The Ecology of Cuvier's beaked whale, *Ziphius cavirostris* (Cetacea: Ziphiidae), in the Bay of Biscay

PhD Dissertation

Submitted by

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Abstract

This dissertation introduces the habitat use and spatial-temporal distribution of Cuvier's beaked whale (*Ziphius cavirostris,* Cuvier, 1823) in the Bay of Biscay, from surveys carried out by the Biscay Dolphin Research Programme between 1995 and 2007. I have analysed the spatio-temporal distribution of Cuvier's beaked whale, using dedicated and opportunistic sightings and the interactions with fixed physical variables (depth, slope and aspect), non-fixed environmental variables (sea surface temperature) in the Bay of Biscay, northeast Atlantic. This study used a differing combination of environmental variables and modelling: GAM (General Additive Model), and ENFA (Ecological Niche Factor Analysis), and PCA (Principal Component Analysis). Geographical Information Systems (GIS) and Remote Sensing were used to achieve this. The habitat preferences of Cuvier's beaked whale showed strong correlations with water depths >1000m and <4000m and steep slopes, associated with the Capbreton canyon, in the southeast Bay of Biscay and the continental shelf slopes in northern Biscay. Areas of high suitability for Cuvier's beaked whale were predicted for the Bay of Biscay and predictions showed high habitat suitability areas over continental shelf slopes and submarine canyons. The variety of modelling techniques used to identify the habitat preferences and to predict areas of high suitability for Cuvier's beaked whale in the Bay of Biscay all proved advantageous. On a global scale, techniques such as these could be applied to help research worldwide for future implementations of protected areas to conserve and maintain this species. The abundance and distribution of Cuvier's beaked whales varied between years and seasons, with an increase in sightings over time and a seasonal distribution shifting north during spring and summer. Stranding records were also analyzed and compared with the sightings data, which identified regional patterns in seasonal distribution between France, the UK and Ireland. In addition to Cuvier's beaked whale, this study investigated other deep-diving cetaceans (Northern bottlenose whale, *Hyperoodon ampullatus*, Sowerby's beaked whale, *Mesoplodon bidens,* Sperm whale, *Physalus macrocephalus,* Pilot whale, *Globicephala melas*) and non-deep diving cetaceans (Fin whale, *Balaenoptera physalus*, and Common dolphin, *Delphinus delphis*) observed in the Bay of Biscay and the English Channel. The Bay of Biscay is the most northerly range of the Cuvier's beaked whale in the eastern north Atlantic and with year round observations, it could be suggested the population may be resident. This raises the question, could Cuvier's beaked whale act as a predictor of increasing water temperatures because of climate change by shifting their distribution further north.

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I herby declare that no part of this thesis has been submitted for a degree to the University of Southampton, or any other University, at any time previously. The material included is the work of the author, except where expressly stated

Jaclyn Smith
Southampton, July, 2010

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- Laboratory for Satellite Oceanography, National Oceanographic Centre: sea surface temperature data
- Ocean colour website: Sea surface temperature.
- The Natural History Museum: Strandings data
- Irish Whale and Dolphin Group: sightings and strandings data

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Chapter 1

Introduction

1. Introduction

1.1 Cetaceans and habitat use

A major goal of ecology is to understand how characteristics of the environment affect the distribution of organisms (MacArthur, 1972). Habitat selection has a strong impact on these distribution patterns by influencing the use of habitat in both time and space. Habitat studies allow us to understand species integration in an ecosystem and to define critical habitat, such as feeding and breeding. If we examine the geographic distribution of a widely ranging species, we find that the distributional range consists of both occupied and unoccupied areas. Those areas actually occupied that meet the requirements for a species' survival and reproduction are its habitat. The correlation of environmental features with sightings data can improve our understanding of cetacean ecology and be indicative of, if any, oceanographic variables that may be affecting cetacean distribution (Kenney and Winn, 1987).

Studies of habitat selection have often focused on terrestrial ecosystems where habitat patches change over comparatively long temporal scales (Redfern *et al.,* 2006). In marine ecosystems, habitats of mobile species such as cetaceans can change over short time spans and fine spatial scales (Bjørke, 2001). This complexity poses unique challenges when trying to model species-habitat relationships. Studying habitat selection by marine mammals therefore generates additional challenges but can also improve our understanding of the general rules governing species distributions. Studying cetacean habitat selection can be extremely challenging as they spend most of their lives under water, and collecting data on free-ranging animals at sea presents numerous logistic and financial challenges (Ingram *et al.*, 2007). In addition, the study of marine ecosystems requires methods for investigating patchiness of cetacean prey and variability of their habitat (Croll *et al.*, 1998). Because of these constraints, early studies of habitat use by whales usually chose easily accessible oceanographic variables and broad spatial scales, while de-emphasizing temporal variability (Bjørke, 2001). In recent years, new developments in remote-sensing (e.g. satellite data) and analytical tools (e.g. geographic information systems, spatial statistics, computer-intensive methods) have led to a rapid increase in the explanatory power of habitat selection models (Redfern *et al.,* 2006). Studies that quantify habitat use and selection can be used to assess the biological requirements of species (Redfern *et al.*, 2006), to predict effects of habitat and climate changes (Thomas *et al.,* 2004), to justify protection of key areas (Hooker *et al.*, 1999c; Cañadas *et al.*, 2002) and to improve conservation planning, as models may be an important tool for mitigating anthropogenic impacts on these species (Redfern *et al.*, 2006).

Over the last decade, oceanography and sea floor topography (physiography) have been increasingly used as an approach to understanding cetacean distribution (Baumgartner, 1997; Davis *et al.*, 1998; Baumgartner *et al.*, 2001; Hooker and Baird, 2001b; Waring *et al.*, 2001; Cañadas *et al.*, 2002; Yen *et al.*, 2004; MacLeod and Zuur, 2005). In particular depth and slope are the key variables. Prior to these studies, Kenny and Winn (1987) compared the distribution of cetaceans near submarine canyons to distributions in adjacent shelf/slope areas. It seems that as well as depth and slope, submarine canyons play an important influence on cetacean distribution throughout the world's oceans, even if modalities and intensities depend on hydrological, topographical, and biological contexts.

The general distribution of cetaceans appears to mirror that of their prey, with their main distribution occurring in areas of increased productivity, including seasonal or unpredictable food chains. The seasonal, monthly, and daily migrations (horizontal and vertical) of prey species are important factors to be considered when establishing the time of year and the time of day cetaceans are sighted. It may be that different areas such as the continental slope and associated canyons, may reach their highest species richness during different times of the month and during different times of the day and, therefore influencing the time and place when cetaceans are observed. As predicted by their feeding ecology, cetaceans tend to have non-uniform distributions at a wide range of spatial scales (Jaquet and Whitehead, 1996). These clumped distribution patterns were first linked to preferential use of certain water depths (e.g. Gowans and Whitehead, 1995, Baumgartner, 1997; Davis *et al.*, 2002) and heterogeneous seabed topography (e.g. Evans, 1971, 1974; Hui, 1985; Selzer and Payne, 1988; Gowans and Whitehead, 1995, Baumgartner, 1997, Davis *et al.*, 2002; Ingram *et al.,* 2007).

The distributions of cetaceans are not directly influenced by the seafloor topography, but are more influenced by hydrological or biological phenomena. For example, bottom relief modifies currents, leading to concentration of organisms. Hydrological features, including eddies and topographically-induced upwellings generate fronts and bring nutrients, which in turn increase primary productivity, and the aggregation of zooplankton from enhanced secondary production. Internal waves, which are produced by complex and steep topography, can also lead to the concentration of prey species. Many papers report evidence that cetaceans occupy the continental slope, especially its upper part and submarine canyons that cut into the slope. Steep slopes and submarine canyons play an important role in influencing the water patterns in and around the surrounding area because of their size and the area they occupy (Hickey, 1995). Submarine canyons can strongly modify flow, shelf-slope exchanges of water and material (Hickey, 1995; Perenne *et al.*, 2001) and this coupling can aid the transport of particulate organic matter that influences productivity. Submarine canyons can also act as funnels for water upwelling from deeper oceanic levels to shallower shelf regions, providing nutrient inputs to the marine ecosystem (Flaherty, 1999) and enhancing productivity.

Physical processes in submarine canyons have received much attention (Shepard *et al.*, 1974; Freeland and Denman, 1982; Noble and Butman, 1989; Breaker and Broenkow, 1994; Allen, 1996; Alvarez and Tintore, 1996), but studies on the ecological processes of canyons are still limited. The morphological features and the geological importance of submarine canyons are well defined. Submarine canyons play an important part in the transport of sediment (Shepard *et al.*, 1974; Gardner *et al.*, 1989) water and biological production into the deep ocean (Vetter and Dayton, 1998) from the continental shelf. They have a large impact on coastal processes (Hickey, 1995), such as the ultimate fate of sediment in suspension or resuspension over the continental shelf (Hickey, 1986; 1995). It is, therefore, important to incorporate the processes on the continental shelf/slope to gain a better understanding of the processes seen within canyons.

1.2 Beaked whales

Beaked whales (Order Odontoceti: Family Ziphiidae) are the second largest group of cetaceans after the Family Delphinidae (Rice, 1998). The Ziphiidae comprise six genera and 21 different species; 14 within the Genus *Mesoplodon*, 2 in the Genus *Hyperoodon*, 2 in the Genus *Berardius* and 3 monospecific genera; *Ziphius*, *Tasmacetus* and *Indopacetus*. Most of what we know has come from the analysis of stranded remains and there are only four beaked whales that are reasonably well known from studies at sea. In some cases, several have yet to be formally described and some species have never been seen alive. The fossil record for beaked whales dates back to the middle of the Miocene age (Mead, 1975; Hooker 2001a), approximately 10 to 15 million years ago (Hooker, 2001a). This makes them one of the oldest families of whales currently found in our oceans.

Beaked whales are deep-water, oceanic animals (Hooker and Baird, 2001b), are often associated with regions characterized by submarine canyons or steep escarpments. They are deep divers and often dive down to depths exceeding 1000m (Tyack *et al.*, 2006; Houston, 1991). As beaked whales are deep-divers they spend little time at the surface (Reeves *et al.*, 2002) and because of this they are difficult to observe (Barlow and Gisiner, 2006; Barlow *et al.*, 2006). The beaked whales appear to have a habitat preference for complex topographic features, such as steep continental slopes and submarine canyons (Whitehead *et al.*, 1997; Hooker and Baird, 1999a, 2002; Frantzis *et al.*, 2003; MacLeod and Zuur, 2005).

Submarine canyons are just one of the underwater topographic features that beaked whales are associated with and submarine canyons are characteristic of many shelf breaks in the world's oceans (Alvarez and Tintore, 1996). The physical and biological oceanography within canyons (Bosley *et al.*, 2004), together with depth, have undoubtedly a significant influence on both the benthic and pelagic ecosystems. It is very likely that these factors influence the distribution and aggregation of species that are preyed upon by beaked whales.

Studies on beaked whales have been carried out in a number of locations including the Northwest Atlantic (Hooker and Baird, 1999a), Bahamas (MacLeod and Zuur, 2005), the Ligurian Basin (D'Amico *et al.*, 2003; Moulins *et al*, 2007), Hawaii (Baird *et al.*, 2004; 2006) and Greece (Frantzis, *et al.*, 2002). These studies have demonstrated beaked whales inhabit primarily deeper and off-shelf waters, notably areas associated with specific bathymetric and/or oceanographic features (Mead, 1989; Whitehead *et al.*, 1997; Davis *et al.*, 1998; Hooker and Baird, 1999a; Waring *et al.*, 2001). Frequently observed species include Cuvier's beaked whale, *Ziphius cavirostris*; the most widespread and cosmopolitan (Heyning, 1989), Sowerby's beaked whale, *Mesoplodon bidens,* observed in cold temperate waters of the North Atlantic (Mead, 1989; Hooker and Baird, 1999b), the northern bottlenose, *Hyperoodon ampullatus,* the largest member of the family that is frequently observed in The Gully, Nova Scotia (Hooker and Baird, 1999a; Hooker *et al.,* 2002), the Blainville's beaked whale, *Mesoplodon densirostris*, from studies off Great Abaco Island, Bahamas (MacLeod *et al.*, 2004a; Macleod and Zuur, 2005) and Baird's beaked whale in the northern Pacific (Ohizumi and Kishiro, 2003). A study carried out by MacLeod *et al.* (2006c) indicates that Cuvier's beaked whale and the Northern Bottlenose whale and are the better known members, as more strandings and sightings of these two species are recorded than any other beaked whale.

1.3 Cuvier's beaked whale

The Cuvier's beaked whale, *Ziphius cavirostris,* (Figure 1.1) was described by George Cuvier in 1823, as a fossil using a partial skull collected in 1803 near Fos-sur-Mer, on the Mediterranean coast of France (Heyning, 1989). Published details of the skull in his monumental 'Recherches sur les Ossements fossils' (1823) describe it as an extinct whale, for which he created the Genus *Ziphius* from the Greek '*Xiphos*', a sword, and a species *cavirostris* for the latin '*cavus*', hollow and rostrum a beak (Heyning, 1989). In 1872, Sir William Turner described a whale from the Shetland Islands and realised he was dealing with a live Cuvier's fossil, and also realised that many new beaked whales described all over the world's beaches were *Ziphius cavirostris* (Heyning, 1989). The Cuvier's beaked whale has a cosmopolitan distribution (Figure 1.2) and is thought to be the most widespread of the beaked whales, found in tropical and temperate waters, although not found in polar waters (Heyning, 1989) below the 10°C isotherm (Houston, 1991). From a recent study by MacLeod *et al.* (2006c), they have shown from a number of sources that the distribution is more extensive than previously suggested, with sightings in sub-polar and even polar waters. However, these sightings are not within its normal range. Distribution was primarily known from strandings, but now they are also known from sightings. Both the sightings and strandings are indicative of their cosmopolitan distribution (MacLeod *et al.,* 2006c).

In recent years, sightings of Cuvier's beaked whale have been reported more frequently in areas with steep and complex underwater topography. These areas include: Japan (Ohizumi and Kishiro, 2003), Greece (Frantzis *et al.*, 2002; 2003; Frantzis, 2004;), Ligurain Sea (Moulins *et al.*, 2007) Northeast Pacific (Ferguson *et al.* 2006) and Australia (Flaherty, 1999), and they are also encountered around oceanic islands, including Hawaii (NMFS, 2003; McSweeney *et al.*, 2007) and Great Abaco, Bahamas (MacLeod *et al.*, 2004a). The global population size is still unknown and to assess their geographical distribution it is important to understand their habitat preferences. What is known from research worldwide to date, however, is that Cuvier's beaked whales are seen in groups ranging between 1-15 individuals and with an average group size of 2.3 (MacLeod and D'Amico, 2006a; Moulins *et al,* 2007) and 3.8 (Falcone *et al*, 2009). Because their population status is largely unknown, migrations are unknown for this species. Their deep-diving behaviour, inconspicuous blows, and tendency to avoid vessels may help explain the rarity of sightings. A breakthrough in the behaviour of Cuvier's beaked whale was determined in the Ligurian

Sea by Tyack *et al.* (2006). The diving behaviour was assessed using the DTAG (Suction cup attached), and Cuvier's beaked whales were found to dive between 1005m (min) and 1265m (max) depth with the duration of dives lasting between 34 to 57 minutes (Aguilar De Soto *et al.*, 2006; Tyack *et al.*, 2006) and 1888m for 85 minutes (Tyack *et al*, 2006).

Figure 1.1: Cuvier's Beaked Whale, *Ziphius cavirostris*.
Photo taken in the Bay of Biscay.

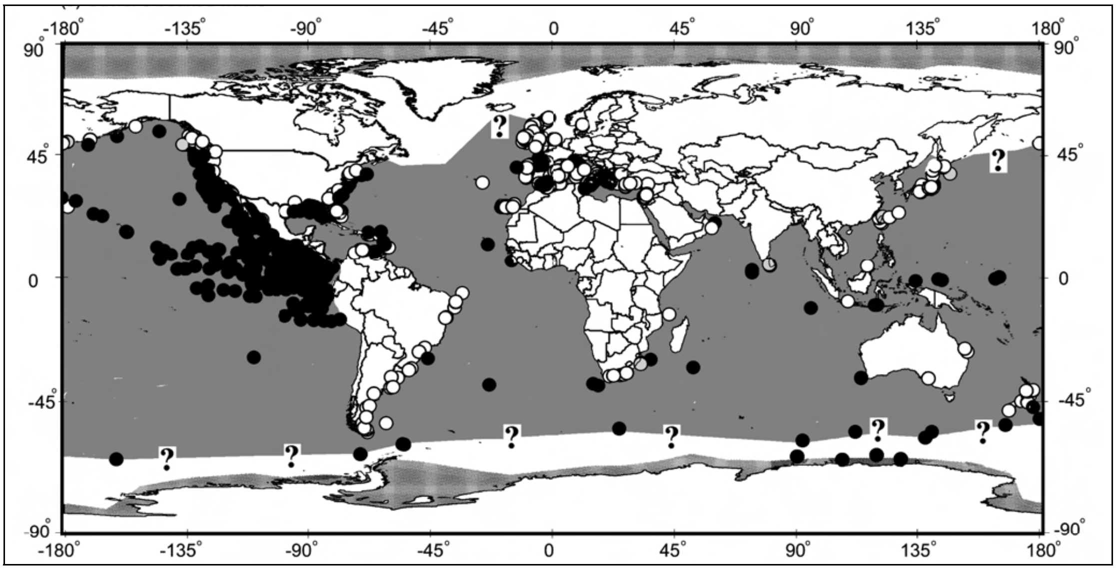


Figure 1.2: Global distribution of Cuvier's Beaked Whale (from MacLeod *et al.,* 2006c)

The strandings of individuals has made it possible to carry out stomach content analysis and necropsy. Prey species found in the stomachs of individual species consist mostly of mesopelagic or deepwater benthic organisms such as squid (Heyning, 1989), which is indicative of their deep diving behaviour. Results from necropsies carried out on the beaked whales stranded in the Canary Islands, also show physiological effects that are consistent with decompression-like sickness: the formation of bubbles within organs. In particular, gas bubble lesions and haemorrhages were found in fourteen necropsied beaked whales, including Cuvier's beaked whale (Jepson *et al.*, 2003; Fernandez *et* al, 2005). This bubble formation or excessive nitrogen supersaturation in tissues, known as the bends or decompression sickness (Mackay *et al.*, 1982), may be in response to behavioural changes to normal dive profiles, such as accelerated ascent rate (Tyack *et al.*, 2006). It is reported that some of the mass strandings events (two or more) of Cuvier's beaked whale might be linked to active sonar and seismic activities that use high power sonar (Simmonds and Lopez-Jurado, 1991; Frantzis, 1998; D'Amico *et al.*, 2003; Jepson *et al.*, 2003; Frantzis, 2004; Freitas, 2004; Martin *et al.*, 2004; Fernandez *et al.*, 2005). For example, twelve whales were found stranded at many locations of the Kyparissiakos Gulf, Greece in 1996 (Frantzis, 1998, 2004), twenty-four whales stranded in the Canary Islands on three occasions (Simmonds and Lopez-Juraco, 1991), fourteen stranded again in the Canary Islands in 2002, close to the site of international naval exercise (Martin *et al.*, 2004), approximately fifteen whales and a dolphin stranded on March 15, 2000, in the northern Bahamas (Report, Joint Interim Bahamas Report, 2001).

Although the Cuvier's beaked whale was hunted in the past, so few were caught that the population was not disturbed, but the greatest threat is thought to be entanglement in fishing gear, ship strikes and possibly trauma from acoustic sources, resulting in strandings related to human-activated sonar (Evans and Miller, 2004). As already mentioned, beaked whales remain the least known of all cetaceans and it is only through the efforts of research over recent years that knowledge of their distribution and habitat usage is being unveiled, although there is still mush that is unknown. While widespread in their distribution, Cuvier's beaked whales appear to inhabit areas of complex underwater topography. Because of their deep diving habits, it is difficult to study them, but finding populations that present themselves year round can only benefit future research to help towards their conservation. The direct link of deaths to naval activity has yet to be fully confirmed, but because there has been links of physiological effects to sonar activity, they may need protection. If this study, along with past and future research, can confirm a resident population of Cuvier's beaked whale in the Bay of Biscay, this may act as a benefit towards future conservation legislation such as marine reserves.

From surveys carried out using fixed route platforms (Williams *et al.*, 2002a), such as the P&O ferry "Pride of Bilbao", it appears that Cuvier's beaked whale does not have a random distribution throughout the Bay of Biscay (study area – see next section), but is associated particularly with the CapBreton Canyon (Williams *et al.*, 2002a). Observations made by the Biscay Dolphin Research Programme (BDRP) have also indicated that northern bottlenose whales are likewise associated with submarine canyons there. It is thought they are spatially and temporally segregated from Cuvier's beaked whale, and it has been suggested they may have different preferences for habitat, prey and/or interact competitively (Williams *et al.*, 2002a).

1.4 Study Area: Bay of Biscay, North East Atlantic

The region of study for this project is the Bay of Biscay (Figure 1.3). The Bay of Biscay is situated geographically between 43 °N to 50 °N and -1 °W to -10 °W in the Northeast Atlantic and is characterised as a temperate open oceanic bay bounded by the Spanish coast to the south, oriented E-W and the French coast to the east, oriented S-N (Koutsikopoulos and Le Cann, 1996). The Bay of Biscay is sometimes described in two parts: the Northern Bay and the Southern Bay. Both areas have variable sea depths, ranging from the shallow continental shelf (less than 100 metres) to the abyssal plain (greater than 4000 metres), with many underwater features such as submarine canyons, seamounts and a steep continental slope. The Armorican shelf in the north of the bay is up to 180km wide, whilst in the south the continental shelf is narrow, only 30 to 40km width (Koutsikopoulos and Le Cann, 1996).

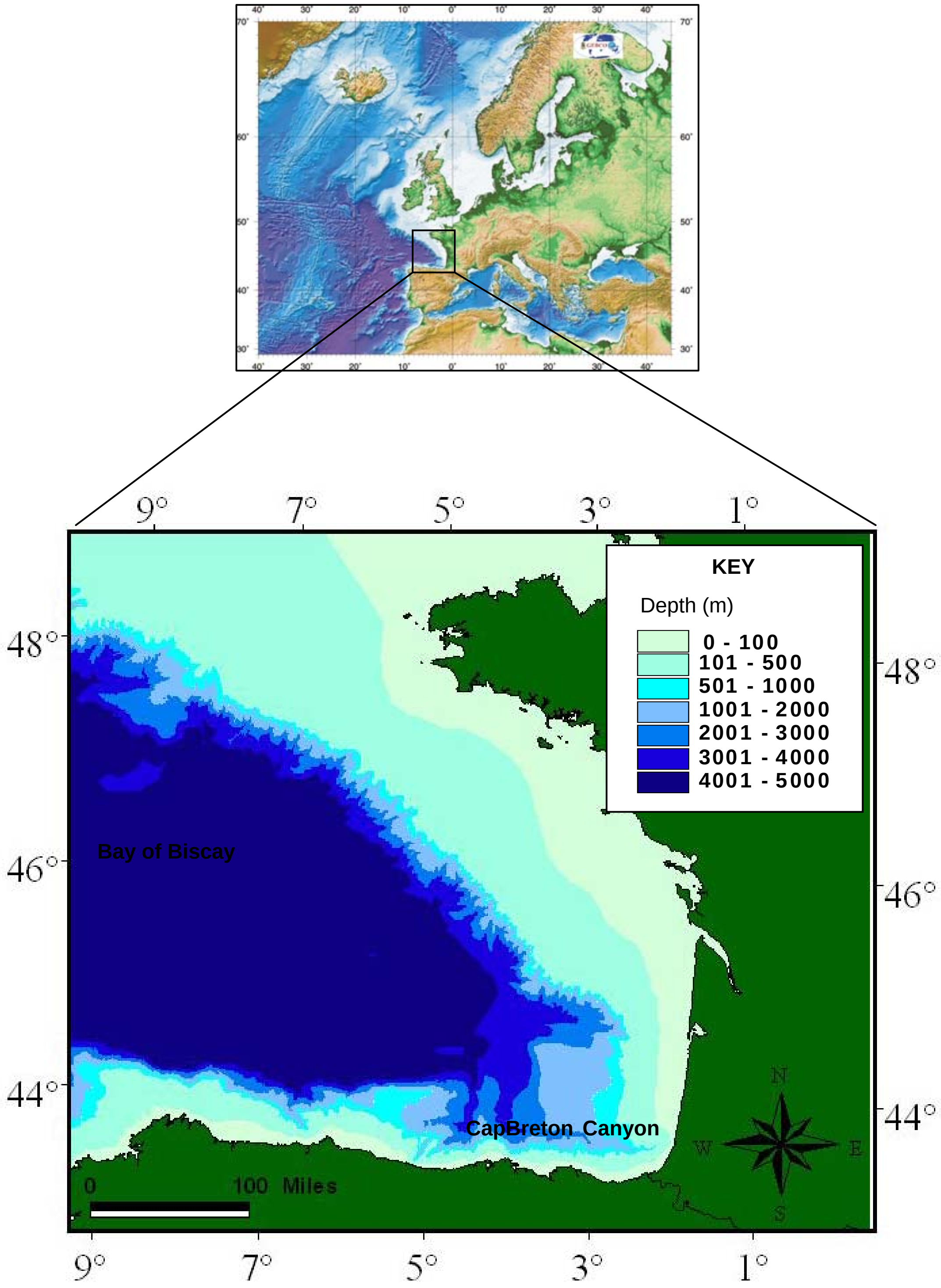


Figure 1.3: Bathymetry map of the study area, northeast Atlantic.
(Top map taken from www.noc.soton.ac.uk)

The CapBreton Canyon, in the southeast corner of the Bay of Biscay, is a major morphological feature that cuts into the continental slope in an E-W direction and the 1000m contour is only 3 km from the coast. The CapBreton canyon has been studied for over a century (Cirac *et al.*, 2001). It is the deepest submarine canyon in the world, the longest off Europe, and its head is located only 250m from the coastline (Cirac *et al.*, 2001). The canyon was formed by the Adour River (SW France), but has been disconnected from the river since 1310 AD (Cremer *et al.*, 2003). The canyon runs westward and parallel to the north coast of Spain for 160 km due to structural control, then turns northward, widens and abruptly disappears in the continental rise by 3500m water depth (Gaudin *et al.*, 2003).

The Bay of Biscay is located between the eastern part of the sub-polar gyre and the subtropical gyre (Planque *et al.*, 2003) and may be affected by both gyres depending on latitude and the general circulation. The general circulation is a weak (~5-10 cm sec^{-1}) (Pingree and Le Cann, 1990) anticyclonic circulation for the oceanic part of the Bay of Biscay (Koutsikopoulos and Le Cann, 1996). In the southern Bay of Biscay, east-flowing shelf and slope currents are common in autumn and winter due to southerly and westerly winds (Valencia *et al.*, 2004). The different circulation and current patterns for the continental shelf and the main Bay are shown in Figure 1.4 On the continental shelf, the circulation is governed by the combined effects of tides, river inputs and, wind so that shelf waters are colder in winter and warmer and less saline in summer (Valencia *et al.*, 2003).

During winter and summer in the Bay of Biscay, the weather is more or less stable and predictable whereas spring and autumn are variable (Valencia *et al.*, 2004). The transition between the seasons shows changes in currents and wind conditions, with particular wind regimes leading to the onset of coastal upwelling (Planque *et al.*, 2003). Between spring and summer, north-easterly winds of medium to low intensity are prevalent, causing frequent coastal upwelling events (Koutsikopoulos and Le Cann, 1996). Between autumn and winter, southerly and westerly winds are dominant, causing frequent downwelling events (Borja *et al.*, 1996). Upwelling is observed along the French and Spanish coasts and the strength of the upwelling corresponds to the winds and water masses (Gill and Sanchez, 2003b).

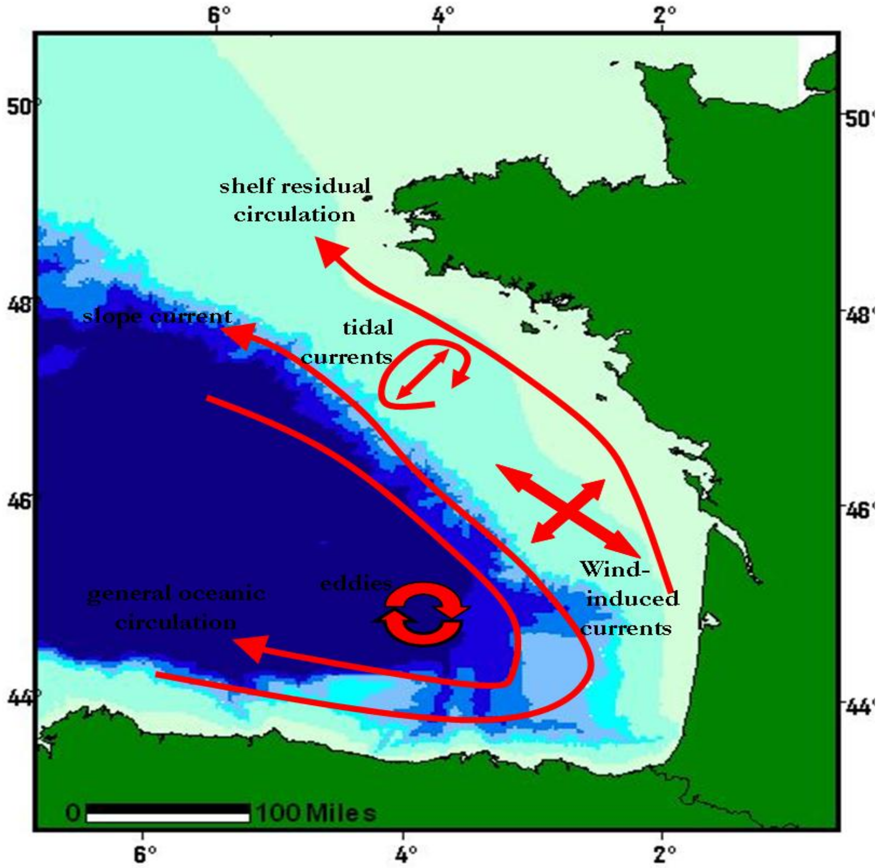


Figure 1.4a: Circulation and current movements in the Bay of Biscay (as described and shown by Koutsikopoulos and Le Cann, 1996).

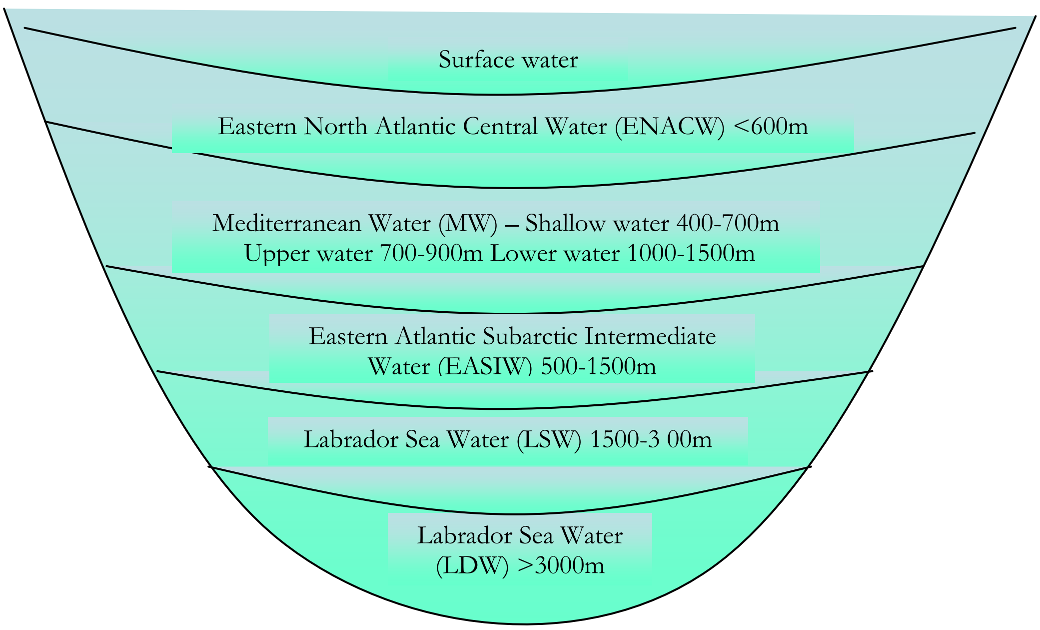


Figure 1.4b: Water masses of the Bay of Biscay. As described by Ospar (2000).

In a study by Gil and Sanchez (2003b), three different hydrographic patterns were found. The first pattern, observed in 1993, 1998, 1999 and 2000, was associated with the distribution of water masses. The second pattern observed in 1994 and 1997 appeared to be linked to a conspicuous front that separated the cold coastal upwelled water from offshore warmer water. The third pattern observed in 1995 and 1996 was the result of the width of the coastal band that did not appear to be continuous along the shelf area and it was thought that it might reflect wind reversals

The water masses observed in the Bay of Biscay can be seen in figure 1.5. This figure is put together from information provided by OSPAR (2000), which is compiled using a number of sources that described the water masses in this region including, Rios *et al.*, 1992; Pollard *et al.,* 1996. Later studies also described similar water masses in the Bay of Biscay (Garcia-Soto *et al.,* 2002; Gil, 2003; Gonzalez-Pola *et al.,* 2005).

The extension of the warm water Iberian poleward current is also observed in the Bay and is now considered a common feature of winter (*Navidad*) circulation (Garcia-Soto *et al.,* 2002) that coincides with the spawning season of pelagic and demersal species due to the higher concentration of nutrients than the surrounding area (Gil, 2003a).

An important feature of the Bay of Biscay is that it is one of the world's strongest generation sites for internal tides (Gerkema *et al.*, 2004). Internal tides and surface tides are amplified by the interaction of bottom topography (New, 1988) and a consequence of these tides is the high phytoplankton abundance and cool water at the surface above the continental shelf break (New, 1988).

The prevailing winds and sea currents make the waters along the continental slope productive and attractive to marine life, including cetaceans and seabirds. The Biscay Channel region is an important area year round for cetaceans, and supports over 30 species out of the 86 species recorded worldwide. The association between seabirds and cetaceans is often made (Evans, 1982; Croll *et al.*, 1998; Yen *et al.*, 2004). Evans (1928) also comments on this association whereby it dates back to the whaling activities in the 1800's.

1.5 Outline of thesis

Based on the literature review, I suggest two hypotheses. First, complex underwater topography has been identified as an important parameter and therefore I expect a clear habitat selection signal (i.e. Cuvier's beaked whale should select environmental characteristics that differ from those of the widely available habitat). Second, because marine habitats are very dynamic, I expect time-varying variables, such as water temperature to be extremely important for habitat selection and seasonal movements because the Bay of Biscay is the most northern limit of the regular range of Cuvier's beaked whale. Therefore, my overall working hypothesis is that two exclusive processes influence the fine-scale distribution of Cuvier's beaked whale: habitat selection and water temperature.

Understanding patterns in the distribution and abundance of species is a fundamental element in ecology. Cetaceans respond to spatial and temporal environmental variability across a range of scales. Therefore, environmental patterns will provide insight into cetacean distribution and abundance, two characteristics of their ecology that must be understood in order to conserve and manage their populations. This thesis contains several elements that constitute original scholarship and contribute to the advancement of knowledge in its field. The main aim of this thesis is to improve our understanding of the environmental factors that influence the distribution of Cuvier's beaked whale in the Bay of Biscay, northeast Atlantic. I was able to quantify habitat selection and predict the distribution of the Cuvier's beaked whale while considering not only the spatial variability but also the temporal dynamics of the available habitat. Beaked whale data are limited, and studying the ecology of Cuvier's beaked whale requires that the most be made of the available data. The goals for my research are twofold:

1.) Provide predictions of habitat use in relation to certain physical and biological components of their environment.

2) Examine spatial and temporal patterns in Cuvier's beaked whale distribution in the Bay of Biscay.

To do this the goal is to answer as many questions as possible by using different techniques, incorporating sightings and strandings data, in new ways to pin point factors affecting the distribution of Cuvier's beaked whale. The results will also highlight the importance for the need of regional studies in the Bay of Biscay. The value of looking at seasonal movements will indeed further our knowledge of what factors may be driving such movements, which in turn will help to interpret how possible climate change effects may affect Cuvier's beaked whale in this region in the future. Another important influence that is looked at is how their distribution is effected over small and large spatial scales, as different environmental variables may be important on a fine scale but not on a large scale, and vica versa.

This is a manuscript-based thesis, containing 6 chapters. Chapters 2, 3, 4, and 5 have been written in manuscript format to facilitate publication in peer-reviewed journals. Therefore, some repetition occurs between chapters, especially in the literature reviews, methods and data sets. Chapters 2 and 3 both focus on habitat use, but differ in the philosophical approach. They aim to compare used vs. available habitats, to test whether habitats are used in proportion to their availability or if preference leads to disproportionate use of certain habitats. In chapter two, I present data on habitat preferences and spatial scales using General Additive Modelling to assess the dedicated survey (presence-absence) data to model Cuvier's beaked whale habitat preferences and distribution from ferry based surveys. Chapter 3 uses Ecological Niche Factor Analysis modelling to show the predictive distribution of Cuvier's beaked whale within the Bay of Biscay using opportunistic (presence-only) sightings data, which identify areas of core/marginal/unsuitable habitats. Such information is crucial to assess the biological requirements of these species and to identify areas of critical importance. Chapter 4 seeks to compare the distribution and habitat preferences of Cuvier's beaked whale to oceanic deep-diving cetaceans using Principal Components Analysis. Chapter 5 looks at the spatial and temporal distribution within the Bay, using sightings and strandings data and this is particularly important as the distribution has changed over the last few years. The final chapter (Chapter six) brings all the chapters together for the final discussion to define the niche occupied by the Cuvier's beaked whale. Here the discussion will lead onto how the results from this study can be used globally and to help their conservation status.

Chapter 2

Habitat Utilisation by the Cuvier's beaked whale, in the Southern Bay of Biscay using Presence/Absence data

2.1 Introduction

Investigations into the relationships between cetaceans and the environment can increase knowledge of cetacean distribution by predicting areas where cetaceans are more likely to occur. The availability of such information would have many potential benefits for example; a greater knowledge of cetacean occurrence in an area would assist in the designation of special areas of conservation for particular species and such information would also be useful in the development of environmental impact assessments.

The distributions and movements of marine mammals are clearly influenced by their oceanic environment. Although such relationships are inherently dynamic, distributions have been related to a range of environmental determinants (Hastie *et al.,* 2005), including sea surface temperature (Jaquet, 1996; Baumgartner *et al*., 2001; Piatkowski *et al*., 2001; Benson *et al.,* 2002; Littaye, *et al*., 2004; Johnston *et al*., 2005; Tynan *et al*., 2005), salinity (Selzer and Payne, 1988; Forney, 2000; Tynan *et al*., 2005), and water depth (Gowans and Whitehead, 1995; Baumgartner, 1997, Davis *et al*., 1998; Carretta *et al*., 2001; Benson *et al*., 2002; Tynan *et al*., 2005; Ballance *et al*., 2006; Wall *et* al., 2006; Praca and Gannier, 2007). However, the importance of these determinants appears to vary among regions and species, a feature that highlights the need to focus studies on the role of oceanography in cetacean habitat selection on a regional basis. Distribution of cetaceans is thought to be primarily influenced by aggregation of suitable prey species (Payne, 1986; Baumgartner, 1997; Davis *et al.,* 1998; Torres *et al*, 2008). The distribution of prey species is often linked to a number of oceanographic features, for example, depth and slope play an important role in directly limiting the distribution of benthic or demersal prey species (Mauchline, 1991). For other cetacean prey species, such as pelagic fish and cephalopods, oceanographic variables could influence their distribution more indirectly, for example, topographically induced upwelling of nutrients, or convergence of surface waters may locally increase primary production and aggregation of zooplankton (Fernandez and Bode, 1991; Tenore *et al*., 1995), leading to the aggregation of suitable prey species for cetaceans. Therefore, it is likely that the distribution of cetaceans is also related to such variables.

Cuvier's beaked whale, *Ziphius cavirostris*, belongs to the family Ziphiidae. In the past, basic assumptions of the distribution of Cuvier's beaked whale were made primarily upon stranded specimens and occasional sightings. Cuvier's beaked whale is probably the most widespread and abundant of all the beaked whale species, ranging throughout temperate and tropical waters, but rarely in polar seas. Since methods of effectively sampling deep-living squid are difficult, it is difficult to relate Cuvier's beaked whale distribution to the distribution of its principal prey species. Stranded specimens however, have provided an insight into the diet of beaked whales from stomach content analysis, and they reveal they predominantly eat squid, pelagic fish, and crustaceans. In response of to the inability to relate the distribution of prey species, studies throughout the past decade have concentrated on finding relationships in distribution to ecogeographical variables (EGVs) and sea surface temperature. Earlier research found that the Cuvier's beaked whale was not randomly distributed within their full range, but was coupled with complex underwater topography, steep slopes and deep waters of the abyssal plains (Williams *et al.,* 2002a; MacLeod *et al.*, 2004a; Baird *et al.*, 2006; Moulins *et al.*, 2007). Modelling of the habitat preference of beaked whales has increased over the past decade to help predict distribution of Cuvier's beaked whales in response to ecogeographical variables (Ferguson, 2005; MacLeod and Zuur, 2005).

Based on sightings the Bay of Biscay is the most northerly regular range of the Cuvier's beaked whale in the NE Atlantic (with the exception of few sightings off Ireland and Scotland) in the northeast Atlantic, however they have been recorded off Sweden and Iceland (Evans *et al.* 2008). With the year-round observations within the Bay of Biscay, it could be suggested the population may be resident, therefore, the Bay of Biscay should be considered as important habitat of the Cuvier's beaked whale. The Bay of Biscay has become well known for the diversity and abundance of cetaceans, since the Biscay Dolphin Research Programme started regular ship board surveys on a passenger ferry in 1995. The Bay of Biscay offers a great diversity of habitats, including the continental shelf and slope, submarine canyons and deep water habitats. The southern Bay of Biscay is dominated by complex submarine canyons. The area is also characterised by the presence of many fronts, localised upwellings and internal wave activity. This variety of habitats supports many of the cetacean species that are found in the wider northeast Atlantic (Reid *et al.,* 2003).

Beaked whale research in various locations worldwide has concentrated on studying their habitat relative to their distribution to increase the knowledge of understanding of critical habitats. Because of their preferred deep-water habitat (Mead, 1989; Carwardine, 1995; Reeves *et al.*, 2002), and their ability to make very long dives, spending little time at the surface (Reeves *et al.*, 2002) they are infrequently encountered (Mead, 1989; Houston, 1991;

Barlow *et al*, 2006). For these reasons little is known for most species. Only three or four out of the 20 species are reasonably well-known from studies at sea and most of what is currently known has come from stranded animals (Dalebout *et al*, 2002; MacLeod *et al.,* 2004b; MacLeod and Zuur, 2005). Sightings of beaked whales show they form fairly discrete populations in different parts of the world (Evans, 1987). As listed by the IUCN (International Union for the Conservation of Nature) the global status and geographical distribution of beaked whales is poorly known (Hooker, 2001a; Reeves *et al*, 2003). For the reasons stated above, it is imperative to use the data available to model beaked whale habitats.

An example of research efforts worldwide supporting this include the Gulf of Mexico, where beaked whales were found over the deepest bottom depths (Davis *et al.*, 1998). In the waters east of Great Abaco in the Bahamas, MacLeod *et al* (2004a) found that Cuvier's beaked whale and Blainville's beaked whale were most often sighted over areas of the seabed that had greater slopes than the rest of the study area. Other studies show beaked whales are commonly seen in waters over the continental shelf slope (ranging 200-2000m) (Waring *et al.*, 2001; Hooker *et al.*, 2002) and submarine canyons (Cañadas *et al.*, 2002; Williams *et al.*, 2002a; D'Amico *et al.*, 2003; MacLeod and Zuur, 2005).

The pioneering work of Hooker *et al.* (2002) carried out on the northern bottlenose whales above a submarine canyon, the Gully, off Nova Scotia, show beaked whales have specific habitat requirements, in particular showing an association with water depth (500-1500m) and relatively steep topography. This study has led to the Gully becoming a Marine Protected Area, yet boundaries and management remain under review (Hooker *et al.*, 2002). Several authors have speculated that the distribution of beaked whales (or cetaceans in general) is likely to be primarily determined by prey availability (Davis *et al.*, 1998; Cañadas *et al.*, 2002; Hooker *et al.*, 1999c; Yen *et al.*, 2004) and Torres *et al.* (2008) showed predictive modelling of prey distribution had a high predictive performance on dolphin habitat selection.

The most commonly used method has been logistic regression or general linear models (GLMs) with a logistic link function of habitat variables. Quantitatively modelling of the habitat preference of beaked whales has shown they were associated with the outer shelf edge (Waring *et al.*, 2001; Hamazaki, 2002). Cañadas *et al.* (2002) and Moulins *et al.* (2007)

used GLMs to examine beaked whale distribution in the Mediterranean Sea and found that functions of depth were better predictors than those of seafloor slope. Another method used is the ecological niche factor analysis (ENFA), whereby beaked whales were mostly seen occupying deeper waters in areas with higher slopes than average, and preferred southward and westward facing slopes (MacLeod, 2005a). MacLeod and Zuur (2005) used both generalised additive models (GAMs) and classification and regression trees (CART) to examine beaked whale habitat associations in the Bahamas and found that depth, seabed slope and seabed aspect were all important factors. Few previous attempts to model beaked whale distribution have been based on data collected over broad geographic areas and few included substantial areas of deep water habitat with low seafloor slope (abyssal plains) (Ferguson *et al.,* 2006). Over the last decade, research on Cuvier's beaked whale distributions have used GLMs to relate distribution to depth and slope (Canadas *et al.,* 2002) and more recently GAMs have been used to predict encounter rates and group sizes in the Eastern Tropical Pacific (ETP) (Ferguson *et al.*, 2006). When looking at why a chosen method is adopted (i.e. GAMs or GLMs), the advantages and disadvantages need to be assessed of both methods. One way to view which method to chose is to look at how sensitive the data set that is being used. Limitations of using GAMs, is that they are sensitive to data input, however, using GLMs, which are more robust in terms of data used, make more assumptions about relationships. It is the latter that is being avoided in this chapter and by using a GAM; this can be overcome, as GAMs assume no prior relationships.

The aim of this chapter is to model Cuvier's beaked whale habitat preferences and distributions from ship line-transect surveys conducted in the Southern Bay of Biscay. The survey covers areas of shallow waters from the continental shelf to deep waters associated with submarine canyons and abyssal plain habitats. Habitat utilisation for Cuvier's beaked whales is investigated by modelling the variation of presence/absence using generalized additive models (GAMs) and by investigating the effects of scale on habitat models. GAMs were chosen to make sure prior assumptions about relationships were correct and because they make no prior assumptions about the form of the relationships. Different spatial scales were investigated because the different oceanic features may be of importance at different scales. For example, the slope may be important on small scales, as the change in steepness can be different at different levels down the slope, but on a large scale the overall slope would be assessed and those small changes would not be seen. In previous studies on beaked whales, only one spatial scale has been investigated: 500m (MacLeod *et al.*, 2004a,; MacLeod and Zuur, 2005; and 9km (Ferguson *et al.,* 2006) and after investigating 3 spatial scales (1km^2, 25km^2, 100km^2) Macleod (2005) used 1km^2 grid cells based on the smallest cell size provided the best model. The aim of this study was to investigate the habitat use of the Cuvier's beaked whale rather than its distribution (chapters 3, 4 and 5), therefore the data from all months and years were combined, and any spatio-temporal variations were not investigated.

2. 2 Methods

2.21Study area

The region of study for this project is the southern Bay of Biscay (Figure 1). The Bay of Biscay is situated between 43 °N to 50 °N and -1 °W to -10 °W, in the Northeast Atlantic and is characterised as a temperate open oceanic bay bounded by the Spanish coast to the south, oriented E-W and the French coast to the east, oriented S-N (Koutsikopoulos and Le Cann, 1996). The Bay of Biscay is often described in two parts: the northern bay and the southern bay. Both areas have sea depths, ranging from the shallow continental shelf (less than 100 metres) to the abyssal plain (greater than 4000 metres), with many underwater features such as submarine canyons, seamounts and a steep continental slope. The Armorican shelf in the north of the bay is up to 180km wide, whilst in the south the continental shelf is narrow, only 30 to 40km width (Koutsikopoulos and Le Cann, 1996).

The CapBreton Canyon, in the southeast corner of the Bay of Biscay, is a major morphological feature that cuts into the continental slope in an E-W direction and the 1000m contour is only 3 km from the coast. The CapBreton is one of the deepest submarine canyons in the world (Gaudin *et al.,* 2003) and the longest off Europe, with its head is located only 250m from the coastline (Cirac *et al.*, 2001). The canyon was formed by the Adour River (SW France), but has been disconnected from the river since 1310 AD (Cremer *et al.*, 2003). The canyon runs westward and parallel to the north coast of Spain for 160 km due to structural control, then turns northward, widens and abruptly disappears in the continental rise by 3500m water depth (Gaudin *et al.*, 2003).

2.22 Field methods

This study is based on data gathered by the Biscay Dolphin Research Programme (BDRP), on board the fixed route platform, Portsmouth-Bilbao ferry 'Pride of Bilbao'. More than 80,000 km have been surveyed during 135 trips, from 1995 to 2006 for the whole survey route and 25,773 km for the southern Bay of Biscay. The height of the platform is 32m and, the speed of the ferry is on average 17knots. Effort-related data are based on twice-monthly survey and observers use the 180° arc in front of the vessel for any cetacean encounters. The dataset contains a record for each sighting and includes species name, total number of species observed, time, position (latitude/longitude) of the encounter, sea state, swell height, visibility, cloud cover (octaves), precipitation, angle, and distance of each sighting from the platform. In order to obtain a good representation of distribution, only data recorded in favourable sea conditions (Beaufort sea state ≤ 3) were taken into account for the data analysis. Beaked whales may go unnoticed because they have long dive times (Aguilar De Soto *et al.*, 2006; Baird *et al.*, 2006; Tyack *et al.*, 2006) and surface without a visible blow or splash (Barlow *et al.*, 2006) and in sea states greater than three the probability of seeing them is reduced, as encounters rates decrease more than 10-fold as sea state increase from 1 to 5 (Barlow *et al.*, 2006). Standard methods were used to record effort, with recordings every 15 to 30 min and/or when there was a change in the weather during an encounter. Other variables recorded included sea state, course, speed, visibility, wind speed and direction, cloud cover and swell height.

The southern Bay of Biscay (outlined by the red box, figure 2.1) was selected as the study area instead of the whole Bay because there were no sightings of Cuvier's beaked whale north of 46°N during dedicated effort surveys. Using the entire area may cause some discrepancies in the analysis because the northern Bay and the English Channel are shallow and even, relative to the deep and complex underwater topography of the southern Bay. The Cuvier's beaked whale is a deep-water species and including the data for shallow water, such as that in the English Channel may obscure the importance of the deep-water habitat.

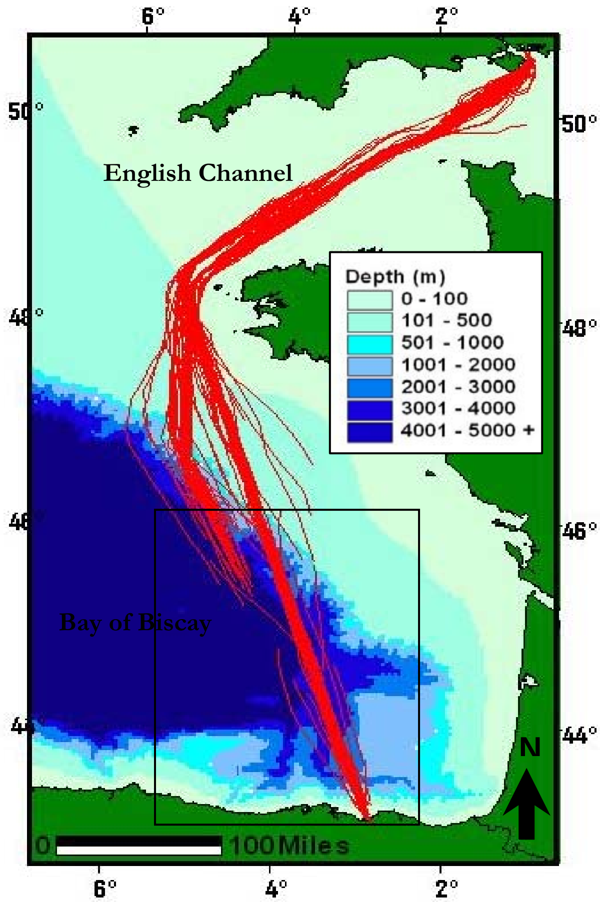


Figure 2.1: Total survey effort completed for the whole ferry route between 1995 and 2006 (red solid lines) and for the study area (solid red lines within the red box) in the Bay of Biscay, northeast Atlantic.

2.23 Analytical methods

2.231Geographic information system (GIS)

In order to explore the effects of spatial scale of habitat preference modelling, a program called MapInfo was used to create base maps with cells sizes of 5km, 10km, 15km, 20km and 25km. These maps were the imported into ArcView 3.2 and superimposed on the study area. Because of the size of the study area under investigation, a grid size smaller than 5km could not be created and grid cells larger than 25km were not used as they encompass a greater area and averaging over a greater area would take out precision of the variation in depth, slope and aspect. Different size grid cells were used in this study to see whether Cuvier's beaked whale preferred different EGVs of different scales. See Appendix 1 for extra maps in sea states 0, 1 and 2 for all grid cell sizes.

A GIS of the study area was constructed using ESRI ArcView 3.2 software. A primary coverage was developed that contained the study area as defined by latitude and longitude, coastline of England, France and Spain and bathymetric contour lines. Data were selected based on data sets of relevant oceanographic features that were acceptable and transferable into a GIS format: Depth, Slope (gradient), Aspect (facing direction of slope), and Sea Surface Temperature (SST), collectively known as EGVs. Grid squares for all 5 grid cell sizes were assigned values for each EGV. The depth values for the central point of the cells were obtained by overlaying the grid onto the GEBCO bathymetry data set. Central depths, including the mean, minimum, maximum, standard deviation (SD), and range were calculated for 10 by 10 grid squares consisting of 500m by 500m grid cells within the 5km grid size; 1000m by 1000m grid cells for 10km; 1500m by 1500m grid cells for 15km; 2000m by 2000m grid cells for 20km; and 2500m by 2500m grid cells for 25km. The slope and aspect were then taken from the depth values in ArcView using the spatial analyst tool. Aspect was initially measured in degrees and then converted from a circular variable (degrees) into two linear components: Sine (Easting) and Cosine (Northing) of the original aspect. The aspect needed to be converted from degrees to circular variables, for example, a cell with an aspect of 359^{o} would give a very different value to a cell with an aspect of 1^{o} even though they are both facing a very similar direction, therefore aspect is separated into an easting and northing. Sine and cosine range from -1 to 1, positive is equal to east and north, while negative is equal to west and south.

As described above, depth, slope and aspect were calculated for each grid cell using GIS tools, while SST data were obtained from the ocean colour web site for satellite imagery (http://oceancolur.gsfc.nasa.gov/ftpsite) and spatially joined to the grid cells. Chl-a variable was not included in the modelling, as over half the sightings were not linked to chl-a value because the data for chlorophyll were only available from the middle of 2002 and as a result caused an error when the models were tested, probably as a result of the reduction in the number of presence cells with SSChl-a. Once all the EGVs were linked to the grid cells, the effort related survey data was joined to the grid to assign each trip a value for depth, slope, aspect, and SST. Each effort related sighting was then manually joined to the correct survey trip, using the date and time. The final spreadsheet contains each trip, sightings, and EGVs, which was then exported out of GIS and imported into Microsoft Excel. Within Microsoft Excel the data were sorted by sightings and each sighting was given a value of 1 (presence) and the rest of the survey data without sightings were given a value of 0 (Absence). This was done to show which grid cells contained sightings (presence) and grid cells that were surveyed but no animals seen (absence).

2.232 Selecting absence cells

A number of absence cells within the study area were removed from the data set, because the model would not work with a high volume of absence cells compared to the small number of presence cells. Selecting a smaller number of absence cells increases the presence-absence ratio, to 25%-75%, respectively, from 1%-99% and 2%-98% (Table 2.1).

The number of absence cells selected to use for each grid size, were chosen by multiplying the presence cells (52) by three, which equals 156 absence cells. To choose 156 absence cells from all absence cells, the total number of absence cells were divided by 156 and the number generated (n) (see Table 2.1) from this was used to select 156 absence cells for each model. To select the 156 absence cells the spreadsheet of absence cells were sorted by year and date and every 'n' cell from the top-down was picked from the absence cells. The data were sorted by year to give an overall mix of all years so there would be no bias in the results by picking absence cells from just one or two years.

Grid cell Size	*Total number of cells*		*% of cells*		*Number generated (n)*
	presence	*absence*	*presence*	*absence*	
5km	52	8257	1	99	53
10km	52	5001	1	99	32
15km	52	3927	1	99	25
20km	52	3361	2	98	22
25km	52	3067	2	98	20

Table 2.1: Total number and percentage of presence-absence cells for the whole study area and the number generated for selecting the smaller number of absence cells.

2.233 Habitat modelling

Habitat use was analysed by applying a generalised additive model (GAM) (Hastie and Tibshirani, 1990), using the graphic user interface for 'R' 2.6 for Windows within the program 'Brodgar'. The model was used to examine whether a significant relationship exists between the distribution of Cuvier's beaked whales and EGVs. The model will be used to understand where Cuvier's beaked whale should be found. The explanatory variables used in the model are physiographic variables (mean, range, SD of depth, slope and SST) and presence/absence of sightings (response variable). Because the data were presence-absence, a GAM with a binomial distribution and logistic link function was used. The models did not contain terms for latitude, longitude, month, and year, as they are better in predicting distribution rather than habitat utilisation.

The Brodgar *forward-backward stepwise* model builds a model by eliminating different variables and investigates how much they improve the fit. The first stepwise selection process started with running all environmental variables (H_1) and the resulting Akaike's Information Criterion (AIC) was used to determine the best model at each step. The stepwise selection began with dropping one of the fixed variables: depth, slope, aspect, and SST. Each time a variable was removed, the model was re-run to see how the AIC is affected from the first step. If the AIC was lower than the first step, the variable was dropped from selection, implying the model is better without it; the lower the AIC, the better the model. If the AIC was higher then the variable was put back into the model and the next variable was removed. This process continued until all variables had been sufficiently tested for the final model predicted by the AIC. The above stepwise selection of variables finds the model that provides the best fit to the given data as expressed by AIC.

Forward/backward stepwise selection of variables, with smoothers, K = 4. K (Knots) represents the amount of movement in the smoothing; a low K (i.e. K=1) would give a near straight line, whereas a higher value of K could see the line travel through each data point, which may not give a clear indication of the relationship. Cross validation was used to choose the most appropriate degrees of freedom (df) in the scope of predictor variables used.

In preparation for building the models, the beaked whale sighting data and oceanographic data were summarized into five different grid sizes, as mentioned above, of on-effort trackline. GAMs were used to relate beaked whale sightings to the summarized fixed geographic variables and temporally dynamic *in situ* oceanographic data described above. A GAM may be represented as:

$$g(\mu) = \alpha + \sum_{j=1}^{p} f_j(X_j)$$ (Hastie and Tibshirani, 1990)

As in generalized linear models (GLMs), the function $g(\mu)$ is known as the link function, and it relates the mean of the response variable given the predictor variables, $\mu = E(Y|X_1,\ldots,X_p)$, to the additive predictor $\alpha + \Sigma_j f_j(X_j)$. GAMs are nonparametric extensions of GLMs: the components $f_j(X_j)$ in the additive predictor may include nonparametric smooth functions of the predictor variables, allowing GAMs to be considerably more flexible than GLMs, which are restricted by the constraints of the linear predictor, $\alpha + \Sigma_j \beta_j X_j$.. Separate GAMs were built to describe and predict the response variable: presence to the explanatory variables described above, for the five grid cell sizes.

An alternative way of analysing the relationship of Cuvier's beaked whale to the EGVs available is by way of univariate tree models. Classification trees were used to explore the relationship between the single response variable (presence) and the multiple explanatory variables (EGVs described above). Trees indicate the relative importance of different explanatory variables. In each case, the statement used to split the grid squares was given above the branching point. The first split (left = yes, and right = no) identifies the variable with the most influence on Cuvier's beaked whale distribution, and the values at the end of the tree contain the proportion of absence cells (left) and presence cells (right), that lie within those conditions. The trees have been pruned to display only the first four branches for clarity.

2.3 Results

2.31 Sightings, survey effort and EGVs

Between 1995 and 2006, 129,176km of systematic effort surveys were conducted for the whole ferry route and 25,773km in the study area. In total 66 groups of Cuvier's beaked whale were encountered during the dedicated surveys, throughout the eleven years. Of these 66, only 53 sightings of the Cuvier's beaked whale were included in the five models, as some sightings were observed during sea states greater than 3.

Table 2.2: The number of different grid cells surveyed, from 1995 to 2006: a) the total number of cells surveyed in the southern bay b) the total number of cells surveyed for the whole

a)

Grid size	5	10	15	20	25
Cells surveyed	443	165	92	60	42
Cells utilised	34	24	19	15	12
% of cells utilised	8	15	21	25	29

b)

Grid size	5	10	15	20	25
Cells surveyed	8309	5053	3979	3413	3119
Cells utilised	52	52	52	52	52
% of cells utilised	1	1	1	2	2

Figures 2.2 to 2.6 show the sightings of Cuvier's beaked whale overlaid onto grid cell sizes of 5, 10, 15, 20 and 25km, respectively. The amount of effort per grid cell is shown and the bathymetry of the area, by showing that they prefer deep-water habitats. The amount of survey effort is relative to the standard route of the ferry after leaving Bilbao, with darker grid cells indicating greater survey effort. The lighter grid cells indicate a lower amount of survey effort, which is due to occasional deviation of the ferry from its normal route. The encounters of Cuvier's beaked whale are greater over areas with more survey effort, therefore the more time spent observing increases the chances of seeing them.

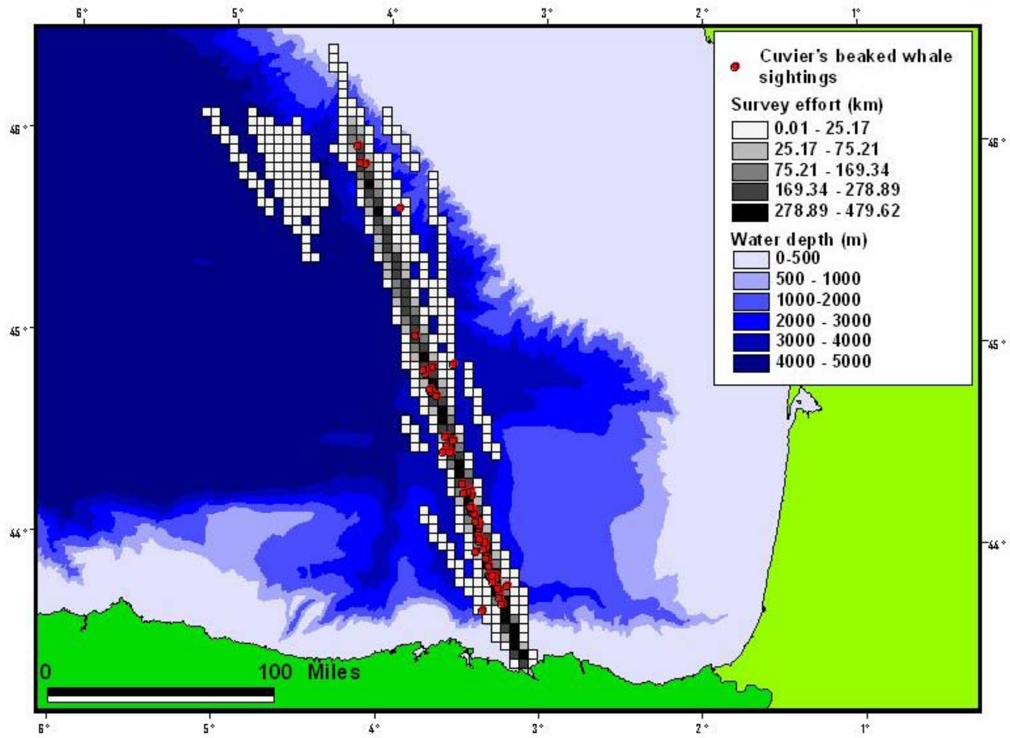


Figure 2.2: Distribution of Cuvier's beaked whale layered above a grid showing survey effort (km) per 5km grid cell. Water depth is shown in metres.

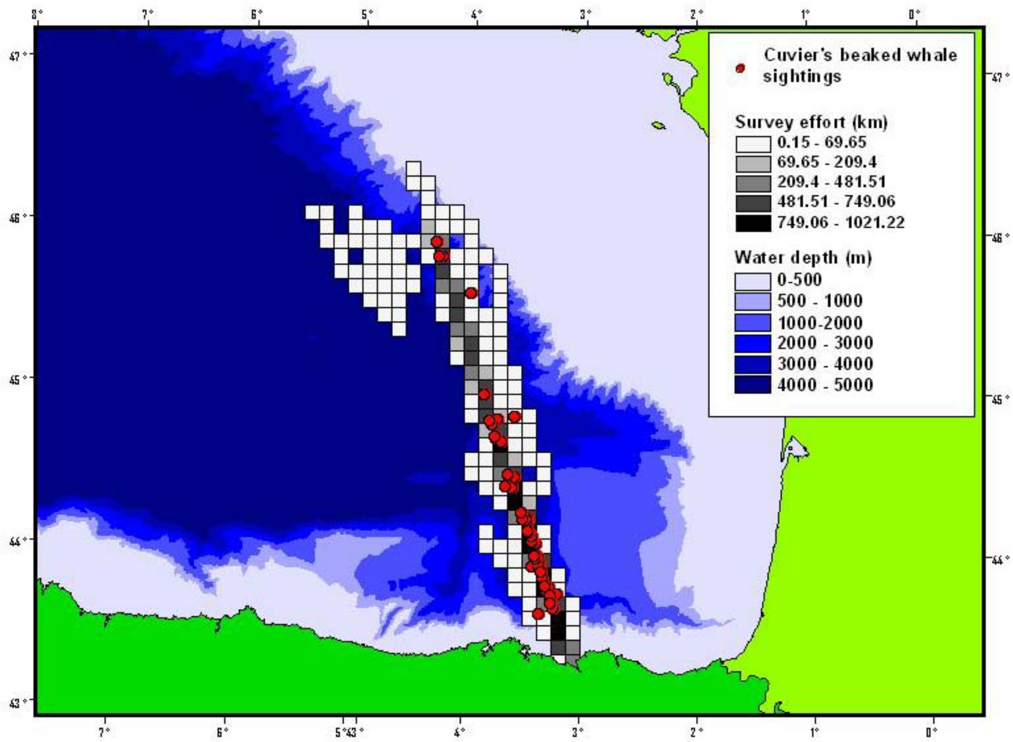


Figure 2.3: Distribution of Cuvier's beaked whale layered above a grid showing survey effort (km) per 10km grid cell. Water depth is shown in metres.

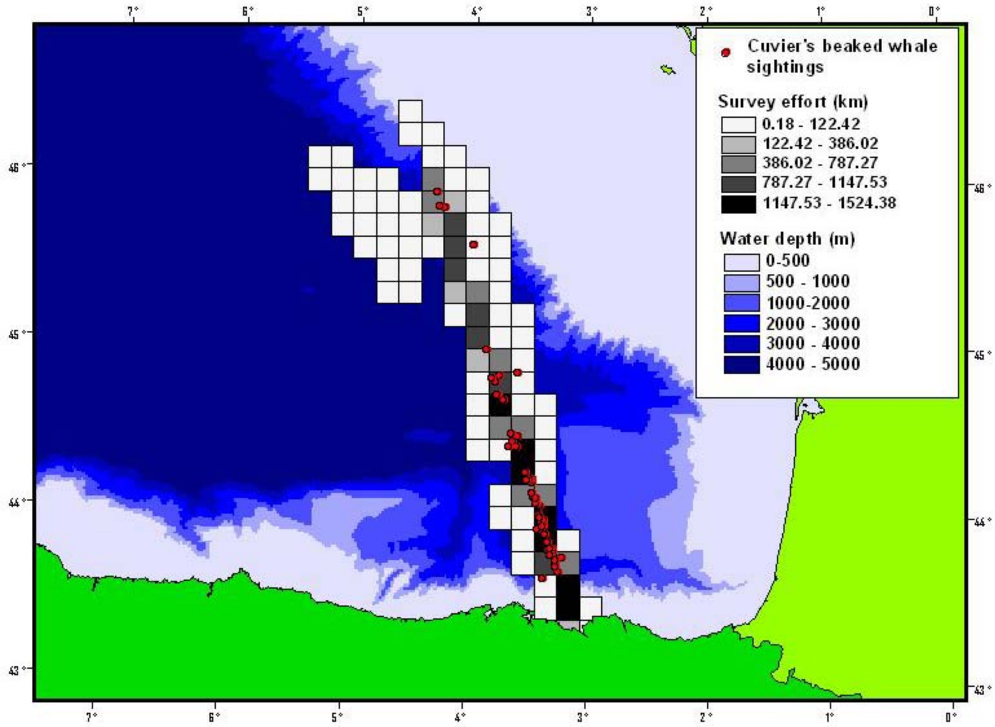


Figure 2.4: Distribution of Cuvier's beaked whale layered above a grid showing survey effort (km) per 15km grid cell. Water depth is shown in metres.

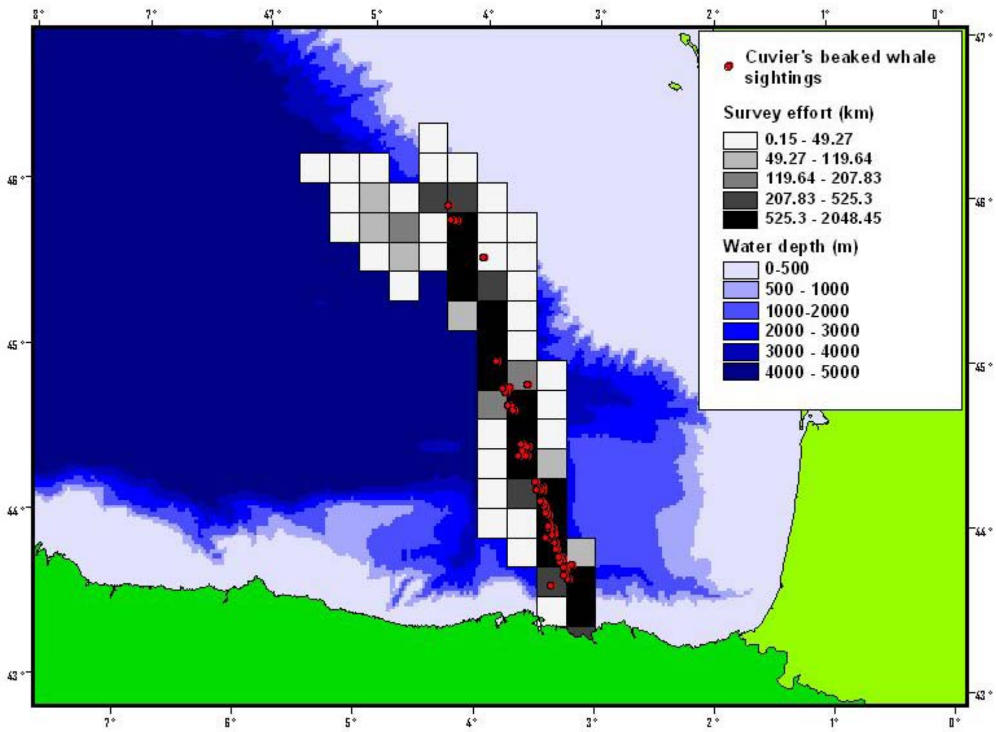


Figure 2.5: Distribution of Cuvier's beaked whale layered above a grid showing survey effort (km) per 20km grid cell. Water depth is shown in metres.

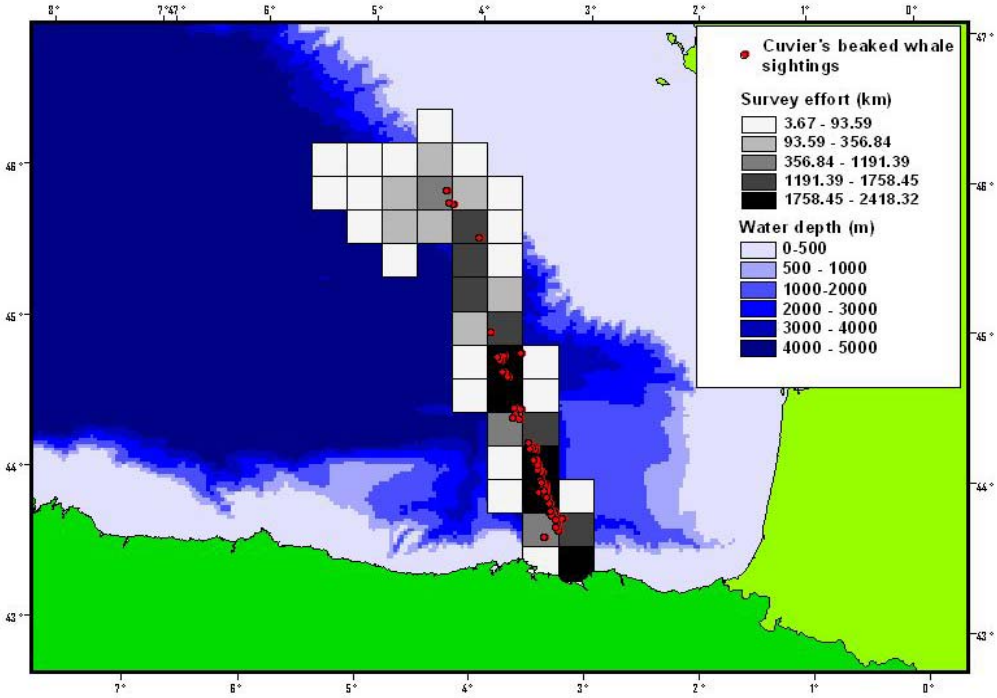


Figure 2.6: Distribution of Cuvier's beaked whale layered above a grid showing survey effort (km) per 25km grid cell. Water depth is shown in metres.

The EGVs investigated in this study were depth, slope (gradient), aspect easting, aspect northing, and sea surface temperature. The mean water depths of grid cells utilised, as an average of all five grid cell sizes, in the southern Bay of Biscay was approximately 2958.91m (range: 158.93-4237.52m; sd: 705.82m). 48% of the encounters were in water depths ranging from 2000 to 3000m, 44% of the sightings were over water depths ranging 3000-4000 meters, whilst only 8% of the whales were encountered in water depths ranging from 1000 to 2000 metres. The gradient varied from 0.270° to 11.72° (mean: 3.62°; SD: 2.59°). The majority of cells where Cuvier's beaked whales were recorded had either a south-east or north-east facing slope, which is likely to be a function of the area surveyed. A summary of statistics for the grid cells surveyed in the southern Bay, for each grid cell size in the study area is shown in Table 2.3.

Table 2.3: Summary statistics of environmental variables for the grid cells surveyed in the Southern Bay of Biscay

5km grid				
	Min	Max	Mean	SD
Depth (m)	488.71	4200.00	2984.59	738.89
Slope (°)	0	21.43	3.98	3.35
Aspect Sin	-1	1	0.44	0.51
Aspect Cos	-1	1	-0.16	0.53
SST (°C)	11.95	23.56	16.89	3.78
SSChl-a (mg m^{-3})	0.16	0.83	0.33	0.21
10km grid				
	Min	Max	Mean	SD
Depth (m)	304.05	4192.29	3008.51	694.41
Slope (°)	0	21.80	3.76	2.93
Aspect Sin	-1	1	0.52	0.39
Aspect Cos	-1	1	-0.18	0.44
SST (°C)	12.00	23.21	16.93	3.74
SSChl-a (mg m^{-3})	0.16	0.79	0.32	0.19
15km grid				
	Min	Max	Mean	SD
Depth (m)	158.93	4237.52	2986.03	724.05
Slope (°)	0	17.18	3.35	2.48
Aspect Sin	-1	1	0.53	0.33
Aspect Cos	-1	1	-0.18	0.33
SST (°C)	12.02	23.61	16.93	3.75
SSChl-a (mg m^{-3})	0.16	0.83	0.32	0.20
20km grid				
	Min	Max	Mean	SD
Depth (m)	210.42	4230.94	2877.27	701.32
Slope (°)	0	15.73	3.51	2.25
Aspect Sin	-1	1	0.60	0.24
Aspect Cos	-1	1	-0.22	0.37
SST (°C)	12.01	23.60	16.94	3.78
SSChl-a (mg m^{-3})	0.16	0.85	0.34	0.21
25km grid				
	Min	Max	Mean	SD
Depth (m)	272.59	4200.00	2938.17	670.41
Slope (°)	0	13.29	3.50	1.94
Aspect Sin	-1	1	0.60	0.26
Aspect Cos	-1	1	-0.23	0.33
SST (°C)	11.99	23.31	16.93	3.74
SSChl-a (mg m^{-3})	0.16	0.80	0.32	0.20

2.32 Habitat preferences of Cuvier's beaked whale in the southern Bay of Biscay

Pairplots were created for the five different grid cell sizes to test the relationships between the average, range, and standard deviation, where possible for depth, slope, aspect sin and aspect cos. This relationship is represented by the dataset using the smaller number of absence cells for the 5km grid cell size (Figure 2.7). In Figure 2.7, the graphs above the diagonal are scatterplots, and the numbers below the diagonal represent (absolute) correlations between the variables. Font size is proportional to the value of the correlation.

The pairplot created for the average depth versus the range of depths per grid cell indicates a weak relationship and therefore both the average and range of depths were used as EGVs in the model. This was also the same for the average/range of aspect sin and cos. For slope, however, the average, log and range of slope all showed a strong linear relationship, which suggests that all three would compute very similar results. The strong linearity among factors allows some factors to be dropped from the analysis and only one of these variables should be used for this reason and in this study; the average slope has been used in the models. The pairplots showed similar relationships between the average, range, and log of the EGVs.

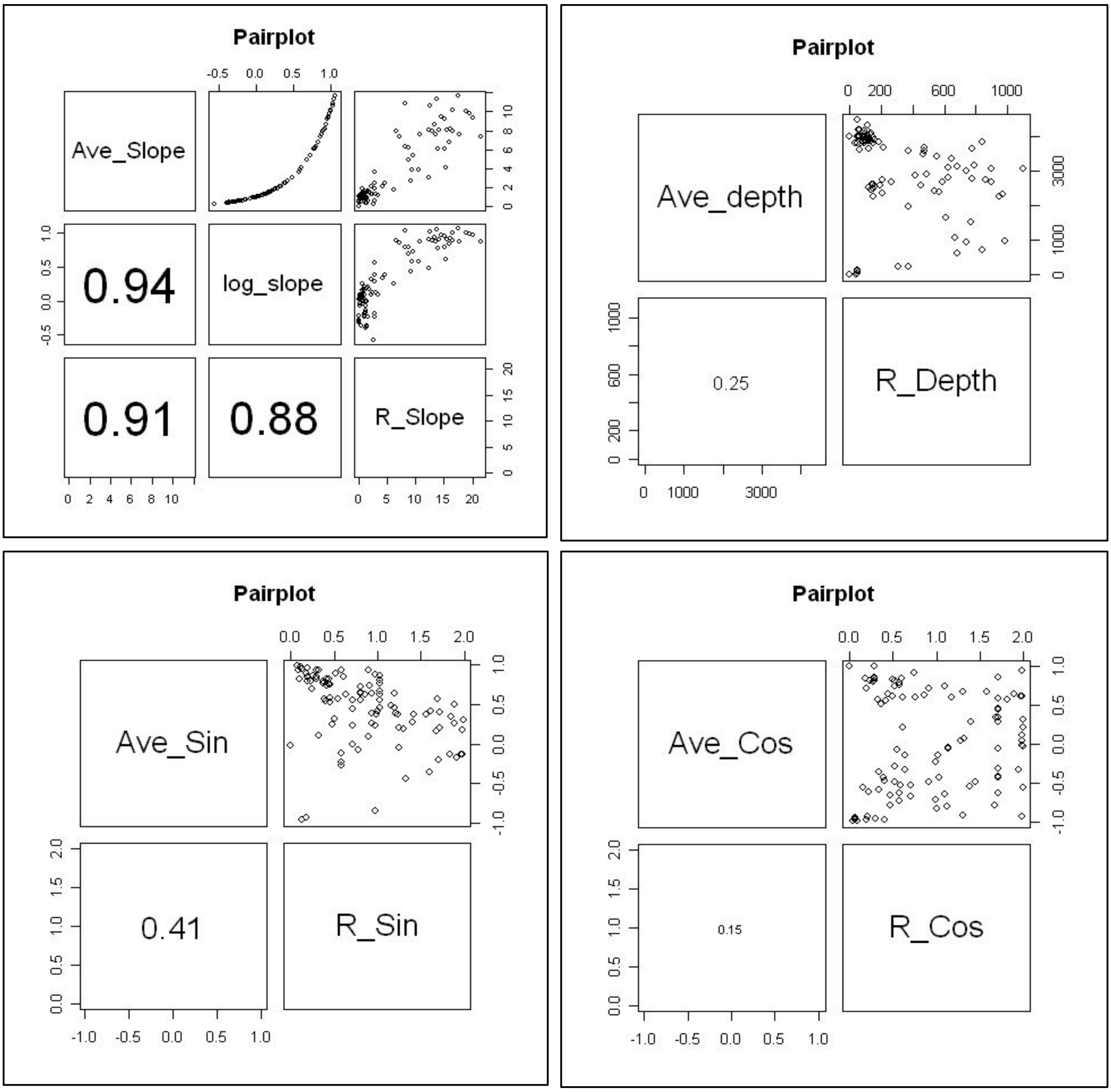


Figure 2.7: Pairplots presented are based upon the 5km grid cell size only (random number).

Table 2.4 shows the results of the AIC values for the five final models used. Together, these EGVs produced the lowest AIC value when the forward-backward stepwise selection was performed. In each model, some of the variables were not significant; however, because they improved the model by lowering the AIC value, they were kept in the model. The overall best model was the 20km model (AIC: 176.83), because the variables explained 31% of the variation of the distribution of Cuvier's beaked whale and subsequently this model is better in explaining the variation in the distribution of Cuvier's beaked whale in relation to the EGVs. The next best model was the 25km, which explained 20.5% of the variation of the whale distribution and the 5, 10, and 15km models explained less than 20%

of the variation in the southern Bay of Biscay. Because more than 60% of the variation is not explained, adding more explanatory variables might improve the models and increase the deviance. The explanatory variance for Cuvier's beaked whale distribution is explained by the deviance (labelled by the software) and shows how much variation in Cuvier's beaked whale can be explained by the final EGVs used in each model. This is the equivalent of the R^2 in linear regression (Ferguson, 2005). For all five models, there was no over-dispersion. Appendix 2 lists the numerical outputs of the forward/backwards selection using the AIC for each of the five models.

Grid cell size	5km	10km	15km	20km	25km
AIC	209.95	203.01	205.32	176.83	201.09
Deviance	16.2%	18.7%	17.9%	31%	20.5%

Table 2.4: The results of the forwards/backwards stepwise selection using the Akaike Information Criteria (AIC) and the variation (deviance) in Cuvier's beaked whale distribution, as a function of the EGVs investigated.

The EGVs shown to be important for Cuvier's beaked whale distribution at 5, 10, 15, 20 and 25km grid cell sizes are shown in Table 2.5, denoted by a star symbol. The variables that had a significant (*p-value* <0.05) effect on the distribution of Cuvier's beaked whale are highlighted in black and the ones that were not significant but kept in the model, because they improved the model by lowering the AIC value, are highlighted blue. Those left blank indicate the EGVs that were removed from the model, because they did not improve it. In some cases the average, a, and/or the range, r, were important. Only the average slope and SST per grid cell were used in the models. The average water depth over which Cuvier's beaked whale were encountered plays an important role in their distribution on all spatial scales tested in this study. In this study, slope was important on smaller spatial scales of 5, 10 and 15km, whereas at 20km and 25km it was not important. The direction of the slope (aspect) is significantly important for the Cuvier's beaked whale on all spatial scales tested, with exceptions at 10km and 15km, where aspect northing and aspect easting is not important, respectively. SST was only significant at 20km, but improved the model at 5 and 10km suggesting that SST is not affect by spatial scales. To assess SST in relation to

Cuviers' beaked whale distribution properly, different factors need to be investigated such as seasonal temperatures. This is not examined here, but see chapter 5.

	5km	*10km*	*15km*	*20km*	*25km*
aDepth	*	*	*	*	*
aSlope	♦	*	*		
aSine				*	♦
rSine	*		*		*
aCos	*	♦		*	
rCos		*			*
SST	♦		♦	*	

Table 2.5: Summary of the EGVs selected for each of the five models.
(***** = EGVs which were significant and ♦ = **EGVs** not significant, but kept in the model)

At 5km, three (depth, range of aspect easting and average of aspect northing) out of the five variables included in the model have a significant influence on the distribution of Cuvier's beaked whale. Average slope (P = 0.1585) and SST (P = 0.2019) were not significant but kept in the model, as they improved the model by lowering the AIC value. At 10km, three out of four variables proved significant for this model; average depth, average slope and the range of aspect (northing). The average aspect (northing) was not significant (P = 0.0711), but it was kept in the model because it improved the model by lowering the AIC value. At 15km, three variables that proved significant for this model are average depth, average slope and the range of aspect (easting). SST was not significant (P = 0.0851), although it did reduce the AIC, therefore improving the model. At 20km, four variables were found to improve the model: average depth, average easting, average northing, and sea surface temperature. They were all found to have a significant effect on the distribution of Cuvier's beaked whale (P = <0.005). At 25km, three out of the four variables used in the final model proved significant (P = <0.005); average depth, range of easting and range of northing. Average northing did not have a significant effect (P = 0.6510) on the distribution of Cuvier's beaked whale, but it did improve the model when the model was run without it; and therefore was kept in the final model.

The average depth per grid cell was significant in all five models. The Cuvier's beaked whale distribution has a non-linear relationship with depth (Figure 2.8). Estimated from the GAM smoother, the optimum value for depth is between 2000m and 300m, for all grid cell sizes. Cuvier's beaked whale distribution has a negative relationship with the average slope, and the GAM smoother indicates a preference for flatter bottoms. This was only evident for grid cell sizes 5, 10 and 15km (Figure 2.8).

The aspect did show to be a significant feature in the distribution of Cuvier's beaked whale for all models as estimated from the GAM smoother, but the aspect also showed to be variable across the scales. The range of aspect easting was significant at 5, 15 and 25km scales, whereas the average aspect easting was only significant at 20km. At a 5km grid cell size, westward facing slopes are favoured (aspect r_sin, Figure 2.9). A preference for east facing slopes is evident for 15km, 20km, and 25km scales (aspect sin, Figure 2.9). At 25km, the 95% confidence bands indicate the aspect could be either east or west when using the average aspect per grid cell, however, this was not significant. The GAM smoother for the range and average of aspect northing were varied across the scales, as the range showed they have a preference for north facing slopes at 10km and 25km, whereas, the average showed they have no particular preference for north or south facing slopes at 5km, 10km and 20km. At the 10km scale, this was not significant for aspect cos.

Sea surface temperature improved three out the five models; 5, 15 and 20km, but was only significant at the 20km scale. Despite not being significant at 5 and 15km, SST was put back into the models because it improved the model by lowering the AIC value. The optimum temperatures estimated by the GAM smoother range 14 to 20°C (Figure 2.8).

In Figures 2.8 and 2.9, the solid line indicates the smoothing curve, using K=4, while the dotted line represents the 95% point wise confidence bands. The degrees of freedom, *df,* for non-linear fits are in the parentheses on the y-axis. The y-axis represents the partial fit of each covariate on the scale of the link-function. The x-axis represents the values of each EGV, and the marks above the x-axis indicate the distribution of observations in all segments (with and without Cuvier's beaked whale).

The classification trees indicate that the first split among the grid cells in relation to Cuvier's beaked distribution is based on the gradient of the slope at 5 and 10km, and aspect at 15, 20 and 25km (Figures 2.10a-e). The variables used in the trees were taken from the final models, as shown in Table 2.6.

Figure 2.8: Estimated smoothing curves and nominal variable for GAM of the habitat preferences of Cuvier's beaked whale in relation to depth (first column) and slope (middle column) and SST (last columns)

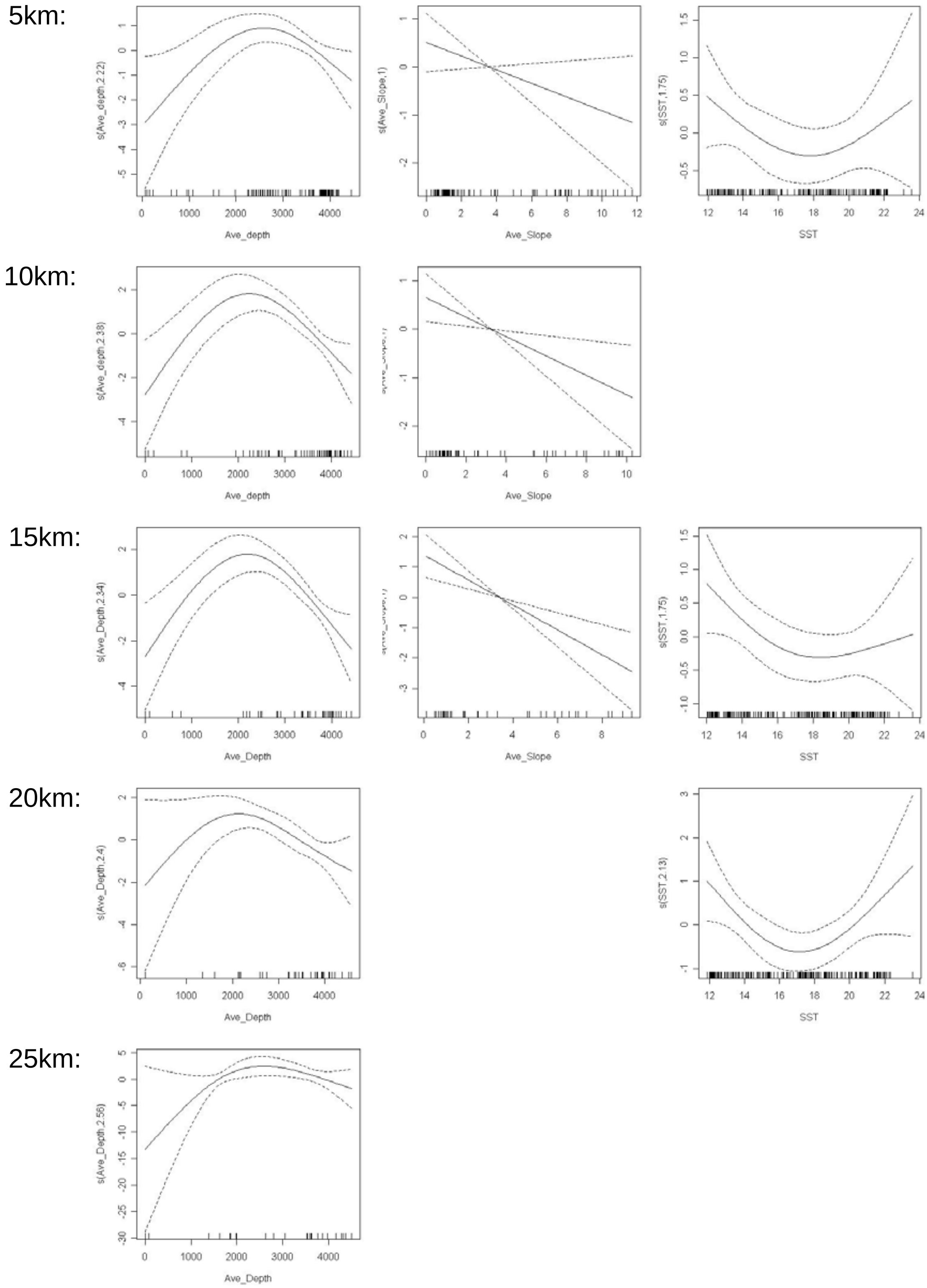
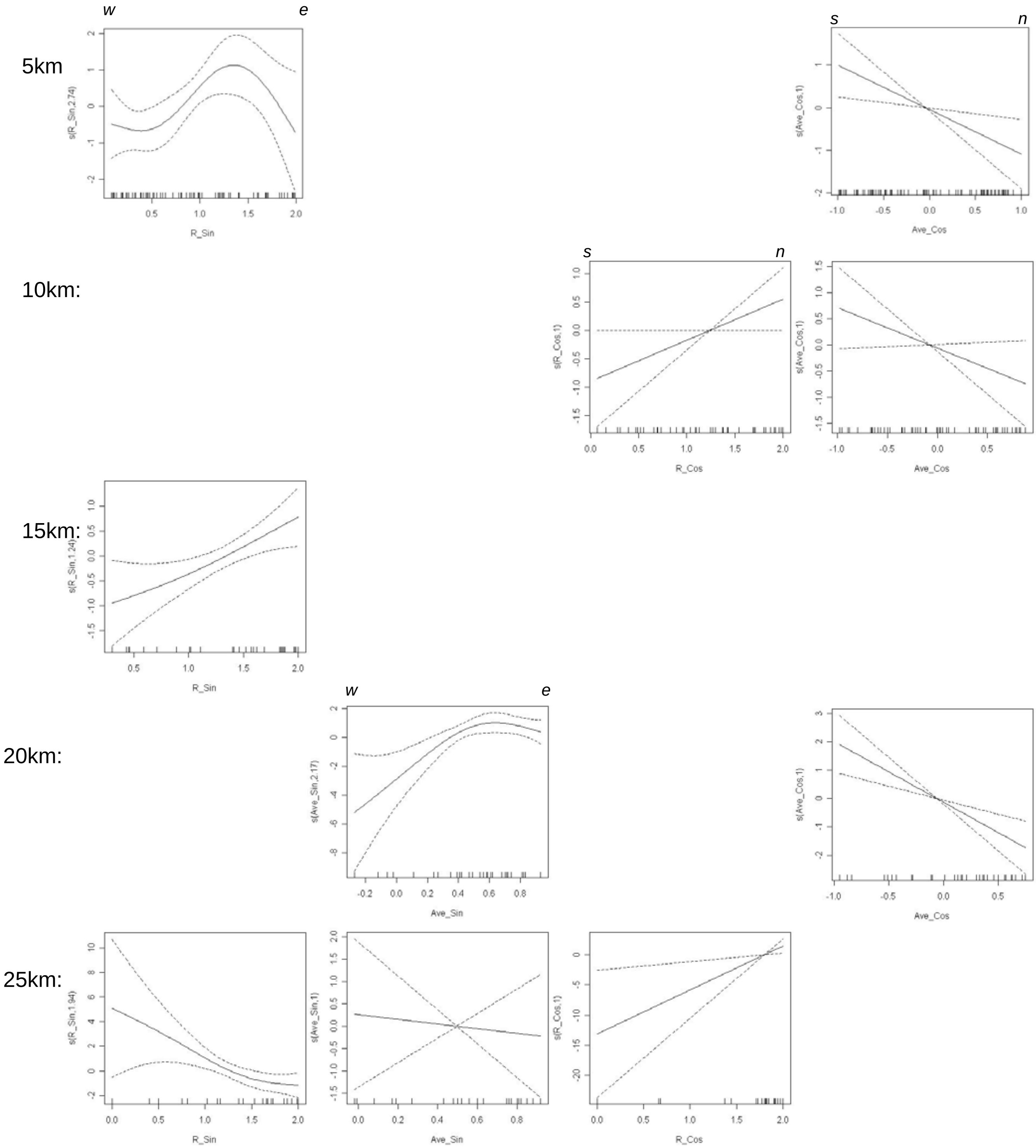
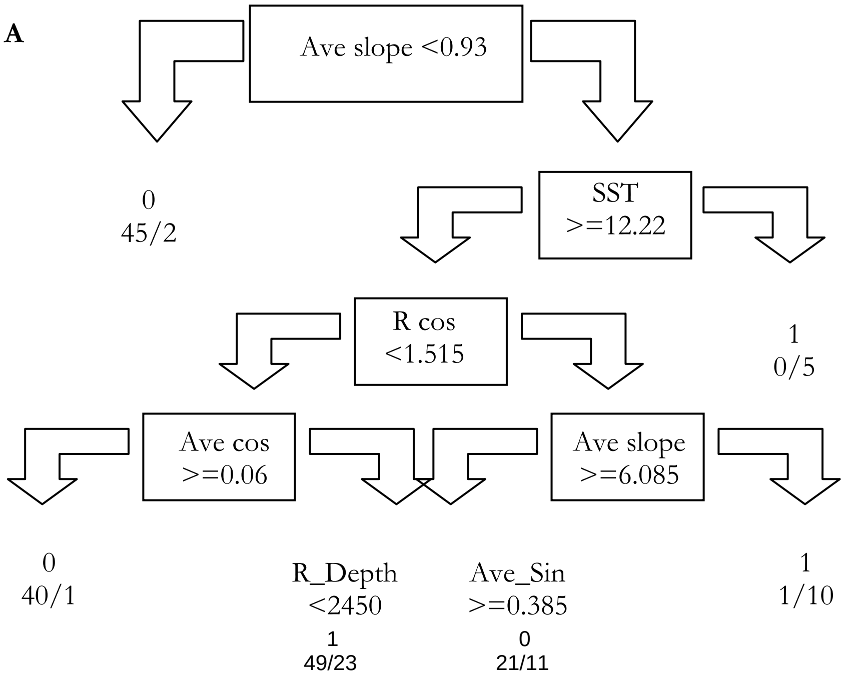
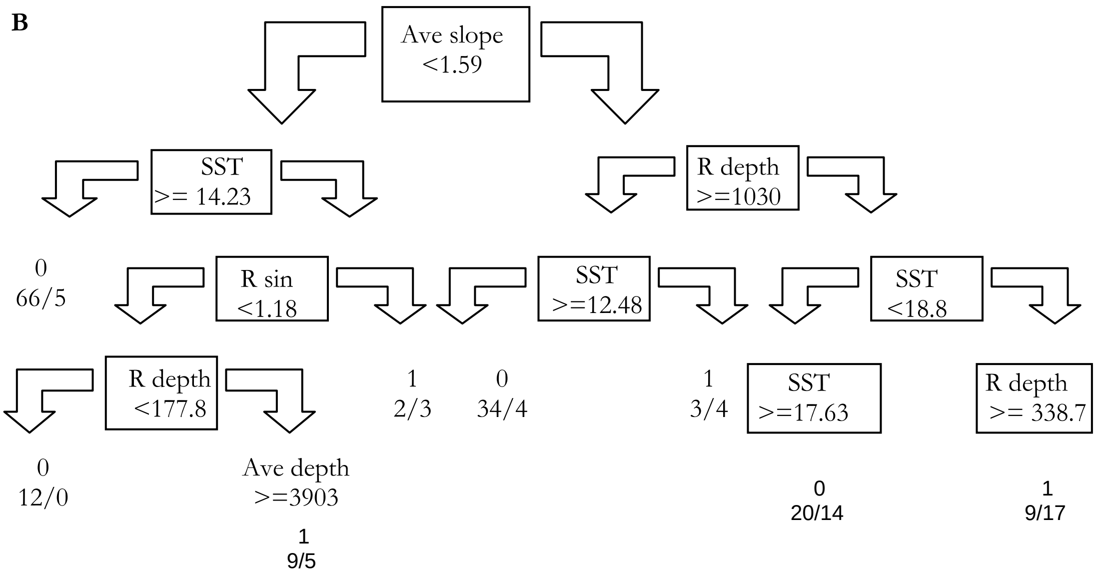


Figure 2.9: Estimated smoothing curves and nominal variable for GAM of the habitat preferences of Cuvier's beaked whale in relation to Aspect easting (first two columns) and Aspect northing (last two columns*)*. The letters *w, e, s* and *n* above the graphs represent west, east, south and north respectively.

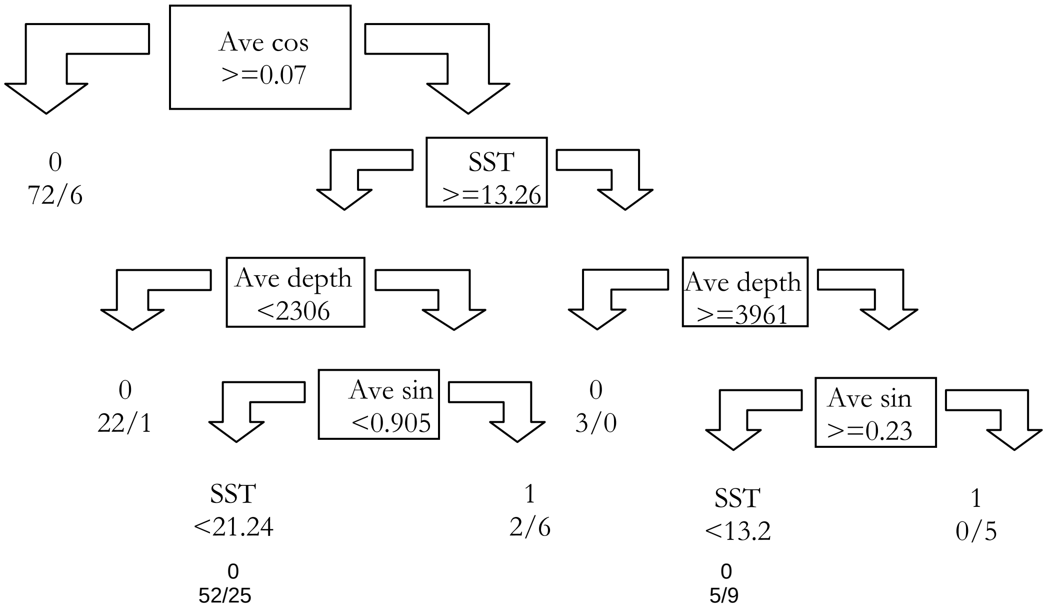


Figures 2.10: Classification trees occurrence of Cuvier's beaked whale in relation to water temperature, depth, seabed slope and seabed aspect. a) 5km grid cell size b) 10km grid cell size c) 15km grid cell size d) 20km grid cell size e) 25km grid cell size.

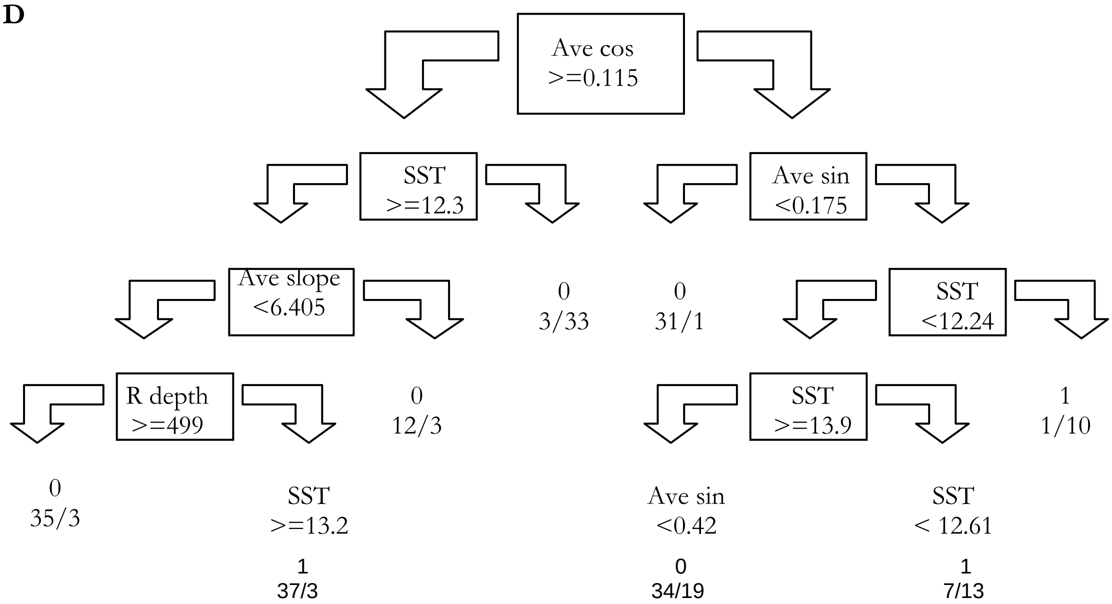




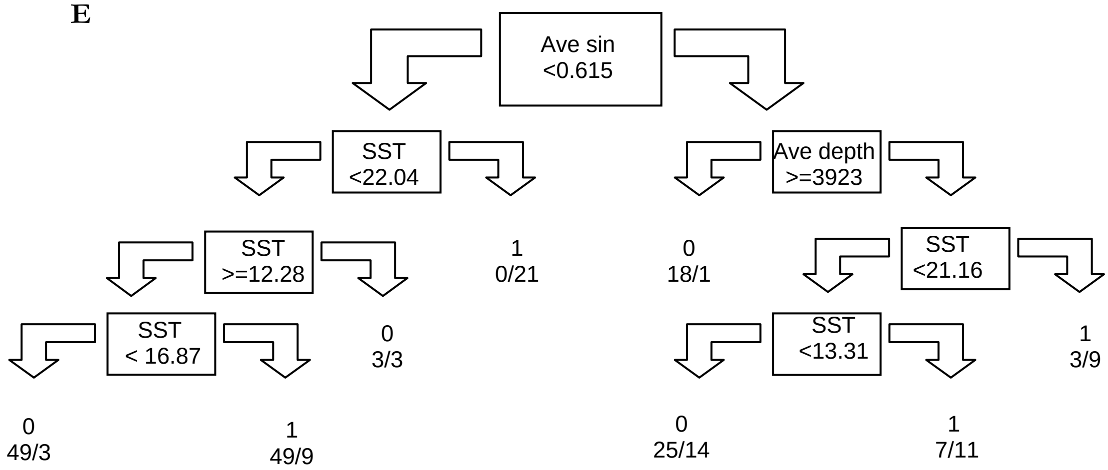
C


Ave cos
>=0.07
0
72/6
SST
>=13.26
Ave depth
<2306
Ave depth
>=3961
0
22/1
Ave sin
<0.905
0
3/0
Ave sin
>=0.23
SST
<21.24
1
2/6
SST
<13.2
1
0/5
0
52/25
0
5/9

D


Ave cos
>=0.115
SST
>=12.3
Ave sin
<0.175
Ave slope
<6.405
0
3/33
0
31/1
SST
<12.24
R depth
>=499
0
12/3
SST
>=13.9
1
1/10
0
35/3
SST
>=13.2
Ave sin
<0.42
SST
< 12.61
1
37/3
0
34/19
1
7/13

E


Ave sin
<0.615
SST
<22.04
Ave depth
>=3923
SST
>=12.28
1
0/21
0
18/1
SST
<21.16
SST
< 16.87
0
3/3
SST
<13.31
1
3/9
0
49/3
1
49/9
0
25/14
1
7/11

2.4 Discussion

The Cuvier's beaked whale models presented here are the first to explore habitat utilisation in the Bay of Biscay. Although it is clear that beaked whale species are associated with continental slopes or topographic features such as submarine canyons (Hooker *et al.*, 1999a,b; MacLeod and Zuur, 2005; Moulins *et al,* 2007; Faclone *et al,* 2009) it is important to increase this understanding in more detail. The analysis presented in this study is important because it supports research that has already been conducted on Cuvier's beaked whale in other parts of the world's oceans.

The sightings of Cuvier's beaked whale were not randomly distributed throughout the southern Bay of Biscay, in the northeast Atlantic. The effort-based surveys show Cuvier's beaked whale has not been encountered north of 46°N, and the only BDRP recorded encounters north of 46°N are based on the opportunistic data (see chapters 3, 4 and 5). The distribution of effort within the study could see a bias of effort coverage, due to the time of day the ferry sails over certain topographic features. However, because of the different features the ferry sails over (continental shelf & slope, abyssal plain and submarine canyons) and the long dataset that this chapter uses I am confident that sightings are reflecting their distribution well in comparison to the effort coverage. Other work does however show records of Cuvier's beaked whale north of Biscay (Rosen *et al.* 2000). Effort-related data from the region north of 46°N were not included in this study because sightings were not seen in water depths less than 1000m and to include data less than 1000m proved insignificant and the analysis did not go any further. Because Cuvier's beaked whale were only sighted in deep waters, it was best to minimize the study area to the southern Bay to obtain clearer comparisons between the habitat use of the Cuvier's beaked whale and the EGVs tested. Factors such as month, year, and latitude were not used in this chapter because this is a habitat study, the spatial and temporal distribution of Cuvier's beaked whale being discussed in Chapter 5.

The majority of sightings, 90%, of Cuvier's beaked whale were concentrated over a significant submarine feature known as the CapBreton Canyon in the southern Bay of Biscay, whilst 10% were sighted over the continental slopes in the northern part of the Bay. The water depth of grid cells surveyed in the southern Bay ranged from 158.93 metres to 4237.52 metres and Cuvier's beaked whale were observed in waters >1000 metres and <4000 metres. Nearly 100% of the sightings were encountered over water depths of 2000 to 3000 metres (48%) and 3000 to 4000 (44%) metres. Despite the slope ranging from 0 to 30.22° within grid cells utilised, the Cuvier's beaked whale was found over seafloors with a mean slope of 3.26°. The results from the GAM found the distribution of Cuvier's beaked whale to be significantly correlated with water depth and slope. Depth significantly affects Cuvier's beaked whale distribution on all scales with preferences for deep water, 2000-4000m depth; however, there is a decline in sightings if the water depth is greater than 4000m. Slope was only significant on scales of 5, 10 and 15km, and showed a preference for flat bottoms. The outputs from the GAM analysis show Cuvier's beaked whales to have a non-linear relationship with depth and a negative near-linear relationship with slope. Is this preference for flatter bottoms indicative of their suction feeding behaviour as suggested by Heyning and Mead (1996)?

The GAM outputs showed that the Cuvier's beaked whales have a preference for westward facing slopes on a small scale (5km), northward facing slopes on small and large scales (10km and 25km) and eastward facing slopes on larger scales 15km, 20km and 25km. Because of the variation across the scales, it is suggested that one of two things could be occurring. The first is that more data is needed to show a more accurate picture of the preferences they have for a particular direction the slope faces or second is that do not have a particular preference for the direction the slopes. If the latter is true this suggests that the depth and steepness of slope plays a major role in their distribution, as shown by the results.

The sea surface temperature of grid cells utilised ranged from 11.95 to 23.61°C, with a mean of 16.92°C. The results from the GAM indicated a non-linear relationship between the Cuvier's beaked whale and sea surface temperature, with a preference for surface waters between 14 and 20°C. Sea surface temperature was only significant for three out the five models, so maybe at the scales where it was not significant, other factors outweighed the significance of sea surface temperature on the distribution of Cuvier's beaked whale. Because of the small number of sightings linked to a SSChl-a value it could not be used in the models and it is therefore difficult to elucidate any relationships. It is noteworthy that Ferguson *et al.* (2006) found no associations between beaked whales and surface chlorophyll concentration in the Eastern Tropical Pacific, which is a biological variable commonly used as a proxy for cetacean prey.

By exploring the models using classification trees, it is interesting to find that despite water depth being significant at all spatial scales, as investigated by the GAM in this study, the slope determines the first split of the tree at 5 and 10km, whereas aspect determines the first split of the tree at 15, 20, and 25km.

2.41 Comparisons with previous habitat modelling studies

At present, only a few published sources are comparable with this study: an early study carried out in the Alboran Sea (Canadas *et al.,* 2002), two studies were carried out off Great Abaco, northern Bahamas (MacLeod *et al.*, 2004a; MacLeod and Zuur, 2005), a study carried out in the Eastern Tropical Pacific (ETP) (Ferguson *et al.*, 2006), a study in the north-western Mediterranean (Moulins *et al.*, 2007) and a more recent study off California (Falcon *et al.,* 2009). The study by MacLeod and Zuur (2005) used a different species of beaked whale, Blainville's beaked whale. The water depths over which Cuvier's beaked whale were encountered in this study compare well with the sightings of Cuvier's beaked whale in water depths of approximately 3400 metres in the Eastern Tropical Pacific (Ferguson *et al.*, 2006), greater than 1000m off Great Abaco, Bahamas (MacLeod *et al.*, 2004a), greater than 1000m in the Mediterranean (Moulins *et al.*, 2007) and greater than 600m in the Alboran Sea (Canadas *et al.,* 2002). It is important to note that Canadas *et al.* (2002) observed beaked whales and Moulins *et al.* (2007) observed Cuvier's beaked whale in water depths shallower than 1000m; 600m and 756m, respectively. I would suggest that the reason for the sightings in shallower waters is that the continental slope in this area starts at a shallower depth than in the Bay of Biscay. Moulins *et al.* (2007) main findings were related to slope rather than aspect and depth, so therefore it would not be uncommon to see them in shallower waters in this area. The GAM results presented in this study show the aspect of the slope to have some importance on the distribution of Cuvier's beaked whale, and, similarly, Moulins *et al.* (2007) found that Cuvier's beaked whale distribution was significantly related to aspect of the seabed in the north-western Mediterranean. The study carried out off Great Abaco, Bahamas showed Blainville's beaked whale distribution was also significantly related to the aspect of seabed (MacLeod and Zuur, 2005). The earlier study in the Bahamas and in the Eastern Tropical Pacific agree with the general descriptions of beaked whale habitats. However, the predictions of Cuvier's beaked whale distribution in the ETP, as suggested by Ferguson *et al.* (2006), have expanded the definition of what is considered a suitable beaked whale habitat by showing they inhabit much deeper waters than other studies. On the other hand, when the later study is looked at in more detail, the ETP is generally deeper than other places studied so in actual fact it does expand on their distribution. Ferguson *et al.* (2006) used a wider study area unlike most beaked whale studies that are conducted in areas limited to the continental slope and shelf waters (Ferguson *et al.,* 2006). In this study, the coverage ranges from shallow waters to deep waters associated with the abyssal plain. Cuvier's beaked whale do inhabit waters over the abyssal plain, but it is thought they are encountered in those areas for transitional purposes from the southern canyons to the northern continental slope because sightings were few.

Unlike the findings made by Canadas *et al.* (2002), where beaked whales preferred steep slopes and MacLeod *et al.* (2004a) where Cuvier's beaked whales were most often sighted over seafloors with greater slopes than the remainder of the study area in the Bahamas, the results here dispute that, as Cuvier's beaked whales show a preference for gentle slopes. The preference for gentle slopes is in agreement with Ferguson *et al.* (2006) and Moulins *et al.* (2007) whose work show that Cuvier's beaked whale seemed to prefer areas with gentle slopes in the Eastern Tropical Pacific and the Northwestern Mediterranean, respectively.

Some useful information on depth preferences for Cuvier's beaked whale has also come from acoustic recording tag (DTAGs) studies. Tyack *et al.* (2006) showed they hunt by echolocation in deep water between 222m and 1888m (maximum dive depth) in the Ligurian Sea and Aguilar Soto *et al.* (2006) showed foraging dives were made to a maximum of 1265m, also in the Ligurian Sea.

What is apparent from these studies and from the present study is that the continental slope is an important variable in their distribution and despite depth also playing a major role; it seems that Cuvier's beaked whale is likely to occur over the continental slope, regardless of the water depth.

2.42 Spatial scales

Ferguson *et al.* (2006) discuss beaked whale habitat use in relation to small and large-scale features where ecological mechanisms affecting beaked whale distribution may be scale-specific, and there may be a specific order in which such mechanisms operating on different scales influence beaked whale distribution. The slope of the seafloor is one variable that may be especially sensitive to the spatial scale of the analysis, for example the steep wall of a submarine canyon is a feature that would appear in an analysis conducted on scales of a few hundred metres to a few kilometres (Ferguson *et al.*, 2006), whereas it would almost disappear in a larger scale analysis (Ferguson *et al.,* 2006). Small-scale features are likely to be important to the success of localized beaked whale foraging; nevertheless, the animals may combine information from larger spatial scales, such as seasonal current movements.

As mentioned in the previous section, the results from this study have been comparable with the findings from studies in other parts of the world's oceans. However, other studies have not compared different spatial scales (grid cell sizes) in their work, using a single grid size. Because no comparisons have been made, it was decided to examine this in the present study and as mentioned above, some EGVs are prominent features in determining the distribution of Cuvier's beaked whale at most scales (water depth and slope), whilst aspect of seabed and sea surface temperature are not significant at all scales. Deciding on using just one scale could therefore significantly change the outcome of the results. So how did the other studies justify using just one grid size? Despite discussing different spatial scales, Ferguson *et al.* (2006) used a grid size based on the finest resolution of the environmental data, which was at 9km segments for the study in the eastern tropical Pacific. Similarly, MacLeod *et al.* (2004a) and MacLeod and Zuur (2005c) also used a single grid cell size for their analysis, 500m by 500m and justified using just one grid size by way of fine scale habitat analysis. In addition, MacLeod (2005) undertook a preliminary comparison of different grid cell sizes ($1km^2$, $25km^2$, $100km^2$) to identify the best model of beaked whale distribution and also found that the fine scale model ($1km^2$) proved the best model. Despite the lack of different spatial scales used in those studies, as mentioned already, findings are comparable, but it would be of interest to see the outcome in the distribution of those species studied over large scales.

2.43 Habitat preferences and hydrography

The sightings of Cuvier's beaked whale are primarily encountered in southern Bay of Biscay and over the submarine canyon, the CapBreton Canyon. It may be that interactions between local deep-water currents and this topographic feature increases local primary productivity and a local increased availability of prey for the Cuvier's beaked whale. The CapBreton Canyon extends far out into the southern Bay of Biscay, from the southeastern corner of France, with other canyons formed around it. This extensive system of canyons, combined with the structure of currents and water masses in and around the southern Bay of Biscay, undoubtedly work together to provide favourable conditions for the Cuvier's beaked whale. Submarine canyons play an important role in influencing the water patterns in and around the surrounding area because of their size and the area they occupy (Hickey, 1995). A combination of EGVs appears to lead to the presence of several cetacean species in the same location in the Gulf of Mexico (Baumgartner *et al.*, 2001). In the southern Bay of Biscay, east-flowing shelf/slope currents are prevalent (OSPAR, 2000) and a common feature in autumn and winter due to southerly and westerly winds (Valencia *et al.*, 2004). The extension of the warm water Iberian poleward (IP) current is now considered a common feature of winter circulation (Garcia-Soto *et al.,* 2002) that coincide with the spawning season of pelagic and demersal species due to the higher concentration of nutrients than the surrounding area (Gill, 2003a). The east flowing current (the Iberian poleward current) parallel to the Spanish coast is likely to help in accumulating prey species such as squid through the canyon system and at the bottom of the slope, providing a favourable habitat for deep diving cetaceans such as Cuvier's beaked whale. Upwelling is seasonal along the French and Spanish coasts and the strength of the upwelling corresponds to the winds and water masses (Gill and Sanchez, 2003b). Upwelling replenishes surface waters by drawing up nutrient-rich water from deep layers stimulating greater productivity of phytoplankton and consequently higher trophic levels in the shallower shelf regions (Flaherty, 1999).

Data on precise distributions of squid in Biscay was not accessible for use in this thesis and so no direct comparisons could be made between where the whales were observed and the location of preferred prey. However, habitat use and seabed topography may be related to the local distribution of their preferred prey. The concentrating effect of currents on prey will be affected by gradient (MacLeod, 2005a). Nesis (1993) suggests that cephalopods; the prominent diet of beaked whales (Evans, 1987; Wang *et al.*, 1995; Lick & Piatkowski, 1998; Santos *et al.*, 2001a,b; MacLeod *et al.*, 2003; Ohizumi and Kishiro, 2003) may become associated with steeply sloping oceanic areas where they are passively carried onto slope areas by oceanic currents. As a result, such species can become concentrated in the near bottom layer and so form an important resource of predators (Nesis, 1993). In steep areas, animals may disperse down slope to flatter areas rather than accumulating on the slope (Nesis, 1993), which would favour the methods of catching prey at depth for Cuvier's beaked whale (Houston, 1991; Heyning and Mead, 1996; Tyack *et al,* 2006).

2.44 Summary

To conclude, the distribution of Cuvier's beaked whale is closely related to seabed topography. Despite the small sample size, the analysis compares well with other studies that have also shown a relationship between Cuvier's beaked whale and ecogeographical variables and, perhaps regardless of the spatial scale, particular EGVs will always be important in determining the distribution of Cuvier's beaked whale.

Understanding Cuvier's beaked whale, and all ziphiid whale, habitats on a global scale may be enhanced by conducting more surveys in areas with similar potential habitats found in this study. Thoughtfully selecting the types of environmental data collected and the scale at which they are collected, will help further investigations of the effects of scale on habitat models. The importance of determining the scale at which environmental predictors define the habitat use of beaked whales is becoming greater and to cover areas that are not biased to key areas have arisen from research efforts into beaked whale distribution. This study has looked at the latter. This study has examined environmental variables at different scales and found: 1) depth and aspect are important at all scales, 2) slope is important on smaller scales and 3) SST is important at small to mid scales. The opportunistic data set (presence-only) for the Cuvier's beaked whale will undoubtedly show relationships better from the increased sample sizes. Chapter 3 examines presence-only data, by combining all the sightings of Cuvier's beaked whale from both dedicated and non-dedicated surveys, to give a larger sample to work with. Using a larger sample size may validate the results found in this study, or it will challenge the results.

Chapter 3

Can opportunistic data be used to understand the distribution of Cuvier's beaked whale?

3.1 Introduction

3.11 General introduction to the Ecological Niche Factor Analysis (ENFA)

The ecological niche is the position or function of an organism/population in a community of plants and animals within an ecological community and a particular area within a habitat occupied by an organism. The niche concept, as defined by Hutchinson (1957), considers the ecological niche of a species as a hypervolume in the multidimensional space as defined by environmental variables, within which the populations of a species can persist. If the niche that a species occupies is related to specific combination of environmental variables that can be identified, this information can be used to provide a picture of where that species is likely to occur and where it is likely to be absent. Understanding the distribution of organisms in relation to their environment is becoming increasingly important in terms of assessing and modelling species distribution (MacLeod *et al.,* 2008), and identifying and protecting essential habitat in terms of assessing and mitigating human impacts upon marine organisms, such as anthropogenic noise (Barlow and Gisiner, 2006).

Ecological Niche Factor Analysis has been developed by Hirzel *et al.* (2002a) to analyse the position of the niche in the ecological space. This technique uses the environmental variables of the location where the animals have been recorded as present to identify the niche occupied by the species. ENFA combines multivariate statistics with the Hutchinson niche concept of an n-dimensional hypervolume defined by the range of ecogeographical variables (EGVs) that a species requires to survive. It assumes that the data represent an unbiased sample of the available habitat. This can easily be applied to areas not covered during data collection, for predictive distribution and to areas where the likelihood of occurrence for a species is unknown (Hirzel *et al.*, 2002a). ENFA could provide an objective way of predicting where marine animals are likely to occur within a given area based upon their ecological niche, and would allow the most to be made of the currently available data to improve the understanding of distribution in relation to EGVs.

ENFA only needs two sets of data 1) presence-only data, which makes ENFA an analysis particularly robust to the quality of data and 2) EGVs to describe the environment. The principle aim is to compare the presence data set (species distribution) and the whole area (global distribution) to a range of EGVs. This process summarizes all predictors into a number of uncorrelated axes, similar to the Principal Components Analysis (PCA) (Reutter *et al.*, 2003), except that the axes have an ecological meaning, marginality and specialisation factors. The position of the niche in the n-dimensional space can be described using two measures. First was the M-specialisation (hereafter termed marginality) and second the S-specialisation (hereafter termed specialisation). Marginality (those variables for which the species niche mostly differs from the available conditions in the global area, Reutter *et al.* (2003)) is represented in the first axis. Positive values (+ve) indicate the species prefers EGV conditions that are higher than the average conditions (Hirzel *et al.*, 2002a). Negative values (-ve) indicated the species prefers EGV conditions that are lower than the average condition (Hirzel *et al.*, 2002a). Specialisation (how restricted the species niche as compared with the available habitat, Reutter *et al.* (2003)) is represented in subsequent axes. The factorial axes coefficients are used to compute the overall marginality (M, varying generally between 0 and 1), specialisation (S, indicating the degree of specialisation when greater to 1) and tolerance (T, inverse of specialisation). Larger values of marginality indicate that the species has habitat requirements that differ from the average condition available (Hirzel *et al.*, 2002a). A high specialisation value indicates the more restricted the range of the focal species with regard to a given EGV. A high tolerance value indicates that within a given study area, the species occupies a relatively wide niche (Hirzel *et al.*, 2002a; Reutter *et al.*, 2003; Engler *et al.*, 2004). Each EGV will vary in the amount of information it explains per factor, as shown by the marginality and specialisation coefficients (Hirzel *et al.*, 2002a).

3.12 Advantages and limitations of the ENFA

The advantage of ENFA over logistic regression techniques such as GAM/GLM is that it requires only presence data rather than presence-absence data (Hirzel *et al.*, 2002a, Reutter *et al.*, 2003). Firstly, they avoid potential bias associated with absence data (uncertainty with potentially inaccurate true/false absences, present but undetectable). Secondly, these presence-only techniques provide scientists with an opportunity to take advantage of data sources that cannot be analysed with GLM/GAM (Mandleberg, 2004). Thirdly, being fundamentally a descriptive analysis, it does not rely on any underlying hypothesis for the data. Lastly, the ENFA relies on the concept of ecological niche and is therefore especially suited to a presence-only design (Hirzel et al., 2002a).

Application of these techniques for studying habitat preference of cetaceans has great potential benefits allowing a wider range of 'opportunistic' data to be included in statistical analysis, thus maximising the use of available data resources. These techniques are increasingly being used to study the distribution and potential habitat of many different organisms for example cetaceans (e.g., Compton, 2004; Mandleberg, 2004), birds (e.g., Hirzel et al., 2004; Ortega-Huerta and Peterson, 2004), mammals (e.g., Dettki et al., 2003), in some plants (e.g., Robertson *et al.,* 2001; Zaniewski et al., 2002), rare or endangered species (e.g., Reutter et al., 2003) and a virtual species (Hirzel *et al.,* 2001). More recently, MacLeod *et al.* (2008) found that not only could presence only techniques be successfully applied to modelling the distribution of cetaceans, but also that they could also provide information on presence/absence models of the species involved.

Despite the numerous advantages of using ENFA, the ENFA has limitations aswell. Firstly, the data set used is not effort related. Secondly, there is a lack of accurate absence data. Thirdly, ENFA is a purely descriptive method and cannot extract causality relations. A fourth limitation is that having only presence only leads to a much narrower variety of modelling techniques. Despite the drawbacks to modeling with presence-only data, these modeling methods are becoming more widely used because of the abundance of presence-only data, as has been described earlier.

3.13 Aim

This study aimed to analyse data collected opportunistically by trained observers during passages across the Bay of Biscay to assess whether it could be used to accurately model the distribution and habitat preferences of cetaceans using ENFA. This is particularly important because while dedicated surveys are undertaken along this route once a month, for less commonly encountered species, such dedicated surveys record too few sightings to allow habitat analysis to be conducted. However, as opportunistic data are collected more frequently, this data set contains a greater number of sightings of such species. Therefore, if the opportunistic data could be used to model the habitat preferences of cetaceans within the Bay of Biscay, this would greatly enhance our abilities to understand the factors which affect the distribution of less frequently encountered species. To investigate this issue, Cuvier's beaked whale was used as a case study. During the monthly dedicated surveys, 53 sightings of Cuvier's beaked whales were recorded between 1995 and 2006 (see chapter 2). In contrast, 402 sightings were available in the opportunistic data set since 2001. Therefore, the opportunistic dataset contains almost ten times as much data collected in half the number of years and provide a potentially valuable dataset for expanding our knowledge of this poorly known species.

3.2 Methods

3.21 Study area and Cetacean sightings

The study area (Figure 3.1) covers part of the English Channel and the Bay of Biscay, along the route of the P&O ferry 'Pride of Bilbao', which operates between Portsmouth, UK and Bilbao, Spain. The Cuvier's beaked whale, *Ziphius cavirostris*, and common dolphin, *Delphinus delphis*, opportunistic sightings data set used for this study was collated from the dedicated and non-dedicated surveys carried out by the Biscay Dolphin Research Programme (BDRP). The opportunistic sightings for common dolphin were used in this study to show that despite extensive survey coverage, certain cetaceans are not found in all areas of the survey route. Because opportunistic sightings are not effort related (amount of time spent observing), using a widespread species such as the common dolphin in comparison to Cuvier's beaked whale, which has a limited distribution, will provide some sort of effort in observation for opportunistic sightings. In total 455 sightings of Cuvier's beaked whales (402 non-dedicated and 53 dedicated) were encountered, and 4262 common dolphins; 2917 non-dedicated and 1345 dedicated.

1. Non-dedicated sightings data (opportunistic data)

The wildlife officer (BDRP) on board the ferry collected the opportunistic sightings data from 2001 to 2006. On every sailing to Bilbao from Portsmouth, a wildlife officer is on board. However, the wildlife officer is not observing at all times, due to other duties, although being on board every trip from 2001, it was in the interest of the charity to start collecting data to monitor the distribution of cetaceans on trips when the survey teams were not present. In doing so, it provides a larger data set to work with when analysing the data, which in turn can help towards the conservation of cetaceans.

2. Dedicated sightings data

The dedicated sightings data were collected by a team of two or three researchers, on twice monthly survey trips from Portsmouth to Bilbao from 1995 to 2006. The first trip is carried out by a Spanish team (AMBAR) and the second an English team. On each trip, the survey starts from first light and finishes at dusk.

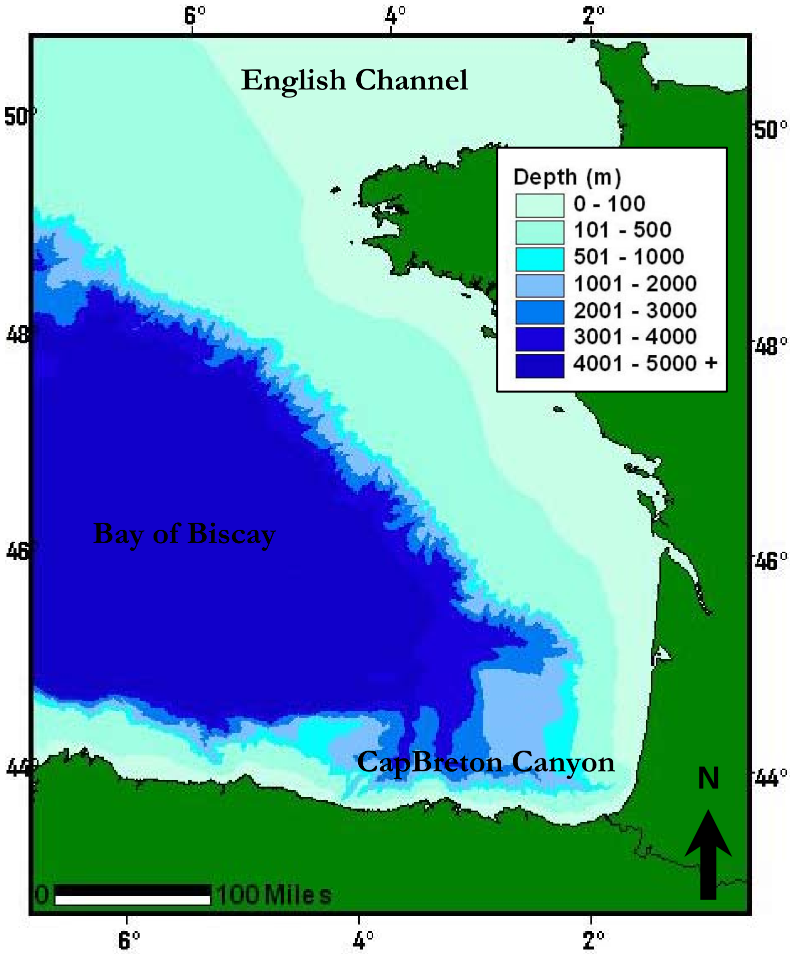


Figure 3.1: Bathymetry map of the study area, Bay of Biscay northeast Atlantic.

3.22 Analytical methods and Ecogeographical Variables (EGVs)

A geographic information system (GIS) consisting of 8,000 10km by 10km grid cells was created using ESRI Map Info software to cover the study area. The grid was imported into ArcView 3.2 and each grid cell was assigned a value for water depth, seabed slope, range of seabed slope and aspect of seabed. Water depth was interpolated from the GEBCO dataset at a 10 by 10km resolution, and slope and aspect were derived using functions within ArcView 3.2 software. Using the map calculation function in ArcView 3.2, aspect of seabed was converted from a circular variable (degrees) into two linear components (radians); Sine (easting) and Cosine (northing) of the original aspect. The opportunistic sightings data were joined to the 10km grid to provide a presence grid to compare against the EGVs during the modelling process.

ENFA and habitat suitability (HS) maps were computed using Biomapper 3 software (Hirzel *et al.*, 2002b) for the Cuvier's beaked whale and only the latter was computed for the common dolphin. BioMapper is a GIS and statistical tool-kit, developed for carrying out ENFA and producing HS maps from the comparison of a species distribution with a number of given EGVs (Hirzel *et al.*, 2002b). A grid for each EGV was imported into Biomapper along with a grid identifying which cells were classified as 'presence' within the model constructing dataset. The EGV grids were standardised using a Box-Cox transformation. After verification that there were no discrepancies between the maps, the ENFA was carried out. Detailed descriptions of the ENFA and its mathematical computations are given in Hirzel *et al.,* 2002a, 2006).

Once the marginality, specialisation, and tolerance factors were computed, MacArthur's broken stick model was used as a guide to select the number of factors that explain the greatest amount of information and to construct the final habitat suitability (HS) map. HS maps are computed by fitting a statistical or numerical model on environmental data and species distribution data (Hirzel *et al.,* 2004). Each cell of the resultant map is given an HS value ranging from 0-100, with 100 being those cells that have the highest suitability. Purely for display purposes, the maps were imported in ArcView 3.2 and reclassified into three categories: unsuitable, marginal and core habitat (0-33, 34-67 and 68-100, respectively) to show where is good habitat and where is not.

3.23 Assessing the predictability of the ENFA based on opportunistic data

The dedicated survey data were used to assess the predictive ability of the ENFA model based on the opportunistic data set. Only survey data collected in sea states of Beaufort 3 or less were used, in order to minimise the possibility of false absences within the dataset (MacLeod and Zuur, 2005). From these data, the 10km by 10km grid cells surveyed were identified. Of these cells, those where Cuvier's beaked whale was recorded during the dedicated surveys were classified as presence cells, while those where Cuvier's beaked whale was not recorded were classified as absence cells. The predicted HSI for each of these cells was then extracted from the ENFA model. A receiver operating characteristics (ROC) plot was then used with effort data to assess the predictive ability of the ENFA model (Zweig and Campbell, 1993, Fielding and Bell, 1997). The ROC plot was obtained by plotting all sensitivity values (true positive fraction) on the *y-axis* against their equivalent (1-specificity) values (false positive fraction) for all available thresholds on the *x-axis*. Sensitivity values indicate the proportion of cells where the model correctly predicted presence in relation to all presence cells in the date set. Specificity values indicate the proportion of cells where the model correctly predicated absence in relation to all absence cells in the data set. The area under curve (AUC) value produced when the ROC plot was made provides a measure of predictive ability (MacLeod *et al.*, 2008) and the AUC value lies between 0 and 1 (Fielding and Bell, 1997). A random model would be expected to have an AUC of 0.5, while a model that was in perfect agreement with the dataset would have an AUC of 1 (MacLeod *et al.*, 2008). The higher the AUC, the greater the predictive ability of the model under consideration and the further it differs from a random model (MacLeod *et al.*, 2008). ROC analysis was conducted using the Analyse-It 'Add-In' to Microsoft Excel produce by Analyse-It, LTD.

3.3 Results

3.31 Habitat suitability of Cuvier's beaked whale

Within the opportunistic dataset, there were 402 sightings of Cuvier's beaked whales in 72 separate grid cells. Based on these data, the ENFA analysis found that the habitat used by Cuvier's beaked whale differed from the general environment within the study area. The marginality value (M) was 1.677, also indicating that the required habitat of Cuvier's beaked whales differs from the average habitat available within the study area. The specialisation value (*S)* was 2.854 indicating that Cuvier's beaked whales are specialised in terms of the habitat they prefer, relative to the available habitats. A relatively low tolerance (1/S) value of $T = 0.350$ is indicative of their specialised habitats, highlighting the lack of sightings over unsuitable habitats.

Out of seven factors calculated, four were retained to create the habitat suitability maps based on the broken stick analysis. These accounted for 54% of the total sum of eigen values (100% of the marginality and 54% of the specialisation). The marginality alone accounted for 34% of this total specialization, a quite important factor meaning that Cuvier's beaked whale display a restricted range on those conditions for which they mostly differ from background Biscay conditions. Marginality coefficients (Table 3.1) showed that Cuvier's beaked whales are essentially linked to EGVs. For the first factor, the most important variable was Slope (coefficients of 0.504), followed by range in Slope (0.500). For the second factor, the most important variable was depth (-0.771) followed by range in slope (0.533). Therefore, factors related to the slope of the seabed and water depth were the most important factors in determining the distribution of Cuvier's beaked whale in the study area. In Table 1, the most important variables can be seen highlighted in bold and the second most important variables are highlighted in italics.

Table 3.1: Variance explained by the first four factors used to calculate the ENFA prediction, and coefficient values for EGVs

	1	*2*	*3*	*4*
Aspect northing	-0.290	-0.029	0.021	-0.097
Aspect easting	0.195	0.132	0.064	0.393
Range aspect northing	0.397	0.193	-0.560	-0.607
Depth	0.333	**-0.771**	-0.024	-0.021
Range aspect easting	0.325	0.025	0.066	0.583
Slope	**0.504**	-0.255	-0.341	-0.293
Range slope	*0.500*	*0.533*	0.749	0.202
Eigen Value	33.620	12.965	4.360	3.164
Accumulated explained variation in specialisation	0.590	0.817	0.894	0.949

The habitat suitability map predicts areas of unsuitable, marginal and core habitats for the Cuvier's beaked whale (Figure 3.2). The highest likelihood of occurrence is within deep waters associated with the continental shelf slope, in both northern and southern Biscay and the lowest likelihood of occurrence in shallower waters of the continental shelf and in deeper waters of the abyssal plain. The opportunistic sightings for Cuvier's beaked whale have been overlaid onto the predictive map in Figure 3.3 to show they are observed over waters that represent the core habitats for Cuvier's beaked whale. This is part due to the fact that all sightings used in the predictive modelling, as seen on the map, came from these core areas to begin with, however, no sightings were observed over shallow waters of the continental shelf, which limits the bias towards the study area concentrating over deep waters and the continental slope.

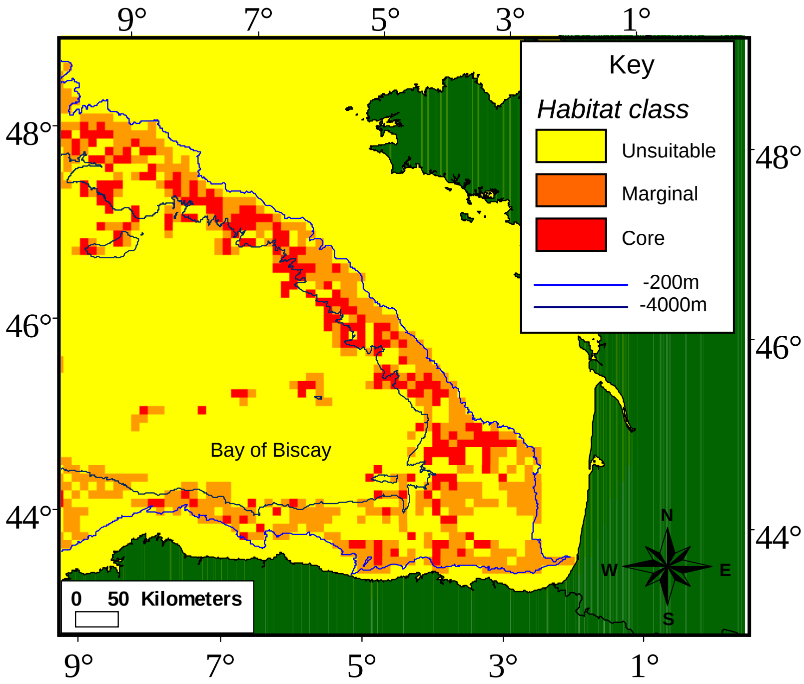


Figure 3.2: HS map for Cuvier's beaked whales in the Bay of Biscay showing unsuitable (yellow), marginal (orange) and core (red) habitats. The 200m and 4000m contour is shown in order to illustrate proximity of high suitability areas over the continental slope.

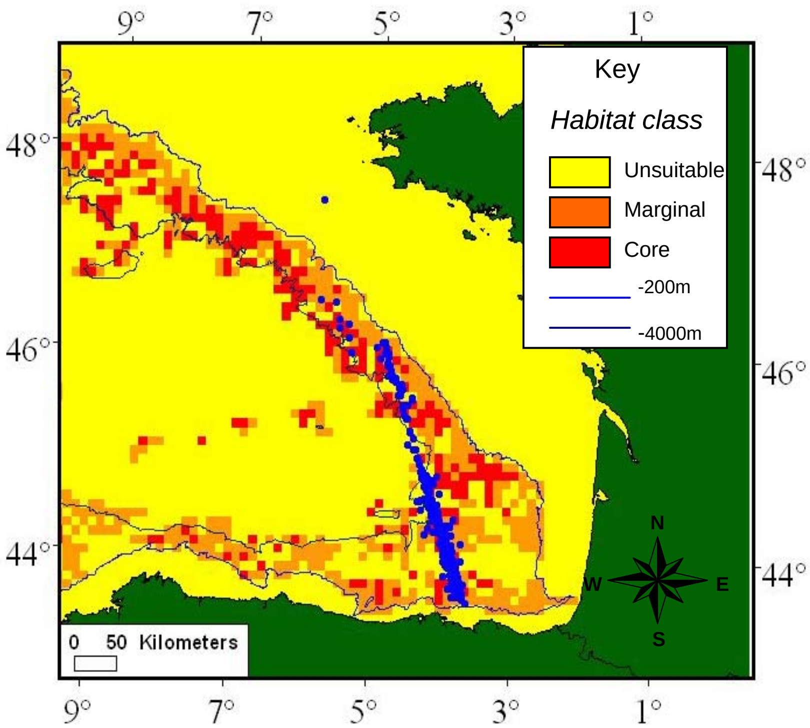


Figure 3.3: HS map for Cuvier's beaked whales in the Bay of Biscay showing unsuitable (yellow), marginal (orange) and core (red) habitats and opportunistic sightings (blue circles). The 200m and 4000m contour is shown in order to illustrate proximity of high suitability areas over the continental slope.

3.32 Would opportunistic data from other species produce a similar predicted spatial distribution?

Opportunistic sightings of the common dolphin were used to construct a habitat suitability model to test whether or not the predicted distribution differs from that of the Cuvier's beaked whale. A habitat suitability map for the common dolphin was built (Figure 3.4) to show the predictive occurrence in the Bay of Biscay, in order to highlight the widespread distribution of common dolphin relative to the Cuvier's beaked whale. It can be seen that for a different species you get a different predicted distribution from the one that has been found for the Cuvier's beaked whale and is not a coincidence resulting from a spatial bias in the data collection. The prediction for Cuvier's beaked whale is not an accident of the spatial coverage of the opportunistic data. Using opportunistic sightings for a widespread and abundant species, such as the common dolphin, highlights extensive survey coverage within the study area yet the Cuvier's beaked whale was not encountered.

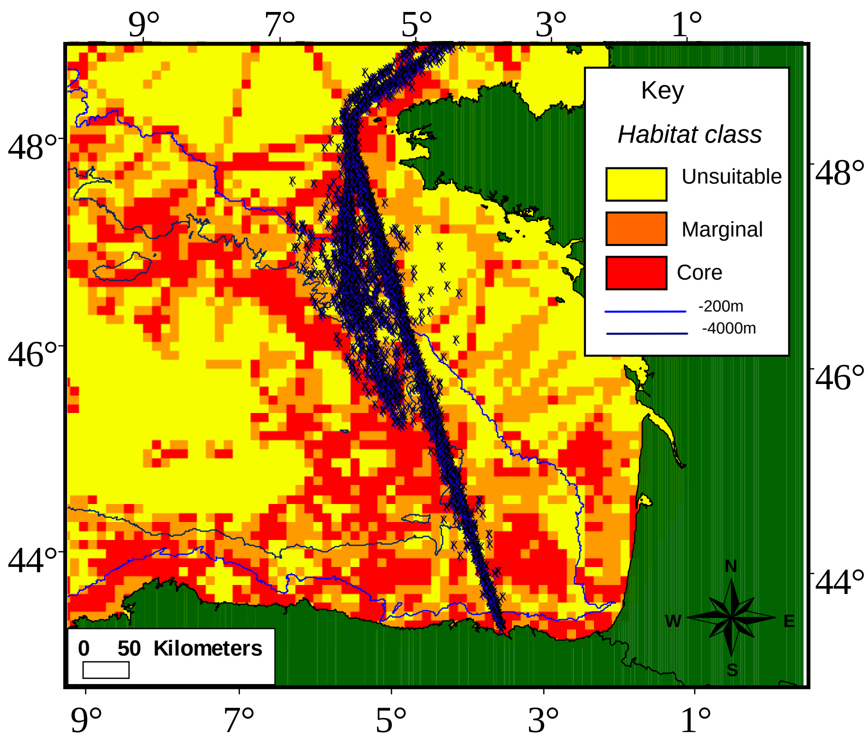


Figure 3.4: Habitat suitability map for the common dolphin (blue circles) in the Bay of Biscay showing unsuitable (yellow), marginal (orange) and core (red) habitats and opportunistic sightings (blue squares). The 200m and 4000m contour is shown in order to illustrate proximity of high suitability areas over the continental slope.

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3.33 Assessing the predictive ability of the ENFA opportunistic data with independent dedicated survey data.

In order to assess the predictive power of the ENFA, the area under curve (AUC) was computed using dedicated survey data of the Cuvier's beaked whale, using a ROC plot. The ROC plot (Figure 3.5) revealed that the predictions of the model differed significantly (AUC: 0.82; $P < 0.0001$; Table 3.2) from random (AUC = 0.5), which indicates it has good predictive abilities. On the other hand, an AUC equal to or less than 0.5 would suggest the predictions were no better than random and sightings would therefore randomly distributed within the study area and therefore would not be able to validate the ENFA model results. Because the dedicated survey data have shown a greater predictive ability than random, it can be used to validate the ENFA model, which used opportunistic sightings. This indicates that opportunistic data can be used to predict Cuvier's beaked whale occurrence in relation to EGVs.

Table 3.2: Area under curve (AUC) for ROC plot of the presence/absence model.

Test	AUC	95% CI	SE	Z	p	CBW = 1
HIS	0.82	0.76 to 0.87	0.027	11.50	<0.0001	have higher values

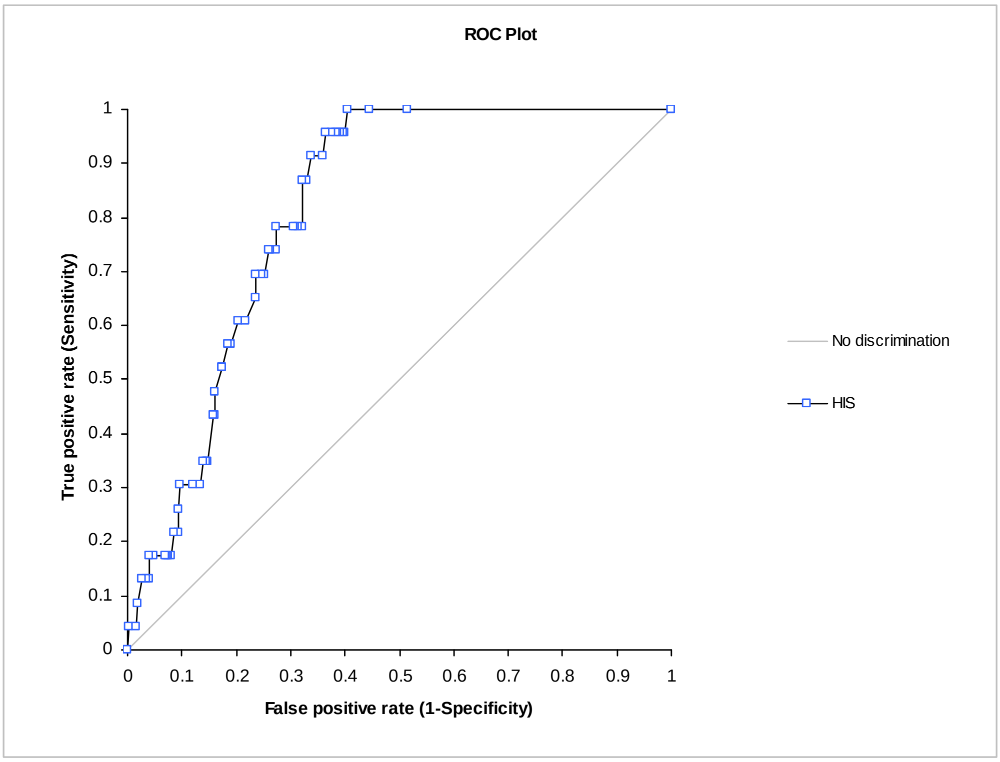


Figure 3.5: ROC plot used to assess the predictability of the modelling approach. Black line – ROC plot for ENFA; Light grey line – Random model with AUC of 0.5.

3.4 Discussion

3.41 Main findings

ENFA produced meaningful habitat predictions and good models of Cuvier's beaked whale distribution, using opportunistically collected data. Therefore, this study suggests that presence-only (opportunistic sightings) models can predict where the Cuvier's beaked whale is most likely to be found in relation to EGVs in the wider Bay of Biscay, and that opportunistic data can be used to understand habitat preferences of rarely seen species when dedicated survey data are limited. The habitat suitability maps marginal and core habitats in the Bay of Biscay to areas with deep water, steep slopes, and submarine canyons, associated with the northern and southern continental slopes. The HS maps produced for the Cuvier's beaked whale are in general agreement with findings from previous studies (Waring *et al.*, 2001; Ferguson *et al.*, 2006; Kiszka *et al.,* 2007; Moulins *et al.*, 2007). The independent dedicated survey data used to assess the predictive ability of this model suggests that it has a high predictive ability. A high value for the AUC indicated a greater predictive ability of the model and the further it differs from a random model (Fielding and Bell, 1997). Taking into account that an AUC value >0.90 is qualified as outstanding (Hosmer and Lemeshow (2000), indicates the validation results from this study (AUC 0.82) are excellent.

The marginality, specialisation and tolerance values computed from the ENFA are representative of the habitats utilized by the Cuvier's beaked whale. Marginality indicates that the required habitat differs from the average habitat and this is notable on the HS map, with greater proportion of unsuitable habitats than core habitats. Specialisation and tolerance go hand in hand, and they imply the Cuvier's beaked whale is specialised in its habitat use and therefore would rarely be seen over waters that are unsuitable; this is represented by the distribution of the sightings overlaid onto the HS map. The M, S and T values are of limited use with regard to a single species and expanding the current ENFA to other beaked whales observed in the study area would allow a comparison of species within the same ecological guild, see chapter 4. This would help identify multi-species core habitat 'hotspots' (Compton, 2004), which may be of high conservation priority and which often occur in the region of prominent habitat features such as submarine canyons.

By comparison to the results obtained by general additive modelling (GAM) in chapter 2, which provided more precision in terms of the preferred water depth, steepness of slope, and the direction in which the slope faces compared with ENFA, ENFA appears useful when absence data are limited or absent, or when a species is rare. From the HS map it is clear they prefer steep slopes and deep water, as shown by marginal and core areas, associated with the northern and southern continental slopes and submarine canyons. The findings in this study are consistent with the findings from the GAM modelling, chapter 2, and it appears that a combination of different techniques may be preferential for predicting species occurrence since the limitations of any one modelling technique can be compensated by the strengths of another model.

3.42 Comparison with previous studies

Few studies have used presence-only techniques to examine distribution and habitat preferences of cetaceans, in comparison to the widely used presence-absence techniques (see, for example, Mandleberg, 2004). One study used a PCA-based technique to model the distribution of four cetaceans in relation to EGVs in the coastal waters of western Scotland (Schweder, 2003). Another compared the ability of three presence only models, including ENFA, to a presence-absence approach to model the distribution of the harbour porpoise, in western Scotland (Mandleberg, 2004), and a third, the most relevant to this study, was modelling beaked whale distribution with ENFA (MacLeod, 2005a). This present study has not directly compared techniques but the presence-only modelling was validated using presence-absence data and they are comparable with the findings in the previous chapter (chapter 2). Mandleberg (2004) found no statistical differences between the presence-only and presence-absence techniques, implying that presence only can be used just as adequately as presence-absence. This was in contrast to previous studies Hirzel *et al.* (2001) used a modelling approach based on a virtual species with predetermined habitat preferences and found GLM predictions to be more accurate than those obtained with ENFA. Brotons *et al.* (2004) supported these results and found GLM predictions of the distribution of a forest bird species to be more accurate than those obtained using ENFA. MacLeod *et al.* (2008) suggests that the findings from the latter study were a result of models for 30 different species rather than direct comparisons of models for individual species. In contrast to the GLM, ENFA produced meaningful habitat predictions for three teuthophagus odontocete species in the northwestern Mediterranean Sea: Risso's dolphin, long-finned pilot whale and sperm whale (Praca and Gannier, 2007).

It was shown by Praca and Gannier (2007) that to assess the effect of global climate change on their distribution and abundance, extensive data sets, or absence data are not needed and ENFA is a useful tool for such objectives. MacLeod *et al.* (2008) also proposed ENFA as a useful tool, as they found presence-only approaches, such as ENFA, can potentially produce models of the distribution of marine species, and, they perform better than random models. Presence-only models do not have a significant poorer performance than presence-absence modelling for the same area, and presence-absence and presence-only models can give similar results, with all predicting the highest likelihood of occurrence in similar areas.

Other previous attempts to model Cuvier's beaked whale distribution have been based upon presence/absence models. Using GLM, Waring *et al* (2001) and Hamazaki (2002) found that Cuvier's beaked whales were associated with deep waters of the outer continental shelf edge along the northeastern coast of US, and using GAM, Ferguson *et al* (2006) found Cuvier's beaked whale distribution in the ETP to be mainly over deep waters. Established methods (e.g. logistic regression, discrimination analysis, GLM) for modelling presence and absence have provided some intuitive answers for habitat preferences, but absences can have three causes: the species is present but not detected, the habitat is suitable but the species is not encountered or no longer present, and/or the habitat is not suitable.

Despite the lack of absence data, which has already been accounted for, another aspect to consider when using presence-only data are the potential inaccuracies with a greater proportion of the presence cells from the dataset falling within the unsuitable habitat category. This, however, cannot be said for the Cuvier's beaked whales, as the ENFA did not fail to recognise any core habitats. Despite the one-off sighting in the area in northern Bay of Biscay classified as unsuitable, it can be seen from the HS map that all the sightings occur over the marginal/core habitats. Presence–only methods do not take into account the areas from which the species might be absent, but this was accounted for in this study by looking at the common dolphin distribution. It has a much wider predicative distribution and, more importantly, the sightings overlaid onto the HS map also highlight extensive survey coverage yet no observations of Cuvier's beaked whale. A habitat suitability map was computed for the common dolphin to see whether a different distribution was observed. The results indicated that for a different species, you get a different predicted distribution from the one that has been found for the Cuvier's beaked whale and it is not a coincidence resulting from a spatial bias in the data collection.

3.43 Advantages of using opportunistic data

ENFA is designed specifically for use with datasets that include adequate absence data, such as opportunistic sightings data and even museum records (Hirzel *et al.*, 2001, 2002a; Reutter *et al.*, 2003). Compton (2004) found ENFA to be good at predicting the distribution of the northern bottlenose whale, *Hyperoodon ampullatus,* in the NE Atlantic and demonstrated through validation that the model was statistically robust.

The first advantage of using opportunistic data is that a wider range of data can be incorporated into habitat models. Secondly, using such data is good for logistic reasons, as data can be pooled together from a number of resources and using techniques such as ENFA allow a wider range of data to be included, therefore maximising the resources available. Thirdly, research can be carried out at relatively low expense on vessels such as passenger ferries or container ships. The latter was used for the collection of opportunistic and dedicated sightings data used in this thesis. Collecting data from such vessels can be a cost-effective way of obtaining sightings data from areas where coverage from dedicated surveys has not been possible, due to the cost of hiring out vessels for such research and that the constant use of other vessels is not always available for effort based surveys. For ecological reasons, the advantage of using opportunistic data will advance the knowledge of the distribution of cetaceans more rapidly, that may otherwise take longer to achieve when trying to build up database from dedicated surveys. In the case of the opportunistic data used in this chapter, it is a much larger data set than the effort data, which in turn can identify much more in the way of predicted habitats. In particular, for the more elusive deep diving species, presence-only methods may then make the best use of available presence data (Brotons *et al.,* 2004), as this present study has achieved for Cuvier's beaked whale. Using opportunistic data can also advance the ability of further research to investigate habitat preferences of beaked whales and other species that are difficult to observe, by targeting other areas based on what has been identified in this study.

3.44 Summary

The analysis presented here identified key areas of habitat suitability within the Bay of Biscay. The results were consistent with previous findings that this species is linked primarily to the continental slopes and submarine canyons. This study shows that one can use opportunistic data to build models of species distribution to make use of a greater number of sightings for less commonly recorded species. To get around the limitations of using opportunistic data, a smaller amount of dedicated survey data can be used to validate the model and check that it is not the result of biases within the opportunistic data. Such surveys can be conducted using platforms of opportunity, providing a cheap and easy way to validate models build from opportunistically collected data. This is particularly useful for beaked whale species because it allows the most to be made of available data while retaining a strict approach to assessing how well the models perform.

Using this approach could enable the predictions of Cuvier's beaked whale distribution globally.

Chapter 4

Inter-specific comparison of habitat use for oceanic deep-diving cetaceans in the Bay of Biscay

4.1 Introduction

An adequate identification of key habitats and core areas where biologically and socially important behaviours concentrate is an important task in understanding a species' ecology. Interspecific comparisons among species and habitats have been extensively undertaken on terrestrial ecosystems, whilst relatively little has been done for the marine ecosystem and in particular for deep diving cetaceans. Deep diving cetaceans include the beaked whales species, sperm whales, *Physalus macrocephalus*, and the long-finned pilot whale, *Globicephala melas*. Studies looking at the use of habitat for such species were completed in the Gulf of Mexico (Davis *et al.,* 1998), Bahamas, east of Abaco (MacLeod and Zuur, 2005c), Mediterranean (Canadas *et al.*, 2002; Moulins *et al*, 2007) and Eastern Tropical Pacific (Ferguson *et al.*, 2006; Falcone *et al*, 2009), as well as over the submarine canyon 'the Gully', off eastern Canada (Hooker *et al.*, 2002). These authors have suggested that the habitat of several cetacean species, including the deep diving whales, could be defined based on physiography, i.e. depth and slope (from Kiszka *et al.*, 2007). In addition to these studies and long before, Heyning (1889) highlighted the importance of topographic features were important in defining habitats for deep diving cetaceans.

The Bay of Biscay and English Channel habitats include the continental shelf (only for the latter), continental slope, abyssal plain, submarine canyons, and seamounts, and the range of different habitats leads to the accumulation of many prey species for cetaceans (plankton, fish and squid), making it an ideal habitat for cetaceans and other wildlife. However, the habitat use and distribution of marine mammals in this region have not been extensively studied and described compared to some other regions of the world's oceans (i.e. the Gulf of Mexico, Davis *et al.,* 1998). The early studies that investigated cetaceans in this region described the frequently encountered cetaceans based on the distribution and abundance of the common dolphin, *Delphinus delphis* (Brereton *et al.*, 1999; Rosen *et al,* 2000), harbour porpoise, *Phocoena phocoena* and minke whale, *Balaenoptera acutorostrata*, (Rosen *et al,* 2000), bottlenose dolphin, *Tursiops truncatus*, (Layhaye and Mauger, 2000; Rosen *et al,* 2000), pygmy killer whale, *Feresa attenuate* (Williams *et al.*, 2002b), pilot whale (Kiszka *et a.,*. 2004), and the first confirmed sighting of the True's beaked whale, *Mesoplodon mirus* (Weir *et al.*, 2004). Dietary segregation between neritic and oceanic populations of common dolphin has also been studied (Layahe *et al.*, 2005). Before these studies, however, Evans (1980) compiled a mammal review of many different cetacean species from a number of sources, identifying waters around the whole British Isles as important areas for these marine mammals.

More recently, a quantitative study by Kiszka *et* al., (2007), has improved the understanding of habitat use among several cetaceans, including deep diving species, in the area by using sightings recorded on two independent ferry-based surveys operating between the UK and Spain, covering the English Channel and the Bay of Biscay. They found the deep diving species (Cuvier's beaked whale, *Ziphius cavirostris*, pilot whale and sperm whale) to occur in deep oceanic waters of the central and southern Bay of Biscay and overall it was shown that bathymetry played a significant role in the distribution and habitat partitioning of all toothed cetaceans examined (Kiszka *et* al., 2007). Buckland *et al.,* (1993) estimated pilot whale abundance for a survey block in the oceanic Bay of Biscay and adjacent waters during a North Atlantic sighting survey in summer 1989. MacLeod *et al.* (2009) looked at the occurrence of striped dolphin in the Bay of Biscay, whereby it was generally recorded in deep waters.

The study by Kiszka *et al* (2007), which explored the distribution and habitat use of toothed cetaceans was based on an effort-related survey, as was an earlier study by Williams *et al.,* (1999). Other studies in the Bay of Biscay using opportunistic sightings have only investigated distribution and abundance and not habitat use. Using opportunistic data provides a larger data set for analysis; especially where sightings are low, for example for beaked whales. This can increase the possibility of finding patterns in distribution that may reflect true distribution of whales and dolphins that are not seen in small data sets. There are, however, many limitations with using presence-only data. For example, unlike sightings from effort-based surveys, the absence of sightings in areas of opportunistic surveys cannot be accepted as true absences. To overcome this problem, opportunistic sightings for species that have a broader range in distribution within the study area could be used to identify observations being made in areas where beaked whales may be encountered and therefore justifying absences of cetaceans from the area.

To compare habitat preferences between species, methods such as Principal Component Analysis (PCA) can be used. PCA has been used in many terrestrial studies and to a lesser extent for marine studies, especially comparing between cetacean species. Using a data set of opportunistic sightings enables the use of PCA because it does not need effort related data. PCA can be used to partition the variance in cetacean habitat use among axes and these axes capture the patterns of species habitat use, using the predictor variables, i.e. ecogeographical variables (EGVs). Techniques such as PCA reduce the dimension of multivariate data to a level that is easier to interpret (Redfern *et al.,* 2006). The first PCA axis represents the greatest variation within the data set, with each subsequent axis representing a smaller amount of variation until 100% of the variation is explained. In order to assess how different sets of data compare in terms of variation in their combined values for all variables, the scores for each principal component for one set of data can be compared to the other. If there is substantial difference in the principal component scores between the data sets on one or more of the principal component axes, this will indicate that they do not consist of data with similar combinations of the variable examined. The PCA can be use to investigate distribution of species in the same area by looking at the niche centre and niche width, which helps to identify species niche overlap.

A detailed study by Kiszka *et al.* (2007) has already highlighted the distribution of cetaceans in Biscay, although their work and most previous studies (mentioned above) concentrated surveys in specific areas, and/or certain times of the year i.e. summer. The Biscay Dolphin Research Programme (BDRP) overcame this limitation of surveys in specific regions by carrying out research on the distribution of cetaceans in the temperate waters of the English Channel and the Bay of Biscay on board the P&O ferry 'Pride of Bilbao', which started in 1995. The ferry covers the waters between Portsmouth in the UK and Bilbao, northern Spain, so the information gathered represents a substantially large area than previous work. The surveys were initially effort based but then in 2003 the wildlife officer for BDRP started monitoring cetaceans and recorded those sightings as casual (or opportunistic) on every trip. Recording sightings on every trip has led to a large data set of opportunistic sightings. There are only two limitations of collecting data on this ferry route; one is that it covers a narrow area along a fixed route and two part of the region is covered at night. However, sightings identified along a fixed route can be extrapolated out from the fixed route to see if patterns in distribution over similar topographic features in Bay of Biscay and English Channel differ. This is not looked at in this chapter.

This chapter is the first study that compares the habitat use between deep diving cetaceans in the Bay of Biscay using multivariate statistics on a large data set. In this study, opportunistic sightings data are used to compare the relative habitat preferences of Cuvier's beaked whale to other deep-diving and non-deep-diving cetaceans recorded on the same surveys in the Bay of Biscay, based on the assumption that the same habitat has been sampled in each case. It is hypothesized that deep diving whales will show a similar habitat use relative to the topographic features. The main objectives for this chapter are first to explore how habitat use compares among deep diving cetaceans in the Bay of Biscay by relating their distribution to three ecogeographical variables: depth, slope and aspect; and secondly, is there a way to relate opportunistic sightings to effort related sightings in the region? The good coverage of sightings data being used for this study should show the range in habitat preference very well for each species under investigation.

4.2 Methods

4.21 Study area and survey methods

The study area covers the English Channel and the Bay of Biscay (Figure 4.1 – map of the Bay of Biscay), along the route of the P&O ferry 'Pride of Bilbao', which operates between Portsmouth, UK and Bilbao, northern Spain every three days. The Biscay Dolphin Research Programme (BDRP) is the onboard charity collecting data on marine mammals and seabirds. On every sailing from Portsmouth to Bilbao, a wildlife officer is on board. However the wildlife officer is not observing at all times due to other duties on board. Because a wildlife officer was on board every trip year round from 2003, it was in the interest of the charity to start collecting data to monitor the distribution of cetaceans either side of the survey teams that survey twice a month. The wildlife officer (BDRP) on board the ferry collected the casual (referred to as opportunistic) sightings data from 2003 to 2007. In doing so, it provided a larger data set to work with when analysing cetacean distribution. For this study, opportunistic sightings recorded by the wildlife officer for the BDRP were explored to look at the habitat use of Cuvier's beaked whale, *Ziphius cavirostris* compared to the northern bottlenose whale, *Hyperoodon ampullatus*, Sowerby's beaked whale, *Mesoplodon bidens*, unidentified beaked whales (or BWsp), sperm whale, *Physalus macrocephalus,* long-finned pilot whale, *Globicephala melas,* common dolphin, *Delphinus delphis,* fin whale, *Balaenoptera physalus,* and striped dolphin, *Stenella coeruleoalba*. Opportunistic sightings were recorded in all sea states, and all sea states were included in the analysis.

4.22 Ecogeographical variables (EGVs)

The EGVs used in this analysis were depth, slope, aspect easting and aspect northing. A 10 by 10km grid was created in MapInfo and exported into ArcView 3.2. The grid was overlaid onto the study area and each grid cell was assigned a cell ID. Depth, slope and aspect were calculated in ArcView GIS 3.2 as coverages of the whole area, and linked to cells within the 10km by 10km grid using the spatial join function. The depth values for the central point of the cells were obtained by overlaying the grid onto the GEBCO bathymetry data set. The slope and aspect were then taken from the depth values in ArcView using the spatial analyst tool. Aspect was initially measured in degrees and then converted from a circular variable (degrees) into two linear components: Sine (Easting) and Cosine (Northing) of the original aspect. The aspect needed to be converted from degrees to circular variables, for example, a cell with an aspect of 359^{o} would give a very different value to a cell with an aspect of 1° even though they are both facing a very similar direction, therefore aspect is separated into an easting and northing. Sine and cosine range from -1 to 1, positive is equal to east and north, while negative is equal to west and south.

After each grid cell was assigned an EGV value, an average for each EGV per grid cell was calculated using the map calculator function. The sightings were then joined to the 10km grid, which then produces a cell ID number next to each sighting. The grid with the EGVs attached was then joined to the sightings data by the cell ID, to link sightings with EGVs. The identification numbers will be referred in the analysis. The database was sorted by species with a column for the average depth, slope aspect easting and aspect northing. This was then imported into Minitab for statistical analysis-see next section.

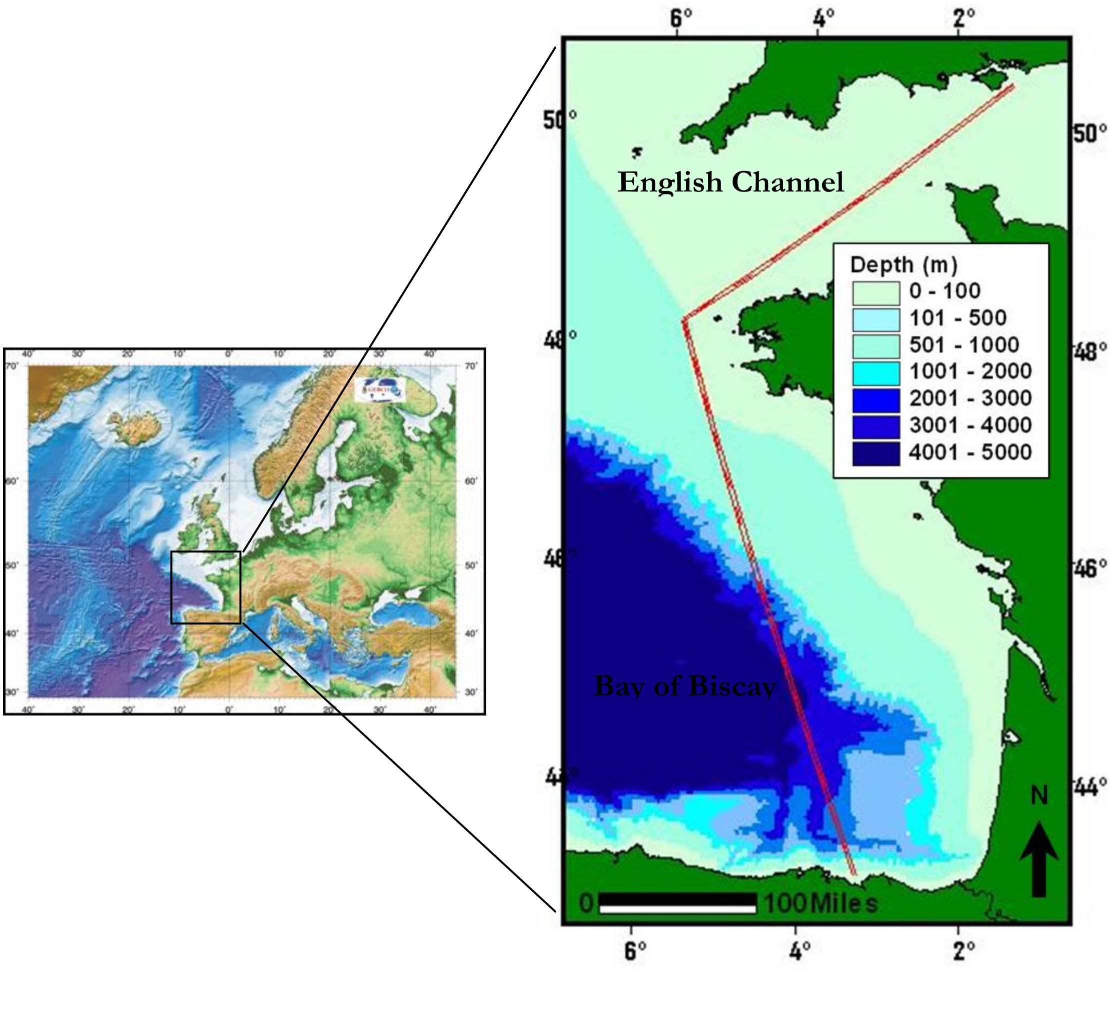


Figure 4.1: Study area, Bay of Biscay, northeast Atlantic. Ships track Portsmouth (UK) to Bilbao (Spain), highlighted in red and water depth is shown in metres. (Left map taken from www.noc.soton.ac.uk)

4.23 Analytical methods

4.231 Principal Components Analysis (PCA)

Standard PCA analyses were conducted using Minitab statistical software (Minitab Ltd) on the cetacean sightings and EGV data using all possible combinations of four variables; depth, slope, aspect easting and aspect northing. The value for each variable for each sighting of all 8 species was standardised by subtracting the mean value of that variable form the actual value for each sighting and then dividing by the standard deviation (see Robertson *et al.*, 2001). This ensures that variables measured on different scales are treated as equal during the PCA process. A PCA was then conducted on these standardised values and a principal component (PC) score was calculated for each axis for each EGV using the appropriate eigen vectors from the PCA. The principal components are independent measures of the variation in the data. The resulting values for each principal component (1, 2, 3 and 4; representing each variable) for each species were added together until the accumulated variation explained by the PC was >80%. The first rule of thumb is the 80% rule; use the principal components that explain 80% (cumulative) of the total variation (Zuur *et al.,* 2008). The PCA compares the distribution for all species described above using depth, slope, and aspect (easting and northing) for localities where the species have been recorded as present. To investigate species niche centre and niche width, principal component 1, 2, 3 and 4 values for each species were standardised (weighted) by multiplying each principal component value by their eigen score. The eigen score was given as the result once the PCA had been run on the data. The average and standard deviation of PC1, 2, 3, and 4 for each species and sightings were used to visualise the species distribution relative to EGVs using ordination plots. The distribution of the principal component scores along an axis will represent the variation in habitat combinations defined by it. After the PC values were standardised, they were added together to give one PC value for each sighting of each species. This final PC value was used in further statistical analyses.

4.232 Niche centre

A Kruskal-Wallis (H statistic) test was used because variance significantly differed between species. The test statistic for the Kruskal-Wallis is H. The Kruskal-Wallis test is a nonparametric test used to compare three or more samples. It is used to test the null hypothesis that all populations have identical distribution functions against the alternative hypothesis that at least two of the samples differ only with respect to location (median). To identify which pairs of species were significantly different, a Mann-Whitney (W statistic) test was carried out on all possible pairs of species (significance is defined as *p-value <0.05*).

4.233 Niche width

The equality of variance statistic (F-test or Levene's test) was used to look at the niche width of each species. Pairwise comparisons were made on all possible pairs of the eight different species. This test determines any significant differences between pairs of species that differ in their niche width. If the value is significant, the conclusion is that, on average, the deviations from the mean in one group exceed those of the other being tested. If the variance is large, it implies a wider niche width. Both the niche centre and niche width were illustrated using a histogram of PC values per species and along with the standard error.

The following diagram shows how species niche centre and niche width can differ.

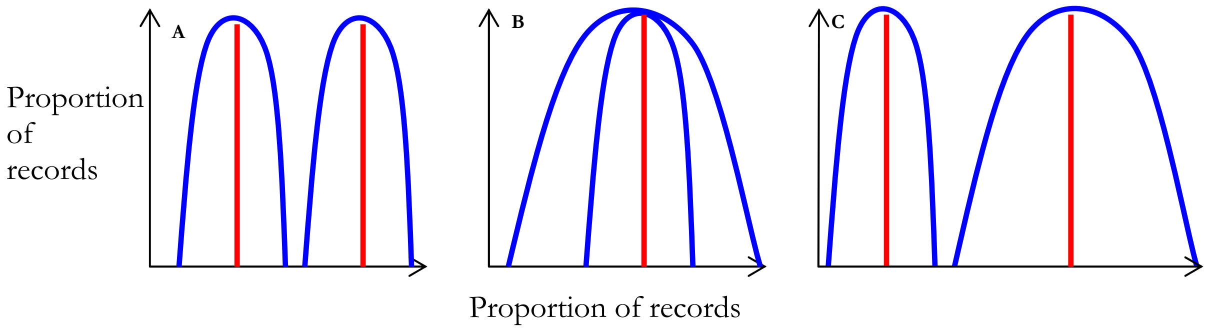


Figure 4.2: Ecological niche diagram to represent species boundaries. (A) Different centre, same width, (B) Same centre, different width and (C) Different niche centre, different width.

4.3 Results

4.31 Distribution of cetaceans in the Bay of Biscay and the English Channel

Between 2003 and 2007 opportunistic sightings were collected on every trip the ferry made between Portsmouth, UK and Bilbao, Northern Spain. A total of 7012 encounters (201672, individuals) were recorded, see Table 4.1 for individual species total numbers. The maps produced (Figures 4.2 to 4.6) highlight the distributions of each species as the sum of the total number of sightings over 5 years for each species. The first map (Figure 4.3) represents all sightings recorded in the English Channel and the Bay of Biscay. Cuvier's beaked whale shows a preference for deep waters >1000m (Figure 4.4). The northern bottlenose whale displays a similar distribution to Cuvier's beaked whale in the Bay of Biscay. Beaked whales predominantly inhabit the deep waters of the Bay of Biscay. Figure 4.5 illustrates the observations for the sperm whale and the pilot whale. The sperm whale appears to have a preference for deep water and steep and complex topography, similar to that of the beaked whales. The pilot whale also shows a preference towards deep water and the continental slope. However, it is also seen in waters further north over the continental shelf and the English Channel. This may be reflected by the prey species consumed by the pilot whale. The common dolphin exhibits a wide distribution, ranging in both shallow and deep waters (Figure 4.6). With the exception of a few sightings in the English Channel, the fin whale is predominantly seen in the Bay of Biscay in waters ranging from 500 to 5000m deep, similarly with the exception of one sighting at the western end of the channel the striped dolphin is observed just in the Bay of Biscay (Figure 4.6).

Table 4.1: The total number of encounters and individuals per species.

Species	*Encounters*	*Individuals*
Cuvier's beaked whale	402	957
Northern bottlenose whale	39	89
Sowerby's beaked whale	15	28
Beaked whale sp.	212	336
Long-finned pilot whale	503	4412
Sperm whale	235	435
Fin whale	1392	2929
Common dolphin	2917	136371
Striped dolphin	1297	56115

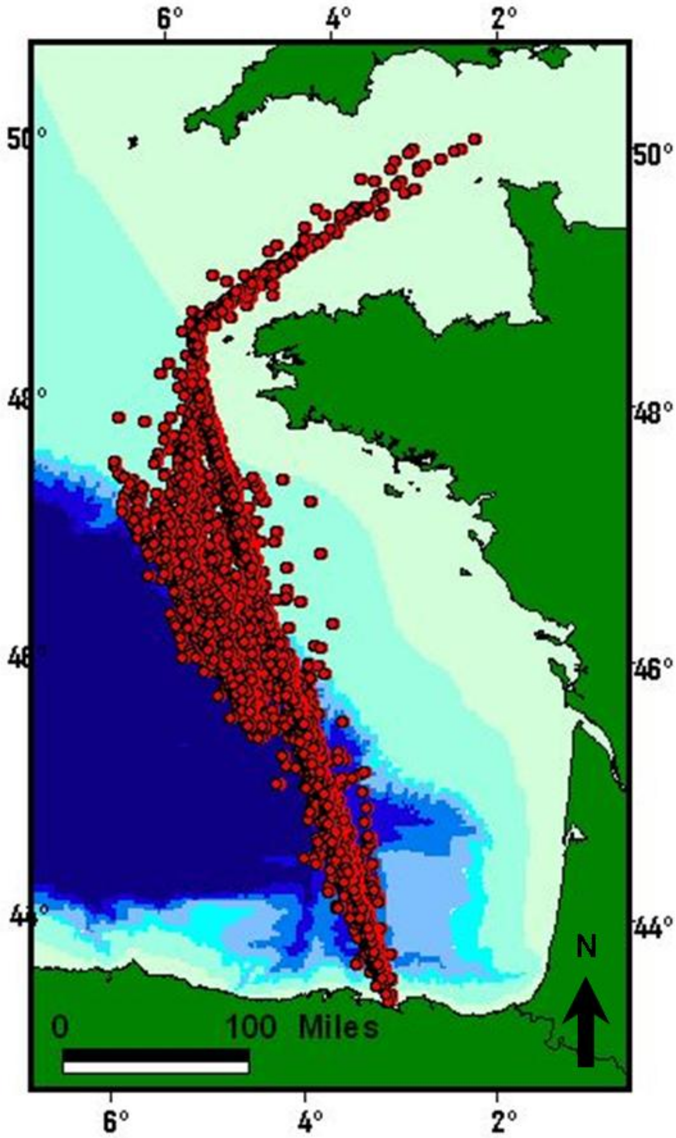


Figure 4.3: Distribution of all cetaceans (red circles.) sightings: Cuvier's beaked whale, northern bottlenose whale, Sowerby's beaked whale, beaked whale spp, sperm whale, pilot whale, common dolphin and fin whale.

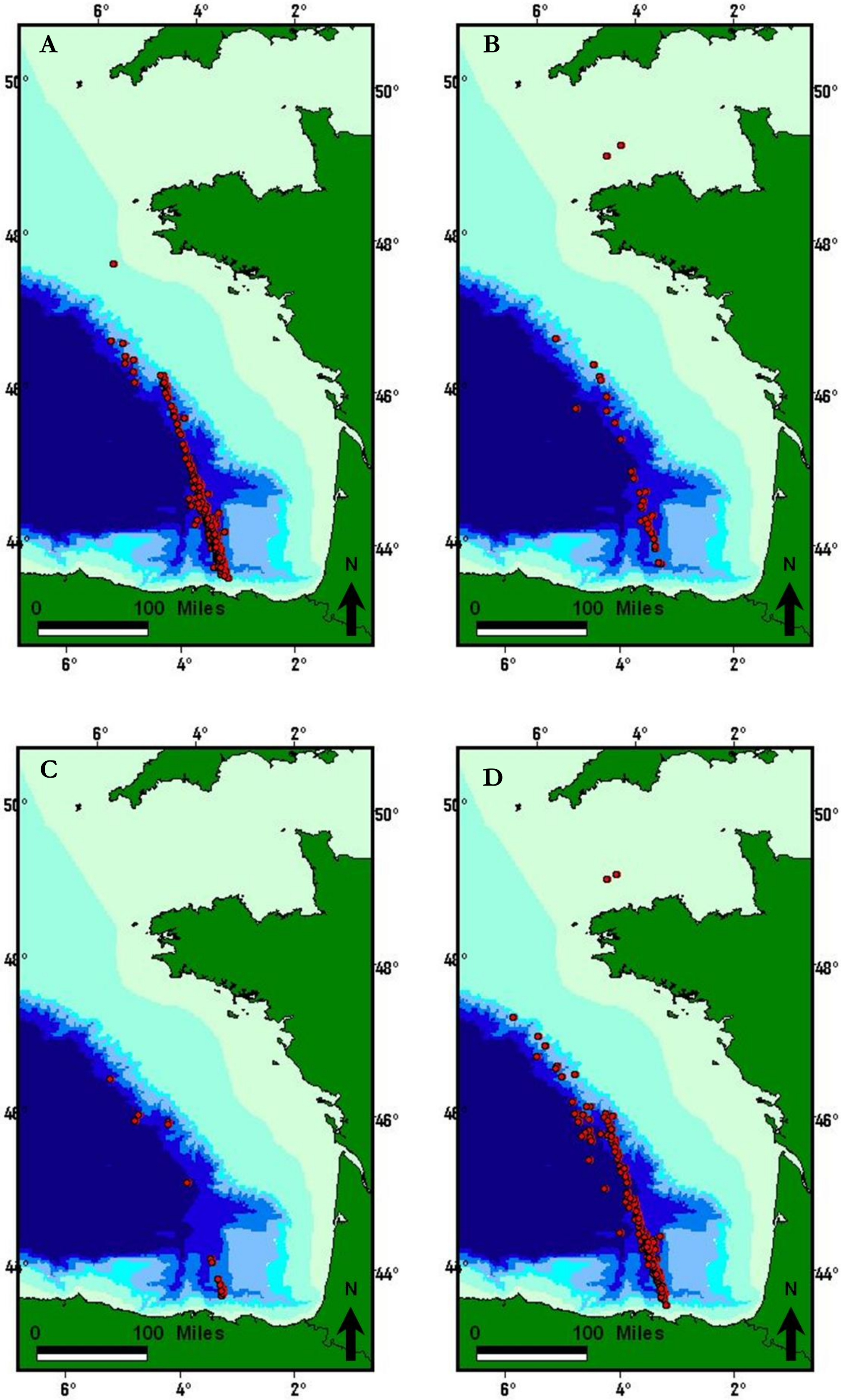


Figure 4.4: Distribution of all beaked whale species: Cuviers' beaked whale (A), northern bottlenose whale (B), Sowerby's beaked whale (C) and beaked whale sp (D), highlighted by red circles.

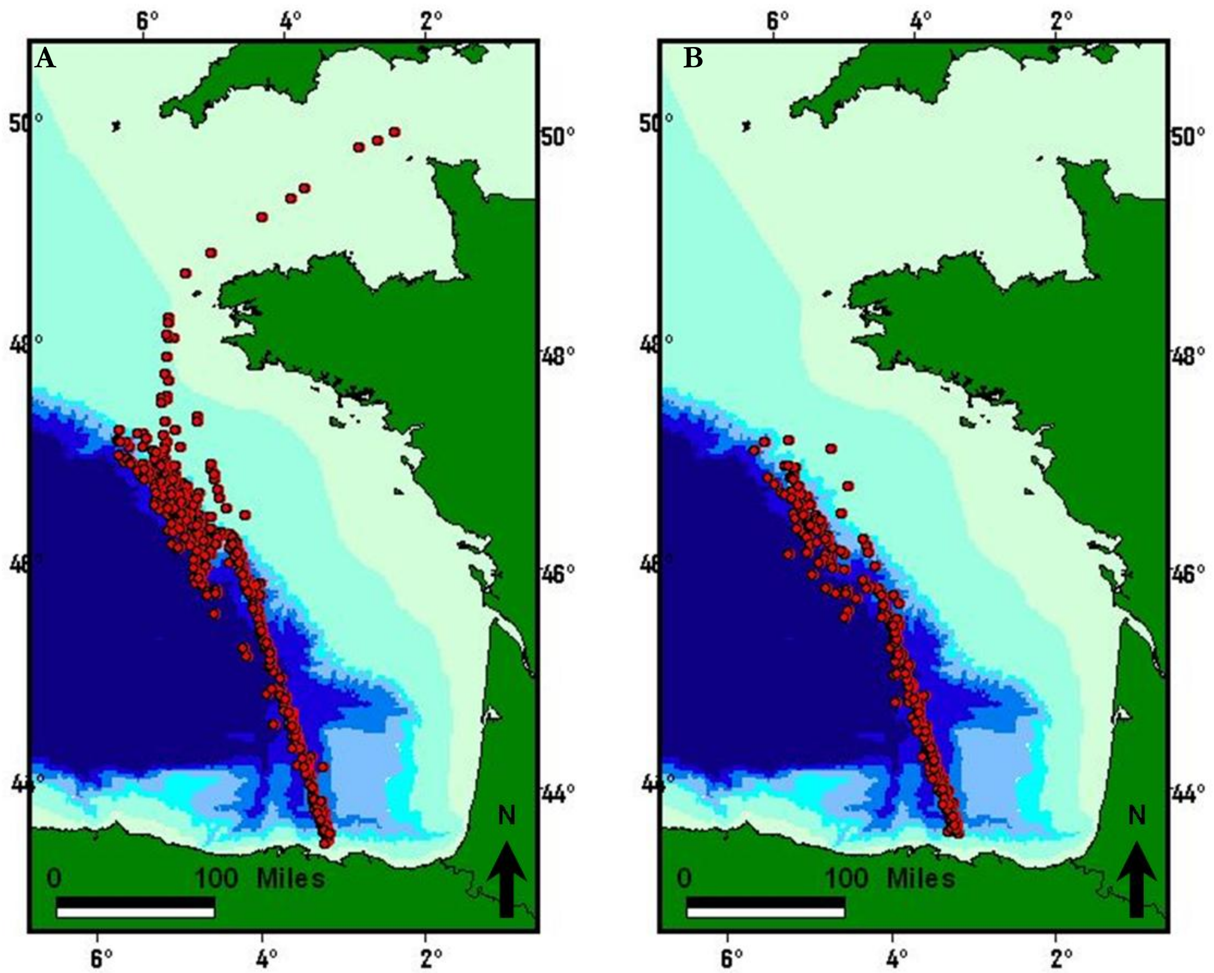


Figure 4.5: Distribution of pilot whale (A) and sperm whale (B), highlighted by red circles.

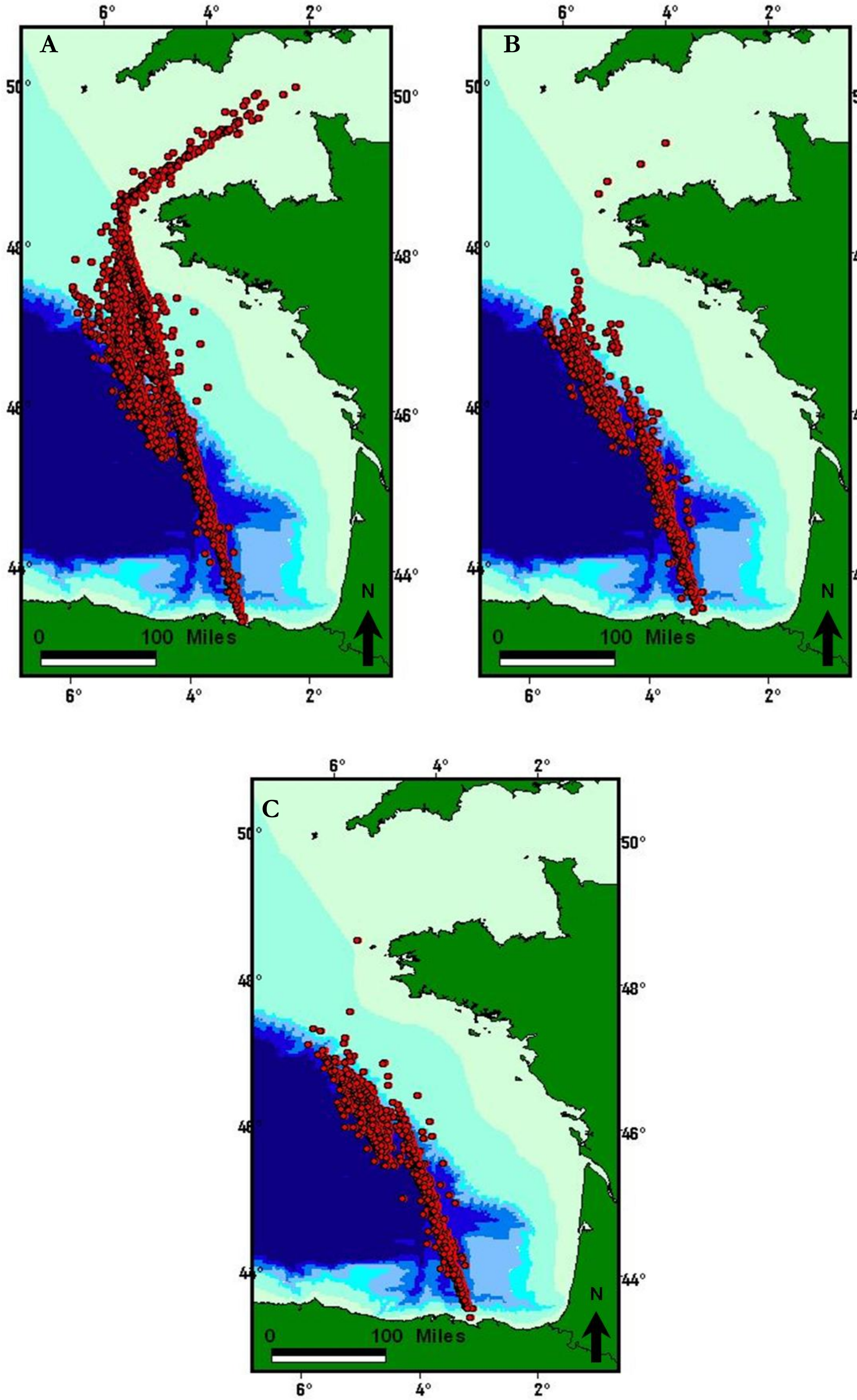


Figure 4.6: Distribution of the common dolphin (A), fin whale (B) and striped dolphin (C), highlighted by red circles

4.32 Analytical findings

4.321 PCA

The habitat use for all species was examined using PCA to look at relative habitat use. The first principal component (PC1) represents the major source of variation in the data (Table 4.2). The most important variable is highlighted in bold, italics highlight the second most important, and the third is underlined. The PC(s) that accumulate the most variation, which account for at least 80% of the variation, are the ones to focus on in terms of the important EGVs. Another way of representing the data is by looking at the number of adequate dimensions that explain distribution. The first of these is associated with the most important variable based on absolute values, the second is associated with the next highest value and so on.

The resulting eigenvalue (Table 4.2) shows the variance on the new factors that were successively extracted. The variances extracted by the factors are called the eigenvalues. This name derives from the computational issues involved. In the sixth row, these values are expressed as a percentage of the total variance and the seventh row contains the cumulative variance extracted. It can be seen that principal component 1 accounts for 35% of the variance, principal component 2 accounts for 66 %, and so on. As expected, the sum of the eigenvalues is equal to the number of EGVs.

The results show that three principal components are needed to explain over 80% of the variation in habitat use and they are a substantial part of the original variation. The data can also be represented adequately in just two dimensions. The first 2 principal components extracted had eigenvalues greater than 1.0 and accounted for over half the total variation present in the data set. Principal component 1, which explained 34% of the variance, indicated that sightings are compared firstly by aspect northing, water depth, and then slope. The former is negative and therefore south facing slopes are used to explain habitat use. Principal component 2, which accounted for 31.1% of the variance, highlights two primary variables, aspect easting, and slope that contributed to driving the differences between species niche. A negative relationship with aspect easting, suggesting west facing slopes are important for habitat use.

EGVs	PC1	PC2	PC3	PC4
Depth	*0.6032*	-0.2270	0.7145	-0.2721
Slope	0.4878	*0.5814*	0.0208	0.6508
Aspect easting	0.0587	**-0.7643**	-0.0486	0.6403
Aspect Northing	**-0.6283**	0.1620	*0.6976*	0.3039
eigenvalue	1.3109	1.2759	0.8078	0.6053
proportion	0.3280	0.3190	0.2020	0.1510
Accumulated variation explained	0.3280	0.6470	0.8490	1.0000

Table 4.2: PCA Eigen vectors and components scores for all species together

The PCA results give an indication of niche differences among the species. Figure 4.7 illustrates that the common dolphin and Sowerby's beaked whale are separated from the other species on the PC1 axis, with the latter separated on the PC2 axis as well, and the Pilot whale is separated from the other species on the PC2 axis. Most importantly, it reveals these three species are dissimilar in their habitat use compared to Cuvier's beaked whale, beaked whale sp, northern bottlenose whale, sperm whale, fin whale and striped dolphin. The primary EGVS that contributed in driving the separation between species are aspect northing, depth, and slope on the PC1 axis and aspect easting and slope on the PC2 axis. The common dolphin lies further down PC1 axis, which indicates that is separated from the other species by a preference for gentle slopes, shallower water, and south facing slopes. Sowerby's beaked whale lies further up the PC1 axis, which indicates it is separated from the other species by a preference for steeper slopes, deeper water, and north facing slopes. The pilot whale is similar to the others on the PC1 axis, but is separated on the PC2 axis, whereby the separation along this axis is reflected by its preference for more east facing slopes and steep slopes.

Cuvier's beaked whale, beaked whale sp, northern bottlenose whale, sperm whale, and fin whale cluster together on the PC graph (Figure 4.7) higher up on the PC1 axis compared to the PC2 axis. This implies that a combination of three most important variables for PC1: slope, aspect northing and depth are the most important. Firstly, a positive relationship with slope indicates this group prefers steeper slopes, secondly a positive relationship with depth indicates this group prefers deep water, and thirdly a negative relationship with aspect northing indicates this group prefers south facing slopes. This relationship can be compared well with the distribution maps produced (Figures 4.3 to 4.6), where each species from this group are predominant in waters of the continental slope, submarine canyons and deep waters of the abyssal plain in the Bay of Biscay.

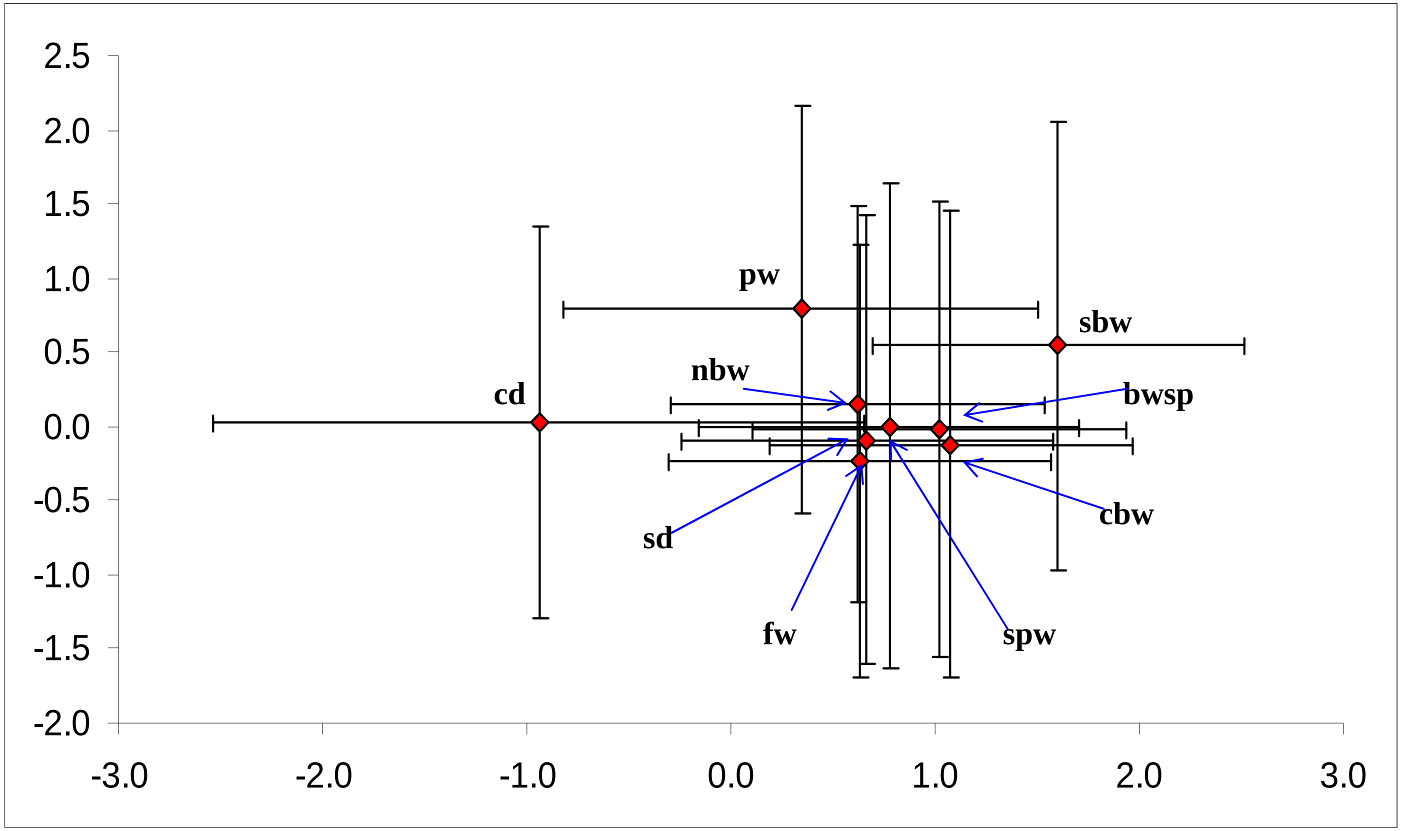


Figure 4.7: PCA scores graph (PC1-*x-axis* v PC2-*y-axis*) for all cetacean sightings. The abbreviations indicate species names: common dolphin-cd, striped dolphin – sd, pilot whale-pw, sperm whale-spw, fin whale-fw, Cuvier's beaked whale-cbw, northern bottlenose whale-nbw, sowerby's beaked whale-sbw, unidentified beaked whale-bwsp).

4.322 Niche centre

A Kruskal-Wallis test was carried out on the PC values for each species, because the variance significantly differed between species pairs (H = 1084.52; *df* = 437; *p-value* = <0.05), (H = 1190.86; *df* = 437; *P-value* >0.05, adjusted for ties). The evidence here suggests rejection of the null hypothesis (H_o): the whales occupy the same habitat. Rejecting the Ho means there is sufficient evidence to conclude that at least two species show a significant difference in the centre of their niche. So which whales occupy different habitats? To find out which species differed in their niche centre, a Mann-Whitney test was run on each pair of species. The results show nineteen out of the thirty-six different pairs of species significantly differed in their niche centre (*P = <0.05,* highlighted in bold) (Table 4.3). The p-values highlighted in red would not be viewed as significant when the Bonferroni correction P=< 0.0014 is applied and only sixteen pairs are significantly different.

4.323 Niche width

To understand how the niche width differed among the 8 species, a 'Pairwise Equality of Variance' test was run on each pair of species (F-test statistic and the *p-value,* Table 4.4). The F-test shows that eleven pairs of species were significantly differed in their niche width. The p-values highlighted in red would not be viewed as significant when the Bonferroni correction P=< 0.0014 is applied and only nine pairs significantly differ when this was added. It has been inferred from these results that two groups are noticeable: group one includes Cuvier's beaked whale, northern bottlenose whale, beaked whale sp, pilot whale, sperm whale, fin whale and, striped dolphin; where by they all significantly differed in their niche width from common dolphin. The second group highlights the pilot whale being significantly different in its niche width from Cuvier's beaked whale, beaked whale sp, common dolphin, fin whale and striped dolphin. This implies the deviations from the mean for the common dolphin exceeded that of the mean for the other six species it was compared against and likewise for the pilot whale versus four other species. This is comparable to the maps, where the common dolphin and pilot whale are regularly observed in the English Channel and the other species are not. This is indicative of their wider niche in this area. The test did not show any differences between the Sowerby's beaked whale and the other species and it also showed the northern bottlenose whale to be significantly different from one other species, the common dolphin (before the Bonferroni correction was applied). This may be because there was no difference in the niche width or because the sample size of the two species compared to the rest was too small to obtain any conclusive results. The latter is more realistic as their habitat preferences are similar to Cuvier's beaked whale and beaked whale sp, so they too should have been significantly different from the common dolphin.

A large variance for the pilot whale and common dolphin versus fin whale, indicates they have a wider niche than the fin whale. Cuvier's beaked whale, beaked whale sp, pilot whale and sperm whale versus fin whale do not appear to have a variance larger than any other value in the table, but they are significantly different from the common dolphin. Because they were significantly different from the fin whale, a large variance was expected, as was the case with the pilot whale and common dolphin versus the fin whale. Nevertheless, the significant difference is evident enough to demonstrate that they have a different niche width.

Figure 4.8 is a histogram plot of the niche centre and niche width of each species, with the columns indicating the niche centre, and standard deviation bars indicate the niche width. This graph helps to identify which species have a wider or narrower niche but same centre, a different niche centre but the same niche width, or if they show similar niche centres and widths. The pairs of species that have similar niche centres are Cuvier's beaked whale and northern bottlenose whale, Sowerby's beaked whale and pilot whale and beaked whale sp, sperm whale, fin whale and striped dolphin. The error bars on the graph show there is overlap in the niche (width) of each species, indicating they occupy the same habitats. Overlap in the niche is most likely due to sufficient prey availability for each species, to sustain all the species investigated. In terms of niche widths the species have placed into three groups; the first group being Cuvier's beaked whale, northern bottlenose whale, Sowerby's beaked whale, beaked whale sp have similar niche widths, the second, pilot whale, sperm whale, fin whale and striped also have similar niche widths and the third is the common dolphin, as it has a wider niche width than the rest. The latter two groups of species have a wider niche width compared to the former group of species.

		W - statistic test								
		CBW	*NBW*	*SBW*	*BWsp*	*PW*	*SpW*	*CD*	*FW*	*SD*
	CBW		67197.50	**61913.50**	94343.50	**125588.50**	97205.00	**785839.50**	293811.50	**25842835.00**
	NBW	0.9365		928.00	4590.00	**7816.50**	4888.00	**79061.00**	27238.50	23173.50
	SBW	**0.0070**	0.0054		**2275.50**	4445.00	2411.00	**36069.50**	**14493.50**	12707.50
p-value	*BWsp*	0.1279	0.4373	**0.0214**		**65702.00**	46920.50	**476226.50**	176570.00	153977.50
	PW	**0.0000**	**0.0033**	0.3338	**0.0001**		**194999.50**	**1249186.00**	**555053.00**	**500469.00**
	SpW	0.0473	0.3009	0.0518	0.6775	**0.0007**		**534377.00**	200505.00	175811.00
	CD	**0.0000**	**0.0001**	**0.0000**	**0.0000**	**0.0000**	**0.0000**		**5386814.00**	**5218710.00**
	FW	0.3343	0.7878	**0.0120**	0.3053	**0.0000**	0.1665	**0.0000**		**1791751**
	SD	**0.0006**	0.2222	0.0500	0.3011	**0.0000**	0.4891	**0.0000**	**0.0001**	

Table 4.3: Comparison of the niche centres of all species using a Mann-Whitney test (significance is defined as *p-value* <*0.05*)

		F- test statistic								
		CBW	*NBW*	*SBW*	*BWsp*	*PW*	*SpW*	*CD*	*FW*	*SD*
	CBW		1.03	1.02	1.00	**0.72**	0.85	**0.52**	0.96	0.95
	NBW	0.940		0.99	0.96	0.70	0.83	**0.51**	0.93	0.92
	SBW	0.956	0.929		0.97	0.70	0.83	0.51	0.94	0.92
p-value	*BWsp*	0.962	0.923	0.968		**0.72**	0.86	**0.53**	0.96	0.95
	PW	**0.001**	0.168	0.454	**0.007**		1.19	**0.73**	**1.33**	**1.32**
	SpW	0.185	0.488	0.736	0.258	0.134		**0.61**	1.12	1.11
	CD	**0.000**	**0.010**	0.142	**0.000**	**0.000**	**0.000**		**1.84**	**1.81**
	FW	0.644	0.807	0.964	0.749	**0.000**	0.229	**0.000**		0.99
	SD	0.544	0.766	0.938	0.661	**0.000**	0.286	**0.000**	0.814	

Table 4.4: Comparison of the niche width of all species using an equality of variance test (significance is defined as *p-value* <*0.05*).

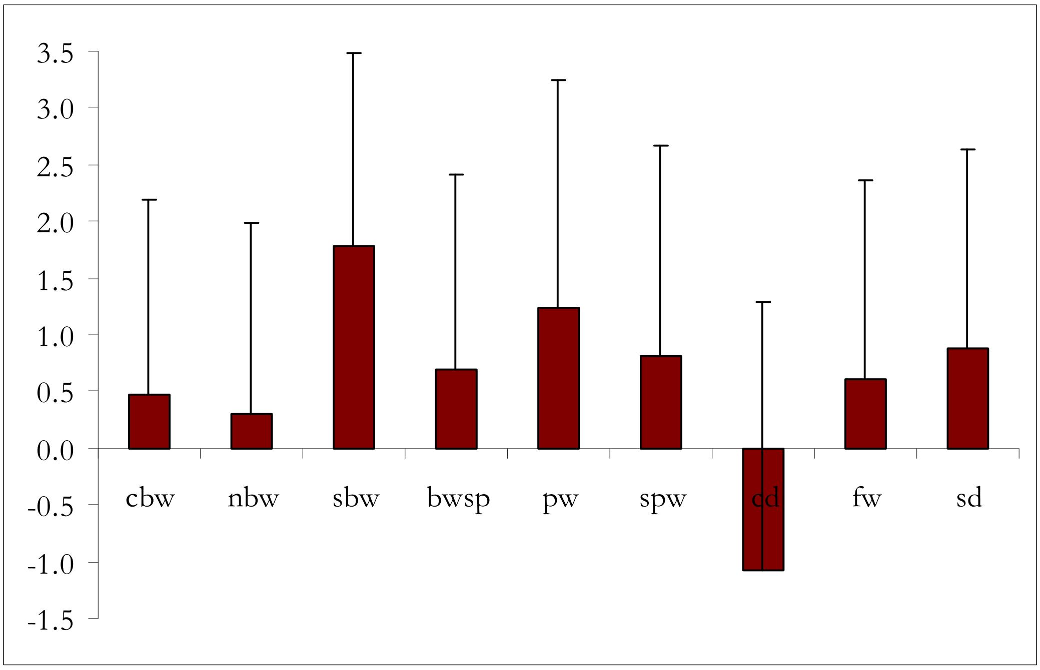


Figure 4.8: Comparison of the niche centre (columns) and niche width (error bars) of each species, as an average of the principal component score (*y-axis*) for each species.

4.4 Discussion

This chapter has explored the habitat preferences of six deep diving species and two non-deep diving species, and the possible determinants of their distribution in the English Channel and the Bay of Biscay. The two non-deep diving species were chosen as they inhabit the deep waters of Biscay and it was of interest to see where how their niche compared to the deep diving species. The results obtained here highlight two important relationships between occurrence and the environment. First, there is clear evidence that some of the animals are not evenly distributed throughout the environment of the English Channel and the Bay of Biscay; and second, there were similarities and dissimilarities in the niche they occupy.

4.41 Comparison of habitat preferences

The waters of the English Channel and the Bay of Biscay have a relatively high diversity of marine mammals, with approximately 30 species being recorded by the Biscay Dolphin Research Programme. This is one of the first studies to compare the habitat preference of deep diving whales in the Bay of Biscay using a long tem data set. The wide coverage from 2003 to 2007 all year round means that full habitat ranges observed are absolute based on the ferry route. `The findings of this study highlight the English Channel and the Bay of Biscay as important habitats for cetaceans and these habitats include the continental shelf, continental slope, submarine canyons, and deep waters of the abyssal plain. All eight species were encountered in the Bay of Biscay and five of them were also encountered in the English Channel (Figures 4.3 to 4.6). The four cetacean species encountered in the English Channel were northern bottlenose whale, pilot whale, fin whale, and common dolphin. In addition, unidentified beaked whales were observed in the English Channel. The common dolphin was observed in large numbers as was the pilot whale to a lesser extent and the other three were only observed on a few occasions in the English Channel, indicating the infrequent use of this habitat. Because of this, they can be placed into two major species groupings: (1) specialists, consisting of Cuvier's beaked whale, northern bottlenose whale, Sowerby's beaked whale, beaked whale sp, sperm whale, fin whale and striped dolphin that prefer offshore waters; (2) the generalists are the common dolphin and pilot whale that prefer both offshore and inshore waters. This suggests that the division between shelf and deep-waters is one of the most important factors in defining where species occur in this region and will have a strong influence on the composition of local marine mammal assemblages in this region. Such divisions between shelf and deep-water species are relatively common in marine mammal assemblages and have been noted in this region before (Evans *et al*, 2003; Reid *et al.*, 2003; Kiszka *et al.*, 2007).

Using opportunistic data meant there were sufficient sightings to investigate the habitat preference of seven species (described above) using PCA. The PCA analysis adequately identified patterns in the habitat preference of those seven species investigated and highlighted their similarities and differences. Using the first two PCs, which accounted for over half of the variation in distribution, slope, depth and aspect were all found to be the important variables responsible for driving the differences between the habitat preferences of those species. The ordination plot identified the common dolphin, pilot whale and Sowerby's beaked whale as separated from the other species investigated; common dolphin and Sowerby's beaked whale by principal component 1 axis and pilot whale by principal component 2 axis. The former two were separated at either end of PC 1 axis; the common dolphin was at the negative end indicating its preference for gentle slopes, shallow water and south facing slopes. In contrast, Sowerby's beaked whale, which was at the positive end, indicating a preference for steeper slopes and deeper water and north facing slopes. The important variable for principal component 2, by which pilot whales were separated from the other species, was a preference for steep slopes and east facing slopes.

The habitat preferences the of Cuvier's beaked whale, northern bottlenose whale, Sowerby's beaked whale, unidentified beaked whales, sperm whale, long-finned pilot whale, common dolphin, and fin whale in the study area was found to be associated with all three EGVs (depth, slope, aspect). The common dolphin occupy the same area as the deep diving cetaceans investigated, but the common dolphin has a broader range in distribution, implying they do not rely solely on those waters occupied by the deep diving species. The relationships found for the continental slope, deep waters and aspect suggests the importance of such physiographic variables combined in cetacean habitat choice within the Bay of Biscay. It is likely that near areas of steep sea floor gradients, dynamic features such as upwelling currents and vertical mixing contribute to the redistribution of nutrients in the water column. Upwelling in particular, promotes a replacement of the lower water layer with the upper one bringing nutrients in the euphotic zone contributing to the primary production enhancement and providing a greater food supply for top predators (Hastie *et al.*, 2004). Areas with steep slopes were expected to concentrate the cetaceans, since areas of high sea floor relief often result in greater nutrient mixing due to topographically induced upwelling (Freeland and Denman, 1982, Allen *et al.*, 2001). Moreover, passively moving organisms can be transported and aggregated, creating "easier conditions" for feeding predators (Allen *et al.,* 2001). The direction in which the slope faces has shown to be important in assessing niche differences of the specie studied. It is likely that the preference for a particular direction goes hand in hand with the movements of the general circulation and currents throughout the year, and the onset of the particular water movements, which no doubt help in aggregating prey in certain areas.

Over the last decade, oceanography and sea floor topography has been used as an approach to understanding cetacean distribution (Evans, 1990; Baumgartner, 1997; Davis *et al.*, 1998; Baumgartner *et al.*, 2001; Hooker and Baird, 2001b; Waring *et al.*, 2001; Cañadas *et al.*, 2002; Yen *et al.*, 2004; MacLeod and Zuur, 2005c). Prior to these studies, Kenney and Winn (1987) compared the distribution of cetaceans near submarine canyons to distributions in adjacent shelf/slope areas. It seems that submarine canyons and shelf slopes have an important influence on cetacean distribution throughout the world's oceans, even if modalities and intensities depend on hydrological, topographical, and biological contexts. Both the southern and northern continental slopes are incised with submarine canyons providing an array of habitats for cetaceans.

4.42 Habitat partitioning and Niche overlap

The eight species when compared were shown to be occupying the same areas, and in particular, regions of overlap existed in the Bay of Biscay for all seven species. Overlap did occur in the English Channel, but to a lesser extent than in the Bay of Biscay. Only two species, the common dolphin and pilot whale, were observed in the English Channel in sufficient numbers to identify the English Channel as a habitat they use, unlike the fin whale, and beaked whale species that have been observed on very few occasions.

To explore the habitat preference of these species further, the niche centre and niche width of each species were investigated. Species were categorized by their niche widths: generalists (a broad niche width) and specialists (a narrow niche width). Having a wide niche means a species needs may be met in a variety of ways whereas having a narrow niche means species needs must be met in a very particular way. It appears that cetacean species can be divided into four groups according to their niche centres: (1) Cuvier's beaked whale, northern bottlenose whale; (2) unidentified beaked whales, sperm whale, fin whale and striped dolphin; (3) Sowerby's beaked whale and pilot whale; (4) common dolphin alone. They can also be divided into three groups according to the niche widths: (1) Cuvier's beaked whale, northern bottlenose whale, Sowerby's beaked whale, unidentified beaked whales; (2) sperm whale, pilot whale, fin whale and striped dolphin; (3) common dolphin. The common dolphin had a different niche centre and wider niche width, which is highlighted by its broad distribution (Figure 4.6) than the rest of the species investigated. Of the species analysed in this study, the beaked whales, sperm whale, fin whale and striped dolphin, are the most ecologically similar. Interestingly, in relation to Cuvier's beaked whale, all species except the northern bottlenose whale have larger niche centres. In addition, the northern bottlenose whale, Sowerby's beaked whale, and beaked whale sp have a narrower niche width than the other species studied. This indicates that the beaked whales are specialists and they appeared to be narrowly restricted to deep water (>1000m) habitats in the Bay of Biscay.

It was then hypothesized that probable habitat and resource partitioning might be occurring. The beaked whales, sperm whale, and pilot whales are known to feed on similar prey which in the study area are likely represented by species of squid, and clearly fin whales and common dolphin are also known to feed in the same areas as them. Thus, the necessity to exploit the same trophic resource in the same area might have led to an extent of segregation in terms of interactions with environmental variables. In addition, habitat partitioning may be occurring and understanding the inter-annual and annual variation would highlight this. It is assumed that at some point, they do occupy the same area at the same time but the extent of this is not known and not investigated in this study. It is widely accepted that the distribution of cetaceans mirrors their feeding habitats (Evans, 1990; Bjørge 2002; Reid *et al.*, 2003; Hastie *et al.*, 2004). Members of the family Ziphiidae and Sperm whale are usually regarded as the main odontocete cephalopod eaters (Clarke, 1996b). Cuvier's beaked whale can prey upon juvenile *Gonatus* sp, which is found closer to the surface (Santos *et al.*, 2001a); the northern bottlenose whale and sperm whale both feed on adult *Gonatus* sp that are found deeper in the water column (Santos *et al.*, 2001b). The diet of Sowerby's beaked whale may differ, as MacLeod *et al.* (2003) have suggested it may rely principally on fish rather than cephalopods as the main component of its diet. Pilot whale feed on both fish (Waring *et al.*, 1990) and cephalopods (Waring *et al.*, 1990; Gannon *et al.*, 1997). In contrast, a member of the mysticetes; the fin whale, predominantly feeds on plankton and some fish, but may take squid accidentally (Clarke, 1996b), and the common dolphin feed on both fish and cephalopods (Lahaye *et al.*, 2005). Similarly, the striped dolphin feed on a combination of oceanic and neritic species including fish and cephalopods, with fish accounting for most of their diet (Spitz *et al.*, 2006).

It was supposed that the deep diving whales and common dolphin and striped dolphin may have occupied different areas in terms of vertical gradient, feeding on prey aggregations also found at different depths. It was also assumed that beaked whales and sperm whales might occupy different areas in terms of vertical gradient, feeding on prey aggregations found at different depths, because of the similarity in ecological niche of these two species (Hooker, 2001). Thus, the necessity to exploit the same trophic resource in the same area might have led to an extent of segregation in terms of interactions with environmental variables and vertical gradient. While little is known about cephalopod distributions in the Bay of Biscay, it is known that cephalopods from the northeast Atlantic occupy different water depths (Collins *et al.*, 2001).

The observed pattern in distribution of the eight species is clearly a result of association with the distribution of their prey, since depth and changes in depth have been shown to concentrate prey. The preferential use of continental slopes has been shown in studies of other cetacean populations (Evans, 1990; Baumgartner, 1997; Wilson *et al.*, 1997; Davis *et al.*, 1998; Ingram and Rogan, 2002; Ballance *et al.*, 2006, Moulins *et al.*, 2007). Areas with steep slopes were expected to concentrate the feeding activities of all cetaceans investigated, since areas of high sea floor relief often result in greater nutrient mixing due to topographically induced upwelling (Fernandez and Bode, 1991; Tenore *et al.*, 1995), which for cetacean species' prey, such as pelagic fish or cephalopods, physiography could play an indirect role through such mechanisms.

On a temporal and more dynamic scale, temperature ranges chosen by Cuvier's beaked whale and northern bottlenose whales with respect to the other species might represent additional partitioning. In this case, the exploitation of resources would be performed differently based on a greater presence of Cuvier's beaked whale and northern bottlenose whales with concurrent increases or decreases in sea surface temperatures in certain seasons. The effect of temperature on changes in distribution is investigated in Chapter 5. The differing distribution across spatial scales suggest potential habitat partitioning, a behavioural strategy to avoid direct competition, also found in other studies (Friedlander *et al.*, 2006). The common area, however, showed that the species were able to cohabit. This may happen where feeding opportunities were greater, i.e. over the steep slopes of the northern and southern continental shelf slopes.

In the present study, a clear trend towards steeper slopes found in the northern and southern parts of the Bay of Biscay were observed for a number of the deep diving species, whereas common dolphins occurred in both deep water and shallow waters, as well as step slopes. The Bay of Biscay is characterised 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 areas (Koutsikopoulos and Le Cann, 1996; Gil and Sanchez, 2003b). The variety of habitats supports many of the toothed cetacean species that are found in the wider northeast Atlantic (Reid, *et al.*, 2003). An important feature of the Bay of Biscay is that it is one of the world's strongest generation sites for internal tides (Gerkema *et al.*, 2004). Internal tides and surface tides are amplified by the interaction of bottom topography (New, 1988) and a consequence of these tides is the high phytoplankton abundance and cool water at the surface over of the continental shelf break (New, 1988). The extension of the warm water Iberian poleward current is also observed in Biscay, and is now considered a common feature of winter circulation (Garcia-Soto *et al.,* 2002) that coincides with the spawning season of pelagic and demersal species due to the higher concentration of nutrients compared with the surrounding area (Gil, 2003a).

To further the understanding of niche overlap and habitat partitioning, looking at the spatio-temporal distribution of these species will highlight the movements of these species to identify the months in which they are abundant and in which area. For example, the large fin and sperm whales are migratory and are not always in the area, Cuvier's beaked whale and northern bottlenose whale may occur with differing water temperatures (see chapter 5) and common dolphins are known year round within the area. Therefore, it is likely that foraging position in the water column helps with this niche overlap.

4.43 Using opportunistic sightings data

Unlike sightings that have been recorded on dedicated surveys, where it can be shown that an animal is absent from the area, the same thing cannot be said for presence only data. One way of possibly relating presence only data to effort could be to use the sightings of other cetaceans observed in same study area, based on the assumption that the survey covered the same area. In this analysis, the sightings of the common dolphin, were chosen to represent areas that have been extensively surveyed, and using these sightings it has found that despite efforts in surveying, the Cuvier's beaked whale was absent from areas over the northern continental shelf in the Bay of Biscay and the English Channel between 2003 and 2007. This compares well with other studies where Cuvier's beaked whale are predominantly found in deeper waters associated with complex underwater topography in other areas: Ligurian Sea, Mediterranean (D'Amico *et al.*, 2003) Greek Seas (Frantzis *et al.*, 2003); Hawaii (McSweeney *et al.*, 2007); north-western Mediterranean (Moulins *et al.*, 2007). In this study, investigating opportunistic sightings for the deep diving whales has greatly increased the chances of detecting patterns in habitat preference that otherwise might have been missed with the effort related survey data.. The effort-based beaked whale sightings dataset is small by comparison to the larger data set of opportunistic sightings, which are recorded on a more regular basis.

4.44 Conclusion

In summary, a clear pattern in habitat preference for the deep diving species and the common dolphin is evident from the opportunistic sightings. This dataset is no doubt a valuable source of information for increasing the understanding of habitat use in beaked whales, sperm whales, pilot whales, common dolphin, fin whale and striped dolphin in the English Channel and the Bay of Biscay. With respect to the marine mammal species examined in this study, there was evidence to suggest that habitat partitioning was occurring between them, as significant differences in the niche centres and widths were found. It may be that it occurs on a temporal scale, at different water temperatures and foraging position in the water column, or that partitioning occurs along niche variables not associated with habitat (i.e. prey size or mode of prey capture) (MacLeod *et al.*, 2007), which were not included in this study. If all possible aspects are not explored, it may be wrongly concluded that niche partitioning is not occurring between species and that other mechanisms are responsible for the structure and composition of marine mammal communities in this area. To increase this understanding further, it is necessary to understand the factors other than the EGVs explored in this chapter that allow deep diving species to occupy the same niche.

Chapter 5

Spatial-Temporal Variation in the Occurrence of Cuvier's beaked whale in the Bay of Biscay

5.1 Introduction

5.11 Spatial and temporal distribution of cetaceans: what causes these movements?

Monitoring spatial and temporal patterns in cetacean distribution and abundance involves a variety of approaches depending upon the target species and the resources available. Information on geographical and temporal distribution guides us in determining whether there are predictable areas and times of concentration that can be used to focus conservation measures in relation to human activity (e.g. noise) and climate change. To conserve species, the need to understand not just habitat, but usage within the habitat over time is essential. In the marine environment, both fixed spatial features such as topography, and variable oceanographic features such as sea surface temperature, may determine species' spatial distributions. Topographic features and oceanographic variables such as water masses, currents, upwelling, topography, and hydrological structures such as SST, Salinity, Chl concentration (Brown and Winn, 1989, Woodley and Gaskin, 1996, Baumgartner, 1997; Hooker *et al.,* 1999a,b) influence the distribution and availability of prey items. The most obvious step to investigate the distribution of a predator and factors affecting its distribution is to study the distribution of its principal prey. In particular for the beaked whales that prey on squid, effective sampling methods of deep-living squid is still in the early stages of development (Collins *et al.*, 2001) and their ecological importance has only become apparent in the last three decades (Clarke, 1996a).

Movements of whales and dolphins can be quite different. Baleen whales (mysticetes) tend to move long distances by migrating between feeding and breeding grounds whereas odontocetes (toothed whales and dolphins) do not have discrete breeding grounds and have more of a variable trajectory. Once the temporal variations are ascertained for each species, inter-specific interactions can more easily be determined, for example investigating seasonal changes can assess the differences in frequency of occurrence of each species in each location. Information on movements of individuals is also required to understand population structure and define stock boundaries. Unbiased information on where animals spend their time can also be used to identify important foraging habitats and to assess the likelihood of repeated exposure to potential anthropogenic impacts, if human activities are spatially heterogeneous.

Cuvier's beaked whale, *Ziphius cavirostris*, has been the subject of intense research over the last few years, due to its tendency to mass strand in the vicinity of naval mid-frequency sonar activities. Cuvier's beaked whale has a cosmopolitan range from temperate to tropical waters, with only a few sightings in polar waters (MacLeod *et al.*, 2006c). Despite having a wide range in distribution, Cuvier's beaked whale is generally associated with submarine canyons (MacLeod and Mitchell, 2006b), continental slopes (Frantzis *et al.,* 2003; Moulins *et al.*, 2007) and around oceanic islands (Baird *et al.*, 2004; 2006). Understanding Cuvier's beaked whale distribution and the factors controlling its distribution is still in its early stages. That very little is known about Cuvier's beaked whale is not to do with the lack of interest, but rather a consequence of the difficulties in studying this species. Originally, most was known from strandings, but now there are a few regions worldwide where Cuvier's beaked whale are seen regularly, including the Bay of Biscay. The Bay of Biscay is the northernmost region in the North East Atlantic where Cuvier's beaked whales are seen year round. From surveys carried out using fixed route platforms (Williams *et al.*, 2002a), such as the P&O ferry "Pride of Bilbao", it appears that Cuvier's beaked whale does not have a random distribution throughout the Bay of Biscay, but is associated with the CapBreton Canyon (Williams *et al.*, 2002a). In addition, observations made by the Biscay Dolphin Research Programme (BDRP) have indicated that northern bottlenose whales are also associated with shelf slopes and submarine canyons. It is thought they are spatially and temporally segregated from Cuvier's beaked whale, and it is suggested they may have different preferences for habitat, prey and/or interact competitively (Williams *et al.*, 2002a).

Mass strandings have been recorded more frequently for Cuvier's beaked whale than for any other beaked whale (Heyning, 1989). Causes of most strandings are unknown, but likely include old age, illness, disease, pollution, exposure to certain strong noises, and perhaps geomagnetic disturbance. Cetaceans, because they communicate and navigate almost entirely using sound, are sensitive to acoustic pollution. Threatening sources of acoustic pollution in marine environments include shipping noise and military sonar. Mass strandings of Cuvier's beaked whale are rare (although individual strandings are quite common), with only seven documented cases of more than four individuals stranding between 1963 and 1995 in the Mediterranean Sea (Frantzis, 1998). In addition, it is listed that 31 mass strandings (more than two) of Cuvier's beaked whale have been recorded worldwide between 1914 and 2002 (Taylor *et al.*, 2004) and Brownell et al. (2004) reported 11 mass strandings of Cuvier's beaked whale and Baird's beaked whale in

Japan from the late 1950s until 2004. It is suggested that several mass strandings of Cuvier's beaked whale may be associated with sources of strong noise such as naval activities that use high power sonar (Simmonds and Lopez-Jurado, 1991; Frantzis, 1998; D'Amico *et al*., 2003; Jepson *et al*., 2003; Frantzis, 2004; Freitas, 2004; Martin *et al*., 2004; Fernandez *et al*., 2005). In particular the bays where the stranding events were recorded in Japan are near to the command base for operations of the US Navy's Pacific 7th Fleet (Brownell et al., 2004). The bubble formation or excessive nitrogen supersaturation in tissues known as the bends or decompression sickness (Mackay *et al*., 1982), found from necropsies on stranded specimens, is thought to be in response to behavioural changes to normal profiles, such as accelerated ascent rate (Tyack *et al*., 2006), which may be due to naval sonar activities. Necropsy findings have also shown that beaked whale auditory anatomy may be susceptible to damage resulting from acoustic pollution (Ketten, 2005).

Strandings have occurred along the northwest coasts of Spain (Santos *et al*., 2001a) and the French Atlantic coast and strandings occur around the United Kingdom and Ireland (Evans, 1980; Berrow and Rogan, 1997; Evans *et al,* 2003; MacLeod *et al.,* 2004b). MacLeod *et al.* (2004b) investigated geographic and temporal variations in detail, using one of the longest continuous time series of stranding records of beaked whales, between 1800 and 2002. In UK and Irish waters, strandings of Cuvier's beaked whales were highest in July and January, with numbers varying from zero on the North Sea coasts to 21 on mid-Atlantic coasts (MacLeod *et al.,* 2004b). The waters around the United Kingdom and Ireland are not areas where Cuvier's beaked whale is sighted frequently and strandings in these areas may represent passively transported individuals (MacLeod *et al.,* 2004b) or individuals that have made navigational errors. Cuvier's beaked whales have also been known to occur in the deeper waters west of Ireland (Pollock *et al.,* 2000; Ó Cadhla *et al*., 2001) and there have been sightings as far north as northern Scotland (Evans *et al*, 2003, 2008). There are no confirmed sightings of Cuvier's beaked whales further north than this in the northeastern Atlantic, although there is a stranding record from Iceland (Evans *et al.,* 2008).

5.12 Oceanographic processes in the Bay of Biscay

The Bay of Biscay is often described in two parts: the northern Bay and the southern Bay. Both areas have variable sea depths, ranging from the shallow continental shelf (less than 100 metres) to the abyssal plain (greater than 4000 metres), with many underwater features such as submarine canyons, seamounts and a steep continental slope. The Bay of Biscay is characterised by a number of physical processes: water masses, currents that are generally weak (Pingree and Le Cann, 1990), varying strengths of upwelling with season (Casas *et al.*, 1997) and it is a generation site of internal tides/waves (Gerkema *et al.*, 2004). The currents are an important variable linked to the mesoscale dynamics. Within the Bay of Biscay hydrological features are influenced by the oceanic processes in the north Atlantic and the coastal processes associated with the French and Spanish coasts (Planque *et al.*, 2003). The extension of the warm water Iberian poleward current is also observed in the Bay and is now considered a common feature of winter (*Navidad*) circulation (Garcia-Soto *et al.,* 2002) that coincides with the spawning season of pelagic and demersal species due to the higher concentration of nutrients than the surrounding area (Gil, 2003a). A summary of water masses, circulation (Figure 5.1) and climatology of the Bay of Biscay is given by Koutsikopoulos & Le Cann (1996) and Ospar (2000).

It is suggested that the hydrographic features observed in the Bay of Biscay may influence the movement of Cuvier's beaked whale directly by changes in water temperatures, or indirectly by prey distribution within the Bay of Biscay. In addition, these features may have some influence on why Cuvier's beaked whales are seen further north than expected. The slope current that makes its way eastward along the Spanish continental slope, ENACW (Pollard *et al.,* 1996), flows northwest along the continental slope to waters north of the Bay of Biscay, including Ireland, UK and Scotland (Pingree, 1993). The northward flow of the shelf currents could actively transport individuals from the Bay of Biscay to waters around the United Kingdom and Ireland (Figure 5.1).

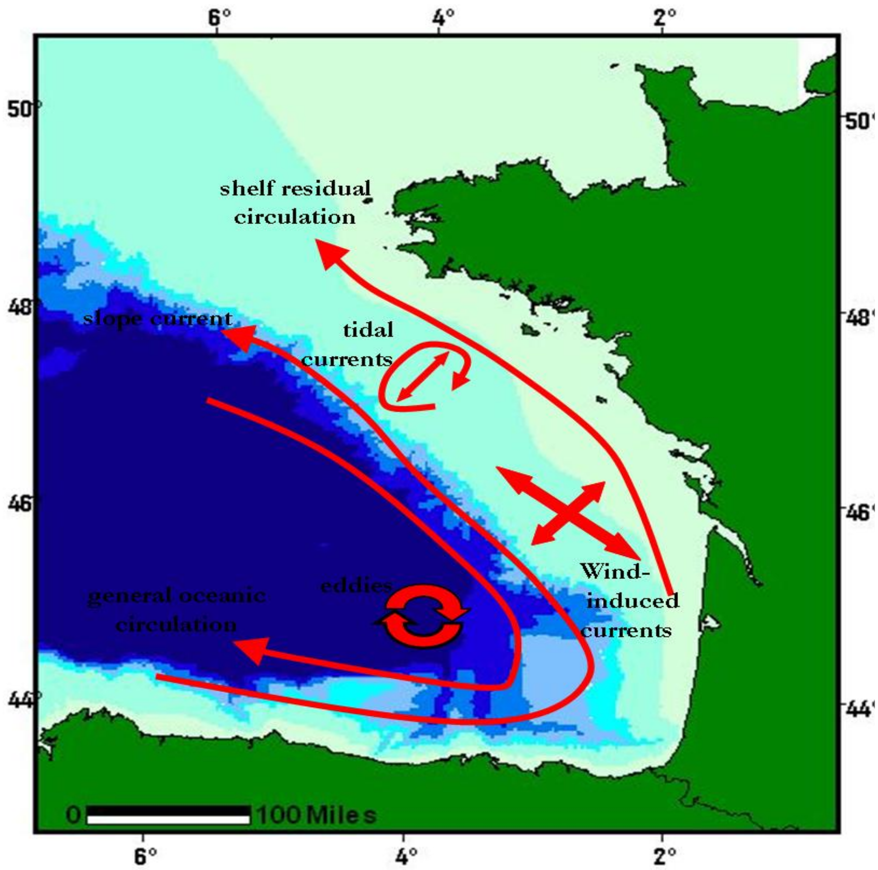


Figure 5.1: Circulation and current movements in the Bay of Biscay (Koutsikopoulos and Le Cann, 1996).

5.13 Aim

In the present study, the main aim is to identify the spatial and temporal distribution of Cuvier's beaked whale in the Bay of Biscay and to compare sighting records from the Bay with strandings records from the UK, Ireland and the Atlantic French coast. It will investigate many aspects that will help to understand the effects of climate change, such as how increasing water temperatures may affect the distribution of Cuvier's beaked whale. With regards to monitoring changes in distribution, MacLeod *et al.* (2005b) assessed how climate change is affecting the cetacean communities of northwest Scotland, with particular reference to distributional range changes as a result of changing water temperatures. With over ten years worth of sightings data from regular surveys across the Bay of Biscay and stranding events dating back to 1904, this enables the evaluation of sightings and strandings based on several different criteria, such as seasonal patterns in distribution. Williams et al. (1999) previously documented significant seasonal variation in the presence and absences of both Cuvier's beaked whale and the northern bottlenose whale, however this study is the first analysis of the seasonal distribution of Cuvier's beaked whale in northwest Europe over a long period. In addition, the Northern bottlenose whale and Sowerby's beaked whale were investigated to show how their distribution changes over time in comparison to Cuvier's beaked whale.

5.2 Methods

5.21 Study area

The main study area covers the English Channel and the Bay of Biscay, along the route of the P&O ferry 'Pride of Bilbao', which operates between Portsmouth, UK and Bilbao, Spain (Figure 5.2). The Bay of Biscay and the English Channel are situated between 43°N to 50 °N and -1 °W to -10 °W, in the Northeast Atlantic. The Bay of Biscay is characterised as a temperate open oceanic bay bounded by the Spanish coast to the south, oriented E-W and the French coast to the east, oriented S-N (Koutsikopoulos and Le Cann, 1996). The Armorican shelf in the north of the bay is up to 180km wide, whilst in the south the continental shelf is only 30 to 40km wide (Koutsikopoulos and Le Cann, 1996). The CapBreton Canyon, in the southeast corner of the Bay of Biscay, is a major morphological feature that cuts into the continental slope in an E-W direction and the 1000m contour is only 3 km from the coast. The CapBreton is one of the deepest submarine canyons in the world (Gaudin *et al.,* 2003) and the longest off Europe, with its head located only 250m from the coastline (Cirac *et al*., 2001). The canyon was formed by the Adour River (SW France), but has been disconnected from the river since 1310 AD (Cremer *et al*., 2003). The canyon runs westward and parallel to the north coast of Spain for 160 km due to structural control, then turns northward, widens and abruptly disappears in the continental rise by 3500m water depth (Gaudin *et al*., 2003).

5.22 Cuvier's beaked whale data

5.221 Sightings data

Dedicated and non-dedicated sightings data for Cuvier's beaked whale used for this study were collected from surveys carried out by the Biscay Dolphin Research Programme (BDRP). In addition, opportunistic data were provided by the Company of Whales (COW), which operates on the ferry from May to September. The non-dedicated sightings will be referred to as opportunistic sightings throughout this chapter. In total, 53 dedicated sightings and 402 opportunistic sightings were analysed. Only effort sightings collected in sea states three or less were used in this study. Each sighting contained information on the date (year, month and season, location, sea state and total number of sightings. In this study the seasons are defined as Spring: April to, June; Summer: July, to September; Autumn: October to December; Winter: January to March. It is important to note the variation of survey effort between seasons over each sector (i.e. English Channel, northern and southern Bay of Biscay) covered by the ferry route. For example, during the winter months the ferry does not reach part of the northern slope in daylight that it reaches in the summer months.

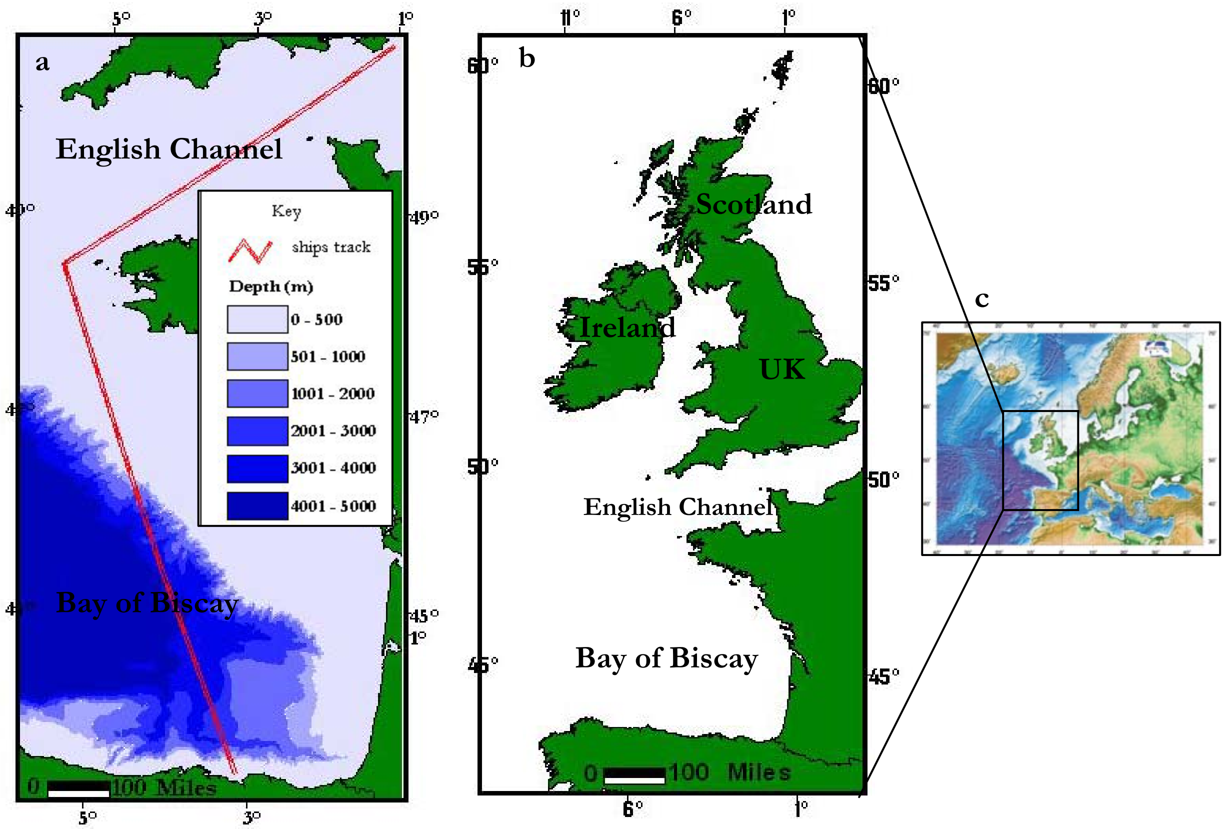


Figure 5.2: Study area (a) Bay of Biscay, northeast Atlantic. Ships track Portsmouth (UK) to Bilbao (Spain), highlighted in red and water depth is shown in meters. Regions of stranding events, map (b). Northeast Atlantic, map (c), taken from www.noc.soton.ac.uk).

1. Non-dedicated sightings data (opportunistic data)

The wildlife officer on board the ferry collected the opportunistic sightings data from 2003 to 2007. On every sailing to Bilbao from Portsmouth, a wildlife officer is on board. However, the wildlife officer is not observing at all times, due to other duties on board. Due to a wildlife officer, being on board every trip from 2003, it was in the interest of the charity to start collecting data to monitor the distribution of cetaceans either side of the survey teams. In doing so, it provides a larger data set to work for analysis, which in turn can help towards the conservation of cetaceans. Opportunistic sightings during for 2000, 2001, and 2002 were also made available from the Company of Whales (COW).

2. Dedicated sightings data

The dedicated sightings data were collected by a team of two or three researchers, on twice-monthly survey trips from Portsmouth to Bilbao from 1995 to 2007. The first trip is carried out by a Spanish team (AMBAR) and the second an English team. On each trip, the survey starts from first light and finishes at dusk.

5.222 Strandings data

Data on Cuvier's beaked whale strandings were compiled from three different sources: the Natural History Museum in London for UK strandings; the Irish Whale and Dolphin Group (IWDG) for strandings around the Republic of Ireland (ROI); and Centre de Recherche sur le Mamifères Marins for strandings along the French Atlantic coasts. In total, 174 strandings were used between 1904 and 2007. Strandings data for the UK and ROI from 1800-2002 were previously analysed by MacLeod *et al.* (2004b) to assess geographic and seasonal variations in beaked whale occurrence around the UK and ROI, and a full description and sources of data can be found in this study.

In addition to Cuvier's beaked whale data, records for northern bottlenose whale and Sowerby's beaked whale strandings were also used in this study from the UK and ROI. These two species were selected for three reasons: 1. The Bay of Biscay is close to the southern limit of the northern bottlenose whale in the northeast Atlantic (MacLeod *et al.,* 2004b); 2. The Sowerby's beaked whale range in distribution is observed further north and south of the Bay of Biscay; 3. Both species from the strandings record have been recorded alive in this area (Williams *et al.* 1999; 2002a).

5.23 Analytical methods

5.231 Geographic information system (GIS)

A GIS of the study area was constructed using ESRI ArcView 3.2 software. A primary coverage was developed that contained the study area as defined by latitude and longitude, coastline of England, France and Spain and bathymetric contour lines (The General Bathymetric Chart of the Oceans, Gebco). A 10km by 10km base map created in MapInfo, was imported into ArcView and overlaid on to the study area. The depth values for the central point of each 10km by 10km cell were obtained using the spatial analyst function and included the mean, minimum, maximum, standard deviation (SD), and range. SST data were obtained from the ocean colour web site for satellite imagery (http://oceancolur.gsfc.nasa.gov/ftpsite) and spatially joined to the grid cells. The effort-related survey data, opportunistic sightings and strandings records were then imported into ArcView. Using the location of each sighting and stranding, maps were constructed to show the spatio-temporal distribution of Cuvier's beaked whale. For further analysis the next step was to join the effort related survey data to the grid to work out the effort (km) per trip and to assign each trip a value for depth. The spreadsheet containing the effort-related survey data was then exported to Microsoft Excel and then manually joined to each effort sighting to the correct survey trip, using the date and time. This was done to calculate the encounter rates (see below). The opportunistic sightings were then joined to the grid and assigned a value for depth, slope, and aspect. Each opportunistic sighting and each effort related trip was also assigned a SST value for its specific month, year and location. The spreadsheets containing the final information on species location and environmental variables were exported out of ArcView and imported into Microsoft Excel for further analysis.

5.232 Spatio-temporal distribution and encounter rates

To investigate the spatial and temporal distribution, both the dedicated and opportunistic sightings and strandings data were investigated per month, season, year, and region within the Bay of Biscay. The region of strandings extends to Ireland and the UK. Trends in the strandings data were compared to sightings data from the Bay of Biscay collected during monthly surveys along a relatively fixed transect conducted by the Biscay Dolphin Research Programme (BDRP) between 1995 and 2007 to assess how the changes in the strandings data may reflect changes in occurrence at sea. To look at variation in strandings over time, a five year running average was calculated for each year between 1904 and 2007 for all three beaked whale species, to account for variations in stranding reporting efforts between years and these values were standardised by the running average for all beaked whale strandings.

Encounter rates for the dedicated sightings were calculated per month per 100km in Microsoft Excel. Encounter rate was defined as

$$\frac{n}{L} \quad \text{X } 100000$$

where *n* is the number of encounters, *L* is the total distance travelled (i.e. survey effort) in metres (m), multiplied by 100000 to convert it into the number of encounters per 100 Kilometre (Km). Further, in order to provide regional differences of encounter rates, three sub-regions were defined:

1. Submarine canyons (CapBreton) and deep oceanic waters of the Bay of Biscay (43°N – 45°N)
2. Shelf slope and deep oceanic waters of the northern Bay of Biscay (45°N – 47°N)
3. Continental shelf waters of the western approaches and English Channel (47°N to 50°N)

For the opportunistic data sightings, the sub-regions were defined as:

1. Submarine canyons (CapBreton) and deep oceanic waters of the Bay of Biscay (43°N–44.5°N).
2. Deep oceanic waters of the Bay of Biscay (44.5°N–45.5°N).
3. Shelf slope and deep oceanic waters of the northern Bay of Biscay (45.5°N–47°N).

These three regions were chosen to highlight the different regions that Cuvier's beaked whale may range over during different seasons, and overall different regions were selected to look at changes in distribution, due to the different use of habitat made by cetaceans (Canadas *et al.*, 2002).

5.233 Statistics

In the program Minitab, Chi-squared tests (χ^2) were used to test the null hypothesis that sightings and strandings did not differ significantly from an even spread between each month, season, year. The sightings data were also examined for regional differences within the Bay of Biscay and the strandings data for geographic variations between France, UK and Ireland.

5.3 Results

The results presented in this chapter show variation in effort-related sightings, opportunistic sightings, strandings data and how satellite data for sea surface temperature can highlight the spatial and temporal distribution of Cuvier's beaked whale in the Bay of Biscay and British Isles. In total, 455 (1088 individuals) Cuvier's beaked whale sightings were included in the analyses (Figure 5.3a): 53 sightings (131 individuals) were included from the effort sightings, in good sea conditions (sea stare $\leq$3) between 1995 and 2007, and 402 (957 individuals) sightings were included from the opportunistic sightings between 2000 and 2007. In total, 174 single stranding records of Cuvier's beaked whales were also included in this analysis between 1904 and 2007, from three countries in the northeast Atlantic. The locations of all Cuvier's beaked whale strandings are shown in Figure 5.3b, with 54 strandings around the UK, 52 from Ireland, and 68 from the French Atlantic coasts. Strandings from the French coasts start later (1971) than records from the UK (from 1916) and Ireland (from 1904).

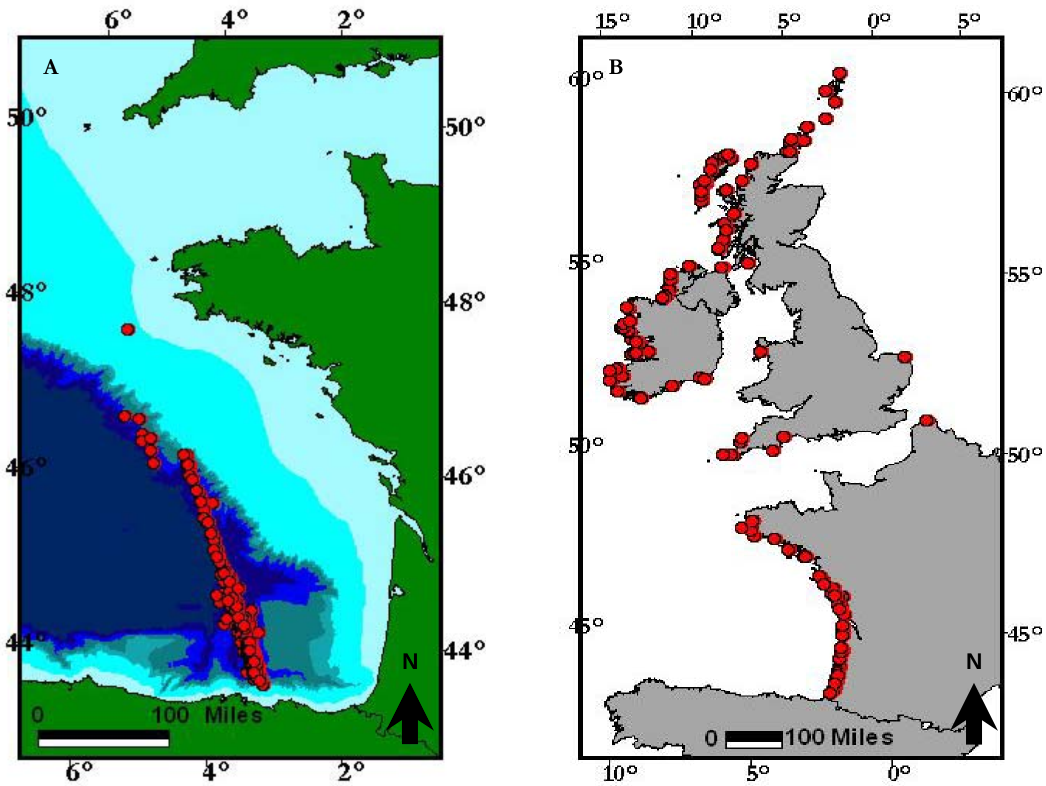


Figure 5.3: Distribution of Cuvier's beaked whale: a) total sightings in the Bay of Biscay, b) total strandings Cuvier's beaked whale around the UK, Ireland and French Atlantic coast.

5.31 Evidence of species variation

5.311 Effort sightings

The spatial distribution of Cuvier's beaked whale appears to concentrate in the southern Bay of Biscay. In particular, the pattern of distribution of this species is associated with the steep and complex underwater topography of the CapBreton Canyon. Only a few sightings have been observed over the deep waters of the abyssal plain and the northern continental slopes. The encounter rate in the southern Bay of Biscay was 0.20 per 100km, 0.02 per 100km in the northern Bay of Biscay and 0.00 per 100km in the English Channel (Table 2). These encounter rates were associated particularly with the steep continental slope in the northern Bay and the CapBreton canyon in the southern Bay, in water depths greater than 1000m and less than 4000m. Cuvier's beaked whales seemed to prefer deep oceanic waters (median = 2982; Q1 = 2415.27; Q3 = 3696.86, min = 788; max = 4087). Depth was classified into 0-1000m, 1000-2000m, 2000-3000m, 3000-4000m and 4000+m and the percentage of sightings was 4%, 2%, 53%, 38%, and 4%, respectively. The majority of sightings were within 2000 to 4000m water depth. Group size of the species was variable, with 2.42 in the southern Bay and 1.84 in the northern Bay.

	southern bay	northern bay	English Channel
Relative Abundance	0.48	0.03	0
Sightings rate	0.20	0.02	0
Ave Group Size	2.42	1.8	0

Table 5.1: Proportion of Cuvier's beaked whale in three-sub regions in the study area.

Sightings of Cuvier's beaked whale reflect a seasonal distribution within the southern Bay of Biscay (Figure 5.4), with a widespread number of sightings observed during spring (n=21 encounters/56 individuals), and summer (n=17/31), encounters and individuals respectively. Numbers start to decline during autumn (n=6/19) and winter (n=10/27), encounters and individuals respectively. The intra-annual pattern of sightings differed significantly from an even spread across all seasons (χ^2 = 8.96, d.f. = 3, $p < 0.05$), but not across all months (χ^2 = 6.43, d.f. = 9, p = 0.696). In addition, the seasonal variation in numbers is highlighted by the sightings rate, relative abundance, and group size per month (Figure 5.5). Despite previous work that indicated Cuvier's beaked whale to be associated with the CapBreton Canyon (Williams *et al.*, 1999), during spring and summer a few sightings are observed over the northern continental slopes of the Bay of Biscay.

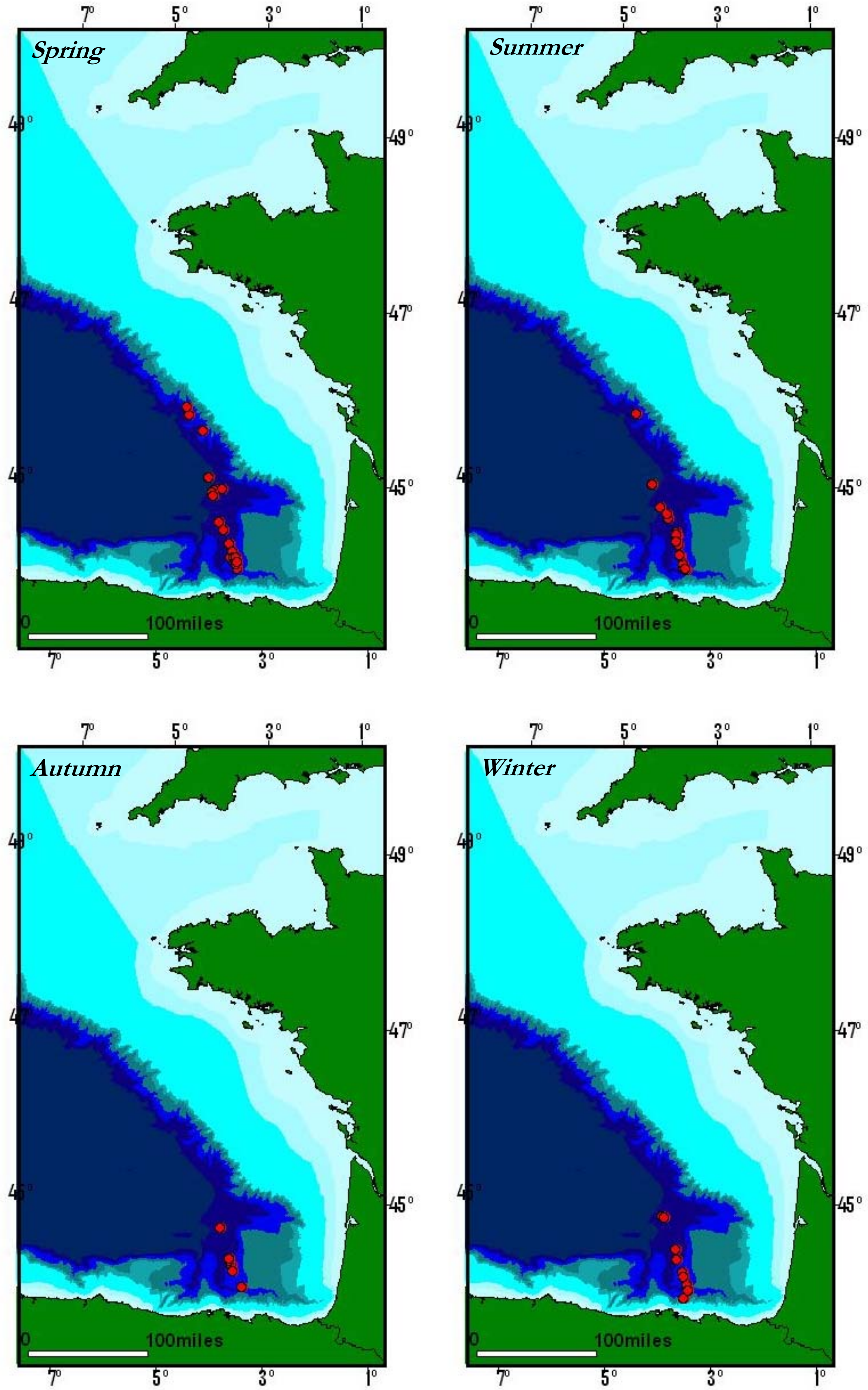


Figure 5.4: Seasonal distribution of Cuvier's beaked whale (red circles) in the Bay of Biscay.

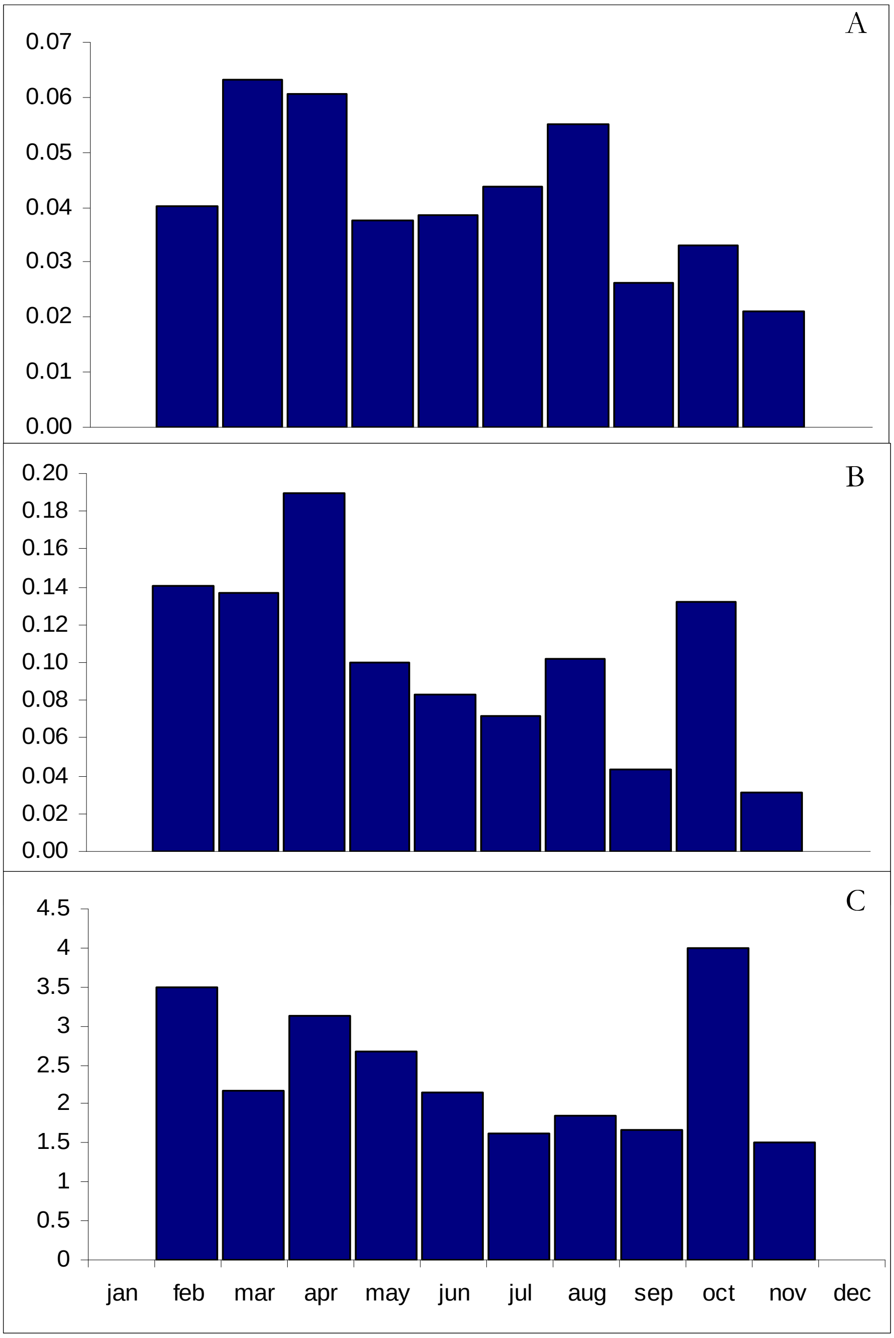


Figure 5.5: Monthly (*x-axis*) sightings rate (*y-axis*): (a) and relative abundance (b), encounters per 100km and group size (c) distribution for Cuvier's beaked whale.

5.312 Opportunistic sightings

The spatial distribution of sightings is reflected in the three regions: southern Biscay (region 1); deep waters of the abyssal plain (region 2); northern Biscay (region 3). The sightings of Cuvier's beaked whale are greater in region one (n=738/301), to a lesser extent in region 2 (n=136/57), and even lower in region 3 (n=81/37), individuals/encounters respectively. The average group size of Cuvier's beaked whale is similar for regions one and two, 2.40 and 2.39 respectively, whereas region three has a slightly smaller average group size of 2.19.

Similar to the effort related sightings, the opportunistic sightings also reveal a seasonal variation in numbers of Cuvier's beaked whale. Sightings were highest in spring (n=125/305) and summer (n=217/517), and lowest in autumn (n=99/43) and winter (n=36/17), individuals and encounters respectively (Figure 5.6). The pattern of sightings differed significantly from an even spread across all seasons (χ^2 = 243.29, d.f. = 3, $p <$ 0.000). This coincides with the higher encounter rate at the beginning of spring observed with the dedicated sightings.

An interesting pattern emerged from the opportunistic sightings, revealing a seasonal northward movement from the south. This northward movement of Cuvier's beaked whale occurs over the deep waters of the abyssal plain and the northern continental slopes. Like the dedicated sightings, most sightings occur in the southern region over the CapBreton Canyon However, sightings have started to increase and become spread out during spring through summer progressing towards the northern continental slope (>1000m) (Figure 5.6). During autumn and winter, the sightings reflect a different pattern that show a decrease in numbers over the northern continental slopes, with a more concentrated distribution over the CapBreton Canyon area (Figure 5.6). The non-dedicated sightings demonstrate this seasonal trend much more clearly than the dedicated data sightings, due to the larger data set. The numbers of sightings per month clearly shows when sightings start to increase in the Bay of Biscay (Figure 5.7), which in turn highlights the seasonal distribution of Cuvier's beaked whale. The intra-annual pattern of sightings differed significantly from an even spread across all months (χ^2 = 26086, d.f. = 11 $p \leq 0.001$). Group size ranged from one to ten (mean = 2.38, s.d. = 1.55) but also showed a seasonal trend (Figure 5.8). During the spring months, the average group size is 3, whilst in the autumn and winter, smaller groups of 1-2 individuals are seen, with an exception in

October when the group size is 3. Larger group sizes seen during spring and autumn suggest a seasonal change in group size.

The depth average corresponding to species positions was 2942.3m ± (range 120.9-4179.6m). Depth was classified into 0-1000m, 1000-2000m, 2000-3000m, 3000-4000m and 4000+m and the percentage of sightings was 0%, 6%, 55%, 35%, and 4%, respectively. These values are similar to the depth average and ranges observed with the effort sightings.

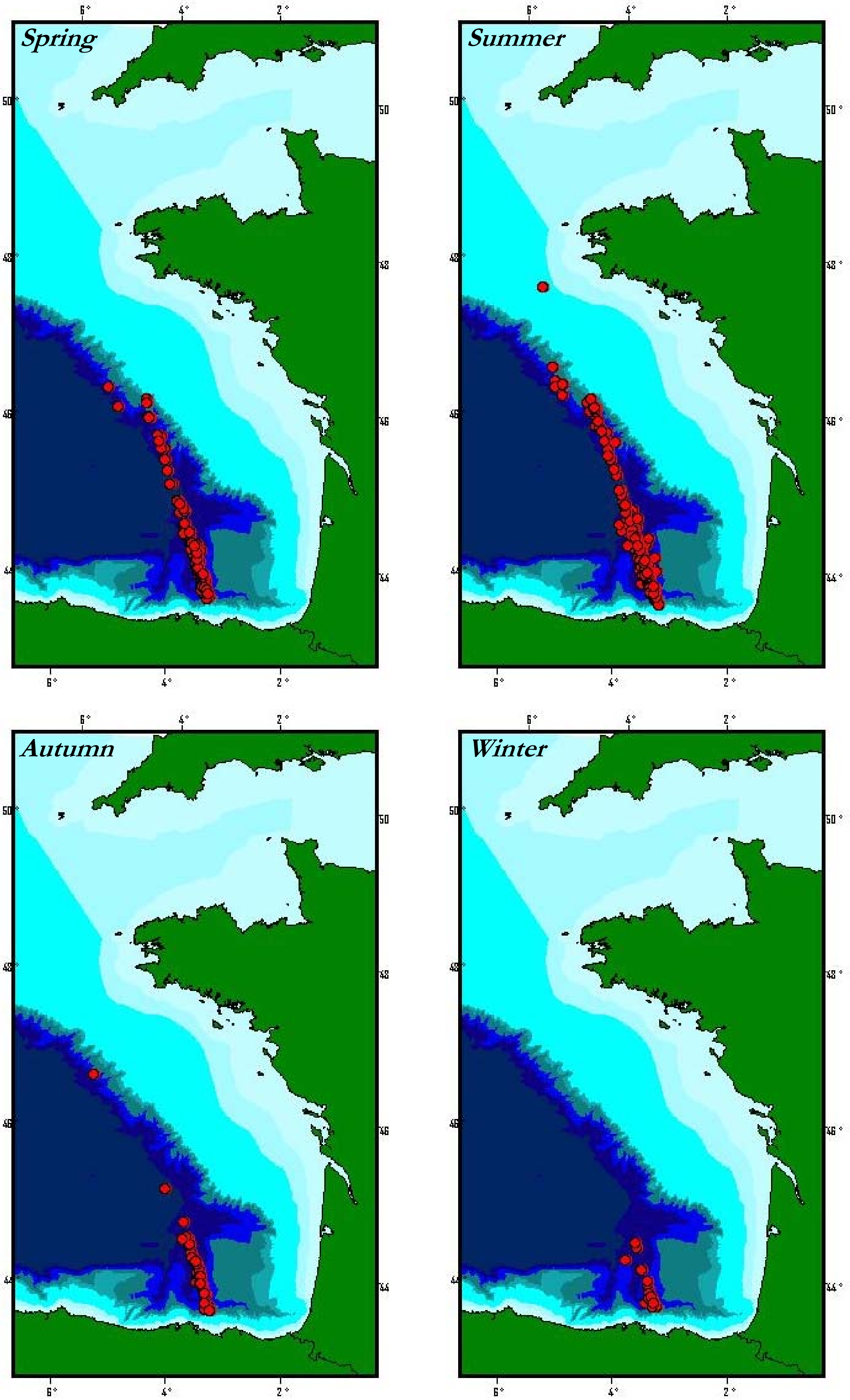


Figure 5.6: Seasonal distribution of Cuvier's beaked whale in the Bay of Biscay (red circles)

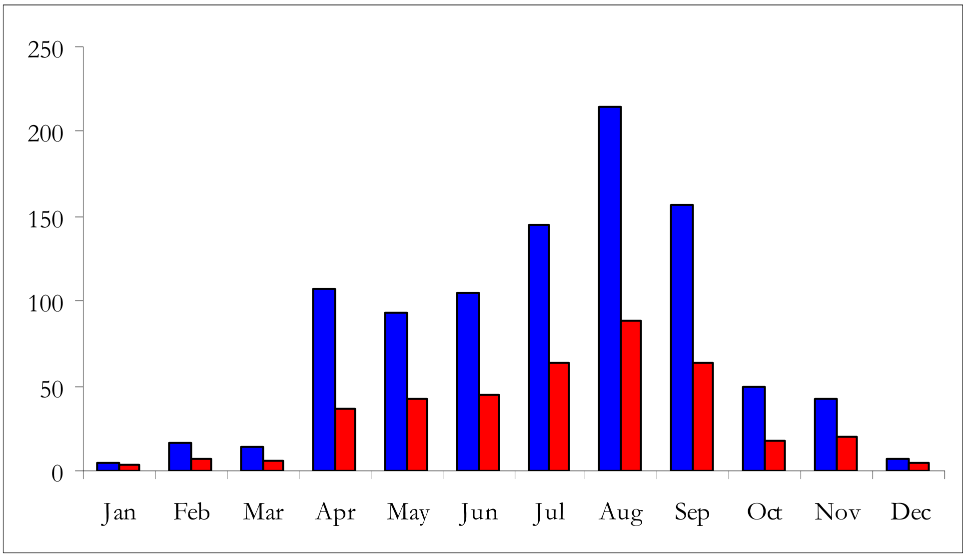


Figure 5.7: Monthly (*x*-axis) distribution of Cuvier's beaked whale. Total number (*y*-axis) of individuals (blue) and total number of encounters (red).

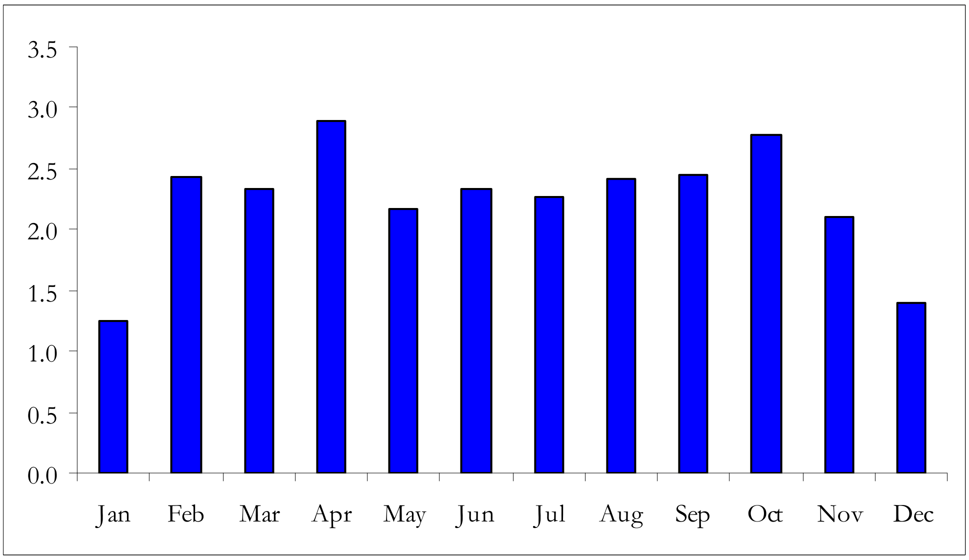


Figure 5.8: Group size (*y*-axis) distribution per month (*x-axis*).

5.313 Strandings data

The analysis of strandings events, as a total of all strandings from the UK, Ireland and France, show Cuvier's beaked whale strandings were highest in winter (Jan-Mar, n=85), and lower in spring (Apr-Jun, n=34), autumn (Oct-Dec, n=33), and summer (Jul-Sep, n=18) (Figure 5.9). The pattern of strandings differed significantly from an even spread across all seasons ($\chi^2 = 60.45$, d.f. = 3 $p < 0.001$) and all months ($\chi^2 = 86.94$, d.f. = 11 $p < 0.001$). The majority of strandings occurred in the winter months. During the spring months and the first month in summer, the data show a consistency in the numbers of strandings and towards the end of summer and the start of autumn, stranding numbers start to decline and are relatively low by comparison to other months (Figure 5.9). In the last two months of autumn, stranding numbers start to increase, followed by a steep rise in strandings during winter, in particular during January and March (Figure 5.9).

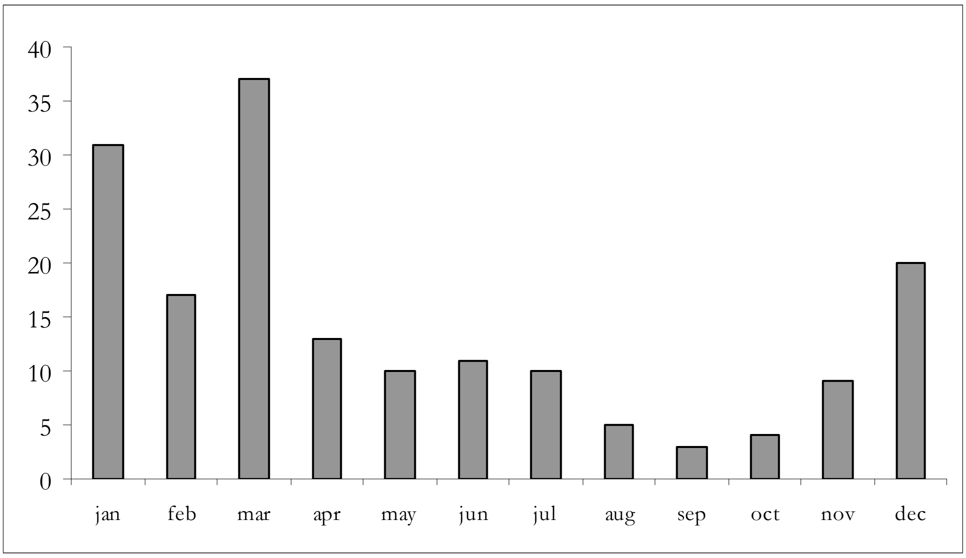


Figure 5.9: Monthly (*x-axis*) variation of total number (*y-axis*) of stranding events from the UK, Ireland, and France.

The seasonal distribution of strandings for the individual countries can be seen in Figure 5.10. The majority of strandings occur in winter on the French coasts, possibly coinciding with sightings observed in the southern Bay during winter but not in northern Biscay. During spring, the numbers of strandings are similar for the UK, Ireland, and France, and during summer, the numbers of strandings are predominantly around the UK, maybe coinciding with the northern movements of sightings of Cuvier's beaked whale during spring and summer. During autumn sightings are higher on the French coasts, compared with the UK and ROI, which concurs with sightings concentrating in southern Biscay during autumn.

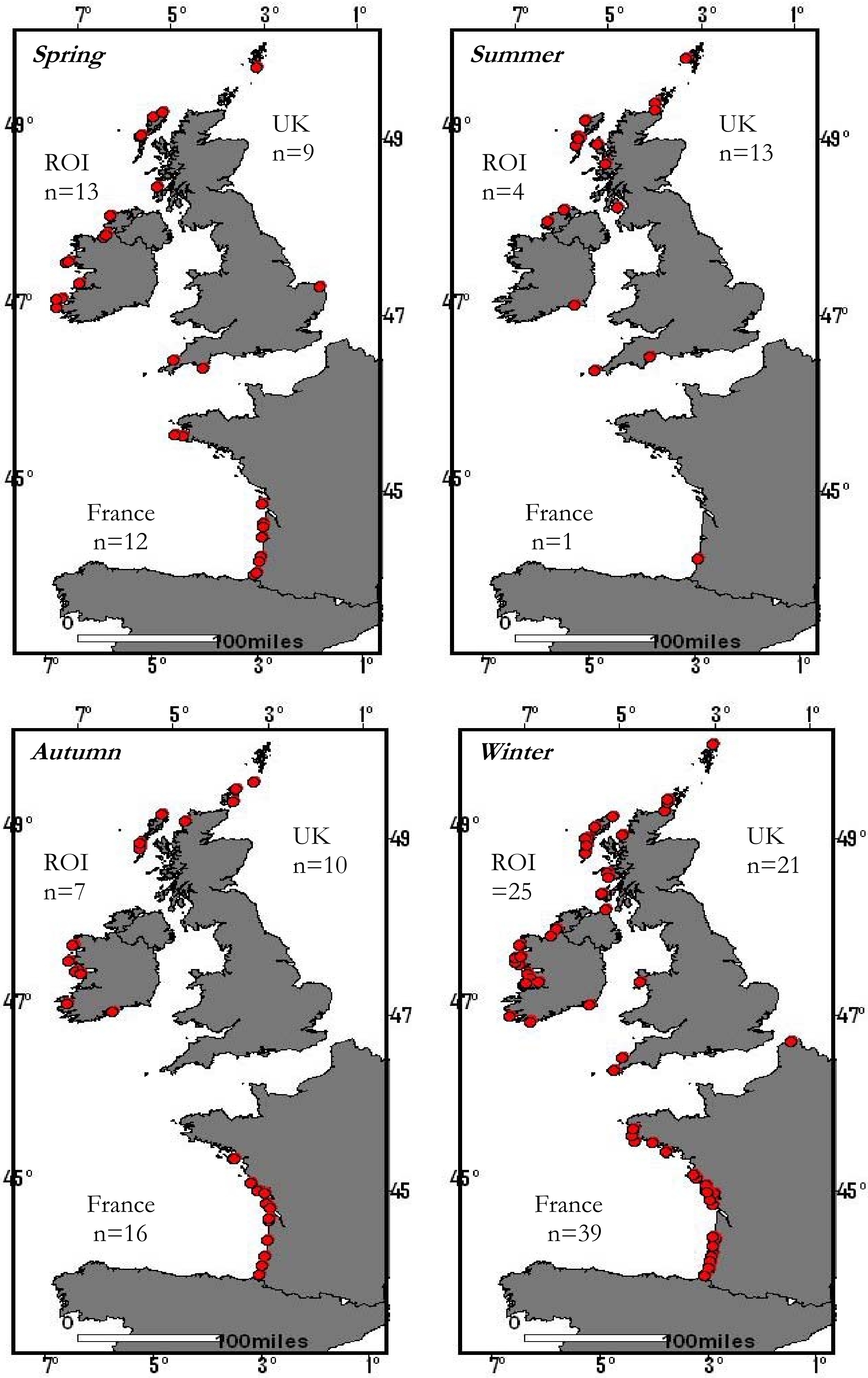


Figure 5.10: Seasonal distribution of strandings around UK, Ireland, and France (n is equal to the number of strandings in each region).

3.32 Interannual changes

5.321 Effort sightings

Between 1995 and 2007, 146 surveys were completed through the English Channel and Bay of Biscay, totalling 140,072 km of survey effort (Figure 5.11a, survey coverage). There was variation in survey effort between seasons and years (Table 5.2), which was due to the amount of daylight hours available and weather conditions. In addition, the amount of survey effort varied between sub-regions; 62% of effort was in the English Channel, 20% was in the northern Bay, and 18% of effort was in the southern Bay (Figure 5.11a). Effort sightings are shown in Figure 11b. The variation in dedicated sightings between 1997 and 2007 ranges from a minimum of 5 individuals to a maximum of 16 individuals (Figure 12). During 1995 and 1996, there were no sightings in good sea states (≤3). 1999 and 2000 were years with very low numbers of Cuvier's beaked whale in comparison to the other years. During 1997, 1998, 2001, 2004 and 2006, sightings of Cuvier's beaked whale were considerably higher in comparison to 2000, 2002, 2003, 2005, and 2006, although overall numbers of Cuvier's beaked whale were not significantly different between years (χ^2 = 13.01, d.f. = 10 $p < 0.223$).

Table 5.2: Observation effort (km) conducted in the English Channel and Bay of Biscay, 1995 – 2007.

Year	***Jan***	***Feb***	***Mar***	***Apr***	***May***	***Jun***	***Jul***	***Aug***	***Sep***	***Oct***	***Nov***	***Dec***
1995								818.56	780.26	813.65	454.21	226.96
1996		786.03		2038.18	1114.37	1249.37	1153.20	1077.46		1464.21	1107.43	698.28
1997	590.35	888.51	974.35	1074.88	1175.58	1309.08	1224.21	1031.05	954.51	871.80	684.08	749.59
1998		868.99	973.51	734.87	1556.17	1222.13	1149.41	1095.62	967.39	846.04	720.78	758.55
1999			955.95	1067.30	1231.30	1266.05	1321.00	1079.76	971.87	1714.88	726.41	760.97
2000		920.78	1023.30		1214.95	1272.06	2130.94	1100.74	954.41	814.67	693.18	718.81
2001		1613.25		979.12	1188.38	2424.18	2346.63	1074.50	902.80	815.87	817.15	591.48
2002		871.54	868.85	1125.58	2183.14	2262.73	1825.04		980.04	637.64	753.17	
2003	739.44	850.12	931.33	1031.93	983.39	1158.48	1158.79	1053.75	1091.38	881.44	653.09	686.07
2004		862.57	888.27	1115.77	1160.32	1106.17	1131.81	1078.95	951.27	840.50	688.38	723.10
2005		855.45	924.28	1937.71	2201.87	2330.64	2385.92	1090.53	936.09	793.40	742.64	690.26
2006		657.41	887.83	983.57	743.49	1277.74	1198.23	1121.23	962.94	827.08	741.35	642.19
2007		799.45	1046.14	1103.52	1215.08	1279.21	1204.17	1085.75	967.49	791.42	714.02	763.55

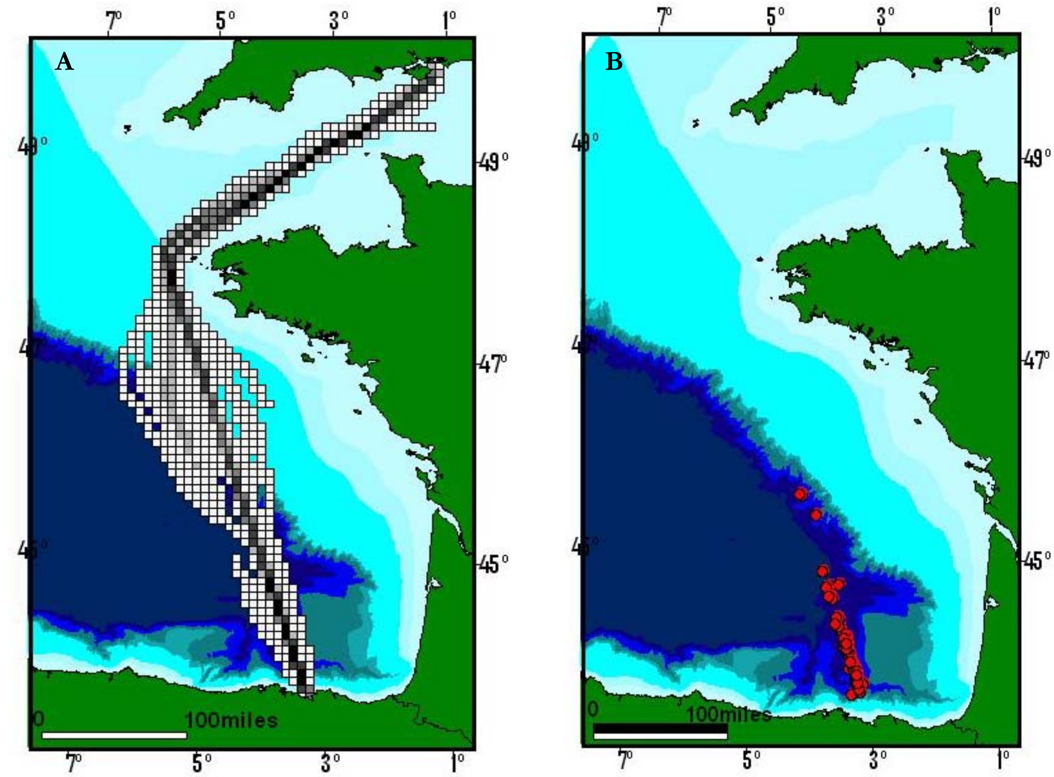


Figure 5.11: Maps showing the survey effort divided in cell units of 10km^2 (A) and Cuvier's beaked whale distribution, highlighted by red circles (B).

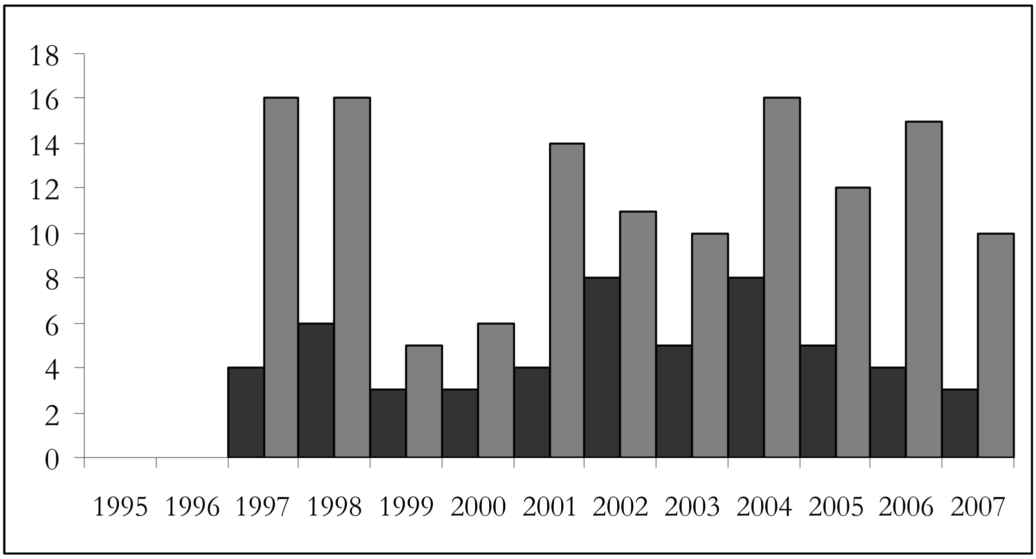


Figure 5.12: Variation in the total number (*y*-axis) of encounters (dark grey) and individuals (light grey) between 1995 and 2007 (*x-axis*)

5.322 Opportunistic sightings

The number of encounters and individuals of Cuvier's beaked whales has steadily increased from 2000 to 2007 (Figures 5.13 and 5.14). The steady increase in numbers from 2000 is most likely due to the increased ability of observers to identify Cuvier's beaked whale, as opportunistic data recording started in 2000. Cuvier's beaked whale sightings were highest in 2003 (n=60/130); 2004 (n=78/159); 2005 (n=69/181); 2006 (n=69/168); 2007 (n=71/185) and lowest in 2000 (n=3/4); 2001 (n=21/56); 2002 (n=31/74); encounters/individuals respectively. Sightings started to increase from 2001 through to 2004, after which encounters with Cuvier's beaked whale during 2005, 2006, and 2007 were showing a decline. The number of individuals, however, increased during these years, indicating that group sizes were larger. The pattern of sightings between years differed significantly from an even spread across all years ($\chi^2 = 108.15$, d.f. = 7 $p < 0.001$).

The sightings appeared to be concentrated in the southern Bay of Biscay during all years, except during 2000 when low numbers were observed everywhere. The seasonal northward shift in sightings of Cuvier's beaked whale, however, has been found in the previous section and this northward movement of Cuvier's beaked whale was observed over the northern continental slope in 2002, 2003, 2004, and 2007. During 2005 and 2006, there were only a few encounters with the Cuvier's beaked whale over the northern slopes (Figures 5.14).

The changes in the proportion of the northern bottlenose whale sightings from 2000 to 2007 were plotted against Cuvier's beaked whale sightings to identify any changes. It is important to note that sighting changes may have been a result of observer effort throughout this time. Only the opportunistic data were used, because the low number of the northern bottlenose whale dedicated sightings meant that no pattern could be visualised on a graph. It can be seen in Figure 5.15 that Cuvier's beaked whale declines from 2000 to 2003, mirrored by slight increases in the northern bottlenose whale and from 2003 to 2004 Cuvier's beaked whale increase and northern bottlenose whale decreases. From 2004 to 2005, both species show a slight increase: from 2005 to 2006 Cuvier's beaked whale show a slight decrease and northern bottlenose whale is still increasing: and from 2006 to 2007, Cuvier's beaked whale increase and northern bottlenose whale decreases.

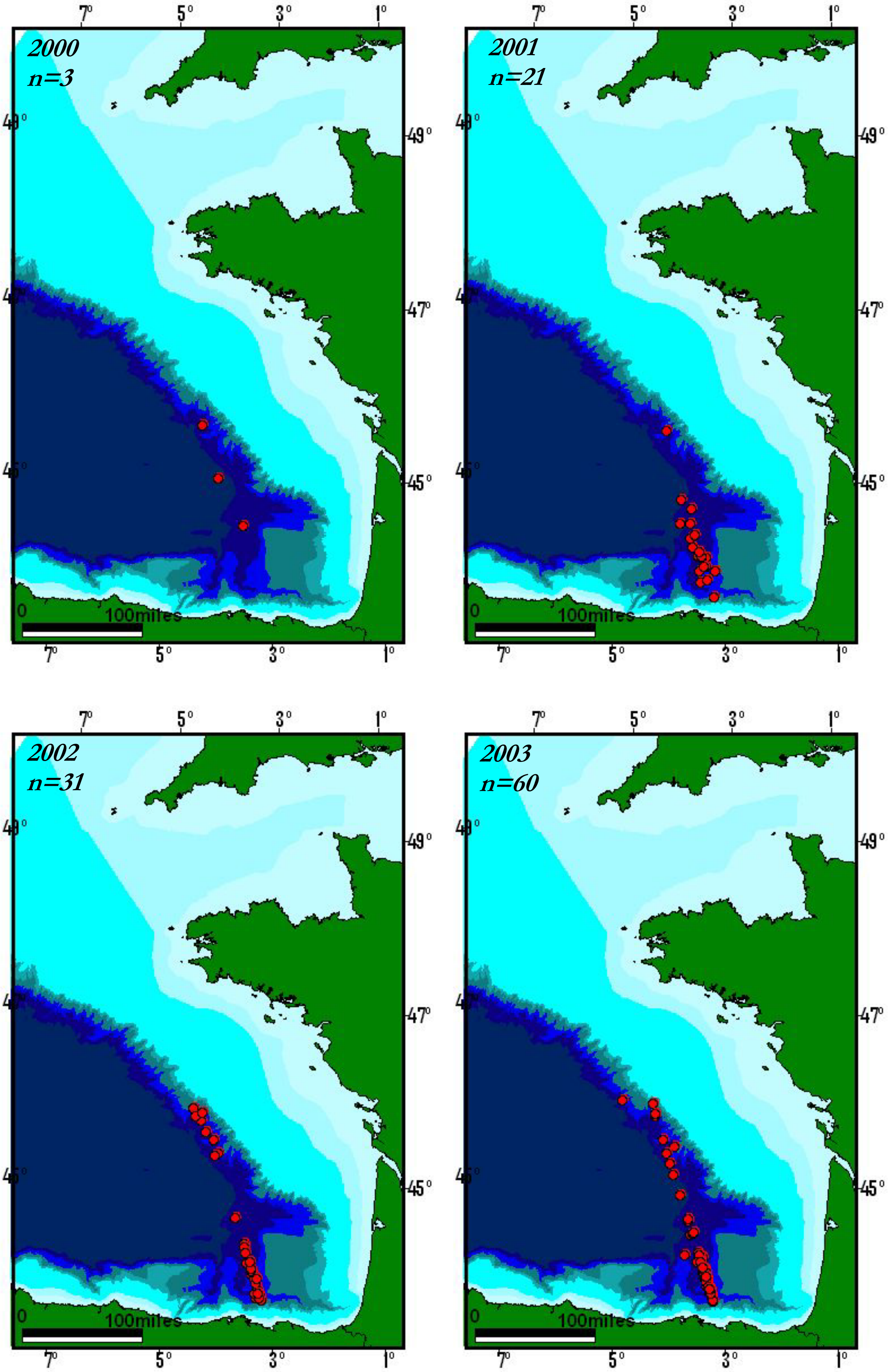


Figure 5.13: Spatio-temporal variation in distribution of Cuvier's beaked whale between 2000 and 2003. Red circles represent sightings and n is equal to the total number of encounters.

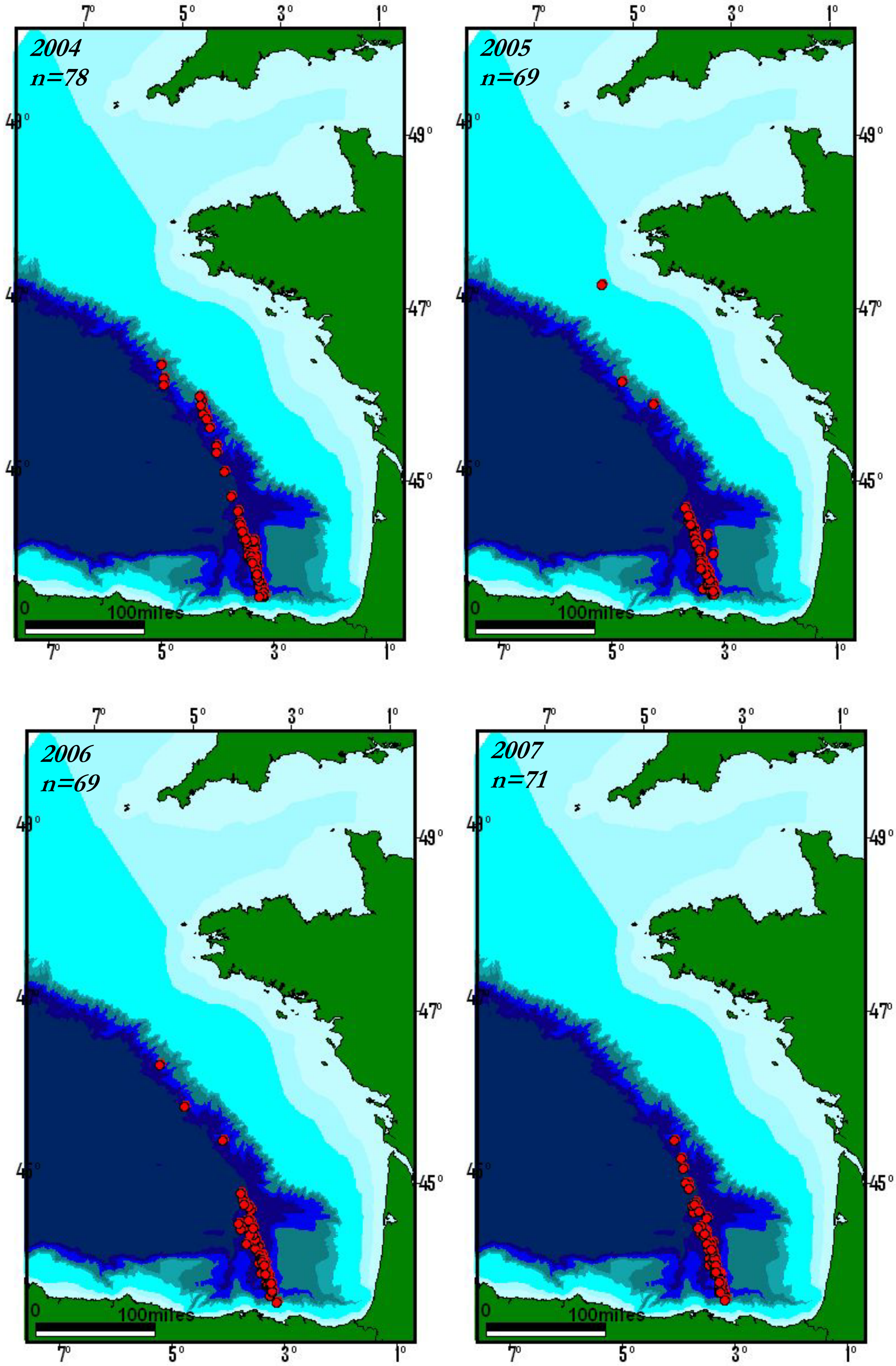


Figure 5.14: Spatio-temporal variation in distribution of Cuvier's beaked whale between 2004 and 2007. Red circles represent sightings and n is equal to the total number of encounters.

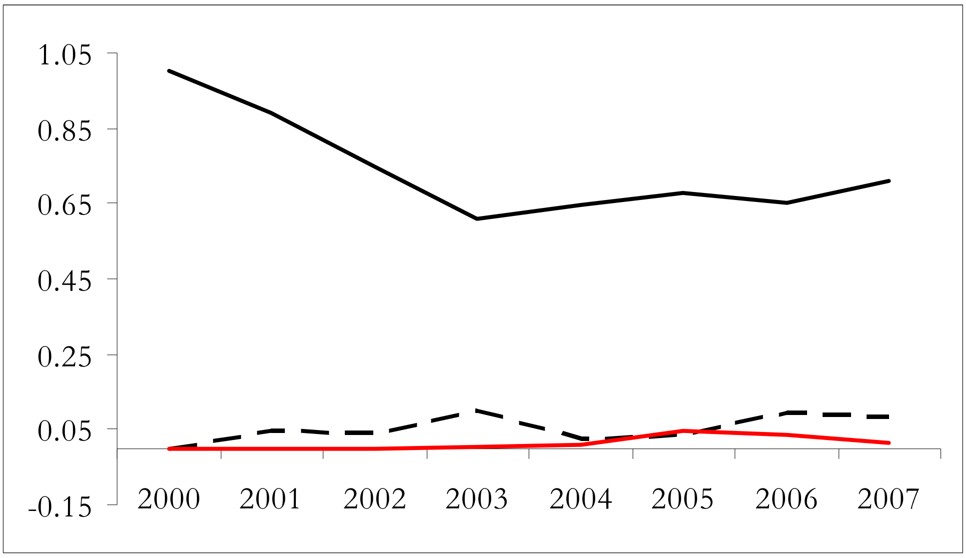


Figure 5.15: Annual variation (*x-axis*) in the total number (*y*-axis) of individuals of Cuvier's beaked whale (solid black line), the northern bottlenose whale (dashed black line) and Sowerby's beaked whale (red solid line)

5.323 Strandings data

The analysis of strandings form 1904 to 2007 found 174 strandings recorded from the UK, ROI and France. During these years an increase in strandings events is notable across the whole time scale (Figure 5.16). Interestingly peaks in stranding events seem to occur in one region at a time, with small peaks in stranding events that overlap between each region. In the late 1970s to the early 1980s, strandings events are much greater than the rest of the years for the French Atlantic coasts. This notable rise in stranding events during this time could be the result of increased attention during the 1970s form published yearly reports by Raymond Duguy for the French coasts from 1972 at the Marine Mammal Research Center (*Centre de Recherche sur les Mammifères Marins*, CRMM).

Over time, the changes in the proportion of Cuvier's beaked whale strandings events were compared to northern bottlenose whale and Sowerby's beaked whale strandings. The findings show that from 1910 to 2005 when Cuvier's beaked whale strandings increase, the northern bottlenose whale strandings decrease and vica versa (Figure 5.17 and 5.18). Over the period from 1995 to 2005, there have been times when this was not seen: from 1996 to 1998 and 2002 to 2003, both species appear to increase at the same time (Figure 5.17 and 5.18). From 2004 to 2006, the northern bottlenose whale findings follows the same fluctuation as Sowerby's beaked whale. Sowerby's beaked whale strandings do not show any particular patterns when compared to the other two species (Figure 5.17 and 5.18).

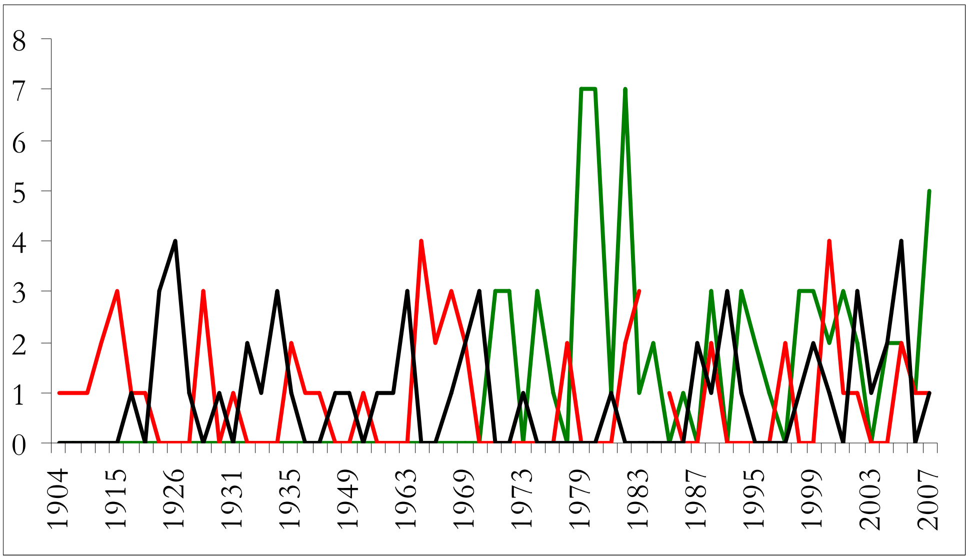


Figure 5.16: Total number (*y-axis*) of strandings events over time (*x*-axis) of Cuvier's beaked whale recorded around the coasts of the UK (black), Ireland (red), and French Atlantic coasts (green).

The changes observed between Cuvier's beaked whale and the northern bottlenose whale is thought to be a result of the preference for different water temperature preferences. It is of common knowledge that the northern bottlenose whales are dominant in cooler waters and Cuvier's beaked whales are dominant in warmer waters with a change in dominance at or close to the latitude of the UK and ROI (MacLeod *et al.,* 2004b; MacLeod, 2005a). In contrast, Sowerby's beaked whale appears to be able to co-exist with both these species and they have a southern range limit that extends further south than the northern bottlenose whale (MacLeod, 2005a). Figure 5.18 represents the strandings in the same period as the sightings data. Figure 5.19 shows the relative strandings rates of both Cuvier's beaked whale versus the northern bottlenose whales. The correlation coefficient was -0.79, suggesting variables change in the opposite direction, as one increases the other decreases and vica versa.

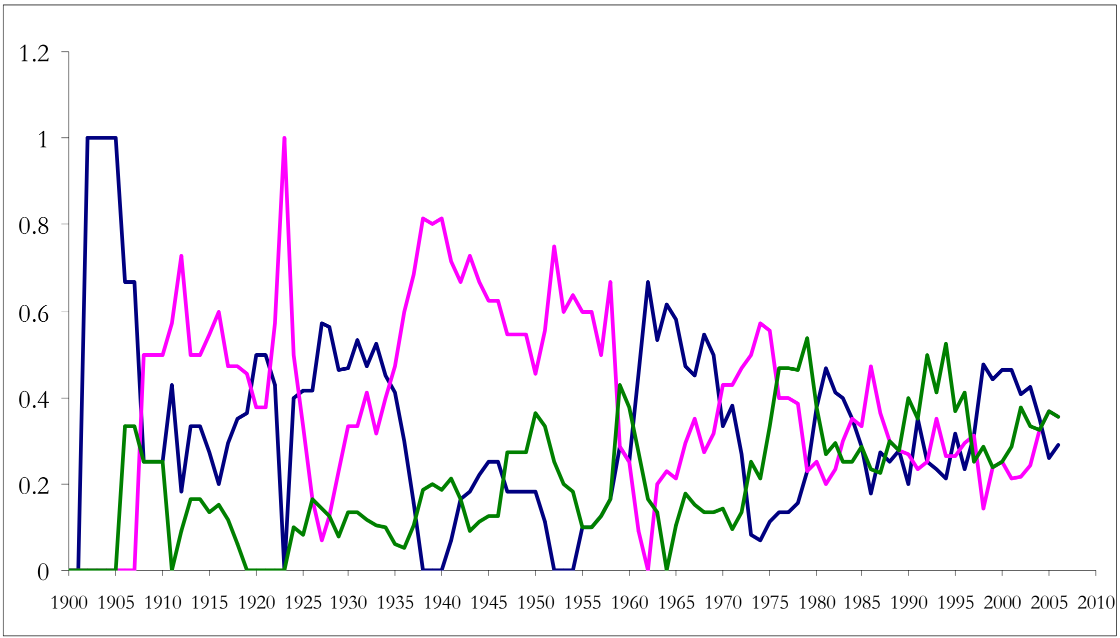


Figure 5.17: Five-year running average for Cuvier's beaked whale (blue), northern bottlenose whale (pink) and Sowerby's beaked whale (green) between 1904 and 2007, as a proportion of all three beaked whales (*y-axis*).

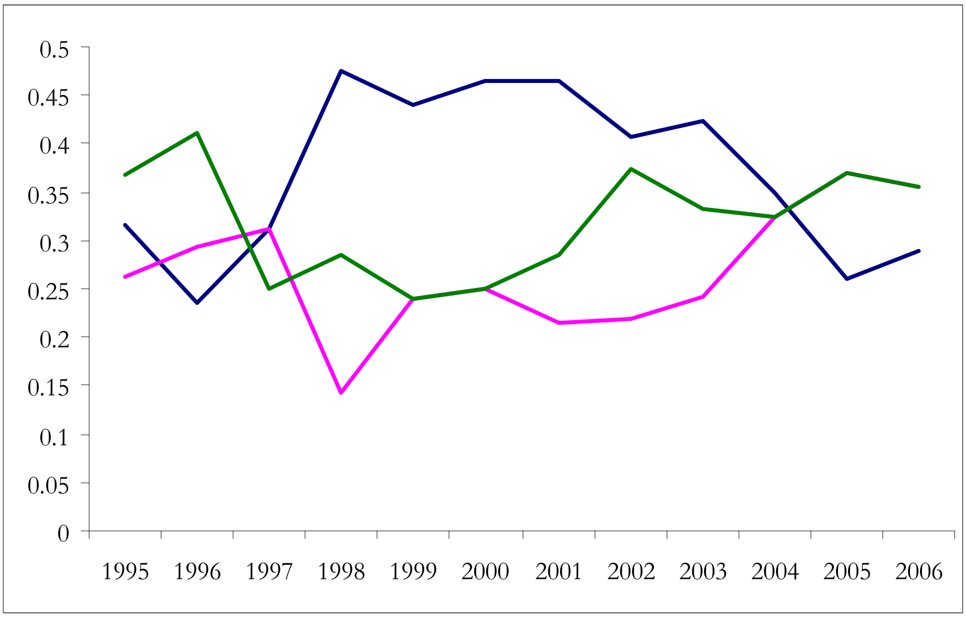


Figure: 5.18: Five-year running average for Cuvier's beaked whale (blue), the northern bottlenose whale (pink) and Sowerby's beaked whale (green) strandings between 1995 and 2007, as a proportion of all three beaked whales (*y-axis*).

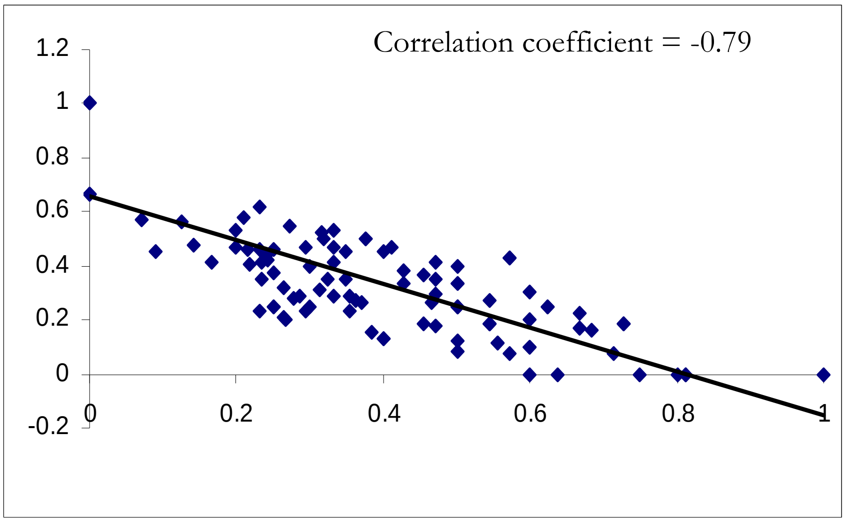


Figure 5.19: Relative strandings rate of Cuvier's beaked whale (*y-axis*) versus the northern bottlenose whale (*x-axis*) between 1900-2007.

5.4 Discussion

The year round sightings of Cuvier's beaked whale, taken over ten years, have provided a unique opportunity to examine the variation in their spatial and temporal distribution within the Bay of Biscay. Sightings data were investigated for the Bay of Biscay between 1995 and 2007, and strandings records were investigated from UK, ROI and French Atlantic coasts 1904 and 2007. Here I discuss the patterns found and then examine how they could be related to changes in water temperature in the Bay of Biscay and around ROI and the UK. The Bay of Biscay is the most northern regular limit of this species in the northeast Atlantic because of its confinement to water temperatures >10°C (Houston, 1991). Theory predicts that this species might expand its distribution by moving north if water temperature increases because of climate change. The year round sightings that are consistent over ten years suggest the population of Cuvier's beaked whale is resident in the Bay of Biscay.

5.41 Spatial and temporal pattern in distribution: sightings and strandings

5.411 Sightings

The results of this study revealed that on a broad scale, sightings of Cuvier's beaked whale indicated a clear preference for deep water that is associated with waters equal to or deeper than 1000m on both the northern and southern continental shelf slopes of the Bay of Biscay. An association is also observed with the CapBreton canyon in the southeast corner of the Bay of Biscay. This was reported by Williams *et al.* (2002a) who suggested a habitat preference for the CapBreton Canyon area, in which the distributions of Cuvier's beaked whale are not random but were instead located over the deep continental slope around the CapBreton Canyon. D'Amico *et al.* (2003) and Moulins *et al.* (2997) in the Ligurian Sea, NW Mediterranean, also found an association between Cuvier's beaked whale and submarine canyons, whilst MacLeod and Mitchell (2006b) identified from a number of sources that the Genoa Canyon is a key area for Cuvier's beaked whale. The preference for deep water is in accord with descriptions of this species in other areas having a preference for deep water and continental slopes, for example eastern tropical Pacific (Ferguson *et al.,* 2006); California (Falcone *et al,* 2009); northeastern US (Kenney and Winn, 1987; Waring *et al.*, 2001); Bahamas (MacLeod *et al.,* 2004a); north-western Mediterranean (Moulins *et al.*, 2007); Hawaii (Baird *at al.*, 2004; 2006); Greece (Frantzis *et al.*, 2003); and Japan (Nishiwaki and Oguro, 1972).

The results from this study have revealed three patterns relating to the distribution of Cuvier's beaked whale. This first and foremost pattern is found in the seasonal distribution of Cuvier's beaked whale, which shows a northward movement from the southern continental slopes and submarine canyons in autumn and winter to the northern continental slope during spring and summer. The second pattern is an increase in the numbers of Cuvier's beaked whale over time. The third pattern is found in both Cuvier's beaked whale and the northern bottlenose whale. In the Bay of Biscay, where these two species are known to overlap in their occurrence, sightings over the last ten years have shown that as one increase the other decreases and vica versa. The stranding findings have also shown this.

While two main locations were southern and northern Biscay, associated with canyons and the continental slopes, a third location over the deep waters of the abyssal plain was observed for this species (water depth 3000-4000m), whereas despite extensive coverage over the shelf and the English Channel, Cuvier's beaked whale were absent. It is suggested that sightings over the deep waters of the abyssal plain are reflecting this area as a transitional zone for Cuvier's beaked whale and not an area they would inhabit on a regular basis. In comparison with this study, Ferguson *et al.* (2006) also found Cuvier's beaked whales over much deeper waters than in any other studies, however the Eastern Tropical Pacific is generally deeper anyway. Further exploration of the opportunistic sightings data showed the movement into the waters over the northern continental slopes as a seasonal event that occurs during spring and summer, whereas in autumn and winter the distribution is mainly in the south over the CapBreton Canyon. Few sightings were recorded in autumn, and no sightings were recorded north of 45°N in winter. It is suggested from the results that it is not a change in habitat for this animal, but more a change in distribution. They appear to migrate from one region with steep slopes and underwater canyons to another region with similar underwater topography - steep slopes with incising submarine canyons. Despite the effort based sightings not showing the northward seasonal movement as clearly as could be seen with the opportunistic sightings, numbers in spring and summer were significantly greater than in autumn and winter, suggesting an overall seasonal shifts within the Bay of Biscay. The group size was also indicative of their seasonality, with group sizes becoming smaller during the winter months. Earlier studies that looked at seasonal changes in Cuvier's beaked whale was by Mitchell (1968) who studied stranded animals and Williams *et al.* (1999) who looked at sightings. Both their work found seasonal patterns in the strandings and sightings, but no obvious pattern of seasonal movements.

Over time, opportunistic sightings data have shown an increase in the numbers of Cuvier's beaked whales. The opportunistic sightings reflect quite large increases in numbers of Cuvier's beaked whales from 2000 to 2007. Numbers were observed to be low in 2000, 2001 and 2002 in contrast to number of encounters and individuals observed from 2003 to 2007, when numbers doubled. One explanation for this is the increase in observer effort, as prior to 2002, there was no wildlife officer on the ferry, and the COW made sightings during spring and summer only of 2000, 2001 and 2002. Another explanation could be the increase in accuracy of the wildlife officers to identify Cuvier's beaked whale over time. By contrast, numbers of effort-based sightings were not observed to increase as much as with opportunistic sightings. This may be due to the effort related surveys only being conducted twice a month, and taking into account the weather which may not always be favourable (sea state $\leq$3), can reduce the chances of encountering beaked whales. It is proposed that the increase in Cuvier's beaked whales in the Bay of Biscay may have been occurring long before the research started. This is supported by the increase in strandings in the last 50 years around France, UK and ROI.

Both the dedicated and opportunistic sightings showed that Cuvier's beaked whales were frequently encountered in the southeastern corner of the Bay of Biscay, over the CapBreton canyon from 1997 and 2007. Opportunistic sightings, however, have shown that Cuvier's beaked whale is more widespread in their distribution than revealed by the effort-based sightings. The seasonal movement of Cuvier's beaked whale from southern Biscay to the northern continental shelf was first observed in 2002 with the opportunistic sightings. Their distribution was thought to be predominantly in southern Biscay, since only a few sightings had been observed over this area in 2000 and 2001 from opportunistic data, and between 1997 and 2007 from dedicated sightings data. Since 2002, encounters with Cuvier's beaked whale over the northern continental slopes in the Bay of Biscay are now a regular event.

5.412 Strandings

The results of the strandings analysis, based on single stranded animals, found region wide seasonal stranding events between the UK, ROI, and France. Stranding events were recorded more frequently in the winter months (Jan-Mar) for all three countries. The seasonal pattern of strandings records, as shown in section 5.11 'species variation', has shown the number of strandings to be greater around the UK and ROI than France during summer, whereas throughout autumn and winter, strandings are greater around France than the UK and ROI. It can also be seen that in winter the number of strandings greatly increase for all regions. In addition to the seasonal patterns, over time, notable peaks in strandings were evident in all regions and analysis shows when strandings were recorded from region they were not recorded in the other regions. However, overlap in strandings did occur between the regions at the same time, but not in great numbers.

Between 1995 and 2003, the proportion of Cuvier's beaked whale strandings were overall higher than the northern bottlenose whale; implying numbers of Cuvier's beaked whale are increasing over time. From 1995, strandings showed an initial decline followed by a rise from 1996 to 1997, after which remain stable until 2003. The steep rise in strandings was mirrored by a decline in the northern bottlenose whale strandings, after which saw a rise then a fall then a steady rise. Between 2003 and 2005, patterns appeared to change, with strandings of Cuvier's beaked whale decreasing and northern bottlenose whale increasing. After 2005, a rise in strandings of both Cuvier's beaked whale and northern bottlenose whale can be seen. Stranding patterns do reflect the changes in proportions of these two species recorded by BDRP in the Bay of Biscay across similar time periods. As strandings of one species go down, sightings go up and vica versa, for example the proportions of sightings show an increase in Cuvier's beaked whale and a decrease of northern bottlenose whale observed during 2003 to 2005.

Looking at the data on a bigger picture, one theory that is postulated is the overall higher numbers of Cuvier's beaked whale sightings and strandings compared to the northern bottlenose whale could be indicative of an expansion of Cuvier's beaked whale range and the contraction of the northern bottlenose whale range in this region. This does however require continued observations.

The findings of this study show there are consistencies between the patterns observed with the three data sets used; dedicated and opportunistic sightings, and strandings records. There are consistencies in seasonal patterns between the opportunistic and dedicated sightings and the strandings data, although the number of sightings from dedicated surveys is relatively low. There are consistencies with the increase of Cuvier's beaked whale sighting and decrease of strandings and vica versa. There are consistencies in the depths at which dedicated and opportunistic sightings were recorded.

5.42 Causes of distribution: physical and biological aspects

Movements of marine mammals represent a response to changes in the marine environment, either the biological requirements of a species, such as prey availability and water temperature, or physical factors such as underwater topography and movements of currents. Together, these factors may trigger the start of seasonal movements, although not all individuals will necessarily respond in the same way. Determining the distribution of Cuvier's beaked whale as well as the patterns found in this study has led to possible explanations that are linked with water temperature and subsequent prey distribution.

In the Bay of Biscay, water temperatures have been found to show an overall warming in the 1990s (Koutsikopoulos *et al.,* 1998), and it has been recognised globally that the 1980s were the warmest of the previous 100 years (Jones *et al.*, 1988). Koutsikopoulos *et al.* (1998) confirm the existence of a long term increasing trend in SST, although this has not been uniform for the entire area. The southeast Bay of Biscay shows a stronger warming trend (Pingree, 1993; Gonzalez-Pola *et al.*, 2005), with a mean increase of 1.4°C from 1972 to 1993. Gonzalez-Pola *et al.* (2005) report evidence of intense warming and salinity modification of intermediate water masses in the southeastern corner of the Bay of Biscay for the period 1992-2003. All water masses below the mixed layer and down to 1000m depth have warmed up during the last decade at rates of two to six times greater than accepted for the North Atlantic during the last half-century (Gonzalez-Pola *et al.*, 2005). Warm winters have been observed because of southerly and westerly winds (Valencia *et al.*, 2003). It has been found that variations in the flow of Eastern North Atlantic Central Water (ENACW) eastward in the south have increased the warming (Gonzalez-Pola *et al.*, 2005). Warm waters are indicative of the intrusion of the ENACW into SE Biscay, that are associated with warm and dry weather conditions (Valencia *et al.*, 2003). In addition, the

Iberian Poleward Current (IPC) off northern Spain is a warm water extension into the southeast Biscay. The IPC starts around Christmas (NAVIDAD), and the development and winter warming were observed exceptionally in January 1990, 1996 and 1998 (Garcia-Soto *et al.*, 2002). A pronounced production of Slope Water Oceanic Eddies (swoddies) are associated with this, which have higher Chl-a concentration spreading warm and productive slope water into the ocean (Garcia-Soto *et al.*, 2002). This is probably related to abrupt slope topography. The eastern boundary poleward warming was found to extend from Portugal to Norway in exceptional NAVIDAD years, forming a narrow warm eastern margin for ENACW. There is a clear seasonal warming effect in the Bay, which is more evident in southern Biscay. Lavin *et al.* (1998) have shown that temperature in the Bay of Biscay follows the expected seasonal warming and cooling pattern, which determines a seasonal process of stratification and mixing of the water column. The seasonal change in water temperature at three regions and the warming of the southeastern corner of the Bay of Biscay is shown in Appendix 3.

5.421 Sightings

The patterns found in this study appear to be consistent with changes in water temperature. One possibly explanation for this movement of Cuvier's beaked whale to the northern continental slopes could be linked to warmer waters during spring and summer over those northern slopes. Findings of remotely sensed sea surface temperature data (Appendix 3) indicate a possible explanation as to why this species is not observed over the northern slopes during winter. The data showed that during the winter months, average SST ranged from 11.32°C to 12.78°C from 1995 to 2006 over the northern slopes. However, unlike waters in the south that rarely go below 10°C in winter, the water temperatures in the north were found to drop below 10°C (see Appendix 3 for this analysis). This species is appears to be largely confined by the 10°C isotherm (Houston, 1991), and with water temperatures dropping below this, it makes the area unfavourable during winter. Winter warming has undoubtedly had an effect on the greater number of Cuvier's beaked whales now observed in the Bay of Biscay, and it is hypothesized that a NAVIDAD event coupled with the ENACW keeps this area warm enough for this species to maintain its position in the southern Bay during the winter months.

The seasonal movement of Cuvier's beaked whale over the northern continental slope was observed during spring and summer from 2002 to 2007, exceptions being 2005 and 2006 when a decline in encounters over the northern slopes was observed. Prior to 2002, during 2000 and 2001 only two sightings were recorded over the northern slopes. It has to be noted that survey coverage at this time was poorer. The low numbers might have also been due to a decrease in temperature in spring from 2001 to 2002, and subsequently 2003 to 2004 (see Appendix 3 for this analysis). Once temperatures started to rise in the summers of 2005 and 2006, Cuvier's beaked whale numbers start to increase in the north in 2007. From the time taken when significant increases or decreases in water temperatures were observed (see Appendix 3 for this analysis) to the time when Cuvier's beaked whale numbers and distribution vary, it appears there might be time lag of approximately two years. This is only an assumption and further analysis is needed. While it seems clear that temperature could affect Cuvier's beaked whale, it is not understood why the distribution should be related to surface water temperature because of their deep diving behaviour. It is suggested that the changes are indirectly related to SST by their prey moving with changes in water temperature and, in turn, Cuvier's beaked whale moving in response to those prey movements. Another theory is they could use warm surface layers to warm up after deep diving in colder waters.

The close association with the CapBreton canyon and the northern shelf slopes may be due to local productivity resulting from upwelling caused by easterly winds in the south and southerly winds in the north, as well as steep topography. Vetter and Dayton (1998) showed that canyons appear to be important as sites of enhanced secondary productivity, providing diverse habitats, and as conduits of coastal detritus to the deep-sea (Shepard *et al.*, 1974; Gardner, 1989). The funnelling of water within canyons can produce complex oceanographic phenomena such as internal waves or upwelling, and it is very likely they may act as conduits for vertical migrating species such as squid, and trap animals swept away during their migrations, allowing an enhanced and near-permanent food supply within the canyon. The continental slope is known to attract cephalopod species for spawning on the bottom, as well as specialized cephalopods adapted to the vertical mixing and canyon topography of this narrow zone (Clarke, 1996b). Water depth and seabed topography can cause 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 (Davis *et al.*, 1998; Cañadas *et al.,* 2002; MacLeod *et al.,* 2004a).

Coastal upwelling in the southern Bay of Biscay is in response to easterly winds that shows a clear seasonal variability, with peak development centred during the spring and summer in southern Biscay (Gil and Sanchez, 2003b). Upwelling increases mesoscale activities such as cyclonic and anticyclonic rings, and meanders of fronts, which enhance nutrients and plankton (Gil and Sanchez, 2003b). How such upwelling would increase the productivity or availability of the deep water prey of beaked whales is unknown. It is likely that the downward flux of primary productivity has an effect on them and subsequently on beaked whales, as it has been speculated by several authors that their distribution (and of cetaceans in general) is likely to be primarily determined by prey availability and distribution (Davis *et al.*, 1998; Cañadas *et al.*, 2002; Hooker *et al.*, 2002; Torres *et al.*, 2009).

Stomach contents analysis of Cuvier's beaked whales included mesopelagic and deep water squid and benthic fish, occurring beyond the 1000m isobath (Heyning, 1989; Blanco and Raga, 2000; Collins *et al.*, 2001; Santos *et al.*, 2001a; Ohizumi and Kishiro, 2003). Stomach contents analysis of Cuvier's beaked whales in Japan (Wang *et al.*, 1995), the western Mediterranean coast (Blanco and Raga, 2000) and in the north-west of Spain (Santos *et al.*, 2001a) found prey items consisting exclusively of cephalopod remains. In addition, the conditions that influence cephalopod distribution would need to be investigated further to understand Cuvier's beaked whale distribution better.

In contrast, a lack of upwelling may affect survival of prey recruits via decreased primary production, and its subsequent effect on zooplankton and higher predators such as beaked whales (and cetaceans in general). This could be in part an explanation for the decline of numbers in some years and during the winter months. The latter is most certainly an effect of reduced SST as well.

5.422 Strandings

It has not been possible to make temperature related assumptions from strandings data recorded before 1996, due to sea surface temperature not being available at the time of analysis. However, variations in the number of Cuvier's beaked whale in different regions, UK, ROI, and France, in different months and seasons may reflect patterns in response to

SST. MacLeod *et al.* (2004b) previously examined strandings from 1800 to 2002 throughout UK and Republic of Ireland, and suggested that they reflect region-wide trends. The use of strandings data from the French Atlantic coasts enabled further investigations into a north-south seasonal movement, coinciding with sightings data.

Even though this species will move within its full range, it is likely that the warming of water temperatures during spring and summer in Biscay and around the UK and Ireland have probably led to Cuvier's beaked whale moving north of Biscay. The northward movement could be due to the narrow band of ENACW that flows north from the Bay of Biscay to Scotland (Pingree, 1993). It could be that the lower number of stranding records in spring, summer and autumn compared to winter reflect the possibility that more are alive at sea rather than stranded in these seasons. It is suggested that once water temperatures start to drop in autumn, Cuvier's beaked whale move south back into the Bay of Biscay. However, strandings still occur in winter around the UK and Ireland. It is possible they are trapped in these cold waters, and therefore cannot survive and are washed ashore. The increase in strandings around the UK and Ireland during winter is most likely to be determined by the fact they are not cool water species and therefore the cool water has adverse effects by causing them to strand more frequently during these months. High numbers of strandings on the French coasts during winter reflect the fact that this species occurs more regularly in Biscay during these months than the UK and ROI. The drop in temperatures in the northern Bay to below 10°C in winter appears to coincide with a decrease of sightings over the northern slopes in the Bay of Biscay in winter and this drop in temperature could be a contributing factor in these strandings. It is of general knowledge that the weather in Biscay can be very rough and unpredictable in winter, which could be another contributing factor to strandings, as rough weather could divert the species onto the continental shelf causing confusion of where they are, as the shelf area is not a habitat they normally frequent. In general, higher number of sightings in the Bay of Biscay compared to the UK and Ireland in winter is a strong indicator as to why stranding numbers are greater on the French Atlantic coasts in winter. It is therefore believed that a rise in strandings particularly around the UK and Ireland is linked to more northerly movement of Cuvier's beaked whale because of increases in water temperatures. If water temperatures rise over the coming years, the range in distribution might expand further north on a more regular basis.

5.43 Cuvier's beaked whale versus Northern Bottlenose Whale

One aspect of this study examines Cuvier's beaked whale relative to the northern bottlenose whale. Both the sightings and strandings reflect similar patterns and the fact that numbers of Cuvier's beaked whale are generally alot higher than the northern bottlenose whale. While the waters of the Bay of Biscay represent the northern-most limit for the usual occurrence of Cuvier's beaked whale in this region, these waters are the southern-most limit for the usual occurrence of northern bottlenose whales. However, both species are observed further north and south of their usual limit; Cuvier's beaked whale has been seen off Scotland (Evans *et al.*, 2008) and the northern bottlenose whale in the Azores (Macleod *et al.*, 2006). The water temperatures observed in the Bay of Biscay (where these two species are known to overlap in their occurrence) and the relative strandings rates of Cuvier's beaked whale versus northern bottlenose whales suggest that changes in water temperature may be responsible for the changes in relative occurrence of the species in this antagonistic pairing. One theory that is postulated is that a northward shift in the ranges of these two species could occur in response to increasing water temperatures and a southward shift when water temperatures cool. An example of range shifts has previously been suggested for white-beaked and common dolphin, also around the UK and Ireland (Evans *et* al, 2003; MacLeod *et al.*, 2005b), with the white-beaked dolphin distribution expecting to contract whilst common dolphins expand northwards in response to increasing sea temperatures (MacLeod *et al.*, 2005b).

The changes in occurrence of these species may reflect changes in other aspects of these ecosystems and changes seen on this study may also be result of competition in the past, and niche differentiation, rather than current competitive interactions. In particular, it may be that such changes in their occurrence reflect changes in the occurrence of preferred prey species. For example, northern bottlenose whales are primarily thought to prey on the cool water squid, *Gonatus fabrici*, while Cuvier's beaked whales often prey on other squid, including many warmer water species (Santos *et al.*, 2001a,b). Therefore, a change in the occurrence of these two species could reflect a change from an ecosystem dominated by cool water species such as *Gonatus fabrici* to one dominated by warmer water species (MacLeod and Smith, in Prep). It is important to remember that such indicators of climate change and increasing water temperatures may only be viable in areas such as the northeast Atlantic where one or more species are currently at the usual limits of their current range.

In addition, the strandings records indicate that Sowerby's beaked whale can co-exist with both Cuvier's beaked whale and the northern bottlenose whale. Unlike patterns identified with Cuvier's beaked whale and the northern bottlenose whale, Sowerby's beaked whale shows no such pattern. This is most likely to be linked to their diet, as they may rely principally on fish rather than cephalopods as the main component of their diet (MacLeod *et al.*, 2003) and therefore pose no threat as competition for prey in these waters. MacLeod et al., (2003), have also investigated the differences in prey sizes and the study showed that *Mesoplodon* species do consume smaller prey than *Ziphius and* Hyperoodon species. In addition, this species also has a more temperate based distribution compared to that of Cuvier's beaked whale and the northern bottlenose whale and the usual limit for the species is not the Bay of Biscay. However, effects of latitude are not explored in this study. Unfortunately, due to insufficient dedicated sightings, no comparisons can be made.

5.44 Implication for Conservation

As there appears to be a relationship between changes in the occurrence of Cuvier's beaked whale, and the northern bottlenose whale and changes in the local climate, both species have the potential to act as indicators of the effects of climate change on oceanic ecosystems. In particular, Cuvier's beaked whale is a widespread species that occurs in most warm temperate to tropical waters of the world (Heyning, 1989; MacLeod *et al.,* 2006c). Therefore, this species could be widely used as an indicator of changes in waters at the poleward ends of its current range as geographic range would be expected to remain within the preferred climatic conditions (Thomas *et al.*, 2004). This study suggests perhaps that Cuvier's beaked whale may become more regular in offshore canyons further north of the Bay of Biscay. This expansion could lead to a greater number of strandings in these waters around Ireland, the UK and French Atlantic coasts because the Bay of Biscay and the west coasts of Scotland are sites of current submarine training exercises (Parsons *et al.*, 2000). Several Cuvier's beaked whale strandings worldwide have been linked to the use of naval sonar (*e.g.* Simmonds and Lopez-Jurado, 1991; Frantzis, 1998; Balcomb and Claridge, 2001; Jepson *et al.,* 2003; Evans and Miller, 2004; Cox *et al.*, 2006), as has been suggested by necropsy results that have shown gas bubble lesions in their liver (Jepson *et al.*, 2003; Fernandez *et al.*, 2005) and haemorrhaging in the inner ears and some cranial spaces (Ketten, 2005). These could be the result of a physiological response from a behavioural response to normal dive profiles on exposure to sonar (Jepson *et al.* 2003). If the strandings were a result of sonar activity, then there is a high probability that stranding events might be recorded more frequently around the UK and Ireland in the future as water temperatures rise and if range moves north of the Bay of Biscay on a more regular basis.

In 2004, the Gully, a large submarine canyon off the coast of Nova Scotia, eastern Canada, was officially designated a Marine Protected Areas (MPA) in Canada (Charles and Wilson, 2009). In particular, this area is known for its resident population of the northern bottlenose whale (Hooker *et al.*, 2002). From ten years worth of data, it can be said without doubt that Cuvier's beaked whale are resident in the Bay of Biscay year round over the Capbreton Canyon and the northern continental slopes. If findings of stranding events in the future can be directly linked to active sonar, then maybe controls to mitigate and monitor when and where testing is carried out in the Bay of Biscay could be put into place.

5.45 Limitations and future work

Interpreting the distribution of living animals from strandings records is problematic with regards to oceanic animals because of the distance they may have been carried, and to infer distributions of stranding events they must be consistent with findings from other avenues of investigation (MacLeod *et al.,* 2004b). This problem has been overcome in this study by using two sets of sightings data (effort-related and opportunistic) of Cuvier's beaked whale at its most northern limit in the northeast Atlantic and comparing those with stranding records for the same period. Looking at the patterns and trends found, it is clear to see that with the use of only one of these data sets, these patterns would not have been observed. Cuvier's beaked whale occurrence over the same submarine canyon (CapBreton Canyon) and continental slopes of the southern Bay of Biscay for ten consecutive years, as identified by the dedicated sightings, is significant. However, incorporating the opportunistic sightings has identified this species showing a seasonal northward movement from the southern part of the Bay over the canyon to the northern continental slopes of the Bay. Investigating strandings events has also highlighted the importance of this region and regions north of Biscay. Cuvier's beaked whale have previously been identified in waters around the UK and Ireland (Evans 1980, 1990, Evans *et al.,* 2003; Reid *et al.,* 2003; MacLeod *et al.,* 2004b; Evans *et al.,* 2008). It is therefore advantageous to use different data sets, because without them it would be difficult to assess their distribution on a region-wide scale.

From what has been found in this study, future research should be focused on a number of areas to assess movements of Cuvier's beaked whale for effects of climate change and increasing water temperatures and sonar activity:

1. Surveying of the northern shelf slopes in winter. This study has indicated that the northern shelf slopes are rarely inhabited during winter by Cuvier's beaked whale. However, the lack of daylight hours during the winter means that the ferry does not reach the northern slopes in favourable viewing conditions and it may be that these animals are present but go unnoticed in the dark. Future research in these months would increase our understanding of their distribution relative to water temperatures and possible climate change effects.

2. Few sightings have been observed off the west coasts of Ireland by the Irish Whale and Dolphin Group (IWDG), and surveying submarine canyons off the west coast of Ireland would again provide more answers for the possible future northward movements of Cuvier's beaked whale in response to increased water temperatures through possible climate change effects. All records of their sightings and strandings are validated and available on: www.iwdg.ie.

5.46 Conclusion

The main findings from this study have shown the Bay of Biscay to be a very important year round habitat for Cuvier's beaked whale, and for all other cetaceans recorded by the Biscay Dolphin Research programme. This work has also shown how important it is to incorporate opportunistic sightings into analysis, especially when it comes to finding out more about inconspicuous and uncommon cetaceans, such as the beaked whales.

Whilst Cuvier's beaked whale distribution can be compared to other studies in terms of preferences for deep wtaer, shallow slopes, and submarine canyons, no comparison can be made with seasonal distribution. After assessing the studies already conducted on Cuvier's beaked whale, I believe that there is sufficient seasonal data to look at seasonal distribution and hopefully this present study can influence this further. Through this work, I have made an important step forward in adding to the knowledge already known of the range and patterns in the movements of *C*uvier's Beaked Whale in the Bay of Biscay and around the UK and Ireland. The opportunistic sightings have helped to broaden the knowledge of their distribution range and habitat use in the region in comparison to what was found with dedicated sightings. Without the use of opportunistic sightings, the seasonal movement observed may have gone unnoticed. Events may be part of a long-term trend, suggesting increasing temperatures with climate change could expand their distribution.

As listed by the IUCN (International Union for the Conservation of Nature), the global status and geographical distribution of beaked whales is poorly known (Reeves *et al,* 2003). Therefore, findings from this study will benefit future research into effective conservation strategies, identifying global seasonal movements, population stability relative to associated global climate change impacts.

Cetaceans are good indicators of climate change as they are at the top of the food chain, so any changes in primary productivity will affect their predator and in time the movements of the whales themselves. As a result, can Cuvier's beaked whale act as a predictor of increasing water temperatures because of global climate change by shifting their distribution to the northern slopes of Biscay, and possibly further north towards deeper offshore canyon regions if water temperatures rise?

Chapter 6

Summary and Conclusions

6. Summary and Conclusions

6.1 Overview of chapters

The present study aimed to examine the ecology of Cuvier's beaked whale in the Bay of Biscay. The main focus was placed on habitat use, spatio-temporal distribution, and the interactions with environmental parameters (*e.g.* sea surface temperature, water depth, slope, and aspect). Chapter 2 explored the habitat use of Cuvier's beaked whale in relation to water depth, slope, and aspect, using General Additive Modelling (GAM). Chapter 3 analysed the opportunistic data against environmental parameters to predict Cuvier's beaked whale distribution across the Bay of Biscay, using Ecological Niche Factor Analysis (ENFA). This chapter integrated effort data results to verify the model output. Chapter 4 explored the inter-specific distribution of deep-diving whales in the Bay of Biscay, using Cuvier's beaked whale as the main focus for comparisons. A Principal Components Analysis (PCA) was conducted to show the habitat use of deep diving and non-deep diving cetaceans, to show how similar or dissimilar they were from each other. Chapter 5 examined the spatio-temporal distribution of Cuvier's beaked whale. The main findings from this showed a seasonal movement that has not been observed and reported for Cuvier's beaked whale sightings in the northeast Atlantic. The following paragraphs will provide a summary of the key findings and how they can be used on a more global perspective, then limitations and future research, followed by a final conclusion.

6.2 Key findings

6.21 Habitat use and modelling

A number of ecological niche factors have been investigated to identify the habitat preferences of Cuvier's beaked whale within the Bay of Biscay. The niche factors included eco-geographic variables (sea surface temperature (Chapters 2 and 5) and habitat factors (water depth, seabed gradient, and aspect). To determine preferences and ranges of these niche factors for Cuvier's beaked whale (Chapters 2, 3, 4 and 5) in the Bay of Biscay, three different models were applied. Using a range of approaches allowed different aspects of Cuvier's beaked whale ecology to be investigated from a number of different angles. This counteracts possible biases and limitations of any one method and provided additional support for conclusions reached. In addition, the niches of other deep-diving and non-deep diving species (Chapter 4) were compared to the niche of the Cuvier's beaked whale.

It must be noted that GAM (Habitat preferences), ENFA (prediction), and PCA (Niche) models do not report the same type or scale of output and predictions and therefore cannot be directly compared with each other. Three techniques were used to look at three different issues. ENFA modelling weights all input variables, so that less important variables are given a lower weighting and contribute less to the final model. PCA modelling involves the user in the selection of different combinations of variables. The choice of input variables can therefore dramatically influence the predictions (Mandleberg, 2004). To reduce bias in the models produced by ENFA and PCA, the choice of eco-geographical variables is very important. Only the variables that are representative of the niche occupied by the species should be included (Mandleberg, 2004). ENFA has also been identified as over-predicting the distribution of a focal species relative to other models such as GLMs (Brotons et al., 2004). However, Hirzel et al. (2001) demonstrated that ENFA can be robust in terms of sample size and with respect to data quality.

In this study, it has been shown that opportunistic sightings (presence-only) can be used just as well as dedicated sightings to model distributions, understand habitat preferences and to produced habitat suitability maps of predicted distribution. All three chapters (2, 3, and 4) identified a strong link between the distribution of Cuvier's beaked whales and its environment. In particular, they all highlighted the importance for water depths ranging >1000m to <4000m, shallow slopes, and the aspect of slope (see chapters 2, 3 and 4). Chapter 2 identified the limits of preferred depth ranges, the steepness of slopes and the particular direction in which the slope faces. South, southeast, east, and north facing slopes appeared to be favoured by Cuvier’s beaked whale. West facing slopes were not favoured on any spatial scale. Chapter 3 provided meaningful habitat predictions of Cuvier’s beaked whale distribution using opportunistically collected data. This suggests that presence-only models can be used to predict where Cuvier’s beaked whale is most likely to occur in relation to ecogeographical variables. From the ENFA modelling, the predicted marginalisation, specialisation and tolerance values identified that the species is most likely to occur in deep waters associated with the continental shelf slope, in both northern and southern Biscay. Findings indicate this species has a high marginality value and as applied to the English Channel and the Bay of Biscay, it requires habitats that differed from the average habitat. This species was also found to have a high specialisation value, which indicates they have a more restricted range with respect to the eco-geographical variables. A relatively low tolerance value was observed for this species that is indicative of their specialised habitats, highlighting the lack of sightings over unsuitable habitats. In chapter 4, a number of different deep diving and non-deep diving cetaceans were included to explore their habitat use in relation to Cuvier's beaked whale. The PCA adequately identified slope as the first factor to separate the species, followed by water depth. It was found that these species could be placed into two major species groupings in the Bay of Biscay: (1) the specialists, consisting of Cuvier's beaked whale, northern bottlenose whale, Sowerby's beaked whale, beaked whale sp, sperm whale, and fin whale that prefer offshore waters; (2) and the generalists are the common dolphin and pilot whale that prefer both offshore and inshore waters. Slope, depth, and east facing slopes were found to be the most important variables responsible for determining the habitat preferences of the seven species. In addition, these species were further grouped according to their individual niche centres and widths. In relation to Cuvier's beaked whale, all species except the northern bottlenose whale have larger niche centres. The beaked whales have narrow niche widths in comparison to pilot whale, sperm whale, fin whale and common dolphin.

Many factors need to be taken into account when trying to understand and determine the distribution of a species. It is hypothesized that probable habitat and resource partitioning might be occurring. The beaked whales, sperm whale, and pilot whales are known to feed on the same prey which in the study area are likely represented by species of squid, and clearly fin whales and common dolphin are also known to feed in the same areas as them. Thus, the necessity to exploit the same trophic resource in the same area might have led to some segregation in terms of interactions with environmental variables. It is widely known in the literature that prey distribution is the main factor determining cetacean distribution (Canadas *et al.* 2002; Hastie *et al.*, 2004; MacLeod *et al.* 2004c; Friedlaender *et al.* 2006; Torres *et al.*, 2009), in addition to movements between breeding and calving areas. An understanding of the inter-annual and seasonal variation in their distribution would also explain more about their distribution relative to each other. It is assumed that at some point, they do occupy the same area at the same time but the extent of this is not known and not investigated in this study. On a temporal and more dynamic scale, temperature ranges chosen by species might represent additional partitioning. In this case, the exploitation of resources would be performed differently based on a greater presence of one species over another with concurrent increasing or decreasing of sea surface temperatures in certain seasons.

Predictive modelling, in which remotely sourced EGVs are used to predict areas of high species diversity, may provide a valuable method for identifying hotspots and focusing future research at a time when short-term findings will have long-term implications for the distribution of Cuvier's beaked whale. If the niche that a species occupies is related to a specific combination of environmental variables that can be identified, then this information, as seen in this study (Chapter 3), can be used to provide a picture of where that species is likely to occur and where it is likely to be absent. As a result, understanding the distribution of organisms in relation to their environment is becoming increasingly important in terms of assessing and modelling species distribution, identifying and protecting essential habitat, and in terms of assessing and mitigating human impacts upon marine organisms. While the use of such spatial modelling is growing rapidly, it is important to remember that in order to model accurately a species distribution from its environmental preferences, the data used to build the model need to be representative of the full range of all available habitat combinations (i.e. adequately sample the entire environmental n-dimensional hyperspace available to a species). If there are large differences between the available habitat combinations and those surveyed, then any model produced may not be a true representation of the actual species distribution.

In addition to the habitat preferences identified for Cuvier's beaked whale distribution, the effects of EGVs on this species were explored over different spatial scales (chapter 2). It was found that EGVs were not important of all scales, except for depth. Using classification trees, slope determined the first split of the tree of small spatial scales (5 and 10km), whereas aspect determined the first split of the tree of larger scales (15, 20, and 25km). Therefore, this means that at different spatial scales, different combinations of EGVs can be used to understand the localised distribution of Cuvier's beaked whale. In previous studies, it has been suggested that the slope of a steep wall of a submarine canyon is a feature that may be important at small scales of a few hundred metres to a few kilometres, but it would almost disappear in large-scale analyses (Ferguson *et al.,* 2006). What has been understood from this study is that, ideally, whale habitat studies should thus use a hierarchical scale framework that takes into account the relative influence of fine, meso-, and broad scale processes. Since studies over broad scales cannot be extrapolated to finer scales, it is best to start off with fine scale studies that can be extrapolated into broad scale ones.

In summary, firstly all three chapters adequately identified the habitat preferences and requirements for Cuvier's beaked whale. Secondly, it has been shown that when dedicated sightings are limited, opportunistic data can be used to understand habitat preferences of Cuvier's beaked whale. In this study, dedicated sightings data were low in comparison to the opportunistic sightings; however, the dedicated survey data suggested that the ENFA model has a high predictive ability. Using such methods can expand on our knowledge of elusive deep-diving species on a global scale. It is important that when opportunistic sightings are used, the model is validated with independent dedicated survey data.

6.22 Seasonal patterns

Seasonal patterns in Cuvier's beaked whale distribution have been previously suggested from sightings in the Bay of Biscay by Williams *et al.*, (1999), and strandings by MacLeod *et al.* (2004b) around the UK and Ireland, and by Mitchell (1968) from the northeast Pacific. However, this study builds upon the former one with a much larger data set. An increase of Cuvier's beaked whale in the Bay of Biscay was observed during spring and summer compared with lower numbers found in autumn and winter. In addition, there is an indication of a seasonal northward movement from the submarine canyons of the southern Bay, to the deep waters of the abyssal plain and the shelf slopes of northern Bay. It is assumed that they show this movement when temperatures warm up and they are following the pattern in seasonal temperature warming/cooling.

The stranding records indicated and concurred with previous studies that this species expands its range north of Biscay by moving north into waters around Ireland and the UK; a movement that probably happens during spring and summer when sea temperatures are warmer. One suggestion for the increase in strandings during the autumn and winter months around the Atlantic coasts of the UK and Ireland is that they become trapped in the cold waters in winter. Together with cooler water temperatures and the fact that their preferred prey may have also moved out of the area, and therefore with little or no food resources, they lack energy to travel back down to warmer waters and strand. Strandings are also greater in winter along the French Atlantic coasts. It is known that water temperatures have increased in the Bay of Biscay over the last two decades (Koutsikopoulos *et al.*, 1998), making it a more favourable habitat all year round for Cuvier's beaked whale. This provides a possible explanation for the greater number of strandings during winter on the French Atlantic coasts. On the other hand, many cetacean species show winter peaks in strandings, and one cannot exclude the possibility that harsher climatic conditions during winter with increased storm frequencies may be responsible for a greater number of animals being washed up on beaches.

In addition to their seasonal distribution, both the sightings and strandings identified that whereas Cuvier's beaked whale records have increased in numbers, northern bottlenose whale records have declined, indicating an extension of Cuvier's beaked whale range and contraction of the range of northern bottlenose whale. Pre 1995, the strandings have also shown periods of increase in northern bottlenose whale strandings, followed by a decrease in Cuvier's beaked whale strandings, which could be the result of competition for resources, or a different response to climatic conditions through prey availability and cooler water temperatures. This could mean that the ecosystem has changed from a cool water ecosystem to a warmer water ecosystem, since Cuvier's beaked whale feed on warmer water species of squid and northern bottlenose whale feed on cooler water species of squid. Changes in distribution could also represent actual evidence for competition, instead of changes due to in water temperature and prey movements.

Overall, an increase in sightings over the last ten years and an increase in strandings over the last 50 years is reported here and is most likely linked to the increase in water temperatures. While it seems clear that temperature could affect Cuvier's beaked whale, it is not understood why the distribution would be related to surface water temperature given their deep diving behaviour. One idea is that they use surface intervals between long dives to undertake essential activities (resting, mating, digestion etc.) (MacLeod, 2005a) and because this species is adapted to warm waters, they may get too cold when they are deep diving and use the surface waters to warm up. Another idea relates to the link to the temperature requirements of their prey, which in turn is reflected in their movements.

6.3 Global perspective

Previously, our knowledge of beaked whales (family Ziphiidae) was limited mainly because of our knowledge of where they occur and because they are deep divers with a tendency to live in deep-sea canyons far from the coast. However, the Spanish coast of the Bay of Biscay is one of the few areas in the world where beaked whales, particularly Cuvier's beaked whale, can be seen within easy reach of a port, as identified by the Biscay Dolphin

Research Program. The Bay of Biscay is the most northerly distribution range of this species, with only a few sightings around Ireland and the UK as far as Scotland and one record off Iceland (Evans *et al.*, 2003; 2008), and strandings in Sweden (Evans *et al.*, 2008). This species is rarely found in waters below 10°C and if water temperatures rise in the future because of climate change, the range of this species could shift north to the continental slopes and submarine canyons west of Ireland, if not further. Cetaceans are top of the food chain and changes in their distributional patterns are indicative of changes happening to the marine ecosystem.

On a global perspective, it is necessary to place the results of this study within a management and conservation context. Studies on beaked whales dating back more than ten years, were mainly based on strandings. Over the last ten years however, studies have dramatically increased because of focused efforts over areas where they are most likely to be found, such as continental slopes, submarine canyons and around oceanic islands. In recent years, beaked whales have been the focus of research interest following a series of mass stranding events associated with the use of military sonar, affecting particularly Cuvier's beaked whale but also Gervais' beaked whale, northern bottlenose whale and Blainville's beaked whale (Evans and Miller, 2004; Cox *et al*, 2006). If Cuvier's beaked whale expands its distribution north of the Bay of Biscay on a more regular basis, then it may come to harm from the effects of sonar testing in waters around Scotland. In addition, naval activity in the Bay of Biscay and further south (Spanish and Portuguese waters), could have potentially harmful impacts on this species and its population in the Bay, so that stranding events may occur more frequently in the future. In addition, two potentially interesting, and relatively non-intuitive, implications of this research are suggested in terms of possible anthropogenic impacts on beaked whales in general and, specifically, on individual species within the study area. These are the possible impacts of anthropogenically-induced global climate change and the exploitation of deep-water marine ecosystems by fisheries.

Beaked whales are the least known of all cetaceans, and increasing our knowledge can help the conservation of these species. Population abundance estimates are unknown in the Bay of Biscay, but since Cuvier's beaked whales have been observed year round over the last 12 years, it is suggested they are resident. Research so far (Evans and Miller, 2004; Cox *et al.,* 2006) plus many others have already concluded that strandings events (single or mass) can result of active sonar activities, so if in the future further active sonar activities appear to be responsible for strandings of these marine mammals, then could areas inhabited by beaked whales year round become protected? One area already established as a marine protected area where no sonar activity is allowed is the Gully, a submarine canyon off Nova Scotia, Canada for the northern bottlenose whale (Hooker *et al.*, 1999c; Charles and Wilson, 2009).

The findings of this study indicates that Cuvier's beaked whales are not evenly distributed throughout the Bay of Biscay, but are instead concentrated in areas of suitable habitat such as the Cap Breton Canyon and the continental shelf slopes. As a result, the potential for effects of anthropogenic activities, such as noise pollution, will vary depending on where those activities occur. If possible, the key habitats for Cuvier's beaked whales identified in this study should be avoided or at least specific mitigation measures taken if they cannot be conducted elsewhere. In the future, it may be that once population estimates for Cuvier's beaked whale are known in the Bay of Biscay, this area could also become a marine protected area.

Further research is required to identify what aspects of oceanic ecosystems are linked to changes in the occurrence within them of apex predators, such as beaked whales. Therefore, while this study suggests that the occurrence of some beaked whale species around the UK and Ireland might be linked to changes in water temperature, those species have the potential to act as indicators of the effects of climate change on the oceanic ecosystems of which they are an important component. Further research is required to determine if these changes do indeed reflect changes in such ecosystems and in what manner they are linked. As indicated from the evidence that SST could be affecting Cuvier's beaked whale distribution in the Bay of Biscay, this species might act as an indicator of global climate change and sea surface temperature could be used as an explanatory variable.

6.4 Limitations and future work

During this study a number of limitations were encountered. The biggest limitation has been the low sample size of dedicated sightings for Cuvier's beaked whale. Initially it was thought that by using a sample size of only 53 sightings, the results would have to be interpreted with great caution. To overcome this problem, opportunistic sightings data were used, with a sample size of 402 sightings. In addition, dedicated sightings were used to verify the presence-only model, ENFA. Both the data sets gave a similar representation of the habitat use and distribution of Cuvier's beaked whale in the Bay of Biscay. For the future, this suggests that opportunistic data (presence-only) can be used just as much as dedicated sightings (presence-absence), especially where dedicated sightings are limited. Evans and Hammond (2004) reviewed a number of methods for surveying and monitoring cetaceans in Europe, and recommended that it was both impractical and unwise to adopt a single methodological approach over all others. They suggested that different approaches can frequently complement one another in providing a more complete picture of the status and distribution of a particular cetacean species (Evans and Hammond, 2004), as has been shown by this study.

In terms of future work, the following points seem worthwhile as part of further investigations:

- Winter surveys over the northern slopes could be carried out to determine if the animals are truly absent, because the ferry does not reach the northern shelf in daylight hours in winter months, therefore affecting observations of Cuvier's beaked whale in this region. Therefore, it cannot be truly said that they are absent.
- Dedicated surveys over the western, southern, and northern shelf slopes, that were not covered in this study, could be carried out to determine Cuvier's beaked whale distribution relative to the predicted distribution within the Bay of Biscay, as identified in chapter 3 of this study.
- Expand research off the ferry line at right angles to the ferry track. The width to expand on off the line could be determined by a buffer zone of the distances (m) at which Cuvier's beaked whales are observed from the vessel. Also running lines east to west through Biscay will help to expand the knowledge of the movements.
- Conduct surveys over the continental shelf and submarine canyons of the Porcupine Bight, west of Ireland and Rockall Trough area, northwest of Ireland, to help identify possibly northward extensions of the range of Cuvier's beaked whale
- Comparing sightings of this study with sightings taken from another route further west, such as the Brittany ferries from Plymouth-Santander, and with sightings from another survey team onboard the Pride of Bilbao - 'ORCA', to see if the results fit with the sightings already recorded.
- Linking the distribution of all beaked whale species found in the Bay of Biscay and in waters around the UK and Ireland to temporally variable parameters such as sea

surface temperature and chlorophyll-a from remote sensing. Both these data sets can be used as proxies for understanding climate change and the effects on the marine mammals and the marine environment in general.

Bibliography

Aguilar De Soto, N., Johnson, M., Madsen, P. T., Tyack, P. L., Bocconcelli, A. and Fabrizio Borsani, J. (2006). Does intense ship noise disrupt foraging in deep-diving Cuvier's beaked whales (*Ziphius cavirostris*)? *Marine Mammal Science.* **22**: 690-699.

Allen, S. E. (1996). Topographically generated, subinertial flows within a finite length canyon. *Journal of Physical Oceanography.* **26**: 1608-1632.

Allen, S. E., Vindeirinho, C., Thomson, R. E., Foreman, M. G. G. and Mackas, D. L. (2001). Physical and biological processes over a submarine canyon during an upwelling event. *Canadian Journal of Fisheries and Aquatic Sciences.* **58**: 671-684.

Alvarez, A. and Tintore, J. (1996). Flow modification and shelf-slope exchange induced by a submarine canyon off the northeast Spanish coast. *Journal of Geophysical Research.* **101**: 12,043-12,055.

Baird, R. W., McSweeney, D. J., Ligon, A. D. and Webster, D. L. (2004). Tagging feasibility and diving of Cuvier's beaked whales (*Ziphius cavirostris*) and Blainville's beaked whale (*Mesoplodon densirostris*) in Hawaii. *Report Hawaii Wildlife Fund, Volcano, HI from SW Fisheries Center, NMFS.*

Baird, R. W., Webster, D. L., McSweeney, D. J., Ligon, A. D. and Schorr, G. S. (2006). Diving behaviour and ecology of Cuvier's (*Ziphius cavirostris*) and Blainville's beaked whales (*Mesoplodon densirostris*) in Hawaii. *Canadian Journal of Zoology.* **84**: 1120-1128.

Balcomb, K. C. and Claridge, D. E. (2001). A mass stranding of cetaceans caused by naval sonar in the Bahamas. *Bahamas journal of Science.* **5**: 2-12.

Ballance, L. T., Pitman, R. L. and Fiedler, P. C. (2006). Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A Review. *Progress in Oceanography.* **69**: 360-390.

Barlow, J., Pitman, R., Ballance, L., Klinger, T., DeMaster, D., Hildebrand, J., Urban, J., Palacios, D. and Mead, J. G. (2004). A call for research to assess risk of acoustic impact on beaked whale populations. Paper presented to the Scientific. Committee at the 56th Meeting of the International Whaling Commission, Sorrento, Italy, SC46/E36.

Barlow, J., Ferguson, M. C., Perrin, W. F., Ballance, L. T., Gerrodette, T., Joyce, G., Macleod, C. D., Mullin, K., Palka, D. L. and Waring, G. (2006). Abundance and densities of beaked and bottlenose whales (Family Ziphiidae). *Journal of Cetacean Research and Management.* **7**: 263-270.

Barlow, J. and Gisiner, R. (2006). Mitigating, monitoring and assessing the effects of anthropogenic sound on beaked whales. *Journal of Cetacean Research and Management.* **7**: 239-249.

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.

Baumgartner, M. F., Mullin, K. D., Nelson May, L. and Leming, T. D. (2001). Cetacean habitats in the northern Gulf of Mexico. *Fisheries Bulletin.* **99**: 219-239.

Benson, S. R., Croll, D. A., Marinovic, B. B., Chavez, P. and Harvey, J. T. (2002). Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Nino 1997-98 and La Nina 1999. *Progress in Oceanography.* **54**: 279-291.

Berrow, S. and Rogan, E. (1997). Review of cetaceans stranded on the Irish coasts, 1901-1995. *Mammal Review.* **27**: 51-76.

Bjørge, A. (2002). How persistent are marine mammal habitats in an ocean of variability? Marine Mammals: Biology and Conservation. P. G. H. Evans and A. R. Raga. Kluwer Academic/Plenum Press. 63-91

Bjorke, H. (2001). Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian sea. *Fisheries Research.* **52**: 113-120.

Blanco, C. and Raga, J. A. (2000). Cephalopod prey of two *Ziphius cavirostris* (Cetacea) stranded on the western Mediterranean coast. *Journal of the Marine Biological Association UK.* **80**: 381-382.

Borja, A., Uriarte, A., Valencia, V., Motos, L. and Uriarte, A. (1996). Relationships between anchovy (*Engraulis encrasicolus*) recruitment and the environment in the Bay of Biscay. *Scientia Marina.* **60**: 179-192.

Bosley, K., Lavelle, J., Brodeur, R., Wakefield, W., Emmett, R., Baker, E. and Rehmke, K. (2004). Biological and physical processes in and around Astoria submarine canyon, Oregon, USA. *Journal of Marine Systems.* **50**: 21-37.

Breaker, L. C. and Broenkow, W. W. (1994). The circulation of Monterey bay and related processes. *In: Oceanography and Marine Biology: An Annual Review.* **32**: 1-64.

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.

Brotons, L., Thuiller, W., Arau´jo, M. B. and Hirzel, A. H. (2004). Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography.* **27**: 437-448.

Brown, C. W. and Winn, H. E. (1989). Relationship between the distribution of right whales, *Eubalaena glacialis*, and satellite-derived sea surface thermal structure in the Great South Channel. *Continental Shelf Research.* **9**: 247-260.

Brownell, R., Yamada, T., Mead, J. G. and Helden, A. L. (2004). Mass stranding of Cuvier's beaked whales in Japan: U.S. Naval acoustic link? *Journal of Cetacean Research and Management.* **7**: 1-10.

Buckland, S. T., Bloch, D., Cattanach, K. L., Gunnlaugsson, T., Hoydal, 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. *Reports of the International Whaling Commission (special issue 14)*. 33-49.

Cañadas, A., Sagarminaga, R. and Garcia-Tiscar, S. (2002). Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep-Sea research*. **49**: 2053-2073.

Caretta, J. V., Taylor, B. L. and Chivers, S. J. (2001). Abundance and depth distribution of Harbour porpoise (*Phocoena phocoena*) in northern California determined from a 1995 ship survey. *Fishery Bulletin*. **99**: 29-39.

Carwardine, M. (1995). Whales, dolphins and porpoises: the visual guide to all the world's cetaceans. Dorling Kindersley.

Casas, B., Varela, M., Canle, M., Gonzalez, N. and Bode, A. (1997). Seasonal variations of nutrients, seston and phytoplankton, and upwelling intensity off La Coruna (NW Spain). *Estuarine, Coastal and Shelf Science*. **44**: 767-778.

Charles, A. and Wilson, L. (2009). Human dimensions of Marine Protected Areas. *ICES Journal of Marine Science*. **66**: 6-15.

Cirac, P., Bourillet, J.-F., Griboulard, R., Normand, A. and Mulder, T. (2001). Le canyon de Capbreton: nouvelles approaches morphostructurales et morphosedimentaires. Premiers resultats de la campagne ITSAS. (canyon of capbreton: new morphostructural and morphosedimentary approaches. first results of the ITSAS cruise). *Earth and Planetary Sciences*. **332**: 447-455.

Clarke, M. R. (1996a). Cephalopods as prey. III. Cetaceans. *Philosophical Transcripts of the Royal Society London*. **351**: 1053-1065.

Clarke, M. R. (1996b). The role of cephalopods in the world's oceans: an introduction. *Philosophical Transcripts of the Royal Society London*. **351**: 979-983.

Collins, M. A., Yau, C., Allcock, L. and Thurston, M. H. (2001). Distribution of deep-water benthic and bentho-pelagic cephalopods from the north-east Atlantic. *Journal of the Marine Biological Association, UK*. **81**: 105-117.

Compton, R. C. (2004). Predicting key habitat and potential distribution of Northern bottlenose whales (*Hyperoodon ampullatus*) in northwest Atlantic ocean. Faculty of Science. Plymouth, University of Plymouth**.**

Cox, T. M., Ragen, T. J., Read, A. J., Baird, R. W., Balcomb, K., Barlow, J., Caldwell, J., Cranford, T., Crum, L., D'Amico, A., D'Spain, G., Fernandez, A., Finneran, J., Gentry, R., Gerth, R., Gulland, F., Hildebrand, J., Houser, D., Hullar, T., Jepson, P. D., Ketten, D., MacLeod, C. D., Miller, P., Moore, S., Mountain, D. C., Palka, D., Ponganis, P., Rommel, S., Rowles, T., Taylor, B., Tyack, P., Wartzok, D., Gisiner, R., Mead, J. and Benner, L. (2006). Understanding the impacts of anthropogenic sound on beaked whales. *Journal of Cetacean Research and Management*. **7**: 177-187.

Cremer, M., Bourillet, J.-F., Cirac, P., Gaudin, M., Gauthier, E., Mulder, T. and Schneider, J.-L. (2003). Morphology and sediment dynamics of the CapBreton canyon (Bay of Biscay, sw France). *Ocean Margin Research Conference, Paris, Abstract 179.*

Croll, D. A., Tershy, B. R., Hewitt, R. P., Demer, D. A., Fiedler, P. C., Smith, S. E., Armstrong, W., Popp, J. M., Kiekhefer, T., Lopez, V. R., Urban, J. and Gendron, D. (1998). An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea research II.* **45**: 1353-1371.

D'Amico, A., Bergamasco, A., Zanasca, P., Carniel, S., Nacini, E., Portunato, N., Teloni, V., Mori, C. and Barbanti, R. (2003). Qualitative correlation of marine mammals with physical and biological parameters in the Ligurian sea. *IEEE Journal of Oceanic Engineering.* **28**: 29-43.

Dalebout, M. L., Mead, J. G., Scott Baker, C., Baker, A. N. and van Helden, A. L. (2002). A new species of beaked whale *Mesoplodon perrini* Sp. N. (Cetacea: Ziphiidae) discovered through phylogenetic analyses of mitochondrial DNA sequences. *Marine Mammal Science.* **18**: 577-608.

Davis, R. W., Fargion, G. S., May, N., Leming, T. D., Baumgartner, M., Evans, E. W., 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 Wursig, B. (2002). Cetacean habitat in the northern oceanic Gulf of Mexico *Deep-Sea Research I.* **49**: 121-142.

Dettki, H., Löfstrand, R. and Edenius, L. (2003). Modeling habitat suitability for moose in coastal northern Sweden: empirical vs process-oriented approaches. *Ambio.* **32**: 549-556.

Engler, R., Guisan, A. and Rechsteiner, L. (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology.* **41**: 263-274.

Evans, W. E. (1971). Orientation behavior of delphinids: radio telemetric studies. *Annals New York Academy of Sciences.* **188**: 142-160.

Evans, W. E. (1974). Radio-telemetric studies of two species of small odontocete cetaceans. Harvard University Press, Cambridge , MA

Evans, P. G. H. (1980). Cetaceans in British Waters. *Mammal Review.* **10**: 1-46.

Evans, P. G. H. (1982). Associations between seabirds and cetaceans: a review. *Mammal Review.* **12**: 187-206.

Evans, P. G. H. (1987). The Natural History of Whales and Dolphins. Christopher Helm Ltd.

Evans, P. G. H. (1990). European cetaceans and seabirds in oceanographic context. *Lutra.* **33**: 95-125.

Evans, P. G. H., Anderwald, P. and Baines, M. E. (2003). UK Cetacean Status Review. Report to English Nature and the Countryside Council for Wales. Sea Watch Foundation, Oxford**:** 160pp.

Evans, P. G. H. and Hammond, P. S. (2004). Monitoring Cetaceans In Europe. *Mammal Review.* **1**: 131-156.

Evans, P. G. H. and Miller, L. A. (eds). (2004). Active sonar and cetaceans. Proceedings of ECS workshop, Las Palmas, Gran Canaria.

Evans, P. G. H., Smeenk, C. S. and van Waerebeek, K. (2008). Genus Ziphius. Mammals of the British Isles: Handbook, 4th edition. S. Harris and D. W. Yalden. The Mammal Society. 690-692.

Falcone, E. A., Schorr, G. S., Douglas, A. B., Calambokidis, J., Henderson, E., McKenna, M. F., Hildebrand, J. and Moretti, D. (2009). Sighting characteristics and photo-identification of Cuvier's beaked whales (Ziphius cavirostris) near San Clemente Island, California: a key area for beaked whales and the military? *Marine Biology.* **156**: 2631-2640.

Ferguson, M. (2005). Cetacean population density in the eastern Pacific ocean: analyzing patterns with predictive spatial models. PhD Thesis, University of California, San Diego.

Ferguson, M. C., Barlow, J., Reilly, S. B. and Gerrodette, T. (2006). Predicting Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whale population density from habitat characteristics in the eastern tropical Pacific ocean. *Journal of Cetacean Research and Management.* **7**: 287-299.

Fernández, E. and Bode, A. (1991). Seasonal patterns of primary production in the central Cantabrian sea (Bay of Biscay). *Scientia Marina.* **55**: 629-636.

Fernández, A., Edwards, J. F., Rodriguez, F., de los Monteros, A. E., Herraez, P., Castro, P., Jaber, J. R., Martin, V. and Arbelo, M. (2005). "Gas and fat embolic syndrome" involving a mass stranding of beaked whales (Family Ziphiidae) exposed to anthropogenic sonar signals. *Veterinary Pathology.* **42**: 446-457.

Fielding, A. H. and Bell, J., F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation.* **24**: 38-49.
Flaherty, T. (1999). Spare a Thought for squid sucking denizens. *Australian Marine Conservation Society Bulletin.* **20**: 9-10.

Forney, K. A. (2000). Environmental models of cetacean abundance: reducing uncertainty in population trends. *Conservation Biology.* **14**: 1271-1286.

Frantzis, A. (1998). Does acoustic testing strand whales? *Nature.* **392**: 29-29.

Frantzis, A. (2004). The first mass stranding that was associated with the use of active sonar (Kyparissiakos Gulf, Greece, 1996). Pp. 14-20 in: Evans, P.G.H and Miller, L.A. (eds). 2004. *Proceedings of the Workshop on Active Sonar and Cetaceans. Las Palmas, Gran Canaria, 8th March 2003, European Cetacean Society Newsletter, No 42. Special Issue.*

Frantzis, A., Alexiadou, P., Paximadis, G., Politi, E., Gannier, A. and Corsini-Foka, M. (2003). Current knowledge of the cetacean fauna of the Greek seas. *Journal of Cetacean Research and Management.* **5**: 219-232.

Frantzis, A., Goold, J. C., Skarsoulis, E. K., Taroudakis, M. I. and Kandia, V. (2002). Clicks from Cuvier's beaked whales, *Ziphius cavirostris* (L). *Journal of the Acoustical Society of America.* **112**: 34-37.

Freeland, H. J. and Denman, K. L. (1982). A topographically controlled upwelling centre off southern Vancouver Island. *Journal of Marine Research.* **40**: 1069-1093.

Freitas, L. (2004). The stranding of three Cuvier's beaked whales *Ziphius cavirostris* in Madeira Archipelago. Pp 28-32 in: Evans, P.G.H. and Miller, L.A. (eds). 2004. *Proceedings of the Workshop on Active Sonar and Cetaceans. Las Palmas, Gran Canaria, 8th March 2003, European Cetacean Society Newsletter, No 42, Special Issue.*

Friedlaender, A. S., Halpin, P. N., Qian, S. S., Lawson, G. L., Wiebe, P. H., Thiele, D. and Read, A. J. (2006). Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the western Antarctic peninsula. *Marine Ecology Progress Series.* **317**: 297-310.

Gannon, D. P., Read, A. J., Craddock, J. E., Fristrup, K. M. and Nicolas, J. R. (1997). Feeding ecology of Long-finned Pilot whales *Globicephala melas* in the western north Atlantic. *Marine Ecology Progress Series.* **148**: 1-10.

Garcia-Soto, C., Pingree, R. D. and Valdes, L. (2002). Navidad development in the southern Bay of Biscay: climate change and swoddy structure from remote sensing and in situ measurements. *Journal of Geophysical Research.* **107**: 10.1029/2001JC001012.

Gardner, W. D. (1989). Baltimore canyon as a modern conduit of sediment to the deep sea. *Deep-Sea Research.* **36**: 323-358.

Gaudin, M., Cirac, P., Trainer, J., Cremer, M., Schneider, J.-L., Bourillet, J.-F., Gonthier, E., Faugeres, J. C., Vittori, J., Crumeyrolle, P. and Griboulard, R. (2003). Morphology and sediment dynamics of the Capbreton canyon (Bay of Biscay, SW France). *Geophysical Research Abstracts.* **5**: 13900.

Gerkema, T., Lam, F.-P. A. and Maas, L. R. M. (2004). Internal tides in the Bay of Biscay: conversion rates and seasonal effects. *Deep-Sea Research II.* **51**: 2995-3008.

Gil, J. (2003a). Changes in the pattern of water masses resulting from a poleward slope current in the Cantabrian Sea (Bay of Biscay). *Estuarine, Coastal and Shelf Science.* **57**: 1139-1149.

Gil, J. and Sanchez, R. (2003b). Aspects concerning the occurrence of summer upwelling along the southern Bay of Biscay during 1993-2003. *ICES Marine Science Symposia.* **219**: 337-339.

Gonzalez-Pola, C., Lavin, A. and Vargas-Yanez, M. (2005). Intense warming and salinity modification of intermediate water masses in the southeastern corner of the Bay of Biscay for the period 1992-2003. *Journal of Geophysical Research.* **110**: C05020.

Gowans, S. and Whitehead, H. (1995). Distribution and habitat partitioning by small Odontocetes in the Gully, a submarine canyon on the Scotian Shelf. *Canadian journal of Zoology*. **73**: 1599-1608.

Hamazaki, T. (2002). Spatio-temporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (From Cape Hatteras, North Carolina, U.S.A. to Nova Scotia, Canada). *Marine Mammal Science*. **18**: 920-939.

Hastie, G. D., Swift, R. J., Slesser, G., Thompson, P. M. and Turrell, W. R. (2005). Environmental models for predicting oceanic dolphin habitat in the northeast Atlantic. *ICES Journal of Marine Sciences*. **62**: 760-770.

Hastie, T. J. and Tibshirani, R. J. (1990). Generalized Additive Models. New York: Chapman and Hall.

Hastie, G. D., Wilson, B., Wilson, L. J., Parsons, K. M. and Thompson, P. M. (2004). Functional mechanisms underlying cetacean distribution patterns: hotspots for Bottlenose dolphins are linked to foraging. *Marine Biology*. **144**: 397-403.

Heyning, J. E. (1989). Cuvier's beaked whale *Ziphius cavirostris* G. Cuvier, 1823. Handbook of Marine Mammals, Vol 4. river dolphins and larger toothed whales. S. H. Ridgway and R. S. e. Harrison. London: Academic Press.

Hickey, B. M. (1986). Suspended particle movement in and around Quinault submarine canyon. *Marine Geology*. **71**: 35-83.

Hickey, B. M. (1995). Coastal submarine canyons. *In, Topographic effects in the Ocean. Proceedings 'Aha Huliko'a. (ed Muller, P and Henderson, D). Hawaii: University of Hawaii, 265pp.* 95-110.

Hirzel, A. H. and Arlettaz, R. (2004). Environmental-envelope based habitat-suitability models. 67-76.

Hirzel, A. H., Hausser, J., Chessel, D. and Perrin, N. (2002a). Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology*. **83**: 2027-2036.

Hirzel, A., Hausser, J. and Perrin, N. (2002b). Biomapper 3.1. Lausanne, lab. for Conservation Biology. *URL: http://www.unil.ch/biomapper.*

Hirzel, A. H., Helfer, V. and Metral, F. (2001). Assessing habitat-suitability models with a virtual species. *Ecological Modelling*. **145**: 111-121.

Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C. and Guisan, A. (2006). Evaluating the ability if habitat suitability models to predict species presence. *Ecological Modelling*. **199**: 142-152.

Hosmer, D. W. L., S. (2000). Applied logistic regression. Wiley.

Hooker, S. K. (2001). Sperm whales and beaked whales. Encyclopedia of Ocean Sciences. J. H. In Steele, Thorpe, S.A and Turekian, K.K (eds). Academic Press. **5:**2865-2872.

Hooker, S. K. and Baird, R. W. (1999a). Deep-diving behaviour of the Northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). *Proceedings: Biological Sciences.* **266**: 671-676.

Hooker, S. K. and Baird, R. W. (1999b). Observations of Sowerby's beaked whales, *Mesoplodon bidens*, in the Gully, Nova Scotia. *The Canadian Field-Naturalist.* **113**: 273-277.

Hooker, S. K. and Baird, R. W. (2001). Diving and ranging behaviour of Odontocetes: a methodological review and critique. *Mammal Review.* **31**: 81-105.

Hooker, S. K., Whitehead, H. and Gowans, S. (1999c). Marine protected area design and spatial and temporal distribution of cetaceans in a submarine canyon. *Conservation Biology.* **13**: 592-602.

Hooker, S. K., Whitehead, H., Gowans, S. and Baird, R. W. (2002). Fluctuations in distribution and patterns of individual range of Northern bottlenose whales. *Marine Ecology Progress Series.* **225**: 287-297.

Houston, J. (1991). Status of Cuvier's beaked whale, *Ziphius cavirostris*, in Canada. *The Canadian Field Naturalist.* **105**: 215-218.

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology.* **22**: 415-427.

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.

Ingram, S. N. and Rogan, E. (2002). Identifying critical areas and habitat preferences of bottlenose dolphins Tursiops truncatus. *Marine Ecological Progress Series.* **244**: 247-255.

Ingram, S. N., Walshe, L., Johnston, D., and Rogan, E. (2007). Habitat partitioning and the influence of benthic topography and oceanography on the distribution of Fin and Minke whales in the Bay of Fundy, Canada. *Journal of the Marine Biological Association of the United Kingdom.* **87**: 149-156.

Jaquet, N. (1996). How Spatial and Temporal Scales Influence Understanding of Sperm Whales Distribution: a Review. *Mammal Review.* **26**: 51-65.

Jaquet, N. and Whitehead, H. (1996). Scale-dependent correlation of Sperm whale distribution with environmental features and productivity in the south Pacific. *Marine Ecology Progress Series.* **135**: 1-9.

Jepson, P. D., Arbelo, M., Deaville, R., Patterson, I. A. P., Castro, P., Baker, J. R., Degollada, E., Ross, H. M., Herraez, P., Pocknell, A. M., Rodriguez, F., Howie, F. E., Espinosa, A., Reid, R. J., Jaber, J. R., Martin, V., Cunningham, A. A. and Fernandez, A. (2003). Gas-bubble lesions in stranded cetaceans. *Nature.* **425**: 575-576.

Jones, P. D., Wigley, T. M. L., Folland, C. K., Parker, D. E., Angell, J. K., Lebedeff, S. and Hansen, J. E. (1988). Evidence for global warming in the last decade. *Nature.* **332:**790

Johnston, D. W., Thorne, L. H. and Read, A. J. (2005). Fin whales *Balaenoptera physalus* and Minke whales *Balaenoptera acutorostrata* exploit a tidally driven island wake ecosystem in the Bay of Fundy. *Marine Ecological Progress Series.* **305**: 287-295.

Kenney, R. D. and Winn, H. E. (1987). Cetacean biomass densities near submarine canyons compared to adjacent shelf/slope areas. *Continental Shelf Research.* **7**: 107-114.

Ketten, D. R. (2005). Beaked whale necropsy findings for strandings in the Bahamas, Puerto Rico, and Madeira, 1999-2002. Woods Hole Oceanographic Institution.

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**: 33-46.

Kiszka, J., Macleod, K., Canneyt, V. and Ridoux, V. (2007). Distribution, relative abundance and bathymetric preferences of toothed cetaceans in the English Channel and Bay of Biscay. *ICES Journal of Marine Science.* 1033-1043.

Koutsikopoulos, C., Beillois, P., Leroy, C. and Taillefer (1998). Temporal trends and spatial structures of the sea surface temperature in the Bay of Biscay. *Oceanologica Acta.* **21**: 335-344.

Koutsikopoulos, C. and Le Cann, B. (1996). Physical processes and hydrological structures related to the Bay of Biscay anchovy. *Scientia Marina.* **60**: 9-19.

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 Ecological Progress Series.* **305**: 275-285.

Lavin, A., Valdes, L., Gil, J. and Moral, M. (1998). Seasonal and inter-annual variability in properties of surface water off Santander; Bay of Biscay, 1991-1995. *Oceanologica Acta.* **21**: 179-190.

Layhaye, 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.

Lick, R. and Piatkowski, U. (1998). Stomach contents of a Northern bottlenose whale (*Hyperoodon ampullatus*) stranded at Hiddensee, Baltic Sea. *Journal of the Marine Biological Association UK.* **78**: 643-650.

Littaye, A., Gannier, A., Laren, S. and Wilson, J. P. F. (2004). The relationship between summer aggregations of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea. . *Remote Sensing of Environmental Data.* **90**: 44-52.

MacArthur, R. H. (1972). Geographic Ecology. New York: Harper & Row.

Mackay, R. S., Lettvin, J. Y., Gruberg, E. R., Rose, R. M., Plotkin, G., Ridgeway, S. H. and Howard, R. (1982). Dolphins and the Bends. *Science.* **216**: 650-651.

MacLeod, C. D. (2005). Niche partitioning, distribution and competition in North Atlantic beaked whales. PhD Thesis, University of Aberdeen, Aberdeen, UK.

MacLeod, C. D., Bannon, S. M., Pierce, G. J., Schweder, C., Learmonth, J. A., Herman, J. S. and Reid, R. J. (2005). Climate change and the cetacean community of north-west Scotland. *Biological Conservation.* **124**: 477-483.

MacLeod, C. D., Brereton, T. and Martin, C. (2009). Changes in the occurrence of common dolphins, striped dolphins and harbour porpoises in the English Channel and Bay of Biscay. *Journal of the Marine Biological Association of the United Kingdom* **89**: 1059-1065.

Macleod, C. D. and D'Amico, A. (2006a). A review of beaked whale behaviour and ecology in relation to assessing and mitigating impacts of anthropogenic noise. *Journal of Cetacean Research and Management.* **7**: 211-221.

MacLeod, C. D., Hauser, N. and Peckham, H. (2004a). Diversity, relative density and structure of the cetacean community in summer months east of Great Abaco, Bahamas. *Journal of the Marine Biological Association, U.K.* **84**: 469-474.

Macleod, C. D. and Mitchell, G. (2006b). Key areas for beaked whales worldwide. *Journal of Cetacean Research and Management.* **7**: 309-322.

MacLeod, C. D., Mandleberg, L., Schweder, C., Bannon, S., M. and Pierce, G. J. (2008). A comparison of approaches for modelling the occurrence of marine animals. *Hydrobiologia.* **612**: 21-32.

Macleod, C. D., Perrin, W. F., Pitman, R. L., Barlow, J., Ballance, L. T., D'Amico, A., Gerrodette, T., Joyce, G., Mullin, K., Palka, D. L. and Waring, G. (2006c). Known and inferred distributions of beaked whale species (Cetacea:Ziphiidae). *Journal of Cetacean Research and Management.* **7**: 271-286.

MacLeod, C. D., Pierce, G. J. and Begona Santos, M. (2004b). Geographic and temporal variations in strandings of beaked whales (Ziphiidae) on the coasts of the UK and the Republic of Ireland from 1800-2002. *Journal of Cetacean Research and Management.* **6**: 79-86.

MacLeod, C. D., Santos, M. B. and Pierce, G. J. (2003). Review of data on diets of beaked whales: evidence of niche separation and geographic segregation. *Journal of the Marine Biological Association UK.* **83**: 651-665.

MacLeod, C. D. and Smith, J.A. (In Prep). Ziphiid strandings and water temperature over a 90 year period: could beaked whales act as a bellwether for the effects of climate change on oceanic ecosystems?

MacLeod, C. D., Weir, C. R., Pierpoint, C. and Harland, E. J. (2007). The habitat preferences of marine mammals west of Scotland (UK). *Journal of the Marine Biological Association, U.K.* . **87**: 157-164.

MacLeod, C. D. and Zuur, A. F. (2005). Habitat utilization by Blainville's beaked whales off Great Abaco, northern Bahamas, in relation to seabed topography. *Marine Biology.* **147**: 1-11.

Macleod, K., Fairbairns, R., Gill, A., Fairbairns, B., Gordon, J., Blair-Myers, C. and Parsons, E. C. M. (2004c). Seasonal distribution of minke whales Balaenoptera acutorostrata in relation to physiography and prey off the Isle of Mull, Scotland. *Marine Ecology Progress Series.* **277**: 263-274.

Mandleberg, L. (2004). A comparison of the predictive abilities of four approaches for modelling the distribution of cetaceans. MRes Thesis, University of Aberdeen, UK.

Martin, V., Servidio, A. and Garcia, S. (2004). Mass strandings of beaked whales in the Canary Islands, 2002. Pp. 33-36 in: Evans, P.G.H and Miller, L.A. (eds). 2004. *Proceedings of the Workshop on Active Sonar and Cetaceans. Las Palmas, Gran Canaria, 8th March 2003, European Cetacean Society Newsletter, No 42. Special Issue*

Mauchline, J. and Gordon, D. M. (1991). Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Marine Ecological Progress Series.* **74**: 169-115.

McSweeney, D. J., Baird, R. W. and MaHaffey, S. D. (2007). Site fidelity, associations, and movements of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales off the Island of Hawaii. *Marine Mammal Science.* **DOI: 10.1111/j.**: 1748-7692.

Mead, J. G. (1975). A Fossil Beaked Whale (Cetacea: Ziphiidae) from the Miocene of Kenya. *Journal of Palaeontology.* **49**: 745-751.

Mead, J. G. (1989). Beaked Whales of the Genus *Mesoplodon*. Handbook of Marine Mammals, Vol 4. river dolphins and larger toothed whales. S. H. Ridgway and R. S. e. Harrison.

Mitchell, E. (1968). Northeast Pacific stranding distribution and seasonality of Cuvier's beaked whale *Ziphius cavirostris. Canadian Journal of Zoology.* **46**: 265-279.

Moulins, A., Rosso, M., Nani, B. and Wurtz, M. (2007). Aspects of the distribution of Cuvier's beaked whale (*Ziphius cavirostris*) in relation to topographic features in the Pelagos Sanctuary (north-western Mediterranean Sea). *Journal of the Marine Biological Association, UK.* **87**:

Nesis, K. N. (1993). Cephalopods of seamounts and submarine ridges. I. Recent advances in fisheries biology. T. Okutami, R. K. O'Dor and T. Kubodera. Tokyo University Press, Tokyo, Japan. 365-373.

New, A. L. (1988). Internal Tidal Mixing in the Bay of Biscay. *Deep-Sea Research.* **35**: 691-709.

Nishiwaki, M. and Oguro, N. (1972). Catch of the Cuvier's beaked Whale off Japan in recent years. *The Scientific Reports of the Whales Research Institute.* **24**: 35-41.

NMFS (2003). Cuvier's beaked whale (*Ziphius cavirostris*): Hawaiian Stock. *http://www.nmfs.noaa.gov/prot_res/PR2/Stock_Assessment_Program/Cetaceans/Cuvier's_Beaked_Whale(Hawaii)/PO00cuviersbeakedwhale_hawaii.pdf.*

Noble, M. and Butman, B. (1989). The structure of subtidal currents within and around Lydonia canyon: evidence for enhanced cross-shelf fluctuations over the mouth of the canyon. *Journal of Geophysical Research.* **94**: 8091-8110.

Ó Cadhla, O., Burt, M. L., Borchers, D. L. and Rogan, E. (2001). Distribution and abundance of cetaceans in western Irish waters and the Rockall Trough. *Abstracts of the Annual European Cetacean Society Conference,* Rome, 2001. Page 11.

Ohizumi, H. and Kishiro, T. (2003). Stomach contents of a Cuvier's beaked whale (*Ziphius cavirostris*) stranded on the central Pacific coast of Japan. *Aquatic Mammals.* **29.1**: 99-103.

Ortega-Huerta, M. A. and Peterson, A. T. (2008). Modelling ecological niches and predicting geographic distributions: a test of six presence-only methods. *Revista Mexicana de Biodiversidad.* **79**: 205-216.

OSPAR (2000). Quality Status Report 2000: Region IV - Bay of Biscay and Iberian Coast. . OSPAR Commission. London.

Parsons, E. C. M., Birks, I., Evans, P. G. H., Gordon, J. C. D., .J.H., S. and Pooley, S. (2000). The possible impacts of military activity on cetaceans in west Scotland *European Research on Cetaceans.* **14**: 185-190.

Payne, P. M., Nicols, J. R., O'Brien, L. and Powers, K. D. (1986). The distribution of the Humpback whale, *Megaptera noveangliae*, on Georges Bank and in the Gulf of Main in relation to densities of the Sand Eel, *Ammodytes americanus. Fishery Bulletin.* **82**: 271-7.

Perenne, N., Lavelle, J. W., Smith, D. C. and Boyer, D. L. (2001). Impulsively started flow in a submarine canyon: comparison of results from laboratory and numerical models. *Journal of Atmospheric and Oceanic Technology.* **18**: 1698-1718.

Piatkowski, U., Pierce, G. J. and Morais da Cunha, M. (2001). Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. *Fisheries Research.* **52**: 5-10.

Pingree, R. D. (1993). Flow of surface waters to the west of the British Isles and in the Bay of Biscay. *Deep-Sea Research II.* **40**: 369-388.

Pingree, R. D. and Le Cann, B. (1990). Structure, strength and seasonality of the slope currents in the Bay of Biscay region. *Journal of the Marine Biological Association U.K.* **70**: 857-885.

Planque, B., Beillois, P., Jegou, A.-M., Lazure, P., Petitgas, P. and Puillat, I. (2003). Large-scale hydroclimatic variability in the Bay of Biscay: the 1990's in the context of interdecadal changes. *ICES Marine Science Symposia.* **219**: 61-70.

Pollard, R. T., Griffiths, M. J., Cunningham, S. A., Read, J. F., Perez, F. F. and Rios, A. F. (1996). Vivaldi 1991 – a study of the formation, circulation and ventilation of Eastern North Atlantic Central Water. *Progress in Oceanography.* **37**: 167-192.

Pollock, C. M. (2000). The distribution of seabirds and marine mammals in the Atlantic Frontier, north and west of Scotland. *Joint Nature Conservation Committee, Aberdeen.*

Praca, E. and Gannier, A. (2007). Ecological niche of three Teuthophageous Odontocetes in the northwest Mediterranean Sea. *Ocean Science Discussion.* **4**: 785-815.

Redfern, J. V., Ferguson, M. C., Becker, E. A., Hyrenbach, K. D., Good, C., Barlow, J., Kaschner, K., Baumgartner, M. F., Forney, K. A., Ballance, L. T., Fauchald, P., Halpin, P., Hamazaki, T., Pershing, A. J., Qian, S. S., Read, A., Reilly, S. B., Torres, L. and Werner, F. (2006). Techniques for cetacean-habitat modelling. *Marine Ecology Progress Series.* **310**: 271-295.

Reeves, R. R., Stewart, B. S., Clapham, P. J. and Powell, J. A. (2002). Sea mammals of the world: a complete guide to whales, dolphins, seals, sea lions and sea cows. London : A & C Black.

Reeves, R.R., B.D. Smith, E.A.Crespo, & G. Notarbartolo di Sciara, eds. (2003). Dolphins, Whales and Porpoises: 2002-2010 Conservation Action Plan for the World's Cetaceans. Switzerland and Cambridge: IUCN/SSC Cetacean Specialist Group. IUCN, Gland.

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.*

Report, J. I. B. (2001). Bahamas marine mammal stranding event of 14-16 March 2000. www.nmfs.noaa.gov/prot_res/overview/Interim_Bahamas_Report.pdf.

Reutter, R. E. and Schluter, D. (2003). Modelling habitat-suitability using museum collections: an example with three sympatris *Apodemus* species from the Alps. *Journal of Biogeography.* **30**: 581-590.

Rice, D. W. (1998). Marine mammals of the world: systematics and distribution. Lawrence: Society of Marine Mammalogy Special Publication, Allen Press.

Robertson, M. P., Caitness, N. and Villet, M. H. (2001). A PCA-based modelling technique for predicting environmental suitability for organisms from presence records. *Diversity and Distributions.* **7**: 15-27.

Rosen, M. J., Evans, P. G. H., Boran, J. R. and Thomas, C. (2000). Cetacean studies in the Celtic Sea, English Channel, and SW North Sea: using training surveys for data collection. *European Research on Cetaceans.* **13**: 383-386.

Santos, M. B., Pierce, G. J., Herman, J., Lopez, A., Guerra, A., Mente, E. and Clarke, M. R. (2001a). Feeding ecology of Cuvier's beaked whale (*Ziphius cavirostris*): a review with new information on the diet of this species. *Journal of the Marine Biological Association UK.* **81**: 687-694.

Santos, M. B., Pierce, G. J., Smeenk, C., Addink, M. J., Kinze, C. C., Tougaard, S. and Herman, J. (2001b). Stomach contents of Northern bottlenose whales *Hyperoodon ampullatus* stranded in the North Sea. *Journal of the Marine Biological Association UK.* **81**: 143-150.b

Schweder, C. (2003). The use of principal component analysis (PCA)-based modelling for constructing predictive models of occurrence for large mobile marine mammals. MSc. Thesis. University of Aberdeen, UK.

Selzer, L. A. and Payne, P. M. (1988). The distribution of White-Sided (*Lagenorhynchus acutus*) and Common dolphin (*Delphinus delphis*) vs. environmental features of the continental shelf of the northeastern United States *Marine Mammal Science.* **4**: 141-438.

Shepard, F. P., Marshall, N. F. and McLoughlin, P. A. (1974). Currents in submarine canyons. *Deep-Sea Research.* **21**: 691-706.

Simmonds, M. P. and Lopez-Jurado, L. F. (1991). Whales and the military. *Nature.* **351**: 448.

Spitz, J., Richard, E., Meynier, L., Pusineri, C. and Ridoux, V. (2006). Dietary plasticity of the oceanic striped dolphin, Stenella coeruleoalba, in the neritic waters of the Bay of Biscay. *Journal of Sea Research.* **55** 309-320.

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.

Tenore, K. R., Alonso-Noval, M., Alvarez-Ossorio, M., Atkinson, L. P., Cabanas, J. M., Cal, R. M., Campos, H. J., Castillejo, F., Chesney, E. J., Gonzalez, N., Hanson, R. B., McClain, C. R., Miranda, A., Roman, M. R., Sanchez, J., Santiago, G., Valdes, L., Varela, M. and Yoder, J. (1995). Fisheries and oceanography off Galicia, NW Spain: mesoscale spatial and temporal changes in physical processes and resultant patterns of biological productivity. *Journal of Geophysical Research.* **100**: 10,943-10,966.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgely, G. E., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L. and Williams, S. E. (2004). Extinction risk from climate change. *Nature.* **427**: 145-148.

Torres, L. G., Read, A. J. and Halpin, P. (2008). Fine-scale habitat modeling of a top marine predator: do prey data improve predictive capacity? *Ecological Applications.* **18**: 1702-1717.

Tyack, P. L., Johnson, M., Aguilar De Soto, N., Sturlese, A. and Madsen, P. T. (2006). Extreme diving of beaked whales. *The Journal of Experimental Biology.* **209**: 4238-4253.

Tynan, C. T., Ainley, D. G., Barth, J. A., Cowles, T. J., Pierce, S. D. and Spear, L. B. (2005). Cetacean distribution relative to ocean processes in the northern California current system. *Deep-Sea research II.* **52**: 145-167.

Valencia, V., Borja, A., Fontan, A., Perez, F. F. and Rios, A. F. (2003). Temperature and salinity fluctuations along the Basque Coast (southern Bay of Biscay), from 1986-2000, related to climatic factors. *ICES Marine Science Symposia.* **219**: 340-342.

Valencia, V., Franco, J., Borja, A. and Fontan, A. (2004). Hydrography of the southeastern Bay of Biscay. In Oceanography and the marine environment of the Basque Country. A. Borja and M. e. Collins. Elsevier B.V. 159-194.

Vetter, E. W. and Dayton, P. K. (1998). Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. *Deep-Sea research II.* **45**: 25-54.

Wang, J. Y., Chou, L. S., Yao, C. J., Neimanis, A. S. and Chou, W. H. (1995). Records of Cuvier's beaked whales (*Ziphius cavirostris*) from Taiwan, Republic of China. *Asian Marine Biology*. **12**: 111-118.

Waring, G. T., Gerrior, P., Payne, P. M., Parry, B. L. and Nicolas, J. R. (1990). Incidental take of marine mammals in foreign fishery activities off the northeast United States, 1977-1988. *Fishery Bulletin, U.S.* **88**: 347-360.

Waring, G. T., Hamazaki, T., Sheehan, D., Wood, G. and Baker, S. (2001). Characterization of beaked whale (Ziphiidae) and Sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast U.S. *Marine Mammal Science*. **17**: 703-717.

Watson, L. (1981). Sea guide to whales of the world. London: Hutchinson

Weir, C. R., Stokes, J., Martin, C. and Cermeno, P. (2004). Three sightings of *Mesoplodon* species in the Bay of Biscay: first confirmed True's beaked whale (*M. mirus*) for the north-east Atlantic? *Journal of the Marine Biological Association, UK*. **84**: 1095-1099.

Whitehead, H., Faucher, A., Gowans, S. and McCarrey, S. (1997). Status of the Northern bottlenose whale, *Hyperoodon ampullatus*, in the Gully, Nova Scotia. *The Canadian Field-Naturalist*. **111**: 287-292.

Williams, A. D., Brereton, T. and Williams, R. (1999). Seasonal variation and topographical preferences of beaked whales in the southern Bay of Biscay. , Abstracts of the 13th Biennial Conference of the Society of Marine Mammalogy, Maui, 29th November - 4th December 1999.

Williams, A. D., Rogers, A., Begona Santos, M. and Brereton, T. (2002a). Association between beaked whales and deep sea canyons. *In: Challenger Society for Marine Science (ed) Challenger Center Conference: Marine Science 2002, Plymouth*. **Book of Abstracts**:

Williams, A. D., Williams, R. and Brereton, T. (2002b). 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, UK*. **82**: 509-511.

Wilson, B., Thompson, P. M. and Hammond, P. S. (1997). Habitat use by Bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology*. **34**: 1365-1374.

Woodley, T. H. and Gaskin, D. E. (1996). Environmental characteristics of north Atlantic Right and Fin whale habitat in the lower Bay of Fundy. *Canadian journal of Zoology*. **74**: 75-84.

Yen, P. P. W., Sydeman, W. J. and Hyrenbach, K. D. (2004). Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *Journal of Marine Systems*. **50**: 79-99.

Zaniewski, A. E., Lehmann, A. and Overton, J. M. (2002). Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling*. **157**: 261-280.

Zuur, A. F., Ieno, E. N. and Smith, G. M. (2009). Analyzing Ecological Data. Springer.

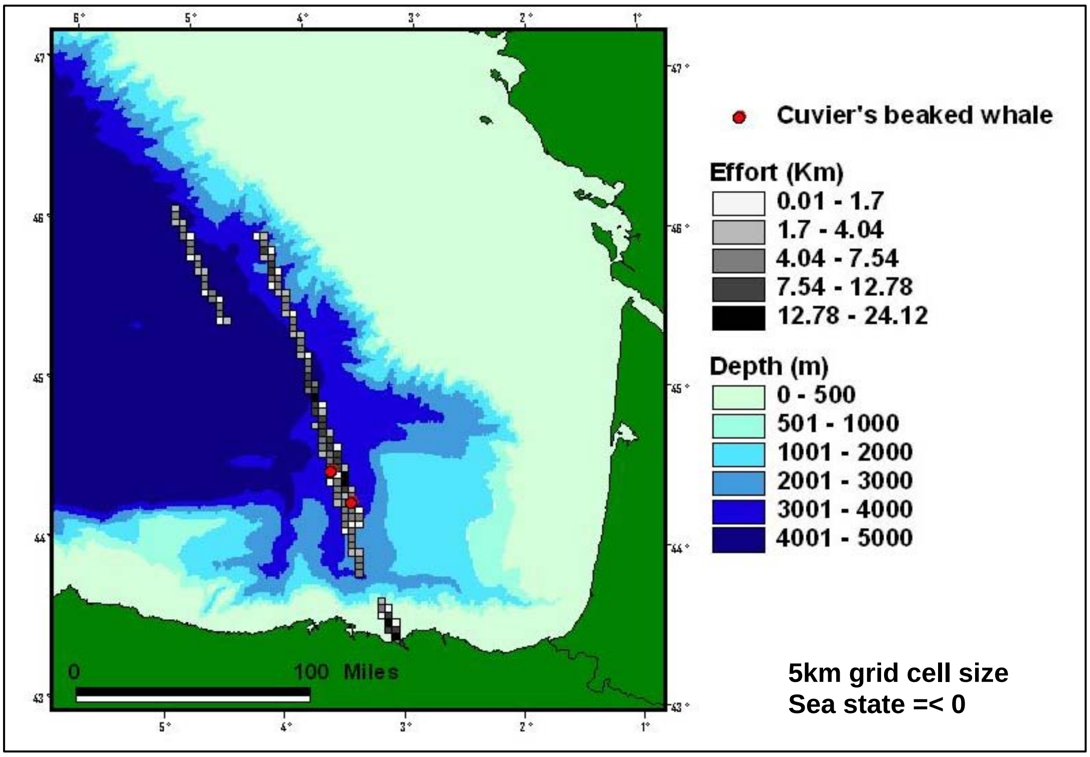
Zweig, M. H. and Campbell, G. (1993). Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clinical Chemistry*. **39**: 561-577.

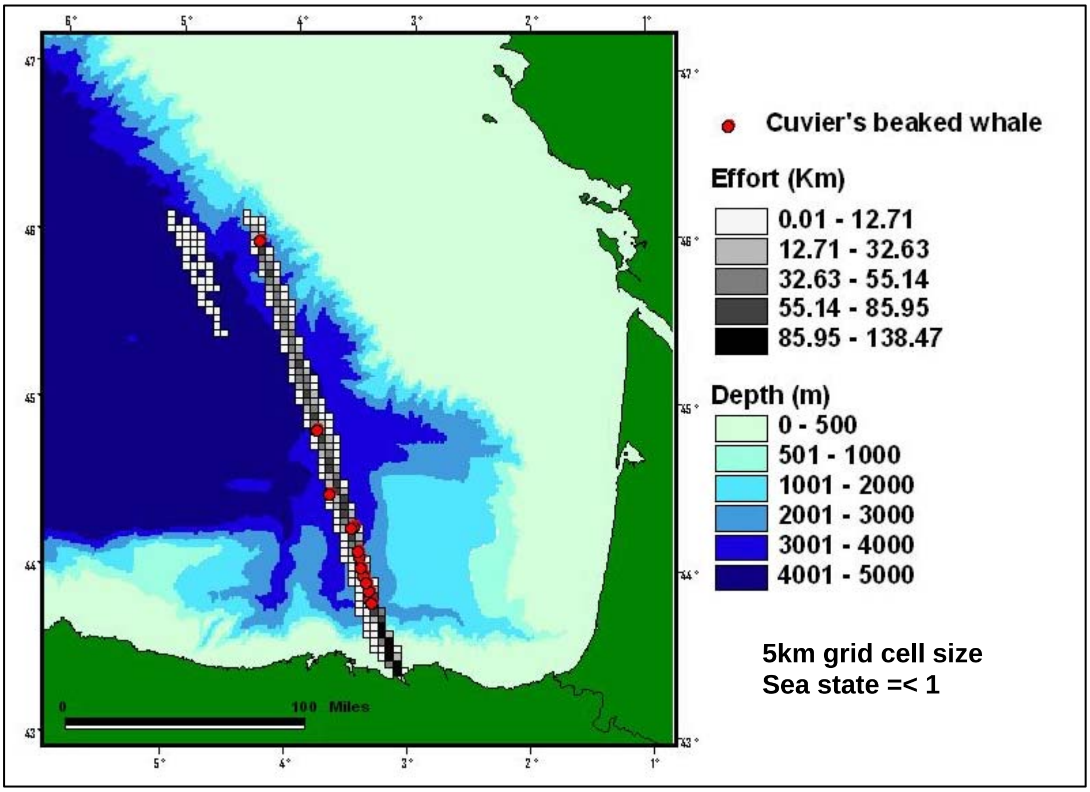
Websites used:
http://oceancolur.gsfc.nasa.gov/ftpsite
www.noc.soton.ac.uk
www.iwdg.ie

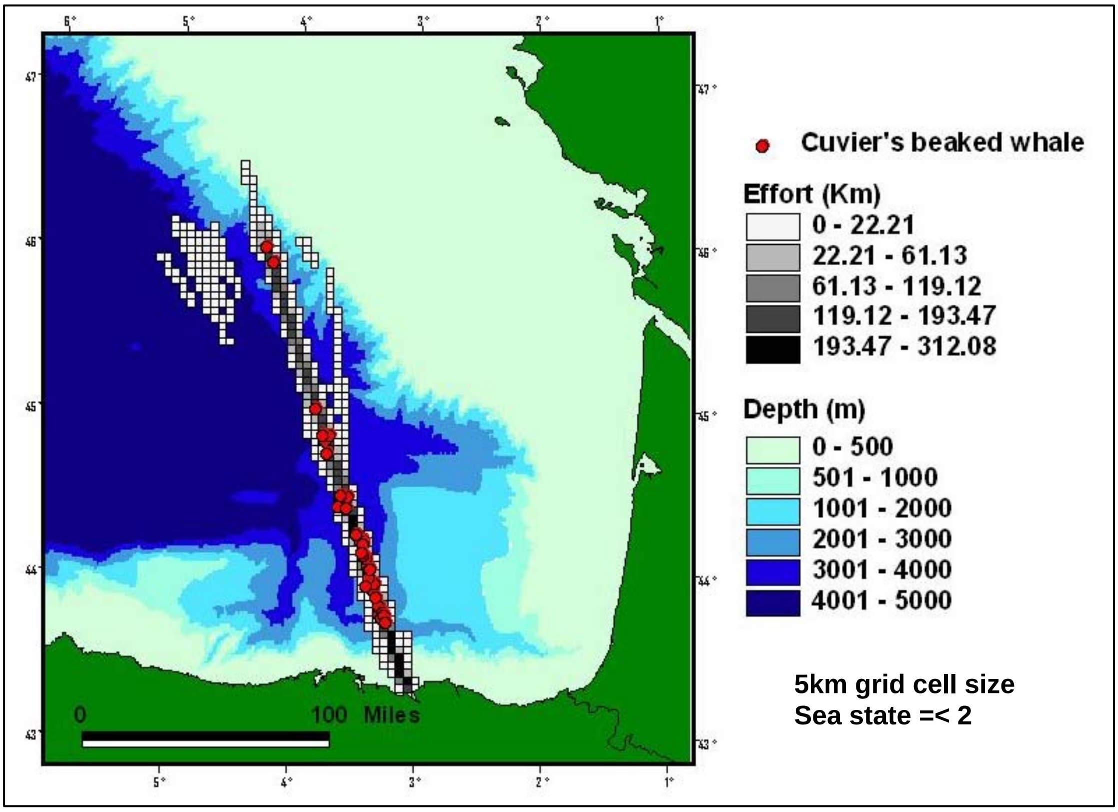
Appendix 1

Below are a series of maps showing the survey effort (km) for each grid cell size (5km, 10km, 15km, 20km, 25km) for sea states 0, 1 and 2.

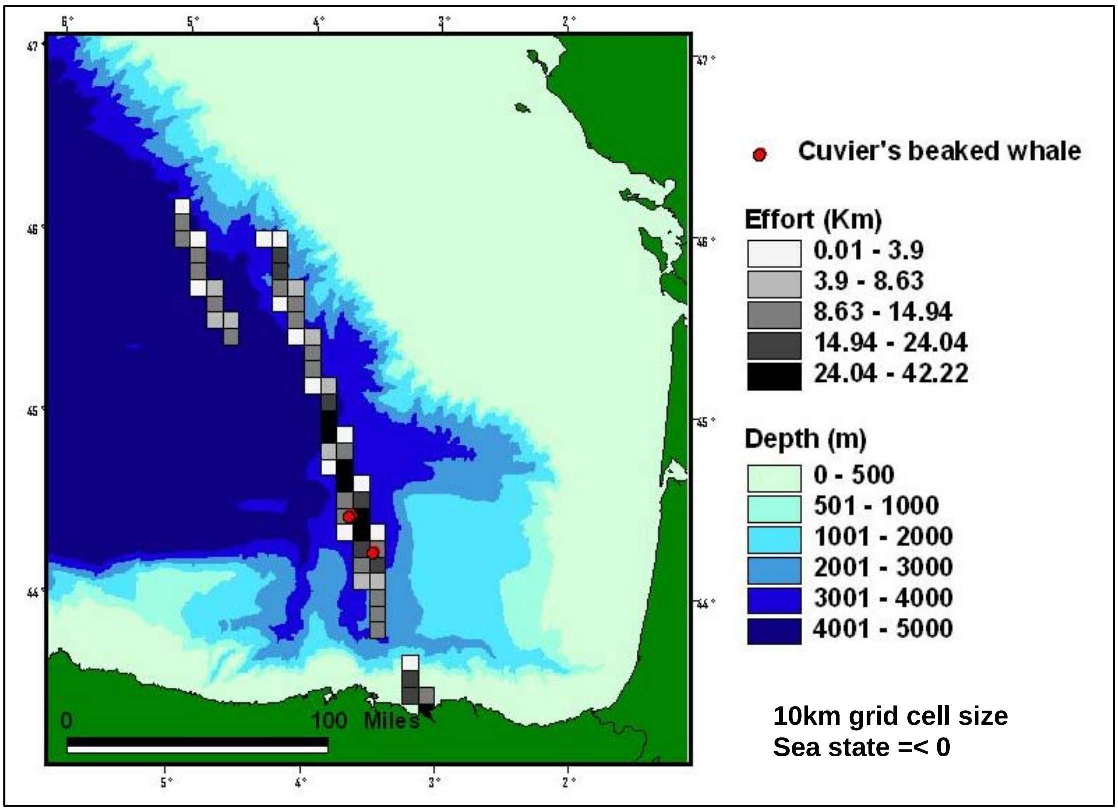
Grid cell size 5km:

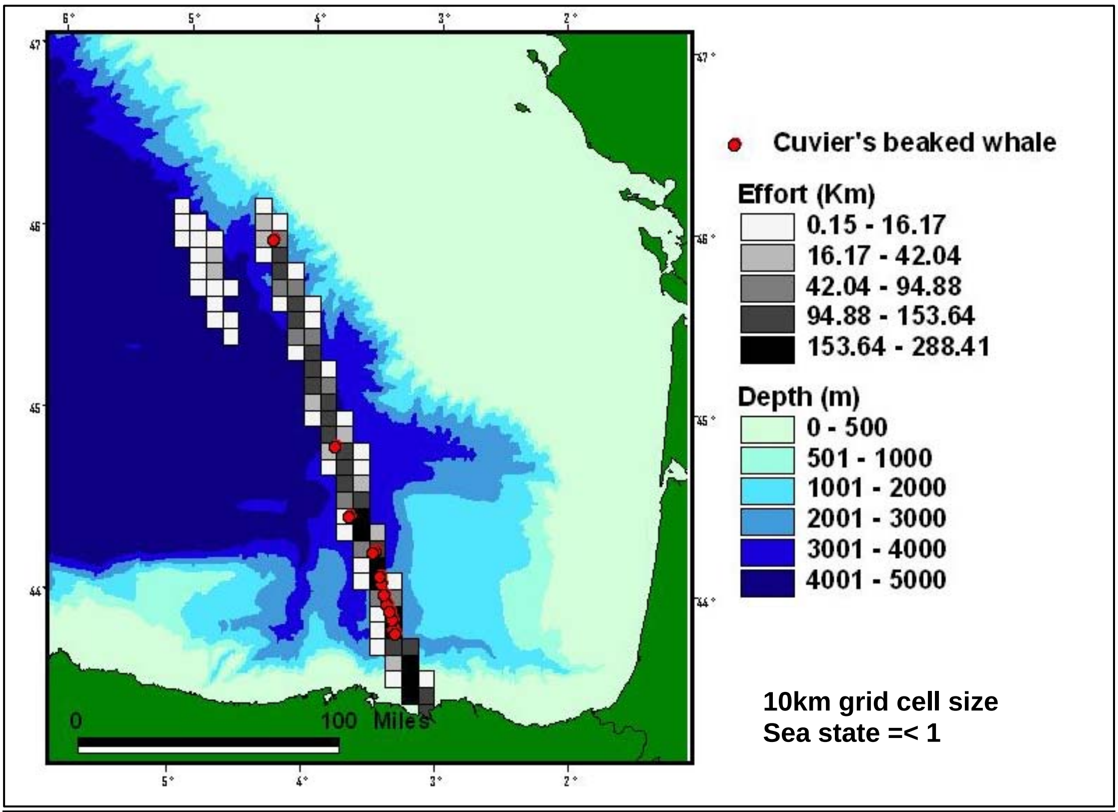


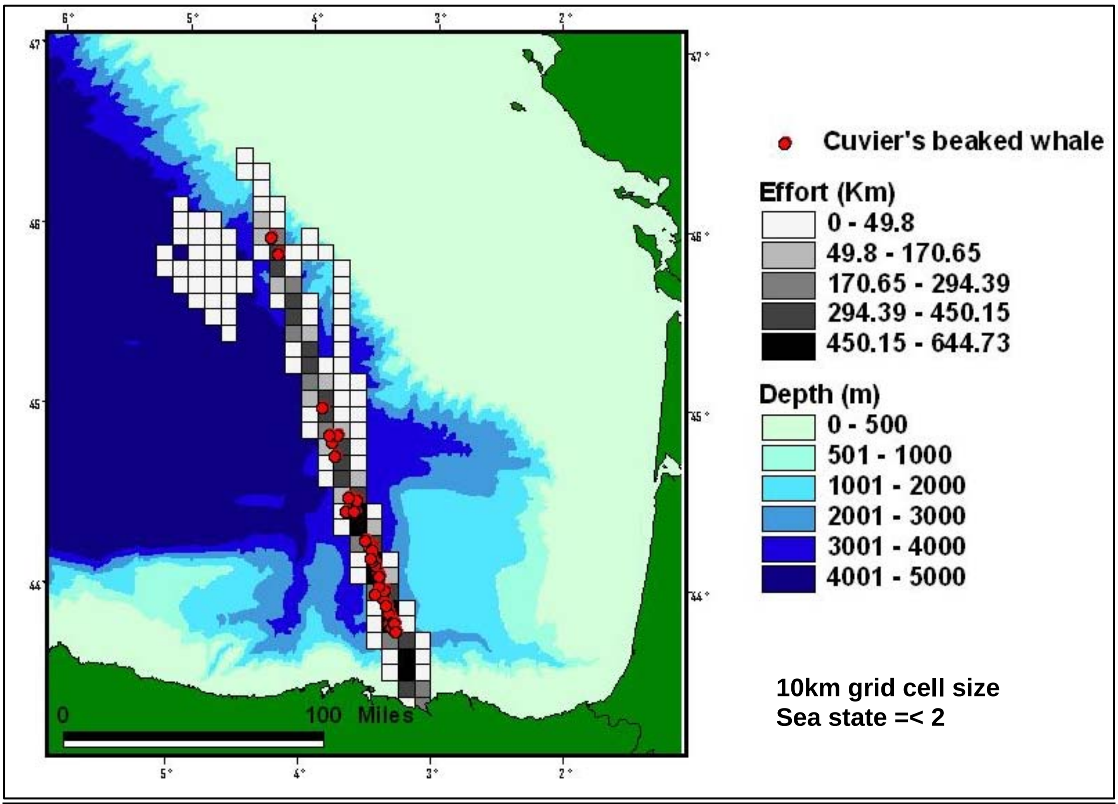




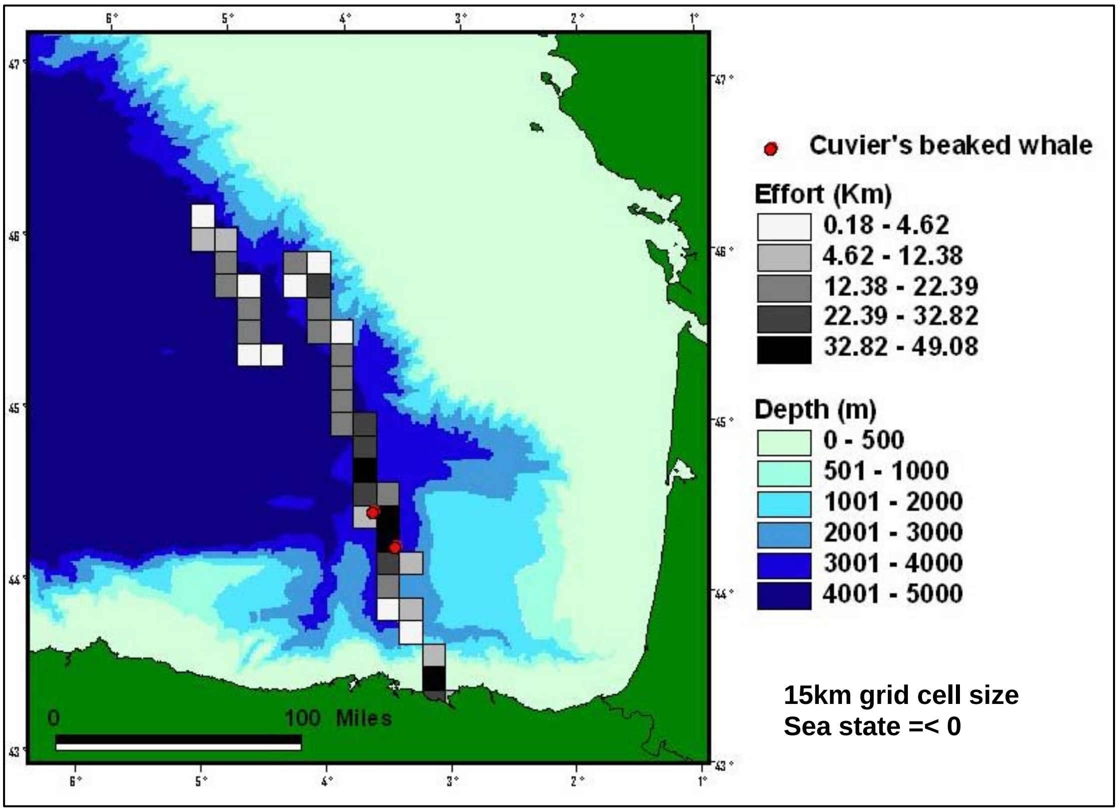
Grid cell size 10km:

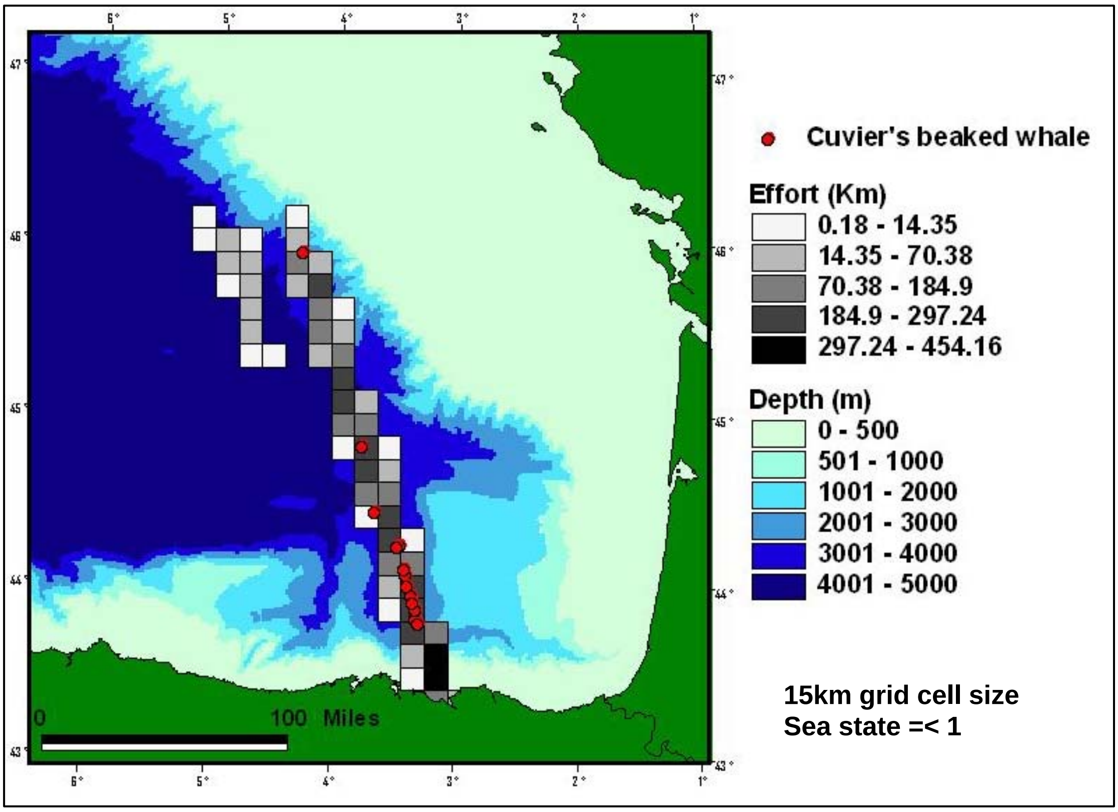


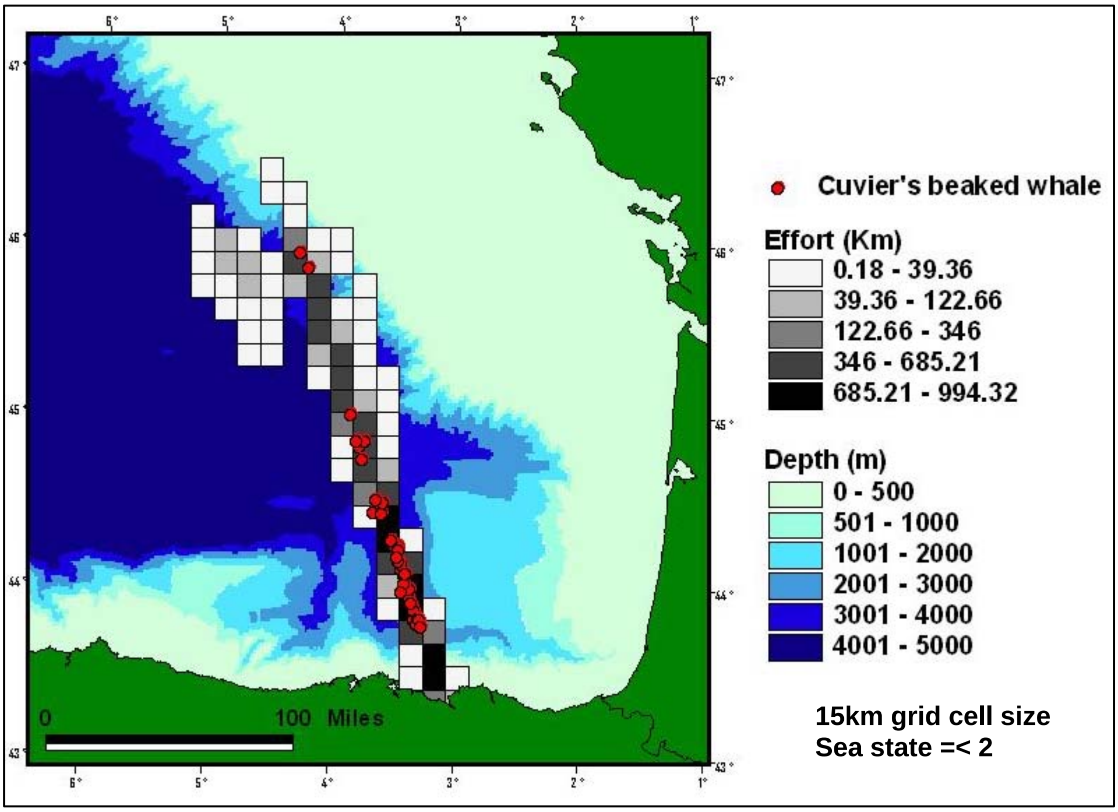

Cuvier's beaked whale
Effort (Km)
0.15 - 16.17
16.17 - 42.04
42.04 - 94.88
94.88 - 153.64
153.64 - 288.41
Depth (m)
0 - 500
501 - 1000
1001 - 2000
2001 - 3000
3001 - 4000
4001 - 5000
0
100 Miles
10km grid cell size
Sea state =< 1


Cuvier's beaked whale
Effort (Km)
0 - 49.8
49.8 - 170.65
170.65 - 294.39
294.39 - 450.15
450.15 - 644.73
Depth (m)
0 - 500
501 - 1000
1001 - 2000
2001 - 3000
3001 - 4000
4001 - 5000
0
100 Miles
10km grid cell size
Sea state =< 2

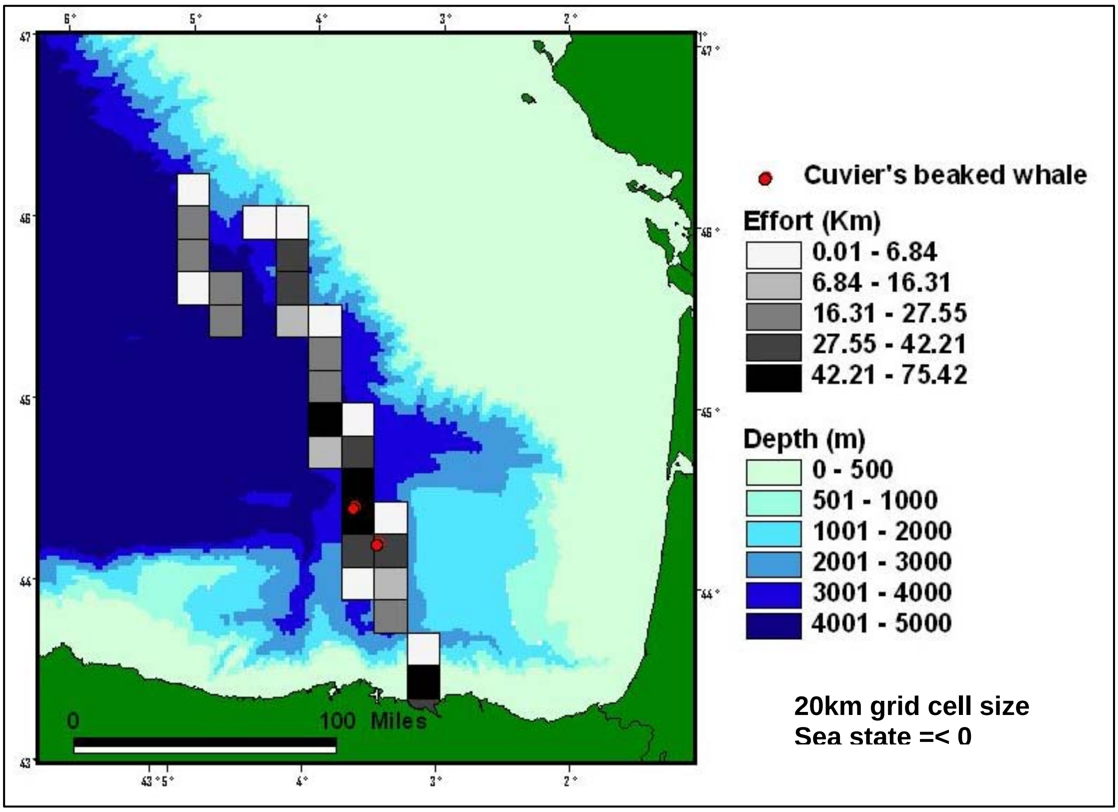
Grid cell size 15km:

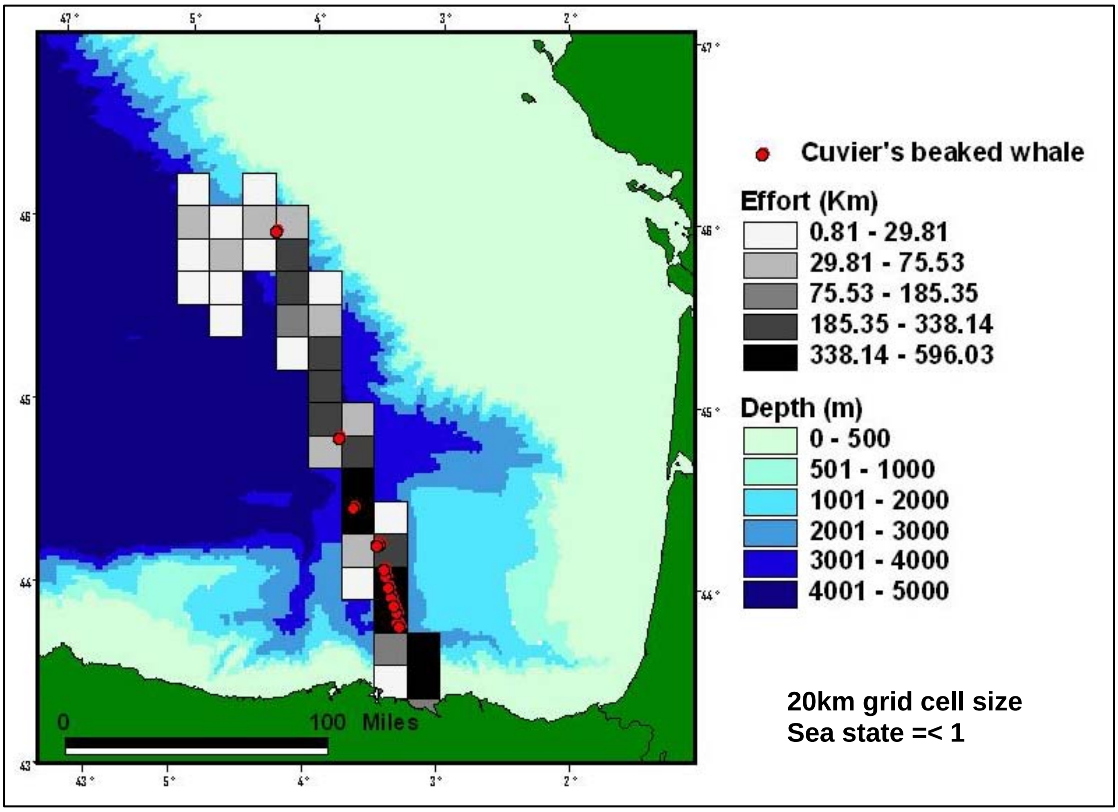


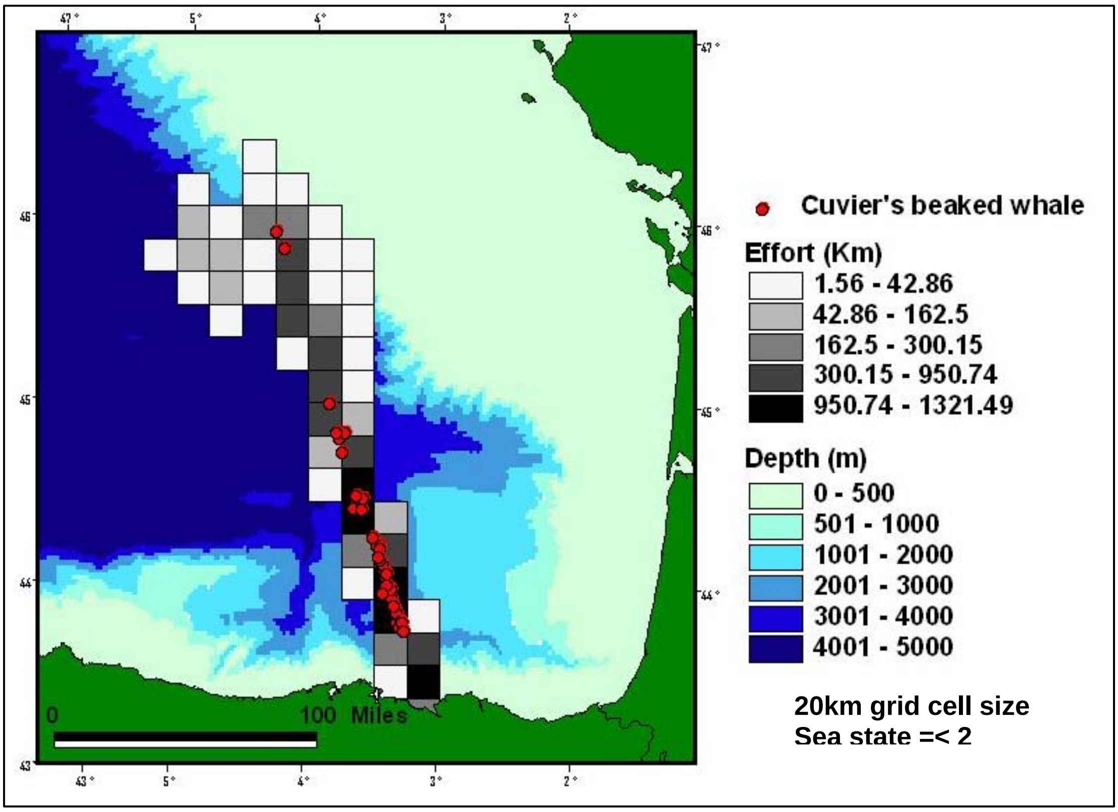




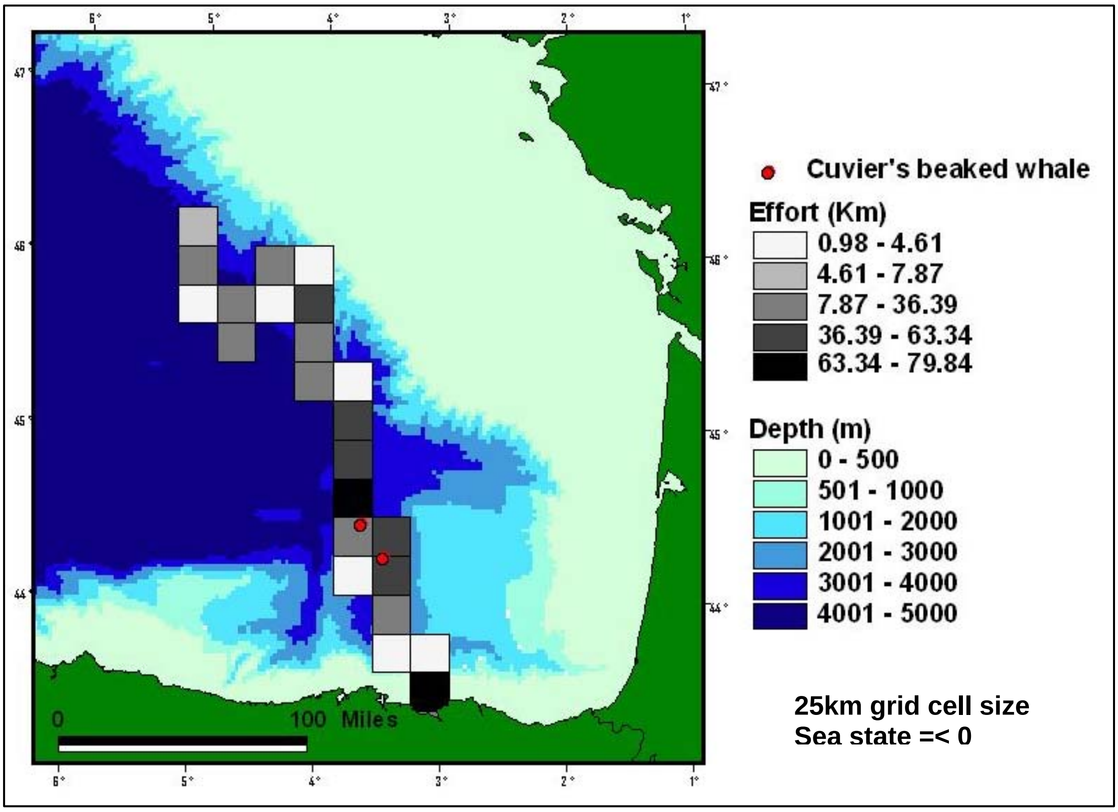
Grid cell size 20km:

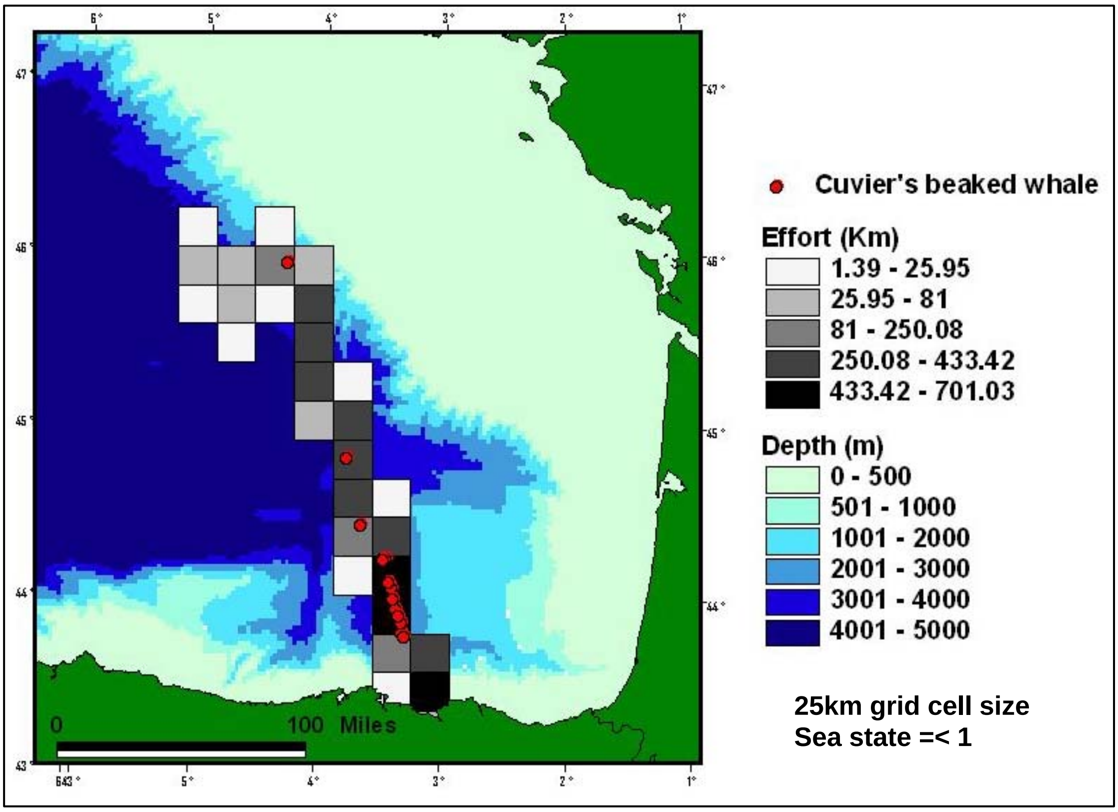


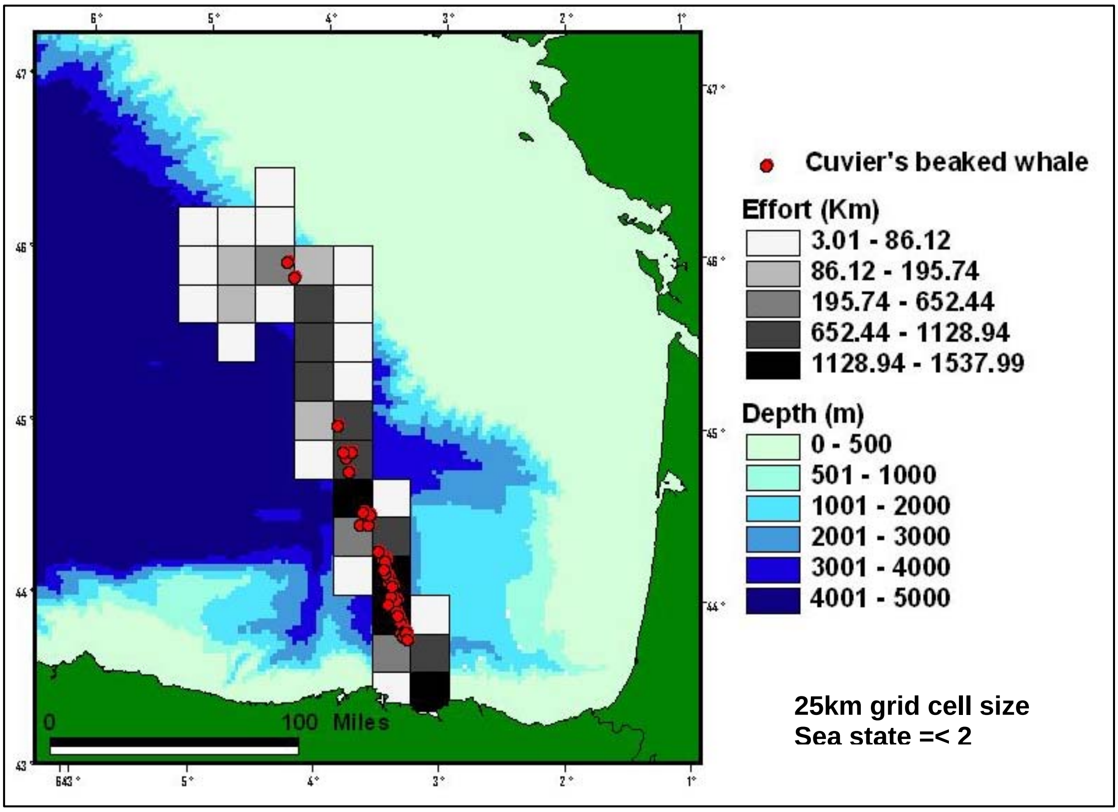

Cuvier's beaked whale
Effort (Km)
0.81 - 29.81
29.81 - 75.53
75.53 - 185.35
185.35 - 338.14
338.14 - 596.03
Depth (m)
0 - 500
501 - 1000
1001 - 2000
2001 - 3000
3001 - 4000
4001 - 5000
0
100 Miles
20km grid cell size
Sea state =< 1


Cuvier's beaked whale
Effort (Km)
1.56 - 42.86
42.86 - 162.5
162.5 - 300.15
300.15 - 950.74
950.74 - 1321.49
Depth (m)
0 - 500
501 - 1000
1001 - 2000
2001 - 3000
3001 - 4000
4001 - 5000
0
100 Miles
20km grid cell size
Sea state =< 2

Grid cell size 25km:







Cuvier's beaked whale
Effort (Km)
3.01 - 86.12
86.12 - 195.74
195.74 - 652.44
652.44 - 1128.94
1128.94 - 1537.99
Depth (m)
0 - 500
501 - 1000
1001 - 2000
2001 - 3000
3001 - 4000
4001 - 5000
25km grid cell size
Sea state =< 2
0
100 Miles

Appendix 2

AIC forwards-backwards (Raw data)

5km AIC outputs

1. All variables
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_depth, k = 4) + s(R_Depth, k = 4) + s(Ave_Slope,
    k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos,
    k = 4) + s(R_Cos, k = 4) + s(SST, k = 4)

```
Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.3844     0.2173   -6.37 1.89e-10 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
               edf Est.rank Chi.sq p-value
s(Ave_depth) 2.310        3 11.735 0.00835 **
s(R_Depth)   1.745        3  5.807 0.12138
s(Ave_Slope) 1.000        1  1.037 0.30849
s(Ave_Sin)   2.100        3  3.880 0.27468
s(R_Sin)     2.924        3  8.050 0.04499 *
s(Ave_Cos)   2.553        3 12.373 0.00621 **
s(R_Cos)     1.000        1  0.727 0.39384
s(SST)       1.679        3  4.082 0.25279
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.164   Deviance explained = 20.6%
UBRE score = 0.081775  Scale est. = 1         n = 197

Dispersion parameter                      =  1
Deviance                                  =  180.49
n          (null degrees of freedom)      =  196
df.residual (residual degrees of freedom) =  180.69
df         (n-df.residual)                =  15.31

Overdispersion (Deviance/df.residual )    =  1

AIC according to formula: -2log(Likelihood) + 2*df   = 213.11
```

2. Minus A_Depth

Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Depth, k = 4) + s(Ave_Slope, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4)

Parametric coefficients:

```
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.2738     0.1968  -6.472 9.65e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Approximate significance of smooth terms:

```
               edf Est.rank Chi.sq p-value
s(R_Depth)   1.000        1  2.348  0.1254
s(Ave_Slope) 2.827        3 11.005  0.0117 *
s(Ave_Sin)   1.543        3  2.711  0.4384
s(R_Sin)     2.892        3 10.734  0.0133 *
s(Ave_Cos)   2.683        3  9.336  0.0251 *
s(R_Cos)     1.000        1  1.373  0.2413
s(SST)       1.715        3  4.208  0.2399
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

R-sq.(adj) = 0.111   Deviance explained = 17.4%
UBRE score = 0.10241 Scale est. = 1   n = 197

```
Dispersion parameter                   =  1
Deviance                               =  187.86
n           (null degrees of freedom)  =  196
df.residual (residual degrees of freedom) =  182.34
df          (n-df.residual)            =  13.66
```

Overdispersion (Deviance/df.residual)   = 1.03

AIC according to formula: -2log(Likelihood) + 2*df   = 217.17

3. Minus R_Depth

Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Slope, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_depth, k = 4)

Parametric coefficients:

```
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.2997     0.2004  -6.484 8.91e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq p-value
s(Ave_Slope) 1.000        1  3.346 0.06735 .
s(Ave_Sin)   1.000        1  0.152 0.69680
s(R_Sin)     2.749        3  6.367 0.09507 .
s(Ave_Cos)   1.398        3  9.957 0.01894 *
s(R_Cos)     1.000        1  0.312 0.57641
s(SST)       1.723        3  4.465 0.21540
s(Ave_depth) 2.259        3 13.557 0.00357 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.123   Deviance explained = 16.7%
UBRE score = 0.08429  Scale est. = 1         n = 197

Dispersion parameter                    =  1
Deviance                                =  189.35
n            (null degrees of freedom)     =  196
df.residual (residual degrees of freedom) =  184.87
df           (n-df.residual)               =  11.13

Overdispersion (Deviance/df.residual )    =  1.02

AIC according to formula: -2log(Likelihood) + 2*df   = 213.61
```

4. Minus A_Slope

```
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) +
    s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_depth, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   -1.234      0.190  -6.494 8.38e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq p-value
s(Ave_Sin)   1.000        1  0.071  0.7899
s(R_Sin)     2.586        3  5.540  0.1363
s(Ave_Cos)   1.000        1  5.913  0.0150 *
s(R_Cos)     1.000        1  0.222  0.6373
```

```
s(SST)       1.836        3  5.183  0.1589
s(Ave_depth) 2.088        3 10.177  0.0171 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.0983   Deviance explained = 14.5%
UBRE score = 0.093503  Scale est. = 1         n = 197

Dispersion parameter                    =  1
Deviance                                =  194.4
n          (null degrees of freedom)    =  196
df.residual (residual degrees of freedom) =  186.49
df         (n-df.residual)              =  9.51

Overdispersion (Deviance/df.residual )    =  1.04

AIC according to formula: -2log(Likelihood) + 2*df   = 215.42
```

5. Minus A_Sin

```
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) +
    s(SST, k = 4) + s(Ave_depth, k = 4) + s(Ave_Slope, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.3005     0.2009  -6.475  9.5e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
               edf Est.rank Chi.sq p-value
s(R_Sin)     2.755        3  6.270 0.09918 .
s(Ave_Cos)   1.481        3 10.018 0.01841 *
s(R_Cos)     1.000        1  0.475 0.49087
s(SST)       1.735        3  4.606 0.20303
s(Ave_depth) 2.267        3 13.435 0.00379 **
s(Ave_Slope) 1.000        1  3.304 0.06911 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.125   Deviance explained = 16.7%
UBRE score = 0.075105  Scale est. = 1         n = 197

Dispersion parameter                    =  1
Deviance                                =  189.32
n          (null degrees of freedom)    =  196
df.residual (residual degrees of freedom) =  185.76
```

df (n-df.residual) = 10.24

Overdispersion (Deviance/df.residual) = 1.02

AIC according to formula: -2log(Likelihood) + 2*df = 211.8

6. Minus R_Sin
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4) +
s(Ave_depth, k = 4) + s(Ave_Slope, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.2586	0.1975	-6.371	1.88e-10	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(Ave_Cos)	1.924	3	8.668	0.03405	*
s(R_Cos)	1.000	1	6.026	0.01410	*
s(SST)	1.864	3	5.435	0.14257	
s(Ave_depth)	2.340	3	15.850	0.00122	**
s(Ave_Slope)	1.000	1	2.838	0.09205	.

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.114 Deviance explained = 14.8%
UBRE score = 0.076347 Scale est. = 1 n = 197

Dispersion parameter = 1
Deviance = 193.78
n (null degrees of freedom) = 196
df.residual (residual degrees of freedom) = 187.87
df (n-df.residual) = 8.13

Overdispersion (Deviance/df.residual) = 1.03
AIC according to formula: -2log(Likelihood) + 2*df = 212.04

7. Minus A_COS
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_depth, k = 4) +
s(Ave_Slope, k = 4) + s(R_Sin, k = 4)

Parametric coefficients:
Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.1779 0.1829 -6.441 1.19e-10 ***
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
edf Est.rank Chi.sq p-value
s(R_Cos) 1.000 1 0.499 0.48008
s(SST) 1.879 3 5.614 0.13195
s(Ave_depth) 2.192 3 13.815 0.00317 **
s(Ave_Slope) 1.000 1 1.317 0.25104
s(R_Sin) 1.624 3 3.705 0.29513

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.0883 Deviance explained = 11.8%
UBRE score = 0.1065 Scale est. = 1 n = 197

Dispersion parameter = 1
Deviance = 200.59
n (null degrees of freedom) = 196
df.residual (residual degrees of freedom) = 188.31
df (n-df.residual) = 7.69

Overdispersion (Deviance/df.residual) = 1.07

AIC according to formula: -2log(Likelihood) + 2*df = 217.98

8. Minus R_Cos
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(SST, k = 4) + s(Ave_depth, k = 4) + s(Ave_Slope, k = 4) +
s(R_Sin, k = 4) + s(Ave_Cos, k = 4)

Parametric coefficients:
Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.286 0.197 -6.526 6.74e-11 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
edf Est.rank Chi.sq p-value
s(SST) 1.747 3 4.618 0.20198
s(Ave_depth) 2.223 3 14.148 0.00271 **
s(Ave_Slope) 1.000 2 3.684 0.15851
s(R_Sin) 2.745 3 10.452 0.01509 *
s(Ave_Cos) 1.000 1 7.368 0.00664 **

```
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.126   Deviance explained = 16.2%
UBRE score = 0.065744  Scale est. = 1         n = 197

Dispersion parameter                  =  1
Deviance                              =  190.52
n          (null degrees of freedom)     =  196
df.residual (residual degrees of freedom) =  187.28
df         (n-df.residual)              =  8.72

Overdispersion (Deviance/df.residual )     =  1.02

AIC according to formula: -2log(Likelihood) + 2*df   = 209.95
```

9. Minus SST

```
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_depth, k = 4) + s(Ave_Slope, k = 4) + s(R_Sin,
    k = 4) + s(Ave_Cos, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.4410     0.2136  -6.746 1.52e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq p-value
s(Ave_depth) 2.266        3 16.217 0.00102 **
s(Ave_Slope) 1.000        2  3.853 0.14569
s(R_Sin)     2.791        3 11.046 0.01148 *
s(Ave_Cos)   1.000        1  8.297 0.00397 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =   0.13   Deviance explained = 16.6%
UBRE score = 0.015849  Scale est. = 1         n = 208

Dispersion parameter                  =  1
Deviance                              =  195.18
n          (null degrees of freedom)     =  207
df.residual (residual degrees of freedom) =  199.94
df         (n-df.residual)              =  7.06

Overdispersion (Deviance/df.residual )     =  0.98
AIC according to formula: -2log(Likelihood) + 2*df   = 211.3
```

10km AIC outputs

1. All variables

Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_depth, k = 4) + s(R_Depth, k = 4) + s(Ave_Slope, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.3345	0.2028	-6.58	4.71e-11	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(Ave_depth)	2.296	3	27.194	5.36e-06	***
s(R_Depth)	1.000	1	0.068	0.794	
s(Ave_Slope)	1.000	1	0.082	0.775	
s(Ave_Sin)	1.000	1	0.640	0.424	
s(R_Sin)	1.000	1	0.010	0.922	
s(Ave_Cos)	1.000	1	2.377	0.123	
s(R_Cos)	1.000	1	0.775	0.379	
s(SST)	1.691	3	3.424	0.331	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.168 Deviance explained = 19.4%
UBRE score = 0.030505 Scale est. = 1 n = 201

Dispersion parameter = 1
Deviance = 185.16
n (null degrees of freedom) = 200
df.residual (residual degrees of freedom) = 190.01
df (n-df.residual) = 9.99

Overdispersion (Deviance/df.residual) = 0.97

2. Minus A_Depth

Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Depth, k = 4) + s(Ave_Slope, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) +

s(SST, k = 4)

Parametric coefficients:

```
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.2361     0.1877  -6.584 4.57e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Approximate significance of smooth terms:

```
               edf Est.rank Chi.sq p-value
s(R_Depth)   1.000        1  2.318 0.12790
s(Ave_Slope) 2.835        3 15.147 0.00170 **
s(Ave_Sin)   1.000        1  0.274 0.60077
s(R_Sin)     1.000        1  2.151 0.14244
s(Ave_Cos)   1.000        1  2.489 0.11467
s(R_Cos)     1.000        1  2.713 0.09954 .
s(SST)       1.930        3  6.295 0.09810 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

R-sq.(adj) = 0.106   Deviance explained = 13.1%
UBRE score = 0.10107 Scale est. = 1   n = 201

Dispersion parameter   = 1
Deviance   = 199.78
n   (null degrees of freedom)   = 200
df.residual (residual degrees of freedom) = 190.23
df   (n-df.residual)   = 9.77

Overdispersion (Deviance/df.residual)   = 1.05

AIC according to formula: -2log(Likelihood) + 2*df   = 221.31

3. Minus R_Depth

Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Slope, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) +
s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_depth,
k = 4)

Parametric coefficients:

```
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.3343     0.2026  -6.585 4.54e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Approximate significance of smooth terms:

```
              edf Est.rank Chi.sq  p-value
s(Ave_Slope) 1.000        1  7.467  0.00628 **
s(Ave_Sin)   1.000        1  0.801  0.37077
s(R_Sin)     1.000        1  0.020  0.88770
s(Ave_Cos)   1.000        1  2.472  0.11591
s(R_Cos)     1.000        1  1.202  0.27292
s(SST)       1.698        3  3.493  0.32169
s(Ave_depth) 2.332        3 27.594 4.42e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.172   Deviance explained = 19.4%
UBRE score = 0.02125  Scale est. = 1         n = 201

Dispersion parameter                    =  1
Deviance                                =  185.21
n          (null degrees of freedom)    =  200
df.residual (residual degrees of freedom) =  190.97
df         (n-df.residual)              =  9.03

Overdispersion (Deviance/df.residual )     =  0.97

AIC according to formula: -2log(Likelihood) + 2*df   = 205.27
```

4. Minus A_Slope

```
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) +
    s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_depth, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.3032     0.1976  -6.596 4.23e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq  p-value
s(Ave_Sin)   1.000        1  1.005 0.316165
s(R_Sin)     1.197        3  2.529 0.469986
s(Ave_Cos)   1.000        1  3.418 0.064486 .
s(R_Cos)     1.000        1  1.578 0.208996
s(SST)       1.763        3  4.031 0.258109
s(Ave_depth) 2.234        3 19.523 0.000213 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

R-sq.(adj) = 0.125 Deviance explained = 15.7%
UBRE score = 0.055637 Scale est. = 1 n = 201

Dispersion parameter = 1
Deviance = 193.79
n (null degrees of freedom) = 200
df.residual (residual degrees of freedom) = 191.81
df (n-df.residual) = 8.19

Overdispersion (Deviance/df.residual) = 1.01

AIC according to formula: -2log(Likelihood) + 2*df = 212.18

5. Minus A_Sin

Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) +
s(SST, k = 4) + s(Ave_depth, k = 4) + s(Ave_Slope, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.336	0.203	-6.582	4.66e-11	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(R_Sin)	1.000	1	0.781	0.3769	
s(Ave_Cos)	1.000	1	2.578	0.1083	
s(R_Cos)	1.005	3	2.268	0.5186	
s(SST)	1.691	3	3.435	0.3294	
s(Ave_depth)	2.323	3	26.967	5.98e-06	***
s(Ave_Slope)	1.000	1	7.772	0.0053	**

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.168 Deviance explained = 19%
UBRE score = 0.015752 Scale est. = 1 n = 201

Dispersion parameter = 1
Deviance = 186.13
n (null degrees of freedom) = 200
df.residual (residual degrees of freedom) = 191.98
df (n-df.residual) = 8.02

Overdispersion (Deviance/df.residual) = 0.97

AIC according to formula: -2log(Likelihood) + 2*df = 204.17

6. Minus R_Sin

Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4) +
s(Ave_depth, k = 4) + s(Ave_Slope, k = 4)

Parametric coefficients:

```
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.3212     0.2011  -6.569 5.08e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Approximate significance of smooth terms:

```
              edf Est.rank Chi.sq  p-value
s(Ave_Cos)   1.000        1  2.795   0.0945 .
s(R_Cos)     1.059        3  6.230   0.1010
s(SST)       1.726        3  3.677   0.2986
s(Ave_depth) 2.299        3 27.057 5.73e-06 ***
s(Ave_Slope) 1.000        2  7.901   0.0192 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

R-sq.(adj) = 0.166 Deviance explained = 18.6%
UBRE score = 0.011203 Scale est. = 1 n = 201

```
Dispersion parameter                     =  1
Deviance                                 =  187.08
n          (null degrees of freedom)     =  200
df.residual (residual degrees of freedom) =  192.92
df         (n-df.residual)               =  7.08
```

Overdispersion (Deviance/df.residual) = 0.97

AIC according to formula: -2log(Likelihood) + 2*df = 203.25

7. Minus A_COS
Family: binomial
Link function: logit
Formula:
Y1 ~ 1 + s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_depth, k = 4) +
s(Ave_Slope, k = 4)

Parametric coefficients:
Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.2663 0.1908 -6.636 3.22e-11 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(R_Cos)	1.678	3	6.660	0.08355	.
s(SST)	1.845	3	4.596	0.20385	
s(Ave_depth)	2.272	3	28.971	2.27e-06	***
s(Ave_Slope)	1.000	1	7.431	0.00641	**

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.175 Deviance explained = 18.2%
UBRE score = 0.012637 Scale est. = 1 n = 201

Dispersion parameter = 1
Deviance = 187.95
n (null degrees of freedom) = 200
df.residual (residual degrees of freedom) = 193.21
df (n-df.residual) = 6.79

Overdispersion (Deviance/df.residual) = 0.97

AIC according to formula: -2log(Likelihood) + 2*df = 203.54

8. Minus R_Cos

Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(SST, k = 4) + s(Ave_depth, k = 4) + s(Ave_Slope, k = 4) +
s(Ave_Cos, k = 4)

Parametric coefficients:
Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.2504 0.1892 -6.61 3.85e-11 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(SST)	1.714	3	3.558	0.3134	
s(Ave_depth)	2.273	3	24.267	2.20e-05	***
s(Ave_Slope)	1.367	3	6.460	0.0912	.
s(Ave_Cos)	1.000	1	1.901	0.1679	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.157 Deviance explained = 17%
UBRE score = 0.022157 Scale est. = 1 n = 201

Dispersion parameter = 1
Deviance = 190.75
n (null degrees of freedom) = 200
df.residual (residual degrees of freedom) = 193.65
df (n-df.residual) = 6.35

Overdispersion (Deviance/df.residual) = 0.99

AIC according to formula: -2log(Likelihood) + 2*df = 205.45

9. Minus SST
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_depth, k = 4) + s(Ave_Slope, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.4077	0.2101	-6.701	2.07e-11	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(Ave_depth)	2.376	3	29.669	1.62e-06	***
s(Ave_Slope)	1.000	2	7.962	0.0187	*
s(Ave_Cos)	1.000	1	3.257	0.0711	.
s(R_Cos)	1.000	1	4.153	0.0416	*

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.168 Deviance explained = 18.7%
UBRE score = -0.02397 Scale est. = 1 n = 208

Dispersion parameter = 1
Deviance = 190.26
n (null degrees of freedom) = 207
df.residual (residual degrees of freedom) = 201.62
df (n-df.residual) = 5.38

Overdispersion (Deviance/df.residual) = 0.94

AIC according to formula: -2log(Likelihood) + 2*df = 203.01

15km AIC outputs

1. All variables

Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Depth, k = 4) + s(R_Depth, k = 4) + s(Ave_Slope,
k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos,
k = 4) + s(R_Cos, k = 4) + s(SST, k = 4)

Parametric coefficients:
Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.6585 0.2928 -5.664 1.48e-08 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
edf Est.rank Chi.sq p-value
s(Ave_Depth) 2.566 3 23.110 3.83e-05 ***
s(R_Depth) 1.000 1 3.501 0.0613 .
s(Ave_Slope) 1.000 1 1.011 0.3146
s(Ave_Sin) 1.000 1 1.410 0.2351
s(R_Sin) 1.000 1 4.923 0.0265 *
s(Ave_Cos) 1.000 1 6.018 0.0142 *
s(R_Cos) 1.000 1 2.806 0.0939 .
s(SST) 1.719 3 6.671 0.0831 .

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.175 Deviance explained = 22.2%
UBRE score = -0.008305 Scale est. = 1 n = 205

Dispersion parameter = 1
Deviance = 180.73
n (null degrees of freedom) = 204
df.residual (residual degrees of freedom) = 193.71
df (n-df.residual) = 10.29

Overdispersion (Deviance/df.residual) = 0.93

AIC according to formula: -2log(Likelihood) + 2*df = 203.3

2. Minus A_Depth
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Depth, k = 4) + s(Ave_Slope, k = 4) + s(Ave_Sin,

```
   k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) +
   s(SST, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.8759     0.3696  -5.076 3.86e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
               edf Est.rank Chi.sq p-value
s(R_Depth)   2.255        3 13.268 0.00409 **
s(Ave_Slope) 2.998        3 13.465 0.00373 **
s(Ave_Sin)   2.804        3  8.571 0.03558 *
s(R_Sin)     1.000        1  2.984 0.08407 .
s(Ave_Cos)   2.848        3 11.274 0.01033 *
s(R_Cos)     1.000        1  5.079 0.02421 *
s(SST)       1.556        3  4.442 0.21755
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.175   Deviance explained = 24.1%
UBRE score = 0.010675  Scale est. = 1         n = 205

Dispersion parameter                      =  1
Deviance                                  =  176.27
n            (null degrees of freedom)    =  204
df.residual (residual degrees of freedom) =  189.54
df           (n-df.residual)              =  14.46

Overdispersion (Deviance/df.residual )    =  0.93

AIC according to formula: -2log(Likelihood) + 2*df   = 207.19


3. Minus R_Depth
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Slope, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) +
   s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_Depth,
   k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.4299     0.2135  -6.698 2.11e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
```

```
              edf Est.rank Chi.sq  p-value
s(Ave_Slope) 1.000        1 13.774 0.000206 ***
s(Ave_Sin)   1.000        1  0.014 0.904269
s(R_Sin)     1.000        1  3.669 0.055430 .
s(Ave_Cos)   1.429        3  7.320 0.062370 .
s(R_Cos)     1.000        1  0.858 0.354202
s(SST)       1.716        3  6.810 0.078208 .
s(Ave_Depth) 2.534        3 21.708  7.5e-05 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =   0.17   Deviance explained = 20.4%
UBRE score = 0.0056608  Scale est. = 1         n = 205

Dispersion parameter                   =  1
Deviance                               =  184.8
n          (null degrees of freedom)   =  204
df.residual (residual degrees of freedom) =  194.32
df         (n-df.residual)             =  9.68

Overdispersion (Deviance/df.residual )   =  0.95

AIC according to formula: -2log(Likelihood) + 2*df   = 206.16
```

4. Minus A_Slope

```
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) +
    s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_Depth, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.3878     0.2106  -6.588 4.44e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq  p-value
s(Ave_Sin)   1.237        3  2.941 0.400860
s(R_Sin)     1.000        1  1.709 0.191102
s(Ave_Cos)   2.874        3 17.807 0.000482 ***
s(R_Cos)     1.000        1  0.882 0.347589
s(SST)       1.915        3  8.477 0.037117 *
s(Ave_Depth) 1.000        1  3.662 0.055667 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.118   Deviance explained = 16.2%
```

UBRE score = 0.046855 Scale est. = 1   n = 205

Dispersion parameter   = 1
Deviance   = 194.55
n   (null degrees of freedom)   = 204
df.residual (residual degrees of freedom) = 194.97
df   (n-df.residual)   = 9.03

Overdispersion (Deviance/df.residual)   = 1

AIC according to formula: -2log(Likelihood) + 2*df   = 214.61

5. Minus A_Sin
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) +
    s(SST, k = 4) + s(Ave_Depth, k = 4) + s(Ave_Slope, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.4276	0.2125	-6.717	1.85e-11	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(R_Sin)	1.000	1	6.201	0.012770	*
s(Ave_Cos)	1.408	3	7.133	0.067768	.
s(R_Cos)	1.000	1	0.819	0.365497	
s(SST)	1.717	3	6.797	0.078663	.
s(Ave_Depth)	2.539	3	21.955	6.67e-05	***
s(Ave_Slope)	1.000	1	13.904	0.000192	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.175   Deviance explained = 20.4%
UBRE score = -0.0039693 Scale est. = 1   n = 205

Dispersion parameter   = 1
Deviance   = 184.86
n   (null degrees of freedom)   = 204
df.residual (residual degrees of freedom) = 195.34
df   (n-df.residual)   = 8.66

Overdispersion (Deviance/df.residual)   = 0.95

AIC according to formula: -2log(Likelihood) + 2*df   = 204.19

6. Minus R_sin
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4) +
    s(Ave_Depth, k = 4) + s(Ave_Slope, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.3286	0.1965	-6.762	1.36e-11	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(Ave_Cos)	1.000	1	3.954	0.046767	*
s(R_Cos)	1.000	2	3.856	0.145475	
s(SST)	1.824	3	7.259	0.064088	.
s(Ave_Depth)	2.215	3	20.640	0.000125	***
s(Ave_Slope)	1.000	1	9.565	0.001983	**

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.153   Deviance explained = 17.4%
UBRE score = 0.013949 Scale est. = 1   n = 205

Dispersion parameter = 1
Deviance = 191.78
n (null degrees of freedom) = 204
df.residual (residual degrees of freedom) = 196.96
df (n-df.residual) = 7.04

Overdispersion (Deviance/df.residual) = 0.97

AIC according to formula: -2log(Likelihood) + 2*df = 207.86

7. Minus A_Cos
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_Depth, k = 4) +
    s(Ave_Slope, k = 4) + s(R_Sin, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.3119	0.1925	-6.815	9.44e-12	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```
Approximate significance of smooth terms:
              edf Est.rank Chi.sq  p-value
s(R_Cos)      1.000        1  0.137 0.711007
s(SST)        1.747        3  6.682 0.082766 .
s(Ave_Depth) 2.296        3 24.250 2.21e-05 ***
s(Ave_Slope) 1.000        1 14.256 0.000160 ***
s(R_Sin)      1.395        3  6.841 0.077133 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.165   Deviance explained =   18%
UBRE score = 0.010578  Scale est. = 1         n = 205

Dispersion parameter                   =  1
Deviance                               =  190.29
n          (null degrees of freedom)     =  204
df.residual (residual degrees of freedom) =  196.56
df         (n-df.residual)              =  7.44

Overdispersion (Deviance/df.residual )    =  0.97

AIC according to formula: -2log(Likelihood) + 2*df   = 207.17


8. Minus R_Cos
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(SST, k = 4) + s(Ave_Depth, k = 4) + s(Ave_Slope, k = 4) +
    s(R_Sin, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.3110     0.1922   -6.82 9.08e-12 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq  p-value
s(SST)        1.749        3  6.619   0.0851 .
s(Ave_Depth) 2.342        3 29.763 1.55e-06 ***
s(Ave_Slope) 1.000        1 15.152 9.92e-05 ***
s(R_Sin)      1.245        3  9.468   0.0237 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.169   Deviance explained = 17.9%
UBRE score = 0.0015427  Scale est. = 1         n = 205
```

Dispersion parameter = 1
Deviance = 190.64
n (null degrees of freedom) = 204
df.residual (residual degrees of freedom) = 197.66
df (n-df.residual) = 6.34

Overdispersion (Deviance/df.residual) = 0.96

AIC according to formula: -2log(Likelihood) + 2*df = 205.32

9. Minus SST
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Depth, k = 4) + s(Ave_Slope, k = 4) + s(R_Sin,
k = 4)

Parametric coefficients:

```
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.3404     0.1968   -6.81 9.75e-12 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Approximate significance of smooth terms:

```
               edf Est.rank Chi.sq  p-value
s(Ave_Depth) 2.439        3 30.272 1.21e-06 ***
s(Ave_Slope) 1.000        1 15.562 7.99e-05 ***
s(R_Sin)     1.544        3  9.799   0.0204 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

R-sq.(adj) = 0.153 Deviance explained = 16.4%
UBRE score = -0.0023634 Scale est. = 1 n = 208

Dispersion parameter = 1
Deviance = 195.54
n (null degrees of freedom) = 207
df.residual (residual degrees of freedom) = 202.02
df (n-df.residual) = 4.98

Overdispersion (Deviance/df.residual) = 0.97

AIC according to formula: -2log(Likelihood) + 2*df = 207.51

20km AIC outputs

1. All variables

Family: binomial
Link function: logit

Formula:
```
Y1 ~ 1 + s(Ave_Depth, k = 4) + s(R_Depth, k = 4) + s(Ave_Slope,
    k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos,
    k = 4) + s(R_Cos, k = 4) + s(SST, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -2.2498     0.4451  -5.055  4.3e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
               edf Est.rank Chi.sq p-value
s(Ave_Depth) 2.178        3 10.834 0.01266 *
s(R_Depth)   2.639        3  5.855 0.11890
s(Ave_Slope) 1.000        1  0.319 0.57198
s(Ave_Sin)   1.000        1  6.046 0.01394 *
s(R_Sin)     1.000        1  9.616 0.00193 **
s(Ave_Cos)   1.000        1  9.203 0.00242 **
s(R_Cos)     1.000        1  0.475 0.49077
s(SST)       2.075        3 10.517 0.01464 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.326   Deviance explained = 35.3%
UBRE score = -0.1368  Scale est. = 1         n = 203

Dispersion parameter                  =  1
Deviance                              =  149.44
n          (null degrees of freedom)     =  202
df.residual (residual degrees of freedom) =  190.11
df         (n-df.residual)            =  11.89

Overdispersion (Deviance/df.residual )    =  0.79

AIC according to formula: -2log(Likelihood) + 2*df   = 175.23
```

2. Minus A_Depth
Family: binomial
Link function: logit

Formula:
```
Y1 ~ 1 + s(R_Depth, k = 4) + s(Ave_Slope, k = 4) + s(Ave_Sin,
```

```
   k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) +
   s(SST, k = 4)

Parametric coefficients:
         Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.8077     0.3015  -5.996 2.03e-09 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq  p-value
s(R_Depth)   1.000        1  0.298 0.585408
s(Ave_Slope) 1.000        1  1.034 0.309154
s(Ave_Sin)   1.000        1 25.456 4.53e-07 ***
s(R_Sin)     1.000        1 11.418 0.000727 ***
s(Ave_Cos)   1.000        1 14.199 0.000164 ***
s(R_Cos)     1.000        1  1.993 0.158063
s(SST)       2.219        3 15.446 0.001472 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.283   Deviance explained = 29.6%
UBRE score = -0.10855  Scale est. = 1         n = 203

Dispersion parameter                    =  1
Deviance                                =  162.53
n            (null degrees of freedom)     =  202
df.residual (residual degrees of freedom) =  193.78
df           (n-df.residual)               =  8.22

Overdispersion (Deviance/df.residual )     =  0.84

AIC according to formula: -2log(Likelihood) + 2*df   = 180.96
```

3. Minus R_Depth

```
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Slope, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) +
   s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_Depth,
   k = 4)

Parametric coefficients:
         Estimate Std. Error z value Pr(>|z|)
(Intercept)   -2.068      0.394  -5.248 1.54e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
```

```
             edf Est.rank Chi.sq p-value
s(Ave_Slope) 2.591        3  4.519 0.21056
s(Ave_Sin)   1.620        3  9.321 0.02531 *
s(R_Sin)     1.000        1  6.233 0.01254 *
s(Ave_Cos)   1.000        1  9.356 0.00222 **
s(R_Cos)     1.000        1  1.078 0.29908
s(SST)       2.059        3 10.275 0.01637 *
s(Ave_Depth) 2.218        3 10.915 0.01219 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =   0.32   Deviance explained = 34.5%
UBRE score = -0.13199  Scale est. = 1         n = 203

Dispersion parameter                    =  1
Deviance                                =  151.23
n          (null degrees of freedom)    =  202
df.residual (residual degrees of freedom) =  190.51
df         (n-df.residual)              =  11.49

Overdispersion (Deviance/df.residual )   =  0.79

AIC according to formula: -2log(Likelihood) + 2*df   = 176.21
```

4. Minus A_Slope

```
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) +
    s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_Depth, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.7945     0.2862  -6.271 3.58e-10 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
             edf Est.rank Chi.sq  p-value
s(Ave_Sin)   1.000        1 32.099 1.47e-08 ***
s(R_Sin)     1.000        1 16.164 5.81e-05 ***
s(Ave_Cos)   1.000        1 11.259 0.000792 ***
s(R_Cos)     1.000        1  2.819 0.093174 .
s(SST)       2.191        3 14.023 0.002874 **
s(Ave_Depth) 1.000        1  6.037 0.014010 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.308   Deviance explained = 31.2%
```

UBRE score = -0.13618 Scale est. = 1   n = 203

```
Dispersion parameter                   =  1
Deviance                               =  158.97
n          (null degrees of freedom)   =  202
df.residual (residual degrees of freedom) =  194.81
df         (n-df.residual)             =  7.19
```

Overdispersion (Deviance/df.residual) = 0.82

AIC according to formula: -2log(Likelihood) + 2*df = 175.35

5. Minus A_Sin
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) +
  s(SST, k = 4) + s(Ave_Depth, k = 4)

Parametric coefficients:

```
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -2.5231     0.4408  -5.724 1.04e-08 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Approximate significance of smooth terms:

```
              edf Est.rank Chi.sq  p-value
s(R_Sin)     1.000        1  1.368 0.242201
s(Ave_Cos)   1.000        1 10.937 0.000943 ***
s(R_Cos)     1.691        3  3.756 0.289043
s(SST)       2.099        3  9.931 0.019161 *
s(Ave_Depth) 2.987        3 26.137 8.93e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

R-sq.(adj) = 0.269 Deviance explained = 28%
UBRE score = -0.084677 Scale est. = 1   n = 203

```
Dispersion parameter                   =  1
Deviance                               =  166.26
n          (null degrees of freedom)   =  202
df.residual (residual degrees of freedom) =  193.22
df         (n-df.residual)             =  8.78
```

Overdispersion (Deviance/df.residual) = 0.86

AIC according to formula: -2log(Likelihood) + 2*df = 185.81

6. Minus R_Sin
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4) +
    s(Ave_Depth, k = 4) + s(Ave_Sin, k = 4)

```
Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.8026     0.2841  -6.346 2.21e-10 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
               edf Est.rank Chi.sq  p-value
s(Ave_Cos)   1.000        1 14.203 0.000164 ***
s(R_Cos)     1.000        1  4.292 0.038290 *
s(SST)       2.148        3 11.313 0.010150 *
s(Ave_Depth) 1.776        3 13.841 0.003130 **
s(Ave_Sin)   2.100        3 19.529 0.000213 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.309   Deviance explained = 31.6%
UBRE score = -0.13266  Scale est. = 1         n = 203

Dispersion parameter                      =  1
Deviance                                  =  158.02
n           (null degrees of freedom)     =  202
df.residual (residual degrees of freedom) =  193.98
df          (n-df.residual)               =  8.02

Overdispersion (Deviance/df.residual )    =  0.81

AIC according to formula: -2log(Likelihood) + 2*df   = 176.07
```

7. Minus A_Cos
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_Depth, k = 4) +
    s(Ave_Sin, k = 4)

```
Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.5425     0.2355  -6.551 5.73e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
Approximate significance of smooth terms:
              edf Est.rank Chi.sq  p-value
s(R_Cos)     2.690        3  7.066 0.069836 .
s(SST)       2.176        3 12.992 0.004655 **
s(Ave_Depth) 1.000        1 14.205 0.000164 ***
s(Ave_Sin)   2.019        3 17.247 0.000629 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.236   Deviance explained = 24.8%
UBRE score = -0.057016  Scale est. = 1         n = 203

Dispersion parameter                    =  1
Deviance                                =  173.66
n           (null degrees of freedom)   =  202
df.residual (residual degrees of freedom) =  194.11
df          (n-df.residual)             =  7.89

Overdispersion (Deviance/df.residual )    =  0.89

AIC according to formula: -2log(Likelihood) + 2*df   = 191.43
```

8. Minus R_Cos

```
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(SST, k = 4) + s(Ave_Depth, k = 4) + s(Ave_Sin, k = 4) +
    s(Ave_Cos, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.6583     0.2494   -6.65 2.94e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq  p-value
s(SST)       2.130        3  10.39 0.015527 *
s(Ave_Depth) 2.397        3  18.62 0.000327 ***
s(Ave_Sin)   2.170        3  12.09 0.007098 **
s(Ave_Cos)   1.000        1  14.68 0.000127 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =    0.3   Deviance explained =   31%
UBRE score = -0.12894  Scale est. = 1         n = 203

Dispersion parameter                    =  1
```

```
Deviance                           =  159.43
n          (null degrees of freedom)     =  202
df.residual (residual degrees of freedom) =  194.3
df         (n-df.residual)              =  7.7

Overdispersion (Deviance/df.residual )    =  0.82

AIC according to formula: -2log(Likelihood) + 2*df   = 176.83
```

9. Minus SST

```
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Depth, k = 4) + s(Ave_Sin, k = 4) + s(Ave_Cos,
   k = 4)

Parametric coefficients:
          Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.8162     0.2861  -6.349 2.17e-10 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
             edf Est.rank Chi.sq  p-value
s(Ave_Depth) 2.638        3  18.29 0.000383 ***
s(Ave_Sin)   2.077        3  10.69 0.013508 *
s(Ave_Cos)   1.000        1  17.80 2.46e-05 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.264   Deviance explained = 27.6%
UBRE score = -0.12141  Scale est. = 1         n = 208

Dispersion parameter                  =  1
Deviance                           =  169.32
n          (null degrees of freedom)     =  207
df.residual (residual degrees of freedom) =  201.29
df         (n-df.residual)              =  5.71

Overdispersion (Deviance/df.residual )    =  0.84

AIC according to formula: -2log(Likelihood) + 2*df   = 182.75
```

<u>25km AIC outputs</u>

1. All variables
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Depth, k = 4) + s(R_Depth, k = 4) + s(Ave_Slope, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.7450	0.3121	-5.591	2.26e-08	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(Ave_Depth)	2.388	3	11.812	0.00806	**
s(R_Depth)	1.000	1	0.201	0.65424	
s(Ave_Slope)	1.000	1	0.512	0.47440	
s(Ave_Sin)	1.000	1	0.081	0.77605	
s(R_Sin)	1.000	1	7.090	0.00775	**
s(Ave_Cos)	1.000	1	1.039	0.30811	
s(R_Cos)	1.000	1	3.583	0.05836	.
s(SST)	1.954	3	5.381	0.14595	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.208 Deviance explained = 23.2%
UBRE score = -0.016321 Scale est. = 1 n = 204

Dispersion parameter = 1
Deviance = 177.99
n (null degrees of freedom) = 203
df.residual (residual degrees of freedom) = 192.66
df (n-df.residual) = 10.34

Overdispersion (Deviance/df.residual) = 0.92

AIC according to formula: -2log(Likelihood) + 2*df = 200.67

2. Minus A_Depth
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Depth, k = 4) + s(Ave_Slope, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) +

```
   s(SST, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   -1.586      0.289  -5.489 4.03e-08 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq p-value
s(R_Depth)   2.064        3  5.846 0.11933
s(Ave_Slope) 1.000        1  0.001 0.97150
s(Ave_Sin)   1.000        1  7.242 0.00712 **
s(R_Sin)     2.418        3  8.658 0.03420 *
s(Ave_Cos)   1.000        1  6.267 0.01230 *
s(R_Cos)     1.000        1  1.548 0.21336
s(SST)       1.893        3  5.575 0.13421
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.184   Deviance explained = 20.4%
UBRE score = 0.015379  Scale est. = 1         n = 204

Dispersion parameter                    =  1
Deviance                                =  184.39
n           (null degrees of freedom)   =  203
df.residual (residual degrees of freedom) =  192.62
df          (n-df.residual)             =  10.38

Overdispersion (Deviance/df.residual )    =  0.96

AIC according to formula: -2log(Likelihood) + 2*df   = 207.14
```

3. Minus R_Depth

```
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Slope, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) +
   s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_Depth,
   k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.7418     0.3171  -5.494 3.94e-08 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq p-value
```

```
s(Ave_Slope) 1.000        1  0.756 0.38459
s(Ave_Sin)   1.000        1  0.091 0.76315
s(R_Sin)     1.000        1  6.717 0.00955 **
s(Ave_Cos)   1.000        1  2.055 0.15172
s(R_Cos)     1.000        1  3.343 0.06749 .
s(SST)       2.003        3  5.796 0.12196
s(Ave_Depth) 2.391        3 11.456 0.00950 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.212   Deviance explained = 23.1%
UBRE score = -0.025167  Scale est. = 1         n = 204

Dispersion parameter                    =  1
Deviance                                =  178.08
n          (null degrees of freedom)    =  203
df.residual (residual degrees of freedom) =  193.61
df         (n-df.residual)              =  9.39

Overdispersion (Deviance/df.residual )    =  0.92

AIC according to formula: -2log(Likelihood) + 2*df   = 198.87


4. Minus A_Slope
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) +
    s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_Depth, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.7821     0.3209  -5.554  2.8e-08 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
               edf Est.rank Chi.sq p-value
s(Ave_Sin)   1.000        1  0.852 0.35593
s(R_Sin)     1.000        1  7.062 0.00787 **
s(Ave_Cos)   1.000        1  4.438 0.03515 *
s(R_Cos)     1.000        1  3.482 0.06205 .
s(SST)       1.997        3  6.151 0.10450
s(Ave_Depth) 2.374        3 12.409 0.00610 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.212   Deviance explained = 22.7%
UBRE score = -0.030602  Scale est. = 1         n = 204
```

Dispersion parameter = 1
Deviance = 179.02
n (null degrees of freedom) = 203
df.residual (residual degrees of freedom) = 194.63
df (n-df.residual) = 8.37

Overdispersion (Deviance/df.residual) = 0.92

AIC according to formula: -2log(Likelihood) + 2*df = 197.76

5. Minus A_sin

Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Sin, k = 4) + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) +
s(SST, k = 4) + s(Ave_Depth, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.8037	0.3239	-5.568	2.58e-08	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(R_Sin)	1.000	1	12.972	0.000316	***
s(Ave_Cos)	1.000	1	4.062	0.043849	*
s(R_Cos)	1.000	1	3.210	0.073180	.
s(SST)	1.989	3	6.035	0.109900	
s(Ave_Depth)	2.317	3	21.374	8.8e-05	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.214 Deviance explained = 22.6%
UBRE score = -0.040315 Scale est. = 1 n = 204

Dispersion parameter = 1
Deviance = 179.16
n (null degrees of freedom) = 203
df.residual (residual degrees of freedom) = 195.69
df (n-df.residual) = 7.31

Overdispersion (Deviance/df.residual) = 0.92

AIC according to formula: -2log(Likelihood) + 2*df = 195.78

6. Minus R_sin
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Cos, k = 4) + s(R_Cos, k = 4) + s(SST, k = 4) +
    s(Ave_Depth, k = 4) + s(Ave_Sin, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.4543	0.2252	-6.458	1.06e-10	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Est.rank	Chi.sq	p-value	
s(Ave_Cos)	1.000	1	5.069	0.024356	*
s(R_Cos)	1.000	1	1.129	0.287973	
s(SST)	1.954	3	5.936	0.114764	
s(Ave_Depth)	2.281	3	9.066	0.028423	*
s(Ave_Sin)	1.000	1	11.101	0.000863	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.178   Deviance explained = 19.1%
UBRE score = -0.00025076 Scale est. = 1   n = 204

Dispersion parameter   = 1
Deviance   = 187.48
n   (null degrees of freedom)   = 203
df.residual (residual degrees of freedom) = 195.76
df   (n-df.residual)   = 7.24

Overdispersion (Deviance/df.residual)   = 0.96

AIC according to formula: -2log(Likelihood) + 2*df   = 203.95

7. Minus A_Cos
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(R_Cos, k = 4) + s(SST, k = 4) + s(Ave_Depth, k = 4) +
    s(Ave_Sin, k = 4) + s(R_Sin, k = 4)

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-2.0393	0.3946	-5.168	2.36e-07	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```
Approximate significance of smooth terms:
              edf Est.rank Chi.sq p-value
s(R_Cos)     1.000        1  6.149 0.01315 *
s(SST)       2.036        3  7.305 0.06278 .
s(Ave_Depth) 2.378        3 14.381 0.00243 **
s(Ave_Sin)   1.000        1  0.046 0.83102
s(R_Sin)     2.050        3 10.197 0.01696 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.206   Deviance explained = 22.3%
UBRE score = -0.025524  Scale est. = 1         n = 204

Dispersion parameter                     =  1
Deviance                                 =  179.87
n           (null degrees of freedom)    =  203
df.residual (residual degrees of freedom) =  194.54
df          (n-df.residual)              =  8.46

Overdispersion (Deviance/df.residual )   =  0.92

AIC according to formula: -2log(Likelihood) + 2*df   = 198.79


8. Minus R_Cos
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(SST, k = 4) + s(Ave_Depth, k = 4) + s(Ave_Sin, k = 4) +
    s(R_Sin, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -1.4952     0.2727  -5.484 4.16e-08 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
              edf Est.rank Chi.sq p-value
s(SST)       2.034        3  7.316 0.06249 .
s(Ave_Depth) 2.313        3 16.332 0.00097 ***
s(Ave_Sin)   1.609        3  2.289 0.51455
s(R_Sin)     1.000        1  1.993 0.15807
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =   0.16   Deviance explained = 17.2%
UBRE score = 0.017638  Scale est. = 1         n = 204
```

```
Dispersion parameter                 =  1
Deviance                             =  191.69
n         (null degrees of freedom)     =  203
df.residual (residual degrees of freedom) =  196.04
df        (n-df.residual)            =  6.96

Overdispersion (Deviance/df.residual )    =  0.98

AIC according to formula: -2log(Likelihood) + 2*df   = 207.6


9. Minus SST
Family: binomial
Link function: logit

Formula:
Y1 ~ 1 + s(Ave_Depth, k = 4) + s(Ave_Sin, k = 4) + s(R_Sin, k = 4) +
   s(R_Cos, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -2.6378     0.5838  -4.519 6.22e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
               edf Est.rank Chi.sq p-value
s(Ave_Depth) 2.560        3 15.068 0.00176 **
s(Ave_Sin)   1.000        2  0.858 0.65107
s(R_Sin)     1.943        3  9.650 0.02179 *
s(R_Cos)     1.000        1  6.729 0.00949 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.179   Deviance explained = 20.5%
UBRE score = -0.033218  Scale est. = 1         n = 208

Dispersion parameter                 =  1
Deviance                             =  186.08
n         (null degrees of freedom)     =  207
df.residual (residual degrees of freedom) =  200.5
df        (n-df.residual)            =  6.5

Overdispersion (Deviance/df.residual )    =  0.93

AIC according to formula: -2log(Likelihood) + 2*df   = 201.09
```

Appendix 3

Sea surface temperature variation in the Bay of Biscay

Over the ten years (1995 – 2007), effort sightings of Cuvier's beaked whale were predominantly recorded in the southern Bay of Biscay coupled to a large underwater feature known as the CapBreton canyon. However, as found in the previous section of this study opportunistic sightings show a seasonal movement from the southern bay to the northern continental slopes. This following section will focus on SST variability in the Bay of Biscay in order to understand these seasonal movements.

The average sea surface temperature was explored at three regions in the Bay of Biscay: 1-southern Biscay (43 to 44.5°N, -2 to -6°W); 2-mid-Biscay (44.5 to 45.5°N, 1- to -2°W); 3-northern Biscay (45.5 to 47°N, -2 to -6°W), between 1995 and 2006. Figure 5.16 shows the fluctuations of the average sea surface temperature between 1995 and 2006. Small fluctuations were observed between 1995 and 2001, followed by a drop in temperature during 2002, then a rise in 2003, after which temperature decreases in 2004 and then rises steadily during 2005 and 2006. The pattern of temperature variation was similar for each region, despite region 1 and 2 showing higher temperatures than region 3 (Figure 5.16).

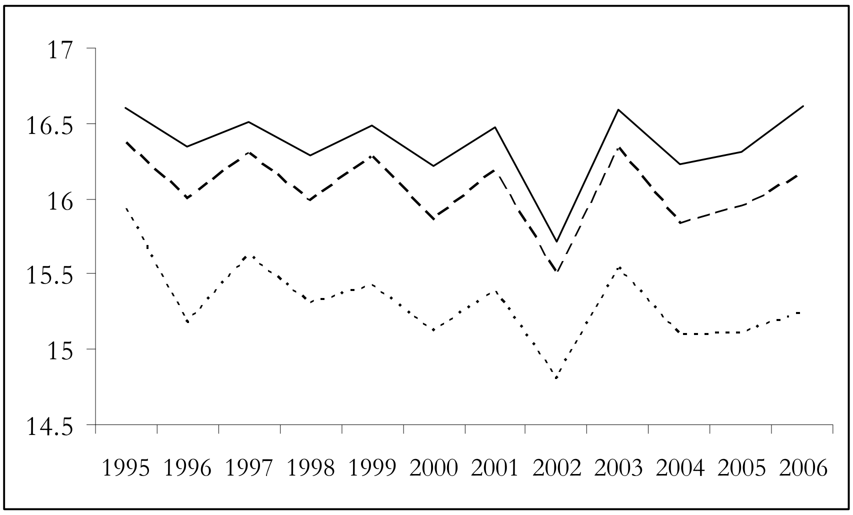


Figure 1: Average SST (y-axis) per year (x-axis) for each region: south (solid line), middle (long dashed line), and north (small dashed line).

As expected sea surface temperatures show the normal seasonal cooling and warming patterns with cooler temperatures in winter and warmer temperatures in summer and during the transitional seasons, spring and autumn, temperatures warm up and cool down, respectively (Figure 1 and 2). These changes in SST are consistent with the work carried out by Valencia *et al.* (2004) that shows winters and summers in the Bay of Biscay are more or less stable and predictable, whereas spring and autumn are variable. In winter, apart from small fluctuations in the early years temperatures remain stable between 1995 and 2006. During spring and summer, SST becomes more variable over the years in comparison to winter months. In spring, notable peaks occur in 2001 and 2003 for all three regions. In the northern region, SST starts to increase from 1996 to 1998, and after which SST declines until 2001, where it mirrors temperature changes in the south and mid regions. In summer, temperatures are higher than in spring. A decrease in temperature is observed between 1995 and 1998, followed by an increase in 1999, after which temperatures drop from 1999 (by approximately 2°C) until 2002 then temperatures rise again by approximately 2°C in 2003. After 2003 temperatures drop in 2004 and then start to increase in 2005 and 2006. During Autumn, overall SST has started to decline. SST drops from 1995 to 1996 and then a high peak in temperature is observed in 1997 after which a steep drop in temperature is observed. Small fluctuations in temperature are observed between 1998 until 2001, after which temperatures appear constant until 2005 then they increase.

The minimum winter temperatures (Figure 3, blue line) show that the temperatures over the northern slopes of the Bay of Biscay, as indicated by the blue line, fluctuate around 10°C. A drop in the minimum sea surface temperature can also be seen from 2004 in the south (black line) and 2005 in the middle (green) and northern (red) areas of the bay.

The colour maps (Figure 4) show an example of the seasonal variation in the sea surface temperature for Bay of Biscay. A regular pattern observed from the satellite images for 1995 to 2003, is an increase in temperature during the spring and summer months. Throughout each year, a general trend in warming of the southeastern corner of Biscay occurs from May to September, after which temperatures start to drop until May the following year. In 1997, 1998, 2001 and 2004, however the temperature increase in southeastern part of Biscay occurs from June to October. In this case, warmer water in May is apparent in the northeastern part of the Bay of Biscay.

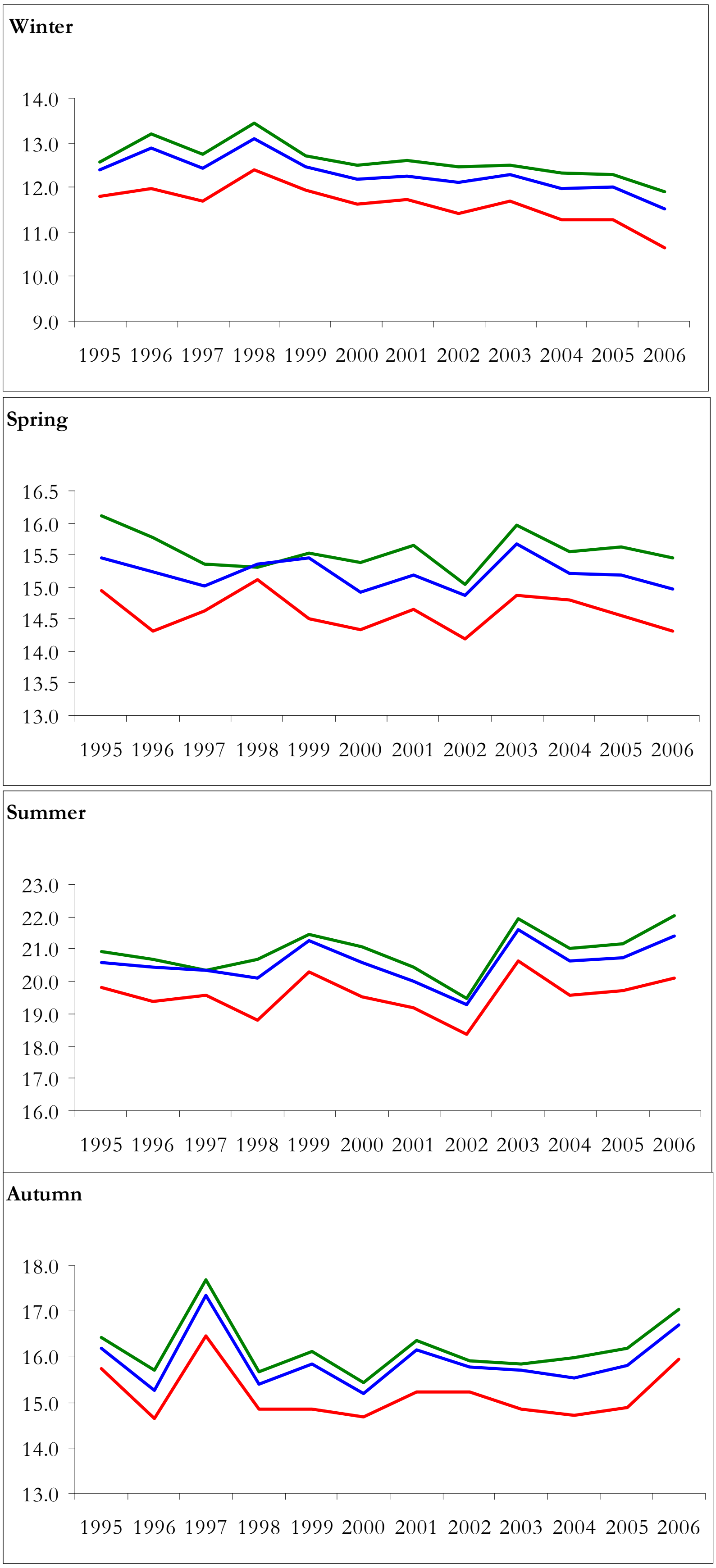


Figure 2: Spatial and temporal variability of sea surface temperature (y-axis) over time (x-axis). Southern Biscay 43-44.5°N (green line); mid Biscay 44.5-45.5°N (blue line); Northern Biscay 45.5-47°N (red line).

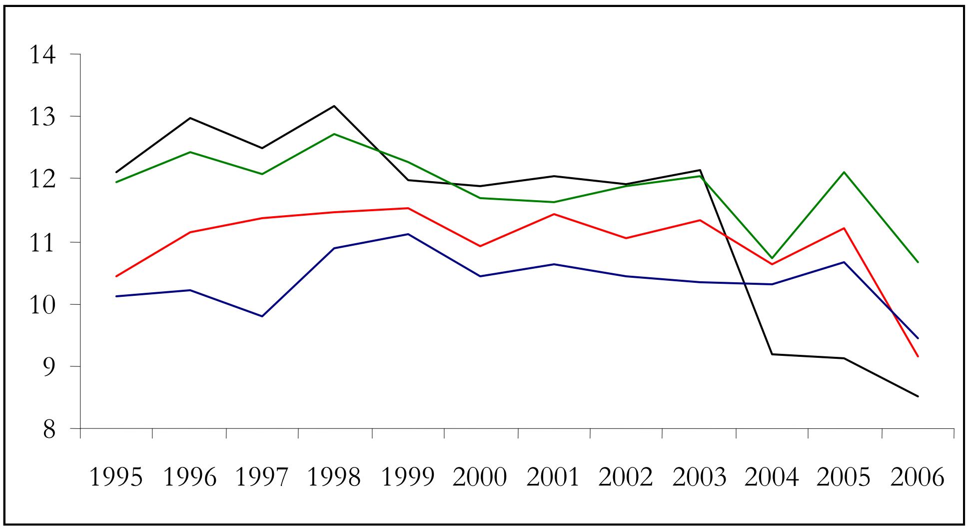


Figure 3: Minimum winter temperatures (y-axis) over time (x-axis) for four regions in the Bay of Biscay. Southern Biscay 43-44.5°N (black line); mid Biscay 44.5-45.5°N (green line); Northern Biscay 45.5-47°N (red line) and 47N to 48N (blue line).

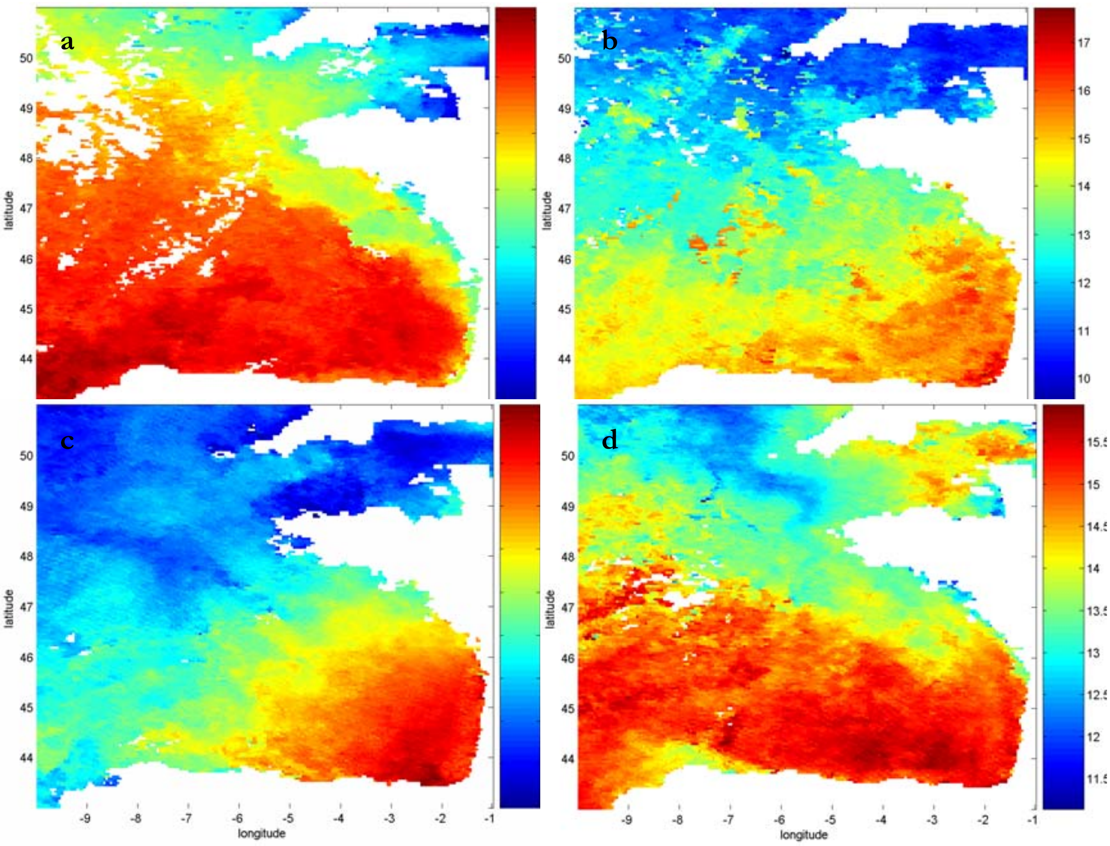


Figure 4: Average sea surface temperature for 2003 in February (a), May (b), August (c), November (d), showing the seasonal warming and cooling.