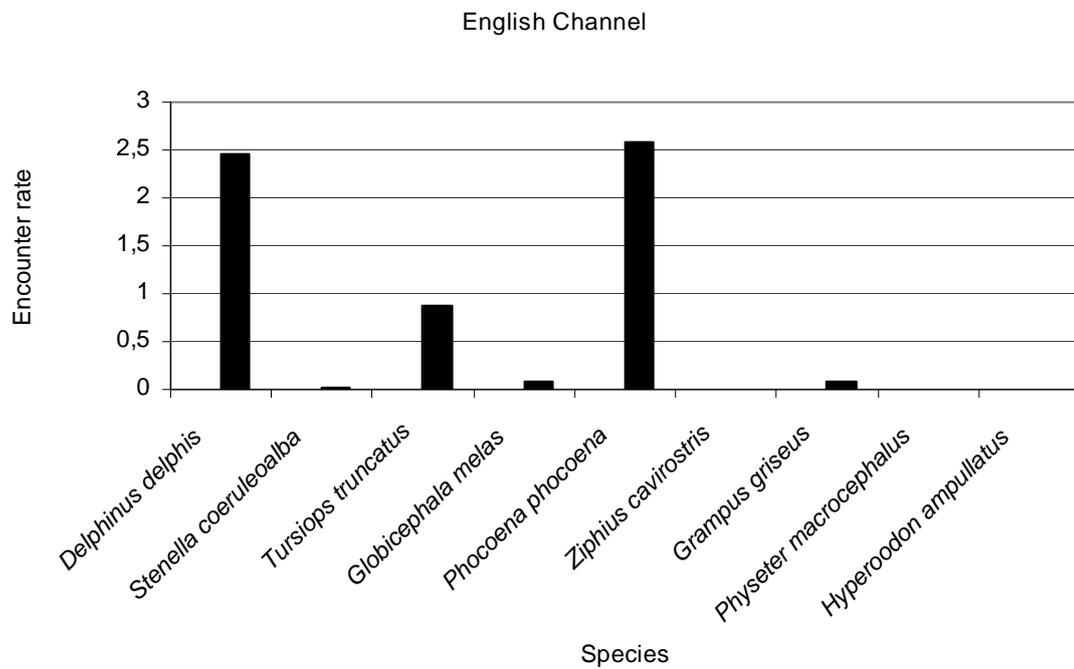


Figure 4: Encounter rates in the western English Channel.

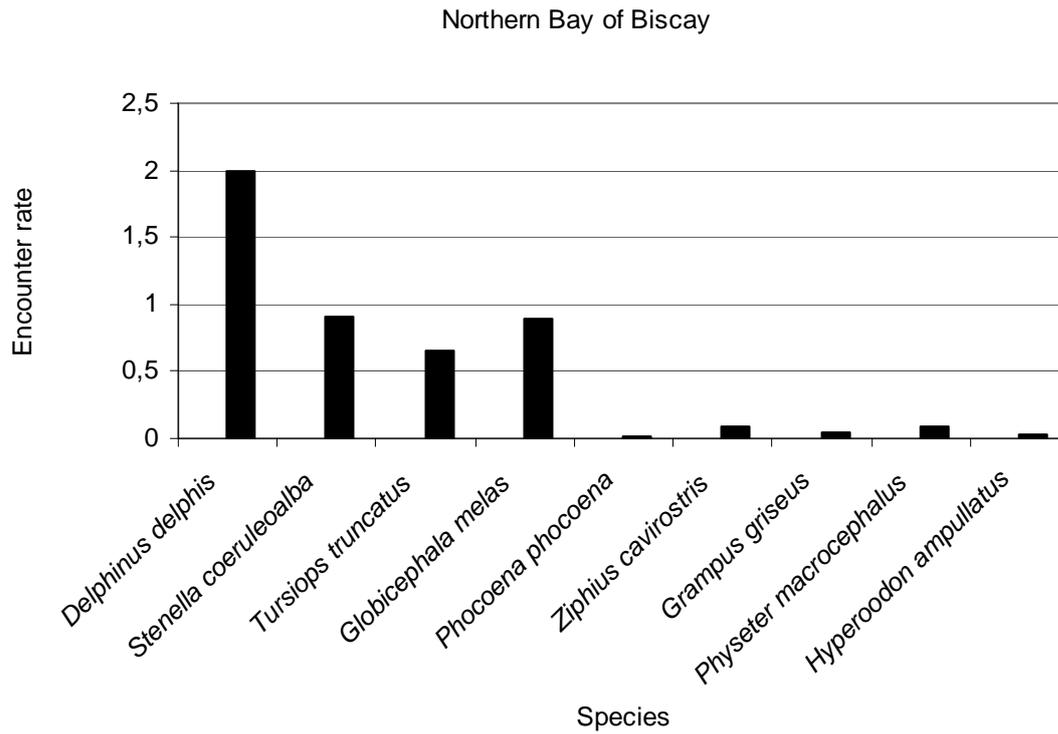


Figure 5: Encounter rates in the northern Bay of Biscay.

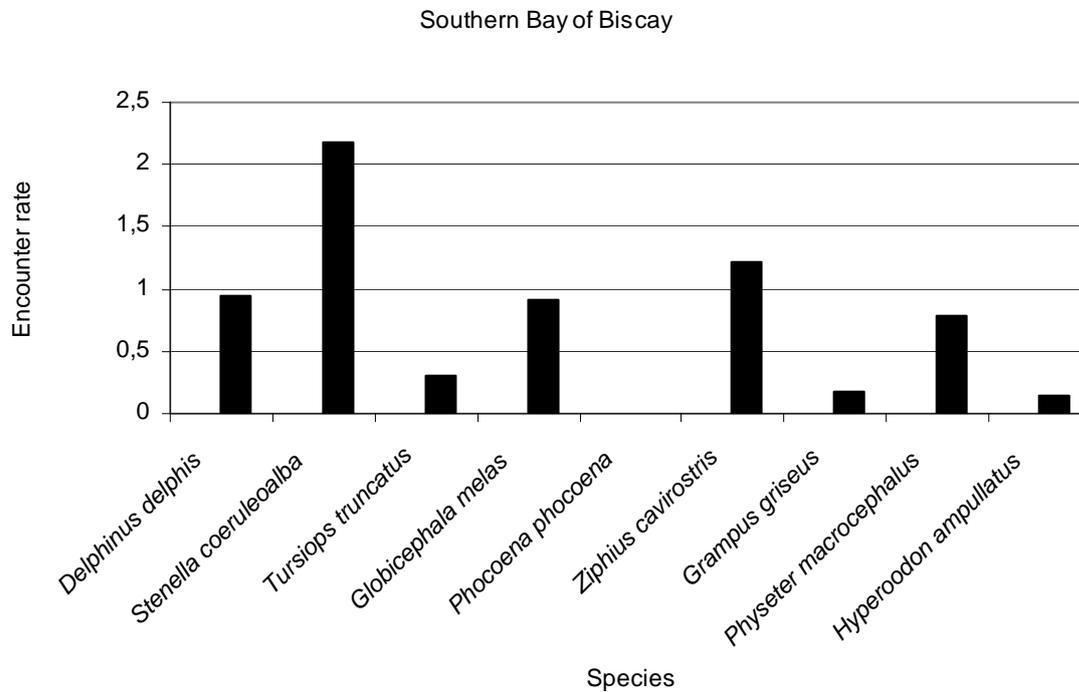


Figure 6: Encounter rates in the southern Bay of Biscay.

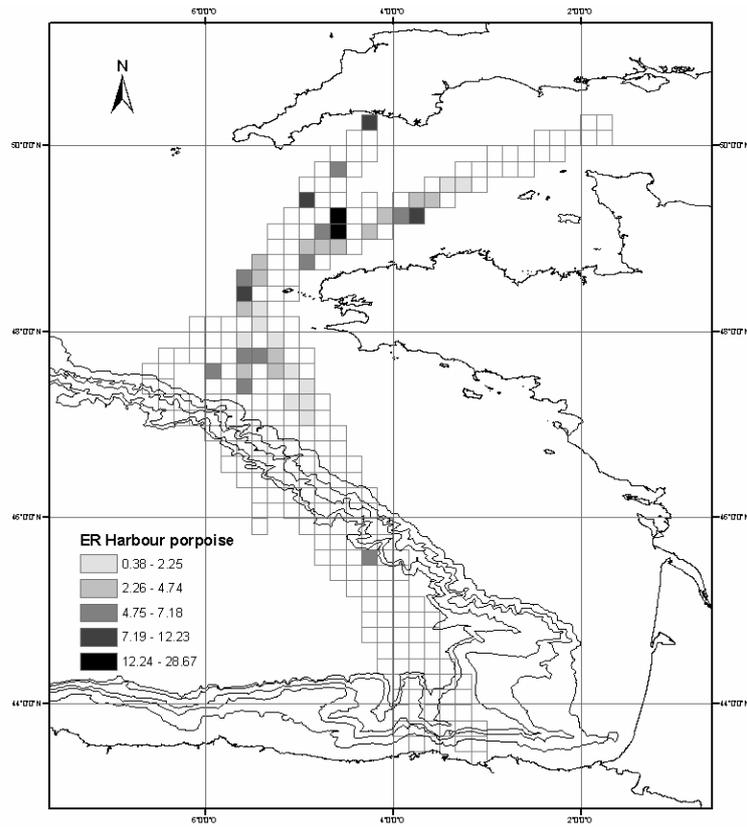


Figure 7: Encounter rates of the harbour porpoise in the English Channel and Bay of Biscay from 1998 to 2002.

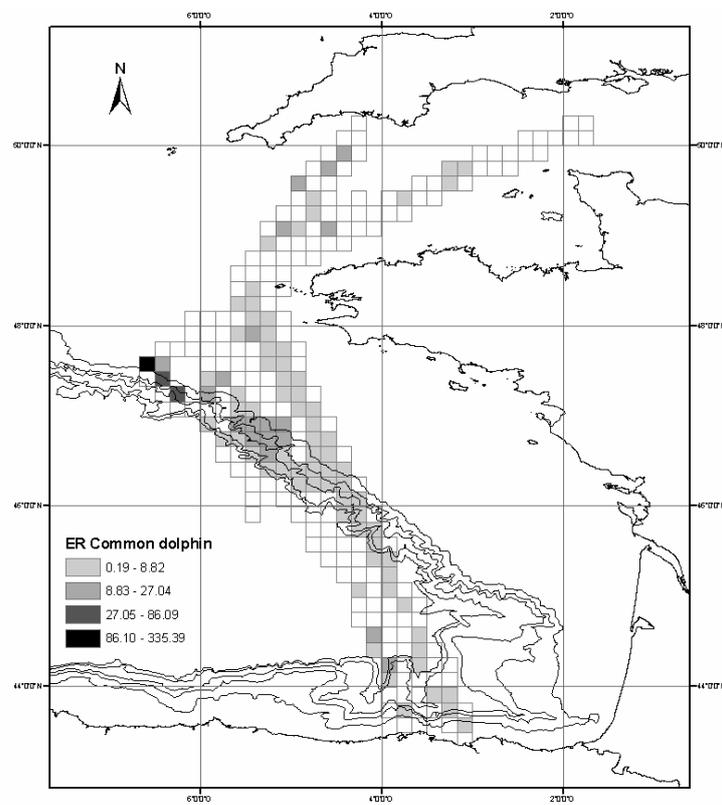


Figure 8: Encounter rates of the common dolphin in the English Channel and Bay of Biscay from 1998 to 2002.

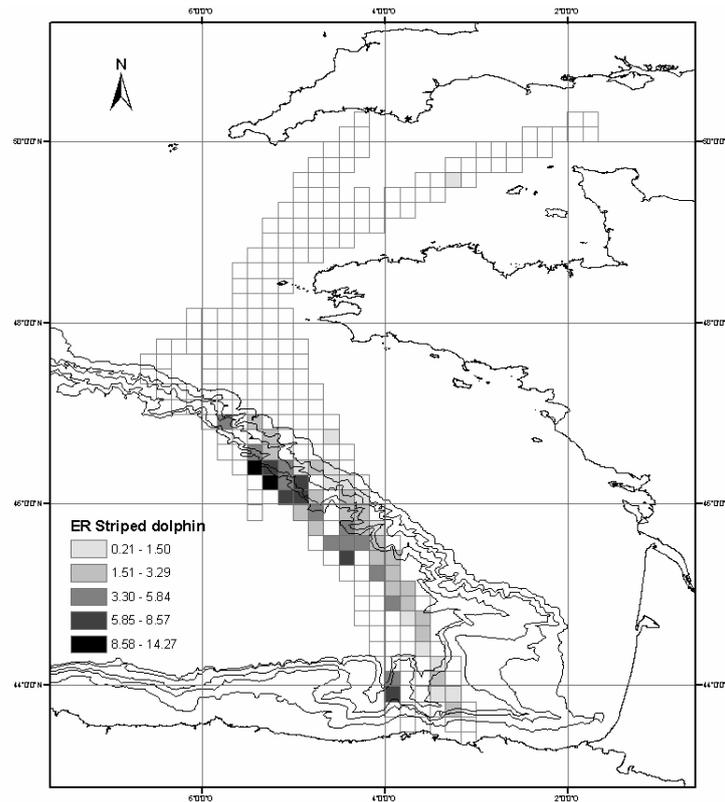


Figure 9: Encounter rates of the striped dolphin in the English Channel and Bay of Biscay from 1998 to 2002.

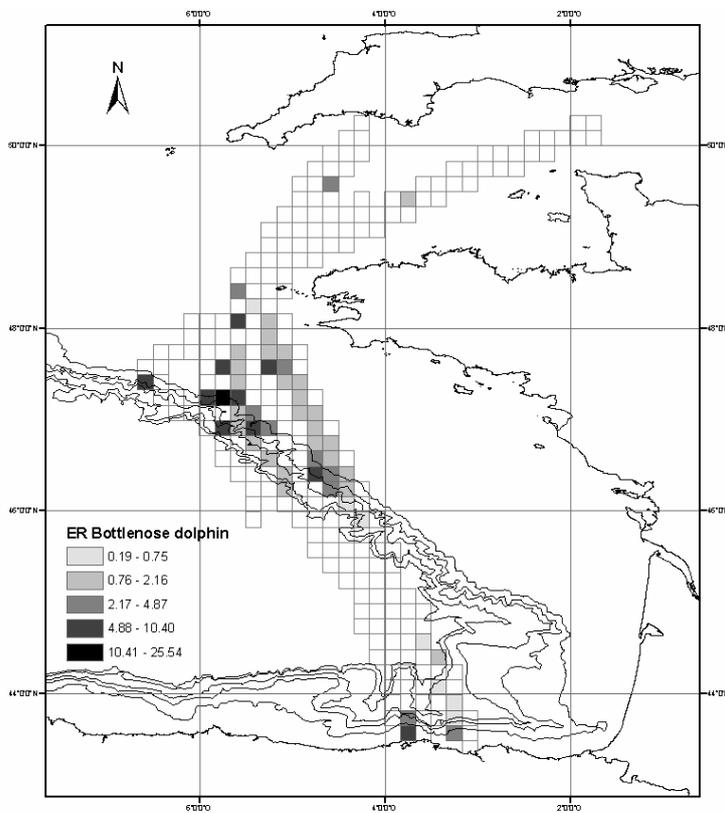


Figure 10: Encounter rates of the bottlenose dolphin in the English Channel and Bay of Biscay from 1998 to 2002.

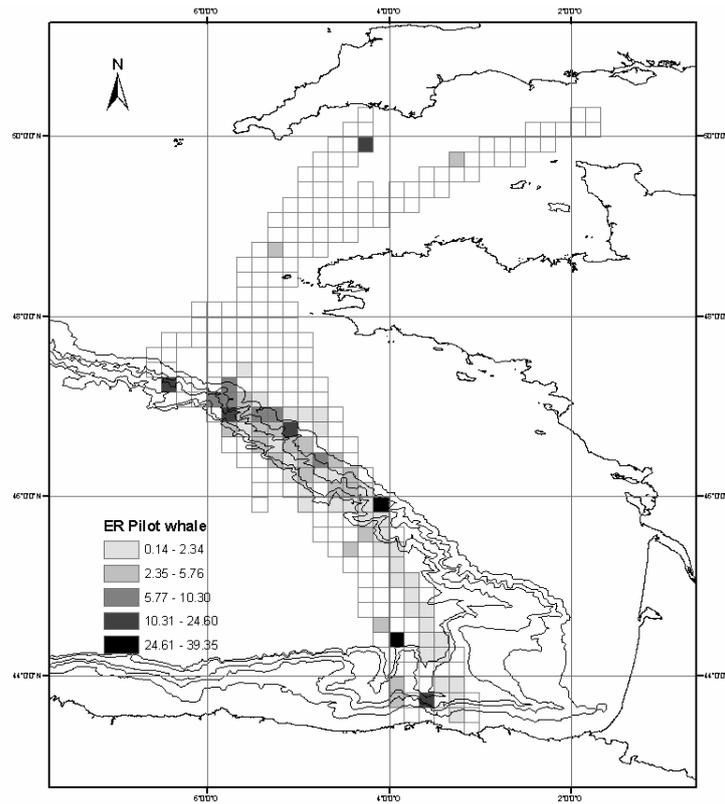


Figure 11: Encounter rates of the long-finned pilot whale in the English Channel and Bay of Biscay from 1998 to 2002.

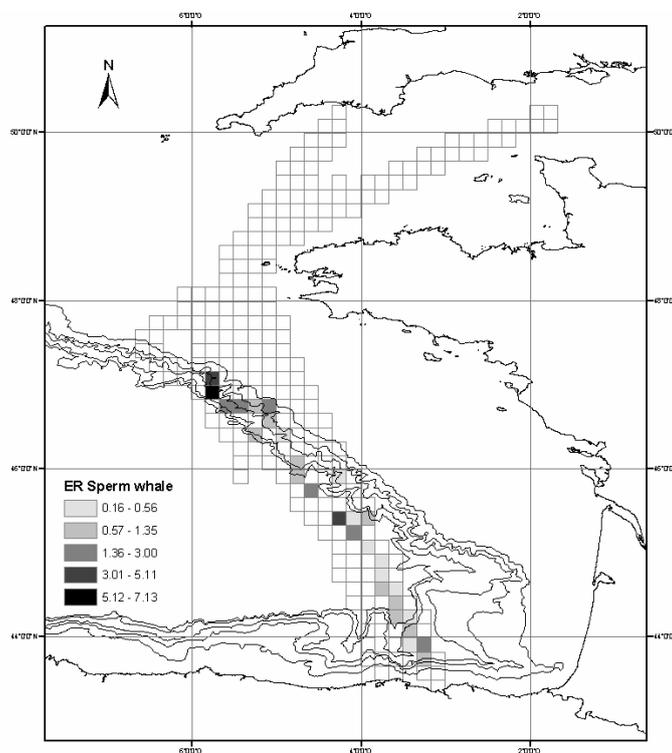


Figure 12: Encounter rates of the sperm whale in the English Channel and Bay of Biscay from 1998 to 2002.

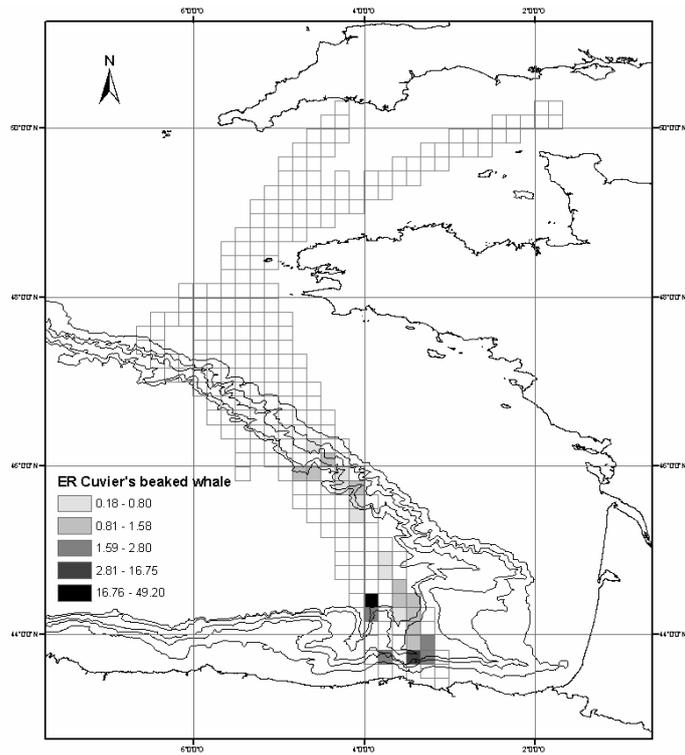


Figure 13: Encounter rates of the Cuvier's beaked whale in the English Channel and Bay of Biscay from 1998 to 2002.