

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

Jeremy Kiszka, Kelly Macleod, Olivier Van Canneyt, Dylan Walker, and Vincent Ridoux

Kiszka, J., Macleod, K., Van Canneyt, O., Walker, D. and Ridoux, V. 2007. Distribution, encounter rates, and habitat characteristics of toothed cetaceans in the Bay of Biscay and adjacent waters from platform-of-opportunity data. – *ICES Journal of Marine Science*, 64: 1033–1043.

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.

Received 12 June 2006; accepted 23 January 2007; advance access publication 5 June 2007.

J. Kiszka, O. Van Canneyt, and V. Ridoux: *Centre de Recherche sur les Mammifères Marins, Université de La Rochelle, 17071 La Rochelle, France, and Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés (CRELA), UMR 6217, CNRS-IFREMER-Université de La Rochelle, Avenue Michel Crépeau, 17071, La Rochelle, France.* K. Macleod and D. Walker: *Organisation Cetacea (ORCA), 7 Ermin Close, Baydon, Wiltshire SN8 2JQ, UK.* Correspondence to J. Kiszka: tel: + 33 546 44 99 10; fax: + 33 546 44 99 45; e-mail: jeremy.kiszka@wanadoo.fr.

Introduction

Distribution and abundance data on cetaceans, particularly those occurring predominantly offshore, are generally difficult to collect. The cost of dedicated surveys on chartered research vessels is generally prohibitive in terms of carrying out regular surveys. For this reason, vessels of opportunity can be used for opportunistic surveying of cetaceans. 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 first, 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 second because there is a paucity of data on the status of cetaceans in this area of considerable interactions, especially with pelagic fisheries (Tregenza *et al.*, 1997; Tregenza and Collet, 1998).

Western European waters provide 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 characterized 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, and includes 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 characterized by the presence of many fronts and localized upwellings attributable to the convergence of various water masses and the steepness of the topography in some sectors (Brylinski, 1997; P. Lazure, Ifremer, Brest, pers. comm., April 2003). The variety of habitats supports many of the toothed cetacean species that are found 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 and 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 (Centre de Recherche sur les Mammifères Marins (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 (95% CI 35 000–108 000) common dolphins (*Delphinus delphis*) and 73 843 (95% CI 36 113–150 990) striped dolphins (*Stenella coeruleoalba*) were estimated in the Bay of Biscay and adjacent waters by Goujon (1996). Buckland et al. (1993) estimated long-finned pilot whale (*G. melas*) abundance as 12 335 individuals (95% CI 3924–38 148) for a survey block in the oceanic Bay of Biscay and adjacent waters during the North Atlantic sighting survey of summer 1989. The surveys of the Small Cetacean Abundance in the North Sea and adjacent waters project conducted during July 1994 failed to record any cetaceans in the English Channel, but harbour porpoise (*Phocoena phocoena*) abundance in the Celtic Sea was estimated as 36 280 (CV 0.57) individuals [Hammond et al., 2002 (This paper has been reviewed, and no abundance estimate for common dolphins is provided. The early version of the paper provides an abundance estimate, but it has been deleted in the published paper. The abundance estimate is only available for the harbour porpoise)].

Preliminary studies suggest that harbour porpoises, and common and bottlenose dolphins are the most frequently encountered species in the English Channel and that they occur year-round. In the Bay of Biscay, common dolphins seem to be the most abundant, followed by striped and 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*) are rarely seen in the Bay of Biscay (Williams et al., 2002; CRMM, unpublished data). The distribution and encounter rates of toothed cetaceans has not been described in detail in the area, and their habitat preferences in terms of physiographical variables such as depth have not been investigated. The distribution of cetaceans is driven by many factors, but the primary influence is probably the aggregation of prey (Hui, 1979; Forcada et al., 1990; Baumgartner, 1997; Davis et al., 1998, 2002; Hooker et al., 1999; Macleod et al., 2004). Those authors also suggested that 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 related to bathymetric preferences of the distribution, encounter rates, and habitat characteristics of toothed cetaceans using data collected on board ferries operating through the English Channel and Bay of Biscay.

Material and methods

Survey method

Two ferry lines operating between the southern coast of the UK and northern Spain (*The Pride of Bilbao*, operating between Portsmouth and Bilbao; and *Val de Loire*, operating between Plymouth and 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 travel at a speed of ~20 knots.

A survey is defined as a return ferry journey between the home port and the destination. Data were collected between July 1998 and September 2002, mainly during summer. The observation effort was significantly greater on the *Pride of Bilbao* than that of *Val de Loire* (see Table 1). At least two or more experienced observers carried out surveys, primarily on the “monkey island”, the deck over the ship’s bridge (at 37 m 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 × 50 binoculars. Environmental data and survey effort were recorded at the start and end of each survey leg and at 30-min 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 (Beaufort <3) were included in the analysis, because cetacean detection capability tends to be biased downwards in conditions worse than that. 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 for this study. Group sizes used to provide mean, standard deviation, and range values were best estimates recorded at sea. Considering the little time spent viewing groups at sea, it is possible that group sizes recorded may not accurately reflect the real group size. Groups were defined as individuals having the same activity and being in close proximity to each other (<5 body widths between individuals). Differences in group size between sub-regions were tested for with a non-parametric Kruskal–Wallis test. All data were collected on pre-prepared data sheets and logged into an Excel database after each survey.

Spatial distribution and encounter rate

To investigate the spatial distribution, encounter rate, and habitat characteristic, maps of encounter rates per cell for the commonest species (≥ 40 encounters) were generated with ArcView 8.2. Encounter rates were calculated for each cell (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 (subsequently referred to as miles, for brevity). Global values of encounter rates were calculated for the whole study area. Further, 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).

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

Year	February	March	April	May	June	July	August	September	October
1998	0	0	0	0	0	465.7	1639.9	747.9	0
1999	0	0	0	0	0	1059.4	532.9	82.2	0
2000	0	0	0	0	0	0	1184.3	0	410.5
2001	0	368.3	0	0	713.5	606.6	277.8	1026.3	0
2002	291.2	98.8	173.91	270.6	422.5	1407.4	1973.1	1617.9	0

Bathymetric preferences

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

Results

Between 1998 and 2002, 147 surveys were completed through the English Channel and Bay of Biscay (Figure 1), totalling 17 873 miles of survey effort. Most survey effort was conducted on the *Pride of Bilbao* ($n = 17\ 075$ miles on the *Pride of Bilbao* and 798 miles 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).

In all, 1008 odontocete encounters were recorded during the surveys, a total of 20 481 animals. 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 bottlenose dolphins, long-finned pilot whales, and harbour porpoises. Three large delphinids, Risso’s dolphin, killer whale, and false killer whale, were rare. The largest toothed whale species encountered were the sperm whale and the four beaked whale species, of which Cuvier’s beaked whale was the commonest.

Distribution, encounter rate, and bathymetric preference

The spatial distribution of sightings is heterogeneous between different species. Group size of the species seen was also highly variable. Delphinids were characterized by larger group size, and the larger species by smaller. Toothed cetaceans were encountered

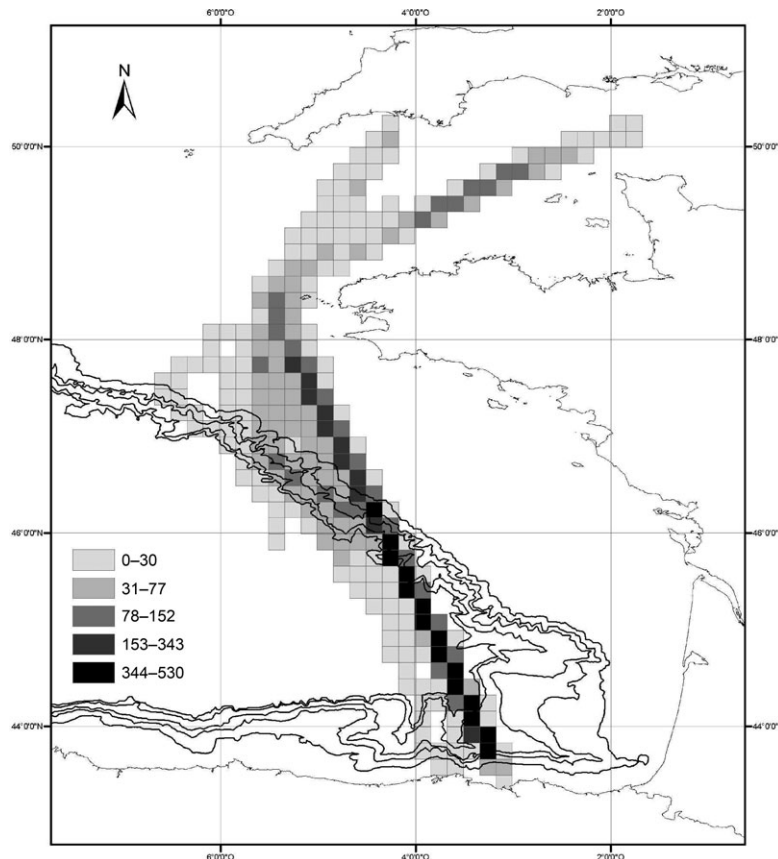


Figure 1. Survey coverage in the English Channel and Bay of Biscay on board both ferries, 1998–2002.

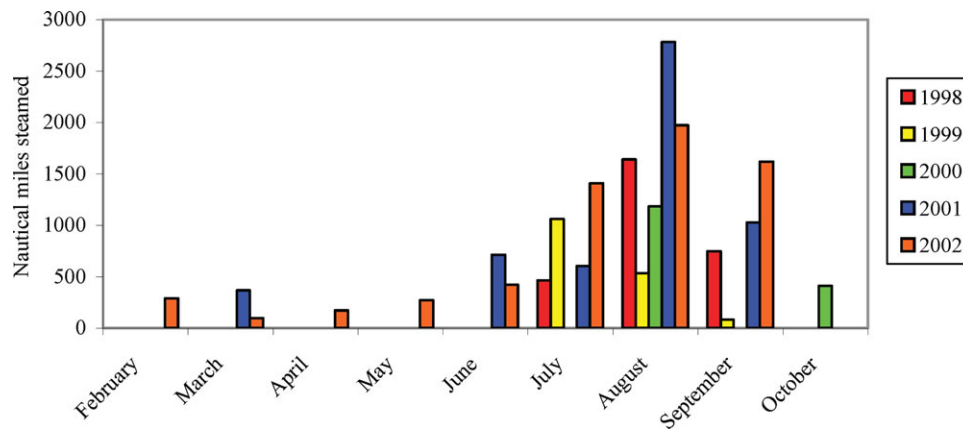


Figure 2. Variation in observation effort on board both ferries by year and season, 1998–2002.

throughout the study area, with greater concentrations of sightings in the Bay of Biscay (Figure 3).

Harbour porpoise

The harbour porpoise was encountered on 114 occasions, a total of 313 individuals. Encounter rate throughout the area was 0.49 per 100 miles steamed. Of the three subareas, encounter rates peaked in the western English Channel and western approaches (Figures 4–6) and was lowest in the northern Bay of Biscay, where there was just one sighting during the study period

(Figure 7), and southern Bay of Biscay, where no sightings were made. Encounter rates were highest off the coast of northern Brittany. Group size was generally small ($\bar{y} = 2.75$; s.d. = 1.8), ranging from 1 to 10 animals. Harbour porpoises showed clear preference for the shallow waters of the western English Channel and its 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 value of the standard deviation.

Table 2. Number of sightings and individuals (and proportions) of each encountered toothed cetacean species, 1998–2002.

Species	Number of sightings	% sightings	Number of individuals	% individuals
Common dolphin	329	32.6	11 297	55.2
Striped dolphin	187	18.6	6103	29.8
Long-finned pilot whale	134	13.3	895	4.4
Harbour porpoise	114	11.3	313	1.5
Bottlenose dolphin	110	10.8	1536	7.6
Cuvier's beaked whale	60	6	146	0.6
Sperm whale	42	4.2	68	0.3
Risso's dolphin	14	1.4	58	0.3
Northern bottlenose whale	9	0.9	32	0.2
Killer whale	5	0.5	16	0.1
False killer whale	2	0.2	13	0.1
Sowerby's beaked whale	1	0.1	3	0.02
True's beaked whale	1	0.1	1	0.005
All species	1008	100	20 481	100

Common dolphin

The common dolphin was the species sighted most often, accounting for >50% of the toothed cetaceans seen ($n = 329$ sightings; 11 297 animals), with an average encounter rate of 1.84 per 100 miles. Regional encounter rates were 2.46, 2, and 0.95 per 100 miles for the western Channel, northern Bay, and southern Bay of Biscay, respectively (Figures 4–6, and 8). Group size was highly variable ($\bar{y} = 38.1$; s.d. = 73.5) ranging from 1 to 600 animals. There was significant variation between group size by subarea, especially between the western Channel and the northern Bay of Biscay (Kruskal–Wallis; $H = 4.38$; $p = 0.036$), as well as between northern and southern Bay (Kruskal–Wallis; $H = 3.975$; $p = 0.04$). Aggregations were largest in the northern Bay of Biscay. Common dolphins were sighted 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).

Striped dolphin

Striped dolphins were the second commonest species recorded, with 187 sightings and 6103 individuals. Over the entire survey region, the encounter rate of the striped dolphin was 1.05 per 100 miles, increasing from 0.03 to 2.18 per 100 miles from the western Channel to the southern Bay of Biscay (Figures 4–6). Encounter rates were most in the central Bay. Group size varied from 1 to 250 animals, with a mean of 32.7 (s.d. = 34.6). Striped dolphins were mainly in the Bay of Biscay (Figure 9) particularly in the south, and were encountered only once in the central English Channel. They were most common in deep oceanic waters of the Bay of Biscay (median = 3552; Q1 = 2633; Q3 = 3975; min = 136; max = 4421).

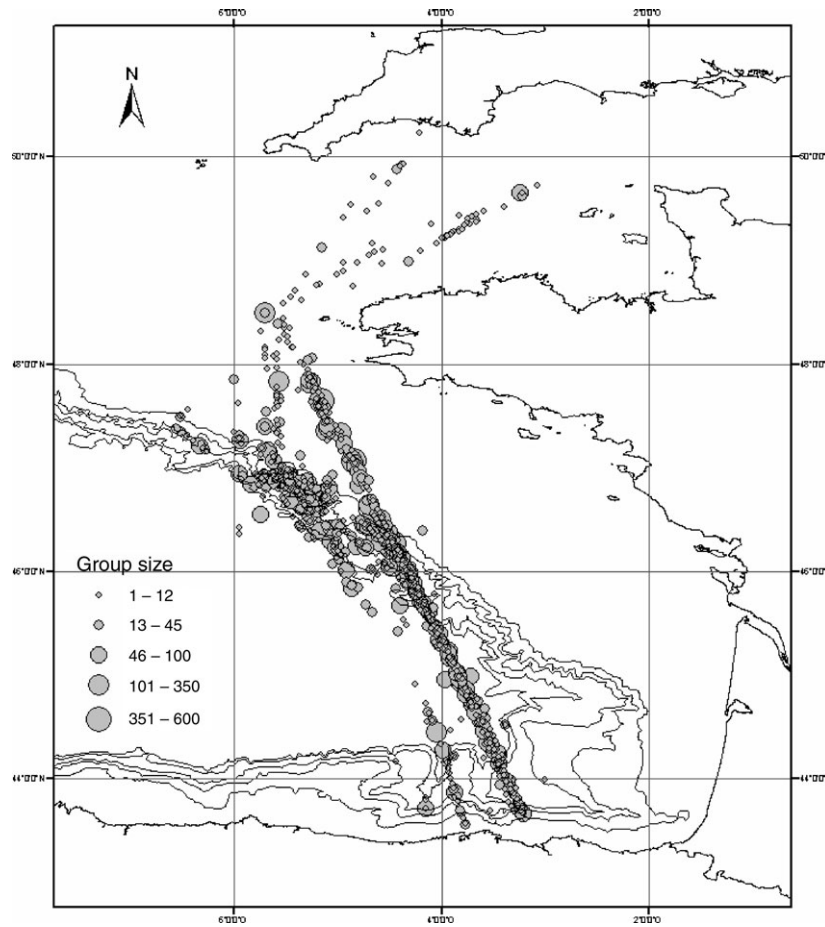


Figure 3. Distribution of monogeneric groups of small cetaceans encountered, 1998–2002 ($n = 1008$).

Bottlenose dolphin

There were 110 sightings of bottlenose dolphins amounting to 1556 individuals. The overall encounter rate was 0.62 per 100 miles, but the rate dropped from 0.87 to 0.66 to 0.31 per 100 miles from the western Channel to the southern Bay of Biscay (Figures 4–6, and 10). Mean group size was 14 (s.d. = 11.9) and was not significantly different between the southern and the 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 = 3920).

Pilot whale

A total of 895 individual pilot whales (probably mainly *G. melas*) was recorded during 134 encounters. Encounter rates were 0.09, 0.89, and 0.92 per 100 miles in the western Channel, northern Bay, and

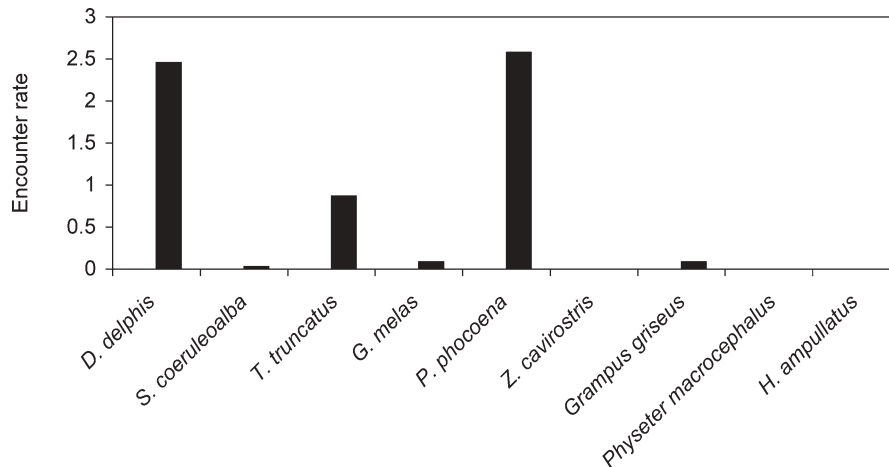


Figure 4. Encounter rates in the western English Channel.

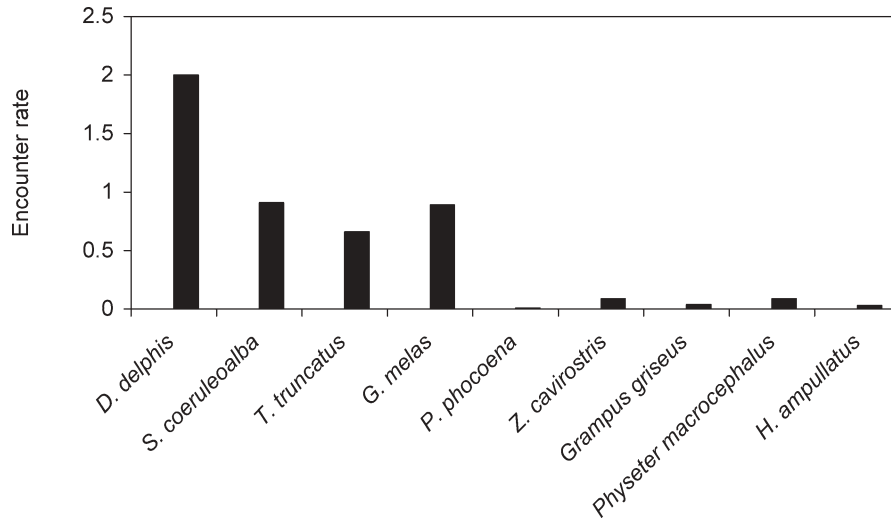


Figure 5. Encounter rates in the northern Bay of Biscay.

southern Bay of Biscay, respectively, and 0.75 per 100 miles overall (Figure 11). Group size was relatively small ($\bar{y} = 6.8$; s.d. = 5.1) with a maximum of 30, and it did not vary between subregions (Kruskal–Wallis; $H = 0.01$; $p = 0.94$). The species is widely distributed in the central and southern Bay of Biscay, but there were just two sightings in the western approaches of the English Channel. Pilot whales showed a clear preference for deep oceanic waters, despite a few sightings being made over the continental shelf (median = 2726; $Q1 = 1088$; $Q3 = 3641$; min = 103; max = 4 237).

Sperm whale

The sperm whale was regularly sighted throughout the study area, with 42 encounters of a total of 68 animals. Group size ranged from one to four ($\bar{y} = 1.6$; s.d. = 0.9). Encounter rates throughout the survey area were 0.23 per 100 miles overall, but higher in the southern Bay of Biscay (0.8), especially in the proximity of the

Santander canyon, than in the northern Bay (0.09 per 100 miles) (Figure 12). No sightings were made in the English Channel. Sperm whales showed a significant preference for deep oceanic waters (median = 3168; $Q1 = 2748$; $Q3 = 3852$; min = 1185; max = 4195).

Cuvier’s beaked whale

The patterns of distribution of this whale were similar to those of the sperm whale; overall occurrence was 0.34 per 100 miles. However, group size was larger and more variable than for the sperm whale ($\bar{y} = 2.4$; s.d. = 1.1). The encounter rate in the northern Bay of Biscay was 0.09 per 100 miles and 1.2 per 100 miles in the southern Bay (Figures 5, 6, and 13), particularly around the Santander canyon. Cuvier’s beaked whales seemed to prefer deep oceanic waters (median = 3238; $Q1 = 2771$; $Q3 = 3770$; min = 685; max = 4259).

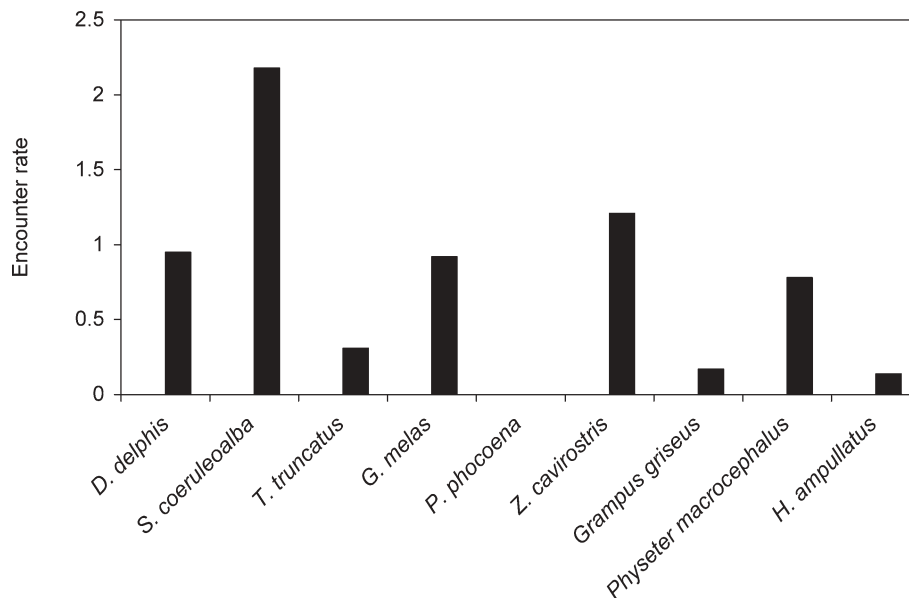


Figure 6. Encounter rates in the southern Bay of Biscay.

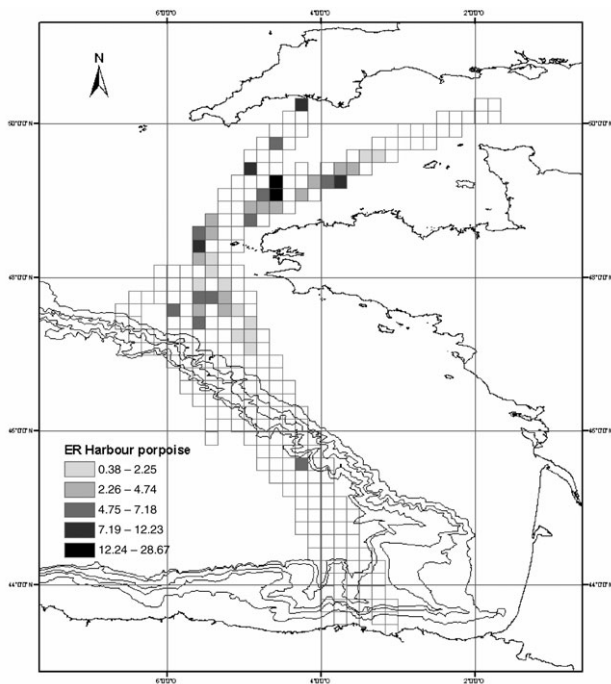


Figure 7. Encounter rates of harbour porpoise in the English Channel and Bay of Biscay, 1998–2002.

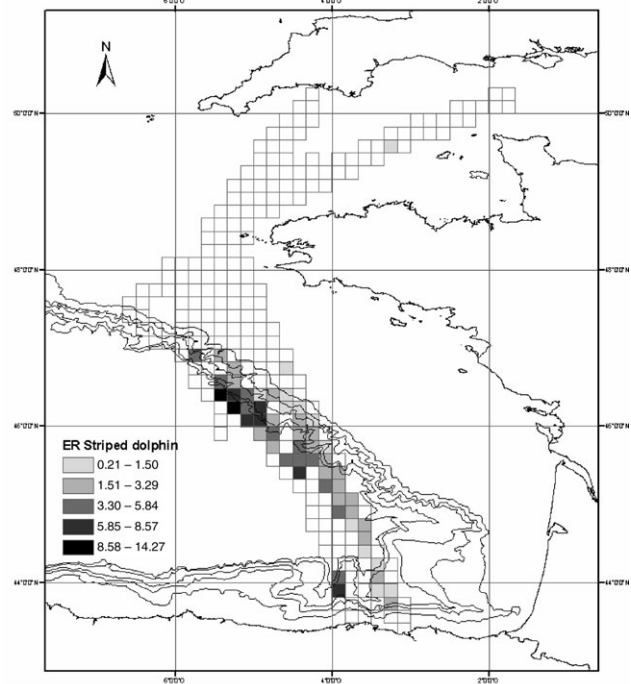


Figure 9. Encounter rates of striped dolphin in the English Channel and Bay of Biscay, 1998–2002.

Less frequently seen species

Risso’s dolphin was rarely seen in the study area, with just 14 confirmed sightings of 58 animals (0.08 per 100 miles) and small group sizes ($\bar{y} = 4$, s.d. = 2.8). The species was sighted more commonly in the central and southern Bay of Biscay, but a few were

recorded in the western English Channel. Risso’s dolphin’s sightings were mainly in deep oceanic waters, but three sightings were also made over shelf waters of the western English Channel (median = 2392; Q1 = 431; Q3 = 2844; min = 81; max = 3852).

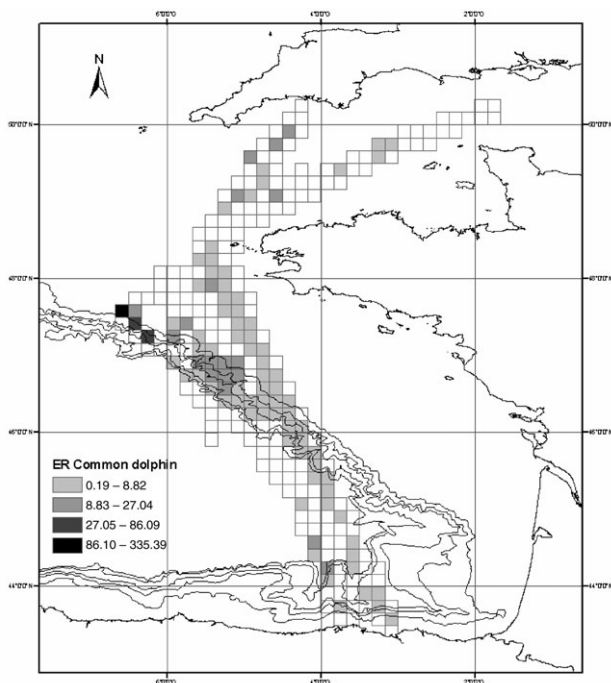


Figure 8. Encounter rates of common dolphin in the English Channel and Bay of Biscay, 1998–2002.

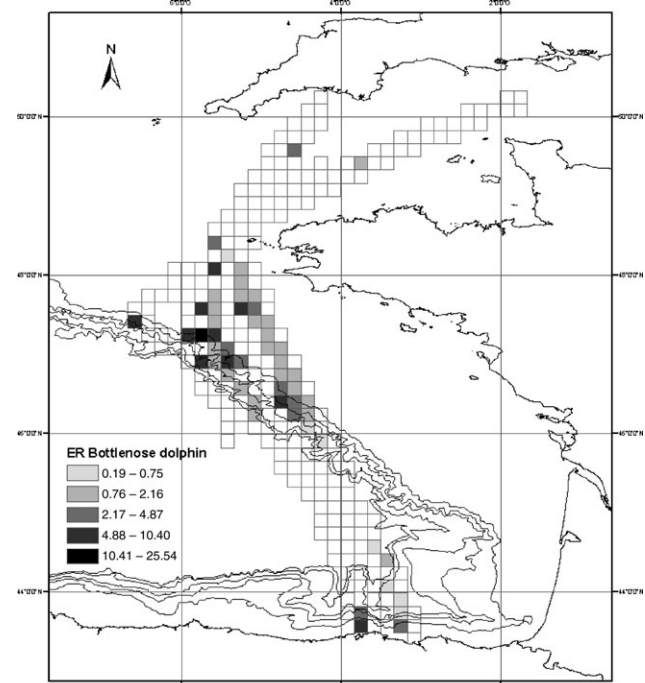


Figure 10. Encounter rates of bottlenose dolphin in the English Channel and Bay of Biscay, 1998–2002.

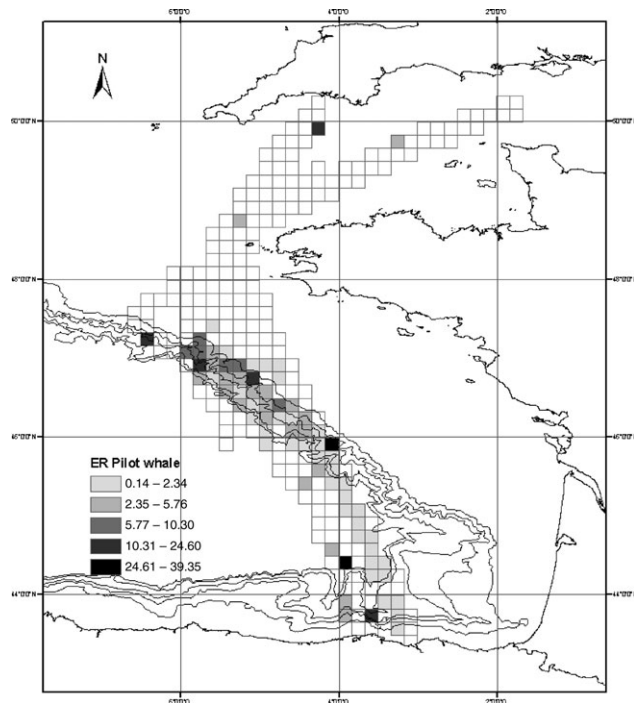


Figure 11. Encounter rates of long-finned pilot whale in the English Channel and Bay of Biscay, 1998–2002.

Nine sightings of northern bottlenose whales were made in deep oceanic waters of the southern Bay of Biscay (median = 3349; Q1 = 1756; Q3 = 3735; min = 972; max = 4470), where the encounter rate was 0.05 per 100 miles. Mean group size was 2.8.

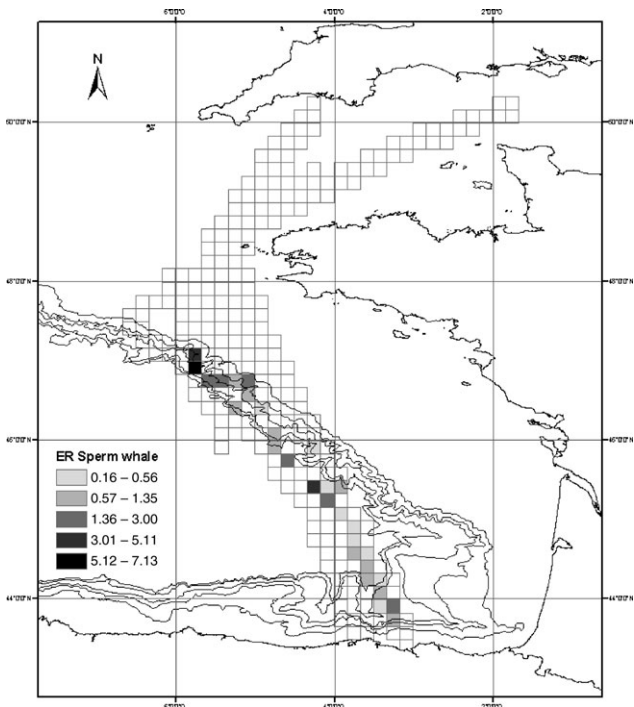


Figure 12. Encounter rates of sperm whale in the English Channel and Bay of Biscay, 1998–2002.

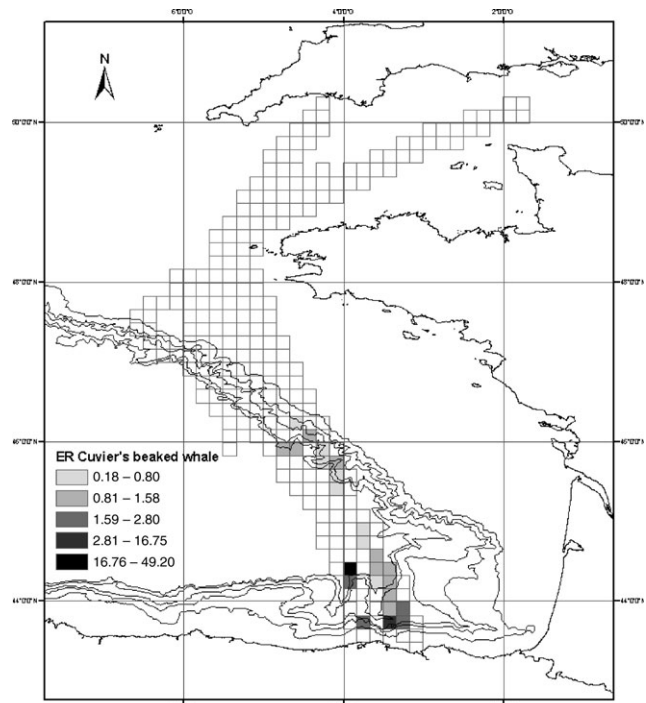


Figure 13. Encounter rates of Cuvier's beaked whale in the English Channel and Bay of Biscay, 1998–2002.

Killer whales were sighted on five occasions in the central and southern Bay, with group sizes ranging from one to five animals (s.d. = 1.6), and two groups of false killer whales were sighted in the same area, with six and seven animals in each. Killer and false killer whale sightings were in deep oceanic waters (>2000 m).

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 (*M. bidens*). Additionally, two unidentified mesoplodon whale groups were encountered in July 1999, involving two and five animals. Both sightings were in deep oceanic waters (>2 000 m).

Discussion

Few studies have been conducted to assess the distribution, encounter rate, 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. For this study, they allowed us to access information in little known offshore areas for low cost. However, their use often incurs limitations and biases in spatial and temporal coverage. Nevertheless, the ferry routes used in this study allowed us to survey several habitat types (shelf, shelf edge, and oceanic ecosystems) and to record data to investigate how toothed cetaceans are distributed in relation to different habitats, particularly at differing depth. The maps on encounter rates (i.e. the integration of effort-related data) presented here help to provide an accurate picture of the spatial distribution of the different cetacean species.

The study area is highly heterogeneous, covering shelf, slope, and oceanic waters. As a result, the diversity of toothed cetaceans in the data set is great, with typically shelf species such as the harbour porpoise and oceanic species such as beaked and

sperm whales being recorded. Delphinids, especially common, striped, and bottlenose dolphins, and pilot whales are particularly common in the Bay of Biscay. In the western English Channel, bottlenose dolphins, common dolphins, and harbour porpoises are the most frequently encountered (Evans, 1980; Kiszka *et al.*, 2004). The greater species diversity of toothed cetaceans in the Bay of Biscay may be attributable to the diverse range of their feeding habitats and prey. The depth and seabed topography of the English Channel is comparatively uniform, whereas that of the Bay of Biscay consists of 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 the Bay 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, e.g. the striped dolphin and Cuvier's beaked whale. Species such as the bottlenose dolphin, common dolphin, Risso's dolphin, and sperm whale tend to range widely throughout the world's oceans, and have been recorded in cold-, warm temperate, as well as tropical waters (Rice, 1998).

Distribution and habitats

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

The harbour porpoise is a typical shelf-water species, restricted in our study area to the shallow waters of the western English Channel and the northern Bay of Biscay. No sightings were made in the southern Bay, even in shelf waters, which suggests absence or low density of the species there. The species is generally considered to be a coastal one, living in shallow waters (Rice, 1998). Sightings of harbour porpoises beyond the edge of the continental shelf have also been made west of the UK (Bloor *et al.*, 1996; Macleod *et al.*, 2003). In the western English Channel and Bay of Biscay, harbour porpoises have been observed essentially over and beyond the continental shelf in water depths <200 m.

The distribution of the common dolphin is very broad in west European waters (Reid *et al.*, 2003). Our study reveals its presence from the English Channel to the southern Bay of Biscay, with more frequent rates of encounter 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 the distribution of the species was linked to regions of high topographic relief. In our data set, we observed an abundance of common dolphins at the shelf edge, a preference that may be related to the concentration of its main prey species in this area, especially *Sardina pilchardus* and *Trachurus trachurus* (Meynier, 2004).

The striped dolphin is considered to be an oceanic species, being sighted primarily off the continental shelf edge (Perrin *et al.*, 1994). Forcada *et al.* (1990) associated it with waters deeper than 1000 m. In the Bay of Biscay, most striped dolphin sightings were made beyond the 2000-m isobath, over the abyssal plain. In the Bay of Biscay, striped and common dolphins exploit different habitats, contrasting with the situation in the eastern tropical Pacific where the two species occur in the same

habitat (Reilly, 1990). The pattern of distribution in relation to depth for common and striped dolphins in the study area is similar to that in the Alboran Sea, in the western Mediterranean (Cañadas *et al.*, 2002).

Bottlenose dolphins were sighted commonly in offshore waters of the Bay of Biscay and the western English Channel, always over the shelf, the slope or in oceanic waters. Coastal and resident populations of bottlenose dolphins around the English Channel have been well documented, but populations living farther offshore have not been studied. In the Northeast Atlantic, offshore bottlenose dolphins are thought to prefer the continental slope area (Skov *et al.*, 1995). In the western Mediterranean, bottlenose dolphins are seen mainly 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, so their distribution may be predicted better by other environmental variables. The wide distribution could be the result of its opportunistic feeding behaviour in the northeast Atlantic, specifically the wide variety of prey on which it feeds (Klinowska, 1991; Spitz *et al.*, 2006).

Pilot whales were recorded generally in small groups, especially in deep waters of the Bay of Biscay, with few incursions into the English Channel. The species sighted in this study is probably the long-finned pilot whale, because the tropical form *G. macro-rhynchus* is rarely seen in the Bay of Biscay, based on stranding records from the Atlantic coast of France (CRMM, unpublished data). Pilot whales are considered to be primarily oceanic and frequently associated with the continental slope (Payne and Heinemann, 1993; Davis *et al.*, 1998; Abend and Smith, 1999; Bernard and Reilly, 1999; Cañadas and Sagarminaga, 2000). However, they can enter shallow coastal waters, at least for short periods. 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 the species is essentially oceanic in the area, being found beyond the 2000 m isobath, but with occasional incursions over the continental shelf. In the northeast Atlantic, pilot-whale sightings are generally over water deeper than 1000 m (Lewis *et al.*, 1998; Stone, 1998).

The sperm whale is a deep oceanic cetacean (Whitehead, 2003), but it is occasionally found over the shelf edge. Males will enter continental shelf waters, albeit rarely, and this is attributed to their opportunistic feeding ecology (Whitehead *et al.*, 1992; Best, 1999; Gregr *et al.*, 2000). In the Bay of Biscay, sperm whales are generally sighted in deep water, rarely over the continental shelf and only occasionally on the upper shelf edge. Highest rates of encounter were in the southern Bay of Biscay, over the Santander canyon. This pattern of distribution is in accord with studies on the species elsewhere (for review, see Whitehead, 2003).

Four species of beaked whale were recorded in this study: Cuvier's beaked whale, northern bottlenose whale, Sowerby's beaked whale, and True's beaked whale. Their presence in the area has been reported previously (Heyning, 1989; Weir *et al.*, 2004). Cuvier's beaked whale was the most frequently encountered species of the group and was most frequently encountered in the deep oceanic waters of the Santander canyon. It has been shown previously that submarine canyons are critical habitats for other species in cold temperate waters, including the northern bottlenose whale in the Gully, northwestern Atlantic (Hooker *et al.*, 1999). 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). Its presence in the Bay of Biscay seems to be irregular and could be linked to lower sea surface temperature.

The other species recorded during the study are not often seen. Risso's dolphin is regularly sighted in the shelf temperate waters off northwest Europe (Reid *et al.*, 2003), but was rare in the western Channel and the Bay of Biscay. However, the species does tend to be sighted seasonally in shallow coastal waters off the western French Channel coasts (Kiszka *et al.*, 2004). Sightings are occasionally made in the English Channel and in the Bay of Biscay, and the species has been sighted in both 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 western European waters (Reid *et al.*, 2003).

The other occasional species in this database are the killer whale and the false killer whale. The killer whale has a worldwide distribution, from tropical to polar pack ice of all oceans, but is most abundant 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, so it is best thought of as a vagrant to the waters of this study (Rice, 1998).

Limitations

Our study has described the main features of distribution and habitat characteristics for several toothed cetacean species. Data were limited for some species, meaning that a relationship between species distribution and depth could not be made. Data collected using platforms of opportunity are a cost-effective means of collecting and monitoring data to assess relative abundance and habitat preferences. However, the spatial coverage throughout the area and the survey effort *per se* is strictly limited and heterogeneous. Therefore, interpretation of species' habitat preferences cannot be inferred beyond the extent of the relatively fixed ferry route. The ferry departs and returns on its crossing at relatively fixed times throughout the year, further restricting and defining the periods available for observations. Moreover, the survey track runs approximately parallel to the central Biscay continental shelf, and that introduces bias into the pattern of sampling. Efforts should be made to extend the survey coverage either through alternative opportunistic platforms or on a dedicated vessel. However, the results presented here do suggest that valuable information can be collected from opportunistic platforms because they have provided some insight into the bathymetric preferences of cetaceans in the western Channel and Bay of Biscay.

Acknowledgements

We thank the Company of Whales, who collected a vast number of the sightings used for this study, and Organisation Cetacea (ORCA), who permitted the use of and supplied the ORCA data to us.

References

- Abend, A. G., and 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 pp.
- 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* Handbook of Marine Mammals, 6, The Second Book of Dolphins and the Porpoises, pp. 245–279. Ed. by S. H. Ridgway, and R. Harrison. Academic Press, London, UK.
- 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. Report 224 of the Joint Nature Conservation Committee, Aberdeen, Scotland. 138 pp.
- Breton, 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* Les Biocénoses Marines et Littorales des Côtes Atlantique, Manche et Mer du Nord: Synthèse, Menaces et Perspectives, pp. 17–20. Ed. by J.-C. Dauvin Laboratoire de Invertébrés Biologie des Marin et Malocologie. Service du Patrimoine Naturel/IEGB/MNHN, Paris, (in French).
- Buckland, S. T., Bloch, D., Cattanch, 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, 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. *et al.* 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. *et al.* 2002. Cetacean habitat in the northern Gulf of Mexico. *Deep Sea Research Part I*, 49: 121–142.
- Duguay, 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. PhD thèse, de l'École Nationale Supérieure Agronomique de Rennes. 239 pp (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. *et al.* 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* Handbook of Marine Mammals, 4, River Dolphins and the Larger Toothed Whales, pp. 289–308. Ed. by S. H. Ridgway, and R. Harrison. Academic Press, London, UK.

- 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, IUCN, Gland, Switzerland. 425 pp.
- 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.
- 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 pp.
- 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.
- 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 UK*, 83: 1187–1192.
- 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 pp.
- Northridge, S., Tasker, M. L., Webb, A., and Williams, J. M. 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 of the International Whaling Commission, 14: 51–68.
- Perrin, W. F., Wilson, C. E., and Archer, F. I. 1994. Striped dolphin *Stenella coeruleoalba* (Meyen, 1833). In *Handbook of Marine Mammals*, 5, The First Book of Dolphins and the Porpoises, pp. 129–159. Ed. by S. H. Ridgway, and R. Harrison. Academic Press, London, UK.
- Quéro, 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 (Ifremer). 229 pp (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 pp.
- 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 4, The Society for Marine Mammalogy. 231 pp.
- 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. *et al.* 2005. Long-term oceanographic and ecological research in the western English Channel. *Advances in Marine Biology*, 47: 1–105.
- Spitz, J., Rousseau, Y., and Ridoux, V. 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. Report 278 of the 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 UK*, 84: 1095–1099.
- Williams, A., Williams, R., Heimlich-Boran, J. R., Evans, P. G. H., Tregenza, N. J. C., Ridoux, V., Liret, C. *et al.* 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 UK*, 82: 509–511.
- Whitehead, H. 2003. *Sperm Whales: Social Evolution in the Oceans*. The University of Chicago Press. 431 pp.
- 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.